

# Evaluation of the Captive Breeding Potential of Reptile and Amphibian Taxa Included in Appendices I and II at CITES CoP19

## Compilation of Taxon-specific Fact Sheets

Beate Pfau, Paul Bachhausen, Ronny Bakowskie, Tobias Eisenberg, Stephan Ettmar, Andreas S. Hennig, Robert Hentschel, Felix Hulbert, Ole Klawonn, Christian Langner, Sebastian Nickl, Maik Schilde, Xaver Wapelhorst, Mona van Schingen-Khan, Laurenz R. Gewiss, Ulrich Schepp and Axel Kwet

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## Imprint

### Cover image:

Portraits of some amphibian and reptile species presented in this document. From upper left to lower right: Lemur leaf frog, *Agalychnis lemur* (© T. Eisenberg), Chiapas giant musk turtle, *Staurotypus salvinii* (© E. Reyes-Grajales), Male brood care in Starrett's Glass Frog, *Hyalinobatrachium vireovittatum* (© T. Leenders), Smooth softshell turtle, *Apalone mutica* (© A.S. Hennig), Giant horned lizard, *Phrynosoma asio* (© K. Kunz), Laos warty newt, *Laotriton laoensis* (© P. Bachmann), Central American wood turtle, *Rhinoclemmys pulcherrima manni* (© X. Wapelhorst)

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## Foreword

On a worldwide scale, Germany and the European Union (EU) are important importers and exporters of live reptiles as well as their parts and derivatives (such as leather), and are therefore responsible for the conservation of traded species.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) ensures that the international trade in protected wildlife is not detrimental to the survival of the species in the wild. Worldwide, international trade in live reptiles and amphibians listed in CITES Appendix I and II mainly involves specimens that labelled as born or bred in captivity. This trade may however involve wild specimens incorrectly labelled as captive-bred to circumvent trade restrictions. Therefore, the CITES source status of certain animals in trade can be questionable and problematic in some cases.

Legal trade in captive-bred specimens may contribute to conservation, e.g. by the establishment of conservation breeding programs, maintenance of genetic diversity of ex-situ populations, reduction of harvest pressure on wild populations, and it can also contribute to the knowledge on the ecology of species.

Illegal trade in wild specimens incorrectly labelled as captive-bred, might however have detrimental impacts on wild populations.

Therefore, the verification of the source code of protected species as a duty of national and international CITES authorities is gaining importance, also in the work of the international Committees of the Convention (e.g. in the frame of the Review of trade in animal specimens reported as produced in captivity according to Res. Conf. 17.7 (Rev.CoP18)\*). As the number of listed species is increasing steadily, this task poses a growing challenge to the responsible authorities.

In order to be in a position to make the obligatory plausibility finding on captive-breeding, detailed information on the reproduction biology and husbandry requirements are of outmost importance. However, specifically for species that are rarely kept, newly listed or described, or generally less studied, the relevant information is often not available in published form. Especially in Germany and Europe, there are numerous specialist keepers with extensive knowledge and experience in the keeping and breeding of rarely kept reptile and amphibian taxa. The German Association for Herpetology (DGHT) was therefore commissioned by the Federal Agency for Nature Conservation (BfN) to compile the relevant data on reproduction for the almost 250 reptile and amphibian taxa that were listed in CITES Appendix I and II at the last CITES CoP19. The present guidance shall assist CITES authorities and contribute to a better implementation of recent listings.

Dr. Andreas Krüß

Head of Department II 1 „Ecology and Conservation of Fauna and Flora“ of the BfN

## Abstract

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) aims to ensure that international trade in specimens of wild fauna and flora does not threaten the survival of the species affected by it. While legal trade in captive-bred specimens may contribute to species conservation, trade in wild specimens falsely labelled to be captive-bred in order to circumvent trade restrictions, can be highly detrimental to wild populations. For this reason and due to the continuously increasing number of captive-bred specimens of CITES-listed species in trade, the verification of the captive breeding of specimens in trade poses an increasing challenge to national and international CITES authorities. In order to check the plausibility of captive breeding, comprehensive information on the reproduction biology and husbandry requirements of the relevant species are crucial.

These documents (with identical content in German and English) summarise the relevant information for those reptile and amphibian species that were included in CITES Appendix I or II at CoP19 in 2022. The introductory chapters first describe the methods used to determine and summarise this information and how it can be applied.

In the following taxon-specific chapters, the subsequent aspects are summarised in a structured form:

- Species dealt with in this chapter from the respective listing proposal, with the valid scientific name and the various common names, as well as a rough estimate of how easily available animals of this species are in Europe,
- **Morphology and taxonomy:** i.e. diagnostic characters of the individual species and, if applicable, further information on taxonomy or distinguishable local forms,
- **Distribution and habitat** of the species and the accepted subspecies,
- **Conservation status and main threats:** Protection status under CITES and the EU wildlife trade regulation, conservation status according to the IUCN Red List or national red lists, protection measures and utilisation in the countries of origin, as well as the main threats to the wild population,
- **Reproduction data** from the natural habitats and additional information from captive breeding,
- **Data on husbandry and captive breeding** both in the countries of origin and in Europe, the USA and Asia, compiled from information from commercial breeders and breeding farms, institutions and, mainly from experienced private breeders; an assessment of the difficulty of keeping and breeding, labelled with a three-letter code A-C, or with an X, if no species-specific information could be obtained,
- **Referenced and further publications** used, and recommended further reading on keeping and breeding the species in this chapter.

The final section of the document contains a list of abbreviations and a detailed glossary.

This guidance is intended to support CITES authorities in the enforcement and especially in making plausibility findings of the captive-breeding of protected species, and thereby to contribute to an improved implementation of the CITES Convention. In addition, the information provided can be used by scientists or for conservation breeding projects.



## Zusammenfassung

Das Washingtoner Artenschutzübereinkommen (CITES) stellt sicher, dass der internationale Handel mit Exemplaren wildlebender Tier- und Pflanzenarten das Überleben der jeweiligen Arten nicht gefährdet. Während ein legaler Handel mit Nachzuchten zum Artenschutz beitragen kann, wirkt sich ein Handel mit Wildexemplaren, die als gezüchtet deklariert werden um Handelsbeschränkungen zu umgehen, oftmals sehr schädlich auf die Wildpopulationen aus. Daher, und auch wegen der kontinuierlich steigenden Anzahl an gezüchteten Exemplaren von immer mehr CITES-gelisteten Arten im Handel, ist die Überprüfung der Zucht eine zunehmende Herausforderung für die nationalen und internationalen CITES-Vollzugsbehörden. Für die Plausibilitätsprüfung von Zuchtangaben sind detaillierte Informationen zu Reproduktionsbiologie und Haltungsansprüchen der betreffenden Arten von größter Bedeutung.

In den vorliegenden Dokumenten (inhaltsgleich in deutscher und englischer Sprache) werden die entsprechenden Angaben für diejenigen Reptilien- und Amphibienarten, die 2022 bei der CITES CoP19 in Anhang I oder II aufgenommen wurden, zusammengestellt. In den einleitenden Kapiteln wird zunächst beschrieben, welche Methoden angewandt wurden, um diese Angaben zu ermitteln und zusammenzufassen, und wie diese Informationen angewendet werden können.

In Taxon-spezifischen Kapiteln sind Angaben zu folgenden Aspekten in strukturierter Form zusammengestellt:

- **Aufzählung der in dem jeweiligen Kapitel behandelten Arten** aus dem jeweiligen Listungsvorschlag, mit den gültigen wissenschaftlichen Bezeichnungen und verschiedenen umgangssprachlichen Namen, sowie einer groben Einschätzung, wie häufig Tiere dieser Art in Europa erhältlich sind,
- **Morphologie und Taxonomie**, d. h. Erkennungsmerkmale der einzelnen Arten und ggf. Hinweise zur Taxonomie bzw. auf unterscheidbare Lokalformen,
- **Verbreitung und Lebensraum** der Arten und der anerkannten Unterarten,
- **Schutzstatus und Gefährdungsfaktoren**: Schutzstatus nach CITES und EU-Artenschutzverordnung, Erhaltungszustand gemäß der Roten Liste der IUCN und ggf. nationaler Roter Liste, Schutz und Nutzung in den Herkunftsländern, sowie die wesentlichen Gefährdungsfaktoren für die Wildpopulation,
- **Reproduktionsdaten**, sofern vorhanden im natürlichen Lebensraum, sowie ergänzende Angaben aus Menschenobhut,
- **Haltung und Nachzucht** in Menschenobhut, sowohl in Herkunftsgebieten als auch in Ländern außerhalb des natürlichen Verbreitungsgebiets, zusammengestellt aus Angaben von kommerziellen Züchtern und Zuchtfarmen, Institutionen und vor Allem von erfahrenen Privatzüchtern; Einschätzung der Schwierigkeit der Haltung und Nachzucht erfolgt mit einem dreistufigen Buchstabencode A-C, bzw. Buchstabe X, wenn keine artspezifischen Informationen ermittelt werden konnten,
- **Zitierte und weiterführende Publikationen**: Verwendete Referenzen und empfohlene weiterführende Literatur zu Reproduktion, Haltung und Nachzucht der Arten in dem jeweiligen Kapitel.

Im Schlussteil des Dokuments findet sich ein Abkürzungsverzeichnis und ein ausführliches Glossar.

Diese Hilfestellung soll die Behörden im Artenschutzvollzug bei der Plausibilitätsprüfung der Zuchtherkunft geschützter Arten unterstützen und damit zu einer verbesserten Umsetzung der CITES-Konvention beitragen. Zusätzlich können die bereitgestellten Informationen von Wissenschaftler\*innen oder auch für Erhaltungszuchtprojekte genutzt werden.

## Introduction

Germany is one of the main importers of live reptiles and amphibians for the pet trade within the EU and worldwide. Especially in the case of amphibians and reptiles, with a particularly large number of species that are difficult to distinguish from one another, correct species identification and the associated implementation of the applicable regulations is often difficult. Currently, the majority of specimens traded are declared as captive-bred, while it is extremely challenging to verify the correct source without the appropriate background knowledge. For example, it is sometimes stated that the specimens were bred in captivity (in farms in the country of origin), while in reality, the animals were caught from the wild or hatched from eggs collected from the wild in order to circumvent trade restrictions for wild specimens.

CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) aims to ensure sustainable international trade in the species listed in its Appendices. According to the convention, commercial trade in wild specimens of Appendix I species is prohibited, while controlled and sustainable trade in specimens from Appendix II species is possible under certain conditions.

In the EU and international, enforcement authorities are increasingly being confronted with the question of the plausibility of alleged captive breeding of reptile and amphibian species listed in the CITES appendices.

In the case of live reptiles or amphibians, genetic testing is generally not feasible in every single case, because such tests would take a long time (i.e. the animals would have to be housed for a long time) and because only few markers or reference datasets are currently available for some of the protected species. Differentiating between wild-caught and captive animals using stable isotope analysis (van Schingen et al. 2016, Hopkins et al. 2022) or X-ray fluorescence analysis (Brandis et al. 2023) is also only possible in exceptional cases to date, as the method would also have to be calibrated for each species or origin and an extensive reference database would have to be created.

Furthermore, such molecular methods are not suitable as practical standard procedures, but are rather used in practice in exceptional cases. In order to verify the plausibility of the source, information on the reproductive biology and husbandry requirements of the respective species is therefore necessary. However, this information is not readily available and published for many species, and in the rarest of cases it is available in a condensed, easy-to-understand form. In particular, newly listed species pose increasing challenges to authorities. At the same time, the number of reptile and amphibian species that were proposed for listing has risen steadily since the last three CITES conferences of the parties, while the responsible authorities are rarely provided with more personnel for processing the increasing number of applications.

In order to support the authorities in verifying breeding information, the essential data on reproduction in human care were compiled for the reptile and amphibian species newly included in the CITES Appendices at CITES CoP19, and the difficulty of husbandry and breeding was assessed. In 2018/2019 and 2022, the DGHT prepared a German and an English document for the Federal Agency for Nature Conservation (BfN) as part of a project to specifically assess the breeding of the amphibian and reptile species newly listed in CITES CoP17 or CoP18 (Langner et al. 2021, Langner et al. 2022, see below 'References for the document'). It has to be noted that these guidance documents are not suitable for determining the legal origin of individual traded animals or the corresponding breeding stock, which must be checked by the

competent authority in each individual case, independently of the plausibility of the breeding. Furthermore, no quantitative information can be derived from this on the frequency of keeping and breeding of the affected taxa in human care.

The information provided here is particularly relevant with regard to paragraphs (1) and (4) of Article 54 of Regulation (EC) No 865/2006.

At CITES CoP19, around 250 species of amphibians and reptiles were added to CITES Appendices I or II, some of which are regularly found in trade, at least in Europe, and of which juveniles are also regularly imported from the countries of origin or from countries with large breeding farms. The current project therefore not only determines the husbandry and reproduction potential of the individual species under ex situ conditions (i.e. mainly in Europe), but also compiles the available information on the protection and use in the countries of origin and the main export countries, in order to be able to better evaluate applications for the import of such animals.

Since the difficulty of husbandry of adult animals, and the difficulty of obtaining offspring and rearing juveniles in good health varies for many reptile and amphibian species, the two factors were assessed separately and each was visually marked by letter symbols (see Methods).

The authors would like to kindly invite authorities to contact the specialists at the DGHT directly if they have any specific questions.

## Methods

### Literature search and selection of references

First, the relevant publications on the various taxa were identified using the usual search engines and databases for scientific literature. University theses and reports from nature conservation organisations are also well indexed by special search engines and bibliographies. However, the 'grey' literature on the husbandry and captive breeding of reptiles and amphibians, which was published in the publications of the societies and associations, is somewhat more difficult to find. For this purpose, the various working groups and the corresponding publishers were contacted – the editorial offices within Europe and the USA are very well connected and often work closely together, so that these publications could also be found and obtained. This resulted in an extensive bibliography for most species.

The individual publications were checked to see if they were quotable and actually worthy of quotation, and selected according to their importance for the creation of the taxon-specific chapters. The relevant reports on reproduction, husbandry and breeding are all included in the bibliography of the chapter, which we therefore named 'referenced and further publications' – reports on geographical distribution etc. are only included here if necessary for understanding the reproduction information so as not to increase the size of the document too much.

## Interviews with keepers and breeders

The authors of the taxon-specific chapters identified keepers and breeders of the respective species in Germany, Europe, North America and Asia. Where possible, the authors of the more recent publications were contacted and information (lecture programmes or conference reports, pet exchange portals, organisational structure, etc.) from the associations and clubs was evaluated. In addition, the corresponding groups on social media and specific personal websites were searched, and, of course, the authors' own notes were reviewed to identify potential breeders to be questioned.

The detailed questionnaires (in German or English) developed for this purpose were sent to experienced breeders, many of whom were already personally known, or they were interviewed in person. The collected questionnaires and informal messages were reviewed by the authors and, if necessary, follow-up questions were asked. In addition, keepers and breeders were called upon via various media to describe their own experiences with the individual species, with anonymous answers also being accepted.

An exchange of knowledge about the husbandry and breeding of many amphibian and reptile species that were included in CITES Appendices I or II at CoP19 and that are popular with terrarium enthusiasts often took place long before their CITES listing in the various working groups or at specialist workshops of the individual associations and clubs – for example, the German Chelonia Group within the DGHT – some of which have existed for more than 50 years. Many of the specialists active at that time can no longer be interviewed directly today, but every effort has been made to include historical knowledge in the present work, wherever possible and meaningful. The number of successful breeders among the participants of past meetings could however only be estimated. In cases where workshop protocols are available, for example, these are mentioned in the bibliography.

In the respective tables on husbandry and breeding of the taxa discussed herein, the number of people interviewed (in addition to the literature) and who provided relevant information is indicated in the tables. A distinction is made between private individuals, commercial breeders and other breeding operations, or institutions such as zoological gardens. As a rule, people who had already succeeded in breeding the respective taxa were contacted first. However, if the people interviewed only kept the taxa but did not breed them, this was indicated accordingly (e.g. difficult or rarely kept species, or when breeding was not desired) in the tables. It is important to note that the number of people interviewed does **not** allow any conclusions to be drawn about the frequency of breeding or husbandry of the respective taxa! On the contrary, an effort was made to contact more breeders of species, in particular when there was previously rather little available information for these species, such as in literature.

## Compilation of taxon-specific chapters

In principle, the taxon-specific chapters follow the order in which proposals were presented at the CoP19.

Each taxon-specific chapter is structured as follows: the scientific names of species in the taxon-specific chapter are based on the nomenclature used in the CITES proposal; any deviations from this approach are explicitly indicated in the text. The selected photos are intended to make it easier to identify the species, but the overview of **morphology and taxonomy** cannot replace dedicated identification literature. Regarding guidance for identification, the authors recommend the existing literature available in the CITES Academy or from TRAFFIC, for example, or specific reference books. The identification literature used is mentioned in the respective taxon-specific chapter.

The information on **distribution and habitat** also only provides a first impression and is intended to help verify the information on geographic origin in the corresponding applications. The information on the protection status and classification into a threat category according to the IUCN Red List corresponds to the status as of summer 2024.

In order to compile the data on **husbandry and captive breeding**, it was first necessary to determine for which species information was already available and for which species there was still a need for investigation. Due to taxonomic changes in recent decades (which, among other things, have led to changes in the CITES listing of some species, e.g. *Cuora galbinifrons* sensu lato), older literature in particular first had to be assigned to the 'correct' species. Furthermore, the authors identified publications that deal with taxa that had not yet been scientifically described at the time of publication or that had only been sufficiently taxonomically processed after the publication of the husbandry or breeding report. This also includes the use of fantasy names, trade names or pseudoscientific names in publications and advertisements. Especially in the case of very long-lived reptiles, e.g. many species of turtles, this often explains the availability of captive-bred specimens shortly after the original description of the species, and also, for example, of captive-bred subsequent generations of taxa that have only recently been described.

The data on age, size and quantity of reproduction and captive breeding were mostly compiled from the questionnaires and the publications – an evaluation of individual questionnaires was only possible for a few taxa for which these questionnaires had been answered very comprehensively.

## Difficulty assessment for captive husbandry and breeding; reviews

For many reptile and amphibian species, the husbandry of adult animals can be technically demanding, but if the conditions are right, breeding might be easy, or vice versa: the animals are easy to keep, but achieving and raising healthy juveniles requires a great deal of experience. Therefore, the degree of difficulty for husbandry and for breeding was assessed separately (see below).

The assessments were made after internal coordination within the team of authors considering the information provided during interviews and from literature, since all relevant fields of herpetoculture are represented here and the specialist authors already have many years of their own experience.



## Authors Team

The taxon-specific chapters were reviewed by the BfN and within the respective author team for lizards, turtles and amphibians, and also, where appropriate, by international specialists for the respective species to ensure accuracy. In addition, further international experts in the field of herpetoculture and the biology of the species concerned were involved for some chapters to ensure maximum objectivity.

The contact persons for the individual topics are:

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**Document Assembly**

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## How to use this document?

As explained above, this publication is intended to support authorities in conducting plausibility checks on the breeding origin of alleged captive-bred animals, and thus to help identify incorrectly labelled animals. Furthermore, the information can be used by zoos, scientists, breeders, etc.

While the publications provide basic information on the husbandry and captive breeding of the species concerned, **no** conclusions can be drawn from regarding the legal origin of individual animals or the affected breeding stock. Furthermore, **no** conclusions can be drawn regarding the frequency of keeping and breeding of the species, as such a quantitative analysis was not the subject of this study.

In the case of import or export applications for live animals into or from the EU, usually a completed application is submitted to the competent authority, which includes the scientific name of the species and an indication of the captive or wild origin (referred to as the source code). The source code indicates whether the animals were taken from the wild or bred in captivity in accordance with CITES Resolution Conf. 10.16 (Rev.)\*, as well as Article 54 of Regulation (EC) No. 865 /2006 (code 'C'), or have other origins (e.g. codes 'U', 'F', and 'R', see below under 'Relevant CITES Source Codes' in the section on acronyms and abbreviations, and in the references to the glossary). In addition, and in case of imports into the EU, the application should include a description of the intended accommodation.

In order to evaluate such an application, it must first be determined whether the species name is correct. To enable the relevant authorities to assess this information, the document is divided into taxonomic groups, either by individual species or, where possible and useful, summarised by species groups. The first chapters of the following 'taxon-specific fact sheets' contain information on taxonomy and the characteristic diagnostic features of the individual species, although this compact presentation cannot replace identification literature. In the individual descriptions, particular attention was paid to the distinguishing features of similar species, especially if they have different protection statuses. In addition, where available, informative photos have been included for comparison purposes, showing the essential characteristics of the taxa. The technical terms necessary for identifying the species are explained in more detail in the glossary.

The following chapters on distribution and habitat, as well as the main threats, and protection status, may be relevant when assessing sustainability (especially for wild specimens). Regulation (EC) No. 338/97, which implements the CITES Convention in the EU, stipulates that the scientific authorities of the importing Member State verify that all imports of specimens of species listed in Annexes A and B are not detrimental to the conservation status and distribution of the population concerned (NDF = Non-Detriment Finding). This applies in particular to imports of wild-caught specimens (source code 'W'), but also to imports of specimens from ranching (source code 'R'), or of specimens that are said to have hatched/been born in a controlled environment but do not meet the criteria for source code 'C' (source code 'F').

Such exports from the countries of origin can have a negative impact on the conservation or growth of the wild population, if the breeding stock is removed from the wild population in a non-sustainable manner. In particular, a correct assessment is important for species for which commercial trade in captive-bred specimens is allowed but where there is an import ban in place on wild-caught specimens. On the other hand, the regulated and sustainable removal of animals can contribute to the conservation of the species in the country of origin, in that the

resulting income contributes to the livelihoods of the local population and thus creates incentives for further research and conservation of the species and its habitats.

The chapters on reproduction data and husbandry and breeding should allow a rough plausibility check of the reported number of captive-bred offspring per breeding female and the conditions under which the breeding was allegedly carried out. This information is particularly relevant in view of paragraphs (1) and (4) of Article 54 of Regulation (EC) No 865/2006. The numerical data on reproduction should be seen in the context of a natural range of variation and not as absolute values. For example, the number of juveniles in human care usually depends on various factors such as the age or size of the breeding female, nutrition, temperature regime, incubation conditions and often also on the breeding group composition. If such influencing factors are already known, they have been mentioned, and often average and likely maximum values have been determined. The variance of the numerical values may depend not only on different husbandry conditions but also on the number of people interviewed.

The fact that the authors were not yet aware that a species had already been bred in the F2 or further generations at the time of writing does not mean that this is fundamentally impossible. For many species, F2 breeding may have taken place in the meantime or may take place in the future under the right conditions, which had simply not yet been published at the time of writing or could be determined using the questionnaires and interviews. The information in this chapter represents the current state of knowledge, based on the experience of the volunteer participants and the literature, while knowledge of the respective species will grow with the experience of the breeders. This document is therefore not intended as a sole basis for decision-making, but as a guide. It does not claim to be complete. In case of doubt, it is always advisable to research the most up-to-date information, and to ask the specialists at the owner associations such as DGHT or VDA. For this reason, the author and the date of completion of single taxon-specific fact sheets are given. Often, reference is also made to other specialists who are willing to provide further detailed information. The expert advisors of the German Nature Protection Agency (BfN) and the corresponding DGHT subgroups are also happy to provide additional information if needed.

## Target species

As with the previous documents, the number of species to be considered is very large: at the 2022 CITES conference, 242 reptile and amphibian species were explicitly named and assigned to the appendices. The profiles will primarily be compiled for these species – but some very similar, newly described or revalidated species that have not (yet) been listed in the CITES Appendices will also be included and assessed.

In the case of reptiles, the species spectrum initially comprises 26 lizard species, including all 22 Horned lizards – *Phrynosoma* spp. as well as the Green Water dragon, *Physignathus cocincinus*, which is so common in captivity, but is threatened in the wild by capture for trade, and two gecko species. In addition, the Adelaide dwarf blue-tongued skink (*Tiliqua adelaidensis*) was listed in Appendix I.

Furthermore, this document includes information on a total of 58 turtle species. These include 31 mud turtles alone (*Claudius angustatus*, *Staurotypus salvinii* and *S. triporcatus*, as well as all species from the genus *Kinosternon* and all musk turtles, *Sternotherus* spp.), the five large-headed species of map turtles, *Graptemys* spp., the American soft-shelled turtles *Apalone* spp. with three species, the snapping (Chelydridae) with a total of five species and also the American Wood turtles *Rhinoclemmys* spp. with nine species, as well as two species of Asian terrapins, which were upgraded from Appendix II to Appendix I, an Asian soft-shelled turtle, and the two Matamoras turtle species.

Among the amphibians, only the Lemur frog (*Agalychnis lemur*) and the Laos newt (*Laotriton laoensis*) are listed individually on the CITES Appendices. However, the family listing of the Central and South American glass frogs (Centrolenidae) poses a particular challenge for the compilation of the fact sheet, as the number of individually named species was 158 when the listing proposals for this CITES conference was submitted, and which has increased since then.

A special feature of these CoP19 reptile and amphibian listings is that although a certain number of species from the fully listed genera are explicitly named in the adapted CITES Appendices, the taxonomic treatment of these genera is still in flux and different local forms are already known among keepers and breeders, which may soon be described or delimited as subspecies or even species and which will of course be included in the fact sheets. By summer 2024, three mud turtle species had already been revalidated and eight glass frog species had been newly described, bringing the number of explicitly named species in this document to 255 (see the species index at the end of the document).



## Evaluating the Captive Breeding Potential

This categorisation illustrates the specialist authors' collective estimate of the degree of difficulty of husbandry and breeding based on the information available. The classifications are listed side by side in each taxon-specific chapter above the 'Husbandry and captive breeding' table to which they refer and are separated by slashes.

### Assessing the degree of difficulty of husbandry:

**A** Due to the standardised basic keeping conditions (temperature, humidity, no hibernation or hibernation that can be carried out in a normal household), a manageable space or room requirement and/or technical effort, the species can also be kept in the living room without any problems for newcomers with appropriate instructions.

**B** The husbandry of this species requires changing basic husbandry conditions during the year (temperature, humidity, precipitation, possibly outdoor keeping and/or hibernation), increased space or room requirements and/or moderate technical effort (e.g. high UV requirements) and in-depth theoretical knowledge.

**C** The husbandry of this species requires changing basic husbandry conditions throughout the year (habitat with extreme environmental conditions), high space or room requirements, and/or it has special husbandry requirements (food specialisation, dangerousness) and/or it requires high technical effort (e.g. permanent cooling). This species therefore appears to be suitable only for specialists.

### Assessing the degree of difficulty of reproduction in captivity:

**A** Reproduction takes place spontaneously or by simple means, incubation is very simple or not relevant due to ovoviviparity/viviparity, rearing is successful under the same husbandry conditions as for the adult animals. Even newcomers usually cope well with breeding and rearing.

**B** Breeding can be easily triggered, incubation of the clutches is easy to achieve after knowledge of species-specific behaviour and/or breeding is successful under similar husbandry conditions as for the adult animals. However, breeding and rearing require experience and a good knowledge of the biology of the species.

**C** Induction of reproduction, incubation of the clutch and/or rearing of the young requires specialised knowledge or is rather difficult, so that this species is usually only bred by specialists.

### Without category:

**X** To the knowledge of the specialist authors, there is no husbandry or breeding experience for this species.

## Sauria

## Agamidae

*Physignathus cocincinus* Cuvier, 1829

| Species                        | Original description | Common name                                                      | Common name International                                                                                                                                                    | Known in the trade |
|--------------------------------|----------------------|------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Physignathus cocincinus</i> | Cuvier, 1829         | Green Water dragon<br>Chinese Water Dragon<br>Asian Water dragon | Grüne Wasseragame<br>Hinterindische Wasseragame<br>Indochinesische Wasseragame<br>Dragon d'eau vert<br>Dragon d'eau chinois<br>Rồng đát<br>ตะกวด / ลั้ง / กิ้งก่ายักษ์<br>鬣蜥 | Yes                |

Fig. 1: *Physignathus cocincinus*

- a adult ♂ *P. cocincinus* in the terrarium (F. Hulbert)
- b adult ♀ *P. cocincinus* in the terrarium (F. Hulbert)
- c *P. cocincinus* hatching (A. Rauhaus, Cologne Zoo)
- d hatchling of the Green Water Dragon (A. Hohmeister).

## Morphology and Taxonomy

With a total length of up to one meter, the Green Water dragon is not only one of the largest species of agama – only surpassed by the sailfin lizards (*Hydrosaurus* spp.) – but also one of the most impressive medium-sized lizards. The equally large Australian water dragon, *Intellagama lesueurii* was described by Gray in 1831 as *Lophura leuseurii*, but was then listed in the same genus as the Green Water dragon for the first time by Gray in 1845 as *Physignathus lesueurii*. It was not until 140 years later that Wells & Wellington established the genus *Intellagama* in their controversial work from 1985, but this was not recognized due to the lack of any justification. However, in 2012 Amey et al. were able to show why *Intellagama lesueurii* is the correct binomial combination for the Australian water dragon. The genus *Physignathus* is therefore monotypic and is only represented by the Green Water dragon, *Physignathus cocincinus*. Interesting in this context is that the genus *Physignathus* is the sister genus to the Australasian radiation and is belongs to the subfamily Amphibolurinae. Thus, the Green Water dragon is the only East Asian species, while all other genera of the subfamily are Indo-Australian (Macey et al. 2000, Hugall et al. 2008).

There are several synonyms for the Green Water dragon, *Physignathus cocincinus*, of which *Physignathus mentager*, described by Günther in 1861 as *Dilophyrus mentager*, was known from herpetoculture (Nietzke 1972, Jauch 1979, Nietzke 1980, Ortner 1982). For some time, individuals with only 6–7 infralabials were considered *Physignathus cocincinus cocincinus*, and individuals with 11 infralabials were considered *Physignathus cocincinus mentager*, whereas *Physignathus cocincinus caudicinctus* was said to have as many as 14 infralabials (Barbour 1912). In the first description of *Physignathus cocincinus caudicinctus*, Barbour noted that the new form is closely related to the other two subspecies and that intermediate stages could occur in the contact zones of the presumably converging distribution areas. Morphological differences depending on the distribution area include, for example, longer snouts in Vietnamese animals (Werning 2004). Kodym (1992) also points out that Vietnamese individuals should not be bred with animals from Thailand, as the former are longer and have more pointed heads and higher dorsal crests. Mertens wrote in a personal message that only one species, *Physignathus cocincinus*, exists on the Asian mainland (Rosenberg 1940).

The terra typica of *P. mentager* is in Siam, today's Thailand, whereas the terra typica of *P. cocincinus* is given as 'Cochinchine'. Cochinchina is the name used in French for the southernmost part of Vietnam and *cocincinus* is the latinised spelling. The terra typica of *P. c. caudicinctus* is given as Laokay, Tonkin (Uetz 2017). The former Tonkin comprised the entire north of Vietnam, today's province of Lào Chai borders directly to China in the central north. If the three Terra typica mentions are placed in relation to each other, they each represent the most extreme distribution point in the west (*mentager*), north (*caudicinctus*) and south (*cocincinus*). It is not surprising that transitional forms occur in such a large area and therefore, based on current knowledge, it makes sense to regard *Physignathus cocincinus* as a polymorphic species with no accepted subspecies.

The maximum length of over 100 cm is rarely reached; the animals usually have a total length of 65–80 cm, with a head-body length of 20–25 cm. While the males usually weigh up to 600 g, the females are significantly smaller and lighter at around 350 g (Werning 2004). There are also reports of males weighing up to 900 g and having a total length of 90 cm (Franke 2009).

The tail accounts for more than  $\frac{2}{3}$  of the total length. While the Green Water dragon is evenly covered with many small scales on its upper side, there are isolated larger tubercles in the

rear lower jaw area and a row of significantly enlarged scales below the infralabials, as well as a transverse gular fold (Ziegler 2002). The tail is clearly compressed at the sides as a rudder tail. Both sexes have a tail, back and neck crest, which is only weakly developed in the females, whereas the males can have very long crests and also skin sails. It is striking here, similar to Green Iguanas of the genus *Iguana*, that males raised in terrariums rarely develop crests as large as those observed in nature. The crest scales, which are also greatly enlarged on the tail, transition into significantly smaller crests from the area of the tail bands.

The basic colour is a strong green, which becomes somewhat duller and greyer with increasing age. The tail is still green at the base and otherwise has alternating brown and beige bands. The bands become wider towards the back; the last quarter is usually dark (Werning 2004). A dark longitudinal stripe runs from the rear edge of the eye to beyond the ear, which can be more or less pronounced. The enlarged scales in the lower jaw area are whitish to cream-colored, in adult males partially strikingly pink. The entire throat area of old males can also be pink or sometimes bluish to purple. Otherwise, the throat is greenish to greenish-yellow, especially in females. Both sexes have a yellowish-orange coloration from the armpit area towards the flank, which is often less pronounced in females. Hatchlings are initially brownish on the upper side and green on the sides. The side stripes are a striking feature, and are cream-colored. These side stripes remain until the adult stage and later take on a slightly bluish hue. Although they fade with age, or increasingly turn into the green tones of the rest of the colouring, they are almost always still slightly visible and recognizable.

## Distribution and Habitat

### Distribution

Distributed from Vietnam through Cambodia, Laos and central Thailand to southern China.

During the last 25 years, intensive field research has been carried out in Vietnam, but prior to this there was little data available on *Physignathus cocincinus* (Ministry of Science, Technology and Environment 1992, Bobrov 1993, Nguyen & Ho 1996, Ziegler 2002, Ziegler 2004, Nguyen, V.S. et al. 2005, Dang et al. 2006, Ananjeva et al. 2007, Dang et al. 2007, Ananjeva et al. 2008a, Ananjeva et al. 2008b, Bobrov & Semenov 2008, Nguyen, S.V. et al. 2009, Nguyen, V.S. et al. 2009, Chúg et al. 2012, Geißler 2012, Hecht et al. 2013, Jestrzowski et al. 2013, Vassilieva et al. 2015, Ziegler et al. 2015, Ngo et al. 2016, Nguyen, V.H. et al. 2017, Nguyen, T.Q. et al. 2018a, Nguyen, T.Q. et al. 2018b, Nguyen, V.H. 2018, Nguyen, V.H. et al. 2018, Ziegler & Nguyen 2019, Gewiss et al. 2020, Pham et al. 2023, Stenger et al. 2023, Ngo et al. 2024). In Vietnam, *Physignathus cocincinus* can theoretically be found throughout the entire country, but only in suitable habitats and usually in small population numbers.

In Thailand, the species is only found in the southeast of central Thailand (Günther 1861a, Günther 1861b, Taylor 1934, Taylor 1963, Stoer 1979, Cox et al. 1998, Chan-ard et al. 1999, Manthey & Manthey 1999, Nabhitabhata et al. 2000, Nabhitabhata & Chan-ard 2005, Cota 2008, Chan-ard et al. 2015, Patawang et al. 2015, Hawkeswood & Sommung 2017).

Recently, some studies have also been conducted in selected protected areas in Cambodia (Stuart & Emmett 2006, Stuart et al. 2006, Grismer et al. 2007, Grismer et al. 2008a, Grismer et al. 2008b, Hartmann et al. 2013, Geissler et al. 2019).

The records of *Physignathus cocincinus* in Laos are only sporadic and are often related to their appearance in food markets (Manthey & Manthey 1999, Stuart 1999, Gilbert 2009, Davenport

& Heatwole 2013, Suzuki et al. 2015, Manthey & Manthey 2017, Schweikhard et al. 2019, Kasper et al. 2020, Zuklin et al. 2021).

The northernmost part of the distribution range of the Green Water dragon is found in the southern Chinese provinces of Guangdong, Guangxi, and Yunnan (Pope 1935, Lin 1984, Zhao & Adler 1993, Zhao et al. 1999, Zang et al. 2008, Das 2010, Wang et al. 2022).

The inclusion in a checklist of lizard species in Malaysia is probably to be regarded as incorrect due to other evidence (Grismer & Quah 2019).

The inclusion in a checklist of lizard species in Malaysia is probably to be regarded as incorrect due to the lack further evidence (Grismer & Quah 2019).

The information from Myanmar, which has been mentioned several times, is not considered to be confirmed due to a lack of voucher specimens or photo evidence. This information has been stated again and again even in recent literature (see Janssen & Sy 2022). The westernmost distribution limit is probably east of Bangkok, Thailand (Stuart et al. 2019). Two photo evidences via iNaturalist suggest that the species may also be found further west in Chaloen Rattanakosin National Park and Kaeng Krachan National Park. However, such single evidences via iNaturalist should be critically scrutinised and can also be attributed to deliberately released animals or specimens in small tourist facilities. Two such photo evidences from the island of Ko Pha-ngan allow this assumption.

The introduced populations in Taiwan (Lee et al. 2019) and Hong Kong SAR (To 2005, Mo 2019, Chan et al. 2020) demonstrate that such targeted or unintentional settlements can lead to stable populations.

### Habitat and Behaviour in the Wild

The primary habitat is along rocky streams in evergreen lowland forests, mixed with deciduous and bamboo forests. *Physignathus cocincinus* can be found at altitudes of 0 to 820 m asl sea level (Gewiss et al. 2020, Nguyen et al. 2018a, Stuart et al. 2006, Ziegler 2002). The habitat is always tied to water; in addition to streams, the animals can also be found along rivers, ponds and pools with dense overgrowth. Undisturbed, natural areas are usually preferred, but they can sometimes also be found near human settlements (Ziegler 2002). A decisive criterion for habitat selection is the presence of forests with dense canopies next to streams (Chang et al. 2020).

The animals prefer to rest on branches and twigs above the water, into which they drop when in danger. Thanks to their pronounced tail paddles, they are excellent swimmers and divers. Water dragons are able to walk short distances bipedally over land. The spatial segregation of the habitat can be assigned to the different age groups. Nguyen et al. (2017) investigated the day and night activity of *Physignathus cocincinus* in Thua Thien Hue Province, Vietnam. A total of 89 individuals were observed during the day and 211 individuals at night. Most of the animals recorded were found in trees. During the day, 71.9% and 96.7% of the total number of specimens recorded were found in trees and bushes, and at night, 96.7%. The Green Water dragon is most active between 10:00 a.m. and 1:00 p.m. At night, the animals climb onto thin branches on or above streams and sleep openly crouched on the branch. The individuals of *Physignathus cocincinus* were found in three types of microhabitats. Juveniles live in the low shrub vegetation below 0.5 m, whereas subadult Green Water dragons are often found in middle high altitude between 1–2 m. Adults inhabit the higher altitudes from about 3 m above water surface (Nguyen et al. 2017).



The population density is related to the altitude of the distribution area. In Nam Dong, Vietnam, 97 individuals were found per 10,000 m<sup>2</sup> at an altitude of less than 100 m asl. Merely 48 individuals lived at an altitude of 100–300 m, whereas at an altitude of 600–800 m asl, only 27 individuals were found per 10,000 m<sup>2</sup> (Nguyen 2018).

Green Water dragons are omnivorous. An analysis of the stomach contents of 187 animals from Thua Thien Hue Province, Vietnam, showed that the majority of the 3066 components examined were invertebrates. Spiders, ants, insect larvae, termites, crickets, grasshoppers and earthworms were the most common, accounting for 5.36% to 35.57%. A total of 43 adult, 70 subadult and 98 juvenile water dragons were examined; 24 stomachs were empty. The proportion of plants was relatively low, with 14 components examined (Nguyen et al. 2018c). Ziegler (2002), on the other hand, found in his field studies in Vietnam that the proportion of vegetarian food in adult animals accounted for about ⅓ of the total. In the introduced population in Taiwan, Ciou (2015) discovered that the prey spectrum of adult *Physignathus cocincinus* includes frogs (*Buergeria robusta*), agamas of the genus *Diploderma*, snakes (*Calamaria pavementata*), and mice (Lee et al. 2019).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 14).

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

VU (Vulnerable A4cd, assessed May 24, 2017).

This species is classified as vulnerable because, although widespread, it is heavily hunted in most parts of its range (Stuart et al. 2019).

### Red List Status in the Range Countries

In the countries of origin, the species was nationally classified as Endangered in China and Thailand, and as Vulnerable in Vietnam (Dang et al. 2007, Jiang et al. 2016, Nabhitabhata & Chan-ard 2005).

### Utilisation within the Natural Range

Initial investigations into the conservation status of *Physignathus cocincinus* in Vietnam showed that between 2010 and 2016, a total of 44,741 animals, mainly from Vietnam, but also from Thailand (as well as 162 animals from Indonesia) were exported to the EU (Nguyen et al. 2018a, Stuart et al. 2019).

The extensive study by Gewiss et al. (2020) also examined the wild population and impact of trade on *Physignathus cocincinus* in Vietnam. The Green Water dragon has been caught in Vietnam for over 20 years for both the local food market and the international pet trade. The researchers conducted field studies in northern Vietnam from 2014 to 2016, comparing undisturbed and disturbed habitats. They found that populations in disturbed areas were significantly smaller than in undisturbed areas. Over the past 20 years, approximately 1.47 million specimens (!) were imported to Europe and the USA, mainly as wild caught. Domestic trade in Vietnam was also extensive, with 51 documented traders and several online shops. The results

showed that the long-term viability of the species in Vietnam is threatened by intensive collection and ongoing habitat loss. Therefore, the authors proposed stricter protection measures, including the possible listing of the species in CITES Appendix II, to regulate international trade. Recent studies examined sexual dimorphism and whether this is a factor in targeted exploitation of *Physignathus cocincinus* in Vietnam (Ngo et al. 2024). Local hunters prefer to catch adult males because they fetch better prices on local markets due to their larger mass, better developed combs and sometimes more striking coloration. This selective hunting presumably leads to an unbalanced sex ratio, which can have a negative impact on the overall population.

In Cambodia, according to a survey of local hunters, the Green Water dragon population has declined by approximately 50% within 18 years (Stuart et al. 2019).

For Laos, the local wildlife trade in food markets is seen as a major threat. For example, wild meat consumption has increased to around 80–90% of the meat consumed in northern Laos since 1990 (Davenport & Heatwole 2013). The commercialization of water dragons preserved in rice liquor as traditional medicine and as a tourist souvenir is also a threat to local populations (Gilbert 2009, Schweikhard et al. 2019, Suzuki et al. 2015).

## Threats

In addition to heavy hunting and collection, habitat loss, degradation and fragmentation due to deforestation, expansion of agricultural land and human settlements, as well as the development of hydropower and infrastructure are further threats. *Physignathus cocincinus* is found almost exclusively in protected areas throughout its range, but only in Thailand the populations in protected areas appear to be secure. It is believed that the decline rates across the entire range of the species have exceeded 30% in the last three generations (Stuart et al. 2019).

## Reproduction

| Topic                   | Details on the reproduction of <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | <p>Distinguishing the sexes in adult animals is very easy. ♂♂ are significantly larger and more massive in their entire stature. The ♀♀ have a crest on the neck, back and tail, but it is relatively weak, whereas in adult ♂♂ it is very prominent and clearly defined. The heads of the ♂♂ are much more angular and broader. The jaw muscles in the ♂♂ are more strongly developed, which makes the cheeks appear swollen (Werning 2004).</p> <p>Femoral pores are present in the ♀♀, but much smaller than in the ♂♂ (Dedekind &amp; Petzold 1982).</p> <p>Dichromatism is somewhat less pronounced. The yellow-orange colouring in the flank area is sometimes less pronounced in the ♀♀. An intense pink colouring of the lower lip shields occurs more frequently in the ♂♂. ♀♀ usually have green-yellow throats, whereas the throats of ♂♂ are green-blue, sometimes purple. The pink colouring of the labial shields can also be seen on the throat.</p> |
| Reproduction            | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sexual maturity         | <p>First secondary sexual characteristics at the age of 3–4 months due to the generally faster growing ♂♂ and the associated larger and broader heads. First male display behaviour can be observed from the age of 5–6 months (Dedekind &amp; Petzold 1982, Kammerer 1999). Clear gender differentiation at the latest at the age of 12–18 months (Franke 2007). Sexual maturity usually occurs at the age of about two to three years.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |



|                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                    | First egg laying by the ♀♀ at 27 months (Liesack 2001). Other keepers have seen first reproduction at the age of about 18 months at a size of about 50–60 TL cm and a weight of 200 g.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Mating and nesting                 | Mating and egg-laying can take place all year round. Franke (2007) often observed mating in the late afternoon hours, between 5 and 6 p.m. Egg-laying phases were always from early spring to late summer.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Reproductive season                | Kammerer (1999) reports mating activities that took place every year in August and September from 1985 onwards. Copulation took place only 1 to 2 times with a duration of about 30 seconds. The first clutch was laid in February of the following year. A second clutch was always laid 4 weeks later. However, this gestation period seems quite long and it can be assumed that sperm storage occurred due to climatic changes during the cold season.                                                                                                                                                                                                                                         |
| Number of eggs/clutches per season | The number of clutches varies from 1 to 3 per year with 4–21 eggs each. In exceptional cases up to 6 clutches per year are possible (Franke 2007).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Egg size/hatchling size            | Eggs 14–16 mm x 25–28 mm, 2.7–3.4 g (Dedekind & Petzold 1982). Kammerer (1999) found that the eggs grew by about 2 mm per week. They were 12 x 20 mm in size when laid, and shortly before hatching they were about 30 x 40 mm in size. Hatchlings TL 13–17 cm, with approx. 5 cm SVL (Werning 1993) and 2,4–3,55 g weight.                                                                                                                                                                                                                                                                                                                                                                        |
| Incubation and hatching            | 60 days at 31°C, 80 days at 27°C (60–104 days in literature).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Sex determination/ Parthenogenesis | The sex determination mechanism is still unknown – the closest relative, <i>Intellagama lesueurii</i> , has temperature dependent sex determination (Matsubara et al. 2019). Parthenogenesis was first documented by a private owner (Franke 2009). Later, Miller et al. (2019) supposedly first demonstrated parthenogenetic reproduction in the Agamidae family. Although this study once again confirmed the ability of <i>Physignathus cocincinus</i> to parthenogenesis, it was neither the first time in the Green Water dragon nor unique in the Agamidae family. The Butterfly dragons of the genus <i>Leiolepis</i> are also capable of parthenogenesis (Hall 1979, Grismer et al. 2014). |
| Sperm storage                      | Several cases of sperm storage are known (Bitter & Bitter 1986, Kammerer 1999, Werning 2003, Hinz 2006, Kast 2007).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |

## Husbandry and Captive Breeding B/A

| Topic                    | Data for <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|--------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction | No special trigger is necessary, as the animals reproduce all year round. Some keepers use a slightly shortened lighting period of 2–3 months, with a slight reduction in temperature. However, in accordance with the natural range, it is important that the temperature does not drop noticeably below 20°C even in the winter months. During this time, the amount of rain is also lower than in the summer months.                                                                                                                                                        |
| Husbandry requirements   | The most important basic requirement and therefore also the biggest problem when keeping water dragons is a sufficiently large terrarium that is set up to meet the animals' needs. For an adult pair, this should be at least 200 x 100 x 150 cm (BNA 2014). Although not the most pragmatic for daily routine work, a depth of 120–150 cm has proven to be effective in order to offer the animals more space to retreat and to have more design options when setting up the terrarium. To keep a group of 1.3, it is best to use containers larger than 300 x 120 x 200 cm. |

| Topic | Data for <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
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|       | <p>When keeping several animals together, it is important to remember that males and females are not compatible with each other and there would be inevitably fights. Even females do not always get along well with each other and the group composition must be closely monitored. Especially during the egg-laying period, ♀♀ can react very quarrelsomely to other ♀♀ during the days-long search and examination of a suitable place to lay their eggs.</p> <p>Furthermore, it must be taken into account that even when kept in pairs, situations can arise in which the ♀ is stressed from the ♂ and has to be separated.</p> <p>For the well-being of water dragons, a sufficiently large water basin is essential. This can easily take up more than half of the terrarium floor space and should also be at least 20 cm deep. Since water dragons like to lie in water for long periods of time, the water basin should be heated. Faeces are often deposited in the water, and regular replacement and filtering is a basic requirement for maintaining health for hygienic reasons.</p> <p>The actual size of the terrarium is not always the most important criterion for keeping and breeding <i>Physignathus cocincinus</i> in a species-appropriate manner. The animals are sometimes kept and bred very successfully and in excellent health in slightly smaller terrariums than suggested. The structure of the equipment used by the animals is a crucial point. <i>Physignathus cocincinus</i> also likes to stay for hours during the day on branches as thick as its body, which should be placed horizontally or diagonally in the terrarium. When keeping several animals together, it is important to ensure that each specimen has its own resting area where it can bask or observe the area. In the wild, Green Water dragons are often found sleeping on thin branches at night (see Ziegler 2002). In the wild, they also use thin branches during the day to bask above the water (see Werning 2004). Additional thin branches in combination with robust plants offer additional space for activity in the terrarium.</p> <p>Caves, as suggested in the EXOPET study (Krautwald-Junghanns 2018), are not necessary, as the animals, as typical tree and shrub dwellers, prefer branches that are placed across or at an angle for sleeping and very rarely retreat into caves on the river bank (Ziegler 2002).</p> <p>When keeping the water dragons, which are extremely capable of jumping, the additional design of the side walls should also be taken into account. Due to the well-known tendency to leap against the glass panes, the animals should not be kept in display cabinet-like terrariums which can be viewed from all sides. Instead, the back and side walls should be designed so that the animals can also use them; back walls made of natural cork with a bark structure, and artificial rock back walls with integrated, additional resting and basking areas have proven to be the best for this.</p> <p>A sand/earth mixture is suitable as a substrate, which is covered with bark mulch and should always be slightly moistened.</p> <p>Robust fig species have proven to be useful as plants, as they are not readily eaten due to their leathery leaves and can also withstand the sharp claws of animals. <i>Ficus rubiginosa</i> (synonym = <i>Ficus australis</i>) is often used in zoological exhibits as it has a significantly firmer foliage than the ubiquitous weeping fig, <i>Ficus benjamina</i>.</p> <p>A temperature of around 23–28°C is desirable in the terrarium. Temperatures of 35–40°C should be achieved under the basking spots. Metal halide lamps are suitable for lighting as they provide a good source of heat while also emitting the required UV radiation. LED bars or T5 tubes can also be used for basic lighting.</p> <p>Humidity during the day 70–80%, at night up to 95%, which usually occurs automatically due to the heated water part.</p> |

| Topic                                                           | Data for <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
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|                                                                 | <p>The juveniles should not be raised in the large display terrarium straight away, as they could otherwise become quite shy (Werning 2004). In the first few months, the growing water dragons can be raised in small groups. From an age of approx. 6–12 months, the ♂♂ must be separated from one another, as otherwise suppression and stress can occur in the group. The juveniles grow quickly and have a high food requirement. Initially, they only eat live food, which should be mineralized and enriched with vitamins at each feeding. All types of insects are greedily devoured, with house crickets (<i>Acheta domestica</i>), steppe and Mediterranean crickets (<i>Gryllus assimilis</i> &amp; <i>G. bimaculatus</i>), and Argentine forest cockroaches (<i>Blaptica dubia</i>) having proven to be good main foods. Larvae and butterflies of the wax moth (<i>Galleria melonella</i>), as well as all kinds of flies, grasshoppers, larvae of mealworms and <i>Zophobas</i>, small snails and earthworms are also used as food for rearing.</p> <p>Adult water dragons, like their young, eat anything they can overpower. In addition to the insects mentioned, they are sometimes given day-old chicks (Ullrich 1979) or mice (Werning 2000b). As they get older, <i>Physignathus cocincinus</i> eat more and more plant-based food, which in can make up to 80% of their diet in the wild (Ziegler 2002). Plant-based food in the terrarium includes sweet fruits such as pears, apples, strawberries, blueberries and melons, as well as the occasional vegetable such as zucchini, cucumber and iceberg lettuce (Franke 2007). Bananas are also very popular (Ullrich 1979). Live fish in the water are usually ignored, or the agamas sometimes have difficulty catching them. Dead fish, however, are readily accepted when presented with tweezers (Werning 2004). Mealworms, <i>Zophobas</i>, waxworms or baby mice should only be fed sparingly due to their high protein and fat content (BNA 2014). However, these energy bombs are ideal for gravid females and directly after the exhausting egg-laying process.</p> |
| General characteristics, difficulties with keeping and breeding | <p>The only difficulty in keeping Green Water dragons is the space they absolutely need. Jumping against the glass panes of the terrarium and the resulting snout injuries were often caused by the small size of the terrarium and the impetuous natural flight behaviour, especially in wild-caught animals. Foekema (1972) already gave the appropriate advice that <i>Physignathus cocincinus</i> requires large and expensive terrariums and should therefore only be imported by order. Fortunately, captive-bred animals are much calmer, but even in this case it occasionally happens that the glass panes are not seen as an obstacle.</p> <p>Providing another large terrarium for the possible separation of suppressed females or those weakened by egg-laying presents an additional difficulty.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Care of the young, technical and time effort                    | Raising the juveniles is completely unproblematic. Young water dragons become tame more easily if they are not raised in terrariums that are too spacious (Werning 2004). Before they reach sexual maturity, the young males must be separated.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Life expectancy                                                 | <p>10–15 years, in exceptional cases up to 25 years.</p> <p>The highest documented age to date was reached by a 24-year-old ♂ (Velenská &amp; Kodym 2002).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Frequency of private breeding and reproduction in zoos          | The first documented captive breeding was in 1965 (Meyer-Holzapfel 1969), then in 1975 (Chester Zoo 1975), and later in 1977 (Ullrich 1979) and 1979 (Dedekind & Petzold 1982).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |

| Topic                          | Data for <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
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| Breeding difficulty evaluation | <p>It is interesting in this context that the Green Water dragon was kept in terrarium conditions relatively late. While the related Australian water dragon, <i>Intellagama lesueurii</i>, had already been known in terrariums for a longer time, Scherpner wrote in the then groundbreaking 'Terrarium Science' (Klingelhöffer 1957), which he revised, what a stroke of luck it was that Rosenberg 'came into possession of a <i>Physignathus</i> from the mainland of the Indies that had not previously been introduced to us'. In 1933, Rosenberg received a single male <i>Physignathus cocincinus</i> from the Hagenbeck Zoo, which developed splendidly despite a severe snout injury. After being kept for over 6 years, the animal was reluctantly killed due to a severe injury from a rhinoceros iguana living with it, because further deterioration would have made the rare specimen of inferior value for the museum collection (Rosenberg 1940). Successful keeping and individual breeding successes in private hands and zoos only occurred in the 1960s and 70s. From the 1980s onwards it became much more frequent (Schliemann 1968, Meyer-Holzappel 1969, Vogel 1969, Bechtle 1971, Foekema 1972, Nietzke 1972, van den Sande 1974, Chester Zoo 1975, Bechtel 1976, Jahn 1978, Stettler 1978, Jauch 1979, Lindstrom 1979, Ullrich 1979, Vit 1979, Kahl et al. 1980, Matz &amp; Vanderhaege 1980, Nietzke 1980, Petzold 1980, Demeter 1981, Blake 1982, Dedekind &amp; Petzold 1982, Howard 1982, Mudde 1982, Ortner 1982, Heselhaus 1983, Obst et al. 1984, Stehr 1984, Blake 1985, Tomey 1985, Bitter &amp; Bitter 1986, Mader &amp; Kerr 1986, Reid 1986, Stolk 1986, Jes 1987, Mader 1987, Martin 1987, Mattison 1987, Blake 1988, Hesselting 1988, Cologne Aquarium at the Zoo 1988, Zimniok 1988, Heselhaus 1989, Zimniok 1989, Bech &amp; Kaden 1990, Mainz 1990, Karbe et al. 1991, Mader 1991, Kodym 1992, Rogner 1992, Vosjoli 1992, Werning 1993, Mader 1994, Rehak 1995, Rezheninova 1995, Werning 1995, Lladó Hädinger 1996, Bartlett &amp; Bartlett 1997, Henkel &amp; Schmidt 1997, Lange 1997, Lladó Hädinger 1998, Bruins 1999, Kammerer 1999, Liesack 1999, Manthey &amp; Schuster 1999, Meek 1999, Dost 2000, Falk 2000, Werning 2000a, Werning 2000b, Werning 2000c, Liesack 2001, Simon 2001, Hernandez-Divers 2002a, Hernandez-Divers 2002b, Drewes 2004, Werning 2004, Engel 2006, Add 2006, Werning 2006, Franke 2007, Kast 2007, Werning 2008, Drewes 2009, Franke 2009, Ngo &amp; Bui 2009, Rohovský 2010, Smith 2013, BNA 2014, Rogner 2015, Werning 2015, Esterbauer 2017, Krautwald-Junghanns 2018, Miller et al. 2019, Fischer 2020, Pachmann 2020, Love 2021).</p> <p>The Green Water dragon is still a commonly kept species in large exhibition facilities and tropical houses of zoological institutions, where natural breeding occurs regularly, as clutches are not always found. Currently (as of September 2024), according to the zoo animal list, there are a total of 182 animals kept in zoological institutions. Of these, 157 are in Europe (in Germany alone in 29 zoos and botanical gardens), 13 in the USA and Canada, as well as 11 in Asia and 1 in Africa (Graf et al. 2024). However, it can be assumed that the list is not complete and that there are significantly more animals kept in public institutions, especially in the USA, than previously thought.</p> <p>At times, the animals were also bred in large numbers by private owners. For example, Kammerer (1999) reported a total of 167 juveniles. In 1987 alone, Liesack (2001) received a total of 8 clutches of 89 eggs from 3 ♀♀, of which only 68 young animals hatched.</p> <p>Due to the high availability of very cheap wild-caught and farm-bred lizards, breeding activity has decreased significantly among some private owners and incubation has only been carried out by pre-order. It is to be hoped that the elimination of imports of wild-caught lizards will lead to a greater interest in healthy offspring and that more owners will once again engage in the very simple breeding of this fascinating agama.</p> <p>Very easy to breed considering the large space required.</p> |

| Topic                                | Data for <i>Physignathus cocincinus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
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| Mortality in the first years of life | Taking into account the high feed requirements and using appropriate UV lighting, raising the juveniles does not cause any problems. Low mortality rate when reared with a diet rich in minerals. With species-appropriate care and timely separation of the ♂♂, over 95% of the animals reach sexual maturity.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| F2 generation bred in captivity      | Yes. There are now several generations of Green Water dragons in breeding. The first documented breeding was in 1965 in the Bern Zoo (Meyer-Holzapfel 1969), then 1977 (Ullrich 1979), 1975 in the Chester Zoo, 1979 in the Berlin Zoo and 1981 in the Hellabrunn Zoo (Dedekind & Petzold 1982). The first explicitly mentioned F2 occurred in 1989 (Kammerer 1999). Werning (2000b) mentions an F3 generation for his 15 years of experience keeping them at the time.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Commercial breeding /ranching        | Reasonably well represented in tropical halls and large exhibition facilities, often 'wild hatchlings' because the eggs are not always found. Very regularly found in private keeping, but due to their size they are more of a pet. Breeding has been suppressed by some private keepers by only hatching the eggs when there is demand. With the formerly very inexpensive wild-caught babies no longer available on the market, the appreciation and demand for healthy offspring has fortunately increased somewhat. Overall, however, there is a noticeable trend that fewer Green Water dragons are being kept than 10–20 years ago. One reason for this is that a large number of other interesting large agama species are now available as healthy offspring. For example, years ago, offspring of various species of the genera <i>Gonocephalus</i> , <i>Hypsilurus</i> , <i>Lophosaurus</i> , and <i>Hydrosaurus</i> were only available in exceptional cases, but today they are in competition with <i>Physignathus</i> due to the frequently limited space available in pet keeping. |
| Interviews/ Surveys/ Consultations   | 10 private holdings (9 breeders, 1 owner), 4 zoos (4 breeding facilities).<br>The responses to the questionnaires represent only a small fraction of the known keepers and breeders.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

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## Gekkonidae

### *Cyrtodactylus jeyporensis* (Beddome, 1878)

| Species                          | Original description | Common name                                 | Common name International | Known in the trade |
|----------------------------------|----------------------|---------------------------------------------|---------------------------|--------------------|
| <i>Cyrtodactylus jeyporensis</i> | (Beddome, 1878)      | Patinghe Indian gecko, Jeypore Indian gecko | Jeypore Gecko             | Yes                |



Fig. 2: Adult gravid ♀ of *Cyrtodactylus jeyporensis* in the habitat, Araku Valley, Andhra Pradesh, India (Ch. Langner)

### Morphology and Taxonomy

*Cyrtodactylus jeyporensis* was scientifically described in 1878 by the British officer and naturalist Richard Henry Beddome based on a single male specimen. The species was considered lost for the next 133 years until it was rediscovered in 2010 by Agarwal et al. (2012). Until a few years ago, *Cyrtodactylus jeyporensis* was traditionally classified within the genus *Geckoella*, established by Gray in 1867. The phylogenetic relationships within the genus *Geckoella* are not considered to be sufficiently clarified. Based on comparisons of morphological characteristics, Bauer (2002) only granted *Geckoella* the rank of a subgenus within *Cyrtodactylus*. A phylogenetic study by Feng et al. (2007) restored the genus status. The members of the genus *Geckoella*, which is endemic to India and Sri Lanka, are now mostly classified in the genus *Cyrtodactylus* (Grismer et al. 2021, Agarwal & Karanth 2014).

With more than 350 species, *Cyrtodactylus* is the most species-rich genus within the order Gekkota and the third largest vertebrate genus after *Pristimantis* and *Anolis*. The assignment of the taxon *Cyrtodactylus jeyporensis* to the genus *Cyrtodactylus* is, as explained above, not undisputed, and it remains to be seen whether this huge collective genus *Cyrtodactylus* will continue to exist in its present form in the future.

*Cyrtodactylus jeyporensis* and most other members of the former genus *Geckoella* have a rather stocky body shape, unlike other bent-toed geckos. Head and torso are not flattened. The tail is carrot-shaped and tail length is only a bit more than  $\frac{2}{3}$  of body length. The toes and fingers of *C. jeyporensis* are bent in an upward curve (bent-toed geckos), clawed and typical for the genus, they miss any adhesive lamellae. The average head-body length of adult specimens was about 50–60mm in 14 specimens measured in the habitat. The tail length was 32–40mm. Regenerated tails were slightly shorter than the originals (Langner, pers. obs.). The dorsal part of the body is covered with large, square or hexagonal, flat scales, arranged evenly next to one another, in a regularly shape like the bricks of a wall. Adult specimens of *C. jeyporensis* have a very distinctive, unmistakable dorsal marking. The basic dorsal colour is orange-brown to light brown. It is interspersed with a striking row of very contrasting large, sometimes almost black to chocolate-brown spots. The spots are round to elongated-oval, sometimes arranged in relatively symmetrical pairs between the shoulder and sacrum. On the back of the head and in the neck area there are partially fused spots with similar dark markings. The flanks have an additional row of four to five dark spots between the bases of forelimbs and hind legs. The spots along the flanks continue to the ventrolateral edge the first two-thirds of the tail. The limbs are slightly lighter coloured than the trunk, with a row of brown bands (forelimbs) or spots (hindlimbs). In comparison to the dorsal side the head is less intense orange or light brown coloured, with partially symmetrical darker markings. The labial scales and sides of the neck are whitish with scattered dark markings. The ventral side is pure white, with dark spots under the chin, on the lateral edges of the neck, and along the flank edges. The basic colouration of the tail is also orange-brown to light brown with five to seven broad dark brown bands. The iris is brass-coloured.

## Distribution and Habitat

### Distribution

*C. jeyporensis* appears to be adapted to the few remaining moist tropical sclerophyll forests in areas above 1,200 meters. These remaining habitats are small and fragmented. Located in the Eastern Ghats in the north of Andhra Pradesh and in southern Odisha. However, the areas in which the geckos were rediscovered are now under enormous pressure from deforestation, mining and agriculture. It is suspected that the taxon may be a relic from climatically more humid periods. As arid areas continued to extend across the Indian subcontinent, the species was probably only able to find suitable refuges in these climatically favoured areas.

Type locality: 'Patinghe Hills' (1280 m above sea level), Jeypore, Madras Presidency, India. The male type specimen was found in the Jeypore Hills, Koraput District, Odisha. Two additional males were found during the rediscovery: One in Deomali, Koraput District, Odisha and the other one in Galikonda, Araku Valley, Visakhapatnam District, Andhra Pradesh, India (Agarwal et al. 2012).



In the latter area, a total of 14 *C. jeyporensis* were observed during two habitat surveys in 2015 and 2016. Seven females and three semi-adult specimens were found for the first time on this occasion (Langner 2022, Langner pers. obs.).

### Habitat and Behaviour in the Wild

The habitat described above consists of a coffee plantation in which trees left standing for shade represented the remainder of the former primary forest. These large solitary trees form a nearly closed canopy, which enabled almost complete shade of the undergrowth, which mainly consists of *Coffea arabica*. The individual trees were also regularly planted with Black pepper (*Piper nigrum*). There was occasional secondary growth of shrubs and trees of various sizes. Small and medium-sized boulders were scattered around in between. At the edge, especially on steeper areas in the upper part, there were also larger rock faces. During fieldwork in the rainy season in mid-July, around 10:30 p.m., the following temperature and humidity data were determined: 23.2°C; 88%. at night, light drizzle set in (Langner 2022). The author was able to observe adult specimens primarily on the ground and in the lower root system of trees. In one case, a male specimen was sitting on a jackfruit tree trunk (*Artocarpus heterophyllus*) covered by moss and lichen covered at a height of about 3.5 m. Two semiadult *C. jeyporensis* were observed climbing on thin branches at a height of 1.5–2 m, in one case in a coffee bush, and in the other case in a bush of *Glochidion* sp. Two females, one juvenile and one male encountered in the wild had regenerated tails (Langner pers. obs.).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 15).

On 26/03/2018, India banned the export of all wild-caught or wild-collected plants of species listed in CITES Appendices I, II and III for commercial purposes (CITES 2018).

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

EN (Endangered B1ab(iii)+2ab(iii), assessed August 08, 2019).

### Threats

The forest habitats in which this species occurs are under extreme anthropogenic pressure (Agarwal et al. 2012). None of the known locations of *Cyrtodactylus jeyporensis* are protected and both localities are heavily deforested. Galikonda and the surrounding hills were converted to coffee plantations and in Deomali there is enormous pressure from continuous conversion to pasture and from firewood removal. The hills in Koraput district are also subject to ongoing bauxite mining. In general, the autochthonous forests in this region have been converted into plantations with non-native tree species, arable land or pastureland, and the remaining forest patches are under extreme threat from firewood harvesting and occasional forest fires. There are plans for bauxite mining in the mountains around the type locality. The original forest cover has already been completely destroyed. Non-native monocultures are being planted for forestry purposes throughout the species' range, predominantly non-native silk oak (*Grevillea robusta*) and *Eucalyptus* sp.

It is assumed that *C. jeyporensis* has already been eradicated at its type locality.

The subpopulation in Deomali is considered to be in immediate danger of extinction due to the rapid deterioration of its habitat, mainly due to deforestation (Mohapatra 2021).

In addition to *Cyrtodactylus jeyporensis*, nine other amphibian and reptile species were recorded in the coffee plantation in Galikonda on an area of less than one hectare during two nighttime inspections within a few hours (Langner 2022).

Given the enormous species richness in a small-scale, intensively used anthropogenic area and the presence of *Cyrtodactylus jeyporensis* and the Skink *Sepsophis punctatus*, two extremely rare reptile species endemic to the Eastern Ghats, the presence of a recently described gecko species endemic to the area (*Hemiphyllodactylus arakuensis*), as well as the presence of a possibly as yet undescribed further *Cyrtodactylus* species from the *C. (Geckoella) nebulosus* complex, it would be imperative to place the area under protection and, if necessary, to re-naturalize it.

It might even be possible to continue to use it extensively in parts of the area in a way that protects the environment, e.g. for the organic cultivation of coffee and pepper, in order to ensure a livelihood for the locals and to increase acceptance of such conservation measures (Langner 2022).

The establishment of a stable, controlled and managed ex situ population under human care, e.g. within the framework of Citizen Conservation, could counteract a potentially impending extinction scenario.

## Reproduction

| Topic                              | Details on the reproduction of <i>Cyrtodactylus jeyporensis</i>                                                                                                                                                                                                                                                                               |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | The species exhibits sexual dimorphism with regard to the significantly enlarged hemipenial pockets of the adult ♂♂.                                                                                                                                                                                                                          |
| Reproduction                       | Oviparous. Two hard-shelled eggs per clutch.                                                                                                                                                                                                                                                                                                  |
| Sexual maturity                    | Starting from the age of 1½–2 years.                                                                                                                                                                                                                                                                                                          |
| Reproductive season                | Spring (March to end of May).                                                                                                                                                                                                                                                                                                                 |
| Number of eggs/clutches per season | 2 eggs per clutch, up to 8 clutches/season. Hatch rate is 100%.                                                                                                                                                                                                                                                                               |
| Egg size/hatchling size            | Hatchlings have a TL of 46 mm and weigh 1.5 g.                                                                                                                                                                                                                                                                                                |
| Incubation and hatching            | 70–86 days at 26–28°C; with fluctuating temperatures in the terrarium room, depending on the season between 20 and 27°C during the day, 23 to 18°C at night. It is recommended to place the eggs individually on bottle caps and deposit these on very moist perlite or vermiculite, and incubate them in a commercially available incubator. |
| Sex determination                  | Genetic sex determination, the sex chromosomes are unknown (Gamble 2010).                                                                                                                                                                                                                                                                     |
| Sperm storage                      | It has been suggested by breeders that sperm can be stored for 2 to 4 clutches after a successful mating.                                                                                                                                                                                                                                     |

## Husbandry and Captive Breeding B/B

| Topic                                                           | Data for <i>Cyrtodactylus jeyporensis</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
|-----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Moderate reduction in temperature and humidity (see husbandry requirements) from December to the end of February in accordance with the natural conditions in East India. In addition, separation of the sexes at this time is beneficial for the regeneration of the females and as a mating stimulus.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Husbandry requirements                                          | <p>According to the German minimum requirements for keeping reptiles the dimensions of the terrarium should be at least 60 x 40 x 60 cm or 50 x 50 x 50 cm (L x W x H). The tanks should offer a large ventilation potential in the lid area. An additional narrow ventilation slit in the area under the front sliding glasses ensures sufficient air exchange. Commercially available LED or fluorescent bulbs are sufficient as lighting for the strictly nocturnal geckos. In summer, the lighting is switched on for 12 hours a day, and in winter for 8 hours a day.</p> <p>The basic temperatures in the terrarium in summer should be around 26–28°C during the day, dropping to room temperature at night, in wintertime between 22–26°C. The humidity should be higher in summer than in winter. Water is sprayed lavishly 2–3 times a week, especially in the rainy season (summer), in winter only once a week, imitating a dry period. The ventilation areas in the lid area should be large enough so that the furnishings can dry completely after misting. Stagnant air must be avoided at all costs. The terrarium needs to be well structured with roots, branches and pieces of bark placed on the floor. A so-called 'wet box' filled with slightly damp moss is also welcomed by the geckos, especially during the skin shedding phase. The terrarium should be densely planted. A variety of common houseplants such as <i>Ficus benjamini</i>, <i>Philodendron spec.</i> etc. are suitable for this. The geckos are fed with commercially available insects such as crickets, house crickets, small cockroaches, grasshoppers, woodlice, etc. of appropriate size. The insects are supplemented with mineral/vitamin mixtures at each feeding. A small water bowl completes the necessary furnishings.</p> |
| General characteristics, difficulties with keeping and breeding | The best results have been achieved by keeping specimens separately. The individual specimens should only be put together briefly for mating during the breeding season.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Care of the young, technical and time effort                    | Offspring are raised individually in smaller containers under identical conditions as the adults. Adequate calcium supplementation is an absolutely essential requirement.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Life expectancy                                                 | Yet unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Frequency of private breeding and reproduction in zoos          | Rare, as the geckos are only kept by a few private keepers. Not known from any zoo.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Breeding difficulty evaluation                                  | Keeping and breeding does not present any difficulties under the conditions described.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Mortality in the first years of life                            | No losses during rearing (individual rearing).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| F2 generation bred in captivity                                 | Yes.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Commercial breeding/ranching                                    | No.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Interviews/ Surveys/ Consultations                              | 8 experienced private breeders.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |

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**Christian Langner (29. 07. 2024)**

### *Tarentola chazaliae* (Mocquard, 1895)

| Species                    | Original description | Common name                      | Common name International                                            | Known in the trade |
|----------------------------|----------------------|----------------------------------|----------------------------------------------------------------------|--------------------|
| <i>Tarentola chazaliae</i> | (Mocquard, 1895)     | Helmeted gecko, Helmethead gecko | Helmkopfgecko<br>Gecko casqué<br>Perenquén de Casco<br>Geco de Casco | Yes                |



Fig. 3: *Tarentola chazaliae*

- a Adult *T. chazaliae* in the wild (U. Prokoph)
- b adult *T. chazaliae* in the wild (Ch. Langner)
- c Head & toe detail of the Helmeted gecko (U. Prokoph)
- d subadult captive bred offspring of the Helmeted gecko (J. Felka).

### Morphology and Taxonomy

The charismatic Helmethead gecko, *Tarentola chazaliae*, is a smaller representative of the genus *Tarentola*, which cannot be confused with any other gecko due to its characteristic ledge on the back of the head. At first glance, its appearance reminds of horned lizards of the genus



*Phrynosoma*. Originally described by Francois Moquard in 1895 as *Geckonia chazaliae*, he already noted a very close relationship to the genus *Tarentola* in the first description of the genus and species. Moquard's laboratory received several specimens of reptiles from Cap Blanc from the ornithologist and zoological collector Raymond Comte de Dumas (1862–1930). As can be read in the first description, the Helmeted gecko was named at the request of Count Dumas after his sailing yacht 'Chazalie', a three-master which sailed as an expedition ship through the Mediterranean, the Atlantic and the Caribbean from 1893 to 1897. The 'Chazalie' ran aground on a sandbank off Cap Blanc, and during the land excursion the type specimen of the Helmeted gecko was collected, among other things.

Presumably due to the distinctive appearance, there are no other synonyms except for the genus *Tarentola chazaliae*. The synonym *Geckonia malazodes*, named as an 'invalid correction' by Uetz & Hallmann (2020), is based on a misinterpretation of the caption in Ahl (1930): While the animals are correctly referred to as *Geckonia chazaliae* in the text by Ahl (l.c.), the caption (*Geckonia* Malazodes, Rio de Oro. Phot. Spaney) leaves room for speculation.

Until molecular genetic studies by Carranza et al. (2002), *Tarentola chazaliae* was a monotypic species within the genus *Geckonia*. In this study, a separate lineage was identified that seemed to be nested with the Macaronesian clade (subgenus *Makariogecko* of the Canary and Cape Verde Islands) (Carranza et al. 2002). Later studies again confirmed the genus affiliation, but found a basic relationship to *Tarentola annularis* and *Tarentola ehippiata* from the subgenus *Sahelogecko* (Rato et al. 2012). Due to the unique morphological features, such as the characteristic 'helmet' and the different body shape and proportions, it seems reasonable to continue the subgenera established by Joger (1984b) (*Tarentola*, *Makariogecko*, *Sahelogecko*, *Saharogecko* and *Neotarentola*) and to place *Tarentola chazaliae* in the subgenus *Geckonia*.

Senfft (1931) begins his report on *Geckonia chazaliae* with the words: 'It seems to me as if our Lord, when creating this strange creature, had first intended to 'produce' a horned lizard, perhaps with the habitus of a *Phrynosoma modestum*, but then thought of something else and modelled a gecko from what had already been created' The comparison to the habitus of the well-known horned lizards could hardly be more apt and describes the appearance of the Helmeted gecko quite well in idyllic words.

Maximum length 115 mm, usually less than 100 mm (Martínez del Marmol et al. 2019). Schleich et al. (1996) report a SVL of 64 mm and a SL of 37 mm. A remarkably large female from Cap Blanc (MNHN 1996.6270) reached a SVL of 74 mm (Ineich et al. 1997). While the tail length of Mediterranean geckos usually corresponds approximately to the head-body length, it is characteristic of Helmeted geckos that the tail length only accounts for a little more than 1/3 of the total length. This species also does not store fat reserves in the tail, as we know from related species or other desert-dwelling geckos of similar habitats, but the fat reserves are formed in the trunk on the belly sides as fat bulges (Schulte 1974). Like all members of the genus *Tarentola*, the Helmeted gecko has a visible claw only on the 3<sup>rd</sup> and 4<sup>th</sup> fingers and toes, while the 1<sup>st</sup>, 2<sup>nd</sup> and 5<sup>th</sup> fingers and toes, which macroscopically appear to have no claws, have a flat, nail-like shield distally. The female animals, however, have a tiny, retractile claw on these toes, which can be described as a clear sexual characteristic (Joger 1984a).

A characteristic feature of *Tarentola chazaliae* is the helmet-like ridge on the back of the head with the distinct occipital tubercles, which is unique to this species. The somewhat grim look is caused by the 5–6 supraocular scales above the eyes, which protrude far to protect the eyes (Seufer 1988). In comparison to the other representatives of the genus, the animals have a



very stocky body shape. As an adaptation to the lifestyle as inhabitants of sandy soils, the toes are also significantly shorter in comparison to other representatives of the genus and also have reduced adhesive lamellae; cf. Bons (1959), González de la Vega (2012), Schleich et al. (1996). In addition, the fingers and toes are very roughly scaled. The fringe-like scales on the sides are not as pronounced as in other psammophilous genera, such as the fringe-fingered lizards of the genus *Acanthodactylus*, but stand out clearly in direct comparison to other representatives of the genus *Tarentola* (see photo in Martínez del Marmol et al. 2019). The function of the fringe-like individual scales is to prevent sinking into loose sand and is adapted to the bottom-dwelling lifestyle in very sandy habitats.

The colouration on the upper side is in different shades of grey and brown, sometimes reddish brown to sand-coloured. The pattern on the upper side is very variable. Pattern and colouration are very individual, but also depending on the mood and time of day (González de la Vega 2012). The belly side is always lighter than the upper side, in a light cream tint, sometimes with delicate speckles. Occasionally animals with no pattern at all occur, which are plain sand-coloured dorsally. A very characteristic pattern element, which often exists even in pale, poorly coloured individuals, are 5 (rarely 6) diamond-shaped, light grey spots across the mid-line of the back. These can be somewhat wider, or narrow and elongated. Sometimes these dorsal spots are interrupted again in the middle, or have a delicate centre line. Very rarely, these dorsal spots can merge into a continuous, light grey vertebral band (Campmany Garcia & Déniz Suárez 2001). In some cases, the light spotting continues on the tail. The striking light grey markings very often alternate with the larger brown spots that precede them along the middle of the back. There are 7–10 darker transverse bands on the tail that are more or less intense, but they are not completely banded, as the underside of the tail is pale and unmarked. Also striking are the always very light ocular scales that immediately surround the eye.

In contrast to the otherwise often different juvenile markings in other species of the genus *Tarentola* which fade with age, the hatchlings of *Tarentola chazaliae* do not have distinctively contrasting, light-and-dark banded tail tips (compare to Hulbert 1995). Juveniles are almost identically patterned to adults when they hatch (see González de la Vega 2012). Sometimes they are coloured in a slightly darker shade of grey, with otherwise identical markings (Seufer 1988). However, this seems to vary greatly from individual to individual. The further darker spots on the back, head and limbs are often not as sharply defined as the light grey dorsal spots and can range from washed out to clearly pronounced. The colour and marking variants bred out by a U.S. breeder cited in Bergmann (2006) are probably due to the high natural variability. The iris is bronze-coloured in varying degrees of brightness, sometimes with pronounced red or brown veins.

The vision of *Tarentola chazaliae* was studied by Roth et al. (2009). They found that these nocturnal animals can distinguish colours even in the weak moonlight, while humans are colour blind under these conditions. The sensitivity is 350 times higher than that of the human eye. In direct comparison with the giant Madagascar day gecko (*Phelsuma grandis*), it was found that the optical system of the diurnal species shows no signs of clearly distinguishable concentric zones. Thus, the optical system of *Phelsuma grandis* is monofocal, whereas the multifocal optical system in *Tarentola chazaliae* is characterized by different concentric zones with different refractive powers. The ability of geckos to see different colours even at night is unique among vertebrates (Bauer 2013).

## Distribution and Habitat

### Distribution

The Helmeted gecko inhabits exclusively a narrow coastal strip, from the northernmost tip of Mauritania to just below Agadir (Inezgane) in Morocco (Mellado & Mateo 1992). The terra typica at Cap Blanc, a long peninsula, which lies half in Western Sahara (Morocco) and half in Mauritania, seems to be the southernmost point of distribution despite other erroneous information. In the literature, ‘central Senegal’ (Rösler, 1995) or even specifically ‘Dakar’ (Schleich et al. 1996) are often mentioned. Referring to the distribution map in the last-mentioned work, there is a correction for Mauritania by Ineich et al. (1998), which indicates that the distribution shown over the entire coastal area of Mauritania is incorrect. Investigations in this 500 km long coastal section of Mauritania could not reveal a single specimen, with the exception of the extreme north, Cap Blanc. It is also pointed out that no specimen collected in this area can be found in any European museum collection. Further research in Mauritania confirmed that *Tarentola chazaliae* is only found in the area bordering Western Sahara (Padial 2006).

A more recent study, which deals with the herpetofauna of the Parc National du Banc d’Arguin, a 120,000 km<sup>2</sup> area along the northern Atlantic coast of Mauritania, was again only able to confirm the occurrence for Cap Blanc (Sow et al. 2014).

Despite sufficient studies in Senegal, Trape et al. (2012) only show a photographic verification from the area around Nouadhibou, which lies north of Cap Blanc on the Mauritanian side of the peninsula. The map shown, as well as the distribution mentioned in the text, also only refers to the area starting south of Agadir as the northernmost distribution limit and names Cap Blanc as the southernmost point.

Wilms et al. (2013) also point to the erroneously named site of Dakar, which has its origins in the work of Bons (1967). Le Berre (1989) already listed individual sites and also only mentions Port Etienne (Nouadhibou) and Cap Blanc in the south. Nevertheless, even in more recent literature, for example Elbahi et al. (2022), Senegal is repeatedly mentioned as the southernmost distribution, without providing more precise information.

Starting from an area from the Souss Valley (south of Inezgane/Agadir) to Cap Blanc in northern Mauritania, the distribution area extends over a coastline of approximately 1,400 km. The northern Souss Valley population is separated from the southern population by a gap of approximately 50 km (Martínez del Marmol et al. 2019).

*Tarentola chazaliae* is usually found within a range of about 5 km, in rare cases up to a maximum of 25 km inland (Harris et al. 2010). With the discovery in Abatteh, about 50 km from the Atlantic Ocean, Helmeted geckos were first found further inland (Bons & Geniez 1996). In the Western Sahara region, a total of 14 specimens were sighted during the night on the stretch from Laâyoune to Smara up to a distance of about 115 km from the ocean (Hasi et al. 1997). Most recently, during a field excursion to the area north of Smara, another specimen was found 144 km inland (Sánchez-Vialas & Aznar-González de Rueda 2016). In this region, near Wadi Saguia el-Hamra, an oceanic climate prevails despite the great distance from the Atlantic. Another species, the fringe-toed lizard *Acanthodactylus aureus*, which also has a coastal distribution, can as well be found in the area around Smara (Bons & Geniez 1996, Geniez et al. 2000).

### Habitat and Behaviour in the Wild

*T. chazaliae* is basically nocturnal, but can also be observed during the day occasionally (Martínez del Marmol et al. 2019). Schleich et al. (1996) cite ants in the stomach contents as evidence of a partially diurnal lifestyle.

In contrast to other desert-dwelling gecko species, they do not actively dig burrows to hide in. These geckos seek shelter under stones during the day or can be found in the tangle of plants of *Euphorbia*, which occurs in the same habitat (Bons 1959). The hollow, dead branches form excellent hiding places. Furthermore, the animals seek shelter under anything that provides the necessary protection. The abundant waste dumped in the countryside which can be found in some parts of the range, is also used as cover (Henkel & Schmidt 2003a). Like almost all geckos, *Tarentola chazaliae* is capable of vocalization. This serves particularly as interspecific communication, but they also emit startle sounds as part of their defensive behaviour (Gramentz 2005). These geckos can be heard calling regularly in the evenings and at night, particularly during mating and egg-laying season. The call is a short, melodic buzzing sound lasting about half a second at a constant frequency (Schulte 1974).

The threatening behaviour of the Helmeted gecko is very pronounced. When the animals are spotted in a hiding place, they usually remain rigid and rely on their cryptic camouflage, which allows them to literally blend in with the ground. However, as soon as the animals notice that they have been discovered, they do not flee, but instead immediately assume a threatening posture and open their mouths wide. Schulte (1974) outlines the threatening behaviour in detail and divides it into 4 phases: 1.) Opening the mouth, 2.) uttering threatening call, 3.) jumping at the supposed enemy & 4.) biting the attacker.

*Tarentola chazaliae* is predominantly insectivorous, but probably also take the smallest vertebrates, such as *Saurodactylus harrisi*, which live in the same microhabitat.

Burmeister from the Bavarian State Collection of Zoology (ZSM) analysed faecal samples of *Tarentola chazaliae* from the area south of Goulmime on behalf of Schleich (Schleich et al. 1996). As expected, no plant material was found, but large pieces of gecko skin. The part of hymenoptera (ants of Formicinae and Myrmicinae), was around 20%. Furthermore, a large specimen of a grasshopper (Caelifera) was found. The main components, at 40%, were round fungus beetles (Leiodidae) and beetles of the family Catopidae. These are small to medium-sized beetles that often live in the nests of small mammals and birds and are rarely found due to their underground lifestyle. A further 10% were Sap beetles (Nitulidae) and 20% of the prey were Wood-borer beetles (Bostrichoidea) of different genera. Finally, 5% were spiders (Aranea) and 5% harvestmen (Opiliones) (Schleich et al. 1996).

During our own investigations in the habitat of *Tarentola chazaliae*, in addition to small beetles and spiders, woodlice (*Porcellio saharaiensis*) and unidentified silverfish (*Zygentoma* sp.) were also frequently observed.

## Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 16).

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

## IUCN Red List Status

VU (Vulnerable A3cd; B1ab(iii,v), assessed 18 July 2004) (Wilms et al. 2013).

## Protection in the Range States

In Morocco, Law No. 29-05 on the protection of wild fauna and flora species and the control of their use applies not only to CITES species but also, through its Category IV, to non-CITES species classified by the IUCN as threatened. Without a permit, any capture, sale, purchase or export is prohibited (Bulletin Officiel 2011).

While the species occurs in some protected areas in Morocco and Mauritania, most of its range is outside protected areas (Wilms et al. 2013). There is no information on specific management plans or further research on the population in Morocco (CITES 2022).

## Threats

The IUCN lists the Helmeted gecko as vulnerable in the Red List due to its limited distribution and the few known locations. In addition, the decline in suitable habitat due to loss of size and quality is used as a criterion, as is the capture of adult specimens for trade (Wilms et al. 2013). Furthermore, the risk status is justified by the fact that the species was known from fewer than 10 locations. In this respect, the level of knowledge has expanded significantly, as Martínez del Marmol et al. (2019) processed almost 70 discovery points on their distribution map. However, Harris et al. (2010) already showed in their distribution map, in addition to the 2 new locations mentioned, around 50 unspecified locations that they had taken from the literature.

The first indication of a lack of trade control and a lack of sufficient data on wild-caught imports of the Helmeted gecko was provided by Affre et al. in 2005. The mention of *Tarentola chazaliae* by Auliya (2003) does not allow any conclusions to be drawn about a continuous appearance in trade, but only contains the indication that this species was offered on exchanges in 1998 and appeared on dealer lists between 1977 and 1999.

Similarly, for the reptile trade in Taiwan, there is only a reference to the occurrence of *Tarentola chazaliae* there, without mentioning its frequency (Shiau et al. 2006).

A report from Sweden is highly alarming. Over 550 wild-caught *Tarentola chazaliae* were confiscated there (The Local 2018). Due to a lack of information about the exact origin of the animals, attempts were made to distribute them to zoological institutions. Unfortunately, of the over 550 Helmethead geckos, only 50 animals could be placed in European zoos. The Swedish authorities then decided to kill the remaining 500 (!) animals; a very controversial approach by the responsible authority in several respects. Given the assumption that Helmethead geckos do not occur in high population densities, the illegal removal of 550 animals was considered highly criminal and certainly caused great harm to the affected populations.

According to own observations, however, the supply of wild-caught *T. chazaliae* has decreased significantly over the last 10 years. At the same time, captive-bred Helmethead geckos have appeared more and more frequently on reptile markets and advertising portals.

## Reproduction

| Topic                              | Details on the reproduction of <i>Tarentola chazaliae</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | <p>Gender differentiation through significantly enlarged hemipenis pouches and equally enlarged postanal tubercles of the ♂♂ compared to the ♀♀. The sexual characteristics are quite clear and very pronounced in adult animals.</p> <p>Otherwise, at first glance, no particularly pronounced sexual dimorphism can be observed. In contrast to other species of the genus, the ♂♂ are not larger, as is the case with some species of the subgenus <i>Makariogecko</i>. In the subgenus <i>Geckonia</i> the ♀♀ tend to be somewhat larger than the ♂♂. The largest animal measured was a ♀ from Cap Blanc (Ineich et al. 1997).</p> <p>The genus characteristic, the 1<sup>st</sup>, 2<sup>nd</sup> and 5<sup>th</sup> fingers and toes appearing to be unclawed. Fingers and toes can be used to determine the sex of subadult and adult animals, as only the males have retractile claws (Joger, 1984a). By gently pulling the flat nail bed backwards, a tiny claw can be revealed on the toes.</p> |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Sexual maturity                    | The animals are usually sexually mature from an age of around 1 to 1½ years and should not be used for breeding any earlier. According to Seufer (1988), the first egg laying (unfertilized) was documented at an age of 9 months, while Bergmann (2006) even states that females become sexually mature at 4 to 6 months and, if given sufficient amount of water and minerals, make good breeding stock and lay eggs all year round. Even if this may work, it is not beneficial for the lifespan of the ♀♀. The extremely rapid growth during rearing, coupled with starting breeding too early and keeping them in warm conditions all year round, does result in higher clutch numbers, but does not correspond to the natural reproductive rhythm with the necessary resting periods.                                                                                                                                                                                                               |
| Gestation period                   | After mating, it takes 10–15 days until eggs are laid (Campmany Garcia & Déniz Suárez 2001).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Reproductive season                | Mating could be observed from spring to autumn.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Number of eggs/clutches per season | Usually 2 eggs per clutch, sometimes only 1 egg.<br>2–5 clutches per season                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Egg size/hatchling size            | Eggs: 7–12 mm x 12–15 mm.<br>Hatchlings: TL ca. 35–40 mm, SVL 20–22 mm, tail length 17–18 mm (Seufer 1988, Wilms 2000). Meiri et al. (2012) state that the hatchling had an SVL 20 mm, while the mother had an SVL of 62.8 mm.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Incubation and hatching            | From 50–56 days at 29–31°C to 85–92 days at 26–27°C. Relative humidity ca. 50–55% (Wilms 2000).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Sex determination                  | Possibly temperature dependent sex determination as in other <i>Tarentola</i> species (see Straková et al. 2024).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Sperm storage                      | Not proven with certainty, but suspected because the egg-laying phase lasts longer than matings have been observed.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |



## Husbandry and Captive Breeding B/B



Fig. 4: *Tarentola chazaliae* captive breeding  
 a high-contrast hatchling (R. van Ham)  
 b hatchling before first skin shedding (J. Felka)  
 c the same animal as above (a), now as adult (R. van Ham)  
 d juveniles of different ages (J. Felka).

| Topic                    | Data for <i>Tarentola chazaliae</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction | <p>A moderate winter dormancy period from December to February with temperatures of 8–10°C can be considered a trigger for reproduction.</p> <p>A fine drizzle of artificial rain (or fogging) in the evening is also important to simulate the humidity (that occurs naturally in the habitat after sunset). However, it is important that the entire terrarium is not heavily wetted, but only partially and very finely dusted. A permanently moist substrate or even wetness must be avoided in any case.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Husbandry requirements   | <p>Desert terrarium with sufficient structure and hiding places. The substrate should be a layer of sand, which is generously mixed with fine shell grit. Either beach sand or sifted river sand has proven to be suitable sand. However, a clay-gravel mixture has also been used successfully in breeding Helmeted geckos.</p> <p>Flat, upside-down clay saucers with an entrance opening that is cut out without sharp edges have proven to be a good hiding place. It is even more decorative if these are roughly covered with beige-coloured concrete to create a more stone-like surface.</p> <p>Flat pieces of bark are also readily accepted. <i>Tarentola chazaliae</i> does not hide under such objects during the day, exclusively, but also likes to sit on or under small dried bushes. Dried thyme bushes have proven to be a decorative and popular terrarium feature in desert terrariums for years. A small plant corner with appropriate succulents is also a good idea and helps to keep a small part of the terrarium moist.</p> |



| Topic                                                           | Data for <i>Tarentola chazaliae</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-----------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                                 | <p>A small water bowl with fresh drinking water should always be available, but you will very rarely see these geckos drinking from open water. <i>Tarentola chazaliae</i> absorbs moisture from food and from dew or sprayed water.</p> <p>Woodlice play an important role in the diet in captivity and were apparently the key in successful keeping and breeding after previous failures (Seufer, 1988; Seufer, personal communication). In particular, <i>Porcellionides pruinosus</i>, erroneously called the 'Cuban woodlice', is an easy to breed isopod from the Mediterranean region that can grow up to 11 mm in size and is very popular with smaller gecko species.</p> <p>Seufer used common woodlice (<i>Porcellio scaber</i>), which are also very easy to breed. However, there are also keepers who do not offer any woodlice at all, but at the same time give large amounts of shell grit and ground cuttlefish. The adequate supply of calcium plays a key role in the successful keeping and breeding of <i>Tarentola chazaliae</i>. Feeding them with firebrats (<i>Thermobia domestica</i>) also seems to be very useful. These food animals are very easy to breed and are therefore available in large quantities, and they are also very readily eaten. A big advantage, especially when raising young <i>Tarentola</i>, is that firebrats, even if they are offered in too large quantities, do not nibble on the young geckos, as is known to happen with house crickets (<i>Acheta domesticus</i>).</p> <p>Considering the natural food spectrum, in which small beetle species make up the main part of the diet, it seems advisable to also offer the lesser mealworm (<i>Alphitobius diaperinus</i>) and four-spotted bean weevil (<i>Bruchus quadrimaculatus</i>), which are regularly available as feeder insects these days. It represents a welcome change in the gecko diet. If offering food, preference should be given to slow-moving food animals. This should be taken into account when feeding house crickets (<i>Acheta domesticus</i>), as well as steppe and Mediterranean crickets (<i>Gryllus assimilis</i> &amp; <i>G. bimaculatus</i>). Small cockroach species of appropriate size, e.g. young of the Argentine forest cockroach (<i>Blaptica dubia</i>), are also a good source of food. Gravid Gecko females can also be fed with wax worms, the larvae of the wax moth (<i>Galleria melonella</i>), before and after egg laying, as they are very nutritious. All feeder animals should be dusted with a mineral-vitamin mixture.</p> <p>The minimum terrarium size for keeping a pair should not be less than 60 x 40 cm, and 80 x 40 cm for keeping a trio. As with other gecko species whose females are larger than the males (e.g. <i>Stenodactylus mauritanicus</i>, <i>Pachydactylus rangei</i>, <i>Tropiocolotes</i> ssp.), a reduced territoriality of the males can be observed. When kept in a 150 cm desert terrarium, several males may be kept together without any obvious territorial fights occurring. However, keeping them in pairs is preferable, as these geckos have also been shown to be solitary in the wild. The basic lighting can be provided by T5 tubes or LED bars. Due to the partial diurnal activity, UVB lighting is recommended (Dobosz 2023). 35-watt metal halide lamps have proven to be effective for this. The lighting can be turned on for 12 hours in the summer months and 8–10 hours during the winter months.</p> |
| General characteristics, difficulties with keeping and breeding | Adequate calcium supply is important all year round and is essential for gravid females. Nighttime lowering of the temperature and sufficient air humidity must be observed. Regular spraying and an adequate air circulation is important (Hamann 2009).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Care of the young, technical and time effort                    | Losses of juveniles do occur, but are rare if they are provided with the appropriate mineral and vitamin-rich food-source. Raising hatchlings should take place clutch wise or in small groups of up to four animals of the same size. Food jealousy can be a trigger for starting to eat. Hatchlings kept alone sometimes refuse to feed. Daily spraying is essential when raising juveniles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Life expectancy                                                 | On average approx. 8 – 10 years. ♂♂ max. 12 years, ♀♀ max. 13 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |

| Topic                                                  | Data for <i>Tarentola chazaliae</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
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| Frequency of private breeding and reproduction in zoos | <p>The keeping of the Helmethead gecko has virtually never played a role in zoological institutions, despite its attractive appearance. The only former keeping locations mentioned in the zoo animal list are the Friedrichsfelde Zoo in Berlin, the Frankfurt Zoo, the Nuremberg Zoo, the Reptile Centre in Malmö, Sweden, the Vivarium in Lausanne, Switzerland, and the Cotswold Wildlife Park in Burford, United Kingdom. The only current keeping (October 2024) is in Prague Zoo in Czech Republic. The zoo's first breeding took place there in 2022 (Graf et al. 2024).</p> <p>Breeding has been carried out annually in private husbandry since 1986 and was first documented by Seufer (1988). Initially, these geckos were described as 'very easy to care for' (Ahl 1930), but he was not able to breed them. Senfft (1931) also kept his animals successfully, but was unable to record any egg laying. It is worth mentioning that Friedel (1967) was the first to note that Helmeted geckos can be bred in terrariums. Friedel observed copulations several times. However, the resulting clutches were destroyed by a turtle living in the same enclosure. Rieppel (1973), on the other hand, was not successful in the long term with his husbandry, but provided good data on the ecology of <i>Tarentola chazaliae</i>. Schulte (1974) also had increased egg laying, but he described that the eggs dried out very quickly and should be placed in moist moss. This is fundamentally wrong. It is likely that Schulte's eggs had a non-calcified eggshell and therefore appeared to have a soft shell. Fertilized eggs of <i>Tarentola chazaliae</i> are generally thin-walled but hard-shelled and must not be placed in moist substrate, but have to be incubated in dry substrate. Contact moisture should always be avoided. A slightly higher humidity can be achieved by placing a separate water container in the incubator or to place i.e. a water filled bottle cap inside the incubation container. To prevent hatchlings from drowning, this should be filled with cotton wool, foam or Seramis granules.</p> <p>Essential is a high supply of calcium is the most important factor in the successful reproduction of <i>Tarentola chazaliae</i>. This can be controlled, for example, by selecting specific food components. For example, Seufer (1988) achieved this by feeding woodlice, <i>Porcellio scaber</i>, which was the decisive success in breeding. When feeding primarily house crickets, <i>Acheta domestica</i>, an adequate supply of calcium can also be ensured by improving the substrate. A high proportion of fine shell grit in the substrate of the terrarium represents a source of calcium that is always available (Van Ham, personal communication).</p> <p><i>Tarentola chazaliae</i> has never been kept frequently and in large numbers in terrariums, but its keeping and occasionally breeding has been continuously documented in the literature for several decades. (Ahl 1930, Friedel 1967, Rieppel 1973, Schulte 1974, Seufer 1988, Rösler 1995, Modry 1996, Ineich et al. 1997, Wilms 2000, Campmany Garcia &amp; Déniz Suárez 2001, Bonetti 2002, Henkel &amp; Schmidt 2003a, Henkel &amp; Schmidt 2003b, Drews 2004, Gramentz 2005, Rösler 2005, Rogner 2005, Bergmann 2006, Hamann 2009, Wirth 2013, Dobosz 2023).</p> |
| Breeding difficulty evaluation                         | Not a species for beginners. If the parameters mentioned are met, adult offspring are completely problem-free terrarium inhabitants.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Mortality in the first years of life                   | Low mortality rate when reared with mineral-rich nutrients. Partial losses due to moulting problems (possibly caused by too low humidity).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| F2 generation bred in captivity                        | Yes, since 1987 F2 (Seufer 1988). There are now several generations of Helmeted geckos in breeding.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Commercial breeding/ ranching                          | No. This species is not frequently kept and bred by private owners.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Interviews/ Surveys/ Consultations                     | 15 (private), of which 13 are breeders and 2 are keepers.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

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## Phrynosomatidae

### *Phrynosoma* Wiegmann, 1828

#### General Information on the Genus *Phrynosoma*

The horned lizards of the genus *Phrynosoma* have always fascinated people. Due to their bizarre appearance, enthusiasts are repeatedly tempted to keep these unusual reptiles. However, due to their dietary specialization and special ecology, keeping and breeding them should only be reserved for very experienced specialists.

Horned lizards are stocky-looking, relatively short-tailed and short-legged lizards from the Phrynosomatidae family within the Iguania. Numerous horn-like projections on the head and back give them a primitive, dragon-like appearance (Powell & Russell 2023).

There are different research approaches to the evolutionary origin of the horn-like head outgrowths and it has been passionately debated repeatedly in the past, for example in the renowned 'Science' magazine (Brodie et al. 2004, Christy 2004, Fouts 2004, Yosef 2004).

Both their scientific and German common names are an allusion to their toad-like body shape. The genus name is derived from the Greek 'phrynos' = toad and 'soma' = body. The name 'Horned toad' is not uncommon in the Anglo-Saxon language, more common is 'Horned lizard'. The rather small iguanas reach body lengths of between eight and 13 cm. The distribution area of these New World lizards extends from southern Canada to northern Guatemala (Hodges 2004, Nieto-Montes de Oca et al. 2014).

In addition to their odd physiognomy, horned lizards also exhibit a whole range of unique behaviours and ecological adaptations.

The first thing to mention here is one of the most spectacular and peculiar defence strategies in the animal kingdom. To ward off enemies, horned lizards are able to spray a targeted jet of blood from the corner of their eyes over a distance of up to 1½ m at the potential attacker. This is achieved by restricting the flow of blood from the head, which increases blood pressure and causes small blood vessels around the eyelids to burst. The blood not only confuses predators, but also apparently tastes extremely disgusting to cats and dogs. The survival rate of the horned lizards after contact with canine predators increases significantly as a result of this behaviour (Sherbrooke & Middendorf 2004). It has been shown that the chemical components in the blood that appear to be responsible for this are already present in the circulating blood and are not added by special glands as previously assumed. It is now assumed that the ingestion of large quantities of poisonous harvester ants (*Messor spec.*) is responsible. Only in three closely related species (*P. mcallii*, *P. modestum*, and *P. platyrhinos*) no blood squirting has been observed to date. However, it is still unclear whether these species only do this very rarely or are incapable of doing so (Sherbrooke & Middendorf 2001).

Sherbrooke & Schwenk (2008) found that these lizards do not bite or chew their food, but swallow it directly, although the harvester ants of the genus *Pogonomyrmex*, which are captured in large numbers, are quite aggressive and can sting painfully. The genus *Phrynosoma* has unique feeding kinematics that are associated with mucus-secreting pharyngeal papillae. When swallowed, the ants are immobilized by the secreted mucus threads and cannot injure the horned lizards in the throat. Studies on freshly killed horned lizards have shown that the ants are rolled up into small balls in the stomach and bound in the mucus.

In particular, the species of horned lizards with pronounced head and occipital spines use another defence strategy. To avoid being grabbed by the head or neck, the lizard crouches or raises its head and points the horned head straight up or backwards. In addition, the body is flattened, tilted and pressed to the ground. This makes the horned lizard appear significantly larger to a potential predator (Sherbrooke 1987a, Baur & Montanucci 1998). Similar to toads, horned lizards move rather sluggishly, often remain motionless and rely on their remarkable camouflage. They are particularly adapted to dry or semi-dry areas. The spines on the back and sides of the lizards are modified scales that also counteract water loss through the skin, while the horns on the head are true horns because they have a bony core. In adaptation to the often desert-like habitat, they lack a urinary bladder (Divers & Camus 2020).

The members of the genus *Phrynosoma* have an interesting similarity with the unrelated Australian agama species *Moloch horridus*. Both the thorny devil (*M. horridus*) and the *Phrynosoma* species have a special structure of the dorsal scales, which allows them to optimally absorb water during rare rainfall events in their very similar arid habitats. There are also striking similarities in other aspects. Both in morphological terms, such as the very spiny external appearance, and in their behavioural repertoire, further parallels can be seen that can be traced back to convergent development (Sherbrooke et al. 2007, Grant & Doherty 2008). The horned lizards of the genus *Phrynosoma* belong to the small family Phrynosomatidae within the Iguania. This family also includes the genera *Callisaurus*, *Holbrookia*, *Petrosaurus*, *Sceloporus*, *Uma*, *Urosaurus*, and *Uta*.

All 17 species of horned lizards currently considered valid occur in Mexico (Uetz et al. 2024, Reptile Database). Ten species are also native to the USA, one species (*P. asio*) reaches the border to Guatemala in the south and two species (*P. douglasii* and *P. hernandesi*) reach Canadian territory in the north.

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 18). *P. coronatum* had already been included in CITES Appendix II in 1992 (CITES 1992), with the subspecies: *P. c. blainvillii* (Gray, 1839), *P. c. coronatum* (Blainville, 1835), *P. c. frontale* (Van Denburgh, 1894a), *P. c. jamesi* (Schmidt, 1922), and *P. c. schmidtii* (Barbour, 1921), which are now partly regarded as separate species, see below.

EU Council Regulation (EC) No 338/97 Annex B.

In Germany, specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List status

*P. asio*: LC (Least Concern, assessed 10 May 2012)

*P. blainvillii*: LC (Least Concern, assessed 12 August 2016)

*P. braconnieri*: LC (Least Concern, assessed 01 March 2007)

*P. cornutum*: LC (Least Concern, assessed 01 March 2007)

*P. coronatum*: LC (Least Concern, assessed 01 March 2007)

*P. ditmarsii*: DD (Data Deficient, assessed 01 March 2007).

*P. douglasii*: LC (Least Concern, assessed 01 March 2007)

*P. goodei*: LC (Least Concern, assessed 13 August 2016)

*P. hernandesi*: LC (Least Concern, assessed 01 March 2007)

*P. orbiculare*: LC (Least Concern, assessed 01 March 2007)  
*P. mcallii*: NT (Near Threatened, assessed 01 March 2007)  
*P. modestum*: LC (Least Concern, assessed 01 March 2007)  
*P. platyrhinos*: LC (Least Concern, assessed 13 August 2016)  
*P. solare*: LC (Least Concern, assessed 01 March 2007)  
*P. taurus*: LC (Least Concern, assessed 01 March 2007)

### Red List Status in the Range Countries

#### Canada

*P. douglasii*: Extirpated since 2018 (COSEWIC 2018). The possibility of reintroducing captive-bred animals should, however, be evaluated (Environment and Climate Change Canada 2017).  
*P. hernandesii*: Imperilled/vulnerable (N2N3) (Environment Canada 2015).

#### Mexico

*P. asio* and *P. braconnieri*: Under special protection (Pr – Sujeta a protección especial) (SEMARNAT 2019)  
*P. cerroense*, *P. mcallii*, *P. orbiculare*, and *P. taurus*: Endangered (Amenazada) (SEMARNAT 2019).

#### USA

The following information has been adapted from Proposal 18 (CITES 2022):

*P. blainvillii*: Vulnerable in California.

*P. cornutum*: Fully Protected in New Mexico, Species of Special Concern in Oklahoma and Colorado, and Threatened in Texas

*P. hernandesii*: Fully Protected in New Mexico, Threatened in Texas, and potentially at risk in Montana

*P. mcallii*: Threatened in California and Arizona

*P. platyrhinos* is not listed as a protected species under the US Endangered Species Act. The states in the US where this species occurs have individual regulations that give the species some protection, but the level of protection varies from state to state and there are currently no federal regulations in place to protect the species nationally.

### Threats

Most *Phrynosoma* species live in desertic habitats. A key factor in the decline of these species is the destruction of natural chaparral habitats with sandy substrates (Leaché et al. 2009) due to urban sprawl, overly frequent fires, increasing droughts due to climate change, the invasion of non-native grasses, air pollution and uncontrolled recreational activities (California Wildfire & Forest Resilience 2022). In addition, the deforestation, primarily for the production of firewood, charcoal and the development of grazing land, of the last remaining oak, pine-oak and cloud forests at high altitudes in Mexico plays a major role. The effects of climate change cannot yet be predicted. However, it is likely that the negative impacts will be particularly severe for the species of horned lizards at higher altitudes, whose options for moving to areas with a cooler climate are limited.



The spread of invasive species caused by human activity should not be underestimated. Ant species introduced from Brazil and Argentina, for example, have a negative effect on members of the genus *Phrynosoma* in California and Texas, as these ants are not eaten by the lizards, but their preferred native ant prey is displaced by the alien ant species (Manaster 2002, Henke & Fair 1998). The use of pesticides, especially insecticides, is increasingly affecting the quantity and availability of insect prey (Henke et al. 1998, Price 1990).

The reason for the CITES listing of the genus *Phrynosoma* is the trade in wild-caught specimens for keeping as pets. Between 2006 and 2015, over 21,393 specimens of nine different species of the genus *Phrynosoma* were exported from the USA, including some specimens of the Mexican species *P. asio*, *P. braconnieri* and *P. taurus*. The proportion of captive-bred specimens was 3.8%, with 822 specimens. A further 487 juveniles were born/hatched in captivity. By far the most frequently exported species was *P. platyrhinos*, with over 20,000 specimens, followed by *P. modestum* (496 specimens). Exports were made to 32 different countries, of which Germany was the main importing country with 3,371 specimens, followed by the Netherlands, England and Japan (all information from CITES 2022b on analyses in LEMIS 2006–2015 and LEMIS 2021).

Mexico also legally exported 602 specimens of the genus *Phrynosoma* for commercial trade between 2019 and 2021, mainly *P. asio* and *P. taurus*. Before that, exports from Mexico were only permitted for scientific research purposes (SEMARNAT 2022 as cited in CITES 2022b).

### Husbandry and captive breeding of *Phrynosoma* species

Some of the husbandry and breeding peculiarities apply equally to all *Phrynosoma* species, so we summarise them here at the beginning of this chapter. The special needs of individual ovoviviparous or viviparous species are discussed in more detail in the corresponding sub-chapters below.

As early as 1973, Baur wrote that an outdoor terrarium is essential for the care and breeding of horned lizards. From today's perspective, the technical equipment, especially with regard to UVB metal halide lamps, is significantly better than in the early days of successful horned lizard keeping. Nevertheless, a temporary outdoor stay should always be aimed for and contributes significantly to the vitality of the animals. However, breeding success in pure indoor keeping is possible under appropriate technical conditions.

As they are desert dwellers, it is important to provide these lizards with a sufficiently sandy substrate. Sand is particularly important for horned lizards, as it not only serves as a walking surface, but the animals also sometimes dig themselves completely into it for protection and to sleep. Small dry shrubs in the terrarium have also proven useful for all horned lizards. Dried thyme plants and similar woody herbaceous shrubbery, are visually appealing. The 'desert shrubs' available in shops are also very suitable. A terrarium for horned lizards can be planted with succulents and tufts of grass, taking into account that a dry, hot climate prevails in the terrariums. Narrow- or round-leaved species are particularly suitable for planting, as they continue to serve as decoration even after their inevitable withering away in the indoor terrarium.

Spacious gauze terrariums, converted cold frames and aviaries have proven to be suitable as outdoor terrariums, as they can be easily secured against external predators. It is ideal if the generously sized outdoor enclosures have a power connection so that additional lighting and heating can be provided during short periods of cloudy and cooler weather. A prerequisite for this is that a transparent cover with UV-permeable twin-wall panels (PLEXIGLAS® ALLTOP) is

used to protect the electrical system from moisture. If it cannot be ensured that the temperatures do not drop too low during the outdoor period, especially in the cooler spring and autumn months, the animals may have to be taken out several times a day. This is not a problem for animals that are accustomed to this procedure and has been practiced for decades (Kunz 2009). A cold hibernation phase is essential for almost all species of horned lizard, whether it is for a balanced hormone household, an intact immune system or even proper growth (Haase 2014a).

The prerequisite for the breeding season beginning in spring and summer is not only the aforementioned hibernation, which can last 3 to 5 months (Haase 2014b), but also the increasing light intensity after hibernation (cf. Schulz 2018c). The summer mating season is triggered by simulating the monsoon season in the natural range. Humidity is increased by frequent misting. However, it is important that the substrate remains dry.

The special requirements of horned lizards and their husbandry, and the associated difficulties, are the main focus of this article. The main diet of all species consists of ants, which make up, in exceptional cases, only 11.3% of the food of *P. ditmarsii*, but up to 88.8% of the food of *P. solare* (Pianka & Parker 1975). The husbandry and breeding of horned lizards entirely without supplying feeder ants is not recommended. Unlike other lizard species from dry areas, which eat large prey items and can fast for several days without any problems, horned lizards must always have access to a sufficient number of small insects. In addition to regular feeding of ants with a low formic acid content, such as yellow meadow ants (*Lasius flavus*) or black garden ants (*Lasius niger*), the animals must be offered 'substitute food' in the form of firebrats (*Thermobia domestica*) and bean beetles (*Bruchus quadrimaculatus*) every day. In particular, the bean beetle has proven to be an enrichment of the food animal supply in recent years, as it is not only very easy to breed, but is also very suitable as food for desert and semi-desert dwellers (Schulz 2018b). While small crickets (*Gryllus* spp.) contain too much fat and too little fibre, young Egyptian migratory locusts (*Locusta migratoria*) or desert locusts (*Schistocerca gregaria*) are a good supplement as food for horned lizards (Schulz 2018a) when they are small enough. The animals' digestive system is susceptible, especially in juveniles. Food that is too large and coarse is fatal, but a high level of fibre is essential (as discussed by Eisenberg 1999 and Baur 1999).

Due to their low territoriality, almost all species of the genus *Phrynosoma* can be kept in groups with several males. The sex ratio should be equal or in favour of females. Pure male groups are also possible. Not only is the level of intraspecific aggressiveness very low, but keeping them together with other species of horned lizards is also entirely possible. Gravid females should be housed individually for a short time before giving birth or laying eggs.

When it comes to husbandry, the aim is to recreate the climatic conditions of the animal's natural habitat as closely as possible. To do this, it is essential to study the relevant meteorological and climatological sources. It should be noted that horned lizards are sensitive to humidity during hibernation. Even during the summer months, care should be taken to ensure that although increased humidity is to be achieved through frequent misting, the substrate must not be wet and must be able to dry quickly.

The ongoing energy and purchase costs for adequate lighting should not be underestimated. The animals are difficult to keep, but it is definitely not impossible. They require a great deal

of time and expertise to be kept successfully. However, with the appropriate training, expertise and experience, the animals can usually be kept and bred successfully. Overall, it can be said that their husbandry is extremely complex.

## Conclusion

Horned lizards have always been considered complicated and demanding to keep and breed. In principle, they are very difficult to care for and keeping and breeding is extremely time-consuming, but almost all species can be kept and bred reasonably well if the appropriate parameters are adhered to. However, these species should only be kept by specialists, as this requires a great deal of sensitivity and knowledge of the species to be cared for. In German-speaking countries in particular, a large proportion of the species have been successfully kept and bred for over half a century. The first horned lizard ever bred in captivity, a *Phrynosoma platyrhinos*, hatched on June 5, 1972 at the house of Bertrand Baur (Baur 1973) in Switzerland (Baur & Montanucci 1998). It was Baur who made a significant contribution to the knowledge of successful keeping and breeding, and inspired many keepers and infected them with enthusiasm for these extraordinary lizards. In particular, species such as *Phrynosoma asio* and *P. platyrhinos* have now taken their place in terrarium keeping, but species such as *P. cornutum*, *P. modestum*, *P. orbiculare*, and *P. solare* are also regularly available as healthy offspring from responsible breeders, whereas most other species are only bred in very small numbers.

## Difficulties in identifying CITES-listed species

In the proposal on CoP19 Prop.18. It is stated that identification at species level is difficult for laypeople, and there is an ongoing, controversial debate about the taxonomy of the genus. Various authors recognize 12 to 21 species (Uetz et al. 2020, Sherbrooke 2020, Köhler 2021). Correct species identification requires the assessment of a number of morphological characteristics such as the number of rows of dorsal scales, the notch between the head horns, as well as their number, the length of the tail, the dorsal stripes, etc. (Sherbrooke 2003). Identification is even more difficult in juveniles, which only develop some characteristics such as the final size of the horns when they reach sexual maturity (Pianka & Parker 1975).

In the present study, the species *Phrynosoma asio*, *P. blainvillii*, *P. braconnieri*, *P. cerroense*, *P. cornutum*, *P. coronatum*, *P. ditmarsii*, *P. douglasii*, *P. goodei*, *P. hernandesii*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, *P. sherbrookei*, *P. solare*, and *P. taurus* currently listed by Uetz et al. (2024) are taken into account. Other species that have recently been synonymized or are now listed as subspecies were not taken into account. The morphological differences between the species, which, as explained at the beginning, are sometimes very difficult to distinguish, are even more complicated here and can often only be verified genetically. In addition, these species play no role in trade or husbandry and there is no information on their lifestyle, biology and husbandry.

For this study, we have decided to divide the genus *Phrynosoma* into two groups. Firstly, the viviparous species and the second, the egg-laying species. This selection was made primarily on the basis of similarities in their way of life, choice of habitat and their (altitude) distribution, not on the basis of common taxonomic relationships. In his studies on the evolution of viviparity in horned lizards, Hodges (2004) makes it clear that viviparous species have no phylogenetic context and that viviparous species are not monophyletic.

### Live-bearing (ovoviviparous) species

| Species                                   | Original description                                               | Common name                  | Common name International                                    | Known in private care or in the trade |
|-------------------------------------------|--------------------------------------------------------------------|------------------------------|--------------------------------------------------------------|---------------------------------------|
| <i>Phrynosoma braconnieri</i>             | Duméril & Bocourt, 1870                                            | Short-tail Horned lizard     | Kurzschwanz-Krötenechse<br>Camaleón de Cola-Corta            | Yes                                   |
| <i>Phrynosoma ditmarsii</i>               | Stejneger, 1906                                                    | Rock Horned lizard           | Camaleón de Roca                                             | Yes                                   |
| <i>Phrynosoma douglasii</i>               | (Bell, 1829)                                                       | Pygmy Short-horned lizard    | Zwerg-Kurzhorn-Krötenechse                                   | Yes                                   |
| <i>Phrynosoma hernandesi</i> <sup>1</sup> | Girard, 1858                                                       | Mountain Short-horned lizard | Berg-Kurzhorn-krötenechse<br>Camaleón Cuernitos de Hernandez | Yes                                   |
| <i>Phrynosoma orbiculare</i>              | (Linnaeus, 1758)                                                   | Mountain Horned lizard       | Mexikanische Kurzhorn-Krötenechse<br>Camaleón de Montaña     | Yes                                   |
| <i>Phrynosoma sherbrookei</i>             | Nieto-Montes De Oca, Arenas-Moreno, Beltrán-Sánchez & Leaché, 2014 | Guerreran Horned lizard      | Guerrero-Krötenechse                                         | Yes                                   |
| <i>Phrynosoma taurus</i>                  | Bocourt, 1870                                                      | Mexican Horned Lizard        | Büffelhorn-Krötenechse<br>Camaleón Toro                      | Yes                                   |

The seven viviparous species are discussed below. In adaptation to their occurrence in higher mountain areas or a distribution far to the north, they have developed a viviparous mode of reproduction over the course of evolution. Important findings on the development of ovoviviparity within the genus *Phrynosoma* can be found in Hodges (2004).

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1 The following species of the *Phrynosoma douglasii* species complex, listed in CoP19 Prop. 18 (CITES 2022b), were synonymised with *P. hernandesi* by Köhler (2021). The little information available on the behaviour, biology and husbandry of these species does not differ from that of *P. hernandesi* and is therefore included there. They do not play a role in the trade or in husbandry.

*Phrynosoma baurii* Montanucci, 2015 (Baur's Short-horned Lizard, San Diego Horned Lizard). Hybridisation of *P. baurii* with *P. hernandesi* was observed by Montanucci (2015);

*Phrynosoma brevirostris* Girard, 1858 (Great Plains Short-horned Lizard);

*Phrynosoma diminutum* Montanucci, 2015 (San Luis Valley Short-horned Lizard)

*Phrynosoma ornatissimum* Girard, 1858 (Desert Short-horned Lizard).





Fig. 5 *Phrynosoma* spp. – live-bearing (ovoviviparous) species part I

- a *P. braconnieri* ♂ Santiago Yolomécatl, Oaxaca, Distr. de Putla, 2,108 m asl (P. Heimes)
- b *P. braconnieri* (J. Schulz)
- c *P. ditmarsis* (A. Duarte)
- d *P. douglassi* (P. Freed)
- e *P. hernandesi* (J. Schulz)
- f *P. orbiculare cortezii* ♀ San Salvador El Seco, Puebla, 2,390 m asl (P. Heimes)
- g *P. orbiculare* (K. Kunz)
- h *P. orbiculare* juveniles (K. Kunz).



Fig. 6: *Phrynosoma* spp. – ovoviviparous species part II

- a *P. hernandesi* (J. Schulz)
- b *P. sherbrookei* ♀ Tenexatlajco, Guerrero, 2,000 m asl (P. Heimes)
- c *P. taurus* ♂ El Aguacate, Puebla, 1,910 m asl (P. Heimes)
- d *P. taurus* adult with a juvenile (J. Schulz).

The seven live-bearing species are discussed below. In adaptation to their occurrence in higher mountain areas or a distribution far to the north, they have developed a viviparous mode of reproduction over the course of evolution. Important findings on the development of viviparity within the genus *Phrynosoma* can be found in Hodges (2004).

### Morphology and Taxonomy

This compilation on morphology and taxonomy is largely based on the Reptile Database (Uetz et al. 2024). Details, additions and deviations are referenced separately.

***Phrynosoma braconnieri*** Duméril & Bocourt, 1870 – As the common name suggests, the Short-tailed horned lizard differs from most of its conspecifics in the genus *Phrynosoma* in its extremely short tail. It is shorter than the head. The temporal spines are about as long as the occipital spines, which makes it significantly different from the also very short-tailed *P. taurus*. Head-body lengths of 60 to 70 mm are given for *P. braconnieri* (Pianka & Parker 1976, Baur & Montanucci 1998, Werning 2014). The head spines are moderately strong and almost the same length; only the two somewhat isolated spines in the centre are somewhat more robust. The cryptic dorsal base coloration allows them excellent camouflage. The spot and stripe pattern, which consists of various shades of brown, varies greatly from individual to individual and allows the animals to virtually ‘blend in’ with the background. This spot pattern often appears particularly along a longitudinal dorsal band. Whereas two fairly broad flank bands



are often almost devoid of markings (Montanucci 1998). Individuals from semi-desert biotopes are usually much lighter coloured than those from pine-oak forests of higher altitude habitats (Montanucci 1979).

***Phrynosoma ditmarsii*** Stejneger, 1906 – The combination of a stubby tail and a strikingly reduced crown of occipital spines makes the species unmistakable. The reduction of the head spines is even more pronounced than in the otherwise quite similar species *P. hernandesii* (Turner et al. 2017). The Rock horned lizard is a medium-sized horned lizard species that reaches 76–90 mm SVL. The dorsal base coloration varies in red, brown, grey or yellowish tones. Dark transverse bands may occur in the posterior dorsal region. The ventral side is whitish with strongly keeled scales. These lizards had a single row of lateral ventral marginal scales that appear blunted pyramidal. The tail is very short. The head is wider than long and has a high postorbital crest that extends from the tip of the orbital bulge to the outer enlarged temporal lobes. The occipital and temporal horns are rounded, strongly reduced. *P. ditmarsii* are long-limbed horned lizards compared to the superficially similar *P. douglasii*. This is interpreted as an adaptation to the rocky habitat (Montanucci 1987). Detailed information on pholidosis can be found in Hodges (1995).

***Phrynosoma douglasii*** (Bell, 1829) – No subspecies are accepted for this species, but see also the notes on *P. hernandesii*. The species name ‘*douglasii*’ honours the Scottish botanist, David Douglas. The species or subspecies of the *P. douglasii* species complex had an eventful taxonomic history. The former subspecies *P. douglasii hernandesii* (Girard, 1858) was elevated to species status by Zamudio et al. in 1997. The former subspecies *P. d. brevirostre*, *P. ornatissimum*, and *P. d. ornatum* were synonymized with *P. hernandesii* by Zamudio et al. in 1997. Montanucci (2015) revalidated *P. brevirostre* and *P. ornatissimum*. Before Leaché et al. (2021), *P. bauri* and *P. brevirostre* were placed in the synonymy of *P. hernandesii*. *P. douglasii brachycercum* was assigned to *P. ornatissimum* by Montanucci in 2015. Currently, for example, Uetz, et al. 2024, Reptile Database does not list any subspecies of *P. douglasii*. As the name pygmy short-horned horned lizard implies, *P. douglasii* is a small species and has a head-body length of about 3–6.5 cm. The body structure has a stocky shape typical of horned lizards with a clearly flattened body structure. The head has an extremely short-spined crown. Compared to the slimmer snouts of most horned lizards, *P. douglasii* has a ‘blunt-nosed’ side profile and relatively short legs. The body is lined with a row of pointed scales. The ventral scales are smooth. The dorsal coloration is grey-beige, yellowish or reddish-brown depending on the season and region. There are also two rows of larger, dark spots on the back. The species is capable of a physiological colour change. During the mating season, when it feels threatened or reacts defensively, its colours become more intense. Detailed pholidosis values can be found, for example, in Montanucci 2015.

***Phrynosoma hernandesii*** Girard, 1858 – The following subspecies are recognised (controversial, see Köhler 2021, Leaché et al. 2021, and Uetz et al. 2024):

*P. hernandesii bauri* Montanucci, 2015

*P. hernandesii brevirostre* Girard, 1858

*P. hernandesii diminutum* Montanucci, 2015

*P. hernandesii hernandesii* Girard, 1858

*P. hernandesii ornatissimum* Girard, 1858

*P. hernandesii ornatum* Girard, 1858

In addition to the nominate form *P. h. hernandesi*, the following subspecies are assigned to *P. hernandesi*, the recognition of which is not undisputed. Some have been repeatedly granted species status in the eventful taxonomic history: *P. (h.) ornatissimum*, *P. h. brachycercum*, *P. h. brevirostre*, *P. h. diminutum*, *P. h. ornatum*, *P. (h.) bauri* (cf. Uetz et al. 2024). The scientific species name is dedicated to the Spanish doctor Francisco Hernández Médico, who was the first to report on horned lizards from the New World in 1651 (Sherbrooke 2003). The mountain short-horned lizard (*Phrynosoma hernandesi*) is often confused with its close relative, the pygmy short-horned lizard (*P. douglasii*). Both have a very similar body structure, although the head spines are less reduced than in *P. douglasii*. Until recently, *P. hernandesi* was considered a subspecies of *P. douglasii* (see taxonomic notes on *P. douglasii*). The two species can easily be distinguished in adult specimens by the considerable difference in size. *P. douglasii* are significantly smaller than *P. hernandesi*. *P. hernandesi* is a very variable species, with different geographical populations differing, sometimes significantly, in colour, pattern and size. Depending on their area of origin, adult *P. hernandesi* reach head-body lengths of around 5 to 13 cm and are flattened, stocky lizards, typical of horned lizards. The body is lined with a row of pointed scales, while the belly scales are smooth. The coloration is predominantly grey, yellowish or reddish-brown tones and there are two rows of large dark spots on the back. The animals can have very variable coloration within a population and cannot be assigned to a geographical subpopulation based on their coloration (Sherbrooke 2003). When they are threatened or show aggressive behaviour, their colours become more intense, similar to *P. douglasii*.

***Phrynosoma orbiculare*** (Linnaeus, 1758) – In addition to the nominative form four other not undisputed subspecies are currently distinguished: *P. o. bradti*, *P. o. boucardii*, *P. o. cortezii*, and *P. o. dugesii* (see Baur & Montanucci 1998, Uetz et al. 2024):

*P. orbiculare bradti* Horowitz 1955

*P. orbiculare boucardii* (Duméril & Bocourt 1870)

*P. orbiculare cortezii* (Duméril & Bocourt 1870)

*P. orbiculare dugesii* (Duméril & Bocourt 1870).

Köhler (2021) synonymized *P. orbiculare orientale* with *P. orbiculare dugesii*. The scientific species name is derived from ‘orbis’ – circular, and refers to the rounded body shape. The dorsal body scales of *P. orbiculare* appear noticeably spiny. The transition to the ventral area is formed by a characteristic single row of lateral abdominal scales. The two occipital spines are strongly developed. They are wider, the same length or slightly stronger than the temporal spines. The ventral scales are smooth and unkeeled. The tail is well developed. (Sherbrooke 2003, Baur & Montanucci 1998). *P. orbiculare* is a medium-sized horned lizard species. It reaches an average head-body length of 6–7 cm. In exceptional cases, body lengths of over 10 cm have been recorded. Males usually remain somewhat smaller than females. The tail measures about 51% of SVL in females and 62% in males (Baur & Montanucci 1998).

***Phrynosoma sherbrookei*** Nieto-Montes de Oca, Arenas-Moreno, Beltrán-Sánchez & Leaché, 2014 – The species was named after Wade C. Sherbrooke in recognition of his numerous and significant scientific contributions to horned lizards (Nieto-Montes de Oca et al. 2014). A conspicuous feature that distinguishes *P. sherbrookei* from most other horned lizard species is its strikingly keeled ventral scales. *P. sherbrookei* differs from *P. asio* and *P. cornutum*, which also have keeled ventral scales, in its significantly smaller body size and shorter tail, among other traits. *P. sherbrookei* is most closely related to the two species *P. braconnieri* and *P. taurus*. It

differs from *P. braconneri* in that the outer temporal part of the skull is extended posterio-dorsally into two temporal spines (in contrast to the outer temporal part of the skull, which is extended posterio-dorsally into three temporal spines in *P. braconneri*). *P. sherbrookei* differs from *P. taurus* in various morphological and pholidosis characteristics (see the details of the first description by Nieto-Montes de Oca et al. 2014) and above all in its smaller adult body size.

***Phrynosoma taurus*** Bocourt, 1870 – *P. taurus* has two outstanding characteristics. In addition to the extremely short tail, this is particularly the buffalo-like, greatly elongated shape of the outer lateral head horns, which look like two fused head spines with two tips. The inner occipital spines are extremely reduced, which leads to the eponymous ‘two-horned’, bull-like appearance. This ‘skull anchor’ gives the species a distinctive appearance within the genus *Phrynosoma*. The horn-like projections above the eyes are also quite pronounced (Sherbrooke 2003). The small to medium-sized species reaches head-body lengths of 6–8 cm and a maximum of approximately 10 cm. The maximum weight determined was 29 g (Baur & Montanucci 1998). The colouration can be very diverse and depends on the population, usually on the conditions of the ground in the respective habitat. Gray, brown and beige-yellow colours usually predominate. The dorsal centre is slightly lighter, as are the spine fringes on the sides of the body (Baur & Montanucci 1998). Detailed descriptions of the morphology and pholidosis can be found in Bocourt (1874), Martin del Campo (1934), and Reeve (1952).

#### Distribution Habitat and Behaviour in the Wild

***Phrynosoma braconneri*** is endemic to Mexico; evidence is available for the states of Oaxaca and Puebla (Zamudio & Parra-Olea 2000, Canseco-Márquez & Gutiérrez-Mayé 2010). Terra typica: Oaxaca, Mexico. The habitat of *P. braconneri* is oak-pine forests and dry scrubland in the Sierra Madre Oriental and the Sierra Madre del Sur at 1,900–2,250 m asl (Montanucci 1979, Zamudio & Parra-Olea 2000, Canseco-Márquez & Gutiérrez-Mayé 2010).

Among the viviparous and high-altitude *Phrynosoma* species, *P. braconneri* has one of the highest documented body temperatures (Lara-Reséndiz et al. 2015). Studies have shown that the body temperature of this species in the field is not related to the air or substrate temperature or to the body size of the animals. Interestingly, in *P. braconneri*, males had higher body temperatures than females (Woolrich-Piña et al. 2012). Díaz-Marín et al. (2019) investigated whether ambient temperature and seasonality have an impact on the body temperature of a *P. braconneri* population. In contrast to the above-mentioned record values, Díaz-Marín et al. (2019), in a study of a population that included nocturnal specimens, found that the measured body temperature values (cloaca) were among the lowest recorded for the genus *Phrynosoma*. It is assumed that the reproductive cycle is similar to that of *P. ditmarsii* (Baur & Montanucci 1998).

***Phrynosoma ditmarsii*** is endemic to the Mexican state of Sonora. The story of the discovery of *P. ditmarsii* is like a detective story and its distribution was an unsolved mystery for a long time. The rock horned lizard, named after the famous first reptile curator of the Bronx Zoo, Raymond Lee Ditmars, was described by Stejneger in 1906. Only three specimens were deposited in herpetological collections and the species remained lost until the early 1970s because nothing was known about its exact distribution other than the vague information ‘Mexican Sonora’ near the border with the United States. By means of stomach content examinations, attempts were made to analyse the exact origin, e.g. through ingested soil particles and eaten ants, and thus to narrow down the area of origin of *P. ditmarsii*. It was not until 1971

that further specimens appeared and for the first time statements could be made about the distribution and lifestyle of this rare species (Roth 1971, Sherbrooke 2003, Baur & Montanucci 1998). Terra typica: Sonora, Mexico, not far from the Arizona border.

The habitat is described as southwest-facing scree slopes with sparse oak or oak-pine forests at altitudes of around 1,400 m asl. The scree slopes are partly heavily overgrown. The vegetation consists of various shrubs, grasses and succulents (Hodges 1995). In spring, temperatures in the habitat rise rapidly, and in May/June it becomes very hot and dry. From July, the monsoon rains typical for the region begin and temperatures drop.

***P. douglasii*** has been recorded in the US states of Washington, Arizona, Colorado, Idaho, California, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Utah, Texas, and Wyoming. The species has also been recorded in Chihuahua, Mexico. Its occurrence in British Columbia, Canada, is now possibly extinct. Terra typica: 'somewhere on the Columbia River, Washington'

The lizards live in rocky and sandy drylands or sparse forests. The habitats are diverse and range, for example in New Mexico, from grassy and bushy semi-deserts at 1,200 m asl (Degenhardt et al. 1996) to alpine tundra at 3,424 m asl (Gehlbach 1965). The habitat of the controversial southern subspecies *P. d. brachycercum* in northern Mexico is below 120 m asl and is described by Montanucci (1981) as open grassland. The diet of *P. douglasii* varies from region to region, depending on seasonal availability and age or gender. Juveniles feed almost exclusively on ants (89%). In adult lizards, the proportion of ants drops to around 72%. In addition to ants, various arachnids, beetles and larvae, woodlice, snails, slugs and earthworms as well as butterflies and their caterpillars have been described as food components. Plant food is also said to be consumed occasionally. Ants make up the majority of the natural food resources of *P. douglasii*, the proportion of a particular prey species can vary greatly seasonally (Lahti et al. 2008). In addition to various mammals and birds such as blue jays (*Cyanocitta cristata*) and shrikes (*Lanius spec.*), larger lizards such as leopard iguanas (*Gambelia wislizenii*) are also mentioned as predators. The start of the activity period after hibernation varies considerably due to the large distribution area and the different altitude distribution. The animals appear after the snow melts between late March and early June. The populations in the north of the distribution area are generally at lower altitudes, for example in Alberta in southeastern Canada, between 700 and 900 m asl. *P. douglasii* becomes sexually mature in the second year. In summer, during the peak phase of its activity, its body temperature is between 33–35°C (Powell & Russel 1984, Prieto & Whitford 1971, Pianka & Parker 1975). However, *P. douglasii* is able to move normally at body temperatures as low as 6°C (Degenhardt et al. 1996).

***P. hernandesii*** is the most widespread species of horned lizard and is found from Mexico to southern Alberta and Saskatchewan. In the US, *P. hernandesii* has been recorded from the states of Arizona, Colorado, Idaho, Montana, Nebraska, Nevada, New Mexico, Oregon, North and South Dakota, Texas, Utah, and Wyoming. In Mexico, it has been recorded from Chihuahua, northeastern Sonora, and Durango. In Canada, it has been recorded from southeastern Alberta and southwestern Saskatchewan. Terra typica: 'New Mexico and Sonora'. The determination of a holotype and thus a terra typica is complex due to the changing taxonomy and recognition of the species or subspecies of *P. hernandesii*. Narrowed down to Santa Fe, New Mexico by Smith & Taylor in 1950, and to Fort Huachuca, Cochise County, Arizona by Montanucci (2015). For more detailed information on the individual subspecies, see Reptile Database (Uetz et al. 2024).

The mountain short-horned lizard inhabits a wide variety of habitats, from semi-arid plains to high mountain regions. In the south in particular, the species is predominantly an inhabitant of dry mountain regions. Depending on its distribution, however, it can be found at altitudes of between 170 and 3,440 m asl. For example, its habitats include short grass prairies on the Grait Plains, prairies and semi-deserts dominated by sagebrush (*Artemisia tridentata*) plant communities, and loose juniper and pine forests. The soil in these habitats can be stony or rocky, but is usually fine, loose soil or sand (Stebbins 2003, Hodges in Jones & Lovich 2009). The greater short-horned lizard has a high cold tolerance and can survive in harsher climates at higher altitudes and further north than most other *Phrynosoma* species. It is the only representative of its genus in the state of Wyoming, which lists *P. hernandesii* as the official 'state reptile.' The proportion of ants in the diet of the mountain short-horned lizard is lower than in most other species, and the proportion of other arthropods such as crickets, beetles, spiders, etc. is relatively high (COSEWIC 2007). *P. hernandesii* are among the most cold-tolerant lizards of all. They have been found active at air temperatures as low as 1.5°C, but can reach body temperatures of 41°C during the hottest season, seemingly surviving unscathed (Hodges in Jones & Lovich 2009). Females tend to establish a series of small territories within a larger area during the active summer period, and move relatively short distances overall. Males, on the other hand, travel longer distances. In Alberta populations, activity has been recorded between April and November (COSEWIC 2007).

***Phrynosoma orbiculare*:** This species is endemic to Mexico. It is recorded from the Mexican federal state, Aguascalientes, Chihuahua, Coahuila, Federal District (Mexico City), Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacan, Morelos, Nayarit, Nuevo Leon, Oaxaca, Puebla, Queretaro, San Luis Potosi, Tlaxcala, Sinaloa, Sonora and Zacatecas. Terra typica: Mexico. Specified as 'Mexico City' by Smith & Taylor in 1950.

*P. orbiculare* occurs in a variety of primary habitats (including dry scrubland, pine-oak forests, oak forests and juniper forests). Mexican short-horned lizards also use secondary habitats such as agricultural areas, e.g. agave and prickly pear fields, as their habitat. They primarily inhabit habitats at altitudes between 1,370 and 3,350 m asl (Sherbrooke 2003, Davis 1953). Baur & Montanucci (1998) report a sympatric occurrence of *P. orbiculare* and *P. douglasii* in a biotope near San José de Barbicora, Chihuahua, Mexico. The proportion of ants in the diet of *P. orbiculare* appears to be subject to major fluctuations. Montanucci (1981) states that 40% are ants, the remaining 60% are beetles and other insects. In another case, the proportion of ants was 82%. Pianka & Parker (1975), on the other hand, found an ant proportion of only 26% in stomach content analyses and otherwise predominantly beetles, and in one case almost exclusively beetles. Little is known about its lifestyle in nature.

***Phrynosoma sherbrookei*:** The species is endemic to Mexico and is so far only known from the Terra typica and two other sites in Guerrero (Nieto-Montes de Oca et al. 2014, Grummer 2014). However, Nieto-Montes de Oca et al. (2014) suspect that the distribution area in Guerrero is significantly larger and could also extend to neighbouring Puebla. iNaturalist (2024) lists 6 sites, some of which are not far from the border with Puebla. Terra typica: Tenexatlajco, municipality of Chilapa de Álvarez, Guerrero, Mexico, in 1,997 m asl. Coordinates: 17.55437°N, 99.26973°W.

The climate at the type site is temperate and subhumid with summer rainfall. The subsoil consists of clay and sedimentary rocks (Inegi 2009). The vegetation is composed of oak forest interspersed with patches of grassland and scrubland with agave species and other herbaceous plants (Rzedowski 1978). The area is heavily affected by agriculture and soil erosion



(Inegi 2009). The type series was collected during the day on a small patch of grassland on a slope with strong erosion (Nieto-Montes de Oca et al. 2014). Field observations of one individual, and faecal analyses of five specimens show that *P. sherbrookei* feeds on ants as is typical for most *Phrynosoma* species. The mean body temperature of 15 specimens was 30.25°C (±1.61°C).

***Phrynosoma taurus*** is endemic to Mexico. There are records from the Mexican states of Guerrero, Morelos, Oaxaca and Puebla. iNaturalist (2024) also lists a record from the federal state of Mexico (Estado de México). Terra typica: Matamoras Izúcar, Puebla, Mexico.

The Buffalo-horned lizard is found in dry shrubland, high deserts and even tropical dry forests. *P. taurus* can also survive in secondary habitats such as traditional managed pastures and extensively managed edges of corn fields (Pianka & Hodges 2007, Baur & Montanucci 1998). According to Sherbrooke (2003), *P. taurus* inhabits a variety of dry habitats. These include seasonally deciduous tropical shrubland and semi-arid areas with lush succulent vegetation such as columnar cacti. Although *P. taurus* generally occurs at lower altitudes (up to 1,500 m asl) than the species *P. braconnieri*, also native to Oaxaca and Puebla, the two species occasionally occur sympatrically. Montanucci (1979) states that *P. taurus* occurs in open oak-thorn bush forests in Guerrero, whereas in Puebla it lives in semi-desert like habitats. Davis & Dixon (1961) state that its habitat is a rocky hilly, open chaparral oak forest. In the areas where the species occurs, most rainfall occurs in the months of May to October, averaging 300–700 mm per year. It is very hot during this time, so that a large part of the moisture evaporates quickly. Temperatures of over 30°C can occur in the habitat all year round (Bauer & Montanucci 1998). In comparison to other members of the horned lizard genus *Phrynosoma*, little is known about this species (Baur & Montanucci 1998). Montanucci (1989c) concludes from the jaw and tooth morphology that the species feeds mainly on ants. Pianka & Parker (1975) also found an average volume percentage of 56% ants in four individuals when examining their stomach contents. Baur & Montanucci (1998) cite Modry (written communication), who was able to identify only remains of ants in faeces samples.

## Reproduction

Unless otherwise stated, the information on reproduction, husbandry and breeding was compiled from the surveys.

| Topic                   | Details on the reproduction of the live-bearing (ovoviviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|-------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | <p>The sexes can be clearly identified in all species of the genus <i>Phrynosoma</i>. Adult ♂♂ are not only a bit smaller and slimmer than the somewhat bulkier ♀♀, but the length of the tail is also proportionally longer. In addition, the base of the tail is significantly thickened by the internal hemipenis pockets of the ♂♂, especially during the mating season.</p> <p>In <i>P. hernandesi</i> adult ♀♀ are conspicuously larger than ♂♂.</p> <p>Another difference between the sexes can be seen in all species (except the oviparous <i>P. coronatum</i>). Below the anal slit, the ♂♂ have a series of significantly enlarged scales. These can be seen even in juveniles, sometimes with the help of a magnifying glass (Baur 1998).</p> |
| Reproduction            | Ovoviviparous: Ovoviviparous reptiles possess embryos that develop inside eggs which remain in the mother's body until they are ready to hatch. Immediately before or during birth, the young hatch from the thin egg membrane.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Sexual maturity         | As a rule, sexual maturity only sets in after the second winter. Depending on when the                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |

|                                                            |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                            | <p>young are born, this is after about 1½ years. ♀♀ are at least 18 months old when getting mature, ♂♂ can reach sexual maturity a little earlier.</p> <p><i>P. braconneri</i> ♀♀ mature from 60 mm SVL on (Baur &amp; Montanucci 1998)</p> <p><i>P. douglassi</i> matures in or after the second year of life</p> <p><i>P. ditmarsii</i>: At least 13 months in both sexes (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Breeding season                                            | <p><i>P. braconneri</i> is possibly active year-round, depending on the area. Births have been observed in both July and January (Baur &amp; Montanucci 1998)</p> <p><i>Phrynosoma ditmarsii</i>: Mating August–October, the juveniles are born in the rainy season, in July–September (Baur &amp; Montanucci 1998)</p> <p><i>P. hernandesii</i>: In Canadian populations, adult females give birth to live young in late July or early August. Litter size varies greatly, and can be 10 or more, but survival of the newborns is reported to be low (COSEWIC 2007)</p> <p><i>Phrynosoma orbiculare</i>: Mating takes place in autumn and winter (Suarez-Rodríguez et al. 2018), or, according to Baur &amp; Montanucci (1998) directly after hibernation. The juveniles are born in the following summer season (Haase 2014b, Schulz 2018c)</p> <p><i>P. sherbrookei</i>: Mating takes place in spring and birth in autumn (Nieto-Montes de Oca et al. 2014).</p> |
| Gestation period of the live-bearing horned lizard species | <p><i>P. braconneri</i>: 3–4 months</p> <p><i>P. ditmarsii</i>: 3–4 months</p> <p><i>P. douglasii</i>: 3–4 months</p> <p><i>P. hernandesii</i>: 3–4 months gestation period in the terrarium, according to Baur &amp; Montanucci (1998) 63 days</p> <p><i>P. orbiculare</i>: 3–4 months gestation period (Haase 2014b, Schulz 2018c), Baur &amp; Montanucci (1998) assume a gestation period of 6–7 months in the wild</p> <p><i>P. sherbrookei</i>: 3–4 months</p> <p><i>P. taurus</i>: 3–4 months gestation period.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Litter size/frequency of litters per year                  | <p><i>P. braconneri</i>: 2–12 juveniles / 1, max. 2 litters per year. In the wild 5–8 juveniles (Baur &amp; Montanucci 1998)</p> <p><i>P. ditmarsii</i>: 2–12 juveniles per litter / 1, max. 2 litters per year. In the wild 9–16 juveniles (Baur &amp; Montanucci 1998)</p> <p><i>P. douglasii</i>: 4–12 juveniles / 1, max. 2 litters per year</p> <p><i>P. hernandesii</i>: 4–12 juveniles / 1, max. 2 litters per year. In the wild on average 16 juveniles per litter (max. 18, Dammann 1949), in Canada usually 10 juveniles and only 1 litter per year (CITES 2022b)</p> <p><i>P. orbiculare</i>: 4–14 juveniles (Schulz 2018c) / 1, max. 2 litters. Baur &amp; Montanucci (1998) report an average litter size of 9–10 juveniles</p> <p><i>P. sherbrookei</i>: 2–12 juveniles</p> <p><i>P. taurus</i>: 2–12 juveniles.</p>                                                                                                                                  |
| Birth weight/size                                          | <p><i>P. hernandesii</i>: 0.9–1.3 g / 24–30 mm (Baur &amp; Montanucci 1998), in Canada 25–32 mm.</p> <p><i>P. orbiculare</i>: 40 mm (Haase 2014b).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Sex determination/parthenogenesis                          | <p><i>P. platyrhinos</i> have genetic sex determination, X/Y sex chromosomes (Koochekian et al. 2022). There are no studies for the ovoviparous species.</p> <p>Parthenogenesis is unknown in <i>Phrynosoma</i> spp.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Sperm storage                                              | <p>So far, little is known about this, only <i>Phrynosoma hernandesii</i>, <i>P. ornatissimum</i> (syn. of <i>P. hernandesii</i>) and <i>P. orbiculare cortezi</i> have been reported to store sperm over a season.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |

## Husbandry and Captive Breeding C/C



Fig. 7: *Phrynosoma* spp. husbandry (all photos J. Schulz)

- a Terrarium system
- b Open-air terrarium in the midday shade
- c Breeding terrarium
- d Tub for raising the smallest juveniles
- e Terrarium for raising the older juveniles
- f Vacuuming ants in the garden
- g *Lasius flavus*, the Yellow Meadow ant, is a good food insect for Horned Lizards
- h *P. orbiculare cortezii* with juveniles.





Fig. 8: *Phrynosoma* spp. outdoor enclosure in southwestern Germany. Outdoor keeping is essential for all *Phrynosoma* species during the summer months (all photos A. & E. Calgua)

- a Outdoor enclosure designed as a cold frame
- b *P. asio* kept in a group
- c Outdoor enclosure designed as a walk-in aviary
- d *P. asio* group basking together in the warmest part of the aviary.

| Topic                  | Data for the live-bearing (ovoviviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Husbandry requirements | <p>In contrast to the egg-laying species, some viviparous horned lizards are usually inhabitants of higher altitudes and therefore have a somewhat different climate. They are kept in spacious dry terrariums with Mediterranean temperatures. Despite their very calm nature, the larger species, such as the most commonly kept viviparous species <i>Phrynosoma orbiculare</i>, require indoor terrariums measuring at least 120 x 60 x 60 cm.</p> <p>For small and medium-sized species, terrariums measuring approximately 100 x 60 x 60 cm are suitable. Most horned lizard species are not territorial and can be kept quite well in small groups, even with several males. This must be taken into account when determining the size of the terrarium.</p> <p>As diurnal inhabitants of dry areas at higher altitudes, lightning for horned lizards can never really be bright enough in the terrarium. UVB metal halide lamps, which are available in a wide range of wattages, have proven to be effective. Suitable products include Solar Raptor from ECONLUX, Premium UVB MD lamp from Reptiles Expert or Bright Sun from Lucky Reptile.</p> |

| Topic                                                         | Data for the live-bearing (ovoviviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|---------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| General characteristics, difficulties in keeping and breeding | <p>While 35 watts and 50 watts are suitable for breeding terrariums, 70 watts and 100 watts are the rule for adult terrariums. In terrariums that are open at the top, which have proven to be particularly effective, the 150 watts versions are more likely to be used, as there is no risk of overheating. In the dry terrarium for viviparous horned lizards, an ambient temperature of 20–25°C is to be aimed for, while the basking spots can get up to 45°C (Haase 2014b, Schulz 2018c).</p> <p>It is important to achieve a nighttime reduction by cooling the terrarium to room temperature below 20°C. T5 tubes and LED bars can be used as additional basic lighting, but only to increase the lighting intensity; they are completely unsuitable as the sole lighting. The lighting duration is up to 14 hours during the mating season in summer and 6 hours in the winter months. During the 3–4 month of hibernation, which is best carried out individually in separate boxes in the refrigerator at 12°C, basic lighting is ideally required for the living plants in the terrarium.</p> <p>In general, hibernation (brumation) in a refrigerator is recommended for horned lizards (see above). If the terrarium room is cold enough in the winter months, the animals can also be hibernated inside the terrarium (see Schulz 2018c for <i>Phrynosoma orbiculare cortezi</i>).</p> <p>As inhabitants of dry high altitudes, it is important to offer the animals not only a sufficient substrate of sand, but also additional structures, as they do not live in completely open habitats like the desert-dwelling species. For <i>Phrynosoma orbiculare cortezi</i>, for example, it has proven useful to mix ⅓ spruce needles with sand (Schulz 2018c).</p> <p>The sand used should not contain any clay so that it does not solidify too much. Washed river sand or pre-packaged play sand are very suitable. When well dried, it should be loose so that the horned lizards can bury themselves half or completely in the typical way. It is particularly important to use finely sieved sand for newly hatched <i>Phrynosoma</i>, as the juveniles have difficulty digging in if the sand is too coarse (cf. Galli &amp; Ruf 2010).</p> <p>Some larger stones and pieces of root can be used as additional furnishings. In the wild, the viviparous horned lizards usually inhabit more structured areas such as grassland and dry forests and do not live in open areas like their desert-dwelling relatives. In addition to the mixing of the sand with spruce needles, the surface can also be covered with dried leaves.</p> <p>In contrast to most other horned lizards, which show a high degree of intraspecific tolerance, considerable aggressive behaviour was observed in <i>P. ditmarsii</i> when kept in communal terrariums. This was very pronounced even in newly born juveniles and, unlike adults, was not limited to aggression associated with feeding activities (Montanucci 1989d). A female was observed hunting and eating an own one-day-old juvenile (Baur &amp; Montanucci 1998). A tendency towards crepuscular activity has also been described in <i>P. ditmarsii</i> based on observations in terrariums. In line with this theory is the detection of some crepuscular and nocturnal arthropods, such as scorpions, as an unusual dietary component in Rock horned lizards (Montanucci 1989d).</p> |
| Care of the young, technical and time effort                  | <p>The effort required for all species is very high and time-consuming. It was stated that a single litter of juveniles can require 30–60 minutes of time per day.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Life expectancy in human care                                 | <p><i>Phrynosoma ditmarsii</i>: One CB male lived to 10 years (Baur &amp; Montanucci 1998)</p> <p><i>Phrynosoma hernandesi</i>: One CB female lived to 8 years; on average the animals live 6–7 years (Baur &amp; Montanucci 1998)</p> <p><i>Phrynosoma orbiculare</i>: maximum &gt; 8 years (data from keeper's interviews); one CB male lived &gt; 5 years (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |



| Topic                                                  | Data for the live-bearing (ovoviviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                             |
|--------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Number of specimens that survive to sexual maturity    | <i>P. braconnieri</i> : ca. 30%<br><i>P. ditmarsii</i> : ca. 60%<br><i>P. hernandesi</i> : ca. 60%<br><i>P. orbiculare</i> : ca. 80%<br><i>P. taurus</i> : ca. 60%.                                                                                                                             |
| Frequency of private breeding and reproduction in zoos | Live-bearing horned lizards are rare to very rare in captivity, but all of them have been bred. However, the many species were more likely to be individual successes by highly specialized keepers.<br>The most common (sub) species kept and bred is probably <i>P. orbiculare cortezii</i> . |
| Breeding difficulty evaluation                         | For all ovoviviparous species of the genus <i>Phrynosoma</i> , the breeding difficulties are rated as high to very high.                                                                                                                                                                        |
| F2 generation bred in captivity                        | <i>P. hernandesi</i> : yes<br><i>P. orbiculare</i> : yes.                                                                                                                                                                                                                                       |
| Commercial breeding/ranching                           | No.                                                                                                                                                                                                                                                                                             |
| Interviews/<br>Surveys/<br>Consultations               | <i>P. braconnieri</i> : 1 breeder<br><i>P. hernandesi</i> : 2 breeders<br><i>P. orbiculare</i> : 6 breeders<br><i>P. taurus</i> : 2 breeders.                                                                                                                                                   |

### Egg-laying (oviparous) species

| Species                                  | Original description | Common name                 | Common name International                                              | Known in private care or in the trade |
|------------------------------------------|----------------------|-----------------------------|------------------------------------------------------------------------|---------------------------------------|
| <i>Phrynosoma asio</i>                   | Cope, 1864           | Giant Horned lizard         | Riesenkrötenechse<br>Camaleón de Grandes Cuernos                       | Yes                                   |
| <i>Phrynosoma blainvilli</i>             | Gray, 1839           | San Diego Horned lizard     | Blainvills Krötenechse<br>Camaleón de Blainville                       | Yes                                   |
| <i>Phrynosoma cerroense</i>              | Stejneger, 1893      | Cedros Island Horned lizard | Lézard cornu de l'île de Cedros<br>Iguana cornuda de la isla de Cedros | Yes                                   |
| <i>Phrynosoma cornutum</i>               | (Harlan, 1825)       | Texas Horned lizard         | Texas-Krötenechse<br>Camaleón Común                                    | Yes                                   |
| <i>Phrynosoma coronatum</i> <sup>2</sup> | (Blainville, 1835)   | Coast Horned lizard         | Kronen-Krötenechse<br>Camaleón del Litoral                             | Yes                                   |
| <i>Phrynosoma goodei</i>                 | Stejneger, 1893      | Sonoran Horned lizard       | Sonora-Wüstenkrötenechse<br>Camaleón de Sonora                         | Yes                                   |
| <i>Phrynosoma mcallii</i>                | (Hallowell, 1852)    | Flat-tail Horned lizard     | Flachschwanzkrötenechse<br>Camaleón de Cola Plana                      | Yes                                   |
| <i>Phrynosoma modestum</i>               | Girard, 1852         | Roundtail Horned Lizard     | Rundschwanz-Krötenechse                                                | Yes                                   |

<sup>2</sup> *Phrynosoma wigginsi* Montanucci, 2004 (Gulf Coast Horned Lizard) was split from *Phrynosoma coronatum jamesi* on 23 June 2010, following taxonomic changes adopted at CoP15.

| Species                       | Original description | Common name          | Common name International                   | Known in private care or in the trade |
|-------------------------------|----------------------|----------------------|---------------------------------------------|---------------------------------------|
|                               |                      |                      | Tapayaxin                                   |                                       |
| <i>Phrynosoma platyrhinos</i> | Girard, 1852         | Desert Horned lizard | Wüsten-Krötenechse<br>Camaleón del Desierto | Yes                                   |
| <i>Phrynosoma solare</i>      | Gray, 1845           | Regal Horned lizard  | Vierhorn-Krötenechse<br>Camaleón Real       | Yes                                   |

## Morphology and Taxonomy

This compilation on morphology and taxonomy is largely based on the Reptile Database (Uetz et al. 2024). Details, additions and deviations are referenced separately.

***Phrynosoma asio*** Cope 1864 – The scientific name ‘asio’ is latinized and means ‘horned owl’. As its common name suggests, the giant horned lizard is one of the largest species in the genus *Phrynosoma* with a SVL of up to 124 mm and a GL of over 200 mm. In terms of head-body length, they are only surpassed in exceptional cases by female *P. cornutum*, which can reach up to 130 mm. The size can vary slightly depending on the distribution area. The animals from the southern parts are significantly larger than those from the north. The largest measured male animal had a SVL of 123 mm, the largest female 124 mm (Baur & Montanucci 1998). Since the SL of males is about  $\frac{2}{3}$  of the SVL, but only about half of the SVL of females, the males can be longer overall than the females. The males are always somewhat slimmer than the more massive females and weigh over 100g when well fed. Gravid females can weigh well over 130 g (Baur & Montanucci 1998). The spines on the head make it easy to distinguish from all other species. The 8 pointed spines on the head are significantly larger than the other head spines (Baur & Montanucci 1998). In addition, the 8 large spines on the head are not only all similar in size, but in contrast to other species, the supraorbital spines in particular are very pronounced and almost as large as the occipital spines. In other species, the occipital spines are usually much more pronounced and the supraorbital spines relatively small. In contrast to most horned lizard species, *P. asio* has the most ‘lizard-typical’ body structure. The body is slightly rounder and slightly longer in cross-section and the tail length is also the longest of all horned lizards in relation to the head-body length.

***Phrynosoma blainvillii*** Gray, 1839 – This species has often been considered a subspecies of *P. coronatum* (Burt 1933, Jennings 1988b, Baur & Montanucci 1998, Köhler 2021). Named after Henri Marie Ducrotay de Blainville but described by Gray in 1839 as *P. blainvillii*. Even if the final ‘e’ is not pronounced in French, at least in German the correct surname should be used, and the species should be named Blainville's horned lizard. *P. blainvillii* has a flattened body typical of horned lizards with long, pointed horns on the top and sides of the head, as well as smaller spines all over the body and tail. Adult specimens can reach head-body lengths of up to 110 mm. They can reach a weight of between 45 and 55 g, with gravid females weighing up to 70 g (Jones & Lovich 2009). They are either reddish-brown, brownish-yellowish or grey in colour. Dorsally there are pairs of darker transverse spots, often with white borders, and a large dark spot is found under each of the two largest occipital horns. The belly is smooth and pale, often interspersed with small dark dots and spots. Some individuals have a contrasting yellowish colour. Females are generally larger than males (Jones & Lovich 2009). The latter have enlarged postanal scales (Tinkham 1951, Powell & Russell 1985).



Fig. 9: *Phrynosoma* spp. – egg-laying (oviparous) species part I

- a *P. asio* (F. Hulbert)
- b *P. asio* (K. Kunz)
- c *P. blainvilli* (P. Clevinger)
- d *P. cerroense* (A. Duarte)
- e *P. cornutum* (K. Kunz)
- f *P. cornutum*, ♀ Viesca, Coahuila 1,250 m asl (P. Heimes)
- g *P. cornutum* (F. Hulbert)
- h *P. cornutum* (J. Schulz).





Fig. 10: *Phrynosoma* spp. – oviparous species part II

- a *P. coronatum*, La Paz, BCS (P. Heimes)
- b *P. mcalli*, Sierra Blanca, El Pinacate, Sonora (P. Heimes)
- c *P. mcalli*, Yuma County, Arizona (R. Nixon)
- d *P. modestum* ♂ Estación El Oro, Mun. Sierra Mojada, Coahuila (P. Heimes)
- e *P. platyrhinos platyrhinos* in the habitat (J. Schulz)
- f *P. platyrhinos calidiarum* (J. Schulz)
- g *P. solare* (K. Kunz)
- h *P. solare*, Valle de Guaymas, Mun. de Empalme, Sonora (P. Heimes).

***Phrynosoma cerroense*** Stejneger, 1893 – This species is sometimes considered a subspecies of *P. coronatum* (Baur & Montanucci 1998, Köhler 2021). But even the subspecies status is sometimes questioned; Grismer (2002) sees the various subspecies of *coronatum*, including *P. cerroense*, as only regional ‘colour forms’. The name ‘*cerroense*’ refers to the island of Cedros, which was incorrectly referred to as ‘Cerros’ in Stejneger’s original description. *P. cerroense* is a medium-sized species from the *P. coronatum* group. It reaches a maximum head-body length of about 85 mm. It is characterized by a black-spotted, smooth-scaled ventral side and two rows of pointed, lateral marginal scales on each side of the body, with the lower one appearing greatly reduced. Three rows of enlarged throat scales on the sides of the throat are another characteristic. Dorsal coloration is steel grey with three pairs of evenly spaced, irregular, dark spots. There are two occipital spines that are three times as long as the basal width and do not touch at the base. In addition, *P. cerroense* has four temporal spines on each side of the head, with the fourth from behind appearing greatly reduced or absent. The tympanum is visible externally. Dark banding is absent on the head (Jennings 1988a).

***Phrynosoma cornutum*** (Harlan, 1825) – The scientific species name *cornutum* means ‘horned’. According to the current view, the previously described subspecies are not recognised as such (see Uetz et al. 2024). Köhler (2021) reclassifies *blainvillii* and *P. cerroense* as subspecies of *P. coronatum*; the Reptile Database does not follow this taxonomic change (Uetz et al. 2024). The Texas horned lizard is, together with *P. asio*, the largest horned lizard. It is slightly shorter in total length, but slightly larger in head-body length than the giant horned lizard. *P. cornutum* shows sexual dimorphism, with females being larger and reaching a maximum head-body length of 130 mm, while males only reach about 95 mm. *P. asio* is somewhat smaller, with a maximum head-body length of 123 mm for females but reaches a greater total length of over 200 mm due to the slightly longer tails. The tail length of *P. cornutum* is only about half the body length, so the total length is slightly shorter. *P. cornutum* is dorsally covered with keeled and granular scales. Two rows of fringe scales form the transition to the ventral area. *P. cornutum* has characteristic spines that are distributed over the entire body, with the largest forming the crown of the head. The two inner spines of the crown are the most pronounced. Additional spines are found on the eyebrows and jaw. The coloration varies depending on the environment, and usually corresponds to the colour of the ground in the respective biotope. Animals in desert-like environments are more yellowish or reddish-brown, in prairies they are more brownish. On the top of the head there are dark lines that extend from the eyes to the tip of the horns. A characteristic, continuous white line extends along the middle of the body. On the sides of this there are noticeably large, often light yellow or white-edged, black circular spots (Jones & Lovich 2009, Baur & Montanucci 1998).

***Phrynosoma coronatum*** (Blainville, 1835) – The scientific species name *coronatum* means ‘crowned’. Recognised subspecies are *P. coronatum coronatum* (Blainville, 1835) and *P. coronatum frontale* Van Denburgh, 1894b. *P. coronatum* is a large species with a rather slender body shape. The strong pair of occipital horns are not in contact at the base. *P. coronatum* has two large dark spots behind the head dorsally followed by three broad dark transverse bands. Several smaller bands run along the tail. The ventral scales are smooth, the scales on the neck are tapered. The head-body length is given as 70–105 mm. Adults reach a weight of 40–70 g. The tail measures slightly more than half the head-body length in males and slightly less than half the head-body length in females. The colour can be various shades of brown, with cream-colored ‘accents’ around the spots and the outer edge of the scales. (Sherbrooke 2003, Baur & Montanucci 1998).



***Phrynosoma goodei*** Stejneger, 1893 – This species is sometimes considered a subspecies of *P. platyrhinos* (Stejneger, 1893, Pianka 1991, Baur & Montanucci 1998, Köhler 2021). The Sonoran Desert Horned Lizard is a medium-sized, flattened species, reaching up to about 95 mm SVL, typical of horned lizards. Thick, spine-like scales protrude from the back of the head. The two central head spines (occipital horns) protrude upwards and backwards, and are significantly longer than the other spines. The bases of the occipital horns do not touch. Several isolated, pointed scales protrude from the back. Each underside of the body is bordered with one or two fringes of enlarged, pointed scales. A row of enlarged, pointed scales protrudes on each side of the throat. The basic coloration is light brown, grey, or brown and usually corresponds to that of the substrate on which this lizard lives. The lower edges of the body are often salmon, peach, or orange. A pair of large dark spots marks the throat. The back is often adorned with paired dark spots. The back of the edge of each body spot is often bordered with white or cream. The underside of the body is often punctuated with sparse dark spots that are denser and more pronounced anteriorly and on the throat. The very similar-looking *P. platyrhinos* often has extensive dark mottling over the entire ventral surface, and its occipital horns point almost straight back, not up and back. The Sonoran Desert horned lizard lacks a dark dorsal stripe, distinguishing it from *P. mcallii*. The bases of the occipital horns of the similar-looking *P. solare* are in contact (Brennan & Holycross 2006).

***Phrynosoma mcallii*** (Hallowell, 1852) – The species epithet honours the discoverer of the species, George A. M'Call, who collected the species in the 1850s (Sherbrooke 2003). It is a medium-sized species that can reach a total length of 120 mm. The body is flattened, as is typical of horned lizards, with scattered, enlarged, pointed scales on the upper body and tail. The skin on the back is mostly smooth with a few scattered small spines. Eight strikingly long horn spines extend from the back of the head. The two middle horns are longer than the rest, slender and pointed. Long and narrow spines are found on the lower jaw and two rows of fringed scales on the sides of the body, with the lower row of scales being smaller than the upper one. The nostrils are located within the canthal crest, the 'muzzle edge'. Long and narrow spines are located on the lower jaw and two rows of spiny fringed scales on the sides of the body, with the lower row of scales smaller than the upper. The tympanic membrane is not externally visible (Funk 1981, Uetz et al. 2024).

***Phrynosoma modestum*** Girard, 1852 – With a total length of only 80–100 mm, *P. modestum* is the smallest and lightest species of horned lizard (Baur & Montanucci 1998). The characteristic spine border on the sides is missing in the round-tailed horned lizard and is therefore easy to distinguish from all other species, despite considerable differences in colour and size depending on the population (Baur & Montanucci 1998). Overall, they are somewhat more inconspicuous and less spiny in appearance, although parts of the head spines, 2 temporal and 2 occipital spines are well developed. 2–4 of the temporal spines that follow forward can also be slightly enlarged.

***Phrynosoma platyrhinos*** Girard, 1852 – *P. platyrhinos calidiarum* (Cope 1896) has been synonymized with *P. p. platyrhinos* in Köhler (2021). The desert horned lizard is a medium-sized, flat-topped species, reaching up to about 95 mm SVL. Thick, spine-like scales project from the back of the head. The two central head spines (occipital horns) project upward and backward and are noticeably longer than the other spines. The bases of the occipital horns do not touch. Several isolated, pointed scales project from the back. Each underside of the body is bordered with one or two fringes of enlarged, pointed scales. A row of enlarged, pointed scales projects on each side of the throat. The dorsal coloration is light brown, grey, or brown,

usually corresponding to the soil on which the lizard lives. The lower edges of the body are often salmon, peach, or orange. A pair of large dark spots marks the neck, and the back is often adorned with paired dark spots. The back of the edge of each body patch is often bordered with white or cream. The belly is often covered with sparse dark spots, which are denser and more pronounced on the front part of the underside and on the neck (Sherbrooke 2003, Brennan & Holycross 2006).

***Phrynosoma solare*** Gray, 1845 – The scientific name of the regal horned lizard is derived from the Latin ‘solaris’ – ‘relating to the sun’. *P. solare* is a medium-sized, up to 117 mm SVL, horned lizard-typically flattened species with a short tail and a crown of flattened, dagger-like horns that protrude from the back of the head. The base of each of the four central horns touches that of the adjacent horn, which distinguishes this species from other horned lizards. Several isolated, pointed scales protrude on the dorsal side. The ventral side is bordered by a single fringe of enlarged, pointed scales. The front of the limbs is covered with enlarged, keeled, pointed, protruding scales. The basic coloration is usually reddish-brown, light brown or grey and usually corresponds to the substrate on which the animal lives. The middle of the back is usually noticeably lighter than the sides of the body. There are often two dark, washed-out, rounded spots on the neck. The underside is pale with small, dark spots. Some specimens have a faint, pale stripe running down the middle of the back (Sherbrooke 2003, Brennan & Holycross 2006).

### Distribution, Habitat and Behaviour in the Wild

***Phrynosoma asio***: The species is distributed along the Pacific side of Mexico, from Jalisco in the northwest of the range to Chiapas in the southeast (Canseco-Marquez et al. 2013). The species appears to be endemic to Mexico and is found in the provinces of Jalisco, Colima, Michoacán, Morelos, Guerrero, Oaxaca and Chiapas. Historically, it may also have been distributed in the Río Grijalva Valley and adjacent areas of Guatemala. The Savana Grande site in Guatemala refers to Günther 1890 (Baur & Montanucci 1998). Despite further research, these historical data could not be verified (Calgua 2000, CITES 2022b). Terra typica: Colima, Mexico.

*P. asio* inhabits dry to semi-arid habitats and is found at altitudes from sea level to 750 m asl (Canseco-Marquez et al. 2013). In the open forests and semi-desert areas, average temperatures range from 25–35°C (Baur & Montanucci 1998). The mating season is during the rainy season from June to September. This is followed by a pronounced dry season with slightly lower temperatures. During this time, many plants dry out and lose their leaves. Temperatures fall slightly towards the end of the year, but then rise again until they reach their peak in the driest time of the year, in April and May (Baur & Montanucci 1998). Information on the behaviour *P. asio* the wild is scarce. According to Baur & Montanucci (1998), the main activity period is from April to October. Davis and Dixon (1961) found several specimens under pieces of bark in great heat. At the end of June, they observed a copulating pair near Chilpancingo, Guerrero. The female died 7 weeks later while laying eggs. One of the authors found two half-grown specimens south of Nueva Italia de Ruiz, Michoacan in July 2010 in a dry forest interspersed with many cacti. A horned lizard was active at around 9:30 a.m. and was looking out from a burrow the size of a mouse hole. The second specimen was found around an hour later, nestled against a larger boulder. It was already very warm and humid in the first half of the morning, despite the overcast sky, as it had rained heavily the previous night. The reddish, clayey soil was saturated with water from the rain, there were rain-filled puddles everywhere and the temperature was already 30°C at around 9:00 a.m. when starting the field trip (Langner pers. obs.).

***Phrynosoma blainvillii***: The distribution is limited to the area around San Diego, California and northern Baja California, in Mexico at altitudes from sea level to 1,135 m asl (Köhler 2021). Terra typica: 'California'. Limited to the San Diego area, California (Klauber 1936).

Literature data on altitude distribution vary greatly. While Köhler (2021) gives altitudes from sea level to 1,135 m asl, Hult & Germano (2015) provide the following information: '*P. blainvillii* occurs in a variety of habitats, for example in semi-arid mountains, chaparral, oak forests, coniferous forests, foothills and valleys at altitudes from sea level to about 1,800 m (Smith 1946, Sherbrooke 2003, Stebbins 2003, Leaché et al. 2009). Jones & Lovich (2009), on the other hand, give the maximum altitude distribution limit as 2,500 m asl level and describe the biotopes as open shrub vegetation. Ants, such as native harvester ants, and a substrate loose enough for these lizards to burrow in should be present. Although this species is usually associated with coastal sage communities, it also inhabits a surprising variety of other habitats. Dense chaparral stands, coniferous, deciduous and mixed forests, and coastal dunes are all potential habitats for the species (Jones & Lovich 2009). According to Jones & Lovich (2009), the males' activity period begins at the end of March after hibernation, females following about a month later. The home range of activity of males during the spring is significantly larger than that of females. Ants make up the majority of the diet.

***Phrynosoma cerroense***: The Cedros horned lizard is found in the central part of Baja California, Mexico (26.7–30.8 latitude) at altitudes from sea level to 845 m asl (Köhler 2021). For some time, *P. cerroense* and *P. coronatum schmidtii* were thought to be sympatric on Cedros Island (Barbour 1921, Reeve 1952). This has been proven incorrect (Banta 1968, Jennings 1985). *P. cerroense* is the only horned lizard native to Cedros Island. *P. coronatum jamesi*, which occurs on the eastern side of Baja California, is a synonym of *P. cerroense*. The distribution area of *P. cerroense* is not only limited to the island of Cedros, but the species can also be found on the central eastern side of Baja California (Baur & Montanucci 1998). Terra typica: Cedros Island, Baja California, Mexico.

Since the species was mostly listed as a subspecies of *P. coronatum* in the past, there are no explicit descriptions of the habitat and lifestyle of *P. cerroense* in the literature. This species has developed special skin structures for moisture harvesting as an adaptation to its very arid habitat (Joel et al. 2021).

***Phrynosoma cornutum***: The Texas Horned Lizard is distributed from southeastern Arizona and northeastern Sonora through New Mexico to eastern Texas, and from Kansas southward to Mexico in the provinces of Durango, Zacatecas, Nuevo León and northern Veracruz. There are also isolated records from northern Colorado, southern Nebraska and southwest Arkansas. *P. cornutum* can be found at altitudes from almost sea level to 1,865 m asl (Köhler 2021). Terra typica: Great Plains east of the Rocky Mountains, restricted to 'Fort Riley, Geary County, Kansas'. Holotype not known (Köhler 2021).

The Texas Horned Lizard lives in various dry to very dry regions with sandy or rocky soil and sparse vegetation, such as deserts, prairies or dune areas. Plants that grow in the preferred habitat include cacti, acacias and drier grasses. Environments with some dead wood piles are preferred. The lizards use these to sun themselves and seek shelter. *P. cornutum* is also more commonly found under bushes that provide cover and shade (Degenhardt et al. 1996, Bartlett and Bartlett 1999, Hammerson 1999, Stebbins 2003). The soil conditions can vary from sandy to stony. When inactive, the animals burrow into the ground, seek out rodent burrows or hide under stones (Hammerson 2007). To escape drowning after heavy monsoon rains, Texas

horned lizards have been observed climbing up trees to about one meter high (Sheffield & Carter 1994). The diverse predators include the desert hawk (*Parabuteo unicinctus*) the road-runner (*Geococcyx californicus*), the grasshopper mice (*Onychomys* spec.) and the whip snake (*Masticophis flagellum testaceus*) (Bauer & Montanucci 1989, Sherbrooke 1990b, Sherbrooke 1991). The proportion of ants in the diet of Texas horned lizards is around 75% (Pianka & Parker 1975, Montanucci 1989c). Surprisingly, the highly poisonous blister beetles (*Megetra cancellata*) are also part of the diet (Cohen & Cohen 1990).

***Phrynosoma coronatum*:** The distribution of the crowned horned lizard extends from Northern California to the Cape region of Baja California, Mexico, at altitudes from almost sea level to 1,655 m asl (Köhler 2021). Terra typica: 'California'. Limited to San Lucas, Baja California, Mexico (Köhler 2021).

*P. coronatum* inhabits very diverse habitats from sea level to 2,000 m asl. The species occurs in a variety of arid and semi-arid habitats. Extensive grasslands are often present, along with scattered cacti, yuccas, mesquite bushes, acacias, juniper trees, and other waist-high desert shrubs and small trees. The ground is often interspersed with sandy areas in which the animals like to burrow. (Sherbrooke 2003, Baur & Montanucci 1998). The main activity period of *P. coronatum* is between March and June. The proportion of ants in the diet of *P. coronatum* is 45% (Pianka & Parker 1975).

***Phrynosoma goodei*:** The Sonoran Desert Horned Lizard is found in southern Arizona and the state of Sonora, Mexico (Köhler 2021). Terra typica: Coastal deserts of the province of Sonora, Mexico, restricted to Puerto Libertad (Köhler 2021).

Information on the habitat and lifestyle of the former *P. platyrhinos* subspecies *P. goodei* is sparse. They are described as terrestrial lizards living in desert areas that bury their eggs in the ground. They spend inactive periods burrowed (Hammerson 2019). In Arizona, *P. goodei* inhabits the Sonoran, Mohave and Great Basin deserts, as well as the lower foothills of an ecoregion known as the 'Interior Chaparral' and the conifer forests of the Great Basin. The species is usually found in relatively flat, open areas with sandy or clay soil, and less frequently in rocky, broad slopes of alluvial material called 'bajadas' at the foot of a slope or mountain (Brennan & Holycross 2006). This diurnal ground dweller is most active in the morning and evening. It seeks protection from the high midday temperatures by burrowing into the ground or retreating into a burrow. *P. goodei* is more likely to try to escape by running away, usually under the nearest bush, than other horned lizards. When this horned lizard is picked up, it often puffs itself up, jabs its horns or flattens its body (Brennan & Holycross 2006).

***Phrynosoma mcallii*:** The flat-tailed horned lizard is found in southern California and southwestern Arizona, as well as adjacent regions in Baja California and Sonora, Mexico, where they can be found from almost sea level to 785 m asl (Köhler 2021). Terra typica: Great Desert of the Colorado, between Vallecita and Camp Yuma, about 160 miles east of San Diego. According to Smith and Taylor (1950), this corresponds to the area between Vallicita [= Vallecito] and Winterhaven [= Fort Yuma, Camp Yuma] (Köhler 2021).

Typical habitats are sandy desert plains with sparse vegetation. These can be low hills or flat areas interspersed with small stones below 300 m asl, which are loosely interspersed with creosote bush (*Larrea tridentata*), ragweed (*Ambrosia artemisiifolia*), bastard indigo (*Amorpha fruticosa*), saltbush (*Atriplex lentiformis*), ocotillo (*Fouquieria splendens*), and tamarisk (*Tamarix ramosissima*) (Turner & Medica 1982, Grismer 2002). Flat-tailed horned lizards are

most likely to be found where the surface soils have some loose or windblown sand. The species is rarely found on dunes (Beauchamp et al. 1998). In Arizona, it is most common in areas with galleta grass (*Pleuraphis jamesii*), sandy soil and many active nests of black harvester ants (*Veromessor pergandei*) (Rorabaugh et al. 1987). *P. mcallii* relies primarily on its excellent cryptic camouflage coloration. It is often immobile and very difficult to spot until it moves. The ground-dwelling lizards rarely sit elevated on rocks or wood (Grismer 2002). They often spend inactive phases buried in loose sand. When approached, they sometimes try to escape into a burrow or under a bush and can achieve a speed that is astonishing for a horned lizard (Wone & Beauchamp 1995). It is believed that *P. mcallii* uses self-dug hibernation caves. They usually hibernate only between 5 and 10 cm from the surface. The greatest measured depth was 20 cm below the surface (Muth & Fisher 1992, Mayhew 1965). This rare species usually occurs in low population densities. The daytime temperatures in the habitat of this species can reach 50°C, the annual rainfall rarely exceeds 100 mm (Baur & Montanucci 1998).

***Phrynosoma modestum*:** The round-tailed horned lizard is found from eastern Arizona through New Mexico to west-central Texas. The distribution area extends southwards to the Mexican states of Aguascalientes and San Luis Potosí. In the large distribution area, the animals occur at altitudes of 380 to 2,595 m asl (Baur & Montanucci 1998, Köhler 2021). Terra typica: Rio Grande west of San Antonio, or between San Antonio and El Paso, Texas. According to Smith & Taylor (1950) restricted to Las Cruces, Dona Ana County, New Mexico (Köhler 2021).

The habitat of *P. modestum* is deserts and semi-deserts, where the animals inhabit stony and gravelly areas, which are covered to varying degrees with shrubs and grasses (Baur & Montanucci 1998). The animals do not dig themselves into the ground so much, but instead sometimes cling to existing stones to rest. This interesting behaviour, known as stone mimicry, which is particularly common in populations from gravelly biotopes, serves to deceive predators (Sherbrooke & Montanucci 1988). In this case, they not only press themselves flat against the ground, but they also bend the back part of their spine into a hump, so that with their legs drawn up and their heads lowered, they look like the pebbles lying around everywhere (Sherbrooke & Montanucci 1988).

***Phrynosoma platyrhinos*:** The desert horned lizard is distributed from Idaho and Oregon in the north southward through Utah, Arizona and California to the northern part of Baja California, Mexico (Köhler 2021). Terra typica: Salt Lake County, Utah.

The range of the desert horned lizard extends across the highland areas of the Sonoran Desert, Chihuahuan Desert, and semi-desert grassland communities. It inhabits valleys, rocky bajadas, and low foothills. It is usually found in relatively flat areas with low shrubs and open, sunny areas. Throughout its range, *P. platyrhinos* is associated with habitats with woody shrubs, cacti, and yuccas in various arid and semi-arid areas of plains, floodplains, and valleys (Sherbrooke 2003, Brennan & Holycross 2006). These horned lizards inhabit all types of desertic shrubland with sand plains, alluvial fans, floodplains, or bushy dune margins (Grismer 2002, St. John 2002, Stebbins 2003). It is most commonly found where there are bare areas between free-standing shrubs. It occurs where summers are hot and winters are cold or mild. However, winter temperatures are generally too low for activity. The altitude of the habitats inhabited by this species ranges from -100 m in Death Valley to 1,980 m asl (Baur & Montanucci 1998). The diet consists mainly of slow-moving insects (e.g. ants and beetles), but sometimes also of spiders and some plant material (e.g. *Lycium* fruits) (Banta 1961, Tanner & Krogh 1973). In general, this lizard is considered an ant specialist (Pianka 1991). In a shrub-steppe bajada in



northwestern Utah, desert horned lizards consumed 14 of the 20 ant species present in the study areas, but showed a clear preference for species with the largest body sizes, including but not limited to harvester ants (Newbold & MacMahon 2009). Desert horned lizards rely primarily on their excellent camouflage coloration to protect themselves from potential predators. They are very difficult to detect as long as they are not moving. However, they are also capable of amazingly fast sprints into the vegetation cover, which is usually nearby (Linsdale 1938). *P. platyrhinos* are not known to use the defence mechanism of blood squirting, which is otherwise common among horned lizards, against potential enemies. Predators include *Falco mexicanus*, *Lanius ludovicianus*, *Gambelia wislizenii* and *Masticophis taeniatus* (Middendorf & Sherbrooke 1992, Sherbrooke & Middendorf 2004).

***Phrynosoma solare*:** The four-horned lizard is found from central Arizona southward through the states of Sonora to central Sinaloa, Mexico. The species can be found from almost sea level to about 1,700 m asl (Köhler 2021). Terra typica: 'California' (in error). Corrected by Schmidt (1953) to 'Tucson, Arizona' (Köhler 2021).

*P. solare* inhabits mainly flat or gently sloping terrain with open desert vegetation such as mesquite trees (*Prosopis* spec.), creosote bushes (*Larrea tridentata*) and saguaro cacti (*Carnegeia gigantea*) (Pianka & Hodges 2007). The four-horned lizard is excellently adapted to a dry, hot climate. The soil in the habitat can occasionally be covered with a fine layer of limestone dust (Suarez et al. 2000). *P. solare* has been shown to inhabit relatively small territories of about 146 meters radius (Parker 1971). *P. solare* can be active year-round, but in winter they are usually only active on unusually warm days. They burrow into the ground to protect themselves from cold or excessively high temperatures. When threatened or captured, *P. solare* occasionally squirts blood from its eyes. Other defensive behaviours include puffing up and butting its horns.

## Reproduction

Unless otherwise stated, the information on reproduction, husbandry and breeding was compiled from the surveys.

In Proposal 18 (CITES 2022b) the following information is given on the reproduction: In the wild, the eggs of the horned lizards are deposited in 2 to 3 layers and each layer is covered with soil (Reeve 1952, Sherbrooke 1981). Once laying is completed, the female refills the hole with excavated soil, rakes the surrounding surface to disguise the nest (Ramsey 1956) and leaves the site (Sherbrooke 1981). Clutch sizes for horned lizards range from 13 to 45 eggs (Milne & Milne 1950, Ballinger 1974, Pianka & Parker 1975, Sherbrooke 1981).

| Topic                   | Details on the reproduction of the egg-laying (oviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
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| Secondary sexual traits | <p>The sexes can be clearly identified in all species of the genus <i>Phrynosoma</i>. Adult ♂♂ are usually not only somewhat smaller and slimmer than the somewhat more massive ♀♀, but the length of the tail is also proportionally somewhat longer. In addition, the base of the tail is significantly thickened by the internal hemipenis pockets of the ♂♂, especially during the mating season.</p> <p>Another difference between the sexes can be seen in all species except <i>P. coronatum</i>. Below the anal slit, the ♂♂ have a series of significantly enlarged scales. These can be seen even in juveniles, sometimes with the help of a magnifying glass (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Reproduction            | Oviparous (egg-laying).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Sexual maturity         | <p>As a rule, sexual maturity is reached at least after the second winter. Depending on the hatching month, this is usually at the age of about 1½ years. ♀♀ at least 18 months, ♂♂ somewhat earlier.</p> <p><i>Phrynosoma asio</i>: Juveniles grow relatively slowly. The hatching weight of one ♀ was 1.2 g, after 2 months the same animal weighed 3 g, after 5 months 11 g. After 9 months several animals weighed about 50–65 g. The animals reach adult weights of about 110–135 g</p> <p><i>P. cornutum</i>: Sexual mature individuals are at least 20 months old and 68 mm in SVL (Baur &amp; Montanucci 1998)</p> <p><i>P. coronatum</i>: In the wild, sexual maturity in <i>P. cornutum</i> is reached in the 2<sup>nd</sup> summer after hatching (Ballinger 1974)</p> <p><i>P. modestum</i>: The animals are sexually mature when their SVL is just over 40 mm. Animals from early clutches can have reached this level by the time of their first hibernation (Baur &amp; Montanucci 1998), meaning they can mate in the following spring</p> <p><i>P. platyrhinos</i> reaches sexual maturity at about 22 months (Tanner &amp; Krogh 1973, Nussbaum et al. 1983)</p> <p><i>Phrynosoma solare</i>: Compared to other <i>Phrynosoma</i> species, <i>P. solare</i> grow very quickly and reproduce in the next season, at an age of about 9 months. In comparison to <i>P. asio</i>, which weigh more than twice as much when fully grown, young <i>P. solare</i> already weigh over 50 g after 7 months, whereas <i>P. asio</i> only weighs about 25 g at the age of 7 months.</p>                                                              |
| Reproductive season     | <p><i>P. asio</i>: First matings have been observed at the end of June. The mating season lasts about 5–6 weeks (Baur &amp; Montanucci 1998). Egg-laying can occur even more than 2 months after mating. This significantly longer than in other horned lizard species (Baur 1979a). Alvarez del Toro (1960) reports egg-laying in September and October in Chiapas and states that clutches contain 7–15 eggs</p> <p><i>P. blainvillii</i>: Nesting occurs in the first half of June (Shaw 1952) Hult &amp; Germano (2015) state that the activity period is from the beginning of April to the beginning of November. According to their data, the hatchlings appear from July on and are most active between August and September (Howard 1974, Zeiner et al. 1988, Jennings and Hayes 1994)</p> <p><i>P. cerroense</i>: Mating from mid-February on, nesting early in March to end of April (Baur &amp; Montanucci 1998). This reference is on <i>P. coronatum</i> in middle Baja California = <i>P. cerroense</i></p> <p>In Texas, the breeding season for <i>P. cornutum</i> begins shortly after the spring and continues until mid-July (Milne &amp; Milne 1950). Matings have been observed at the end of April to early May. The mating season begins three to four weeks after hibernation. The manner of mating is unique for horned lizards. The male bites onto a fold on the side of the female's neck, takes two to three steps forward and turns the female onto her back with a strong movement of his head. He stands over the female now, fixes her and copulation follows. The whole process takes about a quarter of an hour, the</p> |

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|                                        | <p>actual mating takes 6 minutes (Montanucci 1968, Tollestrup 1981, Baur &amp; Montanucci 1998). Egg laying takes place about 40 days after mating. The female digs a tube in loose soil to deposit her eggs. The maximum clutch size is given as up to 49, with 25–30 eggs being the average. The incubation period varies between 40 and 60 days (Baur &amp; Montanucci 1989). Sometimes the clutch is found under stones (Collins 1982). Under terrarium conditions, successful matings have been observed in June (Galli &amp; Ruf 2010)</p> <p><i>P. coronatum</i>: Mating in mid-March, oviposition at the end of April. Mating to oviposition takes about four weeks. 7–21 eggs are laid between mid-June and mid-July. The young hatch after eight to nine weeks (Baur &amp; Montanucci 1998)</p> <p><i>P. mcallii</i>: At the beginning of April, after the end of hibernation, the breeding season begins. 1<sup>st</sup> clutch is laid in May, a 2<sup>nd</sup> clutch can be deposited in July (Pianka &amp; Parker 1975)</p> <p>Females of <i>Phrynosoma platyrhinos</i> produce one or two clutches between April and July and bury their eggs in the soil. Clutch size averages about 7. Incubation lasts about 50–60 days. Hatchlings appear from mid-July to mid-September; time of birth slightly differs throughout the range of the species (Hammerson 2016, cited in CITES 2022b). Hibernation ends in early to mid-March. The mating season usually begins at the end of March. It can last until the end of May. After three to four weeks, an average of 6–8 eggs are laid. The incubation period is given as about 6 weeks (Baur &amp; Montanucci 1998)</p> <p><i>P. solare</i>: The reproductive period begins relatively late, with mating taking place in July. Females generally lay their eggs between June and August (Parker 1971). Between 7 and 33 eggs are laid per clutch. Females usually only lay one clutch per year. Nests are semi-circular, sloping tunnels dug into the ground to allow the egg-laying site to remain in the shade for longer during the day. They usually nest in damp fine silt or sand (Van Devender &amp; Howard 1973). However, egg-laying usually occurs later than this, and most do not occur until late July. Hatchlings can be found relatively late in the year, in September or October (Baur &amp; Montanucci 1998). Various courtship activities are used to attract a female, such as push-ups and head nodding (Langner pers. obs.).</p> |
| Number of eggs/<br>clutches per season | <p><i>P. asio</i>: 4–30 eggs (on average 16–22 eggs) / usually 1 clutch per year, a maximum of 2 clutches are possible (Recchio et al. 2014)</p> <p><i>P. blainvillii</i>: 10–21 eggs (Shaw 1952)</p> <p><i>P. cerroense</i>: 11–16 eggs (Baur &amp; Montanucci 1998). This reference is on <i>P. coronatum</i> in middle Baja California = <i>P. cerroense</i></p> <p><i>P. cornutum</i>: 4–30 eggs / 1 or maximum 2 clutches per year. Up to 29 eggs (Ballinger 1974).</p> <p><i>P. coronatum</i>: 4–30 eggs. 7–21 eggs (Baur &amp; Montanucci 1998)</p> <p><i>P. goodei</i>: 4–8 eggs</p> <p><i>P. mcallii</i>: 4–24 eggs, 3–10 eggs per clutch and 1–2 clutches per year (Pianka &amp; Parker 1975)</p> <p><i>P. modestum</i>: 2–12 eggs per clutch, 6–15 eggs per clutch and 1–2, exceptionally up to 3 clutches (Wernicke &amp; Haase 2014)</p> <p><i>P. platyrhinos</i>: 4–8 eggs, 6–8 (Baur 1973), 2–12 (Fabian 2013) / up to 4 clutches per year (Schulz 2018a)</p> <p><i>P. solare</i>: 4–30 eggs / 1 clutch per year, 13–33 eggs per clutch (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Egg size/<br>hatchling size            | <p><i>P. asio</i>: hatching size 1.2 g, 1.4–2.1 g (Recchio et al. 2014)</p> <p><i>P. blainvillii</i>: Egg size 12.8–15.4 x 10.2–11.1 mm / hatching size CL 35–37 mm (Shaw 1952).</p> <p><i>P. cornutum</i>: Egg size 10 x 16 mm (Baur &amp; Montanucci 1998). Hatching size 2.6–3.6 cm / 1.0–1.3 g (Galli &amp; Ruf 2010). Hatching size 20–32 mm SVL, 30–42 mm CL (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |

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|                                    | <p><i>P. coronatum</i>: Hatching size 27–28 mm SVL, 38–41 mm CL (Baur &amp; Montanucci 1998).</p> <p><i>P. mcallii</i>: Egg size 7–10 x 14–17 mm / hatching size 35–38 mm (Pianka &amp; Parker 1975)</p> <p><i>P. modestum</i>: Freshly laid eggs 0.5–0.7 g (Wernicke &amp; Haase 2014)</p> <p><i>P. platyrhinos</i>: Egg size 15–25 mm / hatching size SVL 20–35 mm, 2–3.2 g (Fabian 2013)</p> <p><i>P. solare</i>: Hatching size 30 mm SVL (Baur &amp; Montanucci 1998).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Incubation and hatching            | <p><i>P. asio</i>: 80–120 day (at +/- 29°C), about 85 days (at 28°C), 93–106 days at 25–26°C (Baur &amp; Montanucci 1998). 100 days at 26°C (Haase 2014), 90–100 days at 25°C (Marchevskaya et al. 2024)</p> <p><i>P. blainvillii</i>: 63–69 days (at 21–35°C) (Shaw 1952), 60 days (Hult &amp; Germano 2015).</p> <p><i>P. cornutum</i>: 58–98 days (at 29°C), 43–53 days (Baur &amp; Montanucci 1998), 60–66 days at 29°C (Galli &amp; Ruf 2010)</p> <p><i>P. coronatum</i>: 60–100 days (at 29°C), 52–58 days (at 27–28°C) (Baur &amp; Montanucci 1998)</p> <p><i>P. goodei</i>: 45–60 days (at 29°C)</p> <p><i>P. mcallii</i>: 60–90 days (at 29°C)</p> <p><i>P. modestum</i>: 55–75 days (at 29°C), 50–70 days at 26–28°C (Wernicke &amp; Haase 2014)</p> <p><i>P. platyrhinos</i>: 45–60 days (at 29°C), 39–40 days (Baur 1973), at least 42 days at 28–29°C (Schulz 2018a), 45–60 days at 26–28°C (Fabian 2013)</p> <p><i>P. solare</i>: 60–100 days, 66 days (at 28°C).</p> |
| Hatch rate                         | <p><i>P. asio</i>: 80–90%, 45–79% (Recchio et al. 2014)</p> <p><i>P. blainvillii</i>: 80%</p> <p><i>P. cornutum</i>: 70–80%</p> <p><i>P. coronatum</i>: 80%</p> <p><i>P. goodei</i>: 80%</p> <p><i>P. mcallii</i>: 80%</p> <p><i>P. modestum</i>: 80%</p> <p><i>P. platyrhinos</i>: 80–100%, 90–100% (Fabian 2013), 100% (Schulz 2018a)</p> <p><i>P. solare</i>: 55–80%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Sex ratio at hatching              | <p><i>P. asio</i>: ca. 50/50% ♂♂/♀♀</p> <p><i>P. blainvillii</i>: ca. 50/50% ♂♂/♀♀</p> <p><i>P. cornutum</i>: ca. 50/50% ♂♂/♀♀</p> <p><i>P. coronatum</i>: ca. 50/50% ♂♂/♀♀; 56% ♂♂/44% ♀♀ (Ruf &amp; Galli 2010)</p> <p><i>P. goodei</i>: 65% ♂♂, 35% ♀♀</p> <p><i>P. mcallii</i>: ca. 50/50% ♂♂/♀♀</p> <p><i>P. modestum</i>: 40% ♂♂, 60% ♀♀</p> <p><i>P. platyrhinos</i>: 65% ♂♂, 35% ♀♀</p> <p><i>P. solare</i>: ca. 50/50% ♂♂/♀♀.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sex determination/ parthenogenesis | <p><i>P. platyrhinos</i> has genetic sex determination with X/Y sex chromosomes (Koochekian et al. 2022).</p> <p>Parthenogenesis is unknown in <i>Phrynosoma</i> spp.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Sperm storage                      | Yes, with the exception of <i>Phrynosoma asio</i> sperm storage for more than one season has been observed.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |



## Husbandry and Captive Breeding C/C



Fig. 11: Breeding *Phrynosoma modestum* and *P. platyrhinos* in human care. (all photos J. Schulz)

- a *P. modestum*, Texas local form, ♀ laying one egg
- b *P. modestum*, clutch
- c *P. modestum*, hatching of a juvenile of the Albuquerque local form
- d *P. modestum*, juveniles in the rearing terrarium
- e *P. platyrhinos*, laying eggs
- f *P. platyrhinos*, the unearthed clutch
- g *P. platyrhinos*, hatchlings
- h *P. platyrhinos*, group of juveniles.



| Topic                  | Data for the egg-laying (oviparous) <i>Phrynosoma</i> species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
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| Husbandry requirements | <p>Oviparous horned lizards are mostly desert dwellers of lower and middle altitudes. They are kept in spacious desert terrariums. For larger species such as <i>Phrynosoma asio</i> or <i>P. cornutum</i>, the terrariums should not be smaller than 150 x 60 x 60 cm. For medium-sized species such as <i>P. platyrhinos</i>, terrariums of around 120 x 60 x 60 cm are suitable. Even the smallest species such as <i>P. modestum</i> should have terrariums of at least 100 x 60 x 60 cm. All horned lizard species are not territorial and can be kept quite well in small groups, even with several males. This must be taken into account when choosing the size of the terrarium.</p> <p>Baur wrote as early as 1973 that an outdoor terrarium was essential for the care and breeding of horned lizards. Spacious gauze terrariums, converted cold frames and aviaries have proven to be suitable outdoor terrariums, as they offer the possibility of protecting them well against external predators. It is ideal if the generously sized outdoor terrariums have a power connection so that additional lighting and heating can be provided even during cloudy and cooler days. From today's perspective, the technical equipment, especially with regard to UVB metal halide lamps, is significantly better than in the early days of successful horned lizard keeping. Nevertheless, a temporary stay outdoors should always be aimed for and contributes significantly to the vitality of the animals. However, success with pure indoor keeping is certainly possible. In one year, over 90 young horned lizards from 5 different species were bred under these conditions. The continuous breeding of <i>P. cornutum</i> over several years in an indoor terrarium is also documented there (Galli &amp; Ruf 2010). Other keepers have also achieved success with pure indoor keeping, be it with <i>P. platyrhinos</i> (Haase 2012) or <i>P. modestum</i> (Wernicke &amp; Haase 2014). As diurnal desert dwellers, horned lizards can never have enough light in their terrarium. UVB metal halide lamps, which are available in a wide range of wattages, have proven to be effective. Suitable products include Solar Raptor from ECONLUX, Premium UVB MD lamp from Reptiles Expert or Bright Sun from Lucky Reptile. While 35 watts and 50 watts are suitable for breeding terrariums, 70 watts and 100 watts are the rule for adult terrariums. In terrariums that are open at the top, which have proven to be particularly effective in some cases, the 150 watts versions are more likely to be used, as there is no risk of heat build-up. In the desert terrarium for horned lizards, an ambient temperature of 25–30°C is the aim, while the sunbathing areas can get up to 45°C. It is important to achieve a reduction in temperature at night by cooling the terrarium to room temperature below 22°C (Schulz 2018a). T5 tubes and LED bars can be used as additional basic lighting, but only to increase the lighting intensity; they are completely unsuitable as the sole lighting. The lighting duration is up to 14 hours during the mating season in summer and 6 hours in the winter months (Marchevskaya et al. 2024). During the 2-month hibernation period, which is best carried out individually in separate boxes in the refrigerator at 12°C (Schulz 2018a), the basic lighting is needed, at best, for the living plants in the terrarium. As desert dwellers, it is important to offer the animals a sufficient substrate of sand. Sand is particularly important for horned lizards, as it not only serves as a running surface, but the animals sometimes bury themselves completely in it for protection and to sleep. A higher substrate is particularly important for oviparous species to enable them to lay eggs in a species-appropriate manner (Baur 1998). Even for the smallest species, <i>P. modestum</i>, the substrate should be at least 15 cm deep (Wernicke &amp; Haase 2014). The sand used should not contain any clay so that it does not cake too much. Washed river sand or pre-packaged play sand are very suitable. When well dried, it should be loose so that the horned lizards can bury themselves half or completely in the typical way. Especially for newly hatched <i>Phrynosoma</i> it is important to use finely sieved sand, as the juveniles have difficulty burrowing if the sand is too coarse (Galli &amp; Ruf 2010).</p> |

As additional furnishings, individual larger stones can be used, although these are more decorative than practical, since most horned lizards do not climb much. However, for the small *P. modestum*, a few stones the size of a nut or plum should be added to the substrate. According to Baur & Montanucci (1998), this species buries itself less often than other species. Hatchlings in particular are too weak to bury themselves in the sand. This species is also known to fall into stone mimicry when threatened and imitate a stone (Sherbrooke & Montanucci 1988). Small dry bushes in the terrarium have proven to be useful for all horned lizards. Small dried thyme bushes and other woody herbaceous plants are visually appealing. The commercially available 'desert bushes' are also very suitable. Small bushes are particularly important for *P. asio*, as the animals sometimes rest in the bushes. But other horned lizard species such as *P. cornutum* also like to use dry bushes for resting (Galli & Ruf 2010). Planting horned lizard terrariums can be done with succulents and tufts of grass, taking into account that the terrariums have a dry, hot climate. Narrow or round-leaved types of grass are particularly suitable as tufts of grass, which continue to serve as decoration in the room terrarium even after they inevitably wither.

For the Giant Horned Lizard, some dried leaves can also be added as terrarium decoration, as these come from dry, warm, light forests and semi-desert areas (Baur & Montanucci 1998).

General characteristics, difficulties with keeping and breeding

*Phrynosoma asio* is the most common horned lizard and, due to its size, the easiest horned lizard to breed. It does not necessarily need ants to be kept successfully, but regular feeding is highly recommended. Some keepers have described keeping and breeding, especially *P. asio*, as uncomplicated and not difficult. However, it should be noted that some of these breeders have 20–30 years of experience in breeding horned lizards and are much more experienced in handling their animals. Other participants describe keeping them as complicated, very high-maintenance but still easily manageable.

The Giant Horned Lizard is the only horned lizard species that does not dig an ovipositor to bury its eggs, but rather digs an open pit 10–15 cm in diameter and about 10 cm deep to lay the eggs. The female then covers up the clutch and tamps the ground firmly (Baur & Montanucci 1998).

The ongoing energy and purchase costs for adequate lighting should not be underestimated.

Long-term care and a long lifespan are hardly possible without the use of ants as food (Wernicke & Haase 2014). *Phrynosoma mcallii* is considered to be a pronounced ant specialist that is hardly able to eat large prey (Baur & Montanucci 1998).

Life expectancy

*P. asio*: 12–18 years (data from keeper's interviews); one male lived to nearly 14 years (Baur & Montanucci 1998)

*P. cornutum*: at least 10 years in both sexes (data from keeper's interviews); one female lived to nearly 12 years (Baur & Montanucci 1998)

*P. coronatum*: at least 10 years in both sexes (data from keeper's interviews); one male lived to nearly 9 years (Baur & Montanucci 1998)

*P. goodei*: at least 10 years

*P. mcallii*: 10–15 years (data from keeper's interviews); one male died from an accident at 5 years of age (Baur & Montanucci 1998)

*P. modestum*: males live for maximum 6–8 years, females maximum 12 years (data from keeper's interviews); one male lived nearly 18 years (Baur & Montanucci 1998)

*P. platyrhinos*: 10–15 years, (data from keeper's interviews); one female lived nearly 6 years (Baur & Montanucci 1998); in the wild only 7–8 years (Medica et al. 1973; Tanner & Krogh 1973)

*P. solare*: at least 10 years in both sexes (data from keeper's interviews); one male lived nearly 11 years (Baur & Montanucci 1998).

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|--------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Frequency of private breeding and reproduction in zoos | <p><i>Phrynosoma asio</i>: First breeding mentioned in 1976 (Baur 1979). Since the late 1980s / mid 1990s there have been several breeding successes by different owners. The Giant Horned Lizard is still the most commonly bred species in private keeping today, but is still rare overall. Extremely rare in zoos</p> <p><i>Phrynosoma blainvillii</i>: CB has been successful on a regular basis, but very rarely.</p> <p><i>Phrynosoma cornutum</i>: One of the more 'common' species in breeding, but still rare</p> <p><i>Phrynosoma coronatum</i>: Rarely, but regularly</p> <p><i>Phrynosoma goodei</i>: Rarely, but regularly</p> <p><i>Phrynosoma mcallii</i>: Rarely, but regularly</p> <p><i>Phrynosoma modestum</i>: One of the more 'common' species in breeding, but still rare</p> <p><i>Phrynosoma platyrhinos</i>: First breeding mentioned in 1972 (Baur 1973, Baur &amp; Montanucci 1998). Offspring are regularly found. After <i>P. asio</i>, the most commonly kept and bred horned lizard</p> <p><i>Phrynosoma solare</i>: Rarely, but regularly.</p> |
| Breeding difficulty evaluation                         | <p>For all oviparous species of the genus <i>Phrynosoma</i>, the breeding difficulties are rated as high to very high. However, with the necessary expertise, all species can be bred.</p> <p><i>Phrynosoma asio</i> and <i>P. platyrhinos</i> are considered the 'entry-level species' in the complex keeping and breeding of horned lizards.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Number of specimens that survive to sexual maturity    | <p><i>P. asio</i>: ca. 80–100%</p> <p><i>P. blainvillii</i>: ca. 60%</p> <p><i>P. cornutum</i>: ca. 60–80%</p> <p><i>P. coronatum</i>: ca. 60%</p> <p><i>P. goodei</i>: ca. 60%</p> <p><i>P. mcallii</i>: ca. 60%</p> <p><i>P. modestum</i>: ca. 60–80%</p> <p><i>P. platyrhinos</i>: ca. 70–80%</p> <p><i>P. solare</i>: ca. 50–70%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| F2 generation bred in captivity                        | <p><i>P. asio</i>: Yes. In our terrariums lives at least the F6 generation</p> <p><i>P. cornutum</i>: yes</p> <p><i>P. coronatum</i>: yes</p> <p><i>P. goodei</i>: yes</p> <p><i>P. mcallii</i>: yes</p> <p><i>P. modestum</i>: yes, at least F3</p> <p><i>P. platyrhinos</i>: yes, at least F5</p> <p><i>P. solare</i>: yes.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Commercial breeding/ranching                           | <p>Yes: Professional breeding of <i>P. asio</i> outside the natural range under indoor and outdoor terrarium conditions (Marchevskaya et al. 2024).</p> <p>For a re-introduction project, over 1000 <i>Phrynosoma cornutum</i> were bred at the Fort Worth Zoo, Texas, until 2021 (Virata 2021).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Interviews/ Surveys/ Consultations                     | <p><i>P. asio</i>: 2 zoos (1 of them with captive breeding), 10 private keepers (9 of them with breeding success)</p> <p><i>P. blainvillii</i>: 2 private keepers and breeders (1 of them with breeding success)</p> <p><i>P. cornutum</i>: 4 private keepers (3 of them with breeding success)</p> <p><i>P. coronatum</i>: 2 private keepers (2 of them with breeding success)</p> <p><i>P. goodei</i>: 2 private keepers (1 of them with breeding success)</p> <p><i>P. mcallii</i>: 3 private keepers with breeding success</p> <p><i>P. modestum</i>: 5 private keepers with breeding success</p> <p><i>P. platyrhinos</i>: 2 zoos (1 of them with captive breeding), 7 private keepers (6 of them with breeding success)</p> <p><i>P. solare</i>: 3 private keepers with breeding success.</p>                                                                                                                                                                                                                                                                             |

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### **Christian Langner & Felix Hulbert (31.12.2024).**

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## Scincidae

### *Tiliqua adelaidensis* (Peters, 1863)

| Species                     | Original description | Common name             | Common name International | Known in the trade |
|-----------------------------|----------------------|-------------------------|---------------------------|--------------------|
| <i>Tiliqua adelaidensis</i> | (Peters, 1863)       | Pygmy Bluetongue lizard | Zwerg-Blauzungen-skink    | Yes                |



Fig. 12: *Tiliqua adelaidensis* (F. Hulbert)

### Morphology and Taxonomy

The genus *Tiliqua* contains seven species, and is based primarily on similar characteristics of tooth morphology. With the exception of the species *T. adelaidensis* discussed here, all congeners are massive lizards that are among the largest and heaviest in the scincid family. These lizards are well-known as blue-tongue skinks, and the largest species can reach total lengths of up to 55 cm. The bright blue color of the tongue is the common name-giving feature in most species. The head is conical, as is typical for skinks. It is heavily armored due to strongly ossified osteodermal scales. The usually massive body appears cylindrical, and the scales are unkeeled in most species. Only the shingleback lizards (*Tiliqua rugosa*) have a greatly enlarged and keeled coat of scales that is reminiscent of a pinecone. Bluetongues have four relatively short legs, each with five toes of equal length. The ear openings are clearly visible. Like all species of the genus, *T. adelaidensis* is omnivorous and viviparous (Fenner et al. 2007). This kind of true viviparous reproduction is rather rare in reptiles. The embryos are supplied with nutrients via a so-called pro- or chorioallantoic placenta (Stewart & Blackburn 1988). Reaching a maximum total length of 18–20 cm, *T. adelaidensis* is by far the smallest species in the genus.

The tail length is approximately 60% of the head-body length. The tail is very thin compared to those of other *Tiliqua* species and tapers abruptly behind the tailbase (Hutchinson & Milne in Hausschild et al. 2000). The English and German common name 'dwarf blue-tongued skink' is misleading, because *T. adelaidensis* is the only member of the genus *Tiliqua* to have a flesh-colored tongue (Herrel in Hausschild et al. 2000). The dorsal basic color varies from pale yellowish-brown to pale blue-gray. In addition to individuals with no markings at all, some specimens also have irregular black stripes and small spots that sometimes merge into an irregular stripe along the vertebral line. Ventrally, the skinks are whitish to cream-colored and predominantly unspotted.

### Distribution and Habitat

The genus *Tiliqua* is limited in its distribution to Australia, New Guinea and some adjacent Indonesian islands. *T. adelaidensis* has the smallest distribution area of the genus. The species was thought to be extinct for several decades and was just rediscovered in 1992. The exact distribution was a mystery and was only solved with rediscovery. In a dissected roadkill of the Elapid *Pseudonaja textilis*, a recently consumed dwarf bluetongue was found as stomach contents (Armstrong & Reid 1992, Oschman (ed.) 1993). This made it possible to determine the distribution area following targeted searches. Data on the habitat and lifestyle were now available for the first time (Hutchinson et al. 1994, Hutchinson & Milne in Hausschild et al. 2000). Specially trained detection dogs have been used very successfully to track down the hidden and difficult-to-detect pygmy bluetongues (Nielsen et al. 2016).

### Distribution

The few habitats of the species known to date extend in a narrow strip, barely 20 km wide, from Kapunda in the Light River Valley, about 77 km northeast of Adelaide, northwards to Peterborough, about 254 km north of Adelaide. The altitudinal distribution range of the species is between 400 and 600 m asl.

Pygmy bluetongues are only known from 31 locations. All sites are on private agricultural land and are mostly surrounded by arable land or other unsuitable habitats. The sole information on total population size is based on Milne et al. (2000) and was estimated at around 5000 animals. 22 new populations have been discovered since, one of which is now considered extinct (Duffy et al. 2012). At selected locations, maximum population densities of 80–100 adult lizards per ha were documented (Hutchinson & Milne in Hausschild et al. 2000).

Type locality: 'Buchsfelde near Adelaide, South Australia' [= Loos, near Gawler, South Australia].

### Habitat and Behaviour

The habitat of *T. adelaidensis* consists mainly of treeless grassland steppe. Most of the original habitat had to make way for agricultural land for livestock and crop farming. The climate is warm, temperate and Mediterranean with moderate annual rainfall of 450–550 mm. Today, only 2% of the original area of this temperate steppe landscape remains. Habitats that have never been ploughed are essential for dwarf bluetongues, as these lizards inhabit a microhabitat that is unique to skinks. *T. adelaidensis* inhabits abandoned spider burrows that run vertically into the ground. Most often, the former burrows of mygalomorph spiders (trapdoor spiders), measuring around 2 cm in diameter, are used, and less frequently (especially by juveniles) the narrower burrows of wolf spiders (Lycosidae). The diurnal lizards appear in the



morning to bask with about two-thirds of their body looking out of their burrow. Dwarf blue-tongues spend most of the day in this position, with their heads raised, watching for potential prey or predators. At the slightest disturbance, they immediately retreat into their burrow (Hutchinson et al. 1994, Hutchinson & Milne in Hausschild et al. 2000, Langner pers. obs. 1993 unpubl.). Research by Ebrahimi & Bull (2012) shows that Dwarf bluetongues not only benefit from the spiders, but can also fall victim to them. In one observed case, an adult *T. adelaidensis* became prey of a wolf spider (Lycosidae).

Bull et al. (2015) described the dynamics of burrow occupancy in a study. They found that there are both 'strays' that only inhabit a spider burrow for a short time, and specimens that occupied a burrow for the entire study period. The proportion of females in the studied population was higher than that of males. Many of the burrows were abandoned in early spring, the time when the males are probably looking for mates. Clayton & Bull (2015) investigated how sheep grazing affects the construction and persistence of spider burrows by comparing burrow dynamics in adjacent grazed and ungrazed grassland habitats of *T. adelaidensis*. It turned out that heavy grazing leads to a decrease in spider burrows and therefore has negative effects on both the lizards and spiders. Ebrahimi et al. (2012a), Ebrahimi et al. (2012b) and Staugas et al. (2013) investigated the acceptance of artificial burrows and found that artificial burrows without an enlarged basal chamber led to a change in behaviour when seeking the hiding place and that in tubes without a widened chamber at the base of the tube, the lizards had to spend more time to get into the preferred 'head-first position'. The authors therefore suggest using tubes with a widened chamber at the lower end when installing artificial hiding places as part of nature conservation measures.

In the wild, mating occurs in the Australian spring and usually takes place between late October and early November (Hutchinson et al. 1994). Gestation lasts about three months. Litter size varies between one and a maximum of four offsprings. The juveniles stay in the mother's burrow for between one and twelve weeks before they move into their own, smaller burrows (Milne 1999, Milne et al. 2002). At about one year of age (SVL 75–85 mm and weight 6–10 grams), males are capable of reproduction in the next spring season. Females can also reproduce at this age, although most females need at least another year to reach reproductive capacity. It is estimated that fewer than 10% of the offspring reach adulthood (Milne 1999). In human care, pygmy blue-tongued lizards can live to at least 18 years of age. Skeletal chronological data from a small number of museum specimens show that some wild specimens were at least eight years old when collected (Duffy et al. 2012). The skinks are omnivorous. In addition to various invertebrates such as caterpillars, beetles, grasshoppers, ants, cockroaches, spiders and snails, soft herbs and seeds of the flax lily (*Dianella* spec.), and flowers and leaves of the introduced plants alfalfa (*Medicago* spec.), as well as unspecified leaf fragments of the family Chenopodiaceae are also mentioned as food plants. In addition to the previously mentioned venomous snake *Pseudonaja textilis*, *Tiliqua adelaidensis* appears to be relatively immune to the potent venom of *P. textilis* (Ehmann 1982, Hutchinson et al. 1994, Milne 1999, Hutchinson & Milne in Hausschild et al. 2000, Fenner et al. 2007, Fenner et al. 2008). Predators also include smaller birds of prey such as *Falco cenchroides* and *Elanus notatus*.



### Conservation Status and Main Threats

CITES Appendix I since 2023 (CoP19 Proposal 19).

EU Council Regulation (EC) No 338/97 Annex A.

In Germany strictly protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

EN (Endangered B2ab(ii,iii,iv,v), assessed 13 June 2017).

### Protection and reintroduction in southern Australia

The pygmy blue-tongued (*Tiliqua adelaidensis*) is classified as endangered both nationally under the Environment Protection and Biodiversity Conservation Act (EPBC) and in South Australia under Schedule 7 of the National Parks and Wildlife Act 1972 (Duffy et al. (2012).

In order to better study the species' habitat and reproduction, sixteen adult pygmy blue-tongue skinks (eight males and eight females) from two separate populations near Burra, South Australia, were captured and transported to Monarto Zoological Park, approximately 150 km south of the natural range, to establish a breeding group (Daniell 2021). The furnishing/planting of the breeding enclosures consisted of natural soil, a few large tussock grass tufts planted in for providing shade, and several artificial hiding places made of 30 cm long round logs with a diameter of 3 cm, which were drilled lengthwise – the inner diameter of the tube was 1.8 cm for adult skinks. These tubes were buried vertically, with the entrance hole at ground level. Since the soil layer in the enclosures was 40 cm deep, the skinks may have dug an enlarged burrow end chamber themselves, but this was not monitored. The skinks could prey on natural food items in these rather natural enclosures. Additionally, they were fed crickets that had been dusted with a calcium-vitamin preparation. The first breeding in this zoo took place in 2016 with 13 juveniles; in the following year, already 18 juveniles were born. Studies in the wild (Milne 2003a) had already shown that such artificial hiding places are well accepted, and that the females that were able to inhabit them were heavier and gave birth to more juveniles than in natural burrows which they had dug themselves. However, the captive-bred animals would have been less fit for release than wild-caught individuals (Daniell et al. 2020), because they had got to know humans as food suppliers at the zoo and showed little avoidance behaviour towards predators.

In the wild, males often mate with several females, but these lizards do not actively avoid mating with closely related individuals (Schofield 2015). The animals usually remain within a population, so there is little genetic exchange between spatially separate populations. The species conservation guide (Australian Government 2023) explicitly states that, while more research is needed on local adaptations, young females should be exchanged between particularly small populations to avoid inbreeding. In addition, genetically managed conservation breeding is expressly called for here: 'Continue efforts to maintain and expand the breeding programme for the dwarf blue-tongue skink at Monarto Zoological Park SA and other potential facilities to ensure the continued survival of the genetic lines of this species. A studbook should be introduced in breeding colonies.' The unsuccessful attempt to establish a breeding group at Adelaide Zoo (CITES 2022) is not mentioned.

In nature, males often mate with several females, but *T. adelaidensis* does not avoid mating with closely related individuals as *T. rugosa* does (Bull & Cooper (1999, Schofield 2015). The

animals usually remain within a population, and even young males do not migrate far, so there is hardly any genetic exchange between the spatially separate populations. The guide to the conservation of the species (Australian Government 2023) explicitly points out that, of course, local adaptations need to be better researched, but that young females should then be exchanged between particularly small populations in order to avoid inbreeding effects. In addition, the guide explicitly calls for genetically managed conservation breeding: ‘Continue efforts to maintain and increase the captive breeding program for the pygmy bluetongue lizard at Monarto Zoological Park SA and other potential facilities, to ensure the persistence of genetic lineages of the species. A stud book should be implemented in captive breeding colonies’. The unsuccessful attempt to establish a breeding group in the Adelaide Zoo (CITES 2022) is not discussed further in this guide.

However, the designation of new protected areas and appropriate biotope management is of the utmost importance for the preservation of the species. Care must be taken to ensure that new populations are settled south of the previous range, because climate change is making survival increasingly difficult for the northern populations (Gardner 2024).

### Threats

The threats to which pygmy bluetongues are currently exposed are diverse. In addition to the risk factors of the onset of climate change, which cannot yet be precisely evaluated, the main threats are disturbances and changes to their natural habitat. Due to the adaptation to a very specific ecological niche (short grass steppe, microhabitat – spider burrows), the habitat requirements are particularly complex. *T. adelaidensis* therefore reacts specifically sensitively to changes and is highly dependent on the preservation of the remaining habitats that should be as unchanged as possible.

While little is currently known about the impacts of climate change on the pygmy bluetongue, monitoring in 2007 and 2008 found significantly lower soil fertility, less grass cover and more bare soil areas than in 2006. These trends may be related to the ongoing drought in the region (Duffy et al. 2012).

Since all known populations of dwarf bluetongues occur exclusively on private land, agricultural activities in particular represent an enormous potential threat. Ploughing, digging or removing the soil layer poses a very high risk, as it directly kills both *T. adelaidensis* and the spiders on whose burrows the lizards depend. Even a single tillage permanently destroys the habitat and prevents long-term repopulation. By breaking up the soil, the burrows dug later by newly settled spiders become unstable and unsuitable for the lizards. So even if a pasture is ploughed just once and regenerates naturally, the original lizard population is lost (Duffy et al. 2012).

The intensity of grazing in pygmy bluetongue habitats also has an impact on population vitality. While moderate grazing is generally compatible with the habitat requirements of *T. adelaidensis*, heavy grazing by livestock is likely to be harmful. ‘Heavy grazing’ can be defined as grazing that leads to destabilization of soil structure. A complete stop of grazing at sites where pygmy bluetongues occur can also be harmful if the current grazing system helps to maintain a suitable habitat structure. Without grazing, it can lead to increased vegetation growth and/or a reduction in the spaces between grass tufts, which can affect foraging and basking opportunities. Other threat factors include the use of pesticides. In addition to reducing the

number of prey items for lizards and spiders, the latter can also be directly affected by insecticides. Herbicide use, in turn, can negatively affect the diversity of food plants. Another factor that can have a negative impact on habitat structure is the spread of alien neophytes. The spread of various plant species associated with excessive fertilization can promote their growth at the expense of the native grasses that are so important for the steppe character (Duffy et al. 2012).

Afforestation, which endangers the tree- and bush-less character of the grassland steppe biocoenosis, as well as the gradual bush encroachment that may occur 'naturally' due to climate change, represent a further serious threat to the few remaining habitats of *T. adalaidensis* (Duffy et al. 2012).

The effects of fire on dwarf bluetongue populations are not fully known. Fires may have once been a natural landscape-shaping process throughout the dwarf bluetongue's range. Given the few remaining populations of *T. adalaidensis* that are isolated from one another, fires could potentially have significant effects (Duffy et al. 2012). Fenner & Bull (2007) compared the situation in a closely monitored population before and after a fire event that occurred in December 2005. The results suggest that the lizards were able to seek shelter from the fire in their deep burrows, as the fire neither killed adult lizards nor affected the fertility of females. While a decrease in foraging activity as well as a deterioration in body condition and a lower survival rate of the young were initially observed after the fire, these effects were only observed in the short term. In the following years, no negative effects were detected.

The fragmentation of the isolated populations and the partially considerable distances between them inevitably lead to a decline in genetic potential. Genetic studies confirm that the exchange between today's populations is low (Smith 2006, Smith et al. 2009).

Studies on shingleback lizards (*Tiliqua rugosa*) have shown that this species is sensitive to smoke emissions in the air. This is interpreted as a natural protective mechanism against the fire events that are common in the Australian bush (Mendyk et al. 2019). Since *T. adalaidensis* is also significantly threatened by bushfires, it would be interesting to see whether they react in a similar way to the related species *T. rugosa*.

Domestic dogs are known to prey on pygmy blue-tongued lizards (Duffy et al. 2012). Introduced foxes (Nielsen & Bull 2016b) and feral domestic cats are also predators that should not be underrated.

Clive & Bull (2018) report roadkill of *T. adalaidensis* on a gravel road. They point out that the threat to this species may increase with the expected expansion of wind turbines near known populations and the associated increase in traffic.

Duffy et al. (2012) point out the risk of illegal smuggling of rare Australian species for the pet trade. Establishing stable captive breeding populations of pygmy bluetongues outside Australia, and the associated availability, could counteract this.

## Reproduction

| Topic                   | Details on the Reproduction of <i>Tiliqua adalaidensis</i>                                                                                                                                                           |
|-------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | The species shows sexual dimorphism in relation to head proportion. In adult ♂♂ the distance from the tip of the snout to the axillae of the forelimbs is about one third of the SVL. In ♀♀ it is about one quarter. |

|                                        |                                                                                         |
|----------------------------------------|-----------------------------------------------------------------------------------------|
| Reproduction                           | Viviparous (combined chorioallantoic & omphaloplacental nutrient supply to the embryo). |
| Sexual maturity                        | From the age of 3–4 years on.                                                           |
| Mating                                 | Spring: Feb./ March (Northern Hemisphere); Oct./Nov. (Southern Hemisphere).             |
| Number of eggs/<br>clutches per season | 1–4 offspring 1 x per year.                                                             |
| Gestation                              | 4–6 months.                                                                             |
| Juvenile size at birth                 | 40–44 mm head-body length; approx. 60 mm total length, 1.5 g.                           |
| Sperm storage                          | Not known.                                                                              |

### Husbandry and Captive Breeding C/C



Fig. 13: Husbandry and breeding of *Tiliqua adelaidensis* (photo author is known to the BfN)  
a newborn Pygmy Bluetongue skink  
b set-up of the breeding terrarium  
c accessories for breeding Pygmy Bluetongue skinks.

| Topic                    | Data for <i>Tiliqua adelaidensis</i>                                                                                          |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction | Moderate resting period below 15°C from November to February. No real hibernation.                                            |
| Husbandry requirements   | Artificial hiding place made of terracotta (see illustration), based on the spider tubes that these skinks inhabit in nature. |

| Topic                                                                                    | Data for <i>Tiliqua adelaidensis</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                                                          | <p>They are constructed in 2 separate parts: a basal spherical chamber with a diameter of about 8 cm and a 20 cm long tube with an open top and a diameter of about 2 cm. The tube/living chamber is almost completely embedded in the substrate (dry sand). One living tube/chamber per skink. The terrarium dimensions are 80 x 60 x 60 (length x width x height). The tanks are open at the top (without cover) and are illuminated with 70W HQI-UV spotlights, which are in operation for 12 hours a day in summer and 7 hours a day in winter.</p> <p>The basic temperature in the terrarium is 28°C during the day, dropping to room temperature at night. The humidity is kept very low. The omnivorous lizards are fed with commercially available feeder insects of appropriate size, which are supplemented with a mineral/vitamin mixture at each feeding, as well as wild herbs, bitter lettuce, flowers, etc.</p> |
| General characteristics, difficulties with keeping and breeding                          | Strictly husbandry in pairs.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Care of the young, technical and time effort                                             | Juveniles are kept under identical conditions as the adults in correspondingly smaller containers.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Life expectancy                                                                          | Unknown, at least 16 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| First report of captive breeding, frequency of private breeding and reproduction in zoos | The species has been regularly bred by private breeders since 2020. The species is rare in husbandry/breeding, as the skinks are kept by only a few enthusiasts. The zoo animal list indicates two zoos in southern Australia that currently keep and breed this species (Graf et al. 2024). In one of the two, Monarto Safari Park, the species has been successfully bred since 2015 (CITES 2022, Daniell et al. 2020).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Breeding difficulty evaluation                                                           | Under the conditions described keeping and breeding does not present any difficulties. The most important item of equipment and indispensable for successful keeping and breeding are the artificial tubes.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Mortality in the first years of life                                                     | Less than 20%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| F2 generation bred in captivity                                                          | One private breeder had the first F2 juveniles in 2024 from an F1 pair which was born in 2021.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Interviews/ Surveys/ Consultations                                                       | 2 experienced private breeders.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |



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**Christian Langner (26. 07. 2024), updated and amended: Beate Pfau (10.01.2025)**

## Testudines

### Chelidae

#### *Chelus* Duméril, 1805

| Species                                | Original description                                                                                                                  | Common name      | Common name International                                                                                                                                                   | Known in the trade |
|----------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Chelus fimbriata</i>                | (Schneider, 1783)                                                                                                                     | Amazon Matamata  | Fransenschildkröte, Matamata-Schildkröte<br>Matamatá Amazonica<br>Cágado, Matamatá amazônica<br>Caripatúa (Colombia)<br>Indigene Namen: Zancudo (Guainía, Colombia): Youyap | Yes                |
| <i>Chelus orinocensis</i> <sup>3</sup> | Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Pires-Farias, Hrbek, Campbell & Fritz, 2020 | Orinoco Matamata | Orinoko-Fransenschildkröte                                                                                                                                                  | Yes                |

Matamata turtles are specialised ambush predators that wait well camouflaged in shallow streams in their area of origin for fish swimming by, which they then suck in through the lightning-fast opening of their large mouth and throat sac. Their snorkel-like nose allows the turtle to breathe without the animal having to leave its hiding place and swim. The bizarre appearance and the prey capture behaviour are described in great detail in many publications.

#### Morphology and Taxonomy

The genus *Chelus* (at that time spelled as '*Chelys*') was named by Duméril (1805), and the only species known was '*Testudo fimbriata*', which had already been described long before by Schneider (1783). Until 2020, the valid name of the Matamata turtle was *Chelus fimbriata* (formerly also *Chelus fimbriatus*), until the 'Orinoco form' (Schmidt 1966), already long known in herpetoculture, was separated and redescribed as *Chelus orinocensis* (Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Pires-Farias, Hrbek, Campbell & Fritz 2020). According to the current CITES nomenclature, both species are now listed as *Chelus fimbriatus* (Fritz & Havaš 2007) although the proposal already referred to two separate species following the 7<sup>th</sup> edition of the taxonomic reference list of the Turtle and Tortoise Taxonomy Working Group (Rhodin et al. 2017).

<sup>3</sup> According to the valid CITES nomenclature (Fritz & Havaš 2007), both species are listed as *Chelus fimbriatus* in the CITES context (UNEP 2024), but the application to include the Matamata in CITES Appendix II (CITES 2022) lists both species names and refers to the 7<sup>th</sup> edition of the taxonomy reference list of the Turtle and Tortoise Taxonomy Working Group (Rhodin et al. 2017), which lists both species separately.





Fig. 14: *Chelus* spp. distinctive features

- a *C. fimbriata*: patterned underside of the neck (M. Rawski)
- b *C. orinocensis*: unicoloured light underside of the neck (O. Klawonn)
- c *C. fimbriata*: high-contrast pattern of the head (B. Pfau)
- d *C. orinocensis*: light underside of the head (O. Klawonn)
- e *C. fimbriata*: rather rectangular shell shape (M. Rawski)
- f *C. orinocensis*: nearly oval shell shape (S. Ettmar)
- g *C. fimbriata* juvenile: high-contrast pattern of the whole underside (M. Rawski)
- h *C. orinocensis* juvenile: unicoloured light underside (O. Klawonn).

The two species differ in the light, yellowish to ochre plastron colouration of *Chelus orinocensis* in contrast to the light to dark brown colouration of the plastron in *Chelus fimbriata*. The underside of the neck is pink in *Chelus orinocensis*, whereas in *Chelus fimbriata* the neck colouration does not differ from the colouration of the limbs. Seen from below, the skin of *Chelus fimbriata* is much darker overall and a dark stripe pattern can be found on the neck. Juveniles

of *Chelus fimbriata* show an intense black-and-red pattern on the entire underside (neck, limbs, plastron, bridge and underside of the carapace shields). Juvenile *Chelus orinocensis* have a light red coloured plastron with a few dark markings.

In adult specimens, the shape of the carapace also provides information about the species. *Chelus orinocensis* usually has an oval carapace, the carapace of *Chelus fimbriata* is almost rectangular.

In the case of confiscations, the young turtles must be identified very quickly so that they can be returned to their respective river system and released back into the wild before they are too weak due to lack of suitable food in captivity. A PCR test has been developed for species identification (Cardeñosa et al. 2021), which can at least be used by specialised officials and provides a result in less than two hours. The further differentiation of the two species into separate populations (Vargas-Ramírez et al. 2020) has apparently not yet been translated into a genetic tool, so that it is currently not possible to actually return confiscated juveniles to their original population.

Within *Chelus fimbriata*, there are morphological differences between the turtles caught in black-water rivers and the turtles caught in white-water rivers (Maia Garcês 2023).

## Distribution and Habitat

### Distribution

*Chelus fimbriata*: Amazonas River basin – Ecuador, Perú, Colombia, Brazil and Bolivia, as well as in the Mahury River basin in Suriname and French Guiana. Type locality: Uprouague (Aprouague) and Remire Island, French Guiana (Vargas-Ramírez et al. 2020). Introduced in Florida (Somma 2023).

*Chelus orinocensis*: Orinoco and Rio Negro River basins, in Brazil, Colombia and Venezuela, also found on Trinidad Island (Cunha et al. 2021). Type locality: Colombia, Vichada, Pto. Carreño, Bitá River (5.7610N/68.5858W WGS84).

*Chelus sp.*: The Matamata turtles from the Essequibo River basin, which is neither connected to the Amazonas nor the Orinoco River basins, are not reliably assignable to either of the two species – their haplotype is close to that of *C. fimbriata*, but morphologically they are closer to *C. orinocensis* (Pritchard 2008, Vargas-Ramírez et al. 2020).

### Habitat

The animals live on the bottom of slow-flowing, usually turbid, streams (black and clear water) with lots of detritus. They sit in ambush in the vegetation and under roots and walk on the bottom of the water. It is a rare sight to see a turtle swim. During the dry season, they retreat to deeper areas of the rivers. They only leave the water to lay their eggs.

The Matamata turtles also tolerate salty water and can use estuaries and beach lakes as stepping stones to reach new habitats (Cunha et al. 2021).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 22). In Appendix II, *Chelus fimbriatus* is explicitly listed and *C. orinocensis* is treated as a synonym (UNEP 2024).

With note received on 21 February 2023, the Cooperative Republic of Guyana entered a reservation with respect to the inclusion of *Chelus* spp in Appendix II of the Convention. In 2023 this country had set the export quota to 123 animals.

EU Council Regulation (EC) No. 338/97 Annex: B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

Both *Chelus* species have not yet been assessed for the IUCN Red List.

For many Central and South American turtle species, a reassessment was prepared in 2024 (invitation to the workshops see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023), which are still in print and expected for 2025. Both species have been classified as Least Concern (LC) (A.G.J. Rhodin pers. comm. 30/08/2024).

### Red List Status in the Range Countries – there is no distinction between the two species

#### Bolivia

Near Threatened (MMAyA 2009, Domic-Rivadeneira et al. 2021), but had been classified earlier as ‘very common’ (Embert 2007).

#### Brazil

Least concern (LC, Vogt et al. 2015, ICMBio 2018).

#### Colombia

Least concern (LC, Morales-Betancourt et al. 2015, Paez et al. 2022).

#### Ecuador

Near threatened (Casi amenazada, Carrillo et al. 2005).

#### French Guiana

Not threatened (LC, MHN, UICN France & Biotope 2017)

#### Perú

Not assessed (SERFOR 2018), the species is said to be ‘common’ (Ique Guerrero et al. 2018).

#### Venezuela

Not assessed (Rodríguez et al. 2015) or not threatened (Trebbau & Pritchard 2016).

From Guyana, French Guiana, and Suriname, no Red List or Libro Rojo could be found, and no assessment of the conservation status is known.

## Utilisation and Protection within the Natural Range

Matamata turtles are so malodorous when newly caught, so peculiar in appearance, and with such an unusual distribution of edible meat (concentrated primarily in the neck, the limbs being small and weak) that most tribal or rural people prefer to eat other, more ‘ordinarily-looking’ turtles for food consumption (Andrade 2008, Pritchard 2008).

Whether the Matamatas, which are offered at relatively high prices in online shops in China (Ji et al. 2020), are fattened for consumption or whether they are only kept as pets is not described, and it also remains unclear where these animals originated from.

### Bolivia

In Bolivia *Chelus fimbriata* meat is used for subsistence, but in the ranking order of preference this species is only ranked 7<sup>th</sup> of the 14 native tortoise and freshwater turtles, despite its size and ease of catching (Domic-Rivadeneira et al. 2021). Obviously neither meat nor eggs are marketed and the species is only ranked 6<sup>th</sup> for the domestic pet market. The conservation priority is assessed as medium (place 11), but the priority for further investigation is rather high (place 5).

Bolivia declared a total ban on the capture, consumption commercialisation and export of wild animals, their by-products and secondary products in the Decreto Supremo 21312 of 27 June 1986, but wildlife smuggling occurs across all the borders that Bolivia shares with Argentina, Brazil, Chile, Paraguay and Perú (Verheij 2019).

### Brazil

Rural people in the Amazon area consume meat and eggs of Matamata turtles (Chaves et al. 2021), but in southern Brazil these turtles are mentioned only rarely as ‘important’ by the local people (Ataides et al. 2021). Their sale at markets has not been documented, as consumption is considered a widespread taboo in Amazonia, where the rural people see these species as ugly and have a common fear of getting sick after eating their meat (Morcatty 2018). Since Matamata turtles do accumulate Mercury and other heavy metals from their prey fish, the level of mercury in their muscle meat is often sufficiently high to pose a potential risk to humans who consume them (Burger et al. 2010, Schneider et al. 2010, Cunha 2015, Schneider & Vogt 2018). In the Rio Negro region, the meat is not consumed, but the carapace scutes are often used to make medicine, and hunted adult animals can be found at markets at a rather high price (Pezzuti et al. 2010).

The export of Matamatas is prohibited in Brazil (Pritchard 2008, referenced in CITES 2022).

### Colombia

In the Comunidad de Zancudo, the meat of the turtles was offered at a local market at a relatively low price compared to the prices paid for caiman (*Palaeosuchus* sp.) meat (Lasso & Morales-Betancourt 2021). Currently, indigenous communities are monitoring the utilisation and availability of *Chelus orinocensis* populations, particularly in the Guaviare River and a tributary of the Inírida River. The reason for this monitoring is the traditional use as food, and its meat is sometimes traded locally. According to CITES CoP19 Proposal 22, the information obtained is to be used to develop management measures that can ensure sustainable utilisation.

W. Lamar (pers. comm.) reported that, in Colombia, ornamental fisheries personnel collect large numbers of juvenile Matamatas in their nets, especially in the vicinity of Puerto Inírida (Guainia) and around Caño Cabuyaro, a tributary of the Upper Meta (Meta/Casanare) (cited



from Pritchard 2008). Breeding or even ranching of Matamata turtles is illegal in Colombia, but there has been considerable illegal trade of obviously wild-caught hatchlings from Colombia to Perú, from where they could be legally exported (Lasso et al. 2018). Probably this was the actual source of the many *C. orinocensis* hatchlings from Perú in the European pet trade in former years.

In 2019, the confiscation of 1,987 *C. fimbriata* at the airport of El Dorado, Bogotá, was reported. These animals were already checked in on a local flight to Leticia; in 2020, another shipment of 2,500 *C. fimbriata* destined for the United States and Japan was uncovered, and in 2021, a shipment of 1,936 *C. orinocensis* on the same airport, but with unknown destination, had been intercepted (Noboa et al. 2024).

The legal export of Matamatas is prohibited in Colombia (Pritchard 2008, referenced in CITES 2022).

### **French Guiana**

Matamata turtles are protected by French legislation but enforcement is inadequate (Métrailler & Le Gratiet 1996).

### **Guyana**

Pritchard (2008) mentioned that an estimated 60 adult Matamatas were exported commercially from Guyana to the United States in 1992, and about a decade earlier several hundred juvenile specimens had been imported into California. Live animals have entered the international trade in significant numbers until 2017, when the establishment of the Wildlife Conservation and Management Commission under the new law had been announced (Sinovas et al. 2017), but no recent information on the enforcement of this new law could be found.

On 23 February 2023 Guyana has entered a reservation to the listing of *Chelus* spp. on CITES Appendix II, and at the time of writing (2023) hatchlings from Guyana have been imported into the EU at rather high prices, see below.

### **Peru**

In rural communities the meat of Matamata turtles is consumed and sold at markets, but it is not valued much (Castro, Revilla & Neville 1976). The shell is used for medicinal purposes. Young Matamata turtles are being kept as pets.

Hatchlings of the native species *Chelus fimbriata* have been exported in large quantities for years, e.g. in 2020 4,472 and in 2018 18,355 animals. Some of these shipments contained *C. orinocensis*, which do not naturally occur in Peru and were probably smuggled from Colombia (see also Lasso et al. 2018). CITES Proposal 22 mentions that a large number of juveniles are legally exported, but the origin, whether they were caught in the wild or hatched in a zoocriadero from the clutches of wild-sourced ♀♀, is unclear. The breeding and trade of these turtles is permitted in Peru; four breeding operations are registered (SERFOR 2022), although three of them are suspected of having obtained animals illegally and one of them was fined for not providing the required information to OSINFOR (Organismo de Supervisión de los Recursos Forestales y de Fauna Silvestre). Prior to the CITES listing, the companies did not have to provide any information on their breeding animals and breeding methods (information summarised from Murillo 2022 and from personal communications from WCS Peru). In the summer of 2024, juveniles that had hatched on such breeding farms in Peru were offered on various internet sales platforms.



Ique Guerrero et al. (2018) summarized the breeding method in a zoocriadero in Loreto, Perú (see tables below).

### Suriname

Suriname is a major Latin American exporter of live reptiles and birds. To the extent that these species are CITES-protected, the trade is governed by the Convention, which entered into force in Suriname on 15 February 1981. Upon acceding to CITES, the government established a quota system to regulate wildlife exports. The Surinamese government has tried to encourage Suriname's wildlife traders to shift to captive breeding, but according to the traders, the costs of establishing the necessary infrastructure are prohibitive (Verheij 2019). Suriname exports tortoises and freshwater turtles, but there is no indication that the captive breeding of any freshwater turtles has even been tried (compare to Sinovas et al. 2017). In the summer of 2024, half-grown matamatas with the indication of origin from Suriname were offered on various internet sales platforms.

### Venezuela

The populations of Matamata in Venezuela do not suffer from hunting pressure, since their meat is not consumed by the people living near the rivers (Hernández & Espin 2003), however the eggs are collected and consumed in this country (Daza Mendizabal & Correa-Viana 2015).

The export of Matamata turtles is officially prohibited in Venezuela, but there might be two or three licenced farms 'producing' hatchlings. The Ministry of Environment does not publish data on these farms or on legal exports of juveniles (O. Hernández pers. comm.). The proposal to list *Chelus* spp. in CITES Appendix II was not supported by Venezuela.

### Regulations in EU member states

In Spain, *Chelus fimbriata* has been classified as potentially invasive and cannot be imported any more since 2021 (Oliva-Paterna et al. 2021).

In France, *Chelus fimbriata* has been classified as dangerous animal species, which can only be kept if the owner had a special 'Certificat de Capacité' and a permit. In French Guiana this species is also specially protected. For some time *Chelus orinocensis* was not included in these two decrees, and this species was therefore imported into France and freely sold. This legal gap was corrected in 2023 (République Française 2023).

### Threats

Habitat loss and degradation, clutch loss due to strong fluctuations in river water levels and predators, and mercury accumulation are the main threats to both species (Cunha 2015, Daga et al. 2020, Daza-Mendizabal & Correa-Viana 2015, Sánchez 2022). Since adult Matamatas are occasionally consumed by humans, they sometimes appear at the meat markets – however, they are not very sought-after because the meat is mainly on the neck and does not look 'white' when cooked, but rather grey. They also have very well-functioning odorous glands, and at least the raw meat probably smells rather unpleasant and requires strong spices for preparation. Some indigenous communities along the rivers also consume the eggs. Juveniles are occasionally offered for sale and then kept as pets.

## Reproduction

Differences in the reproductive data of the two species are not known and are not to be expected due to the very similar climate in the neighbouring distribution areas. It is not always possible to assign the data from the literature to one of the species.

| Topic                              | Details on the reproduction of <i>Chelus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | Sexual dimorphism is not very pronounced. ♂♂ are slightly smaller and have longer tails and two slight concavities in the posterior half of the plastron. In <i>C. fimbriata</i> , ♀♀ usually grow up to 40–50 cm CL, while ♂♂ attain 30–40 cm CL.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Sexual maturity                    | In captivity at 5–7 years, in both sexes. ♀♀ attain sexual maturity in the wild at about 30 cm CL.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Mating and nesting                 | <p>Mating details are unknown.</p> <p>Eggs are laid in loamy or mulch-covered sand on steep river banks, i.e. the large sand-banks that other turtles use for nesting are avoided. To overcome the slope, the ♀♀ climb sideways and support themselves with their head and neck (Pritchard 2008).</p> <p>In the hatchery in Peru, the eggs were usually laid in clay ground with a layer of litter or mud, but pure leaf litter was also accepted. Sometimes the eggs were even laid directly on the surface, but the nest could also be up to 26 cm deep.</p> <p>Under aquarium conditions in captivity, the eggs are sometimes simply laid in the water. However, available land parts are usually accepted if they are elevated. The eggs are buried at a depth of up to 25 cm. Trial burrows often occur beforehand.</p>                       |
| Reproductive season                | <p>In their natural habitats, both species nest at the end of the rainy season (October to December), when the water level in the water bodies begins to recede.</p> <p>In a hatchery in Peru, the eggs of <i>C. fimbriata</i> were laid at night, in almost every month of the year, with most eggs (27%) being laid in June.</p> <p>In aquarium husbandry in Europe, courtship behaviour occurs all year round with egg laying mostly in spring. In the case of multiclutching ♀♀, however, nesting takes place throughout the year.</p>                                                                                                                                                                                                                                                                                                         |
| Number of eggs/clutches per season | <p>In their natural habitat 3–28 eggs/clutch, on average 12.5 eggs (lower Juruá River), in captivity up to 30 eggs have been observed in one clutch.</p> <p>In their natural habitat usually only one clutch per season, in captivity two clutches are common, but depending on the feeding regime even four clutches per season are possible.</p> <p>In a hatchery in Peru, the 30 ♀♀ (and 18 ♂♂) produced a total of 2009 eggs with 3–30 eggs per clutch in the year under observation. In the case of smaller clutches, there are usually several clutches per year.</p>                                                                                                                                                                                                                                                                        |
| Egg size/hatchling size            | Eggs in captivity 50–60 mm in diameter and 20–28 g. In the hatchery in Perú, the hatchlings had an average CL of 48.8 mm (44–52 mm), and an average weight of 13.8 g (11.1–18.6 g).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Incubation and hatching            | <p>In the wild, incubation is &gt; 200 days, hatching is triggered by water contact when the river water level rises again. Accordingly, the hatchlings appear on the surface of the soil at the beginning of the new rainy season, i.e. usually in February or March.</p> <p>In captivity, incubation temperature should be set to 29–30.5°C in an incubator like the one used by Budde (1980). Substrate: moss or coconut fibres, 180–200 days until hatching (in individual cases up to 300 days). The hatching rate is below 30% and there is a high mortality rate among the juveniles. Incubation is the main breeding problem for all South American chelid turtles: It may be necessary to initiate and terminate diapauses by drying out and remoistening the substrate at specific times during incubation (Pfau 2024a, Pfau 2024b).</p> |

|                   |                                                                                                       |
|-------------------|-------------------------------------------------------------------------------------------------------|
| Sex determination | Genetic sex determination, with a micro-XY sex chromosome system in both species (Viana et al. 2022). |
| Sperm storage     | Yes, > 1 year.                                                                                        |

## Husbandry and Captive Breeding C/C

The conditions for keeping and breeding the two species do not differ.

| Topic                                                           | Data for <i>Chelus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Unknown. Possibly, as with many other South American species, the rainy season can be imitated by increased water changes, which could stimulate follicle growth.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Husbandry requirements                                          | <p>Due to their final size and need for movement, these turtles require an enormous amount of space; sufficiently large tanks are usually custom-made, so no minimum dimensions can be suggested.</p> <p>♂♂ of both <i>Chelus</i> species are best kept individually, and ♀♀ kept in groups must also be closely monitored for signs of being stressed. Overall, however, the species can be considered as unaggressive towards conspecifics and turtles of other species. Mixing with other turtle species should be avoided nevertheless, as <i>Chelus</i> spp. appear to be stressed by them.</p> <p>Round-grained, somewhat coarse, sand is recommended as a substrate in the tank, which should be deep enough to allow the animals to at least partially bury themselves, as they otherwise tend to develop shell corrosion on their plastra. The turtles do not need special lighting, but the need for warmth is relatively high (water temperature about 26°C year-round).</p> <p>Live feeder fish of an appropriate size are required for feeding the hatchlings. Adult animals can be fed frozen and thawed whole fish and even pieces of large forage fish and in rare cases will also accept other foods such as dead mice or shrimps. To prevent a thiamine deficiency, the food should be supplemented with vitamin B, and it is recommended to feed the animals individually with long tweezers.</p> |
| General characteristics, difficulties with keeping and breeding | <p>Some keepers have seen shell inflammations or infections and even necrosis in their turtles. Large-volume filters and, if necessary, UV sterilisers should be used to optimise the water in which they are kept.</p> <p>The bite is said to be painful, which is why feeding should not be done by hand but with long feeding tweezers.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Care of the young, technical and time effort                    | When enough live fish of appropriate size are available, care of the juveniles does not require any particular effort. When feeding with frozen fish, however, the time required is high, as each animal has to be encouraged to snap at the food with the help of tweezers moving the fish pieces in front of its mouth.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Life expectancy                                                 | Approximately 40 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Frequency of private breeding and reproduction in zoos          | <p>Rare. Only a few private keepers and zoos have succeeded in breeding the animals to date. The number of hatchlings born in captivity has been so low that only in exceptional cases actually captive bred turtles have been offered in the pet trade so far. Most juveniles in trade are imported from hatcheries in the range countries.</p> <p>The first publication on the reproduction in an European Zoo is from the Aquarium Berlin (Heinroth 1943). Matamata turtles (no species information available) have been or are still bred successfully in two zoos in Venezuela (O. Hernández pers. comm.), but a direct consultation was not possible.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Breeding difficulty evaluation                                  | Breeding all South American chelid turtles continues to be a challenge, even if simply keeping them is basically unproblematic. In the case of <i>Chelus</i> , the space requirements in particular are a major restriction to successful breeding in large numbers.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Mortality in the first years of life                            | The mortality rate of juveniles is high, although the exact causes are not known. At one breeder, some hatchlings were born with a kinked neck and did not survive for                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

|                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                    | long.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| F2 generation bred in captivity    | Yes, but very rarely. As far as known, the first F2 offspring in Europe hatched in 1998 at Hagenbeck Zoo in Hamburg (Richter 1999).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding/ranching       | In the 'farms' (hatcheries) the eggs collected from the wild, or being laid by wild-sourced ♀♀ (considered as 'ranching' in CITES), are being hatched under almost natural conditions, and the fresh hatchlings are immediately sold without initial head-starting. In the zoocriadero in Perú the adult turtles are being kept together in a large group in a rather big pond, and no details on feeding or water change are available (Ique Guerrero et al. 2018). Actual captive breeding at a commercial scale seems highly unlikely, given the husbandry requirements of these turtles.                                                                                 |
| Interviews/ Surveys/ Consultations | Five of the six private individuals with whom it was possible to discuss the current situation already have several years of experience in keeping and breeding Matamatas. In addition, one institution that has been keeping <i>C. orinocensis</i> for several years (as yet without any real breeding success) could also be consulted. Moreover, there has long been great interest in the keeping and breeding of these species in private households (see bibliography), so that private notes on the experience reports with these species, which were discussed at the meetings of the various associations and clubs, were also be analysed and are included herein. |

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**Beate Pfau and Ole Klawonn (09.07.2024).**

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## Chelydridae

## Handling the so-called 'Dangerous' Turtles



Fig. 15: Handling large freshwater turtles

- a *Macrochelys temminckii* – this ♂ is used to being lifted up. The chairman of the working group 'Macrochelys/Chelydra', I. Giebner, with 'Otto' (B. Pfau)
- b *Staurotypus triporcatus* can also bite hard. E. Reyes-Grajales with a wild caught animal during his research on the population of this species in Mexico (E. Reyes-Grajales)
- c *Macrochelys temminckii* ♂ get heavy! R. Praschag pushes him into the fenced-off area in the greenhouse (R. Praschag)
- d *Chelydra serpentina* can bite in almost all directions, but if you hold like this, above the hind legs, nothing bad will happen (B. Pfau).

Common snapping turtles (*Chelydra* spp.) and Alligator snapping turtles (*Macrochelys* spp.) have been categorised as ‘dangerous animals’ in many countries because they are large and strong, have sharp jaws and bite when they feel threatened. However, reports of people being bitten by the turtles while bathing, for example, have not yet been confirmed – *Chelydra* spp., as well as *Macrochelys* spp., are rather shy in the water. However, as the turtles live a predatory life and are quick to bite lively prey such as waterfowl or smaller mammals, bites cannot be completely ruled out if the animals are hand-fed, for example. Other turtle species (some soft-shelled turtles, e.g. *Apalone ferox*) or Mexican Giant musk turtle (*Staurotypus triporcatus*) have also been added to the lists of dangerous animals in some EU member states or in certain German federal states. However, the handling of these animals does not play a major role in the trainings of handling dangerous animals, as injuries caused by these animals can be easily avoided if a few precautionary measures are observed. With calm handling, most turtles in captivity can be accustomed to certain routines, e.g. being lifted up or being urged to an area in the tank that can be closed off so that the keepers can enter the enclosure even if the water has to be drained. To avoid bite or scratch injuries, the large Alligator snapping turtles (*Macrochelys* sp.) can be held by the side of the shell or with one hand on the edge of the shell above the head and the other above the tail, as the neck and legs do not have a large range of mobility. However, adults of these species are very heavy, ♂♂ up to approx. 90 kg – possibly more if overfed – so that many keepers use aids to lift them, e.g. a carrying grid with a pulley on the greenhouse roof. Common snapping turtles (*Chelydra* spp.) have a long, very flexible neck and can bite very quickly and also scratch violently in all directions – apart from the fact that the secretion from the scent glands (Trauth 2012), which are located relatively far forward, in front of the hindleg openings, is difficult to wash off if it comes into contact with the human skin. By holding the turtle by the carapace above the hind legs and turn the ventral side towards you, there will be no bite or scratch wounds or ‘foul scenting’ in humans, and no injuries to the caudal vertebral column in the animal. If it is only a matter of preventing the animal sitting on the ground from biting, a suitably sized suction cup that can hold the turtle's head is also useful (Munscher et al. 2015).



Fig. 16: Handling softshell turtles

- a *Pelodiscus sinensis* at a rescue centre. The animal is used to being taken out and does not attack or bite (B. Pfau)
- b Juvenile *Apalone ferox*. The animal has been taken off the road and feels threatened, biting at everything in sight. Note the range! (B. Pfau).



Soft-shelled turtles are not quite so easy to hold in hand, as their shell is slippery. But even in this case, a firm grip on the rear edge of the carapace, above the hind legs, helps to avoid possible biting and scratching injuries.

### *Macrochelys* Gray, 1856

| Species                                      | Original description                                                            | Common name                        | Common name international                                   | Known in the trade |
|----------------------------------------------|---------------------------------------------------------------------------------|------------------------------------|-------------------------------------------------------------|--------------------|
| <i>Macrochelys suwanniensis</i> <sup>4</sup> | Thomas, Granatosky, Bourque, Krysko, Moler, Gamble, Suarez, Leone & Roman, 2014 | Suwannee Alligator Snapping turtle | Suwannee-Geierschildkröte<br>Tortuga mordedora de Suwannee  | Unknown            |
| <i>Macrochelys temminckii</i>                | (Troost in Harlan 1835)                                                         | Western Alligator Snapping turtle  | Geierschildkröte<br>Tortuga mordedora<br>Tartaruga-aligátor | Yes                |

### Morphology and Taxonomy

The family Chelydridae covers two genera, *Macrochelys* and *Chelydra*, which diverged during the Pliocene or the early Pleistocene. *Macrochelys* is the only turtle genus in which the supra-marginal shields, which are located on the side of the carapace between the marginal shields and the costal shields, have been preserved, as in all other turtles which are still alive today, the marginal shields are directly connected to the costal shields (Ascarrunz & Sánchez-Villagra 2022).

In human care it is possible to breed hybrids of *Chelydra serpentina* and *Macrochelys temminckii* and to raise them (McKeown 1985), and on Facebook, pictures of an animal shop were posted, showing a hybrid of *C. rossignonii* and *M. s. temminckii* (Thế Giới Rùa 2023).

However, there is no record of hybridisation between the two genera in the wild, although the North American species can be found in the same waters and in rather close proximity to each other.

Young *Macrochelys* spp. are brownish in colour and, like young *Chelydra* spp., have ridges on the scales of their three-keeled carapace. A special feature of the genus *Macrochelys*, which is particularly easy to recognise in juveniles, are the 1–5 supramarginal scutes on both sides (Rosenbaum et al. 2023), which are located on the sides of the carapace between the costal and marginal scutes and which are missing in snapping turtles. The carapace shape and colouration of the juveniles is also slightly different, *Macrochelys* juveniles are more orange-brownish in colour and the lateral edges of the dorsal carapace run almost parallel, while juveniles of *Chelydra serpentina* are grey-brownish and have a rounded carapace shape – they also have bright spots on the ventral carapace, which *Macrochelys* juveniles lack. As both *Macrochelys* and *Chelydra* try to bite when being picked up, the length and mobility of the neck can be estimated: *Macrochelys* can only bite forwards and the neck is relatively short, whereas all *Chelydra* species have a very mobile neck and can also bite backwards at least to the middle of the carapace. The neck of *Chelydra* spp. is also very long, i.e. when the neck is stretched forwards, the tip of the nose is about as far away from the front edge of the carapace

<sup>4</sup> According to the valid CITES nomenclature (Fritz & Havaš 2007), both species are listed as *Macrochelys temminckii* in the CITES context (UNEP 2024).



as the entire carapace is long. The risk of confusion of juveniles of both genera in export shipments from the USA emphasised in CITES CoP19 Proposal No. 23 cannot be confirmed.

Larger *Macrochelys* spp. can be distinguished from *Chelydra* spp. of the same size by the fact that the dorsal carapace of *Chelydra* spp. becomes almost smooth, while that of *Macrochelys* spp. remains strongly sculptured. In addition, the eyes of *Macrochelys* spp. are located laterally, whereas in *Chelydra* spp. they are located more on the upper edge of the head. The strong hooked beak of *Macrochelys* spp. is also striking when they threaten with an open mouth.

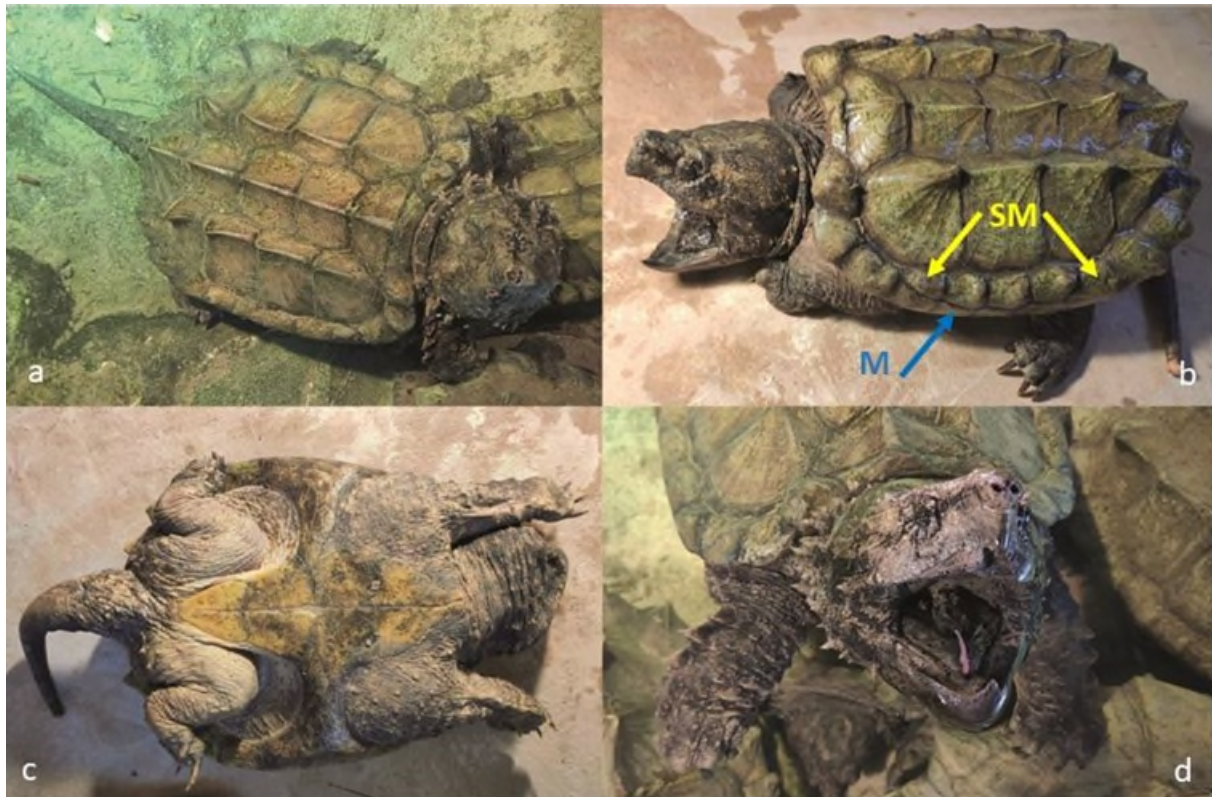


Fig. 17: *Macrochelys temminckii* in a European rescue centre (all photos by J. Soler)

- a Dorsal view, note the jagged rear edge of the carapace
- b Lateral view, SM: supramarginal scutes, M: marginal scutes, below them
- c ventral view, note the reduced plastron
- d The worm-like lingual process is recognisable in the open mouth.

***Macrochelys temminckii*** – carapacial caudal notch usually narrow and triangular or U-shaped, pygal with two serrations, not extending to the marginal shields. However, there are *M. temminckii* with have a semicircular carapacial caudal notch and are almost indistinguishable from *M. suwanniensis*. ♂♂ can reach CL up to 77.5 cm, ♀♀ up to 53.3 cm.

***Macrochelys suwanniensis*** – carapacial caudal notch very wide and lunate, usually without serrations, typically comprising the pygal and the marginal shield #11. ♂♂ can reach CL up to 80.0 cm, ♀♀ up to 49.2 cm.

Until 2014, the *Macrochelys* genus was recognised as monotypic. It was split into initially three species, *M. temminckii*, *M. apalachicola* and *M. suwanniensis* according to genetic studies (Thomas et al. 2014). Afterwards, *M. apalachicola* has been synonymised with *M. temminckii* again (Folt & Guyer 2015). The attempt of Hoser (2013) to describe a species named after himself failed, because the two specimens he declared as holotypes had only been seen alive,

but are not included in the collection of the Natural History Museum of Gainesville, so that they could not be checked for the stated skeletal attributes (Thomas et al. 2014).

Population genetic studies show some genetic structuring in both species. The populations of the river systems manifest some genetic differences (Pearson 2021, Apodaca et al. 2023) and also some minor morphological differences (Rosenbaum et al. 2023), but this does not result to the description of any new subspecies according to the current state of knowledge.

In the CITES CoP19 Proposal No. 23, *M. suwanniensis* and *M. apalachicola* were still seen as synonyms of *M. temminckii* (CITES 2022), hence both recognised species have been implicitly included in Appendix II as *M. temminckii* following the taxonomy of Fritz & Havaš (2007).

### Distribution and Habitat

Alligator Snapping Turtles naturally occur in the southern states of the USA. Fuller, Somma & Cameron (2023) give an overview of the natural distribution and occurrences outside of it. Outside of the natural range, Alligator Snapping Turtles can be found in some European countries, in South Africa and in South- and Southeast Asia (see e.g. GBIF Secretariat 2022, Pleguezuelos 2002, Orueta 2003, Nehring, Rabitsch & Essl 2015, Poch et al. 2020, Esposito et al. 2022).

As many sightings of Alligator Snapping Turtles have been reported quite spectacularly in certain newspapers and it is not easy to assess the actual size of these scary looking turtles seen from distance, some of those observations might have been falsely identified as Common Snapping Turtles (*C. serpentina*, see below). *Macrochelys temminckii* has been assessed as ‘potentially invasive’ and included in the ‘action list’ meaning that there are indications for negative impacts (Nehring et al. 2015). Based on the current state of knowledge, the ecological ‘risk potential’ of Alligator Snapping Turtles as non-native predator for aquatic communities in natural waters outside their natural distribution cannot be fully evaluated. So far, Alligator Snapping Turtles occurrences within the EU are based on individual findings in Germany, France and in the Canary Islands (Nehring et al. 2015), while there are no records of any established, self-sustaining populations. Spain completely banned imports because of some findings in 2021 (Oliva-Paterna et al. 2021).

Some research has been conducted on the distribution and the potential for reproduction in the wild in Southeast Asia (see Kobayashi 2007, Sy 2015, Lee et al. 2019), which led to the comprehensible assessment of their invasiveness – which was estimated to be minor, because so far there is no evidence of any successful reproduction in the wild in these countries.

A new assessment of invasion risk and vulnerability revealed a low risk level for *M. temminckii* (worldwide), with climate change likely to have a negative impact on natural populations. It is therefore appropriate to accurately record the occurrences in the area of origin and the findings outside the natural range, and turtle keepers should be trained in handling these turtles (Nerozzi et al. 2024).

Alligator Snapping Turtles are typically ambush predators, they sit quietly in their hiding place with their mouth open and trying to lure their prey (mostly fish, but also smaller turtles etc) with the help of their wormlike movable tongue appendages directly into their mouth (Hedinger 1963). Aside from that they will also actively take up less mobile or immobile animal prey (crabs, shells, carrion; Denton et al. 2023). Those turtles also eat fruits and nuts, they might even go ashore to find some (Elbers & Moll 2011).

Adult *M. temminckii* are usually found at the bottom of deeper or slow-flowing, larger bodies of water, often in bald cypress forests. In early summer, however, they seek out warmer, shallower areas of water (Soileau et al. 2021). Juveniles prefer smaller bodies of water, or side waters of larger rivers, with plenty of cover from wood and fallen leaves (Spangler et al. 2021). *M. suwanniensis* generally seem to prefer shallow waters (Thomas et al. 2024).

At least the ♂♂ seem to be territorial and fight each other, usually ritual fighting, not real fighting with intentions to hurt each other (Enge et al. 2023). The territories might overlap each other. The ♀♀ also seem to defend their nesting places against other ♀♀ (Thompson & Ligon 2022).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 23). Has already been listed on CITES Appendix III since 2006.

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

Classified as invasive species in Germany according to § 3 BArtSchV since 2002.

The whole genus has been included in the regulations on dangerous animals in several federal states in Germany (Gebhardt-Brinkhaus 2021) and is also subject to certification and authorisation in some EU countries and Switzerland.

### IUCN Red List Status

VU (Vulnerable A1cd, assessed August 01, 1996) – valid for both species that have not been perceived as separate species at that time.

New assessments for the IUCN Red List are in press and expected for 2025 (A.G.J. Rhodin pers. comm. 30/08/2024):

*Macrochelys suwanniensis*: VU

*Macrochelys temminckii*: EN.

### Utilisation and Protection within the Natural Range

Both species were proposed for listing as ‘threatened’ under the Endangered Species Act in 2021 (USFWS 2022). The final listing as endangered species is viewed critically by conservationists, as the corresponding regulations would severely restrict the necessary research into the status of individual populations. *Macrochelys suwanniensis* was given the ‘endangered’ status in 2024 (USFWS 2024).

The two species had been listed on CITES Appendix III since 2006, so that legal exports could be monitored. An import statistic from Hong Kong (HKSAR 2017) shows in the appendix for the year 2012 the impressive number of 28,835 *M. temminckii* imported for the pet trade, and in 2013 this species is still among the top 5 reptile species for Hong Kong with 23,234 live imports. An evaluation of international trade in the years 2020–2023 (UNEP-WCMC 2024) showed that *M. suwanniensis* had not been registered in international trade at all, and that of the 564,062 registered exports of *M. temminckii*, 93% had been classified as live wild-caught specimens; the recipient countries were predominantly in East Asia, and only a few animals had been sent to Spain during this period.

The different federal US states have different regulations for the protection of the *Macrochelys* species. From around 1960 until the 1990s, the turtles were caught in large quantities for consumption and the meat was directly marketed or processed into tinned soup (CITES 1997). Capture is now banned in most states. In 2022, however, the capture of one turtle > 24 cm carapace length per year was still permitted in Mississippi, and in Louisiana even the capture of one turtle per day or per vehicle (without size restriction) is allowed – in each case for personal use, and of course only with a fishing permit. According to CITES CoP19 Proposal No. 23, catch limits are hardly controlled and turtles are illegally caught in unknown numbers to replace the deceased breeding animals in turtle farms, and for consumption. Inclusion in CITES Appendix II and listing under the Endangered Species Act should therefore help to strengthen controls and better enforce the existing national capture bans.

## Threats

Alligator Snapping turtles were classified as ‘Endangered’ in the IUCN Red List in 1988. This status was confirmed in subsequent reassessments. In one of the best-known books on *Macrochelys* spp. (Pritchard 1989), it was already pointed out that excessive utilisation for consumption poses a major threat to the conservation of these turtles, see also Sloan & Lovich (1995). In addition, the threat posed by the use of habitats as recreational waters or transport routes has been pointed out, as people fear these turtles and therefore clean up the waters, i.e. they remove the necessary hiding places for the turtles (see e.g. VanDeWalle 1993). In addition, these mainly carnivorous turtles are also threatened by environmental pollution, in particular by the accumulation of mercury (Rosenbaum 2022).

Both, *M. suwanniensis* and *M. temminckii*, have been classified as endangered species by the U.S. Fish and Wildlife Service (USFWS 2020, USFWS 2021a), although the conservation regulations are clearly not sufficient for habitat protection (USFWS 2021b). In the meantime, there are many initiatives to investigate the status of individual populations and to determine whether population reinforcement measures with captive bred animals may be already necessary (Voves et al. 2023).

## Reproduction

| Topic                   | Details on the reproduction of <i>Macrochelys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|-------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | ♂♂ have longer tails than ♀♀, but the difference is only clearly recognisable from a CL of approx. 30 cm on. ♂♂ become more than twice as heavy as ♀♀, and old ♂♂ often develop light-coloured heads, which in <i>M. suwanniensis</i> usually become distinctly yellow.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Reproduction            | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Sexual maturity         | In the wild at 11–21 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Mating and nesting      | In ♂–♂ mating combats, the larger animal usually wins. The ♀♀ can easily evade the mating attempts of the ♂♂, they actively seek out their mating partner.<br>Eggs are laid on rather steep sandbanks, often directly above the maximum water level line. However, the egg-laying sites are sometimes far away from the water (up to 200 metres). The bottle-shaped nest pit is up to 17 cm deep and around 20 cm in diameter. Sand is favoured and egg-laying sites are usually found near plants. More ♂♂ hatch from eggs laid in sand with foliage cover, i.e. between bushes, than from eggs laid in more open sandy areas. As some former wild rivers have been made navigable and the bank vegetation has been removed, the egg-laying sites are now warmer than |



|                                     |                                                                                                                                                                                                                                                                                                                                                                                     |
|-------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                     | before, which could lead to a lack of ♂♂ in the wild population at this particular site in the long term (see below, sex determination).                                                                                                                                                                                                                                            |
| Reproductive season                 | Mating season in nature is in the winter months, eggs are laid by <i>M. temminckii</i> mid-May to early June, by <i>M. suwanniensis</i> mid-April to early May. In captivity accordingly, as the animals are usually kept and bred under the same climatic conditions as in the wild.                                                                                               |
| Number of eggs/ clutches per season | <i>M. temminckii</i> 16–52 eggs/ clutch (on average 22.4 eggs), usually 1 clutch/ year. If food is scarce in the wild, reproduction can be skipped in a year; if feeding is very plentiful in captivity, two clutches per year may be (rarely) laid.<br><i>M. suwanniensis</i> : Few observations, clutches of 43 and 47 eggs each have been found, with an average mass of 27.9 g. |
| Egg size/ hatchling size            | Eggs almost round, 38–51.8 mm long, hatchlings CL 42 mm and 15.1 g weight.                                                                                                                                                                                                                                                                                                          |
| Incubation and hatching             | In the wild 100–140 days. Hatching occurs in autumn, from August on. In the incubator, at slightly below 30°C ca. 100 days.                                                                                                                                                                                                                                                         |
| Sex determination                   | Temperature dependent, Type II, lower threshold temperature 24,5°C, upper threshold temperature 27,5°C.                                                                                                                                                                                                                                                                             |
| Sperm storage                       | Probable, but not directly observed.                                                                                                                                                                                                                                                                                                                                                |

## Husbandry and Captive Breeding C/B

In Europe, Alligator Snapping turtles (*Macrochelys temminckii*) were quite popular and spectacular terrarium animals in zoos and private collections, as they could be kept outside in summer and in moderately heated water tanks in winter (Hediger 1962, Wermuth 1962, Grossmann 1988, Platt 1994). In the 1970s and 1980s, large numbers were exported from USA to Japan and Europe for sale in pet shops, and even in hardware stores in Germany. In Germany, escaped *M. temminckii* were also reported in the wild early afterwards (Blumenthal 1982).

There is no evidence that Suwannee Alligator Snapping turtles (*M. suwanniensis*) has ever been knowingly exported from the US. As part of this project, no zoos or owners of this species outside Florida could be found – but it is likely that this species had already been bred by turtle breeders in Florida before it was scientifically named.

| Topic                    | Data for <i>Macrochelys temminckii</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|--------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction | Seasonally triggered, probably by temperature.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Husbandry requirements   | Depending on their size and metabolic activity, these turtles require large tanks with regular automated water changes. Adult ♀♀ should have the opportunity to lay their eggs in an appropriately sized sand box – with good feeding, ♀♀ that are kept individually can also produce eggs. ♂♂ should also be given the opportunity to leave the water. Due to the required tank size, the animals are often kept individually, even in zoos. Whether several animals of approximately the same size can be kept together depends on the individuals. If these turtles are kept in groups, they should be closely monitored, as incompatibilities can quickly lead to injuries.<br><br>In a large breeding farm for the purpose of release into the wild, the sex ratio of just under 1:5 (♂:♀) was apparently responsible for the poor fertilisation and low hatching rate of 49%. A ratio of 1:3 or even 1:2 is therefore recommended for breeding groups. New animals should only be added to the group in summer, as the social compatibility between unfamiliar turtles is better when it is hot than in the cooler seasons (Van den Bussche et al. 2018). |



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|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| General characteristics, difficulties with keeping and breeding | <p>Most animals are quite sociable towards their keepers and can also learn that they get food if they show a certain behaviour. Nevertheless, they should always be handled with great care and safety precautions (such as protective fencing) can be useful. Alligator Snapping turtles have enormous biting power and can be surprisingly fast!</p> <p>In some animal shows, only chicken legs or pieces of fish fillet are fed, but this kind of food is not sufficient as a complete diet. To prevent the beak from overgrowing, hard food such as mussels, large snails or larger crabs with shells is required, and around one third of the diet should be plant-based (sweet fruit, berries, but also hard food such as cracked nuts). Whether the low hatching rate in this large-scale hatchery was due to unbalanced feeding (exclusively fish) could not be investigated further.</p>                                                                                                                                                                                   |
| Care of the young, technical and time effort                    | The juveniles can be reared together, and care should be taken to provide sufficient vitamins and minerals, as well as fibre and plant food. When rearing in hard or alkaline water, the tips of the tails may die off, so the water should be acidified for smaller juveniles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Life expectancy                                                 | In captivity 70 years or more, ♂♂ in nature between 11 and 45 years, ♀♀ usually do not live as long as ♂♂.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Frequency of private breeding and reproduction in zoos          | <p><i>M. temminckii</i> has been successfully bred at Tulsa Zoo as early as 1981 (Grimpe 1987). Breeding in European zoos is now very rare, as usually only single animals are kept and the young would be difficult to pass on. The 2<sup>nd</sup> breeding book of the German Chelonia Group (Giebner 1998) lists 27 captive-bred animals from various European breeders and zoos.</p> <p>Keeping and breeding by private people is prohibited in many European countries – however, there are some very successful private breeders within Europe.</p> <p>The production of juveniles for reintroduction projects in the USA is very successful.</p>                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Breeding difficulty evaluation                                  | If breeding animals of matching size are available, or if the turtles are kept separately and mating only takes place under supervision, captive breeding is quite simple.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Mortality in the first years of life                            | Low, but no detailed information is available.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| F2 generation bred in captivity                                 | <p>Very likely in zoos, and probably also by private breeders, but not published.</p> <p>It is likely that the first offspring which had hatched in the large breeding farms in Southeast Asia was raised and used as breeding stock, but more precise information is not available. In the corresponding offers on the Internet, there are repeated references to the fact that different colour forms (leucistic, hypomelanistic, melanistic etc.) have already been produced by these breeding farms, so that the cute hatchlings can be offered at a high price as pets.</p> <p>Since 2018, entries for exports from the USA with source code 'C' can also be found in the CITES Trade Database, and some breeding farms in the southern US States exist since the 1990s, which means that this source code seems plausible.</p>                                                                                                                                                                                                                                                 |
| Commercial breeding/ ranching                                   | <p>The breeding farms in the USA are often, even today, not 'closed' systems, i.e. wild-sourced animals are usually kept there and the breeding stock is supplemented legally or illegally as required (CITES 2022h). It is not known how long the adult animals survive in the breeding ponds, and the exact control mechanisms for these breeding farms are not published, or are only published in a very condensed form, depending on the state.</p> <p>It is unlikely that juveniles are actually caught in the wild for export, as indicated in CITES Proposal No. 23, due to their secretive lifestyle.</p> <p>Breeding as part of species conservation projects is also based on adult wild-sourced animals.</p> <p>In Mexico, hatchlings of <i>M. temminckii</i> were on sale in 2022 for 2,500 pesos (approx. €120) plus shipping costs. Alligator Snapping turtles are also bred in China and neighbouring countries (according to unconfirmed information &gt; 1,400 breeding farms in China alone), but nothing is yet known about the breeding methods used there.</p> |

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|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Interviews/ Surveys/ Consultations | 6 experienced private breeders in Europe and the USA were interviewed, and additionally some reports on keeping were sent. Besides this information from 2 commercial breeders in the USA, and from 1 institution in the southern USA (breeding for the purpose of release into the wild) could be gathered, as well as evidence of breeding in various zoos from their publications. |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

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**Beate Pfau (01.05.2024)**

***Chelydra* Schweigger, 1812**

| Species                                   | Original description | Common name                      | Common name international                                                                                                                                                                                                                                                   | Known in the trade |
|-------------------------------------------|----------------------|----------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Chelydra acutirostris</i> <sup>5</sup> | Peters, 1862         | South American Snapping turtle   | Südamerikanische Schnappschildkröte<br>Tortuga pimpano, tortuga lagarto de Sudamérica, tortuga mordedora costera sudamericana, tortuga pímpano, báchara, bache, guáchara, guachí, icotea caimana, icotea guáchara, mordedora, mordelona, tortugaña, talmana, ba-sch, ba-chí | Rare               |
| <i>Chelydra rossignonii</i>               | (Bocourt, 1868)      | Central American Snapping turtle | Mittelamerikanische Schnappschildkröte<br>Tortuga mordedora espinosa, chiquiguao, servengue, tortuga lagarto, tortuga satán, tortuga toro, sambunango, zambundango                                                                                                          | Rare               |
| <i>Chelydra serpentina</i>                | (Linnaeus, 1758)     | North American Snapping turtle   | Nordamerikanische Schnappschildkröte<br>Tortuga lagarto común, tortuga mossegadora                                                                                                                                                                                          | Yes                |

Snapping turtles are unmistakable with their long tail, which is usually as long as the carapace. The ventral carapace is reduced, the leg openings are large. The individuals are grey brownish in colour and often covered with algae.

For a long time Snapping turtles were considered as a monotypic species, *Chelydra serpentina*, with four subspecies. It was not until 1996 that *C. acutirostris* and *C. rossignonii* were recognised as separate species (Philipps et al. 1996), which are relatively closely related and also resemble each other.

<sup>5</sup> Only the North American Snapping turtle, *Chelydra serpentina*, has been listed on CITES Appendix II (due to the alleged similarity of appearance to *Macrochelys temminckii*). The two other snapping turtle species, *C. acutirostris* and *C. rossignonii*, are in fact not easy to distinguish from *C. serpentina* and they are in the international trade as well. Therefore, they are also covered here.



Fig. 18: Distinguishing characters of *Chelydra* spp.

- a *C. acutirostris*, Ecuador (F. Grünewald)
- b *C. rossignonii*, adult, Mexico (E. Reyes-Grajales)
- c *C. serpentina*, adult, gravid ♀, Maryland, USA. It can be recognised that the rear edge of the carapace is almost smooth and has only flat indentations above the tail (B. Pfau)
- d *C. serpentina*, old animal with smooth carapace, Maryland, USA (B. Pfau)
- e *C. serpentina*, only the lower jaw is pointed, Georgia, USA (B. Pfau)
- f *C. rossignonii* laying eggs in the recuperation centre in Spain. (J. Soler).

### Morphology and Taxonomy

***Chelydra acutirostris*** – The South American snapping turtle usually has two pairs of chin barbels, but in exceptional cases up to six. Their upper jaw protrudes clearly above the lower jaw. The skin appendages on the neck are low and rounded or cylindrical. A broad, light-coloured, often black-edged postorbital stripe can be seen in juveniles. The plastron is dark, but can sometimes also be reddish, the carapace of fresh hatchlings is coffee-brown to black, the barbels have white tips or are completely white. The anterior plastral lobe is > 40% of the carapace length. This is the smallest species of *Chelydra*, ♂♂ reach 41.0 cm CL in the wild, ♀♀ 39.1

cm. In captivity the animals can grow larger, a ♂ in the Parque Historico of Guayaquil even reached 48 cm CL (Grünewald 2008).

***Chelydra rossignonii*** – The Yucatán snapping turtle can be recognised by the conspicuous, long and widened skin appendages on its neck, giving it a shaggy appearance when viewed from the front. Two to three pairs of chin barbels, one pair of which is often conspicuously brightly coloured and long, about the diameter of the eye socket. The light-coloured postorbital stripe of the younger animals is narrow. The carapace colouration is variable, animals from the south of the distribution area are said to have a more ‘gold-coloured’ carapace and smaller chin barbels. The plastron anterior lobe is > 40% of the carapace length. CL: ♂♂ up to 47.0 cm, ♀♀ up to 33.0 cm.

***Chelydra serpentina*** – In the North American snapping turtle, the anterior lobe of the plastron is < 40% of the total plastron length. *Chelydra serpentina* has only two distinct chin barbels. Even in juveniles there is usually no clear postorbital stripe. CL: ♂♂ up to 50.3 cm, ♀♀ up to 39.0 cm.

Stejneger (1918) described the subspecies *C. s. osceola* from Florida and neighbouring areas on the basis of the more cranial elevations on the vertebral scutes and the larger number of skin scales between the eye socket and the soft skin of the neck. However, the main distinguishing feature of the two subspecies should be the skin tubercles in the neck, which should be more conical in *C. s. osceola* and more roundish and wart-shaped in *C. s. serpentina*. More precise morphological and morphometric studies have shown continuous transitions in the characteristics, and genetic studies have also shown so few differences that a subspecies delimitation does not appear to make sense (Feuer 1971, Phillips et al. 1996, Shaffer et al. 2008).

## Distribution and Habitat

### Distribution

***Chelydra acutirostris***: One population occurs from Honduras to Nicaragua, a geographically separated second population from Costa Rica via Panama and the west coast of Colombia (Antioquia, Atlantico, Bolivar, Cauca, Choco, Cordoba, Magdalena, Narino, Sucre, Valle del Cauca) to western Ecuador. Type locality: ‘Guayaquil’ [Ecuador]. Altitudinal distribution from sea level to 1,200 m asl.

***Chelydra rossignonii***: Mexico (Oaxaca, Veracruz, Tabasco, Campeche, Chiapas), Belize, Guatemala, NE Honduras, and also on the island of Utila (for a summary of the distribution data from the literature, see Uetz et al. 2024). Type locality: Marais de Pansos, near the Rio Polochie (Guatemala).

***Chelydra serpentina***: From southern Canada across the eastern USA (westwards to about the Rocky Mountains) to Texas and the Gulf of Mexico. The subspecies *C. s. osceola* described from Florida is no longer recognised. The records for Mexico, near Brownsville, are probably based on released animals. Single individuals or reproducing populations have also been described for various states of the USA outside the natural range, as well as in Canada, in the province of British Columbia (Fuller et al. 2023). Reproducing populations have also been noted for China, Japan and Thailand, and new records are constantly being added from all parts of the world (GBIF Secretariat 2022). The species is also successfully being bred in large numbers in China. Tian et al. (2016) report 8 million animals in captivity and > 4.5 million hatchlings per year for Chinese breeding farms.

*Chelydra serpentina* has been assessed as 'potential invasive' and included in the 'action list' meaning that there are indications for negative impacts (Nehring et al. 2015). No established self-sustaining populations are known in Europe; individual animals have been found in Germany, Austria and Spain (Nehring et al. 2015).

Due to various biological parameters, e.g. the similarity of certain climatic parameters in the area of origin and in the country of import, the lack of shyness towards humans, the large number of eggs per year, etc., the risk that *Chelydra serpentina* from the pet trade could become established in various European countries was assessed as 'serious' (Kopecký et al. 2013, also see the assessment of single animal observations in Esposito et al. 2022 or Kalaentzis et al. 2023).

A more detailed study on the occurrence of *Chelydra serpentina* in France and an assessment of the threat posed to ecosystems by escaped snapping turtles can be found in Maucarrée's master's thesis (2016) – although the snapping turtle has already established itself and reproduced in several places in France, it is not yet known whether this has a negative impact on the ecosystem. The existing reporting obligation for snapping turtles in captivity in France should be properly enforced. Whether the free-living animals need to be permanently removed can only be decided once it is clear whether they have a negative impact on the bio-coenosis in this region, or actually pose a risk to humans.

A new assessment of the invasion risk and danger to humans and also to the respective native fauna revealed a fairly low risk level for *C. serpentina* (worldwide). However, occurrences outside the natural range should be closely monitored and turtle keepers should be trained in handling these turtles and preventing them from escaping into the wild (Nerozzi et al. 2024).

### Habitat

*Chelydra acutirostris*: In the upper reaches of large streams and in smaller rivers in the forest, as well as in ponds and swamps, often hidden in fallen leaves. The turtles can also live in brackish water. May dig in on land during aestivation (in Colombia July to October). 1–35% of its diet consists of fish (Acuña-Mesén 1993). In addition, they eat molluscs, insects, crustaceans, amphibians and carrion, as well as plant food.

*Chelydra rossignonii*: Lives at the swampy edges of shallow still waters and in muddy, slow-flowing smaller rivers, which are often covered with water hyacinths. These turtles are therefore difficult to spot and it is not easy to set turtle traps in these waters. This species has always been considered quite rare compared to *C. serpentina* (Moll & Dodd 1985, Legler & Vogt 2013).

*Chelydra serpentina*: North American snapping turtles can be found in all types of stagnant or slow-flowing, usually turbid, waters with a muddy bottom. Adults can live for long periods in the food-rich brackish water of estuaries. They can also survive for shorter periods in pure seawater and have probably arrived swimming at the various islands where the species is now found. However, juveniles are dependent on freshwater and prefer smaller waters with plenty of cover. The animals prefer to stay in shallow water; snapping turtles are rarely observed in water depths greater than 2.5 metres. Gravid ♀♀ also bask outside the water on driftwood or on the shore, but the animals usually float a few centimetres below the surface of the water to bask. In winter, the turtles can even be observed sunbathing under a closed layer of ice. At temperatures above 7°C, the animals can also migrate overland, usually at night, and some ♀♀ visit certain nesting sites every year, which can be > 10 km away from their home waters. The



animals are territorial in summer, but can hibernate together in suitable places, buried in the mud (Graves & Anderson 1987).

### Conservation Status and Main Threats

*Chelydra serpentina* has been listed on CITES Appendix II since 2023 (CoP19 Proposal 23). *Chelydra* spp. have already been listed on CITES Appendix III since 2016 (ten years later than *Macrochelys* spp.).

With the inclusion of *C. serpentina* in Appendix II, the then implicit CITES listing for *C. acutirostris* and *C. rossignonii* will no longer apply from 2023 on. Accordingly, these two species are currently not included in the appendices of the EU Regulation / the Federal Species Protection Act.

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

Classified as invasive species in Germany according to § 3 BArtSchV since 2002.

*Chelydra serpentina* has been included in the regulations on dangerous animals in several federal states in Germany (Gebhardt-Brinkhaus 2021) and is also subject to certification and authorisation in some EU countries and Switzerland.

With the inclusion of *C. serpentina* in Appendix II, the former implicit CITES listing for *C. acutirostris* and *C. rossignonii* will no longer apply from 2023 on. Accordingly, these two species are currently not included in the appendices of the EU Regulation / the Federal Species Protection Act.

### IUCN Red List Status

*Chelydra acutirostris*: NT in the TFTSG Provisional Red List (van Dijk et al. 2011)

*Chelydra rossignonii*: NT (Near Threatened a A2cd + A4c, assessed July 07, 2023)

*Chelydra serpentina*: LC (Least Concern, assessed August 02, 2010).

For many American turtle species, a reassessment was planned in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). The following assessments, for 2025, are in press (A.G.J. Rhodin pers. comm. 30/08/2024):

*C. acutirostris*: NT

*C. rossignonii*: NT

*C. serpentina*: LC.

## Red List Status in the Range Countries

*Chelydra acutirostris*:

### **Colombia**

Near threatened (NT, Morales-Betancourt et al. 2015), low priority for conservation measures (Forero-Medina et al. 2016).

*Chelydra rossignonii* (included in *C. serpentina*):

### **Ecuador**

Vulnerable (VU, Carillo et al. 2005).

### **Mexico**

Specially protected (Pr, SEMARNAT 2019). This regulation can only be updated with the help of a formal application, which has not yet been submitted. *C. rossignonii* has been categorised as critically endangered using the EVS (Environmental Vulnerability Score) (Wilson et al. 2013). The current status of the population and the population trend are unknown. At the same time, however, *C. serpentina* s. str. is considered invasive in Mexico (CONABIO 2017).

The other range countries of the three species have no Red Lists, or the *Chelydra* spp. were not considered there.

## Utilisation and Protection within the Natural Range

*Chelydra serpentina*:

In the USA, fishing for personal use is usually permitted without restriction, only fishing for commercial purposes must be authorised. In most federal US states, however, the catch is subject to a size limit, i.e. only turtles with a carapace length > 30 cm may be caught – in other words, reproductive adults are deliberately taken with the risk that the turtle population in these states will eventually become endangered (Colteaux & Johnson 2017).

The species had been listed on CITES Appendix III since 2016, so that legal exports could be monitored. An evaluation of international trade in the years 2020–2023 (UNEP-WCMC 2024) showed that of the 11,118,278 registered exports, only 11% had been classified as live wild-caught specimens, and half animals were ranched already; the recipient countries were in East Asia. The LEMIS database lists also 3,958 kg of meat and 2,700 eggs. Since 2020 the export of these turtles has almost come to a halt.

Snapping turtles are still a favourite food within the US. There are many instructions on the internet on how to catch, kill and gut them, and of course how to prepare them. As a rule, a kind of soup or stew is cooked from them, with the eggs, which are still unshelled, being put on top of the soup, i.e. ♀♀ are preferably caught for this. In the USA, however, the meat is sometimes also grilled or deep-fried, and the larger ♂♂ are particularly popular for this. Specialised mail-order butchers offer frozen snapping turtle meat with bones, deboned meat, minced meat and various types of sausage made from turtle meat. Frozen snapping turtle eggs are also available by mail order. Special organs, e.g. turtle penis, can be pre-ordered from these butcheries.

In Canada, fishing for commercial purposes is prohibited, but sometimes turtles are caught for personal use with hook and line, or with baited traps.

*Chelydra acutirostris* and *C. rossignonii*:

In Central and South America, the native snapping turtles are also caught and consumed as soup or stew. However, the meat of North American snapping turtles that have been reared in special breeding farms tends to be offered on the market. The native species are sometimes bred in smaller, often unlicensed breeding farms, and the juveniles are sold as pets and then, when they are no longer so cute, are often fattened up for personal consumption and eventually slaughtered (Grünewald 2008, Legler & Vogt 2013, Ramírez-González & Canseco-Márquez 2015). The eggs are also coveted as food, and some indigenous communities use snapping turtles as traditional medicine (Montuy Pozo et al. 2019, Lasso & Morales-Betancourt 2021).

A species conservation breeding programme for *C. rossignonii* was set up in 2008 in one Unidad de Manejo in Mexico (UMA), and 119 eggs were incubated in the first year, from which 15 juveniles resulted. A study report on the conditions for captive breeding in this UMA (Ruiz López 2011) is quite sobering, and more recent information on species conservation or targeted captive breeding projects could not be found. Zenteno Ruiz et al. (2019) still list five licensed UMAs for Tabasco that breed *Chelydra rossignonii*, Contreras Hernandez (2021) only three (plus one that has specified breeding *C. serpentina*). The turtles produced in these UMAs are usually sold to butchers or restaurants. Snapping turtles are expensive in Mexico, and the Secretaría de Cultura in Tabasco even gives a book value of \$1,800 MXN (approx. €100) per adult snapping turtle for 2022.

Upon enquiry, Mexico's Scientific CITES Authority (Muñoz Lacy 2023) compiled the following data to our questions: The National Commission for the Knowledge and Use of Biodiversity (CONABIO) in Mexico reported that in 2023, five UMAs and five PIMVS (Predios e Instalaciones que Manejan Vida Silvestre, see Glossary) were registered with the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) for *C. rossignonii*, while as many as 15 UMAs and 23 PIMVS were registered for the more prolific *C. serpentina*, although not all of these farms are aimed at breeding. In the years 2013–2022, a total of 5,217 live *C. rossignonii* with CITES permits were exported from two UMAs, of which 18 animals were exported to the US in 2015 and all others to China. In the same period, four UMAs exported 1,335 live *C. serpentina*, 30 of them to Korea in 2019, and all others to China. One of these UMAs is licensed for both species. Why these exports are not listed in the CITES database, and why instead a total of 300 live *C. serpentina* are listed in this database as exports from Mexico to France in 2017–2018, could not be clarified. The original breeder animals of *C. serpentina* appear to have been imported from the USA in 2014 and 2015, SEMARNAT lists 14,000 live animals – these imports are also not included in the CITES Trade Database.

There are hints on the internet (mainly Facebook entries from 2015) that *C. rossignonii* ♂♂ were deliberately mated with *C. serpentina* ♀♀ in small breeding farms in Mexico because the North American snapping turtle ♀♀ lay more eggs. The hybrids inherited the lighter shell colouration of *C. rossignonii* and were then exported and sold in South-East Asia as *C. rossignonii* 'local form from Veracruz'. Whether there is also a domestic market for these turtles in Mexico could not be determined.

In France, only *Chelydra serpentina* have been offered in the pet trade so far, the photos of which cannot be identified. In Spain, snapping turtles with relatively light, reddish, carapace colouration, have been observed again and again in recent years, irrespective of the conditions in which they are kept (J. Soler, pers. comm. Soler, personal communication from the

CRARC rescue centre in Masquefa, Catalonia) or offered on the usual sales platforms, sometimes as captive-bred specimens. The reddish-coloured specimens from Spain identified to date are *C. rossignonii* (E. Reyes-Grajales pers. comm.), hybrids with *C. serpentina* have not yet been observed there.

## Threats

The biggest threats to snapping turtles are the draining and conversion of water or riparian habitats for urban development purposes, habitat fragmentation, illegal logging, burning of native vegetation to create farmland, deliberate and accidental capture in fish traps or injuries caused by swallowed fishing hooks, and the loss of very many clutches due to subsidized predators. Water pollution and injuries caused by boats, as well as losses in road traffic, also play a role.

For *Chelydra rossignonii*, capture for the illegal trade is certainly also a threat, but the extent is difficult to assess as systematic inspections of intermediaries are difficult to organise. Real or feigned confiscation operations and subsequent legalisation of the animals by placing them in a licensed UMA to supplement the breeding stock certainly also play a role in the loss of animals from the wild populations, but this is obviously very difficult to quantify.

## Reproduction

| Topic                   | Details on the reproduction of <i>Chelydra</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | ♂♂ have longer tails than ♀♀, and the distance between the cloaca and the rear edge of the carapace is greater in ♂♂ than in ♀♀.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Reproduction            | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Sexual maturity         | <i>C. acutirostris</i> in Colombia: ♂♂ at 17 cm PL, ♀♀ at 14 cm PL<br><i>C. rossignonii</i> : ♀♀ at 11–16 years<br><i>C. serpentina</i> in Iowa: ♂♂ usually in their 5 <sup>th</sup> year at a PL of 149–155 mm, ♀♀ already can develop fat their 4 <sup>th</sup> –7 <sup>th</sup> year, at 123–175 mm PL, enlarged follicles, ovulation takes place in their 7 <sup>th</sup> or 8 <sup>th</sup> year at the earliest. Nesting ♀♀ have a CL > 28 cm. In Florida ♀♀ are sexually mature at 22 cm CL at 6–8 years of age. In the north of the distribution area of this species, sexual maturity is generally considered to occur at 19 to 21 cm CL, the animals are then usually 11–12 years old, with a minimum of six and a maximum of 17 years.                                                                                                                                                                                                                                                                       |
| Mating and nesting      | <i>C. acutirostris</i> : Mating season in Costa Rica from late April to November, i.e. during the rainy season. Egg laying sites are often near water, in Colombia 2–50 m (Henao & Ruiz-Palma 1996), in Costa Rica 6–79 m from the water's edge (Flausín et al. 1996/1997). The egg pits are usually created in clayey-sandy soil and are only 5–10 cm deep. After oviposition, the site is camouflaged with soil and leaves. The last clutches of the season (in Costa Rica around February) are laid in warm, sunny places. Grünwald (2008) describes that in Ecuador the eggs are often laid in sandbanks directly on the river and that the ♀♀ from riverine habitats often lay simultaneously.<br><i>C. rossignonii</i> : No observations available, probably similar to <i>C. acutirostris</i> .<br><i>C. serpentina</i> : Mating takes place from spring to autumn. Oviposition often occurs on open, sandy ground < 100 m from the water. The ♀♀ often return to the same oviposition site for the next clutch. |
| Reproductive season     | <i>C. acutirostris</i> : In Colombia, oviposition was observed in January (Rueda-Almonacid et al. 2007), February (Medem 1977), April (Young-Valencia, pers. obs. 2022), June (Mosquera & Murillo 2003), September (Henao & Ruiz-Palma 1996, Young-Valencia, pers. obs. 2022) and October (Young-Valencia et al. 2014). In Ecuador, oviposition occurs at                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

|                            |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
|----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                            | <p>the beginning of the dry season, between May and early July (Grünwald 2008). In Costa Rica, oviposition was observed both in February, during the spring dry season (Moll 2010), and later, in September and October (Flausín et al. 1996/1997).</p> <p><i>C. rossignonii</i>: Vitellogenesis from October, oviposition February to April, depending on the rainy season. In the UMA, mating April to November, oviposition May to September with a peak in June.</p> <p><i>C. serpentina</i>: Oviposition in the north of the range often in the first three weeks of June, with the onset of oviposition being triggered by temperature.</p>                 |
| Eggs/clutch, clutches/year | <p><i>C. acutirostris</i>: Costa Rica: 11–38, on average 35.2 eggs per clutch, Colombia: 20–35, on average 27 eggs per clutch, Ecuador: 11–83 (on average 27) eggs per clutch. Probably several clutches per year.</p> <p><i>C. rossignonii</i>: 15–52 eggs per clutch, 1–2 clutches per year between February and April. In the UMA, 11–83 eggs per clutch, only one clutch per year.</p> <p><i>C. serpentina</i>: Usually up to 75 eggs/ clutch, maximum 83 eggs (Bleakney 1957). In the northern parts of the range only one clutch per year.</p>                                                                                                              |
| Egg size/ hatchling size   | <p>The eggs of <i>Chelydra</i> spp. are spherical.</p> <p><i>C. acutirostris</i>: Eggs 28–39 mm in diameter, on average 35.4 mm (Costa Rica), 34–35 mm (Honduras), on average 36.3 mm (Colombia); approx. 20.4 g, hatchlings approx. 32.7 mm CL and 17.4 g.</p> <p><i>C. rossignonii</i>: Eggs 23–35 mm in diameter, 19–20.3 g, hatchlings (incubation temperature 25–29°C) on average 31.8 mm (26.0–36.6 mm), on average 31.8 g (7.2–15.2 g).</p> <p><i>C. serpentina</i>: Eggs rounded, 22.5–34.8 mm in length, 6.42–19.07 g.</p>                                                                                                                               |
| Incubation and hatching    | <p><i>C. acutirostris</i>: 55–125 days in nature (Costa Rica, Ecuador), 94–106 days (Colombia). The hatchlings come to the surface at the end of the rainy season.</p> <p><i>C. rossignonii</i>: &gt; 95 days in the wild, in the UMA in Mexico 55–125 days, at 25°C constant incubation temperature 103 days and at 29°C 75–84 days. Diapause has never been observed in this species, despite the occurrence in the particular climate zone!</p> <p><i>C. serpentina</i> from Wisconsin: at a constant incubation temperature of 25°C 60 days, at constantly 29°C 45 days. In the wild 70–120 days – the hatchlings may overwinter underground in the nest.</p> |
| Sex determination          | <p>Temperature dependent.</p> <p><i>C. rossignonii</i>: In the north of the natural range FMF, lower threshold temperature approx. ca. 21°C, upper threshold temperature approx. 29°C, in southern areas of the range MF, threshold temperature 26.5°C.</p> <p><i>C. serpentina</i>: Northern populations FMF, lower threshold temperature 24.5°C, upper threshold 27.5°C. Southern populations MF, threshold temperature 28.5°C. Even at a constant incubation temperature of 21.5°C, some embryos may develop until hatching – above 31°C, only a few embryos will develop into viable hatchlings.</p>                                                          |
| Sperm storage              | <p>In <i>C. serpentina</i> &gt; 5 years; in the other two species no exact records are available, but certainly several years as well.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |



## Husbandry and Captive Breeding B/A



Fig. 19: *Chelydra* spp. juveniles

- a *C. rossignonii*, plastron, in a recuperation centre in Spain (J. Soler)
- b *C. serpentina*, plastron, subadult wild animal in Georgia, USA (B. Pfau)
- c *C. acutirostris*, juvenile, Ecuador (F. Grünewald)
- d *C. rossignonii*, sculpted carapace, ♀ about three years old, in a recuperation centre in Spain (J. Soler)
- e *C. acutirostris*, plastron, juvenile, Ecuador (F. Grünewald)
- f *C. acutirostris*, juvenile, head markings, Ecuador (F. Grünewald).

| Topic                                                           | Data for <i>Chelydra</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-----------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Increase in temperature. The influence of day length has not been investigated.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Husbandry requirements                                          | All three species are very adaptable and can also be kept in relatively small water tanks. Good filtration and the possibility of leaving the water is recommended. The snapping turtles from the south of the distribution area require the water to be heated.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| General characteristics, difficulties with keeping and breeding | <p><i>C. acutirostris</i> can be kept in pairs or groups, even mixed housing with other turtle species or larger fish is often possible.</p> <p><i>C. rossignonii</i> is said to be aggressive towards conspecifics, and defensive towards humans.</p> <p>There are significant individual differences in the behaviour of <i>C. serpentina</i>, but it is often possible to keep a number of turtles of approximately the same size together.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Care of the young, technical and time effort                    | The effort for rearing is very low. Young Snapping turtles can be reared in large groups. They also accept extruded food pellets shortly after hatching. Frequent water changes and good water filtration are recommended.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Life expectancy                                                 | Certainly > 60 years (in human care as well as in the wild), probably much longer.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Frequency of private breeding and reproduction in zoos          | <p><i>C. acutirostris</i>: A breeding success at Schönbrunn Zoo, Vienna, was published in 2014 (Preininger et al. 2014), the offspring were sold to a breeding group in the US. It is not known whether these animals have already reproduced. Otherwise probably not kept in Europe.</p> <p><i>C. rossignonii</i>: Apparently kept in Spain and possibly in other European countries, but not differentiated here from <i>C. serpentina</i>. Egg laying has been observed, but the eggs are destroyed as the young cannot be given to private keepers. No information is available on breeding conditions in South-East Asia.</p> <p><i>C. serpentina</i>: Now rare in most European countries due to the frequent ban on keeping and breeding. The NBSV's offspring statistics show a total of 280 offspring for the Netherlands and Belgium by 2020 (NBSV 2024). This species is frequently bred in the countries of origin and in Asian countries.</p>        |
| Breeding difficulty evaluation                                  | Breeding is very easy with <i>C. serpentina</i> , and juveniles often hatch from overlooked clutches in the outdoor enclosure.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Mortality in the first years of life                            | Low in captivity, but, due to predation, high in the wild.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| F2 generation bred in captivity                                 | From 1989 onwards, juveniles of <i>C. serpentina</i> were repeatedly reported for the offspring statistics of the AG Schildkröten (Bakowskie in prep.). It is not clear from the statistics whether these offspring, which are now sexually mature, were actually bred on to the F2 generation, but in view of the former popularity of the species, this is likely. For <i>C. acutirostris</i> and <i>C. rossignonii</i> , F2 breeding in captivity in the countries of origin seems possible.                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Commercial breeding/ ranching                                   | <p>In the range countries of <i>C. acutirostris</i> and <i>C. rossignonii</i> adult ♀♀ are often caught and kept in ponds until they lay their eggs. Most of the newly hatched juveniles are then sold. In Mexico, hatchlings of <i>C. rossignonii</i> were on sale in 2022 for 1,000 pesos (approx. €52) plus shipping costs.</p> <p>However, there also seem to be breeders in the USA who breed over several generations. In the corresponding offers on the Internet, there are repeated references to the fact that these farms also breed different colour forms (albinos, leucistic, hypomelanistic, melanistic, cinnamon-coloured etc.) and offer them at high prices as pets. Snapping turtles are also bred in large numbers in China and neighbouring countries, as well as in Indonesia. However, nothing is yet known about the breeding methods used there. <i>C. rossignonii</i> is apparently particularly sought after in China and is known</p> |

|                                    |                                                                                                                                                                                                                                                                                                                  |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                    | as the 'queen of the snapping turtles'. As a speciality, juveniles of hybrids of <i>Macrochelys</i> spp. with <i>Chelydra serpentina</i> and also with <i>C. rossignonii</i> are offered as well.                                                                                                                |
| Interviews/ Surveys/ Consultations | <i>Chelydra serpentina</i> : several private breeders in different European states could be interviewed; for <i>C. acutirostris</i> : one institution in Europe and one in the country of origin provided data; <i>Chelydra rossignonii</i> : literature review on breeding operations in the country of origin. |

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### Beate Pfau (01.05.2024)

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## Emydidae

### *Graptemys* Agassiz, 1857

| Species                     | Original description                              | Common name                                | Common name international                               | Known in the trade |
|-----------------------------|---------------------------------------------------|--------------------------------------------|---------------------------------------------------------|--------------------|
| <i>Graptemys barbouri</i>   | (Carr and Marchand, 1942)                         | Barbour's Map turtle                       | Barbour's Höckerschildkröte<br>Tortuga mapa de Barbour  | Yes                |
| <i>Graptemys ernsti</i>     | (Lovich and McCoy, 1992)                          | Escambia Map turtle                        | Escambia-Höckerschildkröte<br>Tortuga mapa de Escambia  | Yes                |
| <i>Graptemys gibbonsi</i>   | (Lovich and McCoy, 1992)                          | Pascagoula Map turtle, Gibbons' Map Turtle | Pascagoula-Höckerschildkröte<br>Tortuga mapa de Gibbons | Yes                |
| <i>Graptemys pearlensis</i> | (Ennen, Lovich, Kreiser, Selman and Qualls, 2010) | Pearl River Map turtle                     | Pearl-Höckerschildkröte<br>Tortuga mapa del río Pearl   | Yes                |
| <i>Graptemys pulchra</i>    | (Baur, 1893)                                      | Alabama Map turtle                         | Alabama-Höckerschildkröte<br>Tortuga mapa de Alabama    | Rare               |

According to the current taxonomic checklist (Rhodin et al. 2021), the genus *Graptemys* contains a total of 14 species, but the species delimitation is still under discussion (Lindeman 2013, Thomson et al. 2018). Of these, only the five very similar, megacephalic *Graptemys* species were transferred from CITES Appendix III to Appendix II at CoP19; the other species remain in Appendix III. These large-headed map turtles are closely related and live in neighbouring river systems in the south-eastern USA, which flow into the Gulf of Mexico and have been connected several times by past sea level fluctuations.

Sexual dimorphism is extreme in these turtle species: adult ♂♂ usually only have a CL of approx. 10–13 cm, while the ♀♀ can reach approx. 30 cm CL. The sexes occupy separate ecological niches: The ♂♂ live in the more plant-rich side waters of the larger rivers and, like the juveniles, feed mainly on insects and other soft food animals, while the ♀♀ tend to stay in the main river channels and eat mainly mussels and similar hard-shelled animals (other molluscs or crayfish) whereby the basket mussels (*Corbicula* spp.) introduced from Asia play a major role as food items. The head shape of the ♀♀ adapts to the food supply: The more really hard food items are cracked, the more the chewing surfaces widen over the years, so that the head of older ♀♀ becomes disproportionately large (megacephalic). The ♂♂, on the other hand, retain the 'usual' aquatic turtle head proportions throughout their lives.





Fig. 20: megacephalic *Graptemys* spp., adults

- a *G. barbouri*, 2 ♀♀ with very different head markings (R. Praschag)
- b *G. barbouri* breeding pair, ♀ on the left (X. Wapelhorst)
- c *G. gibbonsi* ♂, Chickasawhay River Mississippi (R. Praschag)
- d *G. gibbonsi* ♀ raised in captivity (B. Pfau)
- e *G. ernsti* ♀, Conecuh River (R. Praschag)
- f *G. pearlensis* young ♀ (X. Wapelhorst)
- g *G. pulchra*, Cahaba River, adult megacephalic ♀ (R. Praschag)
- h *G. pulchra* pair captive bred and raised at the photo author's facility, ♀ on the right (R. Praschag).

The carapace of the megacephalic map turtles is oval, serrated along the rear margin, and curved upwards, with the highest point being slightly in front of/cranial to the midpoint. The vertebral shields are raised in the midline and form narrow, sharp projections (i.e. without the conspicuous ‘knobs’ that characterize some other *Graptemys* species). The basic colouration of the carapace is olive green to olive brown, with a dark line along the midline and light markings on the pleural and marginal scutes. The plastron is yellowish and sometimes shows narrow black fringes on the shield seams. The basic skin colour is dark grey, and the legs and tail have light longitudinal stripes.

These turtles are easy to distinguish from other aquatic turtles because they have a striking yellow-green head marking on the top and sides of the head. This head marking is used for species recognition (Myers 2008), but does not usually prevent hybridisation with other *Graptemys* species. In older ♀♀ of the megacephalic species, this head marking becomes muted and the head looks finely freckled.

### Morphology and Taxonomy

The five megacephalic *Graptemys* species, which have been transferred to CITES Appendix II, are morphologically very similar. There are only around ten specialists in the USA who can reliably identify each animal of these species, unless the geographical origin from a river basin is also known (Selman 2022). Indeed, the description of some forms as new species has provoked controversy, as the genetic distance between them is also quite small (Praschag et al. 2017). *G. barbouri* shows the greatest morphological differences to the other species (Lovich & McCoy 1992).

***G. barbouri*** – ♀♀ can reach up to 33 cm CL and 3.3 kg. The heads of ♀♀ *G. barbouri* can grow to a width of 78 mm. ♂♂ grow to a maximum of 13 cm CL, and about 200 g in weight (Ewert et al. 2006), but growth usually stops at around 10 cm (Ernst & Lovich 2009). The dorsal head markings are yellowish to slightly orange on a dark grey background, consisting of a large interorbital blotch connected to postorbital spots; behind the eye sockets there is a heart-shaped or Y-shaped dark pattern with a light concentric pattern in it. There is a transverse or curved bar pattern on the chin, often following the curve of the jaw, and the nape has relatively broad, equally sized stripes. Many animals of this species can be recognised by the following features: Postorbital spots large, light-coloured transverse bar pattern on the chin, C-shaped to almost ring-shaped, thin, yellow, black-edged pattern elements on the costal scutes, the light-coloured stripes on the marginal scutes are narrow. In some animals, often ♂♂, the costal scute pattern is very conspicuous, making the animal’s colouration look close to *G. oculifera*, but they are certainly not hybrids.

***G. ernsti*** – ♀♀ reach about 28.5 cm CL, the ♂♂ 13.1 cm. The head pattern consists of a large interorbital blotch, which is separated from the likewise relatively large postorbital spots on each side of the head by a dark space (a narrow connecting line may occur, however). A nasal trident is almost always visible in front of the yellowish interorbital blotch. Relatively broad stripes of approximately equal size run along the neck, with the two central stripes ending in enlarged ends that are often set off as supraoccipital spots. The chin is spotted with a light-coloured longitudinal bar. Characteristic markings of this species are the nasal trident pattern, the postorbital spots not connected to the interorbital blotch, and the supraoccipital spots.

The markings on the costal shields are reticulated, but with few crossings, and sometimes ring-shaped at the lower edge with a darker centre and a somewhat lighter central spot. Juveniles often have a ‘hump’ on the foremost costal shield, which will disappear later in the course of

growth. The marginal scutes often have smaller, yellow spots within the area circumscribed by the large stripes. The turtles from the three separate river systems of the distribution area differ in the frequency of the nasal trident: in the Conecuh River all turtles show this colouration, in the Yellow River 97.6% and in the Pea River 75% (Ennen et al. 2016). In captivity, these three forms are kept and bred separately due to their slightly different biology (Lechowicz pers. comm. 2023, see also below). Crossbreeds with *G. barbouri* have also been described from the Pea River region (Godwin et al. 2014), which show variants of the nasal trident pattern.

***G. gibbonsi*** – ♀♀ reach 29.5 cm CL and 3.15 kg in weight, ♂♂ 12.4 cm and 340 g in weight. The postorbital spots are large and in older ♀♀ often indented at the posterior margin, resulting in a large upper and a smaller lower lobe pattern which is usually fused with the supramandibular spots. The interorbital blotch may be tridentate and is connected to the postorbital spots by thick lines. There is often a longitudinal bar on the chin. The costal shields with narrow light-coloured lines, and the ring-shaped markings on the lower edge of the costal shields are uniformly filled in dark. The upper side of the dark marginal shields have a relatively straight, broad stripe. The dark line along the spine is usually interrupted behind the serrations.

***G. pearlensis*** – ♀♀ reach 29.5 cm CL, ♂♂ 12.1 cm. The pattern is very similar to that of the closely related *G. gibbonsi*, from which this species was separated in 2010. However, in this species the dark midline is continuous and not interrupted, and the marginal scales bear very broad, almost straight and at the ends widened light stripes (16–21% of the scale width).

***G. pulchra*** – ♀♀ reach 27.3 cm CL, ♂♂ 13 cm. Head markings are mask-like, with the postorbital spots broadly fused with the interorbital blotch. No nasal trident is recognisable. There is a concentric ring pattern on the marginal plates.

## Distribution and Habitat

### Distribution

The exact distribution of these species is difficult to clarify, as they have a very large flight distance and also look very similar, and are therefore difficult to identify through direct observation or photos, and trapping between all the deadwood may be difficult (Lindeman 2013, Lindeman et al. 2020, Selman 2024). Due to the very small genetic distances between the species, it is also likely to be very time-consuming to develop species-specific markers for detection using environmental DNA, which can be used to indirectly prove the presence of the species in a water bodies (Adams et al. 2019).

*Graptemys barbouri*: Mainly distributed in the Apalachicola River basin, as well as in the larger tributaries such as the Chipola, Chattahoochee and Flint Rivers in Alabama, Georgia and Florida. However, new records continue to be established in in other rivers east and west of the Apalachicola system (see also Gregoire 2023). The type locality is the Chipola River near Marianna, Jackson County, Florida.

In the Choctawhatchee River, as well as in the Aucilla, Waciss and Ochlockonee rivers, *G. barbouri* occurs sympatrically with *G. ernsti* and also hybridises with it (Ernst & Lovich 2009). The ultimate cause of this hybridisation likely relates to the existence of a river tapping in the Choctawhatchee-Escambia subregion in Alabama during the Pliocene or Pleistocene, and not, as initially suspected, a release by turtle enthusiasts (Godwin et al. 2013, 2014).



*Graptemys ernsti*: There are records from various rivers that flow into Pensacola Bay, e.g. the Yellow, Escambia, Conecuh and Shoal. The type locality is the Conecuh River, 1 mile upstream from the County Road 4 bridge, 14 km east of East Brewton, Escambia County, Alabama, USA. The species apparently avoids the very tannin-rich waters such as the Blackwater River, likely because few mussels and snails can live here. *G. ernsti* has also been recorded further west, in the Pea and Choctawhatchee Rivers, where it hybridises with *G. barbouri*, see above. Probably released in the St. Johns River on the east coast of Florida (Nelson 2023).

*Graptemys gibbonsi*: Originally described from the Pascagoula and Pearl River systems in Mississippi and Alabama, but now restricted to the Pascagoula River basin following the description of *G. pearlensis* as a separate species. The type locality is in the Chickasawhay River, Leakesville, Greene County, Mississippi, USA.

*Graptemys pearlensis*: This species occurs in the larger rivers of the Pearl and Bogue Chitto Rivers in Louisiana and Mississippi. Type locality is the Pearl River at State Highway 28, near Georgetown, Copiah County, Mississippi. Smith et al. (2020) were also able to detect *Graptemys pseudogeographica* in the Pearl River, which has presumably been released there, but the fear that this species could hybridise with *G. pearlensis* has not been confirmed yet (there is only evidence of hybrids with the syntopically occurring, small-headed *G. oculifera*, which could pose a threat to that species).

*Graptemys pulchra*: This was the first described large-headed *Graptemys*. Type locality is Montgomery, Alabama. Shealy (1976) described its biology in detail and pointed out that there were actually four different ‘forms’, three of which were subsequently described as new species. Currently, only the megacephalic map turtles of the Mobile Bay River systems in Alabama, Georgia, Mississippi and Tennessee are attributed to this species, i.e. the animals in the Black Warrior, Cahaba, Coosa, Tallapoosa, Tensaw and Tombigbee Alabama, and also in tributaries of the Tombigbee River in Mississippi. More recently, *G. pulchra* has also been recorded in a county in Tennessee (Brown 2021), and the species appears to be spreading into the Tennessee River system via the Tennessee-Tombigbee Waterway (Berry et al. 2020). Further investigations into the actual distribution of this species are therefore necessary.

## Habitat

The large-headed *Graptemys* species live in smaller or larger watercourses with plenty of dead wood for basking. It is important that basking sites are far enough away from the bank and offer a good view, as the map turtles immediately dive into the water at the slightest disturbance. They only come to the shore to lay their eggs. The substrate in the water can be muddy, but is often sandy or stony due to the speed of the current. A rich mollusc fauna is important, which is why acidic or tannic waters are avoided, as mussels and water snails are absent here. The ♀♀ tend to live in the main stream with deep water zones, where they can find and feed on mussels or snails and larger crayfish found on the submerged dead wood. The juveniles and the small ♂♂ prefer side waters with little current, preferably also rich in plants, where they can find insects and small crustaceans.

In most rivers where large-headed map turtles are found, there is also a small-headed map turtle species (a so-called sawback turtle, because the projections on the vertebral scutes of these turtles are particularly conspicuous). These species (*G. flavimaculata*, *G. nigrinoda* and *G. oculifera*) occupy a similar ecological niche to the ♂♂ and juveniles of the megacephalic species, but they are not food competitors for the adult ♀♀. These sawback turtles remain

relatively small, even in the ♀♀, and are easier to accommodate in the usual aquariums in private households. They are therefore much more sought-after in the pet trade than those species that have now been listed on CITES Appendix II.

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 24).

All other species of the genus *Graptemys* are still listed in CITES Appendix III since the inclusion of the genus by the USA in 2006.

EU Council Regulation (EC) No 338/97 Annex B.

In Germany, specially protected under Article 7 (2) No 13 BNatSchG.

In some European countries, e.g. France, all *Graptemys* species are classified as potentially invasive and are therefore subject to certification and authorisation.

### IUCN Red List status

*Graptemys barbouri*: NT (Near Threatened, assessed August 01, 2010);

*Graptemys ernsti*: NT (Near Threatened, assessed August 01, 2010);

*Graptemys gibbonsi*: EN (Endangered A2bce+4ce, assessed August 01, 2010);

*Graptemys pearlensis*: EN (Endangered A1bcde+4bcde, assessed August 01, 2010);

*Graptemys pulchra*: NT (Near Threatened, assessed August 01, 2010).

New threat assessments for the IUCN Red List 2025 are in press (A.G.J. Rhodin pers. comm. 30/08/2024), the status of these species will not change.

### Protection and utilization within the United States

*Graptemys barbouri*: U.S. Endangered Species Act: Listed as endangered species due to similarity to *G. pearlensis* (USFWS 2024). NatureServe Global Status G2, in Alabama and Florida S2, in Georgia S3 (Jackson 2014). Also protected in all three states: Classified as a species of high conservation concern in Alabama, a fully justified exemption permit must be obtained for capture and keeping (including for scientific interests). In Florida, the capture and keeping of this and similar-looking species is completely prohibited. In Georgia, the species is classified as endangered, which means that keeping is also prohibited. In an analysis of the ZIMS database, Ahmed et al. (2024) found that nine zoos in the USA keep this species (37 animals in total) and that only one captive-bred animal was reported to this database in 2022.

*Graptemys ernsti*: U.S. Endangered Species Act: Listed as endangered due to similarity to *G. pearlensis* (USFWS 2024). NatureServe Global Status G2, in Alabama and Florida S2 (Jackson 2013). Also protected in both states: Classified as a species of high conservation concern in Alabama, for capture and keeping (also for scientific interests, Lechowicz pers. comm. 2023) a detailed, justified exemption permit must be obtained. Ahmed et al. (2024) were only able to identify one zoo in the USA that keeps four animals (probably juveniles) of this species.

*Graptemys gibbonsi*: U.S. Endangered Species Act: Listed as endangered due to similarity to *G. pearlensis* (USFWS 2024). NatureServe Global Status G2, in Mississippi S2 (Mann 2023). The Mississippi Department of Wildlife, Fish and Park (MDWFP) has stipulated that a maximum of ten animals may be taken (with a licence) per year, but not between 1 April and 30 June; the



keeping of a maximum of four animals of this species may be permitted (with a different licence) (CITES 2022). In an analysis of the ZIMS database, Ahmed et al. (2024) found that four zoos in the USA keep this species (35 animals in total), but that no captive-bred animals have been reported to this database since 2022.

*Graptemys pearlensis*: U.S. Endangered Species Act: Listed as endangered species (USFWS 2024). NatureServe Global Status G2, in Louisiana S3, in Mississippi S2 (Hammerson 2010). The species has no protected status in Louisiana (CITES 2022). The Mississippi Department of Wildlife, Fish and Park (MDWFP) has stipulated that a maximum of ten animals may be taken (with a licence) per year, but not between 1 April and 30 June; the keeping of a maximum of four animals of this species may be permitted (with a different licence) (CITES 2022). The Che- lonian Advisory Group (2015) proposed to the American Association of Zoos and Aquariums to establish a management programme for the two species *G. gibbonsi* and *G. pearlensis* in American zoos, initially to research the husbandry and breeding conditions required and then to find partners for the reintroduction of the offspring. This plan was apparently not pursued further. In an analysis of the ZIMS database, Ahmed et al. (2024) found that two zoos in the USA keep this species (seven animals in total), but that no captive-bred animals have been reported to this database since 2022.

*Graptemys pulchra*: U.S. Endangered Species Act: Listed as endangered species due to similarity to *G. pearlensis* (USFWS 2024). NatureServe Global Status G4, in Alabama S3, in Georgia S3, in Mississippi S2 (Hammerson 2010). Classified as a species of medium conservation interest in Alabama, a detailed and justified special permit must be obtained for capture and keeping (including for scientific purposes). In Georgia, the species is classified as rare and keeping it is therefore prohibited. The Mississippi Department of Wildlife, Fish and Park (MDWFP) has stipulated that a maximum of ten animals may be caught (with a licence) per year, but not between 1 April and 30 June; the keeping of a maximum of four animals of this species may be permitted (with a different licence) (CITES 2022). The species is not protected in Tennessee, where it has now also been observed. In an analysis of the ZIMS database, Ahmed et al. (2024) found that a zoo in the USA keeps five animals of this species, but that no offspring could be obtained from the one adult ♀ in 2022.

## Threats

The following main threats to the map turtle are listed in CITES Proposal No. 24: Hydraulic engineering on the river system, pollution, declining water quality, targeted shooting for recreation, capture for consumption, capture for the pet trade (within the US), disease, and losses to human-subsidized predators. In particular, sediment deposition below the new pulp mills appears to be damaging mussels, the main food source of adult ♀♀, to such an extent that populations of the large-headed species below these industrial operations are declining sharply, while the medium- and small-headed map turtles are hardly affected (see e.g. Hammerson 2010). The Endangered Species Act (USFWS 2024) goes into more detail on the species-specific threat posed by hydraulic engineering measures and environmental pollution, and sets out exactly which permits must be obtained prior to the corresponding interventions. However, as little is known about the status of the populations and their increase or decrease, the effectiveness of these regulations for the conservation of the species in their natural habitat cannot be assessed.

In the individual assessments for the IUCN Red List and in the species chapters in the series ‘Conservation Biology of Freshwater Turtles and Tortoises’, it is also repeatedly pointed out

that motorboats and driving on the sandbanks with four-wheel drive vehicles pose a threat to these turtles and their eggs, and that unauthorised but mostly tolerated wild camping on the nesting beaches also prevents these shy species from laying their eggs. It is also mentioned here that even the large ♀♀ of these map turtles are often captured for the still popular turtle races. The turtles are then labelled (often painted with nail varnish) and placed in the centre of a large circle under a bucket before the start on the very sunny fairground – the turtle that reaches the outer edge of the circle the fastest after the bucket has been lifted is the ‘winner’ and the person who registered it receives a prize (Lee 2012b). The turtles are released somewhere after the festival, stressed and weakened. This probably explains some findings far from the natural distribution area of the respective species. The threat of these popular events to the wild turtle populations nearby have been comprehensively reviewed by Heeb et al. (2024).

### International trade with the megacephalic *Graptemys* spp.

CITES Proposal No. 24 refers to the fact that ‘the international pet trade has become an increasing threat to the large-headed map turtle’ (Ewert et al. 2006, van Dijk 2011a, van Dijk 2011c, van Dijk 2011e). However, this statement is qualified by the fact that, for example, the cited work by Ewert et al. (2006) only refers to a total of 747 *Graptemys barbouri* of unknown age that were already exported in 1997. Furthermore, the IUCN assessments cited merely state that animals ‘also’ occur in international pet trade, but no quantitative metrics are given from which potential negative effects could be derived. Only for *G. ernsti*, it is stated that the species is in high demand in the trade and that capture could possibly jeopardise the wild population. Ewert et al. (2006) also rightly note that the capture of adults ♀♀ would have a greater impact. However, it should be borne in mind that these animals are large and heavy and would therefore incur high freight costs in international trade, while the collection of the eggs and their incubation for export of the hatchlings would have little impact on the population. The fact that wild-caught species are exported from a country of origin does not mean in itself that the wild population is threatened by that (Challender et al. 2022).

In the same paragraph of Proposal No. 24, it is also pointed out that the number of search advertisements for North American turtles, especially for rare species and wild-caught turtles, is increasing in the online trade in Hong Kong SAR (Sung & Fong 2018). At this point and in the corresponding internet reports and market analyses, however, almost exclusively the small-headed ‘sawback turtles’ are mentioned (cf. Chow et al. 2014). An explicit reference to a wanted advertisement for animals of the megacephalic *Graptemys* species could not be found so far, and the search for corresponding legal or illegal offers, even with modern means (cf. Rinne et al. 2023, Soriano-Redondo et al. 2023), has so far been unsuccessful.

The global trade in map turtles can be traced in the CITES trade database as all the *Graptemys* species were included in CITES Appendix III by the US in 2006. An analysis of the US exports in this Database shows that in 2006 only a total of 59 live *Graptemys gibbonsi* (source code ‘C’ or ‘F’) were exported for commercial purposes (purpose code ‘T’). Later, in 2018, altogether 18 living megacephalic *Graptemys* spp. were exported from the US to Austria for captive breeding purposes. The observations and breeding success with these animals were later documented by Reiner Praschag (Praschag 2023a, Praschag 2023b, Praschag 2023c).

An increase in legal exports of wild-caught specimens of these megacephalic species in the legal international trade in recent years, as stated in Proposal No. 24, can therefore not be confirmed. In fact, however, the export of undetermined map turtles (categorised as

*Graptemys* spp.) or (even more frequently) *Graptemys* ‘hybrids’ has increased. This could entail individuals of the megacephalic *Graptemys* species but does not necessarily refer to the now more strictly protected species (cf. also Tlustý et al. 2023). Looking at the exports of wild-caught *Graptemys* species from the USA to Hong Kong SAR, the number is very high, but these are either *G. pseudogeographica*, *G. ouachitensis*, or ‘hybrids’, i.e. animals from the breeding farms that are probably registered as wild-caught due to the peculiarities of the LEMIS database (cf. Lee 2012a, Luiselli et al. 2016, Kolby & Weissgold 2022). The imported large-headed map turtles from the USA are mostly not kept as pets in Hong Kong and China, but are instead reared on farms for consumption or to produce juveniles for later export (CITES 2011, Luiselli et al. 2016).

An evaluation of international trade with megacephalic *Graptemys* spp. from the USA in the not publicly accessible LEMIS Database (UNEP-WCMC 2024), also showed that in the years 2000–2006 a total of 569 *G. barbouri* were exported, mainly to Japan, of which 83% were captive-bred (source code ‘C’). In addition, 1,860 *G. gibbonsi* were exported during the same period, 76% of which were captive-bred, mostly to Japan and Spain.

When the publicly accessible CITES Trade Database is analysed specifically for the large-headed species precisely identified to species-level, it becomes clear that nearly all these animals were bred within the EU (Germany, Austria, Italy or Spain) or in Switzerland (source code ‘C’ or ‘F’). Afterwards these were exported to Hong Kong SAR, as well as China, Taiwan and Japan, which means that there is hardly any direct influence on the wild populations. These animals are mostly descendants of animals that were imported to Germany and Austria in the 1980s and 1990s (cf. Engert 1986, Artner 2001, Praschag 2023a, Praschag 2023b, Praschag 2023c). Despite much attention in recent years (in preparation for the planned ESF studbook, Pfau et al. 2014), no evidence of megacephalic *Graptemys* of unknown origin could be found within the EU and neighbouring countries. Thus, in the authors’ view, the illegal trade in these species does not play a major role in Europe. It can also be seen that a large number of *Graptemys* with source code ‘C’ have been exported from China and neighbouring countries since 2009. Particularly striking is an entry for 2016, where 51,000 ‘*Graptemys* spp.’ were imported from China into the EU (Italy is specified), without specifying a source code, i.e. possibly offspring of different species or hybrids from the many turtle farms there.

A long-term observation of the retail trade in Europe (Schober 2023) shows more clearly that this must have included the large-headed species, which were resold within Europe. Today most large-headed *Graptemys* species can be purchased as captive-bred specimens directly from specialised European breeders.

Only for Japanese zoos is there explicit evidence of a single *Graptemys barbouri* in one zoo and a total of seven *Graptemys pulchra* in two zoos, albeit from 1998 (Kawata 2003). In an analysis of the ZIMS database, Ahmed et al. (2024) were unable to identify any European zoo keeping one of the large-headed *Graptemys* species.

## Reproduction

| Topic                              | Details on the reproduction of the megacephalic <i>Graptemys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | The sexes can be distinguished by tail length at the earliest when the carapace is 5 cm long. The tails of ♂♂ are longer and thicker than those of ♀♀, the cloaca of ♂♂ is behind the end of the carapace when the tail is outstretched. There are also significant size differences in adult specimens. ♀♀ are large-bodied and can reach 4–5 times the body size of ♂♂, which are often identified as juveniles by laypeople.                                                                                                                                                                                                                                                  |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Sexual maturity                    | <p>Data from the field:</p> <p><i>Graptemys barbouri</i>: ♂♂ with 3–4 years and 6.9 cm PL, ♀♀ with approx. 17 cm PL</p> <p><i>Graptemys ernsti</i>: ♂♂ with 3–4 years and 8 cm CL, ♀♀ with 14 years and 22 cm CL</p> <p><i>Graptemys gibbonsi</i>: ♂♂ with 4 years and 8.9 cm PL, ♀♀ with 15–20 years, from 17 cm PL</p> <p><i>Graptemys pearlensis</i>: ♂♂ from 8.9 cm CL, ♀♀ from 17.0 cm PL</p> <p><i>Graptemys pulchra</i>: ♂♂ with 4 years and 8.9 cm PL, ♀♀ from 17 cm PL.</p> <p>Sexual maturity is reached more quickly in captivity under warmer conditions and with frequent feeding, sometimes as early as 2 years of age in ♂♂, ♀♀ usually at 7–15 years of age.</p> |
| Mating and nesting                 | <p>As river dwellers, large-headed <i>Graptemys</i> spp. lay their eggs on sandbanks and on embankments with easy-to-dig soil. Due to the risk of flooding, the eggs are laid well above the highest water level of the river.</p> <p>This must be taken into account when keeping the animals, as they are unlikely to accept nesting places at water level.</p>                                                                                                                                                                                                                                                                                                                |
| Reproductive season                | In the wild May–August, in captivity in Europe April–June/July.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Number of eggs/clutches per season | <p><i>Graptemys barbouri</i>: on average 8.8 (3–15) eggs/clutch and 3–5 clutches/year</p> <p><i>Graptemys ernsti</i>: on average 7.2 (3–12) eggs/clutch and on average 4 (maximum 6–7) clutches/year</p> <p><i>Graptemys gibbonsi</i>: on average 7.5 (6–12) eggs/clutch and 4–6 clutches/year</p> <p><i>Graptemys pearlensis</i>: on average 6.4 (5–12) eggs/clutch and 4–6 clutches/year</p> <p><i>Graptemys pulchra</i>: 6–7 eggs/clutch and 4–7 clutches/year.</p>                                                                                                                                                                                                           |
| Egg size/hatchling size            | <p><i>Graptemys barbouri</i>: Egg size in the wild on average 37.7 (31.0–41.6) mm long and on average 27.3 (22.1–30.8) mm in diameter, in captivity 30–38 mm long. Hatchlings in captivity 30.2–38 mm PL</p> <p><i>Graptemys ernsti</i>: Egg size 38 x 27 mm, hatchlings on average 40.8 (34–44) mm CL</p> <p><i>Graptemys gibbonsi</i>: Egg size 38 x 26 mm, with weight of 13.9–15.5 g, hatchlings on average 31.2 (21.5–35.3) mm PL</p> <p><i>Graptemys pearlensis</i>: Egg size 38 x 26 mm, with 13.9–15.5 g in weight.</p> <p><i>Graptemys pulchra</i>: Egg size 42.5 x 25.7 mm, hatchlings on average 36.5 mm CL, with 10.9 g in weight.</p>                               |
| Incubation and hatching            | 58–84 days, at 25°C 100% ♂♂, at 30°C 100% ♀♀.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Sex determination                  | TSD, threshold temperature for <i>G. barbouri</i> 28.4°C, for <i>G. pulchra</i> 28.5°C.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sperm storage                      | Yes, > 1 year.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |



## Husbandry and Captive Breeding B/B



Fig. 21: megacephalic *Graptemys* spp., captive breeding

- a *G. ernsti* at hatching (C. Lechowicz)
- b *G. barbouri* juvenile in a zoo (B. Pfau)
- c *G. barbouri* ♂ captive bred offspring (X. Wapelhorst)
- d *G. barbouri* juvenile ♀ (R. Hentschel)
- e *G. gibbonsi* captive bred offspring (R. Hentschel)
- f *G. pearlensis* (left) and *G. pulchra* juveniles (R. Praschag).



The five megacephalic *Graptemys* species are so closely related and so similar in their husbandry and breeding requirements that they are treated here as a group.

| Topic                                                           | Data for the megacephalic <i>Graptemys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|-----------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Lowering of the temperature in winter. Mating takes place in autumn and spring.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Husbandry requirements                                          | <p>These river turtles require specific egg deposition areas that are well above the water level. For captive propagation appropriate nesting areas can be, for example, sufficiently large boxes filled with sand which are placed above the water. Gradients for humidity and temperature are recommended, so that the ♀ can choose the exactly right place for her nest (Meier 1997). The proper soil/sand moisture in egg deposition areas is imperative for nesting and seems to be higher than other <i>Graptemys</i> species (Lechowicz pers. comm. 2024).</p> <p>Incubation is difficult for <i>G. ernsti</i>, as the humidity in the incubator must correspond very closely to the natural conditions (personal communication from a very experienced breeder of all five species).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| General characteristics, difficulties with keeping and breeding | <p>Adult ♀♀ prefer deeper nest boxes than the congener sawbacks, as well as more spacious enclosures. If they are kept too crowded, they will survive but lay only few, if any, eggs sporadically (Lechowicz pers. comm. 2024).</p> <p>Large-headed <i>Graptemys</i>-♀♀ tend to escape, especially when looking for a place to lay their eggs. Care should therefore be taken to ensure that they are housed in an escape-proof environment.</p> <p>These turtles can often be kept together with conspecifics of the same size and also with other, similarly calm freshwater turtles with similar requirements, but some ♀♀ are aggressive to other ♀♀ of the same species and must be separated.</p> <p>However, the large-headed ♀♀ in particular can injure other turtles (usually due to food envy) and should therefore be carefully observed, and always be fed separately. Mating should take place under supervision, as ♀♀ that are not willing to mate can attack the much smaller ♂, which can even be fatal for him.</p> <p>As far as difficulty, <i>G. barbouri</i> has shown to be the easiest megacephalic <i>Graptemys</i> species to keep and reproduce in human care. <i>G. ernsti</i> seems to be rather delicate, in particular in regards to successful reproduction (Lechowicz pers. Comm 2024).</p> |
| Care of the young, technical and time effort                    | The juveniles are kept like adults. However, the water level has to be adjusted to their swimming capability, as it is quite possible for juveniles to drown. Good water quality and very good lighting with a sufficient UVB component must be ensured (Wunderlich et al. 2024).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Life expectancy                                                 | Animals over 31 years old have already been documented in zoos. Praschag (2023) had exceeded this duration of keeping several map turtles in captivity by 10 years. There are also specimens in private husbandry in Europe that are significantly older and still alive.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Frequency of private breeding and reproduction in zoos          | The megacephalic <i>Graptemys</i> are only bred by specialists. Due to the size of the ♀♀, more ♂♂ are incubated. These are popular pets due to their small size.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Breeding difficulty evaluation                                  | <p>Breeding is not difficult if they are kept close to natural conditions and the species-specific requirements are taken into account. However, the final size of the ♀♀ deters potential private keepers, as well as the fact that these turtles are not suitable for outdoor keeping in Central Europe and the heating and lighting of the correspondingly large tanks requires a lot of energy.</p> <p>All <i>Graptemys</i> species will successfully hybridize with each other regardless of head width group, especially if the opposite sex of that species is not present (Lechowicz pers. comm. 2024).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |

| Topic                                | Data for the megacephalic <i>Graptemys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|--------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mortality in the first years of life | Low if the animals are kept in clean water and high-quality lighting is provided. The five megacephalic <i>Graptemys</i> species, and only these, are susceptible, as hatchlings, to a fatal condition that starts with a softening of the rear carapace that spreads anteriorly. A dark blemish starts to form on the plastron before the turtle succumbs. It appears to be a calcium deficiency that softens the shell. This has been seen in both wild and captive hatchlings of these five species (Lechowicz pers. comm. 2024). Already in 2011, in the IUCN Red List Assessment of <i>Graptemys barbouri</i> , a 'sometimes-fatal disease condition of unknown aetiology' had been mentioned for parts of the Flint River population (Van Dijk 2011a). It is not yet known whether this the same problem and whether this condition might be caused by a virus. |
| F2 generation bred in captivity      | Yes, in all five species, but due to the long time it takes for the ♀♀ to reach sexual maturity, this has rarely been achieved. In the case of <i>G. barbouri</i> , which has been regularly bred in Europe since 1956, there have already been more subsequent generations.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding/ ranching        | <i>Graptemys barbouri</i> is bred commercially in at least one breeding farm in Spain. It is not known whether the other large-headed <i>Graptemys</i> species are bred in Europe on a larger scale. There are several commercial breeders in the USA who advertise hatchlings of <i>Graptemys barbouri</i> , but these five species are not bred in large numbers by any one individual or farm in the United States. <i>G. pearlensis</i> is successfully bred by more than five breeders in the United States, whereas the other four species are bred by less than five breeders each currently (Lechowicz pers. comm. 2024).                                                                                                                                                                                                                                     |
| Interviews/ Surveys/ Consultations   | Several experienced private breeders for all five species in Europe and the USA could be interviewed personally. However, most of the information on keeping and breeding in Europe was collected and intensively discussed at the various specialist meetings of the associations, in the mailing list of the 'Schmuckschildkröten' working group of the German Chelonia Group and especially at the meeting of the AG <i>Graptemys</i> (Pfau 2014), and can no longer be assigned to individual persons.                                                                                                                                                                                                                                                                                                                                                            |

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## Bataguridae

### *Batagur kachuga* (Gray, 1831)

| Art                    | Original description | Common name                                                                        | Common name international                                                                                                               | Known in the trade |
|------------------------|----------------------|------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Batagur kachuga</i> | (Gray, 1831)         | Red-crowned Roofed turtle, Painted Roofed turtle, Bengal Roof turtle, Sail Terapin | Bengalische Fluss-schildkröte, Rotgekrönte Dachschildkröte, Rotgekrönte Batagurschildkröte<br>Bangladesh: Kori Kaitta, Aadi Kori Kaitta | No                 |



Fig. 22: *Batagur kachuga* in the breeding centre at Madras Crocodile Bank Trust and Centre for Herpetology (all photos N. Whitaker)

- a breeder ♀ on the egg-laying site
- b plastron of a ♂
- c eggs with signs of development (white banding)
- d hatchling.

## Morphology and Taxonomy

For a long time, the genus *Kachuga* included both large river turtles and small species, which are very similar in their ecology to North American map turtles. Praschag et. al (2007) determined the relationships within the genus using molecular methods which led to a split into two different genera. The small-bodied species were placed in the genus *Pangshura*, while the

large river turtles were assigned to the genus *Batagur*. Only one species, *Batagur kachuga* is now the only representative in the genus *Batagur*: the red-crowned Batagur turtle.

*Batagur kachuga* ♀♀ can reach a carapace length of up to 580 mm and a weight of up to 25 kg. ♂♂ specimens, on the other hand, usually only reach half of these dimensions (approx. 290 mm CL).

While the carapace of juvenile specimens is strongly keeled, it flattens out as they grow. The head and soft parts of juveniles, ♀♀ and males outside the mating season are brown-grey in colour. During the mating season, sexually mature ♂♂ develop a splendid head pattern, as is also known from the ♂ specimens of other *Batagur* turtles.

During this time, ♂ *Batagur kachuga* show a brightly coloured head pattern consisting of red, yellow, white and blue stripes. The colour of the top of the head is red, hence the English name. Adult ♂♂ *Batagur sp.* can be easily determined by this striking species-specific colouration.

### **Distribution and Habitat**

The distribution of *Batagur kachuga* lies within the basin of the Ganges in India and extends into parts of Nepal and Bangladesh. However, the occurrence of viable population in Nepal and Bangladesh is still debatable. Its current main distribution area, in which reproducing populations still exist, is within Chambal River that belongs to the National Chambal Sanctuary spanning among Uttar Pradesh, Madhya Pradesh and Rajasthan states of North India.

As a typical riverine turtle, the Red-crowned *Batagur* turtle prefers flowing waters with high sandbanks, which are used for oviposition. The species thermoregulates on exposed mid river rocks.

The diet of *Batagur kachuga* consists predominantly of aquatic plants. Riparian vegetation that protrudes into the water is also fed upon, as well as fruits. Hatchlings and yearlings feed on fish in captivity, and it is assumed that they prefer an omnivorous diet during early life stages.

### **Conservation Status and Main Threats**

CITES Appendix I since 2023 (CoP19 Proposal 25). Had already been included in CITES Appendix II in 2003 (CITES 2002).

EU Council Regulation (EC) No. 338/97: Annex A.

In Germany strictly protected under Article 7 (2) No 13 BNatSchG.

### **IUCN Red List Category**

Critically Endangered – CR (A2cd+4cd, assessed 13 March 2018).

### **Red List Status in the Range Countries**

#### **Bangladesh**

CR (Critically Endangered, Species-ID RE 0004) (Alam 2015).

### **Threats**

Das (1991) describes *Batagur kachuga* as rare throughout its range. Choudhury et. al (2000) consider the population status of the species to be difficult to assess.

Although no reliable data is available, it is assumed that the natural population of *Batagur kachuga* has declined by 90% over the past 50 years. This trend is expected to continue in the coming years.

By 2010, all but one population of the species appears to have become extinct. Only in Chambal River in the national park with the same name, the species benefits from at least a partially effective protection, in that the last known reproducing population exists here. It is estimated that roughly 500 reproductive ♀♀ still live there.

In the rest of the species' former range, however, only scattered individuals are likely to be found.

TSA Foundation India has been running a conservation project on the Chambal River since 2006 (Singh et al. 2024). As part of this project, *Batagur* turtle nests are protected from animal egg predators and human egg collectors. The young turtles are raised under human care until they have attained a weight of up to 1 kg, at which they are released into the wild. The hatching success in the frame of this project appears to be high.

Subsequently, captive breeding colonies in different zoological institutions in India such as Kukrail Gharial Centre and Lucknow Zoo, Kanpur Zoo have been established.

Hatchlings produced at the Madras Crocodile Bank Trust are send back to Uttar Pradesh for release (Whitaker 2009b).

In addition to the exploitation of eggs and the capture and consumption of *Batagur kachuga* in their countries of origin, a major threat to this species is the loss of their habitat. The commercial extraction of sand causes the necessary egg-laying sites to disappear. Furthermore, the modification and development of rivers prevents the turtles from migrating, and destroys their food sources.

To a lesser extent, the live animal trade also poses a further threat to the species (CITES 2022). Individual animals have probably found their way to Southeast Asia, as can be seen from photos on social media. Two confiscations in UPs between 2017-2024 indicates their demand in South-east Asian countries with unknown final destinations.

The authors are not aware of any keepers of this species in Europe or the USA.

## Reproduction

| Topic                              | Details on the reproduction of <i>Batagur kachuga</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | <p>Pronounced sexual dimorphism, ♂♂ only reach half the size of ♀♀. The tails of ♂♂ are proportionally longer and thicker than those of ♀♀.</p> <p>During the mating season, the ♂♂ display brightly coloured head and neck markings consisting of red, yellow, white and blue stripes with a red upper head.</p>                                                                                                                                                                                                                  |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Sexual maturity                    | <p>According to Praschag et al. 2019, one generation is about 25 years. At the Lucknow Gharial Centre, <i>Batagur kachuga</i> reached sexual maturity at the age of 18 years.</p> <p>According to Whitaker &amp; Yelahanka (2021) the onset of the cephalic pigmentation becomes visible at an age of three years. At the same time, prominent mental glands appear in ♂♂.</p>                                                                                                                                                     |
| Mating and nesting                 | <p>Mating occurs at the end of the rainy season (November). At this time, the ♂♂ show the typical courtship colouration. Eggs are laid in March and April.</p> <p>The nest pit is dug in loose sand on the riverbank, about 10 m from the water (1.5–15.4 m), it is about 35 cm deep, and the excavated sand is thrown up to 2 m away. This makes the nest pits very conspicuous (Pareek 2023).</p>                                                                                                                                |
| Reproductive season                | From the end of the rainy season to spring.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Number of eggs/clutches per season | <p>A clutch comprises 11–30 (on average 18) eggs. ♀♀ can lay one to two clutches per year (Praschag et. al 2007, Whitaker &amp; Yelahanka (2021).</p> <p>Pareek (2023) excavated a clutch of 15 eggs and incubated them.</p>                                                                                                                                                                                                                                                                                                       |
| Egg size/hatchling size            | Measured eggs of <i>Batagur kachuga</i> were 64–75 mm long and 38–46 mm wide (Whitaker & Yelahanka 2021).                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Incubation and hatching            | <p>At temperatures of 25.3–34.4°C the eggs took about 47–55 days to hatch (Whitaker 2009a).</p> <p>However, Pareek (2023) indicated an incubation period of 86 days at 29°C, 70 days at 32°C and only 67 days at 35°C. All eggs hatched, and all young survived for more than 5 months, but the young incubated at the intermediate temperature were slightly larger and fitter than those incubated at cooler or warmer temperatures. The animals will be raised until they reach about 1 kg and then released into the wild.</p> |
| Sex determination                  | Probably TSD like the other species of the genus, the threshold temperature is unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Sperm storage                      | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |



## Husbandry and Captive Breeding C/C

| Topic                                                           | Data for <i>Batagur kachuga</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Seasonal fluctuations / rainy season.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Husbandry requirements                                          | <p>Spacious pools heated to tropical temperatures are necessary for keeping. A basking area with approx. 40°C radiant heat is required.</p> <p>♀♀ are compatible with each other.</p> <p>Due to the expected final size, the space requirement is enormous, especially when caring for adult ♀♀. The breeding pond for <i>Batagur kachuga</i> at the Madras Crocodile Bank Trust is measuring 29.5 x 15.52 m, with a maximum depth of 2.7 m (Whitaker 2009a).</p>                                                                                                                    |
| General characteristics, difficulties with keeping and breeding | <i>Batagur</i> turtles can be prone to skin diseases, so good water quality and probably the addition of salt or similar water treatment products is necessary.                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Care of the young, technical and time effort                    | <p>The husbandry parameters are similar to those of adult specimens, although smaller tanks are used. It is possible to raise several juveniles together. Though, the group sizes may not be too large.</p> <p>The optimal water temperature ranges from 20 to 25°C (Singh et al. 2024).</p> <p>Good water quality should always be ensured. (Bio-)Filter for fish tanks can be helpful for keeping up a good water quality (Whitaker 2009).</p> <p>Young turtles may be prone to pneumonia, eye swelling or other infections, if temperatures drop too low (Singh et al. 2024).</p> |
| Life expectancy                                                 | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Frequency of private breeding and reproduction in zoos          | <p>Very rare. There is no information on breeding outside of India (Lucknow Gharial Centre, Madras Crocodile Bank Trust).</p> <p>The Turtle Breeding and Rehabilitation Centre in Sarnath provides veterinary care for injured turtles and incubates their eggs. In 2019, 50 hatchlings were born here (Singh et al. 2019). The juveniles are reared a size suitable for release into the wild – however, no targeted breeding takes place there.</p>                                                                                                                                |
| Breeding difficulty evaluation                                  | Difficult due to the size of the turtles and their requirements for the egg-laying site.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Mortality in the first years of life                            | At the head starting facility in the Chambal River national park, mortality between 2014 and 2020 was low at about 1,9% (Singh et al. 2024).                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| F2 generation bred in captivity                                 | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Commercial breeding/ ranching                                   | According to the available information, there are no commercial breeding or ranching activities.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Interviews/ Surveys/ Consultations                              | Several zoological institutions in India have husbandry experience and provided some information, but only one institution provided data on captive breeding.                                                                                                                                                                                                                                                                                                                                                                                                                        |

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### **Sebastian Nickl (15.08.2024)**

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***Cuora galbinifrons* Bourret, 1940**

| Art                       | Original description | Common name           | Common name international                                                  | Known in the trade |
|---------------------------|----------------------|-----------------------|----------------------------------------------------------------------------|--------------------|
| <i>Cuora galbinifrons</i> | Bourret, 1940        | Flowerback box turtle | Hinterindische Scharnierschildkröte<br>Rùa hộp trán vàng miền bắc<br>黄额闭壳龟 | Yes                |

**Morphology and Taxonomy**

The Asian box turtles of the *Cuora galbinifrons* species group (*Cuora galbinifrons*, *C. bourreti* and *C. picturata*) look very similar, they have similar ecological requirements and are also closely related. Therefore, they had been presented as a group in the document ‘Evaluation of the reproduction potential of selected amphibian and reptile taxa listed in Appendix I and II at CITES CoP18’ (Langner et al. 2022). This chapter is an update of the corresponding chapter in the aforementioned document. Adult turtles of the three species reach a shell length of about 20 cm and a weight of about 1 kg. The plastron has a transverse hinge (hence the German name ‘Scharnierschildkröte’) and can be closed completely. In *Cuora galbinifrons*, it is often completely black or dark brown with a narrow, yellowish edge. The carapace is distinctly domed and smooth. The colouring is very variable, ranging from beige, yellow, orange, brown or dark brown, with a broad dark brown longitudinal band along the centre of the back. This median band completely covers the vertebral scutes and about the upper quarter of the costal scutes. A narrow, yellowish line with black edges often runs along the spine. The lower third of the costal plates are light in colour, often with small black stripes.

Depending on the year of import, the *Cuora galbinifrons* imported for the European and US pet trade could be distinguished by very different colourations, which were further bred separately in the private breeding groups (Becker 2019), while they were mixed in the zoos. A genetic study of the source animals of various breeding groups in zoos and in private collections, as well as samples from northern Vietnam (Ihlow et al. 2023), showed that, although several genetic clades can be distinguished within *Cuora galbinifrons* s. str. Nonetheless, all of these turtles, which are so differently coloured, are all closely related, i.e. both separate breeding and mixing are compatible with conservation breeding. However, the study also showed that some other animals, originally assigned to *C. galbinifrons* s. str. both morphologically and on the basis of the haplotype, were hybrids with *C. bourreti*. It is possible that there is an intergradation zone between these two geographically and genetically neighbouring species, i.e. these hybrids should be removed from the ex-situ breeding groups as a precaution, as the aim here is to breed pure species. Three other animals turned out to be hybrids of the completely allopatric species *C. bourreti* and *C. picturata* and must therefore be excluded from further breeding for conservation in any case. Their origin could not be clarified; they may have come from a breeding farm on Hainan.





Fig. 23: Imported *Cuora galbinifrons* from the pet trade in Germany in the 1990s (all photos H. Becker)

- a Blackish animal
- b Two animals with very differently coloured carapaces
- c 'Yellowish' coloured Flowerback box turtles often have a black dash on the first costal shield
- d A reddish turtle with a distinct speckled pattern on the costal shields
- e A pale, but already fully coloured juvenile
- f This juvenile turtle will grow into a blackish adult
- g Forehead and chin will remain pale yellow in this animal
- h hatching of a blackish juvenile.



The Flowerback box turtle often has yellow, orange or even red colouring elements on the head in both sexes, and sometimes also coloured scales on the otherwise dark forelegs. The lower jaw has often a clear yellow colour. The markings on the head of adult animals change very little over their lifetime, so that a photo of the right side of the head, for example, is well suited for photo documentation. The pupil is round, the iris greenish, yellow or sometimes bright orange or red.

Newly hatched young are usually relatively pale in colour, but the colouring becomes darker and more contrasting with age.

In their conservation priority plan, Horne et al. (2022) call for the genetic studies on *Cuora galbinifrons* to be extended to include animals from Laos, and for all existing ex situ breeding groups to be included in the studies in order to avoid unwanted hybridisation effects between the subspecies and genetically distinct local forms.

## Distribution and Habitat

### Distribution

China (Guangxi and Hainan provinces), northern Laos and Vietnam (provinces of Lao Cai, Yen Bai, Vinh Phuc, Son La, Dien Bien, Hoa Binh, Thanh Hoa, Quang Binh and Nghe An), mostly at altitudes between 500 and 1,000 m asl. Type locality Tam-Dao, Tonkin (today Tam Dao N.P., Vinh Phuc Prov.), Vietnam.

### Habitat

The turtles live terrestrially in evergreen, humid mountain forests with closed canopies, where they are well camouflaged by the colouring of their shells in the thick layer of leaves on the ground. They are well able to swim, and often sit in shallow water for long periods. They have relatively long legs and are good climbers. When feeling threatened, they sometimes literally push themselves off and then roll down the slope to the nearest leaf pile, where they are practically invisible to the human eye. Temperatures above 28°C are hardly tolerated, but in winter brief light frosts can occur at some known sites.

### Conservation Status and Main Threats

CITES Appendix I since 2023 (CoP19 Proposal No. 26) with a zero annual export quota for wild-caught animals from all countries of origin for commercial purposes.

The species had already been listed in CITES Appendix II (CoP11 Proposal No. 36) since 2000. During CoP13, the proposal (Proposal No. 33) to transfer *C. galbinifrons* s. l. (i.e. including the other two species, which were still listed as subspecies at the time) to Appendix I, in accordance with Rule 23.6, could not be accepted due to an overlap with Proposal No. 32 at the time (CITES 2013). The proposed proposal for CoP18 to transfer the species to Appendix I was not submitted in due time (P.P. van Dijk pers. comm.), so that only *Cuora bourreti* and *C. picturata* were transferred to Appendix I at this meeting. The current Proposal No. 26 for CoP19 follows the recommendation of the Animals Committee from 2015 (AC28 2015) to list all three species in Appendix I.

EU Council Regulation (EC) No. 338/97 Annex: A.

In Germany strictly protected under Article 7 (2) No 13 BNatSchG.

## IUCN Red List Status

CR (Critically Endangered A2bd+4bd, assessed Mar 13, 2018).

## Red List Status in the Range Countries

### China

Red List of Chinas Vertebrates (Jiang et al. 2016): CR (A1d+2bcde+3cde+4cd; B1b(iii, iv, v); C1). In China, the species has been included in the highest category of the list of protected terrestrial animal species since 2000. There are also some licensed breeding farms for this species (Hong et al. 2022), while regulations of these farms and the numbers of offspring are unknown. According to the CITES Trade Database, China has recorded a planned number 160 animals as exports with source code 'C' to Japan in 2022, while in fact 80 animals were reported as imports by Japan (UNEP-WCMC 2024). Whether the source code 'C' was correctly assigned for these animals is rather unclear in view of the reproductive biology of the species.

### Laos

In Laos, the species was placed in the highest prohibition category of the Wildlife and Aquatic Species Law (No07/NA 24 December 2007).

### Vietnam

Protected in Vietnam since 2013 (Decree 160/2013/ND-CP) and strictly protected since 2019 (Decree 06/2019/ND-CP) (McCormack et al. 2021), in the Red Data Book Vietnam status EN (Tran et al. 2007).

## Threats

Since the 1990s, the market value of these turtles in China has risen sharply, and the capture and smuggling has increased accordingly. The main threat is the collection for the pet trade and for consumptive use in Asia. Poachers use specially trained dogs to track down the animals (Le et al. 2024). Sometimes, the undergrowth is set on fire to expose the hidden turtles. The collected turtles are usually traded through a network of traders at the local, district and provincial levels before being exported or consumed, which makes it difficult to prosecute the individual perpetrators.

According to estimates, the population has declined by more than 90% in the last 60 years (three generations), which is a direct consequence of over-harvesting. Stable population have only been found in very remote, inaccessible bamboo forests (Pham et al. 2020, Ducotterd et al. 2022). The calculated population density is less than one animal per square kilometre within protected areas with suitable habitats. Since the animals are well camouflaged, they are rarely found by chance, but they are sought specifically with trained dogs. In Vietnam, the trade in turtles is now subject to tighter controls, and open trade in the animal markets has come to a halt since 2006, when some turtle species were placed under national protection. Nevertheless, wild-caught turtles are still being traded illegally, or are still being smuggled in from Laos, albeit in smaller numbers, as the animals have become increasingly rare (Le et al. 2024). Since the listing of the two closely related species *C. bourreti* and *C. picturata* in CITES Appendix I, very high penalties (in one case even 10 years in prison and an additional fine of about €3,500) have been imposed in Vietnam for the illegal trade in these animals. There were several reports on this by Doug Hendrie to the IUCN SSC Tortoise and Freshwater Turtle Specialist Group in 2022 and 2023, see also the status reports in Education for Nature Vietnam

(ENV) (2023), and now similarly high, truly deterrent, penalties for the capture and trade of *C. galbinifrons* s. str. within Vietnam are also on the table.

According to the CITES trade database, the trade in wild-caught specimens from the countries of origin to Europe has come to a complete standstill. There is also no record of any recent smuggling attempts to Europe either. Between 2019 and 2021, a total of 24 captive-bred specimens (source code 'C') were exported from Germany to Switzerland, Taiwan and Japan.

In addition to the use and trade of wild animals, the ongoing destruction of their natural habitat, e.g. the conversion of forest into plantations that do not provide a suitable habitat for the animals, is another significant threat to the three species.

## Reproduction

| Topic                              | Details on the reproduction of <i>Cuora galbinifrons</i>                                                                                                                                                                                                                                                                                           |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | Adult ♂♂ have a longer and thicker tail than adult ♀♀. The difference is only recognisable shortly before sexual maturity is reached, however.                                                                                                                                                                                                     |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                         |
| Sexual maturity                    | At 10–15 years, from 14 cm CL in both sexes.                                                                                                                                                                                                                                                                                                       |
| Mating and nesting                 | The eggs are sometimes laid half-open or only buried relatively shallowly in very soft, moist substrate. Stressed ♀♀ often discard the eggs into the water. In human care, laying mounds made of soft forest soil or similar can be piled up as an incentive for laying.                                                                           |
| Reproductive season                | In captivity in Europe, the first eggs are laid rather shortly after hibernation, approximately in March; the time interval to possible subsequent clutches is variable. The last clutches were laid at the end of September.                                                                                                                      |
| Number of eggs/clutches per season | In the breeding centre at Cuc Phuong in Vietnam, one clutch/year with 1–2 (rarely 3) eggs; in human care in Europe/USA often 2 clutches/year, very rarely also 3 clutches. In private husbandry in Europe, 1–5 eggs/clutch, on average 2 eggs depending on the nutritional status of the ♀, a maximum of 7 eggs within one year has been observed. |
| Egg size/hatchling size            | Eggs about 55 x 30 mm and 20–35 g mass, hatching size about 50 mm CL and 25,5 g.                                                                                                                                                                                                                                                                   |
| Incubation and hatching            | Incubation at very high humidity. At 24–30.5°C incubation period 49–112 days. Controlled incubation at 26–27°C is recommended, then hatching after 70–91 days is to be expected. The eggs of the first clutch of the year hatch faster at a constant incubation temperature.                                                                       |
| Sex determination                  | Whether these turtles have a temperature-dependent sex determination is unknown and is currently being investigated in more detail.                                                                                                                                                                                                                |
| Sperm storage                      | Yes, > 1 year.                                                                                                                                                                                                                                                                                                                                     |

## Husbandry and Captive Breeding C/C

| Topic                                                           | Data for <i>Cuora galbinifrons</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|-----------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | <p>The exact triggers are unknown, but oviposition often begins after a cooler hibernation period, and the ♀♀ are often only willing to mate in late summer or autumn. Some breeders mate the animals in spring and autumn at the equinox.</p> <p>The ♂ must be placed with the ♀ for mating, and they must be separated again immediately after mating or if the ♀ is unwilling.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Husbandry requirements                                          | <p>Very sensitive to stress, avoid touching and moving; animals sometimes only eat when they are not being observed.</p> <p>Strictly singly housed in humid terrariums with a soft floor for burrowing and with cover structures (caves made of wood or cork, if possible, with living plants), shallow water basin for dipping. Privacy screen required to separate the terrarium from other terrariums with turtles of the same species. UV lighting recommended.</p> <p>A varied diet (adult animals with crustaceans, including dried Gammarus, and also with snail and mussel meat, but definitely add fruit and green leaves). Add vitamin/mineral supplements. Some animals also accept pellet food. The juveniles are carnivorous and initially need live food of a suitable size.</p>                                                                                                                                                                                                        |
| General characteristics, difficulties with keeping and breeding | Secure the enclosure to prevent climbing out. For husbandry in glass terrariums, install visual barriers between neighbouring terrariums.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Care of the young, technical and time effort                    | If possible, raise them individually, initially in shallow water with plants or other things they can hold on to, and a small island where they can climb out from the water and dry off. Feed the hatchlings with insect larvae or very small redworms first.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Life expectancy                                                 | Certainly, much more than 30 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Frequency of private breeding and reproduction in zoos          | Relatively rare due to the high husbandry requirements and secretive way of life. Some dedicated private breeders and the international breeding centre in Münster, Germany are successfully breeding this species. In the Turtle Survival Center in the USA the 100th hatchling has been born in 2024.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Breeding difficulty evaluation                                  | For specialists. Some animals temporarily stop reproducing due to stressful experiences (e.g. new tank setup or even visual contact with conspecifics in neighbouring tanks).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Mortality in the first years of life                            | Low if rearing first takes place in shallow water and then at very high humidity. However, underweight hatchlings usually die within the first two years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| F2 generation bred in captivity                                 | Some of the respondents report on captive breeding of animals that had already hatched in human care. However, such breeding successes are still very rare due to the long time to sexual maturity of the captive-bred turtles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Commercial breeding/ ranching                                   | <p>The breeding of these turtles for reintroduction purpose in the Cuc Phuong breeding center in Vietnam has been successful since 2004, but so far only a relatively small number of animals have been successfully raised to release size.</p> <p><i>Cuora galbinifrons</i> is being bred on Hainan, China (Shi &amp; Parham 2000), and species from the species complex may also be mixed there (Ihlow et al. 2023), but further information could not be obtained. The species is said to have been regularly bred in Chinese farms since 2013 (Hong et al. 2022), but here too, breeding success is likely to be rather modest. Tian et al. (2016) do not mention the breeding of this species, and Zhou et al. (2008) only mention breeding attempts. More detailed information about successful breeding farms within China is also not available. TRAFFIC (2013) recommends very close inspection of breeding operations, as this species is not likely to be bred on a commercial scale.</p> |

|                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Interviews/ Surveys/ Consultations | <p>Several experienced private breeders and 3 zoological institutions.</p> <p>Most of the private individuals contacted did not complete the questionnaire and instead referred to the many publications and our personal discussions at conferences. The discussion about captive breeding has been going on for a long time, and &gt; 20 successful breeders from Europe regularly take part in the discussions. In addition, there are discussions with breeders and breeder organisations in the USA, where the species is also regularly bred.</p> |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

The EAZA EEP is managed at the IZS Münster, the AZA Studbook is the responsibility of Lauren Augustine, Philadelphia Zoo (AZA 2022), and the species is regularly bred at the Turtle Survival Alliance (Goldstein 2017, Hagen 2022). Some private breeders in Europe are organised in the ESF studbook, but many breeders have not yet joined any studbook at all. Stenger et al. (2023) list only two breeding institutions with a total of six hatchlings in 2022.

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**Beate Pfau (07.07.2024)**

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***Rhinoclemmys* Fitzinger, 1835**

| Species                          | Original description     | Common name                                                                                                                                  | Common name international                                                                                                               | Known in the trade |
|----------------------------------|--------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Rhinoclemmys annulata</i>     | (Gray, 1860)             | Brown Wood turtle                                                                                                                            | Braune Erdschildkröte<br>Tortuga trueno, tortuga de monte, tortuga de bosque café, montañera                                            | Yes                |
| <i>Rhinoclemmys areolata</i>     | (Duméril & Bibron, 1851) | Furrowed Wood turtle                                                                                                                         | Gefurchte Erdschildkröte<br>Mojina, tortuga de monte mojina                                                                             | Yes                |
| <i>Rhinoclemmys diademata</i>    | (Mertens, 1954)          | Maracaibo Wood turtle                                                                                                                        | Diadem-Erdschildkröte<br>Inguensa                                                                                                       | Yes                |
| <i>Rhinoclemmys funerea</i>      | (Cope, 1875)             | Black Wood turtle                                                                                                                            | Bauchstreifen-Erdschildkröte<br>Tortuga negra                                                                                           | Yes                |
| <i>Rhinoclemmys melanosterna</i> | (Gray, 1861)             | Colombian Wood turtle                                                                                                                        | Kolumbianische Erdschildkröte<br>Tortuga pintadilla, palmera, inguensa, esmeraldeña<br>Indigenous names: Wounann (Bajo San Juan): Khodd | Yes                |
| <i>Rhinoclemmys nasuta</i>       | (Boulenger, 1902)        | Chocoan River turtle, Large-nosed Wood turtle                                                                                                | Ecuador-Erdschildkröte<br>Tortuga de bosque, tortuga de río cho-coana<br>Indigenous names: Wounann (Bajo San Juan): Bambero             | No                 |
| <i>Rhinoclemmys pulcherrima</i>  | (Gray, 1856)             | Painted Wood turtle                                                                                                                          | Prachterdschildkröte<br>Tortuga colourado, tortuga de monte pintada, tortuga pinta, tortuga de rayas rojas                              | Yes                |
| <i>Rhinoclemmys punctularia</i>  | (Daudin, 1801)           | Spotted-legged turtle<br><i>R. p. punctularia</i> : Eastern Spot-legged turtle<br><i>R. p. flammigera</i> : Upper Orinoco Spot-legged turtle | Guyana-Erdschildkröte<br>Aperema, Cágado, Jabuti-Aperema, Jurará, Muçuã, Perema<br>Indigenous names: Warao (Orinoco Delta): Joni-guaku  | Yes                |
| <i>Rhinoclemmys rubida</i>       | (Cope, 1870)             | Mexican Spotted Wood turtle                                                                                                                  | Mexikanische Erdschildkröte<br>Casco Amarillo, tortuga de monte payaso                                                                  | Yes                |



## Morphology and Taxonomy

The genus name *Rhinoclemmys* is derived from the Greek words 'rhinos' (nose, snout, beak, bill) and 'klemmys' (turtle). The name alludes to the protruding snout of some specimens of the type species of this genus, *Rhinoclemmys areolata*.

The genus *Rhinoclemmys* was established by the Austrian zoologist Leopold Fitzinger in 1835 and has retained its nomenclatural meaning to this day (Smith et al. 1974). The entire genus is referred to as Central- and South American Wood Turtles, whereby the nine species are the only representatives of the Old-World Terrapins (Geoemydidae) in the new world. Like many other geoemydids, *Rhinoclemmys* spp. are characterised by their adaptability to different habitat types.

Within the genus, use of habitats ranges from mainly terrestrial in dry areas (*R. rubida*) to mainly aquatic rainforest dwellers (*R. nasuta*), which is also reflected in their feeding and reproductive habits: Most species are opportunistically omnivorous, but, if necessary, also mainly herbivorous. South American wood turtles tend to lay large eggs in smaller numbers per clutch, usually 1–2 eggs, exceptionally 3–4 eggs per clutch. Several clutches can be laid per reproductive cycle.

Within the genus *Rhinoclemmys*, there are only a few morphological differences between the individual species apart from body size. All South American Wood Turtles have a more or less oval-elongated carapace shape and quite strong, barely webbed legs. Carapace and plastron are quite large and not equipped with movable hinges, but *Rhinoclemmys* move skilfully on land and climb over obstacles with ease.

Some species (e.g. *R. funerea*, *R. melanosterna*, *R. nasuta*, *R. punctularia*) are more comfortable in deeper waterbodies than others, but all can swim.

Hybrids between *Rhinoclemmys diademata* and *R. punctularia*, as well as between *R. punctularia* and *R. melanosterna*, were described in Fritz (1995); photos of further species hybrids can be found now and then online in social media. There are also photos of a male hybrid of *Rhinoclemmys funerea* x *Mauremys sinensis*, in a special chelonian hybrids facebook group, but nothing has been published about this animal so far.



Fig. 24: *Rhinoclemmys* spp. adults  
 a *R. annulata* (F. Medem)  
 b *R. areolata* (G. Schaffer)  
 c *R. diademata* (B. Pfau)  
 d *R. funerea* (G. Schaffer)  
 e *R. melanosterna* (G. Schaffer)  
 f *R. nasuta* (F. Medem)  
 g *R. rubida* (G. Schaffer)  
 h *R. punctularia* (S. Ettmar).

Some *Rhinoclemmys* species have similar head markings. These closely related species can be distinguished, for example, using this figure:

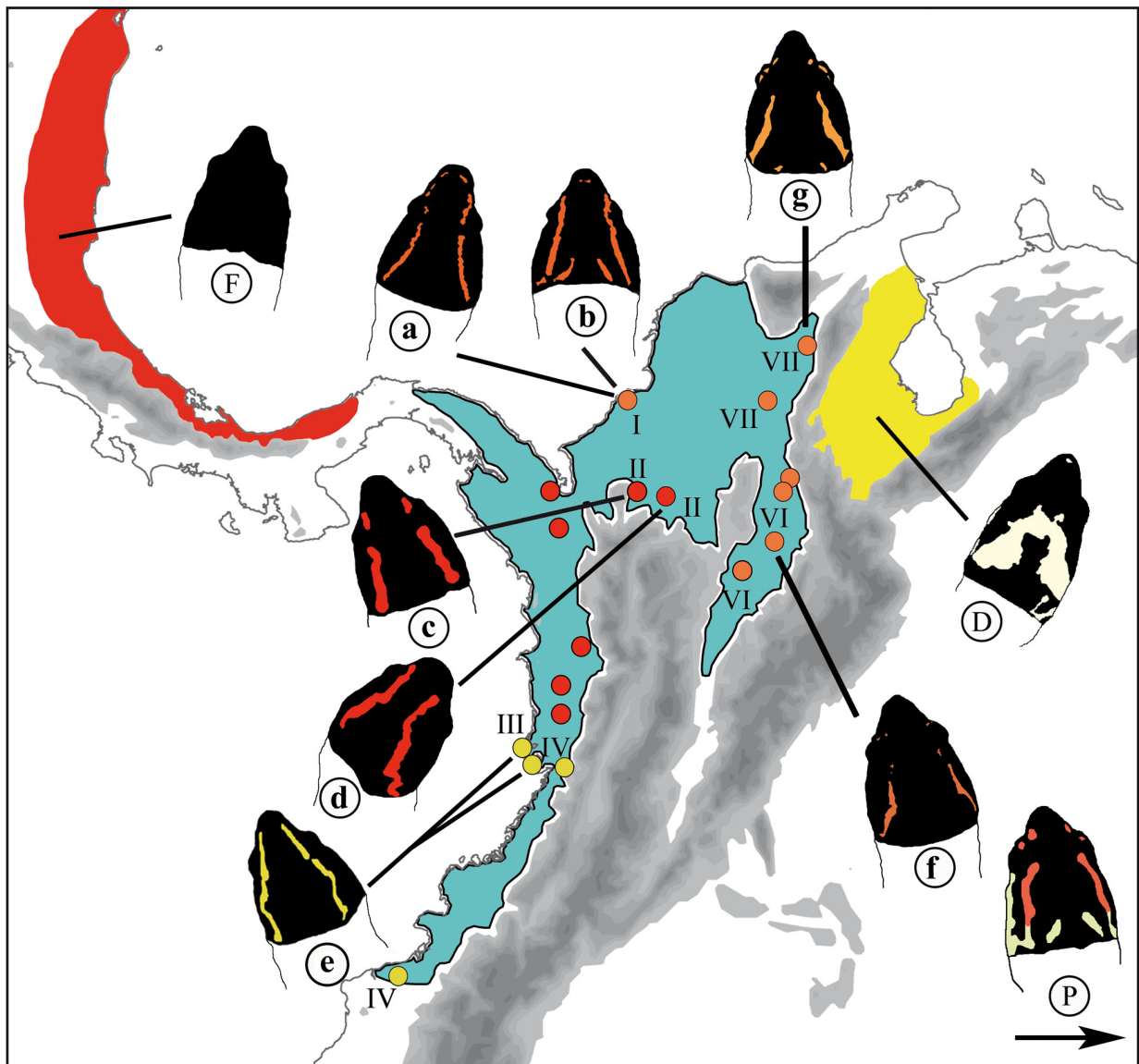


Fig. 25: Geographical variation of head pattern in *Rhinoclemmys melanosterna*. Figured turtles are: (a) MTD T 4885, Cazuela, Lorica, Córdoba, Colombia; (b) MTD T 4888, Sicara, Lorica, Córdoba, Colombia; (c) MTD T 4726, Montelibano, Córdoba, Colombia; (d) MTD T 4569, Qda. Carmelo, Caucasia, Antioquia, Colombia; (e) MTD T 9167, Ladrilleros, Valle del Cauca, Colombia; (f) MTD T 9171, Ciénaga de Barbacoas, Antioquia, Colombia; (g) MTD T 4565, Caño Grande, Cesar, Colombia; F = *R. funerea*; D = *R. diademata*; P = *R. punctularia*. Colour of ranges of *R. funerea*, *R. melanosterna* and *R. diademata* correspond to Figure 1. Roman numerals indicate mitochondrial clades of *R. melanosterna*, coloured circles symbolize different colours of head stripes. Symbols without Roman numerals refer to specimens described by Medem (1962); vouchers are in the collection of the Instituto de Ciencias Naturales, Bogotá, Colombia (reproduced from with permission by the author from Vargas-Ramírez et al. (2013): figure 4).

MTD T numbers refer to samples in the tissue collection of the Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden, Germany.



***R. annulata*** – Unicoloured brown carapace, plastron black throughout with a light (yellow) edge. Head and soft parts are dark brown in colour and have only weakly contrasting, reduced yellow spots.

***R. areolata*** – The head is dark on top, with mostly red spots (in some local forms even with red ‘eyebrows’), chin and throat, as well as the skin of the front legs are light, often yellowish, with dark spots or longitudinal stripes; carapace domed; plastron light coloured, but with a broad, dark (black) longitudinal band, in contrast to *R. pulcherrima*.

***R. diademata*** – No other *Rhinoclemmys* species has the characteristic yellow crown pattern on the top of the head. Plain brown plastron with light-coloured edges of the plastral scutes.

***R. funerea*** – By far the largest species of the genus. Uniformly brown carapace.

***R. melanosterna*** – Appearance very similar to *R. punctularia*, but the iris of *R. melanosterna* is intensely white or light blue in colour. The plastron is black, hence the scientific species name. There are local forms with yellow, orange or distinctly red head stripes, and there has been much discussion about whether the form with the red head stripes could not in fact be a transitional form to the *R. punctularia* found directly to the south (Methner & Wicker 1982, Methner 1989, Fritz 1995, Vargas-Ramírez et al. 2013).

***R. nasuta*** – Carapace unicoloured brown, plastron yellow with reduced black spots. The elongated tip of the nose is unique within the genus. The top of the head and cheeks have a few thick, yellow lines.

***R. pulcherrima*** – The most colourful representative of the genus. Head with grey-green ground colour, on which there is a strongly contrasting pattern of thin red and yellow stripes. Carapace with black-red/yellow ocelli pattern on costal- and vertebral scutes. The plastron has a yellow-reddish base colour with a black central stripe with a reddish border, which varies in width depending on the subspecies. The undersides of the carapace’s marginal shields are intensely red-black in colour. Janzen (1980) points out the similarity of this colouration pattern to the coral snake *Micrurus nigrocinctus*, and considers this to be a possible case of Batesian Mimicry.

A total of four geographically separate subspecies are currently recognised: *R. p. pulcherrima* from Mexico (Guerrero, Oaxaca); *R. p. incisa* from Mexico (Oaxaca), northern Nicaragua, El Salvador; *R. p. manni* from southern Nicaragua and Costa Rica and *R. p. rogerbarbouri* from Mexico (Sinaloa). In addition to plastron colouration (extent and shape of the dark markings on a yellow-orange background) and carapace colouration (extent and contrast of ocelli or dots on the shields), the main distinguishing features are the carapace proportions: While the more northerly subspecies tend to be flatter and broader, the more southerly subspecies tend to appear high-backed and narrower in shape. The two northern forms *R. p. rogerbarbouri* and *R. p. pulcherrima*, which are geographically furthest away from *R. p. manni*, are clearly distinguishable. Distinguishing between *R. p. manni* and *R. p. incisa* is often not easy – especially as intermediate forms or hybrids on subspecies level can be found in the trade. In general, *R. p. incisa* are larger and flatter than *R. p. manni*, which is the most colourful subspecies and therefore often easier to recognise. Based on observations in captive environments, *R. p. incisa* appears to behave more aquatic than *R. p. manni*.

***R. punctularia*** – Upper side of the head black with red dots and stripes; the soft parts and the side of the head have a yellow stripe and dot pattern.

The Guyana wood turtle *R. punctularia* (Daudin 1801) is the type species of the genus and its generic affiliation has rarely been challenged since the middle of the 20th century. Other species, which according to the IUCN TTWG (2021) belong to *Rhinoclemmys*, have also undergone relatively few taxonomic changes in the past, but in the 20th century they were placed in the genera *Chelopus* and *Nicoria*, but mainly in *Geoemyda* Gray 1834, which was long regarded as a collective genus for geoemydid turtles from South America and Asia. Two subspecies of *R. punctularia* have been described, *R. p. punctularia* and *R. p. flammigera*, with *R. p. flammigera* only inhabiting a small area in the Venezuelan state of Amazonas.

***R. rubida*** – Relatively robust head, intensive yellow markings on the top of the head and on cheeks, which are not found in other *Rhinoclemmys*. There are yellow markings on the brown carapace, especially on the costal and vertebral scutes, and a small yellow dot in the centre of carapacial scutes. *R. rubida* also has two subspecies, which are further differentiated in hobbyist circles into different morphotypes, e.g. ‘Guerrero form’.

### Distribution and Habitat

#### Natural occurrence in the following countries:

*R. annulata*: Costa Rica, Ecuador, Honduras, Colombia, Nicaragua, Panama; type locality ‘Esmeraldas, Ecuador’.

*R. areolata*: Belize, Guatemala, Honduras, Mexico; type locality originally given as ‘El Peten Province, Central America’, corrected to ‘Flores, El Peten, Guatemala’ (Dunn & Stuart 1951).

*R. diademata*: Colombia, Venezuela: type locality ‘Maracay, Venezuela’, which may not be correct as this locality is not within the known range (Pritchard 1979). The turtles occur in the south of the Maracaibo Basin from sea level up to 300 m asl.

*R. funerea*: Costa Rica, Honduras, Nicaragua, Panama; type locality ‘Limón (= Puerto Limón), Costa Rica’.

*R. melanosterna*: Ecuador, Colombia, Panama; type locality originally ‘Gulf of Darién: Cherunha, corrected to ‘Boca Chirambira in the delta of the Río San Juan, Choco, Colombia’ (Medem 1958).

*R. nasuta*: Colombia, Ecuador; type locality ‘Bulun, elevation 160 feet, and Río Durango, 350 feet asl’, Esmeraldas Province, Ecuador.

*R. pulcherrima*: Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua; type locality originally ‘Mexico’, corrected to ‘surroundings of San Marcos, Guerrero, Mexico’ (Ernst 1978).

*R. punctularia*: Brazil, French Guiana, Guyana, Surinam, Trinidad and Tobago, Venezuela; type locality Cayenne, French Guiana.

*R. rubida*: Mexico (lowlands of Jalisco, Colima, Michoacan, Oaxaca, Chiapas, western Guerrero); type locality ‘Tuchitan, Tehuantepec, Mexico’ (= Juchitan, Oaxaca, Mexico).



## Habitat

The *Rhinoclemmys* species inhabit aquatic, semi-aquatic or terrestrial habitats. These include rainforests, savannahs, marshland, swampland, ponds, streams and rivers in wet forests, scrubland, wet woodlands and gallery forests. *Rhinoclemmys rubida* is completely terrestrial, *R. annulata* and *R. pulcherrima manni* are predominantly terrestrial, *R. areolata* is semi-terrestrial, and *R. funerea* and *R. nasuta* are classified as aquatic. The two subspecies of *R. punctularia*, as well as *R. diademata*, *R. melanosterna* and the three subspecies of *R. pulcherrima* (except *R. p. manni*) are considered semi-aquatic. The ♂♂ are generally more aquatic than the ♀♀.

There are more detailed studies on habitat usage of *R. diademata*. Main habitats where this species occurs are classified by the IUCN as Endangered (the Maracaibo dry forest) or Critically Endangered (the Catatumbo humid forest) (Oliveira-Miranda et al. 2010). The turtles are affected and threatened by the conversion of primary flooded forest into rice paddies, farmland and pasture, as well as by coal mining, oil extraction and water pollution (Morales-Betancourt et al. 2024).

## Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 27).

EU Council Regulation (EC) No 338/97 Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

## IUCN Red List Status

*Rhinoclemmys annulata*: Vulnerable – NT (Near Threatened, assessed 01 August 1996).

*Rhinoclemmys areolata*: Vulnerable – NT (Near Threatened, assessed 01 March 2007).

*Rhinoclemmys diademata*: Critically endangered – EN (Endangered A2cde+4cde, assessed 22 March 2023).

*Rhinoclemmys funerea*: Vulnerable – NT (Near Threatened, assessed 01 August 1996).

*Rhinoclemmys melanosterna*: Not yet assessed by the IUCN; provisional Red List of the TFTSG: Not endangered – LC (2011).

*Rhinoclemmys nasuta*: Vulnerable – NT (Near Threatened, assessed 01 August 1996).

*Rhinoclemmys pulcherrima*: Not yet assessed by the IUCN; Provisional Red List of the TFTSG: Not Endangered – LC (2010).

*Rhinoclemmys punctularia*: Not yet assessed by the IUCN; provisional Red List of the TFTSG: Not endangered – LC (2011).

*Rhinoclemmys rubida*: Vulnerable – NT (Near Threatened, assessed 01 March 2007), but due to lack of information. In 1996 the species was still classified as VU.

For many Central and South American turtle species, a reassessment was planned in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). The following assessments are in press (A.G.J. Rhodin pers. comm. 30/08/2024) and will be published in 2025:

*Rhinoclemmys annulata* (Brown wood turtle): NT

*Rhinoclemmys areolata* (Furrowed wood turtle): LC

*Rhinoclemmys funerea* (Black wood turtle): LC

*Rhinoclemmys nasuta* (Large-nosed wood turtle): VU

*Rhinoclemmys pulcherrima* (Painted wood turtle): NT

*Rhinoclemmys punctulata* (Spot-legged wood turtle): NT

*Rhinoclemmys rubida* (Mexican wood turtle): VU.

### Red List Status in the Range Countries

#### Brazil

*Rhinoclemmys punctulata*: LC (Menos Preocupante) (Vogt 2016).

#### Colombia

*Rhinoclemmys diademata*: En Peligro (EN B1ab(iii) (Morales-Betancourt et al. 2015)), Vulnerable (CITES 2022).

*Rhinoclemmys nasuta*: Near Threatened (CITES 2022).

#### Costa Rica

*Rhinoclemmys pulcherrima* categorised as a species with a declining population (MINAE 2017).

#### Ecuador

*Rhinoclemmys annulata*: EN

*Rhinoclemmys melanosterna*: EN

*Rhinoclemmys nasuta* EN (CITES 2022)

#### El Salvador

*Rhinoclemmys pulcherrima*: Not endangered (Sin Amenaza) (Pérez-García 2023).

#### Guatemala

*Rhinoclemmys areolata* Environmental Vulnerability Score: High (15) (Griffin et al. 2024).

#### Mexico

*Rhinoclemmys areolata*: A (Amenazada)

*Rhinoclemmys pulcherrima*: A (Amenazada)

*Rhinoclemmys rubida*: Pr (sujeta a protección especial) (SEMARNAT 2019).

#### Venezuela

*Rhinoclemmys diademata*: Vulnerable (CITES 2022).

## Utilisation and protection within the natural range

**Belize:** Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Bolivia:** In ‘Decreto Supremo 21312 of 27 June 1986’, Bolivia imposed a total ban on the capture, preparation, marketing and export of wild animals, their by-products and secondary products. Nevertheless, smuggling of wild animals takes place across all borders that Bolivia shares with Argentina, Brazil, Chile, Paraguay and Peru (Verheij 2019). Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Brazil:** The Brazilian constitution stipulates that all practices that pose a threat to the ecological function, cause the extinction of species or treat animals cruelly are prohibited by law (Article 225, paragraph 1, line VII). This is generally understood to include domestic animal husbandry and export to other countries. Nevertheless, *Rhinoclemmys punctulata* is occasionally kept locally as a pet. Utilisation as bushmeat occurs rarely.

**Costa Rica:** Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food. Export is prohibited.

**Ecuador:** Locally, *Rhinoclemmys* are occasionally kept as pets. Based to their appearance, *R. melanosterna* which appear in international trade probably originate from the Chóco region. There are also reports of them being caught for food. Within their natural range, *Rhinoclemmys* (e.g. *R. annulata*) are often found in settlement areas/parks. At least in Ecuadorian zoos, there are no dedicated breeding programmes in place for any of the *Rhinoclemmys* species.

**El Salvador:** The utilisation of all wild animals is subject to the Wildlife Conservation Act of the Ministry of Environment and Natural Resources (CITES 2022). Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**French Guiana:** The export of *Rhinoclemmys punctulata* from the French overseas department is prohibited by law. Nothing is known about their use as food.

**Guatemala:** *Rhinoclemmys* are occasionally kept as pets locally. Keeping and breeding is permitted, as is the capture and marketing of turtles from wild populations – but authorisation is required in each case. Management plans are in place for the wild populations to prevent over-exploitation. Mayan culture also includes the consumption of turtle soup.

**Guyana:** No local conservation regulations for *Rhinoclemmys* spp.; Guyana is a major Latin American exporter of live reptiles and birds. Exports are permitted for a certain quota under the Wildlife Conservation and Management Act (WCMA) of 2016. In 2018, for example, the state quota for *R. punctulata* was 1,500 animals, but 469 specimens were actually exported (Guyana Wildlife Conservation & Management Commission Report 2018). Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Honduras:** Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Colombia:** Locally, *Rhinoclemmys* are occasionally kept as pets. Some indigenous communities use them as food, but other turtle species are favoured over *Rhinoclemmys* spp.

**Mexico:** According to the Mexican Constitution (Art. 27), all natural resources, including turtles, belong to the country and are therefore protected. The Norma Oficial Mexicana also lists endangered species, which may only be commercialised under certain conditions. *R. areolata*

and *R. pulcherrima* are classified as ‘Threatened’, *R. rubida* as ‘Rare, Endemic’. Despite stringent legislation, protection within the country often only works on paper (Legler & Vogt 2013). Locally, *Rhinoclemmys* are occasionally kept as pets. They are only rarely used as bushmeat.

**Nicaragua:** No local protection regulations for *Rhinoclemmys* spp. Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Panama:** Since May 05<sup>th</sup>, 2023 Panama no longer issues export licences for the export of wild-caught animals for commercial use. No local protection regulations for *Rhinoclemmys* spp. exist. Locally, *Rhinoclemmys* are occasionally kept as pets. Nothing is published about their use as food.

**Suriname:** Suriname is an important Latin American exporter of live reptiles and birds. Where these species fall under the protection of CITES, trade is subject to the Convention, which came into force in Suriname on 15 February 1981. When the government joined CITES, it introduced a quota system to regulate the export of wildlife. The Surinamese government has tried to encourage Surinamese wildlife traders to switch to captive breeding, but according to the traders, the cost of setting up the necessary infrastructure is prohibitive (Verheij 2019). Suriname exports turtles, but there is no evidence that captive breeding of freshwater turtles has even been attempted (cf. Sinovas et al. 2017). There are no local conservation regulations for *Rhinoclemmys* spp. Locally, these turtles are occasionally kept as pets. Nothing is known about their use as food.

**Venezuela:** Groups (usually over ten animals) are kept by private individuals in the Lake Maracaibo area or stored until later consumption and it is assumed that the catch for consumption is increasing due to the ongoing economic crisis in Venezuela (Morales-Betancourt et al. 2024). Export is prohibited.

## Threats

Habitat loss and degradation are probably the biggest problem for all South American Wood Turtles (see red list assessments at [www.redlist.org](http://www.redlist.org)). Due to the fact that both aquatic and terrestrial habitats are used and species such as *R. rubida* or *R. diademata* occur in habitats with pronounced dry and rainy seasons, the absence of flooding or the drying up of waterbodies due to construction or drainage have a particularly dramatic effect on the populations.

Local use as food source is usually negligible compared to other turtle species, but most *Rhinoclemmys* are often kept as pets (and bred uncontrolled, accidentally) within countries of origin, especially in Central America and Brazil (Schaffer, pers. comm., Ettmar, pers. obs.).

Not all species of the genus *Rhinoclemmys* are relevant to the international trade. Until the CITES listing, *Rhinoclemmys pulcherrima manni*, *R. p. incisa* and *Rhinoclemmys punctularia* were most commonly offered legally in the pet trade. The two subspecies of *R. pulcherrima* were offered at relatively favourable prices even by larger pet shop chains in the USA, Europe and Asia (Ettmar, pers. obs.). *R. areolata*, *R. funerea* and rarely *R. rubida* have been found in the trade by a wide margin in terms of quantity. The remaining *Rhinoclemmys* species hardly play a role in the international trade, although *R. annulata*, *R. diademata* and *R. melanosterna* are at least available in hobbyist circles and captive bred offspring have been on offer in Europe.

## Reproduction

| Topic                              | Details on the reproduction of <i>Rhinoclemmys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | In all species of <i>Rhinoclemmys</i> , ♂♂ have a much more voluminous tail than ♀♀, especially in old ♂♂ the plastron is clearly concave. A reliable sex determination is only possible after several years. ♀♀ can grow a bit larger than the ♂♂.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Reproduction                       | All <i>Rhinoclemmys</i> lay hard-shelled eggs. The number of eggs per clutch is low, in many cases only a single, large egg is laid. However, several clutches can be laid per year. <i>R. annulata</i> lays the largest eggs of all turtles in relation to their body mass.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Sexual maturity                    | All <i>Rhinoclemmys</i> reach sexual maturity after several (4–6) years or at a body size that corresponds to the average size.<br><i>R. annulata</i> : With approx. 18 cm CL, or 4–5 years.<br><i>R. melanosterna</i> : At approx. 18 cm CL, or 4–5 years.<br><i>R. p. manni</i> : Animals lay eggs for the first time after 6 years.<br>The generation time in the field is estimated at 10–17 years (Iverson 2024).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Mating and nesting                 | No distinct mating ritual has been described so far. Only <i>R. rubida</i> can mate on land; for all other species, shallow water is required for successful mating.<br>The eggs are not buried deep in the ground but are usually buried under leaves or logs and other decorative items in enclosures.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Reproductive season                | <i>R. funerea</i> , <i>R. nasuta</i> , <i>R. punctularia</i> lay eggs all year round.<br><i>R. annulata</i> , <i>R. areolata</i> , <i>R. diademata</i> , <i>R. melanosterna</i> , <i>R. pulcherrima</i> , <i>R. rubida</i> show seasonal reproduction in the wild due to the alternation between dry and rainy seasons, but egg-laying can also be expected all year round in human care. However, an endogenous seasonal rhythm is usually recognisable.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Number of eggs/clutches per season | 1, rarely 2, or even 3 eggs per clutch in species with relatively small eggs. In the wild, up to 5 clutches are possible ( <i>R. annulata</i> , <i>R. punctularia</i> , <i>R. diademata</i> ), or up to 3 clutches ( <i>R. rubida</i> ) outside of an aestivation period. <i>R. diademata</i> can lay 6–18 eggs per year. <i>R. funerea</i> lays 1–4 clutches with as many as 1–6 eggs per clutch each year. In human care with regular feeding, usually significantly more clutches per year can be expected.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Egg size/hatchling size            | <i>R. annulata</i> : At hatching, juveniles are approx. 50 mm long<br><i>R. p. pulcherrima</i> : The eggs measure on average 5.4 x 3.2 cm. Juveniles are approx. 5 cm in size when they hatch and weigh 20 g.<br><i>R. p. manni</i> : Juveniles are approx. 3.5–4.0 cm in size at hatching and weigh 10–13 g.<br><i>R. punctularia</i> : Eggs are quite large (sometimes over 70 mm long) and round-oval. Hatchlings are approx. 53 x 34 mm in size shortly after hatching. 30 eggs from the Emperor Valley Zoo (USA) measured on average 6.72 x 3.79 cm and weighed 29 to 59 g. Ten resulting hatchlings were 5.8 x 5.0 cm in size.<br><i>R. diademata</i> : The eggs are quite large and oval (5.2–6.6 cm x 3.0–3.2 cm). A hatchling in Pritchard & Trebbau (1984) measured 4.6 x 3.8 cm immediately after hatching but unfolded to a size of 5.0 x 4.5 cm during its first days of life.<br><i>R. rubida</i> : In the literature, hatchling size is given as approx. 50 mm. <i>R. p. perixantha</i> : Juveniles are approx. 4.5–5.0 cm in size at hatching and weigh approx. 20 g.<br><i>R. areolata</i> : Egg size approx. 60 x 31 mm; hatchlings are approx. 52 mm long.<br><i>R. funerea</i> : Approx. 68 x 35 mm egg size; hatchlings are approx. 55 mm long.<br><i>R. melanosterna</i> : Hatchlings are approx. 50 mm long.<br><i>R. nasuta</i> : Approx. 67–70 x 35–39 mm egg size. |
| Incubation and hatching            | The embryonic development duration for almost all <i>Rhinoclemmys</i> is around 90 days. In the wild, juveniles usually hatch at the start of the rainy season, which is why the individual incubation period can vary by a few weeks (embryonic aestivation). In hu-                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |



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|-------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                   | <p>man care the embryonic development also takes longer under dry incubation conditions (R. Wicker pers. comm.). In addition, some taxa within the group need to break through an initial diapause, which significantly extends the incubation period.</p> <p><i>R. annulata</i>: For successful incubation, it is necessary to break the diapause, which can extend the incubation period to up to 9 months. Under semi-natural conditions in Ecuador, the eggs experience temperatures of around 20°C for a few weeks at a breeder, but during the rainy season the temperatures rise to around 35°C.</p> <p><i>R. areolata</i>: approx. 70 days at 30.0°C to 101 days at 25.5°C. A shorter incubation period of 64 days could also be observed at fluctuating temperatures (R. Wicker pers. comm.).</p> <p><i>R. funerea</i>: approx. 80 days at 30°C.</p> <p><i>R. melanosterna</i> has a direct embryonic development without initial diapause.</p> <p><i>R. p. manni</i>: The incubation period is 99–102 days at a temperature of approx. 30°C. In southern Europe, it has been observed that in late autumn, healthy juveniles hatched from eggs laid in spring in outdoor enclosures.</p> <p><i>R. p. pulcherrima</i>: Incubation lasts a total of approx. 120–140 days, at an initial temperature of 20°C and dry substrate to break the diapause for approx. 3 weeks, followed by incubation at approx. 30°C and moistened substrate.</p> <p><i>R. punctularia</i>: The incubation period is approx. 90 days.</p> <p><i>R. rubida perixantha</i>: The incubation period is approx. 80–100 days at an initial temperature of 25°C (incubation in the terrarium) and then approx. 30–31°C in the incubator.</p> |
| Sex determination | <p>According to Ewert et al. (2004), the sex of all <i>Rhinoclemmys</i> is determined by temperature (TSD). Only <i>R. areolata</i> was systematically analysed, but the information on TSD type I (predominantly ♂♂ at lower temperatures, ♀♀ at higher temperatures) or TSD type II (predominantly ♀♀ at very low temperatures, predominantly ♂♂ at temperatures of 25–27°C, predominantly ♀♀ again above this temperature) is contradictory in the various publications analysed.</p> <p>For the other <i>Rhinoclemmys</i> species, no information is available on the pivotal temperatures for temperature-dependent determination.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Sperm storage     | Probably yes, but not observed.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |

## Husbandry and Captive Breeding B/B

*Rhinoclemmys nasuta* **X**, as there are no breeding attempts known. Husbandry and breeding parameters probably similar as for the other species.



Fig. 26: *Rhinoclemmys* – captive breeding

- a *R. pulcherrima manni* in a zoo (B. Pfau)
- b *R. p. manni* juvenile with clear carapacial pattern (X. Wapelhorst)
- c *R. p. manni* colourful juvenile (G. Schaffer)
- d *R. p. manni* juveniles, coral snake mimicry (G. Schaffer)
- e *R. rubida* Hatching, the hatchling is still pale (M. Schilde)
- f *R. rubida*, some days after hatching, the juvenile has unfolded and is trying to hide (M. Schilde).

| Topic                                                           | Data for <i>Rhinoclemmys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | <p>An endogenous seasonal rhythm appears to be present in all species, which can be synchronised in breeding animals, for example, by the length of daylight hours.</p> <p><i>R. annulata</i>, <i>R. melanosterna</i>, <i>R. rubida</i>: Maintaining rainy and dry periods in the terrarium to synchronise the hormonal cycles of ♂♂ and ♀♀.</p> <p><i>R. pulcherrima</i> and <i>R. punctularia</i> lay eggs all year round in human care and mate all year round.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Husbandry requirements                                          | <p><i>R. areolata</i>, <i>R. pulcherrima</i>: Low requirements, simulation of rainy and dry seasons useful for breeding management (laying breaks); 50:50 ratio of land to water in the terrarium.</p> <p><i>R. nasuta</i>, <i>R. funerea</i>: Low requirements, 10:90 ratio of land to water in the terrarium. Large enclosures necessary due to the body size of the animals.</p> <p><i>R. diademata</i>, <i>R. melanosterna</i>, <i>R. punctularia</i>: Low requirements of captive bred animals, 30:70 ratio of land to water in the terrarium.</p> <p><i>R. annulata</i>, <i>R. rubida</i>: slightly higher demands on lighting, 90:10 ratio of land to water in the terrarium.</p> <p>Due to their origin, <i>Rhinoclemmys</i> species need heated tanks in temperate regions, i.e. energy consumption can be high depending on where they are kept – keeping them in outdoor enclosures is usually not possible in Central Europe, or only for a few weeks in summer. All <i>Rhinoclemmys</i> species also need loose soil for digging in the land part. They like to bury themselves in soil, i.e. they dig themselves in or scoop substrate onto their carapax. When they then enter water basin, they will take substrate with them and the water section will be filthy soon. It therefore makes sense to provide a sufficiently sized drain valve in the water section, or to alternatively find a simple way of emptying the water basin completely and refilling it with less soiled water. The time and effort required to care for the animals is relatively high.</p> |
| General characteristics, difficulties with keeping and breeding | <p>In general, it should be noted that wild-caught <i>Rhinoclemmys</i> spp. are often infested with endoparasites, which must be treated under quarantine conditions after arrival. Acclimatisation must be carried out patiently and carefully, as adult wild-caught specimens are particularly sensitive to stress.</p> <p><i>R. areolata</i>, <i>R. pulcherrima</i>: None</p> <p><i>R. diademata</i>: Apparently mainly ♀♀ have been hatched so far among hobbyists, ♂♂ are only rarely offered.</p> <p><i>R. funerea</i>: This species is easy to keep but is only suitable for larger aqua-terraria due to its large size and swimming behaviour.</p> <p><i>R. punctularia</i>, <i>R. rubida</i> are considered difficult to acclimatise (Ettmar &amp; Altenburger 2020). The fertilisation rate of <i>R. rubida</i> eggs has so far been rather low and there is a relatively higher mortality rate in the developmental phase before hatching compared to other <i>Rhinoclemmys</i>.</p> <p><i>R. annulata</i>, <i>R. nasuta</i>: Unknown.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Care of the young, technical and time effort                    | <p>Hatchlings of <i>R. pulcherrima</i> are already relatively large after leaving their eggs and are not as fragile as other species. Initially, offering live food is recommended as this stimulates their motivation to start feeding. Greens such as dandelion and chicory and sweet fruit are accepted quite quickly as well. For the first few months, it is recommended that they are kept purely in water at a water level of around 5 cm. If hatchlings are raised under too dry conditions, their carapace will not grow properly. Further, it is easier to feed pellets in water. At the age of 6 months at the earliest, they should be offered a land section (about half the area of the terrarium). The animals can be reared in such a setup for a further two years before they are moved to a terrarium for adult turtles.</p> <p>At Salvador Zoo, juveniles of <i>R. punctularia</i> up to approx. 12 cm carapace length are reared purely aquatic, also together with other turtle species, before they are placed in an enclosure together with adults (Ettmar 2021).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |

| Topic                                                  | Data for <i>Rhinoclemmys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
|--------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                        | Juveniles of <i>R. annulata</i> and <i>R. melanosterna</i> are much more aquatic in their behaviour than adults. For healthy growth, the humidity should always be high and due to their origin from heavily wooded areas, rearing enclosures should not overheat or be shaded.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Life expectancy                                        | <p><i>R. annulata</i>: Apparently one specimen in human care lived to be over 30 years old.</p> <p><i>R. areolata</i>: 19.3 years (AnAge 2023). R. Wicker (pers. comm.) received a ♀ in 1976 that was still laying eggs in 2024.</p> <p><i>R. melanosterna</i>: 37 years 9 months (Iverson 2014), in human care &gt; 40 years</p> <p><i>R. pulcherrima</i>: 20.4 years (AnAge 2023) or 20 J 5 months (Slavens &amp; Slavens 2000)</p> <p><i>R. rubida</i>: 11.8 years (AnAge 2023). R. Wicker (pers. comm.) received a ♂ in 1984, which is still alive in 2024</p> <p>Overall, it can be assumed that all <i>Rhinoclemmys</i> can live to be over 40 years old in human hands, although there are no verifiable sources to date.</p>                                                                                                                                                                                                                                                                                                                                                                             |
| Frequency of private breeding and reproduction in zoos | <p><i>R. annulata</i>, <i>R. areolata</i>, <i>R. diademata</i>, <i>R. rubida</i>: Rare in Europe, both in private collections and in zoos. Hardly any breeding reports available, but if captive bred specimens are available, breeding is easily possible:</p> <p>Breeding reports for <i>R. areolata</i> exist (Artner 2009).</p> <p><i>R. melanosterna</i> was first bred in 1990 (R. Wicker, pers. comm.). There are a few (private) specialists worldwide who keep and breed the species.</p> <p><i>R. diademata</i> has been occasionally bred in Europe since at least 2015 (Fuchs 2016).</p> <p><i>R. nasuta</i>: Not kept in Europe, no breeding reports.</p> <p><i>R. pulcherrima</i>, <i>R. punctularia</i>: Are kept in some zoos, many private keepers and breeders. One of the first breeding reports was published by Pauler (1980)</p> <p><i>R. diademata</i>, <i>R. melanosterna</i>, <i>R. punctularia</i>, <i>R. pulcherrima incisa</i> and <i>R. p. manni</i>, as well as <i>R. rubida perixantha</i> have been recorded in the DGHT captive breeding statistics since 1986 (Horn 1988).</p> |
| Breeding difficulty evaluation                         | <p><i>R. diademata</i>: Threshold temperature for hatching ♂♂ must be determined experimentally, most offspring so far are ♀♀.</p> <p>Other <i>Rhinoclemmys</i>: Depending on the geographical origin, the simulation of rainy and dry seasons may be necessary as a trigger for reproduction.</p> <p><i>R. nasuta</i>, <i>R. funerea</i>: The required size of the enclosures makes accommodation difficult for hobbyists and thus a wider distribution within the hobby but does not pose a problem for specialists and zoos (Hofstra 2004).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Mortality in the first years of life                   | <p><i>R. pulcherrima</i>: Hardly any mortality in juveniles, hardly any deformities in carapace growth, provided the juveniles are kept moist enough. In <i>R. p. pulcherrima</i>, mortality in juveniles is approx. 15%.</p> <p>In the much more stress-sensitive <i>R. rubida</i> it is approx. 25%.</p> <p><i>R. punctularia</i>: Hardly any mortality in juveniles if kept correctly.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| F2 generation bred in captivity                        | Probable in all <i>Rhinoclemmys</i> species, but not yet documented in some cases. In private breeding, <i>R. areolata</i> , <i>R. diademata</i> , <i>R. melanosterna</i> , and all subspecies of <i>R. pulcherrima</i> (Methner (1989) noted that <i>R. melanosterna</i> had already been bred to F2 by R. Wicker, for all other species mentioned here, R. Wicker confirmed the F2 breeding in a personal communication). For <i>R. pulcherrima</i> , F2 breeding was already published in 2004 (Schilde 2004).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Commercial breeding/ ranching                          | <p><i>R. annulata</i>, <i>R. funerea</i>, <i>R. melanosterna</i>, <i>R. nasuta</i>, <i>R. rubida</i>: not to our knowledge.</p> <p><i>R. areolata</i>, <i>R. pulcherrima</i>: yes (Mexico), perhaps also in several Meso-American countries.</p> <p><i>R. diademata</i> is bred in large numbers in a zoo in Venezuela for reintroduction into the wild.</p> <p><i>R. punctularia</i> is bred in moderate numbers in the zoo of Salvador (Bahia/Brazil).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |



| Topic                              | Data for <i>Rhinoclemmys</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Interviews/ Surveys/ Consultations | Several private individuals could be interviewed directly or answered the questionnaire, including > 10 very experienced breeders of these turtles in various European countries, who usually do not travel to the special workshops due to language problems. The zoos that have mentioned breeding any <i>Rhinoclemmys</i> species did not respond to our enquiries. The recent very well-attended ISV <i>Rhinoclemmys</i> Workshop with more than 20 participants is worth mentioning (Ettmar & Altenburger 2020), because in this workshop the captive breeding of all <i>Rhinoclemmys</i> species, except <i>R. nassuta</i> , in Europe was discussed. There have also been specialist meetings on these chelonians at other European associations since around 1990, which have also been attended by zoo experts. Therefore, the number of people/institutions that have contributed to this collection of information cannot be specified in detail. |

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**Stephan Ettmar (15.08.2024)**

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## Kinosternidae

### *Claudius angustatus* Cope, 1865

| Species                    | Original description | Common name                | Common name international                                                                                                                                                                                                          | Known in the trade |
|----------------------------|----------------------|----------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Claudius angustatus</i> | Cope, 1865           | Narrow-bridged Musk turtle | Großkopf-Schlammschildkröte<br>Chopontil (Veracruz),<br>taimán (Tabasco),<br>joloque (Tabasco),<br>taimame (Campeche),<br>tortuga caimán (Chiapas),<br>tortuga vampiro (Chiapas),<br>tortuga rayo (Chiapas),<br>tortuga almizclera | Yes                |

### Morphology and Taxonomy

*Claudius* is a monotypic genus, *C. angustatus* is the only species.

The extremely reduced carapace is characteristic of this turtle species. The plastron is roughly cruciform and leaves the leg attachments exposed. The carapace is also relatively small, the highest point is very far forward and the connection between the carapace and plastron consists only of elastic connective tissue. The head is large and cannot be retracted under the carapace in adults, but juveniles can at least partly retract their heads.

The jaws are very strong, with a hook-like tip on the upper jaw and two tooth-like hooks next to it. Two barbels can be recognised on the chin. The neck is long and very agile, making the animals really strong in defence. They threaten potential predators with their mouths wide open and then bite quickly.

The basic colour of the carapace is variable, from beige to olive to dark brown. Darker spots or stripes are usually present on the carapace shields, but there are also animals with a completely un-patterned carapace. The pattern on the top of the head is also variable. In adults, the carapace is light in colour and the limbs are slightly darker on the upper side than on the underside. Juveniles have a yellow spot on each shield of the plastron, which is framed in black. The shell and skin colouring are influenced by the light conditions at the bottom of the waters in which the turtles live.

Melanistic (very dark or completely black) animals are rarely found in the wild, but various colour forms are now bred in captivity.



Fig. 27: *Claudius angustatus*

- a swimming in the aquarium (S. Ettmar)
- b at hatching (S. Ettmar)
- c upper jaw has 'teeth' (B. Pfau)
- d defensive threatening (P. Pfau)
- e melanistic individual (O. Klawonn)
- f exceptionally light-coloured animal (O. Klawonn).

No subspecies have been described for *C. angustatus*. In Europe, however, two different sized forms are kept and bred separately: The 'small form' was first imported in the 1990s from Tlacotalpan, Veracruz, Mexico, in the far north of its range. The ♀♀ had a CL of at most 11 cm, the ♂♂ of 12 cm, and they have not grown since. The offspring of these animals grow slowly, but seem to grow a little larger than the imported parents. In her research on the shells in the waste pits of the fish shops on the Rio Papaloapan in Tlacotalpan, López Gómez (2009) also found only the remains of very small *C. angustatus*, she therefore assumed that only juveniles had been caught and eaten there. In the 'large form', the ♂♂ often reach 18 cm (and approx. 1 kg); the previously known maximum size of a ♂ grown in human care is > 20 cm CL. The ♀♀

reach up to 14 cm CL (at approx. 500 g). The exact origin of these turtles kept in the EU is not known.

In his genetic studies, Rivera Arroyo (2016) found no sharp differences between this small form from the north of its range and other *C. angustatus* populations, but he did find a difference between the ‘western’ and ‘eastern’ populations: the western populations, to which the ‘small form’ would also belong, seems to tolerate lower temperatures (20.4°C), while the other populations require temperatures well above 24°C.

A genetic mapping of *C. angustatus* is currently being carried out in Mexico to enable the re-introduction of confiscated specimens into the original population (CITES 2022). Morphological characteristics will also be recorded if possible, so that it may be elucidated if there is a smooth transition from small to large populations, or whether a taxonomic revision of the species might be needed.

## Distribution and Habitat

### Distribution

Mexico: Central Veracruz, northern Oaxaca, Chiapas, Campeche, Quintana Roo and Tabasco. There is also one record from the northern part of the Yucatán peninsula, near Celestún (Calderon Mandujano et al. 2001). This species occurs in the northeast of Guatemala and in Belize (CITES 2022, Munscher et al. 2022, Augustine et al. 2024). The species was known to live from sea level to 611 m asl, but new locality records have extended the known range into the Altas Montanas in northwestern and southwestern Veracruz in Mexico, where the species has been found up to 820 m asl, albeit in connection with the cultivation of sugar cane (Contreras-Calvario et al. 2024). The type locality is ‘Tabasco, Mexico’.

### Habitat

These turtles live in shallow, muddy waters at a depth of about 0.5–1.5 m (Vogt 1997). *C. angustatus* is a bottom-crawling species that thrives in seasonal ponds, flooded fields, flooded forest, marshlands, and occasionally along the margins of shallow lakes. ‘At the beginning of the dry season (March) they bury themselves in the loose soil or mud, often under vegetation as the water is receding, and remain in aestivation until summer rains flood their seasonal microhabitat again in mid-June to late July. Legler found *Claudius* in flooded forest pools, with *Kinosternon acutum*, in Belize (late June 1966). Most of the ecological data presented in this account are from a population at Lerdo de Tejada in wetlands inundated by the Rio Augustin (Papaloapan drainage, 19°39'N, 95°34'W), near Alvarado, Veracruz. The area is 30 m above sea level’ (cited from Legler & Vogt 2013). Depending on the local climate, the onset of the rainy season or the dry season may vary.

The turtles enter aestivation at the beginning of the dry season. ‘As the water level dropped, the turtles buried themselves 8–12 cm deep in the bottom substrate and remained there until disturbed. Aestivation is solitary’ (cited from Legler & Vogt 2013). Depending on the local climate, the turtles spend several months, sometimes even more than half a year, in dry dormancy (aestivation). The maximum duration of two years of dry dormancy stated in Proposal No. 28 (CITES 2022) is likely to be due to an extreme weather event.

The proposal also states that these turtles are territorial and aggressive towards conspecifics, but Hausmann (1968) already points out that in captivity the animals can be quite tolerant of conspecifics, threatening a lot but usually only biting in defence or under stressful conditions.

Oviposition takes place during the rainy season, until about September (Vogt 1997). The usually 2–3 (maximum 6) eggs of a clutch are superficially buried between plant material (Flores-Villela & Zug 1995) or in the root area of plants. It is assumed that a ♀ in nature lays only one or two clutches per year (Cervantes-López et al. 2021), but Vogt (1997), who has monitored very nutrient-rich waters, even indicates up to five clutches per year.

Their natural diet consists of snails, worms, small fish, crustaceans and mussels, with a small amount of plant material (Flores-Villela 1980). Although Vogt (1997) states that crayfish (*Procambarus* spp.) and large freshwater prawns (*Macrobrachium* spp.) are popular food items in the Pantanos de Lerda de Tejeda, the species is still not a food specialist for crayfish, as the stomach contents also included beetles, butterfly caterpillars, water bugs and other aquatic insects, as well as plant parts.

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 28).

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

NT (Near Threatened, assessed 2019-11-13).

For many Central and South American turtle species, a reassessment was planned in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). For 2025 a new assessment, with category EN, is in press (A.G.J. Rhodin pers. comm. 30/08/2024).

### Red List Status in the Range Countries

#### Guatemala

Endangered (CONAP 2021).

#### Mexico

Critically Endangered (P – En peligro de extinción; SEMARNAT 2019).

### Utilisation and Protection within the Natural Range

Campbell (1998) states that *Claudius angustatus* is eaten in Belize and Guatemala and that this species is preferred to the approximately equally large *Kinosternon* sp. because these turtles ‘stink more’. However, it is not possible to say to what extent the turtles are caught for consumption.

In Mexico, *C. angustatus* is usually offered for sale as a live specimen from controlled breeding for the pet trade and for consumption. The first captive breeding report for Mexico which could be found is by Espejel González (2004), but she did not refer to the husbandry conditions. Only later, Legler & Vogt (2013) mention that ‘The flesh of *Claudius* is savory and popular in southeastern Mexico. Growth is fast, and the ratio of edible parts to total body mass is the highest of any Mexican turtle studied by Vogt (unpublished data). This attribute would be favorable in a turtle farm environment’. They then give more details on the conditions in that farm where Espejel González (2004) had examined the incubation conditions – the turtles are

'kept in earthen tanks, allowed to aestivate naturally, and fed a natural diet of insects and fresh crustaceans (scraps from markets). Reproductive output of 39 captive ♀♀ versus 17 wild ♀♀ did not differ. This facility is judged to be successful'. No more data on the breeding success in this facility are available.

In 2020, five breeding farms for this species were registered in Mexico, with the numbers of hatchlings rising sharply from 2015 onwards. The highest number of registered offspring to date was 4,841 hatchlings in 2018, although fewer than 2,000 juveniles were legally exported in that year and the following year. However, Reynoso (2021) was able to show that not all of these animals were actually captive-bred, but that wild-caught animals have probably been used to supplement the numbers, and he also suspects that most of the animals offered for sale in Europe and Asia are actually wild-caught. He justifies this conclusion with husbandry and breeding difficulties and states that this species mainly feeds on crayfish (*Procambarus* sp.), which have not yet been bred commercially. In addition, mortality of the turtles in the breeding farms is high and the reproductive rate is low. However, he only refers to the situation in Mexico, because although he cites some reports of breeding in Europe, he obviously could not evaluate them.

Adult *C. angustatus* for consumption are less commonly offered in Mexico, as it takes a long time to grow and fatten a specimen under the husbandry conditions which usually prevail in the breeding facilities there (CITES 2022). This makes this type of meat less profitable than the meat of, for example, *Staurotypus triporcatus*. However, some breeding farms also offer prepared turtle dishes in their affiliated restaurants, often with green sauce – a traditional Easter dish (Pfau et al. 2021). The cultural significance of eating these small turtles, as well as how they are prepared, is described in Ocampo-González et al. (2018) and Montuy Pozo et al. (2019). In addition, products from this species of turtle are considered to be particularly effective traditional medicine; the shell is used to make a cough remedy and the eggs are said to have an aphrodisiac effect (Vogt 1997, Morales Mavil et al. 2010). In the illegal domestic trade, it is mainly the meat of the turtles that is sold, and a dish with turtle meat can cost between 600 and 800 pesos (30–40 €) (Reynoso et al. 2016). Most of the specimens sold for consumption in the illegal trade are fresh wild-caught specimens (CITES 2022).

In China, and probably also in other countries in East Asia, these small, original-looking turtles are popular as pets. They are also offered for sale at fairly high prices in online shops (Ji et al. 2020). Therefore, attempts are repeatedly made to smuggle large numbers of live *C. angustatus* out of the country by air – in May 2020, 4,216 turtles of this species, together with about 10,000 turtles of other species, were confiscated at Mexico City airport (CITES 2022, PROFEPA 2020). Cantú & Sanchez (2024) also list this species as the third most frequently confiscated reptile; according to their records, 7,294 *Claudius angustatus* were confiscated in Mexico between 2019 and 2023 alone. Since the confiscating authorities have no experience in caring for the animals, it can be assumed that they either did not survive for long, or that they were made available to a UMA to expand the breeding stock there, thus legalising them and indirectly returning them into the trade chain (E. Reyes-Grajales in a mail to the IUCN SSC Tortoise and Freshwater Turtles group, dated June 2023).



## Threats

Proposal 28 (CITES 2022) cites the collection of wild specimens for consumption and for the illegal pet trade as the main factors endangering the species. The animals for consumption are mainly collected at the beginning and end of the rainy season, when the water levels are low and the turtles are easy to catch; the end of the aestivation at the end of the dry season is a particularly critical time, because then the developing eggs for the first clutches of the next nesting season are also ‘harvested’ as well. They are considered a special delicacy. The numbers of confiscated turtles in the domestic trade and at the borders, for illegal export, are extremely high (CITES 2022). Although the legal regulations in Mexico are strict, it is obviously very difficult to detect the packaged animals and, above all, to prosecute the traffickers, so that the number of unreported cases is likely rather high.

Loss of habitat due to urban development and changes in farming methods (burning during the dry season and deep ploughing of the ground of the now dry water bodies where the turtles have buried themselves) is only mentioned in second place. Sugar cane cultivation should also be viewed critically, because although new water bodies are created due to the necessary flooding of the fields, the use of pesticides in these cultures is extremely high, posing a threat to the turtles that still live there (Vogt 1997, Contreras-Calvario et al. 2024).

## Reproduction

| Topic                              | Details on the reproduction of <i>Claudius angustatus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | Relatively weakly pronounced. The ♂♂ have a larger tail. In some holders, ♂♂ have developed a ‘buffalo back’, i.e. a carapace that is higher at the front. Age melanism in ♂ is also reported. A larger final size of carapace and head is another male sexual characteristic, but it does not always occur prominently.                                                                                                                                                                                                                                                               |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Sexual maturity                    | At 10 cm CL. Juveniles raised in human care usually start laying eggs at an age of 4 years. Under good husbandry conditions the juveniles grow fast and attain sexual maturity much earlier than under the usual conditions in the facilities in Mexico.                                                                                                                                                                                                                                                                                                                               |
| Mating and nesting                 | In human care, mating only under supervision is recommended (two breeders report that deaths occurred during longer periods of unsupervised mating). Not all animals are willing to mate, especially old animals from the wild often cannot be persuaded to mate in human care.<br><br>About four weeks after mating, the first clutch of eggs is laid. The species is not choosy when it comes to choosing a place to lay its eggs. Sand or a sand/earth mixture has proven to be practical. The nest boxes should be filled with sand, depth of the substrate should be about 15 cm. |
| Reproductive season                | Mating takes place August–September, nesting November–July.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Number of eggs/clutches per season | 6 clutches per year are possible, 5–6 eggs/clutch.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Egg size/hatchling size            | Egg size is 30,5 x 17,5 mm, hatchling CL 29–30 mm.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Incubation and hatching            | 70–225 days, diapause!                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Sex determination                  | Genetic (XX/XY) sex determination, no heteromorphic sex chromosomes. Temperature influences on sex determination have been observed.                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Sperm storage                      | Probable, but no direct observations.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |

## Husbandry and Captive Breeding **A/B**

| Topic                                                           | Data for <i>Claudius angustatus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|-----------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Aestivation before the (supervised) introduction of the mating partners is recommended but not absolutely necessary.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Husbandry requirements                                          | This species is easy to keep if the heating requirements of the animals are met (at least 24°C) and if they are kept individually. Due to their small size, the species can be kept in standard aquariums. Aestivation recommended.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| General characteristics, difficulties with keeping and breeding | <p>Single housing, breeding under supervision. The species tends towards obesity. The animals should be fed very sparingly outside of the breeding season.</p> <p>Not all animals are willing to mate. ♂ hatchlings are somewhat less common than ♀ hatchlings. Incubation of the eggs is lengthy and difficult due to the fact that sometimes a diapause is required and sometimes not. If the hard-shelled eggs are incubated in a substrate that is too moist, they will crack. The number of eggs that develop into a healthy juvenile is often low, sometimes as low as one third.</p> <p>The specialisation on a certain <i>Procambarus</i> sp. (CITES 2022) could not be confirmed, but stressed, wild-caught specimens often accept crayfish pieces as their first meals. After acclimation they will certainly also eat the normal food for carnivorous freshwater turtles.</p> |
| Care of the young, technical and time effort                    | Individual rearing. Juveniles have quite high demands on water quality. If the water is not changed sufficiently, whitish rashes may develop in the throat and around the eyes. These rashes can be treated very well by adding leaves of the Indian almond tree. In rare cases, the juveniles also suffered from problems with the anal bladder and were then no longer able to dive. This problem could not be treated successfully so far. Since the animals grow very quickly, the breeding containers must be adapted accordingly. UV lighting improves breeding results, even though the animals do not actively bask and usually rest hidden in the thicket.                                                                                                                                                                                                                      |
| Life expectancy                                                 | At least 40 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Frequency of private breeding and reproduction in zoos          | Frequently kept in private households, some single individuals have been kept in European and US zoos.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Breeding difficulty evaluation                                  | Because the incubation with diapause is tricky, the breeding difficulty is rated as B = requires experience of the breeder. Due to the high productivity, the high number of non-developing eggs does not pose a serious problem.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Mortality in the first years of life                            | With very good water quality (up to daily water changes), the species can be raised with practically no losses under laboratory conditions. Alternatively, the young can be raised with significantly less effort in bioactive setups (substrate, planting, filtering).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| F2 generation bred in captivity                                 | Has certainly been bred up to F3 generation, and perhaps even to further generations, in Europe.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Commercial breeding/ ranching                                   | The breeding farms in Mexico do not yet seem to be breeding very successfully. There are a few large breeders in the USA and Far East. Most of the animals sold in the EU come from private breeders.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Interviews/ Surveys/ Consultations                              | Several very experienced private breeders of this species in Europe could still be interviewed in person. However, since the species has been frequently bred in Europe since the 1980s, it was no longer possible to ask all the breeding pioneers directly, and only their numerous publications were available. Most of the actual information on keeping and breeding has been collected and intensively discussed at the specialist meetings of the various European associations, they cannot be assigned to individual persons.                                                                                                                                                                                                                                                                                                                                                   |

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**Maik Schilde and Ole Klawonn (22.08.2024)**

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**Kinosternon Spix, 1824**

| Species                        | Original description                                                                                      | Common name                                            | Common name international                                                                                                                                       | Known in the trade |
|--------------------------------|-----------------------------------------------------------------------------------------------------------|--------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Kinosternon abaxillare</i>  | Baur in Stejneger, 1925                                                                                   | Central Chiapas Mud turtle                             | Chiapas-Klapp-schildkröte<br>Casquito pardo, tortuga cantado                                                                                                    | Rare               |
| <i>Kinosternon acutum</i>      | Gray, 1831                                                                                                | Tabasco Mud turtle                                     | Spitzschnauzen-Klappschildkröte<br>Tortuga pecho quebrado de Tabasco, tortuga de pantano de Tabasco, pochitoque jaguactero o negro, montera, chechagua de monte | Yes                |
| <i>Kinosternon alamosae</i>    | Berry & Legler, 1980                                                                                      | Alamos Mud turtle                                      | Alamos-Klapp-schildkröte<br>Casquito de Álamos, casquito de noroeste, tortuga pecho quebrado de Álamos, tortuga de agua                                         | Rare               |
| <i>Kinosternon albogulare</i>  | Duméril & Bocourt 1870 <sup>6</sup>                                                                       | White-throated Mud turtle                              | Weißkehl-Klapp-schildkröte                                                                                                                                      | Yes                |
| <i>Kinosternon angustipons</i> | Legler, 1965                                                                                              | Narrow bridged Mud turtle, Central American Mud turtle | Zentralamerikanische Klappschildkröte<br>Tortuga de pantano Centroamericana, tortuga de barro de puente estrecho                                                | Yes                |
| <i>Kinosternon baurii</i>      | Garman, 1891                                                                                              | Striped Mud turtle                                     | Dreistreifen-Klapp-schildkröte<br>Tortuga del fango estriada, tortuga de barro rayada                                                                           | Yes                |
| <i>Kinosternon chimalhuaca</i> | Berry, Seidel & Iverson, 1997                                                                             | Jalisco Mud turtle                                     | Jalisco-Klapp-schildkröte<br>Tortuga de pantano jalisciense                                                                                                     | Yes                |
| <i>Kinosternon cora</i>        | Loc Barragán, Reyes-Velasco, Woolrich-Piña, Grünwald, Venegas de Anaya, Rangel-Mendoza & López-Luna, 2020 | Cora Mud turtle                                        | Cora-Schlammschildkröte<br>Casquito cora, chacuanita cora                                                                                                       | Rare               |

<sup>6</sup> Species revalidated according to the revision of *Kinosternon scorpioides* (Iverson & Berry 2024). According to Rhodin et al. (2021), the taxonomic reference used for Proposal No. 29, *K. scorpioides* is a species complex that was only subdivided into separate species after CITES CoP19. Therefore, this species is still treated as *K. scorpioides* in the CITES context.

| Species                        | Original description                                     | Common name             | Common name in-ternational                                                                                                                                                | Known in the trade |
|--------------------------------|----------------------------------------------------------|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Kinosternon creaseri</i>    | Hartweg, 1934                                            | Creaser's Mud turtle    | Creaser's Klapp-schildkröte, Yucatán-Klappschildkröte<br>Casquito de Creaser, tortuga de pantano yucateca                                                                 | Yes                |
| <i>Kinosternon cruentatum</i>  | Duméril & Bibron in Duméril & Duméril, 1851 <sup>7</sup> | Red-cheeked Mud turtle  | Rotwangen-Klapp-schildkröte                                                                                                                                               | Yes                |
| <i>Kinosternon dunni</i>       | Schmidt, 1947                                            | Dunn's Mud turtle       | Dunn's Klapp-schildkröte<br>Tortuga de pantano Colombiana                                                                                                                 | Rare               |
| <i>Kinosternon durangoense</i> | Iverson, 1979d                                           | Durango Mud turtle      | Durango-Klapp-schildkröte<br>Casquito de Durango, casquito de los presones                                                                                                | Rare               |
| <i>Kinosternon flavescens</i>  | Agassiz, 1857                                            | Yellow Mud turtle       | Gelbliche Klapp-schildkröte<br>Casquito amarilla                                                                                                                          | Yes                |
| <i>Kinosternon herrerae</i>    | Stejneger, 1925                                          | Herrera's Mud turtle    | Herrera-Klapp-schildkröte<br>Tortuga casquito pecho quebrado, tortuga pecho quebrado de Herrera, casquillo de herrera, galapago, pochitoque                               | Yes                |
| <i>Kinosternon hirtipes</i>    | Wagler, 1830                                             | Rough-footed Mud turtle | Raufuß-Klapp-schildkröte<br>Tortuga pecho quebrado pata rugosa                                                                                                            | Yes                |
| <i>Kinosternon integrum</i>    | LeConte, 1854                                            | Mexican Mud turtle      | Mexikanische Klapp-schildkröte<br>Tortuga pecho quebrado mexicana, casquito de burro, tortuga de agua, tortuga de río                                                     | Yes                |
| <i>Kinosternon leucostomum</i> | Duméril & Bibron in Duméril & Duméril, 1851              | White-lipped Mud turtle | Weißlippen-Klapp-schildkröte<br>Tortuga pecho quebrado labios blancos, tortuga candado amarilla, abaniquillo de Hidalgo, pochitoque septentrional, tortuga del fango boca | Yes                |

<sup>7</sup> Species revalidated according to the revision of *Kinosternon scorpioides* (Iverson & Berry 2024). According to Rhodin et al. (2021), the taxonomic reference used for Proposal No. 29, *K. scorpioides* is a species complex that was only subdivided into separate species after CITES CoP19. Therefore, this species is still treated as *K. scorpioides* in the CITES context.

| Species                          | Original description                                 | Common name                                                                            | Common name in-ternational                                                                                                                                                          | Known in the trade |
|----------------------------------|------------------------------------------------------|----------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
|                                  |                                                      |                                                                                        | blanca, tortuga cofre, tapaculo, tacán<br>Tapacul (name of the Wounann, Bajo San Juan)                                                                                              |                    |
| <i>Kinosternon mexicanum</i>     | LeConte, 1854 <sup>8</sup>                           | Pacific Coast Red-cheeked Mud turtle                                                   | Pazifik-Rotwangen-Klappschildkröte                                                                                                                                                  | Unclear            |
| <i>Kinosternon oaxacae</i>       | Berry & Iverson, 1980                                | Oaxaca Mud turtle                                                                      | Oaxaca-Klappschildkröte<br>Tortuga pecho quebrado oaxaqueña, casquito de Oaxaca                                                                                                     | Yes                |
| <i>Kinosternon scorpioides</i>   | (Linnaeus, 1766) <sup>9</sup>                        | Scorpion Mud turtle                                                                    | Skorpionsklappschildkröte<br>Tortuga pecho quebrado escorpión, tortuga barrosa, tortuga estuche, muçuã, tapaculo, tacán<br>Indigener Name der Warao (Delta del Orinoco): Joni-guaku | Yes                |
| <i>Kinosternon sonoriense</i>    | Le Conte, 1854                                       | Sonora Mud turtle, Sonoyta Mud turtle                                                  | Sonora-Klappschildkröte<br>Tortuga pecho quebrado sonorese, tortuga pecho quebrado de Sonoyta                                                                                       | Rare               |
| <i>Kinosternon steindachneri</i> | Siebenrock, 1906                                     | Florida Mud turtle                                                                     | Florida-Klappschildkröte<br>Tortuga pecho quebrado de Florida                                                                                                                       | Yes                |
| <i>Kinosternon stejnegeri</i>    | (Hartweg, 1938)                                      | Arizona Mud turtle                                                                     | Arizona-Klappschildkröte<br>Casquito de suroeste, tortuga de los charcos                                                                                                            | Rare               |
| <i>Kinosternon subrubrum</i>     | (Bonnaterre, 1789)                                   | Eastern Mud turtle, Common Mud turtle, Pennsylvania Mud turtle, Mississippi Mud turtle | Gewöhnliche Klappschildkröte, Mississippi-Klappschildkröte<br>Tortuga de lodo oriental, tortuga de pantano común                                                                    | Yes                |
| <i>Kinosternon vogti</i>         | López Luna, Cupul-Magaña, Escobedo-Galván, González- | Vallarta Mud turtle                                                                    | Vallarta-Klappschildkröte                                                                                                                                                           | Rare               |

<sup>8</sup> Species revalidated according to the revision of *Kinosternon scorpioides* (Iverson & Berry 2024), has been referred to as 'pacific population within *K. cruentatum*' in Schilde (2001).

<sup>9</sup> The previous subspecies were recognised as separate species after the revision (Iverson & Berry 2024). According to Rhodin et al. (2021), the taxonomic reference used for Proposal No. 29, *K. scorpioides* is a species complex that was only subdivided into separate species after CITES CoP19.



| Species | Original description                                                                   | Common name | Common name in-ternational                          | Known in the trade |
|---------|----------------------------------------------------------------------------------------|-------------|-----------------------------------------------------|--------------------|
|         | Hernández, Centenero-Alcalá, Rangel-Mendoza, Ramírez-Ramírez & Cazares-Hernández, 2018 |             | Chacuanita de Puerto Vallarta, casquito de Vallarta |                    |

### Morphology and Taxonomy

The mandatory nomenclature for the CITES listings is Fritz & Havaš (2007), which distinguishes 18 species of *Kinosternon*. However, the 9<sup>th</sup> edition of the taxonomic checklist of the world's turtles (Rhodin et al. 2021) was already used for the preparation of the proposal. According to this checklist, 22 species are listed in CITES Appendices I and II. The inclusion of *Kinosternon* spp. in Appendix II (except for the species, *K. cora* and *K. vogti*, included in Appendix I) was on genus level including automatically all species. However, any special protection for individual subspecies in the countries of origin is generally not covered by the convention.

*Kinosternon scorpioides* was revised following the entry into force of the CITES CoP19 listings and the publication of the CITES nomenclature reference for the genus (Hurtado-Gómez et al. 2024, Iverson & Berry 2024). The previous subspecies *K. s. albogulare* and *K. s. cruentatum* (only the populations on the Atlantic side of the distribution area) were raised to species rank, and *K. mexicanum* (from the Pacific side), previously synonymised with *K. s. cruentatum*, was described as the fourth independent species (see below: Distribution).

The outstanding morphological feature of the genus is the special structure of the plastron. It is the only turtle genus that has two hinges across the plastron. Most species have the ability to completely close the shell with the moveable front and rear plastral lobes.

The species differ mainly in the shape of the carapace, but also in colouration and habitus.

For differentiation of the species see Schilde (2001, 2025). An identification key for adult animals of the species known at that time is also included in Annex IV of Proposal No. 29 (CITES 2022).

Some species have striking colourations: *Kinosternon cruentatum*, for example, has specimens with bright red heads in both sexes, and most (but not all!) *K. cruentatum* have red or reddish patterns on the sides of the head. As with many aquatic turtles, the colouration also depends on the living conditions: Animals kept over a light background or with dim lighting are lighter and usually less contrastingly coloured than turtles in their natural habitat, and the reddish head colouration in turtles from the *K. scorpioides* complex can be enhanced by feeding carotenoid-rich foods (Pfau & Wiechert 2003, May 2003, 2009). Colouration cannot be used to identify the species.

Species hybrids have not been observed in the wild, and hybrids of two species have only rarely been bred in captivity – *K. baurii* x *K. subrubrum* (Farkas & Sasvari 1993, Fritz 1995) or *K. subrubrum* x *K. flavescens* (Philippen 2003). There are occasional reports in the social media about hybrids of North American *Kinosternon* species with various *Sternotherus* species.



Fig. 28: North American Mud turtles

- a *Kinosternon baurii*, Florida Keys (M. Schilde)
- b *K. subrubrum hippocrepis* (M. Schilde)
- c *K. subrubrum subrubrum* (M. Herz)
- d *K. subrubrum* without indication of subspecies (S. Ettmar)
- e *K. flavescens* (M. Schilde)
- f *K. subrubrum* without indication of subspecies, mating (X. Wapelhorst)
- g *K. baurii*, ♂ (right) and ♀ (left) (X. Wapelhorst)
- h *K. baurii* hatchling (R. Hentschel).





Fig. 29: Mud turtles from Central America

- a *Kinosternon acutum* (M. Schilde)
- b *K. creaseri* (M. Schilde)
- c *K. scorpioides* (M. Schilde)
- d *K. cruentatum*, Guatemala locale at a breeder's home in Europe (B. Pfau)
- e *K. leucostomum* Veracruz, unusual reddish colour of the light head stripes (M. Schilde)
- f *K. oaxacae* (M. Schilde)
- g *K. herrerae* (M. Schilde)
- h *K. integrum* (M. Schilde)
- i *K. cruentatum*, Guatemala locale, ♂ (left) and ♀ (right) (B. Pfau)
- j *K. cora*, hatchling freshly emerged from the egg (H. Prokop).



Fig. 30: Mud turtles from tropical climates

- a *Kinosternon durangoense* (J.B. Iverson)
- b *K. hirtipes tarascense* (M. Schilde)
- c *K. sonoriense* (S. Ettmar)
- d *K. stejnegeri* (M. Schilde)
- e *K. alamosae* (J.B. Iverson)
- f *K. sonoriense*, note the white barbels (S. Ettmar).

## Distribution and Habitat

### Distribution

*Kinosternon abaxillare*: Limited to the central valley of Chiapas in Mexico, the basin of the Grijalva River, and neighbouring northwestern Guatemala. Type locality: Tuxtla (Gutierrez), near the Chiapas River, Chiapas, Mexico (Baur in Stejneger 1925).

*Kinosternon acutum*: Central Veracruz, Tabasco, south of the Yucatán Peninsula (Mexico) to Belize and north of Guatemala. Type locality: Not known; Gray (1844) later stated 'Central



America'; Schmidt (1941) restricted it to 'British Honduras', Smith & Taylor (1950) indicated 'Cosamaloapam, Veracruz', Mexico as the type locality.

*Kinosternon alamosae*: Distributed in Mexico from Hermosillo, Sonora, in the Pacific coastal lowlands to Guasave, Sinaloa. Terra typica: Rancho Carrizal, 7.2 km north and 11.5 km west of Alamos, Sonora, Mexico, 27° 05' N, 109° 03' W.

*Kinosternon angustipons*: Distributed in the Caribbean lowlands from the Río San Juan on the border of Nicaragua and Costa Rica southwards to the Bocas del Toro Province in Panama. Terra typica: Los Diamantes, Limón Province, Costa Rica.

*Kinosternon baurii* occurs from the Florida Keys across the entire Florida peninsula and along the Atlantic coast to Maryland, USA. Type locality: Brackish water ponds on Key West, Monroe County, Florida, USA.

*Kinosternon chimalhuaca* occurs in Jalisco and Colima (Mexico) south of the Río San Nicolas and east to the Río Cihuatlán along the Pacific coast (approx. 150 km). Type locality: A clear pond located 30 m southeast of Mexico Highway 80, 1.9 km northeast of Barra de Navidad, Jalisco, Mexico (19° 15' N, 104° 43' S [sic]).

*Kinosternon cora* lives in the Pacific coastal plain of the Mexican states of Sinaloa and Nayarit. Terra typica: Sinaloa: Ejido La Concepción (La Concha), Municipio de Escuinapa (22.531758°, -105.450767 at 10 m asl).

*Kinosternon creaseri* is widespread on the northern and central Yucatán peninsula, Mexico. Terra typica: One mile south of the hacienda, Chichen Itza, Yucatán.

*Kinosternon dunni* only occurs in the Colombian district of del Choco from the Río San Juan to the Río Baudó along the Pacific coast, perhaps even further southward to the Valle de Cauca. These turtles inhabit streams and swamps in the catchment areas of the Rio Docampadó, Rio San Juan and Rio Atrato. A specimen from Acandi, Chocó, might represent a natural population of this species in an Atlantic drainage (Rentería-Moreno et al. 2012). Terra typica: Pizarro, Choco, Colombia.

*Kinosternon durangoense*: The species occurs in isolated populations in southern Chihuahua, western Coahuila and eastern Durango (Mexico). Terra typica: 8 km from Ceballos, Lago de los Palomas, Durango, Mexico.

*Kinosternon flavescens*: Mainly in the USA: Northwestern Illinois, eastern Iowa, northeastern Missouri, Nebraska south to Texas, New Mexico, southeastern Arizona to the Río Panuco Basin in Veracruz (Mexico). Terra typica: Waco, Texas. The formerly specially protected subspecies *K. f. spooneri* from Illinois is now considered as belonging to the nominate subspecies.

*Kinosternon herrerae*: Mexico, from southern Tamaulipas, northern Veracruz, eastern San Luis Potosí, Hidalgo and Puebla. Occurs from the Río Tamesi and Río Panuco in Tamaulipas to the Río Acton in Veracruz. Terra typica: Xochimilco, Valley of Mexico' (in error [= inadvertent misstatement]); to 'La Laja, Veracruz', Mexico, by Smith & Taylor (1950), later corrected to 'Tampico', Tamaulipas, Mexico, by Smith & Brandon (1968).

*Kinosternon hirtipes*: Southwest Texas (USA) and northern Chihuahua to Chapala, Zapotlán, San Juanico, Pátzcuaro and the Valley of Mexico. Terra typica: 'Mexico'; restricted by Schmidt (1953) to 'lakes near Mexico City' (= lakes near Mexico City). *K. h. hirtipes*: Mexico (Valley of Mexico, Distrito Federal, Mexico, Morelos). *K. h. chapalaense*: Mexico (Jalisco and Michoa-



cán). *K. h. magdalense*: Mexico (Magdalena Valley in Michoacán). *K. h. megacephalum*: Mexico (Coahuila) – extinct. *K. h. murrayi*: USA (Big Bend area in Texas), Mexico (Coahuila, eastern Chihuahua, Zacatecas, northern Jalisco, northern Michoacán, Sinaloa). The subspecies *K. h. tarascense*: Mexico (around Lake Pátzcuaro in Michoacán) could not be differentiated by genomic analysis from *K. h. murrayi*, extending the range of that subspecies to the southern Mexican plateau across the Rio Lerma drainage (Weaver et al. 2022).

*Kinosternon integrum*: southern Sonora, southern Chihuahua, Sinaloa on the central plateau from Durango southwards to central Oaxaca and south-west Tamaulipas (Mexico). Terra typica: 'Mexico', later restricted by Smith & Taylor (1950) to 'Acapulco, Guerrero', Mexico.

*Kinosternon leucostomum*: The huge distribution area extends on the Atlantic side of Central America from central Veracruz to Colombia and on the Pacific side from Costa Rica to Ecuador. Terra typica: 'N. Orleans; Mexique; Río Sumasinta (Amer. Centr.)', delimited by Schmidt (1941) to the Río Usumacinta, El Peten, Guatemala. *K. l. leucostomum* occurs along the Gulf of Mexico and on the Atlantic side from Belize, Guatemala, Honduras and Mexico to Nicaragua. On the southern border of Nicaragua and the northern border of Costa Rica there is a transition zone to *K. l. postinguinale*, which then occurs from the whole of Costa Rica southwards to Ecuador.

*Kinosternon oaxacae*: River systems of the Río Colotepec and Río Tonameca on the Pacific coast of Oaxaca, Mexico. Terra typica: 11.6 km north of Pochutla (San Pedro Pochutla) along Mexican Highway 175 (approx. 235 m asl), Oaxaca, Mexico (15° 46' N, 96° 28' W).

*Kinosternon scorpioides*: From Mexico to northern Peru across large parts of South America to northern Argentina. Terra typica: Suriname. A genetic analysis (Hurtado-Gómez et al. 2024) revealed that some of the previously described subspecies should be independent species. Iverson & Berry (2024) first analysed the northern populations: The species name *Kinosternon scorpioides* was retained for turtles from Panama, Colombia, Ecuador, French Guiana, Guyana, Brazil, Argentina, Paraguay, Bolivia, Peru and Suriname, as well as Trinidad, although some populations could well still be separated out as separate species. The now independent *Kinosternon albogulare* occurs from Nicaragua, El Salvador, Honduras, Costa Rica, Panama and the offshore Isla Cañas to Isla San Andrés, which belongs to Colombia. *Kinosternon cruentatum* occurs in three separate populations: In the Tampico area in the north of Mexico's Gulf Coast, around Veracruz further south, and throughout the Yucatán Peninsula, i.e. also in Belize and parts of Guatemala. *K. mexicanum*, originally classified as *K. c. cruentatum* but now recognised as a separate species, inhabits the Pacific coast of Mexico from the province of Oaxaca southwards to El Salvador.

*Kinosternon sonoriense*: Colorado River and Bill Williams River in Arizona and California east to the Gila River in New Mexico (USA) and south to the Río-Yaqui Basin in Mexico. Terra typica: Tucson, in Sonora (Arizona, USA). *K. s. sonoriense* occurs in Mexico and the USA (Arizona and New Mexico), in California it is considered extinct. *K. s. longifemorale* lives only in a small desert river, the Sonoyta, in the border region of Arizona (USA) and Sonora (Mexico).

*Kinosternon steindachneri*: Florida, USA, south of the Suwannee River and Jacksonville to the southern tip of the peninsula, but not on the Florida Keys. Terra typica: Orlando (Orange Co.), Florida, USA.

*Kinosternon stejnegeri*: Sonora, Mexico and in south-west Arizona, USA. There are common occurrences with *Kinosternon sonoriense longifemorale* in the Quitobaquito Springs, Arizona,

and a few localities together with *Kinosternon alamosae* in Sonora (Legler & Vogt 2013). Terra typica: Llano, Sonora.

*Kinosternon subrubrum*: The species is distributed over large parts of the USA. Its northernmost occurrence is on Long Island, New York, and the range extends to Florida and the Gulf Coast. Westwards it occurs as far as Texas, Indiana and Illinois. An isolated population lives in north-west Indiana. Terra typica: Originally unknown; Schmidt (1953) places it 'near Philadelphia, Pennsylvania (USA). *K. s. subrubrum* occurs in the eastern part of the species' range to east of the Mississippi River, while *K. s. hippocrepis* is distributed along the Mississippi River and west of it. The intergradation zone of the two subspecies extends from just south of St. Louis to the Gulf of Mexico, and to about Pensacola in the Panhandle of Florida.

*Kinosternon vogti*: Jalisco, Mexico, as far as known so far restricted to the urban area of Puerto Vallarta. Terra Typica: 'urban stream in Puerto Vallarta, Jalisco, Mexico (WSG84, 20°38'24.99'N, 105°13'55.57'W), 10 m asl'.

### Habitat

Mud turtles are active hunters and opportunists that search the bottom of the water for food. Their diet is mainly carnivorous consisting of small animals such as arthropods, molluscs, fish, worms, etc. However, plant food is also occasionally consumed.

Mud turtles live in swamps, shallow, temporary or permanent ponds, they also inhabit slow-flowing streams and rivers and artificial reservoirs. Some species inhabit water bodies within desert-like or sandy grassland areas, others live in water bodies within evergreen or deciduous forest areas. Most species live at altitudes of 0 to 1,700 m asl, only some populations of *K. sonoriense*, *K. integrum* and *K. hirtipes* have been found in the mountains at altitudes of up to around 2,000 m asl.

### Conservation Status and Main Threats

All *Kinosternon* species are included in the CITES Appendices since 2023 (CoP19 Proposal No. 29). *K. cora* and *K. vogti* are included in Appendix I, all other *Kinosternon* spp. in Appendix II.

On 23 February 2023, Guyana entered a reservation against the genus listing of *Kinosternon* species in CITES Appendix II, i.e., the CITES provisions for these species will not be implemented in that country. For the native species *Kinosternon scorpioides*, Guyana published an export quota of 250 animals on 23 September 2023.

EU Council Regulation (EC) No. 338/97: *Kinosternon cora* and *K. vogti*: Annex A, all other *Kinosternon* spp: Annex B.

In Germany, *Kinosternon cora* and *Kinosternon vogti* are strictly protected under Article 7 (2) No 14 a) BNatSchG, all other *Kinosternon* spp. are specially protected under Article 7 (2) No 13 BNatSchG.

In France, *Kinosternon* species (with the exception of *K. subrubrum* and *K. flavescens*) are subject to certification and authorisation (République Française 2024).

## IUCN Red List Status

*Kinosternon abaxillare*: VU (Vulnerable A2cd+4cd, assessed 15 December 2020)

*Kinosternon acutum*: NT (Lower Risk/near threatened, assessed 01 August 1996)

*Kinosternon alamosae*: DD (Data Deficient, assessed 01 March 2007)

*Kinosternon angustipons*: VU (Vulnerable B1+2c, assessed 01 August 1996)

*Kinosternon baurii*: LC (Least Concern, assessed 01 August 2010)

*Kinosternon chimalhuaca*: LC (Least Concern, assessed 01 March 2007)

*Kinosternon cora*: Has not yet been assessed by the IUCN, TFTSG Provisional Red List (2020): VU (Vulnerable).

*Kinosternon creaseri*: LC (Least Concern, assessed 01 March 2007)

*Kinosternon dunni*: VU (Vulnerable B1+2c, assessed 01 August 1996)

*Kinosternon durangoense*: DD (Data Deficient, assessed 01 March 2007)

*Kinosternon flavescens*: LC (Least Concern, assessed 01 August 2010)

*Kinosternon herrerae*: NT (Near Threatened, assessed 01 March 2007)

*Kinosternon hirtipes*: LC (Least Concern, assessed 01 March 2007)

*Kinosternon integrum*: LC (Least Concern, assessed 01 March 2007)

*Kinosternon leucostomum*: Has not yet been assessed by the IUCN

*Kinosternon oaxacae*: DD (Data Deficient, assessed 01 March 2007)

*Kinosternon scorpioides*: Has not yet been assessed by the IUCN

*Kinosternon sonoriense*: NT (Near Threatened, assessed 21 March 2011)

*Kinosternon sonoriense longifemorale*: CR (Critically Endangered A3c, assessed 10 March 2016)

*Kinosternon steindachneri*: LC (assessed as a subspecies of *K. subrubrum* 23 March 2011)

*Kinosternon stejnegeri*: LC (Least Concern, assessed 01 March 2007)

*Kinosternon subrubrum*: LC (Least Concern, assessed 23 March 2011)

*Kinosternon vogti*: CR (Critically Endangered A4cde, assessed 11 March 2022).

A reassessment was planned in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). The following assessments, to be published in 2025, are in press (A.G.J. Rhodin pers. comm. 30/08/2024):

*Kinosternon baurii*: NT

*Kinosternon flavescens*: LC

*Kinosternon sonoriense*: VU

*Kinosternon steindachneri*: DD

*Kinosternon stejnegeri*: NT

*Kinosternon subrubrum*: LC.

The classifications of the different species in the national Red Lists of the countries of origin can be found in detail in the CITES CoP19 Proposal No. 29 (CITES 2022).

### Utilisation and Protection within the Natural Range

*Kinosternon* spp. are caught on a large scale for the local trade and for consumption. Legler & Vogt (2013) discuss the economic, social and cultural significance in more detail. Throughout the species' range in Central and South America, there are farms where they are bred for legal trade. They are an important source of protein for the rural population and are generally considered to promote fertility (CITES 2022).

#### Brazil

*K. scorpioides* is mainly bred and then consumed by the poorer rural population, mostly fed with waste from the fruit canning industry and from slaughterhouses or seafood processing (summary in Pfau & Pempelfort 2018).

#### Costa Rica

Only animals from registered breeding farms may be traded. In 2021, there were 33 registered facilities, most of which kept *K. angustipons*, *K. leucostomum* and *K. scorpioides* (probably *K. albogulare*, which is now recognised as a separate species), mainly for the purpose of environmental education (26%) and in zoos or zoological gardens (24%). Some farms (10%) also breed these turtles and sell the juveniles (Arias Ortega et al. 2016), whereby it is very likely that animals from illegal collections from the wild are also sold. Nothing is known about their use as food. Export is prohibited.

#### El Salvador

The utilisation of all wild animals is subject to the Wildlife Conservation Act of the Ministry of Environment and Natural Resources. Between 2013 and 2020, 46 *K. scorpioides* (but probably the now revalidated *K. mexicanum*) were exported from here, 76% of which to the USA and the rest to the Far East (CITES 2022).

#### French Guiana

Capture is prohibited since 1986 (CITES 2022).

#### Guatemala

The keeping and breeding of turtles is permitted, as is the capture and marketing of turtles from wild populations – but both are subject to authorisation. Management plans are in place for the wild populations to prevent over-exploitation. Mayan culture also includes the consumption of turtle soup, but it is not known whether the relatively small native *Kinosternon* spp. are still consumed in large quantities today.

Many of the *K. cruentatum* kept in Europe are the descendants of animals that were originally exported from Guatemala. Whether *K. mexicanum* are also bred in Guatemala, and whether this species was also exported from there, cannot be ascertained.

#### Mexico

Various *Kinosternon* species were already commercially exploited in Mexico before 1980, especially the meat and eggs of *Kinosternon hirtipes* (Flores-Villela 1980). In 2022, according to Proposal No. 29 (CITES 2022), there were 31 Unidades de Manejo (UMAs) registered with the DGVS SEMARNAT as breeding farms: 21 for *K. leucostomum*, six for *K. integrum*, three for *K.*

*acutum*, three for *K. scorpioides* and one each for the following species: *K. abaxillare*, *K. creaseri*, *K. flavescens*, *K. herrerae*, *K. hirtipes*. It is not known whether there have been any breeding successes worth mentioning for all of the species. In addition to these abovementioned UMAs, there are 20 facilities in Mexico that keep wild animals outside their natural habitat (PIMVS): eight of these keep *K. leucostomum*, seven *K. integrum*, four *K. scorpioides*, two *K. acutum* and one *K. alamosae*, *K. chimalhuaca*, *K. flavescens* and *K. hirtipes*. In most cases, they do not breed themselves, but the farms can obtain juveniles from the UMAs.

The keeping and breeding of the various *Kinosternon* species, whose hatchlings are sold in the UMAs and PIMVS, in private households is usually tolerated, and there are also pet shops and markets that usually sell hatchlings of various tortoise and freshwater turtle species (Pineda-Vázquez et al. 2022). In the week before Easter, various dishes made from boiled, or more rarely grilled, *Kinosternon* spp. are offered in southern Mexico – either in the gastronomic establishments of the UMAs, where mostly captive-bred *K. leucostomum* are prepared, or in specialised restaurants, where illegally wild caught turtles, e.g., of *K. hirtipes*, are often used. The corresponding photos and recipes are easy to find on social media.

In Mexico, the various *Kinosternon* species are therefore traded legally on a large scale, but there is also ongoing illegal trade, often of wild-caught animals in large quantities. In the IUCN SSC Tortoise and Freshwater Turtle Specialist Group, there were several discussions on confiscated turtles, for example those nearly 15,000 turtles, mainly kinosternids, which were already boxed for the transport to China, and confiscated on a Mexican airport, or the 14,000 reptiles and birds, among them many mud turtles, which were found, packed in sales containers, and confiscated in a south Mexican house, or those 250 turtles found in suitcases and sacs in a crashed truck. Cantú & Sanchez (2024) report that between 2019 and 2023, *Kinosternon leucostomum* was the most frequently seized reptile, with a total of 13,718 specimens, and *K. herrerae* was the fourth most frequently seized reptile species, with 3,723 specimens; *K. scorpioides* is in seventh place in these statistics with 269 specimens.

Pfau et al. (2021) discuss some of the recent cases and how to uncover the smugglers and determine the species and verify their origin and local form by forensic methods. There are now also well-organised, regular gangs that collect animals of particularly sought-after, rare species, especially in southern Mexico, or buy them cheaply from the rural population and then smuggle them to the Far East (Felbab-Brown 2022).

According to proposal No. 29, no commercial breeding facilities have yet been licensed for *K. vogti* and *K. cora*, the two species listed on CITES Appendix I.

For *K. vogti*, the ‘Proyecto Casquito de Vallarta’ has now been initiated, which includes, besides research and conservation activities in the natural habitat (Loc-Barragan et al. 2022, Praschag 2023 a, b), in situ breeding at the University of Guadalajara (CUC) to reinforce the natural population, as well as ex situ breeding in Austria for research on the reproduction biology (Blanck & Praschag 2024).

A research project has also been set up for *K. cora* by the CICODEC organisation (Ciencia y Conservación para el Desarrollo de las Comunidades A.C.). The initial aim of the project is to gain a more precise understanding of the natural history of the 47 wild animals of this species that are known to exist. The project team will, in collaboration with the local population, also sample other suitable habitats in the coastal plain of Nayarit and Sinaloa, in order to better plan and implement the necessary conservation measures for this species (Loc-Barragán 2024).



## Nicaragua

There are no known national regulations on protection or trade restrictions for *Kinosternon* species. Géczy et al. (2017) explicitly point out that the so-called *Kinosternon cruentatum* (but probably in reality *K. albogulare*) and *K. leucostomum*, which also originates from there, are freshly wild-caught specimens.

## Perú

In 2019/2020, Peru exported a total of 239 live *K. scorpioides* from farms in the Loreto region (CITES 2022).

## USA

The regulations of the federal states vary greatly, in most cases capture for the trade is prohibited, or subject to authorisation, or only permitted outside fixed closed seasons, and some species may not be bred in captivity in some states, or there are restrictions on the number of individuals that may be kept privately, and sometimes even the transport of live or dead animals is subject to authorisation.

In Arizona, the subspecies *K. sonoriense longifemorale*, which endemic to this region, is classified as endangered under the Endangered Species Act (ESA) and is therefore specially protected. There was also a cross-border conservation project between the nature park in Arizona and two nature parks in Mexico for the conservation of this species (Long 2018), but this can no longer be continued due to the construction of the border fence, as direct cooperation between the two nature parks is no longer possible without a border crossing. The unique spring biotope in these parks is being severely damaged by the extraction of large quantities of water – the water is needed for the concrete for the foundations of the border fence (Olivera 2023). The prospects for the conservation of these turtles in the USA are not good, and great efforts would also have to be made in Mexico to ensure that these turtles (and other endangered species in this habitat) do not become extinct (Grageda Garcia 2023).

There are repeated reports of arrests or convictions when pet dealers have attempted to declare wild-caught *Kinosternon baurii* as captive-bred and export them to Europe and the Far East (see e.g. U.S. Attorney's Office, Southern District of Florida 2024). Whether these animals were actually sent to Europe appears doubtful, as there has been no evidence of *Kinosternon* spp. of unclear origin in recent years, and the prices for healthy captive-bred and adult animals are not high enough to make smuggling worthwhile (see below). In the Far East, on the other hand, *Kinosternon* spp. are highly sought after (at somewhat higher prices than in Europe), but a genuine overview of the market there is almost impossible to obtain. Easter & Carter (2024) have analysed the LEMIS database and report a total of only ten confiscated export specimens of *Kinosternon* spp. destined for export between 1999 and 2018, and also very small numbers of animals that were legally exported to Europe, while the figures for legal exports to the Far East were much higher.

A more recent analysis of legal international exports from the USA, from the LEMIS database in the years 2020–2023 (UNEP-WCMC 2024), showed that 92,581 live *K. baurii* were exported during this period, mainly to East Asia. 37% of these were registered as wild-caught and 29% as captive-bred. For *K. flavescens*, there are a total of 17,089 export records, almost exclusively to East Asia, of which 65% were wild-caught. *K. sonoriense* was only exported in 2015 and 2016, a total of 23 live animals, of which 91% were captive-bred. The number of exported *K. subrubrum*, almost exclusively to East Asia, increased significantly from 2020 onwards, a total

of 82% of these animals were registered as wild-caught. No database entries were found for *K. hirtipes*, *K. steindachneri*, and *K. stejnegeri*.

## Threats

The main threat is the loss of habitats (deforestation, burning for pasture, urban sprawl and habitat fragmentation due to road construction, and of course the drying up and/or pollution of water bodies). The already very rare *Kinosternon vogti* in particular is threatened by the construction of a road that cuts through its small remaining habitat and by a planned hotel project (Praschag 2023), but other species also suffer from similar construction projects. Collection for use as food or traditional medicine, or to a lesser extent for jewellery making or local pet keeping, also plays a role. Especially in the case of the newly described species, targeted capture for illegal trade is also contributing to the decline of the species in the wild.

## Reproduction

| Topic                              | Details on the Reproduction of <i>Kinosternon</i> spp.                                                                                                                                                                                                                                                                                    |
|------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | Adult ♂♂ with a considerably larger tail. ♂♂ of many species have clasping organs on the back of their legs.                                                                                                                                                                                                                              |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                |
| Sexual maturity                    | North American species at about 4–7 years<br>Species from arid areas in Mexico and tropical species at about 5–8 years.                                                                                                                                                                                                                   |
| Mating                             | North American species: in autumn before hibernation or after the end of hibernation in spring<br>Species from arid areas in Mexico and tropical species: before or after aestivation/brumation.                                                                                                                                          |
| Nesting season                     | North American species: April to October<br>Species from arid areas in Mexico: May to September<br>Tropical species: September to June.                                                                                                                                                                                                   |
| Number of eggs/clutches per season | North American species: In the wild 1–9 eggs/clutch, up to 4 clutches/year, in human care sometimes even more<br>Species from arid areas in Mexico: In the wild 1–9 eggs/clutch, up to 2 clutches/year, in human care possibly more<br>Tropical species: In the wild 1–9 eggs/clutch, up to 4 clutches/year, in human care possibly more. |
| Egg size/hatchling size            | North American species: eggs about 22–32 x 13–19 mm, hatchlings about 20–30 mm CL<br>Species from arid areas in Mexico: eggs about 25–35 x 13–19 mm, hatchlings about 20–30 mm CL<br>Tropical species: eggs about 25–35 x 13–19 mm, hatchlings about 20–30 mm CL.                                                                         |
| Incubation and hatching            | North American species: 80–130 days in the wild<br>Species from arid areas in Mexico: 120–345 days, depending on embryonic diapause and/or embryonic aestivation<br>Tropical species: 120–345 days, depending on embryonic diapause and/or embryonic aestivation.                                                                         |
| Sex determination                  | TSD Ia or TSD II.                                                                                                                                                                                                                                                                                                                         |
| Sperm storage                      | North American species: yes<br>Species from arid areas in Mexico: probably yes<br>Tropical species: yes.                                                                                                                                                                                                                                  |

## Husbandry and Captive Breeding **A–B/A–C**

Three species groups can be distinguished among the *Kinosternon* species, which have very similar requirements for keeping and breeding:

**North American mud turtles:** *K. baurii*, *K. flavescens*, *K. subrubrum*, *K. steindachneri*. Assessment of difficulty for husbandry **A** breeding **A**

**Mexican mud turtles from arid regions:** *K. alamosae*, *K. durangoense*, *K. hirtipes*, *K. sonoriense*, *K. stejnegeri*. Assessment of difficulty for husbandry **B** breeding **C**

**Tropical mud turtles:** *K. abaxillare*, *K. acutum*, *K. albogulare*, *K. angustipons*, *K. chimalhuaca*, *K. cora*, *K. creaseri*, *K. cruentatum*, *K. dunni*, *K. herrerae*, *K. integrum*, *K. leucostomum*, *K. mexicanum*, *K. oaxacae*, *K. scorpioides*, *K. vogti*. Assessment of difficulty for husbandry **A** breeding **C**.

The most common species that are kept and regularly bred in Europe are *Kinosternon acutum*, *K. baurii*, *K. leucostomum*, species from the *K. scorpioides* species complex and *Kinosternon integrum*. All other *Kinosternon* species have also been bred in human care, but not quite as frequently.

If the species group is not specified in the following table, the corresponding information applies to all *Kinosternon* spp.

| Topic                                                           | Data for <i>Kinosternon</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | North American species: 2–3 months hibernation/brumation at about 10°C.<br>Species from arid areas in Mexico: 2–3 months aestivation.<br>Tropical species: Not all these species need a dormancy period.                                                                                                                                                                                                                                                                                                                                                                       |
| Husbandry requirements                                          | North American species: low requirements, water temperature 20–25°C, basking place 35–40°C.<br>Species from arid areas in Mexico: rather high, water temperature 26–28°C, basking place up to 45°C; several months of aestivation in dry substrate are mandatory.<br>Tropical species: water temperature 23–28°C, basking place 35–40°C.                                                                                                                                                                                                                                       |
| General characteristics, difficulties with keeping and breeding | Usually not compatible with conspecifics, mating under supervision is recommended.<br>North American and tropical species: ♂♂ should better be kept individually, ♀♀ can sometimes be kept in a group. In the case of the species from arid areas in Mexico, the ♀♀ should always be kept individually.                                                                                                                                                                                                                                                                        |
| Care of the young, technical and time effort                    | Low effort, juveniles should be kept at a relatively low water level and provided with climbing opportunities (underwater plants, roots, etc.) so that they can easily reach the water surface.                                                                                                                                                                                                                                                                                                                                                                                |
| Life expectancy                                                 | North American species: regularly 50 years and more, no decline in reproductivity has been observed.<br>Species from arid areas in Mexico: No exact empirical values available – long-lived.<br>Tropical species: Experience is not available for all species; individual animals of various species from this group have lived > 80 years in captivity.                                                                                                                                                                                                                       |
| Frequency of private breeding and reproduction in zoos          | Rarely kept in zoos, as these turtles are rather inconspicuous and sometimes incompatible with other species.<br>North American species in private households: frequently kept and sometimes also bred – but breeding is not always attempted due to the long incubation period. <i>K. baurii</i> has been regularly listed in the breeding statistics of the German Chelonia Group since 1991. The NBSV's offspring statistics include 477 offspring of this species until 2020, as well as 45 <i>K. flavescens</i> , 146 <i>K. subrubrum</i> and 4 <i>K. steindachneri</i> . |

|                                      |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|--------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                      | <p>Species from arid areas in Mexico and tropical species: Most species are rarely kept, but are then often selectively bred. <i>Kinosternon acutum</i>, <i>K. leucostomum</i> and the species from the <i>K. scorpioides</i> species complex are frequently kept and bred. <i>K. acutum</i> has regularly appeared in the offspring statistics of the AG Schildkröten since 1990, with new breeders joining in regularly. The offspring statistics of the NBSV until 2020 lists 40 juveniles of <i>K. acutum</i>, 127 of <i>K. cruentatum</i>, 89 of <i>K. leucostomum</i>, 58 of <i>K. scorpioides</i>, and <i>K. sonoriense</i> was bred in the Netherlands for the first time in 2022, 6 juveniles hatched. No breeding statistics are available for other European countries, but there is a lively exchange between breeders in different countries.</p> <p>Of particular interest are the details for the two species that were placed directly on CITES Appendix I: While only one ♂ specimen of <i>K. vogti</i> was known to have lived in Europe for around ten years before this species was scientifically recognised, and then sold to Far East because no ♀ could be found for breeding attempts, several specimens of <i>K. cora</i> (under various fantasy names) lived in Europe from around 1980 onwards, although they were initially only bred very rarely because the conditions for successful incubation were not yet known. It was not until around 2020, when this species was scientifically recognised and the exact place of origin was revealed, that breeding became more regular.</p> |
| Breeding difficulty evaluation       | <p>North American and tropical species: Easy, a diapause may be required.</p> <p>Species from arid areas in Mexico: Difficult due to pronounced diapause of the embryo and often subsequent aestivation in the egg, i.e. the required substrate or air humidity is not constant during incubation.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Mortality in the first years of life | Low.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| F2 generation bred in captivity      | <p>North American species: Yes for all species, frequently.</p> <p>Species from arid areas in Mexico and tropical species: Mostly unknown, but for some <i>K. hirtipes</i> subspecies, subsequent captive generations have already been recorded. Due to frequent taxonomic changes, it is not always easy to trace the breeding history of the tropical species over more than one generation on the basis of older publications or oral traditions.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Commercial breeding/ ranching        | <p>North American species: Some commercial breeders, for example in Alabama.</p> <p>Species from arid areas in Mexico: A few licensed breeding facilities in Mexico.</p> <p>Tropical species: Some species are being bred on a larger scale in their countries of origin.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Interviews/ Surveys/ Consultations   | <p>For almost all species several experienced private breeders throughout Europe could be interviewed, only for <i>K. vogti</i> one private breeder in the EU has been asked for his experiences. In addition, some private individuals with many years of experience in keeping the species, but who were unable to assemble breeding groups, contributed to this collection of information. Additional information comes from discussions in the long-established working groups in Europe, and from the literature (see below). Many <i>Kinosternon</i> species are obviously also being bred in China in large numbers and colour morphs, but the breeders could not be personally contacted via facebook.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |

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**Maik Schilde (25.07.2024)**

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***Staurotypus* Wagler, 1830**

| Species                        | Original description | Common name               | Common name international                                                                    | Known in the trade |
|--------------------------------|----------------------|---------------------------|----------------------------------------------------------------------------------------------|--------------------|
| <i>Staurotypus salvinii</i>    | Gray, 1864           | Chiapas Giant Musk turtle | Salvin's Kreuzbrust-Schildkröte<br>Guao de Tres Lomos, crucilla, tortuga almizclera crucilla | Yes                |
| <i>Staurotypus triporcatus</i> | (Wiegmann, 1828)     | Mexican Giant Musk turtle | Große Kreuzbrust-Schildkröte<br>Guao                                                         | Yes                |

**Morphology and Taxonomy**

The special morphological feature of the genus *Staurotypus* is: A strongly reduced plastron, which is cross-shaped and loosely connected by connective tissue, and three distinct longitudinal keels on the dorsal carapace.

Only two species are distinguished, which can be easily identified as adults by their final size and colouration: *Staurotypus salvinii* remains smaller (♂♂ of the large form from the Pacific coast of Mexico can reach approx. 25 cm CL, ♀♀ remain smaller; the smaller form from Guatemala to El Salvador only reaches about 20 cm even in ♂♂) and has a brown or grey head with, in younger animals, small, orange spots and without stripes on the light jaw edges (rarely pale spots). *S. triporcatus* grow significantly larger (up to about 38 cm CL) and have an almost black head with larger, very light spots and spotted or striped jaw edges. Juveniles of *S. triporcatus* are usually vividly patterned in contrasting black and white, whereas *S. salvinii* juveniles are rather dark.

The distinguishing features of the two species are detailed in CITES CoP19 Proposal No. 30 (CITES 2022).

**Distribution and Habitat**

Giant Musk turtles are mainly active hunters and opportunists, feeding on snails and mussels in particular. Overall, the food spectrum includes arthropods, molluscs, fish, worms, etc. However, plant food is also occasionally consumed, whereby *S. salvinii* can have up to 25% plant material in its stomach in the wild (Dean 1980). Stomach content analyses in the field are hardly possible with the even more defensive and larger *S. triporcatus*, which can also crack molluscs with its strong jaws (Vogt & Guzman 1988).

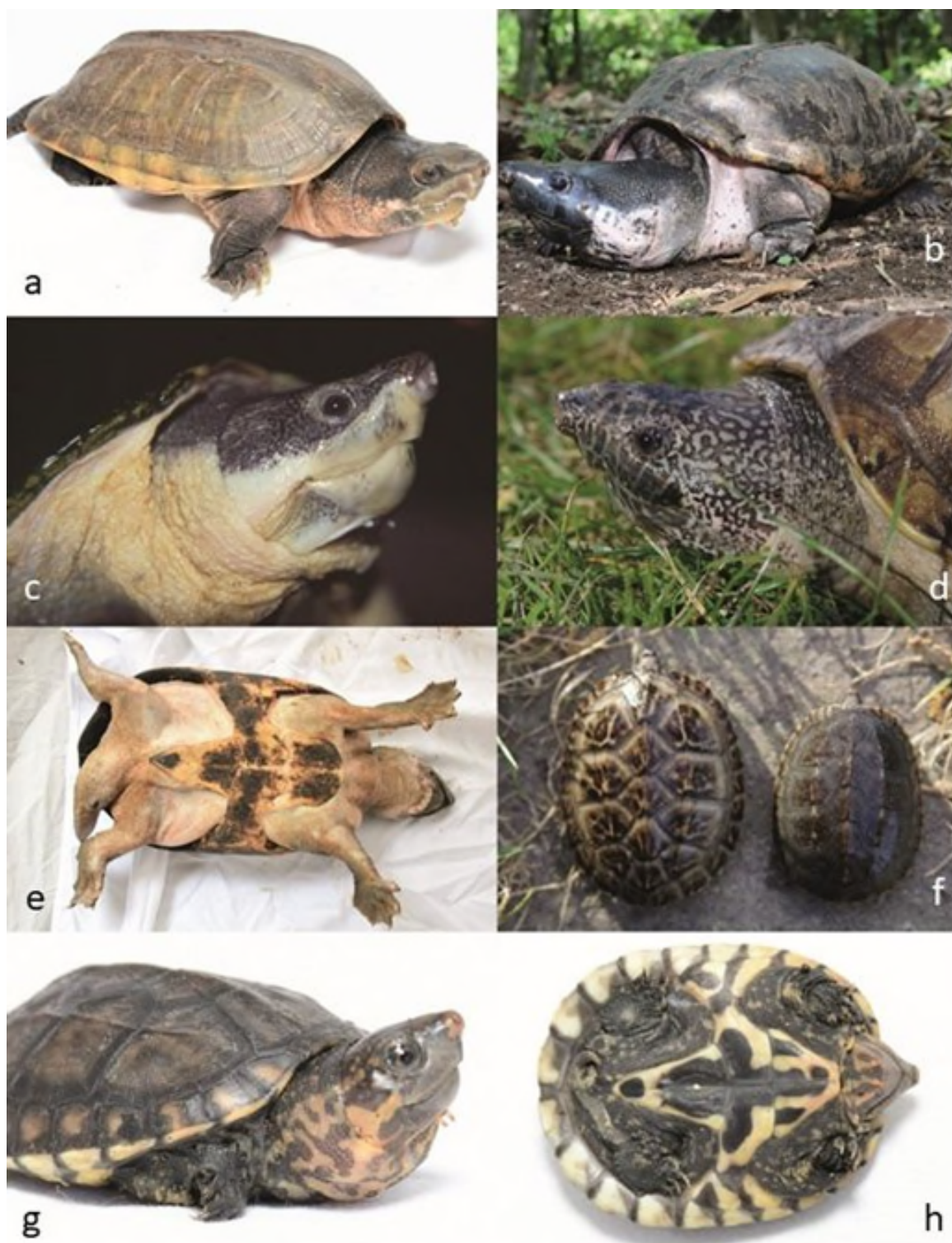


Fig. 31: *Staurotypus* spp. distinctive features

- a *S. salvinii* from a mangrove habitat in Chiapas, showing the reddish skin colouration caused by tannins (E. Reyes-Grajales)
- b *S. triporcatus* in the natural habitat (E. Reyes-Grajales)
- c *S. salvinii* (M. Schilde)
- d *S. triporcatus* showing the patterned head and the striped jaws (M. Schilde)
- e Plastron view of *S. salvinii* (E. Reyes-Grajales)
- f Juveniles of *S. triporcatus* on the left, and *S. salvinii* on the right (M. Schilde)
- g *S. salvinii*, juvenile (E. Reyes-Grajales)
- h *S. salvinii*, juvenile, plastron view (E. Reyes-Grajales).

*Staurotypus salvinii*: This species is widespread in the lowlands of the Pacific side of Central America from eastern Oaxaca via Chiapas (Mexico) through southern Guatemala to El Salvador. Type locality: Huamuchal, Guatemala (today the correct locality name is 'Huamúchil, Oaxaca, Mexico').

*Staurotypus triporcatus*: The distribution area extends from central Veracruz, Tabasco, Campeche, the southernmost part of the Yucatán Peninsula via Belize, the north of Guatemala to north-west Honduras. Type locality: Río Alvarado, Veracruz (Mexico).

*Staurotypus salvinii* inhabits permanent or temporary, stagnant or slow-flowing, usually turbid, water bodies.

*Staurotypus triporcatus* prefers permanent waters such as larger lakes, lagoons, canals, mangrove swamps, rivers and their oxbow lakes. This species also occurs in brackish water.

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal No. 30).

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

Article 7 (2) No 13 Giant Musk turtles have been classified as 'dangerous' in some European countries, e.g. France, and therefore require in these cases a certificate of competence and an authorisation for keeping them.

### IUCN Red List Status

*Staurotypus salvinii*: Near Threatened (NT, assessed 01 August 1996).

*Staurotypus triporcatus*: Near Threatened (NT, assessed 01 August 1996).

For many Central and South American turtle species, a reassessment was planned in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). The following assessments for *Staurotypus* spp., are in press and will be published in 2025 (A.G.J. Rhodin pers. comm. 30/08/2024):

*Staurotypus salvinii*: EN

*Staurotypus triporcatus*: VU.

### Red List Status in the Range Countries

#### Guatemala

*Staurotypus salvinii*: Categoría 2 – Endangered (En peligro, CONAP 2021)

*Staurotypus triporcatus*: Categoría 2 – Endangered (En peligro, CONAP 2021).

#### Mexico

*Staurotypus salvinii*: Sujeta a protección especial – specially protected (SEMARNAT 2019)

*Staurotypus triporcatus*: Amenazada – vulnerable (SEMARNAT 2019).



## Utilisation and Protection within the Natural Range

The large *Staurotypus triporcatus*, in particular adults, are still caught in the wild for consumption, because they are a traditional Easter dish. As a result, the wild populations in the easily accessible areas are in significant decline – whether this is also the case within the protected areas is not known. *S. salvinii* is also very important to the rural population as a source of meat and natural medicine (Ávila-Nájera et al. 2018).

Capturing live animals for the trade is still an important source of income for the local population, as the repeatedly published confiscation reports demonstrate (CITES 2022). The laws and regulations for the protection of wild populations are difficult to enforce (Masés-García 2021, Felbab-Brown 2022, Méndez & Olivera 2022), and there are still seizures of large numbers of wild-caught animals, mainly *S. triporcatus*, destined for illegal export (CITES 2022). Cantú & Sanchez (2024) report that a total of 931 *S. triporcatus* and 211 *S. salvinii* were confiscated in Mexico between 2019 and 2023, which puts them in sixth and eighth place in the statistics for the most frequently confiscated reptile species in the country.

A first reference to the breeding of *S. triporcatus* in Mexico (Tejeda 2002) points out that this is illegal and that most of the allegedly bred animals are eaten directly because breeding is not worthwhile. A workshop on the breeding of Mexican freshwater turtles in the UMAs (Unidades de Manejo de Vida Silvestre) was held as early as 2009, at which the breeding methods for the most economically valuable species were discussed (Zenteno Ruiz 2009), later the requirements for the breeding centres were specified in more detail (Carrillo Lázaro 2018) and now the six largest breeding farms for *S. triporcatus* in Tabasco are well documented (Zenteno Ruiz et al. 2019b) and a breeding centre for *S. salvinii* in Chiapas has also been mentioned (Contreras-Hernández et al. 2021). Until 2022 a total of 14 UMA/PIMVS had been licensed for the breeding of *S. triporcatus*; no more recent information could be found for *S. salvinii* (CITES 2022).

In commercial breeding facilities, the animals are fed with offal, fish meat, trout pellets and fruit, and the large animals are kept individually or in pairs in small tanks. No published information on the incubation methods in these farms could be found. The hatchlings are reared in larger groups until they are ready for sale, as can be inferred from the corresponding YouTube video (Spyder Ña 2013).

Legal exports of live animals mostly go to China (86%), followed by Hong Kong SAR (11%), Japan (2%) and the USA (1%) (CITES 2022). Most legal exports of the two species now probably consist of offspring from these breeding farms or from unlicensed private breeders. There is no obvious evidence of wild-caught specimens on photos of imports to Europe that are openly offered on the internet (cf. Stärk et al. 2018).

The authors of the proposal No. 30 (CITES 2022) still assumed that these species are not bred in Southeast Asia (see also Reynoso et al. 2021), and there is also no indication on captive breeding of these species in the large review of turtle breeding in People's Republic of China (Tian et al. 2016). However, at least the more sought-after of the two species, *Staurotypus triporcatus*, is reported to be farm-bred in China in the meantime (Hong et al. 2022), and Malaysia and South Korea are also export countries for this species. *Staurotypus triporcatus* is now also offered for sale at relatively moderate prices on internet pet portals in China (Ji et al. 2020).



## Threats

The main threat to *S. triporcatus* is the capture of large, i.e. already reproducing, animals for direct consumption and the sale of meat at local markets. The animals are easily caught at the beginning and end of the rainy season when the water level is low (Reynoso Rosales 2021).

Habitat loss due to the utilisation of natural habitats for agriculture and livestock farming also poses a major threat to both species. In particular, the burning of old vegetation before tillage/grazing poses a major threat to both species. In agricultural areas, the animals can still survive for a while if the water bodies are preserved, but many water bodies are completely disappearing due to road construction to develop the areas (CITES 2022) and the animals often fall victim to traffic and the tillage machineries used.

For *S. salvinii*, the removal of large mangrove areas to create direct access to the sea for new large hotel developments is significant, as some populations have already become extinct in such areas on the Pacific coast of Mexico (Reyes-Grajales 2023, pers. comm.).

## Reproduction

| Topic                              | Details on the reproduction of <i>Staurotypus</i> spp.                                                                                                                                                                                                                                                                                |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | Adult ♂♂ have considerably longer, thicker tails.                                                                                                                                                                                                                                                                                     |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                            |
| Sexual maturity                    | In captivity both species are reproductively active at approx. 6–8 years, in the wild <i>S. triporcatus</i> may already be sexually mature at 4–5 years, ♂ > 18 cm, ♀ > 22 cm CL.                                                                                                                                                     |
| Mating and nesting                 | Mating season is August to September, sandy soil is chosen for nesting.                                                                                                                                                                                                                                                               |
| Reproductive season                | <i>S. salvinii</i> : Oviposition from October on<br><i>S. triporcatus</i> : Vitellogenesis May–June, oviposition August–March.                                                                                                                                                                                                        |
| Number of eggs/clutches per season | <i>S. salvinii</i> in the wild 2–12 eggs per clutch, up to 3 clutches per year, in human care possibly more<br><i>S. triporcatus</i> in the wild 3–22 eggs per clutch (on average 9,8), up to 6 clutches per year, in human care possibly more.                                                                                       |
| Egg size/hatchling size            | <i>S. salvinii</i> approx. 38–43 x 18–21 mm, hatching in the wild March to April, at the end of the dry season<br><i>S. triporcatus</i> approx. 42 x 24 mm, 12–17 g, hatching in the wild from June on, at the beginning of the rainy season. Hatchlings 8–12 g and 51–58 mm CL.                                                      |
| Incubation and hatching            | <i>S. salvinii</i> 80–224 days<br><i>S. triporcatus</i> 108–260 days until hatching. Initial diapause (if the eggs have been laid in very wet ground with low oxygen content) up to 80 days, after that the embryonic development begins.                                                                                             |
| Sex determination                  | Genetic sex determination, X/Y sex chromosomes.<br>A temperature effect was also observed in one breeding group of <i>S. salvinii</i> (Ewert & Nelson 1991), but whether this was the offspring of an animal after sex reversal or whether this breeding group was the smaller form from Guatemala had not been investigated further. |
| Sperm storage                      | Possibly, but no direct observations available.                                                                                                                                                                                                                                                                                       |

## Husbandry and Captive Breeding B/B

Both species have nearly the same husbandry requirements, merely adult *S. triporcatus* need larger tanks than adult *S. salvinii*. due to their considerably larger size.

| Topic                                                           | Data for <i>Staurotypus</i> spp.                                                                                                                                                                                                                                                                                                       |
|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Annual rhythm with dry period as in the region of origin.                                                                                                                                                                                                                                                                              |
| Husbandry requirements                                          | Water level for adults approx. 40 cm, 26–28°C water temperature, a basking place is not absolutely necessary.                                                                                                                                                                                                                          |
| General characteristics, difficulties with keeping and breeding | Both sexes can be rather intolerant towards conspecifics, keeping each animal individually is strongly recommended. Mating under supervision.                                                                                                                                                                                          |
| Care of the young, technical and time effort                    | The effort is low. Keeping the juveniles at a relatively low water level and providing climbing opportunities (underwater plants, roots, etc.) are required so that they can easily reach the water surface.                                                                                                                           |
| Life expectancy                                                 | 50 years or more.                                                                                                                                                                                                                                                                                                                      |
| Frequency of private breeding and reproduction in zoos          | Commonly kept and bred by private keepers, but rather rare in zoos, since the animals have to be kept solitary. One hatchling of <i>S. salvinii</i> has been reported for Dortmund Zoo in 2020 and one in 2021 (KiZooDo 2020).                                                                                                         |
| Breeding difficulty evaluation                                  | Demanding due to pronounced diapause of the embryo and often subsequent aestivation in the egg.                                                                                                                                                                                                                                        |
| Mortality in the first years of life                            | Low.                                                                                                                                                                                                                                                                                                                                   |
| F2 generation bred in captivity                                 | Yes, both species have frequently been bred to F2 and subsequent generations.                                                                                                                                                                                                                                                          |
| Commercial breeding/ ranching                                   | <i>S. triporcatus</i> farming in Mexico is rather common, <i>S. salvinii</i> is rarely farmed.                                                                                                                                                                                                                                         |
| Interviews/ Surveys/ Consultations                              | > 15 experienced breeders in the EU took part in the collection of information. All of them have been breeding successfully with at least one of the two species for several years. In addition, 4 private individuals who are currently rearing subadults for their own breeding groups have also contributed with their experiences. |

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**Maik Schilde und & Ronny Bakowskie (01.05.2024)**

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***Sternotherus* Bell in Gray, 1825**

| Species                         | Original description                     | Common name                         | Common name international                                                                                                                               | Known in the trade |
|---------------------------------|------------------------------------------|-------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Sternotherus carinatus</i>   | (Gray, 1856)                             | Razorback Musk turtle               | Gekielte Moschusschildkröte, Dach-Moschusschildkröte<br>Gekielde muskusschildpad                                                                        | Yes                |
| <i>Sternotherus depressus</i>   | Tinkle & Webb, 1955                      | Flattened Musk turtle               | Flache Moschusschildkröte<br>Platte muskusschildpad                                                                                                     | Rare               |
| <i>Sternotherus intermedius</i> | Scott, Glenn & Rissler, 2017             | Intermediate Musk turtle            | Alabama-Moschusschildkröte                                                                                                                              | Rare               |
| <i>Sternotherus minor</i>       | (Agassiz, 1857)                          | Loggerhead Musk turtle              | Kleine Moschusschildkröte, Zwerg-Moschusschildkröte<br>Kleine muskusschildpad                                                                           | Yes                |
| <i>Sternotherus odoratus</i>    | (Latreille in Sonnini & Latreille, 1801) | Common Musk turtle, stinkpot turtle | Gewöhnliche Moschusschildkröte<br>Cinosterne odorant<br>Tartaruga del muschio comune<br>Tortuga Almizclera<br>Gewone muskusschildpad<br>Klapavka obecná | Yes                |
| <i>Sternotherus peltifer</i>    | Smith & Glass, 1947                      | Stripeneck Musk turtle              | Nackenstreifen-Moschusschildkröte                                                                                                                       | Yes                |

The accepted CITES standard nomenclature is Fritz & Havaš (2007) with four *Sternotherus* species. Since this publication, there have been significant taxonomic changes in the genus including the description of *Sternotherus intermedius* and the inclusion of *Sternotherus peltifer* as a subspecies of *Sternotherus minor*. Here, the nomenclature according to Rhodin et al. (2021) with six *Sternotherus* species is used.

At first glance, *Sternotherus* spp. appear similar to the Mud turtles (*Kinosternon* spp.), but the *Kinosternon* species usually have two distinct transverse hinges in the plastron (the posterior hinge has been secondarily lost in *K. herrerae*, for example), while *Sternotherus* spp. only have one (the anterior) rather indistinct hinge and cannot close their shell as most *Kinosternon* spp. can. The carapace of most *Kinosternon* species is not keeled (exception for example *K. s. scorpioides* with three distinct keels even in adults) and no skin is visible between the plastron plates.





Fig. 32: *Sternotherus* spp., adults

- a *S. carinatus* (X. Wapelhorst)
- b *S. intermedius* (X. Wapelhorst)
- c *S. minor*, large form (X. Wapelhorst)
- d *S. minor*, 5 year old male with enlarged head from crushing hard-shelled prey (X. Wapelhorst)
- e *S. peltifer* (H. Pempelfort)
- f *S. odoratus*, young ♀ with the typical stripe pattern on the cheeks (R. Hentschel).

## Morphology and Taxonomy

***Sternotherus carinatus*** – The Razorback musk turtle has no gular shield. It has the most pronounced dorsal keel of all musk turtles and is the largest among the musk turtles. In the wild, adults have a straight carapace length of 10–16 cm (Iverson 1999), but in human care the ♂♂ can grow up to 20.9 cm in carapace length, and are usually much larger than the ♀♀ (14.0 cm).

***S. depressus*** – The Flattened musk turtle has the lowest shell of all musk turtles. They live in crevices between the large stones in the riverbed. As juveniles, *S. depressus* still have a keel in the middle of the back shell and flared carapace margins, but no lateral keels. They have a reticulated pattern on the neck and head. ♂♂ of *S. depressus* reach 9.9 cm, while the ♀♀ grow slightly larger at 12.5 cm (Melancon et al. 2011).

***S. intermedius*** – The Intermediate musk turtle has a dark-spotted head on a lighter background, with a slightly hinted stripe pattern on the side of the head and neck. There may be a single gular shield or two separate ones. There is a keel on the vertebral plates, but the lateral keels on the carapace are usually reduced or absent. There are two barbels on the chin (Scott 2016, Scott et al. 2018). Adult *S. intermedius* can grow to a carapace length of 7.3–8.9 cm.

***S. minor*** – Juvenile Loggerhead musk turtles have three low keels on the carapace, one along the vertebral column, and another one on each side on the costal plates. However, in adult turtles, the keels are often no longer visible. On the head, there are dark spots on a light background. At the front of the plastron, there is a single gular. On the throat, there are two barbels. In the wild, these turtles have a CL of 80–135 mm, with the ♀♀ growing larger than the ♂♂ (Iverson 1977). In Europe, there are two forms which are being bred separately, the so-called small form and the large form. The vast majority of specimens belong to the small form and rarely reach more than 10 cm in carapace length. The large form regularly reaches 13–15 cm.

***S. odoratus*** – The only rather grey musk turtle, the other species are brownish. Younger specimens with two distinct yellow stripes on the head – one runs from the tip of the nose above the eye to the neck, the other from the lower edge of the eye past the corner of the mouth to the throat. Sometimes there is a third stripe from the tip of the lower jaw to the throat, or a light pattern on the chin. These patterns are no longer visible in older animals. Four barbels on chin and throat. Southern populations can be smaller (animals from Florida with an average CL of 6–7 cm) and usually brighter and much more patterned than the rather uniformly dark northern populations (Indiana & Ontario with an average CL of 10 cm) (Scott pers. comm. 2024). The maximum carapace length is 16.0 cm, with male *S. odoratus* remaining smaller with a maximum of 13.7 cm.

***S. peltifer*** – In the Stripeneck musk turtle, juveniles have a medial keel on the carapace, but no lateral keels (Scott et al. 2019, Welc 2021). There is a line-like pattern on the head and neck, particularly on the lateral portions of the neck behind the head, and the top of the head may exhibit some reticulation pattern, but not discrete spots. There are two gular scutes (the specimens kept in Europe often have only one) and two barbels on the chin. The maximum carapace length is 11.7 cm for ♀♀ and 10.0 cm for ♂♂.

**Key to the genus *Sternotherus* (after Ernst & Lovich 2009, modified):**

- 1a)** Two light stripes on the head, four barbels on the chin and throat, non-overlapping vertebral carapace plates: ***Sternotherus odoratus***
- 1b)** no light stripes on the side of the head, only two barbels on the chin, overlapping vertebral carapace plates: **2**
- 2a)** gular shield absent, pronounced dorsal keel: ***Sternotherus carinatus***
- 2b)** single or paired gular shield present, dorsal keel not strongly developed, often two dorso-lateral keels in juveniles: **3**
- 3a)** carapace broad and flattened, sides sloping at an angle greater than 100°, mean angle/carapace height ratio is 8:1 or greater: ***Sternotherus depressus***
- 3b)** carapace not strongly flattened, sides sloping at an angle of less than 100°, mean angle/carapace height ratio is 5:1 (in specimens with a dorsal keel): **4**
- 4a)** head with dark spots on a light background; three keels in juveniles, often no longer visible in adults; single gular shield: ***Sternotherus minor***
- 4b)** reticulated pattern, with more spots on the head and fine stripes on the neck; three keels in juveniles, often no longer visible in adults, single or paired gular scutes: ***Sternotherus intermedius***
- 4c)** linear pattern on the head and neck; dorsal keel present in juveniles, but no lateral keels, two gular scutes: ***Sternotherus peltifer*.**

**Distribution and Habitat****Distribution**

Musk turtles originated in North America. While *Sternotherus odoratus* is found as far north as Canada, the other species are restricted to the United States. There are some unconfirmed sightings from Chihuahua, Mexico, maybe that this species is now extirpated there.

*S. carinatus*: Alabama, Arkansas, Louisiana, Mississippi, Oklahoma, Texas.

*S. depressus*: Alabama, in the Black Warrior River basin upstream of Bankhead Dam.

*S. intermedius*: Alabama and Florida, Choctawhatchee River and Escambia River with their tributaries.

*S. odoratus*: Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, Rhode Island

*S. peltifer*: Alabama, Georgia, Louisiana, Mississippi, North Carolina, Tennessee, Virginia.

## Habitat

Musk turtles mainly inhabit permanent waters, and less frequently seasonal wetlands that regularly dry out. *S. odoratus* is really the only pond/lake/marsh dwelling member of the genus, even if it also can be found in springs and rivers. Flowing water is the primary habitat for the rest of the genus (again with some exception). The boundary between *S. depressus* and *S. peltifer* in the Black Warrior River is rock (*depressus*) to sand (*peltifer*) bottom. *S. carinatus* inhabits predominantly rivers and streams with strong currents and soft bottoms that have pools with deep water. However, they can also be found away from flowing water, for example in cattle watering holes. *S. intermedius*, *S. peltifer*, and *S. minor* can mostly be found in waters with soft bottoms, such as ponds, lakes and swamps with proliferating aquatic plants. Many of the famous spring runs in Alabama, Mississippi and Florida with these species are sand bottomed, and watching *S. minor* is one of the attractions for snorkelers in the clear spring rivers of Florida.

## Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal 31).

EU Council Regulation (EC) No 338/97 Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

In some European countries, e.g. France, *Sternotherus odoratus* is classified as potentially invasive and are therefore subject to certification and authorisation.

## IUCN Red List status

*Sternotherus carinatus*: LC (Least Concern, assessed 01 August 2010)

*Sternotherus depressus*: CR (Critically Endangered A2bce+4bce, assessed 06 August 2023)

*Sternotherus intermedius*: Not assessed; in the TFTSG Provisional Red List (2018): LC (Least Concern)

*Sternotherus minor*: LC (Least Concern, assessed 01 August 2010)

*Sternotherus odoratus*: LC (Least Concern, assessed 03 August 2010)

*Sternotherus peltifer* (included as a subspecies to *Sternotherus minor*): LC (Least Concern, assessed 01 August 2010).

A reassessment was planned in 2024, to be published in 2025 (A.G.J. Rhodin pers. comm. 30/08/2024). The following categories are expected:

*Sternotherus carinatus*: LC

*Sternotherus depressus*: CR

*Sternotherus intermedius*: DD

*Sternotherus minor*: LC

*Sternotherus odoratus*: LC

*Sternotherus peltifer*: DD.

## Utilisation and protection within the natural range

In breeding farms for the pet trade, musk turtles play a less important role than larger turtles with a higher reproduction potential. Nevertheless, various species (*S. carinatus*, *S. minor*, *S. odoratus* and *S. peltifer*) are farmed and sold, including some colour morphs (albino, pastel, etc.) (Alabama Turtle Farmer 2024, Bonin 2004, Boudreaux's Turtle Farm 2024, Dark Hammock Turtle 2024). *Sternotherus* spp. do not play a significant role as human food or for medicinal purposes today. Trade in wild-caught animals for the pet trade has been documented in particular for the non-endangered species *S. carinatus* and *S. odoratus*.

At the state level, *Sternotherus* spp. are partially protected, often it is prohibited or requires a permit to collect animals, and in some cases the number of specimens that may be kept privately is limited.

The collection and trade of *S. depressus* is prohibited in the United States; this species has been listed as an endangered species in the Endangered Species Act since 11 June 1987. Unfortunately, this protection does not prevent the river from being developed and from mining with wastewater discharge, so that the endangerment of the population in the natural range is rather intensified. The species is farmed in the United States (Food and Drug Administration 2015) and a total of 640 captive-bred *S. depressus* were exported from the United States between 2013 and 2019 (CITES 2022).

In Canada, collecting, trading and possession of *S. odoratus* is prohibited in the two provinces where the species occurs.

An analysis of international trade from the USA from the LEMIS database in the years 2000–2006 (UNEP-WCMC 2024) showed that a total of 994,492 live *S. carinatus* had been exported mainly to East Asia, but some animals were also exported to Germany. 51% of these were wild-caught, and 120,087 *S. minor*, of which 39% were wild-caught and 38% farmed animals. The recipient countries were almost exclusively in East Asia. Additionally, 1,695,989 *S. odoratus* were exported, of which 65% were wild-caught. Of these turtles, about  $\frac{2}{3}$  were sent to East Asia, but quite a few were also sent to the UK. Even *S. depressus* is included in this analysis: A total of 1,238 animals of this species were exported, 95% of which were classified as ranched, in 2002, 2006 and 2018. Almost half of them were sent to Germany as the first country of import, the rest mainly to China, and some animals were also exported directly to Japan.

## Threats

The greatest threat to musk turtles is habitat loss and degradation, especially for species with comparatively small ranges (particularly *S. intermedius* and *S. depressus*). Musk turtles are susceptible to pollution (chemicals, industrial effluents, runoff from mining, forestry, agriculture and road transport) and sedimentation (e.g. from open-cast mining, sand extraction) of their home waters, which leads to a reduction in the abundance of aquatic insects and molluscs, which form their food source. In addition, sediments can make the hiding places of musk turtles in rock crevices inaccessible.

This applies somewhat less to the adaptable and comparatively hardy *S. odoratus* than to the other musk turtles. Deadwood removed for shipping leads to the loss of particularly popular basking places.

Since musk turtles rarely stray far from the water, they are less at risk from traffic than other turtles. However, the danger posed by road traffic can be relevant for ♀ *Sternotherus* sp. looking for places to lay their eggs (Aresco 2005a, b, Dodd 1990, Dodd 2008, Iverson & Meshaka 2006, Lindeman 2008, Melancon et al. 2013, Zappalorti & Iverson 2006).



The construction of dams has altered the habitat of *S. depressus* to such an extent that they have come into contact with *S. peltifer*, creating a hybrid zone. Originally, the habitats of the two species were separated by the insurmountable fall line (Scott et al. 2019). *S. depressus* is strongly adapted to the layered rocks found only in the Black Warrior River, which are used as hiding places. As a result of hybridisation, this hiding behaviour is lost, and the turtles are easier to find for predators (e.g. herons, centrarchid fish, river otters, racoons, etc.).

## Reproduction

| Topic                              | Details on the reproduction of <i>Sternotherus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | The sexes can be distinguished by the length of the tail, but this is only possible in animals > 4 cm CL. The tails of the ♂♂ are longer and thicker than those of ♀♀, and when the ♂ tail is stretched out, their cloaca is behind the edge of the carapace. ♂♂ only have a pointed nail at the tail tip that is not present in ♀♀. Male <i>Sternotherus</i> spp. have two conspicuous patches of scales on the inner surface of each hind leg.                                                                                                    |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sexual maturity                    | <i>Sternotherus carinatus</i> : with 4–11 years, ♀♀ 8.5–10 cm CL, ♂♂ 10–12 cm CL<br><i>S. depressus</i> : ♀♀ with 7.0–8.3 cm CL at the age of 5–15 years, ♂♂ at the age of 4–12 years with 6.0–7.0 cm CL<br><i>S. intermedius</i> : ♂♂ 4 years old, ♀♀ 5–7 years old<br><i>S. minor</i> : ♂♂ 5.5–6 cm CL at 2–5 years old, ♀♀ 7–9 cm CL at 3–8 years old<br><i>S. odoratus</i> : ♀♀ 2–11 years and 5.7–8 cm SVL, ♂♂ 4.7–7.0 cm at the age of 1–7 years<br><i>S. peltifer</i> : ♂♂ 3–4 years, ♀♀ 9–10 cm at the age of 4–7 years.                    |
| Mating and nesting                 | Mating both in the autumn before hibernation and afterwards in the spring, in Florida year-round. Oviposition in nature in rather shallow nest pits, often at the base of plants or next to fallen tree trunks, usually close to water, but sometimes up to 45 m away.                                                                                                                                                                                                                                                                              |
| Reproductive season                | April–October, nesting from May–July, <i>S. odoratus</i> as early as April, in Florida partly from September–July. Egg deposition in the land section of the aquaterrarium possible all year round.                                                                                                                                                                                                                                                                                                                                                 |
| Number of eggs/clutches per season | <i>Sternotherus carinatus</i> : 2–4 clutches/year with 1–7 eggs each<br><i>S. depressus</i> : 1–3 clutches/year with 1–4 eggs each<br><i>S. intermedius</i> : 3–4 clutches/year with 2–6 eggs each<br><i>S. minor</i> : 1–6 clutches/year with 1–5 eggs each<br><i>S. odoratus</i> : 1–6 clutches/year with 1–13 eggs each<br><i>S. peltifer</i> : 2–5 clutches/year with 1–6 eggs each.                                                                                                                                                            |
| Egg size/hatchling size            | <i>Sternotherus carinatus</i> : eggs 26.0–36.0 mm x 14.4–18.2 mm, hatchlings 23.0–31.0 mm and 3.4–4.2 g<br><i>S. depressus</i> : eggs 25.0–33.1 mm x 15.0–18.0 mm, hatchlings 25–33 mm and 1.5–2.3 g<br><i>S. intermedius</i> : hatchlings: 21.0–27.0 mm, 2–4 g<br><i>S. minor</i> : eggs 21.2–35.0 mm x 12.7–20 mm, hatchlings 20.0–30.0 mm and 1.5–5 g<br><i>S. odoratus</i> : eggs 18.2–35.0 x 11.2–18.9 mm, hatchlings 17.2–36.0 mm and 0.81–5.0 g<br><i>S. peltifer</i> : eggs 18.2–24.1 mm x 13.0–19.0 mm, hatchlings 22.0–30.0 mm and 2–4 g. |
| Incubation and hatching            | <i>Sternotherus carinatus</i> : 65–150 days<br><i>S. depressus</i> : 45–122 days<br><i>S. intermedius</i> : 80–120 days<br><i>S. minor</i> : 50–141 days<br><i>S. odoratus</i> : 44–121 days                                                                                                                                                                                                                                                                                                                                                        |

|                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                   | <i>S. peltifer</i> : 67–160 days.                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Sex determination | TSD II, in general 22 or 30°C for more ♀♀, 26°C for more ♂♂.<br><i>Sternotherus carinatus</i> : threshold temperatures 25,4 and 28,7°C<br><i>Sternotherus depressus</i> : no information available<br><i>S. intermedius</i> : mostly ♂♂ at 26°C, ♀♀ at 29°C<br><i>S. minor</i> : threshold temperatures 24,6 and 26,2°C<br><i>S. odoratus</i> : threshold temperatures 24,2 and 26,7°C<br><i>S. peltifer</i> : mostly ♂♂ at 25–26°C, ♀♀ at 28–30°C. |
| Sperm storage     | Yes, at least one season, probably longer.                                                                                                                                                                                                                                                                                                                                                                                                          |

### Husbandry and Captive Breeding **A–B/A–B**

*Sternotherus carinatus*, *S. intermedius*, *S. minor*, *S. odoratus* and *S. peltifer*: Husbandry **A**, captive breeding **A**

*Sternotherus depressus*: Husbandry **B**, captive breeding **B**.

The most commonly bred species in Europe are *S. minor*, *S. odoratus* and *S. peltifer*. Some breeders report that they do not hatch all clutches of *S. odoratus*, as demand is lower than supply. Presumably due to its size, *S. carinatus* is bred less often, but is often kept. *S. depressus* and *S. intermedius* are rarely bred due to their limited availability.

Since the *Sternotherus* species can hybridize with each other, they should be kept separate in human care. The husbandry requirements of the species are very similar, therefore they will be treated together below, unless otherwise indicated.

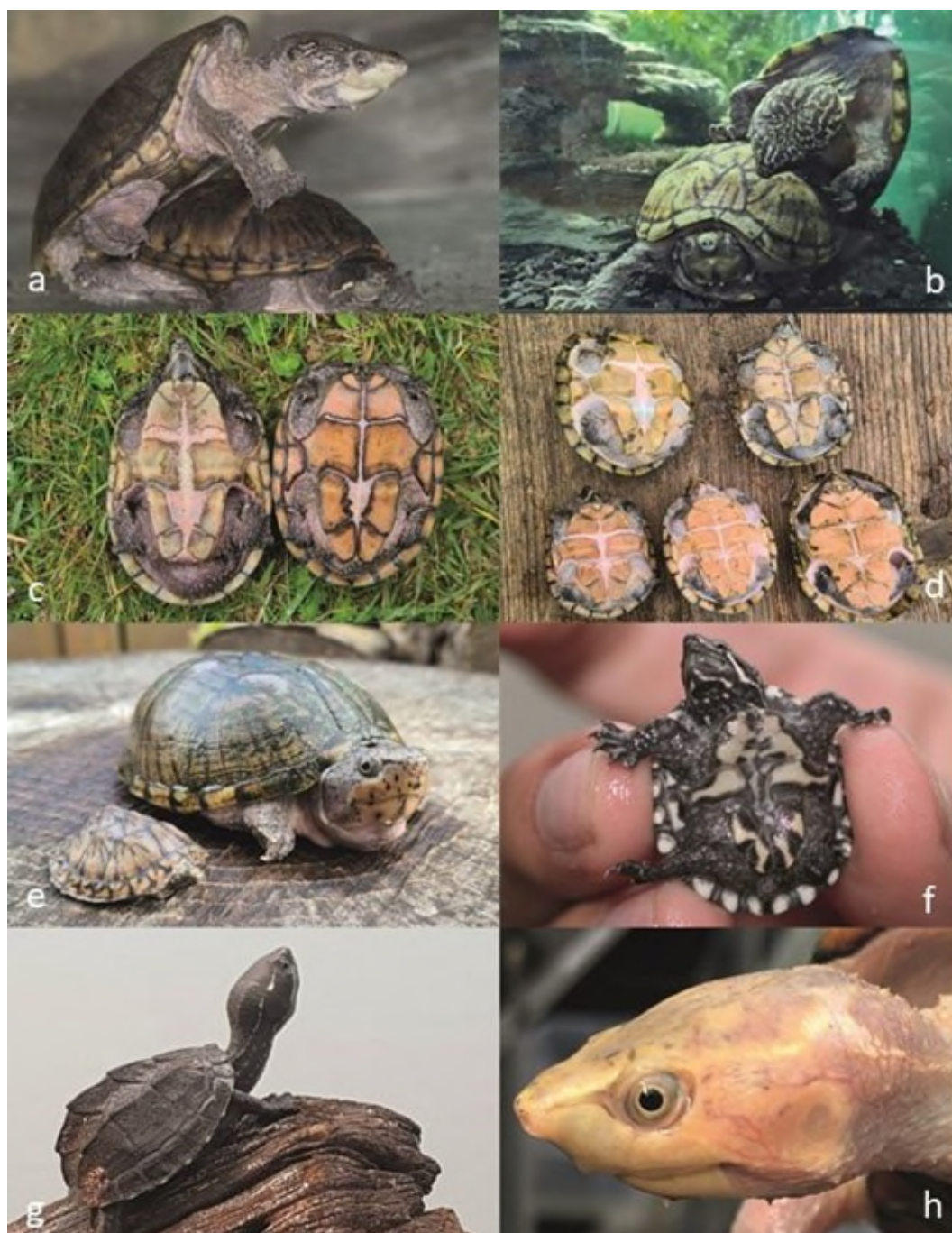


Fig. 33: *Sternotherus* reproduction

- a *S. odoratus* mating, the ♂ no longer shows the distinct head stripes of smaller/younger animals (R. Hentschel)
- b *S. intermedius* mating, the ♂ shows the typical head pattern (X. Wapelhorst)
- c Sexual differences of adult *Sternotherus odoratus*, ♂ left (X. Wapelhorst)
- d Plastron views of adult *Sternotherus*, upper row: *S. carinatus* and *S. odoratus*, below *S. peltifer*, *S. minor* and *S. intermedius* (X. Wapelhorst)
- e *S. minor* juvenile and adult ♂ (X. Wapelhorst)
- f *S. odoratus* hatchling. The hatchlings of *Sternotherus* (as well as of *Kinosternon*) species are really tiny (R. Hentschel)
- g *S. odoratus* juvenile, still with the typical carapace keels. Musk turtles are skilled climbers (R. Hentschel)
- h *S. odoratus*, isabella coloured morph (R. Hentschel).

| Topic                                                           | Data for <i>Sternotherus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | 2–5 months of hibernation at 4–15°C possible, but not absolutely necessary; a temperature reduction to 18–20°C in winter is sufficient; the length of daylight appears to be more important. In Florida, musk turtles are active year-round.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Husbandry requirements                                          | Generally easy to keep, can even be bred without UV light or a heat lamp and by feeding exclusively on commercial feed. Aquariums from 50 x 30 cm upwards can suffice. Only <i>S. depressus</i> is more sensitive to stress and has slightly higher demands in terms of water quality and hiding places (crevices).<br>Water temperature during the active period 20–30°C.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| General characteristics, difficulties with keeping and breeding | <p>About half of the respondents keep their musk turtles alone and only put them together for mating. Occasionally kept in combination with other species (<i>Chrysemys</i> sp., <i>Clemmys guttata</i>, <i>Cuora</i> sp., <i>Graptemys</i> sp., <i>Mauremys</i> sp., <i>Pseudemys</i> sp.), but due to the possibility of hybridisation, it is not recommended to keep them together with <i>Kinosternon</i> sp. or other <i>Sternotherus</i> species.</p> <p>Keeping several ♂♂ together in one aquarium does not work for any species. ♀♀ of <i>S. carinatus</i>, <i>S. minor</i> and <i>S. odoratus</i> are often compatible, sometimes several ♀♀ can be kept together with one male. If kept in groups, pay attention to compatibility and separate if necessary. For <i>S. intermedius</i> and <i>S. peltifer</i>, single keeping is generally recommended.</p> <p>Water level usually 15–30 cm, sometimes more than 50 cm. Temperature on basking area 25–45°C. A small nesting box (from 15 x 15 x 10 cm filled with at least 10 cm of slightly damp sand) is sufficient. Incubation at 20–30°C in vermiculite, perlite, Seramis, sand or gravel.</p> <p>For all musk turtle species, the tank must be very well secured against climbing out, as these turtles are very skilled escape artists. In addition, a longer stay in dry surroundings can cause damage to the health of musk turtles that have, for example, fallen on the floor of the living room (Sachsse, pers. comm.).</p> |
| Care of the young, technical and time effort                    | For <i>Sternotherus depressus</i> , <i>S. peltifer</i> and <i>S. intermedius</i> , individual rearing is often practised by breeders. For <i>S. carinatus</i> , <i>S. minor</i> and <i>S. odoratus</i> , group rearing can work. Containers with a base area of 15 x 20 cm or larger, water level at first usually 5–10 cm, up to 25 cm possible, even for hatchlings, if plants to cling on are available. Water temperature 20–28°C, temperature on the basking area 20–40°C.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Life expectancy                                                 | 30–50 years, perhaps more.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Frequency of private breeding and reproduction in zoos          | <p>All species are rare in zoos, and some are no longer kept in private collections. There is little targeted breeding, with the zoo in Frankfurt am Main occasionally breeding <i>S. carinatus</i>.</p> <p><i>S. carinatus</i>: Probably less frequently bred than other musk turtles due to their final size. They have been bred in Germany at least since the 1980s (Horn cited in Becker 1992).</p> <p><i>S. depressus</i>: rarely kept and therefore rarely bred, considered the most delicate of the musk turtles, bred in Europe at least since the 1972 (Sachsse 1973). The Turtles Survival Center is assembling a group for ex situ breeding (C. Hagen pers. comm. 2024).</p> <p><i>S. intermedius</i>: individual captive breeding successes, possibly some specimens are kept unrecognised as '<i>S. minor</i>'.</p> <p><i>S. minor</i>: bred regularly at least since the 1970s, probably the second most frequently bred musk turtle.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |

| Topic                                | Data for <i>Sternotherus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|--------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                      | <p><i>S. odoratus</i>: First documented European captive breeding in the 1960s (Olexa 1969), regularly published since then (e.g. Polder 1978, Hendrischk 1979, Budde 1982, Ophorst 1986, Gad 1987, Feder 1989, Knappik 1989, König 1999, Hennig 1999, Hofer &amp; Artner 2001, Budde 2002, Hennig 2002, Debry 2005, Thierfeldt &amp; Höfler-Thierfeldt 2005, Nad &amp; Schaffer 2009, Odorizzi 2010, Kalter 2011, Hofmann 2013, Hennig 2020). Regarded as one of the easiest water turtle species to breed.</p> <p><i>S. peltifer</i>: breeding activities in Germany at least since the 1990s.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Breeding difficulty evaluation       | Easy, sometimes juveniles hatch without further intervention from the terrestrial part of the aquaterrarium.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Mortality in the first years of life | Low, many breeders reported that 80–100% of the hatchlings could be raised to adulthood.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| F2 generation bred in captivity      | Yes, for all species. For the more frequently bred species F3 and further generations.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Commercial breeding/ ranching        | Two respondents stated that they commercially breed several species of musk turtle in Europe. In addition, there are several breeding farms in North America and Asia that also breed musk turtles (usually <i>Sternotherus odoratus</i> or <i>S. carinatus</i> , but also <i>S. minor</i> and <i>S. peltifer</i> ) in addition to other freshwater turtles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Interviews/ Surveys/ Consultations   | 33 completed questionnaires, almost half of them for <i>S. odoratus</i> , only one questionnaire for <i>S. intermedius</i> , no questionnaire for <i>S. depressus</i> , but an experienced breeder of this species could be interviewed personally. For the other species, individual questionnaires were returned ( <i>S. minor</i> : 7, <i>S. peltifer</i> : 5, <i>S. carinatus</i> : 4). Some people filled out questionnaires for several species. Some questionnaires were completed by people who did not breed, either because they only had a single animal or because they were not interested in breeding. Two people stated that they were commercial breeders, and no questionnaires were received from zoos or other institutions. Additional information was obtained from discussions at various turtle meetings in Germany and Austria and from the literature. Some turtle enthusiasts stated that they did not complete a questionnaire because so much is already known and published about musk turtles. In addition, many people reproduce musk turtles without paying partial attention to breeding and without recording reproduction data. |

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### **Xaver Wapelhorst (20.10.2024)**

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## Trionychidae

### *Apalone* Rafinesque, 1832

| Species                  | Original description | Common name              | Common name international                                          | Known in the trade |
|--------------------------|----------------------|--------------------------|--------------------------------------------------------------------|--------------------|
| <i>Apalone ferox</i>     | (Schneider, 1783)    | Florida Softshell turtle | Florida-Weichschildkröte<br>Tortuga de Carapazón Blando de Florida | Yes                |
| <i>Apalone mutica</i>    | (LeSueur, 1827)      | Smooth Softshell turtle  | Glattrand-Weichschildkröte<br>Tortuga de Concha Blanda Espinosa    | Yes                |
| <i>Apalone spinifera</i> | (LeSueur, 1827)      | Spiny Softshell turtle   | Dornrand-Weichschildkröte<br>Tortuga de Carapazón Blando Lisa      | Yes                |

The genus *Apalone* contains the following currently recognised species and subspecies:

*Apalone* Rafinesque, 1832 – North American Softshell Turtles

*Apalone ferox* (Schneider, 1783) – Florida Softshell Turtle

*Apalone mutica* (LeSueur, 1827) – Smooth Softshell Turtle

*Apalone mutica mutica* (LeSueur, 1827) – Midland Smooth Softshell Turtle

*Apalone mutica calvata* (Webb, 1959) – Gulf Coast Smooth Softshell Turtle

*Apalone spinifera* (LeSueur, 1827) – Spiny Softshell Turtle

*Apalone spinifera spinifera* (LeSueur, 1827) – Eastern Spiny Softshell Turtle

*Apalone spinifera aspera* (Agassiz, 1857) – Gulf Coast Spiny Softshell

*Apalone spinifera atra* (Webb & Legler, 1960) – Black Spiny Softshell Turtle, Cuatro Ciénegas Softshell Turtle

*Apalone spinifera emoryi* (Agassiz, 1857) – Texas Spiny Softshell Turtle

*Apalone spinifera guadalupensis* (Webb, 1962) – Guadalupe Spiny Softshell Turtle

*Apalone spinifera pallida* (Webb, 1962) – Pallid Spiny Softshell Turtle





Fig. 34: *Apalone* spp. distinctive features

- a *A. ferox* is the largest of the North American softshell turtles (A.S. Hennig)
- b North American softshell turtles, for example *A. ferox*, are strong swimmers (A.S. Hennig)
- c *A. spinifera*, with the 'thorny' carapacial rim (A.S. Hennig)
- d *A. mutica*, juveniles with smooth carapacial rim (A.S. Hennig)
- e juvenile *A. spinifera* (A.S. Hennig)
- f juvenile *A. mutica* (A.S. Hennig)
- g typical head shape of an adult *A. ferox* (A.S. Hennig)
- h hatchling *A. ferox* with the 'snorkel' still bent upwards (W. Helm).

## Morphology and Taxonomy

Three species are currently recognised within the genus *Apalone*: *Apalone ferox*, the Florida soft-shelled turtle, *A. mutica*, the smooth soft-shelled turtle, and *A. spinifera*, the spinous soft-shelled turtle. The latter was described by LeSueur in 1827 as *Trionyx spiniferus*; the same author described the smooth soft-shelled turtle as *Trionyx muticus*. Even before that, in 1783, Schneider had described a soft-shelled turtle found in Georgia as *Testudo ferox*.

When several synonyms subsequently emerged for all three species, Boulenger (1889) established the generic name *Trionyx* for all American soft-shelled turtles. Together with some Asian species, they were classified in this genus for a long time (Wermuth & Mertens 1961, Stebbins 1985, Obst 1988, Ernst et al. 1994), although Carr (1952) used the genus name *Amyda*. Carr (1952), like Neill (1951) and Crenshaw & Hopkins (1955), only recognised two species: *ferox* and *mutica*; in contrast, he assigned *spinifera* and its subspecies to *ferox* as subspecies – until the clarifying work of Schwartz (1956) and Webb (1962).

Meylan (1987) split *Trionyx* into nine genera and introduced the name *Apalone*, which had already been proposed by Rafinesque in 1832. Ernst & Barbour (1989) followed this division and applied the generic name *Apalone* to the North American soft-shelled turtles.

Kizirian & Webb (1990) and Webb (1990), on the other hand, doubted the reorganisation established by Meylan (1987); Webb (1990) considered it to be premature, but a first step towards a better understanding of the relationships within the genus *Trionyx*. In Ernst et al. (1994), Ernst and Barbour followed Webb's view and no longer used *Apalone*, but *Trionyx* again; some of the genera established by Meylan (1987) were demonstrably valid, while others rather had the rank of a subgenus. However, in Ernst & Lovich's 2009 reissue of the 1994 work, *Apalone* is finally used.

On the one hand, there is no alternative hypothesis regarding the relationships within the genus *Trionyx*, and on the other hand, the North American species differ morphologically and biologically from the closest related species – so the generic name *Apalone* ultimately prevailed for the North American soft-shelled turtles (e.g. Iverson 1992, Conant & Collins 1998, Fritz & Havaš 2006).

A similar situation applies to the subgenus of the Florida soft-shelled turtle mentioned by Meylan (1987): *Apalone (Platypeltis) ferox*. This status is mentioned by Iverson (1992) and adopted by Vetter (2004), but is not considered by the majority (including Ernst et al. 1994, Weisrock & Janzen 2000, Fritz & Havaš 2006, Meylan & Moler 2006). *Apalone ferox* has no subspecies, but genetic differences have been found between populations in peninsular Florida and southeastern South Carolina on the one hand and animals from the Apalachicola River in northwestern Florida on the other (Weisrock & Janzen 2000).

The black softshell turtle, *Apalone spinifera atra*, was originally described as *Trionyx ater* (Webb & Legler 1960). However, there is little molecular difference between the form restricted to the Cuatro Ciénegas basin in Mexico and *A. s. emoryi*, which occurs in the Mexican-Texan border area, among other places. Therefore, it is not justified as a species, and it is also listed as a subspecies of *Apalone spinifera* (McGaugh pers. comm., Fritz & Havaš 2006).

After studying *A. spinifera* throughout its entire range, McGaugh et al. (2008) placed the subspecies *A. s. hartwegi* in the synonymy of *A. s. spinifera*. Since then, *A. spinifera* has had only six subspecies for the time being.

***Apalone ferox*** – The grey-brown to olive-coloured carapace of the Florida soft shell turtle (*A. ferox*), with its more or less present dark, large spots, can reach a length of over 60 cm in ♀♀, while ♂♂ grow to around 33 cm in length (Ernst & Lovich 2009). Adult specimens have a white to grey plastron. The grey, brown to olive-coloured carapace shows numerous small, round, elongated ‘bumps’ that are arranged lengthwise. Head and extremities are whitish grey to dark brown. Behind the eyes there is a cream-coloured or yellow stripe that runs in a Y-shape in front of the eyes in younger animals and extends to the elongated tip of the snout, which is typical of soft-shelled turtles. The bulging ‘lips’ on the upper jaw are also brightly coloured. In younger specimens, the legs and feet show a few cream-coloured and yellow stripes in a longitudinal direction. The large webbing between the toes is clearly pronounced. In addition to size, the sexes also differ in the shape and size of the tail: in ♂♂ it is longer and wider, and the cloaca is further away from the base of the tail than in ♀♀. Juveniles still have a whitish to canary-yellow reticulated pattern on a dark ground on their carapace and skin, their plastron is lighter coloured on the front half and darker on the back half.

***Apalone mutica*** – Barko & Briggler (2006) mention a maximum carapace length of 26.6 cm for ♂♂ *A. mutica*, Ernst & Lovich (2009) give 35.6 cm for ♀♀. Moler (2006a) gives a maximum length of 28.7 cm for *A. m. calvata*. The olive to light brown carapace of the smooth soft-shelled turtle (*A. mutica*), which has dark spots or short lines, has an orange-light brown border and appears to be extremely flat in comparison to the other *Apalone* species. It is very smooth, hence the name – the carapace of an *A. spinifera*, on the other hand, feels like fine sandpaper, while the carapace of an *A. ferox* feels very rough with its coarse structure. This way, you can literally ‘feel’ the species. The colouring of the plastron varies from white to grey. The head, neck and extremities are light brown, orange and olive on top and light or white in colour on the underside. A black-edged yellow stripe runs from each eye to the neck. There are pronounced webs between the claws. ♂♂ differ from ♀♀ not only in the smaller size of the adult animals but also in the longer and thicker tail. Two subspecies are distinguished: juvenile specimens of the nominate form have a pattern of dark dots and short lines between the eyes and snout tip, as well as two weakly pronounced, light stripes. The pale temporal stripe is edged in black. *Apalone mutica calvata* has large, round spots on its carapace. There are no stripes on the upper side of the snout. The black lines bordering the temporal stripes are not as thin as in the nominate form, but considerably broader. Fine markings can be seen on the thick ‘upper lips’, which are typical of soft-shelled turtles.

***Apalone spinifera*** – The carapace of the spiny soft-shelled turtle (*A. spinifera*), which is covered with many tiny spines (like sandpaper), can reach up to 54.0 cm in ♀♀ and a maximum of 21.6 cm in ♂♂ (Halk 1986). However, the known maximum sizes differ from subspecies to subspecies. The carapace is olive-coloured to brown in colour and has black ocelli or dark spots. A clearly visible dark line marks the frequently light-coloured edge of the carapace. The plastron is whitish to pale yellow in colour; it can have numerous dark spots, which merge into larger dark areas on the rear half of the carapace with increasing age. The colour of the skin varies in numerous shades of olive green, white and brown. A black-edged, yellow to whitish-coloured stripe extends from the snorkel-like tip of the nose over the eyes and along the temples to the back of the head. Many dark spots, reticulations or even larger grey-brown areas cover the head, neck, legs and tail – the variability and the changes in colour and pattern that occur as the animal grows make it difficult to identify the *spinifera* subspecies correctly. In addition, there are colour differences between the sexes. Without knowing the exact origin of the animals, identification is usually difficult. The nominate form has large, black ocelli on the



carapace. *Apalone s. aspera* shows at least two, often three lines along the edge of the carapace; however, these often consist only of several short and longer lines. The light stripes behind the eyes merge on the sides of the head with the stripes that also start at the mouth and are whitish to cream-coloured (in *A. s. spinifera* these run parallel to each other). *A. s. pallida* have a pale brown carapace with numerous small, light-coloured tubercles on the rear half. The dark carapace of *A. s. guadalupensis* has light elevations, as in the aforementioned subspecies, but also small black ocelli, which are distributed over the entire carapace. A striking feature of *A. s. emoryi* is the slightly curved black line between the eyes. The hind ocular stripes are often interrupted, leaving only a light elongated spot.

### Distribution and Habitat

*Apalone ferox*: The range of *Apalone ferox* extends from southern South Carolina, southern Georgia and southernmost Alabama across all of Florida (see Ernst & Lovich 2009). The Florida Keys in the south of the peninsula are not part of the natural range, but the species has been introduced to Big Pine Key (Iverson & Etchberger 1989). This species lives in all freshwater habitats. Ernst & Lovich (2009) found specimens in shallow drainage canals and deep rivers, as well as in swamps, lakes and streams. The species can also be found in brackish water near river mouths. Conant & Collins (1998) also mention water-filled road ditches. The species prefers waters with sandy or muddy bottoms. Due to the warm winters on the Florida peninsula, *A. ferox* is active throughout the year; during cold spells it is inactive. In the western and northern parts of its range, there is a period of inactivity during cold winters. During the day, Florida soft-shelled turtles often lie buried in the substrate of the water; if the water is shallow, they can stretch their heads to the water surface from such a hiding place thanks to their long necks in order to breathe. Such periods of rest alternate with foraging and active basking on sandbanks, on the shore or on tree trunks and large stones that protrude from the water. It is also common to see the animals floating on the surface of the water and basking (Ernst & Lovich 2009).

*Apalone mutica*: While the range of *A. m. calvata* is relatively small, extending only from southeastern Louisiana through southern and eastern Mississippi and southern Alabama to the westernmost tip of Florida (the Escambia and Pearl River basins), the natural occurrences of the nominate subspecies cover much larger areas: ranging from southern Minnesota, the Dakotas, and Ohio in the north, south to Tennessee, Louisiana, northern Alabama, and western Mississippi, west to Texas and New Mexico (including the drainage basins of the Mississippi, Missouri, Ohio, Arkansas and Red River; Iverson & Etchberger 1989, Iverson 1992, Conant & Collins 1998, Ernst & Lovich 2009). They colonise large flowing waters (such as the Kansas River, Ohio River, Mississippi, Missouri, Pearl River) as well as their tributaries and outflows. The nominate form is also known from still water bodies. They prefer to live in waters with sandy bottoms, some rocks and aquatic vegetation (see Ernst & Lovich 2009). In Indiana, Ewert (1979a) observed adult ♀♀ in seasonally flooded oxbow lakes and directly in the rivers; males were usually found in the rivers. Plummer (1977) found that ♂♂ inhabited all areas of the Kansas River, although they were most abundant in shallow water near sandy shores or sandbars. Adolescent ♀♀, on the other hand, tended to spend more time near the sandbars more than adult ♀♀; the latter only visited them during the nesting season. Hatchlings preferred small, shallow, warm pools that were separated from the main body of water by sandbars. The same author also notes that the species will bask on either sandy or muddy shores just a few metres from the water, or on rocks and logs (Fitch & Plummer 1975, Plummer & Shirer 1975). According to Williams and Christiansen (1981), occurrences of *A. m. mutica* in

Iowa are concentrated along rivers; ponds are also usually visited, but only if they are at least connected to nearby rivers by flooding. *Apalone mutica* and *A. spinifera* occur sympatrically in large parts of their range. In Iowa, for example, they have been observed basking together on riverbanks. However, while the former species is only found in the larger river areas, *A. spinifera* can be found much further upriver, in the narrower sections of the river. Lindeman (2001) also noted different 'preferences' when choosing places to bask: among the soft-shelled turtles he observed in Kentucky, Mississippi and Louisiana, he discovered 38 *A. mutica* basking on the riverbank, but only three *A. spinifera*. The latter species prefers to bask on deadwood protruding from the water. In shallow water, *A. mutica* has also been observed basking in the water (Williams & Christiansen 1981). The animals let themselves drift on the surface or benefit from the shallow water warming up faster in the sun. The diurnal, agile *A. mutica* is usually active in Kansas from May to September, but can also leave the wintering site in the bottom of the water as early as late March or April (Plummer & Shirer 1975, Plummer 1977). When not basking or otherwise active, they spend much time buried at the bottom of the water; they choose a depth that allows them to reach the water surface with their nose to breathe. Adult ♀♀ are more active than subadult ♀♀ and also more active than males; they also have a larger home range (Plummer & Shirer 1975). Juvenile *A. mutica* often fall prey to a variety of vertebrates, including large fish and turtles, snakes, water birds and various mammals (Ernst & Lovich 2009).

*Apalone spinifera*: The range of *A. spinifera* extends from northern Mexico across the central and eastern United States to southeastern Canada. That of *A. s. spinifera* extends north to the Great Lakes, Minnesota and South Dakota. The northwesternmost foothills are in Wisconsin, the northeastern most in the southeast of the Canadian provinces of Ontario and Quebec. There is a large isolated population in Montana, and a small isolated population between this and the territories described above. To the south, the populations extend as far as northern Louisiana and northeastern New Mexico, and as far as western Virginia, North Carolina and Tennessee. This is where the range of *A. s. aspera* begins. Bordering the Mississippi River drainage basin to the west, its range extends to the Gulf Coast and across northern Florida to southern North Carolina in the east. Populations of *A. s. pallida* live west of the Mississippi River. Their range is bounded by the Brazos River in eastern Texas in the west and the Gulf Coast in the south. In the northeast, the range boundary runs along the Red River drainage basin in Louisiana and Oklahoma. The small range of *A. s. guadalupensis* is restricted to south-central Texas (watershed of the Nueces River and Guadalupe/San Antonio River). *Apalone spinifera emoryi* lives in the Rio Pecos (Texas, New Mexico) and Rio Grande (the border river between Texas and Mexico) drainage basin. To the northwest, there are occurrences in the Colorado River drainage basin. The very small range of *A. s. atra* is located in the Cuatro Ciénegas Basin in the Mexican state of Coahuila. In the Mississippi River basin and in Texas, the adjacent ranges of the respective subspecies overlap over a large area. In these intergradation zones, mixed populations occur (Iverson 1992, Conant & Collins 1998, Moler 2006b, Ernst & Lovich 2009). Depending on the distribution area, *A. spinifera* is active throughout the year (in the south) or only from April to October (in the north). The more northerly the location, the shorter the period of activity (Ernst & Lovich 2009). In Lake Champlain (at the northern limit of the species' range, the species' northernmost location), the species does not leave hibernation until early May and returns at the end of August (Galois et al. 2002). The diurnal turtles sleep at night buried in the bottom substrate of the water or under the branches of sunken trees. When buried in mud or sand, they like to choose a location in shallow water that allows them to reach the water surface to breathe by stretching their necks and craning their heads



(Ernst & Lovich 2009). The small (30–40 mm) hatchlings have fish, snakes, wading birds, mammals and other turtles as predators. Adult specimens are eaten by alligators, and humans of course (Webb 1962, Ewert 1979b, Ernst & Lovich 2009).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (CoP19 Proposal No. 32), except for *Apalone spinifera atra*, which already had been listed in Appendix I when the CITES Convention came into force in 1975.

EU Council Regulation (EC) No. 338/97 *Apalone spinifera atra* Annex A, all other *Apalone* Annex B.

In Germany, *Apalone* spp. are specially protected under Article 7 (2) No 13 BNatSchG. *Apalone spinifera atra* is strictly protected under Article 7 (2) No 14 a) BNatSchG.

Although *Apalone* spp. have occasionally been observed in various European countries and outside their natural range in North, Central and South America, these turtles are not considered invasive to date.

### IUCN Red List Status

*Apalone spinifera atra*: CR (Critically Endangered A1ace+2c, assessed 03 August 1996).

*Apalone ferox*: LC (Least Concern, assessed 01 August 2010).

*Apalone mutica*: LC (Least Concern, assessed 01 August 2010).

*Apalone spinifera*: LC (Least Concern, assessed 26 December 2023) (Doody et al. 2024).

A re-evaluation has taken place for many American turtle species in 2024 (for invitations to the workshops, see IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 2023 and Stanford & Rhodin 2023). In 2025 two new assessments will be published (A.G.J. Rhodin pers. comm. 30 August 2024). *Apalone mutica* and *A. spinifera* continue to be considered LC (least concern) in it. A re-evaluation for *Apalone spinifera atra* is not currently planned.

### Breeding farms

A short note on husbandry and captive breeding of the *Apalone* species was published as early as 1973 (Anon. 1974), but the turtles were not bred in large numbers at that time. After that, North American soft-shelled turtles have already been bred in turtle farms for the pet trade for decades. In particular, *Apalone ferox* and *Apalone spinifera* were regularly bred in large and small farms in the southern United States. These were sold on the domestic market as food and pets, as well as to recipients in Asia, Europe and Mexico. In 1997, for example, the USA exported 6,494 *Apalone* specimens to Japan, 2,735 to Mexico, 1,000 to Taiwan, 412 to Spain, 361 to Italy, 230 to China and 25 to Hong Kong SAR, see in the CITES Trade Database, (UNEP-WCMC 2024) in the references for the document section below. In total, the USA exported during that year 7,781 *Apalone ferox*, 200 *Apalone mutica*, 1,485 *Apalone spinifera* and 5,487 specimens which were not determined to species level (Franke & Telecky 2001). Later, exports increasingly focused on China: The listing of the relevant species in CITES Appendix III allows conclusions to be drawn about extensive *Apalone* exports from the USA to this country, e.g. 25,790 *Apalone ferox* in 2017, 63,605 in 2018, 32,706 in 2019, and 10,000 specimens in 2020. In addition, there were exports to Mexico (9,300 in 2019) and to a much lesser extent to EU countries, among others; Germany is not documented as a direct importing country. *Apalone mutica* never played a commercial role in Europe. In particular in Asia (China, Hong

Kong), the use of turtles in the traditional Chinese medicine, in addition to the consumptive trade, has been and continues to be an important reason for the immense import of turtles, including *Apalone* species, and the production of soft-shelled turtles on Chinese turtle farms, which has been going on for decades.

An analysis of international trade from the USA from the LEMIS database in the years 2000–2023 (UNEP-WCMC 2024) showed that a total of 2,7022,036 live *A. ferox* were exported, mainly to East Asia, but a few also to Mexico and Italy. Of these, 58% were exported as wild-caught and 37% as captive-bred. The LEMIS database also recorded the export of 702,028 live eggs, 3,600 possibly preserved eggs and 1,710 kg of meat of *A. ferox*. Export entries for this species declined significantly after 2014, and from 2020 there are no more entries in this database. For *A. mutica*, exports already had declined significantly from 2006 on, with the last database entries being from 2012. A total of 36,605 *A. mutica* animals were exported, 79% of which were captive-bred. In addition to countries in East Asia, Mexico and the Netherlands were also recipient countries. For *A. spinifera*, exports have declined significantly from 2013, but there are still individual entries. A total of 704,721 animals of this species were exported alive. 51% of the animals were recorded as ‘ranchered’ and 32% as captive-bred. Recipient countries were mostly in East Asia while Mexico was also among the recipients and a few animals went to Italy.

Tian et al. (2016) mention that *Apalone ferox* was first imported to China more than 20 years ago; Shi & Qingle (2005) cite the 1990s as the period when the first specimens were imported (see above). Yuan et al. (2013) note that the Florida soft-shelled turtle has since been successfully bred in China. In 2016, more than ten million specimens were kept on farms and six million hatchlings were produced each year (Tian et al. 2016). Currently, Chinese turtle farms produce an estimated one billion *Apalone* hatchlings per year, mainly *Apalone ferox* and *Apalone spinifera* (Ting & Blanck, pers. comm. 6-2024).

Yu et al. (2019) identify *Apalone ferox* and *Apalone spinifera* as important commercial species. Many hatchlings are sold as pets in ornamental fish markets in China. When they get too large for the aquarium in the living room, they are often released; the Florida soft-shelled turtle can be found in the Yellow River (China) (Yu et al. 2019).

## Threats

Populations of *Apalone* species, as well as other North American aquatic turtles, are affected by human activities. The greatest threat is habitat destruction (Ernst & Lovich 2009): wetlands (including marshes, ponds, and other bodies of water) are drained (Gregory & Campbell 1984, Mitchell 1994, 2001), and rivers and streams are modified (e.g., by dredging the river bottom) and channelised (Mitchell 1994, 2001). Over the past 200 years, more than 53% of the wetlands in the United States have been eliminated (Meffe & Carroll 1994), and wetland habitats continue to be destroyed, altered, or left as isolated fragments of the landscape (Tiner 1987).

For example, Galois et al. (2002) attribute the high level of activity in a population of *A. s. spinifera* on the US-Canadian border to habitat fragmentation. The reduced availability of suitable habitat (e.g. sites for oviposition and hibernation) means that the turtles have to travel further and be more active.

Furthermore, ♀♀ of North American water turtles are often run over by cars when crossing roads in search of a suitable oviposition site (a similar problem to the mortality of amphibians during migration in Germany). For example, Lake Jackson in Florida is divided by a four-lane

highway. In particular, when the smaller area of the lake that is cut off by the highway dries up, the amphibians and reptiles living there, including water turtles such as *A. ferox*, migrate. Many individuals fall victim to traffic when crossing the highway (e.g. Aresco 2003).

In addition, *A. ferox* is the most intensively hunted freshwater turtle in Florida; nevertheless, it is still common overall (Meylan & Moler 2006). Hatchlings of this species are sold primarily to the pet trade, while other age groups are sold on the food market: specimens between 3.5 and 4.5 kg are slaughtered and sold as frozen meat, specimens below the stated weight are killed, eviscerated and frozen whole, smaller animals are sold live (Moler & Berish 1995).

The very small range of *A. s. atra* in the Cuatro Ciénegas basin in the Chihuahuan desert in Mexico is extremely vulnerable to disturbance. With the construction of canals and the connection to the natural occurrences of *A. s. emoryi* that this created, the subspecies can intermix with the *A. s. atra* that is native to the Cuatro Ciénegas Basin (see Vetter 2004, or Cerdá-Ardura et al. 2008, among others).

In Canada, *A. spinifera* is classified as 'threatened'. Habitat loss has severely reduced the historic range of this species. The use of the habitats by humans for development and leisure activities prevents the soft-shelled turtles from accessing nesting and wintering sites, as well as basking areas and feeding grounds. The risk of predation on juvenile specimens remains, and the reproductive rates are reduced by the conditions mentioned. Populations are isolated by dams and other infrastructure. Finally, the turtles collide with motorboats and drown in traps used for fishing (COSEWIC 2002).

## Reproduction

### Reproduction of *Apalone ferox* in the wild

Webb (1962) mentions that ♂♂ with a plastron length of 12 cm or more are sexually mature. The ♂♂ of various sizes caught for more recent studies (Meylan et al. 2002) were all sexually mature – the smallest specimen with a plastron length of 15.2 cm. Hamilton (1947) states that the minimum carapace length for sexually mature ♀♀ is about 22 cm, whereas Iverson (1985) assumes 28–30 cm based on his research.

In southern Florida, the nesting season begins in mid-March and lasts until July (Lardie 1983, Iverson 1985), and from June to July in the northern and western parts of the range. Preferred nesting sites are sunny and have sandy soil (Ernst & Lovich 2009). Like the red-bellied turtle, *Pseudemys nelsoni*, the Florida soft-shelled turtle occasionally lays its eggs in alligator nests (Deitz & Jackson 1979, Jackson 2006). Clutches can range in size from 4–24 eggs (usually 17–22); the eggs are roundish and range in diameter from 24–33 mm (Goode 1983, Iverson 1985, Ernst & Lovich 2009). Two to possibly more than six clutches may be deposited per year (Iverson 1985). Development takes 56–83 days (usually 60–70), depending on incubation temperature (Goff & Goff 1935, Lardie 1973, Goode 1983, Iverson 1985).

The nests can be predated by crows, skunks, bears, raccoons and foxes, among others. Juvenile *A. ferox* are preyed upon by large water turtles and fish, snakes, birds of prey and water birds, as well as various mammals (Pope 1939, Hamilton 1947, Woodin & Woodin 1981, Beissinger 1990, Ernst & Lovich 2009).

Members of the genus *Apalone* are subject to genetic sex determination, known as genotypic sex determination (GSD). Bull & Vogt (1979) and Janzen & Paukstis (1991) demonstrate this for *A. spinifera*. Ernst & Lovich (2009) come to the same conclusion and mention in this context

Ewert & Nelson (1991), who incubated eggs of *Apalone mutica* at 27–33°C and obtained approximately equal numbers of ♂♂ and ♀♀. The sex ratio of turtle eggs with GSD is approximately 1:1 within a clutch, regardless of the constant or fluctuating incubation temperature (see also Pieau & Dorizzi 2005). Ewert (1979b, pers. comm. in Meylan & Moler 2006) reports on a clutch of *A. ferox* with 26 eggs, from which 13 ♂♂ and 13 ♀♀ hatched.

### Reproduction of *Apalone spinifera* in the wild

The ♂♂ reach sexual maturity in their fourth year of life, when they usually reach plastron lengths of 80–85 mm. ♀♀ become sexually mature in their ninth year of life, with plastron lengths of 140–150 mm. Mating takes place from April to June and in August. During this time, the ♂♂ actively search for mating partners, both in the water and on the sunny basking spots. They ‘check’ each basking turtle by sliding their snout under the edge of the carapace. If they come across a male soft-shelled turtle, it reacts aggressively and opens its mouth threateningly. Sunbathing ♀♀ not only threaten but also bite ♂♂ looking for a mate; therefore, male specimens show fresh injuries on the edge of the carapace in spring. When a ♀ leaves the basking site and glides into the water, several males may try to mount the potential mate (Plummer 1977).

From late May into July, up to 33 eggs (Ernst & Lovich 2009) are buried in a clutch; in Kansas there are usually 11–14 (Plummer 1977), in the more northerly distribution areas 18–22 (e.g. Vogt 1981). A second clutch per year is possible (Ernst & Lovich 2009). The sites are usually within 30 m (4–90) of the water's edge, in sunny places such as high sandbars, and less often in permanently vegetated places (e.g., Anderson 1958, Webb 1962, Fitch & Plummer 1975). The nest pits are 15–30 cm deep (Goldsmith 1945, Ernst & Lovich 2009). The nests can be predated by fly larvae, crows, moles, raccoons, skunks and dogs; however, the main problem is periodic flooding of the sandbars selected as nesting sites (Muller 1921, Goldsmith 1945, Webb 1962, Fitch & Plummer 1975, Plummer 1976). After an incubation period of about 44–82 days (depending on incubation temperature), the hatchlings, which are about 30–45 mm in size and weigh about 3–7 g, will leave the nest (Ernst & Lovich 2009).

### Reproduction of *Apalone spinifera* in the wild

Sexual maturity occurs in males *A. spinifera* as early as 8–10 cm plastron length, and in ♀♀ as early as 18–20 cm (Webb 1956, 1962). Mating occurs in April and May. The egg-laying season begins in late May and lasts until August; two clutches per year are possible. The ♀♀ can migrate up to 100 m inland to lay their eggs, but most nests (each 10–25 cm deep) are built in sunny places relatively close to the water, including on gravel and sand banks.

The eggs, which measure 28 mm in diameter on average, weigh 10–11 g. Most clutches contain 12–18 buried eggs, but 4–39 eggs per clutch are possible (Webb 1962, Ernst & Barbour 1972, Minton 1972, Robinson & Murphy 1978, Vogt 1981, Miller et al. 1989). If the nests are not plundered by skunks or raccoons, the turtles hatch after an incubation period of 82–84 days (in Wisconsin).

| Topic                   | Details on the reproduction of <i>Apalone</i> spp.                                                                                                                                                |
|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits | Adult ♂♂ are (significantly) smaller and lighter than ♀♀. In ♂♂, the tail is longer and broader than in the ♀ specimens, and the cloacal opening is further from the base of the tail than in ♀♀. |

|                                    |                                                                                                                                                                                                                 |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Reproduction                       | Oviparous.                                                                                                                                                                                                      |
| Sexual maturity                    | <i>Apalone ferox</i> : 15 (♂♂) or usually 22–30 cm plastron length (♀♀); <i>A. mutica</i> : 8–8.5 cm (♂♂) or 14–15 cm (♀♀); <i>A. spinifera</i> : 8–10 cm (♂♂) or 18–20 cm (♀♀).                                |
| Mating and nesting                 | Mating takes place most often after hibernation; for oviposition, the turtles mostly check out sunny sand sites, <i>A. ferox</i> occasionally deposits the eggs in alligator nests in the field.                |
| Reproductive season                | <i>Apalone ferox</i> : March to August; <i>A. mutica</i> : May to July; <i>A. spinifera</i> : May to August.                                                                                                    |
| Number of eggs/clutches per season | <i>Apalone ferox</i> 4–40 eggs, 2–7 clutches/year; <i>A. mutica</i> 1–33 eggs, 2–3 clutches/year; <i>A. spinifera</i> 3–39 eggs, 1–3 clutches/year.                                                             |
| Egg size/hatchling size            | <i>Apalone ferox</i> : round eggs, diameter 24–33 mm, 9.8–12.1 g; <i>A. mutica</i> : oval to spherical eggs, diameter 18–27 mm, 3.4–9.1 g; <i>A. spinifera</i> : spherical eggs, diameter 22–32 mm, 6.7–11.9 g. |
| Incubation and hatching            | <i>Apalone ferox</i> 56–80 days; <i>A. mutica</i> 44–82 days; <i>A. spinifera</i> 75–85 days.                                                                                                                   |
| Sex determination                  | Genetic, ZZ/ZW chromosome system.                                                                                                                                                                               |
| Sperm storage                      | Possible.                                                                                                                                                                                                       |

## Husbandry and Captive Breeding B/A

| Topic                                                           | Data for <i>Apalone</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Cooler winter temperatures (specimens from the southern US states, e.g. <i>A. ferox</i> ) or brumation at around 6–9°C.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Husbandry requirements                                          | <p>Adult specimens should be kept in aquaria from 150–200 cm in length (♀♀). For the smaller-sized ♂♂ of <i>A. mutica</i> (max. carapace length &lt; 20 cm) and <i>A. spinifera</i> (approx. 20 cm), correspondingly smaller tanks. Sunbathing area with radiant heat of approx. 45°C at certain points, if necessary supplemented with LED light bars for general illumination. Sand-filled, sufficiently large land area for the ♀♀ to lay their eggs. Seasonal keeping in outdoor terrariums/pools possible.</p> <p>Water temperatures of 25–30°C during the day in the summer months, with air temperatures slightly higher; at night, reduce to room/greenhouse temperature.</p> <p>Overall, easy to keep; a lot of space is needed for adult ♀♀. Usually calm animals, not aggressive towards the owner.</p> <p>Individual housing of overly intrusive ♂♂ or dominant specimens.</p> |
| General characteristics, difficulties with keeping and breeding | An essential part of the husbandry is a deep layer of clean, non-abrasive sand on the bottom of the aquarium where the animals will remain completely buried for long time periods, only the head sticking out for breathing.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Care of the young, technical and time effort                    | Several juveniles can be raised together in well-structured, smaller tanks (sand as substrate, robust [floating] plants, roots, branches) in the first year of their lives; separate larger specimens as they grow at different rates. Place a spotlight over a basking place, or keep them outdoors in summer. Feed them a varied diet with invertebrates (live, frozen, dried), pellets and much more.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Life expectancy                                                 | More than 20 years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Frequency of private breeding and reproduction in zoos          | <i>Apalone</i> species are not commonly kept (lack of interest in these species, space-intensive, not very attractive in zoos due to their burying behaviour); breeding of <i>A. spinifera</i> has regularly taken place at Frankfurt Zoo (1991–2010), <i>A. ferox</i> has been regularly bred in private husbandry for years.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |



| Topic                                | Data for <i>Apalone</i> spp.                                                                                                                                                                                                                                                                                                                                                                         |
|--------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Breeding difficulty evaluation       | Easy, and comparable to other soft-shelled turtle species. The only limiting factor is the space required, with appropriately sized tanks.                                                                                                                                                                                                                                                           |
| Mortality in the first years of life | Low under the species-appropriate husbandry conditions.                                                                                                                                                                                                                                                                                                                                              |
| F2 generation bred in captivity      | Not yet published in Europe; F2 or higher generations most certainly bred in the USA and in Chinese farms.                                                                                                                                                                                                                                                                                           |
| Commercial breeding/ranching         | Regularly and in large numbers in turtle farms in the USA and China.                                                                                                                                                                                                                                                                                                                                 |
| Interviews/ Surveys/ Consultations   | 25 private breeders in Europe and the USA and 2 zoos; most of them had experiences with more than one species and/or subspecies. Additionally, information was obtained from discussions at the various meetings of the turtle keeper associations in Europe and an intensive discussion of the Radiata editors about the conditions for farm breeding in Louisiana with Feldmann & Feldmann (2018). |



Fig. 35: *Apalone* spp. husbandry and breeding

- a *A. ferox*, ♂ plastron view (A.S. Hennig)
- b *A. ferox*, ♀ plastron view (A.S. Hennig)
- c *A. ferox*, freshly laid eggs in the nest (W. Helm)
- d *A. ferox* hatchlings (X. Wapelhorst)
- e *A. spinifera* in the garden terrarium (A.S. Hennig)
- f *A. ferox* hatchling with the typical black plastron (W. Helm).

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**Andreas S. Hennig (15.08.2024)**

***Nilssonia leithii* (Gray, 1872)**

| Species                  | Original description | Common name                                       | Common name international                                                                                                                                        | Known in the trade |
|--------------------------|----------------------|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|
| <i>Nilssonia leithii</i> | (Gray, 1872)         | Leith's Softshell turtle, Nagpur Softshell turtle | Leiths Pfauenaugen-Weichschildkröte, Vorderindische Weichschildkröte<br>Tamil: Parisal amai, Seravi amai, Thoni amai<br>Kannada: Pale poo<br>Telugu: Nadi tabelu | No                 |



Fig. 36: *Nilssonia leithii* (S. Singh / TSA India).

**Morphology and Taxonomy**

*Nilssonia leithii* is a large species of soft-shelled turtle from the Indian subcontinent. At around 63.5 cm, the ♂♂ grow larger than the ♀♀ which attain a CL of 54.8 cm (Moll & Vijaya 1986, Deepak & Vasudevan 2009). Das et al. (2014) report an average total carapace length of 63.3 cm for five specimens from the Kali River, Karnataka, India. An adult male from the same river was measured to have a total length of 72 cm. A supposedly record-sized ♀ caught in the Tungabhadra River near Kalagatta in 2011 and confiscated by the local forest officials had (according to the officials) a CL of 160 cm, carapace width of 110 cm and a weight of about 130 kg (Murthy 2011). However, after examining the photos provided by Murthy (2011), the specimen was found to belong to *Chitra indica*.

Like all soft-shelled turtles of its genus, *Nilssonia leithii* is characterized by 4 to 6 eyespots in the area of the dorsal carapace. These fade with increasing age, which makes it difficult to clearly determine the species of adult, older individuals. The ground colour of the carapace is

usually grey or greyish-olive, but in 2022 an aberrantly coloured, golden, turtle could be rescued (Vaghela 2025).

The plastron of Leith's softshell turtle is cream-colored, its greenish head may have some black markings, and the corners of the mouth show a yellow or reddish-orange dot. Such dots can also appear on the forehead of juvenile specimens.

Originally described by Gray (1872) as *Trionyx leithii*, the species was listed in this genus for more than 100 years. Meylan (1972) placed the large soft-shelled turtles of India in the genus *Aspideretes*. On the basis of genetic analyses, Praschag et al. (2007) placed them in the genus *Nilssonia* (and thus closer to the Burmese soft-shelled turtle, *Nilssonia formosa*). Liebing et al. (2012) were able to show that *Nilssonia leithii* is the sister taxon of *Nilssonia gangetica*.

Neither subspecies nor geographic variations of *Nilssonia leithii* are known.

### Distribution and Habitat

The distribution of Leith's softshell turtle is limited to the Indian subcontinent. It extends from the southern Ganges River valley, Andhra Pradesh to Karnataka and Tamil Nadu in the south (Vasudevan et al. 2019). Older distribution data in the literature from locations further north are based on confusion with other species.

Like all species of its genus, this species is mainly found in larger rivers. These are primarily the rivers originating in the flat hilly country of central India, which flow east and west towards the sea. Isolated findings are also known from (artificial) water reservoirs.

The discovery of a specimen in the Chalakudy River, near the village of Perinjanam in Kerala, suggests the possibility of using estuaries as at least a temporary habitat. Few specimens have been recorded from near Pune in Maharashtra in last five years.

The diet of *Nilssonia leithii* consists of fish, crustaceans, freshwater molluscs and, in juveniles, mosquito larvae (Das 2001). Specimens kept in a temple pond in the village of Kotapalli in the state of Andhra Pradesh also consumed hibiscus flowers and bananas (Das et al. 2014).

### Conservation Status and Main Threats

CITES Appendix I since 2023 (CoP19 Proposal 33). Had already been included in CITES Appendix II in 2014 (CITES 2013).

EU Council Regulation (EC) No. 338/97: Annex A.

In Germany strictly protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Category

Critically Endangered – CR (A2cd+4cd, assessed 13 March 2018).

### Threats

For a long time, *Nilssonia leithii* was considered a widespread and common species, although individual populations were in decline (Choudhury et al. 2000). However, more comprehensive data presented in 2005 and 2010 at the Red List Workshop in Lucknow, India, showed a different picture: over the past 30 years, the species' population had declined by 90%. Comprehensive field studies from the following years confirmed this assessment (Das et al. 2014). Leith's softshell turtle is already rare in protected areas, and populations in unprotected areas are in drastic decline.

*Nilssonia leithii*, like many other turtle species (especially soft-shelled turtles), is exploited on a large scale for human consumption in its country of origin. At the beginning of the 2000s, a turtle cost between 100 and 300 rupees on the local market, the equivalent of around 2 to 5 euros (Kumar 2004). Later in the 2000s, the national domestic trade also seems to have intensified, with turtles being exported from southern India to further north-eastern states. It appears that this trade has now increasingly shifted from live specimens to calipee (dried, processed carapacial cartilage) in recent years (Murthy 2011, Das et al. 2014, CITES 2022, Roopa et al. 2024). Local hunters stated in interviews that they no longer actively searched for *Nilssonia leithii* as this effort was no longer worthwhile due to its rarity. By 2011, the species was considered very difficult to find, with no viable population known (Praschag et al. 2021). In addition to the turtles themselves, their eggs are also traded as food.

Environmental pollution, the commercial extraction of sand, the alteration of river courses and the construction of hydropower plants and dams in the habitat of *Nilssonia leithii* are further factors in the decline of their populations throughout their range (Praschag et al. 2021).

## Reproduction

| Topic                              | Details on the reproduction of <i>Nilssonia leithii</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual traits            | The tails of male specimens are longer and thicker at the base than those of ♀♀.                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Reproduction                       | Oviparous.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Sexual maturity                    | Praschag et al. (2021) estimate that sexual maturity occurs at 7–8 years, and therefore assume a generation time of 21–24 years.                                                                                                                                                                                                                                                                                                                                                                                        |
| Mating and nesting                 | Information on the mating of <i>Nilssonia leithii</i> is not available.<br>Egg deposition is reported to take place in the sandbanks of inhabited rivers.                                                                                                                                                                                                                                                                                                                                                               |
| Reproductive season                | ♀♀ with mature eggs in their bodies were observed in the months of January and June. In Sharavathi Valley Wildlife Sanctuary, egg-laying occurred in the months of April and May. The turtles probably burrow for aestivation after laying eggs in summer (Praschag et al. 2007).<br>At the Moyar River, newly hatched hatchlings were found in June (Das et al. 2014).<br>Vardia & Tonapi (1992) state that the breeding season for the turtles in eastern India correlates with the monsoon season (June to October). |
| Number of eggs/clutches per season | It is possible that two clutches are laid per year, around December/January, and then again in June (Praschag et al. 2007). Nothing is known about the number of eggs per clutch.                                                                                                                                                                                                                                                                                                                                       |
| Egg size/hatchling size            | Eggs found in Pune, western India, were spherical and had a diameter of 29.8–31.1 mm (Das et al. 2014, Vardia & Tonapi 1992).                                                                                                                                                                                                                                                                                                                                                                                           |
| Incubation and hatching            | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Sex determination                  | As in all Trionychidae probably genetic.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Sperm storage                      | Likely, but not reported so far.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |



## Husbandry and Captive Breeding **C/X**

| Topic                                                           | Data for <i>Nilssonia leithii</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|-----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Husbandry requirements                                          | Spacious, heated water tanks with sufficient water depth for swimming are suitable for keeping them. Tropical water and air temperatures must be reached all year round. A basking area where approx. 40°C radiant heat is achieved is absolutely essential. As with many other soft-shelled turtles, these turtles should be kept individually. The water section should not be too strongly lit and should provide sufficient cover for the turtles. In human care, <i>Nilssonia leithii</i> prefer to eat carnivorous food such as worms, shrimps, fish or molluscs (Varghese & Tonapi 1986), but occasionally the turtles also accept plant-based food (Das et al. 2014). Specimens kept in a temple pond in Andhra Pradesh were fed with hibiscus flowers ( <i>Hibiscus rosa-sinensis</i> ) and bananas ( <i>Musa domestica</i> ). |
| General characteristics, difficulties with keeping and breeding | The potential adult size and the temperature requirements of the species pose the greatest difficulty.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Care of the young, technical and time effort                    | Juveniles can initially be fed with mosquito larvae. They are kept similarly to adult specimens, although smaller tanks are used. Young soft-shelled turtles are sensitive and can be prone to fungal skin infections, so attention must always be paid to good water quality. Even hatchlings should already be housed individually.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Life expectancy                                                 | Unknown. The Madras Crocodile Bank has maintained an adult ♀ of <i>Nilssonia leithii</i> for more than ten years. TSA Foundation India is planning to build up a reserve population in various zoos in the distribution area (CITES 2022), and posted a photo of a very small juvenile on Facebook in 2016, but nothing is known about the husbandry conditions and whether offspring have already been bred.                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Frequency of private breeding and reproduction in zoos          | Very rare. There are no known active breeding projects in India and no known breeding outside India.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Breeding difficulty evaluation                                  | The large adult size of the species and the required housing temperatures represent a major challenge for keeping them in human care. A sufficiently large land area is required for laying eggs.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Mortality in the first years of life                            | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| F2 generation bred in captivity                                 | To the best of our knowledge, this has not taken place so far.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding/ranching                                    | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Interviews/ Surveys/ Consultations                              | The information comes from conservation projects and from the literature.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

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**Sebastian Nickl (15.08.2024)**

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## Anura

### Centrolenidae

#### General Information on Glass Frogs (Centrolenidae Taylor 1951)



Fig. 37: Ventral view of a ♀ *Hyalinobatrachium fleischmanni*. The right and left ovaries with attached follicles are clearly visible. Also note the yellowish tips of the toes, the centrally located abdominal vein and the transparent peritoneum (parietal peritoneum) in this genus, whereas the heart, anterior half of the liver and gastrointestinal tract are covered by a white peritoneal coating (visceral peritoneum) (T. Eisenberg).



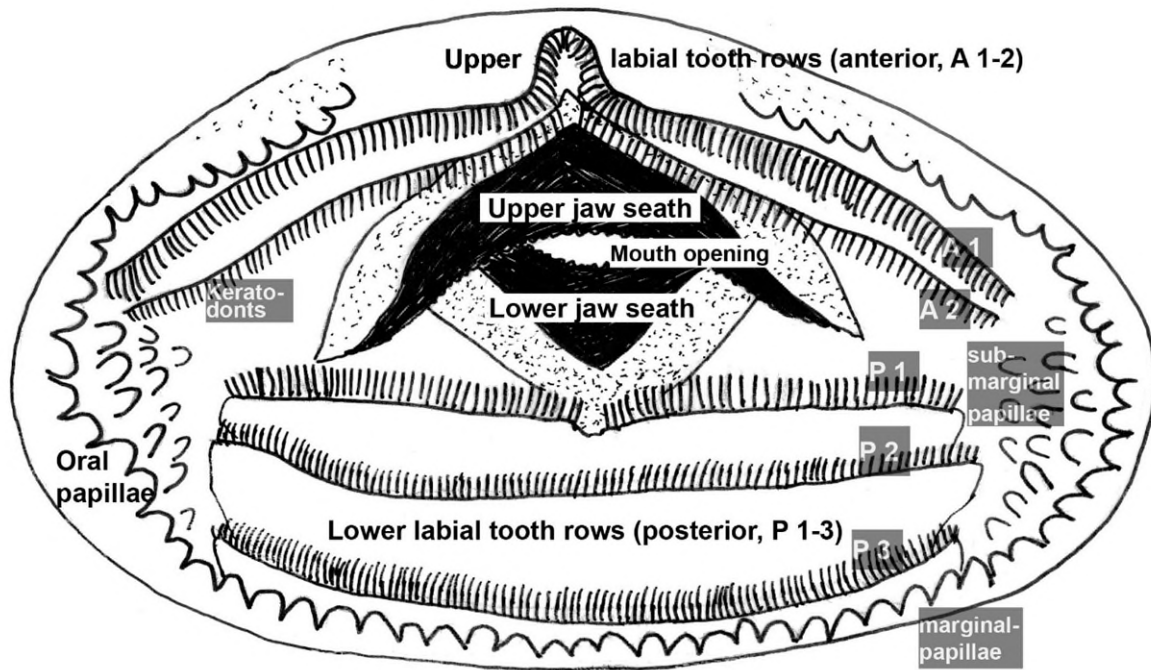


Fig. 38: Mouth field of a tadpole using the example of *Scinax perereca* (Hylidae) (A. Kwet). Note two upper teeth rows (anterior; A 1–2) and three lower teeth rows (posterior; P 1–3) between the upper and lower beak as well as marginal and submarginal papillae surrounding the mouth field.

### Morphology and Taxonomy

The glass frog family received its name because of the ventral – and sometimes even the dorsal (see Fig. 38) – transparency of their skin, through which the organs of the abdominal cavity can be partially recognised from outside. Most glass frogs are coloured green on the upper side, which provides them with masterful camouflage on their perches, the leaves. In some species, the green colouring caused by bile salts can even be found in the bones. Members of this group are also united by a special skin pigment that reflects infrared radiation in the same way as plants, which also serves as camouflage. Most glass frogs are considerably smaller than 30 mm head to body length (SVL), only the Colombian *Centrolene geckoidea* reaches 77 mm.

The Neotropical family of glass frogs (Centrolenidae) occurs from Central America across large parts of South America (tropical Central America, tropical Andes, Sierra Nevada de Santa Marta in Colombia, Cordillera de la Costa in Venezuela, Tobago, Guiana Shield, Amazon Basin, Atlantic Forests of Brazil).

The family was comprehensively revised in 2009, so that at the time of writing it contains 166 species in twelve genera (Guayasamin et al. 2009, AmphibiaWeb 2023). It thus forms a clade descended from the most recent common ancestor of the species *Centrolene geckoidea* Jiménez de la Espada 1872, *Centrolene tayrona* Ruiz-Carranza & Lynch 1991b and *Hyalinobatrachium fleischmanni* (Boettger 1893). All glass frogs are characterised by similarities in the bony structures of the extremities (widened medial process on metacarpus III, an intercalary element between distal and penultimate phalanges, a complete or partial fusion of tibial and fibular) or the trunk (8 presacral vertebrae, no ribs, arciferal pelvic girdle), reproductive biol-



ogy (eggs are laid outside the water) or other anatomical structures (ventral parietal peritoneum partially or completely transparent, anteriorly directed eyes at an angle of 45° to the body axis, a feature that may enable binocular vision). Some of the above features are hypothesised to be synapomorphies for glass frogs, but other putative synapomorphies relating to myology, osteology, colouration and larval development are discussed, which are less relevant to the understanding and purpose of this paper.

The concept of a total of twelve genera, some of them newly defined, has become generally accepted and is also applied in the following chapters in order to express the differences between species and species groups as clearly as possible. However, characteristics that can only be determined microscopically on the specimen or after dissection have only been mentioned in passing or have not been taken into account in the interest of the flow of the text. Information on the specifics of the genus can be found in the individual chapters. However, a genuine identification key would go beyond the scope of this work due to the regularly occurring similarities between taxa, especially, as many species determinations can only be confirmed by means of molecular biological analyses. This was achieved in the cited revision on the basis of a selection and analysis of mitochondrial and nuclear genes, so that the following genera and the monophyly of the family are described on the basis of morphological and genetic data, in part also on the basis of ecological data (lifestyle, bioacoustics, embryology). The sister taxon of the family Centrolenidae is the family Allophrynidae.

*Centrolene* is the type genus of the family Centrolenidae. With the exception of *Espadarana andina*, *Nymphargus balionotus*, *Sachatamia albomaculata* and *S. ilex*, species of the subfamily Centroleninae are characterised by a crista medialis on the humerus, which is absent in all members of the second subfamily Hyalinobatrachinae, whereas it is particularly pronounced in *Ikakogi* spp. as the third 'basic group'. Another characteristic of Centroleninae and *Ikakogi* spp. is a relatively long prepollex, which is short in Hyalinobatrachinae. The fighting behaviour of the ♂♂ was also investigated for some species of the Centroleninae and evaluated as a primary homology of the clade: According to this, two fighting ♂♂ hang belly to belly with only their feet attached to the leaf and try to push each other off the leaf. In contrast, the 'amplexus-like' or 'wrestling behaviour' of the Hyalinobatrachinae is considered primitive. Most representatives of the Centroleninae still have lobed livers (3–5 lobes), green bones in life (white in *Nymphargus rosadus* and *N. anomalus*); ♂♂ usually call from the upper sides of the leaves, and ♀♀ usually also spawn on the upper sides (exceptions: *Centrolene antioquiense*, *C. notostictum*, *C. peristictum*, *Cochranella spinosa*, *Hyalinobatrachium eurygnathum*), and ♂♂ of at least some genera have a hook (humeral spine) on the upper arm. Seven of the nine genera of the Centroleninae are still grouped together in the tribe Cochranellini (*Chimerella*, *Cochranella*, *Espadarana*, *Rulyrana*, *Sachatamia*, *Teratohyla*, and *Vitreorana*) (Guayasamin et al. 2009).

Glass frogs can be found in the foliage of trees and bushes above forest streams and rivers, at least during their reproductive phase. Depending on the species, tropical to subtropical lowland to mountain rainforests or cloud forests are inhabited. The eggs of the glass frogs are always laid in simple to complex clutches outside and above mostly flowing waters on leaves or rocks, so that the hatching tadpoles have an important developmental advantage over spawn deposited in the water. The exact place of deposition, namely the upper or lower side of the leaf, plays an important role in the classification of different species. The clutches of different genera differ in the maternal jelly parts of the clutch surrounding the yolk mem-

branes and range from simple clumps of eggs with only small amounts of jelly to eggs embedded in large jelly-like structures. Species with paternal brood care often lay ‘simple’ clutches (flat layer of eggs touching each other with no jelly between them [monolayer]), which are deposited on the underside of leaves. In species without paternal care, clutch forms range from simple egg clumps to eggs embedded in a complex jelly matrix attached to a variety of substrates (e.g. upper leaf surfaces, stones in splash zones, moss, branches). The configuration of these jelly components determines the ability of a clutch to absorb and store water during incubation, which increases embryo survival. While the survival of clutches without a jelly-like matrix around the eggs depends on the prevention of dehydration by parental brood care (as in *Hyalinobatrachium* and some *Centrolene* species), clutches exposed to rain with a gelatinous matrix absorb water faster and survive longer without rehydration as in species without paternal brood care in the genera *Chimerella*, *Cochranella*, *Espadarana*, *Nymphargus*, *Sachatamia*, *Teratohyla* and *Vitreorana* (Valencia-Aguilar et al. 2024).

Before the developing embryos hatch from the clutch and complete their metamorphosis in the stream below, they are cared for more or less intensively by the parents, each of different sexes, through brood care. This behaviour, in which the clutch is exclusively moistened and possibly defended by the ♂ over a longer period of time, has developed twice independently of each other within the two genera *Centrolene* and *Hyalinobatrachium*. Permanent brood care carried out exclusively by ♀♀ was recently described in the genus *Ikakogi* and thus in the third basal clade with an as yet unresolved status (incertae sedis) (Valencia & Delia 2016). In the other genera, transitional forms exist in which the ♀♀ remain sitting on the clutch for a few hours immediately after laying the eggs, i.e. only temporarily in a kind of ‘brooding behaviour’, in order to provide moisture during the most sensitive phase. The brood care behaviour of the parents and the nature of the clutch have also been taken into account in the systematic classification.

In all the species studied, brood care was essential, particularly in the first few days, but was no longer absolutely necessary in the later phase. All species showed a caring behaviour, which in the case of simple (single-layered) clutches with a high fluid requirement, as in *Hyalinobatrachium* spp. is achieved by prolonged brood care. In some other genera (*Cochranella*, *Teratohyla*), extremely shortened brood care takes place in the form of initial brood care behaviour carried out exclusively by the ♀ immediately and for a few hours after egg deposition. The clutches of the latter genera are usually placed on the rain-exposed upper side of the leaf, so that they dry out particularly easily and suffer embryonic damage in the absence of rain (< 5 mm daily during the first three days). In species with longer brood care (e.g. *Hyalinobatrachium*) this is prevented by the ♂. The clutch structure influences the fluid intake and the need for rehydration: clutches rich in jelly absorb faster and more water than simple, single-layered clutches (jelly-rich clutches of *Cochranella granulosa* absorbed a maximum of 12.72 g of water, while those of *H. fleischmanni* absorbed only 4.9 g). At maximum saturation after initial brooding-only care behaviour, these clutches withstand desiccation longer than simple clutches, which is why continued parental brood care no longer seems necessary in the jelly-rich type. Thus, there was an almost consistent, statistically verified relationship between the evolutionary transition to simple clutches and an increasing length of brood care behaviour (usually as a combination of guarding and repeated moistening (‘guarding-and-brooding care’) exclusively by the ♂ (exceptions: *Sachatamia* spp. clutches are simple clutches that are not permanently cared for, although they are often laid in the splash zone; *H. fleischmanni* do not practise guarding, only moistening [prolonged brooding-only care])). Another exception are the

simple, low-jellied clutches of *Ikakogi tayrona*, for which prolonged brood care is provided exclusively by the ♀. A further fluid-storing factor in the form of the presence of empty egg cases in the clutch, which are particularly abundant in clutches rich in jelly, could have the same function in glass frogs as in phyllomedusine tree frogs (McDiarmid 1978, Hayes 1991, Savage 2002, Delia et al. 2017a, 2020).

### Particular difficulties in identifying CITES-listed glass frog species

Partial translucency, especially of the ventral skin, is also known from other anurans from different continents, although there are no closer relationships to the glass frogs, for example in *Boana cinerascens*, *B. nympha*, *Hyloscirtus phyllonathus*, *Tlalocohyla celeste* (Hylidae), *Hyperolius jackie* (Hyperoliidae), *Boophis boppa* (Boophinae), *Feihyla kajau* (Rhacophoridae). This makes it difficult for the competent authorities and customs to differentiate morphologically between glass frogs and non-CITES-listed species. In order to enable adequate implementation of CITES listings, States Parties are therefore encouraged in accordance with Res. Conf. 19.4 to develop and share guidance on the identification of CITES-listed species and, where practicable, non-listed species.

### Conservation Status

All species of the Centrolenidae family are included in CITES Appendix II since 2023 (Cop19 Proposal 34).

EU Council Regulation (EC) No. 338/97: Annex B.

In Germany all glass frogs of the Centrolenidae family are specially protected under Article 7 (2) No 13 BNatSchG.

### Husbandry and Captive Breeding, Interviews

Certain conditions are required for keeping and breeding glass frogs in captivity, which are summarised here in general terms from my own experience or particularly detailed breeding reports and survey data. More detailed information can be found in the following, taxon-specific chapters.

Micro crickets (*Acheta domesticus*, *Gryllus assimilis*, *G. bimaculatus*), *Drosophila* spp., bean weevils (*Acanthoscelides obtectus*), pea aphids (*Acyrtosiphon pisum*) or various springtail species (especially for juveniles) have proven to be effective as food for glass frogs in the terrarium; feeding with fruit flies alone does not appear to be sufficient. They are fed once (Redbond et al. 2019) to several times (T. Eisenberg, unpublished data) per week. All feeder insects are dusted with a mineral-vitamin preparation, e.g. Repashy Calcium plus (Repashy Superfoods, Oceanside, CA, USA) or Nutrobal (Vetark Ltd., Winchester, UK), before feeding (Redbond et al. 2019, Eisenberg in prep., Papenfuss & Eisenberg in prep.).

The terrariums are illuminated for approx. twelve hours and the temperatures should be between 24 and 26°C during the day. Redbond et al. (2019) controlled the climate according to a climate table from the area of origin in Costa Rica. Apart from higher day and night temperatures in the local summer, which cannot always be avoided but to which the animals are also temporarily exposed in their natural habitat (T. Eisenberg, unpublished data), relatively uniform husbandry conditions should be maintained all year round.

Keeping several ♂♂ and ♀♀ together has proven to be advantageous. The calls of several ♂♂ stimulate reproduction. Rank order fights between rivaling ♂♂ only occur very rarely and only in certain species during the breeding season, but should not be permanent.



Fig. 39: Technical equipment for keeping and breeding glassfrogs (all photos by T. Eisenberg)

- a Measurement and control technology: switching relays as clock generators for pulsating irrigation systems
- b Switch panels for alternating use of different pumps of the irrigation system to enable pulsatile irrigation for individual terrarium groups
- c View into the humid chamber – the leaves with the eggs are attached above the water surface. A mist nozzle or an ultrasonic nebulizer regularly moistens the clutches with water. It is important that the leaf surfaces are allowed to dry for some time afterwards so that the eggs do not slip into the water prematurely. This clutch treatment is essential for the incubation of *Cochranella granulosa* clutches
- d Aquarium system for rearing glass frog tadpoles: one species is reared in each compartment. Note the airlift sponge filters for aeration and filtration of the water as well as numerous shelters for the larvae.

The terrarium should be as high as possible, at least 50–60 cm (up to 100 cm for larger species). The width and depth should be adjusted accordingly. Terrarium or paludarium sizes of



e.g. 50 x 50 x 50 to 60 x 50 x 80 cm (L x W x H) are suitable for groups of 3–4 ♂♂ and 3–5 ♀♀ for most species.

Even if the care works without a permanent shallow water section, such a section has generally proved its worth – it is constantly supplied with fresh water by an automatic sprinkler system. Suitable plants (e.g. *Spatiphyllum cochlearispathum*, *Philodendron laciniatum*, *P. heteraceum*, *P. erubescens* and *Monstera acuminata*, anthuriums, etc.) with smooth, not too fleshy leaves should be placed above the water and land sections. As the frogs also spawn over land, the larvae may find the water by darting movements of their bodies.

The author's terrariums have a double bottom disc glued in at an angle, which drains into a frontal moat with a floor drain. The back and side walls of the containers are covered with Xaxim sheets or Hygrolon® gauze, on which all plants and mosses grow epiphytically. No bottom substrate was used, but moss grows on parts of the bottom disc, which is still covered with larger stones. Other authors recommend stones, leaves and a substrate of gravel and soil (Redbond et al. 2019) or artificial material. The terrariums are best connected to a sprinkler system with spray nozzles, which is operated with varying frequency throughout the year. LED light bars or 35 W full spectrum lamps with UV component (e.g. Bright Sun UV Jungle, Import Export Peter Hoch GmbH, Waldkirch) are used above the wire gauze for lighting (T. Eisenberg, unpublished data).

After laying the eggs, removing the entire leaf from the terrarium has proven to be a good way of ensuring hygienic breeding.

Mating can be initiated by frequent spraying via the sprinkler system or continuous rain, which is achieved with a circulation pump. A body of flowing water, as propagated by Redbond et al. (2019), is not absolutely necessary for egg laying.

Rearing of juvenile frogs: 25 x 20 x 60 cm rearing terrariums with a water ditch and epiphytic *Philodendron* vines without substrate (Eisenberg in prep., Papenfuss & Eisenberg in prep.).

176 known glass frog keepers and breeders were contacted directly for the survey and reminded; the questionnaire was also publicised via the DGHT-AG Anuren mailing list and as a form in the Facebook group 'Glass Frog Breeding COOP' (approx. 3,500 members at the beginning of 2024) and the WhatsApp group 'Dendrobaten Germany' (201 members).

Specific information on individual genera or species can be found in the individual taxon-specific chapters. A vertical line between the keeper details ('|') represents the respective answers from the keeper survey. Unless otherwise indicated, the statements refer to information provided by one keeper (n=1).

#### **Tobias Eisenberg (15.08.2024)**

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## References on the Centrolenidae

The publications on glass frogs usually refer to several species, which are now often even assigned to different genera; they have therefore been compiled here in a general bibliography.

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***Celsiella* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                      | Original description          | Common name                | Common name international | Known/ documented in international trade |
|------------------------------|-------------------------------|----------------------------|---------------------------|------------------------------------------|
| <i>Celsiella revocata</i>    | (Rivero, 1985)                | El Tovar Glass Frog        |                           | No                                       |
| <i>Celsiella vozmedianoi</i> | (Ayarzagüena & Señaris, 1997) | Magdalena Giant Glass Frog |                           | No                                       |



Fig. 40: *Celsiella vozmedianoi*, Peninsula de Paria, Sucre, Venezuela  
(C. Barrio Amorós/Fundación AndígenA)

**Morphology and Taxonomy**

The genus *Celsiella* is named after the Venezuelan herpetologist Josefa Celsa Señaris and is the sister taxon to the genus *Hyalinobatrachium*, with which it forms the subfamily Hyalinobatrachinae.

In the comprehensive revision of the family of glass frogs, the genus *Celsiella* was newly described and – at the time of writing this paper – contains only two species (Guayasamin et al. 2009). These are characterised by the following features: (1) no humeral spines, (2) a three-lobed liver covered by a transparent peritoneum, (3) ventral parietal peritoneum white in

front, transparent behind, (4) bones pale green to green in life, (5) dorsal colouration in preservative cream-coloured, (6) ♂♂ without conspicuous spines on the back, (7) nuptial excrescences in ♂♂ inconspicuous, (8) vomer without dentary processes and teeth, (9) ♂♂ call and ♀♀ spawn on the upper side of the leaves (*C. vozmediano*) or on the upper and lower sides (*C. revocata*). The genus *Celsiella* is morphologically similar to the genera *Nymphargus*, *Rulyrana* and *Sachatamia*, none of which spawn on the undersides of leaves (Señaris & Ayarzagüena 2005, Guayasamin et al. 2009).

The two species in this genus are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unambiguous species identification):

*Celsiella revocata*: medium-sized glass frog with dorsal deep green colouration with small yellowish white dots on dorsum and posterior half of head, patchy melanophores on entire dorsum including legs and arms, upper lip with very distinct white band, fingers and toes yellowish, white line from outer edge of ankle to fifth toe disc, a white band separates the flanks of the abdomen (opaque) from a transparent ventral region, SVL ♂♂ 21.8–25.2 mm, ♀♀ unknown, head slightly wider than long, mouth region short, rounded in dorsal view and slightly oblique in lateral view, iris with strong grey marbling, tympanum inconspicuous, Bones light green, ventral parietal peritoneum white in anterior third with lateral extensions, transparent central zone (translucent), peritoneum on pericardium white, liver and visceral peritoneum transparent. The two species in this genus had previously been included in the genera *Centrolenella*, *Hyalinobatrachium* and *Cochranella* (Ruíz-Carranza & Lynch 1998, Señaris & Ayarzagüena 2005, Guayasamin et al. 2009).

*Celsiella vozmediano*: medium-sized glass frog with dorsal green colouration and numerous, larger white dots on the head, bright melanophores on the entire dorsum including legs and arms, upper lip with very distinct white band, fingers and toes whitish, fingers I and II yellowish, transparent flank region reveals white parietal peritoneum, SVL ♂♂ 27.8–28.4 mm, ♀♀ unknown, head slightly wider than long, mouth region short, truncated in dorsal and lateral view, iris with grey marbling and white dots, tympanum conspicuous, ventral parietal peritoneum white in the anterior third, remaining parts transparent, peritoneum on pericardium white, liver and visceral peritoneum transparent (Señaris & Ayarzagüena 2005).

### Distribution and Habitat

*Celsiella revocata*: Primary forests of the southern foothills of the central parts of the Cordillera de la Costa (Distrito Capital and state of Aragua) and from Cerro Azul, Fila La Blanquera in Serranía del Interior (state of Cojedes), Venezuela (1,200–1,800 m asl). Habitat: in the vegetation near streams in humid high mountain rainforests, possibly also in secondary forests (Señaris & Ayarzagüena 2005).

*Celsiella vozmediano*: Like *C. revocata*, this species is also endemic to Venezuela and is only known from Cerro El Humo and the surroundings of Las Melenas, Sucre state (750–800 m asl, possibly also up to an altitude of 1,200 m in the cloud forest). Habitat: on vegetation above mountain streams or in their vicinity (Ayarzagüena & Señaris 1996, Señaris & Ayarzagüena 2005, Guayasamin et al. 2009).

## Conservation Status and Main Threats

### IUCN Red List Status

*Celsiella revocata*: VU (Vulnerable, B1ab(iii), assessed 2020-02-27)

*Celsiella vozmediano*: EN (Endangered, B1ab(ii,iii,v), assessed 2019-11-13).

### Red List Status in the Range Countries

Neither species is on the Venezuelan Red List.

### Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local applications of pesticides, fertilisers and pollution, disease, climate change and increased UV-B radiation.

*Celsiella revocata*: Although the species was frequently found around the type locality in the 1960s and 1970s, it was categorised as vulnerable due to its relatively limited and fragmented distribution area (two populations). The continuous decline in spatially and qualitatively suitable habitats in large parts of its distribution area in the Cordillera de la Costa due to deforestation and environmental pollution is also causing a declining population trend (Señaris & Lampo 2022).

*Celsiella vozmediano*: categorised as endangered due to the very small distribution area of only 148 km<sup>2</sup>, also declining population trend due to the same causes as for *C. revocata* (Señaris & Rivas 2022).

### Reproduction

| Topic                       | Details on the reproduction of <i>Celsiella</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | In both species the ♂♂ call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Sexual maturity             | Not specified in the literature, probably 6–12 months as with other representatives of the Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Calls                       | <i>C. revocata</i> : Calls consisting of one modulated note, but occasionally also two calls emitted in close succession, dominant frequency 3,540–4,140 Hz (Señaris & Ayarzagüena 2005).                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Mating and spawning         | Both species: Axillary amplexus in the vegetation above small forest streams.<br><i>C. revocata</i> : ♂♂ were found calling during the rainy season on the upper and lower leaf surfaces at a height of 0.8–8 m above the water, spherical clutches are also placed on both leaf surfaces, ♂♂ practise brood care (Señaris & Ayarzagüena 2005).<br><i>C. vozmediano</i> : ♂♂ call from the tops of leaves, where ♀♀ also place their clutches, ♂♂ perform brood care, in which brooding behaviour to provide moisture has been observed (Ayarzagüena & Señaris 1996, Señaris & Ayarzagüena 2005, Delia et al. 2017b). |
| Reproductive season         | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Eggs/clutch, clutches/year  | <i>C. revocata</i> : 28–52 eggs/clutch (Señaris & Ayarzagüena 2005).<br><i>C. vozmediano</i> : spherical clutch with 20 eggs at the tip of a leaf, approx. 1.5 metres                                                                                                                                                                                                                                                                                                                                                                                                                                                 |

|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | above the water (Señaris & Ayarzagüena 2005).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Size of eggs and larvae at hatching               | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Development time from egg laying to metamorphosis | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Details on the larvae                             | <p><i>C. revocata</i>: Tadpole with spiraculum in the posterior third of the body; cloacal opening in the form of a long tube (Señaris &amp; Ayarzagüena 2005).</p> <p><i>C. vozmediano</i>: Before hatching, tadpoles have a deep yellow body with a white tail and a reddish ring in between. The following description is based on a batch of five tadpoles at stage 25, which were obtained from the development of a clutch found: Body length 3.6–4.6 mm, tail length 9.6–11.6 mm, body height 1.8–2.3 mm, body width 2.2–2.6 mm, width of oral disc 1.2–1.3 mm, dorsally compressed body, laterally oval, small, dorsolaterally located eyes, tail musculature does not reach the distal end of the tail, distal tail end rounded, dorsal fin originates at the junction between body and tail, the ventral fin originates at the body, oral disc ventral, bordered below and laterally by a single row of marginal papillae, fully keratinised rows of denticles with free edges, horn beak with saw edges (Señaris &amp; Ayarzagüena (2005).</p> |

### Husbandry and Captive Breeding **X**

On the *Celsiella* species there is no husbandry information available.



**Centrolene Jiménez de la Espada, 1872**

| Species                              | Original description                                        | Common name                                                                | Common name international             | Known/ documented in international trade |
|--------------------------------------|-------------------------------------------------------------|----------------------------------------------------------------------------|---------------------------------------|------------------------------------------|
| <i>Centrolene acanthidiocephalum</i> | (Ruiz-Carranza & Lynch, 1989)                               | Santander Giant Glass Frog                                                 |                                       | No                                       |
| <i>Centrolene altitudinalis</i>      | (Rivero, 1968)                                              | Mountain Giant Glass Frog                                                  |                                       | No                                       |
| <i>Centrolene antioquiensis</i>      | (Noble, 1920)                                               | Antioquia Giant Glass Frog                                                 |                                       | No                                       |
| <i>Centrolene azulae</i>             | (Flores & McDiarmid, 1989)                                  | Blue Giant Glass Frog                                                      |                                       | No                                       |
| <i>Centrolene ballux</i>             | (Duellman & Burrows, 1989)                                  | Burrowes' Giant Glass Frog, Golden-flecked Glass Frog, Gold-dust Glassfrog |                                       | No                                       |
| <i>Centrolene buckleyi</i>           | (Boulenger, 1882)                                           | Buckley's Giant Glass Frog, Buckley's Glass Frog                           | Rana de cristal altoandina de Buckley | No                                       |
| <i>Centrolene camposi</i>            | Cisneros-Heredia, Yáñez-Muñoz, Sánchez-Nivicela & Ron, 2023 | Campos' Glassfrog                                                          |                                       | No                                       |
| <i>Centrolene charapita</i>          | Twomey, Delia & Castroviejo-Fisher, 2014                    | Charapita Glassfrog                                                        |                                       | No                                       |
| <i>Centrolene condor</i>             | Cisneros-Heredia & Morales-Mite, 2008                       | Condor Glassfrog                                                           | Rana de cristal del Cóndor            | No                                       |
| <i>Centrolene daidalea</i>           | (Ruíz-Carranza & Lynch, 1991c)                              | Alban Cochran Frog                                                         |                                       | No                                       |
| <i>Centrolene ericsmithi</i>         | Cisneros-Heredia, Yáñez-Muñoz, Sánchez-Nivicela & Ron, 2023 | Smith's Glassfrog                                                          |                                       | No                                       |
| <i>Centrolene geckoidea</i>          | Jiménez de la Espada, 1872                                  | Pacific Giant Glass Frog, Gecko Glassfrog                                  |                                       | No                                       |
| <i>Centrolene heloderma</i>          | (Duellman, 1981)                                            | Bumpy Glassfrog, Pichincha Giant Glass Frog, Warty Glassfrog               |                                       | No                                       |
| <i>Centrolene hesperia</i>           | (Cadle & McDiarmid, 1990)                                   | Basecamp Giant Glass Frog                                                  |                                       | No                                       |
| <i>Centrolene huilensis</i>          | Ruiz-Carranza & Lynch, 1995c                                | Huila Glassfrog                                                            | Rana de cristal del Huila             | No                                       |
| <i>Centrolene hybrida</i>            | Ruiz-Carranza & Lynch, 1991b                                | Eastern Giant Glass Frog                                                   |                                       | No                                       |
| <i>Centrolene lemniscata</i>         | Duellman & Schulte, 1993a                                   | Rioja Giant Glass Frog                                                     |                                       | No                                       |
| <i>Centrolene lynchi</i>             | (Duellman, 1980)                                            | Lynch's Glassfrog, Lynch's Giant Glassfrog                                 | Rana de cristal de Lynch              | No                                       |
| <i>Centrolene medemi</i>             | (Cochran & Goin, 1970)                                      | Medem's Glassfrog, Medem Giant Glass Frog                                  |                                       | No                                       |

|                                 |                                                                |                                                |                                                            |    |
|---------------------------------|----------------------------------------------------------------|------------------------------------------------|------------------------------------------------------------|----|
| <i>Centrolene muelleri</i>      | Duellman & Schulte, 1993a                                      | Muller's Giant Glass Frog                      |                                                            | No |
| <i>Centrolene notosticta</i>    | Ruiz-Carranza & Lynch, 1991b                                   | Cordillera Giant Glass Frog                    |                                                            | No |
| <i>Centrolene paezorum</i>      | Ruiz-Carranza, Hernández-Camacho & Ardila-Robayo, 1986         | Colombian Giant Glass Frog                     |                                                            | No |
| <i>Centrolene peristicta</i>    | (Lynch & Duellman, 1973)                                       | Tandapi Giant Glass Frog, Dappled Glassfrog    | Rana de cristal de Tandapi                                 | No |
| <i>Centrolene petrophilum</i>   | Ruiz-Carranza & Lynch, 1991b                                   | Boyaca Giant Glass Frog                        |                                                            | No |
| <i>Centrolene pipilata</i>      | (Lynch & Duellman, 1973)                                       | Amazon Giant Glass Frog, Peeping Glassfrog     |                                                            | No |
| <i>Centrolene quindianum</i>    | Ruiz-Carranza & Lynch, 1995c                                   |                                                |                                                            | No |
| <i>Centrolene robledoii</i>     | Ruiz-Carranza & Lynch, 1995c                                   |                                                |                                                            | No |
| <i>Centrolene sabini</i>        | Catenazzi, von May, Lehr, Gagliardi-Urrutia & Guayasamin, 2012 | Sabin's Glassfrog                              |                                                            | No |
| <i>Centrolene sanchezi</i>      | Ruiz-Carranza & Lynch, 1991b                                   | Sánchez's Giant Glassfrog, Sánchez's Glassfrog | Rana de cristal de Sánchez                                 | No |
| <i>Centrolene savagei</i>       | (Ruiz-Carranza & Lynch, 1991c)                                 | Savage's Glass Frog, Savage's Cochran Frog     |                                                            | No |
| <i>Centrolene solitaria</i>     | (Ruiz-Carranza & Lynch, 1991c)                                 | Lonely Cochran Frog                            |                                                            | No |
| <i>Centrolene venezuelensis</i> | (Rivero, 1968)                                                 |                                                | Ranita de cristal Venezolana, ranita verde de labio blanco | No |
| <i>Centrolene zarza</i>         | Székely, Córdova-Díaz, Hualpa-Vega, Hualpa-Vega, Székely, 2023 | Zarza Glassfrog                                |                                                            | No |

The genus name *Centrolene* is probably derived from the Greek 'kentron' (= tip or spur) and 'olene' (= elbow), in reference to the conspicuous humerus spine present in adult ♂♂ of the type species. Phylogenetically, the genus represents the clade of the common lineage of the two species *Centrolene geckoidea* Jiménez de la Espada, 1872 and *Centrolene peristicta* Lynch & Duellman, 1973. The sister genus is *Nymphargus*.

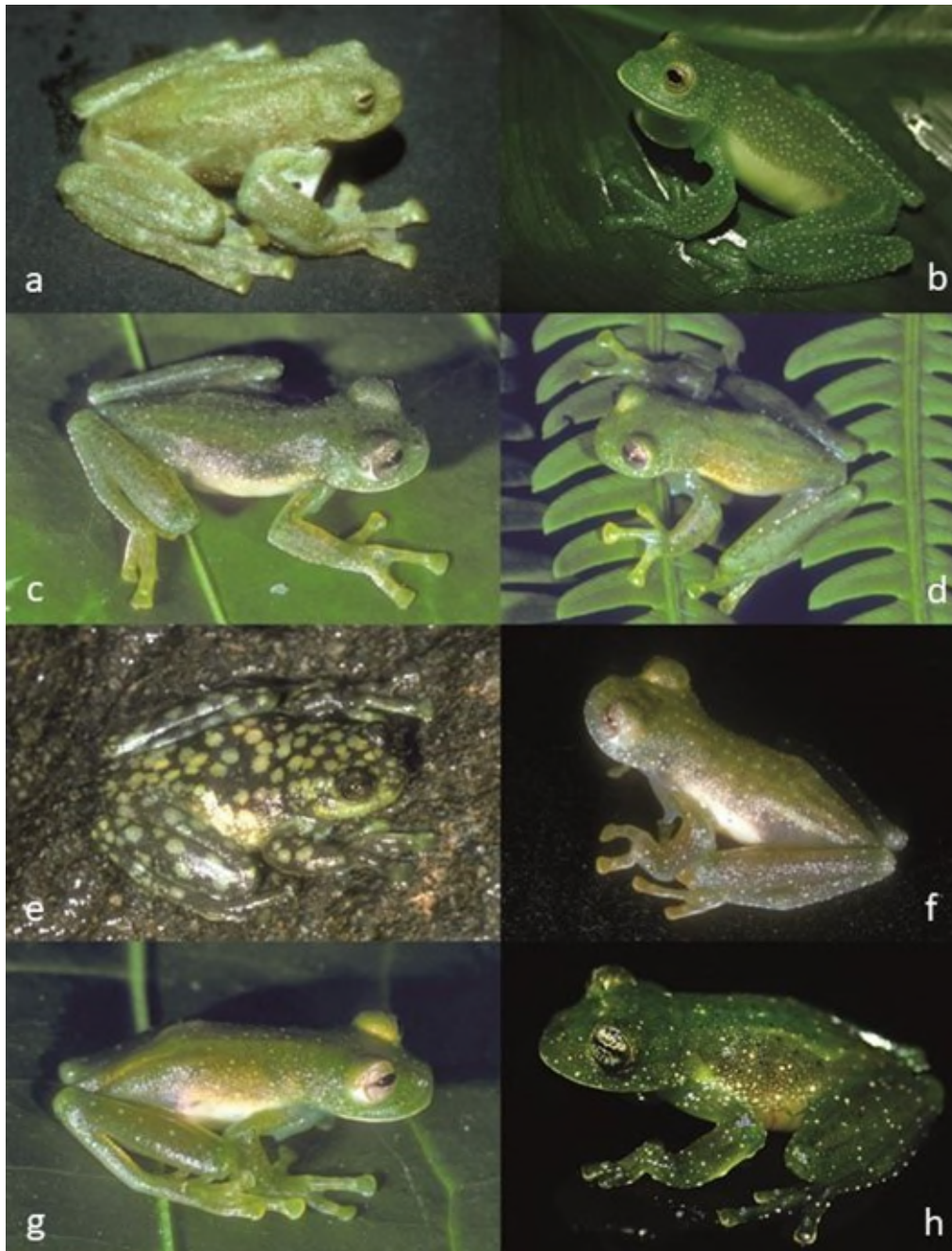


Fig. 41: *Centrolene* species

- a *C. geckoidea* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001082)
- b *C. heloderma*, NW-Ecuador (A. Plewnia)
- c *C. huilense* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001094)
- d *C. lynchi* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001101)
- e *C. medemi* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001104)
- f *C. pipilatum* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001109)
- g *C. sanchezi* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001131)
- h *C. savagei* Tatamá-Nationalpark (A. Plewnia).

## Morphology and Taxonomy

Representatives of the genus can be distinguished by the following characteristics: (1) humeral spine present in adult ♂♂ of all species except *C. charapita*, *C. daidalea*, *C. savagei* and possibly *C. solitaria*, (2) three-, four- or five-lobed liver, which is covered by a transparent hepatic peritoneum, (3) a ventral parietal peritoneum, which is coloured white in the anterior region by iridophores, whereas the posterior region is transparent/translucent, (4) the bones are pale to bright green in life, (5) the back turns lavender-coloured (with or without dots) in preservative, (6) the back of the ♂♂ bears small spiky skin elevations (so-called spiculae) during the reproductive period; not present in *C. antioquiense*, *C. hybrida*, (7) conspicuous nuptial excrescences in ♂♂, (8) ♂♂ usually call from the upper sides of leaves, and ♀♀ also lay their clutches on the upper sides of leaves along streams (exceptions: *C. geckoidea* calls from the spray zone behind waterfalls and spawns on rocks, *C. peristictum* calls and spawns on lower leaf surfaces, while *C. antioquiense* calls on upper leaf surfaces but spawns on lower leaf surfaces), (9) articulated connection between quadratojugals and maxillae. The presence of pronounced humeral spines in most adult male representatives of the genus distinguishes this group from most other clades, only the genera *Espadarana* and *Ikakogi* also possess them. *Ikakogi*, on the other hand, has white bones, a distinctive crista medialis on the humerus and female brood care. The morphological similarity between the genera *Centrolene* and *Espadarana* is remarkable due to the lack of a clear distinguishing feature. While enamelled pericloacal tubercles are typical in *Centrolene*, these have not yet been described in *Espadarana*. Furthermore, most species of the genus *Centrolene* have no denticles on the vomer (present in *C. condor*, *C. daidaleum*, *C. geckoidea*, *C. savagei*, *C. solitaria*), whereas all *Espadarana* species have these denticles. Humeral spines are also found in individual representatives of other genera (e.g. *Nymphargus grandisonae*, *Chimerella mariaelenae*, *Cochranella litoralis*, *Vitreorana gorzulae*), but these are morphologically different from those in *Centrolene* and therefore probably not homologous (Guayasamin et al. 2009).

Many species in this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for definitive species identification):

*Centrolene acanthidiocephalum*: large glass frog with lime, lemon to deep green dorsal colouration and few orange ocelli surrounded by a brown halo, smooth dorsal skin with tiny bumps and conical spines on the head of the ♂♂, slightly protruding, slightly whitish upper lip, infracloacal ornamentation consisting of a zone of small cream-coloured tubercles, humeral spines prominent in ♂♂, SVL 30.0–33.3 mm (body mass 2.2–2.7 g; ♂♂ 31.3 ± 0.8 mm; n=15, ♀♀ 31.4 ± 0.9 mm; n=4), head with small eyes, mouth region elongated, slightly pointed dorsally, inclined anteroventrally laterally, no denticles present on the vomer, anterior parietal and pericardial peritoneum white, transparent hepatic and visceral peritoneum. Related species: *C. geckoidea* and *C. charapita* (putative, i.e. probable, sister taxa), furthermore *C. daidalea*, *C. savagei*, *C. antioquiense*, *C. peristicta* (Ruiz-Carranza & Lynch 1989, Rios-Soto & Rada 2018, Carvajal-Cogollo et al. 2023).

*Centrolene altitudinalis*: medium-sized glass frog with dark green (yellowish green during the day) dorsal colouration with small white or cream-coloured spots, granular dorsal skin with tiny spines on the head of the ♂♂, pronounced yellowish white line on the edge of the upper lip, fingers and toes yellowish, humeral spines of ♂♂ moderately large, iris grey, SVL ♂♂ 21.5–24.5 mm, ♀♀ unknown), head slightly broader than body, eyes very large, anterolaterally aligned, mouth region truncate from dorsal, inclined anteroventrally from lateral, no tooth processes and no vomer teeth, tympanum moderately large, ¾ visible, dorsolaterally aligned,

anterior parietal (about  $\frac{2}{3}$ ) and pericardial peritoneum white, transparent hepatic and visceral peritoneum, liver four-lobed. Related species: *C. buckleyi*, *C. venezuelensis*, *C. hesperia*, *C. lemniscata* (Señaris & Ayarzagüena 2005, Guayasamin et al. 2020).

*Centrolene antioquiensis*: see *C. peristicta* (sister species), but with somewhat less pronounced integument on the hands. Similar species: *C. lynchi*, *C. peristicta*, *C. pipilata*, *Nymphargus truebae* (Guayasamin et al. 2020).

*Centrolene azulae*: medium sized glass frog with uniform dark green dorsal colouration with very small (~ 1 mm) yellow spots, dorsal and ventral skin slightly granulated, dorsum with some scattered low warts; Ventral colouration slightly bluish green on chin, silvery white on chest and front half of body, transparent with bluish green tinge behind, iris iridescent yellow with numerous wavy black lines, SVL of ♂♂ unknown, ♀ 27.5 mm [holotype], head much wider than body, eyes very large, a yellow line around each eye, mouth region truncate from dorsal, slightly protruding from lateral, 2–3 teeth present on vomer, tympanum directed dorsally, anterior parietal peritoneum white, transparent visceral peritoneum. Status: incertae sedis within the Centroleninae, as molecular data are not available and morphological and behavioural characters do not provide clear evidence of genus affiliation (possibly synonym of a previously described species; Flores & McDiarmid 1989, Guayasamin et al. 2009, 2020).

*Centrolene ballux*: small glass frog with lime-green dorsal colouration with characteristic golden spots and small warts on the dorsal surface, dorsal skin smooth, ventral skin smooth to granular, anal opening directed posteriorly, humeral spines large in ♂♂, upper lip white, iris copper to bronze coloured with fine black reticulation, SVL ♂♂ 19.2–22.2 mm, ♀♀ 21.0–23.3 mm, head slightly wider than body, eyes moderately large, directed anterolaterally, mouth region dorsally and laterally truncate, no teeth present on vomer, tympanum partially visible, anterior parietal peritoneum white (heart not visible), transparent peritonea on stomach, intestines, testes, kidneys, urinary and gall bladder, four-lobed liver. Similar species: *C. lynchi*, *C. peristicta*, *C. robledo*, *Nymphargus buenaventura*, some populations of *N. griffithsi* (Duellman & Burrowes 1989, Hutter & Guayasamin 2012, Guayasamin et al. 2020).

*Centrolene buckleyi*: medium-sized to large glass frog with uniform green colouration with or without scattered white spines or tubercles, dorsal skin slightly granular, ♂♂ with or without spines, gular region pale green, belly yellowish white in anterior half, translucent in the rear half, heart not visible, a white line separates the back from the lower flanks, which are whitish cream in colour, ventrolateral edge of the arm and tarsus white, edge of the upper lip white, small white tubercles near the cloacal opening, whitish grey iris with small black reticulations and a brown horizontal line, humeral spines large in ♂♂, SVL ♂♂ 26.5–30.9 mm, ♀♀ 29.3–34.4 mm, mouth region rounded dorsally, slightly sloping laterally, no teeth present on the vomer, tympanum partially or completely hidden under the skin, when visible it is almost vertically orientated, supratympanic fold distinct, anterior parietal peritoneum white (pericardium silvery-white), transparent peritonea on stomach, intestines, testes, kidneys, urinary and gall bladder, four- or five-lobed liver. It is a species complex, Amador et al. (2018) provided molecular evidence that *C. buckleyi* consists of at least three species, none of which is most closely related to the others, one species in southern Ecuador, two (including *C. buckleyi* sensu stricto) in northern Ecuador and another in the central Andes of Colombia, although the distributional limits are currently unknown. Two specimens from Huancabamba in the department of Piura in northern Perú, which were previously attributed to this species, are in fact metamorphs of another species. All records of this species from Venezuela that were previously assigned to



this taxon are now assigned to *C. venezuelensis*. Similar species: *C. ballux*, *C. condor*, *C. heloderma*, *C. hesperia*, *C. lemniscata* (Perú), *C. altitudinalis*, *C. venezuelensis* (Venezuela; Duellman & Wild 1993b, Guayasamin et al. 2008a, 2020, Amador et al. 2018, Frost 2024).

*Centrolene camposi*: large glass frog with uniform green colouration with light yellowish green low round tubercles, melanophores on the dorsal surfaces of the hands and feet and at the base of finger IV, toe IV and toe V, dorsal skin slightly granular, ♂♂ with tiny spines and spines, ventral skin granular, thick yellowish white labial stripe, opening into a faint yellowish line between lip and anterior ¼ of the body, yellowish green flanks, two distinct tubercles near the cloacal opening, iris with white background, towards the centre flesh-coloured, fine brown reticular structures, humeral spines clearly developed in ♂♂, SVL ♂♂ 29.1–31.2 mm, ♀♀ unknown, mouth region rounded to slightly pointed dorsally, slightly sloping laterally, no teeth or dentary processes present on the vomer, lower ¾ of tympanum visible, supratympanic fold present and low, anterior parietal peritoneum white (pericardium silvery-white), transparent peritonea on stomach, intestine, (five-lobed) liver, testes, kidneys, urine and gall bladder. Related species: *C. condor*. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. heloderma*, *C. hesperia*, *C. lemniscata*, *C. venezuelensis* (Cisneros-Heredia et al. 2023).

*Centrolene charapita*: large glass frog with dark green colouration of dorsal and dorsolateral surfaces with yellow or pale green spots of varying size (ocelli) bearing shiny, ‘enamelled’, tubercles and microspiculae (tiny spines) forming a dark green network (darker around the ocelli), upper lip, fingertips and toes I, II and III shiny white, ventral side, flanks, upper arms unpigmented, jagged, enamelled ulnar and tarsal folds, low enamelled tubercles over the orbits forming an irregular lateral band from the head to the middle of the body and to the dorsoposterior margin of the upper arm, ventral skin on abdomen and thighs coarsely areolate, while all other ventral surfaces are smooth, conspicuous cloacal ornament of folded skin bearing four large, shiny tubercles protruding forward (valves), surrounded by various lower tubercles with or without shiny ‘enamelling’, iris white to light grey with a net structure of yellow shades and black dots, humeral spines not present in ♂♂, SVL ♂♂ 34.7–37.0 mm, ♀♀ unknown, mouth region in the Peruvian population blunted to slightly rounded in dorsal view and in profile, in the Ecuadorian population, the mouth region is round in dorsal view and oblique in profile, a tooth-like projection on each vomer bearing a row of 4–6 small vomer teeth, tympanum covered by skin and not visible, anterior parietal peritoneum (⅓) white, transparent peritonea on pericardium, (trilobed) liver, testes, kidneys, urine and gall bladder, white peritonea on stomach and intestines. Related species: *C. geckoidea* (sister species). Similar species: *C. daidaleum*, *C. paezorum*, *C. savagei*, *C. solitaria*, *C. huilense*, *C. muelleri*, *Cochranella mache*, *Cochranella resplendens*, *Vitreorana parvula*, *Nymphargus ocellatus* (Twomey et al. 2014, Páez-Rosales & Pinto 2017, Guayasamin et al. 2020).

*Centrolene condor*: medium sized glass frog with bluish green colouration with many small yellowish white spots and dark bluish black to brown spots and dots, dorsal skin chagrined with low tubercles and abundant spiculae, ventral skin granular, light labial stripe, subcloacal area granular with several shiny tubercles, shiny ulnar and metatarsal folds, followed by a row of distinct enamelled (shiny) tubercles along the outer edge of the tarsus, Iris creamy yellow with fine dark reticulation, humeral spines in ♂♂ small and curved, SVL ♂♂ 23.2–27.6 mm, ♀♀ unknown, mouth region slightly pointed from dorsal, slightly sloping from lateral, horizontal toothed vomer processes present, tympanum visible, vertical, with slight dorsolateral orientation, anterior parietal and pericardial peritoneum white, transparent peritonea on stomach, intestines, liver, testes, kidneys, urinary and gall bladder. Related species: *C. camposi*; possibly

species complex. Similar species: *C. altitudinale*, *C. buckleyi*, *C. hesperia*, *C. lemniscata*, *C. pipilata*, *C. venezuelensis* (Cisneros-Heredia & Morales-Mite 2008, Guayasamin et al. 2020).

*Centrolene daidalea*: small to medium sized glass frog with pale green colouration with darker areas together with black and white dorsal spots, dorsal skin granular with whitish tubercles, outer margin of hand, forearm and tarsal region with pronounced fold, eyes small and anterolaterally aligned, humeral spines absent, SVL ♂♂ 20.0–24.1 mm, ♀ 25.5 mm (n=1), head width corresponds to body width, but wider than long, mouth region rounded from dorsal, inclined anteroventrally from lateral, toothed vomer processes present (Ruiz-Carranza & Lynch 1991c, Rada et al. 2007, Stuart et al. 2008).

*Centrolene ericsmithi*: medium-sized glass frog with bright green colouration, melanophores on the dorsal surfaces of the hands and feet and at the base of finger IV, toe IV and toe V, dorsal skin chagrined, ♂♂ with tiny spines, ventral skin granulated, thin, yellowish labial stripe with a row of white bumps between lip and arm base and a yellowish line between arm base and groin, shiny elbow, metatarsal and tarsal folds, subcloacal area shiny, strongly granular with two slightly larger subcloacal tubercles and cloacal sheath, iris with flesh-coloured background, fine brown reticular structures, humeral spines clearly developed in ♂♂, SVL ♂ 27.3 mm (n=1), ♀♀ unknown, mouth region rounded dorsally and laterally, no teeth or tooth processes present on the vomer, tympanal ring barely visible, anterior parietal peritoneum white (pericardium silvery-white), transparent peritonea on stomach, intestines, liver, testes, kidneys, urinary and gall bladder. Related species: *C. sabini* and an undescribed *Centrolene* sp. From south-eastern Ecuador. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. heloderma*, *C. hesperia*, *C. lemniscata*, *C. sabini*, *C. venezuelensis* (Cisneros-Heredia et al. 2023).

*Centrolene geckoidea*: Largest glass frog with dull green to dark grey colouration with greenish or bluish shiny tubercles, throat greenish yellow, edge of upper lip yellow, belly cream or yellowish cream, ulnar, tarsal and cloacal tubercles creamy white, white spots on flanks, dorsal surfaces of both sexes covered with tubercles, spines only visible in ♂♂, melanophores on dorsal surfaces of hands and feet, hands and feet darker than the rest of the limbs, adhesive discs very large (gecko-like), oval and transverse, toe tips very broad and blunt, subcloacal area without paired enlarged tubercles, elbow fold with small, white bumps, inner tarsal fold low, short, outer tarsal fold low, with small, white tubercles, prominent integument present but reduced between fingers I, II and III, iris greenish golden with fine black reticulation, humeral spines prominent and pointed in ♂♂ (perforating own skin in some individuals), SVL ♂♂ 70.2–80.7 mm, ♀♀ 61.8–72.9 mm, mouth region truncated dorsally and laterally, 4–5 teeth present on the vomer, tympanic membrane visible and small, almost vertically orientated, anterior parietal (two thirds to complete) and pericardial peritoneum white, transparent peritonea on stomach, intestines, (four-lobed) liver, testes, kidneys, urinary and gall bladder. It has been surmised that the type locality ‘banks of the Río Napo in Ecuador’ is incorrect. Similar species: *C. paezorum*. The molecular phylogenetic tree reported by Twomey et al. (2014) places *C. geckoidea* as the sister species of *C. charapita*. However, the derived tree by Guayasamin et al. (2020) shows that *C. geckoidea* clusters as a sister species to all other *Centrolene* species.

*Centrolene heloderma*: medium-sized to large glass frog with green, dark green to bluish green colouration of back and limbs and white to white-blue tubercles, tubercles on back with stronger blue colouration, tubercles around cloaca, heel and skin over ulna especially white, throat yellow (lighter around mouth opening), skin on back granulated, coarse-grained on the flanks, belly and back of the thighs, smooth on the rest of the body, cloacal opening in the

upper part of the thighs pointing downwards, two large and many small tubercles below the cloaca, ♂♂ with tiny thorns and spines, narrow white labial stripe, outer elbow fold distinct, white, inner tarsal fold low, short, outer tarsal fold long, with low white tubercles, iris yellow to pale gold with fine, black, continuous lines (reticulations or net-like cross-connections) running through it, humeral spines clearly developed in ♂♂, SVL ♂♂ 26.8–31.5 mm, ♀ 32.3 mm (n=1), mouth region rounded dorsally, directed obliquely forwards from the lateral, eyes small, directed laterally rather than forwards, no teeth or tooth processes present on the vomer, tympanum completely visible, anterior three quarters of the ventral parietal peritoneum white (pericardium silvery-white), transparent peritonea on stomach, intestines, (four-lobed) liver, testes, kidneys, urinary and gall bladder. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. condor*, *C. lemniscatum*. Recent relationship studies place *C. heloderma* in a group with *C. altitudinalis*, *C. nostosticum*, *C. buckleyi*, *C. ballux*, *C. lynchi*, *C. muelleri*, *C. sabini*, *C. venezuelensis*, *C. hesperia* and *C. huilense* (Duellman 1981, Hutter et al. 2013b).

*Centrolene hesperia*: medium-sized glass frog with leaf-green colouration with pale green spines with white tips on upper sides of limbs, head and body, light cream-coloured upper lip stripe runs laterally along the body to the groin and separates the dorsal colour from the yellowish cream-coloured ventral colouration, dorsal skin texture chagrined in ♂♂, smoother in ♀♀, ventral skin granulated, ventral sides of throat and thighs green, feet, interdigital membranes and ventral surfaces of thighs coloured yellow, white rump spot, skin under the cloacal opening thickened, glandular, a pair of tubercles ventral to the cloacal opening, ♂♂ with tiny thorns and spines, ulnar and tarsal crests present, iris greyish white with black reticulation, humeral spines clearly developed in ♂♂, SVL ♂♂ 23.0–27.3 mm, ♀♀ 24.7–28.8 mm, mouth region blunted dorsally, blunt to moderately oblique from lateral, eyes small, slightly directed anteriorly, no teeth or tooth processes present on vomer, tympanum not visible, anterior three quarters of ventral parietal peritoneum white (pericardium silvery-white), transparent peritonea on stomach, intestine. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. lemniscata*, *C. venezuelensis* (Guayasamin et al. 2020).

*Centrolene huilensis*: medium-sized glass frog with green dorsal colouration with dark green to dark lavender and white spots, white tubercles on the ventrolateral edges of finger V, forearm, elbow, toe V, tarsus and heel, in ♂♂ spines and tubercles, upper lip white, lower flanks with numerous small white tubercles, elbow and tarsal folds with white tubercles, dorsal skin texture fine-grained with many small tubercles and folds, foot three-quarters covered with interdigital membranes, one pair of tubercles ventral to the cloacal opening, iris cream-coloured with a slight yellow tinge and thin black reticulated lines, yellowish cream-coloured ring around the eye socket, humeral spines at ♂♂ medium sized, curved towards the rear, SVL ♂♂ 23.6–26.7 mm, ♀♀ 28.7–31.0 mm, head as broad as body, mouth region short, rounded dorsally, slightly bevelled laterally, no teeth present on vomer, lower ¾ of tympanum visible, anterior half of ventral parietal peritoneum white, transparent peritonea on stomach, intestine, (lobed) liver, kidneys, gall bladder and urinary bladder. Similar species: *C. peristicta*, *C. daidalea*, *C. condor*, *C. lynchi*, *C. muelleri*, *C. pipilata*, *C. savagei*, *C. solitaria*, and *Nymphargus truebae* (Ruiz-Carranza & Lynch 1995c, Mendoza-Henao et al. 2019, Guayasamin et al. 2020).

*Centrolene hybrida*: small glass frog with light to dark green dorsal colouration with yellow spots, white spots on lateral parts of head and forearm, palms and feet are yellow, dorsal skin texture smooth with small spines in ♂♂, abdomen and thighs granular, throat smooth, one pair of tubercles ventral to cloacal opening, iris greyish yellow with black reticulated pattern, humeral spines present in ♂♂ and visible from the outside, SVL ♂♂ 20–21.9 mm, ♀♀ 20–23.1

mm, eyes large and directed anterolaterally, head wider than body, mouth region short, roundish dorsally (Ruiz-Carranza & Lynch 1991b, AmphibiaWeb 2023).

*Centrolene lemniscata*: medium-sized glass frog with medium green dorsal colouration and yellow-green spots, dorsal skin texture with small spines in ♂♂, upper lip white (labial stripe extends laterally above the base of the arm to the groin), lower flanks green, outer edges of forearm and foot as a narrow white stripe, toes pale yellow-green, ventral sides of flanks, thighs and belly granular, otherwise smooth, two pairs of tubercles ventral to the cloacal opening, iris silver-bronze coloured with black spots, humeral spines present in ♂♂, SVL ♂ 27.0 mm (n=1), ♀♀ unknown, head almost as broad as body, mouth region truncated dorsally, rounded laterally, eyes large, no teeth present on vomer, tympanic membrane indistinct, posterolaterally orientated, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach and intestine. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. hesperia*, *C. venezuelensis*, *Rulyrana saxiscandens*. Taxonomic note: no molecular data available (Duellman & Schulte 1993b, Guayasamin et al. 2020).

*Centrolene lynchi*: medium-sized glass frog with green dorsal colouration with tiny yellowish white and small diffuse black dots, dorsal skin texture in ♂♂ and ♀♀ slightly granular, in ♂♂ with low tubercles corresponding to white spots and spines, knobbed tubercles on the sides of the head, flanks creamy white, tips of toes yellow, fingers and toes pale yellow, elbow and outer tarsal folds with thin white line or with low white bumps, upper lip white, ulnar fold present and white, outer tarsal fold absent, inner tarsal fold small, ventral surface of the thighs with a pair of enlarged tubercles, a pair of tubercles ventral to the cloacal opening, iris bronze-coloured with black reticulation, pronounced humeral spines present in ♂♂, SVL ♂♂ 23.3–26.5 mm, ♀♀ 24.6–25.0 mm, mouth region rounded or blunted dorsally, truncated to slightly sloping from lateral, toothed vomer process without teeth, tympanic membrane almost vertically orientated with a slight lateral and posterior inclination,  $\frac{1}{2}$  to  $\frac{2}{3}$  of the ventral parietal and pericardial peritoneum white, transparent peritonea on stomach, intestine, (four-lobed) liver, kidneys, gall bladder and urinary bladder. Closely related species: *C. sabini* and an undescribed *Centrolene* sp. Similar species: *C. muelleri*, *C. peristicta*, *C. pipilatum*, *C. quindianum*, *Nymphargus truebae*, *N. garciae*. Taxonomic notes: *C. gemmata* and *C. scirtetes* have been synonymised with *C. lynchi* (Duellman 1980, Twomey et al. 2014, Guayasamin et al. 2020).

*Centrolene medemi*: medium-sized to large glass frog with a unique pattern for glass frogs in the form of an olive green back with large cream-coloured dots (at night the back is black with bluish green dots), melanophores cover the fingers and toes, dorsal skin texture in ♂♂ and ♀♀ smooth to slightly granular, in ♂♂ with small spines on dorsum and flanks, flanks cream-coloured, large disc on finger III (> 80% of eye diameter), extensive integument on fingers (except fingers I–III) and toes, interdigital membranes pale yellow, small tarsal and ulnar folds, a pair of slightly enlarged tubercles ventral to the cloacal opening, iris dull grey-bronze with tiny black dots, pronounced humeral spines present in ♂♂, SVL ♂♂ 25.5–30.8 mm, ♀♀ 34.7–44.3 mm, mouth region rounded dorsally, truncated to slightly protruding laterally, dentate vomer process with or without teeth, each process with 0–4 teeth, tympanic membrane small (< 20% of eye diameter), dorsal third of tympanic membrane covered by supratympanic fold, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach, intestine, (four-lobed) liver, kidneys, testes, gall bladder and urinary bladder. Taxonomic notes: genus assignment is uncertain (incertae sedis; Guayasamin et al. 2009, 2020, Díaz-Ricaurte & Rada 2020b).

*Centrolene muelleri*: medium sized glass frog with green dorsal colouration with dark greenish black spots and yellowish tubercles, dorsal skin texture smooth with dorsolateral rows of tubercles, large, conical tubercles on dorsal surfaces of head, body and limbs, tubercles on dorsal surfaces of forelimbs, thighs, lower legs and tarsals, flanks smooth dorsally, granular ventrally, skin on belly and ventral surfaces of thighs coarsely granular, remaining ventral surfaces smooth. Skin fringes on limbs, low, wavy (fringed) skin fold on outer edge of forearm and tarsus, a pair of slightly enlarged tubercles ventral to cloacal opening, humeral spines present in ♂♂, SVL ♂ 23.5 mm (n=1), ♀♀ unknown, head distinct, slightly wider than long, mouth region truncated dorsally, inclined anteroventrally laterally, no teeth present on vomer, tympanic membrane distinct, posterolaterally orientated with slight inclination dorsally, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach and intestine. Similar species: *C. lynchi*, *C. hesperia*, *C. huilense*, *C. pipilatum*. Taxonomic notes: contradictory phylogenetic topologies, possibly due to undescribed species and ambiguous voucher specimens (sister species *C. lynchi* or *C. huilense*; Duellman & Schulte 1993a, Catenazzi et al. 2012, Twomey et al. 2014).

*Centrolene notosticta*: small glass frog with light green dorsal colouration with many thin and thick yellow spots corresponding to the locations of the small spines on the epidermis, skin very granular on posteroventral side of the legs, forearms of ♂♂ more robust than those of ♀♀, tarsal folds and tubercles absent, a pair of slightly enlarged tubercles ventral to the cloacal opening, moderately large humeral spines present in ♂♂, iris cream-bronze coloured, SVL ♂♂ 19.4–22.7 mm, ♀♀ 20.8–24.9 mm, head wider than body, mouth region rounded dorsally, blunted laterally, large eyes, anterolaterally aligned, no teeth present on the vomer, tympanic membrane small, supratympanic fold slightly thickened. Related species: *C. altitudinalis*. Similar species: *Espadarana audax* (Ruiz-Carranza & Lynch 1991b, Rojas-Runjaic et al. 2012, Viuche-Lozano et al. 2018, Barrio-Amorós et al. 2019).

*Centrolene paezorum*: large glass frog with green dorsal colouration, dorsal skin texture granular with numerous small tubercles and subconical tubercles on the sides of the head, on the lateral trunk and laterally on the exposed dorsal surfaces of the limbs, gular region, thorax, abdomen and ventral surfaces of the limbs areolate, ulnar margin of the forearm with a row of 6–7 confluent white tubercles with a wrinkle-like appearance, extending over the forearm and tapering progressively over the ulnar margin of the hand to the outer finger, tarsal fold absent, no skin appendages on elbow or heel, prominent integument present (see below), cloacal region densely covered with white glands, humeral spines in ♂♂ unknown, iris cream-coloured with truncated sinuous lines and brown spotting, SVL in ♂♂ unknown, ♀ 44.5 mm (holotype), mouth region rounded dorsally, obliquely truncated laterally, eyes relatively small, no teeth present on vomer, tympanic membrane almost completely visible, directed dorso-laterally and slightly inclined posteriorly. Similar species: *C. geckoidea*. Taxonomic note: *C. paezorum* is only known from a single ♀ and is said to be smaller than *C. geckoidea*, with no teeth on the vomer and smaller integuments on fingers and toes. It remains to be clarified whether *C. paezorum* is a more recent synonym of *C. geckoidea* because no molecular data is currently available (Ruiz-Carranza et al. 1986, Guayasamin et al. 2020).

*Centrolene peristicta*: small glass frog with yellowish green dorsal colouration with tiny white or yellow dots and diffuse grey spots, dorsal skin texture granular, without spines in both sexes, upper lip white, area under the eye with small white bumps, dorsal flank region green with tiny white dots, ventral flank cream-coloured with tiny white spots, belly yellow-cream, fingers and toes dull greenish yellow, elbow fold with thin white line or with small white



bumps, outer tarsal fold with small white bumps, small white bumps just behind the cloaca, extensive membranes between most fingers and toes, toe discs dilated and blunted, one pair of enlarged subcloacal tubercles present, small, curved humeral spines present in ♂♂, iris white-grey with yellow tint and thin black reticulation, thin yellow line surrounding pupil, SVL ♂♂ 17.9–21.2 mm, ♀♀ 20.8–20.9 mm, mouth region rounded dorsally, rounded or blunted laterally, toothed vomer process without denticles, tympanic membrane moderately large, almost vertically orientated with a slight lateral and posterior inclination, supratympanic fold distinct, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach (partially), intestine (partially), (four-lobed) liver, kidneys, gall bladder and urinary bladder. Similar species: *C. antioquiensis* (sister species), *C. huilense*, *C. daidalea*, *C. condor*, *C. lynchi*, *C. muelleri*, *C. pipilata*, *C. savagei*, *C. solitaria*, *Nymphargus truebae* (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Centrolene petrophilum*: medium-sized to large glass frog with dark green dorsal colouration, hands, feet, abdomen light yellow, axillary region greenish blue, upper lip and ulnar region edged in white, ♂♂ with spines on the rostral and lateral sides of the head, abdomen and femora with many small tubercles, tarsus without dermal tubercles or skin folds, humeral spines present in ♂♂, SVL ♂♂ 25–30 mm, ♀♀ 27.4–31.4 mm, head width corresponds to body width, head wider than long, mouth region rounded from dorsal and lateral. Similar species: *C. acanthidiocephalum* (sister species). Taxonomic note: Genus uncertain (incertae sedis; Ruiz-Carranza & Lynch 1991b, Guayasamin et al. 2009).

*Centrolene pipilata*: small glass frog with green dorsal colouration with small black and yellowish white spots, dorsal skin texture chagrined, in ♂♂ with spines ending in white spots, upper lip white, region below the eye with small white tubercles, which are spiny in the ♂♂, flanks dorsally green with tiny white spots, ventrally whitish cream coloured, elbow fold with thin white line, outer tarsal fold with low white tubercles, small white tubercles immediately behind the cloaca, a pair of enlarged subcloacal tubercles present, large, wide humeral spines present in ♂♂, normally pointing forwards, iris greyish white with thin black reticulated lines and a yellow tint around the pupil, SVL ♂♂ 19.7–22.6 mm, ♀♀ 22.6–23.6 mm, mouth region rounded dorsally, rounded or blunted laterally, no teeth present on vomer, tympanic membrane moderately large, almost vertically orientated with slight lateral and posterior inclination, supratympanic fold distinct, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach, intestine, (four-lobed) liver, kidneys, gall bladder and urinary bladder. Similar species: *C. sanchezi*, *C. huilense*, *C. hybrida* (sister species), *Nymphargus truebae* (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Centrolene quindianum*: medium-sized glass frog with greenish yellow dorsal colouration with many black spots evenly distributed over head and body, some have cream-coloured shoulders, SVL ♂♂ 21.1–29.9 mm, ♀♀ 22.8–29.7 mm, head as broad as body, mouth region rounded from dorsal, blunted from lateral, no teeth present on vomer, tympanic membrane small, only lower three quarters visible. Taxonomic note: genus uncertain (incertae sedis; Ruiz-Carranza & Lynch 1995c, Rios-Soto et al. 2017a).

*Centrolene robledo*: small to medium sized glass frog with some dark green or blue shading along with white patches along the tibial region or legs and a white stripe along the flanks, ulnar and tarsal tubercles and folds absent, dorsal skin texture fine-grained, medium sized, backward curved humeral spines present in ♂♂, SVL ♂♂ 19.9–24.4 mm, ♀♀ 23.4–25.9 mm, head wider than body, no teeth present on vomer, tympanic membrane small, only three-quarters visible, anterior half of ventral parietal peritoneum white, transparent peritonea on

viscera. Taxonomic note: genus uncertain (incertae sedis; Ruiz-Carranza & Lynch 1995c, Guayasamin et al. 2009).

*Centrolene sabini*: large glass frog with greenish-yellowish dorsal colouration with yellowish spots and dots. The back is covered with yellowish green spiny tips, in ♂♂ with spines, pronounced yellowish white labial stripe continuing into a lateral stripe, ulnar and inner tarsal folds low, outer tarsal fold absent, a pair of enlarged subcloacal tubercles present, humeral spines present in ♂♂, iris silvery bronze or cream coloured with fine black reticulations, SVL ♂♂ 29.6–31.2 mm, ♀♀ unknown, mouth region rounded from dorsal, blunted from lateral or inclined anteroventrally, no teeth present on vomer, tympanic membrane small, posterolaterally orientated, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach, intestine, (four-lobed) liver. Similar species: *C. lemniscatum*, *C. buckleyi*, *C. altitudinale*, *C. ballux*, *C. notostictum*, *C. peristictum*, *C. pipilata*, *C. quindianum*, *C. sanchezi*, *C. venezuelensis*. Related species: *C. lynchi*, *C. muelleri* (Catenazzi et al. 2012).

*Centrolene sanchezi*: small glass frog with green dorsal colouration with small white spots, presence of white tubercles in an area from below the eye to the base of the arm, upper lip white, dorsal skin texture chagrined, with spines in ♂♂, ulnar and inner tarsal folds low or absent, outer tarsal fold absent, one pair of enlarged subcloacal tubercles present, small humeral spines present in ♂♂, iris pale bronze coloured with black reticulation, SVL ♂♂ 18.9–22.3 mm, ♀ 20.9 mm (n=1), mouth region rounded from dorsal, blunted to rounded from lateral, no teeth present on vomer, tympanic membrane almost vertically aligned, dorsal edge of tympanic membrane ring covered by supratympanic fold, anterior half of ventral parietal and pericardial peritoneum white, transparent peritonea on stomach, intestine, (four-lobed) liver. Similar species: *C. pipilata*. Related species: *C. pipilata* plus *C. hybrida* (sister clade). Taxonomic note: *C. bacata* and *C. guanacarum* were placed in the synonymy of *C. sanchezi* (Ruiz-Carranza & Lynch 1991b, Guayasamin et al. 2020).

*Centrolene savagei*: small to medium-sized glass frog with pale green dorsal colouration with white, yellow and green spots; small blue spots are usually also present, upper lip white, dorsal skin texture smooth with small white rounded tubercles on rump and flanks of head, skin on belly and undersides of thighs granular, ulnar, outer and inner tarsal folds low, each with a row of tubercles, subcloacal white warts and tubercles present, no humeral spines present in ♂♂, iris greyish-yellowish with dark brown reticulation SVL ♂♂ 19.0–24.2 mm, ♀♀ 23.3–26.3 mm, head wider than long and as wide as body, mouth region rounded dorsally and laterally, small eyes, anterolaterally directed, teeth present on vomer, tympanic membrane large and conspicuous, supratympanic fold covers posterior margin, ventral parietal peritoneum, pericardium and large intestine white (extends almost to liver). Similar species: *C. daidaleum* (sister species; Ruiz-Carranza & Lynch 1991c, Guayasamin et al. 2009, Vargas-Salinas et al. 2014, 2017).

*Centrolene solitaria*: small glass frog with pale green dorsal colouration with white and dark green spots, upper lip white, dorsal skin texture finely granulated and with small tubercles matching the white spots, white tubercles on margin of forearm, feet and cloaca, forearm, hand, ankle and foot lined with short tubercles, no humeral spines present in ♂♂, iris cream-coloured with a horizontal stripe, pupil surrounded by an orange ring, SVL ♂ 19.3 mm (n=1), ♀♀ unknown, mouth region blunt and rounded dorsally, elliptical teeth present on vomer, tympanic membrane small. Similar species: *C. daidaleum*, *C. savagei*, *Cochranella mache*, *Cochranella resplendens*. Taxonomic note: no molecular data available (Ruiz-Carranza & Lynch 1991c, Guayasamin et al. 2009).

*Centrolene venezuelensis*: medium-sized to large glass frog with light green dorsal and flank colouration with cream-coloured spots on extremities, throat light green, belly cream-coloured, thighs greenish yellow, toes yellowish, upper lip yellowish cream-coloured, dorsal skin texture smooth to slightly granular, with spicules of varying sizes, with or without ulnar and tarsal folds and/or tubercles on forearm and tarsus, whitish line on outer edge of forearm, paired subcloacal white tubercles present, humeral spines present in ♂♂, relatively thick, rounded and curved at distal end (alignment between 25–30° to the upper arm axis), iris golden coloured with black reticulation, SVL ♂♂ 23.4–33.8 mm, ♀ 30.6 mm (n=1), head slightly wider than body, mouth region short, rounded from dorsal, obliquely truncated from lateral, large eyes, anterolaterally aligned, no teeth present on the vomer, tympanic membrane conspicuous, especially in the lower part directed dorsolaterally, anterior half of the ventral parietal and pericardial peritoneum white, transparent peritonea on viscera, liver four-lobed. Similar species: *C. altitudinalis*, *C. buckleyi*, *C. hesperia*, *C. lemniscata*. Taxonomic notes: Myers & Donnelly (1997) raised the subspecies *Centrolene buckleyi venezuelensis* (Rivero 1968) to species level without justification. Señaris & Ayarzagüena (2005) supported this decision on the basis of morphological and acoustic differences to the typical *C. buckleyi* populations. More recent phylogenetic studies support the validity of this species (Guayasamin et al. 2009, 2020, Castroviejo-Fisher et al. 2014).

*Centrolene zarza*: medium sized glass frog with light green dorsal colouration with many whitish raised dots and spots of various sizes, melanophores on the dorsal surfaces, except fingers IV and toes IV and V, fingers and toes yellowish, usually without melanophores, dorsal skin texture chagrined, with raised, partly shiny tubercles corresponding to white spots, ventral skin coarsely areolate, ventral surfaces of the thighs below the cloaca with a pair of large, round, flat tubercles (subcloacal tubercles), cloacal region bordered ventrally by many shiny, white tubercles, outer edge of the forearms and tarsus with a row of ‘enamelled’ (shiny) tubercles, which often continue into the outer edges of finger IV and/or toe V, fingers and toes with broad lateral margins, moderately developed interdigital membranes between the outer fingers and toes, small, protruding humeral spines present in ♂♂, iris white or yellowish white with thick and thin black reticulations, rounded dots on the upper and lower sides of the iris and no eye ring, SVL ♂♂ 23.2–26.2 mm, ♀♀ 25.5–27.0 mm, mouth region rounded in dorsal view, oblique in profile, dentary processes of vomer ovoid, in transverse row with 3–5 teeth each, tympanic ring and large tympanic membrane recognisable, weak supratympanic fold slightly obscuring upper margin, anterior half of ventral parietal peritoneum white, all visceral peritonea, including pericardium, transparent. Related species: undescribed *Centrolene* sp. (*C. aff. condor* Ca04 in Guayasamin et al. 2020). Similar species: *C. condor*, *C. pipilata*, *C. solitaria*, *C. altitudinalis*, *C. buckleyi*, *C. ballux*, *C. heloderma*, *C. daidalea*, *C. sanchezi*, *Cochranella resplendens*, *Nymphargus posadae* (Guayasamin et al. 2020, Székely et al. 2023).

### Distribution and Habitat

The genus *Centrolene* is endemic to the northern Andes from the Cordillera de Mérida in Venezuela across the Andes of Colombia and Ecuador to the Cordillera de Huancabamba in northern Perú (1,100–3,500 m asl). With few exceptions, the forest types found at these altitudes form the habitat for reproduction, in which the larvae of the *Centrolene* spp. develop in streams (Guayasamin et al. 2009).

*Centrolene acanthidiocephalum*: Andean forests of the Santuario de Fauna y Flora Guanentá, Alto del Río Fonce (Virolín and El Encino), municipalities of Charalá and Gámbita on the western slope of the Cordillera Oriental, Departamento de Santander, Colombia (1,750–2,100 m asl). In the vegetation and on rocky edges along streams in the cloud forest. The frogs called from bushy and herbaceous vegetation, especially from leaves of the genera *Heliconia* and *Asplundia*, at a height of no more than 3 m above the ground (Ruiz-Carranza & Lynch 1989).

*Centrolene altitudinalis*: This species is known from the forested areas of the basin of the Río Albarregas at Monte Zerpa (type locality), La Joya, north-east of Mérida city and from the Caño Seco stream in the Finca El Cedral-Altos de San Luis in the state of Mérida, Venezuela (1,900–2,400 m asl). High gradient rivers in the catchment area of the Río Albarregas, stream habitats in humid montane tropical forests. It appears to show little or no tolerance to habitat destruction (Señaris & Ayarzagüena 2005).

*Centrolene antioquiensis*: known from the departments of Antioquia, Caldas and Tolima on the western flank of the central Andes in Colombia, possibly further records from Urrao on the eastern flank of the western Andes (1,730–2,450 m asl). Habitat: montane, sub-Andean forests along river courses. The species requires a gallery forest above the streams for reproduction (Rivera-Correa 2010).

*Centrolene azulae*: known only from the type locality: km 184, 3.3 km west of Fundo Nuevo Mundo, an isolated cloud forest of the Cordillera Azul between Tingo Maria and Pucallpa, in the department of Huánuco, central Perú (1,500 m asl). Stream habitats in montane tropical forests where the trees are generally widely spaced and separated by 2–3 m high bushes. Within these areas there are also humid depressions and small ravines with slightly higher (4–9 m) elfin forest (Flores & McDiarmid 1989).

*Centrolene ballux*: known from six localities in the cloud forests of the provinces of Carchi, Imbabura, Pichincha and Santo Domingo de los Tsáchilas (Ecuador) and one locality in the department of Nariño (Colombia) on the Pacific slopes of the Cordillera Occidental of the Andes. Occurrence in the valley of the Río Saloya in Ecuador possibly extinct, but sporadic records in the Reserva Las Galarías and at the Río Canchupi (1,700–2,340 m asl). Habitat in humid mountain forests, individual specimens can be found at night in the vegetation along rivers, streams and roadside ditches, rests on leaf surfaces of ferns or bushes and trees 0.5–8 m above small bodies of water (Duellman & Burrowes 1989, Hutter & Guayasamin 2012).

*Centrolene buckleyi*: widespread in the Andes of Colombia and Ecuador (states of Azuay, Bolívar, Carchi, Cotopaxi, Imbabura, Loja, Napo, Pichincha, Zamora Chinchipe, Sucumbíos, Chimborazo), as far north as Perú (Huancabamba, Departamento Piura). This species is known with certainty only from the Cordillera Oriental and the Cordillera Occidental of the Ecuadorian Andes. Subpopulations from Colombia are considered to be *C. aff. buckleyi* and probably belong to another species that will probably be split off from this taxon in the near future. Altitudinal distribution 2,050–3,300 m asl. The species lives in mountain forests, in Andean scrub and in paramos. During the day it has been found on terrestrial bromeliads and epiphytes near or away from streams in secondary forests and grasslands. At night, individuals were actively found in terrestrial bromeliads and in vegetation above streams, ponds and swamps in primary and secondary forests. The ♂♂ fight dangling upside down while clinging to vegetation with their hind legs and each other's bellies. One ♂ was found on a leaf shoot near a clutch of eggs (not on the leaf itself) about 1.6 m above the stream (Bolívar-García et al. 1999, Guayasamin et al. 2008a, 2020, Amador et al. 2018).

*Centrolene camposi*: known only from the type locality (La Enramada) in the province of Azuay, near the border with the province of El Oro, on the southwestern slopes of the Cordillera Occidental of the Andes of Ecuador (2,900 m asl). This ecosystem is characterised by trees with a height of more than 15 m, densely covered with epiphytes such as bromeliads, mosses and orchids, both known individuals were found along a steep stream (Cisneros-Heredia et al. 2023).

*Centrolene charapita*: only known from two individuals at the type locality near the village of La Oliva, behind the village of Muyo (49 km north of Bagua), Amazonas region, Perú and from the Reserva Natural Maycu, Zamora Chinchipe province, Ecuador. The species probably occurs in the intermediate areas between the two known localities (680–1,220 m asl). Habitat in primary and secondary tropical lowland and mountain forests near water sources. Individual specimens have been found on vegetation at the edge of streams and rivers up to 5 m asl (Twomey et al. 2014, Páez-Rosales & Pinto 2017).

*Centrolene condor*: recorded at the type locality ‘Destacamento Militar Cóndor Mirador’, western slopes of the Cordillera del Cóndor, Zamora Chinchipe province, Ecuador (1,750–1,850 m asl). The species inhabits primary and secondary elfin forests. The ♂♂ have been heard between the leaves of the river vegetation a few centimetres above the water (Cisneros-Heredia & Morales-Mite 2008).

*Centrolene daidalea*: humid forests on the western slope of the Cordillera Oriental of Colombia in the departments of Boyacá, Cundinamarca, César and Santander, between 1,600 and 2,060 m altitude; also reported from the eastern slope of the Sierra de Perija, Zulia, Venezuela, from 800–1,832 m asl. This species inhabits vegetation near streams in premontane, montane and cloud forests and has also been observed in secondary forests. Individuals have been found 1.5 metres above the water, actively calling from the leaves of bushes, along streams and the main courses of rivers. In the departments of Santander and Norte de Santander, this species was found frequently and abundantly along degraded streams near unpaved roads and pastures. In Venezuela, almost all small streams where individuals were found were surrounded by primary forest, with high humidity, abundant ferns and Helioconiaceae, Araceae and Cyclanthaceae plants. Frogs often call and spawn on ferns, in Manastara individuals were found on shrubs and coffee plants in secondary forests, especially on ferns and Cyclanthaceae in Cerro Las Antenas (Ruiz-Carranza & Lynch 1991c, Rada et al. 2007, Stuart et al. 2008, Cardozo-Urdaneta & Señaris 2012).

*Centrolene ericsmithi*: see *C. camposi*; ♂♂ call from the upper side of the leaves.

*Centrolene geckoidea*: in the three Andean Cordilleras of Colombia (Cordillera Occidental, Central and Oriental; in the departments of Antioquia, Valle del Cauca, Caldas, Quindío, Risaralda, Tolima, Boyacá and Caquetá), south to the Pacific slope of the Andes in Ecuador (provinces of Carchi and Pichincha) (1,750–2,525 m asl). This species lives in cloud forests, where it can be found on vegetation next to running water or on rocks in streams and behind waterfalls. It is very susceptible to deforestation and does not survive in degraded habitats. The eggs are laid on rocks in the splash zone of fast-flowing streams and waterfalls. It is a very territorial species and the ♂♂ guard the eggs.

*Centrolene heloderma*: occurs on the western side of the Cordillera Occidental in Colombia in the departments of Cauca, Valle del Cauca and Risaralda, south to the valleys of Tandayapa and Saloya in Ecuador, provinces of Pichincha and Santo Domingo (1,900–2,400 m asl). Habitat in higher altitudes of cloud forests in treetops and dependent on old forests. The species is



very difficult to spot and is more likely to be heard than seen. During the rainiest months from December to April, it usually stays in vegetation zones 1–7 metres above the ground. Occasionally it moves away from streams, most likely to migrate to other areas (Duellman 1981, Coloma et al. 2004, Hutter & Guayasamin 2012, Arteaga 2013).

*Centrolene hesperia*: known from forested slopes of the Río Zaña watershed on the Pacific side of the Cordillera Central in the Cajamarca region of northern Perú (1,500–1,800 m asl). Habitat in streams in montane forests, at night the individuals sit on the upper sides of the leaves above the streams, also during the day they rest on the upper sides of the leaves. Breeding of this species apparently begins with the onset of rainfall (January). ♂♂ call and ♀♀ spawn on the upper sides of the leaves 0.5–3 m above the streams. Reproductive activity (based on the number of clutches observed in some stream sections) is estimated to be high compared to other species of the genus (Cadle & McDiarmid 1990).

*Centrolene huilensis*: known only from a small stream at the type locality in the municipality of San José de Isnos on the eastern slope of the Cordillera Central in the Department of Huila, Colombia, also reported from the Reserva Yanayacu, Province del Napo, Ecuador (1,980–2,190 m asl). The species occurs in vegetation near water sources or in streams in sub-Andean forests. It depends on gallery forests to lay its eggs and is therefore very sensitive to the destruction of its forest habitat (Mendoza-Henao et al. 2019, Guayasamin et al. 2020).

*Centrolene hybrida*: on the eastern slopes of the eastern Andes in the states of Boyacá, Cundinamarca and Caquetá, Colombia (1,420–2,020 m asl). The species occurs in the vegetation along streams in montane forests. It tolerates a certain degree of habitat change.

*Centrolene lemniscata*: known from the eastern slopes of the central Andes (Cordillera Central), in the Río Nieva watershed in the San Martín and Amazonas regions of northern Perú. The species could be much more widespread, although the actual extent of its occurrence is hardly known. Altitudinal distribution 2,000–2,280 m asl. Habitat: Streams in premontane rainforest and cloud forest. Eggs are laid at the top of leaves above streams (IUCN SSC Amphibian Specialist Group 2019b).

*Centrolene lynchi*: originally only known from the Pacific slope of the Cordillera Occidental of the Andes in Ecuador. However, as *C. scirtetes* and *C. gemmata* have been placed in synonymy with this species, its distribution area has also been extended to southern Colombia. In Colombia, the species has so far only been recorded from a single locality in the department of Nariño (Reserva La Planada); previously, an occurrence on the western side of the Cordillera Occidental in the department of Risaralda, Colombia, was also reported, but these specimens correspond to *C. quindianum*. The species probably also occurs between the known localities, but is rare and difficult to detect (1,140–1,852 m asl). Habitat in cloud forests including secondary forests, along streams where they require forest vegetation overhanging the water, not in degraded habitats. ♂♂ can engage in aggressive fights, attacking their rivals by hanging upside down and clinging to leaves and branches with their feet. After laying eggs, brood care is carried out by the ♂, one ♂ can look after three different clutches at the same time, which suggests polygynous reproduction (Duellman & Burrowes 1989, Dautel et al. 2011, Guayasamin et al. 2010, 2020).

*Centrolene medemi*: Known from the eastern and western slopes of the Cordillera Oriental in the Colombian and Ecuadorian Andes, has been recorded from several localities in Colombia, including the type locality of Mocoa in the department of Putumayo, Florencia in the depart-

ment of Caquetá, on the eastern slope of the Cordillera Oriental, and Icononzo in the Department of Tolima on the western slope of the Cordillera Oriental, as well as from a stream near the Reventador volcano on the Amazonian slopes of the Ecuadorian Andes in the Province of Napo. Based on museum specimens collected in the 1990s, the species is now also known from the vicinity of the Parque Nacional Natural Cordillera de Los Picachos in San Vicente del Caguán, Departamento Caquetá (790–1,800 m asl). Habitat along streams in montane cloud forests, also in secondary forests, provided the vegetation near the streams is lush. The adults were found at night on rocks, crevices and rocky cliffs along the streams; the juveniles were found in palm leaves or crevices (Suárez 1999, Guayasamin et al. 2006c).

*Centrolene muelleri*: known from three localities on the watershed between the Huallaga and Marañón rivers in the southern part of the Department of Amazonas and from the type locality in the Department of San Martín, Perú (1,830–2,050 m asl). Habitat along streams in the cloud forest, individual specimens were found at night along rivulets and streams, the ♂♂ were seen calling from the tops of leaves 0.5–2.5 m above the water. This species appears to be tied to undisturbed habitats with relatively dense canopy; however, the Gocta site is open, lying deep in a ravine (Duellman & Schulte 1993a, Twomey et al. 2014).

*Centrolene notosticta*: In Colombia, the species occurs on both slopes of the Cordillera Oriental in the Departments of Cundinamarca, Boyacá, Santander and Norte Santander. In Venezuela, this glass frog has been recorded at a site in the eastern part of the Sierra de Perijá (State of Zulia) in Campamento Guacharaca, Caño Tétari Kopejoacha, in the basin of the Río Negro (1,600–2,440 m asl). Habitat in the vegetation at the edge of streams in cloud forests. It is not found outside of primeval forests (Rojas-Runjaic et al. 2012, Viuche-Lozano et al. 2018, Barrio-Amorós et al. 2019).

*Centrolene paezorum*: only known from the type locality: Municipality of Inza in the Department of Cauca on the eastern slope of the Cordillera Central of the Colombian Andes. Presumably the species is more widespread, but this has yet to be confirmed (3,030 m asl). The holotype was found at night on the leaf of a bromeliad species of the genus *Puya* ('achupalla') in the sub-Andean Forest, a few metres from a rocky ravine and about 50 cm above the ground (Ruiz-Carranza et al. 1986).

*Centrolene peristicta*: Occurs along the western slope of the Cordillera Occidental in Colombia, from Urrao south to the northwestern slopes of the Andes in Ecuador (Pichincha and Carchi Provinces) (1,350–1,820 m asl). It is a species of undisturbed cloud forest that has not been found in secondary habitats (Guayasamin et al. 2020).

*Centrolene petrophilum*: known from six localities on the eastern flank of the northern part of the Cordillera Oriental, Departamento Boyacá, Colombia (1,600–2,200 m asl). Habitat in the vegetation next to or above streams in cloud forest, but can also occur in secondary forest. The species lays its eggs on rocks next to streams, the larvae develop in the water.

*Centrolene pipilata*: on the Amazonian slopes of the Andes in the Río Salado, Río Azuela and 16 km from Santa Rosa in the Provinces of Napo and Sucumbíos, Ecuador (1,300–1,910 m asl). Habitat near streams in cloud forest, has been observed above 3 m above the ground, not found in anthropogenic habitats.

*Centrolene quindianum*: known from Colombia, where the species occurs in the Andean Cordillera from southern Antioquia to Filandia and Salento in the Department of Quindío as well as in Ucumari and Pereira in the Department of Risaralda on the western flank of the Cordillera

Central. The species has also been recorded 3.5 km north of the town of Manizales near the Aguasclaras stream (1,900–2,050 m asl). Habitat in vegetation next to streams in sub-Andean forests. The species has also been found in gallery forests near pine plantations and rural areas (Ruiz-Carranza & Lynch 1995c, Rada and Guayasamin 2008, Rojas-Morales et al. 2011).

*Centrolene robledo*: north of the Cordillera Central in the Department of Antioquia, on the eastern flank of the Cordillera Central in the Departments of Risaralda and Valle del Cauca and on the western flank of the Cordillera Central in the Departments of Caldas and Tolima in Colombia (800–2,940 m asl). Habitat in the vegetation next to streams in the cloud forest, also found in secondary forests near bodies of water. However, no individuals have been found outside the forest.

*Centrolene sabini*: known only from two streams along the road in the Kosñipata Valley in the upper Manu National Park on the Amazonian slopes in the south-east of the Peruvian Andes, where this species apparently occurs only in a narrow altitudinal and geographical range in southern Perú, and it is not known whether it is more widespread (2,750–2,800 m asl). Habitat along fast-flowing streams in montane forests.

*Centrolene sanchezi*: This species was previously only known from the type locality on the eastern flank of the Cordillera Oriental, Florencia, in the Department of Caquetá, Colombia. Following the synonymisations of *C. bacata* and *C. guanacaram* (see above), it is now known from five isolated localities on the Amazonian slopes of the Andes of Ecuador and Colombia and from one locality on the eastern slope of the Colombian Cordillera Central (1,800–2,350 m asl). Habitat in cloud forests, individual specimens have been found in the vegetation above streams in both primary and secondary forests. The species requires gallery forests for oviposition and is unable to survive in disturbed habitats (Guayasamin et al. 2020).

*Centrolene savagei*: Occurs on the western slope of the Cordillera Central in the Departamentos Quindío and Risaralda, on the eastern slope of the Cordillera Central in the Departamento Caldas and on the western slope of the Cordillera Occidental in the Departamento Valle del Cauca in Colombia (1,400–2,410 m asl). Habitat in sub-Andean forests on vegetation near flowing waters such as streams. The species also occurs in secondary forests and disturbed habitats, provided there is sufficient riparian vegetation.

*Centrolene solitaria*: Initially only known from the type locality on the eastern flank of the Cordillera Oriental, Florencia, in the Department of Caquetá, Colombia, the species has been recorded from two new localities in Fuente De Lavapatas and Pitalito in the Department of Huila. It is possibly even more widespread (1,318–1,730 m asl). Habitat in treetops of the cloud forest and secondary forest. At the Fuente de Lavapatas site, however, the species has also been recorded in the low vegetation along large, fast-flowing streams near forests (Ruiz-Carranza & Lynch 1991c, Malambo et al. 2017).

*Centrolene venezuelensis*: Venezuelan Andes from Táchira to Mérida; Sierra de Perijá, Zulia, Venezuela, possibly as far as Colombia (2,100–3,050 m asl). Habitat along streams, ponds and swampy habitats in humid montane tropical and bamboo forests. The species appears to show a certain resilience to disturbance (Señaris & Ayarzagüena 2005, Rojas-Runjaic et al. 2012).

*Centrolene zarza*: currently only known from the Refugio de Vida Silvestre El Zarza, Zamora Chinchipe Province, southern Ecuador (1,434–1,480 m asl). Habitat in an evergreen, low montane forest ecosystem, (locally) common species, all specimens were found at night on the upper leaf surfaces of vegetation at two small streams (Székely et al. 2023).

## Conservation Status and Main Threats

### IUCN Red List Status

- Centrolene acanthidiocephalum*: DD (Data Deficient, assessed 2017–03–07)
- Centrolene altitudinalis*: EN (Endangered, B1ab(iii), assessed 2020–02–10)
- Centrolene antioquiense*: NT (Near Threatened, assessed 2016–08–02)
- Centrolene azulae*: DD (Data Deficient, assessed 2018–03–23)
- Centrolene ballux*: EN (Endangered, B1ab(iii,v), assessed 2016–07–18)
- Centrolene buckleyi*: CR (Critically Endangered, A2ce+3ce, assessed 2021–01–25)
- Centrolene camposi*: has not yet been assessed by the IUCN
- Centrolene charapita*: EN (Endangered, B1ab(iii), assessed 2021–01–15)
- Centrolene condor*: EN (Endangered, A3c; B1ab(iii,v), assessed 2020–11–12)
- Centrolene daidalea*: LC (Least Concern, assessed 2020–06–29)
- Centrolene ericsmithi*: has not yet been assessed by the IUCN
- Centrolene geckoidea*: CR (Critically Endangered, D, assessed 2016–08–02)
- Centrolene heloderma*: VU (Vulnerable, B1ab(iii,v), assessed 2016–08–02)
- Centrolene hesperia*: EN (Endangered, B1ab(iii), assessed 2018–03–30)
- Centrolene huilensis*: EN (Endangered, B1ab(iii), assessed 2018–12–14)
- Centrolene hybrida*: LC (Least Concern, assessed 2018–12–19)
- Centrolene lemniscata*: DD (Data Deficient, assessed 2018–03–28)
- Centrolene lynchi*: EN (Endangered, B1ab(iii), assessed 2021–01–13)
- Centrolene medemi*: EN (Endangered, D, assessed 2018–12–14)
- Centrolene muelleri*: DD (Data Deficient, assessed 2017–03–29)
- Centrolene notosticta*: LC (Least Concern, assessed 2020–07–02)
- Centrolene paezorum*: DD (Data Deficient, assessed 2017–03–07)
- Centrolene peristicta*: LC (Least Concern, assessed 2016–08–05)
- Centrolene petrophilum*: EN (Endangered, B1ab(iii)+2ab(iii), assessed 2016–08–02)
- Centrolene pipilata*: CR (Critically Endangered, B1ab(iii), assessed 2016–07–19)
- Centrolene quindianum*: VU (Vulnerable, B1ab(iii), assessed 2016–08–02)
- Centrolene robledo*: LC (Least Concern, assessed 2014–08–15)
- Centrolene sabini*: VU (Vulnerable, D2, assessed 2017–04–18)
- Centrolene sanchezi*: EN (Endangered, B2ab(iii), assessed 2021–01–20)
- Centrolene savagei*: LC (Least Concern, assessed 2016–08–02)
- Centrolene solitaria*: EN (Endangered, B1ab(iii), assessed 2018–06–29)
- Centrolene venezuelensis*: LC (Least Concern, assessed 2020–04–30)

*Centrolene zarza*: has not yet been assessed by the IUCN.

### Red List Status in the Range Countries

#### Colombia

Libro Rojo de los Anfibios del Valle del Cauca (Castro-Herrera & Bolívar-García 2010)

NatureServe Status S1 (Critically Imperiled):

*Centrolene buckleyi*

*Centrolene geckoidea*

NatureServe Status S1S2:

*Centrolene grandisonae*

NatureServe Status S2 (Imperiled):

*Centrolene heloderma*

NatureServe Status S3 (Vulnerable):

*Centrolene peristictum*

NatureServe Status SU (Unclassifiable):

*Centrolene savagei*

#### Ecuador

Amphibians of Ecuador Anfibios de Ecuador (Centro Jambatu (2011–2020) V1.23)

PE (possibly extinct – Posiblemente extinta):

*Centrolene geckoidea*

CR (critically endangered):

*Centrolene ballux*

*Centrolene buckleyi*

*Centrolene charapita*

*Centrolene heloderma*

*Centrolene lynchi*

*Centrolene medemi*

*Centrolene pipilata* (endemic species)

EN (endangered):

*Centrolene condor* (endemic species)

*Centrolene sanchezi*

NT (not threatened):

*Centrolene peristicta*

DD (data deficient):

*Centrolene huilensis*



**Perú**

Libro Rojo de la Fauna Silvestre Amenazada del Perú (SERFOR 2018)

EN (En Peligro):

*Centrolene azulae*

*Centrolene audax*

*Centrolene hesperium*

VU (Vulnerable):

*Centrolene buckleyi*

*Centrolene muelleri*

**Threats**

The main threats are associated with habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local application of pesticides and fertilisers, pollution, disease, climate change and increased UV-B radiation.

*Centrolene acanthidiocephalum*: The data situation is insufficient as there is no up-to-date information on the size of the population, population status, ecological requirements and threats. This species may be in serious decline, but population declines cannot be quantified and further field research is urgently needed to confirm the persistence of this species.

*Centrolene altitudinalis*: a rare species that is endangered due to its range of only 729 km<sup>2</sup> and its susceptibility to habitat degradation, which may be further weakened by regular flooding, invasive alien fish species and the possible influence of the chytrid fungus.

*Centrolene antioquiensis*: categorized as near threatened by the declining size and quality of its habitat in the central Colombian Andes, namely deforestation due to agriculture, livestock farming and water pollution (Rivera-Correa 2010).

*Centrolene azulae*: Uncertainty about the size of occurrences, population status and ecological requirements. No further information is available since the 2004 assessment. The species is only known from a single ♀ specimen collected in 1966; there is also uncertainty about its taxonomic status.

*Centrolene ballux*: categorised as endangered, as the distribution area is limited and the species occurs in several non-contiguous locations classified as threatened. The size and quality of the habitat as well as the number of sexually mature specimens is continuously declining, mainly due to agricultural activities, deforestation and introduced trout (Hutter & Guayasamin 2012).

*Centrolene buckleyi*: categorised as critically endangered because this formerly abundant species is thought to have declined by at least 80% in the last ten years (2011–2020) and is expected to decline by at least 80% in the next ten years (2021–2031) due to impacts such as chytridiomycosis, neozoa (trout), habitat degradation due to agriculture, livestock farming and climate change (Ortega-Andrade et al. 2021).

*Centrolene camposi*: factors such as habitat loss, degradation and fragmentation due to legal and illegal logging, the expansion of agricultural and mining activities, are insufficiently researched, which is why the IUCN Red List category 'Data Deficient' at national and global level was used in the initial description (Cisneros-Heredia et al. 2023).

*Centrolene charapita*: categorized as endangered due to a range of only 614 km<sup>2</sup> and the known decline in the extent and quality of the habitat on the eastern slopes of the Andes in southern Ecuador and northern Perú. Throughout its range, the habitat continues to be lost due to agriculture, logging, road construction and human settlement. In the Cordillera del Condor, mining poses a serious threat.

*Centrolene condor*: Considering that the species is only known from a few locations in an isolated mountain range (Cordillera del Cóndor) characterised by extensive mining (copper, gold) and road construction activities and the associated deforestation and pollution, the species is considered endangered.

*Centrolene daidalea*: in view of its wide distribution and presumably large population, this species is not classified as endangered despite adverse anthropogenic influences.

*Centrolene ericsmithi*: s. *C. camposi*.

*Centrolene geckoidea*: categorised as critically endangered (possibly extinct) as this once widespread species appears to have suffered a drastic population decline in the 1990s, resulting from the apparent disappearance of most or all of its population, possibly due to chytridiomycosis, exotic predators in the rivers and pollution from spraying with poisons from illegal crops. In addition, the species is suffering from continuous habitat loss and degradation throughout its range due to agriculture, logging and human settlements. If there is still a population, it probably has fewer than 50 sexually mature individuals. In Ecuador, all subpopulations now appear to be extinct, as the species could no longer be detected in recent surveys. In Colombia, the species was common in the 1980s to 1990s; however, it was no longer recorded in more recent surveys in many of the places where it used to occur. The last record in Colombia dates back to 1997 (Lynch & Grant 1998).

*Centrolene heloderma*: categorised as vulnerable because its abundance is limited, it is threatened in several locations, and the extent and quality of its habitat and the number of sexually mature specimens are continuously declining due to agricultural development, fire, deforestation and human colonisation, climate change and the introduction of exotic predatory fish. The 2004 assessment speculated that the sharp population decline was caused by a shift in cloud cover on the mountain slopes due to climate change, resulting in lower humidity in the species' high-altitude range (likely exacerbated by habitat fragmentation). Efforts are underway to increase populations of this species in protected areas in Colombia, and the IUCN Red List has called for the conservation of a captive population of these frogs (Coloma 2004, AmphibiaWeb 2023).

*Centrolene hesperia*: categorised as endangered because the estimated range is only 309 km<sup>2</sup>, the species occurs in two locations classified as endangered and the extent and quality of its habitat on the Pacific side of the Cordillera Central in Perú continues to decline.

*Centrolene huilensis*: categorised as endangered because its range of 3,775 km<sup>2</sup> is fairly small, it occurs in several locations classified as endangered and the extent and quality of its habitat in the Colombian and Ecuadorian Andes is continuously declining, mainly due to deforestation for livestock farming. Declining population trend.

*Centrolene hybrida*: not categorised as endangered due to its relatively large distribution area, tolerance to habitat changes and a stable, presumably large population

*Centrolene lemniscata*: Due to ongoing uncertainties regarding its taxonomic status, extent of occurrence, population status and threats, this species is categorised as 'Data Deficient'. It is not clear what the main threats to this species are. There is a general regional destruction and loss of habitat due to increasing agricultural activities, selective logging and human colonisation. This species may also be endangered by chytridiomycosis.

*Centrolene lynchi*: categorised as endangered due to its limited range of 4,268 km<sup>2</sup>, the presence of five localities in threatened sites and the continuous decline in the extent and quality of its habitat due to agricultural activities, deforestation and other human-induced threats. The main threats to this species include deforestation due to agricultural activities (including the cultivation of illegal crops in Colombia), logging and human colonisation. Another likely threat is the introduction of exotic predatory fish species into the rivers. Chytridiomycosis cannot be ruled out either, given the apparent disappearance of this species from parts of its range in the 1980s and 1990s.

*Centrolene medemi*: categorised as endangered due to a drastic decline in populations and the apparent disappearance of the species since the 1990s. Populations are thought to have declined sharply more than ten years ago, possibly due to the spread of the chytrid fungus. It is likely that this species has only survived in small numbers, possibly with fewer than 250 adult individuals. The species was still considered common in the 1990s, but the last observation of this species dates back to the mid-1990s in the Parque Nacional Natural Cordillera Los Picachos, Departamento Caquetá. In Ecuador, it is only known from a single specimen collected in March 1975 (Guayasamin et al. 2006c).

*Centrolene muelleri*: this species is listed as 'Data Deficient' due to the ongoing uncertainty about the size of the population, population status and threat factors. In general, there is a progressive regional habitat loss due to increasing agricultural activities, selective logging and human settlement. The valleys between the mountains in the region are intensively farmed. This species was described in 1993 from a single specimen collected in 1989 and was known only from this holotype until 2007. Six further specimens were recorded during two expeditions at the foot of the Gocta waterfall in Amazonas in 2007 and 2011, and a further specimen was collected 7.4 km south-east of Puente Vilcaniza in 2011. The estimated distribution area is 233 km<sup>2</sup> and it is assumed that all individuals of this species occur in only three locations which were classified as threatened. The specimens from the Gocta waterfall could also represent an undescribed species, but are still included in this assessment pending a detailed taxonomic analysis (Twomey et al. 2014).

*Centrolene notosticta*: In view of its wide distribution, the presumably large population and the remaining suitable habitats throughout its range, the species is not categorised as endangered. However, habitat loss due to livestock farming and agriculture is a threat to this species, which is also disappearing from streams where trout have been introduced, such as El Rasgon. However, the species is still widespread and has been sighted frequently in recent times.

*Centrolene paezorum*: This species is categorised as 'Data Deficient' due to ongoing uncertainty about its abundance, population status, ecological requirements and threats. In the region where it occurs, water pollution from agriculture and human disturbance due to the cultivation of illegal crops are considered a problem. However, further field studies are needed to clarify how these threats affect the species, especially with regard to a possible population

decline. There is no information on the population status of this species, which is only known from one specimen (an adult ♀) to date.

*Centrolene peristicta*: Although the species is relatively widespread and probably has a large population on the western slopes of the Cordillera Occidental in Colombia and Ecuador, its overall population appears to be declining; it is therefore categorised as least concern. The main threats to this species are deforestation and habitat fragmentation, mainly due to agricultural activities, including farming and ranching, pollution from agriculture, hydroelectric development and deforestation. Although the species tested positive for the chytrid fungus, it showed no signs of population decline during a two-year monitoring study in Reserva Las Galarias, Ecuador (Guayasamin et al. 2014).

*Centrolene petrophilum*: categorised as endangered as its range is only 139 km<sup>2</sup>; most populations are found in locations classified as threatened due to ongoing deforestation caused by agricultural activities (livestock farming and agriculture) and mining. It was a common species until the mid-1980s, but was not detected again in 2010 and 2011 (Colombia Red List Assessment Workshop August 2016).

*Centrolene pipilata*: critically endangered because its distribution in north-eastern Ecuador is very limited (size of occurrence: 48 km<sup>2</sup>) and it only occurs in a single location, where the extent and quality of its habitat is continuously decreasing due to activities related to the construction of a dam and other human-induced activities. The lack of observations since 1977, despite research, means that the species may already be extinct. An oil pipeline runs through the distribution area of this species, which could be destroyed if the active El Reventador volcano were to erupt.

*Centrolene quindianum*: categorised as vulnerable, as the range and quality of the habitat continue to decline due to the expansion of livestock farming and agriculture. However, the species can also occur in disturbed biotopes as long as there is sufficient riparian vegetation. It is a locally widespread species that is rare in most of its range. It is assumed that the population is declining overall (Rojas-Morales & Escobar-Lasso 2013).

*Centrolene robledo*: currently not endangered, as its range is estimated at 43,139 km<sup>2</sup> and there were no signs of ongoing decline at the time of this assessment. The species is considered widespread, populations are fragmented, and the area and quality of habitat are continuously declining. However, these threats are spread over a relatively large geographical area. In addition, the species is known from several protected areas.

*Centrolene sabini*: categorised as vulnerable in view of the continuing uncertainty about the size of the population, population status and ecological requirements. Classified as vulnerable under IUCN criterion D2 (very small threatened range), as landslides in the only valley from which the species is known could have devastating effects. The extent of the occurrence is only 10 km<sup>2</sup> based on the only known location, which may still be an overestimate, and the very limited distribution and small population size make this species vulnerable to stochastic events (randomly occurring natural disasters). Amphibian communities in Upper Manu National Park have collapsed over the last decade during an epidemic of *Batrachochytrium dendrobatidis*, which is likely the cause of the local extinction of most sympatric glass frog species (Catenazzi et al. 2011, 2012).

*Centrolene sanchezi*: categorised as endangered because its range is limited (estimated at 20–500 km<sup>2</sup>), the species occurs in five locations classified as endangered and the extent and

quality of its habitat on the Amazonian slopes of the Andes in Ecuador and Colombia is in continuous decline. The main threat to this species is the severe loss of its habitat due to the expansion of agriculture and livestock farming. In Colombia, the cultivation of illegal crops poses an additional threat, while in southern Ecuador, mining poses a further threat. This species is considered rare. The ongoing decline in the quality and extent of this species' habitat indicates a downward trend in the population (Guayasamin et al. 2020).

*Centrolene savagei*: categorised as least concern, as the estimated range is 33,534 km<sup>2</sup> and the population trend appears stable. The species also occurs in protected areas, is not affected by any known major threats and is able to adapt to some disturbed situations. Local threats include habitat loss due to agricultural activities and settlements.

*Centrolene solitaria*: categorised as endangered, as its range is only 784 km<sup>2</sup>, it occurs in two to three locations classified as threatened and the extent and quality of the forest habitat required by the species continues to decline. The greatest threat to this species is the loss of habitat caused by the expansion of agriculture (subsistence farming, fish farming, coffee plantations) and livestock farming, as well as the cultivation of illegal crops. Due to the continuing decline in the size and quality of the habitat, the population is thought to be in decline.

*Centrolene venezuelensis*: not endangered, as its range is large and its decline is currently not fast enough to classify it in a higher threat category. The main threats to this species are the loss and degradation of its habitat due to the expansion of urban and agricultural boundaries. Forests are being cleared for the cultivation of subsistence crops and for livestock farming. Pollution from fertiliser run-off is widespread. In addition, alien predatory fish have been introduced into many streams. Nevertheless, a rare species, all but one record is of adult ♂♂ found during calling (Señaris & Ayarzagüena 2005).

*Centrolene zarza*: has not yet been assessed by the IUCN. Although it is a locally distributed species living in a nationally protected area, the authors of the original description recommend a classification as 'critically endangered' based on the 'B1ab(i,ii,iii) + 2ab(i,ii,iii)' IUCN criteria (range probably < 7 km<sup>2</sup>, known only from a single location, habitats affected by legal or illegal mining activities in the near future (Székely et al. 2023).



## Reproduction

| Topic                       | Details on the reproduction of <i>Centrolene</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂: call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Calls                       | <p><i>C. acanthidiocephalum</i>: Description of the advertisement calls (n=17) of two ♂♂ (SVL 31.5 and 32.3 mm) at an air temperature of 12.2°C: call consisting of 2–6 pulses with a mean call duration of <math>410.0 \pm 79.5</math> ms, mean call length <math>72.3 \pm 8.0</math> ms, call intervals <math>35.2 \pm 10.3</math> ms, mean dominant frequency <math>5,338 \pm 116.57</math> Hz (Carvajal-Cogollo et al. 2023).</p> <p><i>C. altitudinalis</i>: The ♂♂ call from the upper side of leaves at a height of 1.5–3 metres. The call was recorded on 20 April 1995 between 20–21 h (air temperature 13–16.5°C) at the type locality of the species. The advertisement call consists of two or three pulses (72.7% of the analysed calls two tones). Call length 375–831 ms, dominant frequency 4,700–4,920 Hz (with considerable secondary frequencies), 2.4–3.8 calls/min, call intervals 20–58 s (Señaris &amp; Ayarzagüena 2005).</p> <p><i>C. antioquiensis</i>: The advertisement call consists of one to four multiple pulsed tones that sound like a ‘trii’ to the human ear. The number of consecutive notes per call is <math>2.5 \pm 0.3</math> (1 to 4) with an interval between notes of 715.4–746.0 ms. Single notes last 44.0–46.3 ms, the number of pulses per tone is 5–12, the pulse rate is 157.1–172.9/s. The pulses are not uniform in amplitude and length; the first pulses are similar, while the last has the longest duration and the lowest amplitude. Dominant frequency 6,965–7,020 Hz (Duarte-Marín et al. 2022).</p> <p><i>C. ballux</i>: ♂♂ emit a single high-pitched trill as an advertisement call during the rainy season. ♂♂ call from the top of the leaves; the call is emitted sporadically and consists of a single short tone (328.5–420.4 ms) with 7–9 pulses; mean dominant frequency maximum 4,833 Hz (range 4,440–4,640 Hz); the tones are frequency modulated (Márquez et al. 1996, Guayasamin et al. 2020).</p> <p><i>C. buckleyi</i>: The ♂♂ call from the top of the leaves, description of an advertisement call from the highlands of Ecuador: calls in series, every 45–67 s, each call has a single, strongly pulsed tone with a duration of 0.248–0.288 s, slight frequency modulation, with an initial dominant frequency at 2,816–2,941 Hz and a dominant final frequency at 3,222–3,255 Hz (Bolívar-García et al. 1999, Guayasamin et al. 2006b).</p> <p><i>C. condor</i>: ♂♂ call from the top of the leaves; the advertisement call has a duration of 650–700 ms (n=3) and resembles a trill of two pulsed notes. The first note is strikingly longer (435–510 ms) than the second (101–102 ms); the time between notes is 66–118 ms and the dominant frequency is 2,620–2,970 Hz (Almendáriz &amp; Batallas 2008).</p> <p><i>C. daidalea</i>: two different call types that differ in the number of notes they contain. In about 50%, the call consisted of two tonal notes with a total duration between 587 and 7,629 ms; the first note is slightly shorter with an average duration of 26 ms than the second note with 46 ms, the time between them varies from 519–910 ms. The other half of the calls analysed correspond to a single tone, the total duration of which varies from 519–910 ms. In both cases, the dominant frequency of the calls is between 5,699 and 6,466 Hz, call interval 4–11 calls/min, call pauses 4.2–40.5 s (Cardozo-Urdaneta &amp; Señaris 2012).</p> <p><i>C. geckoidea</i>: ♂♂ (El Queremal, Valle del Cauca, Colombia) calling behind waterfalls or within or near splash zones of fast-flowing streams. The advertisement call is a loud, high-frequency, trilling whistle that lacks a consistent pattern of amplitude modulation. The call is weakly to moderately pulsed and has a duration of 155–373 ms. The calls were rarely emitted at intervals of 1.48–5.05 min. However, the ♂♂ usually call less frequently (i.e. less than once per hour). The dominant frequency is 3,468–4,187 Hz and is modulated (Grant et al. 1998).</p> |

*C. heloderma*: advertisement call short (133–188 ms), with two tones per call; tones strongly pulsed; dominant frequency at 4,393–4,823 Hz (Guayasamin et al. 2020).

*C. hesperia*: short, two-tone, high-frequency call (recorded 8 May 1987): Total duration 0.12 s, 1<sup>st</sup> note with 2–3 pulses, 2<sup>nd</sup> note with 1–2 pulses, dominant frequency 3,300–4,000 Hz, call frequency 2/s (Cadle & McDiarmid 1990).

*C. huilensis*: Call consists of two rapid high-pitched notes, individuals call from the top of the leaves 1.5–4 metres above the water. The advertisement call consists of one or two tones that sound like a ‘tic’ to the human ear. The 1<sup>st</sup> tone has a call duration of  $27.63 \pm 11.37$  ms and a dominant frequency of  $4,785.5 \pm 336.42$  Hz, while the 2<sup>nd</sup> tone has a duration of  $30.9 \pm 11.85$  ms and a dominant frequency of  $4,940.2 \pm 266.34$  Hz. Both notes have a limited amplitude modulation, with the highest energy in the centre of the note. The notes are separated by an interval of  $9.75 \pm 1.28$  ms (Mendoza-Henao et al. 2019, 2021).

*C. hybrida*: Individuals call from the tops of leaves at a height of 20 cm to 5 m above the water. The advertisement calls were recorded between 20:00 and 23:50 on clear nights in the vegetation above small and medium-sized streams at the edge of areas cleared for cattle. The call is a short, high-pitched sound that resembles a ‘tic’ to the human ear. The entire sound lasted  $19.9 \pm 9.7$  ms and had a dominant frequency of  $6,072.9 \pm 106.0$  Hz. In most cases, the call consisted of a single tone, but in a few cases, the animals produced calls with up to five tones after intervals of  $1,322.3 \pm 87.6$  ms. The highest energy is produced in the first third of the sound.

*C. lynchi*: ♂♂ call from the tops of leaves in trees or from branches above streams, at the type locality they were 2.5–4 m above the water. The call is relatively short and consists of a tonal note followed by one to three high-pitched notes (9.0–138.0 ms apart), the mean dominant frequency is 4,995–5,599 Hz. The aggression call differs significantly in structure from the advertisement call, which consists of a single short tone with two pulses: call length 140.0–156.0 ms, dominant frequency 4,823–4,910 Hz (significantly lower than that of the advertisement call; Dautel et al. 2011, Guayasamin et al. 2020).

*C. notosticta*: Description of the advertisement call from the Galilea natural forest (Villarrica, Tolima, Colombia) based on three recordings in June 2016 and January 2017 from the upper leaf surface, at a mean air temperature of 16.0–17.6°C and a relative humidity of 89–96% at a height between 2.0 and 4.0 m above streams: The advertisement call consists of two multiple pulsed tones (note 1: 7–8 pulses; note 2: 2 pulses; n=18 calls), with ascending (note 1) and descending (note 2) amplitude modulation and a call frequency of 0.6 calls/min. The calls are  $188.39 \pm 24.44$  ms long (139–238 ms), the duration of the first tone is  $96.82 \pm 18.72$  ms (74–130 ms, n=18 calls), the duration of the second tone is  $34.41 \pm 8.71$  ms (19–50 ms, n=18 calls). The interval between the two tones is  $58.15 \pm 17.52$  ms (36–90 ms). The two tones have a dominant frequency of  $4,400 \pm 280$  Hz with a range between 4,000 Hz (5% frequency) and 4,800 Hz (95% frequency). Two additional overtones are visible at 8,000 Hz and 13,000 Hz (Viuche-Lozano et al. 2018).

*C. peristicta*: The advertisement call consists of a short and pulsed sound that resembles the chirping of a cricket. The call has a duration of 0.036–0.087 s and a dominant frequency of 6,471–7,278 Hz. The repetition rate varies between 2–20 calls/min (Salgado & Guayasamin 2018).

*C. quindianum*: The advertisement call consists of two different call types. The most common call consists of two tones with amplitude modulation and a dominant frequency of  $4,678.1 \pm 156.0$  Hz; the other call type consists of 3–5 tones with high amplitude modulation and a dominant frequency of  $4,568.5 \pm 61.4$  Hz (Rios-Soto et al. 2017a).

*C. robledo*: Recording of advertisement calls (n=10) on branches of bushes at a height of 30 cm, which sound like a ‘trii’ to the human ear. A single tone consisting of  $13.7 \pm 1.3$  (12–15) pulses. Each pulse lasts  $4.2 \pm 0.5$  ms (4–5.7 ms), and the pulse rate per s is  $64.3 \pm 10.8$  (48.2–86.9). The amplitude of the pulses increases gradually in the first half of the note (amplitude modulation:  $13.9 \pm 8.3\%$  [3.1–26–9%]), while it decreases steadily towards the end of the note (amplitude modulation towards the end:  $19.7 \pm$

14.7% [2.8–46.3%]). Call length  $216.5 \pm 29.6$  ms (161–253 ms), the mean dominant frequency is 3,270 Hz (Duarte-Marín et al. 2023.).

*C. sabini*: The advertisement call consists of 8–14 high-pitched notes with dominant frequencies between 2,597 and 3,919 Hz. All recorded calls showed consistent patterns of amplitude modulation. The call lengths recorded at only 12°C varied from 3,089–7,563 ms when the call contained only a series of 6–11 tones, and from 8,537–10,111 ms when the first series of tones was followed by a second series of three tones. These two series of tones were separated by call intervals of 1,459–1,652 ms. The call intervals within the series averaged 258 ms (Catenazzi et al. 2009, 2012).

*C. sanchezi*: Calls are produced in series that can be relatively long (618–3,085 ms), each individual call may contain one or two notes; the repetition rate is 3–9 notes per call series. The notes sometimes occur in pairs (i.e., the spacing is much shorter than in the rest of the call). Each individual call is very short with a duration of 6–21 ms. The tones are strongly pulsed and have one or two amplitude peaks during the tone, with the second amplitude peak generally weaker than the first. The pulses within a tone have a frequency of 83–200 pulses/s. The dominant frequency of the peak amplitude is 5,719–6,188 Hz (Guayasamin et al. 2020).

*C. savagei*: The advertisement call consists of 1–3 ‘beeps’ lasting  $16.65 \pm 2.98$  ms (10–22 ms), with the frogs in Yotoco and Filandia emitting one- or two-part calls, while the species in Alto Bonito-Águila emits up to three-part calls. Successive sounds are separated by intervals of  $348.77 \pm 33.67$  ms (302–442 ms). The average call length is  $0.501 \pm 0.26$  s (0.018–1.057 s). The call rate is  $0.112 \pm 0.03$  calls/s (0.061–0.198 calls/s). The dominant frequency of the call is  $6,214 \pm 334$  Hz (5,822–7,211 Hz). The maximum sound pressure level of the advertisement call, which was measured 50 cm in front of two ♂♂, reached 75.4 and 78.6 dB. In addition, a call type following an amplexus in *C. savagei* is described in which the clasping was interrupted. Here, the ♂♂ seem to interrupt the amplexus for no apparent reason and start calling again. The vocal playback after the amplexus included two types of acoustic signals. One type of signal consisted of a tone similar to a ‘beep’ that lasted on average  $11 \pm 6$  ms and whose mean dominant frequency was  $5,684.8 \pm 0.0$  Hz. This signal is similar to the advertisement call described above. The second type of signal consisted of a single tone with  $31 \pm 0.7$  pulses. Each pulse lasted an average of  $7.2 \pm 1$  ms, followed by short intervals averaging  $3.1 \pm 0.7$  ms; the mean call duration was  $156 \pm 28.2$  ms, and the mean dominant frequency was  $5,871.2 \pm 101.8$  Hz. The temporal structure of this signal was similar to the courtship call emitted before amplexus formation by a ♂ of *C. savagei* in a population of the western Andes of Colombia (Díaz-Gutiérrez et al. 2013, Vargas-Salinas et al. 2014, Rios-Soto et al. 2017b).

*C. venezuelensis*: The advertisement call recorded at 13°C consisted of 2–4 notes, the call length was 1,035.5–1,199.8 ms, and the notes were modulated in packets, the first note was always the shortest (11.9–23.9 ms): 1<sup>st</sup> note: 11.9–23.9 ms (dominant frequency 1: 3,900–4,170 Hz, 2<sup>nd</sup> note: 25.6–61.4 ms, 3<sup>rd</sup> note: 30.4–68.2 ms). Note: 11.9–23.9 ms (dominant frequency 1: 3,900–4,170 Hz), 2<sup>nd</sup> note: 25.6–61.4 ms, 3<sup>rd</sup> note: 30.4–68.2 ms, 4<sup>th</sup> note: 33.7–65.4 ms (dominant frequency 2–4: 4,250–4,400), intervals: 256.2–392 ms (Señaris & Ayarzagüena 2005).

*C. zarza*: ♂♂ call from the tops of leaves, advertisement calls at the type locality (03.09.2022) at a height of several metres, in the vegetation at the edge of a small stream: high, pulsed single tone with three clearly distinguishable pulses, call length 0.242–0.318 s, pulse length 0.072–0.159 s, average pulse rate 11.8/s, dominant frequency 5,041–5,487 Hz. ♂♂ courtship calls (14 October 2020, in plastic bag, in the presence of ♀♀): multi-tone call (usually 5–6 notes/call), note structure like advertisement call (three pulses), call length 0.581–1.905 s, call interval 40.2–596.9 s, call rate  $\sim 0.23$  calls/min. or  $\sim 14$  calls/hour, dominance frequency 4,915–5,411 Hz (Székely et al. 2023).

#### Mating and spawning

All species: Axillary amplexus in the vegetation above small forest streams.

*C. acanthidiocephalum*: Three adult ♂♂ were found in November 2018 and April 2021 on the underside of leaves at the edge of unvegetated streams at a height of  $130 \pm 64$

cm above the water in two gallery forests, one of which was disturbed by livestock. At the time of the observations, air temperature was  $14.96^{\circ}\text{C} \pm 4.14^{\circ}\text{C}$  and relative humidity was  $80.6\% \pm 3.77\%$ . The ♀♀ lay their eggs in the apical zone of the leaves. The morphology of the clutch resembles a single layer of eggs with an empty centre, giving it a ring-shaped appearance (U-shaped; Ruiz-Carranza & Lynch 1989, Rios-Soto & Rada 2018, Carvajal-Cogollo et al. 2023).

*C. altitudinalis*: The eggs are laid on leaves above streams; after prolonged rainfall, a clutch was found about two metres above the stream on 4 June 1995 at an air temperature of  $16.5^{\circ}\text{C}$  (clutch 3.1 cm from the tip of the leaf, round to ovoid shape, diameter 2.3 cm, 20 well-developed eggs; Señaris & Ayarzagüena 2005).

*C. antioquiensis*: Two adult ♂♂ were recorded calling (37 calls) on the upper or lower surface of leaves at a height of 2–4 m; one ♂ was found near two clutches with 35 and 36 eggs. The eggs are laid on the underside of leaves that protrude above the water (Duarte-Marín et al. 2022).

*C. buckleyi*: A ♂ was observed near a clutch of 18 eggs in the Las Gralarias reserve in March 2008. The eggs are laid on the upper side of the leaves. Nocturnal activity on terrestrial bromeliads and vegetation 30–160 cm above streams, ponds and swamps in primary and secondary forests. Lynch & Duellman (1973) surmised that the species could reproduce in torrential mountain streams like other glass frogs, but also in bromeliads or swamps. They based this statement on the observation of a clutch of eggs on the inner leaf of a bromeliad in an area where *C. buckleyi* is common. The ♀♀ take over the short-term parental care of the clutch (hydration immediately after egg laying), ♂♂ show no parental care (Guayasamin et al. 2020).

*C. daidalea*: All clutches (n=24, found in Río Las Antenas) were found on leaf bundles, mainly of ferns (67%), followed by Arecaceae (21%) and Cyclanthaceae (12%). More than half (58.3%) of the clutches were located in the posterior third of the leaf (near the petiole), followed by the middle third (25%) and finally a few clutches deposited on the anterior third (16%) near the tip. The clutches were located at heights between 4–142 cm, most of them on leaves directly above the water of the stream (92%) and only 8% on rocky substrate. The clutches contained an average of 21.8 pale green eggs/clutch (3–32). Most clutches were found in April and May. 58% of the clutches were guarded by the ♂, which completely covered the eggs with its body and sat on them both during the day and at night. No parental care was observed in 42%. Of the 24 egg masses examined, 12% were categorised as ‘unhealthy’, most of which experienced sudden loss of part of the clutch, possibly due to a sharp rise in water levels following heavy rainfall. A further 33% showed irregular egg laying, possibly as a result of predators (Cardozo-Urdaneta & Señaris 2012).

*C. geckoidea*: ♂♂ and ♀♀ were found clinging to vertical or overhanging rock surfaces in the splash zone behind waterfalls. The ♂♂ remain in one’s habitat and have been observed in the same location for up to a month. The clutches were laid on rocks in the splash zone and contained 89–112 black eggs, which were stuck to the rocks by a brittle jelly, which is unknown in other members of the Centrolenidae. An ‘empty space’ could be seen in the centre of the attached clutch (possibly the eggs are laid while the ♀ rotates in a circle). During the night, the ♂♂ were observed sitting on or near up to four clutches while calling. During the day, ♂♂ were also observed sitting near or on clutches on the rock face behind a waterfall or hidden in spaces between rocks (Grant et al. 1998).

*C. heloderma*: Reproduction takes place during the rainy season. The ♂♂ call while sitting on the undersides of the leaves. The call is loud and high-pitched and serves to attract the ♀♀ and alert other ♂♂ to the presence of a rival, which can be described as a shrill ‘peeping’. The ♀♀ produce clutches of up to 29 eggs containing brownish embryos. They lay their eggs on the undersides of leaves high above the water level. Like many other centrolenids, the ♂♂ fight by dangling upside down, clinging to the vegetation with their hind legs and turning their ventral sides towards each other (Duellman 1981, Guayasamin et al. 2009, Guayasamin et al. 2014).

*C. hesperia*: light green to white eggs in a single, loosely arranged layer deposited on the upper surface of leaves, usually on the distal quarter of the leaf near the tip. Clutches were found on ferns, *Melastoma* sp., leaves of a small palm, elephant ears (Araceae) and other understory plants along stream margins, in some cases clutches were attached to aerial roots of epiphytes. The original description (Cadle & McDiarmid 1990) notes: 'One clutch, taken from a leaf 1.5 m above the water at 21:14 on 7 May, contained 26 light green Gosner stage 1 eggs, measuring about 2.2 mm in diameter and possibly laid shortly before that evening. Another clutch was collected during 29 January and contained 38 eggs in stages 4 and 5 with a diameter of 2.5–2.7 mm. A roosting ♂ was found on the tip of a leaf near a clutch. This clutch of 38 eggs was attached to the top of a fern frond (*Polystichum* sp.) and had 16 empty egg jellies on its upper edge. All clutches examined had empty egg jellies on the side closest to the leaf stalk. As these jelly shells are always positioned at the upper edge of the clutches, it is assumed that they reinforce the attachment of the clutch to the leaf or may serve as an additional water source during development due to their hygroscopic properties. The size of 12 clutches in the 'dry season' (2–9 May) varied between 16 and 30 eggs (mean  $20.7 \pm 4.4$ ). This is significantly smaller than the size of 15 clutches laid at the beginning of the 'rainy season' (29 January): Clutch size 19–42 eggs (mean:  $33 \pm 6.9$ ). Some observations indicate that egg losses due to desiccation occur after the rainy season. Reproductive activity declined rapidly after mid-May, by which time the regular rainfall had ceased, the fog characteristic of the site was less intense and persistent, and humidity was lower. The last viable clutches were observed on 25 May, when three clutches with advanced larval development were discovered along the stream where most of the earlier activity had taken place. On 26 May, two desiccated clutches were found along another stream on the same palm frond where viable clutches had been seen earlier in the month. Two desiccated clutches and no fresh egg masses were observed on 15 June. ', short-term brood care by the ♀ (hydration of the clutch especially in species that lay their eggs on the upper side of the leaves), ♂♂: ventral side to ventral side dangling from the hind legs, the presence of humeral spines serves less of an advantage in amplexus, but these could have a function as secondary sexual characters used by ♂♂ to defend their territory against other ♂♂ (analogous to horns in territorial mammals) (Cadle & McDiarmid 1990, Guayasamin et al. 2020).

*C. huilensis*: ♂♂ call from the upper side of the leaves at a height of 1–1.5 m (Mendoza-Henao et al. 2019, Guayasamin et al. 2020).

*C. lynchi*: ♂♂ fight while hanging upside down on leaves; at Reserva Las Gralarias (Lucy's Creek) the ♀♀ laid clutches of 21–24 neon green eggs on the vegetation in the territories of the ♂♂, most clutches were deposited on large leaves or ferns above a fast-flowing stream at a height of 165–600 cm. In most cases the eggs were laid on the upper side of the leaves, but in exceptional cases also on the underside. A single ♂♂ was observed with three clutches at the same time, which suggests polygynous reproduction. The initial assumption that ♂♂ perform prolonged parental brood care has since been refuted: Only the ♀♀ participate in (short-term) brood care (to hydrate the clutch) immediately after egg laying (Dautel et al. 2011, Guayasamin et al. 2020).

*C. medemi*: The eggs in the oviduct of a ♀ were dark brown in colour (KU 164493). It appears that the ♀♀ of this species lay their eggs on rocks, as has been observed in other saxicolous species living in similar microhabitats (e.g. *C. geckoidea*, *C. petrophilum*, *Rulyrana adiazeta*, *R. susatamai* and *Sachatamia orejuela*; Ruiz-Carranza & Lynch 1991a).

*C. muelleri*: ♂♂ called from the tops of leaves at 2–2.5 m above the water at night after a heavy rainfall, ♂♂ were seen struggling while dangling from the edge of leaves. One clutch was found on the upper surface of a leaf and consisted of 46 white eggs surrounded by clear jelly. On the second occasion, several individuals were found in a small rivulet about 0.5 m above the water that flowed into the Río Gocta near the splash zone. A third animal called from the top of a leaf about 1.5 metres above the water of a torrential cloud forest stream. This stream flowed through an apparently



undisturbed highland forest and was full of large rocks and deep pools with a strong current (Duellman & Schulte 1993a).

*C. notosticta*: on 28 April 1983 at the type locality 'El Encino' many pairs were observed in amplexus on the undersides of leaves with 13–20 greenish-pale yellow eggs. On 15 August 1986, a ♂ was observed in Tona on the underside of a fern frond, apparently guarding the clutch. In May 2009, the species was common in Campamento Guacharaca, almost all ♂♂ were found calling between 19–22 h on the upper side of ferns and Heliconiaceae on the banks of a small, fast-flowing stream (Rojas-Runjaic et al. 2012).

*C. peristicta*: ♂♂ call from both sides of the leaves, the ♀♀ spawn on the undersides of the leaves of palms, ferns, heliconias, anthuriums and other plants at a height of 0.7–5 m above the water (2.70 m + 1.04 m, range 0.7–5.3 m, n=25). After the ♀♀ have laid their eggs, they leave the territory. The ♂♂, on the other hand, can stay with the clutch and guard it. One and the same ♂ can take care of several clutches at the same time. Each clutch is the result of mating with a different ♀, the eggs of other ♀♀ can be adopted as well ('alloparental care'; Salgado & Guayasamin 2018, Valencia-Aguilar et al. 2021).

*C. petrophilum*: inhabits vegetation in rocky habitats. ♂♂ sit calling on the sides of the rocks and defend these calling sites because the ♀♀ also lay their eggs there. ♀♀ have been seen both on nearby plants and directly on the rocks. The sexual dimorphism in this species can be recognised by the fact that the ♀♀ are larger and lack head spines.

*C. pipilata*: ♂♂ call from the upper side of leaves, eggs are also laid on the upper side of leaves; all individuals were found at night on vegetation along watercourses, in captivity one ♀ laid a clutch of 18 eggs (Lynch & Duellman 1973, Guayasamin et al. 2020).

*C. quindianum*: An observation of two pairs in amplexus dates from 14 November 2015. The first pair was on a moss-covered branch 4 m above the water at 19:25. At 21:06, another calling ♂ tried to dislodge the ♂ in amplexus from the back of the ♀. The pair moved away and were then pursued by the single ♂, which held the already mated ♂ by the legs. After almost an hour, the pair moved to another branch and the single ♂ remained attached to the original branch for 16 minutes. A few minutes later, the ♂ started calling again and was observed at 23:22 in amplexus with another ♀ at a height of 3 m above the stream and 40 cm away from the first pair. The latter spawned at 02:20 after a total observation time of about 7 hours. Before laying the eggs, the ♂ began to move its legs in a circle above the ♀; during egg-laying the ♂ lifted the rear part of its body, the ♀ then quickly ejected its eggs. After laying the eggs, the ♂ continued to move its legs above the ♀ for a few seconds (with repetitions at intervals of approx. 10 min, for a total of almost 2 h until approx. 04:30 h). After the ♂ had completed the amplexus, it remained in the vicinity of the ♀ for 25 min; later it moved away. The ♀ remained on the eggs and moved its legs in a circle over the clutch. The second pair spawned at 02:53; the egg-laying behaviour showed the same sequence as the first pair. At around 03:15 the ♂ completed amplexus and remained next to the ♀ until 04:30. The ♀ also ejected its eggs quickly and finished laying in less than a minute; it initially remained on the eggs and moved its legs in a circular motion. Both ♀♀ remained sitting over their eggs for at least 3 hours until the observations were finished. By the following midday, the ♀♀ had disappeared. During the observation of a total of 15 clutches, no further brood care was observed during their development (Rios-Soto et al. 2017a).

*C. sabini*: ♂♂ were active at night at temperatures between 11 and 12.7°C, the ♂♂ call from the upper side of the leaves, the ♀♀ lay eggs on the upper side of the leaves (Catenazzi et al. 2012).

*C. sanchezi*: found at night on leaves 130–300 cm above streams in primary and secondary forests, ♂♂ calling from the upper sides of leaves. One ♂ was found near two clutches, one on the underside, the other on the upper side of a single leaf (Guayasamin et al. 2020).

|                            |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
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|                            | <p><i>C. savagei</i>: ♂♂ call after the daily rainfall to attract the ♀♀. After the eggs are laid, the clutches are guarded by the ♂♂ until they hatch. Larger ♂♂ have a higher chance of mating than smaller ♂♂ (due to rivalry competition [intrasexual selection], not due to the choice of ♀♀ [intersexual selection]). Paternal brood care protects the offspring from at least two sources of danger, namely dehydration and predators, and appears to be more pronounced at night than during the day. The tendency to brood care decreases from egg laying to hatching as the embryos develop. Embryonic mortality was higher in clutches abandoned naturally by the ♂ than in clutches cared for by ♂♂. Most ♂♂ that cared for the eggs, but none of the non-brood-caring ♂♂, showed defensive behaviour such as biting and kicking against the predator stimulus. Characteristic defence postures, cloacal fluid release and the production of deterrent secretions were also observed. Preliminary results also suggest that brood-caring ♂♂ have a higher tolerance to threatening stimuli before fleeing than non-brood-caring ♂♂. After ♂♂ removal, the motivation to return to the clutch was higher in brood-caring ♂♂ than in unpaired ♂♂, and the motivation to return decreased with the distance of relocation. Furthermore, the availability of reproductive territories (limited resource) had an influence on this behaviour (Escobar-Lasso &amp; Rojas-Morales 2012, Vargas-Salinas et al. 2014, Ospina-L et al. 2020, Navarro-Salcedo et al. 2021).</p> <p><i>C. venezuelensis</i>: The ♂♂ call from the upper side of leaves, between a few centimetres and 2 m above the water. The clutches are laid on the upper side of the leaves (Señaris &amp; Ayarzagüena 2005, Rojas-Runjaic et al. 2012).</p> |
| Reproductive season        | <p><i>C. ballux</i>: Reproductive activity in the rainy season (December–April; Guayasamin et al. 2020).</p> <p><i>C. daidalea</i>: Records especially in March to June 2009 (Cardozo-Urdaneta &amp; Señaris 2012).</p> <p><i>C. hybrida</i>: In May 1981, 1983 and October 1985, some ♀♀ with eggs were collected, while others were observed laying their eggs on the underside of leaves and fern fronds about 1–3 m above the water surface (AmphibiaWeb 2023).</p> <p><i>C. peristicta</i>: Clutches were recorded in the Galarías Reserve in February, March and April (Salgado &amp; Guayasamin 2018).</p> <p><i>C. quindianum</i>: Calling and oviposition dominated in months with higher rainfall and lower temperatures, especially in October and November. Interestingly, reproduction took place longer in two syntopic glass frog species (<i>C. savagei</i>, July to December, <i>N. grandisonae</i>, August to December; Rios-Soto et al. 2017a).</p> <p><i>C. sanchezi</i>: In February 2013, calling ♂♂ were heard at the Yanayacu Biological Station (Guayasamin et al. 2020).</p> <p><i>C. savagei</i>: Gravid ♀♀ were collected in June 1981, August 1989 and November 1990 with cream-coloured eggs, clutches were recorded in March, April and June 2006 (Ruiz-Carranza &amp; Lynch 1991c, Vargas-Salinas et al. 2007).</p> <p><i>C. zarza</i>: calling ♂♂ were heard in January, March, June, October and November, but intense activity (many ♂♂ called from lower altitudes, 50 cm to 3 m above the streams) was recorded between October and March (Székely et al. 2023).</p>                                                                                                                                                                                                                         |
| Eggs clutch, clutches/year | <p><i>C. acanthidiocephalum</i>: Clutches with 80 eggs (possibly from several egg depositions) were found in November 2018 on the apical part of the upper side of a fern leaf (Dryopteridaceae) at a height of 110 cm above the water. Other sources speak of clutches with an average of 35 eggs (21–48; n=5). No adults were found in the vicinity of the eggs. The clutch had a single-layer arrangement and was U-shaped, as previously described for this species. The eggs were grey-brown at the animal pole and whitish at the vegetative pole, with a darker yolk in the eggs in the upper part of the clutch. The eggs were in different embryonic stages, with some of them hatching as larvae that moved by small jumps on the leaf and then fell on the water surface (Ruiz-Carranza &amp; Lynch 1989, Rios-Soto &amp; Rada 2018, Carvajal-Cogollo et al. 2023).</p> <p><i>C. ballux</i>: ♀♀ lay clutches of 18–21 eggs on the upper side of leaves. The eggs are gelatinous, clear and sometimes green in colour. ♂♂ were found in the vicinity of the</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | <p>clutches, although brood care would be atypical for this genus (Duellman &amp; Burrowes 1989, Hutter &amp; Guayasamin 2012, Guayasamin et al. 2020).</p> <p><i>C. charapita</i>: A clutch of 34 eggs was found on a leaf 2.20 metres above the stream (Páez-Rosales &amp; Pinto 2017).</p> <p><i>C. huilensis</i>: average 46.6 eggs/clutch (44–49; n=3; Mendoza-Henao et al. 2019).</p> <p><i>C. peristicta</i>: The average number of eggs per clutch was 22.9 (n=40, range 6–41). The eggs hatched after 17–27 days (mean: 21.4 + 3.2, n=12; Salgado &amp; Guayasamin 2018).</p> <p><i>C. pipilata</i>: The eggs have a clear jelly and pale green yolk colour (Lynch &amp; Duellman 1973).</p> <p><i>C. quindianum</i>: The clutches contained an average of <math>26 \pm 2.6</math> eggs (22–29; n=8); the oviposition substrate consisted mostly of moss-covered branches, and one clutch was found on a leaf. The yolk of most clutches was yellow, in one case green (Rios-Soto et al. 2017a).</p> <p><i>C. sabini</i>: clutches contained 35–45 eggs (n=5; Catenazzi et al. 2012).</p> <p><i>C. sanchezi</i>: The clutches consisted of 14–18 pale yellowish green eggs (Guayasamin et al. 2020).</p> <p><i>C. savagei</i>: The clutches (18 eggs on average) were laid on the upper sides of leaves at a height of 80–300 cm above the stream (Vargas-Salinas et al. 2007).</p> <p><i>C. zarza</i>: Two clutches at Gosner stage 19 were found at the type locality on 9 June 2021. Both clutches were located on the upper side of a leaf ~ 3 m above the stream. The clutches contained 13 and 33 embryos; no adults were observed guarding the eggs or staying nearby, so parental brood care is probably not taking place (Székely et al. 2023).</p> |
| Size of eggs and larvae at hatching               | <p><i>C. quindianum</i>: The mean diameter of eggs per developmental stage were as follows: Stages 1–6 (<math>3.13 \pm 0.33</math> to <math>4.82 \pm 0.43</math> mm), Stages 13–18 (<math>5.26 \pm 0.63</math> to <math>7.80 \pm 0.53</math> mm), Stages 19–25 (<math>5.27 \pm 0.51</math> to <math>7.54 \pm 1.20</math> mm [min–max]). No dead embryos were observed, but predation by spiders (Rios-Soto et al. 2017a).</p> <p><i>C. savagei</i>: The eggs had an average diameter of 4.58 mm when they were 1–2 days old and 6.4 mm at the time of hatching (Vargas-Salinas et al. 2007).</p> <p><i>C. venezuelensis</i>: oocytes of different sizes (diameter between 0.9 and 2 mm) were found in the ovaries of a dissected ♀; the larger oocytes had a dark brown pole and a yellowish creamy colouration, while the smaller oocytes were completely yellowish (Señaris &amp; Ayarzagüena 2005).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Development time from egg laying to metamorphosis | <p>Glass frog ♀♀ lay their eggs on substrates outside the water along streams, after several days or weeks (often &gt; 20 days), the eggs hatch and the embryos fall into the water where they complete their development (Cisneros-Heredia &amp; McDiarmid 2007).</p> <p><i>C. daidalea</i>: more than five months from hatching to metamorphosis (Rada et al. 2007).</p> <p><i>C. lynchi</i>: The eggs develop into hatching larvae in 23–29 days (Dautel et al. 2011, Guayasamin et al. 2020).</p> <p><i>C. quindianum</i>: In the observation of five clutches, the time to hatching was 28–32 days (Rios-Soto et al. 2017a).</p> <p><i>C. savagei</i>: Hatching took place 10–12 days after egg laying and was not synchronised (Vargas-Salinas et al. 2007).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Details on the larvae:                            | <p><i>C. acanthidiocephalum</i>: In life, the back is cream-coloured with brown melanophores gathered around the interocular space and most of the yolk sac. The eyes are dark, and the distal part of the body is translucent cream-coloured, the belly is brown, the caudal musculature beige with a stripe of brown melanophores extending longitudinally over most of the proximal region; the caudal fins are cream-coloured with scattered brown melanophores mainly in the proximal region. The morphology of the tadpoles is described on the basis of 12 larvae at Gosner stage 22–23: Body spherical in lateral view (as wide as high at posterior end) and wedge-shaped in dorsal view (wider distally than proximally). Eyes arranged and orientated dorsolaterally, nose with oval openings arranged anterolaterally, closer to the tip of the mouth than to the eyes.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

Oral disc not developed in all specimens examined. Long tail, about 65% of total length, wider proximally than distally. Dorsal and ventral fins begin at the tail/body junction, increase in size towards the distal end of the tail and gradually end in a rounded tip. The fins reach their maximum height in the distal two-thirds of the tail (Carvajal-Cogollo et al. 2023).

*C. altitudinalis*: Description of larvae (n=6) in stage 25 according to Gosner (1960): yellowish green body (transparent green in the tail musculature), body length 3.8–5.3 mm, tail length 9.8–12.2 mm, body height 1.8–2.7 mm, body width 2.5–3.7 mm, body compressed in dorsal view, oval in lateral view, eyes small, silhouetted dorsolaterally, short, visible on the left side, cloacal opening on the right side, caudal musculature does not reach the distal end of the tail, distal end rounded, upper fin margin as wide as the lower one, originates at the junction between body and tail, the lower fin margin originates at the body. Oral disc bordered ventrally, inferiorly and laterally by blunt, umbilical papillae, formula of ceratodont row 1/2–3. Body dorsally and laterally light brown marbled, rest transparent, internal organs visible; caudal musculature light brown marbled (Señaris & Ayarzagüena 2005).

*C. daidalea*: Gosner stage 36: Total length 36.69 mm, body length 9.69 mm, body elongate and depressed, mouth region subacuminate in dorsal profile and tapering in lateral view, eyes medium sized, arranged dorsally, nostrils very small, arranged anterodorsally and much closer to the eye than at the end of the rostrum, spiraculum short, located on the left side in the posterior and ventral region of the body, cloacal opening caudal, medial-marginal and right-sided, forming a short free tube, tail long and robust, with rounded distal end, upper fin margin reaches its greatest height shortly after the middle of the tail, oral disc large, transangular and anteroventrally located, bordered by a row of small, blunt marginal papillae on the sides and in the posterior region. Lateral papillae anterior, blunt, anterior disc fold with smooth surface, middle part of oral disc with well-developed suprakeratostoma, without medial division, thin and arcuate with fine margins and small, distinct serrations, U-shaped and denticulate. Dental formula 2/2 (possibly additional weak fold with small row of blunt papillae), upper lip: with two incomplete rows of denticles of short length located at sides and corners of mouth. Lower lip: two rows of keratodonts P1 and P2 of different length and development (P1 large and evenly developed, P2 short, medially interrupted and poorly developed in relation to the previous row). Colouration: body coloured yellow to brown, caudal musculature has the same colour, with translucent fin margins, heart and hyobranchial apparatus bright red (Hoffmann 2010a, Rada et al. 2007).

*C. geckoidea*: fresh tadpole (total length 22.3 mm) with typical centrolenid body shape, the upper rows of teeth are missing in the mouth, but there are two lower rows of teeth (P1 with wide medial gap), maxillary sheath thick with tiny serrations, mandibular sheath thin and poorly keratinised, a row of large subconical marginal papillae borders the ventrolateral and posterior oral disc. Tadpoles at Gosner stage 22, one month after hatching, have two incomplete rows of teeth on the upper lip and three rows of teeth on the lower lip. Three months after hatching, all rows of teeth were lost and only skin furrows were still recognisable. The dorsal surfaces of the body and the tail muscles were black in colour, the belly was not pigmented (Lynch et al. 1983, Rueda-Almonacid 1994).

*C. heloderma*: Tadpoles have a worm-like body shape with C-shaped eyes positioned on the upper side. The tadpoles feed on external food sources and are fossorial, i.e. they live buried in the bottom of flowing streams (Cisneros-Heredia 2006).

*C. hesperia*: Tadpoles were reared to stage 25 (Gosner 1960): Total length 14.9 mm, tail length 10.2 mm, centrolenid-typical, fusiform body, rounded mouth region, eyes small, sickle-shaped, arranged dorsally, nostrils slightly closer to the eye than to the tip of the mouth, lower fin margin in the middle of the tail slightly lower than the upper fin margin, rounded tip of the tail, spiraculum small, oval and left posterolateral, oral disc anteroventral: a uniserial row of about 22 large marginal papillae laterally and posteriorly, maxillary sheaths narrow, weakly keratinised and serrate, labial tooth rows barely visible and incompletely keratinised, A2 with wide medial gap, the short

sections located almost lateral to the anterior maxillary sheath. Labial tooth row formula 2(2)/3 (Cadle & McDiarmid 1990).

*C. huilensis*: Larvae up to stage 17 sensu Gosner (1960) are creamy light green (yolk remains), from the 18<sup>th</sup> Gosner stage the embryos become light grey, while the jelly takes on a whitish to smoky cloudy colour and increases in volume (Mendoza-Henao et al. 2019).

*C. quindianum*: The mean total length of the hatchlings was  $9.5 \pm 1.5$  mm (7.6–11.8 mm; n=9). The dorsal and ventral colouration of the hatchlings (stage 25) was translucent pink with grey spot patterns (Rios-Soto et al. 2017a).

*C. savagei*: At the time of hatching, the embryos had reached Gosner stage 24 and had a mean total length (body + tail) of 11.92 mm. A tadpole at Gosner developmental stage 39 had an elongated, somewhat flattened (wider than high) body in profile and was oval in dorsal view. Total length 33.1 mm, body length 9.8 mm, body width 5.9 mm, body height 4.8 mm, mouth region truncated in dorsal view, rounded in profile, lateral line system with neuromasts recognisable, especially in the anterior part of the body, eyes arranged dorsolaterally, nasal openings small, elliptical and dorsally directed, spiraculum posterolateral, short and left-sided, diameter 0.7 mm, cloaca short, medial, opening posteriorly, oral disc directed anteroventrally, width of oral disc 3.0 mm, marginal and uniserial papillae around the oral disc, the longest papillae on the lower labium, five submarginal papillae are present on each side of the maxillary sheath, marginal papillae are interrupted dorsomedially in the anterior labium and form a wide gap, maxillary sheath completely keratinised, with a serrated edge and a pronounced arch in the middle, mandibular sheath keratinised, V-shaped and with a serrated edge, wide denticulation short and directed straight medially. Tooth row formula 1(1)/2(2) (tooth row A1 interrupted medially, located laterally on both sides of the maxillary sheath, forming a wide gap; Díaz-Gutiérrez et al. 2013, Vargas-Salinas et al. 2007, 2017).

*C. venezuelensis*: elongated, flattened body, tail longer than  $\frac{2}{3}$  of the total length, tail musculature strongly developed, upper fin margin as broad as the lower one, eyes in dorsal position, spiraculum small, left-sided, posterior, cloaca medial, oral disc in anteroventral position, surrounded by two rows of small papillae, oral dentition formula: 6(1-I)I (1-1)7 (Rada 1990).

*C. zarza*: The tadpoles hatched in the laboratory after five days and survived for more than six months, until 2 January 2022. They initially developed well, but stopped their development at Gosner stage 31 (around 20 November) and died in January 2022 without having completed their metamorphosis. It is possible that the tadpoles died due to inadequate rearing conditions, or their death was caused by chytridiomycosis. Gosner stage 31: Total length 26.9–34.7 mm, body length 8.2–10.4 mm (about 30% of total length), body elongate, oval and flattened, wider than high, snout rounded in dorsal view, oblique and rounded in profile, eyes arranged dorsally and C-shaped (at least up to Gosner stage 31), nostrils dorsal, protruding, very small and directed forwards, spiracles short, single, left-sided, posterolateral, tail long with slightly pointed end, upper fin margin begins approximately in the middle of the tail length, oral disc large (width ~ 65% body width), not raised, near the tip of the mouth, directed anteroventrally, projecting ventrally but not laterally, marginal papillae single-rowed, large, distributed around the oral disc (~ 43–47 papillae), a large part of the anterior (upper) margin of the oral field has no papillae (instead a rolled fold with a smooth surface), but a row of submarginal, flattened papillae near the maxillary sheath, maxillary sheath broadly arched, mandibular sheath slightly U-shaped, serrated margin, Labial tooth row formula 0/2(1), P1 with medial gap and a row of submarginal, flattened, papilla-like ridges (consisting of seven or eight papillae), in the lower part of the mouth field in Gosner stage 26 (in Gosner stage 31 all tooth rows have been lost, and only the dental ridges (dermal) were still present next to the submarginal papilla ridge; unclear whether physiological). Colouration: Gosner stage 24 slightly pinkish, but with green colouration of the abdomen, Gosner stage 25: more distinct pink colouration, Gosner stage 26: almost red, Gosner stage 31: body only slightly pink, tail almost brown (Székely et al. 2023).



## Husbandry and Captive Breeding **X**

No husbandry information is available for any of the species.

***Chimerella* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                       | Original description                                                     | Common name              | Common name international      | Known/ documented in international trade |
|-------------------------------|--------------------------------------------------------------------------|--------------------------|--------------------------------|------------------------------------------|
| <i>Chimerella corleone</i>    | Twomey, Delia & Castroviejo-Fisher, 2014                                 |                          |                                | No                                       |
| <i>Chimerella mariaelenae</i> | (Cisneros-Heredia & McDiarmid, 2006)                                     | Maria Elena's Glass-frog | Rana de cristal de María Elena | No                                       |
| <i>Chimerella mira</i>        | Köhler, Venegas, Castillo-Urbina, Glaw, Aguilar-Puntriano & Vences, 2023 |                          |                                | No                                       |

The genus name *Chimerella* comes from the Greek word 'chimaira'. In Greek mythology, the chimera is a creature made up of parts of several animals. The name was chosen in reference to the peculiar combination of morphological characteristics of *Chimerella mariaelenae*. The ending -ella is a diminutive form. Phylogenetically, the genus represents a clade of the common lineage of the species *Centrolene mariaelenae* Cisneros-Heredia & McDiarmid 2006 and species that are more closely related to *C. mariaelenae* than to other genera within the Cochranellini. The sister genus in this case is uncertain, the mitochondrial dataset supports a clade in which *C. mariaelenae* is related to all other genera of the Cochranellini, whereas the nuclear and overall topological data diverge from this mitochondrial hypothesis.

**Morphology and Taxonomy**

Members of the genus can be distinguished by the following characteristics: (1) adult ♂♂ with small humeral spines, (2) lobed liver covered by a white hepatic peritoneum, digestive tract white, (3) ventral parietal peritoneum completely transparent, (4) interdigital membranes absent between inner fingers or basal, between the outer fingers moderately pronounced, (5) pale green bones in life, (6) dorsum lavender coloured with small dark spots in the preservative, (7) dentary process of vomer present but without denticles, (8) ♂♂ call from the upper sides of the leaves.

The *Chimerella* species are the only glass frogs that possess a small humeral spine in adult ♂♂, a transparent ventral parietal peritoneum and white pericardial, hepatic and visceral peritonea. The aforementioned features are otherwise only found in one species from the Guiana Shield (*Vitreorana gorzulae*). Based on the morphological similarity (i.e. transparent ventral parietal peritoneum and white hepatic peritoneum), Cisneros-Heredia & McDiarmid (2006) argued that *Chimerella mariaelenae* is part of a group (the *gorzulai* species group sensu Duellman & Señaris 2003) endemic to the Guiana Shield. These authors presented their hypothetical clade as evidence of a biogeographical connection between the Andes and the Guiana Shield. The relationships of *C. mariaelenae* and other genera within the Cochranellini do not receive strong support in the topologies obtained from the complete and nuclear datasets. However, the phylogeny does not support the Andean-Guiana Shield biogeographic connection hypothesis. If the mitochondrial topology were correct, this would imply that the most recent common ancestor of the Cochranellini group was similar in morphology and behaviour to species of the genera *Chimerella* and *Vitreorana* (Guayasamin et al. 2009).



Fig. 42: *Chimerella* species

- a *C. mariaelenae*, Nangaritza Canton, Province Zamora Chinchipe in southern Ecuador (A. Sanchez Vialas)
- b *C. mariaelenae*, Nangaritza Canton, Province Zamora Chinchipe in southern Ecuador (A. Sanchez Vialas)
- c *C. mariaelenae*, Puyo, Ecuador (A. Plewnia)
- d *C. mariaelenae*, Puyo, Ecuador (A. Plewnia)
- e *C. mira* (J. Köhler)
- f *C. mira* (J. Köhler).

The three species of this group are easily distinguishable, but *Chimerella* spp. can sometimes be difficult to distinguish from other genera (molecular identification is recommended for unequivocal species identification):

*Chimerella corleone*: small glass frog with green dorsal colouration, with scattered yellowish green spots and dusted with tiny dark melanophores, hands and feet light green, tips of fingers and toes pale orange, dorsal skin finely chagrined, ventral skin granular, cloacal ornament consisting of two round, low, unpigmented bumps lateral to the cloaca, enamelled margins

on the postaxial margin of finger IV, metacarpal fold and enamelled margins on the postaxial margin of toe V absent, elbow fold present, white, tarsal fold present as a line of low white bumps on lateral margin of tarsal bone, prepollex not enlarged, obscured, iris silvery-white with dark grey reticulation, SVL ♂♂ 18.8–20.0 mm, ♀ 21.0 mm (n=1), mouth region blunted in dorsal view, rounded in lateral view, tympanic membrane and tympanic ring clearly recognisable, with a slight posterior inclination, ventral parietal peritoneum transparent (no bib-like spot visible), liver bulbous with two rounded lobes, liver, heart and visceral peritonea white, urinary bladder unpigmented. Similar species: *Hyalinobatrachium* spp., *C. mariaelenae* (sister species), *Vitreorana antisthenesi*, *Vitreorana eurygnatha*, *Vitreorana gorzulae*, *Vitreorana parvula*, *Teratohyla ameliae*, *Teratohyla pulverata* (Twomey et al. 2014).

*Chimerella mariaelenae*: small glass frog with yellowish green dorsal colouration and small grey to black spots, dorsal surfaces of fingers and toes without melanophores, except some at the base of toe V, dorsal skin chagrined, ♂♂ with tiny dorsal spines (only visible under 250x magnification), Cloacal ornamentation consisting of two round, low, unpigmented bumps lateral to the cloaca, upper arms thin and half as wide as the robust forearms, ulnar and tarsal folds absent, concealed prepollex, finger I slightly longer than finger II, interdigital membranes extended between the toes, iris white with numerous dark spots, pupil surrounded by a reddish to orange ring edged with a dark grey to blue ring, SVL ♂♂ 17.9–19.7 mm, ♀ 20.8 mm (n=1), mouth region blunted in dorsal view, blunt to slightly protruding in lateral view, tympanic membrane oriented posterolaterally with a slight dorsal inclination, ventral parietal peritoneum transparent, iridophores in the pericardium and in the peritonea of the digestive tract, bulbous liver and testes, kidneys and urinary bladder without iridophores. Similar species: *Hyalinobatrachium* spp., *C. corleone* (sister species), *Vitreorana gorzulae*, *Teratohyla ameliae*. Taxonomic note: Type species of the genus *Chimerella* (Cisneros-Heredia & McDiarmid 2006, Guayasamin et al. 2020).

*Chimerella mira*: small glass frog with yellowish green dorsal colouration and small round scattered pale yellowish spots, dorsal surfaces of limbs yellowish cream coloured, with scattered melanophores, dorsal surfaces of fingers and toes without melanophores, except on toes IV and V, dorsal skin finely chagrined with few tiny scattered dorsal tubercles, ventral skin granular, cloacal ornamentation consisting of two round, low, unpigmented tubercles lateral to the cloaca, enamelled seams present on the postaxial edge of finger IV, ulnar fold diffuse, tarsal fold absent, enlarged tubercles on the ventrolateral margins of arm and tarsus absent, concealed prepollex, not enlarged, prepollex spine not protruding, finger I slightly longer than finger II, interdigital membranes between the toes extended, iris silvery-white with fine black spotting and a dark brown central stripe consisting of fine dots, SVL ♂♂ 18.1–19.6 mm, ♀♀ unknown, mouth region blunted in dorsal view, blunt in lateral profile, eardrum and eardrum ring distinct, round, supratympanic fold weakly pronounced, dentary processes of vomer and vomer denticles absent, ventral parietal peritoneum transparent, iridophores in pericardium and peritonea of digestive tract, bilobed liver and testes (partially), kidneys and urinary bladder without iridophores. Similar species: *Hyalinobatrachium* spp., *C. corleone*, *C. mariaelenae*, *Vitreorana gorzulae* (Köhler et al. 2023).

## Distribution and Habitat

The genus *Chimerella* occurs on Amazonian Andean slopes in Ecuador, 1,400–1,820 m asl, in the provinces of Napo, Tungurahua, Morona Santiago and Zamora Chinchipe, Ecuador, possibly also in neighbouring southern Colombia. It has also been recorded from the vicinity of San José in the Cainarachi Valley near Tarapoto, Departamento San Martín, Perú, at 610 m asl (Guayasamin et al. 2009, 2020, Twomey et al. 2014, Frost 2024).

*Chimerella corleone*: known only from the type locality, a stream near the village of San José in the Cainarachi Valley near Tarapoto, in the department of San Martín, Perú. It is not known whether the species is restricted to the vicinity of this locality or whether it is possibly more widespread (610 m asl). All individuals were found on low herbaceous vegetation growing along vertical rock faces in the splash zones of waterfalls in a tropical lowland forest (Twomey et al. 2014).

*Chimerella mariaelenae*: known from about 20 localities on the slopes of the Cordillera Oriental and the Amazon region in the provinces of Sucumbios, Napo, Orellana, Morona Santiago and Zamora Chinchipe, Ecuador. The species also occurs in the Cordillera Kampankis, Zona Reservada Santiago-Comaina, Amazonas region, Perú, and possibly in neighbouring southern Colombia (813–1,820 m asl). Habitat on leaves up to 5 m above small streams and ponds in primary or older secondary evergreen mountain and cloud forests as well as on pastures and forest edges. The species can use temporary (seasonal) springs with flowing water during the breeding season. Outside the reproductive season, the species appears to colonise the canopy region of trees (Cisneros-Heredia & McDiarmid 2006, Catenazzi & Venegas 2012, Batallas-Revelo & Brito 2016, Guayasamin et al. 2020).

*Chimerella mira*: only known from the banks of the Río Patay Rondos (type locality), a medium-sized tributary of the Río Monzon, which in turn is part of the Huallaga River, province of Leoncio Prado, department of Huánuco, Perú (798 m asl). Lives in intermittently flooded marshland with small standing bodies of water, shrub vegetation and younger trees. ♂♂ were found on the upper sides of leaves about 0.5–2.5 m above the ground and called during light rain (Köhler et al. 2023).

## Conservation Status and Main Threats

### IUCN Red List Status

*Chimerella corleone*: DD (Data Deficient, assessed 2018-03-23)

*Chimerella mariaelenae*: LC (Least Concern, assessed 2018-02-06)

*Chimerella mira*: has not yet been assessed by the IUCN.

### Red List Status in the Range Countries

#### Ecuador

Lista Roja Anfibios del Ecuador (Ortega-Andrade *et. al.* 2021)

*Chimerella mariaelenae*: Near threatened (Casi amenazada Criterio B1b(iii)).



## Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local applications of pesticides, fertilisers and pollution, diseases, climate change and increased UV-B radiation.

*Chimerella corleone*: due to the continuing uncertainty about the size of the population, the ecological requirements and the threats, this species is listed with ‘insufficient data’. The threats to this species are therefore unknown. It is currently only known to occur within the boundaries of the Área de Conservación Regional Cordillera Escalera, which offers a certain degree of protection. Little is known about the population status of this species, but it appears to be locally rare. Although a large section of the stream was worked on 12 nights, animals could only be found near waterfalls. In addition, the lower part of this stream was extensively searched in 2004–2006 without the species being encountered there (Twomey et al. 2014).

*Chimerella mariaelenae*: categorised as not endangered because the species is widespread, it occurs in an area with extensive suitable habitat that does not appear to be significantly threatened, it can adapt to some extent to habitat changes and it has a presumably large population. When the species was described, it was considered rare, but further research has shown that it is locally common. A healthy subpopulation of this species occurs in the Cordillera Kampankis, Zona Reservada Santiago-Comaina, Perú, where 50 individuals were observed during a one-hour search in 2011 (Catenazzi & Venegas 2012).

*Chimerella mira*: Since the size of the population, the actual distribution area and thus potential threats are still unknown, the authors propose the IUCN status ‘Data Deficient’ (Köhler et al. 2023).

## Reproduction

| Topic                       | Details on the reproduction of <i>Chimerella</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|-----------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂: call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Calls                       | <p><i>C. corleone</i>: advertisement call consisting of a high-pitched tone pair (sometimes three tones), call duration 0.39 s, tone duration 0.013–0.020 s, call pauses 5–15 min, dominant frequency of the first tone 7,629 Hz and the second tone 7,425 Hz, the highest frequency known for this family (Twomey et al. 2014).</p> <p><i>C. mariaelenae</i>: The typical advertisement call is variable and ranges from a short to moderately long call (range 231–1,761 ms), usually two tones, but some calls can have up to 10 tones, each tone is extremely short at 4–7 ms and has a single amplitude peak. The dominant frequency measured at the amplitude peak is 6,718–8,010 Hz (Batallas-Revelo &amp; Brito 2016, Guayasamin et al. 2020).</p> <p><i>C. mira</i>: The calls consist of 2–3 high-frequency, pulsed tones with considerable amplitude modulation (‘trii’ calls sensu Duarte-Marín et al. 2022), usually 3–4 clearly separated pulses at the beginning of each note, followed by about 10–12 less clearly separated pulses (pulse rate ~ 200 pulses/s), tone length 42–85 ms, 160–239 ms interval duration between the tones within the calls, repetition rate about 1.5–1.9 calls/min, dominant frequency 5,543–6,135 Hz. The calls were emitted at somewhat irregular intervals and occurred in ‘waves’, with several ♂♂ calling almost synchronously (Köhler et al. 2023).</p> |

|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mating and spawning                               | <p>All species: Axillary amplexus in the vegetation above small forest streams.</p> <p><i>C. corleone</i>: The ♂♂ call from horizontal branches and the tops of broad-leaved herbs 2–4 metres above the ground. In captivity, one pair laid 18 pigmented eggs in a smoky, cloudy, viscous jelly on the lower edges of a leaf that was placed in the tank. Two other clutches corresponding to this species were found at a waterfall on the edges of the underside of a leaf, about 2 metres above the water surface. Eggs of the clutch had a pigmented animal pole; the vegetative pole is cream coloured (Twomey et al. 2014).</p> <p><i>C. mariaelena</i>: Unpigmented, white eggs in clear jelly were deposited on the upper surfaces of leaves, short-term maternal brood care occurred (Guayasamin et al. 2020).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Reproductive season                               | <i>C. mariaelena</i> : Reproductively active individuals were observed near the Cascada San Rafael in Quebrada Pangayacu in August 2012.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Eggs/clutch, clutches/year                        | <i>C. corleone</i> : see above at ‘Mating and spawning’.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Size of eggs and larvae at hatching               | No data in the literature.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Development time from egg laying to metamorphosis | Glass frog ♀♀ lay their eggs on substrates outside the water along streams, after several days or weeks (e.g. > 20 days) the embryos hatch and fall into the water where they complete their development (Cisneros-Heredia & McDiarmid 2007).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Details on the larvae                             | <p><i>C. mariaelena</i>: Description based on a specimen at Gosner stage 39, reared under laboratory conditions: Body elongate and oval compressed, wider than high, mouth region rounded in dorsal and lateral view, lateral line organ visible (several parallel dots perpendicular to the long axis of the body), short, single, left spiraculum posterolaterally on the body, cloacal tube short and abdominal, free opening directed posteriorly, tail long, with rounded tip, myotomes visible over the entire length of the tail, dorsal fin beginning approximately in the middle of the tail, ventral fin has its origin near the base of the caudal muscle, oral disc not enlarged and surrounded by 49 marginal, unilateral papillae (only ventral and lateral papillae present), upper and lower jaw sheaths almost straight and completely keratinised, with serrated edge, labial tooth row formula 2(1)(2)/3; gap in tooth row A1 could be artificial (due to tooth loss). Brownish dorsal colouration, area at the eye without pigmentation, reddish colouration on the anterior half of the (transparent) dorsum, anterior, outermost part of the head grey, iridophore clusters on the back along the spine, iris bronze-coloured (Terán-Valdez &amp; Guayasamin 2014).</p> |

## Husbandry and Captive Breeding X

As far as the author is aware, none of the *Chimerella* species has yet been kept in captivity.

***Cochranella* Taylor, 1951**

| Species                           | Original description                                     | Common name                                                             | Common name international | Known/ documented in international trade |
|-----------------------------------|----------------------------------------------------------|-------------------------------------------------------------------------|---------------------------|------------------------------------------|
| <i>Cochranella duidaeana</i>      | (Ayarzagüena, 1992)                                      | Duida Cochran Frog                                                      |                           | No                                       |
| <i>Cochranella erminea</i>        | Torres-Gastello, Suárez-Segovia & Cisneros-Heredia, 2007 |                                                                         |                           | No                                       |
| <i>Cochranella euhystrix</i>      | (Cadle & McDiarmid, 1990)                                | Ridge Cochran Frog                                                      |                           | No                                       |
| <i>Cochranella euknemos</i>       | (Savage & Starrett, 1967)                                | Fringe-Limbed Tree Frog, San Jose Cochran Frog, Slope Snouted Glassfrog |                           | No <sup>10,11</sup>                      |
| <i>Cochranella geijskesi</i>      | (Goin, 1966)                                             | Wilhelmina Cochran Frog                                                 |                           | No                                       |
| <i>Cochranella granulosa</i>      | (Taylor, 1949)                                           | Granular Glassfrog, Grains Cochran Frog                                 |                           | Yes                                      |
| <i>Cochranella guayasamini</i>    | Twomey, Delia & Castroviejo-Fisher, 2014                 |                                                                         |                           | No                                       |
| <i>Cochranella litoralis</i>      | (Ruiz-Carranza & Lynch, 1996b)                           | Litoral Glassfrog                                                       |                           | No                                       |
| <i>Cochranella mache</i>          | Guayasamin & Bonaccorso, 2004                            | Ecuadorian Blue Glass Frog, Mache Glassfrog                             | Rana de cristal de Mache  | No                                       |
| <i>Cochranella nola</i>           | Harvey, 1996                                             | Bell Glass Frog                                                         |                           | No                                       |
| <i>Cochranella ramirezi</i>       | Ruiz-Carranza & Lynch, 1991c                             | Ramirez's Cochran Frog                                                  |                           | No                                       |
| <i>Cochranella resplendens</i>    | (Lynch & Duellman, 1973)                                 | Resplendent Cochran Frog, Resplendent Glassfrog                         |                           | No                                       |
| <i>Cochranella riveroi</i>        | (Ayarzagüena, 1992)                                      | Rivero's Cochran Frog                                                   |                           | No                                       |
| <i>Cochranella xanthocheridia</i> | Ruiz-Carranza & Lynch, 1995b                             |                                                                         |                           | No                                       |

<sup>10</sup> an extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists two holders, El Valle Amphibian Conservation Center (Panama) and Baltimore Aquarium (USA, possibly not any longer), of *C. euknemos* up to 2010 (T. Eisenberg, unpublished data).

<sup>11</sup> According to our own experience, the species is currently not kept in private ex situ care.



Fig. 43: *Cochranella* species

- a *C. euknemos*, Costa Rica, picture taken at the Costa Rican Amphibian Research Center (CRARC) (T. Eisenberg)
- b *C. granulosa* from the surrounding of Golfito, Costa Rica (T. Eisenberg)
- c *C. granulosa*, underside, note the two clearly visible seminal ducts (Wolffian ducts) indicating male sex (T. Eisenberg)
- d *C. granulosa*, underside (T. Leenders)
- e *C. granulosa* from southwestern Costa Rica in a private reserve near Piedras Blancas National Park (T. Leenders)
- f *C. nola*, Bolivia (J. Köhler).

## Morphology and Taxonomy

The genus *Cochranella* was named in honour of Doris M. Cochran, former curator of the Smithsonian Institution, who focused her research mainly on the herpetofauna of the West Indies and South America, especially Brazil and Colombia. Phylogenetically, the genus represents the clade of the common lineage of the species *Centrolenella granulosa* Taylor 1949, *Centrolene litoralis* Ruiz-Carranza & Lynch 1996 and *Cochranella nola* Harvey 1996. The sister genus is uncertain in this case, at least according to the analysis of the combined mitochondrial dataset, the closest relationship with the genus *Espadarana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009 is supported. Members of the genus can be distinguished by the following characteristics: (1) conspicuous humeral spines absent in adult ♂♂ (small spine in *C. guayasamini*, *C. litoralis*), (2) digestive tract white (translucent in *C. duidaeana*, *C. erminea*, *C. euhystrix*, *C. guayasamini*, *C. nola*, *C. riveroi*), lobed liver covered by a translucent liver peritoneum, (3) a ventral parietal peritoneum, which is coloured white in the anterior region by iridophores, whereas the posterior region is transparent/translucent, (4) moderate to strong interdigital membranes between digits III and IV, (5) bones green in life, (6) dorsum lavender-coloured in preservative, with or without spots, (7) dentary processes of vomer and vomer denticles present (absent in *C. duidaeana*, *C. euhystrix*, *C. litoralis*), (8) the ♂♂ call from the upper side of leaves, the ♀♀ lay their eggs on the upper side of leaves above watercourses, (9) articulated connection between quadratojugal and maxillary bones. *Cochranella* differs from *Rulyrana* by a mostly white peritoneum (translucent in *Rulyrana*). Three species of *Centrolene* (*C. daidaleum*, *C. savagei* and *C. solitaria*) bear remarkable resemblance to some species of *Cochranella* (*C. mache*, *C. resplendens*); these *Centrolene* species differ mainly by a concentration of iridophores (similar to a line) separating the upper and lower flanks of the body (absent in *Cochranella*). They also occur in different biogeographical areas; all species of *Centrolene* are restricted to the tropical Andes, while *C. mache* and *C. resplendens* occur only in the lowlands ( $\leq 1000$  m asl). The monophyly of *Cochranella* is supported by ribosomal (12S, 16S), combined mitochondrial, combined nuclear data and complete datasets (Wägele 2005, Guayasamin et al. 2009).

Many species in this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unambiguous species identification):

*Cochranella duidaeana*: medium-sized glass frog with uniform green dorsal colouration, lip greenish yellowish, dorsal skin slightly granular with small spines, especially in the tympanum region, ventral skin areolate and cream-coloured, pericloacal region strongly tuberculated, forelegs with strong forearms without humeral spines, humeral folds and/or tubercles, thick fingers and toes, ulnar and tarsal tubercles absent, iris yellowish green, SVL ♂♂ 21.5–25.1 mm, ♀♀ unknown, mouth region rounded in dorsal view and slightly sloping in lateral view, eyelids blackish due to transparency of skin revealing dark eyeball, vomer teeth and dentary processes absent, tympanic membrane inconspicuous, anterior half of ventral parietal peritoneum white, pericardium white (but with transparent lower end), peritonea on viscera and trilobed liver transparent. Taxonomic note: The species has not yet been evaluated in any phylogenetic analysis. Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (Guayasamin et al. 2009, 2020).

*Cochranella erminea*: small to medium sized glass frog with blue to olive green dorsal colouration, with abundant enamelled (bright white) spots on flat tubercles and scattered larger dark blue spots on the tubercles, upper lip bright white, ends of finger and toe tips yellow, dorsal skin chagrined with numerous small and scattered large tubercles, pericloacal region



with abundant white shiny tubercles (granular skin), pair of subcloacal tubercles absent, low row of enamelled tubercles on ulna and outer tarsus, extensive interdigital membranes between fingers III and IV, iris light to slate grey with fine dark grey reticulated lines (pinkish reddish in northern Perú), SVL ♂♂ unknown, ♀ 23.6 mm (n=1), mouth region slightly sloping anteroventrally in profile, rounded in dorsal view, tympanic membrane ovoid, inclined dorsally to dorsolaterally, tympanic ring distinct, supratympanic fold weak, anterior half of ventral parietal peritoneum white, pericardium white, peritonea on digestive tract, gall bladder, urinary bladder, kidneys and trilobed liver transparent. Similar species: Based on the three combined main features presence of extensive interdigital membranes between digits III and IV, absence of white pigment on the visceral peritonea and a characteristic dorsal colouration with a combination of abundant enamelled spots and few dark dorsal spots, the species can be distinguished from the following species: *Centrolene muelleri*, *C. duidaeana*, *C. euhystrix*, *C. geijskesi*, *C. guayasamini* (sister taxon), *C. nola*, *C. riveroi*, *C. xanthocheridia*, *Espadarana prosoblepon*, *Nymphargus megistus*, *Nymphargus mixomaculatus*, *Rulyrana adiazeta*, *Rulyrana flavopunctata*, *Rulyrana saxiscandens*, *Rulyrana spiculata*, *Rulyrana susatamai*, *Sachatamia albomaculata*, *Sachatamia orejuela*, *Sachatamia punctulata*, *Teratohyla spinosa* (Torres-Gastello et al. 2007, Guayasamin et al. 2009, Twomey et al. 2014, Frost 2024).

*Cochranella euhystrix*: large glass frog with dark greenish black colouring at night and dark green to brownish dorsal colouring during the day, with lighter green spines on the head (especially eyelids and lips), back and limbs in ♂♂, which are lighter than the dorsal ground colour and give the back a finely spotted appearance (♀♀ much smoother), fingers and toes greenish yellow, dorsal skin spiny in ♂♂, smoother in ♀♀, ventral side greenish with yellow spots on the anterior ventral region, a pair of tubercles ventral to the cloacal opening, ulnar and tarsal folds absent, interdigital membranes pronounced, toe discs dilated, iris grey with fine black irregular reticulations, SVL ♂♂ 28.5–31.3 mm, ♀♀ 31.1–33.6 mm, head wider than body and wider than long, mouth region slightly truncated in profile (slightly rounded in some ♀♀), truncated in dorsal view, vomer teeth and dentary processes absent, tympanic membrane distinct, two-thirds completely visible, dorsomedially inclined, posterolaterally directed, usually smooth or with low spine, anterior half of ventral parietal peritoneum white, pericardium white, peritonea on digestive tract and liver transparent. Taxonomic note: The species has not yet been evaluated in any phylogenetic analysis. Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (Cadle & McDiarmid 1990, Guayasamin et al. 2009).

*Cochranella euknemos*: medium-sized to large glass frog with deep blue-green dorsal colouration with many raised, medium-sized yellowish white tubercles, ivory-coloured white margin along the lip, arm and leg margins, ventral side pale yellowish white, distinct fleshy margin along the posteroventral margin, running from the elbow to finger disc IV, undersides of palms and fingers smooth, with lateral fleshy margins, extensive interdigital membranes between fingers III and IV and on all toes, hind limbs long, also with a distinct fleshy margin posteroventrally from the heel to toe disc V, belly and undersides of thighs strongly granulated, below the cloaca distinct fringe-like ridge with two raised nodules and a row of small nodules (white subcloacal ornaments), iris ivory-coloured with very fine network, SVL ♂♂ 21–25 mm, ♀♀ 25–32 mm, mouth region long, rounded in dorsal view, strongly truncated in profile, eyes relatively small, eardrum round, laterally directed, anterior half of ventral parietal peritoneum white, pericardium and digestive tract white, liver peritoneum transparent. Similar species: *C.*

*granulosa*, *Sachatamia albomaculata*, *Teratohyla pulverata* (Savage & Starrett 1967, Savage 2002, Kubicki 2007).

*Cochranella geijskesi*: medium-sized to large glass frog with uniform dark green dorsal colouration, no tarsal crest, no skin appendage on the heel, interdigital membranes between fingers III and IV and toes almost fully developed, iris golden with grey reticulations, SVL 36.1 mm (sex unknown), mouth region rounded in dorsal view, eyes large, eardrum moderately pronounced, about half the diameter of the eye. Similar species: *Espadarana prosoblepon*. Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (Goin 1966, Ouboter & Jairam 2012, Guayasamin et al. 2009).

*Cochranella granulosa*: large glass frog with deep dark green to blue-green dorsal colouration, with yellowish or bluish granules (without spines) and faint to distinct blue to black spots in many individuals/populations, yellowish green hands and feet, abdominal skin areolate, without a pair of enlarged subcloacal tubercles, pale or whitish lip in populations from Central America, ulnar fold low, inner and outer tarsal folds low and thin, extensive interdigital membranes between fingers III and IV and all toes, iris yellow to golden coloured with few, faint brownish stripes, SVL ♂♂ 22.5–29.0 mm, ♀♀ 29–32 mm, mouth region truncated in dorsal view, slightly sloping in lateral profile, eardrum dorsolaterally aligned, with slight inclination to the rear, tympanic ring visible, low supratympanic fold, slightly less than the anterior half of the ventral parietal peritoneum white, liver tetralobed, liver peritoneum without iridophores, peritoneum of the digestive tract with white iridophores. Similar species: *C. litoralis*, *C. euknemos*, *Teratohyla spinosa*, *Espadarana prosoblepon* (some populations). Taxonomic note: Type species of the genus *Cochranella* (Savage 2002, Kubicki 2007, Guayasamin et al. 2020).

*Cochranella guayasamini*: medium-sized glass frog with dorsal and dorsolateral green colouration with yellow tones and tiny melanophores (absent in the upper lip), upper lip margin white (enamelled), hands and feet yellowish green with yellowish fingers and toes (without melanophores), eyelid margins bright yellow, ventral surfaces yellow-green, dorsal skin and that of the flanks smooth, skin on abdomen and thighs coarsely areolate, remaining abdominal surfaces smooth, cloacal ornamentation of folded skin with small, non-enamelled tubercles and two paired round tubercles, folds on limbs absent, extensive interdigital membranes between fingers III and IV and all toes, adult ♂♂ with small humeral spines, iris reddish bronze with black reticulation, black or grey spots and a black ring bordering the iris, yellow pupil ring absent, SVL ♂♂ 22.5–24.5 mm, ♀♀ unknown, mouth region rounded in dorsal view, rounded and slightly inclined in profile, tympanic membrane visible, not covered by skin, laterally slightly inclined dorsally, tympanic ring low, no supratympanic fold, anterior half of ventral parietal peritoneum white, peritonea of stomach, intestine, trilobed liver, kidney and gonads mostly transparent, but with some small and isolated traces of iridophores. Similar species: *Nymphargus balionotus*, *Nymphargus chancas*, *Espadarana durrellorum* (Twomey et al. 2014).

*Cochranella litoralis*: small glass frog with pale yellow-green dorsal colouration, with small grey to black dots and faint yellow to cream dorsolateral stripes, dorsal skin smooth in anterior region, chagrined in sacral region, without spines, no pair of enlarged subcloacal tubercles, ulnar and tarsal folds absent or low and inconspicuous, without white colouration, moderate interdigital membranes between fingers III and IV and all toes, adult ♂♂ with small pointed humeral spines, iris bright orange to red, SVL ♂♂ 19.4–20.0 mm, ♀♀ unknown, mouth region blunted in dorsal and lateral view, no teeth on the vomer, eardrum of moderate size, almost

vertically orientated, eardrum ring mostly visible, supratympanic fold covers posterodorsal margin, anterior half of ventral parietal peritoneum white, iridophores in pericardium and gastrointestinal peritoneum, no iridophores on lobed liver, testis, gall bladder, urinary bladder and kidneys. Similar species: *C. guayasamini*, *Espadarana prosoblepon*, *Nymphargus griffithsi* (Guayasamin et al. 2020).

*Cochranella mache*: medium-sized to large glass frog with dark olive-green to lavender-blue or pale blue dorsal colouration and small yellow to orange spots, large dull to bright yellow spot on top of head, upper lip with thin white border, white tubercles visible on skin folds of hind and fore extremities, dorsal skin chagrined with tubercles, corresponding to the pale spots, ♂♂ with numerous tiny spines, abdominal skin granular, several round enamelled tubercles around the cloaca, cloacal fold and a pair of enlarged subcloacal tubercles present, ventrolateral margins of finger IV, forearm, elbow, toe V, tarsus and heel with dermal enamelled folds and bumps, inner fingers and toes white or unpigmented, extensive interdigital membranes between fingers III and IV and all toes, iris whitish cream to beige with thin brown reticulation, white to golden ring around pupil, SVL ♂♂ 22.0–27.0 mm, ♀♀ 28.0–33.4 mm, mouth region slightly pointed in dorsal view, gradually bevelled in lateral view, eardrum almost vertically aligned, slightly laterally and posteriorly inclined, low supratympanic fold visible, anterior third of ventral parietal peritoneum white, iridophores in peritoneum of pericardium, gastrointestinal tract and gonads as well as kidney capsules (in some individuals), peritoneum of tri- or tetralobulated liver transparent or with small, isolated spots due to iridophores. Similar species: *Centrolene daidalea*, *Centrolene savagei*, *Centrolene solitaria*, *Cochranella resplendens*, *Cochranella euknemos*. Taxonomic note: The species is very similar to *C. euknemos* (sister species) and further taxonomic studies are needed to define the limits (Guayasamin & Bonaccorso 2004, Cisneros-Heredia et al. 2008a, Guayasamin et al. 2020).

*Cochranella nola*: small to medium sized glass frog with uniform light green dorsal colouration, eyelids, upper lip and flanks white, dorsal skin granular with numerous spines of equal size, skin on hands and feet smooth, ventral skin and ventral surfaces of thighs areolate, without paired enlarged subcloacal tubercles or para- and subcloacal folds, arms short, circumference of the upper arm about half that of the forearm, ulnar fold and tubercles absent, skin ridges and tarsal tubercles absent, short tarsal fold present, fingers green, in some individuals with a red spot on the fingers, extensive interdigital membranes between fingers III and IV and all toes, eyes large, iris pale grey with fine black reticulation, SVL ♂♂ 20.7–21.1 mm, ♀♀ 24.4–25.7 mm, head wider than body, mouth region truncated in dorsal and lateral view, eardrum small, anterior half of ventral parietal peritoneum white, heart, trilobulated liver and stomach not visible through the skin, viscera yellowish. Similar species: *Rulyrana spiculata*, *Rulyrana saxiscandens*, *Teratohyla midas* (Harvey 1996, Köhler 2000, Lötters & Köhler 2000).

*Cochranella ramirezi*: medium-sized glass frog with pale green to pale greenish yellow dorsal colouration and a net-like pattern of cream-coloured spots, dorsal skin granular with larger bumps that coincide with the cream-coloured spots, no skin folds on the forearms or tarsals, SVL ♂♂ 25.6–27.4 mm, ♀ 27.4 mm (n=1), head as wide as body and wider than long, mouth region rounded in dorsal and lateral view, tympanic membrane small, anterior half of ventral parietal peritoneum white, stomach and viscera not visible through skin. Taxonomic note: Ruíz-Carranza & Lynch 1991c and Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (AmphibiaWeb 2023).

*Cochranella resplendens*: medium to large sized glass frog with dark green dorsal colouration with numerous small white to bluish white spots, upper lip, bumps on forearm and foot and warts on cloaca white, dorsal skin chagrined with raised and needle-shaped warts corresponding to the white spots, ventral skin granular, a pair of slightly enlarged subcloacal warts and an enlarged cloacal fold present, ventrolateral margins of finger IV, forearm, elbow, toe V, tarsus and heel with skin folds and enamelled bumps, extensive interdigital membranes between fingers III and IV and all toes, iris whitish cream to beige, with fine grey to brown reticulation; pale yellow ring around the pupil, SVL ♂♂ 26.5–26.6 mm, ♀♀ unknown, mouth region round when viewed dorsally and slightly sloping in lateral profile, eardrum almost vertical with slight lateral and posterior inclination, tympanic ring partially visible, low supratympanic fold visible, anterior three quarters of the ventral parietal peritoneum white, iridophores in the pericardium and peritoneum covering the viscera and stomach, liver, kidney capsules, gall bladder and urinary bladder without iridophores. Similar species: *C. mache*, *C. granulosa* (sister species), *Centrolene daidalea*, *Centrolene savagei*, *Centrolene solitaria*. Taxonomic note: *C. phryxa* has been synonymised with *C. resplendens* (Lynch & Duellman 1973, Ruiz-Carranza et al. 1996, Cisneros-Heredia & McDiarmid 2005, Guayasamin et al. 2020).

*Cochranella riveroi*: small to medium sized glass frog with unknown dorsal colouration in life (in alcohol with a pink or purple uniform shade), dorsal skin texture strongly granular with small spines (in the ♂♂ the density is greater than in ♀♀), throat, chest and ventral surfaces of the arms with smooth skin, ulnar and tarsal folds and tubercles absent, pericloacal region strongly tuberculate with a pair of larger tubercles, SVL ♂♂ 21.6–22.1 mm, ♀ 25.0 mm (n=1), head slightly wider than body and wider than long, mouth region rounded in dorsal view, oblique in lateral view, eyes large, anterolaterally directed, tympanic membrane, especially in lower part rounded and dorsolaterally directed, anterior two thirds of ventral parietal peritoneum and pericardium white, peritonea covering viscera and four-lobed liver, without iridophores. Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (Ayarzagüena 1992, Señaris & Ayarzagüena 2005, Guayasamin et al. 2009).

*Cochranella xanthocheridia*: medium-sized glass frog with dark green dorsal colouration, dorsal skin texture finely granulated, tarsal and ulnar folds absent, SVL ♂♂ 22.7–24.4 mm, ♀♀ unknown, head slightly wider than body, mouth region slightly ovoid in dorsal view, truncated in lateral view, anterior half of ventral parietal peritoneum and pericardium white. Similar species: *Rulyrana susatamai*. Guayasamin et al. (2009) consider this taxon as incertae sedis within the genus *Cochranella* sensu lato until more data are available (Ruiz-Carranza & Lynch 1995b, Guayasamin et al. 2009).

### Distribution and Habitat

The genus *Cochranella* is found in the lowlands and mountains at altitudes below 1,750 m in Central America (*C. granulosa*, *C. euknemos*), in the Pacific lowlands and cloud forests of Colombia (*C. euknemos*, *C. litoralis*, *C. mache*, *C. ramirezi*, *C. xanthocheridia*) and Ecuador (*C. litoralis*, *C. mache*), in Venezuela (*C. duidaeana*, *C. riveroi*) or in the Guiana Shield region (*C. geijskesi*), on the Amazonian slopes of the Andes of Bolivia (*C. nola*), in the Amazon lowlands of Ecuador (*C. resplendens*), Perú (*C. erminea*, *C. euhystrix*, *C. guayasamini*, *C. nola*, *C. resplendens*), Brazil and Bolivia (*C. resplendens*) (Guayasamin et al. 2009).

*Cochranella duidaeana*: This species is only known from its type locality on the southern part of the Cerro Duida peak in the state of Amazonas in Venezuela. Cerro Duida is one of the

largest sandstone plateaus in the Guiana Shield, with a concave 1,000 km<sup>2</sup> peak which slopes from south (2,358 m asl) to north (500–800 m asl). It is mainly drained by the Caño Negro, a stream that flows into the Cunucunuma River near the northern flank of the plateau. Cerro Duida is part of the Duida-Marahuaca massif, a large complex of quartzites and sandstones belonging to the Roraima group, in the central-eastern part of the state of Amazonas (2,140 m asl). The known locality of this species is located in the higher elevations of Cerro Duida in an undisturbed, remote area. The specimens were found at night among branches and leaves of bushes of the genera *Gongylolepis* sp. (Asteraceae), *Stenopadus* sp. (Asteraceae) and *Retiniphyllum* sp. (Rubiaceae) in the dense foliage along a small stream that originates from the runoff of the neighbouring peat bogs (Ayarzagüena 1992, Señaris & Ayarzagüena 2005).

*Cochranella erminea*: widespread in the eastern Andes of Peru, occurring from about 5–12° southern latitude in the regions of Cusco, Junín, San Martín and Amazonas in Perú. However, the species seems to be only patchily distributed within this region; despite frequent searches in this area, it has not been recorded from the mountains around Tarapoto (349–923 m asl). The species inhabits a variety of habitats, ranging from primary premontane forests to relatively disturbed, low-lying foothill forests. The area around the type locality has been little affected by humans and is covered with primary lowland forest, dominated by dense or semi-dense forest with bamboo patches. Habitat strongly linked to streams, on vegetation by waterfalls or next to streams at a height of up to 1.8 metres above the ground. The species can also use temporary (seasonal) water sources during the breeding season. Outside the breeding season, it appears to stay in the treetops (Torres-Gastello et al. 2007, Rodríguez Mercado 2012, Twomey et al. 2014).

*Cochranella euhystrix*: currently known only from the type locality, near Chorro Blanco, 2.5–4.5 km north-east of Monte Seco, watershed of the Río Zaña, Cajamarca region, Perú (1,800–2,650 m asl). Habitat: montane tropical forests, individuals were mainly found on vertical rock faces in the splash zones of waterfalls, on rock ledges (upper and lower surfaces) in or around waterfalls and on wet boulders covered with liverwort and moss in the centre of the river. Many individuals were found on outcrops in 6–8 m high waterfalls. Breeding was only observed in permanent streams at high altitudes. As all individuals were on rock faces in or near waterfalls and no clutches were found on vegetation, the authors assume that these are usually laid on rocks (Cadle & McDiarmid 1990).

*Cochranella euknemos*: known from scattered localities from central Costa Rica and Panama to western Colombia (Departamentos Chocó, Antioquia and Risaralda). Some records from the Colombian departments of Antioquia and Chocó have been assigned to *C. mache*; records from the Colombian department of Risaralda are considered uncertain in this assessment until they can perhaps be assigned to another species (90–1,650 m asl). Habitat in humid lowland, foothill and mountain forests, restricted to wooded streams, in bushes and trees along forest streams, drainage ditches or drying stream beds (Kubicki 2007, Jaramillo-Martinez et al. 2015).

*Cochranella geijskesi*: for a long time only known from the type locality on the southern slope of the Wilhelmina Mountains in Suriname. Meanwhile, the species is also distributed from the Raleigh Valley, the Sipaliwini Nature Reserve and the Mitaraka Massif in southern Suriname as well as in southern French Guiana, probably also in neighbouring Amapá, Brazil (about 200 m asl). The type locality is in primary forest (Fouquet et al. 2015, 2019, Lescure et al. 2022).

*Cochranella granulosa*: Humid lowland and premontane slopes of the Atlantic Cordillera from eastern Honduras to central Panama and on the Pacific side from northern Costa Rica to south-



west Panama and neighbouring Chocó, Colombia, apparently also isolated record from the private reserve El Jardín de los Sueños, Cotopaxi, Ecuador (40–1,500 m asl). Habitat in humid lowland, gallery and mountain forests. The species normally feeds on arthropods in the vegetation, but has also been found foraging on the ground (Savage 2002, Kubicki 2007, Zumbado-Ulate & Acosta-Chaves 2012, Guayasamin et al. 2020).

*Cochranella guayasamini*: known from the San Martín and Amazonas regions of Perú. Before 2011, this species was only known from northern San Martín, but a record from the Cordillera de Campanquis in the Amazonas region extended its known range from the original locality by 400 km to the north-west (250–1,150 m asl). The species is found in a variety of habitat types, including heavily disturbed areas and even primary forests. The highest density is found at 1,120 m asl near Abra Tangara in a stream flowing through a cattle pasture with low bushes at the edges (Twomey et al. 2014).

*Cochranella litoralis*: known only from a few localities in the south-west of Colombia (Departamentos Cauca and Nariño) to the centre-west of Ecuador (Province of Esmeraldas, Santo Domingo de los Tsáchilas and Los Ríos). The locality in Cauca requires confirmation. Altitudinal distribution 100–220 m asl. The species occurs in tropical lowland rainforests of the Pacific. It has also been found in secondary forests during afforestation. The Ecuadorian specimens were found in primary forests away from streams. The species reproduces explosively after heavy rainfall (IUCN SSC Amphibian Specialist Group 2019b).

*Cochranella mache*: initially only known from the Cordillera Mache-Chindul in the province of Esmeraldas, Ecuador. However, new information has extended its range to the north-west of Colombia, based on the re-identification of specimens from Colombia and new distribution records. The species is now known from western Colombia to north-western Ecuador and is thus endemic to the evergreen forests of the Chocó region. The newly documented locations in Colombia include the municipalities of Dabeiba and Frontino in the department of Antioquia and Buenaventura in the department of Valle del Cauca (40–1,030 m asl). Habitat in the tropical rainforests of the lowlands and foothills, individual specimens have been found at night on vegetation at a height of 1–1.6 m above the ground near streams in primary and old secondary forests, in Colombia also in Andean forests. The species seems to be restricted to small streams and rivulets in primary and secondary forests in lowland and foothill forests. Although individuals have been observed in different forest layers up to a height of 6 m, *C. mache* prefers the vegetation in the mid-altitude.

*Cochranella nola*: known from the provinces of Florida and Ichilo in the department of Santa Cruz, the departments of La Paz and Cochabamba in Bolivia and from the Bahuaja Sonene National Park (Puno region), the Amarakaeri Communal Reserve (Madre de Dios region) and Kosñipata, Cusco, in southern Perú in the buffer zone of the Manu National Park. The recoveries from La Paz and Cochabamba and all records from Perú represent a significant expansion of the distribution area since the last assessment (500–1,750 m asl). Habitat near streams in humid montane and premontane forests, especially in the forests of the Amazon region, in semi-humid montane forests and in the forests of the Yungas. A multiple opening of the mouth of an individual in the evening hours described by Arrivillaga (2019) does not seem to represent a threatening behaviour as assumed in the publication, but is more reminiscent of the initiation of the evening moulting process (T. Eisenberg, own observation; Harvey 1996, Köhler 2000, Lötters & Köhler 2000).

*Cochranella ramirezi*: known from several localities in the departments of Antioquia (Parque Nacional Natural Las Orquídeas) and Chocó (Opogado, Jurado and Bahía Solano) on the western flank of the western Andes in Colombia. Now also described from the Quebrada Oscurana in the department of Córdoba. In view of its occurrence in the immediate vicinity of the border with Panama, it is possible that it also occurs in Panama (20–855 m asl). Habitat in lowland rainforests in the vegetation along streams. This species is restricted to streams with heavy forest cover.

*Cochranella resplendens*: known from the Amazon basin of Colombia, Ecuador, Perú and Bolivia. A disjunct population of the species was recently found on the eastern slope of the central Andes in the department of Antioquia, Colombia, at much higher altitudes. In Ecuador, the species has been recorded from localities in the provinces of Morona Santiago, Napo, Orellana, Pastaza and Sucumbíos; in Ecuador, the potential distribution area is 77,793 km<sup>2</sup> within the ecoregions of Amazonian tropical rainforest and eastern foothill forest (190–1,100 m [other occurrences], 1,309–1,699 m [Andean Colombia] asl). Last record also from Amapá, Brazil. Habitat in tropical primary and secondary rainforests in the lowlands and in the pre-montane zone as well as in sub-Andean forests near streams. The species has not been found in modified habitats and can use temporary (seasonal) water sources during the breeding season. Outside the breeding season, the species appears to inhabit the forest canopy (Lynch & Duellman 1973, Ruiz-Carranza et al. 1996, Cisneros-Heredia & McDiarmid 2005, Twomey et al. 2014, Guayasamin et al. 2020, Costa-Campos et al. 2020).

*Cochranella riveroi*: known only from its type locality on the summit of Cerro Aracamuni in the state of Amazonas in Venezuela. It seems possible that it also occurs in the neighbouring Cerro Avispa, but this has yet to be confirmed. Cerro Aracamuni and Cerro Avispa are granite mountains in the northern part of the Neblina massif with a combined slope area estimated at 658 km<sup>2</sup> and a combined summit area ( $\geq 1,500$  m asl) of 238 km<sup>2</sup> (1,600 m asl). The summit of Aracamuni is mostly covered by dense meadows on peaty soils and low shrub vegetation, with small areas of forest in the hollows along the streams. The meadows are mainly characterised by *Stegolepis* spp. (Rapateaceae), Eriocaulaceae, Bromeliaceae, Xyridaceae, Liliaceae and Sarracenaceae. The only known specimens of this species were found in terrestrial bromeliads. A photographic record also indicates that it lays its clutches in bromeliad leaves (a very unusual place for centrolenid reproduction [cf. *Centrolene buckleyi*]), where they are guarded by one of the parents (Ayarzagüena 1992, Señaris & Ayarzagüena 2005).

*Cochranella xanthocheridia*: this endemic species in Colombia was previously only known from the Departamentos Risaralda and Antioquia on the western flank of the Cordillera Occidental. It has now also been recorded in the Municipio de Tierra Alta, Departamento Córdoba, in the northern part of the Cordillera Occidental (480–2,060 m asl). Habitat in the vegetation next to streams in sub-Andean and Andean forests. The species has not been recorded outside of forests (Ruiz-Carranza & Lynch 1995b, Romero-Martínez et al. 2008).

## Conservation Status and Main Threats

### IUCN Red List Status

*Cochranella duidaeana*: VU (Vulnerable, D2, assessed 2019-09-30)

*Cochranella erminea*: LC (Least Concern, assessed 2017-04-20)

*Cochranella euhystrix*: CR (Critically Endangered, B1ab(iii), assessed 2018-03-30)

*Cochranella euknemos*: LC (Least Concern, assessed 2019-09-11)  
*Cochranella geijskesi*: LC (Least Concern, assessed 2017-11-15)  
*Cochranella granulosa*: LC (Least Concern, assessed 2019-09-04)  
*Cochranella guayasamini*: LC (Least Concern, assessed 2018-03-23)  
*Cochranella litoralis*: VU (Vulnerable, B1ab(iii), assessed 2018-12-14)  
*Cochranella mache*: NT (Near Threatened, A4ac, assessed 2017-02-27)  
*Cochranella nola*: LC (Least Concern, assessed 2019-09-24)  
*Cochranella ramirezi*: NT (Near Threatened, B1ab(iii), assessed 2019-01-15)  
*Cochranella resplendens*: LC (Least Concern, assessed 2017-04-19)  
*Cochranella riveroi*: VU (Vulnerable, D2, assessed 2019-09-28)  
*Cochranella xanthocheridia*: VU (Vulnerable, B1ab(iii), assessed 2017-02-27).

### Red List Status in the Range Countries

#### Ecuador

*Cochranella mache*: It is categorised as critically endangered on Ecuador's national Red List (Cisneros-Heredia et al. 2010, Ortega-Andrade et al. 2013, Guayasamin et al. 2020).

#### Perú

*Cochranella euhystrix*: Im Libro Rojo de la Fauna Silvestre Amenazada del Perú als CR – En Peligro Critico eingestuft (SERFOR 2018).

#### Venezuela

*Cochranella riveroi*: The species is listed as NT (Near Threatened) in the most recent Red List of the Venezuelan fauna ([http://wikieva.org.ve/index.php/Cochranella\\_riveroi](http://wikieva.org.ve/index.php/Cochranella_riveroi)).

### Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local spraying of pesticides, fertilisers and pollution, disease, climate change and increased UV-B radiation.

*Cochranella duidaeana*: categorised as vulnerable as its estimated range is only 117 km<sup>2</sup> despite intensive exploration in the Duida-Marahuaca massif and the species is only known from a single location on the summit of Cerro Duida. Longer and more frequent droughts, extreme temperatures and habitat degradation due to climate change could lead to this species reaching the status of 'threatened with extinction' or 'extinct in the wild' within a very short time. Like most amphibian taxa in Pantepui, this species is likely to be threatened by stochastic events such as drought and temperature extremes. Altitudinal Range Shift (ARS) and Species-Area Relationship (SAR) models predict that in a scenario with a 4°C temperature increase by the end of 2100, around 25% of the endemic vascular plants and 98% of the summit habitat on Cerro Duida will be lost. This means that a significant part of this species' habitat could disappear within the next 80 years. In addition, viruses, bacteria and fungi as pathogens pose

a potential threat to this species. No further information is available on past or current population sizes or trends (Nogué et al. 2009, Vegas-Vilarrúbia et al. 2012, Señaris & Rojas-Runjaic 2019).

*Cochranella erminea*: due to its relatively wide distribution, tolerance to a certain degree of habitat modification and a presumably large population, the species is not classified as endangered (Torres-Gastello et al. 2007, Rodríguez Mercado 2012, Twomey et al. 2014).

*Cochranella euhystrix*: categorised as critically endangered due to its distribution in an area of only 75 km<sup>2</sup>, as it only occurs in a single location classified as endangered and the area and quality of its habitat in the Cajamarca region in the northern Peruvian Andes is in continuous decline. The type locality is located on an abandoned logging road. In the region, there is destruction and loss of habitat for livestock farming and through selective logging. Based on satellite imagery of the type area and surrounding area in 2017, severe habitat loss and fragmentation is evident outside the protected area, and forest loss is also visible within the boundaries. Little information is available on the population size and development of this species. During intensive field surveys in 2006–2007, no individuals were discovered on 74 search days. No individuals were recorded during extensive surveys in El Refugio de Vida Silvestre Bosques Nublados de Udimá in 2010 and 2011 either. Due to the continuing decline in the extent and quality of the habitat, it is assumed that the population is in decline (Cadle & McDiarmid 1990, von May et al. 2008).

*Cochranella euknemos*: not categorised as least concern in view of its wide distribution and presumably large population. In Panama, the species is generally threatened by habitat loss, but over all there are no major threats. Declines were observed at certain sites in Panama in 2007 following the detection of *Bd* in 2006; thus, chytridiomycosis may be a problem for this species. The causes of the apparent historical decline in Costa Rica are not known. Some logging activities were documented at one of the sites on the north-eastern slope of Volcán Turriabla in 2011, but these have probably since ceased. The species is considered rare in Costa Rica and has not been recorded in the country since a single individual was observed in the Barva transect in 1986. In 2011, three subpopulations were discovered on the northern and eastern slopes of Volcán Turriabla in Costa Rica. The species was last recorded near Volcán Turriabla in 2013, as only a few surveys have been carried out in this area recently, partly due to difficult access. As of 2019, the species was no longer recorded during numerous visits to the type locality. In Panama, this species has a patchy distribution and is considered rare. In Colombia, the species is relatively common. Declining population trend (Kubicki 2007, Woodhams et al. 2008).

*Cochranella geijskesi*: classified as not endangered because, although its range is only 2,144 km<sup>2</sup>, there are no current threats and it occurs in an area that is both isolated and protected.

*Cochranella granulosa*: due to its wide distribution, its tolerance to a certain degree of habitat modification and its presumably large population, this species is not categorised as endangered. It can occur in suitable, even modified habitats (with some trees remaining) and is usually found in bushes and trees along forest streams. The species is threatened by both severe habitat loss due to deforestation (from urban expansion, agriculture and logging) and water pollution. Due to the continuing decline in the extent and quality of the habitat, the population is thought to be in decline.

*Cochranella guayasamini*: categorised as not endangered because, although the species' range is 9,231 km<sup>2</sup>, it occurs in an area with extensive suitable habitat that does not appear

to be significantly threatened, it can adapt to habitat disturbance and there is probably a large, stable population.

*Cochranella litoralis*: categorised as vulnerable because its distribution is 7,161 km<sup>2</sup>, the species occurs in only about six sites classified as threatened, the population is highly fragmented and the extent and quality of its habitat in the Colombian and Ecuadorian Andes is continuously declining, mainly due to deforestation for agricultural expansion and logging activities. It is probably not tolerant of changes or disturbances in its habitat and is apparently rare, but this is probably also due to its arboreal lifestyle and reproductive habits (explosive reproduction). In 2015, surveys in the immediate vicinity of the type locality in the department of Nariño, Colombia, revealed large populations of this species. Due to the continuing decline in the extent and quality of the habitat, it is assumed that the population is in decline.

*Cochranella mache*: A population decline of approximately 30% over a 10-year period (2015–2025) has been observed and projected, due to ongoing habitat conversion and habitat degradation in its range, so the species is categorised as near threatened under criterion A4. It has not been found in recent secondary forests, small isolated patches of forest or in agricultural or suburban areas and is therefore considered sensitive to habitat disturbance. Deforestation in western Ecuador is extensive and the remaining forests are highly fragmented. Habitat destruction is mainly caused by unsustainable logging, uncontrolled expansion of agricultural land and replacement by non-native plantations. Probable threats to the species in Antioquia are habitat loss due to mining and deforestation. The species appears to be rare throughout its range, even in well-preserved areas, although this could be due to the fact that the species lives in the forest canopy and is difficult to locate there, or that it is affected by a gradual population decline. In Colombia, the species is only known from six specimens. It is assumed that the population is highly fragmented and the distances between the subpopulations are considered too great for dispersal within one generation. The population is also in decline (Cisneros-Heredia et al. 2010, Ortega-Andrade et al. 2013, Guayasamin et al. 2020).

*Cochranella nola*: not categorised as endangered in view of its wide distribution and presumably large population. The species does not occur in open or cultivated areas, but it has been found in forests that were once selectively logged and are now regenerating. Deforestation and illegal gold mining are the biggest threats to the species, destroying and degrading its riverine habitat. The start of gold mining in Peru's Amaraeri Communal Reserve in 2014 could pose a threat, but satellite images show that management efforts have curbed further expansion within the protected area. Throughout its range, localised habitat loss is occurring due to livestock farming, agriculture, logging, hydropower exploitation and water abstraction for agriculture and domestic use. Water pollution from agriculture is another problem. Under suitable environmental conditions, the species is easy to observe and is locally abundant. However, due to the continuing decline in the extent and quality of the habitat, it is suspected that the population is in decline (Köhler 2000).

*Cochranella ramirezi*: categorised as near threatened, as the population is 26,318 km<sup>2</sup>, the species occurs in about 10 locations classified as threatened and the extent and quality of its forest habitat in Colombia is continuously declining. The main threats are deforestation and habitat degradation due to agricultural development (including the cultivation of illegal crops), logging, human settlements and agrochemical pollution. It is a rare species and not much is known about its population status. Due to the continuing decline in the extent and quality of the habitat, the population is thought to be in decline.



*Cochranella resplendens*: due to its wide distribution, presumably large population and occurrence in an area with extensive remaining suitable habitats, the species is categorised as not threatened. It is threatened by habitat fragmentation and habitat loss due to the expansion of agriculture (including the planting of illegal crops), deforestation and water pollution. *C. resplendens* is a rare species. Since its description in 1973, only eight other specimens have been reported. The rarity is not due to insufficient sampling effort, as exactly 7,765 specimens of amphibians and reptiles were collected at the type locality (Santa Cecilia) during fieldwork from 1967–1972, but no additional specimens of this species. However, detailed examinations of the tree crowns could reveal that the species is more common in small areas. It is not known from any protected area and the status in Ecuador is ‘insufficient data’ (Guayasamin et al. 2020).

*Cochranella riveroi*: categorised as vulnerable because its distribution is only 109 km<sup>2</sup>, the species is only known from a single location on the summit of Cerro Aracamuni and this distribution is at risk due to habitat loss and deterioration of living conditions caused by climate change. Longer and more frequent periods of drought, temperature extremes and habitat degradation due to climate change could lead to the extinction of this species within a very short time. Furthermore, if mining activities in neighbouring regions were to expand into its range, this species would have to be placed on the endangered species list immediately. Like most amphibian taxa in the Pantepui, this species is also endangered by stochastic threat processes such as extreme temperatures and droughts caused by climate change. Altitudinal Range Shift (ARS) and Species Area Relationship’ (SAR) models predict that under a 4°C rise scenario, all endemic vascular plants (16 spp.) on the summit of Cerro Aracamuni will disappear by the end of 2100. This means that the entire habitat of this species could be lost by 2100. In addition, pathogens pose a potential threat to this species, which is only known from three specimens collected in October 1987: two adult ♂♂ and one ♀. There is no information on its past or current population size or trends (Ayarzagüena 1992, Rödder et al. 2010, Vegas-Vilarrúbia et al. 2012, Rull et al. 2019).

*Cochranella xanthocheidia*: categorised as vulnerable because the species' range is 16,635 km<sup>2</sup>, it occurs in four locations classified as vulnerable and the extent and quality of its forest habitat in the Western Cordillera of Colombia continues to decline. The main threats are habitat fragmentation and loss due to the expansion of agriculture and logging, as well as water pollution. Another major threat is mining, which destroys forest areas and pollutes water bodies. The species is only known from seven specimens, five of which were collected in the years 1980–1990 and the last two in the years 2004–2005. The last survey of the species in the vicinity of the site was in 2010 and there have been no more recent surveys elsewhere. It is assumed that the population is declining.

## Reproduction

| Topic                       | Details on the reproduction of <i>Cochranella</i> spp.                                                                                                                            |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂ call from a singular subgular vocal sac.                                                                                                                                       |
| Sexual maturity             | <i>C. granulosa</i> : ♂♂ can be identified by first calls at an age of 6–8 months. First reproductive activities were registered at 8–15 months (T. Eisenberg, unpublished data). |
| Calls                       | <i>C. duidaeana</i> : ♂♂ called between 7 and 9 pm at an ambient temperature of only 13–14°C with a short, pulsed note from the top of the leaves, 1.5–2 m above the ground       |

(Señaris & Ayarzagüena 2005).

*C. erminea*: single call (Pongo de Rentema [5°18'3.86 'S, 78°23'44.57 'W, 682 m asl], temperature 21.4°C): two sharp, rapid successive notes. The first begins softly and increases in amplitude over time (amplitude modulated), call length 313 ms, 14 pulses, dominant frequency 4,870 Hz. This is followed by a single chirp that sounds 173 ms after the first tone, call length 54 ms, 3 pulses, dominant frequency 4,866 Hz. For the human ear, the call was given as a 'zzzzzzzzt ZT'. Calls from other populations (Juanjui and from the type locality) all sound similar, with the only noticeable difference being that the number of trailing chirps can vary between zero and two. The call is similar to that of *C. granulosa*, which has a 'pulsed main tone followed by 0–5 shorter pulsed secondary tones' (Ibáñez 1991). The call is also similar to that of *C. guayasamini*, although the latter emits a two-tone call only in groups (often only one tone when alone), whereas *C. erminea* typically uses a two-tone call. Furthermore, in *C. guayasamini* the first and second notes are of equal length and are not amplitude modulated. The ♂♂ call from the tips of the leaves, typically in groups of 2–5 individuals, although single calling ♂♂ have also been observed. When calling in groups, the ♂♂ appear to make their calls in succession, and the calls of different ♂♂ usually do not overlap. At one site, the ♂♂ called sequentially downstream, with the chorus beginning with an ♂ sitting upstream and ending with a ♂ sitting downstream (Twomey et al. 2014).

*C. euhystrix*: ♂♂ called from rocky outcrops or vertical places near waterfalls at about 2,600 m asl on 2 June. A single ♂ called from a large boulder 20 cm above a stream at 1,800 m asl on 6 May. The call is a short click or chirp, usually heard as two sounds in rapid succession. Occasionally a call consisted of only a single note. In January 1989, no individuals were heard calling, but this may have been due to the noise of the heavily swollen streams during the rainy season (Cadle & McDiarmid 1990).

*C. euknemos*: ♂♂ call during the rainy season from low trees or bushes overhanging fast-flowing streams. The call is similar to that of *C. granulosa* and consists of one, two or three unmelodic notes that are repeated quickly and sound indistinctly like 'creep, creep, creep'. The call has a dominant frequency of 4,300 Hz, average call length of 0.1 s, call pause of 0.15 s and a total length (2 tones) of 0.35 s (Savage & Starrett 1967, Kubicki 2007).

*C. granulosa*: ♂♂ call from the top of leaves 5–10 m above the water and are therefore not easy to find. In populations where syntopically occurring glass frogs are absent, lower perches are also occupied. The call is very characteristic and loud. Each call usually consists of three, sometimes up to five notes ('reet-reet-reet'), with the first note being slightly longer than the others, the average duration of a three-note call is 0.8–0.9 s, the dominant frequency is 3,700–4,500 Hz. A call is followed by a pause of a few minutes. The calls often take place in choirs, in which one ♂ begins and ♂♂ close to it immediately join in. The calls can thus swell into call waves that spread up to 600 metres along the river (Savage 2002, Kubicki 2007).

*C. guayasamini*: ♂♂ call from the tops of leaves, description of calls from the Cainarachi Valley at temperatures of 20–24°C: The advertisement call consists of 1–2 sharp humming tones with a duration of 0.166–0.208 s (note length), 9–10 pulses at a dominant frequency of 6,080–6,180 Hz and pulse rate of 48–54 pulses/s. The two-note call includes a second, slightly longer, 0.5 s buzz that is appended to the end of the first note. One of the most striking aspects of the calls of this species is their complex calling behaviour. Individual ♂♂ were encountered, but they only called infrequently (e.g. once every 10–15 minutes). In contrast, the ♂♂ called much more frequently in dense congregations (every 1–5 minutes). The calling behaviour also becomes more complex in group situations, as the ♂♂ tend to switch to individual calls. In a calling duel between two ♂♂, each giving a two-part call, the second ♂ began its call immediately after (and slightly overlapping with) the first note of the first ♂, while the second notes of the two ♂♂ overlapped more. This situation becomes much more complex in larger groups (usually 3–6 calling ♂♂), as individual ♂♂ can make either monophonic or

biphonic calls. It seems that one ♂ leads the chorus and its call is quickly followed by a cascade of calls from other ♂♂ nearby. In the field, this creates the impression of a continuous 'wave' during the chorus, which makes it extremely difficult to localise individual calling ♂♂ (similar to *C. granulosa*). The calling behaviour of *C. guayasamini*, *C. erminea* and *C. granulosa* appears to be similar in that the ♂♂ call once in discrete bursts (presumably in response to their neighbour's call) and then remain silent until the next call. As a strong overlap of calls can affect the temporal information of calls and reduce the ability of ♂♂ to attract mates, the overlap of calls between these *Cochranella* spp. could have an effect against frog-eating enemies (e.g. bats) that hinders their detection (Twomey et al. 2014).

*C. mache*: ♂♂ call from the top of the leaves or branches of trees and shrubs, the advertisement call consists of two tones separated by an interval of 0.107–0.130 s, each tone has a duration of 0.029–0.049 s. The dominant frequency is 5,383–5,426 Hz, the call frequency is 1.46 calls/min (Ortega-Andrade et al. 2013, Guayasamin et al. 2020).

*C. nola*: ♂♂ call from rocks, the species epithet is derived from the Latin noun *nola*, which means little bell and refers to the high-pitched call. The call consists of a single sharp 'pink' and can be heard about once every 30 seconds (Harvey 1996).

#### Mating and spawning

All species: Axillary amplexus in the vegetation above small forest streams.

*C. duidaeana*: Eggs are presumably laid on the upper side of the leaves. However, according to field observations, a clutch was discovered in an earth bromeliad (*Brocchinia* sp.) on one of the rising slopes of Cerro Marahuaka between 1,700 and 1,800 m asl. It contained about 19 greenish eggs arranged in a single layer. The tadpoles would therefore slide into the water reservoir measuring about 200 ml at the base of the bromeliad, whose water values (high conductivity, low pH of 3.1–5.2 and low oxygen content of 1.52–2.66 ppm) are considered unfavourable for the development of the tadpoles (Señaris & Ayarzagüena 2005).

*C. erminea*: spherical cluster of pigmented eggs dangling from leaf tips (Twomey et al. 2014).

*C. euknemos*: The paratype of an adult ♀ contained black and white eggs similar to those of *C. granulosa*. The clutches were found at the same time as the calling ♂♂. The eggs are deposited in gelatinous masses on the upper side of the front half of the leaf, the clutches contain 40–70 black and white eggs and 'swell' after the rain until they hang down in a cone shape over the leaf tip (Savage & Starrett 1967, Hayes 1991, Kubicki 2007, Leenders 2016).

*C. granulosa*: Dark eggs, which are previously visible through the transparent abdominal skin (medially in front of the cloaca), are laid on the upper surfaces of leaves many metres above the water on the front half of the leaf. Immediately after the eggs are laid, a short period of maternal brood care follows for a few hours, presumably to provide moisture, after which the jelly swells – also due to the high humidity – over the next few days until the clutch hangs down over the folded leaf tip, reaching the shape and size of a large pine cone (in contrast to *C. euknemos*, the jelly remains clear). The 40–104 eggs initially orientate themselves with the dark animal pole facing upwards, the white vegetative pole shrinks visibly to a light dot during the multicellular stage over the next few days and then disappears completely. Territorial fights of the ♂♂ last for hours, as they try to push each other belly to belly and with their arms entwined from a leaf, which they only hold on to with their feet. Very rarely, standing water in the form of small ponds was also used for reproduction (Kubicki 2007, Hoffmann 2010a).

*C. guayasamini*: ♀♀ lay their eggs on the tops of leaves along streams. The eggs are golden yellow with clear jelly, clutch size 16–38 eggs (Twomey et al. 2014).

*C. mache*: ♀♀ lay clutches of around 30 brown eggs on the upper surfaces of leaves (Guayasamin et al. 2020).

*C. nola*: The clutches are laid on stones along streams (Harvey 1996).

*C. resplendens*: Clutches are laid on the upper side of leaves, with short-term maternal brood care (hydration), similar to the clutches of *C. euknemos* and *C. granulosa*, but

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|                                                   | <p>the eggs are initially yellowish brown. On the Río Napinaza, a clutch of 74 embryos was found on the upper side of a leaf (Guayasamin et al. 2020).</p> <p><i>C. riveroi</i>: The only known adult ♀ (paratype) was found with 21 well-developed eggs in her ovaries, which were 2.3–2.5 mm in diameter, with a dark brown animal pole and light maroon vegetative pole (Señaris &amp; Ayarzagüena 2005).</p> <p><i>C. xanthocheridia</i>: The eggs are laid on the upper surface of leaves (Ruiz-Carranza &amp; Lynch 1995b).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Reproductive season                               | <p><i>C. duidaeana</i>: The species is only known from three adult ♂♂ collected at the end of the rainy season, in November 1991. According to the field notes made during the collection of this type series, advertisement calls were frequently heard when it rained and the species seemed to be abundant (Ayarzagüena 1992, Señaris &amp; Ayarzagüena 2005).</p> <p><i>C. euhystrix</i>: see table row Calls.</p> <p><i>C. euknemos</i>: Calls were heard from August to October at the type locality Canton de Coronado (Savage &amp; Starrett 1967).</p> <p><i>C. mache</i>: The frequency of sightings depends on rainfall and is higher during the rainy season (February-May), breeding seems to be restricted to the rainy season (Ortega-Andrade et al. 2013, Guayasamin et al. 2020).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Eggs/clutch, clutches year                        | <i>C. euknemos</i> : see table row Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Size of eggs and larvae at hatching               | <p><i>C. granulosa</i>: Egg size: 1 mm in diameter (T. Eisenberg, unpublished data); larval size: see table Husbandry and rearing.</p> <p><i>C. riveroi</i>: see table row Mating and spawning.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Development time from egg laying to metamorphosis | Glass frog ♀♀ lay their eggs on substrates outside the water along streams, after several days or weeks (e.g. > 20 days) the larvae hatch and fall into the water, where they complete their development (Cisneros-Heredia & McDiarmid 2007).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Details on the larvae                             | <p><i>C. euknemos</i>: The tadpoles have long tails, elongated bodies and are pale in colour; a series was kept and reared until the tadpoles reached a size of 24 mm (Savage &amp; Starrett 1967, Hoffman 2010).</p> <p><i>C. granulosa</i>: Tadpoles have a flattened body and slender tail, in early stages they have a dark brown pigmentation, which changes from light brown to bright red in the course of ontogenesis. The oral disc develops during the first days of life and then consists of initially about 10, later about 20–40 marginal papillae and a labial tooth row formula of 2/3. Later, all five tooth rows are well developed as are the toothed jaw sheaths, the upper jaw forms a smooth M-shape, the lower sheath is V-shaped. Centrolenid larvae are generally described as fossorial, i.e. they burrow into the substrate of the reproductive waters. Such zones are not only characterised by low flow velocities, but also by decomposition processes, which take place with increasing depth with the participation of anaerobic bacteria. A relative lack of oxygen can be assumed in these ecological niches. Hoffmann (2010b) describes precisely this phenomenon, as well as a pale dark blue (cyanotic) basic colour of the larvae, while the normal phenotype consists of the typical red colouration of glass frog larvae. In two different rearing experiments, the tadpoles in question were reared once in oxygen-rich water (+O<sub>2</sub>) and once under hypoxic (oxygen-poor) conditions (-O<sub>2</sub>) and their development, growth and survival rate were recorded: Larvae in the +O<sub>2</sub> group showed a pale colour, whereas larvae in the -O<sub>2</sub> group grew faster, were more active and stood out with a bright red colour. This is explained by an oxidative conversion of ammonium from the larvae's faeces and urine to nitrate, whereas this reaction does not take place under O<sub>2</sub> deficiency. Presumably, the nitrate produced in the +O<sub>2</sub> larvae is reduced to nitrite by bacteria in the larvae's intestines, after the absorption of which so-called methaemoglobin is formed in the blood from the normal blood pigment haemoglobin. This was eight times higher in the +O<sub>2</sub> larvae – and therefore in the toxic range for other vertebrates – and, in the author's opinion, provided the reason for the observed growth depression. In contrast, the -O<sub>2</sub> larvae swim more, consume more energy and appear to have better food utilisation than their well-aerated conspecifics</p> |

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despite a slightly lower food intake (Hoffmann 2010a, b).

*C. guayasamini*: The following description is based on three tadpoles of stages 26, 35 and 39 according to Gosner (1960), which originate from a collected clutch and were artificially reared: Total length 28.9–36.5 mm, body length 9.5–11.8 mm, body width 4.6–5.6 mm, maximum tail height in the middle of the tail to the end of the tail, body colour translucent white in life, then red, finally grass green. General characteristics: Body round to elongate, eyes dorsal, becoming more lateral as development progresses, spiraculum lateral on left side, cloaca medial, tail musculature uniformly white, maxillary and mandibular sheaths narrow and dentate, lateral process of maxilla of medium length, distal tips slightly curved forwards, oral disc not notched at the edge, marginal papillae complete on the ventral side, while they are completely absent on the dorsal side, submarginal papillae absent, labial tooth row  $\frac{1}{3}$  present in all stages examined, no gaps (Twomey et al. 2014).

*C. resplendens*: (based on a tadpole in Gosner stage 36): Body elongate, oval compressed, wider than high, mouth region rounded in dorsal and lateral views, eyes on dorsal surface of head (initially C-shaped, round after stage 35), spiraculum posterolateral on left side of body, cloaca short and abdominal, directed caudally, dorsal fin beginning about halfway down tail, ventral fin begins almost at the base of the caudal muscle and reaches its maximum height behind the middle of the tail, oral disc not very pronounced, marginal papillae in a single row (larger on the lower lip, upper lip with papillae only at the lateral ends), upper jaw sheath completely keratinised with serrated edge, slightly curved, lower jaw sheath keratinised, U-shaped, with serrated edge. Labial tooth row formula 2(2)/3; A2 with medial gap. Dorsally, the tadpole is mostly red, with some clusters of iridophores forming an interorbital line and a central band from behind the eyes almost to the end of the body (dorsally, the foremost part of the body is pale yellow (Terán-Valdez et al. 2009, Guayasamin et al. 2020).

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### Husbandry and Captive Breeding of *Cochranella granulosa* B/C

All other species *Cochranella* spp. **X**, as they have not yet been introduced into captivity. Husbandry and breeding parameters probably similar for many species.

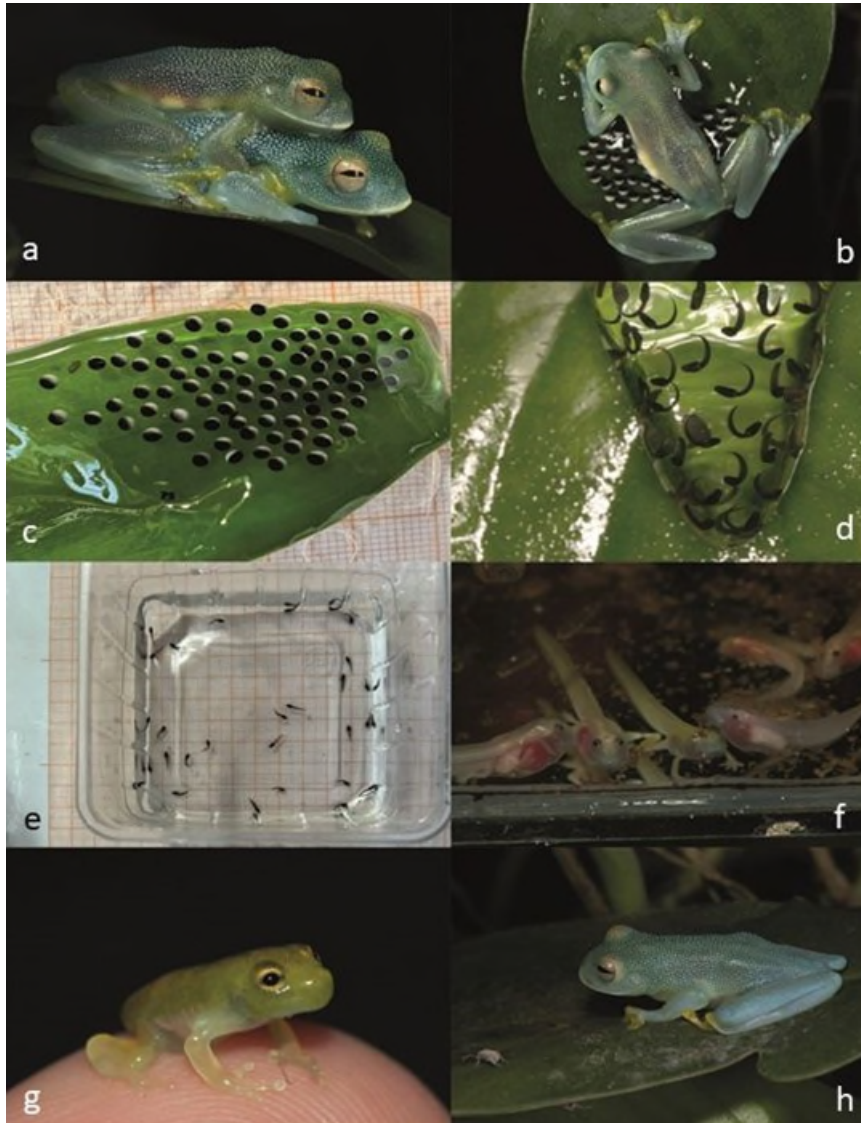


Fig. 44: *Cochranella granulosa*, captive breeding

- a amplexus (T. Eisenberg)
- b female 'brooding' behaviour on the eggs. The female remains for some hours after oviposition on the eggs to transfer liquid through the skin and from the bladder through the cloaca in order to make the jelly absorbing water (T. Eisenberg)
- b freshly laid clutch that has been removed from the rain chamber for external incubation. Note the monolayer structure at first that needs to absorb lots of water (T. Eisenberg)
- d clutch of eggs in advanced state of development. Note the blackish embryos and the cone appearance of the clutch under natural conditions (T. Eisenberg)
- e freshly hatched tadpoles remaining in shallow water until they are reared in the described aquaria (T. Eisenberg)
- f well-fed tadpoles in different developmental stages (R. Stuster)
- g froglet that has just succeeded metamorphosis (R. Stuster)
- h adult frog before eating a dusted bean beetle (T. Eisenberg).

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Cochranella granulosa</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
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| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p data-bbox="448 286 1396 1059">Special notes on the genus <i>Cochranella</i>: Removing the entire leaf from the terrarium has proven to be a good way to ensure hygienic rearing. With <i>C. granulosa</i>, the incubation of the clutches in accordance with natural conditions is the decisive factor for successful breeding, as the eggs usually only develop if the jelly can swell after laying the eggs due to a limited supply of liquid (rainwater or high humidity) and swell into the cone-like, free-hanging shape. If there is too much moisture, the clutch detaches from the leaf and can fall into the water; if there is too little moisture, the jelly does not swell and dries up. In both cases, as with other artificial approaches (e.g. horizontal incubation in a petri dish), the result is increased death of the embryos, which is manifested by a fungal infestation that quickly destroys the entire clutch. While the mere husbandry of <i>C. granulosa</i> can be regarded as unproblematic, controlled breeding is associated with considerable difficulties even for experienced keepers, so that the period between egg laying and hatching of the larvae urgently requires further optimisation. In the author's opinion, the problems described above make the breeding of this species one of the most complicated of all available glass frog species. Once again, it seems important to imitate the natural spawning conditions as closely as possible: The yield could be increased by hanging the leaf in a horizontal position so that the swelling clutch can form over the tip of the leaf as a free-hanging shape while still adhering to a broad support surface on the leaf. In the author's opinion, this is best achieved by regular moistening using an ultrasonic nebuliser or a sprinkling nozzle. If, on the other hand, the leaf was to be hung vertically, the shear forces would appear to be too great to fix the clutch to the leaf so that it would fall off more easily. It is very important that the entire leaf is allowed to dry after wetting to improve the adhesion of the clutch to the leaf.</p> <p data-bbox="448 1070 1396 1160">The analyses of the keeper surveys (nine keepers or breeders of <i>Cochranella granulosa</i>) revealed the following information on the housing conditions for the breeder animals:</p> <ul data-bbox="448 1171 1396 2054" style="list-style-type: none"> <li>– Sex ratio mostly with several ♂♂ (1.3   3.2   2.1   2.2   1.2 and 3.3).</li> <li>– Air and water temperature (°C): 18–28 (n=1)   20–28 (n=1)   20–25 (n=5)   22–30 (n=1), water section not specially heated in each case.</li> <li>– Humidity (rel.%): 70–100 (n=8), during the day 50–60 (n=2).</li> <li>– Lighting/type/day-night cycle: LED light bar (n=6) and additionally 35 W full spectrum lamps (n=1), with UV component (n=2) or with night light LED (n=1), daylight length 12–14 hours (n=7).</li> <li>– Container size (length x width x height in cm): 35 x 50 x 50   45 x 45 x 60 (n=2)   50 x 50 x 50   60 x 70 x 70   70 x 50 x 60   60 x 60 x 100 cm.</li> <li>– Proportion of water in the total area (%): 0–100 (often as a moat, complete soil area can be flooded during irrigation).</li> <li>– Soil substrate: organic (island of aquarium gravel, pine bark, leaves (n=2), inorganic (foam, filter sponge, soil mat, Epiweb; n=5) or no substrate, but many fist-sized moss-covered river pebbles (n=1).</li> <li>– Furnishing/planting: <i>Philodendron</i> (n=9), as well as other tropical plants such as anthuriums, <i>Monstera</i> spp., vanilla, bromeliads (<i>Neoregelia</i> sp.), various vines, all of which grow epiphytically on cork, coconut, tree fern slabs or Hygroton® gauze.</li> <li>– Water depth (cm): 0–4 (n=4)   5–8 cm (n=3).</li> <li>– Number of animals per container: 2–10.</li> <li>– Feed/feeding intervals: every night (n=1)   2x/week (n=4)   3x/week (n=3).</li> <li>– Supplementation (minerals/vitamins): unspecified (n=2)   Repashy Calcium plus (n=1)   Repashy Supervit, Repashy Vit A (n=2)   Ranarium Rana Vit, Dendrocare (n=1)   Amphib (Herpetal; n=1).</li> <li>– Aggression between several ♂♂ or ♀♀: temporary during the breeding season between ♂♂ (n=1)   none (n=6).</li> </ul> |

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| Life expectancy                                                          | <i>C. granulosa</i> : Maximum age of the animals kept (in years): ca.1.5 (n=1)   8 (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Triggers for reproduction                                                | <p><i>C. granulosa</i>: Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): Rain chamber (tempered to approx. 25°C; n=2)   more humid husbandry and (intensive) sprinkling in normal terrarium (n=2)   sprinkling, spontaneous egg laying, temperature reduction (n=1)   8 s sprinkling every 15 min from 8–2 pm, higher room temperature of approx. 24°C; feeding crickets (size 2) with spirulina &amp; Repashy Bug Burger, filter switches on at night from 10–4 pm (first clutch after 3 weeks with filter installed), feeding insects with Vit. A supplement once a month (n=1)   Basic nutritional requirements: food-enriched crickets ('gut-loaded'), whose gut contents contain glycosaminoglycans (GAGs), and tropical isopods. Seafood such as clams and mussels are a source of GAGs, as are essential fatty acids contained in seeds, nuts and extracted oils. Higher levels of palmitoleic acid in the feed, e.g. from well-fed feeder insects, are also important for glass frogs. Supplements for feeder insects include preparations containing vitamins, calcium and minerals (n=1).</p> <p>First offspring (CB) in the year: 2012 (n=1)   2015 (n=1)   2021 (n=2)   2023 (n=1).</p> <p>Frequency of breeding since then (number of clutches): 2 to &gt; 50.</p> <p>Where are the eggs laid (leaves/glass/objects)? Leaves, glass (n=5).</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (upper side, lower side, tip of the leaf)? <i>Philodendron</i>, <i>Monstera karsteneanum</i> &amp; <i>Monstera adansonii</i>; leaf tip on upper leaf surface (n=5).</p> <p>How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): initially adjacent, not overlapping, but eggs lying together, monolayer, then swelling of the clutch to cone shape (=complex; see above; n=5).</p> <p>Number of clutches per ♀ in one oviposition: 1 (n=5).</p> <p>Number of clutches/♀/year (min.–max.): 1–2 (n=3)   3–5 (mostly induced, rather not spontaneous; n=2).</p> <p>Number of eggs/clutch (min.–max.): 10–45   20–40   20–40   22–64   36–84 (n=10).</p> |
| Number of fertilised eggs per clutch (min.–max.)                         | 5–40   0–40   up to 100%, individual eggs not fertilised   > 95%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Number of embryos hatched per clutch (min.–max.)                         | 5–30   variable, 15–39   0–40   usually < 10%, rarely more.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Hatching rate (number of hatched larvae/number of eggs)                  | <p>Hatching rate (number of hatched larvae/number of eggs) or &lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%:</p> <p>&lt; 25%   50%   &lt; 25% to &gt; 75%   usually &lt; 10%, rarely more.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Size of juvenile frogs (freshly metamorphosed; min.–max. [in mm])        | 10 mm (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Number of metamorphosed juvenile frogs per year                          | approx. 20 (n=1)   0–50 (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Number of rearing losses up to the 3 <sup>rd</sup> month                 | < 1%* (n=2)   not assessable due to group rearing of many clutches in a confusing aquarium, practically no rearing losses after metamorphosis.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Husbandry conditions (larvae) /Technical requirements for larval rearing | <p><i>C. granulosa</i>: for general information on larval rearing see above (chapter General Information on Glass Frogs).</p> <p>Total length of newly hatched larvae (in mm): 7–12 (n=1)   8–9 (n=1).</p> <p>Duration of the larval period (oviposition to metamorphosis; min.–max. [in months]): 5–7 (n=1)   5–8 (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |

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|                                                                         | <p>Special conditions and requirements for larval rearing (including technology and daily time requirements):</p> <ul style="list-style-type: none"> <li>– Water temperature (in°C): 20–25 (n=1)   25 (n=1)   22–28 (n=2).</li> <li>– Lighting/type/day-night cycle: Daylight (n=3)   50 W LED strip and daylight (n=1).</li> <li>– Container size (length x width x height in cm): 30 x 20 x 20   40 x 30 x 30   50 x 13 x 29   40 x 20 x 20 cm (n=1 each).</li> <li>– Substrate/furnishing/planting: Lava granules or no substrate at all, clay bricks and clay flower pots as hiding places   Java moss/lava granules of various grain sizes, foliage, river pebbles   1 cm cleaned gravel (n=1 each).</li> <li>– Water depth (in cm): 15   17   18   20 (n=1 each).</li> <li>– Number of animals per container: 5–30   18   10–50   5–100 (n=1 each).</li> <li>– Filter (type, performance): Airlift sponge filter (n=3)   Nano corner filter, 2W (n=1).</li> <li>– Special requirements (e.g. water values): acidified with humic acids (n=1).</li> <li>– Larval food: various fish foods, spirulina tablets (n=1)   spinach, Repashy fish food, TetraMin catfish tablets (n=2)   food tablets for carnivorous and herbivorous fish, cooked mushrooms, spinach, lettuce (n=1).</li> <li>– Frequency of water changes: 90% 1x/week (n=1)   50–80% 1x/week (n=1)   1x/month (n=2).</li> <li>– Type of water (rainwater, tap water, RO water, etc.): 50% reverse osmosis (RO) water:50% tap water (n=1)   100% tap water (n=1)   90% RO water:10% tap water (n=1)   rainwater (n=1).</li> </ul> |
| Number or percentage of offspring that become adults or sexually mature | After metamorphosis > 95% (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Age/size at sexual maturity                                             | <p>♂♂: start calling after approx. 3–4 months (n=1)   1.5 a with approx. 25 mm (n=1)   8–15 months (n=1).</p> <p>♀♀: 1.5 a with &gt;30 mm (n=1)   8–18 months (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Indicators for reaching sexual maturity                                 | Transabdominally visible ovaries, vasa deferentia, transabdominally visible dark follicles in front of the cloaca (n=1)   ovaries, call of the ♂♂ (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sex ratio of the offspring (♂♂:♀♀)                                      | 3:1 (n=1)   ~1:1 (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Evidence of deformities or diseases                                     | None (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Mortality of larvae up to metamorphosis                                 | Mortality of larvae up to metamorphosis (< 25%; 25–50%; > 50–75%; > 75%) or estimated: high/low: < 25% (n=2)   Low, air filtration, high mortality rate in established tanks – better survival rate in freshly established tanks (rainwater; n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Mortality in the first months/years of life after metamorphosis         | Low (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Routine testing for amphibian diseases and parasites                    | No (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

|                                                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Quarantine (type and extent)                                    | No (n=2)   yes, for 1 (n=2), for 2 (n=1), for 4–6 months (n=2) <sup>12</sup> .                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| General characteristics, difficulties with keeping and breeding | <p>General characteristics, difficulties with keeping and breeding: low (n=1)   or medium difficulty (n=1)   husbandry unproblematic, but a delicate species due to the above-mentioned clutch losses during incubation (n=3).</p> <p>Assessment of the frequency of husbandry: rare (n=3)   more frequent (n=1).</p> <p>Personal assessment of the difficulty of husbandry: medium difficulty   high level   difficult (compared to other glass frogs).</p> <p>Further notes: Amplexus was observed several times in spring while the ♂♂ were calling during the day (n=1)   need crickets, oven fish, bean beetles, feeding only with flies leads to emaciation (n=1)   correct incubation of clutches is <i>the</i> decisive factor (n=1)   relatively robust glass frogs (n=1).</p>                                                                                                                                                                                                             |
| Frequency of private breeding and reproduction in zoos          | An extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists numerous entries between 2005 and 2022 as holders of <i>C. granulosa</i> (T. Eisenberg, unpublished data).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Reproduction in captivity up to F2 generation                   | Yes (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding                                             | No (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Interviews/ Surveys/ Consultations                              | All nine participants in the survey on <i>Cochranella granulosa</i> stated that they were private owners. All participants were certain that the species was correctly identified, whereby the species identification was mostly carried out by the breeder, in collaboration with other specialists or based on their own expertise. With the exception of two sources, one of which received its animals as so-called ‘farm-breds’, all the animals kept were identified as captive-bred. Two breeders have been keeping their animals continuously since 2011 and 2012, while the others have been husbandries since 2018–2023. Three keepers have not yet been successful with breeding (only once no breeding ambitions were stated), although one of these sources has already seen successful development of the clutches. The remaining six breeders, on the other hand, have successfully bred their offspring, and three of them also indicated regular breeding up to the F2 generation. |

<sup>12</sup> Small, sterile terrariums (e.g. 30 x 60 x 20 cm with front and lid wire gauze ventilation) with climbing plants (*Philodendron* spp.) without substrate are suitable for this purpose. A moat with overflow serves as a water reservoir. The quarantine should last at least 8 weeks and up to 6 months. During this time, PCR tests are carried out for *Batrachochytrium dendrobatidis*, *Batrachochytrium salamandrivorans*, *Ranavirus*, *Chlamydia* and *Brucella* as well as coproscopic tests for parasites (T. Eisenberg, unpublished data).



**Espadarana Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                       | Original description       | Common name                                                       | Common name international       | Known/ documented in international trade |
|-------------------------------|----------------------------|-------------------------------------------------------------------|---------------------------------|------------------------------------------|
| <i>Espadarana andina</i>      | (Rivero, 1968)             | Andes Giant Glass Frog                                            |                                 | No                                       |
| <i>Espadarana audax</i>       | (Lynch & Duellman, 1973)   | Napo Giant Glass Frog, Daring Glass-frog                          | Rana de cristal de espina curva | No                                       |
| <i>Espadarana callistomma</i> | (Guayasamin & Trueb, 2007) | Beautiful Eyes Glass-frog                                         |                                 | No                                       |
| <i>Espadarana durrellorum</i> | (Cisneros-Heredia, 2007c)  | Durrell's Glassfrog                                               |                                 | No                                       |
| <i>Espadarana prosoblepon</i> | (Boettger, 1892)           | Emerald Glass Frog, Nicaragua Giant Glassfrog, Variable Glassfrog | Rana de cristal variable        | Yes                                      |

**Morphology and Taxonomy**

The generic name *Espadarana* honours Marcos Jiménez de la Espada, a Spanish zoologist who was a member of the Comisión Científica del Pacífico, which explored the Americas between 1862 and 1865. His work 'Vertebrados del Viaje al Pacífico Verificado de 1862 a 1865 por una Comisión de Naturalistas Enviada por el Gobierno Español – Batracios' is an indispensable reference work for anyone interested in the amphibians of South America. Jiménez de la Espada described the first centrolenid, *Centrolene geckoidea*, in 1872. In Spanish, the word Espada means 'sword', which we associate with the humeral spines present in the adult ♂♂ of the species of this genus. *Espadarana* is a combination of the words Espada and Rana (frog) and is female.

Phylogenetically, this genus embodies the clade of the common lineage of the two species *Centrolenella andina* Rivero 1968 and *Hyla prosoblepon* Boettger 1892. The sister genus in this case is uncertain, at least according to the analysis of the mitochondrial dataset, the closest relationship with the genus *Cochranella* Taylor 1951 is supported, while the analysis of nuclear genes does not provide significant support for relationships between genera within the Cochranellini.

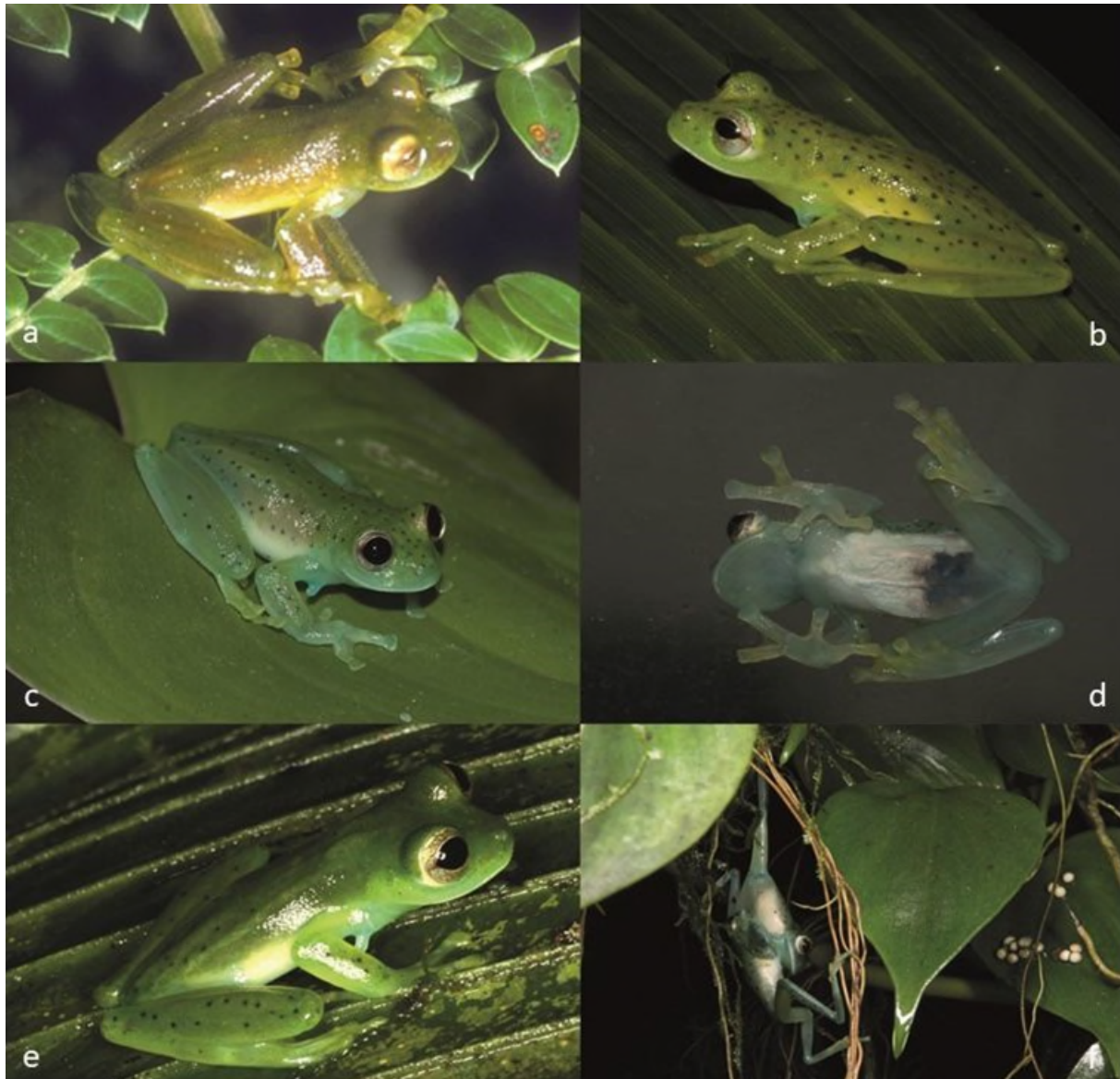


Fig. 45: *Espadarana* species

- a *E. audax* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001058)
- b *E. prosoblepon*, male individual from the surrounding of Braulio Carillo National Park, Costa Rica. Note the humeral spine on the upper arm (T. Eisenberg)
- c *E. prosoblepon*, male individual with prominent humeral spine in captivity (R. Stuster)
- d *E. prosoblepon*, underside of a female specimen. Note the dark eggs visible through the skin in front of the cloaca (R. Stuster)
- e *E. prosoblepon*, male individual from El Copé, Panama (T. Eisenberg)
- f *E. prosoblepon*, two male individuals during intraspecific competition. The dominant male is defending its territory by wrestling and trying to push the invader off the leaf (T. Eisenberg).

Members of the genus can be distinguished based on the following characteristics:

(1) conspicuous humeral spines present in adult ♂♂, (2) lobed liver covered by a translucent hepatic peritoneum, digestive tract translucent, (3) a ventral parietal peritoneum coloured white in the anterior region by iridophores, whereas the posterior region is transparent/translucent, (4) moderate interdigital membranes between digits III and IV, (5) bones green in life,

(6) back in preservative lavender coloured, with or without spots, (7) dentary process of the vomer with denticles, (8) the ♂♂ call from the upper side of leaves or twigs, the ♀♀ lay their eggs on the upper side of leaves above watercourses (in *E. prosoblepon* egg laying was observed on the upper and lower side of leaves), (9) articulated connection between quadratojugal and maxillary bones. The presence of conspicuous humeral spines in the adult ♂♂ of *Espadarana* species distinguishes this genus from most other centrolenids. The two other genera that have this characteristic are *Centrolene* and *Ikakogi*. In *Ikakogi*, however, the ♀♀ guard the clutches and the bones are white in life. *Centrolene* species usually have shiny pericloacal warts, which according to Guayasamin et al. (2009) are absent in *Espadarana*; in addition, most *Centrolene* lack teeth on the vomer, whereas all *Espadarana* species have vomer denticles; however, DNA data are required to unambiguously assign species to one of these two clades. Only the species of the genera *Centrolene*, *Espadarana* and *Ikakogi* have distinct humeral spines in ♂♂ (i.e., the crista ventralis on the humerus is expanded into a conspicuous spine). Other species have small (*Chimerella mariaelenae*, *Nymphargus grandisonae*, *Vitreorana gorzulae*), hidden (*Sachatamia ilex*) or absent spines (*Celsiella*, *Hyalinobatrachium*, most species of *Nymphargus*). The monophyly of *Espadarana* is strongly supported by 12S, 16S, ND1, POMC, combined mitochondrial, combined nuclear and complete datasets (Guayasamin et al. 2009).

Many species in this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unequivocal species identification):

*Espadarana andina*: Small to medium-sized glass frog with apple-green to dark green dorsal colouration, with or without dark blue-purple spots on head, back and extremities (northernmost populations less intensely spotted compared to southern populations), dorsal skin granular, with small spines, especially in the tympanum region, upper lip white, fingers and toes light yellowish green, humeral spines in adult ♂♂ of moderate size, relatively thick, with a rounded distal end, ventral skin areolate and strongly tuberculated around the cloaca, throat smooth, ulnar and tarsal folds absent, two infracloacal tubercles, iris greyish with dark grey to black speckles, SVL ♂♂ 21.6–26.4 mm, ♀♀ 24.7–29.5 mm, mouth region narrow (subovoid) in dorsal view, slightly sloping in lateral view, tympanic membrane moderately large, dorsally directed, anterior two thirds of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver without iridophores. Similar species: *E. prosoblepon*, *E. audax*. Taxonomic note: Type species of the genus (Señaris & Ayarzagüena 2005, Guayasamin et al. 2009, Cabanzo-Olarte & Ortega-Chinchilla 2018).

*Espadarana audax*: small to medium-sized glass frog with pale green dorsal colouration and small yellow spots, dorsal skin chagrined with small spines in ♂♂, ventral skin on abdomen and thighs granular, other surfaces smooth, paired subcloacal tubercles, chest white, fingers and toes pale yellow, humeral spines in adult ♂♂ short, bent inwards distally, ulnar fold present, inner tarsal fold present, outer tarsal fold absent, iris pale bronze coloured with black reticulation, SVL ♂♂ 21.6–25.5 mm, ♀♀ 24.5–28.8 mm, head much wider than body, mouth region round in dorsal view, truncated in lateral view, lower four fifths of tympanic membrane visible, dorsolaterally directed, anterior two thirds of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver, testes, kidneys, gall bladder and urinary bladder without iridophores. Related species: *E. durrellorum*. Similar species: *E. durrellorum*, *Centrolene notosticta*, *Nymphargus buenaventura*, *Nymphargus siren*, *Nymphargus humboldti*, *Rulyrana flavopunctata*, *Teratohyla midas*. Taxonomic note: *E. fernandoi* has

been synonymised with *E. audax*, but the species may belong to a species complex (Lynch & Duellman 1973, Guayasamin et al. 2009, 2020, Cisneros-Heredia & Guayasamin 2014).

*Espadarana callistomma*: medium-sized glass frog with uniform green dorsal colouration, dorsal skin chagrined with small spines in ♂♂, ventral skin on abdomen and lower flanks areolate, paired enlarged subcloacal tubercles, upper lip whitish cream-coloured, flanks white, conspicuous blue-green humeral spines in adult ♂♂, ulnar and inner tarsal fold low, outer tarsal fold absent, interdigital membranes between fingers III and IV and on foot strongly pronounced, iris silvery-white with black reticulated lines, SVL ♂♂ 26.7–29.6 mm, ♀♀ 29.5–31.8 mm, head as broad as long, mouth region truncated in dorsal and lateral view, large, anterolaterally aligned eyes, eardrum small, vertically aligned, with lateral inclination, tympanic ring covered above by supratympanic fold, anterior two-thirds of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestines, (four-lobed) liver, testes, kidneys, gall bladder and urinary bladder without iridophores. Related species/evolutionary relationships: *E. prosoblepon* is paraphyletic compared to *E. callistomma*, although *E. callistomma* is monophyletic. The most likely explanations for the observed pattern are: (i) the divergence between the two species is recent and mutual monophyly has not yet been achieved, (ii) *E. callistomma* is a synonym of *E. prosoblepon*, or (iii) *E. prosoblepon* is a species complex that needs to be further subdivided. In view of the available morphological and acoustic data, Guayasamin et al. (2020) favour the first and third hypothesis. Similar species: *E. andina*, *E. prosoblepon* (some populations), *Sachatamia ilex* (♀♀ not distinguishable; Guayasamin & Trueb 2007, Guayasamin et al. 2020).

*Espadarana durrellorum*: medium sized glass frog with uniform green dorsal colouration, dorsal skin chagrined with small spines in ♂♂, ventral skin granular, distinct cloacal sheath with two large, rounded, flat subcloacal tubercles and two folds on the sides of the (caudally directed) cloacal opening, humeral spines short and straight, with sharp tip in adult ♂♂, ulnar fold, inner tarsal fold and outer tarsal fold absent, forearm strong, diameter of the upper arm about  $\frac{2}{3}$  of the diameter of the forearm, iris golden with thin dark reticulation, SVL ♂♂ 25.7–26.1 mm, ♀♀ 25.7–29.3 mm, mouth region rounded in dorsal view, blunted in lateral view, tympanic ring distinct, dorsolaterally aligned, very weak supratympanic fold above the tympanic membrane, anterior two thirds of the ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver, testes, kidneys, gall bladder and urinary bladder without iridophores. Similar species: *E. audax* (sister species), *Centrolene heloderma*, *Centrolene buckleyi*, *Centrolene hesperia*, *Centrolene hybrida*, *Centrolene venezuelensis*, *Centrolene lemniscata*, *Sachatamia ilex*, *Ikakogi tayrona* (Cisneros-Heredia 2007c, Guayasamin et al. 2020).

*Espadarana prosoblepon*: medium-sized glass frog with green dorsal colouration and small black spots (however, very variable dorsal colouration, including individuals with both black and yellow spots [also dark spots surrounding yellow spots and forming false ocelli], only yellow, only black or no spots at all), dorsal skin chagrined, both sexes may have tiny spines on the flanks and in the area of the tympanic membrane, upper lip whitish cream coloured, one pair of enlarged subcloacal tubercles, humeral spines large, flat and protruding in adult ♂♂, ulnar and tarsal folds absent or low and inconspicuous, without white colouration, iris varies from greyish white to pale bronze with fine dark reticulation, to silvery white with strong black reticulation, SVL ♂♂ 23.2–27.5 mm, ♀♀ 25.3–27.8 mm, mouth region blunted in dorsal and lateral view, eardrum small, almost vertically aligned, with slight lateral and posterior inclination, tympanic ring mostly visible, with supratympanic fold covering its posterodorsal margin,



anterior half to two thirds of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver, testes, kidneys, gall bladder and urinary bladder without iridophores. Similar species: *E. andina*, *E. callistomma*, *Centrolene buckleyi*, *Cochranella litoralis*, *Vitreorana ritae*, *Nymphargus cochranae*, *Nymphargus megacheirus*, *Sachatamia ilex*. Evolutionary relationships: see *E. callistomma* (Guayasamin et al. 2020).

### Distribution and Habitat

The genus *Espadarana* occurs at altitudes below 2,500 m asl in the lowlands and mountains of Central America (*E. prosoblepon*), in the Amazon lowlands of Colombia (*E. audax*) and Ecuador (*E. audax*, *E. durrellorum*) or in the Pacific lowlands of Colombia and Ecuador (*E. callistomma*, *E. prosoblepon*) as well as in the cloud forests of the Andes in Colombia, the Cordillera de Mérida and the Serranía del Perijá in Venezuela (*E. andina*) (Guayasamin et al. 2009).

*Espadarana andina*: found in the Venezuelan Cordillera de Mérida and the Serranía de Perijá as well as in Colombia on the western slopes of the Cordillera Oriental (Departamentos Norte de Santander to Cundinamarca) and in the Serranía de los Motilones (505–2,500 m asl). Habitat in cloud forests and montane evergreen dry forests along mountain streams. The species appears to be little affected by habitat loss in the landscape and survives even when there are only small rows of trees along streams (Señaris & Ayarzagüena 2005).

*Espadarana audax*: formerly only known from a few places in the Amazonian slopes of the Andes: Río Salado and Cascada de San Rafael, Napo Province, Ecuador, and 35 km south-west of San Francisco, Departamento Putumayo, Colombia. However, the species is now also known from the Reserva Biológica Narupa (Napo Province) and from Nangaritza and Machinaza (Cordillera del Cóndor) in Ecuador and the Serranía de los Churumbelos, Departamento Cauca, in Colombia. After the synonymy of *E. fernandoi* with *E. audax*, the species now also occurs on the western slope of the Abra Tangarana in San Martín, Perú (800–1,900 m asl). Habitat in primary cloud forest. The holotype was found in a bromeliad in the spray zone of a waterfall on a cliff (AmphibiaWeb 2023).

*Espadarana callistomma*: described in Ecuador from the tributaries of the Río Bogotá in the province of Esmeraldas and from the Río La Carolina on the Ibarra-Lita Road near Jijón and Caamaño. In Colombia known from the departments of Valle del Cauca (Bahía Malaga, Buenaventura, Bajo Calima) and Chocó (Condoto, probably in other places in Chocó). Altitudinal distribution 20–500 m asl. Habitat: Streams in evergreen lowland forests (Guayasamin & Trueb 2007, Ospina-Sarria et al. 2010).

*Espadarana durrellorum*: known from the foothills of the Cordillera Oriental in Ecuador, provinces of Zamora Chinchipe, Orellana, Napo and Sucumbios (300–1,267 m asl). Individual specimens were found at night on the upper leaf surface of small trees at a height of 3–4 m above small streams. The species has also been observed in secondary forest mosaic areas and in pastures. It can use temporary (seasonal) streams during the breeding season. In the non-reproductive period, the species appears to inhabit the forest canopy.

*Espadarana prosoblepon*: widespread from eastern Honduras, Nicaragua, Costa Rica and Panama to the Pacific slopes of Colombia and Ecuador. The species also occurs in Colombia on the northern and eastern flanks of the Cordillera Oriental south of Caldas in the Magdalena Valley, and there is a more recent record from the Río Barbas River basin on the western slopes of the Cordillera Central. Two other localities in Ecuador have been included in the distribution area: Tandapey in the province of Pichincha and Paramba in the province of Imbabura, which



is due to the synonymy of *Cochranella ocellifera* with *E. prosoblepon*. The subpopulation from Pilalo on the eastern slope of the Cordillera Oriental of the Ecuadorian Andes probably belongs to an undescribed species. Altitudinal distribution from sea level to 2,200 m asl. Habitat in the low vegetation in the tropical forests of the lowlands and the montane cloud forests, mostly in original forest areas. Occasionally, however, the species can also be found in disturbed habitats. It often occurs with strong site fidelity near rivers and streams and is therefore more common at higher altitudes. The species feeds on a variety of small arthropods, including beetles, moths, spiders and mites. As a defence mechanism, this glass frog, like many other amphibians, produces a pungent odour when seized. It is one of the few species for which information on the probability of survival is available. McCaffery & Lips (2013) report that the mean annual survival probability is 0.46 (0.41–0.52, 95% CI) (excluding the influence of the chytrid fungus). These authors also provide data on the abundance of several populations from Panama. Spiders of the genus *Cupiennius* have been identified as predators of the species (Cisneros-Heredia & Yáñez-Muñoz 2007b, Robertson et al. 2008, Guayasamin et al. 2009, 2020, Cortas & Vallejos 2021).

### Conservation Status and Main Threats

#### IUCN Red List Status

*Espadarana andina*: LC (Least Concern, assessed 2020-07-01)

*Espadarana audax*: LC (Least Concern, assessed 2018-03-14)

*Espadarana callistomma*: LC (Least Concern, assessed 2018-12-14)

*Espadarana durrellorum*: LC (Least Concern, assessed 2016-07-16)

*Espadarana prosoblepon*: LC (Least Concern, assessed 2019-09-04).

#### Red List Status in the Range Countries

##### Central America

Environmental Vulnerability Score Category (Johnson et al. 2015)

*Espadarana prosoblepon* – L (Low)

##### Colombia

Libro Rojo de los Anfibios del Valle del Cauca (Castro-Herrera & Bolívar-García 2010)

NatureServe Status S3 (Vulnerable):

*Espadarana prosoblepon*

##### Costa Rica

All Centrolenidae of Costa Rica are classified as LC (Not Endangered) (Chaves et al. 2014).

##### Ecuador

Amphibians of Ecuador/Anfibios de Ecuador (Centro Jambatu (2011–2020) V1.23)

EN (Endangered):

*Espadarana audax*

## Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other possible threats include local application of pesticides, fertilisers and pollution, diseases, climate change and increased UV-B radiation.

*Espadarana andina*: not endangered due to its wide distribution, tolerance of habitat changes and presumably large overall population. This species has disappeared from streams where trout have been introduced. Overall, there are currently no major threats. It is a rare species, but there are several recent records.

*Espadarana audax*: In view of its wide distribution and presumably large population, the species is not categorised as endangered. The southern part of the range is threatened by mining activities, but most of the range is unaffected and the species occurs in several protected areas. Habitat destruction and degradation due to agriculture, logging and mining are local threats to this species in Ecuador. In Colombia, the Cauca locality is protected, but there is extensive deforestation in the Putumayo locality (Colombia Red List Assessment Workshop in August 2016). In Ecuador, the species is locally distributed (Ecuador Red List Assessment Workshop in July 2016). In Colombia, the species is only known from a single specimen from 1974 and another from 1998, and in Perú it is only recorded from a single location.

*Espadarana callistomma*: in view of its wide distribution and presumably large population, it is not categorised as endangered. If future studies reveal that this species is restricted to the lowlands of the Chocó ecoregion, a reassessment of its endangerment category is recommended in view of the high rate of deforestation in this area. The species is sensitive to habitat disturbance. However, it is locally widespread in the places where it has been found. It does not appear to be very common in Colombia, which is probably due to insufficient surveys in the Chocó. Due to the continuing decline in the extent and quality of the habitat, the population is thought to be in decline.

*Espadarana durrellorum*: not categorised as endangered in view of its relatively wide distribution and presumably large population. Habitat destruction in the foothills of the Cordillera Oriental is extensive. The northern distribution area is affected by oil extraction and is heavily populated, the central area is characterised by deforestation and livestock farming, and the southern part is affected by mining activities. The species can be considered rare. Due to the continuing decline in the extent and quality of the habitat, the population is suspected to be in decline.

*Espadarana prosoblepon*: not categorised as endangered in view of its wide distribution and presumably large population. The main threats are deforestation for agricultural development, illegal harvesting, logging, human settlement and pollution from spraying of illegal plants. The declines recorded in Costa Rica could be due to chytridiomycosis, although this is not certain as the species is said to have a strong resistance to *Batrachochytrium dendrobatidis*. The species is common and widespread in many parts of its range in Costa Rica and Nicaragua, and moderately common in Honduras and Colombia. It is also common in Panama, although it is declining in El Copé. It is widespread in Ecuador, but no individuals have been recorded in Tandapey (since 1973 despite repeated visits) and Paramba (since its discovery), suggesting that it may be locally extinct. The species appears to be more common at higher altitudes, probably due to the presence of more stream habitats (Woodhams et al. 2006, Guayasamin et al. 2020).

## Reproduction

| Topic                       | Details on the reproduction of <i>Espadarana</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
|-----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂ call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Calls                       | <p><i>E. andina</i>: the ♂♂ call from the upper side of the leaves, the call consists of a pulsed tone (5–6 pulses), call length 25.3–48 ms, dominant frequency between 5,470 and 5,900 Hz. However, a warning call from a Colombian population has also been described as a relatively short call characterised by a single tone: call length 36 ms, dominant frequency 4,371–5,467 Hz (Señaris &amp; Ayarzagüena 2005, Cabanzo-Olarte &amp; Ortega-Chinchilla 2017, 2018).</p> <p><i>E. audax</i>: ♂♂ call from the tops of the leaves, the calls are produced in series, each series consists of four or five calls, each call consists of a single, pulsed tone, the dominant frequency is 5,426–6,718 Hz (Guayasamin et al. 2020).</p> <p><i>E. callistomma</i>: ♂♂ call from the upper side of the leaves, each call consists of three to four pulsed tones, call length 0.28–0.44 s, 9.1–11.0 notes/s, not frequency modulated, dominant frequency at 5,343–5,812 Hz (Guayasamin et al. 2020).</p> <p><i>E. prosoblepon</i>: ♂♂ call from the upper side of leaves or small branches. The following description is based on the call of an individual from the Río Sune Chico (908 m, Cordillera Chontilla, Pachijal-Mashpi) in the province of Pichincha, Ecuador (4 July 2012, air temperature 18.8°C): Calls every 4–7 minutes, two pulsed tones each, call length 0.207–0.223 s, tone length 0.032–0.054 notes/s, tone interval 0.130–0.137 s, frequency modulated; dominant frequency 5,712–5,825 Hz (beginning) or 6,196–6,394 Hz (end), overtones also frequency modulated, they show complex spectral patterns. The call of the species from Monteverde, Costa Rica, shows some differences to the call described: Call sequence at irregular intervals (17 calls/h), two to five short ‘peeps’ (when encountering another frog within 15 cm, the ♂♂ often emit a series of rapid, short peeps), calls also during amplexus and immediately after egg laying, a rapid series of three, sometimes four to five tones, average tone length 0.03 s, dominant frequency 5,500–5,800 Hz. Typical call series have an average total length of 0.5 s (three-tone series) or 0.75 s (four-tone series). Furthermore, a stress call in rivalling ♂♂ has been described, which consisted of two short ‘beeps’ with amplitude and frequency modulation (1<sup>st</sup> and 2<sup>nd</sup> beep [dominance frequency] 47 ms [5,350.7 Hz] and 51 ms [5,684.8 Hz]). Predatory bats (e.g. <i>Trachops cirrhosus</i>) are sometimes unable to correctly locate the exposed ♂♂ because the periodic calls are often synchronised by other ♂♂ nearby (Jacobson 1985, Kubicki 2007, Rios-Soto et al. 2017b, Guayasamin et al. 2020).</p> |
| Mating and spawning         | <p>All species: Axillary amplexus in the vegetation above small forest streams.</p> <p><i>E. andina</i>: Calling, mating and oviposition sites are located between 70 and 140 cm above the surface of the stream. Breeding usually takes place in the months with higher rainfall compared to the dry season. Numerous clutches have been observed in various stages of development. In all cases, the clutches were laid on the upper side of leaves close to the apex. There is no evidence of brood care by ♂♂ or ♀♀, although the ♂♂ rest near the clutches. The ♂♂ show fighting behaviour in the form of clutching belly to belly. Possible causes of embryonic mortality include the presence of parasitic flies in the jelly (families Otitidae, Tipulidae; Cabanzo-Olarte et al. 2013, Cabanzo-Olarte &amp; Ortega-Chinchilla 2017, 2018).</p> <p><i>E. audax</i>: Eggs are laid in moss on branches, short-term female brood care, one ♀ had dark brown eggs in its oviducts (Guayasamin et al. 2020).</p> <p><i>E. callistomma</i>: ♀♀ lay pigmented eggs on the upper side of leaves usually 100–200 cm above the water surface (Guayasamin et al. 2020).</p> <p><i>E. durrellorum</i>: The only known clutch was observed in a twig, 2 m above the water of</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

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|                                                   | <p>a river (Cisneros-Heredia 2007c).</p> <p><i>E. prosoblepon</i>: Eggs are deposited on the upper surface of leaves, moss-covered stones or branches along streams in primary to slightly degraded forests and sporadically even on pastures. Breeding reaches its peak in the rainy season, when the ♂♂ often engage in aggressive territorial fights. When a ♂ invades an occupied territory, the resident ♂ emits a rapid series of calls. If the intruder continues to approach, a fight ensues in which both ♂♂ dangle upside down while clinging to the vegetation with their hind legs and maltreating each other with their arms and upper arm spines. This can result in wounds on the back and phalanges. It is rumoured that the upper arm spines are used in combat to stab the opponent. The fight is over when the loser falls from the fighting area or signals his submission by pressing his body against the surface of the leaf. The ♂♂ initiate the amplexus by jumping onto the back of approaching ♀♀. Activity patterns during mating in Colombia revealed an average of <math>35.4 \pm 4.79</math> eggs/clutch (<math>n=29</math>), a positive correlation of activity of both sexes with precipitation rate, a mating success of the ♂♂ that is independent of body size but dependent on calling activity, a higher number of eggs/clutch in large ♀♀, oviposition after an average of <math>3.76 \pm 1.74</math> hours after the first observation of the amplexus (in 93.1% of cases in fronds of <i>Selaginella geniculata</i> at an average height of <math>1.58 \pm 0.44</math> m). After oviposition, the ♂ left the site, while the ♀ remained between 30 and 45 minutes, partially covering the eggs with its body. ♂♂ removed from the calling group often found their way back to their original location (Kubicki 2007, Krohn &amp; Voyles 2014, Basto-Riascos et al. 2017, Rios-Soto et al. 2017b, Gómez-Murcia et al. 2023).</p> |
| Reproductive season                               | <i>E. andina</i> : The species was found calling from January to March, May to June and September to December (Cabanzo-Olarte & Ortega-Chinchilla 2018).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Eggs/clutch, clutches/year                        | <p><i>E. andina</i>: The clutches collected consisted of 10–68 (not varying between wet and dry seasons) pale green, greenish yellow or light-yellow eggs arranged in a single layer ('monolayer') (Señaris &amp; Ayarzagüena 2005, Cabanzo-Olarte et al. 2013, Cabanzo-Olarte &amp; Ortega-Chinchilla 2018).</p> <p><i>E. callistomma</i>: Clutches contained 32–39, average 35 eggs, diameter about 2.1 mm, animal pole dark brown (interpretation: UV protection and/or pigmented area warms up more in sunlight, reflecting [faster] development in cooler areas), vegetative pole light brown, development time under laboratory conditions 12 days from 32-cell stage to hatching of tadpoles. Detailed information on embryonic development in Salazar-Nicholls &amp; del Pino (2015).</p> <p><i>E. prosoblepon</i>: The ♀♀ lay 20–52 eggs, which have a dark brown to black colouration (animal pole) and light brown colouration (vegetative pole), on the upper side of leaves, moss-covered stones or branches above the water. The ♀♀ take over the short-term parental brood care (up to 131 minutes), but once they have left the clutch, neither parent returns to the clutch. Genetic polymorphisms in egg pigmentation cause the animal pole to contain less melanin. Dark eggs are discussed in connection with camouflage and UV protection (Guayasamin et al. 2020, Salazar-Nicholls et al. 2021).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Size of eggs and larvae at hatching               | <p><i>E. andina</i>: The eggs had a diameter of 0.5–1 mm (Cabanzo-Olarte &amp; Ortega-Chinchilla 2018).</p> <p><i>E. callistomma</i>: see table row Number of eggs/clutch.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Development time from egg laying to metamorphosis | <p>Glass frogs ♀♀ lay their eggs on substrates outside the water along streams; after several days or weeks (e.g. &gt; 20 days), the eggs hatch and the embryos fall into the water, where they complete their development (Cisneros-Heredia &amp; McDiarmid 2007).</p> <p><i>E. callistomma</i>: see table row Number of eggs/clutch.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Details on the larvae                             | <i>E. andina</i> : the tadpole has the following sizes (in mm): Body length 3.8–5, tail length 7.7–10.6, body height 1.63–2.31, body width 2.13–3.13, oral disc width 1.13–1.56, body depressed globular in dorsal view, oval in lateral view, eyes small, located dorso-laterally, small nostrils, rounded, directed anterolaterally, spiraculum left-sided, short,                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |

laterally visible tube, abdominal cloacal opening, right-sided, short, caudal musculature does not reach the end of the tail, distal end rounded, caudal fin margin less broad than the caudal musculature, upper fin margin less broad than the lower one, dorsal fin margin begins at the junction between body and tail, ventral margin of the pelvic fin on the body, oral disc ventral, bordered by blunt marginal papillae, without intramarginal papillae, horn beak completely keratinised, margins free with small notches, upper beak M-shaped, lower beak in broad U-shape, keratodont row formula 1/3, body dorsally and laterally light brown, the rest transparent, caudal musculature with light brown marbling on and in the depressions of the myomeres, rest cream-coloured, caudal fins transparent (Señaris & Ayarzagüena 2005).

*E. callistomma*: The tadpoles are brown in life (Salazar-Nicholls & del Pino 2015).

*E. prosoblepon*: The embryos are black, but quickly turn yellow. When the tadpoles hatch and fall into the river, they are red in colour. At stage 25, the larvae have a left-sided spiraculum, a simple oral disc with medium-sized jaw sheaths, 2/3 rows of teeth and a single row of marginal papillae with a wide dorsal gap. The second anterior (upper) row of teeth (A2) also has a wide gap. After hatching, the tadpoles usually hide under leaf litter or sand at the bottom of streams (Starrett 1960, McCranie & Wilson 2002, Savage 2002).

### Husbandry and Captive Breeding of *Espadarana prosoblepon* B/B

All other species *Espadarana* spp. **X**, as to the author's knowledge they have not yet been introduced into captivity. Husbandry and breeding parameters probably similar for many species.



Fig. 46: *Espadarana prosoblepon* captive breeding

- a spawning (R. Stuster)
- b larvae (T. Eisenberg)
- c metamorph (R. Stuster)
- d skin shedding (R. Stuster).



| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Espadarana prosoblepon</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
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| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p>The analyses of the keeper surveys (six keepers or breeders of <i>Espadarana prosoblepon</i>) yielded the following information on the housing conditions for the breeder animals:</p> <ul style="list-style-type: none"> <li>– Sex ratio mostly with several ♂♂, with three breeders working with group sizes between one and five pairs over time (1.1–5.5 [n=3]   1.1 [n=1]   2.3 [n=1]   not specified.</li> <li>– Air and water temperature (°C): 18–28 during the day, 22–24 at night   18–28   20–28   20–25   22   21–26, water section not specially heated, partly not available.</li> <li>– Humidity (rel.%): 70–100 (n=5), no measurements taken, but not spraying/misting for months is not a problem as long as water can evaporate from the bottom of the terrarium.</li> <li>– Lighting/species/day-night cycle: LED light bar (n=2) or fluorescent lamps (n=2), with UV component (n=2), daylight length 12–14 h (n=5) or 6.5 h.</li> <li>– Container size (length x width x height in cm): 30 x 20 x 20 (laboratory)   40 x 60 x 60   50 x 50 x 50 (n=2)   60 x 60 x 60   100 x 60 x 60   70 x 50 x 100 cm.</li> <li>– Proportion of water in the total area (%): 0–100 (often as a moat, complete soil area can be flooded during irrigation).</li> <li>– Bottom substrate: organic (island of aquarium gravel, pine bark, leaves, inorganic (foam, filter sponge (n=2) or no substrate (n=3), additionally individual fist-sized moss-covered river pebbles (n=1), paper towel (n=1).</li> <li>– Furnishing/planting: <i>Philodendron</i> (n=6), also other tropical plants such as anthuriums, <i>Monstera</i> spp., vanilla, bromeliads (<i>Neoregelia</i> sp.), various vines, which either grow epiphytically on cork, coconut, tree ferns or Hygrolon® gauze or in pots.</li> <li>– Water depth (cm): 0–4 (n=4)   7–9 cm (n=1).</li> <li>– Number of animals per container: 1–10.</li> <li>– Feed/feeding intervals: every night   1 x/ week   2 x/ week (n=3)   3 x/ week (n=2).</li> <li>– Supplementation (minerals/vitamins): yes, but not specified (n=2)   calcium, omega-3 fatty acids, vitamins   Repashy Calcium plus   Repashy Supervit, Repashy Vit A   Ranarium Rana Vit, Dendrocare   Herpetal Amphib.</li> <li>– Aggression between several ♂♂ or ♀♀: temporary during the breeding season between ♂♂ (n=3)   none (n=2).</li> </ul> |
| Life expectancy                                                                                              | Maximum age of the animals kept (in years): 6   6–7   7–8.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Triggers for reproduction                                                                                    | <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): Feed pollinated crickets and fruit flies regularly. Terrarium floor covered with water only, with the exception of one or more (depending on tank size) upturned clay pots, each with a pot of <i>Epipremnum aureum</i> placed on top to create islands (these often quickly overgrow the tanks so that there are plenty of places to hide, spawn and hunt)   rain chamber (tempered to approx. 22–25°C)   more humid husbandry and sprinkling in the normal terrarium (n=2)   spontaneous release of clutches (n=2)   ambient noise (with calling) from the natural habitat.</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom or tip of the leaf)? Leaves (n=3), leaves and glass panes (n=2), <i>Philodendron</i> leaves were the most frequently used deposition sites, whereby the clutches were mostly placed in the centre on the upper side of the leaf (n=4), in one breeder on both sides of the leaf and additionally on moss cushions, stems and twigs.</p> <p>How is the clutch structured? Simple layer (monolayer), complex clutch, other (how?): Single-layer clutch with eggs embedded in abundant sticky jelly (n=3), which develop into a complex clutch by swelling and then hang down from the leaf or branch structure (n=2).</p> <p>Number of clutches per ♀ in one oviposition: 1 (n=5).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |

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|                                                                           | <p>Number of clutches/♀/year (min.–max.): 2–5 (n=1)   4–6 (n=1)   one clutch every 14 d (n=1; mostly induced by irrigation, occasionally spontaneous).</p> <p>Number of eggs/clutch (min.–max.): 20–30   approx. 20–40   30–60   13–34 (n=6).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Number of fertilised eggs per clutch (min.–max.)                          | 27–60 (90–100%)   5–30   10–30   20–30   0–100%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Number of embryos hatched per clutch (min.–max.)                          | 27–60   5–25   5–30   12–18   0–100%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Hatching rate (number of hatched larvae/number of eggs)                   | <p>Hatching rate (number of hatched larvae/number of eggs) or &lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%: &gt; 75%:</p> <p>initially close to 100%, later in some ♀♀ partly 0% (n=2)   &lt; 25–100%   &gt; 50–75%   &gt; 75%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Size of juvenile frogs (freshly metamorphosed; min.–max. [in mm])         | 7–8 mm   about 10 mm   10–12 mm.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Number of metamorphosed juvenile frogs per year                           | 10–100   0–30.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Number of rearing losses up to the 3 <sup>rd</sup> month                  | 0%   < 1%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Husbandry conditions (larvae) / Technical requirements for larval rearing | <p>For general information on larval rearing see above (chapter General Information on Glass Frogs).</p> <p>Total length of newly hatched larvae (in mm): 7   10   10–11   10–12.</p> <p>Duration of larval period (oviposition to metamorphosis; min.–max. [in months]): 3–5 (n=1)   2–6 (n=1; shortest time 56 days, Eisenberg, unpublished data).</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements): observed differences in location: successful rearing in plastic tubs with some moss and weekly water changes (aged water with some rooibos tea) no longer worked at the new location, but then rearing was successful again in a small, well-established aquarium; the time to metamorphosis was much longer, but the young were also larger. The tadpoles were mainly fed with food for tropical fish, but (wet) cat food was also eagerly accepted (n=1)   hygienic husbandry with frequent cleaning of the terrarium and the tadpole water (daily). Need for special lamps with UV-A and UV-B light, daily feeding (n=1)</p> <p>– Water temperature (in°C): Room temperature   19–22   20–25   22–28 (n=2).</p> <p>– Lighting/type/day-night cycle: indirect by daylight (n=3)   50 W LED strip (12 h) and daylight/UV fluorescent lamps (6.5 h).</p> <p>– Tank size (length x width x height in cm): 30 x 20 x 20 (n=2)   40 x 20 x 20   40 x 25 x 25   50 x 13 x 29 cm.</p> <p>– Substrate/furnishing/planting: Gravel, wood and aquarium plants (mainly mosses)   lava granules or no substrate at all, clay bricks and flower pots as hiding places, Java moss (n=2)   lava granules of various grain sizes, leaves, river pebbles   sand, coarse gravel, leaves.</p> <p>– Water depth (in cm): 18 (n=2)   20   25.</p> <p>– Number of animals per tank: 5–30   20–25   10–50   5–100 (n=2).</p> <p>– Filter (type, performance): Airlift sponge filter (n=2)   Nano corner filter, 2W   no filter (n=2).</p> <p>– Special requirements (e.g. water values): acidified with humic acids   dissolved oxygen above 6 mg/l and water with a temperature between 19 and 22°C.</p> |

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|                                                                         | <p>– Food for the larvae: various fish foods, wet cat food   spinach, Repashy fish food Super Green, Tetramin catfish tablets (n=2)   food tablets for carnivorous and herbivorous fish, cooked mushrooms, spinach, lettuce.</p> <p>– Frequency of water changes: only topping up the aquarium water without changing the water   every 2–4 d   50–80% 1 x/ week   90% 1 x/ week   1 x/ month (n=2).</p> <p>– Type of water (rainwater, tap water, RO water, etc.): 50% reverse osmosis (RO) water: 50% tap water   100% tap water (n=2)   90% : 10% tap water   50% tap water: 50% distilled water   stream water (laboratory).</p> |
| Number or percentage of offspring that become adults or sexually mature | ~50%   > 99% (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Age/size at sexual maturity                                             | ♂♂: at 5–6 months   at 8–10 months,<br>♀♀: at 7–8 months   at 10–12 months.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Indicators for reaching sexual maturity                                 | Calls, amplexus, ovipositions/ovaries/calls, vasa deferentia, transabdominally visible dark follicles in front of the cloaca.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Sex ratio of the offspring (♂♂:♀♀)                                      | ~1:1 (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Evidence of deformities or diseases                                     | One missing eye formation in one frog out of hundreds (n=1)   none (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Mortality of larvae up to metamorphosis                                 | Mortality of larvae up to metamorphosis (< 25%; 25–50%; > 50–75%; > 75%) or estimated: high/low:<br>0–70%   < 20%   25–50%   50–75%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Mortality in the first months/years of life after metamorphosis         | Very low (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Routine testing for amphibian diseases and parasites                    | No (n=4)   annual testing for <i>B. dendrobatidis</i> using real-time PCR (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Quarantine (type and extent)                                            | No (n=2)   yes, for 1 (n=1), for 4–6 months (n=1) <sup>13</sup> .                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| General characteristics, difficulties with keeping and breeding         | Larval rearing sometimes difficult/relatively robust glass frogs.<br>Assessment of the frequency of husbandry: rare (n=5).<br>Personal assessment of the difficulty of breeding in husbandry: very easy to keep, but breeding can be complicated (n=2)   relatively easy (compared to other glass frogs)   easy husbandry.                                                                                                                                                                                                                                                                                                           |
| Frequency of private breeding and reproduction in zoos                  | see Assessment of the frequency of husbandry; an extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists two (extinct) entries between 1996 and 2005 as holders of <i>E. prosoblepon</i> (T. Eisenberg, unpublished data).                                                                                                                                                                                                                                                                                                                                                                   |

<sup>13</sup> Small, sterile terrariums (e.g. 30 x 60 x 20 cm with front and lid wire gauze ventilation) with climbing plants (Philodendron spp.) without substrate are suitable for this purpose. A moat with overflow serves as a water reservoir. The quarantine should last at least 8 weeks and up to 6 months. During this time, PCR tests are carried out for *Batrachochytrium dendrobatidis*, *Batrachochytrium salamandrivorans*, *Ranavirus*, *Chlamydia* and *Brucella* as well as coproscopic tests for parasites (T. Eisenberg, unpublished data).

|                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|-----------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Reproduction in captivity up to F2 generation | Yes (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Commercial breeding                           | No (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Interviews/ Surveys/ Consultations            | <p>Six participants took part in the survey on <i>E. prosoblepon</i>. Five of them stated that they were private owners, one participant from Costa Rica kept the frogs for research purposes in the laboratory at the Universidad Nacional (UNA) there. Six participants were certain or very certain that the species was correctly identified, whereby the species identification was mostly made by the dealer   in collaboration with other specialists   based on their own knowledge and the latest literature   based on the origin of the animals or based on the known location of the animals or the parents. Almost all of the animals kept were labelled as captive-bred, and on one occasion they were wild-caught. The duration of husbandry was stated as between one and 14 years, although two keepers have since ceased husbandry and the animals kept for research purposes were not used for further breeding. All other keepers stated that they were endeavouring to breed offspring, with all of them having successfully laid eggs at least once and more than 30 times. The first offspring were bred in 2010   2011   2020   2021   2023.</p> |

***Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991**

| Species                                  | Original description                                                                                                       | Common name                            | Common name international          | Known/ documented in international trade                                        |
|------------------------------------------|----------------------------------------------------------------------------------------------------------------------------|----------------------------------------|------------------------------------|---------------------------------------------------------------------------------|
| <i>Hyalinobatrachium adespinosai</i>     | Guayasamin, Vieira, Glo & Hutter, 2019                                                                                     | Adela's Glassfrog                      |                                    | No                                                                              |
| <i>Hyalinobatrachium anachoretus</i>     | Twomey, Delia & Castroviejo-Fisher, 2014                                                                                   |                                        |                                    | No                                                                              |
| <i>Hyalinobatrachium aureoguttatum</i>   | (Barrera-Rodriguez & Ruíz-Carranza, 1989)                                                                                  | Sun Glassfrog                          | Rana de cristal de manchas doradas | Yes                                                                             |
| <i>Hyalinobatrachium bergeri</i>         | (Cannatella, 1980)                                                                                                         | Berger's Glass Frog                    |                                    | No                                                                              |
| <i>Hyalinobatrachium cappellei</i>       | (Van Lidth de Jeude, 1904)                                                                                                 | Banded-Limb Glassfrog                  |                                    | Yes, allegedly kept sporadically in the USA, imports to Europe only included ♂♂ |
| <i>Hyalinobatrachium carlesvilai</i>     | Castroviejo-Fisher, Padial, Chaparro, Aguayo & De la Riva, 2009                                                            | White-Hearted Glass Frog               |                                    | No                                                                              |
| <i>Hyalinobatrachium chirripoi</i>       | (Taylor, 1958)                                                                                                             | Suretka Glass Frog, Chirripó Glassfrog |                                    | No                                                                              |
| <i>Hyalinobatrachium colymbiphyllum</i>  | (Taylor, 1949)                                                                                                             | Plantation Glass Frog                  |                                    | No                                                                              |
| <i>Hyalinobatrachium diana</i>           | Kubicki, Salazar & Puschendorf, 2015                                                                                       | Diane's Bare-Hearted Glassfrog         |                                    | No                                                                              |
| <i>Hyalinobatrachium duranti</i>         | (Rivero, 1985)                                                                                                             | Durant's Glass Frog                    |                                    | No                                                                              |
| <i>Hyalinobatrachium esmeralda</i>       | Ruíz-Carranza & Lynch, 1998                                                                                                |                                        |                                    | No                                                                              |
| <i>Hyalinobatrachium fleischmanni</i>    | (Boettger, 1893)                                                                                                           | Fleischmann's Glass Frog               | Fleischmanns Glasfrosch            | Yes                                                                             |
| <i>Hyalinobatrachium fragile</i>         | (Rivero, 1985)                                                                                                             | Fragile Glass Frog                     |                                    | No                                                                              |
| <i>Hyalinobatrachium guairarepanense</i> | Señaris, 2001                                                                                                              | El Ávila Glass Frog                    |                                    | No                                                                              |
| <i>Hyalinobatrachium iaspidiense</i>     | (Ayarzagüena, 1992)                                                                                                        | Yuruani Glass Frog, Jaspe Glass Frog   |                                    | Yes (CITES 2022); imports to Europe only included ♂♂                            |
| <i>Hyalinobatrachium ibama</i>           | Ruíz-Carranza & Lynch, 1998                                                                                                |                                        |                                    | No                                                                              |
| <i>Hyalinobatrachium kawense</i>         | Castroviejo-Fisher, Vilà, Ayarzagüena, Blanc & Ernst, 2011                                                                 |                                        |                                    | No                                                                              |
| <i>Hyalinobatrachium mashpi</i>          | Guayasamin, Brunner, Valencia-Aguilar, Franco-Mena, Ringler, Medina Armijos, Morochz, Bustamante, Maynard & Culebras, 2022 | Mashpi Glassfrog                       |                                    | No                                                                              |



|                                        |                                                                                                                            |                                                                         |                          |                                                      |
|----------------------------------------|----------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------|--------------------------|------------------------------------------------------|
| <i>Hyalinobatrachium mesai</i>         | Barrio-Amorós & Brewer-Carías, 2008                                                                                        | Sarisariñama Glass Frog                                                 |                          | No                                                   |
| <i>Hyalinobatrachium mondolfii</i>     | Señaris & Ayarzagüena, 2001                                                                                                |                                                                         |                          | Yes (CITES 2022 [based on unverifiable information]) |
| <i>Hyalinobatrachium muiraquitana</i>  | Oliveira & Hernández-Ruz, 2017                                                                                             | Muñoz's Glassfrog                                                       |                          | No                                                   |
| <i>Hyalinobatrachium munozorum</i>     | (Lynch & Duellman, 1973)                                                                                                   | Upper Amazon Glass Frog<br>Munoz's Glassfrog                            |                          | No                                                   |
| <i>Hyalinobatrachium nouns</i>         | Guayasamin, Brunner, Valencia-Aguilar, Franco-Mena, Ringler, Medina Armijos, Morochz, Bustamante, Maynard & Culebras, 2022 | Nouns' Glassfrog                                                        |                          | No                                                   |
| <i>Hyalinobatrachium orientale</i>     | (Rivero, 1968)                                                                                                             | Eastern Glass Frog                                                      |                          | No                                                   |
| <i>Hyalinobatrachium orocostale</i>    | (Rivero, 1968)                                                                                                             |                                                                         |                          | No                                                   |
| <i>Hyalinobatrachium pallidum</i>      | (Rivero, 1985)                                                                                                             | Guacharaquita Glass Frog                                                |                          | No                                                   |
| <i>Hyalinobatrachium pellucidum</i>    | (Lynch & Duellman, 1973)                                                                                                   | Andean Glassfrog,<br>Río Azuela Glass Frog                              | Rana de cristal fantasma | No                                                   |
| <i>Hyalinobatrachium talamancae</i>    | (Taylor, 1952)                                                                                                             | Talamanca Glass Frog                                                    |                          | No                                                   |
| <i>Hyalinobatrachium tatayoi</i>       | Castroviejo-Fisher, Ayarzagüena & Vilà, 2007                                                                               |                                                                         |                          | No                                                   |
| <i>Hyalinobatrachium taylori</i>       | (Goin, 1968)                                                                                                               | Taylor's Glass Frog                                                     |                          | No                                                   |
| <i>Hyalinobatrachium tricolor</i>      | Castroviejo-Fisher, Vilà, Ayarzagüena, Blanc & Ernst, 2011                                                                 |                                                                         |                          | No                                                   |
| <i>Hyalinobatrachium valerioi</i>      | (Dunn, 1931)                                                                                                               | Reticulated Glass Frog,<br>Valerio's Glass Frog,<br>La Palma Glass Frog | Genetzter Glasfrosch     | Yes                                                  |
| <i>Hyalinobatrachium vireovittatum</i> | (Starrett & Savage, 1973)                                                                                                  | Starrett's Glass Frog                                                   |                          | No                                                   |
| <i>Hyalinobatrachium viridissimum</i>  | (Taylor, 1942)                                                                                                             | Northern Glassfrog                                                      |                          | No                                                   |
| <i>Hyalinobatrachium yaku</i>          | Guayasamin, Cisneros-Heredia, Maynard, Lynch, Culebras & Hamilton, 2017                                                    | Yaku Glassfrog                                                          |                          | No                                                   |

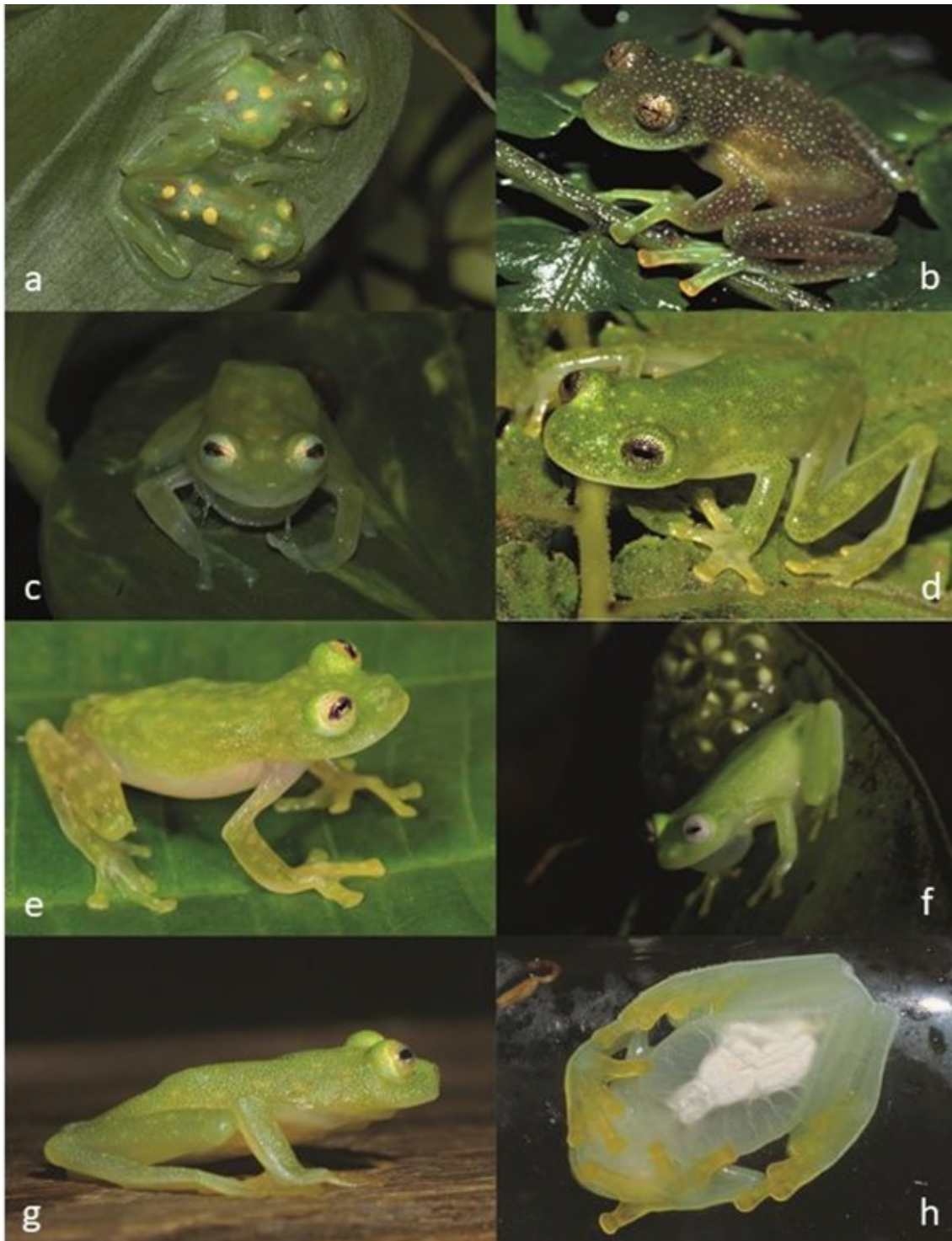


Fig. 47: *Hyalinobatrachium* species

- a *H. aureoguttatum*; note the greenish eggs visible through the dorsal skin in the female at the top of the picture (R. Stuster)
- b *H. bergeri*, Bolivia (J. Köhler)
- c *H. capellei*; this frog is eating its skin while moulting at the beginning of the activity period (R. Stuster)
- d *H. carlesvilai*, Peru (J. Köhler)
- e *H. columbiphyllum*, Costa Rica (T. Leenders)
- f *H. diana*, Costa Rica (C. Barrio Amorós)
- g *H. fleischmanni* (A. Kwet)
- h *H. fleischmanni*, underside (A. Kwet).



Fig. 48: *Hyalinobatrachium* species II

- a *H. lemur* (M. Dobiey)
- b *H. pellucidum* (C. Koch)
- c *H. talamancae* (T. Leenders)
- d *H. tatayoi* (T. Leenders)
- e *H. valerioi* (F. Hulbert)
- f *H. vireovittatum* (T. Leenders).

### Morphology and Taxonomy

The genus name *Hyalinobatrachium* is composed of the Greek words 'hyalos' (= glass) and 'batrachion' (= frog) and is characterised by the following features:

In the comprehensive revision of the Centrolenidae (Guayasamin et al. 2009), the genus *Hyalinobatrachium* was redefined on the basis of morphological and molecular data and found to be monophyletic. The genus, which belongs to the subfamily Hyalinobatrachinae, currently contains 38 species. Most *Hyalinobatrachium* spp. are characterised by the following features: (1) no humeral spines, (2) digestive tract and bulbous liver covered by a white (iridophore-



studded) peritoneum, (3) completely transparent ventral parietal peritoneum, (4) white bones in life (exceptions: green in *H. mesai* and *H. taylori*), (5) dorsal colouration fades to white or cream in preservative, (6) ♂♂ without conspicuous spiny dorsal structures during the reproductive period, (7) if present, nuptial excrescences small and restricted to the inner margin of finger I in ♂♂, (8) no tooth-like projection and no denticles on the vomer (ploughshare-like bone), (9) ♂♂ usually call from the underside of the leaf (exception *H. taylori*), and ♀♀ also lay single-layered clutches on the underside of leaves, (10) complete fusion of the forearm bones (tibial and fibular). The genus can be easily distinguished from most other glass frog genera by features (1) and (3), only *Vitreorana* and some *Teratohyla* spp. show some of the features mentioned. However, *Teratohyla* spp. and *Vitreorana* spp. usually have green bones and both genera call and spawn on upper leaf surfaces. Some members of the sister genus *Celsiella* call (*Celsiella revocata*, *Centrolene peristicta*) and spawn (*Celsiella revocata*, *Centrolene antioquiense*, *C. peristictum*) equally on the undersides of leaves. Further characteristics of the Hyalinobatrachinae (*Hyalinobatrachium* and *Celsiella*) include (1) an amplexus-like clasping of two ♂♂ during intra-species territorial behaviour, in which the opponent is thrown off the leaf by hind leg kicks, (2) ♂♂ of *C. revocata* also call from the undersides of leaves, (3) ♀♀ of *C. revocata* spawn on the upper and lower leaf surfaces, (4) male brood care (guarding and moisturising the clutch) in numerous *Hyalinobatrachium* spp, but also in *C. vozmediano*i. The members of the genus *Hyalinobatrachium* have a wide distribution area, which includes tropical Central America, the tropical Andes, the Cordillera de la Costa in Venezuela, the island of Tobago, the upper Amazon basin and the Guiana Shield up to altitudes of 2,500 m asl.

The species in this group can be identified by the following combination of characteristics (although molecular identification is recommended for definitive species identification):

*Hyalinobatrachium adespinosai*: yellow-green to bright green dorsal colour with grey-black and some yellow spots, SVL ♂♂ 20.5–22.2 mm, ♀♀ unknown. Head wider than long, mouth region truncated in plan and profile, eyes small, anterolaterally aligned, iris pale yellow, tympanum faintly visible through the skin, tongue round, glottis extends along the base of the mouth parallel to the tongue, no glands on the underside of the upper jaw, finger and toe discs round, interdigital membranes slightly pronounced (variable), slender hind legs, transparent peritoneum on pericardium, kidneys, gall bladder and urinary bladder, kidneys round and bean-shaped, peritoneum on liver and intestinal tract white, morphologically similar to *H. anachoretus* (larger interdigital skin) and *H. pellucidum* (sister species) as well as *H. esmeralda*, but distinguishable by call parameters (Guayasamin et al. 2019a).

*Hyalinobatrachium anachoretus*: apple-green dorsal colour with irregular diffuse yellow dots and small, dark green melanophores, arms and legs pale green and mottled yellow (without melanophores), finger and toe discs pale orange, flanks white, granulated dorsal skin, especially laterally on the head, SVL ♂♂ 20.6–21.4 mm, ♀♀ unknown. Mouth region truncated in plan and profile, iris creamy white with irregular dark spots, especially around the pupil, tympanum barely visible through the skin, transparent peritoneum on pericardium, gall bladder and urinary bladder, distinct central ventral vein, medial third of kidneys transparent, lateral two thirds covered in white, white peritoneum on liver, testes and gastrointestinal tract. Similar species: *H. colymbiophyllum*, *H. chirripoi*, *H. bergeri*, *H. carlesvilai*, *H. esmeralda*, *H. ibama*, *H. mondolfii*, *H. munozorum*, *H. pellucidum*, *H. adespinosai* (Twomey et al. 2014).

*Hyalinobatrachium aureoguttatum*: small greenish yellow glass frog, SVL ♂♂ 20.4–24.0 mm, ♀♀ 22.9–23.9 mm, head wider than long, short, rounded mouth region in top view, mouth truncate in profile, rostral margin rounded and slightly protruding, visceral peritoneum white

on stomach, intestines and testes, transparent peritoneum on kidneys, gall bladder and urinary bladder, heart visible red (variable), iris centrally silver, marginally yellow with numerous black dots, dorsally 2–7 large yellow spots (diameter 0.5–2.1 mm) and with or without brown spots (in Colombian populations) to distinguish from all other *Hyalinobatrachium* spp. , resembles *H. tatayoi* (but eardrum clearly separated from the surrounding skin and a ventrally visible red heart), broad fingers (length  $II < I < IV < III$ ), sister species *H. valerioi*.

*Hyalinobatrachium bergeri*: see *H. carlesvilai*, but pericardium at least partially transparent and a dark grey ring around the pupil present, SVL ♂♂ 20.3–22.4 mm, occurs sympatrically and in high density with *H. carlesvilai*, both species are very similar, phylogenetically different populations, possibly also other cryptic undescribed species.

*Hyalinobatrachium cappellei*: medium-sized, lime-green glass frog with yellow and brownish spots, SVL ♂♂ 18.6–24.9 mm, ♀ 21.3 mm (n=1), mouth region truncated and dorsal, head broad, iris yellow with brown spots, sometimes with incomplete, reddish-brownish ring around the pupil, tympanum indistinct, pericardium translucent to white. In addition to *H. cappellei*, three other species, *H. crurifasciatum*, *H. eccentricum* and *H. igniocus*, were previously distinguished on the basis of colour variations on the body and iris, but these could not be confirmed on a molecular basis. The sister clade to *H. cappellei* consists of *H. iaspidiense* and *H. tricolor* (Castroviejo-Fisher et al. 2011).

*Hyalinobatrachium carlesvilai*: green glass frog with fine yellow speckles and tiny melanophores, SVL ♂♂ 20.6–23.9 mm, ♀♀ 23.2 mm (n=1), mouth region truncated dorsally and in profile, iris cream-coloured with small dark spots. Tympanum indistinct, peritoneum on pericardium, liver and viscera covered with white iridophores, confusion with *H. munozeorum* and *H. bergeri* in the past, also similar are *H. fleischmanni* and *H. tatayoi* (Castroviejo-Fisher et al. 2009).

*Hyalinobatrachium chirripoi*: medium-sized, dorsally green glass frog with yellow spots, SVL ♂♂ 24–26 mm, head wider than long, mouth region indented to blunt at tip in top view, round in profile, iris golden coloured, nostrils open in fleshy protuberances and end in clearly raised ridges, tympanum indistinct, finger I longer than finger II, interdigital membranes especially between fingers II and III clearly developed (in contrast to the closely related *H. colymbiophyllum*), finger and toe discs truncate, liver and digestive tract covered by white peritoneum, pericardium transparent (Savage 2002).

*Hyalinobatrachium colymbiophyllum*: medium-sized, dorsally light green frog with yellow spots, SVL ♂♂ 23–27 mm, ♀♀ 24.5–29 mm, protruding eyes, mouth region truncate in profile, dorsally with notched tip, iris gold-coloured, nostrils open in fleshy protuberances and end in clearly raised ridges, tympanum indistinct, peritoneum of the pericardium transparent, limbs white underneath, finger I longer than finger II. Very similar to *H. chirripoi*, distinguishing feature: interdigital membranes weakly developed especially between fingers II and III (Savage 2002).

*Hyalinobatrachium diana*: medium-sized, lime-green glass frog without yellow dots, dorsal granules slightly lighter, SVL ♂♂ 27.8–29.4 mm, ♀♀ 28.0 mm (n=1), head width slightly larger than body width, mouth region round dorsally, eyes aligned frontally, iris white with tiny dark spots, especially around the pupil, nostrils arranged sideways, tympanum not visible, skin on skull, body and legs rough on the upper side, smooth on the chin, hands and feet pale greenish yellow, dorsally in the pelvic region (mostly left of the medians) under the skin an elongated to round black structure, whose meaning is unclear, liver and digestive tract covered by white



peritoneum, heart, vena cava and vessels of the lungs visibly blood-filled from ventral side, gall bladder yellow and transparent, arms relatively short with large hands, interdigital membranes between fingers I and II absent, between fingers II and III slightly and fingers III and IV moderately pronounced, legs relatively long, sister species to *H. chirripoi* and *H. colymbiphylum* (Kubicki et al. 2015).

*Hyalinobatrachium duranti*: dorsal colouration light to apple green, mottled with fine, almost black or dark brown dots and yellowish zones, two light yellow dorsolateral lines that appear to be under the skin, same fine punctation on upper side, dorsal skin slightly granular, SVL ♂♂ 21.1–23.8 mm, ♀♀ 22.4–24.6 mm, head wider than long and wider than body, eye margins light yellowish, light brown iris, arms and legs light green, translucent with fine speckles, abdomen very light and translucent green, yellowish fingers, all internal organs covered with white peritoneum (Señaris & Ayarzagüena 2005).

*Hyalinobatrachium esmeralda*: small glass frog with light green dorsum with yellowish speckles, dorsal skin very finely granular, SVL ♂♂ 18.4–22.3 mm, ♀♀ 21.2–22.4 mm, iris golden coloured with brown spots, tympanum barely visible, peritoneum of pericardium translucent, visceral peritoneum white, rutting nuptial excrescences not visible, similar to *H. cappellei* (Ruiz-Carranza & Lynch 1998).

*Hyalinobatrachium fleischmanni*: small to medium-sized glass frog with pale green dorsal colouration and yellow-greenish spots, SVL ♂♂ 19.2–25.5 mm, ♀♀ 23–32 mm, flattened body, broad head, rounded mouth region, frontally aligned eyes, iris gold-coloured with horizontal elliptical pupil, heart, anterior half of liver and gastrointestinal tract covered by white peritoneum, fingertips yellow (Wild 2003a, Leenders 2001, 2016, Guyer 2005, Savage 2002).

*Hyalinobatrachium fragile*: small to medium-sized species, green dorsal colouration with tiny yellow dots and occasional dark melanophores, SVL ♂♂ 18.9–21.6 mm, ♀♀ 19.1–24.5 mm, head as wide as body or slightly wider and broader than long, iris golden yellow, tympanum not visible, translucent pericardium, white liver and visceral peritoneum (Señaris & Ayarzagüena 2005).

*Hyalinobatrachium guairarepanense*: dorsal colouration in life light green, SVL ♂♂ 21.4–23.6 mm, head slightly wider than body, mouth region in dorsal view and in profile roundish blunted, iris very light yellow, small but visible tympanum, pericardial, visceral and hepatic peritoneum white (Señaris & Ayarzagüena 2005).

*Hyalinobatrachium iaspidiense*: pale green dorsal colouration with bright lime green spots and many smaller irregular black dots and melanophores, white stripes on the forearms and legs, SVL ♂♂ 20 mm, head wider than body, mouth region round in top view, truncate in profile, iris white with black melanophores, bones pale green, pericardium transparent, peritoneum on liver and gastrointestinal tract white, dorsal skin slightly granulated, tympanum not visible, similar species: *H. fleischmanni*, *H. igniocus*, *H. taylori*, the species *H. nouraguense* was synonymised with *H. iaspidiense*. Despite morphological similarity of the individuals within the large distribution area, preliminary genetic analyses indicate cryptic species (Lescure & Marty 2000, Barrio-Amorós & Brewer-Carias 2008, Guayasamin et al. 2008a, Yáñez-Muñoz et al. 2009).

*Hyalinobatrachium ibama*: dorsum pale yellowish green in life with yellow speckles and fine black spots, dorsal skin granular, SVL ♂♂ 19.9–23.4 mm, ♀♀ 21.3–23.5 mm, mouth region rounded in dorsal view, truncate in lateral view, head as wide as body, wider than long, eyes

small, directed anterodorsally, iris golden coloured with fine brown speckles, protruding nostrils, tympanum inconspicuous, small, not prominent, visceral and pericardial peritoneum white, hands and feet yellow (Ruiz-Carranza & Lynch 1998).

*Hyalinobatrachium kawense*: small glass frog with green ground colour and small yellow as well as tiny to small black spots, dorsal skin smooth, ventral skin granulated, SVL ♂♂ 19.9–20.0 mm, ♀ 20.0 mm (n=1), mouth region truncate dorsally and in profile, iris gold-coloured towards the pupil, a black and white network at the edge, tympanum not visible, pericardial, hepatic and visceral peritoneum white, all others transparent, tips of fingers and toes white. Similar species: *H. carlesvilai*, *H. fleischmanni* and *H. tatayoi* (Castroviejo-Fisher et al. 2011).

*Hyalinobatrachium mashpi*: small, apple to yellow-green glass frog above with pale yellow dots (may fuse dorsally between eyes as an interorbital line), SVL ♂♂ 19.7–20.9 mm, ♀♀ unknown, mouth region truncated dorsally, slightly protruding in profile, tympanum almost horizontally extended, peritonea on pericardium (red heart visible), gall and urinary bladder transparent, those on liver, testes and gastrointestinal tract white, iris golden yellow with tiny lavender-coloured melanophores. Similar species: *H. aureoguttatum*, *H. talamancae*, *H. valerioi*, *H. vireovittatum* and *H. nouns* (Guayasamin et al. 2022).

*Hyalinobatrachium mesai*: small, pale green glass frog, dorsally and on limbs with large lime green spots studded with homogeneous black melanophores and larger black spots, SVL ♂♂ 20.0 mm, mouth region rounded in dorsal view, blunted in lateral view, iris white with an abundance of black melanophores, tympanum not visible, tympanic region almost vertically aligned, bones pale green in life (important distinguishing feature), pericardium transparent, liver and intestinal peritoneum white. Similar species: *H. iaspidiense*, *H. mondolfii*, *H. orientale*, *H. cappellei*, *H. taylori* (Barrio-Amorós & Brewer-Carias 2008).

*Hyalinobatrachium mondolfii*: light green glass frog with tiny yellow dots, fore and hind extremities uniformly green, slightly lighter than dorsal, finger and toe discs greenish yellow, SVL ♂♂ 20.3–22.5 mm, ♀♀ unknown, head slightly broader than body, wider than long, mouth region rounded in dorsal view and oblique in lateral view, eyes small and not very pronounced, directed anterolaterally, iris golden to yellowish bronze in colour with very fine reticular structures, dorsal skin very granular, pericardium, visceral and hepatic peritoneum white. Similar species: *H. munozorum* (Señaris & Ayarzagüena 2001).

*Hyalinobatrachium muiraquitán*: small light green glass frog with small yellow dots and tiny black melanophores (also on arms and legs), SVL ♂♂ 19.2–19.6 mm, ♀♀ 20.0–21.8 mm (data contradictory), mouth region round dorsally, truncate in profile, tympanum hidden behind skin fold, peritonea on pericardium and liver white, on gall bladder yellowish, all others transparent, iris golden yellow with grey melanophores on pupil, finger and toe discs yellow (exception: toe I white). Sister species: *H. mondolfi*, *H. munuzorum*, other similar species: *H. cappellei*, *H. iaspidiense* (Oliveira & Hernández-Ruz 2017).

*Hyalinobatrachium munozorum*: small, light green frog with yellow and tiny dark brown to black dots on dorsum, dorsal skin slightly granular, SVL ♂♂ 19.9–21.9 mm, ♀♀ 20.9–23.6 mm, mouth region blunt when viewed dorsally, rounded when viewed laterally, iris pale golden with tiny dark dots, tympanum usually small because covered by skin fold, peritonea on pericardium (in some individuals the iridophore layer is thin), liver, digestive tract and testes white, urinary bladder transparent, bones green, toe discs blunted. Sister species: *H. mondolfii*, other similar species: *H. carlesvilai*, *H. bergeri*, *H. iaspidiense*, *Chimerella mariaelenae*,

*Teratohyla ameliae*, meanwhile *H. ruedai* has been placed in the synonymy of *H. munozorum* (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Hyalinobatrachium nouns*: small, apple to yellow-green glass frog with light yellow dots above (may fuse dorsally between the eyes as an interorbital line), SVL ♂♂ 19.1–21.3 mm, ♀♀ unknown, mouth region truncate dorsally, slightly protruding in profile, tympanum almost horizontally extended, peritonea on pericardium (red heart visible), gall and urinary bladder transparent, those on liver, testes and gastrointestinal tract white, iris golden yellow with tiny lavender-coloured melanophores. Morphologically indistinguishable from the species *H. mashpi*, from which it is only separated by a (linear) distance of 18.9 km across the Río Intag-Guayllabamba valley. Similar species: *H. aureoguttatum*, *H. talamancae*, *H. valerioi*, *H. vireovittatum* and *H. mashpi* (Guayasamin et al. 2022).

*Hyalinobatrachium orientale*: small glass frog with green dorsal colouration, with or without small yellow dots and black melanophores, SVL ♂♂ 19.8–22.4 mm, ♀♀ 23.6 mm (n=1), head slightly wider than the body and wider than long, pale yellow iris, invisible eardrum. Venezuelan populations were subdivided into *H. orientale* and *H. orocostale* on the basis of phylogenetic, morphological and bioacoustic studies. Populations from Venezuela and Tobago differ genetically, which has led to the differentiation of the two subspecies *H. orientale orientale* (mainland) and *H. orientale tobagense* (Hardy 1984, Jowers et al. 2014).

*Hyalinobatrachium orocostale*: s. *H. orientale*. Formerly placed in the synonymy of *H. orientale*, now independent. Sister species: *H. fragile*, *H. orientale* (Castroviejo-Fisher et al. 2009, Jowers et al. 2014).

*Hyalinobatrachium pallidum*: small glass frog with green dorsal colouration and small fine speckled melanophores and yellowish round interspaces, SVL ♂♂ 21.9–22.4 mm, ♀♀ unknown, head wider than body, with pronounced postcephalic constriction, rostrum short, truncate in dorsal and lateral view, iris yellow-bronze, also speckled with melanophores, tympanum small but visible, pericardium transparent, peritonea on liver and gastrointestinal tract white. Closely related species: *H. ibama* (Guayasamin et al. 2009, Castroviejo-Fisher et al. 2014).

*Hyalinobatrachium pellucidum*: small glass frog with pale green, granulated dorsal colouration and diffusely distributed yellow dots, fingers and toes yellow, SVL ♂♂ 19.8–22.0 mm, ♀♀ 21.6–22.0 mm, mouth region truncate in dorsal view, iris bronze-coloured, tympanum partially visible, liver and gastrointestinal tract covered by white peritoneum, urinary bladder and pericardium translucent (red heart visible). Similar species: *H. munozorum*, *H. yaku*. *H. lemur* (now synonymised with *H. pellucidum*; Castroviejo-Fisher et al. 2009, Frost 2024).

*Hyalinobatrachium talamancae*: medium-sized glass frog with a canary yellow dorsum and a greenish network that looks like yellow spots on a green background (smaller on head and nuchal area), a green dorsal median stripe on the back but no yellow paravertebral stripes, SVL ♂♂ 24–26 mm, ♀♀ 25–27 mm, broad head, mouth region rounded in profile, dorsally slightly pointed, iris gold-coloured with small black spots, nostrils prominent, tympanum indistinct, peritoneum on pericardium transparent (red heart visible), peritonea on liver and gastrointestinal tract white. Similar species: *H. fleischmanni*, *H. vireovittatum* (Savage 2002, Kubicki 2006).

*Hyalinobatrachium tatayoi*: small glass frog with green dorsal colouration and interspersed light yellow to greenish dots and spots, SVL ♂♂ 19.2–21.2 mm, ♀♀ 21.9 mm (n=1), mouth

region round in frontal view, truncate from lateral, large and prominent eyes, iris white to light yellow, tympanum almost completely obscured, peritoneum of pericardium and gastrointestinal tract white, tips of fingers and toes yellow. The species *H. tatayoi*, formerly endemic to Venezuela, now includes many populations previously classified as *H. fleischmanni* (from the Costa Rican lowlands to South America). Sister species: *H. fleischmanni*, other similar species: *H. munozorum*, *H. pellucidum*, *H. valerioi*, *H. chirripoi*, *H. viridissimum* (Castro-Viejo-Fisher et al. 2007, Mendoza-Henao et al. 2020).

*Hyalinobatrachium taylori*: small glass frog with dark green dorsum with light green spots usually with a white spot in the middle of each spot, finger and toe tips orange, SVL ♂♂ 18.1–19.4 mm, ♀♀ 20.6 mm (n=1), mouth region short, rounded from dorsal, truncate in profile, eye medium sized, iris grey with reticulate blackish brown to bronze reticulum, nostrils more lateral than superior, not protruding, tympanum very indistinct, about one third of the eye diameter, pericardial peritoneum white with small transparent areas, visceral and hepatic peritonea white, all other peritonea transparent, green bones (Goin 1968, Señaris & Ayarzagüena 2005, Castro-Viejo-Fisher et al. 2011).

*Hyalinobatrachium tricolor*: small glass frog with light green dorsum and larger irregular lime green spots, numerous brown tubercles and tiny melanophores, SVL ♂♂ 20.3–21.0 mm, ♀♀ unknown, mouth region truncate in top view and profile, tympanum covered by skin, pericardial peritoneum transparent, peritonea on liver and gastrointestinal tract white, all other peritonea including pericardium transparent, iris yellow with dark grey spots, tips of fingers and toes white. Similar species: *H. iaspidiense* (Castroviejo-Fisher et al. 2011).

*Hyalinobatrachium valerioi*: small glass frog with green back with large round yellow spots and small black dots (resembles an egg clutch in appearance), SVL ♂♂ 19.5–24.0 mm, ♀♀ 22.5–26 mm, head broad, mouth region truncate from dorsal and lateral, eyes not prominent, iris golden coloured, tympanum indistinct, heart translucent red from the outside, although pericardium, liver and gastrointestinal tract are covered by whitish peritonea, finger discs truncate. In Ecuador probably part of a species complex, sister species: *H. aureoguttatum* (McDiarmid 1978, Savage 2002; Leenders 2001, 2016, Solis et al. 2008, Guayasamin et al. 2020).

*Hyalinobatrachium vireovittatum*: medium-sized glass frog with green upper side and moderately large yellow spots and a distinct green mid-dorsal longitudinal stripe, which is laterally bordered by two yellow paravertebral stripes, SVL ♂♂ 21.5–23.0 mm, ♀♀ 24.0–25.0 mm, head wider than long, mouth region truncated dorsally and laterally, eyes not prominent, iris golden-coloured, tympanum indistinct and oriented dorsally, peritonea of liver and gastrointestinal tract white, pericardium transparent, finger discs truncated (Savage 2002, Leenders 2001, 2016).

*Hyalinobatrachium viridissimum*: small to medium-sized glass frog with green dorsal colouration and numerous yellow dots, fingers and toes yellow, SVL ♂♂  $21.7 \pm 1.6$  mm, ♀♀  $22.4 \pm 0.6$  mm, mouth region semicircular to round from dorsal, truncated laterally, iris creamy yellow to golden coloured with a dark reticulated pattern, visceral and pericardial peritoneum white (exceptions in some Mexican populations in Chiapas and Oaxaca). Separated from *H. fleischmanni* as a so-called northern clade on the basis of genetic, morphological and bioacoustic data as an independent species, exact boundary line currently unclear (especially in El Salvador). The morphological differences are altogether too little discriminatory to be considered here. Similar species: *H. fleischmanni*, *H. tatayoi*, *H. munozorum* (Mendoza-Henao et al. 2019, 2020).

*Hyalinobatrachium yaku*: small glass frog with apple to yellow-green dorsal colouration and numerous yellow dots and grey-black pigment cells on head and body, few dark green dots along midline between occiput and anterior half of body, decreasing in size posteriorly, SVL ♂♂ 20.8–22.3 mm, ♀♀ 21.1 mm (n=1), head wider than body, mouth region truncated laterally, iris silvery-yellow with a ring-shaped dark reticular pattern around the pupil, surface between eyes and slightly protruding and oval nostrils concave, visceral peritoneum white, peritonea on urinary bladder, kidneys and pericardium transparent (red heart and central vein visible). Reference is made to a possible sexual dimorphism, according to which ♀♀ are smaller than ♂♂ (eye diameter of ♂♂ 2.4–2.5 mm versus 1.6 mm in a ♀, leg lengths possibly smaller than in ♂♂). Sister species: *H. pellucidum*, other similar species: *H. anachoretus*, *H. talamancae* and *H. vireovittatum* (Guayasamin et al. 2017).

### Distribution and Habitat

*Hyalinobatrachium adespinosai*: only known from the type locality (Río San Jacinto, Tungurahua Province, Ecuador, 1,795 m asl). All individuals were found on leaf undersides along the river, which had several rapids in this area. The species lives in the canopy region, 4–16 m above the ground, and is therefore difficult to find, common species at the site (many calls) (Guayasamin et al. 2019a).

*Hyalinobatrachium anachoretus*: known from the vicinity of the type locality on the eastern slope of the Abra Patricia (watershed between the catchments of the Río Marañón and the Río Huallaga), from the vicinity of Puente Nieva, 2 km by road from the type locality, in the San Martín region and from El Tingo within the Concesión de Conservación Alto Huayabamba in the San Martín region, Perú (2,000–2,050 m asl). Cool cloud forests in the rainy highlands of the Alto Mayo River basin (Twomey et al. 2014).

*Hyalinobatrachium aureoguttatum*: western slopes of the Cordillera Occidental and eastern Cordillera Central in the departments of Chocó, Risaralda, Antioquia and Valle del Cauca, Colombia, Esmeraldas, Ecuador and Panama (Darién province) (45–1,560 m asl). Habitat in *Heliconia* spp. in primary and secondary forests at 1–7 m above smaller streams. Areas in Colombia are very rainy (7,000 mm rainfall/year), average temperature 25°C, relative humidity 78%, flow velocity 0.5 m/s (Valencia-Aguilar et al. 2012).

*Hyalinobatrachium bergeri*: Amazonian side of the Andes from the department of Cuzco, Perú, southwards to the departments of Cochabamba, La Paz (near Coroico) and Santa Cruz, Bolivia. In Perú, cloud forests of the Cordillera Oriental (Kosñipata, Marcapata and Puente Fortaleza (Cusco region), Tutumbaro (Ayacucho region), Santo Domingo de Carabaya (Puno region) and Chancas (Pasco region) are colonised (300–1,980 m asl). Tree-dwelling species that is distributed along streams and riverbanks from the lowlands to primary and secondary mountain rainforests and cloud forests.

*Hyalinobatrachium cappellei*: near clear, fast-flowing streams on tepuis and the Gran Sabana plateau of southern and eastern Venezuela to central Guyana, French Guiana and Suriname, also recorded from Amapá, Mato Grosso and the central state of Amazonas, Brazil, and from southern Colombia (municipalities of Cartagena del Chairá and Solano), from sea level to 3,500 m asl (Thompson et al. 2018). On leaves of trees and bushes near streams in mossy forests with evergreen hard-leaved vegetation, highland savannahs and tropical rainforests with palms and heliconias (Noronha & Rodrigues 2018).



*Hyalinobatrachium carlesvilai*: Amazonian Andes of Peru and Bolivia, Perú: 29 km north-east of Tingo María, the Valle de Marcapata and upper Tambopata, Departamentos San Martín, Ucuyali, Huánuco, Cusco and Puno. Bolivia: Chapare and Carrasco provinces (Cochabamba department) and Amboró National Park (Ichilo province, Santa Cruz department). Further records in the northern part of Mato Grosso (near Aripuanã) as well as Acre and Amazonas, Brazil (300–2,230 m asl). Occurs in tropical humid lowland, premontane and mountain rainforests (Castroviejo-Fisher et al. 2009).

*Hyalinobatrachium chirripoi*: low to medium altitudinal distribution of the Atlantic foothills in eastern Olancho and Colón, Honduras, southeastern Costa Rica, eastern Panama across western and central Colombia to northwestern Ecuador (Esmeraldas), expected (but unconfirmed) in northeastern Nicaragua (0–700 m asl). Habitat in humid primary and secondary lowland forests, in bushes and trees along forest streams and on cattle pastures in Costa Rica (Kubicki 2004, McCranie 2007, Ibañez et al. 2000, Ruiz-Carranza et al. 1996, Solís et al. 2004, Frost 2024).

*Hyalinobatrachium colymbiphyllum*: Atlantic coast near Catamacas, Departamento de Olancho, Honduras, possibly (but unconfirmed) in north-eastern Nicaragua, central and southeastern Costa Rica, western slopes of the Cordillera Occidental in Colombia (Departamentos Antioquia, Boyaca, Caldas, Choco, Cordoba, Risaralda, Tolima and Valle del Cauca) and the province of Colón, Panama (6–1,800 m asl). Humid lowland and mountain rainforest, on leaf undersides of trees and bushes along small forest streams (Kubicki 2007, McCranie & Wilson 2002, McCranie 2007, Solís et al. 2008, Ruiz-Carranza et al. 1996, Jaramillo et al. 1998, Ibañez et al. 2000, Savage 2002). Escalante et al. (2007) document the predation of the species by the northern cat-eyed snake *Leptodeira ornata*.

*Hyalinobatrachium diana*: Only known from three Caribbean Mountain foothills between Santa Clara and the headwaters of the Río Victoria in the provinces of Heredia and Limón and in the Parque Nacional Braulio Carrillo, Costa Rica (400–900 m asl). Habitat: Primary and secondary humid and premontane forests (Kubicki et al. 2015).

*Hyalinobatrachium durantii*: Forests of the central Cordillera de Mérida, Venezuela (1,830–2,400 m asl). In the vegetation above and near fast-flowing streams in mountain cloud forests. In a study on the local seasonal frequency distribution in the natural habitat cloud forest, positive correlations were found for this species with precipitation and relative humidity and negative correlations with temperature, whereas no statistically significant differences were found between the seasons (Señaris & Ayarzagüena 2005, Villa et al. 2019).

*Hyalinobatrachium esmeralda*: eastern Andean area of the Colombian Cordillera Oriental in the department of Boyacá (municipality of Pajarito), known around the type locality Cerro Yutajé in closed cloud forest with moss-covered trees above a small waterfall on a stream, now also recorded in Garagoa (Boyacá), Acacias, Las Salinas (Meta) and Chamesa (Casanare) (1,600–1,750 m asl). In the vegetation (also secondary) above streams at 2.5–3 m altitude (Ruiz-Carranza & Lynch 1998).

*Hyalinobatrachium fleischmanni*: former distribution from Guerrero and Veracruz, Mexico through Central America to Colombia (Pacific lowlands south of Valle del Cauca, central Valle de Magdalena, western foothills of the Cordillera Oriental), Ecuador, Venezuela, Guyana and Surinam. Records from Ecuador have since been placed in the synonymy of *H. petersi*, previous records from Venezuela have been described as *H. guairarepanensis*, the representatives from

Mexico, Guatemala, Belize to north-western Honduras have been described as *H. viridissimum*, further South American populations have been separated as *H. tatayoi* and *H. cappellei*. The current distribution area of *H. fleischmanni* therefore now extends from the Mosquitia coast in eastern Honduras and Nicaragua southwards to the Cordillera de Tilarán and Cordillera de Central in Costa Rica (countries Costa Rica, El Salvador, Honduras, Nicaragua) (25–1,740 m asl). Like other representatives of the genus arboricolous, near streams with medium to high flow velocity in lowland rainforest, sometimes on pastures and other influenced habitats, also in tropical and subtropical mountain forests, dependent on sufficient primary and secondary vegetation (Señaris 2001, Barrio-Amorós 2004, Castroviejo-Fisher et al. 2011, Wild 2003a, Savage 2002, Mendoza-Henao et al. 2020). According to Méndez-Narváez & Warkentin (2022), compared to other terrestrially spawning anurans, the species compensates for the drying out of clutches, which is associated with potentially lethally elevated ammonia levels, by increasing urea excretion. In addition to the camouflaging green base colour, which reflects the same infrared wavelength as green leaves due to skin pigments, another camouflage behaviour in *H. fleischmanni* was recently described scientifically: This species can increase its transparency two to threefold during sleep by storing almost 90% of the red blood cells in the liver (Taboada et al. 2022).

*Hyalinobatrachium fragile*: Cordillera de la Costa (Aragua, Carabobo and Vargas), Sierra de Aroa and Macizo de Nirgua (Yaracuy) and in the mountains in the northern state of Cojedes, Venezuela (100–1,400 m asl). Habitat: primary and secondary gallery forests along permanent or temporary streams (Rivero 1985, Señaris & Ayarzagüena 2005, Lotzkat 2007, Castroviejo-Fisher et al. 2009, Rojas-Runjaic et al. 2018, Barrio-Amorós et al. 2019).

*Hyalinobatrachium guairarepanensis*: central part of the Cordillera de la Costa, northern Venezuela, since 2014 also recorded on the Río Chacaíto in the Waraira Repano National Park (El Ávila) (720–1,200 m asl; possibly up to 1,900 m [Rivero 1961]). On vegetation above mountain streams (Señaris et al. 2018, Barrio-Amorós et al. 2019).

*Hyalinobatrachium iaspidiense*: Guiana region of Venezuela (Sarisariñama-Tepui, Quebrada de Jaspe, Estado Bolívar, Serranía de Imataca, Delta Amacuro), central Guyana, Suriname (Sipaliwini, Nickerie, Marowijne), French Guiana, Ecuador (Sucumbios, Napo), Perú (Lago Preto-Paredón, Ramon Castilla Province, Loreto) and Brazil (Amazonas, Amapá, Pará, Mato Grosso). Possibly much wider distribution in the Amazon region between Ecuador, Perú and the Guiana region as well as in Colombia (25–1,000 m asl). Habitat: Lowland and highland rainforests, associated with forest streams, mostly on the upper leaf surfaces of bushes and trees about 1–7 m above the water (Lescure & Marty 2000, La Marca & Señaris 2004, Barrio-Amorós & Brewer-Carias 2008, Guayasamin et al. 2008a, Kok & Castroviejo-Fisher 2008, Yáñez-Muñoz et al. 2009).

*Hyalinobatrachium ibama*: western foothills of the Cordillera Oriental, Boyacá, Charalá, Gámbita and Tona, Departamento Santander, Colombia, apparently still an allopatric population in San Isidro, Barinas, Venezuela (1,479–2,200 m asl). Habitat: riparian habitats of primary forests (Ruiz-Carranza & Lynch 1998).

*Hyalinobatrachium kawense*: known from two localities in floodplain forests near Rivière de Kaw, on the Mitaraka Massif and near Mitán, French Guiana, in a forest on Mount Apalagadi, Sipalawini Nature Reserve, Suriname, and near Memora, Amapá, Brazil, possibly more wide-

spread, from sea level to 100 m asl. Habitat: swamp forests, presumably dependent on undisturbed habitats, ♂♂ call from 3–4 m above the water from the upper side of *Montrichardia* and *Pachira aquatica* leaves (Castroviejo-Fisher et al. 2011, Fouquet et al. 2015, 2019).

*Hyalinobatrachium mashpi*: banks of the Mashpi River in the province of Pichincha (Reserva Mashpi Lodge [Río San Vicente, Río Laguna], Reserva Amagusa [Río Amagusa, Río Mashpi Chico], Reserva Tayra), Ecuador, possibly (unconfirmed) also in Colombia (Departamentos de Risaralda and Valle del Cauca), altitudinal distribution 976–1,137 m asl. Habitat: leaf undersides of vegetation above a steep stream, 3–14 m above the ground (Guayasamin et al. 2022).

*Hyalinobatrachium mesai*: only known from the terra typica on the slopes of the Sarisariñama-Tepui, Jaua-Sarisariñama National Park, Bolívar, Venezuela (420 m asl), which is difficult to access. Habitat: on stream-associated vegetation in unspoilt woodland (Barrio-Amorós & Brewer-Carías 2008).

*Hyalinobatrachium mondolfii*: initially only described from the Venezuelan Guiana Shield, states of Monagas and Delta Amacuro, from the floodplain of the Orinoco Delta. Since then, also recorded from San Antonio, Bolivia, Loreto and Madre de Dios, Perú, Amazonas and Caquetá, Guyana, Surinam, French Guiana and from the states of Acre, Amazonas, Pará, Amapá in Brazil. Distribution possibly more extensive in Amazonia, records from Pará are now counted as *H. muiraquitana*. Altitudinal distribution 100–300 m asl. The species occurs in the tropical lowland rainforest and in alluvial areas and sits on the undersides of leaves 1–8 m above the ground. The vegetation in the streams of the Caño Acoima corresponds to an evergreen wet forest, 20–30 m high, partly flooded. Tree species such as *Licania densiflora*, *Eschweilera decolorans*, *Gustavia poeppigiana*, *Virola surinamensis* predominate (Señaris & Ayarzagüena 2001, IUCN SSC Amphibian Specialist Group 2022b).

*Hyalinobatrachium muiraquitana*: only two forest areas in the municipalities of Vitória do Xingu and Altamira, Pará, in Brazil, current distribution area only 193 km<sup>2</sup>, altitudinal distribution unknown. Habitat: foliage over fast-flowing forest streams (Oliveira & Hernández-Ruz 2017).

*Hyalinobatrachium munozorum*: a few localities in the upper Amazon lowlands and in the foothills and cloud forests in Colombia (Parque Nacional Natural de Chiribiquete in Caquetá, Meta), Ecuador, Perú (Huanuco and Cusco), Brazil (Acre, Amazonas) and northern Bolivia (Pando) (190–1,840 m asl). Habitat: primary and secondary forests, on leaves of shrubs and trees, some specimens have also been found away from streams, e.g. at a pond or a large fallen tree in a forest clearing (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Hyalinobatrachium nouns*: only known from the neighbouring reserves Río Manduriacu and Bosque Protector Los Cedros, Toisán Mountains, Imbabura, Ecuador (1,177–1,420 m asl). Habitat: tropical premontane moist forest and cloud forest, leaf undersides above the stream at 1–6 m above the ground (Guayasamin et al. 2022).

*Hyalinobatrachium orientale*: Serranía del Turimiquire (Monagas) and Serranía de Paria (Sucre) in the eastern areas of the Cordillera de la Costa, Venezuela, as well as northeastern watercourses Dead Bay, Main Ridge and Hermitage on Tobago (13–1,200 m asl). Habitat: neotropical primary and secondary moist forest in bushes and trees along streams (Castroviejo-Fisher et al. 2008, Byrne et al. 2020).

*Hyalinobatrachium orcostale*: Cerro Platillón (type locality) and surrounding area (Hacienda La Canopia, Villa de Cura, San Juan de los Morros, Guárico, Venezuela). This species is re-

stricted to higher altitudes of the Cordillera del Interior, the southernmost part of the Cordillera de La Costa, which is isolated from the Sierra del Litoral by drier valleys (800–1,200 m asl). Habitat: on vegetation above or along mountain forest streams (Castroviejo-Fisher et al. 2009).

*Hyalinobatrachium pallidum*: western, southern and eastern foothills of the Cordillera de Mérida (Mérida, Táchira, Barinas), Sierra de Perijá (Zulia), Venezuela, and western foothills of the Cordillera Oriental, Colombia (1,130–1,832 m asl). Habitat: primary and secondary humid mountain and cloud forests, on vegetation above or near fast-flowing streams up to 6 m asl (Señaris & Ayarzagüena 2005, Barrio-Amorós 2006).

*Hyalinobatrachium pellucidum*: Caquetá, Colombia, Río Azuela (Sucumbíos) as well as other states (Napo, Morona Santiago, Zamora Chinchipe) in Ecuador to San Martín and Cusco in Perú (532–1,740 m asl). Habitat: Bosque Piemontano Oriental, primary and secondary premontane and cloud forests, individuals were found on the upper leaf surfaces of shrubs and trees approx. 1.5–4 m above the stream.

*Hyalinobatrachium talamancae*: Cartago, eastern Guanacaste, southern Heredia, central Limón, Costa Rica, now also La Nevera, Ngöbe-Buglé, Panama (475–1,600 m asl). Adapted to smooth-leaved vegetation over mountain streams of medium and high inclination in tropical wet or premontane forest (Savage 2002, Kubicki 2006, Hertz et al. 2011).

*Hyalinobatrachium tatayoi*: Venezuelan Cordillera de Perija on the northern border between Colombia and Venezuela, dry forests in the middle and upper Valle de Magdalena in the Caribbean lowlands to the department of Tolima, Caribbean lowlands of the Cordillera de Talamanca of Costa Rica and Panama, Darién-Choco region through Colombia to the province of Esmeraldas, Cordillera Occidental to about 20 km south of Naranjal in Ecuador (0–1,640 m asl). Habitat: in the vegetation above rivers and streams in primary and secondary forests up to 10 m above the water, well adapted to anthropogenic changes (Guayasamin et al. 2020).

*Hyalinobatrachium taylori*: Guiana shield in southern and central Suriname, Guyana, French Guiana, southeastern Venezuela and Amapá, Brazil, and about 1,500 km from this population at the Roncadeira waterfall (450–550 m asl; municipality of Palmas, Taquaruçu, Brazil) (30–1,850 m asl). In tropical rainforest and in the montane forests of Guyana, vegetation along small rocky permanent streams in primary forest, usually in high vegetation layers (2–30 m) above the water (Lescure & Marty 2000).

*Hyalinobatrachium tricolor*: recorded in Crique Wapou, Réserve Naturelle des Marais de Kawroua, in Crique Wapou Blanc, Saut Grand Machicou, Mitán as well as in the Kaw Mountains, French Guiana and in the Serra do Navio, Amapá, Brazil (2–200 m asl). Habitat: lowland forest streams in unaltered habitat, the species is not easy to find and difficult to collect, is more easily identified by call (Castroviejo-Fisher et al. 2011).

*Hyalinobatrachium valerioi*: from central Costa Rica to the Pacific coast of Ecuador, western Andes in the Valle de Magdalena (0–1,500 m asl). Habitat: lowland humid and rain forests as well as premontane forests, on vegetation along small streams. In its habitat, this species is attacked by frog-biting midges (Diptera, Corethrellidae) of only 0.6–2.5 mm in size, which are attracted by the frog calls. Although some midge species identified only on a morphological basis appear to parasitise several frog species, there are also indications of specialisations and numerous undescribed frog-biting midge species (Savage 2002; Leenders 2001, 2016, Lunau 2021, Virgo et al. 2022).

*Hyalinobatrachium vireovittatum*: scattered occurrence within the premontane zone of southwestern Costa Rica from the foothills of Tenorio Volcano, Guanacaste, to the vicinity of Barú Volcano, Puntarenas (Cordillera Central and Cordillera de Talamanca), as well as in western, central and eastern Panama (El Valle, Coclé, Cerro Bruja, Serranía de Majé) (800–1,957 m asl). Habitat and lifestyle see *H. fleischmanni*. Similar species: *H. talamancae* (Savage 2002, Kubicki 2007).

*Hyalinobatrachium viridissimum*: Humid and cloud forests of the Pacific coast in Guerrero, Mexico, to southern Guatemala and Atlantic coast from central Veracruz, Tabasco and Chiapas, Mexico, via central Guatemala and Belize to northern Honduras, possibly also in Santa Ana and Cabañas, El Salvador (20–1,275 m asl). In the vegetation above small and medium-sized streams of primary and secondary forests including coffee plantations (Mendoza-Henao et al. 2020).

*Hyalinobatrachium yaku*: known from a few localities in the Ecuadorian lowland rainforest in the catchment area of the Río Kallana, Kichwa community, Kallana, Pastaza, at the Timburi-Cocha Research Station near San José de Payamino and in Orellana near Ahuano, Napo. Possibly also distributed further into Perú (300–360 m asl). Habitat: vegetation above rainforest streams in primary and secondary, very humid forests, one of the above-mentioned localities was 30 m from the water in bushes, ferns and grasses (Guayasamin et al. 2017).

## Conservation Status and Main Threats

### IUCN Red List Status

*Hyalinobatrachium adespinosai*: DD (Data Deficient, assessed 2021-03-12)

*Hyalinobatrachium anachoretus*: EN (Endangered, B1ab(iii), assessed 2018-03-23)

*Hyalinobatrachium aureoguttatum*: LC (Least Concern, assessed 2019-08-14)

*Hyalinobatrachium bergeri*: LC (Least Concern, assessed 2019-09-25)

*Hyalinobatrachium cappellei*: LC (Least Concern, assessed 2021-04-13)

*Hyalinobatrachium carlesvilai*: LC (Least Concern, assessed 2021-04-13)

*Hyalinobatrachium chirripoi*: LC (Least Concern, assessed 2020-12-16)

*Hyalinobatrachium colymbiphyllum*: LC (Least Concern, assessed 2019-08-14)

*Hyalinobatrachium diana*: LC (Least Concern, assessed 2019-09-10)

*Hyalinobatrachium duranti*: EN (Endangered, B1ab(iii), assessed 2020-05-06)

*Hyalinobatrachium esmeralda*: EN (Endangered, B1ab(iii), assessed 2016-08-02)

*Hyalinobatrachium fleischmanni*: LC (Least Concern, assessed 2021-11-16)

*Hyalinobatrachium fragile*: NT (Near Threatened, B1ab(iii), assessed 2020-02-29)

*Hyalinobatrachium guairarepanense*: EN (Endangered, B1ab(ii,iii,iv,v) + 2ab(ii,iii,iv,v), assessed 2020-02-17)

*Hyalinobatrachium iaspidiense*: LC (Least Concern, assessed 2021-04-13)

*Hyalinobatrachium ibama*: LC (Least Concern, assessed 2020-08-19)

*Hyalinobatrachium kawense*: LC (Least Concern, assessed 2017-11-15)



*Hyalinobatrachium mashpi*: has not yet been assessed by the IUCN

*Hyalinobatrachium mesai*: DD (Data Deficient, assessed 2020-06-22)

*Hyalinobatrachium mondolfii*: LC (Least Concern, assessed 2021-04-13)

*Hyalinobatrachium muiraquitana*: DD (Data Deficient, assessed 2021-04-13)

*Hyalinobatrachium munozorum*: LC (Least Concern, assessed 2021-04-13)

*Hyalinobatrachium nouns*: has not yet been assessed by the IUCN

*Hyalinobatrachium orientale*: VU (Vulnerable, B1ab(iii), assessed 2020-06-08)

*Hyalinobatrachium orcostale*: EN (Endangered, B1ab(iii), assessed 2020-02-12)

*Hyalinobatrachium pallidum*: NT (Near Threatened, B2ab(iii), assessed 2020-05-07)

*Hyalinobatrachium pellucidum*: NT (Near Threatened, A4c, assessed 2021-04-07)

*Hyalinobatrachium talamancae*: LC (Least Concern, assessed 2019-08-14)

*Hyalinobatrachium tatayoi*: LC (Least Concern, assessed 2021-11-16)

*Hyalinobatrachium taylori*: LC (Least Concern, assessed 2020-02-26)

*Hyalinobatrachium tricolor*: LC (Least Concern, assessed 2017-11-15)

*Hyalinobatrachium valerioi*: LC (Least Concern, assessed 2019-09-04)

*Hyalinobatrachium vireovittatum*: LC (Least Concern, assessed 2019-09-11)

*Hyalinobatrachium viridissimum*: LC (Least Concern, assessed 2021-10-20)

*Hyalinobatrachium yaku*: EN (Endangered, B1ab(iii), assessed 2021-03-12).

### Red List Status in the Range Countries

#### Central America

Environmental Vulnerability Score Category (Johnson et al. 2015)

*Hyalinobatrachium talamancae* – H (High)

*Hyalinobatrachium vireovittatum* – H (High)

*Hyalinobatrachium aureoguttatum* – M (Medium)

*Hyalinobatrachium chirripoi* – M (Medium)

*Hyalinobatrachium colymbiphyllum* – M (Medium)

*Hyalinobatrachium valerioi* – M (Medium)

*Hyalinobatrachium fleischmanni* – L (Low)

#### Colombia

*H. aureoguttatum*: common species in Colombia, rare in Panama, stable trends (Panama Red List Assessment Workshop August 2019, Colombia Red List Assessment Workshop August 2016).

**Costa Rica**

All Centrolenidae of Costa Rica are classified as LC (Not Endangered) (Chaves et al. 2014).

**Guatemala**

*Hyalinobatrachium fleischmanni* VU – Vulnerable (CONAP 2022)

**French Guiana**

La Liste rouge des espèces menacées en France. Faune vertébrée de Guyane – Amphibiens et Reptiles (MNHN, UICN France & Biotope 2018).

*Hyalinobatrachium cappellei* LC – Least Concern

*Hyalinobatrachium iaspidiense* LC – Least Concern

*Hyalinobatrachium kawense* DD – Data Deficient

*Hyalinobatrachium mondolfii* LC – Least Concern

*Hyalinobatrachium* sp. (Species not yet described when this Red List was compiled) LC – Least Concern

*Hyalinobatrachium taylori* LC – Least Concern

*Hyalinobatrachium tricolor* DD – Data Deficient

**Ecuador**

Amphibians of Ecuador/Anfibios de Ecuador (Centro Jambatu (2011–2020) V1.23)

CR (Critically endangered):

*Hyalinobatrachium pellucidum* (endemic species)

EN (Endangered):

*Hyalinobatrachium chirripoi*

*Hyalinobatrachium mashpi* (endemic species)

*Hyalinobatrachium nouns* (endemic species)

VU (Vulnerable):

*Hyalinobatrachium valerioi*

**Mexico**

*Hyalinobatrachium viridissimum* – SEMARNAT NS (No Status), Environmental Vulnerability Category Score 10 (Medium) (García-Padilla et al. 2022)

**Venezuela**

*Hyalinobatrachium guairarepanense* EN (Endangered, B1ab(iii) (Señaris et al. 2015)).

**Threats**

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other possible causes of endangerment include the local application of pesticides, fertilisers and environmental pollution, diseases, climate change and increased UV-B radiation.

*Hyalinobatrachium anachoretus*: small distribution areas harbour a particular risk of negative population trends due to the reasons mentioned above. In the vicinity of the distribution area in the northern Peruvian Andes, road construction, deforestation, agriculture and slash-and-burn agriculture play a role, which is why a declining population is assumed (Twomey et al. 2014).

*Hyalinobatrachium aureoguttatum*: common species in Colombia, rare in Panama (Colombia Red List Assessment Workshop August 2016, Panama Red List Assessment Workshop August 2019). Local threats include habitat fragmentation and loss due to agriculture, mining and water pollution.

*Hyalinobatrachium bergeri*: no known threats from Bolivia or in Marcapata and Kosñipata, Perú; in central Perú, pollution from agricultural herbicide run-off plays a role; in the Valle de Kosñipata, Manu National Park, the chytrid fungus has also been detected. Numerous records in March and April 2000 in Madidi National Park, whereas similar monitoring in Cotapata National Park between September 1999 and February 2000 classifies the species there as rare.

*Hyalinobatrachium cappellei*: assumed large and stable population, large distribution area with suitable habitats and no known major threats. Possible population declines due to deforestation, urban expansion and agriculture (Noronha et al. 2012). A threat from the pet trade appears questionable on the basis that only *H. fleischmanni* is available in trade. According to one report, the species is occasionally kept in captivity in the USA (T. Eisenberg, unpublished data).

*Hyalinobatrachium carlesvilai*: assumed large and stable population due to wide distribution, potential threats are habitat loss due to deforestation and eutrophication of water bodies by agricultural crops, livestock farming, expansion of human settlements and hydropower plants (Cisneros-Heredia et al. 2010).

*Hyalinobatrachium chirripoi*: some populations in Honduras, Panama, Colombia and Ecuador are threatened by habitat loss due to increasing agriculture and forestry, slash-and-burn agriculture and water pollution – in Honduras also due to a hydroelectric power plant – but otherwise tolerant to anthropogenic habitat change (Solís et al. 2004).

*Hyalinobatrachium colymbiophyllum*: assumed large and stable population due to wide distribution, individual populations may be affected by habitat loss due to deforestation. In Monteverde, Costa Rica, and in El Copé, Panama, there were population collapses in the 1990s – partly following infections with *Batrachochytrium dendrobatidis* – which have since partially recovered (Solís et al. 2008).

*Hyalinobatrachium diana*: little data available, currently apparently not threatened, but future threat likely due to the small distribution area, habitat loss and climate change (Kubicki et al. 2015).

*Hyalinobatrachium duranti*: small overall range, sometimes habitat loss (expansion of agriculture and settlements) and changes (deliberately introduced allochthonous predatory fish species), widespread distribution of the frog fungus (*Batrachochytrium dendrobatidis*), therefore listed as endangered. Elsewhere (Río Albarregas, El Chorotal, La Mucuy), it is a species which is frequently recorded during the rainy season (Señaris & Ayarzagüena 2005).

*Hyalinobatrachium esmeralda*: small overall range, only four localities with susceptibility to habitat loss (livestock farming, illegal farming) and declining population trend, therefore listed

as endangered. Species apparently tolerant of environmental pollution due to sewage discharges near the town of Santa María (Boyacá; Ruiz-Carranza & Lynch 1998).

*Hyalinobatrachium fleischmanni*: common species in the remaining large distribution area, local threats result from habitat loss due to deforestation, agriculture, human settlements and environmental pollution, in some museum specimens the chytrid fungus was also detected (Leenders 2001, 2016).

*Hyalinobatrachium fragile*: categorised as near threatened due to its limited distribution area, occurs at twelve sites where habitat loss (due to deforestation and fragmentation) cannot be ruled out. Although the species is very common in some places (Sierra de Aroa, Yaracuy, and Carabobos mountain region), declines in vegetation in the Cordillera de La Costa, the spread of the chytrid fungus and gold mining activities are having a negative impact.

*Hyalinobatrachium guairarepanensis*: In the initial description, specimens that had already been preserved for some time were processed. In the years 1997–1998, intensive but unsuccessful searches for this species were again carried out at the terra typica locations. It was not until 2014 that new evidence was found elsewhere. Due to this, the relatively limited overall distribution area and the existing or impending habitat loss and fragmentation as a result of agriculture and forestry, urban expansion and the chytrid fungus, this species is classified as endangered with a declining population trend (Señaris & Ayarzagüena 2005, Guayasamin et al. 2009, Señaris et al. 2018, Barrio-Amorós et al. 2019).

*Hyalinobatrachium iaspidiense*: despite the large distribution area, local threats due to habitat loss as a result of deforestation, agriculture and mining (gold, diamonds; AmphibiaWeb 2023).

*Hyalinobatrachium ibama*: despite the large distribution area, local threats due to habitat loss as a result of agriculture and environmental pollution; a declining population trend is suspected.

*Hyalinobatrachium kawense*: Although the species also occurs in protected areas, a certain threat is posed by regional gold mining in French Guiana, populations with few individuals, declining population trend (Castroviejo-Fisher et al. 2011, Fouquet et al. 2015).

*Hyalinobatrachium mashpi*: no formal classification to date, the original description publication recommends categorisation as critically endangered due to the small distribution area and the threat of habitat loss (agriculture, mining) (Guayasamin et al. 2022).

*H. mesai*: no direct threats known, insufficient data available.

*Hyalinobatrachium mondolfii*: large distribution area with stable population trend, however there is a great risk of habitat pollution due to oil extraction, but also due to agriculture and forestry, particularly in the Orinoco delta (IUCN SSC Amphibian Specialist Group 2022b).

*Hyalinobatrachium muiraquitana*: known from two non-protected, agriculturally utilised forest fragments, additionally expanded fish farming and hydropower plants there, currently insufficient data, proposal for IUCN status threatened with extinction if an assumed further distribution does not materialise.

*Hyalinobatrachium munozorum*: assumed stable population trend, presumably the relatively few sightings are due more to the hidden lifestyle in the canopy region of trees than to an unstable population, possibly local habitat loss due to agriculture and human settlements (Guayasamin et al. 2020).

*Hyalinobatrachium nouns*: see *H. mashpi*; distribution area is permanently threatened by illegal agriculture and mining (Guayasamin et al. 2022).

*Hyalinobatrachium orientale*: declining population trend and habitat loss in Venezuela due to urbanisation, expansion of agriculture, deforestation, slash-and-burn agriculture and infectious diseases (*Batrachochytrium dendrobatidis*) contributed to 'vulnerable' status, more stable trend in Tobago (IUCN SSC Amphibian Specialist Group 2020b).

*Hyalinobatrachium orocostale*: listed as endangered due to habitat loss and fragmentation, population trend not sufficiently known, presumably declining due to isolated habitat fragments, although the species was very common at terra typica with 5–10 ♂♂ per 25 m stream transect (Castroviejo-Fisher et al. 2009).

*Hyalinobatrachium pallidum*: listed as near threatened due to a limited number of suitable habitats and anthropogenic habitat utilisation. At the terra typica locations very high population density of 155 calling ♂♂ in a 300 m stream transect at the beginning of the rainy season, possibly more widespread distribution.

*Hyalinobatrachium pellucidum*: categorised as near threatened due to a sufficiently large distribution area that cannot be adequately protected and a declining population trend. A decline of 20–25% over the 10-year period (2015–2025) is feared due to habitat loss as a result of deforestation, expanding agriculture and mining (Cisneros-Heredia 2008).

*Hyalinobatrachium talamancae*: although the type locality has since been converted to cattle pasture, the population trend is stable and the species occurs in numerous protected areas (Kubicki et al. 2004).

*Hyalinobatrachium tatayoi*: wide distribution, high tolerance to water pollution and habitat changes (e.g. below mining camps), stable population trend (Mendoza-Henao et al. 2020).

*Hyalinobatrachium taylori*: wide distribution, presumably large, stable population, lives in areas with minimal human impact, precise information on the size of the population is lacking, assumed stable population trend.

*Hyalinobatrachium tricolor*: wide distribution, remaining suitable habitats, stable population trend.

*Hyalinobatrachium valerioi*: not endangered, wide distribution, tolerates habitat modifications, but not frequently found, Costa Rican populations appear stable, in Panama there appears to be a decreasing population trend, patchy distribution in Panama, Colombia and Ecuador. In addition to agricultural and forestry-related threats and human settlement expansion, animals have also been removed from parts of the distribution area (Costa Rica) for the pet trade in the past. These removals were sustainable and not at a population-threatening level. An established set of polymorphic microsatellite markers can be used to analyse relationships (Savage 2002, Kubicki 2007, 2008, Solis et al. 2008, Ringler et al. 2014).

*Hyalinobatrachium vireovittatum*: wide distribution and assumed large population, suspected impairment in anthropogenically influenced habitats, in Panama deforestation also in protected areas as well as danger from agriculture and human settlements (Stuart et al. 2008).

*Hyalinobatrachium viridissimum*: widespread distribution, assumed large population, stable population trend, no assessment in a conservation category due to lack of complete data.



*Hyalinobatrachium yaku*: rare species, declining population trend, currently listed as both insufficient data (AmphibiaWeb) and endangered (IUCN), there are threats from environmental pollution, particularly from oil extraction, road construction and mining (Guayasamin et al. 2017).

## Reproduction

| Topic                       | Details on the reproduction of <i>Hyalinobatrachium</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|-----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | <p>All species: ♂♂: calls from single subgular vocal sac, Wolffian ducts mostly recognisable on the ventral side, nuptial excrescences more or less pronounced dorsomedially on finger I. ♂♂ take care of the brood and guard the clutch.</p> <p><i>H. chirripoi</i>: ♂♂ gland-rich nuptial excrescences on the bunion on the back and outside of the base of the thumb (Savage 2002).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Sexual maturity             | Not stated in the literature, probably 6–12 months as with other members of the Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Calls                       | <p><i>H. adespinosai</i>: pulsed call, tonal voice, cricket-like, call length 0.38–0.44 s (longer and with more pulses per note than <i>H. anachoretus</i>). Dominant frequency 4,645–5,203 Hz, call pauses 2–11 s (n=9; Guayasamin et al. 2019a).</p> <p><i>H. anachoretus</i>: similar to <i>H. adespinosai</i>, pulsed call with 5–6 pulses, call length 0.32–0.37 s, dominant frequency 4,670–4,800 Hz without frequency modulation (Twomey et al. 2014).</p> <p><i>H. bergeri</i>: see <i>H. carlesvilai</i>, but completely tonal without pulsed note, constant frequency 3,775.20–4,337.90 Hz, dominant frequency 4,489.60–4,659.91 Hz (Castroviejo-Fisher et al. 2009).</p> <p><i>H. cappellei</i>: the advertisement call is emitted from the top of leaves 1–5 m above water and is characterised as a ‘peeeep’ sound lasting 0.319 s on average. The mating call sounds like ‘Peeeee...fiii’ and lasts 1.077 s on average.</p> <p><i>H. carlesvilai</i>: courtship call consists of one note, the first third pulsed, the remaining two thirds tonal, call length 0.102–0.152 s, dominant frequency 4,617.33–4,915.36 Hz (Castroviejo-Fisher et al. 2009).</p> <p><i>H. chirripoi</i>: the advertisement call is an insect-like high-pitched buzzing (Kubicki 2004). The advertisement call consists of a single, strongly pulsed note (duration 230–270 ms) with 14–16 amplitude peaks, dominant frequency 4,565 Hz (Guayasamin et al. 2020).</p> <p><i>H. colymbiphyllum</i>: the advertisement call consists of a single long trill lasting 600–800 ms and repeated after a pause, dominant frequency 4,400–4,600 Hz. ♂♂ are territorial and call very consistently from the same place throughout the entire breeding season. When a rival enters the territory, the calling frequency increases three to fourfold. If the intruder does not move away, a physical confrontation ensues until the inferior frog is gripped, pressed onto the leaf and flees (Savage 2002).</p> <p><i>H. diana</i>: advertisement call: very fast, long, metallic whistle, weak intensity, note length 0.40–0.55 s, dominant frequency: 3,350–3,440 Hz at 22.7°C (Kubicki et al. 2015).</p> <p><i>H. durantii</i>: the call was recorded in La Mucuy on the Río Albarregas at air temperatures of 13–18°C: modulated note that begins with a sudden increase in frequency and then remains stable, call length 37–62 ms, dominant frequency: 3,810–4,370 Hz, continuous call (4–6/min), call pauses 5–17 s (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. fragile</i>: advertisement call: single tonal note with amplitude modulation, call length 0.12–0.15 s, frequency 3.12 calls/min, dominant frequency 3,774.78–3,931.89 Hz, call pauses 6.85–19.86 s (Wen et al. 2012).</p> <p><i>H. guairarepanensis</i>: the advertisement call was recorded at an air temperature of about 21°C and described as a chirping sound. Modulated sound with emphasis on the first half, call length 185–205 ms, dominant frequency 3,902–3,944 Hz, continuous</p> |

call with approx. 5–8 calls/min (Señaris & Ayarzagüena 2005).

*H. iaspidiense*: the call is shrill and usually consists of a single note (length 0.17 s), sometimes two notes (call interval 9.3 s), dominant frequency 4,700 Hz (Barrio-Amorós & Brewer-Carias 2008).

*H. kawense*: the call consists of a single, shrill, widely audible note, first half with rapid frequency rise with 6–11 pulses, second half tonal, call length 0.08–0.09 s, dominant frequency 5,622.5–6,065.9 Hz (Castroviejo-Fisher et al. 2011).

*H. mashpi*: the call consists of a single pulsed note, call length 0.37–0.46 s, dominant frequency 5,250–5,600 Hz (Guayasamin et al. 2022).

*H. mesai*: the recorded call is a high-pitched, single note with a dominant frequency of 4,700 Hz (fundamental frequency 4,300 Hz) and a duration of 0.17 s. The interval between two calls is 9.3 s, usually one-note calls, sometimes two-note calls (Barrio-Amorós & Brewer-Carias 2008).

*H. mondolfii*: at an air temperature of about 22°C, the continuous call consisted of a relatively short, modulated, weakly pulsed tone of 182–212 ms duration and call intervals of 6.14–11.7 s, dominant frequency 5,070–5,146 Hz, about 7–8 calls/min (Señaris & Ayarzagüena 2001).

*H. munozorum*: the call consists of a single note, call length 145–178 ms, notes are mostly tonal but with 1–7 low amplitude peaks, dominant frequency 5,719–5,906 Hz (Guayasamin et al. 2020).

*H. orientale*: a long, modulated note, the advertisement call of the island and mainland populations, in contrast to the closely related species *H. orocostale*, has a higher dominant frequency of 4,240–4,520 Hz with an average call length of 0.239 s (Castroviejo-Fisher et al. 2009).

*H. orocostale*: call similar to *H. orientale*, but shorter call length of 0.17–0.20 s, lower dominant frequency of 3,383–3468 Hz (Castroviejo-Fisher et al. 2009).

*H. pallidum*: the call consists of a short, pulsed note with a dominant frequency of 3,640–3,710 Hz (Cardozo-Urdaneta & Señaris 2012).

*H. pellucidum*: the call consists of a single tonal note without frequency or amplitude modulation, call length 0.12–0.18 s, average frequency 15.6 calls/min, call pauses 2.57–7.37 s, dominant frequency 4,863–5,408 Hz (Wen et al. 2012).

*H. talamancae*: the call is a single protracted, non- to slightly pulsed, non-frequency but amplitude-modulated whistle, call length approx. 0.3 s, initial frequency 4,300 Hz, which rises to 4,900 Hz and then falls to 4,600 Hz. The call is repeated every 10 seconds. The advertisement call can usually be heard at night (occasionally during the day on cloudy days) from the underside of the leaf in an upright sitting position with the ♂ looking at the base of the leaf. In contrast, calling ♂♂ for territory defence (and also pairs in amplexus) are often also on the upper side of the leaf with a view of the leaf tip. However, a more recent study has produced interesting findings that could possibly also apply to other species. Chaves-Acuña et al. (2024) found in this species that the call frequency, but not the call length and dominance frequency, differed between frogs engaged in brood care and territorial disputes and those not involved in brood care. The latter called more frequently than the caring ♂♂, whereas ♂♂ interactions triggered the highest call frequencies. The authors raise the question of whether this could also have consequences for the selection of sexual partners, as ♀♀ could thus already take into account the reproductive success of caring ♂♂ in mate choice through acoustic call differences (Kubicki 2006, Chaves-Acuña et al. 2024).

*H. tatayoi*: the call most frequently heard during the rainy season consists of a single ascending ‘wheet’, call length 150–300 ms, frequency 4–19 calls/min, dominant frequency 3,800–4,500 Hz, below 93% relative humidity the calling activity decreases significantly (Guayasamin et al. 2020).

*H. taylori*: advertisement call very characteristic, but not easy to record due to calling groups of many individuals, consists of modulated 5–8 notes with a significant increase in frequency, first note longest, call length 0.652–1.052 s, dominant frequency 4,010–4,350 Hz (Señaris & Ayarzagüena 2005).

*H. tricolor*: advertisement call consisting of four tonal notes, call length 0.19–0.20 s, dominant frequency 4,628–4,903 Hz (Castroviejo-Fisher et al. 2011).

*H. valerioi*: the call resembles a short repeated ‘sheet’, call length 200–250 ms, dominance frequency initially 7,000 Hz, rising to 7,500 Hz, then falling to 7,200 Hz, call frequency every 7–10 s, a beeping sound is emitted when another ♂ approaches, sometimes by the territory holder and opponent. If the intruder does not leave the territory immediately, a kind of wrestling match ensues, in which the attacker is usually held down by the defending ♂ (Savage 2002, Wild 2003b, Guayasamin et al. 2020).

*H. vireovittatum*: the call resembles a repeated soft and swelling ‘wheel’, with a call length of 400–500 ms, dominance frequency starts at 5,000 Hz and rises to 5,400 Hz (Savage 2002).

*H. viridissimum*: the advertisement call consists of a single pulsed note, call length  $187.6 \pm 21.6$  ms, dominant frequency  $4,549 \pm 130$  Hz. A distinctive mating call was recorded when approached by a presumably female conspecific in San Vicente de Benitez, Guerrero, Mexico: 1–9 individual pulses, sometimes followed by a long note, emitted in call groups with call pauses of  $536.3 \pm 209.2$  ms, mean dominance frequency  $4,441 \text{ Hz} \pm 88.8 \text{ Hz}$ , highly variable call length of  $110.1 \pm 47.5$  ms and clear complexity and frequency modulation compared to the advertisement call (Mendoza-Henao et al. 2020).

*H. yaku*: The advertisement call consists of a single tonal note, dominant frequency 5,219–5,329 Hz, pulse rate 44,100 Hz/s, call length 0.27–0.4 s (Guayasamin et al. 2017).

#### Mating and spawning

*H. anachoretus*: three clutches near calling ♂♂, reproductive mode presumably as in other species of the genus. Although the species is very commonly heard in some nights, it is sometimes almost impossible to observe the animals directly, despite ideal weather conditions. Clutches on the undersides of leaves (Twomey et al. 2014).

*H. aureoguttatum*: ♂♂ calling from water accumulations in heliconias, mating and oviposition in heliconias (Barrera-Rodriguez & Ruiz-Carranza 1989). The eggs are glued to the undersides of leaves, larvae develop and fall into the stream bed below. According to Valencia-Aguilar et al. (2012), there is no intraspecific aggression between the ♂♂ despite small distances of only 0.3–0.5 m within the same plant. ♂♂ guard, clean and supply 1–5 clutches with liquid at the same time and stay near them during the day and at night. ♀♀ leave the laying sites immediately after laying their eggs. Between 2–6 ♂♂ per 10 m stream segment were detected, which proved to be site-loyal with regard to subsequent clutches. In addition to the favoured Heliconiaceae (*Heliconia*), oviposition plants also included Araceae (*Anthurium*, *Philodendron*), Cyclantaceae (*Cyclanthus*), Marantaceae (*Calathea*), Musaceae (*Musa*) and Sapotaceae with a general preference for large leaves (Valencia-Aguilar et al. 2012). Valencia-Aguilar et al. (2024) found, among other things, a reduced relative testis size in this species, combined with an assumed smaller sperm count as a trade-off and adaptation between paternal brood care and reproductive effort. Brood care reduces the risk of clutch piracy after mating by ♂♂ of the same species (so-called ‘sneakers’) and thus the risk of genetic competition (Vieites et al. 2004).

*H. bergeri*: eggs are glued to the undersides of leaves; larvae develop in the stream bed below. In Tutumbaro (Perú), the species reproduces in an area of cloud forest influenced by humans in a river valley overgrown with bamboo, ferns and *Colocasia* spp. (Araceae). calling ♂♂ were found about one metre from the stream, the ♂♂ call from the underside of the leaves about 1–3 m above the ground.

*H. cappellei*: activity peaks in the middle of the night. During the reproductive phase, the ♂♂ call from the top and undersides of leaves from dense vegetation 1–6 m above the ground, then ♀♀ approach, and both sexes go into amplexus on contact. The entire process from courtship to egg-laying takes about eight hours. Fast-flowing streams and pond-like lateral recesses are used, although quieter sections of stream seem to be favoured. The dimensions of suitable spawning waters are given as 1–2 metres wide, up to 1 metre deep and with a sandy, partly rocky bottom and banks up

to 4 metres high. ♀♀ lay their gelatinous clutches of greenish eggs on the underside of leaves hanging over streams. They then need a 2–3 week break before they are ready to spawn again. ♂♂ guard up to three clutches of eggs of different ages until the tadpoles fall into the water after hatching (see also *H. chirripoi*). The ♂♂ often stay close to the clutch during the day and cover the eggs with their bodies at night, using ventral contact to give the clutch fluid. They also defend the clutch against typical egg predators such as cockroaches, moths, bush crickets and ants (Castroviejo-Fisher et al. 2011, Noronha & Rodrigues 2018, Noonan & Bonett 2003, Valencia-Aguilar et al. 2020).

*H. carlesvilai*: ♂♂ call at dusk from the underside of leaves in vegetation 1–3 m above streams and rivers (Castroviejo-Fisher et al. 2009).

*H. chirripoi*: adult ♀♀ lay greenish white eggs in a layer on the undersides of smooth leaves above streams, ♂♂ call under palm leaves 1–4 m above the water and engage in brood care, which experimentally also includes other females' clutches ('alloparental care'), provided that the ♂ in question had just cared for a clutch itself. This behaviour, in which the ♂ cares for the other clutch with the same intensity as for its own clutch(es) after 2–3 days, could also be significant in nature, as the chance of successful mating in *H. cappellei* increases with the number of clutches cared for (Kubicki 2004, Valencia-Aguilar et al. 2020, 2021).

*H. colymbiphyllum*: clutches are deposited on the underside of the leaf by the calling ♂. Occasionally the ♂ sits on the clutch and touches it with its abdomen and pelvic region, presumably to transfer fluid (see also 'brooding behaviour' in *H. fleischmanni*). According to some authors, clutches are not guarded by the ♂ during the day, only at night (but refuted in Delia et al. 2017a). Day-active wasps can then attack clutches by repeatedly removing individual eggs and flying away with them. In an analysis of brood care behaviour across many species of the Centrolenidae family, it was found for *H. colymbiphyllum* and *H. fleischmanni* that removing the ♂♂ from the clutch increased embryonic mortality, particularly as a result of desiccation (*H. fleischmanni*) or desiccation and predation (*H. colymbiphyllum*, *Centrolene peristictum*, *Centrolene aff. savagei*). The duration of brood care was 4–18 days in *H. colymbiphyllum* and 2–16 days in *H. fleischmanni*. In Panama, embryos of both species reached hatching maturity about 7 days after egg laying, although hatching can be delayed up to 19–20 days.

*H. diana*: typical for many glass frogs: after heavy rainfall, otherwise dry stream branches are connected to existing streams and used as spawning habitat, so that ♂♂ and clutches can also be found in areas above drying, possibly even totally dry substrate. ♂♂ guard and defend clutches found 0.5–5 m above the ground (Kubicki et al. 2015).

*H. durantii*: ♂♂ call from the undersides of leaves, approx. 2–6 m above the ground, ♀♀ also spawn on the undersides of especially anthuriums, *Palicourea* sp., palms or ferns, ♂♂ guard and defend the single-layered clutches (Señaris & Ayarzagüena 2005).

*H. esmeralda*: clutches of cream-coloured eggs deposited on the underside of leaves and petioles of vegetation (Ruiz-Carranza & Lynch 1998).

*H. fleischmanni*: according to some authors, clutches are not attended by the ♂ during the day, only at night (refuted in Delia et al. 2017a). However, one ♂ can care for several clutches on different, nearby leaves at the same time. Brood care behaviour, i.e. the intimate belly-abdomen contact of the ♂ with the clutch, was investigated in more detail in *H. colymbiphyllum* and *H. fleischmanni* (and *H. viridissimum*): Dew or raindrops are first collected on the upper side or tip of the leaf using the pelvic patch (an anatomical structure ventrally in front of the cloaca, see glossary) and presumably stored in the urinary bladder. Even nests of other species (*Teratohyla pulverata*), which are not guarded, can be visited repeatedly over many nights as a water reservoir for 20–40 minutes and used for their own water supply and to hydrate their own clutch. The ♂ 'broods' for between approx. 15 and 45 minutes at a time and also appears to promote embryonic development by swinging and rotating movements and

with the aid of its extremities. The authors were able to show in *H. fleischmanni* (and *H. viridissimum*) that the ♂♂ also care for individual fallen eggs or provide a kind of manual hatching aid. In contrast, feeding on or sorting out dead embryos was never observed (Delia et al. 2017a).

*H. fragile*: ♂♂ call and ♀♀ spawn on the undersides of leaves approx. 1–3 m above the ground, ♂♂ guard and defend the clutch (Señaris & Ayarzagüena 2005).

*H. guairarepanensis*: ♂♂ call on upper and lower leaf surfaces 1–5 m above the ground, ♀♀ spawn on upper leaf surfaces, ♂♂ guard and defend the clutch (Señaris & Ayarzagüena 2005).

*H. iaspidiense*: ♂♂ usually call on upper leaf surfaces and defend the clutch, ♀♀ spawn on lower leaf surfaces (La Marca & Señaris 2004).

*H. ibama*: ♂♂ call in the vegetation at the edge of streams at a height of about 2–3 m and defend their clutches, ♀♀ spawn on the undersides of leaves of e.g. *Dicranopygium* sp., heliconias and some arum plants (Ruiz-Carranza & Lynch 1998).

*H. kawense*: ♂♂ call from upper and lower leaf surfaces, ♀♀ attach clutches as monolayers with whitish eggs to leaf undersides, territorial behaviour and brood care of ♂♂ unknown, ♂♂ form calling groups of about 10 individuals every 100 m along the river (Castroviejo-Fisher et al. 2011).

*H. mashpi*: ♂♂ call in the vegetation at the edge of streams and defend their clutches, ♀♀ spawn on the undersides of leaves (Guayasamin et al. 2022).

*H. mesai*: ♂♂ call from upper leaf surfaces (e.g. heliconias) 2 m above the ground and 2 m from small streams in the forest, other ♂♂ stayed high in the trees and bushes (Barrio-Amorós & Brewer-Carias 2008).

*H. mondolfii*: ♂♂ may guard several clutches at the same time (Señaris & Ayarzagüena 2001).

*H. muiraquitana*: ♂♂ descend to heights of up to 40 cm to call, ♀♀ lay their eggs on the undersides of leaves (Oliveira & Hernández-Ruz 2017).

*H. munozorum*: ♂♂ call from the upper and lower sides of leaves about 2 m above the ground, ♀♀ lay their eggs on the underside of leaves, brood care unknown (Lynch & Duellman 1973, Guayasamin et al. 2020).

*H. orientale*: reproductive activities and egg-laying most frequently during the rainy season and preferably in fast-flowing streams, mating and egg-laying (mostly on *Heliconia* leaves, but also on philodendron and palms up to 6 m high) last approx. 5 hours, the pair remain on the upper and lower leaf surfaces, but spawn on the underside. After laying the eggs, the ♂ stay with the clutch and thus optimise the development time, which is strongly influenced by egg size, temperature, precipitation and predation by arthropods (Murphy et al. 2012, Delia et al. 2014, Nokhbatolfigohahai et al. 2015).

*H. orocostale*: ♂♂ call on leaf undersides, approx. 3–10 m above the water, ♀♀ also attach clutches to leaf undersides, ♂♂ practise brood care (Rivero 1968).

*H. pallidum*: ♂♂ usually call on leaf undersides, sometimes on the upper side, ♀♀ also lay on leaf undersides of Cyclanthaceae, Araceae and Arecaceae plants, ♂♂ undertake brood care (Señaris & Ayarzagüena 2005).

*H. talamancae*: ♂♂ usually call from the undersides of leaves, sometimes also on the upper side, from vegetation hanging above the water at a height of 2–5 m, mating takes place in the first hours after dark, ♂♂ mainly care for their clutches at night (sometimes also during the day) (Kubicki 2006).

*H. tatayoi*: Calling activity begins at dusk (from 7 pm) and decreases towards midnight in the populations of Chocó and Magdalena in Colombia. In Ecuador, the ♂♂ call from the top of the leaves at dusk, followed by a retreat to the underside of the leaves after dark. During heavy rainfall, the species can also be heard calling in the early morning between 4.40 and 5.30 am. Eggs are laid on the undersides of leaves. ♂♂ call from the undersides of the leaves of epiphytes and ferns, the eggs are laid on the underside



of the leaves in a single gelatinous layer, the clutch is looked after by the ♂ at night, especially in the dry season, the ♂♂ can look after one or more clutches at the same time, among rivaling ♂♂ there are physical fights in which one ♂ tries to jump on the back of the other, both squirm and kick, during these fights the call changes to a quiet 'priiip' (Savage 2002, Kubicki 2007, Delia et al. 2010, Mendoza-Henao et al. 2020).

*H. taylori*: ♂♂ call from the upper sides of leaves, eggs are laid on the upper and lower sides of leaves, sometimes resulting in astonishingly high densities of 10 calling ♂♂, which sit 30–40 cm apart (Señaris & Ayarzagüena 2005).

*H. tricolor*: ♂♂ were found at altitudes of 4–5 m above 0.5–1.5 m wide streams and called from leaf undersides in the immediate vicinity of clutches, ♀♀ laid single-layer clutches on leaf undersides (Castroviejo-Fisher et al. 2011).

*H. valerioi*: ♂♂ are territorial and call from leaf undersides (smooth-leaved plants of the families Araceae, Arecaceae, Cyclanthaceae, Heliconiaceae and Marantaceae), after mating the ♀ lays the eggs in a sticky jelly as a simple (single-layered) clutch on leaf undersides up to 6 m above the water, the ♀♀ leave the deposition site soon after insemination. In contrast, the ♂ guards the eggs during the day and at night, aggressively attacking other approaching ♂♂. The ♂♂ continue to call during brood care, attract further ♀♀ and can simultaneously care for up to seven clutches on one leaf. ♂♂ released 450 metres away from the clutch were able to find their way back to their clutch. In the natural habitat in Costa Rica, polygynandrous mating behaviour was observed in *H. valerioi*, which demonstrates a low level of sexual selection in both sexes. According to this, both sexes are not choosy in their choice of partner, the ♀♀ lay a clutch of eggs every three weeks on average, while ♂♂ inseminate one every fortnight or so. Under outdoor conditions, the tadpoles hatch from the clutches after 13.9 ± 8.6 days and fall into the water below to complete their development. However, it is now also known that glass frog tadpoles of different genera can accelerate hatching from the clutch in the event of predation, but delay it by more than twice the minimum required development time in dry conditions. During the day the ♂ is turned towards the clutch, sometimes touching it, at night the ♂ remains close by but only sometimes assumes the guarding position, at night a 'brooding behaviour' is also shown to moisten the eggs, for this purpose the ♂ touches the clutch with its rear ventral side and empties its urinary bladder over it. The diurnal phase of brood care also serves as a defence against wasps, which eat individual eggs from the clutch. By mimicking the habitus with a clutch, the wasp could even be directed to the ♂, which optimises defence or even feeding. Other egg predators are spiders, ants and certain leafhoppers (from the Copiphoridae family; McDiarmid 1978, Savage 2002, Wild 2003b, Guyer & Donnelly 2005, Kubicki 2007, Vockenhuber et al. 2008, 2009, Mangold 2014, Mangold et al. 2015, Delia et al. 2019).

*H. vireovittatum*: ♀♀ lay clutches of green eggs on the underside of the leaves, ♂♂ only brood at night by moistening the clutches by emptying the urinary bladder, as in other members of the genus (Savage 2002, Vargas-Salinas et al. 2014).

*H. viridissimum*: (see also brood care behaviour in *H. fleischmanni*), ♂♂ call during twilight until after midnight from low to very high perches mostly from leaf undersides (rarely from upper sides) at a height of 1–10 m above the water, cream-coloured eggs are laid on leaf undersides, which are subsequently cared for by the ♂. During the day the ♂ rests next to the eggs, at night it sits on the clutch three to five times to provide moisture (see also comments on this in *H. colymbiphyllum* and *H. fleischmanni*). In the absence of an important predator (*Trachops cirrhosus*, a bat that recognises the call of *H. fleischmanni* [now *H. viridissimum*]), an increased number (22.5%) spawned on leaf surfaces. Another predator of clutches of eggs was described as the Blunthead Tree Snake (*Imantodes cenchoa*) (Delia et al. 2010, 2013, Díaz-García et al. 2023).

*H. yaku*: ♂♂ call and guard clutches on the underside of leaves, no aggressive behaviour known among ♂♂ of the same species or between ♂♂ and predators (Guayasamin et al. 2017).

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| Reproductive season            | <p><i>H. adespinosai</i>: ♂♂ call from July to August.</p> <p><i>H. anachoretus</i>: the authors assume that the reproductive phase ends with the end of the rainy season in May (Twomey et al. 2014).</p> <p><i>H. aureoguttatum</i>: ♂♂ call from July to August (Barrera-Rodriguez &amp; Ruiz-Carranza 1989).</p> <p><i>H. cappellei</i>: ♂♂ call during the rainy season from November to April (Castroviejo-Fisher et al. 2011).</p> <p><i>H. chirripoi</i>: a ♂ guarding a clutch of eggs was observed on 15/07/2001 (Kubicki 2004).</p> <p><i>H. colymbiphyllum</i>: breeding season during the rainy season from May to November (Savage 2002).</p> <p><i>H. ibama</i>: pairs were caught in October 2005 and September 2006 (Rada et al. 2007).</p> <p><i>H. mashpi</i>: ♂♂ calling especially in the months of April to June and August to November (rainy season from February to May, dry season from June to October; Guayasamin et al. 2022).</p> <p><i>H. nouns</i>: reproductive activity was observed from November to March. In the Río Manduriacu reserve, a ♂ was found during the rainy season in February at a height of 6 m, calling from the underside of a leaf, where it was found right next to a clutch of eggs. At the same location, metamorphs were found in October and November on leaves 50–150 cm above the water (Guayasamin et al. 2022).</p> <p><i>H. valerioi</i>: reproductive activity coincides with the rainy season (May to late October).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Eggs / clutch, clutches / year | <p><i>H. adespinosai</i>: ♂♂ guards clutches of 22 embryos (Guayasamin et al. 2019a).</p> <p><i>H. anachoretus</i>: clutch size 19–25 eggs (Twomey et al. 2014).</p> <p><i>H. aureoguttatum</i>: ♂ guards the clutch by remaining at a distance of approx. 5 cm from the eggs. Clutch size 25–42 greenish eggs/clutch (Barrera-Rodriguez &amp; Ruiz-Carranza 1989) or 27–49 (Valencia-Aguilar et al. 2012).</p> <p><i>H. cappellei</i>: The number of eggs per clutch is between 4 and 32 with an average of 17.2 eggs (Noronha &amp; Rodrigues 2018). Other authors report 10 (Noonan &amp; Bonett 2003) to 22 eggs with up to five clutches on the underside of a leaf (Rodrigues et al. 2010). During observations in the natural habitat, a clutch of 21 underdeveloped eggs was observed on 03/03/2023 and collected on 15/03/2023. The larvae hatched on 16 March after 13–15 days. The first metamorphosis took place on 01/05/2023 after only 45 days. Ten further individuals metamorphosed by 20.05.2023. A further clutch of 19 eggs was discovered on 21.05.2023, which already showed early developments. The larvae hatched on 28/05/2023 and the first metamorphosis again took place after only 45 days on 13/07/2023. Nine further individuals made the landfall between 14 July and 12 August 2023, three juveniles died. On 29/08/2023, at least two tadpoles in good condition (stage 30) were still in the water. These juveniles did not grow so well, perhaps due to the heat of the summer (Philippe Gaucher, personal communication).</p> <p><i>H. carlesvilai</i>: ♂♂ guard clutches of 27–32 eggs on the underside of leaves (Castroviejo-Fisher et al. 2009, Cisneros-Heredia et al. 2010).</p> <p><i>H. chirripoi</i>: ♂♂ guard clutches with 53–80 eggs on the underside of the leaf, brood care also during the day (Kubicki 2004, Guayasamin et al. 2020).</p> <p><i>H. colymbiphyllum</i>: clutches usually contain 50 eggs (maximum 75; Savage 2002).</p> <p><i>H. diana</i>: clutch size of 31–68 eggs (Kubicki et al. 2015).</p> <p><i>H. durantii</i>: clutch of 20–29 white-green eggs, clutch size 2 x 2.0–3.2 cm, arranged in a circle (Señaris &amp; Ayarzagüena 2005).</p> <p><i>Hyalinobatrachium esmeralda</i>: clutch with approx. 35–45 eggs (Ruiz-Carranza &amp; Lynch 1998).</p> <p><i>H. fragile</i>: clutch with 20–25 eggs.</p> <p><i>H. guairarepanensis</i>: clutch with 20–26 eggs (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. iaspidiense</i>: clutch of 22 eggs (La Marca &amp; Señaris 2004).</p> <p><i>H. ibama</i>: clutches with 12–19 pale cream to greenish embryos (Ruiz-Carranza &amp;</p> |

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|                                                   | <p>Lynch 1998) or egg masses, each containing between 15 and 25 creamy yellow eggs. Of the ♂♂ caught, about 90% guarded one or two egg masses. In the field, not only was exclusive care by the ♂♂ observed both during the day and at night, but in the cases where two clutches were present (n=7), it was also observed that the ♂ sat on the youngest clutch (Rada et al. 2007).</p> <p><i>H. kawense</i>: ♀♀ lay clutches of up to 33 eggs on the underside of leaves (Castroviejo-Fisher et al. 2011). During deforestation work in the natural habitat in 2020, a clutch of 29 freshly laid eggs was collected, from which the larvae hatched after a period of 9–10 days. The first frogs completed metamorphosis after only 50–58 days, with only nine tadpoles remaining by this time. The young were reared for two months until these animals also disappeared. The following year, another clutch of 19 eggs was laid on 9 January 2021 and left in place. Some hatched in the stream on 18/01/2021 (eight individuals), the rest on 19/01/2021 (11 individuals). In 2023, another clutch of 23 tadpoles was found on 28/02/2023, from which the larvae presumably hatched on 06/03/2023. The first observed metamorphosis took place on 01/05/2023 after only 55 days. The following 17 individuals metamorphosed between 2 and 19 May 2023. At least two further individuals were found outside the water, killed by ants. The last three tadpoles were no longer detectable (Philippe Gaucher, personal communication).</p> <p><i>H. mashpi</i>: examined clutches contained 31–34 eggs (n=3; Guayasamin et al. 2022).</p> <p><i>H. mondolfii</i>: clutch with 25–32 greenish white eggs laid in a single oval layer (approx. 30 x 15 mm surface) (Señaris &amp; Ayarzagüena 2001).</p> <p><i>H. muiraquitana</i>: clutch of 11 eggs in a jelly nest (Oliveira &amp; Hernández-Ruz 2017).</p> <p><i>H. orientale</i>: average clutch sizes comprised 14–36 eggs (Nokhbatolfoghahai et al. 2015).</p> <p><i>H. pallidum</i>: clutches with 20–33 eggs (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. talamancae</i>: the clutches consist of 20–30 eggs, which are laid in the centre of the leaf on the underside. The clutches are typical of the genus, consisting of a single layer (monolayer) with surrounding jelly. The eggs are initially greenish white and change colour from pale pink to brownish during development (Kubicki 2006).</p> <p><i>H. tatayoi</i>: clutches contain 20–35 greenish white eggs (Mendoza-Henao et al. 2020).</p> <p><i>H. taylori</i>: clutches with 26–38 small and pale green eggs (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. tricolor</i>: clutch with 22 eggs (n=2; Castroviejo-Fisher et al. 2011).</p> <p><i>H. valerioi</i>: one clutch contains 22–40 greenish eggs (Vockenhuber et al. 2009, Kubicki 2007, Guayasamin et al. 2020).</p> <p><i>H. viridissimum</i>: clutches consist of 22–23 pale green to cream-coloured eggs in single-layer clutches (Mendoza-Henao et al. 2020).</p> |
| Size of eggs and larvae at hatching               | <p><i>H. aureoguttatum</i>: black spotted larvae were in Gosner stage 25 at hatching (Valencia-Aguilar et al. 2012).</p> <p><i>H. colymbiphyllum</i>: egg diameter approx. 1.5 mm (without jelly; Savage 2002).</p> <p><i>H. durantii</i>: eggs with a diameter of 1 mm (at oviposition) or 4–5 mm (developed), transparent with light green embryos (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. orientale</i>: average egg diameter 1.86 mm (Nokhbatolfoghahai et al. 2015, Lehtinen &amp; Georgiadis 2012).</p> <p><i>H. valerioi</i>: egg diameters are given as 2 mm diameter, with jelly coating it is 3–4 mm (T. Eisenberg, own measurements).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Development time from egg laying to metamorphosis | <p><i>H. aureoguttatum</i>: the larvae hatch during or after heavy rainfall after an average of 17.1 days. Hatching success possibly high due to permanent guarding (96.5% hatching rate [in <i>H. valerioi</i> – also with permanent 24 h guarding – 50.4%, in <i>H. fleischmanni</i> – only at night with guarding – 32%]; Valencia-Aguilar et al. 2012).</p> <p><i>H. chirripoi</i>: ♂♂ guard the clutch for 2–3 weeks until hatching (Valencia-Aguilar et al. 2021).</p> <p><i>H. ibama</i>: during ex situ development, the hatching time of the tadpoles was about 20</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |

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|                       | <p>days, the larvae did not start feeding until one week after hatching and fed on the yolk still in the body during this time. It took more than five months from hatching to metamorphosis (Rada et al. 2007).</p> <p><i>H. orientale</i>: embryonic mortality appears to vary throughout the year, with most damage occurring during the rainy season (Lehtinen &amp; Green 2019).</p> <p><i>H. talamancae</i>: the larvae hatch after 15 days (Kubicki 2006).</p> <p><i>H. valerioi</i>: under field conditions, the tadpoles hatch from the clutch after <math>13.9 \pm 8.6</math> days and fall into the water below to complete their development. However, it is now also known that glass frogs of different genera can accelerate hatching from the clutch in the event of predation, but delay it by more than twice the minimum development time required in dry conditions (Vockenhuber et al. 2008, 2009).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Details on the larvae | <p><i>H. aureoguttatum</i>: the description is based on a larva in stage 35 (Gosner 1960). Total length 34.0 mm, body length 10.4 mm, tail length 24.5 mm, body elongate, slightly oval, wider (4.5 mm) than high (3.1 mm), mouth region rounded dorsally and laterally, lateral line organ inconspicuous, eyes dorsal, spiraculum short and left-directed, large anteroventral oral disc, marginal (ventral and lateral) sawn papillae, maxillary sheath in M-shape, mandibular sheath in U-shape, LTRF (labial tooth row formula) 2(2)/3 rows of teeth, A1/A2 with 259 and 110 teeth, P1/P2/P3 with 158, 206 and 206 teeth, anterior half of body grey, posterior half of body and tail red (Ibáñez et al. 1999, Teran-Valdez et al. 2009).</p> <p><i>H. cappellei</i>: descriptions of the larvae can be found in Myers &amp; Donnelly (1997) as <i>H. crurifasciatum</i>, in Noonan &amp; Bonett (2003) as <i>H. igniocolus</i> and in Señaris &amp; Ayarzagüena (2005).</p> <p><i>H. chirripoi</i>: larva pale brownish red at hatching, hatching at Gosner stage 25–26, unusual pattern on the back: two rows of brown pigmented, cobweb-like spots run over the entire body, which meet at the tip of the mouth to form a semicircle, another row of pigmented spots extends dorsally over the tail muscles, body, gills and heart red, tail cream-coloured to yellow, strong length growth from Gosner stage 25–41, so that this species has the longest known larvae of the Centrolenidae, oral disc bulging, limited to a dorsal gap by a single row of teeth with 45 marginal papillae (LTRF 2(2)/3), edges of the two jaw sheaths bordered by many narrow teeth (Hoffmann 2010a, Guayasamin et al. 2020).</p> <p><i>H. colymbiphyllum</i>: the larvae are small and measure only 9.5 mm at Gosner stage 25. The body is elongated, the tail is long with a tapering tip, fin margins transparent. Dorsal colouration chocolate brown, underside lighter (reddish), tail musculature with dark spots. The mouth is ventral with a complete oral disc, horn beak and 2/3 rows of teeth with many denticles present, lower beak finely toothed, around the oral disc there is a single row of papillae except for the upper part (Savage 2002, Jaramillo et al. 1997).</p> <p><i>H. durantii</i>: small, dorsolaterally located eyes, small, rounded, anterolaterally directed nostrils, tail musculature does not reach the distal end of the tail, distal end of the tail rounded; narrow caudal fin fringes, the upper one as wide as the lower one, dorsal fin margin begins after the connection between body and tail, ventral margin on the body (Señaris &amp; Ayarzagüena 2005).</p> <p><i>H. fleischmanni</i>: descriptions of the larva can be found in Savage (2002), Hoffmann (2010a) and Salazar-Nicholls &amp; Pino (2014) or see under <i>H. viridissimum</i>.</p> <p><i>H. ibama</i>: body light grey with a white or cream tail, dorsal, lateral and ventral body surfaces translucent with some scattered grey spots and melanophore clusters on the rostrum and body; ventrally, the gut is brown to green translucent, heart visible through the body wall and covered by a thin layer of whitish iridophores, body elongated and depressed, slightly wider than high, eyes medium sized, dorsally arranged, nostrils very small, anterodorsal and much closer to the end of the rostrum than to the eye, tail long and robust, with a rounded distal end, its length is 2.34 times the body length, dorsal fin margin reaches its greatest height just behind the centre of the tail and originates at the base of the caudal musculature, origin of the ventral fin margin at the cloaca, oral disc small, positioned anteroventrally, bordered by a row of</p> |

small marginal papillae, slightly blunt and decreasing in size towards the sides and posterior region. In Gosner stage 24 whitish body colour, eyes are barely visible as black dots, separation on the sides of the body: grey towards the back and translucent towards the abdomen and tail, translucent ventral view, heart visible (red colour). In the first months of development there is no strong increase in size, but the eyes become more visible from stage 29 (12 weeks); one month later the heart is still visible and red in some larvae of the younger stages, but the more developed larvae (around Gosner stage 36) have white iridophores in the pericardium, a constant and typical feature of frogs after metamorphosis. Five months later (Gosner stage 41), the larvae change colour and take on a more intense white hue. Head shape changes from a round to a blunt shape, eyes already well developed with horizontal pupil, nostrils clearly recognisable, the body becomes wider and the forelegs are visible under the skin (Rada et al. 2007).

*H. orientale*: tadpoles in Gosner stage 25 had a length of approx. 11 mm, were bright green and transparent with yolk sac residues. When they hatched over land, they were able to cover distances of up to 40 cm by leaping upwards (Lehtinen & Georgiadis 2012).

*H. tatayoi*: information on embryonic development and larvae can be found under *H. viridissimum*.

*H. taylori*: description of the tadpole based on Gosner stage 25 (n=9) from a clutch at the Quebrada de Jaspe, collected 5 m above the water: Body length 3.06–3.32 mm, tail length 6.44–7.63 mm, body height 1.25–1.56 mm, body width 1.88–2.13 mm, flattened spherical body from dorsal, oval in lateral view, small eyes located dorsally, spiraculum in the last left third of the body and pointing posteriorly (Señaris & Ayarza-güena 2005).

*H. valerioi*: when hatching, the larva is 12 mm long, it has brown spots on the upper side and on the tail, the fins are transparent, the underside is bright red. Elongated body and tail, body slightly flattened, caudal fin fringe small, tail tip rounded, complete oral disc with beak and 2/3 rows of teeth, edge of lower beak finely serrated, a single row of papillae on lateral and ventral edge of oral disc (Savage 2002).

*H. viridissimum*: two six-day-old larvae had body lengths of 3.1 and 3.4 mm with total lengths of 10.5 and 11.2 mm. Ten eight-day-old larvae had body lengths of 3.1–3.8 mm and total lengths of 10.4–12.6 mm. Further description of one of these larvae: dorsally oval head and body, greatest width at the middle body, tooth rows 2/2, second upper row only laterally pronounced, a row of relatively large papillae around the mouth opening, upper horn beak describes a broad arch, lower beak more prominent with narrower arch. In comparison with larvae of about the same size of *H. fleischmanni* from Costa Rica the following differences can be observed: *H. fleischmanni* shows a blunter mouth region seen from the lateral side, which is inclined ventrally, furthermore three well-developed lower rows of teeth, upper beak directed medially. Three pale-green metamorphs with a small tail had SVLs of 11.6, 12.3 and 12.5 mm (Duellman & Tulecke 1960).

### Husbandry and Captive Breeding of *Hyalinobatrachium aureoguttatum*, *H. fleischmanni*, and *H. valerioi* **B/B–C**

Assessment of difficulty for *Hyalinobatrachium aureoguttatum* **B** breeding **C**,

Assessment of difficulty of husbandry of *H. fleischmanni* and *H. valerioi* **B** breeding **B**.

All other species *Hyalinobatrachium* spp. **X**, as they have not yet been kept in human care. Husbandry and breeding parameters probably similar for many species.



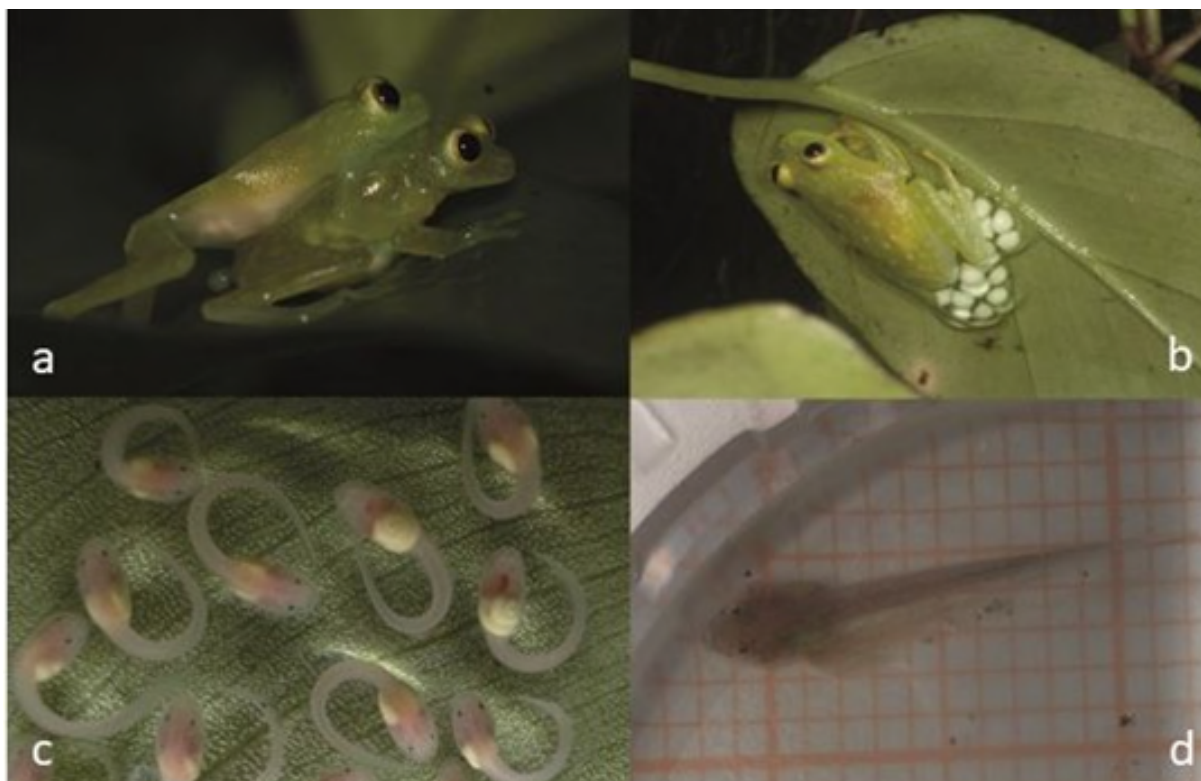


Fig. 49: Captive breeding of *Hyalinobatrachium fleischmanni*

- a mating. Note the eggs visible through the lateral skin of the female (R. Stuster)
- b ♂ with freshly laid eggs (T. Eisenberg)
- c young tadpoles still in the eggs (T. Eisenberg)
- d freshly hatched tadpole. Note the mycel of *Saprolegnia* sp. at the spiracle opening that caused subsequent death of larvae from this clutch (T. Eisenberg).



Fig. 50: Captive breeding of *Hyalinobatrachium valerioi*

- a brooding ♂ in the natural habitat near Sueño Azul, Horquetas, Costa Rica. Note a second clutch in advanced development on the left edge of the picture, which is also being cared for (T. Eisenberg)
- b feeding tadpoles (T. Eisenberg)
- c juvenile in metamorphosis (M. Weber)
- d young frogs (T. Eisenberg).

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Hyalinobatrachium</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|--------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p>According to Redbond et al. (2019), daytime temperatures in the natural habitat in Costa Rica were 23–24°C in October–February (up to 17°C at night) and 24–26°C in March–April. Automatic irrigation was paused between December and March to simulate a dry period (only two manual sprays); in March, spraying was carried out three times a day for 30 s, in April for 60 s. The spray water was provided with locally collected rainwater, and humidity was increased by using a misting system via two nozzles in the vivarium, controlled by an automatic timer and allowing adjustable misting duration. The water had a temperature of 19–23°C and the following parameters: pH 6.8–7, KH: 3–6 °d (carbonate hardness) and GH: 8 °d (Redbond et al. 2019). Information on the housing conditions was provided as follows:</p> <p><b><i>H. aureoguttatum</i>:</b></p> <ul style="list-style-type: none"> <li>– Sex ratio: 1.3   5.2   6.4.</li> <li>– Air and water temperature (°C): 20–25   23   20–28, water section not specially heated, partly not available.</li> <li>– Humidity (rel.%): 70–100 (n=3).</li> <li>– Lighting/type/day–night cycle: LED light bar (n=3)   no UV component (n=3)   day-light length 12–14 h (n=3).</li> <li>– Tank size (length x width x height in cm): 40 x 60 x 60   60 x 70 x 70   70 x 50 x 100 cm.</li> </ul> |

- Proportion of water in the total area (%): 0–100 (often as a moat, complete floor area can be flooded during irrigation).
- Soil substrate: Filter sponge, pine bark, leaves | soil mat | no substrate, plus individual fist-sized moss-covered river pebbles.
- Furnishing/planting: *Philodendron* (n=3), also other tropical plants such as anthuriums, *Monstera* spp., vanilla, bromeliads (*Neoregelia* sp.), various vines, which either grow epiphytically on cork, coconut, tree ferns or Hygrolon® gauze or in pots.
- Water depth (cm): 0–4 (n=3).
- Number of animals per container: 4–10.
- Feed/feeding intervals: 2x/week (n=3).
- Supplementation (minerals/vitamins): yes, but not specified | Repashy Calcium plus | Ranarium Rana Vit, Dendrocare.
- Aggression between several ♂♂ or ♀♀: none (n=3).

#### ***H. fleischmanni*:**

- Sex ratio mostly with more ♂♂ than ♀♀ (17.2 | 3.0 | 6.4 | not specified).
- Air and water temperature (°C): 20–28 | 25–29 during the day, 21–24 at night | 22 | 23, water section not specially heated, partly not available.
- Humidity (rel.%): 70–100 (n=4).
- Lighting/type/day-night cycle: LED light bar (n=3) or fluorescent lamps (n=2), with UV component (n=1), daylight length 12–13 h (n=3) or 6.5 h.
- Container size (length x width x height in cm): 30 x 20 x 20 (laboratory) | 40 x 60 x 60 | 60 x 70 x 70 | 50 x 60 x 120 cm.
- Proportion of water in the total area (%): 0–100 (often as a moat, complete soil area can be flooded during irrigation).
- Soil substrate: organic (gravel, tree fern, leaves, moss) | inorganic (soil mat) | no substrate, but additionally individual fist-sized moss-covered river pebbles | paper towel.
- Furnishing/planting: *Philodendron* (n=4), also other tropical plants such as anthuriums, *Monstera* spp., vanilla, bromeliads (*Neoregelia* sp.), various vines, which either grow epiphytically on cork, coconut, tree fern or Hygrolon® gauze or in pots.
- Water depth (cm): 0–4 (n=2) | 15 cm (n=2).
- Number of animals per container: 3–19.
- Feed/feeding intervals: every night | 2x/week (n=3).
- Supplementation (minerals/vitamins): yes, but not specified (n=2) | calcium, omega-3 fatty acids, vitamins | Repashy Calcium plus.
- Aggression between several ♂♂ or ♀♀: none (n=4).

#### ***H. valerioi*:**

- Sex ratio: 1,0,3 (n=2) | 1,1 | 2,1 | 3,1 | 4,4 | 2,5,3 | 2,1 | 2,5 | 1,1,1 | 6,4 | not specified.
- Air and water temperature (°C): 23–27, at night up to 19 | 23.5–29, water temperature 24–26 | approx. 20–26 (night/day; water 23–25) | 23–25 (night/day; water 22–24) | 25–28 | 19–23 (maximum 27) | 19–29 | 24 | Summer daytime 22–27, nighttime 20–24, winter daytime 22–26, nighttime 18–21 | 18–28 | 20–28.
- Humidity (rel.%): 70–100 (n=8) | 50–70 (dry season) to 100 (irrigation) | 50–75 | 60 during the day, 90–100 at night | not specified.
- Lighting/type/day-night cycle: LED light bars (n=4) | fluorescent lamps (n=4) | with UV component (n=2), daylight length 12–14 h (n=10) | lighting in seasonal rhythm | not specified.
- Container size (length x width x height in cm): 30 x 30 x 50 | 30 x 50 x 50 | 40 x 60 x 60 | 45 x 45 x 60 | 50 x 50 x 50 (n=3) | 60 x 40 x 80 | 60 x 45 x 90 | 60 x 50 x 80 | 70 x 30 x 70 cm | not specified.
- Proportion of water component in the total area (%): 0–100 (often as water ditch, complete floor area can be flooded during irrigation, water component not always

|                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|---------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                           | <p>present; n=10)   not specified (n=2).</p> <p>– Soil substrate: Cork sheets with a coating which is suitable for drinking water-use, on polystyrene sheets   flocked rigid foam   coarse-grained coconut fibres mixed with fine coconut fibres, peat moss and bark. Good drainage for even watering. This mixture may not be suitable for feeding insects such as crickets, as they hide in the substrate   foam filter fabric (10 ppi, geotextile fabric, magnolia leaf litter, i.e. no soil)   epiweb submerged during irrigation   pine bark   foam   no substrate, plus individual fist-sized moss-covered river pebbles (n=4)   not specified.</p> <p>– Furnishing/planting: <i>Philodendron</i> (n=9), also other tropical plants such as mosses, ferns, anthuriums, <i>Monstera</i> spp., vanilla, bromeliads (<i>Neoregelia</i> sp.), various vines, which either grow epiphytically on cork, coconut, tree fern panels or Hygrolon® gauze or in pots   back and side walls made of cork insulating panel, manzanita wood, fake rocks on the floor; plants: <i>Anthurium forgetti</i>, <i>Philodendron chinchamayense</i>, <i>Neoregelia</i> sp., <i>Campyloneurum angustifolium</i>, Cyclanthaceae, <i>Philodendron verrucosum</i>, <i>Philodendron chinchamayense</i>, <i>Gesneria reticulata</i>   not specified.</p> <p>– Water depth (cm): 0–4 (n=6)   5–20 (n=3)   not specified (n=3).</p> <p>– Number of animals per tank: 3–10   not specified (n=4).</p> <p>– Food/feeding intervals: <i>Drosophila</i>, aphids, firebrats, Jamaican field crickets (<i>Gryllus assimilis</i>) 2x/week (n=3)   3x/week (n=4)   4–5x/week (n=3)   30% 5–6 mm enhanced crickets ('gut-loaded' with carnivore fish food pellets soaked in almond milk, dusted with spirulina), 40% <i>Drosophila hydei</i>, 10% <i>Drosophila melanogaster</i>, 10% pea aphids, 10% springtails   not specified (n=2).</p> <p>– Supplementation (minerals/vitamins): yes, but not specified (n=4)   Repashy Calcium plus at every feeding, 1–2x/month Nekton Rep   Repashy Vit A once every 2 weeks   Repashy Calcium plus at every feeding, Repashy Vit A once a month   Repashy Supervit twice a week, Repashy Vit A once a month   Herpetal Amphib   <i>Drosophila</i> feeding with multivitamin, vitamin A, sepia   not specified (n=2).</p> <p>– Aggression between several ♂♂ or ♀♀: none (n=7)   leaves with clutches are (rarely) defended against other ♂♂ (n=3)   not specified (n=2).</p> |
| Life expectancy           | <p>Maximum age of the animals kept:</p> <p><i>H. aureoguttatum</i>: 6 years   not specified (n=2).</p> <p><i>H. fleischmanni</i>: 6 years   not specified (n=3).</p> <p><i>H. valerioi</i>: 2   5–8   6–7 (n=3)   8   not specified (n=6).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Triggers for reproduction | <p><b><i>H. aureoguttatum</i>:</b></p> <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical equipment, animal care activities): Rain chamber (tempered to approx. 22–25°C)   very strong irrigation</p> <p>First offspring (CB) in the year: 2019   2023</p> <p>Frequency of CB since then: 10x   not specified (n=2).</p> <p>Where are the eggs laid (leaves/panes/objects)? Leaves (n=2).</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (upper side, lower side, tip of leaf)? <i>Philodendron</i>, underside of leaves (n=2).</p> <p>How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): Monolayer (n=2).</p> <p>Number of clutches per ♀ in one oviposition: 1 (n=2).</p> <p>Number of clutches/♀/year (min.–max.): 2–8   not specified (n=2)</p> <p>Number of eggs/clutch (min.–max.): approx. 20–40   11–49 (n=6)</p> <p><b><i>H. fleischmanni</i>:</b></p> <p>Triggers (stimuli) for reproduction: rain chamber (tempered to 28°C), 2 x 4 h continuous irrigation, one ♀ laid a clutch during a summer thunderstorm/strong pulsatile irrigation only via the irrigation system (e.g. rain every 15–30 min for 30 s over several</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |

days using Easy Timer interval control (Lucky Reptile) or wifi switching relays (Shelly Plugs).

First offspring (CB) in the year: 2016 | 2020.

Frequency of CB since then: 3x | >10x.

Where are the eggs laid (leaves/panes/objects)? Leaves (n=2) | panes.

On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom, tip of leaf)? *Philodendron*, *Monstera*, underside of leaves (n=2).

How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): Monolayer (n=2) | adjacent, non-overlapping but connected eggs (monolayer); the clutch increases in volume during incubation and can then detach somewhat spherically from the leaf surface.

Number of clutches per ♀ in one oviposition: 1 (n=2).

Number of clutches/♀/year (min.–max.): 1–2 | 4–6 (probably significantly more).

Number of eggs/clutch (min.–max.): 17–24 (n=3) | 26–34 (n=3).

***H. valerioi*:**

Triggers (stimuli) for reproduction: regular spontaneous release of clutches (n=3) | slightly more humid husbandry, more rain or circulation pump (n=3) | spawning period begins every year in late autumn without any change in any parameters and lasts until approx. March | higher irrigation intensity and slightly higher temperatures in spring (n=2) | Basic diet: vitamins and minerals sprinkled on the fruit flies, algae powder (spirulina, chlorella and saltwater algae) mixed with approx. 5–10 per cent calcium by volume. Enhanced ('gut-loaded') fruit flies with activated baker's yeast at each feeding | 8 s spraying every 15 min from 8–2 pm, higher room temperature +/-24°C, feeding small crickets with spirulina & Repashy Bug Burger, filter (sprinkler) switches on at night from 10–4 pm (first clutch after 2 weeks with filter installed); feeder insects with vitamin A supplement once a month | not specified (n=2).

First offspring (CB) in the year: 2012 | 2013 | 2016 (n=2) | 2017 | 2019 | 2022 | 2023 (n=3).

Frequency of CB since then: 1–5x (n=4) | 6–10x (n=3) | >30x | >100x | not specified (n=3).

Where are the eggs laid (leaves/panes/objects)? Leaves (n=10) | panes (n=3) | flower pot | not specified (n=2).

On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom, tip of leaf)? *Philodendron*, *Monstera*, *Calathea*, *Anthurium*, underside of leaves (n=10) | not specified (n=2).

How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): Monolayer (n=8) | (occasionally) multi-layered, complex clutch (n=3) | not specified (n=2).

Number of clutches per ♀ in one oviposition: 1 (n=9) | not specified (n=3).

Number of clutches/♀/year (min.–max.): 1 (n=2) | approx. 3 | 4–5 | 4–6 | 5–8 | 5–10 | 0–12 | not specified (n=4).

Number of eggs/clutch (min.–max.): 10–30 | 10–35 | 15–25 | 15–39 | 25–30 (n=4) | 20–40 | not specified (n=3).

|                                                  |                                                                                                                                                                                                                                                                     |
|--------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Number of fertilised eggs per clutch (min.–max.) | <i>H. aureoguttatum</i> : 10–20   mostly > 95%.<br><i>H. fleischmanni</i> : up to 100%, individual eggs not fertilised   25–30   mostly > 95%.<br><i>H. valerioi</i> : low (0)   10–20   0–35   20–40   0–100%   80–90%   mostly > 95% (n=2)   not specified (n=4). |
| Number of embryos hatched per clutch (min.–max.) | <i>H. aureoguttatum</i> : 5–15   usually > 95%.<br><i>H. fleischmanni</i> : none   18–23   > 95%.<br><i>H. valerioi</i> : 0   0–10   0–35   20–40   0–100%   80–90% (n=2)   mostly > 95%   not specified (n=4).                                                     |
| Hatching rate (number of                         | Hatching rate (number of hatched larvae/number of eggs) or < 25%; 25–50%; > 50–75%; > 75%:                                                                                                                                                                          |



|                                                                                        |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
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| hatched larvae/<br>number of eggs)                                                     | <p><i>H. aureoguttatum</i>: &lt; 25%   usually &gt; 95%.</p> <p><i>H. fleischmanni</i>: 0   ~50   &gt; 75%.</p> <p><i>H. valerioi</i>: 50% (n=2)   &gt; 75% (n=2)   80%   &gt; 90%   0–100%   not specified (n=5).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Size of juvenile<br>frogs (freshly meta-<br>morphosed; min.–<br>max. [in mm])          | <p><i>H. aureoguttatum</i>: about 10 mm   not specified (n=2).</p> <p>Freshly metamorphosed juvenile frogs show a green ground colour without yellow dorsal spots (T. Eisenberg, unpublished data).</p> <p><i>H. fleischmanni</i>: about 10 mm   not specified (n=3).</p> <p><i>H. valerioi</i>: 4–7 (n=2)   8–12 (n=3)   &gt;12–16 mm (n=2)   not specified (n=5).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Number of meta-<br>morphosed juve-<br>nile frogs per year                              | <p><i>H. aureoguttatum</i>: 4   0–60.</p> <p><i>H. fleischmanni</i>: 0–60   not specified (n=3).</p> <p><i>H. valerioi</i>: about 14   0–50   20–50   60–80   200–300   not specified (n=7).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Number of rearing<br>losses up to the 3 <sup>rd</sup><br>month                         | <p><i>H. aureoguttatum</i>: &lt; 1%   not specified (n=2).</p> <p><i>H. fleischmanni</i>: &lt; 1%   not specified (n=3).</p> <p><i>H. valerioi</i>: low (0–15%; n=3)   0–60%   about 95%   not specified (n=7)</p> <p>In contrast to the predators mentioned above, damage caused by snails is not always recognised and prevented (T. Eisenberg, unpublished data).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Husbandry condi-<br>tions (larvae)<br>/Technical<br>requirements for<br>larval rearing | <p>Water containers with plant and algae growth have proven effective for rearing the larvae. The development time of the tadpoles at water temperatures of 23–25°C is between five and seven months (Kubicki 2007, Redbond et al. 2019). Individual stragglers, which sometimes take significantly longer than a year, are not uncommon (Eisenberg in prep., Papenfuss &amp; Eisenberg in prep.). Aeration with diaphragm pumps prevents the formation of a residue film and enriches the water with oxygen. When using a filter, the initially tiny size of the larvae must be taken into account, which is why simple airlift filters have proved their worth. Although the larvae are constantly on the move and graze on all surfaces, they are rarely seen actively feeding. Larvae can be fed on algae growth, blanched lettuce, the finest fish food (Repashy Super Green or Superpig (Repashy Ventures Inc, Oceanside, CA)) or feeding gels. In contrast to many other genera of the Centrolenidae family, larvae of the genus <i>Hyalinobatrachium</i> are dependent on plant-based food. Their nutritional status can be easily followed through the skin by the bulging, dark-coloured intestinal cone. Small frogs can initially be housed in small rearing containers and transferred to larger terrariums as they grow (Eisenberg in prep., Papenfuss &amp; Eisenberg in prep.).</p> <p>Redbond et al. (2019) describe egg laying and male brood care in a clutch of <i>H. valerioi</i> and the rearing of the larvae in the terrarium: Clutch size 28 eggs, first hatching of larvae after 15 days, hatching rate 26/28, fertilisation rate 27/28, rearing tank 15 x 20 x 13 cm with 3 L of stagnant tap water with bubble stone, later 28 L with filter (only 15/26 still present), in places with gravel, sand, and oak leaves as substrate in which the larvae could burrow into the substrate, water temperature 22–28°C (mostly 25–28°C), weekly water change 25%, regular determination of water values: Nitrite(&lt; 0.3 mg/l), nitrate(&lt; 100 mg/l) and ammonia (below detection limit), pH: 6.8–7, KH: 3–6°, GH: 8°, 1<sup>st</sup> metamorphosis 147 days after hatching.</p> <p><b><i>H. aureoguttatum</i>:</b></p> <p>Total length of freshly hatched larvae in mm: 10–11   not specified (n=2).</p> <p>Duration of larval period (oviposition to metamorphosis; min.–max.): 5   7–8 months.</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements): not specified (n=3).</p> <p>– Water temperature: 20–25   20–28.</p> <p>– Lighting/type/day-night cycle: no lighting (daylight)   50 W LED strip (12 h) and daylight.</p> <p>– Tank size (length x width x height in cm): 30 x 20 x 20   50 x 13 x 29.</p> <p>– Substrate/furnishing/planting: Lava granules or no substrate at all, clay bricks and clay flower pots as hiding places, Java moss   lava granules of various grain sizes, foliage, river pebbles.</p> |

- Water depth: 18/20 cm.
- Number of animals per tank: 10–30.
- Filter (type, capacity): Airlift sponge filter/Nano corner filter, 2W.
- Special requirements (e.g. water values): none (n=3).
- Larval food: Spinach, Repashy fish food Super Green (herbivorous!) | food tablets for carnivorous and herbivorous fish, cooked mushrooms, spinach, lettuce.
- Frequency of water changes: 50–80% 1x/week | 90% 1x/week.
- Type of water (rainwater, tap water, RO water, etc.): 90% reverse osmosis (RO) water: 10% tap water | 100% tap water.

***H. fleischmanni:***

- Total length of newly hatched larvae in mm: 10–12 | 12–13.
- Duration of larval period (oviposition to metamorphosis; min.–max.): 4–6 months | not specified (n=3).
- Special conditions and requirements for larval rearing (including technology and daily time requirements): not specified (n=3).
- Water temperature: 19–22 | 25 | 20–28.
  - Lighting/type/day-night cycle: no lighting (scattered light) | 50 W LED strip (12 h) and daylight/UV light for 6.5 h.
  - Tank size (length x width x height in cm): 30 x 20 x 20 | 40 x 30 x 30 | 50 x 13 x 29.
  - Substrate/furnishing/planting: Lava granules or no substrate at all, clay bricks and clay flower pots as hiding places, Java moss (n=2) | 1 cm cleaned gravel.
  - Water depth: 15 | 18 | 20 cm
  - Number of animals per tank: 18–100
  - Filter (type, capacity): Airlift sponge filter (n=3).
  - Special requirements (e.g. water values): none (n=2) | water with dissolved oxygen above 6 mg/l.
  - Larval food: Spinach, Repashy fish food Super Green (herbivorous!) | various fish foods, spirulina tablets (n=2).
  - Frequency of water changes: every 2–4 d/90% | 1x/week | every 3–4 weeks.
  - Type of water (rainwater, tap water, RO water, etc.): 100% rainwater | 100% tap water | 100% stream water (laboratory).

***H. valerioi:***

- Total length of freshly hatched larvae in mm: < 7 (n=3) | 10 | 11–13 (n=2) | not specified (n=6).
- Duration of larval period (oviposition to metamorphosis; min.–max.): 3–7 | 4 | 4–6 | ca. 5 | 5–11 | 5–12 months | not specified (n=6).
- Special conditions and requirements for larval rearing (including technology and daily time requirements): Mating success occurred soon after the animals were transferred. Initially there was no success with rearing of the tadpoles, but after changing the food, substrate and water, it has worked much better since then (no long-term experience yet) | Last year 4 ♀♀ laid eggs, but the calls of the ♂♂ could not be heard. After installing the filter, the ♂♂ can be heard throughout the night | n. A. (n=9).
- Water temperature: 20–24 | 20–29 (n=2) | 22–28 | 23–25 | 26 | 28 | not specified (n=5).
  - Lighting/type/day-night cycle: no lighting (daylight/scattered light; n=3) | LED strip (12 h; n=3) | not specified (n=6).
  - Tank size (length x width x height in cm): 12 x 20 x 6 | 20 x 30 x 20 | 25 x 40 x 12.5 | 40 x 20 x 20 | 40 x 25 x 25 | 60 x 30 x 30 | 71 x 15 x 15 | 40 L per 30 larvae | not specified (n=2).
  - Substrate/furnishing/planting: Lava granules or no substrate at all, clay bricks and flower pots as hiding places, Java moss (n=4) | sand, foliage, river pebbles (n=3) | not specified (n=5).
  - Water depth: 4 | 6–7 | 12–18 cm (n=6) | not specified (n=5).

|                                                                         |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|-------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                                         | <p>– Number of animals per tank: 10–15   20   24–30   30   50 (n=2)   100   not specified (n=5).</p> <p>– Filter (type, capacity): no filter (n=2)   airlift sponge filter (n=4)   small internal filter   not specified (n=5).</p> <p>– special requirements (e.g. water values): none (n=3)   approx. 8° dH/pH, GH nitrate (as shown above)   acidified with humic acids   not specified (n=6).</p> <p>– Larval food: Spinach, Repashy fish food Super Green (herbivorous! n=2)   algae, detritus, Repashy Super Green   SeraMicron Nature, rearing food   initially algae   spirulina, later Crusta Gran (Dennerle), Aquatic Frog &amp; Tadpole Food (Zoomed)   finest fish flake food, crushed catfish tablets and natural algae growth in the tank   various types of maintenance fish foods, dried <i>Daphnia</i>   algae-based fish food with some fish components   not specified (n=4).</p> <p>– Frequency of water changes: almost daily for the small larvae, then every 1–2 weeks   30–50% 1–3x/week (n=4)   1x/month   as required to maintain the above-mentioned water parameters, avoidance of rapid pH changes   not specified (n=5).</p> <p>– Type of water (rainwater, tap water, RO, etc.): 50% reverse osmosis (RO) water:50% tap water   100% tap water (n=3)   mixture of RO and acidified (dried and then soaked oak leaves) stagnant tap water   50% tap water:50% distilled water   tap water   RO water 1:1 (approx. 7 °dH; n=2)   not specified (n=4).</p> |
| Number or percentage of offspring that become adults or sexually mature | <p><i>H. aureoguttatum</i>: 99%   not specified (n=2).</p> <p><i>H. fleischmanni</i>: 99%   not specified (n=3).</p> <p><i>H. valerioi</i>: ca. 5%   40–100%   &gt; 80%   99%   100%   not to be rated, as all offspring were passed on as subadults (n=2)   not specified (n=5).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Age/size at sexual maturity                                             | <p><i>H. aureoguttatum</i>: 12–18 months   not specified (n=2).</p> <p><i>H. fleischmanni</i>: 12 months   not specified (n=3).</p> <p><i>H. valerioi</i>: from a SVL of 15 mm   from a SVL of 23 mm   after 7–8 months (n=2)   after approx. one year for ♂♂ and one and a half years for ♀♀   not specified (n=7).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Indicators for reaching sexual maturity                                 | <p><i>H. aureoguttatum</i>: ventrally visible ovaries and vasa deferentia   not specified (n=2).</p> <p><i>H. fleischmanni</i>: calls, ventrally visible ovaries (vasa deferentia difficult to recognise in this species)   calls   not specified (n=2).</p> <p><i>H. valerioi</i>: ventrally visible eggs   growth complete, egg formation at ♀♀ and calls at ♂♂ (n=2)   calls, sperm ducts, ovaries (n=2)   not specified (n=7).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Sex ratio of the offspring (♂♂:♀♀)                                      | <p><i>H. aureoguttatum</i>: ~1:1   not specified (n=2).</p> <p><i>H. fleischmanni</i>: ~1:1   not specified (n=3).</p> <p><i>H. valerioi</i>: ~1:1   ~40% ♂♂   ~60% ♂♂   3,1   not specified (n=8).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Evidence of deformities or diseases                                     | <p><i>H. aureoguttatum</i>: none   not specified (n=2).</p> <p><i>H. fleischmanni</i>: none   not specified (n=3).</p> <p><i>H. valerioi</i>: none (n=6)   malformed front legs (with restricted locomotor function) to a small extent or only in the first clutch (n=2)   not specified (n=4).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Mortality of larvae up to metamorphosis                                 | <p>Mortality of larvae up to metamorphosis (&lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%) or estimation: high/low:</p> <p><i>H. aureoguttatum</i>: low   not specified (n=2)</p> <p><i>H. fleischmanni</i>: 100%   normally low, in individual breeding groups the larvae hatched, but developed a fungal infection (saprolegniasis) of the spiracle and died after a short time, therefore 0–100%   not specified (n=2).</p> <p><i>H. valerioi</i>: low (0–15%; n=4)   25–50% (n=2)   &gt; 75%   0–100%   not specified (n=4).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Mortality in the first months/years of life after metamorphosis         | <p><i>H. aureoguttatum</i>: &lt; 1%   not specified (n=2).</p> <p><i>H. fleischmanni</i>: &lt; 1%   not specified (n=3).</p> <p><i>H. valerioi</i>: low (&lt; 1%; n=2)   15%   0–60%   ca. 95%   not specified (n=7).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Routine testing for                                                     | <p><i>H. aureoguttatum</i>: no (n=3).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |

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| amphibian diseases and parasites                                | <p><i>H. fleischmanni</i>: no (n=4).</p> <p><i>H. valerioi</i>: annual <i>Bd</i> examination using qPCR   annual parasite check (n=2)   no (n=6)   not specified (n=3).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Quarantine (type and extent)                                    | <p><i>H. aureoguttatum</i>: no (n=1)   yes, 4–6 months (n=2).</p> <p><i>H. fleischmanni</i>: no (n=1)   yes, 1 month (n=1)   yes, 4–6 months (n=2).</p> <p><i>H. valerioi</i>: no (n=2)   yes, but no specific information given (n=1)   for at least 1 month (n=2)   for at least 1,5–2 months (n=4)   for at least 4–6 Monate   not specified (n=3)<sup>14</sup>.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| General characteristics, difficulties with keeping and breeding | <p><b><i>H. aureoguttatum</i>:</b></p> <p>Medium to high degree of difficulty (compared to other glass frogs)   require house crickets or banded crickets of appropriate size, firebrats, bean beetles – feeding only with flies leads to emaciation.</p> <p>Assessment of the frequency of husbandry: rare (n=3).</p> <p>Personal assessment of the difficulty of husbandry: medium to high degree of difficulty   husbandry unproblematic, breeding not easily triggered, rarely spontaneous egg laying, therefore intensive irrigation (see biotope information) required. Further notes: Husbandry of one or two pairs is significantly less productive than in larger groups (10 individuals).</p> <p><b><i>H. fleischmanni</i>:</b></p> <p>Medium to high degree of difficulty (compared to other glass frogs)   require house crickets or banded crickets of appropriate size, firebrats, bean beetles – feeding only with flies leads to emaciation.</p> <p>Assessment of the frequency of husbandry: rarely kept   rarely in the UK, more often only after imports, which are accompanied by high losses   medium frequency (compared to other glass frogs).</p> <p>Personal assessment of the difficulty of breeding in husbandry: husbandry unproblematic, (continuous) breeding: medium difficulty level.</p> <p>Further comments: In husbandry, high mortality rate when tank is set up, better chance of survival after reorganisation (rainwater)   The terrarium must be cleaned daily, for tadpoles it is important to change the water every time it is cloudy. It is also important to use special lamps with UVA and UVB light. In addition, the terrarium must be cleaned every two days (laboratory)   The search for ♀♀ is very difficult.</p> <p><b><i>H. valerioi</i>:</b></p> <p>Difficulties in ensuring optimal growing conditions for the plants (high humidity leads to rotting of the plants), individuals are nocturnal, ensure that tadpoles fall into the water after hatching, cleaning of tanks, feeding with insects   many losses (development of clutches, rearing of small larvae)   husbandry of adults is relatively easy. The difficulty in breeding is to prevent the spawn from becoming mouldy. Experience has shown that excessively low night temperatures lead to mould growth. I therefore remove the leaf with the clutch and transfer it to a cricket box containing 5 mm water with tadpole tea (alder cones). The clutch is placed in the water several times a day for a few minutes so that the jelly is always fully absorbed. The leaf is then attached so that the clutch is not in the water. The box is placed in an incubator at 27–28°C. The hatching rate has been significantly higher since then, sometimes with a high mortality rate among the young, especially when they are very small and if they do not eat enough baby crickets. Not all small animals accept springtails. They seem to be sensitive to heat and dirty environments   No difficulties in husbandry, but breeding is</p> |

<sup>14</sup> Smaller, sterile terrariums (e.g. 40 x 45 x 38 cm with 15 x 45 cm wire gauze ventilation) with climbing or potted plants (*Philodendron hederaceum*, *Spathiphyllum cochlearispathum*) are suitable for this purpose. The substrate used is either the simple glass bottom (T. Eisenberg, unpublished data) or a base made of paper towels that is changed weekly. A moat with overflow (Eisenberg in prep., Papenfuss & Eisenberg in prep.) or stagnant (chlorine-free) tap water in bowls that is freshly changed daily is used as a water reservoir (Redbond et al. 2019). The quarantine should last at least 8 weeks and up to 6 months.

|                                                        |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|--------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                        | <p>somewhat more difficult   Very robust species, none of the aforementioned problems with the author   not specified (n=5).</p> <p>Assessment of the frequency of husbandry: the most frequently kept and bred captive-bred glass frog (n=5)   rare   animal losses due to (I) too humid environment, (II) lack of hygiene and (III) insufficiently good food (i.e. feeding mainly with fruit flies)   not specified (n=5).</p> <p>Personal assessment of the difficulty of breeding in husbandry: more difficult than other anuran species (e.g. poison dart frogs)   Once you have a basic programme/protocol in place, they are easy to keep. It also helps, but is not essential, if there is previous experience with husbandry of smaller frogs at elevated humidity   good for beginners, although there are few (one?) published husbandry reports   (very) easy (n=3)   medium difficulty (n=2)   higher difficulty   not specified (n=2).</p> <p>Further comments: Larval rearing with filter, stones, algae and wooden exit aids for shore leave/ventilation necessary   Rearing takes place in a 10 litre glass aquarium without substrate at approx. 27°C. Filtration is not used as there is a risk of the tiny larvae being sucked in by the filter   Good quality food is essential, but the species is generally easy to keep   Keep water parameters at zero to minimum ammonia, minimum nitrite and nitrates below 20 ppm, total hardness at 3 to maximum 4°, pH 6.5–6.8 (tolerance range 6–7.5), pH as stable as possible without major changes   not specified (n=6).</p> |
| Frequency of private breeding and reproduction in zoos | <p><i>H. aureoguttatum</i>: rare (n=3); an extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists 45 entries as holders of <i>H. aureoguttatum</i>, all of which are registered in zoos in the USA. However, only 17 entries indicate living individuals (T. Eisenberg, unpublished data).</p> <p><i>H. fleischmanni</i>: common (n=10); an extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists 24 entries as holders of <i>H. fleischmanni</i> reported in zoos in the USA, Taiwan, Japan and Belgium. However, only 12 entries indicate living individuals (T. Eisenberg, unpublished data).</p> <p><i>H. valerioi</i>: common (n=10); an extract from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists 44 entries as holders of <i>H. valerioi</i> reported in zoos in the USA and Canada. However, only 14 entries indicate living individuals (T. Eisenberg, unpublished data).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Reproduction in captivity up to F2 generation          | <p><i>H. aureoguttatum</i>: yes (n=1), no (n=2)</p> <p><i>H. fleischmanni</i>: yes (n=1), no (n=3)</p> <p><i>H. valerioi</i>: yes (n=5), no (n=7).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding                                    | <p><i>H. aureoguttatum</i>: no (n=3)</p> <p><i>H. fleischmanni</i>: no (n=4)</p> <p><i>H. valerioi</i>: no (n=12).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Interviews/ Surveys/ Consultations                     | <p><i>H. aureoguttatum</i>: Three participants took part in the survey on <i>H. aureoguttatum</i>, all of whom are private owners. Based on their own knowledge and in co-operation with other specialists, all participants were very certain that the species was correctly identified. All husbandries identified the animals kept as captive-bred. The duration of husbandry to date was three, five and six years, all husbandries are still current and are being continued. All keepers stated that they were endeavouring to breed offspring, and at least two keepers succeeded in doing so one to two years after the start of husbandry. One keeper reported a total of more than ten clutches.</p> <p><i>H. fleischmanni</i>: Four participants took part in the survey on <i>H. fleischmanni</i>. Three of them stated that they were private keepers, one participant from Costa Rica kept the frogs for research purposes in the laboratory at the Universidad Nacional (UNA) there. Four participants were certain or very certain that the species was correctly identified, whereby the species identification was mostly carried out in collaboration with other specialists/based on their own knowledge and the latest literature/based on the origin of the animals or based on the known location of the animals or the parents. Half of the keepers identified the animals they kept as captive-bred, twice they were wild-caught. The longest husbandry was documented with minor interruptions over</p>                                                               |



16 years to date, the other three husbandries have existed for seven, four and two years. Two keepers stated that they were endeavouring to breed offspring and had already achieved this several times, one keeper only kept ♂♂ and the animals kept for research purposes were not used for further breeding.

*H. valerioi*: Twelve participants took part in the survey on *H. valerioi*. All but one stated that they were private keepers, one participant was from a zoological institution. All participants were very certain that the species had been correctly identified, whereby the species identification was mostly carried out in collaboration with the dealer/with other specialists/based on their own knowledge and the latest literature/based on the origin of the animals or based on the known location of the animals or the parents. All keepers identified the animals kept as captive-bred. The longest husbandry has been documented continuously for 16 years to date, while four of the other husbandries have between eight and twelve years of experience. Correspondingly, seven husbandries remained with experience of between one and five years. Ten husbandries had already made successful attempts at breeding, while the remaining two husbandries had only existed since 2023 and were therefore too short.

*Ikakogi* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009

| Species                | Original description                                                                             | Common name                | Common name international | Known/ documented in international trade |
|------------------------|--------------------------------------------------------------------------------------------------|----------------------------|---------------------------|------------------------------------------|
| <i>Ikakogi ispacue</i> | Rada, Dias, Pérez-González, Anganoy-Criollo, Rueda-Solano, Pinto-E., Mejía Quintero et al., 2019 |                            |                           | No                                       |
| <i>Ikakogi tayrona</i> | (Ruiz-Carranza & Lynch, 1991)                                                                    | Magdalena Giant Glass Frog |                           | No                                       |

Fig. 51: *Ikakogi tayrona*

- a adult animal (R. Stuster)
- b San Lorenzo, Colombia (A. Plewnia)
- c underside. Note the bright seminal ducts in the male (left) and the eggs visible through the skin in the female animal (right) (A. Plewnia)
- d developing eggs (A. Plewnia).

**Morphology and Taxonomy**

The generic name *Ikakogi* is composed of the indigenous word 'Ika' (or 'Ijka') and the Kogi people, descendants of the Tayrona, who inhabit the area of the Sierra Nevada de Santa Marta in Colombia. This mountain range is considered isolated and older than the Andes.

In the comprehensive revision of the family of glass frogs, the genus *Ikakogi* was newly described, but as a phylogenetically basal lineage with an uncertain position ('incertae sedis') and complementary (sister taxa to all other members of the Centrolenidae, i.e. phylogenetically independent alongside the subfamilies Hyalinobatrachinae and Centroleninae (Guayasamin et al. 2009)). The status remains to be clarified by further genetic analyses.

The genus currently contains two species, which are characterised by the following features: (1) the humerus bears conspicuous hooks or spines, as well as an extremely enlarged crista medialis over the entire bone – compared to other Centrolenidae, (2) white bones in life, (3) ventral parietal peritoneum white anteriorly, transparent posteriorly, (4) hepatic and visceral peritoneum transparent. Distinctive humeral spines (the bony crista ventralis expands into a conspicuous hook-shaped spine) in ♂♂ are otherwise only found in species of the genera *Centrolene* and *Espadarana*, less pronounced in *Chimerella mariaelenae*, *Nymphargus grandisonae*, *Vitreorana gorzulae*, completely concealed in *Sachatamia illex* and absent in *Celsiella*, *Hyalinobatrachium* and most *Nymphargus* spp. In addition, unique among glass frogs, the ♀♀ in both species carry out brood care until the larvae hatch by moisturising and guarding the clutches. The clutches can be deposited on both the upper and lower leaf surfaces (Ruiz-Carranza & Lynch 1991b, Guayasamin et al. 2008a, 2009).

The two species in this group cannot be distinguished from each other by morphological characteristics, but can be distinguished from other genera (although molecular identification is recommended for unequivocal species identification):

*Ikakogi ispacue*: large glass frog with bright green dorsal colouration and some very small black dots and yellowish parts on legs and around toes, flanks creamy yellow with small row of white, varnished-looking dots, smooth dorsal skin, ventral side incl. limbs pale green to creamy white, limbs pale green to creamy white, glandular skin on belly and pelvic side, slender limbs, SVL ♂♂ 28.7–30.2 mm, ♀ 29.5–30.6 mm, head wider than long, mouth region round from dorsal, truncated from lateral, eyes large (approx. 3.5 mm), tympanum not visible, parietal peritoneum transparent, bones mainly white, parts of them light green, large subgular vocal sac and humeral spines in ♂♂. Similar species (based on differences in genetics, bioacoustics and larval morphology; adults morphologically indistinguishable), because the species epithet means 'twin of' in the indigenous Kogi language: *I. tayrona* (Rada et al. 2019).

*Ikakogi tayrona*: s. *I. ispacue*, SVL ♂♂ 28.2–30.6 mm, ♀ 28.2–30.6 mm (Ruiz-Carranza & Lynch 1991b, Guayasamin et al. 2008a, 2009).

### Distribution and Habitat

*Ikakogi ispacue*: Records from the Río San Salvador near Palomino, Wimangaga, Dibulla, Guajira in the northern Sierra Nevada de Santa Marta and in the river basin of the Río Tapias near Riohacha, Monte Cheturrycuak, sitio La Cueva, Dibulla, Guajira, Colombia (950 m asl). Habitat in subtropical forests near small streams, adults are found on leaves 1–2 m above the ground (Rada et al. 2019).

*Ikakogi tayrona*: northern part of the Sierra Nevada de Santa Marta, Serranía San Lorenzo, Magdalena, Santa Marta, Colombia (700–2,500 m asl). Habitat: on vegetation along streams in humid gallery forests at about 2–3 m above the ground (Ruiz-Carranza & Lynch 1991b).

## Conservation Status and Main Threats

### IUCN Red List Status

*Ikakogi ispacue*: not listed

*Ikakogi tayrona*: VU (Vulnerable, B1ab(iii), assessed 02 August 2016).

### Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local spraying of pesticides, fertilisers and pollution, diseases, climate change and increased UVB radiation.

*Ikakogi ispacue*: not yet assessed by the IUCN and not included in the Colombian Red List.

*Ikakogi tayrona*: categorised as vulnerable due to its limited range and as a result of habitat loss (agriculture, deforestation, water pollution) and a declining population trend (Pérez-González, Castañeda-Bonilla & Rueda-Solano (2018).

### Reproduction

| Topic                       | Details on the reproduction of <i>Ikakogi</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|-----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | All species: ♂♂: Calls from single subgular vocal sac, Wolffian ducts mostly recognisable on the ventral side (see Fig. 1B in Rada et al. 2019), nuptial excrescences more or less pronounced dorsomedially on finger I. ♀♀ take care of the brood and guard the clutch.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Calls                       | <i>I. ispacue</i> : ♂♂ call from the tops of leaves at low altitudes along streams, the call consists of a single, short, high-frequency trill with 11–20 pulses, dominant frequency 2,928–3,273 Hz (Rada et al. 2019).<br><i>I. tayrona</i> : the advertisement call consists of 3–4 unpulsed notes and is slightly longer than in <i>I. ispacue</i> at $269 \pm 31$ (203–316) ms, dominant frequency 2,650–2,870 Hz (Vargas-Salinas et al. 2015, Rada et al. 2019).                                                                                                                                                                                                                                                                                                                                                         |
| Mating and spawning         | Both species: axillary amplexus in the vegetation above small forest streams.<br><i>I. ispacue</i> : ♀♀ lay their eggs on the upper and lower leaf surfaces above the water. ♀♀ perform brood care by looking after and guarding the clutch.<br><i>I. tayrona</i> : brood care at night and sometimes also during the day by ♀♀ (permanent contact, ‘brooding behaviour’, in which the eggs are moistened and oxygenated by resting phases as well as rotation and pendulum movements and yolk stratification is counteracted), which show a higher risk tolerance compared to ♂♂, ♀♀ removed from the clutch and released at 50 m did not return to their clutches, ♂♂ defend their territories but not the clutches, multiple clutches suggest more than one clutch per reproductive season per ♀♀ (Valencia & Delia 2016). |
| Reproductive season         | Both species: clutches were examined from April to October (Rada et al. 2019).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Eggs/clutch, clutches/year  | <i>I. ispacue</i> : clutches contain 44–62 light cream to greenish eggs in transparent jelly, which change colour to reddish to pink as the embryos develop. The clutch takes on a ring-shaped structure because there is less jelly and no eggs in the centre (Rada et al. 2019).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |

|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Size of eggs and larvae at hatching               | Unknown.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Development time from egg laying to metamorphosis | <i>I. tayrona</i> : development time from oviposition to hatching: 16–18 days (Valencia & Delia 2016).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Details on the larvae:                            | <p><i>I. ispacue</i>: larval body elongate and elliptical when viewed dorsally, laterally the body is elliptical and flattened, in Gosner stage 25 total length of 36.4 mm, body length 10.7 mm. Eyes and nostrils directed dorsally, body reaches its greatest width in the centre, where the short, left-directed spiraculum opens. Body colour reddish to pinkish with some greyish dots, especially between the eyes, brownish longitudinal stripe in the midline, caudal fins transparent. The oral disc occupies 47.6% of the body width and is bordered by a single row of 64 marginal papillae, no submarginal papillae. Maxillary sheaths serrated and keratinised and curved without an 'M' shape. The larvae are found amidst foliage and sand in small pools near the shore. Due to the long and laterally compressed heads of the larvae, the skull roof and strong cartilage parts at the front as well as the lack of lungs, they are able to burrow, an adaptation to their fossorial way of life in the stream (Rada et al. 2019).</p> <p><i>I. tayrona</i>: extensive measurements and variability of larvae, postmetamorphs/juvenile frogs measure 13.9 mm SVL (Rada et al. 2019).</p> |

### Husbandry and Captive Breeding **X**

There is no husbandry information available on the species of the genus *Ikakogi*.



***Nymphargus* Cisneros-Heredia & McDiarmid, 2007**

| Species                          | Original description                                   | Common name                                                    | Common name international        | Known/ documented in international trade |
|----------------------------------|--------------------------------------------------------|----------------------------------------------------------------|----------------------------------|------------------------------------------|
| <i>Nymphargus anomalus</i>       | (Lynch & Duellman, 1973)                               | Napo Cochran Frog, Anomalous Glassfrog                         |                                  | No                                       |
| <i>Nymphargus armatus</i>        | (Lynch & Ruiz-Carranza, 1996)                          |                                                                |                                  | No                                       |
| <i>Nymphargus balionotus</i>     | (Duellman, 1981)                                       | Mindo Cochran Frog, Mottled Glassfrog                          |                                  | No                                       |
| <i>Nymphargus bejaranoi</i>      | (Cannatella, 1980)                                     | Bolivian Cochran Frog                                          |                                  | No                                       |
| <i>Nymphargus buenaventura</i>   | (Cisneros-Heredia & Yáñez-Muñoz, 2007)                 | Buenaventura Glassfrog                                         |                                  | No                                       |
| <i>Nymphargus cariticommatus</i> | (Wild, 1994)                                           | Unadorned Glassfrog                                            |                                  | No                                       |
| <i>Nymphargus caucanus</i>       | Rada, Ospina-Sarria & Guayasamin, 2017                 |                                                                |                                  | No                                       |
| <i>Nymphargus chami</i>          | (Ruiz-Carranza & Lynch, 1995a)                         |                                                                |                                  | No                                       |
| <i>Nymphargus chancas</i>        | (Duellman & Schulte, 1993)                             | Perú Cochran Frog                                              |                                  | No                                       |
| <i>Nymphargus cochranae</i>      | (Goin, 1961)                                           | Cochran Frog, Cochran's Glassfrog                              |                                  | No                                       |
| <i>Nymphargus colomai</i>        | Guayasamin & Hutter 2020)                              | Coloma's Glass Frog                                            |                                  | No                                       |
| <i>Nymphargus cristinae</i>      | (Ruiz-Carranza & Lynch, 1995a)                         |                                                                |                                  | No                                       |
| <i>Nymphargus garciae</i>        | (Ruiz-Carranza & Lynch, 1995b)                         | García's Glassfrog                                             | Rana de cristal de Garcia        | No                                       |
| <i>Nymphargus grandisonae</i>    | (Cochran & Goin, 1970)                                 | Giant Glass Frog, Red-Spotted Glassfrog, Grandison's Glassfrog | Rana de cristal sarampiona       | No                                       |
| <i>Nymphargus griffithsi</i>     | (Goin, 1961)                                           | Ecuador Cochran Frog, Pepper Glassfrog, Griffith's Glassfrog   | Rana de cristal de Ecuador       | No                                       |
| <i>Nymphargus humboldti</i>      | Guayasamin, Cisneros-Heredia, McDiarmid & Hutter, 2020 | Humboldt's Glassfrog                                           |                                  | No                                       |
| <i>Nymphargus ignotus</i>        | (Lynch, 1990)                                          | Lynch's Cochran Frog                                           |                                  | No                                       |
| <i>Nymphargus lasgralarias</i>   | Hutter & Guayasamin, 2012                              | Las Gralarias Glassfrog                                        | Rana de cristal de Las Gralarias | No                                       |
| <i>Nymphargus laurae</i>         | Cisneros-Heredia & McDiarmid, 2007                     | Laura's Glassfrog                                              |                                  | No                                       |
| <i>Nymphargus lindae</i>         | Guayasamin 2020                                        | Linda's Glassfrog                                              |                                  | No                                       |
| <i>Nymphargus luminosus</i>      | (Ruiz-Carranza & Lynch, 1995)                          |                                                                |                                  | No                                       |
| <i>Nymphargus luteopunctatus</i> | (Ruiz-Carranza & Lynch, 1996b)                         |                                                                |                                  | No                                       |
| <i>Nymphargus manduriacu</i>     | Guayasamin, Cisneros-Heredia, Vieira,                  | Manduriacu Glassfrog                                           |                                  | No                                       |

|                                 |                                                                 |                                                 |                              |    |
|---------------------------------|-----------------------------------------------------------------|-------------------------------------------------|------------------------------|----|
|                                 | Kohn, Gavilanes, Lynch, Hamilton & Maynard, 2019b               |                                                 |                              |    |
| <i>Nymphargus mariae</i>        | (Duellman & Toft, 1979)                                         | María's Glassfrog, Maria's Giant Glass Frog     |                              | No |
| <i>Nymphargus megacheirus</i>   | (Lynch & Duellman, 1973)                                        | Santa Rosa Cochran Frog, Large-handed Glassfrog |                              | No |
| <i>Nymphargus megistus</i>      | (Rivero, 1985)                                                  | Urrao Cochran Frog, Greater Andean Glassfrog    |                              | No |
| <i>Nymphargus mixomaculatus</i> | (Guayasamin, Lehr, Rodríguez & Aguilar, 2006)                   |                                                 |                              | No |
| <i>Nymphargus nephelophila</i>  | (Ruiz-Carranza & Lynch, 1991b)                                  | Florencia Cochran Frog                          |                              | No |
| <i>Nymphargus ocellatus</i>     | (Boulenger, 1918)                                               | Spotted Cochran Frog                            |                              | No |
| <i>Nymphargus oreonympha</i>    | (Ruiz-Carranza & Lynch, 1991b)                                  | Caqueta Cochran Frog                            |                              | No |
| <i>Nymphargus phenax</i>        | (Cannatella & Duellman, 1982)                                   | Tutumbaro Cochran Frog                          |                              | No |
| <i>Nymphargus pijao</i>         | Montilla, Arcila-Pérez, Toro-Gómez, Vargas-Salinas & Rada, 2023 | Pijaos' Glassfrog                               |                              | No |
| <i>Nymphargus pluvialis</i>     | (Cannatella & Duellman, 1982)                                   | Pistipata Cochran Frog                          |                              | No |
| <i>Nymphargus posadae</i>       | (Ruiz-Carranza & Lynch, 1995a)                                  | Posada's Glassfrog                              |                              | No |
| <i>Nymphargus prasinus</i>      | (Duellman, 1981)                                                | Río Calima Cochran Frog                         |                              | No |
| <i>Nymphargus rosada</i>        | (Ruiz-Carranza & Lynch, 1997)                                   |                                                 |                              | No |
| <i>Nymphargus ruizi</i>         | (Lynch, 1993)                                                   | Ruiz's Cochran Frog                             |                              | No |
| <i>Nymphargus siren</i>         | (Lynch & Duellman, 1973)                                        | Río Coca Cochran Frog, Siren Glassfrog          | Rana de cristal del río Coca | No |
| <i>Nymphargus spilotus</i>      | (Ruiz-Carranza & Lynch, 1997)                                   |                                                 |                              | No |
| <i>Nymphargus sucre</i>         | Guayasamin, 2013                                                | Sucre's Glassfrog                               |                              | No |
| <i>Nymphargus truebae</i>       | (Duellman, 1976)                                                | Trueb's Cochran Frog                            |                              | No |
| <i>Nymphargus vicenteruedai</i> | Velásquez-Álvarez, Rada, Sánchez-Pacheco & Acosta-Galvis, 2007  |                                                 |                              | No |
| <i>Nymphargus wileyi</i>        | (Guayasamin, Bustamante, Almeida-Reinoso & Funk, 2006b)         | Wiley's Glassfrog                               |                              | No |



Fig. 52: *Nymphargus* species

- a *N. anomalus* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001141)
- b *N. balionotus* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001143)
- c *N. cariticommatatus* (A. Plewnia)
- d *N. megacheirus* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001173)
- e *N. ocellatus* (J. Köhler)

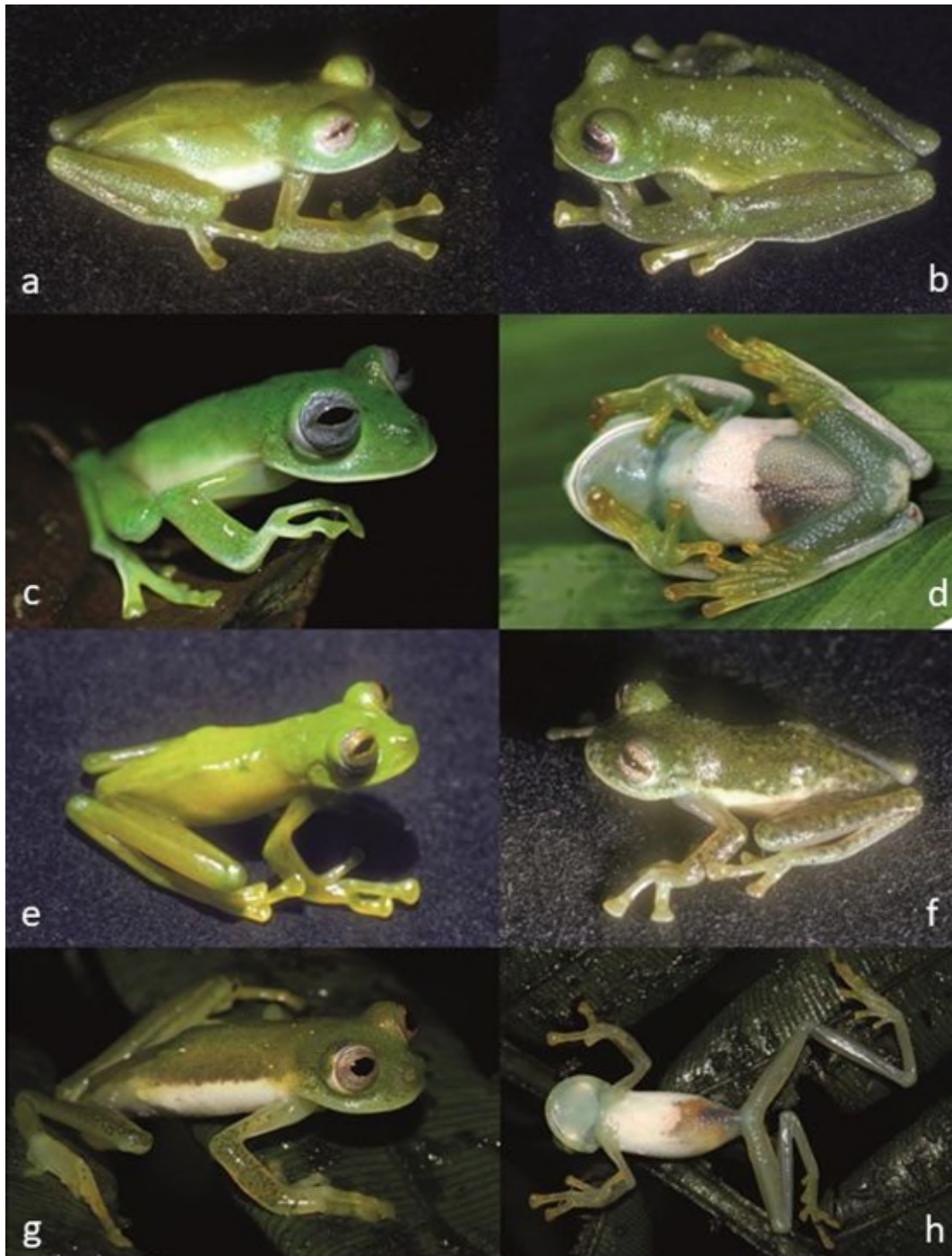


Fig. 53: *Nymphargus* species II

- a *N. phenax* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001177)
- b *N. pluvialis* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001181)
- c *N. aff. posadae*, upper side (A. Plewnia)
- d *N. posadae*, underside (C. Koch)
- e *N. prasinus* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001185)
- f *N. truebae* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 1201)
- g *N. siren*, upper side (A. Sanchez Vialas)
- h *N. siren*, underside (A. Sanchez Vialas).



## Morphology and Taxonomy

The genus name *Nymphargus* is composed of the Greek 'nýmpgae' in allusion to the nymphs, and 'argus' in allusion to the mythological Greek Argus, nephew of the nymph Io, a giant with a hundred eyes that became the ocelli in the peacock's tail. The name alludes to the ocelli found on the backs of at least five species of the genus (*N. anomalus*, *N. cochranæ*, *N. ignotus*, *N. lauræ* and *N. ocellatus*) (Cisneros-Heredia & McDiarmid 2007).

Phylogenetically, the genus reflects the clade of the closest common relatives of the species *Nymphargus* (*Cochranella*) *cochranæ* and *Nymphargus* (*Centrolenella*) *bejaranoi*. The sister genus is *Centrolene*.

Members of the genus *Nymphargus* can be distinguished by the following characteristics: (1) reduced interdigital membranes of the outer fingers III and IV, (2) no hooks or humeral spines on the humerus (exceptions: ♂♂ of *N. grandisonæ*, *N. armatus* and some populations of *N. griffithsi*), (3) three- to four-lobed liver covered by a translucent hepatic peritoneum, (4) ventral parietal peritoneum white in front, translucent behind, (5) bones green intra vitam (white in *N. anomalus*, *N. caucanus*, *N. chancas* and *N. rosada*), (6) dorsum lavender-coloured in the preservative medium, with or without dots, (7) dorsum of ♂♂ usually with conspicuous dorsal spines during the rainy season and (8) with conspicuous nuptial excrescences on the hands, (9) ♂♂ call from leaf upper surfaces, ♀♀ also lay their clutches on leaf upper surfaces above and along streams.

Morphologically similar species of the genera *Celsiella*, *Rulyrana* and *Sachatamia* (Guayasamin et al. 2009).

Many species in this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unequivocal species identification):

*Nymphargus anomalus*: medium sized glass frog that stands out due to its deviating (anomalous) light brown colouration compared to the green ground colour of other glass frogs, light brown back with several ocelli, skin bears raised tubercles on the back and is covered with spines, ocelli are located on the raised tubercles, ventral side cream-coloured, SVL ♂♂ 24.1 mm, head with large protruding eyes, slightly wider than the rest of the body, mouth region blunt from dorsal and lateral, no teeth on the vomer, tympanum covered by supratympanic fold, less than one third of tympanic membrane visible, white bones, parietal peritoneum white anteriorly, transparent hepatic and visceral peritoneum, interdigital membranes between outer fingers and on feet, no interdigital membranes between first and second fingers and rudimentary interdigital membranes between second and third toes, lateral seams present on fingers, finger and toe discs round and blunted, larger on fingers than on toes. Similar species: The species differs from *E. prosoblepon* in the absence of extensive interdigital membranes, a blunt snout and a partially visible tympanum, and from *N. cochranæ* in the absence of prevomer teeth (AmphibiaWeb 2023, Cisneros-Heredia & McDiarmid 2007, Lynch & Duellman 1973).

*Nymphargus armatus*: medium-sized glass frog, pale green with darker green spots on top, yellowish on flanks, SVL ♂♂ 23.3–24.8 mm, ♀♀ 23.9–24.5 mm, head as broad as body, mouth region blunted and short in dorsal and lateral view, eyes anterolateral, moderately large, iris pale grey with a copper-coloured spot around the pupil and black spots above and grey reticulation below the pupil, no teeth on the vomer, tympanum present, directed posterolaterally, in contrast to the majority of representatives of the genus presence of humeral spines in ♂♂



(besides *N. grandisonae* and some populations of *N. griffithsi*), anterior parietal and pericardial peritoneum white, visceral peritoneum transparent, heart not visible, finger discs blunted, prominent ('armed') nuptial excrescences in ♂♂ (eponymic). According to the original publication, very similar to *N. griffithsi* and *N. balionotus* (Lynch & Ruíz-Carranza 1996).

*Nymphargus balionotus*: small glass frog with lime green to metallic green dorsum and rusty or coppery brown dorsolateral stripes up to the middle third of the dorsum, conspicuous rusty to brown-coppery spots, few to many dark spots on the dorsal surface, arms and legs, 1–2 bright yellow spots in the centre of the dorsum are not always present, one bright yellow spot always on the upper eyelids, SVL ♂♂ 19.0–21.0 mm, ♀♀ 21.7–22.0 mm, mouth region truncated dorsally, no teeth on the vomer, tympanum small and directed ventrally, no sexual dimorphism or chromatism, but in ♂♂ a humeral spine (rudimentary humeral hook), pericardial peritoneum white, visceral peritoneum transparent. The species was described as *Centrolenella balionota*, later also assigned to the genera *Centrolene* and *Cochranella* before being placed in *Nymphargus*. Related species: *N. manduriacu*, *N. chancas* and *N. mariae* (Guayasamin et al. 2019b, 2020).

*Nymphargus bejaranoi*: medium-sized glass frog with dark green upper side and tiny white dots, dorsal skin covered with small spiculae (delicate thorny pointed skin structures, heterogeneous, also on upper eyelid and lip), ventral side granulated, fingers orange-green, SVL ♂♂ 23.8–24.4 mm, ♀♀ unknown, head slightly broader than body, mouth region rounded in dorsal view, slightly truncated in lateral view, eyes medium sized, directed anterolaterally, iris metallic yellow with black spots, no teeth on vomer, lower two thirds of tympanum visible, anterior parietal and pericardial peritoneum white, visceral peritoneum transparent (Cannatella 1980).

*Nymphargus buenaventura*: small glass frog, dorsum light green with pale yellow or cream-coloured dots on entire dorsal surface, including arms and legs, abdomen cream-coloured, hands and feet yellowish green with light yellow discs and melanophores on outer fingers and toes, iris yellowish silver with fine brown reticulation, SVL ♂♂ 20.9–22.4 mm, ♀♀ unknown, blunt mouth region seen dorsally and laterally, lower half of tympanic ring distinct, oriented dorsolaterally with dorsoventral inclination, vomer denticles absent, liver four-lobed, humeral spine absent, upper half of parietal peritoneum white, remaining peritoneum transparent with the exception of the renal capsules, which are covered by iridophores. This last feature is shared with three other species, *N. cariticommatu*s, *N. griffithsi* and *N. wileyi*. Due to its morphological similarity to these three species, *N. buenaventura* was considered part of the *Nymphargus* group without molecular examination. Possibly synonymy or species complex with *N. griffithsi* (Cisneros-Heredia & Yáñez-Muñoz 2007).

*Nymphargus cariticommatu*s: small glass frog, dorsal surface of head, body and limbs green with small yellow dots. Fingers and toes on the back yellow, iris silvery-white with dark grey reticulation, ♂ 23.5 mm, ♀ 25.7 mm (n=1 each), mouth region rounded from dorsal, blunted from lateral, no teeth on vomer, moderately large, conspicuous tympanum, dorsal surface slightly granular, with tiny spines in ♂♂, anterior two-thirds of ventral parietal peritoneum white, posterior third transparent, pericardium silvery-white, translucent peritoneum covering intestines, stomach, testes, gall bladder and urinary bladder, oesophagus white, kidneys covered with white peritoneum except for a few patches, liver tetralobulated, three ventral lobes partially covering a smaller lobe, liver peritoneum translucent, humeral spine absent, ♀♀ show slightly more membranous appendages on hands and feet than ♂♂. Similar species: *N. wileyi*, *N. griffithsi*, *N. buenaventura* and *N. chancas* (Guayasamin et al. 2020).

*Nymphargus caucanus*: medium sized glass frog with light brown upper side with dark spots, dorsal skin smooth without spines or tubercles, no humeral spine at ♂♂, SVL ♂♂ 23.6–26.0 mm, ♀♀ 25.1–25.9 mm, mouth region blunted in dorsal and lateral view, iris golden to copper-coloured with fine dark reticulated lines, no teeth on vomer, tympanum visible, anterior parietal and pericardial peritoneum white, visceral peritoneum transparent, liver four-lobed, colour of bones white. Species with similar dorsal pattern: *N. anomalus*, *N. ignotus* and *N. rosada* (Rada et al. 2017).

*Nymphargus chami*: large glass frog with green upper side and many white tubercles, no humeral spine in ♂♂, SVL ♂♂ 30.5–34.6 mm, ♀ 37.6 mm (n=1), head much wider than body and wider than long, Mouth region blunted and anteroventrally inclined in dorsal and lateral view, teeth present on vomer, tympanum visible to  $\frac{3}{4}$ , anterior parietal peritoneum white, visceral peritoneum transparent (Ruiz-Carranza & Lynch 1995b).

*Nymphargus chancas*: medium-sized glass frog with dorsal colouration varying between a dull yellow-green, mandarin yellow to a greyish olive, numerous small orange to yellow dots, dorsal skin slightly granular, ♂♂ with numerous small spines, iris white with a contrasting black horizontal line, no humeral spine, SVL ♂♂ 24.7–25.7 mm, ♀♀ unknown, mouth region blunted in dorsal and lateral view, no teeth on vomer, tympanum almost vertically aligned, with a slight lateral and posterior inclination visible, anterior parietal and pericardial peritoneum white, translucent peritoneum on kidneys, intestines, stomach, gall bladder and urinary bladder, liver lobed, covered by translucent peritoneum, colour of bones white (green according to Duellman & Schulte (1993)). Closely related to *N. mariae* and *N. grandisonae* (Guayasamin et al. 2009, Castroviejo-Fisher et al. 2014, AmphibiaWeb 2023).

*Nymphargus cochranae*: medium-sized to large glass frog with green dorsal colouration and dark blue or black dots, missing membranes on the hands and missing humeral spines, but tiny spines in ♂♂. The blue dots often form black or dark blue ocelli surrounding orange dots, ventral side almost white, except for the posterior third which is transparent, iris greyish white with fine black reticulation, the area immediately around the pupil is brownish yellow in colour, SVL ♂♂ 24.0–26.2 mm, ♀♀ 27.8–30.3 mm, mouth region blunted in dorsal and lateral view, teeth present or absent on vomer, tympanum small, anterior two-thirds of parietal peritoneum white, transparent peritoneum on four-lobed liver. Related species: *N. lindae*, possibly also *N. griffithsi* and *N. lasgralarias* (possible species complex to be verified in low altitude Colombian populations). Similar species with dorsal ocelli pattern: *N. anomalus*, *N. lindae*, *N. ignotus*, *N. laurae*, *N. ocellatus* and *N. megacheirus* (dorsal dots with spines; Lynch & Duellman 1973, Guayasamin et al. 2020).

*Nymphargus colomai*: medium-sized glass frog with dull yellow-green, tangerine-yellow, brown or olive-grey dorsum, no humeral spines, dorsal skin slightly granulated, with numerous tubercles and spines on the ♂♂, iris white with a contrasting black transverse stripe and numerous small yellow to orange spots, SVL ♂♂ 24.7–25.7 mm, ♀♀ unknown, mouth region blunted in dorsal and lateral view, few teeth present or absent on vomer, tympanum small, anterior half of parietal and pericardial peritoneum white, translucent peritoneum on liver, kidneys, intestines, stomach, gall bladder and bladder. Similar species: *N. cariticommatus*, *N. chancas* (preserved), *N. humboldti*, *N. siren* and *N. sucre*. Sister species: *N. mariae* (Guayasamin et al. 2020).

*Nymphargus cristinae*: large glass frog with light green dorsum and many or few fine black dots (greater concentration on limbs), no humeral spines, SVL ♂♂ 26.0–31.1 mm, ♀ 29.7 mm

( $n=1$ ), head wider than body and wider than long, mouth region pointed in dorsal view, blunt in lateral view, teeth present or absent on vomer, tympanum small, eyes large, directed anterolaterally, anterior half of parietal and pericardial peritoneum white, translucent peritoneum on gut and stomach (Ruíz-Carranza & Lynch 1995a, Pérez-González & Rada 2018).

*Nymphargus garciae*: large glass frog with green back with mostly dark green to blue as well as fine cream-coloured spots, white upper lip, no humeral spines, hands and feet yellowish green, dorsal surfaces finely granular with many small tubercles, with spines in ♂♂, iris greyish white with thin black reticulation, SVL ♂♂ 24.9–29.9 mm (Ecuador) resp. 25.1–27.7 mm, ♀♀ 25.9–28.4 mm (Colombia), head slightly wider than body and wider than long, mouth region rounded in dorsal view, blunted in lateral view, no teeth present on vomer, tympanum small, almost vertically orientated, with slight posterior inclination, anterior half of parietal peritoneum as well as those of pericardium and kidneys white, translucent peritoneum on four-lobed liver, urinary bladder, intestine and stomach. Similar species: *Centrolene buckleyi*, *N. megacheirus*, *N. nephelophilus* and *N. oreonympha* (possibly the latter two with *N. garciae* one species with geographical variation). Sister species: *N. vicenteruedai* (Ruíz-Carranza & Lynch 1995b, Guayasamin et al. 2020).

*Nymphargus grandisonae*: medium-sized to large glass frog with green dorsal colouration with red dots and widened toe discs, upper lip margin white, gular area pale green, flanks and belly completely white (combination of the presence of iridophores in the parietal peritoneum and in the urinary bladder), small humeral spines present in ♂♂, dorsal surfaces slightly granulated, tiny spines in ♂♂, iris yellowish grey, SVL ♂♂ 25.1–29.3 mm, ♀♀ 28.9–30.7 mm, mouth region rounded in dorsal view, blunted in lateral view, teeth usually present on vomer, tympanum partially concealed, almost vertically orientated, almost entire parietal peritoneum and those of pericardium and urinary bladder white, kidneys covered dorsally and laterally by iridophores, translucent peritoneum on four-lobed liver, ventral kidneys, testes, gall bladder, intestines and stomach. Species with similar colouration: *Boana punctata* (but larger and with red dorsolateral lines). Related species: *N. colomai* and *N. mariae*. The name *Centrolenella grandisonae* was erroneously used by Lynch & Duellman (1973), who confused *N. grandisonae* with *Centrolene lynchi*. Duellman (1980) corrected this error and described both species in detail (Ruiz-Carranza & Lynch 1991a, Guayasamin et al. 2008b, 2009, Castroviejo-Fisher et al. 1991).

*Nymphargus griffithsi*: small to medium sized glass frog with varying dorsal colouration from uniform green to green with small dark spots and small yellow dots, dorsal skin slightly granular, ventral surfaces mostly greenish white, iris varies from white to creamy beige with brown to black dots forming a thin web; in some animals the pupil is yellow in colour, in ♂♂ no humeral spines, but humeral ridges present in some individuals, SVL ♂♂ 22.5–24.2 mm, ♀♀ 22.5–27.9 mm, mouth region blunted in dorsal and lateral view, no teeth on the vomer, lower half of tympanic ring distinct, dorsally orientated with a dorsoventral inclination, anterior half of ventral parietal peritoneum white, posterior half transparent, peritonea on pericardium and renal capsules white, all other peritonea transparent, liver four-lobed. Similar species: *N. buenaventura*, *N. cariticommatus*, *N. lasgralarias*, *N. pijao* and *N. wiley*, possibly belonging to a species complex (Ruiz-Carranza & Lynch 1998, Guayasamin et al. 2020, AmphibiaWeb 2023).

*Nymphargus humboldti*: medium-sized glass frog with green back and small yellow spots, dorsal skin slightly granular, with tiny spines in ♂♂, upper lip white, front part of the abdomen (approx. 60% of the belly) white, rear part transparent, iris greyish cream with a slight yellow tinge and fine black reticulation, eye ring yellow, in ♂♂ no humeral spines, SVL ♂♂ 23.3–25.2

mm, ♀♀ 25.5–27.4 mm, mouth region blunt in dorsal and lateral view, also slightly rounded in lateral view, teeth present on vomer, tympanic membrane almost vertically aligned, anterior half of ventral parietal peritoneum white, posterior half transparent, peritoneum on pericardium white, peritonea on intestine, stomach, kidneys, gall bladder and urinary bladder transparent, liver tetralobulated. Similar species: *N. cariticommatum*, *N. luminosus*, *N. siren* (sister species), *N. spilotus*, *Espadarana audax*, *Rulyrana flavopunctata*, *R. mcdiarmidi* and *Teratohyla midas* (Guayasamin et al. 2020, AmphibiaWeb 2023).

*Nymphargus ignotus*: medium-sized glass frog with light brown to pale olive-coloured back and black ocelli with orange or yellow centres, dorsal skin slightly granular with raised tubercles, dorsal surfaces of all fingers and toes speckled with a few melanophores, fingers and toes yellow, throat and ventral surfaces of hind limbs light green; chest and ventral surfaces of forelimbs pink, anterior part of abdomen (approx. 50–75% of abdomen) white, posterior part transparent, rear part transparent, iris whitish grey with golden tinge and black reticulation, no humeral spines in ♂♂, SVL ♂♂ 22.2–25.4 mm, ♀♀ 24.2–25.0 mm, mouth region blunted in dorsal and lateral view, eyes large, directed anterolaterally, no teeth present on vomer, tympanic membrane anterolaterally orientated, lower three quarters visible, anterior part of ventral parietal peritoneum white, posterior half transparent, peritoneum on pericardium white, peritonea on intestine, stomach and liver transparent, liver tetralobulated. Similar species: *N. anomalus*, *N. cochranæ*, *N. rosada*. Different populations showed polymorphisms in the dorsal colour patterns, which are used to distinguish central populations (Dagua, La Cumbre, El Cairo and Cali [Pichindé, type locality]) from northern populations (San José del Palmar, Misstrató, Pueblo Rico, Frontino and Urrao). The colour pattern of the central populations is the typical *N. ignotus* with a light brown to pale green, olive-coloured back and well-defined black ocelli surrounding orange or yellow spots. However, the northern polymorphisms include individuals with a light brown to pale brown dorsum and widely distributed dark brown spots, some of which are interspersed with orange or yellow spots and eventually form poorly demarcated ocelli (Lynch 1990, Rada et al. 2017, AmphibiaWeb 2023).

*Nymphargus lasgralarias*: medium-sized glass frog with uniformly green dorsum with small melanophores and yellowish white flanks, fingers and toes yellow with faint green tinge, iris golden with several dark spots and a slight reticulation, in ♂♂ no humeral spines, but low and barely visible ulnar and tarsal folds, SVL ♂♂ 24.6–26.5 mm, ♀♀ unknown, mouth region truncated in dorsal view, slightly protruding in lateral view, no teeth on vomer, tympanic membrane small, anterior half of ventral parietal peritoneum white, posterior half transparent, peritonea on pericardium and kidney capsules pale white, all other peritonea transparent, liver tetralobulated. Similar species: *N. buenaventura*, *N. cristinae*, *N. griffithsi*, *N. prasinus* and *N. wileyi* (Hutter & Guayasamin 2012, Guayasamin et al. 2020, AmphibiaWeb 2023).

*Nymphargus lauræ*: small glass frog with green back and yellow spots bordered by black ocelli, dorsal skin slightly granular with raised tubercles, iris whitish with thin dark network and central dark spots, towards pupil a yellow ring, in ♂♂ no humeral spines, SVL ♂♂ 19.9–22.1 mm, ♀ 22.3 mm (subadult), head slightly wider than long and wider than body, mouth region blunted in dorsal and lateral view, no teeth on vomer, tympanic membrane small, anterior two-thirds of ventral parietal peritoneum white, posterior half transparent, all other peritonea transparent. Similar species: *N. anomalus*, *N. cochranæ*, *N. lindae* and *N. ignotus*. Closely related species: *N. siren* (sister species), *N. humboldti* as well as *N. megacheirus* and *N. anomalus* (Cisneros-Heredia & McDiarmid 2007, Guayasamin et al. 2020, AmphibiaWeb 2023).

*Nymphargus lindae*: small glass frog with dark lavender to black ocelli enclosing yellow or orange dots, dorsal skin slightly granulated, with tiny spines in ♂♂, upper lip white, iris white with slight pale yellow tinge and fine black reticulation, no humeral spines in ♂♂, SVL ♂♂ 23.0–26.3 mm, ♀♀ 27.2–27.8 mm, mouth region truncated in dorsal view, truncated to rounded in lateral view, teeth present on vomer, tympanic membrane small and concealed, almost vertical, approximately anterior two-thirds of ventral parietal and the pericardial peritoneum white, posterior half transparent, peritonea of viscera, stomach, kidneys, liver, gall bladder and urinary bladder transparent, tetralobular liver. Similar species: *N. anomalus*, *N. cochranae* (sister species), *N. laurae*, *N. ocellatus* and *N. ignotus* (Guayasamin et al. 2020, AmphibiaWeb 2023).

*Nymphargus luminosus*: large glass frog with green dorsal side and many yellow spots evenly distributed over head and body, dorsal skin fine-grained with small subconical tubercles, many very small folds, in ♂♂ no humeral spines, SVL ♂♂ 27.8–30.0 mm, ♀♀ 32.7 mm, head much wider than body, wider than long, teeth present on vomer, tympanum small and oval (Ruíz-Carranza & Lynch 1995b, Cisneros-Heredia & McDiarmid 2007, AmphibiaWeb 2023).

*Nymphargus luteopunctatus*: large glass frog with green dorsal side and yellow spots outlined in black, no humeral spines in ♂♂, SVL adults 33.1 mm, mouth region rounded in dorsal view, blunted in lateral view, head slightly wider than body, wider than long, teeth present on vomer, tympanum small and only two thirds visible (Ruíz-Carranza & Lynch 1995b, Cisneros-Heredia & McDiarmid 2007, AmphibiaWeb 2023).

*Nymphargus manduriacu*: medium-sized glass frog with a grey-green back covered with yellow spots. These spots are sometimes surrounded by melanophores forming diffuse black rings (similar to false ocelli), dorsal skin slightly granular, upper lip unpigmented, in ♂♂ with tiny spines, in ♂♂ no humeral spines, inner fingers and toes yellow, iris light grey with pale yellow outline of pupil, SVL ♂♂ 24.0–25.7 mm, ♀ 28.8 mm (n=1), mouth region blunted in dorsal view, blunted to slightly rounded in lateral view, no teeth present on vomer, tympanum small and barely visible, anterior half of ventral parietal and the pericardial peritoneum white, posterior half transparent, most visceral peritonea unpigmented, lobed liver. Similar species: *N. buenaventura*, *N. ignotus*, *N. luminosus* and *N. spilotus*. Sister species: *N. balionotus* (Guayasamin et al. 2019b, 2020).

*Nymphargus mariae*: medium to large sized glass frog with parrot green ground colour with relatively large yellow-green spots, blotches and interorbital bars and dark green reticulate markings on the upper side of the limbs, dorsal skin with low, very flat tubercles corresponding to light spots prominent behind the eyelid, above the tympanic membrane, in the cheek region and below the eye with protruding, somewhat rounded spines, all skin surfaces with very fine grain, eyes protruding and aligned anterolaterally at an angle of about 45 degrees to the longitudinal axis of the head, eyes light blue-green with a transverse green-brown bar running from the centre corner of the eye through the iris to the lateral corner of the eye, in ♂♂ no humeral spines, no interdigital membranes, iris grey-cream with a transverse brown longitudinal stripe and a fine dark reticulum, pale yellow outline of the pupil, conspicuous paired arrangement of 6 tubercles and many folds below the cloacal opening, SVL ♂♂ 23.4–30.2 mm, ♀♀ 25.1–32.8 mm, head wider than body, mouth region truncated in dorsal view, rounded in lateral view, teeth present on vomer, lower three quarters of tympanum hidden under a moderately developed supratympanic fold, anterior half of ventral parietal and pericardial peritoneum white, posterior half transparent, peritonea of intestine, stomach, liver, gall bladder and urinary bladder unpigmented, lobed liver. Similar species: *Rulyrana flavopunctata*, *Teratohyla*



*midas*, *N. cariticommatus*, *N. humboldti*, *N. siren* and *Sachatamia albomaculata* as well as *Centrolene medemi*. *N. puyoensis* has been synonymised (Duellman & Toft 1979, Guayasamin et al. 2009, Cisneros-Heredia & Guayasamin 2014).

*Nymphargus megacheirus*: medium-sized to large glass frog with green dorsal colouration and small blue to black, slightly raised dots, ventral surface almost completely white with the exception of the posterior third, which is transparent. Upper lip and elbow fold white, named after the large hands of this species, iris grey-bronze coloured, all skin surfaces with fine grain, numerous spines present in ♂♂ (in ♀♀ only on the head, in the tympanic region and on the limbs), no humeral spines in ♂♂, SVL ♂♂ 26.8–31.5 mm, ♀♀ 31.2–32.9 mm, Mouth region blunted in dorsal and lateral view, no teeth present on vomer, three quarters of tympanum visible, anterior two thirds to three quarters of ventral parietal and the pericardial peritoneum white, posterior part transparent, the peritonea of viscera, stomach, testes, kidneys, (four-lobed) liver, gall bladder and urinary bladder transparent. Similar species: *N. cochranæ*. Sister species: *N. anomalus* (Guayasamin et al. 2020).

*Nymphargus megistus*: large glass frog with green dorsal colouration and black spots, iris pale grey with greyish reticulation, dorsal skin with abundant, evenly distributed conical spines in ♂♂ present (in ♀♀ dorsal skin with almost flat tubercles and sparse spines only on head, in the tympanic region and on the limbs), ventral skin granular, in ♂♂ no humeral spines, atypical species of the genus *Nymphargus*, in which all species have a reduced interdigital membranes between the third and fourth fingers. In *N. megistus* the interdigital membranes between the fingers are more pronounced, SVL ♂♂ 30.8–37.4 mm, ♀♀ 36.9–40.0 mm, mouth region subovoid in dorsal view, rounded in lateral view, teeth present on the vomer, small tympanum visible, anterior half of the ventral parietal and the pericardial peritoneum white, posterior part transparent, the peritonea of viscera, stomach, (four-lobed) liver transparent. Sister species: *N. grandisonae* (Trageser et al. 2021).

*Nymphargus mixomaculatus*: medium-sized glass frog with pale green dorsum with tiny white and larger black spots, iris silvery-white with dark purple reticulation, dorsal skin granular with tiny spines present (corresponding to the tiny white spots), no humeral spines in ♂♂, SVL ♂♂ 22.8–25.0 mm, ♀ 26.3 mm (n=1), mouth region truncate in dorsal view, slightly protruding to truncate in lateral view, no teeth present on the vomer, tympanic membrane visible under the skin, dorsolaterally orientated with a posterior tilt, anterior half of the ventral parietal and the pericardial peritoneum white, posterior part transparent, the peritonea of viscera, stomach, (four-lobed) liver and kidneys transparent. Similar species: *N. bejaranoi*, *N. chancas*, *N. ocellatus*, *N. phenax*, *N. pluvialis* and *N. truebae* (Guayasamin et al. 2006a, Venegas & García Ayachi 2021).

*Nymphargus nephelophila*: small to medium sized glass frog with yellowish pale green dorsum and black speckles, in ♂♂ no humeral spines, SVL ♂♂ 22.6–24.1 mm, ♀♀ unknown, mouth region truncated in dorsal and lateral view, no teeth present on vomer, tympanic membrane visible to  $\frac{3}{4}$ , anterior half of ventral parietal peritoneum white, posterior part transparent, peritonea of viscera and stomach transparent (Ruiz-Carranza & Lynch 1991b).

*Nymphargus ocellatus*: large glass frog with dark green dorsum and light green, black-edged ocelli, dorsal skin smooth, ventral skin granulated, skin on flanks and (partially) ventral side white, fingers long with prominent adhesive discs, SVL (sex unknown) 29.0 mm, head wider than long, mouth region rounded in dorsal view, tympanic membrane clearly visible. Closely related species: *N. pluvialis*, *N. posadae* (Boulenger 1918, Castroviejo-Fisher et al. 2014).

*Nymphargus oreonympha*: medium-sized glass frog with yellow-green to pale green dorsum and diffuse black broad dorsal spots, dorsal skin with many small tubercles in ♂♂, no humeral spines in ♂♂, SVL ♂♂ 24.0–26.3 mm, ♀ 26.4 mm (n=1), head wider than long and wider than body, mouth region slightly ovoid in dorsal view, slightly truncate in lateral view, no teeth present on vomer, tympanic membrane small (Ruiz-Carranza & Lynch 1991b, Rada et al. 2017).

*Nymphargus phenax*: small glass frog with dark green back and tiny creamy white spots (ending in tiny spines), skin on dorsal side finely spiny, spines also on limbs, eyelids, tympanic region and posterior part of upper lip, skin on belly and thighs granular, flanks smooth, upper lip white, finger discs broad, iris silvery-white with black reticulation, in ♂♂ no humeral spines, SVL ♂♂ 20.2–22.1 mm, ♀♀ unknown, head slightly wider than body, mouth region truncated in dorsal and lateral view, no teeth present on the vomer, lower four fifths of the tympanic membrane visible, exact morphological shape of the peritonea cannot be determined from the original description (Cannatella & Duellman 1982).

*Nymphargus pijao*: small to medium-sized glass frog with green dorsal colouration with punctiform accumulations of melanophores (black dots) and/or small yellow dots (in the form of low warts), dorsal skin smooth with numerous spines (microspiculae) in ♂♂, ventral surfaces granulated, iris colouration silver-white or faintly golden with fine reticulations and small spots on the upper and lower sides, in ♂♂ no humeral spines, SVL ♂♂ 22.1–27.3 mm, ♀♀ 24.6–28.6 mm, mouth region blunted in dorsal and lateral view, teeth on vomer absent or only 1–2 teeth present, tympanic membrane visible, anterior half of ventral parietal peritoneum white, posterior half transparent, peritonea on pericardium white, all other peritonea transparent, liver tetralobulated. Similar species: *N. buenaventura*, *N. cariticommatus*, *N. lasgrallarias*, *N. wiley*. Closely related species are: *N. griffithsi*, *N. humboldti*, *N. laurae*, *N. siren* (Ruiz-Carranza & Lynch 1998, Guayasamin et al. 2020, Montilla et al. 2023).

*Nymphargus pluvialis*: medium-sized glass frog with green dorsum and pale cream-coloured dorsal spots, skin on dorsal surface of body and limbs with fine spines of various sizes, spines also on upper eyelids, dorsal surface of mouth, upper lip below eye and on heels and anal region, skin of abdomen and ventral thighs granular, labial stripes and finger discs cream-coloured, iris pale bronze-coloured with black spots, in ♂♂ no humeral spines, SVL ♂♂ 24.9–26.5 mm, ♀♀ unknown, head slightly wider than body, mouth region truncated in dorsal and lateral view, no teeth present on the vomer, lower three quarters of tympanic membrane visible, anterior half of ventral parietal peritoneum white, posterior part transparent, peritonea of viscera and stomach transparent (Cannatella & Duellman 1982).

*Nymphargus posadae*: large glass frog with green dorsum and some cream-coloured tubercles, no spines visible, upper lip white, lower lip with thin white margin, iris white with thin dark grey reticulated lines, in ♂♂ no humeral spines, SVL ♂♂ 30.7–34.1 mm (♂♂ from Yanayacu Biological Station [Ecuador] are smaller [SVL 30.7–31.9, n=3] than those from Colombian localities), ♀♀ 30.2–33.3 mm, head slightly wider than body and wider than long, mouth region blunt to round in dorsal view, slightly oblique in lateral view (inclined anteroventrally), no teeth present on vomer, but dentate process, tympanic membrane small, anterior half of ventral parietal and pericardial peritoneum white, posterior part transparent, the peritonea of liver, intestines, stomach, kidneys, gall bladder and urinary bladder transparent. Similar species: *Centrolene buckleyi*. Sister species: *N. pluvialis* (Ruiz-Carranza & Lynch 1995a, Guayasamin et al. 2020).

*Nymphargus prasinus*: large glass frog with unicoloured bright green dorsum, no spines visible, dorsal skin smooth, no humeral spines in ♂♂, SVL ♂♂ 33.0–34.5 mm, ♀♀ unknown, head wider than body, mouth region round in dorsal view, truncate in lateral view, teeth present on vomer, ventral parietal peritoneum white, more details missing in original description (Duellman 1981).

*Nymphargus rosada*: medium-sized glass frog with a light brown back and evenly distributed orange-coloured dots in adults; green with orange dots in metamorphs and juveniles, skin on the dorsal surface of the body in ♂♂ granular and covered with fine spines, throat and ventral limbs are greyish, fingers and toes yellow, edge of upper lip with very thin line of iridophores (light), iris golden to copper-coloured with fine dark speckles, no humeral spines in ♂♂, SVL ♂♂ 24.1–26.9 mm, ♀♀ 25.8–28.5 mm, mouth region blunt in dorsal and lateral view, no teeth present on the vomer, tympanic membrane small, anterior half to three quarters of the ventral parietal and pericardial peritoneum white, posterior part transparent, the peritonea on (four-lobed) liver, intestines and stomach transparent, bones white (colour change in the course of ontogenesis, initially pale green). Similar species: *N. anomalus*, *N. ignotus* (Ruiz-Carranza & Lynch 1997, Rada et al. 2017).

*Nymphargus ruizi*: medium-sized glass frog with black, olive-coloured to yellowish olive-green back and black spots on head, body and limbs, skin on dorsal surface of body smooth except for some large spiny tubercles on upper eyelids, sides of the head, in the flank region and sometimes on the limbs (almost only in ♂♂, rarely in ♀♀), belly and inner two fingers cream-coloured to pale yellow, large, anterolaterally directed eyes, large hands, all fingers with large adhesive discs, iris copper-coloured to reddish metallic yellow with black to bronze reticulation and black horizontal stripe, in ♂♂ no humeral spines, in ♂♂ large white nuptial excrescences, SVL ♂♂ 24.3–26.4 mm, ♀♀ 23.9–29.5 mm, head as wide as body, mouth region blunt in dorsal and lateral view, no teeth present on vomer, lower four fifths of tympanic membrane visible, anterior part of ventral parietal and pericardial peritoneum white, posterior part transparent, further details missing. Similar species: *N. megacheirus* (Lynch 1993).

*Nymphargus siren*: small glass frog with green dorsal colouration and small yellow dots, in some individuals narrowly edged in black, dorsal skin slightly granular, in ♂♂ usually with spines (may be related to reproductive activity), iris whitish cream, with yellow tint around the pupil and fine, dark grey reticulation, in ♂♂ no humeral spines, SVL ♂♂ 19.8–22.6 mm, ♀♀ 22.5–23.3 mm, mouth region blunt in dorsal view, blunt to slightly protruding in lateral view, vomer with toothed tooth processes, some individuals may have up to two teeth, tympanic membrane almost vertical, with slight posterior and lateral inclination, upper quarter of tympanic ring covered by supratympanic fold, tympanic membrane clearly demarcated from surrounding skin, anterior half of ventral parietal as well as pericardial peritoneum white, posterior part transparent, the peritonea on (lobed) liver, kidneys, gall bladder, urinary bladder, stomach and intestine transparent. Similar species: *N. humboldti* (sister species), *Espadarana audax*, *Rulyrana flavopunctata*, *Teratohyla midas* (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Nymphargus spilotus*: medium-sized glass frog with deep green dorsal colouration and small yellow spots, dorsal skin very finely granular and without tubercles, hands and feet yellowish, throat and limbs ventrally green, no humeral spines in ♂♂, SVL ♂♂ 25.3–26.4 mm, ♀♀ 27.6–28.5 mm, head slightly wider than body, wider than long, mouth region blunt in dorsal and lateral view, dentary processes and vomer denticles on prominent odontophores present in ♂♂ (with 2–4 teeth on each dentary process), less distinct in ♀♀, tympanic membrane small,

slightly inclined dorsolaterally, anterior half to two thirds of ventral parietal peritoneum white, posterior part transparent, no information on remaining peritonea and iris. Similar species: *N. luminosus* (Ruiz-Carranza & Lynch 1997).

*Nymphargus sucre*: small glass frog with predominantly brownish yellow dorsal colouration and bright yellow dots, rough dorsal skin, with numerous tiny spines in ♂♂, no humeral spines in ♂♂, iris white with tiny dark dots, fine reticulation and a yellow ring around the pupil, SVL ♂♂ 21.6–22.3 mm, ♀ 24.3 mm (n=1), mouth region blunt in dorsal and lateral view, dentate processes present on vomer but not bearing teeth, visible tympanic membrane almost vertically aligned, about a quarter of the eye diameter, anterior half of the ventral parietal peritoneum white, posterior part transparent, the peritonea on (trilobed) liver, kidneys, gall bladder, urinary bladder, stomach and intestine transparent. Similar species: *N. anomalus*, *N. chancas*, *N. colomai*, *N. ignotus*, *N. rosada*. Related species: *N. cariticommatus* (sister species; Guayasamin 2013, Guayasamin et al. 2020).

*Nymphargus truebae*: small glass frog with green dorsum with greenish black and creamy white spots, smooth, somewhat granular dorsal skin, with numerous tiny spines (especially on sides of head and behind eye), in ♂♂ no humeral spines, eyes large, protruding, directed more forward than to the side, iris pale gold with black reticulation, margin of upper lip and flanks cream-coloured, tips of toes yellowish green, SVL ♂♂ 22.6–24.8 mm, ♀ 24.8 mm (n=1), head clearly wider than body, mouth region round in dorsal view, blunted in profile, no teeth or dentary processes present on vomer, lower three quarters of tympanic membrane visible, anterior half of ventral parietal peritoneum white, posterior part transparent, peritonea on stomach and intestine transparent (Duellman 1976).

*Nymphargus vicenteruedai*: medium-sized glass frog with green back with yellow spots on head, body and limbs, dorsal skin weakly granular with numerous, evenly distributed, pointed, tiny spines (in the ♂♂) resp. weakly covered with small spicules (♀♀, especially along the tympanic region), throat and ventral surfaces of the limbs greenish blue, in ♂♂ no humeral spines, eyes large, directed at an angle of approx. 45° anterolaterally and protruding beyond the outer edge of the upper lip, iris gold-coloured with fine black reticulation, narrow golden ring around the pupil, edge of the upper lip white, fingers and toes yellow, SVL ♂♂ 23.3–26.9 mm, ♀ 27.8 mm (n=1), head wider than body, mouth region blunted in dorsal view and in profile, no teeth or odontophores present on vomer, tympanic ring indistinct or barely pronounced, if present, directed posterodorsally, anterior half to three quarters of ventral parietal and pericardial peritoneum white, posterior part transparent, the peritonea on trilobed liver, stomach and intestine transparent. Similar species: *N. bejaranoi*, *N. chami*, *N. luminosa*, *N. posadae*, *N. phenax*, *N. pluvialis*, *N. prasinus*, *N. siren*, *N. spilotos*, *N. wileyi* (Velásquez-Álvarez et al. 2007).

*Nymphargus wileyi*: medium-sized glass frog with uniform pale green dorsum, dorsal skin granular with numerous tiny spines in ♂♂, no humeral spines in ♂♂, iris copper-white with black reticulation, edge of upper lip white, SVL ♂♂ 24.0–26.2 mm, ♀ 27.1 mm (n=1), mouth region blunt in dorsal view and blunt to protruding in profile, no teeth or odontophores present on vomer, tympanum almost vertically aligned, with slight posterior and lateral inclination, tympanic membrane unpigmented and clearly demarcated from the surrounding skin, anterior half of the ventral parietal and pericardial peritoneum white, posterior part transparent, the peritonea on four-lobed liver, intestine, stomach, testes, gall bladder and urinary bladder transparent, peritoneum around the kidneys white with unpigmented patches. Similar species: *N. sucre* (sister species), *N. cariticommatus* (sister species), *Espadarana durrello-rum* (Guayasamin et al. 2006b, 2020).

## Distribution and Habitat

The genus *Nymphargus* is endemic to the Andes and its foothills in Colombia, Ecuador, Peru and Bolivia. Most species are restricted to habitats above 1,000 m asl, only *N. cochranae*, *N. laurae* and *N. puyoense* occur in lower regions of the Amazonian foothills of the Andes.

*Nymphargus anomalus*: known only from four localities (Volcán Sumaco, Río Azuela, Río Yana Challuwa Yaku, surroundings of Río Jacinto) on the Amazonian slopes of the Ecuadorian Andes, provinces Napo, Pastaza and Tungurahua (1,668–1,795 m asl). Habitat: Tropical cloud forest, near flowing water, 1.5 m above the ground (Frost 2024, Lynch & Duellman 1973).

*Nymphargus armatus*: the species is only known from the foot of Cerro Ingles, near Vereda Las Amarillas, Municipio El Cairo, in the department of Valle del Cauca, Colombia (2,160 m asl). Although every stream within a 5 km radius of the type locality was searched, the species was not recorded, indicating that it has a very restricted distribution range.

*Nymphargus balionotus*: occurs in the western foothills of the Cordillera Occidental of the Andes of Ecuador to Colombia, about 51 frogs of this species were described in the species description from the provinces of Carchi, Imbabura and Cotopaxi, Ecuador, later also from Cauca and Valle del Cauca, Colombia (460–1,540 m asl). These areas are characterised by intact evergreen humid lowland rainforests and cloud forests with a canopy below 25 m and rich epiphyte growth. The species occurs on vegetation along streams and is found on leaf tops. The frequency of sightings is correlated with high rainfall intensity and is correspondingly rarer in the dry season and in areas with little rainfall (Maynard et al. 2020, Guayasamin et al. 2020).

*Nymphargus bejaranoi*: occurs in the eastern foothills of the Bolivian Andes, departments of Cochabamba (51.8 km south-west of the municipality of Tunari), Santa Cruz (Sehuencas, La Siberia region, La Yunga) and Chuquisaca (El Palmar) (1,500–2,400 m asl). Habitats in humid mountain forests including cloud and yungas forests, on vegetation near small streams and waterfalls (Cannatella 1980, Köhler 2000).

*Nymphargus buenaventura*: only known from four localities in the provinces of Azuay (Luz María) and El Oro (Reserva Buenaventura, Marcabelí, Cascadas de Manuel) in southwestern Ecuador (667–1,770 m asl). The type locality is covered by evergreen rainforest, the frogs are found in the leaves of bushes and low trees, 1–3 m above the streams. The species possibly uses seasonal flowing waters for reproduction, during the rest of the time it seems to inhabit the canopy region of the surrounding forest (Cisneros-Heredia & Yáñez-Muñoz 2007, Yáñez-Muñoz et al. 2014, Guayasamin et al. 2020).

*Nymphargus cariticommatatus*: distributed on the Amazonian slopes of the southern Andes of Ecuador (provinces of Morona Santiago and Zamora Chinchipe) (2,200–2,350 m asl). The species lives in primary cloud forests and has been observed on shrubs or ferns at a height of 150–200 cm near flowing streams.

*Nymphargus caucanus*: known from the type locality (Hacienda El Tambito-Fundación Proselva, Inspección de Policía 20 de Julio, Municipio de El Tambo) and the Parque Nacional Natural Munchique, both on the western slope of the Cordillera Occidental, Departamento Cauca, Colombia (1,700 m asl). Habitat in primary mountain rainforests along unpolluted streams, where ♂♂ of this species call on upper leaf surfaces at 1–2 m altitude (Rada et al. 2017).

*Nymphargus chami*: known from the western side of the Cordillera Occidental and eastern foothills of the Cordillera Central in Colombia in the Departamentos Antioquia and Risaralda



(type locality Mistrató district, Puerto de Oro, western slope), now also Departamentos Córdoba and Caldas (Parque Nacional Natural Selva de Florencia) (800–1,280 m asl). In the riparian vegetation next to clear streams in very humid tropical forests and cloud forests. The species has also been found up to 200 m away from a stream (IUCN SSC Amphibian Specialist Group 2019b). Adults have been found in vegetation at the edge of crevices (Ruiz-Carranza & Lynch 1995b).

*Nymphargus chancas*: the species is distributed from northeastern San Martín (Perú) to southeastern Ecuador (1,000–1,470 m asl). All individuals were found in vegetation at heights of 100–170 cm along small, fast-flowing streams surrounded by dense vegetation in cloud forests. A small microhabitat consisting of shallow, moist areas with a constant water source is assumed (Duellman & Schulte 1993, Twomey et al. 2014, Castroviejo-Fisher et al. 2014, Ron 2018).

*Nymphargus cochranae*: distributed in northern and southern Ecuador and southern Colombia on the Amazonian slopes of the Andes (Napo, Orellana, Pastaza, Tungurahua, Zamora Chinchipe, Sucumbíos, Morona Santiago). The observation in the Serranía de Churumbelos (Departamento Cauca) is the first record in Colombia ([300–]1,170–1,960 m asl). Occurs in mountain rainforests along streams with steep gradients, at night during the rainy season the ♂♂ call from the upper side of leaves near fast-flowing rivers (Lynch & Duellman 1973, Salaman & Donegan 1998).

*Nymphargus colomai*: only known from its type locality in the Cordillera del Cóndor in the province of Zamora Chinchipe, Ecuador (1,260 m asl). In vegetation at an altitude of 100–170 cm above fast-flowing mountain streams (Guayasamin et al. 2020).

*Nymphargus cristinae*: known from two localities: 1) Vereda El Maravillo, Río Encarnación, Tambo de Ana house, Quebrada La Clara and 2) Vereda El Chuscal, Las Juntas and La Nevera creeks, west side of Cordillera Occidental, Departamento Antioquia, Colombia (2,330–2,490 m asl). Adults in vegetation about 1.50 m above the water in sub-Andean primary forests, canopy over streams required (Ruíz-Carranza & Lynch 1995b).

*Nymphargus garciae*: mountain rainforests on the eastern slope of the Cordillera Central in Colombia (Departamentos Cauca, districts of Belalcazar and Inzá, Huila, San José de Isnas and Tolima) and in the Cordillera Oriental of the Ecuadorian Andes (Colombia: 1,900–2,700 m asl, Ecuador: 2,550–3,012 m asl). Adults were found on vegetation and stones along streams, the species requires gallery forests and is sensitive to changes in habitat, ♂♂ calling from the top of leaves, call, territorial behaviour, egg-laying site, parental care and tadpole unknown (Guayasamin et al. 2020).

*Nymphargus grandisonae*: distributed on the western slopes of the Cordillera Occidental in Colombia, from the department of Antioquia south to the Pacific slopes of the northern Andes, and central Ecuador (provinces of Carchi, Cotopaxi, Pichincha, Santo Domingo de los Tsáchilas) (1,140–3,200 m asl). In the vegetation along streams or swamps in primary and secondary forests as well as on grassland edges (pastures, roadsides) at the edge of the forest (Guayasamin et al. 2020).

*Nymphargus griffithsi*: widespread in Ecuador and Colombia on the western slopes of the Andes (Pacific Colombian foothills of the Cordillera Occidental [Antioquia, Chocó, Cauca, Valle del Cauca, Nariño and Risaralda] and Quindío south to Cotopaxi in neighbouring Ecuador and on the eastern foothills of the Cordillera Central in the department of Caldas) (1,000–2,650 m

asl). Found in the river vegetation, during the rainy season the ♂♂ call at a height of 0.5–9 m above the water level, ♂♂ carry out territorial fights by holding on to branches with their legs belly up (Duellman & Savitzky 1976, Guayasamin et al. 2020).

*Nymphargus humboldti*: known from a few localities in the eastern foothills of the northern and central Andes in the provinces of Napo and Pastaza, Ecuador (1,738–2,400 m asl). Habitat in tropical humid forests near rivers and fast-flowing streams. The ♂♂ call on the upper side of leaves (Guayasamin et al. 2020).

*Nymphargus ignotus*: cloud forest on the western slope of the Cordillera Occidental of the departments of Chocó, Antioquia, Cauca, Valle de Cauca and Risaralda, Colombia (1,280–2,050 m asl). Habitat on leaves above streams at 50–200 cm above the ground (Rada et al. 2017).

*Nymphargus lasgralarias*: western slope of the Ecuadorian Andes in the provinces of Pichincha and Cotopaxi (Río Chalguyacu, Five Frog Creek, Heloderma Creek, Hercules Giant Tree Frog Creek, Kathy's Creek and Lucy's Creek) (1,850–2,300 m asl). Breeding habitat in smaller, permanent streams (about 3 m wide) in primary montane forests with little disturbance, ♂♂ typically calling from the tops of small ferns, leaves and long palm leaves about 1–6 m above the streams (Hutter & Guayasamin 2012).

*Nymphargus laurae*: known in Ecuador from the type locality (near the town of Loreto, on the northern Amazonian lowland slopes of Sumaco Volcano in the Cordillera Oriental, Orellana Province, 500 m asl) and from the Colonso-Chalupas Biological Reserve, eastern slopes of the Cordillera Oriental, Napo Province (500–[700–1,500]–2,200 m asl). Habitat in the evergreen premontane and cloud forest with a large variety of trees of the families Melastomataceae, Solanaceae, Myrsinaceae, Aquifoliaceae, Araliaceae, Rubiaceae. Trees there grow up to 15–25 metres tall, with gnarled trunks and branches and dense and compact crowns covered with epiphytes, including orchids, bromeliads, arums and ferns. This ecosystem is usually covered by fog either permanently or in the early morning and late afternoon, the average annual rainfall is 4,620 mm and the average annual temperature is 28.7°C (Cisneros-Heredia & McDiarmid 2007, Sánchez-Carvajal et al. 2021).

*Nymphargus lindae*: occurs in streams near Miazí Alto, Cordillera del Cóndor, Zamora Chinchipe province, Ecuador (1,200 m asl). Widespread species, ♂♂ were observed calling on leaves and branches 30–400 cm above a stream. One pair in amplexus, and two other ♂♂ were observed fighting on a branch; the ♂♂ not in amplexus constantly approached the large ♂ and tried to kick it away (Guayasamin et al. 2020).

*Nymphargus luminosus*: occurs on the western side of the Cordillera Occidental, Departamento Antioquia, Colombia (1,140–1,430 m asl). The adults are found on the vegetation in forest clearings at an altitude of 1–2 m above the ground, rather rare, possibly also due to the way of life in the canopy region (Ruíz-Carranza & Lynch 1995b, Frost 2024).

*Nymphargus luteopunctatus*: type locality in the department of Cauca, El Tambo district, Vereda La Playa, Finca La Playa-La Primavera, western slope of the Cordillera Occidental, Colombia, possibly also in neighbouring Ecuador (1,200–1,500 m asl). Habitat on vegetation above streams in primary forest (Ruíz-Carranza & Lynch 1995b, Frost 2024).

*Nymphargus manduriacu*: occurs in the Río Manduriacu reserve, Imbabura province, Chocó bioregion and tropical Andes on the Pacific slope of the Andes of Ecuador, possibly also further north in the Cotacachi-Cayapas reserve (1,175–1,275 m asl). Habitat in dense low montane

forest near small 0.5–4 m wide freshwater streams and waterfalls. This area is characterised by high precipitation and humidity above 90% and temperatures between 18–20°C (Guayasamin et al. 2019b, 2020).

*Nymphargus mariae*: known from the type locality, 1 km west of Puyo, Pastaza province, Ecuador, there by synonymisation (see above), also in the provinces of Sucumbíos, Orellana, Napo, Pastaza and Morona Santiago and in the Serranía de Sira, Huánuco, Perú (300–1,550 m asl). The species is known from moss- and bromeliad-covered cloud and humid forests (Guayasamin et al. 2009).

*Nymphargus megacheirus*: endemically distributed in four localities in the Amazonian Andes in Ecuador (Napo province near the Río Azuela and Río Salado) and in the Cordillera Oriental of Colombia (municipalities of Mocoa, Putumayo and San Vicente del Caguán, Department of Caquetá) (1,300–1,750 m asl). During the rainy season, the ♂♂ call from the vegetation from the tops of leaves hanging over fast-flowing streams in primary cloud forest (Guayasamin et al. 2020).

*Nymphargus megistus*: western slopes of the Cordillera Occidental in the departments of Antioquia, Risaralda, Valle de Cauca and Chocó, Colombia, as well as in the Río Manduriacu reserve, Imbabura province, and near Mindo, Pichincha province, northwestern Ecuador (1,550–2,100 m asl). During the rainy season, the adults stay near streams, where the ♂♂ call on branches 1.5–1.8 m above the ground. In the dry season, the adults migrate to more distant areas of the cloud forests without permanent water (Rada & Guayasamin 2008, Trageser et al. 2021).

*Nymphargus mixomaculatus*: in the north of the Reserva Comunal Chayu Nain (Utcubamba province, Departamento Amazonas) and the Bosque de Protección Alto Mayo (Moyobamba province, Departamento San Martín) to the type locality near Caserío Carpish de Mayobamba (Departamento Huánuco, Huánuco province, Perú (2,650–3,180 m asl). Breeding habitat in bushes and trees along small, fast-flowing cloud forest streams (Guayasamin et al. 2006a).

*Nymphargus nephelophila*: eastern slopes of the Cordillera Oriental in Colombia. The type locality is in the department of Caqueta, Florencia district, Vereda Gabinete, 3.1 km below the crest of the Alto Gabinete (1,660–2,190 m asl). Collected in vegetation 2 m above the ground in cloud forest (Ruiz-Carranza & Lynch 1991b).

*Nymphargus ocellatus*: Amazonian slopes of the Andes in central and southern Peru (Pasco region along the Cordillera Oriental: 1) Huancabamba (type locality), 2) Chacos in the southern buffer zone of the Yanachaga-Chemillen National Park) (1,200–1,992 m asl). Habitat in secondary mountain and cloud forest on vegetation approx. 1.4 m above the ground (Frost 2023).

*Nymphargus oreonympha*: only known from the type locality in the department of Caquetá, in the district of Florencia, 8.6 km east of Alto Gabinete on the western slope of the Cordillera Oriental of Colombia (2,040–2,270 m asl). Habitat along streams in primary cloud forest (Ruiz-Carranza & Lynch 1991b).

*Nymphargus phenax*: the species is currently only known from the type locality (Tutumbaro, Río Piene, Departamento Ayacucho, Perú) and a locality 45 km away (river basin of the Río Apurimac, Ayacucho), possible occurrences in Bolivia are discussed. Altitudinal distribution 1,837–1,840 m asl. The occurrence is in a disturbed cloud forest in a river valley with bamboo, ferns and elephant ear plants (*Xanthosoma*), but no tree ferns and only a few bromeliads. The frogs were calling at night from the tops of leaves within 1 metre of a slow-moving river. On

the two days the specimens were collected, the temperature was 14.0–28.5°C and total precipitation was 13.5 mm (Cannatella & Duellman 1982, Köhler 2000).

*Nymphargus pijao*: both slopes of the Cordillera Occidental and the western slope of the Cordillera Central in the departments of Antioquia, Cauca, Chocó, Quindío, Risaralda and Valle del Cauca, Colombia (type locality: Sopladero stream, 40 km north-west of Corregimiento Uribe, Cabaña La Romelia, Parque Nacional Natural Munchique, El Tambo municipality, Cauca department) (1,480–2,430 m asl). Habitat: in stream-associated vegetation. In the habitat ('Cascadas de Río Verde' Nature Reserve, Córdoba, Quindío, Colombia) a defensive behaviour was described, which is said to serve predator avoidance (disinterest) and in which the captured frogs bent their heads, pulled their limbs to their bodies and maintained this position even after manipulation. In addition, one animal lay on its back and showed half-closed eyes and dead posture behaviour. All frogs also emitted a conspicuous odour. While the defensive behaviour first described had already been described in *V. parvula* (as *V. uranoscopa*), the death reflex is the first evidence in the Centrolenidae family (Toledo et al. 2010, Arcila-Pérez et al. 2017, Montilla et al. 2023, Lopez-Molina et al. 2023).

*Nymphargus pluvialis*: known from the area of the type locality (Departamento Cuzco, Perú) and the humid mountain forest of La Paz, Bolivia (1,820 m asl). The type locality, the Cooperativa Pistipata, consists of coffee and tea plantations with remnants of cloud forest. The frogs were found near a bridge over the Río Umas-Bamba (Río Santa Maria). They were calling on a rainy night on bushes and from the tops of leaves above the water bordering the river (Cannatella & Duellman 1982).

*Nymphargus posadae*: eastern slopes of the Cordillera Central in Colombia, in the departments of Caldas, Huila and Cauca, in Ecuador in cloud forests on the Amazonian Andean slopes, in the provinces of Sucumbíos, Napo and Zamora Chinchipe and in north-eastern Peru on the south-western slopes of the Cordillera del Condor (1,100–2,800 m asl). Adults on vegetation and rocks at the edge of stream incisions (Ruiz-Carranza & Lynch 1995a, Guayasamin et al. 2020).

*Nymphargus prasinus*: on the Pacific slope of the Cordillera Occidental in the Departamentos Valle del Cauca, northwards through Chocó and Risaralda to Antioquia, Colombia (900–1,450 m asl). The species occurs in rainforests and sub-Andean forests and is often found in the vegetation along streams (restricted to streams with tree crowns). It lays its eggs on the upper side of leaves (Duellman 1981; Frost 2024)

*Nymphargus rosada*: on the eastern slope of the Colombian Central Cordillera along the Magdalena Valley in the departments of Caldas (municipalities of Pensilvania and Samaná), Tolima (municipalities of Ortega and Falan) and Antioquia (municipalities of Anorí and Santo Domingo) (1,100–2,450 m asl). The species occurs in sub-Andean forests in the vegetation along streams. It requires gallery forests for reproduction and is restricted to the small remnant forests that still exist in its distribution area (Ruiz-Carranza & Lynch 1997, Guzmán & Salazar 2012).

*Nymphargus ruizi*: at medium altitudes on the western slopes of the Cordillera Occidental and on the eastern slope of the Farallones de Cali in the departments of Cauca, Risaralda and Valle del Cauca, Colombia (2,190–2,850 m asl). This species occurs in the vegetation and moss cushions at the edge of streams or in the splash zones of small waterfalls (0.1–1.0 m from the water) in the sub-Andean forests. It is restricted to gallery forests as it requires overhanging branches as spawning habitat (Lynch 1993).

*Nymphargus siren*: cloud forests on the Andean Amazonian slopes of the Cordillera Oriental in the provinces of Napo and Orellana, Ecuador, and in the department of Putumayo, Colombia, up to the province of Ayacucho, southern Peru (1,410–2,000 m asl). The species lives near streams in the cloud forest, ♂♂ calling from the upper sides of the leaves (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Nymphargus spilotus*: on the eastern slope of the Colombian Central Cordillera in the department of Caldas (municipality of Samaná) (1,850–1,940 m asl). This frog species is found in sub-Andean primary forests in the vegetation along streams. It is not expected to tolerate habitat disturbance well (Frost 2024).

*Nymphargus sucre*: only known from its type locality in Ecuador (a stream on the Plan de Milagro-Gualaceo Road, Morona Santiago province, in the evergreen cloud forests of the Andes) (2,140–2,160 m asl). ♂♂ were observed calling at night on the tops of leaves 90–130 cm above a stream. It is assumed that the brownish-yellow dorsal colouring of this species represents a certain adaptation to its habitat and enables it to camouflage itself on dead leaves during the day (Guayasamin 2013, Guayasamin et al. 2020).

*Nymphargus truebae*: only known from a few localities in Valle Kosñipata, Departamento Cuzco, Perú, occurrence in Bolivia not yet confirmed beyond doubt (1,400–1,900 m asl). The formerly quite common species lived along small streams and near waterfalls in the primary and secondary Amazon cloud forest with some tree ferns and bromeliads as well as lush undergrowth of mosses and ferns. In the past, individuals have been observed calling at night on the tops of fern leaves along the banks (Duellman 1976, De la Riva et al. 2000, Köhler 2000, Torres-Gastello et al. 2007).

*Nymphargus vicenteruedai*: known only from the type locality on the western slope of the Cordillera Oriental in the Quebrada Aguas Claras, Santuario de Fauna y Flora Guanentá-Alto Río Fonce, Departamento Santander, Colombia (2,525–2,700 m asl). Habitat: Undisturbed high Andean forests with many epiphytes and water sources associated with streams (Velásquez-Álvarez et al. 2007).

*Nymphargus wileyi*: known only from the cloud forests near the Yanayacu Biological Station, Napo Province, Ecuador (2,100 m asl). Habitat: apparently restricted to primary forest, specimens have been found at night on leaves 120–220 cm above permanent streams (Guayasamin et al. 2006b, 2020).



## Conservation Status and Main Threats

### IUCN Red List Status

- Nymphargus anomalus*: EN (Endangered, B1ab(iii), assessed 2021-04-14): Critically Endangered – CR (AmphibiaWeb 2023)
- Nymphargus armatus*: CR (Critically Endangered, D, assessed 2016-08-02)
- Nymphargus balionotus*: EN (Endangered, B1ab(iii), assessed 2019-07-03)
- Nymphargus bejaranoi*: EN (Endangered, A2ace; C2a(i) assessed 2019-09-25)
- Nymphargus buenaventura*: EN (Endangered, B1ab(iii), assessed 2021-02-17)
- Nymphargus cariticommatu*: EN (Endangered, B1ab(iii), assessed 2021-03-17)
- Nymphargus caucanus*: EN (Endangered, B1ab(iii), assessed 2018-06-28)
- Nymphargus chami*: NT (Near Threatened, B1ab(iii), assessed 2018-06-29)
- Nymphargus chancas*: EN (Endangered, B1ab(iii), assessed 2020-12-22)
- Nymphargus cochranae*: LC (Least Concern, assessed 2021-03-17); Vulnerable – VU (AmphibiaWeb 2023)
- Nymphargus colomai*: Stark EN (Endangered, A3c; B1ab(iii,v), assessed 2020-11-10)
- Nymphargus cristinae*: EN (Endangered, B1ab(iii), assessed 2019-02-12)
- Nymphargus garciae*: VU (Vulnerable B1ab(iii), assessed 2016-08-02)
- Nymphargus grandisonae*: LC (Least Concern, assessed 2021-04-05)
- Nymphargus griffithsi*: LC (Least Concern, assessed 2016-08-02)
- Nymphargus humboldti*: DD (Data Deficient, assessed 2021-01-27)
- Nymphargus ignotus*: LC (Least Concern, assessed 2016-08-02)
- Nymphargus lasgalarias*: EN (Endangered, B1ab(iii), assessed 2021-03-17)
- Nymphargus laurae*: EN (Endangered, B1ab(iii), assessed 2021-04-13); Critically Endangered – CR (Guayasamin et al. 2020, AmphibiaWeb 2023).
- Nymphargus lindae*: EN (Endangered, A3c; B1ab(iii,v), assessed 2020-11-13)
- Nymphargus luminosus*: EN (Endangered, B1ab(iii), assessed 2016-08-03)
- Nymphargus luteopunctatus*: EN (Endangered, B1ab(iii), assessed 2018-06-29)
- Nymphargus manduriacu*: CR (Critically Endangered, B1ab(iii)+2ab(iii), assessed 2020-08-05)
- Nymphargus mariae*: LC (Least Concern, assessed 2018-03-14)
- Nymphargus megacheirus*: CR (Critically Endangered, C2a(i), D, assessed 2021-01-13)
- Nymphargus megistus*: EN (Endangered, B1ab(iii), assessed 2016-07-18)
- Nymphargus mixomaculatus*: CR (Critically Endangered, B1ab(iii), assessed 2017-04-18)
- Nymphargus nephelophila*: DD (Data Deficient, assessed 2016-07-29)
- Nymphargus ocellatus*: DD (Data Deficient, assessed 2017-04-18)

*Nymphargus oreonympha*: LC (Least Concern, assessed 2018-12-14)  
*Nymphargus phenax*: EN (Endangered, B1ab(iii), assessed 2018-03-30)  
*Nymphargus pijao*: has not yet been assessed by the IUCN  
*Nymphargus pluvialis*: EN (Endangered, B1ab(iii), assessed 2019-09-24)  
*Nymphargus posadae*: LC (Least Concern, assessed 2018-03-20)  
*Nymphargus prasinus*: VU (Vulnerable, B1ab(iii), assessed 2016-08-02)  
*Nymphargus rosada*: VU (Vulnerable, B1ab(iii), assessed 2016-08-02)  
*Nymphargus ruizi*: VU (Vulnerable, B1ab(iii), assessed 2016-08-02)  
*Nymphargus siren*: EN (Endangered, A4c, assessed 2020-11-13)  
*Nymphargus spilotus*: NT (Near Threatened, assessed 2018-06-29)  
*Nymphargus sucre*: CR (Critically Endangered, B1ab(iii)+2ab(iii), assessed 2021-03-17)  
*Nymphargus truebae*: CR (Critically Endangered, A2abce, D, assessed 2017-04-18)  
*Nymphargus vicenteruedai*: DD (Data Deficient, assessed 2018-12-11)  
*Nymphargus wileyi*: CR (Critically Endangered, B1ab(iii), assessed 2021-02-02).

### Red List Status in the Range Countries

#### Colombia

Libro Rojo de los Anfibios del Valle del Cauca (Castro-Herrera & Bolívar-García 2010)

NatureServe Status S2 (Imperiled):

*Nymphargus armatus*

*Nymphargus ruizi*

NatureServe Status S2S3:

*Nymphargus ignotus*

NatureServe Status S3 (Vulnerable):

*Nymphargus griffithsi*

*Nymphargus prasinus*

#### Ecuador

Amphibians of Ecuador/Anfibios de Ecuador (Centro Jambatu (2011–2020) V1.23)

CR (Critically Endangered):

*Nymphargus anomalus* (endemic species)

*Nymphargus balionotus*

*Nymphargus manduriacu*

*Nymphargus megacheirus*

EN (Endangered):

*Nymphargus colomai* (endemic species)

*Nymphargus lindae* (endemic species)

VU (Vulnerable):

*Nymphargus garciae*

*Nymphargus griffithsi*

## Perú

Libro Rojo de la Fauna Silvestre Amenazada del Perú (SERFOR 2018)

EN (Endangered):

*Nymphargus mariae*

VU (Vulnerable):

*Nymphargus pluvialis*

NT (Near Threatened):

*Nymphargus ocellatus*

*Nymphargus siren*

## Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other possible threats include local application of pesticides, fertilisers and pollution, disease, climate change and increased UVB radiation.

*Nymphargus anomalus*: declining population trend, hardly any sightings since its description in 1971. Population declines presumably due to agricultural utilisation of the habitat.

*Nymphargus armatus*: critically endangered (estimated less than 50 individuals), only known from the type locality, distribution area only 51 km<sup>2</sup>, despite several searches not found since 1997, possibly affected by chytridiomycosis (IUCN SSC Amphibian Specialist Group 2017).

*Nymphargus balionotus*: the species is listed as endangered on the IUCN Red List, and there is only one known reproducing but declining population in Ecuador. The main threats to the species are climate change and habitat loss. Causes of habitat loss include mining and agricultural expansion in the area, as well as pollution and the introduction of exotic predatory fish. The fungus *Batrachochytrium dendrobatidis* is also suspected to be a threat (Guayasamin et al. 2020).

*Nymphargus bejaranoi*: categorised as endangered due to a negative population trend with more than 50% declines in records within ten years. This is explained by the occurrence of the chytrid fungus in the region, climate change, the construction of hydroelectric dams and other habitat losses. Estimated relict population consisting of 2,500 adults, sometimes extinct populations at known locations or only individual records.

*Nymphargus buenaventura*: listed as endangered due to the rather small and highly fragmented distribution area and the increase in agricultural activities, deforestation and mining (Guayasamin et al. 2020).

*Nymphargus cariticommatus*: listed as endangered due to its moderately large and continuously dwindling range and the increase in agricultural activities, deforestation and mining (Guayasamin et al. 2020).

*Nymphargus caucanus*: categorised as endangered, declining population trend because the range is small, the species occurs in two locations classified as threatened and the size and quality of its habitat continues to decline due to the expansion of agriculture and illegal cultivation.

*Nymphargus chami*: declining population trend due to agriculture and forestry.

*Nymphargus chancas*: declining population trend due to a small range that is subject to continuous loss of quality due to agriculture, forestry and human settlements (IUCN SSC Amphibian Specialist Group 2022c).

*Nymphargus cochranae*: despite isolated threats due to habitat loss as a result of deforestation and mining, stable to slightly declining population trend in a large distribution area.

*Nymphargus colomai*: categorized as endangered due to its small range with poor prospects and declining population trend (mining, pollution; Guayasamin et al. 2020).

*Nymphargus cristinae*: declining population trend due to the very small distribution area and anthropogenic activities (Pérez-González & Rada 2018).

*Nymphargus garciae*: categorized as vulnerable, declining population trend due to the relatively small distribution area and habitat loss due to anthropogenic activities. In Colombia, this is a rare species that has not been found in Ecuador since 1984.

*Nymphargus grandisonae*: currently not endangered due to its large distribution range and a certain tolerance to habitat changes, individual populations show a declining trend (Guayasamin et al. 2020).

*Nymphargus griffithsi*: currently not endangered due to the large distribution area and a certain tolerance to habitat changes, individual populations show a decreasing trend (Guayasamin et al. 2020).

*Nymphargus humboldti*: unclear data situation due to the not yet conclusively clarified distribution area and easy confusability, especially with *N. siren* (Guayasamin et al. 2020).

*Nymphargus ignotus*: currently stable to declining population trend, localised habitat losses due to land fragmentation and other human activities.

*Nymphargus lasgralarias*: declining population trend due to the small distribution area, habitat loss due to land fragmentation and other human activities (neozoa, chytridiomycosis; Guayasamin et al. 2020).

*Nymphargus laurae*: only one animal was found at the time of the original description and only two more have been scientifically analysed since then, meaning that this species is very rare and highly endangered. In addition to the small distribution area, modelling of the habitat shows massive and continuous habitat destruction in the past (Sánchez-Carvajal et al. 2021).

*Nymphargus lindae*: population losses of 50% are expected over the next ten years due to a small distribution and extreme pollution of habitats by copper and gold mining of this species, which is still common today (Guayasamin et al. 2020).

*Nymphargus luminosus*: small distribution area, habitat loss and fragmentation negatively affect the population trend (Ruíz-Carranza & Lynch 1995b).

*Nymphargus luteopunctatus*: suspected declining population trend due to the small distribution area, habitat loss due to land fragmentation and other human activities, rare species that also occurs in an inaccessible former guerrilla region (Ruíz-Carranza & Lynch 1995b).

*Nymphargus manduriacu*: critically endangered due to its very small range (0.4–4 km<sup>2</sup>), habitat destruction and pollution from livestock, agriculture and mining (gold, copper).

*Nymphargus mariae*: in the lowest protection category due to its wide distribution range and despite local population declines with a presumed downward trend (Cisneros-Heredia & Guayasamin 2014).

*Nymphargus megacheirus*: critically endangered due to a very small range and numerically small populations, declining trend due to anthropogenic habitat impact (climate change; Guayasamin et al. 2020).

*Nymphargus megistus*: small distribution area, habitat loss and fragmentation negatively impact the population trend.

*Nymphargus mixomaculatus*: a little-known species of glass frog that is endemic to Perú and is currently only known from its type locality in the Cordillera del Carpish in central Peru, Departamento Huánuco. According to the IUCN, the species has been categorised as critically endangered according to criterion B1ab(iii), as the extent of the occurrence is estimated at 10 km<sup>2</sup>, only one site is known and there has been a continuous decline in the area and quality of the habitat (Guayasamin et al. 2006a, IUCN SSC Amphibian Specialist Group 2018a).

*Nymphargus nephelophila*: very incomplete data basis, areas under the influence of human activities, no systematic studies since 1992 (Guayasamin 2013).

*Nymphargus ocellatus*: incomplete data basis, small distribution area and unclear attribution to other species make a reassessment appear necessary, the extent of susceptibility to disturbance is also not precisely known, assumed declining population trend (IUCN SSC Amphibian Specialist Group 2018b).

*Nymphargus oreonympha*: negative anthropogenic influences in the region primarily affect lower altitudes, currently stable population trend.

*Nymphargus phenax*: categorised as endangered due to anthropogenic influences and a relatively small distribution area; the five specimens analysed to date were collected in 1975 and 2010.

*Nymphargus pijao*: unknown.

*Nymphargus pluvialis*: endangered due to its small range, agricultural utilisation of habitats and their fragmentation. Since 2000–2007, various Peruvian populations have become extinct, possibly correlated with the occurrence of chytridiomycosis. No sightings in Bolivia since 2003.

*Nymphargus posadae*: the species has a relatively large distribution area and occurs in several protected areas.

*Nymphargus prasinus*: vulnerable due to continuous habitat destruction and a relatively limited distribution area, declining population trend.



*Nymphargus rosada*: the distribution area of 12,317 km<sup>2</sup> is relatively limited, in the known localisations there is a continuous deterioration in the extent and quality of the habitats due to human activities, with a currently still stable population trend.

*Nymphargus ruizi*: generally rare species that is threatened by agriculture and forestry, mining and a small distribution area.

*Nymphargus siren*: habitat loss due to illegal agriculture, forestry and mining, the spread of chytridiomycosis and a population decline of more than 50% observed since 2015 or predicted by 2025 justify the categorisation as endangered. At one point illegal trade is also cited as a cause, but not explained in more detail (IUCN SSC Amphibian Specialist Group 2022d). To the best of our knowledge, however, this species has never been of commercial relevance.

*Nymphargus spilotos*: despite an unknown population trend, slightly optimistic prospects due to a well-managed protected area in Las Orquídeas National Park.

*Nymphargus sucre*: an extremely small distribution area (5 km<sup>2</sup>), a single occurrence there and the feared anthropogenic use of this area give rise to fears of extinction of this species (Guayasamin et al. 2020).

*Nymphargus truebae*: classified as critically endangered in view of the 2000–2005 collapse of the entire known population in the buffer zone of the terra typica in south-east Peru, possibly due to chytridiomycosis detected in the area. Since then, several expeditions to the region have been unsuccessful in terms of further sightings. If the species still exists, it is likely that it has only survived in small numbers (feared to be less than 50 individuals).

*Nymphargus vicenteruedai*: lack of data on range extent, population status, ecological needs and threats. The terra typica is located in a protected zone. No further records since the nine specimens collected in 2004–2005 for the original description.

*Nymphargus wileyi*: an extremely small distribution area (10 km<sup>2</sup>), only two known populations and the feared anthropogenic utilisation of these areas give reason to fear the extinction of this species. Since the six specimens collected in 2001–2004 for the original description, only three further records have been published (Guayasamin et al. 2020).

## Reproduction

| Topic                       | Details on the reproduction of <i>Nymphargus</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂: call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Calls                       | <p><i>N. armatus</i>: the call is a soft, 'exhaled' whistle reminiscent of <i>Centrolene geckoidea</i>.</p> <p><i>N. balionotus</i>: the call is a high-frequency chirp consisting of a single pulsating tone: call duration 105–130 ms, call pauses 20.9–84.2 s, dominant frequency 9,733–10,250 Hz (Maynard et al. 2020).</p> <p><i>N. bejaranoi</i>: the call consists of 6–7 pulses, the first six repeated at regular (9 ms) intervals, the last one cancelled, mean call length 202.3 ms, mean dominant frequency 3,887–4,113 Hz (Márquez et al. 1996).</p> <p><i>N. caucanus</i>: the advertisement call resembles a 'tic' to the human ear and consists of a single tone with amplitude modulation, i.e. with one or two amplitude peaks. When two amplitude peaks are present, the first peak is slightly higher than the second. The sound lasted <math>60 \pm 1.5</math> ms (60–61 ms), and its dominant frequency was 4,210–4,280 Hz. The call exhibits an increasing frequency modulation (onset: 4,130–4,180 Hz, then</p> |

4,210–4,280 Hz), intervals between calls 3,210–8,571 ms (Duarte-Marín et al. 2023).

*N. cochranæ*: described as a single, high-pitched tone (Lynch & Duellman 1973).

*N. grandisonæ*: the advertisement call consists of a single tone, call length 0.013–0.158 s, 18–22 pulses per tone, dominant frequency at 3,100–4,048 Hz. 1) Advertisement call: used to communicate the location of a ♂ to other ♂♂ nearby and at the same time to attract ♀♀, 2) Courtship call: communicative call at close range (0.5–1 m) in the presence of a ♀, 3) Territorial call: Modification of the advertisement call; emitted by a ♂ territory holder in response to the presence of another intruding ♂; the intruding ♂ may or may not emit a response call; effective over long distances, 4) Encounter call: further variation of the advertisement call; emitted during interactions between ♂♂ in close range of antagonists before or during the fight over short distances, 5) release call: during the fight, in which one ♂ clinches another ♂, accompanied by vibrations, 6) distress call: usually emitted during antagonising intraspecific interactions or in emergency situations (random, loud, variable beeps during the fight; Hutter et al. 2013a, Guayasamin et al. 2020).

*N. griffithsi*: ♂♂ call from the top of leaves hanging over streams, the call is tonal and consists of a single tone or multiple pulsed (i.e. two or more pulses) calls, call length 0.103–0.148 s, 1.1–1.9 calls per minute, dominant frequency 3,790–4,307 Hz (Hutter & Guayasamin 2012, Arcila-Pérez et al. 2017).

*N. ignotus*: the call consists of a series of chirps. Five ♂♂ called (73 calls) from the upper side of leaves on shrubs at a height of 1–2 m. The advertisement call consists of a pulsed tone that sounds like a high-pitched ‘trii’. The number of pulses per note was 1–4, with a pulse duration of 3–14 ms, and the pulse rate was 58.1–98.8 per second. The entire tone (call) lasted 22–40 ms. The dominant frequency of the call was 4,030–4,500 Hz. This species emits single calls, but also groups of 3–10 calls (Lynch 1990, Duarte-Marín et al. 2023).

*N. lasgralarias*: call with pulsed (1–3) note, calls sound like a pulsating ‘click’ or ‘tick’, call length 0.016–0.044 s, 2–10 calls/min, often in series of 1–5 calls (0.033–2.541 s), calls not or only weakly modulated, dominant frequencies 3,445–3,962 Hz (Hutter & Guayasamin 2012).

*N. manduriacu*: the call consists of a single tone with 8–12 pulsed notes, similar to a high-pitched chirp, call length 0.093–0.118 s, dominant frequency 4,052–4,447 Hz, call intervals 3.9–8.6 s (Guayasamin et al. 2019b).

*N. mariae*: the call consists of a single tone with a duration of 0.015–0.018 s, call pauses 1.733–1.940 s, dominant frequency 3,234–4,299 Hz (Guayasamin et al. 2020).

*N. oreonympha*: the calls consist of a series of 2–4 peeps (‘tic’). The structure of the call is tonal and unpulsed, call length  $14.3 \pm 2.2$  ms, dominant frequency  $4,085 \pm 134.5$  Hz (Ruiz-Carranza & Lynch 1991b, Mendoza-Henao et al. 2021, Duarte-Marín et al. 2022).

*N. pijao*: two different calls were described from a population formerly belonging to *N. griffithsi* and are characterised by the following features: Advertisement call, recorded at 1,926 m asl in the Reserva Bellavista, municipality of Pijao, southern part of Quindío, western slope of the central Andes of Colombia: calls (SVL 25.16–28.10 mm; n=7) recorded between 19:00–01:00 h: pulsed tone with one or more distinct amplitude peaks and modulations, call length  $0.023 \pm 0.0069$  s, dominance frequency 3,620–3,790 Hz, duration and dominant frequency of the advertisement call did not correlate with the temperature during the call. The stress call was described from a population at 1,913 m asl in the Finca El Jardín, Vereda San Rafael, municipality of Calarcá, Quindío (n=7): pulsed, high-frequency tone with amplitude and frequency modulation, mean duration  $0.395 \pm 0.152$  s, mean dominant frequency  $5,130 \pm 2,480$  Hz (2,410–11,890 Hz; Arcila-Pérez et al. 2017).

*N. pluvialis*: the call is a shrill ‘bree-ee-ee-ee-eep’ (Cannatella & Duellman 1982).

*N. rosada*: the call sounds like a high-pitched ‘tick’. The calls recorded at 17–18°C were tonal in structure, call length 47–82 ms, dominant frequency 3,610–4,650 Hz (Rada et al. 2017, Duarte-Marín et al. 2022).

*N. siren*: the typical advertisement call is short and consists of a single, usually pulsed tone. Call length 20–42 ms, 1–3 amplitude peaks, with the first peak being more pronounced than the others, 24–130 pulses/s, dominant frequency 4,737–6,029 Hz (Guayasamin et al. 2020).

*N. spilotus*: the advertisement call sounds like a ‘tic’ and consists of a non-pulsed tone with a duration of 167.7–172.7 ms and frequency modulation (rapid increase in frequency at the beginning of the call), dominant frequency 3,990–4,180 Hz (Duarte-Ma-rín et al. 2022).

*N. truebae*: the call is a series of short, cricket-like chirping sounds (Duellman 1976).

*N. vicenteruedai*: the advertisement call consists of a single ‘tic’ (Velásquez-Álvarez et al. 2007).

#### Mating and spawning

All species: Axillary amplexus in the vegetation above small forest streams.

*N. anomalus*: ♂♂ call from leaf clusters, ♀♀ lay their eggs on mossy twigs.

*N. armatus*: ♂♂ called from the tips of the leaves hanging over the stream and from the vegetation growing on the rock faces of the gorge. Three clutches were found on the tops of leaves. One ♂ was on an isolated fern frond with a clutch of eggs. The other clutches were not clearly assigned to a specific ♂. The clutches are pale yellow, egg cases are clearly delimited, numerous empty (egg-less) tiny gelatinous cases appear to be filled with water. Clutches with similar structures have also been described in various *Centrolene* spp., *Nymphargus griffithsi* and *Teratohyla pulverata* (Rada et al. 2017).

*N. balionotus*: clutches are deposited on the undersides of leaves as well as on mosses, rocks and branches in the shore area, ♂♂ call on leaves at a height of 1–5 m (Díaz-Ricaurte & Guevara-Molina 2020, Guayasamin et al. 2020, Maynard et al. 2020).

*N. bejaranoi*: ♂♂ call from low perches in the vegetation at a height of approx. 1.5 m (Márquez et al. 1996).

*N. ignotus*: the clutches are laid on the upper side of the leaves, 50–180 cm above the water, but not at the leaf tip, but usually in the centre of the leaves. Each clutch contains 15–23 brown eggs (n=2), with the animal pole conspicuously darker and the vegetative pole weakly pigmented. The egg cases are clearly demarcated and there are numerous empty (egg-less) tiny cases that appear to be filled with water. Clutches with similar structures have also been described in various *Centrolene* spp., *N. griffithsi* and *Teratohyla pulverata* (Rada et al. 2017).

*N. cariticommatus*: ♂♂ call from the upper side of the leaves, the eggs are laid on the upper side of the leaves (Wild 1994, Ramírez et al. 2009).

*N. cristinae*: clutches are laid on the leaves and contain brownish yolks on the upper side and cream-coloured yolks on the underside, which develop into brown embryos (Pérez-González & Rada 2018).

*N. garciae*: dissected gravid ♀ with numerous eggs, which had brownish yolks on the upper side and cream-coloured yolks on the underside (Guayasamin et al. 2020).

*N. grandisonae*: reproduction in primary and secondary forests as well as on shrubs along streams and standing water in cloud forests (Guayasamin et al. 2020), ♀♀ lay their eggs on the upper side of leaves near watercourses, short-term maternal brood care, no parental brood care by ♂♂, territorial, ♂♂ very site-faithful over longer periods of time, ♂♂ show complex fighting behaviour, including the following variants: (1) dangling amplexus-like wrestling, (2) dangling belly-to-belly wrestling, (3) amplexus-like wrestling, (4) head-to-belly wrestling and (5) inverted dangling amplexus. As a result of the struggles, ♂♂ usually exhibit injuries likely caused by humeral spines. Ron (2018) reports a fight between *N. aff. grandisonae* and *Espadarana prosoblepon*. A pair observed in amplexus on 17 April 2014 at 8:25 pm in the municipality of Pijao in the central Andes of Colombia was located on the top of a large leaf 260 cm above the water surface. Until 3:08 am continuous observation, the pair moved around the leaf before moving to other leaves and then returning to the location of the first observation. The ♂ (SVL 27.94 mm) repeatedly lifted its abdomen from the back of the ♀ (SVL

32.64 mm), but always maintained the axillary amplexus position. At 23:33, the pair returned to the original observation site, but this time the ♀ turned its body and its posterior part was near the edge of the leaf; minutes later, oviposition began. The ♀ laid several eggs while moving forward; at the same time, the ♂ also moved forward, but also lifted the rear part of its body and moved its legs rhythmically in circular movements, presumably to release its sperm and help fertilise the eggs through the leg movements. The synchronised forward movement of the pair lasted several centimetres until egg deposition was complete. Later, the ♂ moved away from the ♀'s back and jumped onto another leaf (~20 cm away from the ♀); during the following eleven minutes, the ♂ emitted 13 acoustic signals that sounded similar to the advertisement call of this species. The ♀ remained motionless on the leaf for a short time (seconds) before moving slightly backwards and covering the clutch with its body. It remained there on the eggs for more than 25 minutes. It is not known whether this maternal care behaviour promotes fertilisation or increases the hydration of the eggs. Another study on reproduction over a four-year period in a population in the central Andes of Colombia found relationships with rainfall and ambient temperature in that the number of calling ♂♂ was seasonal and particularly high in the months with the highest rainfall. The main significant cause of embryonic mortality in the clutches was related to the infestation by a *Cladochaeta* fly (Guevara-Molina & Vargas-Salinas 2014, Guayasamin et al. 2020, Villegas-Mora et al. 2020).

*N. griffithsi*: ♂♂ show dangling territorial behaviour, eggs are laid on leaf tips on overhanging streams, short-term maternal care, parental brood care by ♂♂ is absent (Guayasamin et al. 2020).

*N. ignotus*: during the rainy season, numerous individuals were studied along a stream in Corregimiento de Bitaco (Municipio de La Cumbre, Valle del Cauca, 1,900 m asl) in April and August. Reproductive activity especially in the months with more rain (April to the end of August). Reproductive behaviour includes the following aspects: (1) very territorial calling ♂♂ congregate punctually in the riparian vegetation, with a density of 12–31 ♂♂ in a 115-metre transect; (2) the mating success of individual ♂♂ varies, and (3) the ♀♀ come asynchronously to the breeding sites. Clutches are laid on the upper surface of leaves, 50–180 cm above the water, but not at the tip of the leaf, but usually in the centre of the leaves.

*N. lasgralarias*: ♀♀ undertake short-term brood care, brood care by ♂♂ not present (Delia et al. 2017).

*N. luminosus*: lays cream-coloured eggs on the upper side of leaves in the tree crown (Ruíz-Carranza & Lynch 1995b).

*N. manduriacu*: ♂♂ call from the tops of leaves 0.5–4 m above the ground from the dense epiphytic vegetation (Guayasamin et al. 2019b).

*N. megacheirus*: ♀♀ examined had mature, pigmented (dark) eggs in the oviduct (Lynch & Duellman 1973, Ruiz-Carranza et al. 1996).

*N. oreonympha*: ♂♂ call from semi-overgrown vegetation 1–3 m above the ground (Ruiz-Carranza & Lynch 1991b).

*N. pijao*: Arcila-Pérez et al. (2017) describe three pairs in the axillary amplexus on 11 October 2016 at 7:25 pm: The animals were located on the upper sides of leaves between 20 and 60 cm above the water. One pair was observed until oviposition (SVL ♂ 26.2 mm, ♀ 29.8 mm). This pair moved around, higher and higher in the vegetation, reaching a leaf height of about 1.7 m above the stream at 11:54 pm. Later, the pair moved to the end of a leaf and started climbing on both sides of the leaf (between 0:42 and 3:20 am). Before laying the eggs, the ♂ began to move its legs in a circular motion over the ♀. The ♂ lifted the rear part of its body and the ♀ pushed out its eggs while the pair moved forwards. The ♀ laid a clutch of 50 eggs. The oviposition lasted seven minutes (3:20–3:27 am). The ♂ continued to move its legs over the ♀ for a few seconds after laying the eggs. At 3:37 am the ♀ lifted its cloaca, moved over the clutch and covered it with its body. The ♂ remained on the ♀'s back until 3:44 am, after

which the ♀ covered the eggs with its body for more than 60 minutes. After this time, neither the ♂ nor the ♀ returned to visit the clutch. We monitored this clutch until hatching, which occurred 25–26 days after egg deposition. We analysed a total of eight clutches with an average number of  $42 \pm 6.63$  eggs (range: 35–50). All clutches were located at the distal tip of leaves, either on the upper (n=1) or lower side (n=7) at an average height of  $1.62 \text{ m} \pm 0.184 \text{ m}$  (range: 1.32–1.91 m). Immediately after oviposition, the diameter of eggs from a clutch in stages 1–6 averaged  $2.10 \pm 0.08 \text{ mm}$  (mean  $\pm$  SD, n=9 eggs). The egg size of three clutches with embryos in stages 19–25 was  $3.52 \pm 0.34 \text{ mm}$  (mean  $\pm$  SD, n=24 eggs). As clutches hydrate, they have a spherical mass structure with a yellow yolk. The clutches were observed on leaves of plants of the families Araceae, Arecaceae, Orchidaceae, Piperaceae and Thelypteridaceae at ~1.3–1.9 m above the water (Montilla et al. 2023).

*N. pluvialis*: the clutches were located at the tips of the upper leaf surfaces (Cannatella & Duellman 1982).

*N. posadae*: ♂♂ called in June from the upper side of fern fronds at a height of 110–220 cm and on rocks along a stream, eggs were found in ♀♀ (embryos brown, pigmented animal pole [dark brown] and unpigmented vegetative pole [cream-coloured]), but without indication of the deposition site (Ruiz-Carranza & Lynch 1995a, Guayasamin et al. 2020).

*N. rosada*: ♀♀ lay their eggs on the upper side of leaves hanging over streams, 50–100 cm above the water. The clutches are laid at the top of the leaves, 50–80 cm above the water. On 18 February 2008, fighting behaviour was documented dangling upside down while both ♂♂ held on to the vegetation with their hind legs, touching each other belly to belly (Rada et al. 2017).

*N. ruizi*: a pair in amplexus was found 1 m above the ground on a leaf of a plant. Juveniles were found in the same microhabitat as the adults. The eggs are said to be black in colour (Lynch 1993).

*N. vicenteruedai*: ♂♂ were found calling loudly on the leaves of plants 1–2 m above the water, close to (30 cm) but not in contact with the clutches (Velásquez-Álvarez et al. 2007).

*N. wileyi*: ♂♂ call from the tops of leaves and are territorial, they usually stay close to clutches located at the top of leaves, distances between clutches and ♂♂ can be up to 20 cm. However, ♂♂ were never observed on the same leaf as the clutch. In addition, in several clutches there was no ♂ nearby; these observations indicate that there is no pronounced parental care (Guayasamin et al. 2020).

#### Reproductive season

*N. buenaventura*: calling and breeding activities were described in December 2003 and July 2006.

*N. chancas*: specimens were collected during the presumed reproductive season in June 2011 (IUCN SSC Amphibian Specialist Group 2022c).

*N. grandisonae*: reproduces in the rainy season (December–April), the amplexus takes place in the territories of the ♂♂ (Guayasamin et al. 2020).

*N. griffithsi*: during the rainy season (December to April) at night on vegetation 50–900 cm above streams, waterfalls and small rivers in primary and secondary cloud forests. Reproductive activity peaks in February to April. The ♂♂ are very territorial and show aggressive interactions with conspecifics; during fights, ♂♂ have been observed clinging to a branch with their hind legs and dangling upside-down belly to belly (Guayasamin et al. 2020).

*N. lasgralarias*: breeding was observed from April to July, ♂♂ calling from the tops of leaves located near the watercourse (Hutter & Guayasamin 2012).

*N. laurae*: the rainy season extends from March to July, with 448 mm average monthly rainfall and 23.5°C average monthly temperature. The dry season is between August and January, with 353 mm average monthly rainfall and an average monthly temperature of 23.9°C (Cisneros-Heredia & McDiarmid 2007, Sánchez-Carvajal et al. 2021).



|                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|-------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                     | <p><i>N. manduriacu</i>: particular activity was recorded in February 2018, March 2019, October 2016, November 2019 and December 2019. With the exception of October, when one individual was found away from the stream, all these months fall within the rainy season. However, low detection rates in February 2014, April 2017, May 2013 and November 2012 along the same stream (Guayasamin et al. 2019b).</p> <p><i>N. siren</i>: larger numbers of calling ♂♂ of this species were found during field surveys on 07.04.1972 (13 individuals), 18.03.1975 (15 individuals; both at the type locality) and 15.07.1977 (21 individuals), 3.2 km NNE of Oritoyacu (Guayasamin et al. 2020).</p> <p><i>N. truebae</i>: the species used to be common and could be observed throughout the year, but especially during the peak of the rainy season (December to March; Duellman 1976).</p> <p><i>N. vicenteruedai</i>: reproductive activity, which can be determined by the number and regularity of calling ♂♂, is limited to the rainy season between April and May (Velásquez-Álvarez et al. 2007).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Eggs/clutch, clutches/year          | <p><i>N. balionotus</i>: clutch with 17 eggs (Maynard et al. 2020).</p> <p><i>N. buenaventura</i>: clutches were found on the upper leaf surfaces of epiphytes at a height of approx. 1 m and contained 38 eggs. It is assumed that ♂♂ take over brood care.</p> <p><i>N. grandisonae</i>: clutches contain 30–71 eggs (Guayasamin et al. 2020).</p> <p><i>N. griffithsi</i>: ♀♀ lay clutches of 14–22 eggs on leaves. These later expand into a hanging gelatinous mass; eventually the tadpoles hatch and fall into the stream below (Guayasamin et al. 2020).</p> <p><i>N. lasgralarias</i>: clutches contain 12–36 eggs, are deposited on the upper sides of the leaves at the leaf margin and hang when the eggs have fully developed (Hutter &amp; Guayasamin 2012).</p> <p><i>N. manduriacu</i>: clutches were discovered on leaf surfaces and contained 26–32 embryos (Guayasamin et al. 2019b).</p> <p><i>N. pijao</i>: see corresponding chapter in Mating and spawning.</p> <p><i>N. rosada</i>: clutches contain 28–39 dark (animal pole) and white (vegetative pole) eggs (n=4). The clutches develop into dark brown embryos (Rada et al. 2017).</p> <p><i>N. vicenteruedai</i>: the spherical egg masses contain 20–30 eggs, which develop into yellow embryos (Velásquez-Álvarez et al. 2007).</p> <p><i>N. wileyi</i>: the number of eggs/clutches varies between 19 and 28, eggs and embryos in early stages of development are whitish, one ♂ can fertilise up to four clutches in one reproductive season (Guayasamin et al. 2020).</p> |
| Size of eggs and larvae at hatching | <p><i>N. chami</i>: in one ♀, eggs were found in the abdominal cavity (yolk cream-coloured), and the oviducts were very thick and twisted (AmphibiaWeb 2023).</p> <p><i>N. grandisonae</i>: the clutch consisted of 61 eggs with a mean diameter of 2.12 mm ± 0.24 (n=20; Guevara-Molina &amp; Vargas-Salinas 2014).</p> <p><i>N. ignotus</i>: each clutch (single-layer egg masses) contains 15–23 brown eggs (n=2), with the animal pole conspicuously darker and the vegetative pole weakly pigmented. The egg capsules are clearly demarcated, and there are numerous empty (egg-less) tiny cases that appear to be filled with water. Clutches with similar structures have also been found in other members of the Centrolenidae. Clutch parasitism in this species mainly by fly larvae (about 50%). Some clutches were also found up to 80 cm away from streams, suggesting that the hatching tadpoles have the ability to survive on wet ground until they reach streams by moving downhill (when it rains) towards the water (Lynch 1990, Villa &amp; Valerio 1982, Restrepo &amp; Naranjo 1999, Rada et al. 2017).</p> <p><i>N. manduriacu</i>: one metamorph was uniformly green with some light spots (Guayasamin et al. 2019b).</p> <p><i>N. pijao</i>: see corresponding chapter in Mating and spawning.</p> <p><i>N. spilotus</i>: the two ♀♀ examined carried small cream-coloured eggs in their bodies (Ruiz-Carranza &amp; Lynch 1997).</p>                                                                                              |

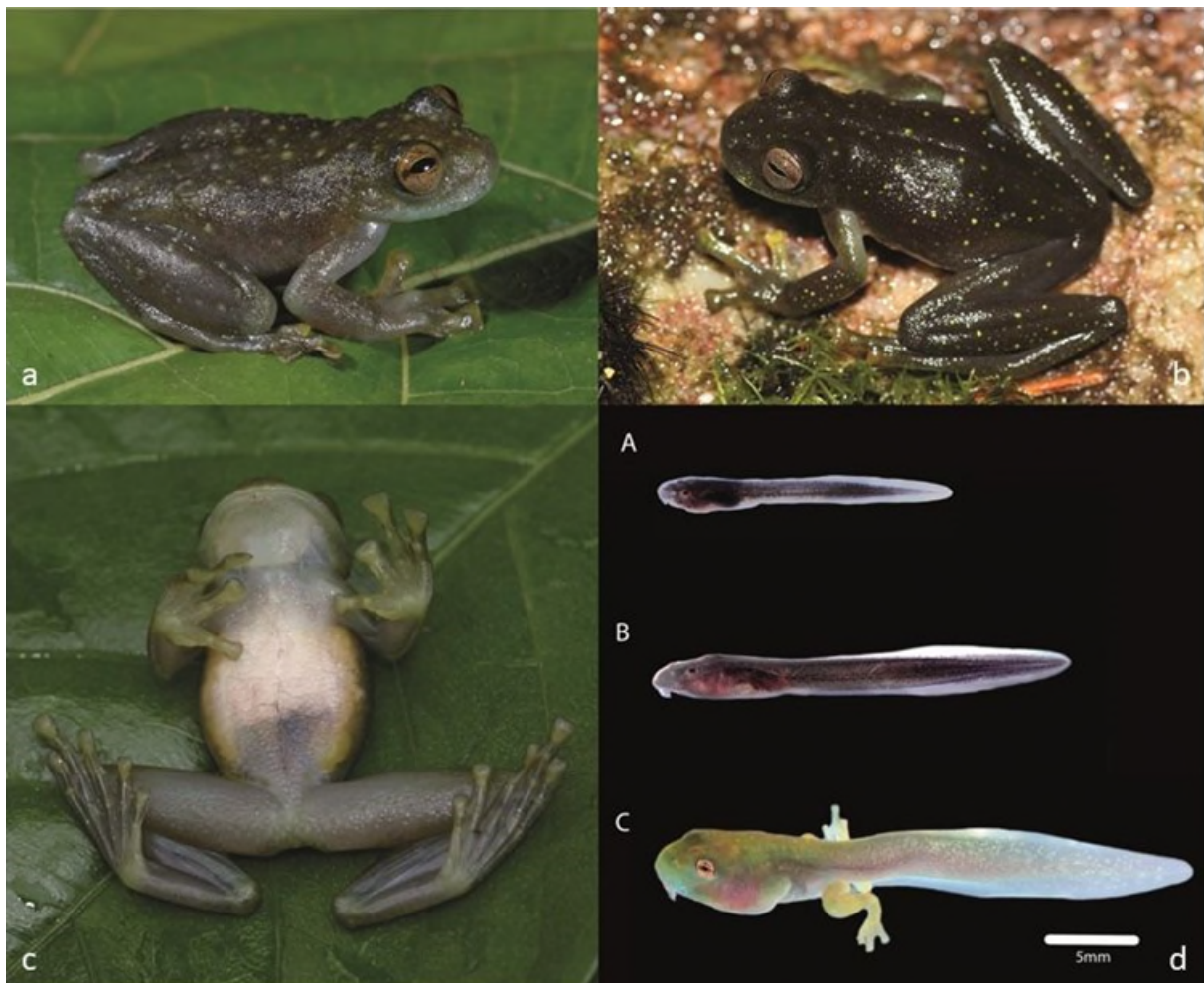
|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Development time from egg laying to metamorphosis | <i>N. pijao</i> : see corresponding chapter in Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Details on the larvae                             | <p><i>N. balionotus</i>: metamorphs measured 11.7 and 15.4 mm (Maynard et al. 2020).</p> <p><i>N. grandisonae</i>: characteristic features include an M-shaped maxillary sheath, a small gap in row A2 and an oral disc not notched at the edge, cream colouration in life (Gosner stage 36), hyobranchial apparatus (Hoffmann 2010a) and heart pinkish, caudal musculature reddish cream, caudal and ventral fins translucent with small dark spots at the distal end of the tail (Ospina-Sarria et al. 2011, Guayasamin et al. 2020).</p> <p><i>N. pijao</i>: mouth region of body rounded in lateral and dorsal view, spiraculum on left side, located posterolaterally, tail long, low, dorsal fin slightly higher than ventral fin, oral disc anteroventral, labial tooth row formula 2(2)/3(1) and occasionally 2(2)/3(1)(2) or 2(2)/2(1), maxillary sheath arcuate, mandibular sheath U-shaped, tadpoles are almost translucent, convoluted viscera visible through the skin, liver orange-pink, heart, hyobranchial sinus (Hoffmann 2010a) and other parts of the circulatory system pink (Arcila-Pérez et al. 2017, Montilla et al. 2023).</p> <p><i>N. vicenteruedai</i>: translucent tadpoles, tooth row formula 2/3, median spiraculum (Velásquez-Álvarez et al. 2007).</p> |

### Husbandry and Captive Breeding **X**

No husbandry information is available for any of the species.

***Rulyrana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                       | Original description                               | Common name                                           | Common name international           | Known/ documented in international trade |
|-------------------------------|----------------------------------------------------|-------------------------------------------------------|-------------------------------------|------------------------------------------|
| <i>Rulyrana adiazeta</i>      | (Ruiz-Carranza & Lynch, 1991d)                     | Western Cochran Frog                                  |                                     | No                                       |
| <i>Rulyrana flavopunctata</i> | (Lynch & Duellman, 1973)                           | Yellow-Spotted Glassfrog, Yellow-Spotted Cochran Frog | Rana de cristal de puntos amarillos | No                                       |
| <i>Rulyrana mcdiarmidi</i>    | (Cisneros-Heredia, Venegas, Rada & Schulte, 2008c) | McDiarmid's Glassfrog                                 | Rana de cristal del Río Jambue      | No                                       |
| <i>Rulyrana saxiscandens</i>  | (Duellman & Schulte, 1993a)                        | Tarapoto Cochran Frog                                 |                                     | No                                       |
| <i>Rulyrana spiculata</i>     | (Duellman, 1976a)                                  | Cuzco Cochran Frog                                    |                                     | No                                       |
| <i>Rulyrana susatamai</i>     | (Ruiz-Carranza & Lynch, 1995a)                     |                                                       |                                     | No                                       |

Fig. 54: *Rulyrana* species

- a *R. mcdiarmidi* (A. Sanchez Vialas)
- b *R. mcdiarmidi* (M. Dobiey)
- c *R. mcdiarmidi*, underside (C. Koch)
- d *R. mcdiarmidi*, larvae at different developmental stages (J.C. Sánchez).

## Morphology and Taxonomy

The genus name *Rulyrana* was chosen in honour of the two herpetologists Pedro Miguel Ruiz-Carranza and John Douglas Lynch, who made significant contributions to the understanding of the diversity, biology and evolution of Colombian glass frogs.

The name *Rulyrana* is an arbitrary combination of the two initial letters of Ruiz and Lynch (Ruly) and the word rana (= frog). Ruly also happens to be the nickname of the friend and colleague Martín Bustamante, whose work in the protection of amphibians was also honoured by the first author of J. M. Guayasamin.

Phylogenetically, this genus represents the clade of the common lineage of the two species *Cochranella adiazeta* Ruiz-Carranza & Lynch 1991d, and *Centrolenella flavopunctata* Lynch & Duellman 1973.

The sister genus is uncertain in this case, according to the analysis of the mitochondrial dataset this would be the genus *Teratohyla* Taylor 1951, while when considering nuclear genes, the genus *Sachatamia* is supported, but only with little significance.

Members of the genus can be distinguished by the following characteristics: (1) no humeral spines present in adult ♂♂, (2) lobed liver covered by a translucent hepatic peritoneum, digestive tract translucent, (3) a ventral parietal peritoneum coloured white in the anterior region by iridophores, whereas the posterior region is transparent/translucent, (4) moderate to strongly developed interdigital membranes between fingers III and IV, (5) bones green in life, (6) dorsum lavender-coloured in preservative, with or without spots, (7) dentary process of vomer present, vomer denticles usually present (present or absent in *R. spiculata* and *R. flavopunctata*), (8) the ♂♂ call from the upper surface of leaves or rocks, the ♀♀ lay their eggs on the upper surface of leaves or rocks. The main features that distinguish *Rulyrana* from other genera are moderate to extensive interdigital membranes between fingers III and IV, the ventral parietal peritoneum, which is white anteriorly and translucent posteriorly, and the absence of humeral spines in adult ♂♂. However, the genus *Sachatamia* cannot be distinguished morphologically from *Rulyrana*. Ideally, these two taxa should be united in a single genus, as suggested by the nuclear dataset and Bayesian analysis of the entire dataset. However, the mitochondrial phylogeny shows that *Rulyrana* and *Sachatamia* do not form a monophyletic group. Given this incongruence between the datasets, both genera are recognised to be monophyletic in all datasets (nuclear, mitochondrial, combined). Should further work show that *Rulyrana* and *Sachatamia* indeed form a natural group, it would be advisable to consider *Sachatamia* as a synonym of *Rulyrana*. At present, however, the classification of the species into one of these two genera requires the use of molecular data. The monophyly of the genus *Rulyrana* is supported by 12S, RAG1, POMC, combined nuclear, combined mitochondrial and complete datasets (Guayasamin et al. 2009).

Many species in this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unequivocal species identification):

*Rulyrana adiazeta*: small to medium-sized glass frog with light green to green dorsal colouration, dorsally tiny conical spines (more numerous in ♂♂), no ulnar or tarsal folds present, SVL ♂♂ 22.5–24.7 mm, ♀♀ 23.3–28.8 mm, head as broad as body, mouth region rounded dorsally, truncated laterally, anterior half to two thirds of ventral parietal peritoneum white (Ruiz-Carranza & Lynch 1991d).

*Rulyrana flavopunctata*: small to medium sized glass frog with green to dark green (to almost black) dorsal colouration with small yellow spots, dorsal skin chagrined, dorsal tiny conical spines in ♂♂, ventral skin areolate, ulnar fold low or absent, inner tarsal fold low, short, outer tarsal fold absent, a pair of slightly enlarged subcloacal tubercles, iris pale greyish white, with or without golden tinge, with dark grey or brown spots or fine reticulation, SVL ♂♂ 21.0–23.9 mm, ♀♀ 24.0–27.4 mm, mouth region rounded dorsally and laterally, tympanic membrane visible, supratympanic fold low, anterior half of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, urinary bladder, (lobed) liver and kidneys without iridophores. Similar species: *R. mcdiarmidi*, *Espadarana audax*, *Nymphargus siren*, *Nymphargus humboldti*, *Nymphargus mariae*, *Teratohyla midas*. Taxonomic notes: The morphological differences between *R. flavopunctata* and *R. mcdiarmidi* are only slight (body size, skin texture, colour pattern), and the two species are genetically indistinguishable. It is possible that *R. mcdiarmidi* is a geographic variant of *R. flavopunctata* or that the two species have recently diverged. Information on call variation and other traits is needed to clarify the species status of *R. mcdiarmidi* (Lynch & Duellman 1973, Guayasamin et al. 2020).

*Rulyrana mcdiarmidi*: medium-sized glass frog with green to dark olive-green dorsal colouration with various darker shades and creamy yellow or light yellowish orange or light green spots (♂♂ with smaller dorsal spots than ♀♀), abundant melanophores on all fingers and toes, dorsal skin smooth, chagrined, with numerous tubercles, ventral skin coarsely granular, subcloacal areas coarsely granular, with numerous low, flat tubercles, other cloacal ornamentation absent, ulnar fold prominent, low, short inner tarsal fold, iris olive-brown to brown with thin dark reticulated lines, SVL ♂♂ 22.8–26.9 mm, ♀♀ 25.4–30.2 mm, mouth region rounded to truncated from dorsal and lateral, tympanic ring distinct, orientated dorsolaterally, weak supratympanic fold, ventral parietal peritoneum completely white or with translucent posterior part, heart not visible, all other peritonea on stomach, intestine, urinary bladder, (lobed) liver and kidneys without iridophores. Similar species: *R. flavopunctata*, *Espadarana audax*, *Nymphargus siren*, *Nymphargus humboldti*, *Nymphargus mariae*, *Teratohyla midas*. Taxonomic notes: see *R. flavopunctata* (Cisneros-Heredia et al. 2008b, Twomey et al. 2014, Guayasamin et al. 2020).

*Rulyrana saxiscandens*: small to medium sized glass frog with dark green to black dorsal colouration (occasionally with lime green spots), melanophores present or absent on the ventral surface of the legs and tarsi, dorsal skin smooth, chagrined or finely spiny, skin on belly and ventral surfaces of thighs coarsely granular, other ventral surfaces smooth, subcloacal areas without cloacal ornamentation, ulnar fold and tubercle absent, inner tarsal fold present or absent, iris dark to light bronze, possibly correlated with dorsal colour (darker individuals tend to have darker irises), SVL ♂♂ 20.8–23.2 mm, ♀♀ unknown, head strong, about as broad as long, mouth region round in dorsal view with truncated upper edge, bluntly rounded in profile, tympanic membrane distinct, dorsolaterally orientated with slight posterior inclination, ventral parietal peritoneum half to completely white, heart not visible, remaining visceral peritonea without iridophores. Taxonomic notes: *R. saxiscandens*, '*Cochranella*' *croceopodes* and *R. tangarana* are considered synonymous based on available morphological, bioacoustic and phylogenetic data, so the latter have been declared junior synonyms of *R. saxiscandens* (Duellman & Schulte 1993a, Twomey et al. 2014).

*Rulyrana spiculata*: small to medium sized glass frog with dark green dorsal colouration, dorsal skin smooth, with tiny white spines on dorsum of body and dorsal and lateral surfaces of head,



melanophores dark green to fingertips, skin on abdomen and proximal surfaces of thighs areolate, other surfaces smooth, a pair of enlarged round subcloacal tubercles, ulnar glandular fold from wrist along entire length of forearm, similar inner tarsal fold centred from metatarsus almost to heel, inner fingers and toes yellow to yellowish green, iris dull bronze-coloured with fine black reticulation, SVL ♂♂ 19.8–23.1 mm, ♀♀ 24.0–27.7 mm, head slightly wider than body, mouth region round in dorsal and lateral view, lower three quarters of tympanic membrane visible, directed dorsolaterally, slightly inclined backwards, ventral parietal peritoneum punctate white, heart not visible, remaining visceral peritonea without iridophores, three-lobed liver (Duellman 1976a, Harvey & Noonan 2005, Chávez et al. 2019).

*Rulyrana susatamai*: medium-sized glass frog with dark green dorsal colouration with many fine yellow spots, dorsal skin smooth with small tubercles, ulnar and tarsal folds absent, SVL ♂♂ 22.3–25.6 mm, ♀♀ 26.9–27.4 mm, head slightly wider than body, Mouth region subovoid in dorsal view, truncate in lateral view, three quarters of the tympanic membrane visible, anterior ventral parietal peritoneum half to two thirds white, remaining visceral peritonea without iridophores (Ruiz-Carranza & Lynch 1995a).

### Distribution and Habitat

The genus *Rulyrana* is widespread on the Amazonian slopes of the Andes in Ecuador and Perú (*R. flavopunctata*, *R. spiculata*) as well as on the western slopes of the Andean Cordillera in Colombia (*R. adiazeta*) and the eastern slopes of the Cordillera Central in Colombia (*R. susatamai*). Altitudinal distribution 70–2,060 m asl. The forest types found at these altitudes form the habitat for reproduction, in which the larvae of *Rulyrana* representatives develop in streams (Guayasamin et al. 2009).

*Rulyrana adiazeta*: on the eastern slope of the Cordillera Oriental in the departments of Cundinamarca, Boyacá, Santander and Tolima in Colombia. Now also known from the municipalities of Charalá and San Vicente de Chucuri in the department of Santander (1,130–2,060 m asl). Habitat in vegetation next to streams in premontane moist forest and also in secondary forest (Rada & Guayasamin 2008).

*Rulyrana flavopunctata*: lower Amazonian slopes of the eastern Andes in Ecuador (Napo, Morona Santiago, Pastaza, Sucumbíos, Tungurahua) and Colombia (Boyacá, Casanare, Meta, Putumayo, Caquetá, Norte de Santander), possibly in neighbouring northern Perú and in the extreme southwest of Venezuela (70–1,850 m asl). The species is an inhabitant of primary and secondary cloud forest, where it is usually found at the edge of streams. It also appears to occur on nearby pastures, which suggests a certain tolerance to habitat degradation.

*Rulyrana mcdiarmidi*: previously only known from two localities in the provinces of Morona Santiago and Zamora Chinchipe in south-east Ecuador and two localities in Cajamarca in north-east Peru. Today, the species is thought to be distributed in the courses of the Utcubamba and central Marañón rivers in Perú (Amazonas, San Martín, Cajamarca regions) and in the eastern foothills of southern Ecuador (Morona Santiago, Zamora Chinchipe provinces) or even beyond (680–1,810 m asl). Occurs in a variety of habitats ranging from pristine rainforests to disturbed, scrubby habitats. The frogs are found on rocks at the edges and in the splash zone of waterfalls (Cisneros-Heredia et al. 2008b, Twomey et al. 2014, Koch et al. 2018).

*Rulyrana saxiscandens*: previously only known from a locality on the southern slope of the northwest-southeast mountain range immediately north of the province of Tarapoto, Departamento San Martín, in northern Perú. After synonymisation with other taxa (see above), the

species is now distributed in the Cordillera Escalera, approximately between the towns of Tarapoto and Moyobamba, in the Departamento San Martín in northern Perú (possibly somewhat more widespread, but still limited). Altitudinal distribution 517–1,047 m asl. Habitats along small streams, torrential rivers to splash zones of waterfalls in submontane and lowland rainforests. The species has never been recorded in heavily disturbed habitats, but occurs in secondary forests. The type locality is a rocky gorge into which two streams fall. The sides of the gorge consist of almost vertical rock faces and the bottom is strewn with huge boulders. About 50 metres beyond the falls, the two streams merge and the resulting wider stream flows over, under and around these boulders, many of which have a thin layer of moss on them. Small trees, ferns and other plants also grow in patches on the floor of the gorge. Some of the frogs were perched on ferns, but most were directly on the rocks about 10 cm from the waterline. Several individuals were also on the bare, wet undersides of the boulders above the stream. When disturbed, the frogs quickly ran over the rocks instead of jumping away (Duellman & Schulte 1993a, Twomey et al. 2014).

*Rulyrana spiculata*: previously known from only two locations in Perú: Kosñipata Valley (Cusco region) and Perene Valley (Pasco region). There are now also confirmed records from the Reserva Comunal El Sira in Perú and northern Bolivia (1,000–1,700 m asl). Habitat in montane primary and secondary tropical forests near streams. Individual specimens have been observed calling at night on the tops of the leaves of herbaceous plants near a small stream. In the area around the Río Cosiipata, which is characterised by cloud forest, many streams cascade down the steep slopes on the north side. The species does not occur there in disturbed areas (Duellman 1976a, Harvey & Noonan 2005, Chávez et al. 2019).

*Rulyrana susatamai*: known from the departments of Tolima, Caldas, Huila and Antioquia on the eastern flank of the Cordillera Central in Colombia (400–1,650 m asl). Habitat in sub-Andean forests on vegetation along streams. The species requires gallery forests for oviposition and is sensitive to any disturbance of its habitat (Ruiz-Carranza & Lynch 1995a, Rada & Guayasamin 2008).

## Conservation Status and Main Threats

### IUCN Red List Status

*Rulyrana adiazeta*: VU (Vulnerable, B1ab(iii), assessed 2016-08-03)

*Rulyrana flavopunctata*: LC (Least Concern, assessed 2021-04-07)

*Rulyrana mcdiarmidi*: NT (Near Threatened, A4c, assessed 2021-05-12)

*Rulyrana saxiscandens*: EN (Endangered, B1ab(iii), assessed 2017-04-19)

*Rulyrana spiculata*: NT (Near Threatened, A2ace, assessed 2019-04-04)

*Rulyrana susatamai*: NT (Near Threatened, B1ab(iii), assessed 2016-07-07).

### Red List Status in the Range Countries

#### Perú

Libro Rojo de la Fauna Silvestre Amenazada del Perú (SERFOR 2018)

EN (Endangered):

*Rulyrana saxiscandens*

## Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other possible threats include local application of pesticides, fertilisers and pollution, disease, climate change and increased UV-B radiation.

*Rulyrana adiazeta*: categorised as vulnerable because, although the estimated distribution area is 19,109 km<sup>2</sup>, the species occurs in four locations classified as endangered and the extent and quality of forest habitat in the Eastern Cordillera of Colombia continues to decline. There is no information on how tolerant this species is to habitat disturbance. The main threat is habitat loss due to the expansion of agriculture (livestock farming and arable farming). It is currently still a common species. However, due to the continuing decline in the extent and quality of the habitat, it is assumed that the population is declining (Colombian Red List assessment workshop in August 2016).

*Rulyrana flavopunctata*: categorised as not endangered due to its wide distribution and presumably large, stable overall population. Small-scale livestock farming and deforestation as well as water and soil pollution due to illegal harvesting in Colombia pose local threats. According to forecasts, almost half of the habitats suitable for this species have been destroyed in Ecuador. However, the species is widespread in suitable habitats. Localised declines may occur due to habitat loss, but the overall population is considered relatively stable.

*Rulyrana mcdiarmidi*: categorised as near threatened as the population is estimated to decline by 20–25% over a ten-year period (2015–2025) due to widespread habitat loss across much of its range as a result of industrial agriculture, logging and mining. It is thought that this species is dependent on well-maintained, unpolluted rivers and that changes in hydrological parameters are likely to affect its survival. The habitat is under threat of destruction from agricultural expansion, deforestation, urban development, mining (and associated pollution) and water retention projects that alter the hydrological cycle. Extensive, large-scale copper and gold mining projects and the associated deforestation and pollution are leading to a serious loss of habitat in the Cordillera del Cóndor.

*Rulyrana saxiscandens*: categorised as endangered because its range is limited to 1,588 km<sup>2</sup>, the species occurs in two locations classified as endangered and the extent and quality of its forest habitat is continuously declining. The main threat to this species is habitat loss due to agriculture, livestock farming, logging and human settlements. The species' type locality is also home to a waterfall that is regularly visited by tourists from the region, which could potentially have a negative impact. The species' existing habitat is highly fragmented, which is why the population is thought to be in decline (Duellman & Schulte 1993a, Twomey et al. 2014).

*Rulyrana spiculata*: categorised as near threatened, as a population decline of almost 30% has been observed in the last ten years, due to the progressive transformation and degradation of the habitat in the distribution area and chytridiomycosis. The prevalence of *Batrachochytrium dendrobatidis* in the Kosñipata Valley is highest in areas that largely overlap with the former range of this species, where most sympatric river-dwelling amphibians have disappeared, probably in the period 2000–2006. In the Perene Valley, the species is threatened by agriculture (coffee, tea and coca cultivation) and human colonisation. In Bolivia, the habitat continues to be lost due to small-scale agriculture and deforestation. Since 1999, the species has not been sighted above 1,100 m asl, despite intensive surveys along previously colonised

streams in 2008, 2009 and 2012–2016. However, it is known that relict subpopulations still occur in the Kosñipata Valley in streams between 1,000 and 1,100 m asl.

*Rulyrana susatamai*: categorised as near threatened because, although its range covers 21,050 km<sup>2</sup>, it only occurs in 8–10 locations and the extent and quality of its forest habitat outside protected areas in the Central Cordillera of Colombia is continuously declining. The main threats are habitat fragmentation and loss due to agricultural expansion, logging and water pollution. It is a widespread species, but the majority of populations are found in subpopulations restricted to remnant forests and isolated by the surrounding matrix of pastures and agricultural use; therefore, the overall population of the species is considered highly fragmented, declining and a priority for conservation (Mendoza & Arita 2014).

## Reproduction

| Topic                       | Details on the reproduction of <i>Rulyrana</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|-----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂ call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Calls                       | <p><i>R. flavopunctata</i>: each call consists of a single short note, which to the human ear resembles a 'trii', with a duration of 3–8 or up to 30 ms. The notes are clearly pulsed; the first pulse of each note has the highest amplitude. The pulses within a note have a rate of 125–333 pulses/s. The dominant frequency of a note is 5,857–7,580 Hz (Guayasamin et al. 2020, Mendoza-Henao et al. 2021).</p> <p><i>R. mcdiarmidi</i>: the call sounds similar to that of <i>R. saxiscandens</i> and consists of a single, piercing 'zip' of short duration. Several ♂♂ called from a vertical rock face of a small waterfall or on small branches, about 1 m above the edge of the stream. This species concentrates on fast-flowing sections of the stream, but despite the background noise, the calls could be heard up to a distance of about 50 metres. Adults and juveniles were all found on rocks or vegetation, typically within 2 m of the water surface (Twomey et al. 2014).</p> <p><i>R. saxiscandens</i>: the species was found at night on low riparian vegetation (calling ♂♂ were heard up to a height of ~4 m) or on boulders and rock faces along streams. The call consists of a short, high-pitched 'zip' that sounds every few seconds. The following parameters were obtained at temperatures of 20–23°C: Call length 0.028–0.056 s, sounds consisting of 7–12 pulses (mean 8.2 pulses), pulse rate 179–250 pulses/s, dominant frequency 6,568–6,915 Hz (Duellman &amp; Schulte 1993a, Twomey et al. 2014).</p> <p><i>R. spiculata</i>: call of a ♂ at a height of 1.2 m above a roaring steep stream (12/02/1999 at 10:45 pm, near San Pedro on the Cusco-Pilcopata road, 1,525 m asl): short, single high-frequency tone with very simple structure, average call length 182.71 ± 2.23 ms, call intervals 3.25–6.64 s, call not amplitude modulated, number of pulses per call very variable (2–11), pulse frequency 11–60 Hz, average dominant frequency 4,528 Hz (Catenazzi et al. 2009).</p> <p><i>R. susatamai</i>: ♂♂ called from 8–3:40 pm on nights with light rain from the tops of the leaves above small streams at heights of about 2–5 metres. The call is a single multi-pulsed tone that resembles a 'trii' to the human ear, call length 58.7 ± 6.58 ms or 71 ± 10 ms (range: 60–80 ms), dominant frequency 5,967.2 ± 163.6 Hz, 7–10 pulses at a rate of 143.3 pulses/s and a visible harmonic at 12,000 Hz (Mendoza-Henao et al. 2021, Galindo et al. 2020).</p> |
| Mating and spawning         | <p>All species: Axillary amplexus in the vegetation above small forest streams.</p> <p><i>R. adiazeta</i>: in low vegetation near waterfalls and on the moist surfaces of rocks (Ruiz-Carranza &amp; Lynch 1991d).</p> <p><i>R. flavopunctata</i>: most individuals were found in a deep ravine where the ♂♂ sat on</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |

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|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | <p>small plants in the splash zone of a small waterfall ♂♂ were calling from the top of leaves or rocks at the Río Tayuntza (Morona Santiago province, Ecuador), clutches were found on rock faces during the rainy season; parental brood care is not known (Guayasamin et al. 2020).</p> <p><i>R. mcdiarmidi</i>: Arpi Lojano et al. (2023) report on an ex situ husbandry of the AMARU Amphibian Conservation Centre in a paludarium (79 x 40 x 38 cm [length x width x height]) after two pairs were removed due to a mining project in the community of Tundayme, Pangui, Zamora Chinchipe, Ecuador. The following sections use the data from this work. On 17 March 2022, at 4:00 pm, a pair was observed in the amplexus near a flat stone in the 21 l water section of the paludarium. During the night, at around 11:00 pm, the clutch was deposited on this stone about 10 cm above the water surface. The clutch contained 96 eggs and the ♂ was observed only 5 cm away from the clutch for 12 days. From the 15<sup>th</sup> day onwards, hatching took place within the following three days.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Reproductive season                               | <p><i>R. adiazeta</i>: the large eggs are spotted black and were found between December 1978 and January 1979 (Ruiz-Carranza &amp; Lynch 1991d).</p> <p><i>R. flavopunctata</i>: at several small streams between Mera and the Río Alpayacu, the ♂♂ called from the tops of the leaves on 2, 14 and 24 July 1968 (Guayasamin et al. 2020).</p> <p><i>R. spiculata</i>: specimens of the species were collected in November 2013 and 2014 and in March 2014 (Chávez et al. 2019).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Eggs/clutch, clutches/year                        | <p><i>R. mcdiarmidi</i>: All clutches deposited ex situ (n=5) were found at night on the above-mentioned rock (see table row Mating and spawning) above the water surface and contained 89–120 eggs/clutch (average 98.8, standard deviation 14.3). The eggs are spherical, light grey in colour with dark edges. In some cases bicoloured eggs were observed, sometimes light and dark grey, in other cases completely white (pale grey: 82.2%, bicoloured 15%, white 2.8%; however, the white eggs were subsequently found to be unfertilised). The embryos reached Gosner stage 17 within the clutch in four days, in which the first synchronised movements were observed. After 15 days (Gosner stage 25), the first embryos hatched (Gosner 1960, Arpi Lojano et al. 2023).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Size of eggs and larvae at hatching               | <p><i>R. mcdiarmidi</i>: see table row Development time from egg laying to metamorphosis.</p> <p><i>R. spiculata</i>: Dissected gravid ♀♀ had ovaries filled with black pigmented eggs, the largest of which was 1.8 mm in diameter. In order not to damage the preserved specimens, the eggs were not counted (Harvey &amp; Noonan 2005).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Development time from egg laying to metamorphosis | <p><i>R. mcdiarmidi</i>: Arpi Lojano et al. (2023) give morphometric data of tadpoles in ex situ husbandry and further report: between the 25<sup>th</sup>–28<sup>th</sup> Gosner stage increase in total length (this process takes about 24 days), later stages take up to four days for each developmental stage, individuals reach their maximum size at stage 39, from this point on the total length begins to decrease, the hind limbs incl. toes and the fingers of the forelimbs (visible as light-coloured fingertips under the skin) develop until stage 39, the development of the forelimbs is completed at stage 40 when they are externally visible. At stage 41, the snout becomes blunt and the eyes with a horizontal pupil are fully developed, the body width increases by 8% and the forelegs are clearly visible under the skin. The first larvae complete their development from hatching to land-fall (in the Gosner stage 42–46) in about 80–108 days. Colouration of the tadpoles: Stages 25–28: back dark grey, belly translucent, tail dark grey with some scattered light grey spots on the tail ends, stages 28–40: back light grey to reddish ochre, tail uniformly light grey, stage 40: body greenish yellow with diffuse yellowish spots on tail and back and scattered small dark spots on back and limbs, tail part: dull golden areas. Completion of metamorphosis (Gosner stage 46) after a further 12 days. The first animals of this generation reached sexual maturity at 23 months and had their first fertile clutch on 9 June 2023. However, when asked, the authors stated that these were earlier offspring of the same breeding generation, which were not identical to the individuals described above, sexual maturity may therefore be reached</p> |



much earlier (Arpi Lojano, personal communication). While Rada et al. (2007) reported a period of more than five months from hatching to metamorphosis in *Centrolene daidalea* and *Hyalinobatrachium ibama*, the time to metamorphosis in *R. mcdiarmidi* was three months (95% of the group; 95–97 days, with clear differences in size at Gosner stages 26, 35 and 42). The differences in development times may be species-specific, but time and variability appear to be more related to the availability and nutritional content of the diet. However, in this study it was observed that individuals changed their food preferences throughout larval development. Protein requirements are highest in the later larval stages, so the transition between developmental stages appears to depend on sufficient food resources. The authors advocate the ex-situ husbandry of amphibians, which allows the precise identification of relevant aspects of behaviour and morphology in order to document larval development and ontogeny. Larval development and survival in human care depend on the species and the technical possibilities. By recording such information, it is now also possible to assess variations in larval size and temporal fluctuations in situ. Ex situ husbandry also opens up the possibility of establishing protocols for the care and reproduction of other glass frog species in order to study their reproductive behaviour and aspects of larval ecology (Arpi Lojano et al. 2023).

Details on the larvae

*R. mcdiarmidi*: Spiraculum short, cloacal opening short, tail long and robust with sub-acute tip and myotomes over the entire length, caudal fin margin extends over the entire tail, its maximum height is reached after the middle of the tail, medium-sized oral disc with 28 papillae, completely keratinised, straight upper beak with 29 teeth, U-shaped lower beak with 32 teeth, tooth formula 2(2)/3, colouration brown to reddish ochre, in later stages yellowish green with diffuse yellowish green spots on the dorsum (Arpi Lojano et al. 2023).

### Husbandry and Captive Breeding **X**

No husbandry information is available for any of the species.

***Sachatamia* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                        | Original description                                           | Common name                                                                                              | Common name international   | Known/ documented in international trade |
|--------------------------------|----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------|-----------------------------|------------------------------------------|
| <i>Sachatamia albomaculata</i> | (Taylor, 1949)                                                 | Yellow-flecked Cascade Glassfrog, White-Spotted Glassfrog, White-Spotted Cochran Frog, Cascade Glassfrog |                             | Yes                                      |
| <i>Sachatamia electrops</i>    | Rada, Jeckel, Caorsi, Barrientos, Rivera-Correa & Grant, 2017b |                                                                                                          |                             | No                                       |
| <i>Sachatamia ilex</i>         | (Savage, 1967)                                                 | Ghost Glass Frog, Limon Giant Glass Frog, Holly's Glassfrog                                              |                             | Yes                                      |
| <i>Sachatamia orejuela</i>     | (Duellman & Burrows, 1989)                                     | Orejuela's Glassfrog, El Tambo Cochran Frog                                                              | Rana de cristal de Orejuela | No                                       |
| <i>Sachatamia punctulata</i>   | (Ruiz-Carranza & Lynch, 1995a)                                 |                                                                                                          |                             | No                                       |

CITES Proposal 34 (CITES 2022) cites a thwarted attempt to illegally export 20 specimens of the species *Sachatamia ilex* from Costa Rica, among others (however, neither source cited supports this claim [Altherr 2014, Fendt 2014]). The same source also cites the US LEMIS database (2017), according to which a total of 891 individuals of *S. ilex* were legally imported into the United States between 2004 and 2016, mainly from Costa Rica and Panama – however, the LEMIS database also includes captive-bred specimens and only has the default value 'wild caught' if the exact source code for these captive-bred specimens was not given (cf. Luiselli et al. 2016 for turtles, or Kolby & Weissgold 2022 for animal products). An excerpt from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists one keeper (USA) of *S. ilex* in 2005 and 2006 (T. Eisenberg, unpublished data); according to our own experience, *S. ilex* is not currently maintained in private ex situ husbandry.

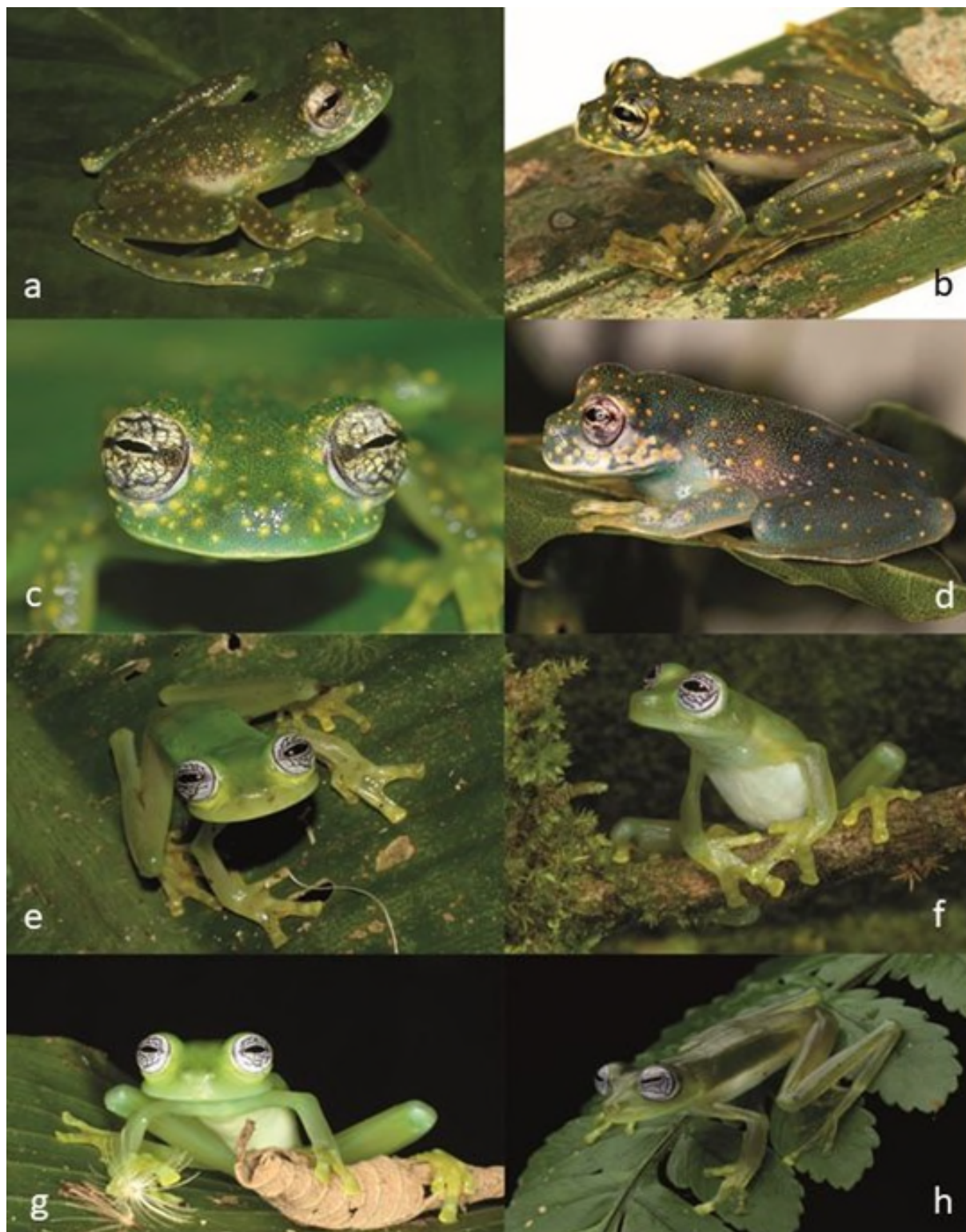


Fig. 55: *Sachatamia* species

- a *S. albomaculata*, specimen from near Las Horquetas, Costa Rica (T. Eisenberg)
- b *S. albomaculata* (T. Leenders)
- c *S. albomaculata* (J. Sens)
- d *S. albomaculata* (M. Weber)
- e *S. ilex*, specimen from near Las Horquetas, Costa Rica (T. Eisenberg)
- f *S. ilex* (T. Leenders)
- g *S. ilex*, specimen from Costa Rican Amphibian Research Center (T. Eisenberg)
- h *S. ilex* (T. Leenders).

## Morphology and Taxonomy

The genus name *Sachatamia* comes from the Quechua words 'sacha', meaning 'forest', and 'tamia', meaning 'rain', and refers to the tropical rainforest where this indigenous people live. Phylogenetically, the genus represents the clade of a common lineage of the two species *Centrolenella albomaculata* Taylor 1949 and *Cochranella orejuela* Duellman & Burrowes 1989. The sister genus is uncertain in this case, at least according to the analysis of the mitochondrial dataset, the closest relationship with the genera *Rulyrana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009 and *Teratohyla* Taylor, 1951 is supported, while the analysis of nuclear genes and the complete dataset supports the closest relationship between the genera *Sachatamia* and *Rulyrana*, albeit with low reliability of the data.

Members of the genus can be distinguished by the following characteristics:

(1) conspicuous humeral spines present in adult ♂♂ (*S. ilex*) or absent (*S. albomaculata*, *S. electrops*, *S. orejuela*, *S. punctulata*), (2) lobed liver covered by a translucent hepatic peritoneum, digestive tract translucent, (3) a ventral parietal peritoneum coloured white in the anterior region by iridophores, whereas the posterior region is transparent/translucent, (4) moderate interdigital membranes between fingers III and IV, (5) bones green in life, (6) dorsum in preservative lavender-coloured, with or without spots, (7) dentary process of the vomer with denticles, (8) the ♂♂ call from the upper side of leaves or stones, the ♀♀ lay their pigmented eggs on the upper side of leaves or stones above watercourses, (9) articulated connection between quadratojugals and maxillary bones.

Although phenotypic characteristics distinguish *Sachatamia* from most Centrolenidae, there are no clear differences between this genus and *Rulyrana*; however, geographically, *Rulyrana* is found on the central and Amazonian slopes of the Andes, while *Sachatamia* is found in Central America, the South American Chocó and the central Andes.

The monophyly of *Sachatamia* is strongly supported by 16S, ND1, combined mitochondrial and complete datasets (Guayasamin et al. 2009, 2020).

Many species of this group are comparatively similar but can be distinguished from other genera (molecular identification is recommended for unequivocal species identification):

*Sachatamia albomaculata*: medium sized glass frog with dark green dorsal colouration and small (Central America) resp. small and large (Central and South America) yellow spots, dorsal skin chagrined, with small spines in ♂♂, belly cream-coloured, ventral skin areolate, a pair of enlarged subcloacal tubercles, which are more pronounced in ♀♀, iris silvery-white to yellow with black reticulation, SVL ♂♂ 22.1–24.7 mm, ♀♀ 26.7–29.0 mm, mouth region round to truncate in dorsal view, truncate in lateral view, dorsal margin of tympanic membrane covered by supratympanic fold, anterior half of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver, testes, kidneys, gall bladder and urinary bladder without iridophores. Taxonomic note: Type species of the genus (Guayasamin et al. 2009, 2020).

*Sachatamia electrops*: medium-sized glass frog with lime-green dorsal colouration and yellow and blue spots, dorsal skin in ♂♂ coarse-grained, with or without tiny spines and low tubercles corresponding to the yellow spots, in ♀♀ chagrined without spines, skin on belly and ventral thighs granular, a pair of large round, flat tubercles on the ventral side of the thighs below the cloaca, subcloacal skin granular, enamelled, interdigital membranes between the fingers I-III absent, interdigital membranes of the outer fingers III-IV pronounced, interdigital membranes

between the toes reduced, ulnar fold present, low, tarsal fold absent, iris colouring silvery to copper-coloured with dark spots and reticular structures as well as a conspicuous silvery-white, crescent-shaped spot (exclusive and distinct diagnostic feature; *electrops* is derived from the Greek nouns elektron [= electric] and ops [= eye]), SVL ♂♂ 21.8–23.3 mm, ♀ 25.3 mm (n=1), mouth region truncated in dorsal and lateral view, tympanic membrane visible, supratympanic fold present, anterior half to two thirds of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver without iridophores. Related species: *S. punctulata* (sister species). Similar species: *S. punctulata*, some populations of *Espadarana prosoblepon*, *Centrolene daidaleum*, *Centrolene lynchi*, *Centrolene peristictum*, *Centrolene savagei*, *Centrolene solitaria* (Rada et al. 2017b).

*Sachatamia ilex*: medium-sized to large glass frog with uniform dark green dorsal colouration, throat and belly creamy white, dull yellow hands and feet, upper lip white, pointed upper arm spine in ♂♂ embedded in the arm musculature (not easily visible from the outside), dorsal skin smooth to chagrined, without spines, abdominal skin areolate, no pair of subcloacal tubercles on the ventral side of the thighs below the cloaca, interdigital membranes absent between digits I and II, reduced between digits II and III, pronounced between III and IV, elbow fold absent or low and inconspicuous, inner tarsal fold low, short, outer tarsal fold absent, iris colouration white to pale yellow or greenish yellow with thick, contrasting black reticulations, SVL ♂♂ 27.0–29.0 mm, ♀♀ 28.0–35.0 mm, mouth region truncated in dorsal and lateral view, tympanic membrane almost vertically aligned, pigmented but clearly demarcated from the surrounding skin, relatively small, conspicuous supratympanic fold, anterior two-thirds of the ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver, kidneys, testes, gall bladder and urinary bladder without iridophores. Related species: *S. orejuela* (sister species). Similar species: *Espadarana prosoblepon* (spotless populations), *Espadarana callistomma*, *Nymphargus prasinus*, *Teratohyla spinosa* (Leenders 2001, 2016, Savage 2002, Guayasamin et al. 2020).

*Sachatamia orejuela*: medium-sized to large glass frog with uniform olive-green dorsal colouration, throat translucent, with light green tinge, belly whitish cream-coloured, dorsal skin chagrined with small spines in ♂♂, ventral skin areolate, no pair of subcloacal tubercles on ventral side of legs below cloaca, in ♂♂ the cloacal region is covered with tiny spines, interdigital membranes between fingers I and II basal, between fingers II and III moderately pronounced and between fingers III and IV strongly pronounced, ulnar and tarsal folds absent, iris dark grey with yellow ring around the pupil, SVL ♂♂ 27.3–28.3 mm, ♀♀ 29.6–33.8 mm, mouth region truncated in dorsal view, protruding in lateral view, tympanic membrane small, conspicuous supratympanic fold, anterior half of ventral parietal peritoneum white, heart not visible, peritonea on stomach, intestine, (four-lobed) liver without iridophores. Related species: *S. ilex* (sister species). Similar species: *Nymphargus prasinus*, *S. ilex*, *Teratohyla spinosa*, *Espadarana prosoblepon* (spotless populations; Duellman & Burrowes 1989, Guevara-Molina & Rada 2018, Guayasamin et al. 2020).

*Sachatamia punctulata*: medium-sized to large glass frog with dark green dorsal colouration and abundant yellow or orange dots evenly distributed on head and trunk, outer edges of forearm, hand, tarsus with discrete whitish line, hands and feet yellow, perianal region yellowish cream, throat bluish green, belly yellowish, dorsal skin smooth with small spines in ♂♂, ventral skin and ventral surface of thighs granular, white cloacal ornamentation consisting of small, not enlarged granules, no subcloacal tubercles, ulnar and tarsal folds absent, iris whitish beige with dark brown to black reticulum, SVL ♂♂ 24.5–27.3 mm, ♀♀ 30.1–31.6 mm, mouth



region slightly ovoid in dorsal view, truncate in lateral view, small eyes, anterolaterally directed, tympanic membrane large, visible in the lower two thirds, dorsally and laterally orientated, laterally oriented, anterior half of the ventral parietal peritoneum white, heart not visible. Related species: *S. albomaculata* (sister species). Similar species: *Rulyrana flavopunctata*, *Teratohyla midas* (Rojas-Morales et al. 2014).

### Distribution and Habitat

The genus *Sachatamia* occurs at altitudes below 1,500 m asl in the rainforests of Central America (Honduras, Nicaragua, Costa Rica, Panama) and South America (Colombia, Ecuador). In South America, *S. albomaculata*, *S. ilex* and *S. orejuela* occur in the Pacific lowlands, while *S. electrops* is restricted to the northern and *S. punctulata* to the eastern slopes of the Cordillera Central of the Colombian Andes (Guayasamin et al. 2009).

*Sachatamia albomaculata*: known from the northern centre of Honduras, Nicaragua, Costa Rica, Panama, the western part of Colombia (departments of Chocó and Antioquia) and the north-western part of Ecuador (provinces of Esmeraldas and Imbabura). Altitudinal distribution from sea level up to 1,500 m asl. Habitat in humid lowland and high mountain forests, in bushes and trees along forest streams, populations can also survive along streams in pastures with minimal riparian vegetation.

*Sachatamia electrops*: endemic to the northern part of the Cordillera Central in Colombia and currently known from seven sites in the department of Antioquia (municipalities of Alejandría, San Roque and San Carlos) (800–1,630 m asl). Habitat in sub-Andean and montane Andean forests near streams. The individuals are active at night in bushes and ferns at the edge of streams with low water levels (Rada et al. 2017b).

*Sachatamia ilex*: this species is known from scattered localities in humid lowland and premontane areas from southern Nicaragua and northern Costa Rica to western Panama, western Colombia (Departamentos Chocó and Valle del Cauca) and northwestern Ecuador (provinces Esmeraldas and Pichincha) as well as from the caldera of the Río Grande de Tárcos in central Costa Rica on the Pacific side (30–1,420 m asl). This hard-to-find species inhabits riparian vegetation in humid primary and secondary forests of the lowlands and mountains and is usually observed in bushes and trees along forest streams.

*Sachatamia orejuela*: known from the Pacific slopes of the Andes in southern Colombia and north-west Ecuador. In Colombia, the species occurs in the departments of Nariño (Reserva La Planada and Quebrada La Carbonera), Valle del Cauca (Campo Alegre and in the Parque Nacional Natural Farallones de Cali) and Cauca (Parque Nacional Natural Munchique) on the western slope of the Cordillera Occidental. In Ecuador, it occurs in the provinces of Esmeraldas, Imbabura, Pichincha and Santo Domingo de los Tsáchilas (500–1,250 m asl). Habitat in premontane and montane rainforest. Mostly found at night on rocks along steep stream banks or within streams in the splash zone of cascades. As with other species adapted to splash zones (e.g. *Centrolene geckoidea*, *Centrolene paezorum*, *Centrolene petrophilum*, *Centrolene medemi*), the hand and foot webs of this species are very pronounced compared to glass frogs, which do not occur in this microhabitat. This species is a specialist in humid forest areas, preferring to live in the cracks between rock faces along streams. It is unlikely that this species tolerates disturbance in its habitat as it has always been recorded in primary forests. It has been observed that spiders of the genus *Clubiona* hunt the young of *S. orejuela*. Parental brood care is unknown (Duellman & Burrowes 1989, Yáñez-Muñoz & Cisneros-Heredia 2008, Almeida-Reinoso & Coloma 2012, Guayasamin et al. 2020).

*Sachatamia punctulata*: known from the departments of Tolima, Antioquia and Caldas on the eastern flank of the Central Cordillera in northern Colombia (360–1,400 m asl). Habitat in the vegetation along streams in low and medium tropical forests. Food composition: Blattodea (Blattidae), Coleoptera (Chrysomelidae), Diptera (Cimicidae, Drosophilidae, Muscidae, Simuliidae), Hymenoptera (Formicidae) and Lepidoptera (Noctuidae), which indicates that this species is an insectivorous generalist (Cortés Bedoya 2010, Frost 2024).

## Conservation Status and Main Threats

### IUCN Red List Status

*Sachatamia albomaculata*: LC (Least Concern, assessed 2019-12-09)

*Sachatamia electrops*: EN (Endangered, B1ab(iii), assessed 2018-10-10)

*Sachatamia ilex*: LC (Least Concern, assessed 2019-11-14)

*Sachatamia orejuela*: LC (Least Concern, assessed 2018-07-03)

*Sachatamia punctulata*: VU (Vulnerable, B1ab(iii), assessed 2016-08-04).

### Red List Status in the Range Countries

The Red Lists of the areas of origin refer to the IUCN category; individual assessments were not carried out for *Sachatamia* species.

### Threats

The main threats are associated with possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local application of pesticides, fertilisers and pollution, disease, climate change and increased UV-B radiation.

*Sachatamia albomaculata*: not classified as endangered due to its wide distribution and presumably large population.

*Sachatamia electrops*: listed as endangered as the distribution area is only 574 km<sup>2</sup>, the species occurs in two locations classified as endangered and the extent and quality of its habitat is continuously declining. This species is not tolerant of habitat disturbance and requires native riparian forests. The landscape in this region has been heavily modified by human activities such as agriculture, cattle grazing, urbanisation, gold mining and, more recently, the construction of large infrastructure projects. Due to the continuing decline in the extent and quality of the habitat, the population is thought to be in decline (Rada et al. 2017b).

*Sachatamia ilex*: not endangered in view of its wide distribution and presumed large population. The generalised loss of habitat due to small-scale deforestation poses a local threat. This species has apparently not experienced chytridiomycosis-related declines in El Copé, Panama, although it is reported to be susceptible to *Batrachochytrium dendrobatidis* infections. Decreasing trend (Woodhams et al. 2006, Crawford et al. 2010).

*Sachatamia orejuela*: not classified as endangered in view of its wide distribution and presumably large population. The species is threatened by the expansion of the cultivation of illegal crops and by water pollution from chemicals used in their cultivation. In Colombia, it is abundant wherever it occurs. However, due to the continuing decline in the extent and quality of its habitat, the overall population is thought to be in decline.

*Sachatamia punctulata*: The distribution area of this species is limited to the Central Cordillera of Colombia; its range covers 16,558 km<sup>2</sup> and its population is considered to be highly fragmented with a decreasing trend. The extent and quality of the habitat is continuously declining due to agricultural and mining activities. The species is therefore categorised as vulnerable. It requires original gallery forests to lay its eggs and is very sensitive to habitat disturbance. The species is therefore restricted to forest remnants throughout its range, and there are hardly any connections between the known sites due to the inhospitable habitat there. In some areas of its range, water is also diverted for small hydroelectric power stations. It is a rare species.

## Reproduction

| Topic                       | Details on the reproduction of <i>Sachatamia</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|-----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂: Calls from paired ( <i>S. albomaculata</i> / <i>S. orejuela</i> ) or single (other species) subgular vocal sacs (Brunner & Guayasamin 2020).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Calls                       | <p><i>S. albomaculata</i>: ♂♂ calls from the tops of leaves and rocks along streams and in the splash zone of waterfalls; the calls consist of a fast, high-pitched single tone ('tik'), with a call length of 0.001–0.002 s; the dominant frequency is 6,100–7,100 Hz (Guayasamin et al. 2020).</p> <p><i>S. electrops</i>: a high-pitched 'tic' sound to the human ear (recordings not available; Rada et al. 2017b).</p> <p><i>S. ilex</i>: ♂♂ call from the top of leaves near watercourses, each call is frequency modulated and consists of a single tone with a duration of 0.077–0.086 s, the dominant frequency starts at 6,562–6,937 Hz, rises to 7,406–7,500 Hz and then falls to 6,562–6,843 Hz (Guayasamin et al. 2020).</p> <p><i>S. orejuela</i>: the recorded ♂ called in a deep stream gorge at a height of 1.5 metres. The advertisement call is a pulsed tone with a duration of 191.8 ± 23.8 ms (157–212 ms), sounding like a 'trii'. The number of pulses per call was 48.2 ± 6.7 (38–58), and the duration of the pulses was 1.6 ± 0.5 ms (1.6–1.7 ms). The pulse rate was 254.5 ± 46.0/s (188.7–339.2/s). The dominant frequency of the call was 6,700 ± 0.130 Hz (6,550–6,890 Hz). In addition to similar call parameters for intraspecific communication, another team of authors describes a waving behaviour of the ♂♂ using the front and rear extremities as well as a head bobbing, which was alternated every second to minute. It is assumed that the high-frequency call and motor behaviour are an adaptation to communicate in the vicinity of loud waterfalls and thus occupy an otherwise inaccessible acoustic niche (Brunner &amp; Guayasamin 2020, Duarte-Marín et al. 2023).</p> <p><i>S. punctulata</i>: calls were recorded from rocks and on vegetation up to 4 m high between 1 and 3 am. The call consists of a series of pulsed harmonic tones (1–5 tones) with a call length of 17.6 ± 4.2 ms, an interval of 97.2 ± 16.1 ms and a dominant frequency of 5,611.7 ± 213.9 Hz, with no amplitude modulation detected. To the human ear, the call sounds like a 'trii'. Each tone shows up to 3.74 ± 1.62 pulses at a rate of 220 pulses/s (Mendoza-Henao et al. 2021).</p> |
| Mating and spawning         | <p>All species: axillary amplexus in the vegetation above small forest streams.</p> <p><i>S. albomaculata</i>: eggs are laid on the tops of leaves or on rocks; short-term maternal brood care (hydration immediately after egg deposition for a few hours), longer-term parental brood care not present (Guayasamin et al. 2020). Barría et al. (2023) describe a fighting behaviour between ♂♂ and a mismating (amplexus) with a ♂ <i>Smilisca sila</i>.</p> <p><i>S. electrops</i>: in bushes and ferns at the edge of a gently flowing stream (approx. 5 m wide), the ♂♂ call from the upper sides of leaves and branches at a height of approx. 50–250 cm, oviposition takes place on the upper side of leaves, approx. 50 cm above the water (Rada et al. 2017b).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |

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|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | <p><i>S. punctulata</i>: ♂♂ called between 8 and 9 pm above a height of 3 m and then descended into the vegetation. Individuals were observed on rocks and herbaceous, bushy vegetation at the edge of streams near small waterfalls inside secondary forests, perching 0.25–1.7 m above the 2.5–3.5 m wide stream, ♀♀ on rocks at low altitude, ♂♂ on fern fronds and other plants (<i>Cyclanthus</i> sp.; Rojas-Morales et al. 2014).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Reproductive season                               | <p><i>S. albomaculata</i>: activity especially during the rainy season, oviposition preferably on leaves. At the beginning of the dry season (December 2001 and 2002), reproductive behaviour and oviposition sites shifted to rocks in the wet splash zone of two waterfalls or directly on the Río Jaris, Costa Rica, to extend the reproductive phase during part of the dry season. Pairs in amplexus were found in February 2021 directly on the rocks at the edge of a stream near the northern border of the Braulio Carillo National Park in Costa Rica (T. Eisenberg, own observation; Puschendorf et al. 2004).</p> <p><i>S. ilex</i>: on 10 November 1999 at Hacienda La Joya (north-west Ecuador), a ♂ called near two gravid ♀♀, indicating reproductive activity. When fighting, the ♂♂ hang vertically in the vegetation by the tips of their toes and grab each other's chests, crossing their arms. The ♂♂ can hang in this position for several minutes to hours, trying to push the feet of the other ♂ away so that it loses its grip on the vegetation. During this fighting behaviour, the two ♂♂ make soft calls (Guayasamin et al. 2006c, Kubicki 2007).</p> <p><i>S. orejuela</i>: individuals were observed from February to April 2019, with only one animal found calling. In Ecuador, this species was the only one of five glass frog species that did not reproduce between January and March (Maynard et al. 2020, Brunner &amp; Guayasamin 2020).</p> <p><i>S. punctulata</i>: ♀♀ with eggs inside were sighted in May 2009 and February 2010, ♀♀ contained light, cream-coloured eggs of different sizes; larger eggs had a black animal pole and a cream-coloured vegetative pole. A ground beetle (<i>Dyscolus</i> [<i>Dyscolidion</i>] cf. <i>punctatostriatum</i>) was described as a potential predator, which consumed 78 eggs from a clutch on 22 October 2014 between 10 pm and midnight (Rojas-Morales et al. 2014, Burbano-Yandi et al. 2018).</p> |
| Eggs/clutch, clutches/year                        | <p><i>S. albomaculata</i>: the eggs are black and white in the oviduct and shortly after laying. The clutches are characterised by the fact that there is often a gap without eggs in the middle of the mass (see <i>S. ilex</i>). The clutches consist of 37–81 eggs. The karyotype is <math>2n=20</math> (Duellman 1967, Savage 2002, Kubicki 2007).</p> <p><i>S. electrops</i>: four clutches with 32–53 eggs on the upper sides of leaves above watercourses, eggs pale cream-coloured (only species of the genus, all other species have dark eggs; Rada et al. 2017b).</p> <p><i>S. ilex</i>: clutches consist of 12–25 eggs. It has been observed that <i>Drosophila</i> species parasitise the clutches. The brown eggs are deposited in a single layer on the upper leaf surface. Sometimes a clutch has a small hole in the centre, resembling a donut, because the pair turns from the centre during oviposition. Parental brood care is unknown (Kubicki 2007, Hoffmann 2010a).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Size of eggs and larvae at hatching               | <p><i>S. albomaculata</i>: egg size 2 mm in diameter (jelly 4 mm; T. Eisenberg, unpublished data); larval size: see table husbandry and captive breeding.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Development time from egg laying to metamorphosis | <p><i>S. punctulata</i>: an individual malformation in a population in Quebrada Soto 2, Montebello village, Norcasia municipality, Caldas department, Colombia, was reported by Martínez &amp; Botero (2019). The metamorph found next to the stream showed a characteristic deformity of the hind limbs, and a detailed examination revealed that the frog had a shortened right tibia-fibula (hemimelia) and a bony triangle on the right thigh (taumelia). It remains to be clarified whether these are spontaneously occurring mutations or toxic or infectious causes. The malformed individuals account for two per cent of the sampled population (one finding and <math>n=50</math>; between October 2016 and November 2017), which is in line with the expected frequency of malformations.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Details on the larvae                             | <p><i>S. albomaculata</i>: the tadpole was described in detail by Hoffmann (2010a): The embryos in Gosner stage 22 are light brown, the hatchlings in stage 25 are dark grey-</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |

brown. The ventral colouration is lighter due to the yellow yolk visible through the skin. The larvae are among the most strongly pigmented centrolenids in Costa Rica. While the hatchlings resorb their yolk sac, the oral disc remains incomplete. More developed tadpoles (stages 25–37) have the typical dorsoventrally compressed body shape, which together with the larvae of *S. illex* and *Teratohyla spinosa* are the most compressed centrolenid larvae in Costa Rica. The oral disc is very similar to that of *S. illex*; it is not notched at the margin and has a single row of 24–40 marginal papillae with a distinctly wide anterior labium (dorsal fissure), a feature also present in *S. illex*, wide dorsal fissure, papillae often flattened, irregular and sometimes absent. The upper jaw is gently curved, the lower jaw broad and V-shaped. The labial tooth row formula is probably 2(2)/3, but most tadpoles lack the A1 tooth row, if present, the A2 is short and usually consists of a few teeth in short rows along the lateral margins of the upper jaw. Three ridges can be recognised on the lower lip, all or some of which bear teeth. Whether these irregularities in the labial tooth rows result from laboratory rearing or are typical for the species remains to be clarified (Hoffmann 2010a).

*S. illex*: when hatching, the larvae have a dark grey-brown dorsal colouration. The body is almost circular in cross-section and with a length of about 12 mm longer than other centrolenid larvae in Costa Rica. In tadpoles that live off their yolk reserves, the oral discs are incomplete. As development progresses (Gosner stages 28–40), the body becomes flattened and dense dorsal pigmentation develops, giving the larvae a black-brown base colour. There is also a slight purple colouration due to the underlying vascularised organs. The lateral body pigmentation decreases towards the ventral side, the colouration of the tail corresponds to that of the back and gradually decreases towards the ventral side. The snout is rounded in dorsal view and pointed in lateral view. The anteroventral oral disc has marginal papillae only on the lateral and ventral edges. The anterior lip forms the upper lip and is evenly wide, the oral disc is not notched at the edge. The labial tooth rows A1 and A2 are absent due to the lack of an anterior oral region. P1 is normally fully developed, P2 is shorter, and P3 has no or very few teeth (Hoffmann 2010a).

### Husbandry and Captive Breeding of *Sachatamia albomaculata* B/C

All other species of *Sachatamia* spp. **X**, as to the best of our knowledge they have – with some exception of *S. illex* – not yet been kept in captivity. Information on husbandry are not available for *S. illex*. Husbandry and breeding parameters probably similar for many species.



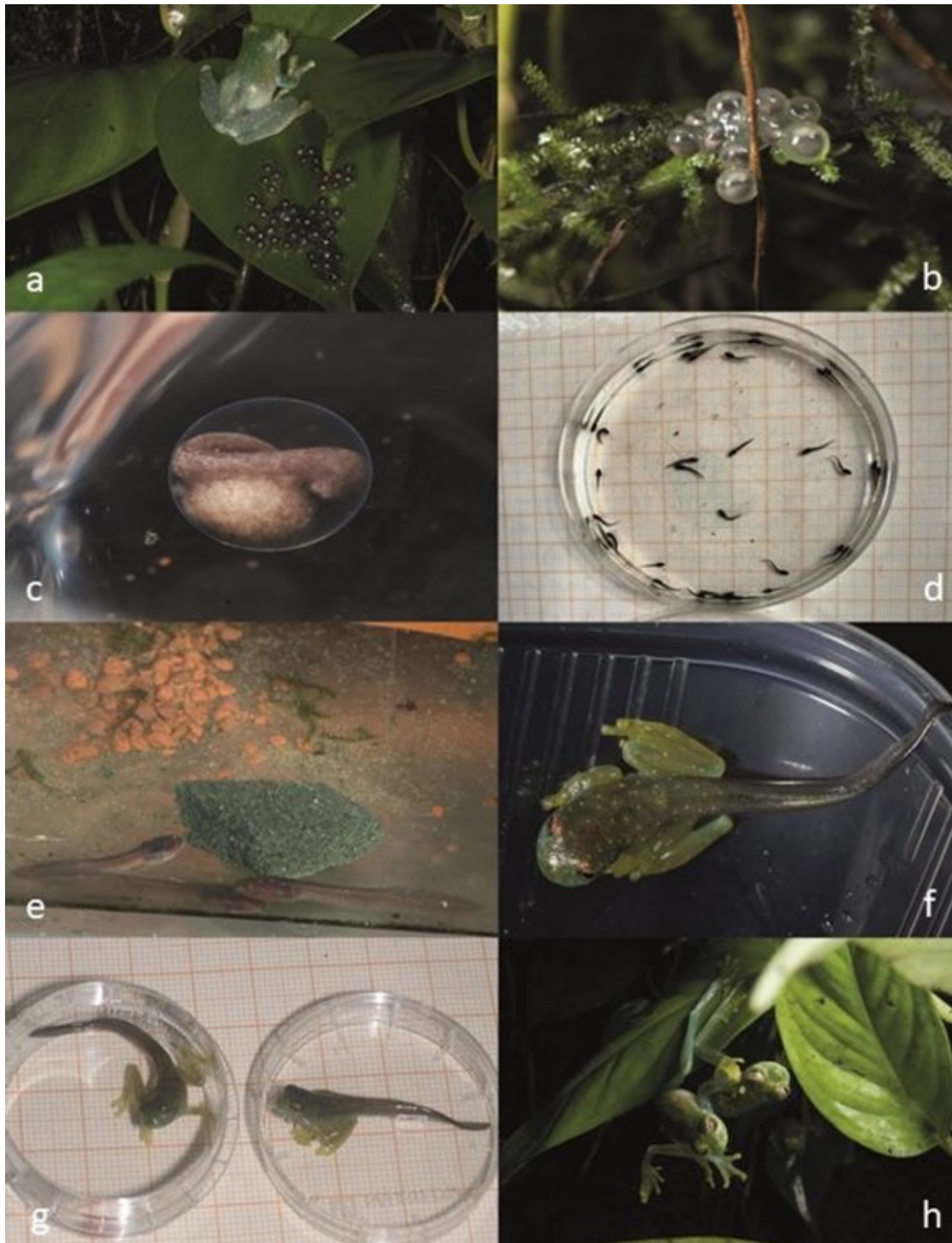


Fig. 56: *Sachatamia albomaculata* captive breeding

- a spawning (T. Eisenberg)
- b eggs are most often laid on upper leaf surfaces and rarely on moss or stones (T. Eisenberg)
- c embryonal development (M. Weber)
- d recently hatched larvae (T. Eisenberg)
- e larva, feeding (T. Eisenberg)
- f metamorphling, immediately after metamorphosis (T. Blees)
- g metamorphs of this species are much longer than most other centrolenid species (T. Eisenberg)
- h fighting in two male individuals (T. Eisenberg).

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Sachatamia albomaculata</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|--------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p>Accordingly, three participants stated that they were private owners. All were certain that the species had been correctly identified, whereby the species identification was usually carried out by the dealer or in collaboration with other specialists. All kept animals were labelled as captive-bred. The duration of husbandry was stated as &gt;2–12 years, in most cases a sex ratio of 2.2–6.2 was kept, all participants were aiming for successful offspring, all three were successful.</p> <p>Information on specific husbandry and captive breeding was provided as follows:</p> <p>Housing conditions (breeder animals):</p> <ul style="list-style-type: none"> <li>– Air and water temperature: 18–28°C   20–28°C   20–25°C.</li> <li>– Humidity: 70–100%   80–100%   70–90%</li> <li>- Lighting/type/day/night cycle: not specified   LED light bar and hourly 35 W full spectrum lamps with UV component   LED light bar (all: 12:12 hours).</li> <li>- Tank size (length x width x height in cm): 50 x 50 x 50   60 x 60 x 60   75 x 50 x 100 cm.</li> <li>- Percentage of water in the total area: 10%   5%   0%.</li> <li>- Substrate: Foam   no substrate, but lots of fist-sized river pebbles covered in moss   filter sponge, pine bark, leaves.</li> <li>- Furnishing/planting: <i>Philodendron</i>   <i>Philodendron</i>, <i>Anthurium</i> spp., <i>Monstera</i> spp., Vanilla plants, and various vines   <i>Philodendron</i>, <i>Anthurium</i> spp., bromeliads, and various vines.</li> <li>- Water depth: 4 cm   1–2 cm   0 cm.</li> <li>- Number of animals per container: not specified   8   4.</li> <li>- Food/feeding intervals: 1–2x/week   2x/week   every 3 days 1–2 x/ week   2 x/ week   every 3 days.</li> <li>- Supplementation (minerals/vitamins): not specified   Repashy Calcium plus   Ranarium Rana Vit, Dendrocare.</li> <li>- Aggression between several ♂♂ or ♀♀: more frequent, and strong between ♂♂   temporarily during the breeding season between ♂♂   none.</li> </ul> |
| Life expectancy                                                                                              | Maximum age of the animals kept: approx. 10 years   > 6 years   not specified.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Triggers for reproduction                                                                                    | <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): more humid husbandry and watering (n=2)   not clearly inducible, higher activity in the winter months, despite reduced watering.</p> <p>First offspring (CB) in the year: 2011   2018   2022.</p> <p>Frequency of CB since then: &gt;30 clutches   &gt; 50 clutches   2 clutches.</p> <p>Where are the eggs laid (leaves/panes/objects)? Leaves, panes   leaves, rarely stones (despite offer) or moss   leaves.</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom, tip of leaf)? <i>Philodendron</i>   <i>Philodendron</i>/<i>Anthurium</i> (all: always on the upper side of leaves).</p> <p>How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): Monolayer   monolayer (without additional jelly between the eggs), sometimes donut-shaped with central recess (see above)   monolayer.</p> <p>Number of clutches per ♀ in one egg laying: 1   1   1.</p> <p>Number of clutches/♀/year (min.-max.): 2–5   10–12   1–2.</p> <p>Number of eggs/clutch (min.-max.): 20–40   32–60 (n=10)   10–30.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Number of fertilised eggs per clutch (min.–max.)                                                             | 0–35   usually all   5–15.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |

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|-----------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Number of embryos hatched per clutch (min.–max.)                            | 0–35   nearly all   5–10.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Hatching rate (number of hatched larvae/number of eggs)                     | Number of hatched larvae/number of eggs or < 25%; 25–50%; > 50–75%; > 75%:<br>> 75%   > 75%   < 25%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Size of juvenile frogs (freshly metamorphosed; min.–max. [in mm])           | 8–10 mm   17–18 mm   not specified.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Number of metamorphosed juvenile frogs per year                             | not specified   0–50   5.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Number of rearing losses up to the 3 <sup>rd</sup> month                    | not specified   <sup>15</sup>   1                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Husbandry conditions (larvae)<br>/Technical requirements for larval rearing | <p>The general parameters for rearing the larvae are described above in the general section.</p> <p>The larvae of <i>S. albomaculata</i> are omnivorous. Small frogs can initially be housed in small rearing containers and transferred to larger terraria as they grow (Eisenberg in prep., Papenfuss &amp; Eisenberg in prep.).</p> <p>Total length of newly hatched larvae: 8–10 mm   8–10 mm   not specified.</p> <p>Duration of larval period (oviposition to metamorphosis; min.–max.): not specified   6–11   6–7 months.</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements):</p> <ul style="list-style-type: none"> <li>– Water temperature: 22–28°C   22–28°C   20–25°C.</li> <li>– Lighting/type/day/night cycle: Daylight   50 W LED strip   daylight.</li> <li>– Tank size (length x width x height in cm): 40 x 20 x 20 cm   50 x 13 x 29 cm   30 x 20 x 20 cm.</li> <li>– Substrate/furnishings/planting: not specified   lava granules   lava granules or no substrate at all, clay bricks and flower pots as hiding places, Java moss   lava granules in various grain sizes, foliage, river pebbles.</li> <li>– Water depth: 18 cm   17 cm   20 cm.</li> <li>– Number of animals per tank: 10–50   5–100   5–30.</li> <li>– Filter (type, capacity): Airlift sponge filter   Airlift sponge filter   Dennerle Nano corner filter, 2 W.</li> <li>– special requirements (e.g. water values): acidified with humic acids   regular water changes (1–2 x/ week in the case of the author) appear to be of particular relevance, otherwise increased mortality among the tadpoles. Also a stronger filter in bigger tadpoles   not specified.</li> <li>– Larval food: spinach, Repashy fish food   spinach, Repashy fish food, Tetramin catfish tablets   food tablets for carnivorous and herbivorous fish, cooked mushrooms, spinach, lettuce.</li> <li>– Frequency of water changes: 1 x/ month   90% 1–2 x/ week   50–80% 1 x/ week.</li> <li>– Type of water (rainwater, tap water, RO water, etc.): 50% reverse osmosis (RO) water: 50% tap water   100% tap water   90% RO water: 10% tap water.</li> </ul> |

<sup>15</sup> not measurable due to group rearing of many clutches in a complex aquarium, practically no rearing losses after metamorphosis.

|                                                                         |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|-------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Number or percentage of offspring that become adults or sexually mature | Not specified   after metamorphosis > 95%   80%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Age/size at sexual maturity                                             | ♂♂: not specified   10–12 moths   not specified.<br>♀♀: not specified   12–15 months   not specified.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Indicators for reaching sexual maturity                                 | Transabdominally visible ovaries/seminal ducts   Transabdominally visible dark follicles in front of the cloaca/seminal ducts, call of the ♂♂, from 16–18 months larger SVL of the ♀♀   calls, ovaries.                                                                                                                                                                                                                                                                                                                                                                                                  |
| Sex ratio of the offspring (♂♂:♀♀)                                      | not specified   no sufficient data basis, in one case 6:0 at n=6   1:1.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Evidence of deformities or diseases                                     | occasionally rickets   no deformities (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Mortality of larvae up to metamorphosis                                 | Mortality of larvae up to metamorphosis (< 25%; 25–50%; > 50–75%; > 75%) or estimated: high/low:<br>~50%   from < 25% to > 75%, the cause of these unsatisfactory losses appears to be related to a low water change frequency. Although no deviations in the water quality could be detected with the aid of water chemistry measurement tests, visible larval losses occurred repeatedly at protracted intervals, particularly among the oldest developmental stages. With weekly intervals, the losses were greatly reduced to > 50–75% in the first few weeks, with no losses at later times.        |
| Mortality in the first months/years of life after metamorphosis         | low   low   low.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Routine testing for amphibian diseases and parasites                    | no   no   no.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Quarantine (type and extent)                                            | no   yes   no.<br>Small, sterile terrariums (e.g. 30 x 60 x 20 cm with front and lid wire gauze ventilation) with climbing plants ( <i>Philodendron</i> spp.) without substrate are suitable for this purpose. A moat with overflow serves as a water reservoir. The quarantine should last at least 8 weeks and up to 6 months. During this time, PCR tests are carried out for <i>Batrachochytrium dendrobatidis</i> , <i>Batrachochytrium salamandrivorans</i> , <i>Ranavirus</i> , <i>Chlamydia</i> and <i>Brucella</i> as well as coproscopic tests for parasites (T. Eisenberg, unpublished data). |
| General characteristics, difficulties with keeping and breeding         | General characteristics, difficulties with keeping and breeding: none   husbandry unproblematic, but a delicate species due to the above-mentioned larval losses   more susceptible to stress than other glass frogs.<br>Assessment of the frequency of husbandry: rare   very rare   very rare.<br>Personal assessment of the difficulty of husbandry: medium difficulty   high level   difficult (compared to other glass frogs).<br>Further comments: none in each case.                                                                                                                              |
| Frequency of private breeding and reproduction in zoos                  | An excerpt from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists 21 entries between 2005 and 2020 as keepers of <i>S. albomaculata</i> , including at least three zoos and three private keepers. The status of most husbandries is unclear/unknown/extinct, with only one zoo in the USA listing 128 living individuals (T. Eisenberg, unpublished data).                                                                                                                                                                                                             |
| Reproduction in captivity up to F2                                      | yes   yes   yes.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

## generation

Commercial breeding no | no | no.

Interviews/ Surveys/ Consultations 3 private breeders participated and answered to the questionnaire.

**Teratohyla Taylor, 1951**

| Species                       | Original description                  | Common name                                                              | Common name international    | Known/ documented in international trade |
|-------------------------------|---------------------------------------|--------------------------------------------------------------------------|------------------------------|------------------------------------------|
| <i>Teratohyla adenocheira</i> | (Harvey & Noonan, 2005)               |                                                                          |                              | No                                       |
| <i>Teratohyla ameliae</i>     | (Cisneros-Heredia & Meza-Ramos, 2007) | Amelia's Glassfrog                                                       |                              | No                                       |
| <i>Teratohyla midas</i>       | (Lynch & Duellman, 1973)              | Midas' Glassfrog, Santa Cecilia Cochran Frog, Centrolène à Points Jaunes | Rana de cristal del Aguarico | No                                       |
| <i>Teratohyla pulverata</i>   | (Peters, 1873)                        | Dusty Glassfrog, Chiriqui Glass Frog                                     |                              | Yes                                      |
| <i>Teratohyla spinosa</i>     | (Taylor, 1949)                        | Dwarf Glassfrog, Spiny Cochran Frog, Minute Spiny Glassfrog              | Rana de cristal de Espinosa  | Yes <sup>16</sup>                        |

**Morphology and Taxonomy**

The genus name *Teratohyla* is derived from the Greek 'teras', which means monster, riddle or wonder, and the word 'hyla', which is traditionally associated with tree frogs and goes back to the mythological Greek boy Hylas. Phylogenetically, this genus embodies the clade of the common lineage of the two species *Centrolenella spinosa* Taylor, 1949 and *Hyla pulverata* Peters, 1873. The sister genus in this case is uncertain, the results of different genetic analyses (ML, Bayes) of the mitochondrial dataset support a clade consisting of the genera *Teratohyla* and *Rulyrana*. The topology of the analysis of nuclear genes shows *Teratohyla* as a sister taxon to a clade consisting of the genera *Chimerella*, *Espadarana*, *Cochranella*, *Rulyrana* and *Sachatamia*, but with only a weak level of coverage.

<sup>16</sup> an excerpt from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists no keepers for *T. pulverata* and four keepers (only one active husbandry in the USA) of *T. spinosa* until 2021 (T. Eisenberg, unpublished data)





Fig. 57: *Teratohyla* species

- a *T. midas*, Peru (J. Köhler)
- b *T. midas* (W.E. Duellman. Courtesy of University of Kansas Digital Archive, KUDA 001174)
- c *T. pulverata* (T. Leenders)
- d *T. pulverata* (T. Eisenberg)
- e *T. spinosa* (F. Hulbert)
- f *T. spinosa*, Costa Rica (T. Eisenberg).

Members of the genus can be distinguished by the following characteristics: (1) humeral spines absent in adult ♂♂, (2) liver covered with a translucent (*T. adenocheira* [partially], *T. midas*, *T. spinosa*) or white (*T. pulverata*, *T. amelia*) liver peritoneum, digestive tract translucent (*T. spinosa*) or white (*T. adenocheira*, *T. amelia*, *T. midas*, *T. pulverata*), (3) ventral parietal peritoneum white in the anterior region (anterior) and transparent in the posterior region (posterior) (*T. adenocheira*, *T. midas*, *T. spinosa*) or completely transparent (*T. amelia*, *T. pulverata*), (4) moderate to strong interdigital membranes between fingers III and IV, (5) bones pale to dark green in life, (6) dorsum cream-coloured, lavender to dark lavender in preservative, with or without spots, (7) dentary process of vomer present, with or without denticles,

(8) ♂♂ call from the upper sides of the leaves, ♀♀ lay their eggs on the leaf tips (*T. pulverata*) or along the margins of the undersides of the leaves (*T. spinosa*), (9) prepollex protruding (*T. spinosa*) or not protruding (*T. adenocheira*, *T. amelie*, *T. midas*, *T. pulverata*). By the presence of a ventral parietal peritoneum that is white anteriorly and transparent posteriorly, a liver covered by a transparent hepatic peritoneum, moderate to extensive interdigital membranes on the hands and the absence of humeral spines, *T. adenocheira*, *T. spinosa* and *T. midas* resemble the species of *Sachatamia* and *Rulyrana*; however, *T. spinosa* is small (SVL < 21 mm) and has a distinct, spiny prepollex that is clearly separated from finger I, and *T. adenocheira* and *T. midas* have a white digestive tract. The other two species of the genus *Teratohyla*, *T. pulverata* and *T. amelie*, have a completely transparent ventral parietal peritoneum and a white hepatic and visceral peritoneum and can be confused with *Hyalinobatrachium*, *Vitreorana* and *Chimerella*. The species of the genus *Hyalinobatrachium*, however, have white bones (for exceptions see chapter *Hyalinobatrachium*) and a cream-coloured dorsal colouration (lavender-coloured in *Teratohyla*); the ♂♂ of *Chimerella* have a small humeral spine (absent in *Teratohyla*), and the species of the genus *Vitreorana* (for exceptions see chapter *Vitreorana*) have white bones (absent in *Teratohyla*). The species of the genus *Vitreorana* (for exceptions see chapter *Vitreorana*) are restricted to the Cordillera de la Costa of Venezuela, the Guiana Shield and the Atlantic Rainforest of Brazil (*Teratohyla* is restricted to Central America, the Pacific and the Amazon lowlands of South America, only *T. midas* reaches French Guiana). The clade *Teratohyla* is one of the few examples within the family Centrolenidae in which the uplift of the Andes is assumed to be the cause of allopatric speciation. According to this dating, the Eastern Cordillera formed a continuous area between 12.9 and 11.8 million years ago, but probably became an important barrier for lowland species during the early Pliocene (5.3–3.6 million years ago). If this dating is correct, the sister species of *Teratohyla* evolved independently over a long period of time. Despite this long isolation, the general morphology of the sister species (*T. midas* and *T. spinosa*; *T. pulverata* and *T. amelie*) has been maintained. Moreover, the sister species still inhabit the lowlands (< 1,000 m) of the tropical rainforests on opposite sides of the Andes, suggesting that the niche has been preserved. The monophyly of *Teratohyla* is supported by the mitochondrial (Bayes), nuclear (Bayes and ML) and complete (Bayes, ML, MP) datasets (Guayasamin et al. 2009).

Many species of this group are comparatively similar, but can be distinguished from other genera (molecular identification is recommended for unequivocal species identification):

*Teratohyla adenocheira*: small to medium-sized glass frog with green dorsal colouration and yellow spots, skin glands white and scattered over the entire body, these fuse to form white folds on the lips, dorsal skin and throat smooth, ventral skin weakly areolate, white glands below the cloaca, paired enlarged tubercles and para- and subcloacal folds absent, arms short, upper arms slender compared to forearms, smooth skin folds along postaxial edge of forearm, hand and foot, prepollex not enlarged and without spines, finger I much longer than finger II, iris yellowish green, SVL ♂♂ 22.0–23.1 mm, ♀♀ 24.0–27.7 mm, head wider than body, eyes large and widely spaced, mouth region round in dorsal view, blunt in profile, dentary process of vomer and denticles present, lower three quarters of the tympanic membrane and tympanic ring clearly visible, parietal peritoneum and pericardium white, visceral peritonea of the gonads, stomach and large intestine white, urinary bladder translucent, liver trilobed (the posterior part of the left lobe of the liver is visible through the ventral skin. Taxonomic note: *T. midas* (sister species; Harvey & Noonan 2005, Guayasamin et al. 2020).

*Teratohyla ameliae*: small glass frog with uniform green to bluish green dorsal colouration, numerous melanophores on all fingers and toes, upper lip white, throat greenish, other ventral surfaces transparent, dorsal skin texture chagrined, ventral and subcloacal surfaces granular, a pair of enlarged subcloacal tubercles, small, non-enameled ulnar fold, low, non-enameled inner tarsal fold, obscured prepollex, finger I longer than finger II, iris cream-brown, SVL ♂♂ 18.1–19.3 mm, ♀♀ unknown, mouth region blunt in dorsal view, rounded in profile, dentary process of vomer without denticles, tympanic ring distinct, dorsolaterally orientated and inclined posteriorly, completely transparent ventral parietal peritoneum, all visceral peritonea (including heart) covered with iridophores, liver white, bulbous (Cisneros-Heredia & Meza-Ramos 2007, Twomey et al. 2014, Guayasamin et al. 2020).

*Teratohyla midas*: small to medium-sized glass frog with green dorsal colouration with or without small yellow dots, usually concentrated on the upper flanks, upper lip and anterior ventral side white, transparent posteriorly, dorsal skin smooth, ♂♂ with tiny spines visible only under magnification (250 x), ventral skin areolate, a pair of enlarged subcloacal tubercles, melanophores usually cover fingers and toes, ulnar and tarsal folds absent, concealed prepollex, finger I slightly longer than finger II, iris silvery-white with pale yellow tint, faint brown transverse stripe and grey reticulate pattern, yellow ring around the pupil, SVL ♂♂ 19.0–22.5 mm, ♀♀ 20.9–26.8 mm, mouth region blunt in dorsal view, blunt to bluntly rounded in profile, vomer with dentary process bearing 0–4 denticles (denticles always present in ♀♀), tympanic membrane moderately large, almost vertically aligned, with slight lateral and posterior inclinations, only the upper edge of the tympanic ring is covered by supratympanic fold, white parietal peritoneum covering the anterior 40–50% of the abdomen, white pericardium and gastrointestinal peritoneum, translucent peritonea on lobed liver, gall bladder and urinary bladder. Similar species: *Nymphargus cariticommatatus*, *Nymphargus siren*, *Nymphargus humboldti*, *Rulyrana flavopunctata* (Lynch & Duellman 1973, Twomey et al. 2014, Guayasamin et al. 2020, Gagliardi-Urrutia et al. 2022).

*Teratohyla pulverata*: medium sized glass frog with green dorsal colouration with tiny (as if powdery) white spots and dots, upper lip white, small white dots visible under the eye, dorsal skin chagrined, ♂♂ with tiny spines visible only under magnification (250 x), ventral skin granular, without a pair of enlarged subcloacal tubercles, melanophores partially covering the dorsal surface of finger IV, absent on fingers I–III, ulnar, metacarpal, metatarsal and tarsal folds with low, enamelled tubercles present, obscured prepollex, fingers I and II about the same length, iris greyish white with thin dark grey reticulated lines and tiny yellow spots, yellow to cream-coloured ring around the pupil, SVL ♂♂ 22.0–24.5 mm, ♀♀ 25.3–28.3 mm, mouth region rounded in dorsal view, sloping in lateral profile, vomer with dentary process bearing two to four teeth, tympanic membrane visible, relatively small, tympanic ring visible, with the exception of the upper margin which is covered by the supratympanic fold, completely transparent ventral parietal peritoneum, white liver and gastrointestinal peritonea (heart, liver, digestive tract, testes and gall bladder covered in white, urinary bladder and kidneys transparent). Similar species: *T. ameliae* (sister species; Savage 2002, Kubicki 2007, Guayasamin et al. 2020).

*Teratohyla spinosa*: small glass frog with uniform green dorsal colouration, dorsal skin smooth, without spines, ventral skin smooth to slightly areolate, missing pair of enlarged subcloacal tubercles, melanophores only on dorsal surfaces of finger IV (sometimes finger III) and toes IV and V, ulnar fold low, tarsal folds absent, prepollex spiny (name *spinosa*), which is clearly set off from finger I, extensive interdigital membranes between fingers III and IV and the toes,

finger I slightly longer than finger II, iris silvery-white to yellowish white, with distinct black reticulation, SVL ♂♂ 18.0–19.7 mm, ♀♀ 19.7–20.7 mm, mouth region truncated in dorsal view, truncated to slightly protruding in lateral profile, vomer with tooth-like projections bearing or lacking denticles, tympanic membrane with pronounced lateral inclination, upper edge of the tympanic ring covered by supratympanic fold, white parietal peritoneum of the anterior 50–60% of the abdomen, white pericardium, no iridophores in the peritonea covering the intestines, stomach and kidneys, transparent peritoneum around lobed liver, gall bladder and urinary bladder. Similar species: *Sachatamia ilex*. Taxonomic note: Type species of the genus, sister species to the clade *T. midas* and *T. adenocheira* (speciation probably due to uplift of the Andes) (Savage 2002, Kubicki 2007, Guayasamin et al. 2020).

### Distribution and Habitat

The genus *Teratohyla* occurs in the lowlands of Central America and in the Pacific and Amazonian lowlands of South America below 1,000 m (Guayasamin et al. 2009).

*Teratohyla adenocheira*: known from the extreme north-eastern tip of Santa Cruz, Bolivia, in the Serranía de Huanchaca, Parque Nacional Noel Kempff Mercado. The species is also widespread in Brazil in northern Mato Grosso, in extreme south-western Pará on the border with Mato Grosso and in eastern Rondônia (130–350 m asl). The Serranía de Huanchaca is a sandstone cliff of the Brazilian Shield. Mean annual temperature at the type locality 25–26°C (annual fluctuations between 3 and 38°C), average annual precipitation 1,400–1,500 mm, dry season from June to August. At the time of the original description, it was assumed that this frog probably requires pristine aquatic habitats and primary rainforest with a closed canopy. However, one specimen was found in secondary forest on the trunk of a palm tree. Individual specimens were also encountered on vegetation along a sandy stream bed whose watercourse had seasonally receded to pools. It is assumed that this is a stream spawner with fossorial larvae.

*Teratohyla ameliae*: eastern Andean foothills from central Ecuador (Pastaza province) to central Perú, approximately between 1–7° south latitude, with an isolated record in southern Perú (near Puerto Maldonado, Tambopata province) (349–1,037 m asl). The species inhabits primary and secondary tropical lowland rainforests. Outside the reproductive season, the species appears to live in the forest canopy; during the breeding season, it may use temporary (seasonal) springs and streams with running water (Cisneros-Heredia & Meza-Ramos 2007, Twomey et al. 2014).

*Teratohyla midas*: Amazon basin in northeastern Ecuador, eastern Perú, southern Colombia (Amazonas and Caquetá), French Guiana and in Brazil in western Rondônia, Amazonas, Amapá and western Acre, probably also found in northern Amazonian Bolivia (0–600 m asl). Habitat in primary and secondary, even slightly disturbed tropical forests (including seasonally flooded forests). The individuals live on leaves and branches (Cisneros-Heredia & McDiarmid 2007, Twomey et al. 2014, Guayasamin et al. 2020).

*Teratohyla pulverata*: Caribbean slopes in northern and eastern Honduras and Nicaragua, Pacific slopes and lowlands in Costa Rica and Panama to the departments of Chocó and Valle del Cauca in Colombia and northwestern Ecuador, provinces of Esmeralda and Pichincha, from sea level to 960 m asl. Habitat in riparian vegetation in humid primary forests of the lowlands and mountains. Salazar-Saavedra et al. (2017) describe an impressive infestation with four fly larvae from the Sarcophagidae family (dorsal myiasis), which were also visible ventrally.

*Teratohyla spinosa*: Caribbean slopes in the north-east of Honduras, Nicaragua and Costa Rica, Pacific slopes of Costa Rica, along the lowlands through western Colombia to the northern and central Pacific lowlands of Ecuador (0–800 m asl). Habitat along streams in the low vegetation of the humid primary forest in the lowlands. The species is observed in bushes and trees along riverbanks. The species has not been found in degraded areas.

### Conservation Status and Main Threats

#### IUCN Red List Status

*Teratohyla adenocheira*: LC (Least Concern, assessed 2021-04-13)

*Teratohyla ameliae*: LC (Least Concern, assessed 2018-03-20)

*Teratohyla midas*: LC (Least Concern, assessed 2021-04-13)

*Teratohyla pulverata*: LC (Least Concern, assessed 2019-09-04)

*Teratohyla spinosa*: LC (Least Concern, assessed 2019-09-05).

#### Red List Status in the Range Countries

##### Central America

Environmental Vulnerability Score Category (Johnson et al. 2015)

*Teratohyla pulverata* – M (Medium)

*Teratohyla spinosa* – M (Medium)

##### Costa Rica

All Centrolenidae of Costa Rica are classified as LC (Not Endangered) (Chaves et al. 2014).

##### French Guiana

La Liste rouge des espèces menacées en France. Faune vertébrée de Guyane – Amphibiens et Reptiles (MNHN, UICN France & Biotope 2018).

*Teratohyla midas* LC – Least Concern

#### Threats

The main threats are listed as possible habitat loss due to water management activities, agriculture and forestry, deforestation, slash-and-burn agriculture and human settlements. Other potential threats include local application of pesticides, fertilisers and pollution, disease, climate change and increased UV-B radiation.

*Teratohyla adenocheira*: in view of the wide distribution, the presumably large population and the remaining suitable habitats throughout the species' range, it is not categorised as endangered. However, habitat degradation and fragmentation is occurring in its range due to human activities, particularly livestock farming and agriculture. Originally, this species appeared to be rare, as no individuals were found on numerous subsequent visits after the original description. However, the renewed records from 2009 and 2012 revealed an extension of the occurrence as far as Brazil, and the larger range may indicate that this species may have a larger population than previously thought. In Bolivia, the species is probably very rare. Due to the continuing deterioration in the quality and extent of its habitat, populations are thought to be



declining (Toledo et al. 2009, de Oliveira et al. 2012, Bolivia Red List Assessment Workshop 2019).

*Teratohyla ameliae*: due to its relatively wide distribution, tolerance to a certain degree of habitat change and the presumably large overall population, the species is not classified as endangered. All known sites in Perú are close to roads, and the sites in the Amazon region correspond to secondary forests and overgrown cocoa plantations, so a certain degree of tolerance to disturbance is confirmed. There are no known major threats to this species, although habitat destruction by agriculture is evident in nearby areas. The species is known from fewer than 15 specimens and its population status is unknown. Although there are no estimates of relative abundance, the species appears to be rare even in the places where it has been found. In northern Perú (Amazonas), it has been recorded on several visits at least one year apart, so it is more common there compared to southern Perú (Cusco), where it appears to be a very rare species (Cisneros-Heredia & Meza-Ramos 2007, Twomey et al. 2014).

*Teratohyla midas*: due to its wide distribution, the presumably large population and the remaining suitable habitats throughout its range, the species is not classified as endangered. There are no major threats; it is a widespread, adaptable species that still has large areas of suitable habitat. The overall population status is considered stable.

*Teratohyla pulverata*: not classified as endangered in view of its wide distribution and presumably large population. Habitat loss due to deforestation and water pollution are local threats, but no major threats have been described for this species.

*Teratohyla spinosa*: not classified as endangered due to its wide distribution and presumably large population. The main threats are deforestation for agricultural development, logging and human settlement, and pollution from herbicide and pesticide use. The population is currently considered stable.

## Reproduction

| Topic                       | Details on the reproduction of <i>Teratohyla</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|-----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | ♂♂ call from a singular subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Sexual maturity             | Not specified in literature, probably at 6–12 months like many other Centrolenidae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Calls                       | <p><i>T. ameliae</i>: ♂♂ call from the tops of the leaves (next to their clutches). The calls are emitted every 10–30 s. Each call consists of a single pulsed tone lasting 0.011–0.014 s; each call has three to four pulses. The dominant frequency is between 4,984–7,085 Hz.</p> <p><i>T. midas</i>: ♂♂ calls from the tops of the leaves. The calls are emitted in series, 16 calls were recorded in 3 minutes, call pauses of 10.2–15.1 s, each call is short and consists of a single tone that has a length of 0.073–0.092 s (or 0.15–0.16 s). The tones usually consist of three or four well-differentiated pulses. The predominant frequency peaks at 7,210–7,390 Hz (or 7,030–7,060 Hz; Twomey et al. 2014, Guayasamin et al. 2020).</p> <p><i>T. pulverata</i>: ♂♂ call from the upper side of the leaves. The call consists of a rapid high-pitched ‘tik’, which is usually repeated several times with a pause of about 1 s between calls, the dominant frequency is 5,700–6,200 Hz (Kubicki 2007).</p> <p><i>T. spinosa</i>: ♂♂ call from the tops of the leaves, each call (every 12–35 s) usually has two pulsed tones (range 1–3 tones, 5–15 pulses per tone; described to the human ear as ‘creep, creep, creep’, followed by a longer pause), the dominant frequency is 6,469–6,937 Hz (or 6,800–7,200 Hz; Guayasamin et al. 2020).</p> |

|                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|-------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mating and spawning                 | <p>All species: axillary amplexus in the vegetation above small forest streams.</p> <p><i>T. amelie</i>: clutches are deposited in a single layer on the upper surfaces of <i>Heliconia</i> leaves about 80 cm above small streams in unspoilt lowland evergreen forests.</p> <p><i>T. midas</i>: the species has been found throughout the year on leaves of bushes, shrubs and trees along small streams in the Amazon rainforest, depositing eggs on the upper surface of leaves along streams. Amplexus started with the axillary and nuchal position for about 150 min, during which time the ♀♀ moved over several leaves or branches with the ♂♂ on their backs, searching for potential oviposition sites. As soon as egg-laying began, the ♂♂ made circling movements with their hind legs until the ♀♀ had laid all their greenish eggs. Then the ♂♂ left the site and the ♀♀ lifted their abdomen twice, moving backwards until they covered the eggs and remained in this position for about 60 minutes ('brooding', hydration). A total of 25 clutches were recorded at an average height of <math>2.9 \text{ m} \pm 1.7</math> (1.1–7.0 m). All clutch substrates were leaves with an average size of <math>8.0 \text{ cm width} \pm 12.1</math> (2.5–60.0 cm, <math>n=21</math>) and <math>20.0 \text{ cm length} \pm 25.8</math> (2.9–103.0 cm, <math>n=21</math>). The clutches contained an average of <math>21.6 \text{ eggs} \pm 6.0</math> (12–38 eggs, <math>n=21</math>), and were on average <math>18.8 \text{ mm wide} \pm 19.0</math> (5.5–31.4 mm, <math>n=22</math>) and <math>23.6 \text{ mm long} \pm 23.1</math> (8.2–46.9 mm, <math>n=22</math>). Fifteen of the 25 clutches were observed on leaves of <i>Selaginella</i> sp. and a smaller number on other substrates (e.g. leaves of <i>Heliconia</i> sp., ferns; Diaz-Ricaurte et al. 2016, Guayasamin et al. 2020).</p> <p><i>T. pulverata</i>: clutches are laid on the upper side of the leaves, short-term maternal brood care (hydration) occurs. This reduces the mortality associated with dehydration, predation and fungal infections. In contrast to other glass frog eggs, the jelly surface is initially furrowed and fissured. The eggs are yellowish green in colour and are laid in a single layer on the upper surface of leaves. The colouring persists for the first five days of development, then changes to pink over the next five days and finally to darker shades of red during the remainder of the development period. The number of eggs per clutch was 23–59 eggs (<math>n=62</math>). The development from egg laying to hatching of the last egg took 6–24 days. There was a positive correlation between hatching and nocturnal rainfall. The survival rate per clutch was 85% to 4% (<math>n=59</math>); 42% of the clutches hatched without embryonic mortality. Embryo mortality was mainly caused by flooding (5% or 128 eggs). Desiccation caused mortality in July and August, while flooding caused mortality in September. Hatching of embryos in clutches with high mortality occurred earlier than that of embryos in clutches with low mortality, perhaps in response to avoiding fungal infection on rotting embryos or predation (Hawley 2006, Delia et al. 2017b).</p> <p><i>T. spinosa</i>: in contrast to other members of the genus, eggs are laid on the underside of the leaves near the leaf edge at a height of 0.5–2.5 m above the water and sometimes above the bank, short-term maternal care available (hydration). When laid, the eggs are greenish white, the embryos are initially yellow and become darker as they develop, reaching a dark grey, brownish or reddish-brown colour when they hatch. The clutches contain 15–25 eggs, with each egg and its jelly case having a diameter of 5–7 mm, clutch dimensions about <math>21 \times 25 \times 7 \text{ mm}</math>. ♂♂ sometimes injure themselves during territorial fights with the eponymous (<i>spinosa</i>) needle-pointed prepollex on the innermost finger. Such scratches are visible for many weeks and then heal, sometimes forming scars (Guayasamin et al. 2020, Barría et al. 2024).</p> |
| Reproductive season                 | <i>T. pulverata</i> : see table row Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Eggs/clutch, clutches/year          | <i>T. midas</i> , <i>T. pulverata</i> , <i>T. spinosa</i> : see table row Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Size of eggs and larvae at hatching | <p><i>T. pulverata</i>: egg size: 1.5 mm in diameter, coating (jelly): 2.5 mm in diameter (T. Eisenberg, unpublished data); size of the larvae: see also table row Mating and spawning.</p> <p><i>T. spinosa</i>: egg size: 2.5 mm in diameter, coating (jelly): 4–5 mm in diameter (T. Eisenberg, unpublished data); size of the larvae: see also table row Mating and spawning.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Development time                    | <i>T. pulverata</i> : see also table row Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |

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|----------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| from egg laying to metamorphosis | <i>T. spinosa</i> : see also table row Mating and spawning.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Details on the larvae:           | <p><i>T. pulverata</i>: at hatching (Gosner stage 24–25) the tadpoles have a dark red colouration due to the dorsal star-shaped pigment spots, the reddish viscera and musculature. Young larvae have an almost circular body cross-section, while later larval stages change to a typical flat shape. Tooth row formula: 2/3, A2 widely spaced in the centre with a wide gap, P3 is slightly shorter than the equally sized P1 and P2. The maxillary sheath forms a smooth arch and has pointed teeth, the mandibular sheath is smooth and V-shaped. Marginal papillae are present on both sides of the oral disc, the papillae are arranged in a single row, but have a wide dorsal gap on the upper lip, eye position dorsal (Hoffmann 2004, 2010a).</p> <p><i>T. spinosa</i>: at hatching in Gosner stage 25 total length about 11 mm, body elongate, depressed, oral disc ventral, nostrils and crescent-shaped eyes dorsal, spiraculum left lateral, cloacal opening median, tail long with rounded tip, caudal fin margin reduced, oral disc complete, medium sized, with a row of marginal papillae (21–45) lateral and ventral, wide dorsal gap over mouth, LTRF probably 2/3 (highly variable), but when rows are present, the tooth rows are weaker and sometimes irregular (A1 often not recognisable, A2 usually present but often only visible as traces of denticles at the lateral ends of the tooth ridge), jaw sheaths robust and well developed, upper broadly arched, lower V-shaped, both with sharp serrations along their entire length. Body and tail greyish brown dorsally, lighter ventrally, bright yellow yolk mass initially colours the posterior half of the body and covers the liver and intestines, tail musculature mostly brown except for a pale area anteroventrally, fin seams opaque with scattered dark spots (Starrett 1960, Hoffmann 2010a, Guayasamin et al. 2020).</p> |

### Husbandry and Captive Breeding of *Teratohyla pulverata* and *T. spinosa* B/B

All other species *Teratohyla* spp. **X**, as they have not yet been introduced into captivity. Husbandry and breeding parameters probably similar for many species.

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Teratohyla pulverata</i> and <i>T. spinosa</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
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| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p><i>T. pulverata</i>, <i>T. spinosa</i>: for general information on husbandry see in the introductory chapter for the Centrolenidae.</p> <p>Special notes on the genus <i>Teratohyla</i>: For hygienic rearing, removing the entire leaf from the terrarium has proved successful. For both species, incubation of the clutches is relatively simple in petri dishes in saturated humidity with horizontal storage. The clutch can remain on the leaf or it can be carefully detached from it with the fingers. In the Petri dish, the clutch should only be surrounded by a little water, never completely covered. Individual mouldy eggs, which are usually preceded by the death of the embryos, can be removed from the clutch with a scalpel, scissors or biopsy punch to prevent the fungal infection from spreading to the well-developing neighbouring eggs. The freed spoilt egg can then be sucked out together with the jelly using a syringe with a button cannula. While the husbandry of both species does not cause any difficulties, the induction of egg laying and thus breeding is somewhat more difficult with <i>T. spinosa</i> than with <i>T. pulverata</i>. In the latter, egg-laying often occurs spontaneously.</p> <p>The analyses of the keeper surveys yielded the following data:</p> <p><b><i>T. pulverata</i>:</b></p> <p>All four participants stated that they were private keepers. All participants were certain that the species was correctly identified, whereby the species identification was mostly carried out by the breeder in collaboration with other specialists or on the basis of their own expertise. With the exception of one source, whose animals were declared as wild-caught by the importer, all three other husbandries were labelled as captive-bred. One breeder kept his animals continuously from 1991 until today, the</p> |

others since 2014 and 2018, whereby only one husbandry ended in 2020 and thus after only two years, the other two breeders also continued the husbandry until today. Groups of 2.2, 2.3 or 3.3 animals were mostly kept. All keepers attempted breeding and usually received clutches one year after the start of husbandry, which were usually fertilised.

Information on specific husbandry and breeding conditions was provided as follows:

Housing conditions (breeding animals):

- Air and water temperature (°C): 18–28 | 20–28 | 21–26 | 23 (n=1 each), water section not specially heated in each case.
- Humidity (rel.%): 70–100 (n=4).
- Lighting/type/day-night cycle: LED light bar (n=2) | fluorescent lamps (n=2) and additionally 35 W full spectrum lamps with UV component (n=1) | daylight length 12–13 hours (n=4).
- Tank size (length x width x height in cm): 40 x 60 x 60 | 50 x 50 x 50 | 60 x 60 x 60 | 60 x 70 x 70 (n=1 each).
- Proportion of water in the total area (%): 0–100 (often as a moat, complete floor area can be flooded when sprinkling).
- Soil substrate: natural (clay, gravel), artificial (foam, soil mat, or no substrate, but many fist-sized moss-covered river pebbles (n=1 each).
- Furnishing/planting: *Philodendron* (n=4), as well as other tropical plants such as anthuriums, *Monstera* spp., vanilla, bromeliads (*Neoregelia* sp.), various vines, all of which grow epiphytically on cork, coconut, tree fern or Hygrolon® gauze sheets.
- Water depth (cm): 0–4 (n=4).
- Number of animals per container: not specified | 4 | 6 | 6–8 (n=1 each).
- Food/feeding intervals: food animals used were springtails, drosophila, firebrats, banded crickets, bean beetles and aphids, fed 1–2 x/ week (n=1) | 2 x/ week (n=1) | 2–3 x/ week (n=2).
- Supplementation (minerals/vitamins): yes, not specified (n=3) | Repashy Calcium plus (n=1).
- Aggression between several ♂♂ or ♀♀: not specified (n=1) | none (n=3).

#### ***T. spinosa*:**

Three keepers of this species took part in the survey. All were private keepers and very confident with the species identification based on the reasons given above. Again, one source stated that they had obtained animals declared as wild-caught, the others were captive-bred from the first source. The husbandries had existed since 2017, 2018 and 2021 and in each case up to the time of writing. Group sizes of 2.2, 3.3 and 5.3 animals were reported. All keepers attempted breeding, and two of them were successful two and four years later respectively; one keeper has not yet succeeded in breeding. The clutches were generally fully fertilised.

Information on specific husbandry and breeding conditions was provided as follows:

Keeping conditions (breeding animals):

- Air and water temperature (°C): 18–28 | 20–28 | 23, water section not specially heated in each case.
- Humidity (rel.%): 70–100 (n=3).
- Lighting/type/day-night cycle: LED light bar (n=2) or fluorescent lamps (n=1), daylight length 12–13 hours (n=3).
- Tank size (length x width x height in cm): 40 x 60 x 60 | 50 x 50 x 50 | 60 x 70 x 70.
- Proportion of water in the total area (%): 0–100 (often as a moat, complete floor area can be flooded during irrigation).
- Soil substrate: artificial (foam, soil mat) or no substrate, but many fist-sized moss-covered river pebbles (n=1 in each case).
- Furnishing/planting: *Philodendron* (n=3), as well as other tropical plants such as anthuriums, *Monstera* spp., vanilla, bromeliads (*Neoregelia* sp.), various vines, all of which grow epiphytically on cork, coconut, tree fern or Hygrolon® gauze sheets.

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|                                                  | <p>– Water depth (cm): 0–4 (n=3).</p> <p>– Number of animals per container: not specified   4   6   4–8 (n=1 each).</p> <p>– Food/feeding intervals: food animals used were springtails, drosophila, firebrats, banded crickets, bean beetles and aphids, fed 1–2 x/ week (n=1)   2 x/ week (n=1)   2–3 x/ week (n=1).</p> <p>– Supplementation (minerals/vitamins): yes, not specified (n=2)   Repashy Calcium plus (n=1).</p> <p>– Aggression between several ♂♂ or ♀♀: none (n=3).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Life expectancy                                  | <p>Maximum age of the animals kept (years):</p> <p><i>T. pulverata</i>: not specified (n=2)   6 (n=1)   8 (n=1).</p> <p><i>T. spinosa</i>: not specified (n=1)   5 (n=1)   8 (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Triggers for reproduction                        | <p><b><i>T. pulverata</i>:</b></p> <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): Rain chamber (with 2 x 4 h continuous sprinkling and 28°C water temperature; n=1)   sprinkling, spontaneous egg laying (n=3).</p> <p>First offspring (CB) in the year: 1992 (n=1)   2015 (n=1)   2019 (n=1)   2020 (n=1).</p> <p>Frequency of breeding since then (number of clutches): 2 to &gt; 50.</p> <p>Where are the eggs laid (leaves/panes/objects)? leaves (n=4)   panes (n=1).</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (upper side, lower side, tip of leaf)? <i>Philodendron</i>, <i>Monstera</i> spp.; upper leaf surface (n=3)   lower leaf surface (n=1).</p> <p>How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): initially adjacent, non-overlapping but connected eggs, monolayer, then swelling of the clutch to form a complex shape, which can then hang from the leaf (n=4).</p> <p>Number of clutches per ♀ in one oviposition: 1 (n=4).</p> <p>Number of clutches/♀/year (min.–max.): not specified (n=1)   1 (n=1)   2–5 (mostly spontaneous; n=2).</p> <p>Number of eggs per clutch (min.–max.): not specified   18–19   15–35   7–58 (n=7).</p> <p><b><i>T. spinosa</i>:</b></p> <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): not specified   irrigation   heavy irrigation, rarely spontaneous egg laying.</p> <p>First offspring (CB) in the year: not specified   2020   2021.</p> <p>Frequency of breeding since then (number of clutches): not specified   &gt;10 (n=2).</p> <p>Where are the eggs laid (leaves/panes/objects)? not specified   leaves (n=2).</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom, tip of leaf)? <i>Philodendron</i>, <i>Monstera</i> spp.; underside of leaves (n=2).</p> <p>How is the clutch structured? Single eggs, simple layer (monolayer), complex clutch, other (how?): not specified   complex   initially adjacent, non-overlapping but connected eggs, monolayer, then swelling of the clutch to a complex form, which can then hang down from the leaf.</p> <p>Number of clutches per ♀ in one oviposition: not specified   1 (n=2).</p> <p>Number of clutches/♀/year (min.–max.): not specified   2–5 (n=2).</p> <p>Number of eggs/clutch (min.–max.): not specified   10–20   11–23 (n=6)</p> |
| Number of fertilised eggs per clutch (min.–max.) | <p><i>T. pulverata</i>: not specified   18–19   0–35   usually &gt; 95%, clutches of individual ♀ generally infertile.</p> <p><i>T. spinosa</i>: not specified   0–20   usually &gt; 95%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Number of embryos hatched per                    | <p><i>T. pulverata</i>: not specified   17–19   0–35   usually &gt; 95%.</p> <p><i>T. spinosa</i>: not specified   0–20   usually &gt; 95%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |



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| clutch (min.–max.)                                                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Hatching rate<br>(number of<br>hatched larvae/<br>number of eggs)                      | <p>Number of hatched larvae/number of eggs<br/>or &lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%:<br/> <i>T. pulverata</i>: not specified   0–75%   &lt; 25–100%   usually &gt; 95%.<br/> <i>T. spinosa</i>: not specified   &gt; 50–75%   usually &gt; 95%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Size of juvenile<br>frogs (freshly meta-<br>morphosed; min.–<br>max. [in mm])          | <p><i>T. pulverata</i>: not specified (n=3)   5–8 (n=1).<br/> <i>T. spinosa</i>: not specified (n=2)   5–6 (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Number of meta-<br>morphosed juve-<br>nile frogs per year                              | <p><i>T. pulverata</i>: not specified (n=2)   20 (n=1)   40–60 (n=1).<br/> <i>T. spinosa</i>: not specified (n=2)   0–50 (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Number of rearing<br>losses up to the 3 <sup>rd</sup><br>month                         | <p><i>T. pulverata</i>: not specified (n=2)   low (n=1)   &lt; 1% (n=1).<br/> <i>T. spinosa</i>: not specified (n=2)   &lt; 1%<sup>17</sup> (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Husbandry condi-<br>tions (larvae)<br>/Technical<br>requirements for<br>larval rearing | <p><b><i>T. pulverata</i>:</b><br/> for general information on larval rearing see in the introductory chapter for the Cen-<br/> trolenidae.<br/> Total length of freshly hatched larvae (in mm): not specified (n=2)   5–7 (n=1)   7–8<br/> (n=1).<br/> Duration of larval period (oviposition to metamorphosis; min.–max. [in months]): not<br/> specified (n=3)   5–8 (n=1).<br/> Special conditions and requirements for larval rearing (including technology and daily<br/> time requirements):<br/> – Water temperature (in°C): not specified (n=1)   25 (n=1)   22–28 (n=2).<br/> – Lighting/type/day-night cycle: not specified (n=1)   Daylight (n=2)   50 W LED strip<br/> and daylight (n=1).<br/> – Container size (length x width x height in cm): not specified (n=1)   40 x 20 x 20   40<br/> x 30 x 30   50 x 13 x 29.<br/> – Substrate/furnishings/planting: not specified   sand, coarse gravel, leaves   1 cm<br/> cleaned gravel   no substrate, clay bricks and flower pots as hiding places, Java moss  <br/> lava granules of various grain sizes, leaves, river pebbles.<br/> – Water depth (in cm): not specified   15   17   18.<br/> – Number of animals per tank: not specified   18   10–50   &lt; 100.<br/> – Filter (type, capacity): not specified   Airlift sponge filter (n=3).<br/> – Special requirements (e.g. water values): not specified (n=3)   acidified with humic<br/> acids (n=1).<br/> – Larval food: various fish foods, spirulina tablets (n=1)   spinach, Repashy fish food,<br/> Tetramin catfish tablets (n=2)   algae, detritus, Repashy Super Green (n=1).<br/> – Frequency of water changes: not specified   90% 1 x/week   every 3–4 weeks, oth-<br/> erwise only topping up   1 x/month.<br/> – Type of water (rainwater, tap water, RO water, etc.): Tap water/Aqua dest. 1:1  <br/> 50% Reverse osmosis (RO) water: 50% tap water   100% tap water   100% rainwater.<br/> <b><i>T. spinosa</i>:</b><br/> for general information on larval rearing see in the introductory chapter for the Cen-<br/> trolenidae.<br/> Total length of freshly hatched larvae (in mm): not specified   5–6   9–11.<br/> Duration of larval period (oviposition to metamorphosis; min.–max. [in months]): not</p> |

<sup>17</sup> not measurable due to group rearing of many clutches in a confusing aquarium, practically no rearing losses after metamorphosis.

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|                                                                         | <p>specified (n=2)   3.5–8 (n=1).</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements):</p> <ul style="list-style-type: none"> <li>– Water temperature (in°C): not specified (n=1)   25 (n=1)   22–28 (n=1).</li> <li>– Lighting/type/day-night cycle: not specified (n=1)   Daylight (n=1)   50 W LED strip and daylight (n=1).</li> <li>– Container size (length x width x height in cm): not specified (n=1)   40 x 20 x 20   50 x 13 x 29.</li> <li>– Substrate/furnishings/planting: not specified (n=1)   no substrate, clay bricks and flower pots as hiding places, Java moss   lava granules of various grain sizes, foliage, river pebbles (n=1).</li> <li>– Water depth (in cm): not specified   17   18.</li> <li>– Number of animals per tank: not specified   10–50   &lt; 100.</li> <li>– Filter (type, capacity): not specified (n=1)   Airlift sponge filter (n=2).</li> <li>– Special requirements (e.g. water values): not specified (n=2)   acidified with humic acids (n=1).</li> <li>– Food of the larvae: not specified (n=1)   spinach, Repashy fish food, Tetramin catfish tablets (n=2).</li> <li>– Frequency of water changes: not specified   90% 1 x/week   1 x/month.</li> <li>– Type of water (rainwater, tap water, RO water, etc.): not specified   50% RO water: 50% tap water   100% tap water</li> </ul> |
| Number or percentage of offspring that become adults or sexually mature | <p><i>T. pulverata</i>: not specified   no data available, since the animals have been passed on to other keepers as subadults   20%   99%.</p> <p><i>T. spinosa</i>: not specified (n=2)   99% (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Age/size at sexual maturity                                             | <p><i>T. pulverata</i>: not specified (n=2)   25 mm   12–18 months.</p> <p><i>T. spinosa</i>: not specified (n=2)   8–12 months.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Indicators for reaching sexual maturity                                 | <p><i>T. pulverata</i>: not specified (n=2)   transabdominally visible ovaries, vasa deferentia, calls of the ♂♂ (n=2).</p> <p><i>T. spinosa</i>: not specified (n=1)   ovaries (n=1)   transabdominally visible ovaries, vasa deferentia, calls of the ♂♂ (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Sex ratio of the offspring (♂♂:♀♀)                                      | <p><i>T. pulverata</i>: not specified (n=3)   ~1:1 (n=1).</p> <p><i>T. spinosa</i>: not specified (n=2)   ~1:1 (n=1).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Evidence of deformities or diseases                                     | <p><i>T. pulverata</i>: not specified   none (n=2)   occasionally rickets.</p> <p><i>T. spinosa</i>: not specified (n=1)   none (n=2).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Mortality of larvae up to metamorphosis                                 | <p>Mortality of larvae up to metamorphosis (&lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%) or estimated: high/low:</p> <p><i>T. pulverata</i>: 50–75%   100%   high   low.</p> <p><i>T. spinosa</i>: not specified   25–50%   &lt; 1%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Mortality in the first months/years of life after metamorphosis         | <p><i>T. pulverata</i>: not specified (n=2)   low   &lt; 1%.</p> <p><i>T. spinosa</i>: not specified (n=2)   &lt; 1%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Routine testing for amphibian diseases and parasites                    | <p><i>T. pulverata</i>: no (n=3), annually <i>Batrachochytrium dendrobatidis</i> using PCR (n=1).</p> <p><i>T. spinosa</i>: no (n=3).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Quarantine (type and extent)                                            | <p><i>T. pulverata</i>: not specified (n=1)   yes, for 1 (n=1)   for 4–6 months (n=2).</p> <p><i>T. spinosa</i>: not specified (n=1)   yes, for 4–6 months (n=2).</p> <p>Small, sterile terrariums (e.g. 30 x 60 x 20 cm with front and lid wire gauze ventilation)</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |

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|                                                                 | <p>with climbing plants (<i>Philodendron</i> spp.) without substrate are suitable for this purpose. A moat with overflow serves as a water reservoir. The quarantine should last at least 8 weeks and up to 6 months. During this time, PCR tests are carried out for <i>Batrachochytrium dendrobatidis</i>, <i>Batrachochytrium salamandrivorans</i>, <i>Ranavirus</i>, <i>Chlamydia</i> and <i>Brucella</i> as well as coproscopic tests for parasites (T. Eisenberg, unpublished data).</p>                                                                                                                                                                                                                                                                                                                                                                                                                     |
| General characteristics, difficulties with keeping and breeding | <p><b><i>T. pulverata</i>:</b><br/> not specified (n=2)   require house crickets or banded crickets of appropriate size, firebrats, bean beetles – feeding only with flies leads to emaciation (n=2).<br/> Estimation of the frequency of captive husbandry: rare (n=4).<br/> Personal assessment of the difficulty of breeding in captive husbandry: not specified (n=2)   no (n=1)   resp. medium difficulty (n=1).<br/> Further remarks: not specified (n=4).</p> <p><b><i>T. spinosa</i>:</b><br/> Not specified (n=1)   require house crickets or banded crickets of appropriate size, firebrats, bean beetles – feeding only with flies leads to emaciation (n=1).<br/> Estimation of the frequency of captive husbandry: rare (n=2)   very rare (n=1).<br/> Personal assessment of the difficulty of breeding in captive husbandry: medium difficulty (n=3).<br/> Further remarks: not specified (n=3).</p> |
| Frequency of private breeding and reproduction in zoos          | <p><i>T. pulverata</i>: see assessment of the frequency of husbandry; an excerpt from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists no entries between 2008 and 2021 as holders of <i>T. pulverata</i> (T. Eisenberg, unpublished data).</p> <p><i>T. spinosa</i>: see assessment of the frequency of husbandry; an excerpt from the Zoological Information Management Software (ZIMS) dated 16 November 2023 lists four entries between 2008 and 2021 as holders of <i>T. spinosa</i> (T. Eisenberg, unpublished data).</p>                                                                                                                                                                                                                                                                                                                                                  |
| Reproduction in captivity up to F2 generation                   | <p><i>T. pulverata</i>: yes (n=2).<br/> <i>T. spinosa</i>: yes (n=2).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Commercial breeding                                             | <p><i>T. pulverata</i>: no (n=4).<br/> <i>T. spinosa</i>: no (n=3).</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Interviews/ Surveys/ Consultations                              | <p><i>T. pulverata</i>: 4 answers from private breeders about this species.<br/> <i>T. spinosa</i>: 3 answers from private breeders about this species.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |

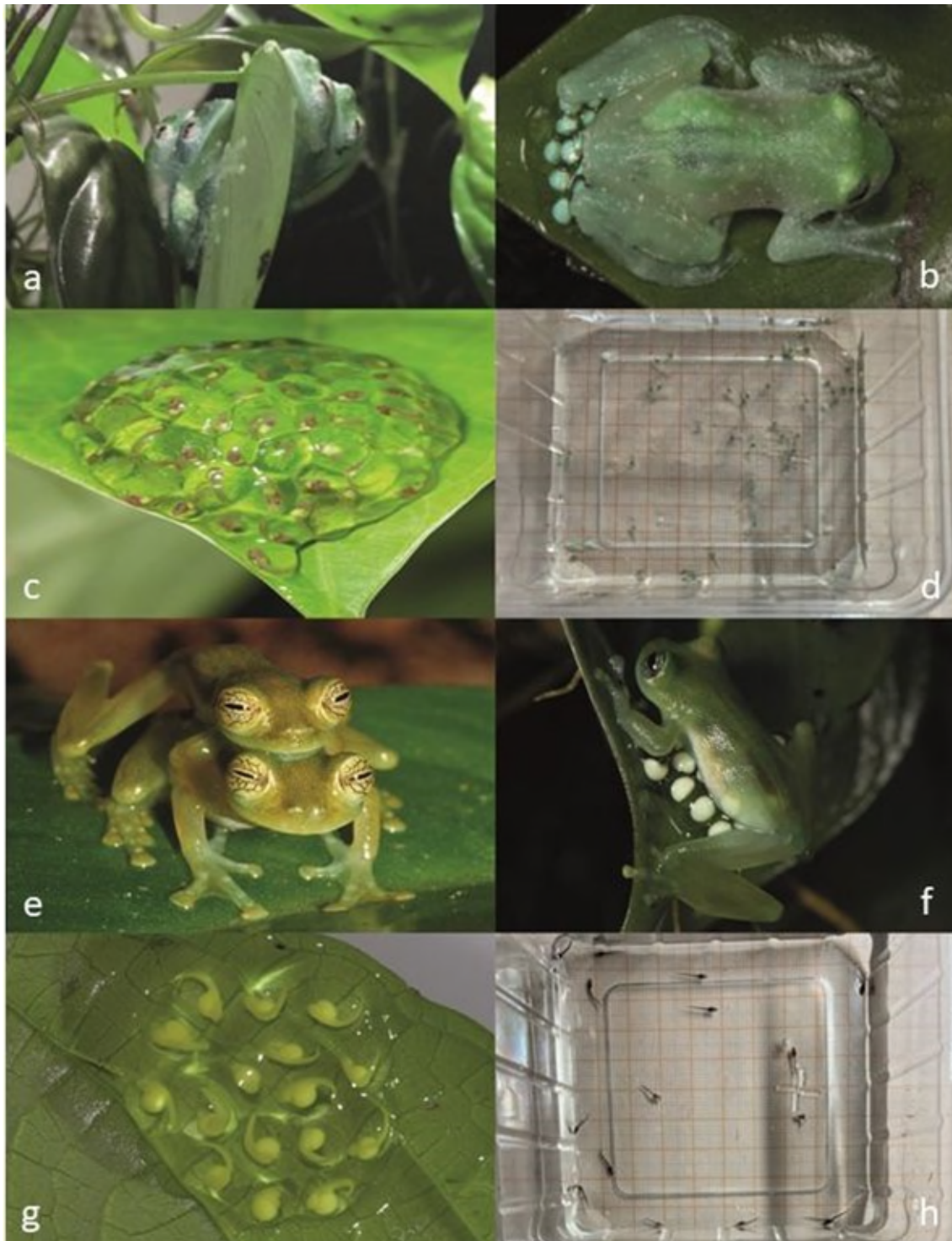


Fig. 58: *Teratohyla* breeding

- a *T. pulverata*, 2 pairs in amplexus in the terrarium (T. Eisenberg)
- b *T. pulverata* in the author's terrarium, ♀ after egg laying during short-term brood care ('brooding' to provide the clutch with moisture). Note that the follicles for the following clutch in the left ovary are visible dorsally through the skin (T. Eisenberg)
- c *T. pulverata*, clutch with developing larvae (T. Leenders)
- d *T. pulverata*, larvae (T. Eisenberg)
- e *T. spinosa* (K.-H. Jungfer)
- f *T. spinosa*, also in short-term brood care by the female (T. Eisenberg)
- g *T. spinosa*, Costa Rica, egg clutch (J. Sens)
- h *T. spinosa*, larvae (T. Eisenberg).

**Vitreorana Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009**

| Species                        | Original description                                                    | Common name              | Common name international                                                                    | Known/ documented in international trade |
|--------------------------------|-------------------------------------------------------------------------|--------------------------|----------------------------------------------------------------------------------------------|------------------------------------------|
| <i>Vitreorana antisthenesi</i> | (Goin, 1963)                                                            | Aragua Glass Frog        |                                                                                              | Yes                                      |
| <i>Vitreorana assuh</i>        | Zucchetti, Rojas-Padilla, Dias, Solé, Orrico & Castroviejo-Fisher, 2023 |                          |                                                                                              | No                                       |
| <i>Vitreorana baliomma</i>     | Pontes, Caramaschi & Pombal, 2014                                       |                          |                                                                                              | No                                       |
| <i>Vitreorana castroviejoi</i> | (Ayarzagüena & Señaris, 1997)                                           |                          | Ranita de Cristal de Castroviejo                                                             | No                                       |
| <i>Vitreorana eurygnatha</i>   | (Lutz, 1925)                                                            | Río Glass Frog           | Ra-de-vidro, perereca-de-vidro, pere-requinha-verde de ventre transparente com focinho curto | No                                       |
| <i>Vitreorana franciscana</i>  | Santana, Barros, Pontes & Feio, 2015                                    |                          |                                                                                              | No                                       |
| <i>Vitreorana gorzulae</i>     | (Ayarzagüena, 1992)                                                     | Bolivar Giant Glass Frog | Ranita de cristal de Gorzula                                                                 | No                                       |
| <i>Vitreorana helenae</i>      | (Ayarzagüena, 1992)                                                     | Venezuela Cochran Frog   |                                                                                              | No                                       |
| <i>Vitreorana parvula</i>      | (Boulenger, 1895)                                                       | Lages Glass Frog         | Perereca-de-vidro                                                                            | No                                       |
| <i>Vitreorana ritae</i>        | (Lutz, 1952)                                                            | Rita's Glassfrog         | Rana de Cristal de Rita, perereca-de-vidro, Rana de cristal de puntos negros                 | No                                       |

**Morphology and Taxonomy**

The genus *Vitreorana* is characterised by the following features:

In the comprehensive revision of the Centrolenidae (Guayasamin et al. 2009), the genus *Vitreorana* was newly described on the basis of morphological and molecular data and found to be monophyletic. The genus, which belongs to the subfamily Centroleninae and the tribe Cochranellini, currently contains eleven species. Most *Vitreorana* spp. are characterised by the combination of a completely transparent ventral parietal peritoneum and the absence of humeral spines, a white visceral peritoneal covering over the liver (white hepatic peritoneum; only partially veiled in *V. ritae*) and the same over the gastrointestinal tract (white gastrointestinal peritoneum; opaque in *V. eurygnatha*). However, these features are not genus-specific, but are also present in members of the genera *Hyalinobatrachium*, *Chimerella* and some species of the genus *Teratohyla*. All *Vitreorana* spp. have green bones, lavender dorsal colouration in the preservative and lay their eggs mostly on upper leaf surfaces (exceptions *V. eurygnatha* and *V. parvula*, which lay eggs on upper and lower surfaces). In *Hyalinobatrachium*



spp. the bones are mostly white (green in *H. mesai* and *H. taylori*), preserved specimens are cream-coloured on the upper side, and oviposition always takes place on the underside of leaves. Although *Chimerella mariaelenae* resembles the species *V. gorzulae*, the two species are not closely related. *Vitreorana* differs from *Teratohyla* in its geographical distribution.



Fig. 59: *Vitreorana* species

- a *V. antisthenesi*, Palmichal, Colombia (César Barrio Amorós/Fundación AndígenA)
- b *V. castrovieji* (César Barrio Amorós/Fundación AndígenA)
- c *V. gorzulae* (César Barrio Amorós/Fundación AndígenA)
- d *V. helenae*, Chivatón, Colombia (César Barrio Amorós/Fundación AndígenA)
- e *V. parvula* (A. Kwet)
- f *V. parvula*, calling male in the habitat (A. Kwet).

The species in this group can be identified by the following combination of characteristics (although molecular identification is recommended for unequivocal species identification):

*Vitreorana antisthenesi*: medium-sized species (SVL ♂♂ 21.4–27 mm), mouth region blunt in profile, reticulation of iris purple to lavender, green ground colour with yellow spots, white peritoneum on gastrointestinal tract.

*Vitreorana assuh*: largest species of the genus, SVL 30.9 mm (♂♂) and 34.1 mm (♀♀), morphologically similar to *V. franciscana*, but with denticles on the vomer, enamelled iridophores on the pericardium, peritoneum on liver and urinary bladder.

*Vitreorana baliomma*: small, slender, dorsally leaf-green glass frog species with small white spots and SVL of 16.4–21.2 mm; ♀♀ with  $20.55 \pm 0.8$  mm on average slightly larger than ♂♂ ( $18.18 \pm 0.6$  mm), ventral side transparent, light green, organs covered by white peritoneum (iridophores), urinary bladder uncovered (in contrast to syntopic *Vitreorana* spp.), hands and feet yellow-green, smooth skin, mouth region truncated in top view, rounded in profile, head wider than long, single subgular vocal sac, horizontal pupil, round tympanum, fingers III > IV > I > II, weakly developed nuptial excrescences in ♂♂ on finger I, cream-coloured after preservation, lavender melanophores in the iris (in contrast to black to lavender reticulation in *V. eurygnatha* and *V. parvula*).

*Vitreorana castroviejoi*: green ground colour with yellow speckles, white peritoneum on gastrointestinal tract, lobed liver.

*Vitreorana eurygnatha*: small, smooth-skinned glass frog (SVL 17–23 mm), mouth rounded, upper lip fold absent, nostrils wide rostral, no teeth present on vomer, eyes prominent, pointing forwards, tympanum almost completely or partially concealed, single subgular vocal sac, large finger and toe discs.

*Vitreorana franciscana*: SVL 21.9–24.1 mm, leaf green ground colour with yellowish shading, hands and feet yellowish, slender body, mouth region slightly ovoid from dorsal, iris light brown with black reticulation, no teeth present on vomer, outer tarsal and ulnar ridges with low, small, thickened tubercles, cloacal region bordered by tubercles, white peritoneum on heart, liver, urinary bladder, kidneys and testes, bulbous liver, transparent peritoneum on gastrointestinal tract, no humeral spines in adult ♂♂.

*Vitreorana gorzulae*: small dark green glass frog (uniform or with tiny pale spots depending on population), SVL ♂♂ 19.2–22.5 mm, ♀♀ 20.9–22.0 mm, mouth region truncate in dorsal view, iris silvery copper-coloured with dark brown to black reticulum, small tympanum, no teeth present on the vomer, parietal peritoneum transparent except for a small white area, white peritoneum on heart, trilobed liver and other viscera, transparent peritoneum on urinary bladder, hands and feet green to blue-green, tips of fingers and toes yellow, ♂♂ bear humeral spines.

*Vitreorana helenae*: morphologically similar to *V. ritae*, iridophores cover parietal peritoneum in anterior third, white peritoneum on gastrointestinal tract.

*Vitreorana parvula*: small to medium-sized *Vitreorana* species (SVL 17–25.8 mm), grey-brown reticulated dorsal pattern with white speckles, dorsal skin smooth or weakly granulated, finger and toe discs truncate, larger than tympanum, glandular tissue on inner side of finger I, distinct forearm fold, mouth region round in dorsal view and spatulate-truncate in profile, head length corresponds to head width, upper lip with a skin fold, eyes aligned forwards (arranged latero-dorsally), tympanum small, covered on the upper side, diameter approx.  $\frac{1}{2}$ – $\frac{1}{3}$  of eye diameter,

♂♂ with single subgular vocal sac, abdomen smooth with transparent ventral side (parietal peritoneum) with visible but white-covered abdominal organs, liver bulbous. Taxonomic note: *V. uranoscopa* was recently transferred to the synonymy of *V. parvula* (Zucchetti & Castroviejo-Fisher 2024).

*Vitreorana ritae*: small glass frog (SVL 19 mm), large head, mouth region rounded and blunted, teeth present on vomer, large eyes (diameter [1 mm] has same length as distance mouth tip to eye), frontally orientated, upper eyelid black, tympanum very small (almost 1/4 of eye diameter), short groin from posterior corner of eye reaches above tympanum, fingers without intermediate membranes, finger discs very large (1 mm), legs very long and broad, smooth skin, colour in alcohol pale yellow with black dots on head and pelvic region. Taxonomic note: *V. oyampiensis*, once synonymised by Guayasamin et al. (2009), is still regarded as a separate species and not as a synonym according to other authors (Fouquet et al. 2019), but this requires a final revision.

### Distribution and Habitat

Members of the genus occur up to an altitudinal distribution of 1,900 m asl in the Cordillera de la Costa, Venezuela (*V. antisthenesi*, *V. castroviejoi*), the Guiana Shield (*V. gorzulae*, *V. helenae*, *V. ritae*) and Amazonian Colombia and Ecuador (*V. ritae*) as well as in the Atlantic forests of Brazil (*V. assuh*, *V. baliomma*) and Argentina (*V. eurygnatha*, *V. parvula*).

*Vitreorana antisthenesi*: this species is known from primary and secondary forests (cloud and gallery forests) on the northern slopes and in the central regions of the Cordillera de la Costa (states of Aragua and Carabobo), Cerro Azul (state of Cojedes) and the Serranía del Interior (state of Yaracuy) in northern Venezuela between almost sea level and 1,200 m asl.

*Vitreorana assuh*: only known from the type locality; a stream in the Serra das Lontras National Park, southeastern state of Bahia, Brazil, central corridor of the Atlantic Forest, at 450 m asl.

*Vitreorana baliomma*: Brazil, northern Atlantic rainforests. 10 different localities have been documented in the states of Bahia, Minas Gerais, Sergipe and Alagoas; the species tolerates altered habitats and has also been recorded in fragmented secondary forests and cocoa plantations. During the breeding season in marginal vegetation near streams between 98–620 m asl. Species found quite frequently in suitable habitats.

*Vitreorana castroviejoi*: Venezuela, Sucre: Cerro El Humo and headwaters of the Río Tacarigua (northern slope of the Paria Peninsula) and Macuro, in the east of this mountainous area at 580–800 m asl, possibly higher.

*Vitreorana eurygnatha*: Brazil, in the states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Santa Catarina and São Paulo, from sea level to 1,700 m asl.

*Vitreorana franciscana*: south-eastern Brazil (São Francisco River, Serra da Canastra National Park, Vargem Bonita, Minas Gerais): 850–900 m asl.

*Vitreorana gorzulae*: Guyana; Venezuela, possibly also Brazil (Roraima), 450–1,850 m asl.

*Vitreorana helenae*: Venezuela: Quebrada de Jaspe (San Ignacio de Yuruan) and Salto Karuay in Bolívar, in eastern Venezuela. Also known from Guyana: Kaieteur National Park and from Brazil: Pacaraima; possibly more widespread. Altitudinal distribution 440–1,000 m asl.

*Vitreorana parvula*: north-eastern Argentina (Misiones), eastern Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo [Lages,

Urubici and São Bento do Sul in the Serra do Mar and Planalto]), possibly also in Paraguay. Altitudinal distribution from sea level up to 1,500 m asl. The regional climate in the Araucaria forests is subtropical and also includes frost and snow in winter.

*Vitreorana ritae*: known from two localisations in the Amazonian lowlands (below 300 m asl) of the Orellana Province, in eastern Ecuador, Colombia (Amazon), Perú (Loreto) Bolivia (Roraima, Pando), eastern Surinam, French Guiana, Brazil (Roraima and Amapá south to the far west [Amazon and municipalities of Cotriguaçu and Sinop, Mato Grosso] and east to Amapá and central Pará), possibly also in southern Guyana and neighbouring Venezuela. Altitude up to 300 m asl. The now lost holotype was collected at the end of the rainy season (April or June 1950) in the high Río Solimões region. There is information that the locality in the cleared forest resembled a clearing closely bordered by trees and lianas.

### Conservation Status and Main Threats

#### IUCN Red List Status

*Vitreorana antisthenesi*: VU (Vulnerable B1ab(iii), assessed February 10, 2020);

*Vitreorana assuh*: has not yet been assessed by the IUCN

*Vitreorana baliomma*: LC (Least Concern, assessed April 09, 2021)

*Vitreorana castroviejo*: EN (Endangered B1ab(ii,iii), assessed November 13, 2019)

*Vitreorana eurygnatha*: LC (Least Concern, assessed April 09, 2021)

*Vitreorana franciscana*: LC (Least Concern, assessed January 01, 2022)

*Vitreorana gorzulae*: LC (Least Concern, assessed June 26, 2020)

*Vitreorana helenae*: VU (Vulnerable B1ab(iii), assessed June 29, 2020);

*Vitreorana parvula*: VU (Vulnerable B1ab(iii), assessed April 09, 2021);

*Vitreorana ritae*: LC (Least Concern, assessed April 13, 2021).

#### Red List Status in the Range Countries

##### Argentina

*Vitreorana parvula*: Not known (Insuficientemente Conocida).

##### Brazil

*Vitreorana eurygnatha*: Presumably threatened (regional: Minas Gerais State Red List: Not Listed. Sao Paulo State Red List: Not listed. Río de Janeiro State Red List: Presumably threatened).

*Vitreorana parvula*: Not listed (regional: Río Grande do Sul: Vulnerable, Paraná: Data Deficient, São Paulo: Probably endangered, Río de Janeiro: Endangered).

## French Guiana

*Vitreorana ritae*: Least Concern (LC).

## Venezuela

*Vitreorana castroviejoi*: Near Threatened (NT).

## Threats

The main threats are indicated as possible habitat loss due to agriculture, deforestation, slash-and-burn agriculture and human settlements (*V. antisthenesi*). Most of the area of the Brazilian Atlantic rainforest has been heavily deforested and fragmented. Nevertheless, populations of *V. baliomma* appear to be tolerant of anthropogenic activities, as the holotype was found in a cocoa plantation with remaining shade trees. Other possible causes of endangerment are local applications of pesticides, fertilisers and pollution, diseases, climate change and increased UVB radiation (*V. baliomma*). Furthermore, knowledge of population trends or damaging influences sometimes remains rudimentary, e.g. cities have expanded in the natural distribution area so that large parts are not under special protection.

## Reproduction

| Topic                       | Details on the reproduction of <i>Vitreorana</i> spp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|-----------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | <i>V. eurygnatha</i> , <i>V. parvula</i> : nuptial excrescences rich in glands at the base of finger I.<br><i>V. baliomma</i> : nuptial excrescences with superficial glands on the edge of finger I.<br>All species: ♂♂: calls from single subgular vocal sac, Wolffian ducts mostly recognisable on the ventral side.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Sexual maturity             | keine Angaben in der diesbezüglichen Literatur zu finden                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Calls                       | All species: axillary amplexus in the vegetation above small forest streams.<br><i>V. baliomma</i> : ♂♂ calls on upper leaf surfaces at a height of 0.3–4 m. Calls of single ♂ or choirs of up to 6 ♂♂; two different call types: A. common call: normal as a sequence, but also independent; with increasing amplitude, dominant frequency 4,694–5,081 Hz (always seven repeated segments: pulse, specific amplitude modulation at a rate of 35.3–37.8 pulses/s, duration 185–198 ms. B. follows type A, 217–249 ms, 4 or 5 pulses, 98–116 ms, dominant frequency 4,694–5,038 Hz. The number of calling frogs is positively correlated with humidity.<br><i>V. eurygnatha</i> : lives and reproduces within forests in small streams (1–2 m wide). ♂♂ call at night on low vegetation or bushes, sporadic advertisement call (call duration 0.04–0.1 s). Adult frogs are regularly found in low densities (1–2 individuals per linear metre of stream).<br><i>V. franciscana</i> : ♂♂ call from 6–2 pm from the tops of leaves at a height of 0.5–1.5 m, advertisement call consists of 6–8 pulsed notes ( $7 \pm 1.4$ ), call length 2.9–3.5 s, dominant frequency 4,136.6–4,490 Hz.<br><i>V. gorzulae</i> : seasonal reproduction, ♂♂ call from the top of leaves, advertisement call (only heard at short distance) with single pulsed note ('chirp'), 3–7 pulses/call, call length 0.02–0.05 s, dominant frequency 4,416.97–5,157.48 Hz.<br><i>V. parvula</i> : the advertisement call has a call length of 0.013–0.084 s at 1–5 pulses/note, call intervals were 0.194–37.2 s, peak dominance frequency was 3,962.1–5,062.5 Hz (Haga et al. 2014). The reproductive biology is presumably similar to that of the other representatives of the genus. |
| Mating and spawning         | <i>V. baliomma</i> : ♀♀ circle a calling ♂ and jump towards it, pair in amplexus moves over upper and lower leaf surfaces, presumably the ♀ chooses the optimal oviposition site,                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |



|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | <p>the pair often turns 180 or 360° on the leaf. A gelatinous clutch (13.1–43.2 mm in diameter) is laid above the water on the upper or lower leaf surface. Particularly large leaves are used for this purpose. Immediately after laying the eggs, the ♀ can carry out short-term brood care (rear end of the body is repeatedly placed over the clutch; average duration 110 min). This behaviour may optimise the fertilisation and moistening of the clutch.</p> <p><i>V. eurygnatha</i>, <i>V. franciscana</i>: eggs are laid on the tops of leaves hanging above the water.</p> <p><i>V. gorzulae</i>: clutches are laid on moss-covered branches or between two leaves, which hang 1.5–2.0 m above the water. No brood care by ♂♂.</p> <p><i>V. ritae</i>: no information is available on habitat requirements, reproductive biology, calling and tadpoles.</p> |
| Reproductive season                               | <p><i>V. baliomma</i>: reproductive behaviour and calling dependent on rainfall intensity and humidity, especially between May and August.</p> <p><i>V. eurygnatha</i>: breeding during the rainy season from August to January.</p> <p><i>V. franciscana</i>: breeding during the rainy season from August to December.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Eggs clutch, clutches/year                        | <p><i>V. baliomma</i>: 7–22.</p> <p><i>V. eurygnatha</i>: few eggs laid on the upper leaf surfaces.</p> <p><i>V. franciscana</i>: 42–53 eggs/clutch.</p> <p><i>V. gorzulae</i>: clutch with 15–22 eggs.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Size of eggs and larvae at hatching               | <i>V. baliomma</i> : 2,18 ± 0,23 mm in diameter.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Development time from egg laying to metamorphosis | no data available from the literature.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Details on the larvae                             | <p><i>V. baliomma</i>: The tadpoles are fossorial (adapted to burrow into the soil substrate in places).</p> <p><i>V. eurygnatha</i>: anteroventral oral disc with a row of marginal papillae without teeth, body ovoid, muscular tail, eyes and nostrils dorsal, tadpoles sometimes burrow into the streambed close to the current (Leite Pezzuti et al. 2024).</p> <p><i>V. parvula</i>: larva (described as <i>V. uranoscopa</i>) in life with red body and dorsal greenish tones as well as a fine network of golden dots, especially in the area of the spiraculum. Abdomen and caudal musculature reddish, fins transparent, dorsally more pigmented (Leite Pezzuti et al. 2024).</p>                                                                                                                                                                            |

## Husbandry and Captive Breeding of *Vitreorana antisthenesi* B/B

All other species *Vitreorana* spp. **X**, as they have not yet been introduced into captivity. Husbandry and breeding parameters probably similar for many species.

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Vitreorana antisthenesi</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|--------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | <p>The analyses of the keeper surveys (two breeders of <i>Vitreorana antisthenesi</i>) yielded the following information:</p> <p>Housing conditions (breeding animals):</p> <ul style="list-style-type: none"> <li>– Sex ratio 1.1 (n=1)   not specified.</li> <li>– Air and water temperature (°C): 18–28   22–25.</li> <li>– Humidity (rel.%): 70–100 (n=2).</li> <li>– Lighting/type/day-night cycle: Daylight length 12 h (n=2).</li> <li>– Container size (length x width x height in cm): 38 x 50 x 50   50 x 50 x 50 cm.</li> <li>– Proportion of water in the total area (%): 10–80.</li> <li>– Substrate: organic (pressed cork)   inorganic (foam).</li> <li>– Furnishing/planting: <i>Philodendron</i>   small <i>Aglaonema</i>.</li> <li>– Water depth (cm): 4   8.</li> <li>– Number of animals per tank: initially 2, later maximum 2 ♂♂.</li> <li>– Feed/feeding intervals: 2 x/ week (n=2).</li> <li>– Supplementation (minerals/vitamins): yes, but not specified   Korvimin ZVT.</li> <li>– Aggression between several ♂♂ or ♀♀: no   ♂♂ fight against each other.</li> </ul> |
| Life expectancy                                                                                              | Maximum age of the animals kept (in years): 4   4.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Triggers for reproduction                                                                                    | <p>Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): irrigation   'running' water through internal filter.</p> <p>On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom, tip of leaf)? Leaves   leaves and panes, <i>Philodendron</i> leaves were the most frequently used deposition sites, with the clutches being laid on the upper side of the leaves.</p> <p>How is the clutch structured? Simple layer (monolayer), complex clutch, other (how?): Single-layer clutches, rarely partly in two layers (n=2).</p> <p>Number of clutches per ♀ in one oviposition: 1 (n=2). Number of clutches/♀/year (min.–max.): 2–3   5–6. Number of eggs per clutch (min.–max.): 20–30   35–42.</p>                                                                                                                                                                                                                                             |
| Number of fertilised eggs per clutch (min.–max.)                                                             | 0–30   30–40.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Number of embryos hatched per clutch (min.–max.)                                                             | 0–20   10–15.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Hatching rate (number of hatched larvae/ number of eggs)                                                     | <p>Hatching rate (number of hatched larvae/number of eggs) order &lt; 25%; 25–50%; &gt; 50–75%; &gt; 75%:</p> <p>Not specified   25–50%.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Size of juvenile frogs (freshly metamorphosed; min.–max. [in mm])                                            | 5–7 mm (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Number of meta-                                                                                              | approx. 10 (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

|                                                                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|---------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| morphosed juvenile frogs per year                                         |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Number of rearing losses up to the 3 <sup>rd</sup> month                  | few (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Husbandry conditions (larvae) / Technical requirements for larval rearing | <p>for general information on larval rearing see above (chapter general Information on glass frogs).</p> <p>Total length of newly hatched larvae (in mm): approx. 7 mm (n=1). Duration of the larval period (oviposition to metamorphosis; min.–max. [in months]): 4–5 months (n=1).</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements): small aquarium, stones from stream and some mulm (n=1).</p> <ul style="list-style-type: none"> <li>– Water temperature (in°C): 22–28   22–25.</li> <li>– Lighting/type/day-night cycle: indirect through daylight   12 h lighting.</li> <li>– Container size (length x width x height in cm): 40 x 20 x 20   38 x 50 x 50 (terrarium adults).</li> <li>– Substrate/furnishings/planting: not specified   see adults.</li> <li>– Water depth (in cm): 18   see adults.</li> <li>– Number of animals per tank: 10–50   5–10.</li> <li>– Filter (type, capacity): Airlift sponge filter   sponge internal filter and membrane pump.</li> <li>– Special requirements (e.g. water values): acidified with humic acids   not specified.</li> <li>– Larval food: spinach, Repashy fish food Super Green   Tabi Min (sparsely), dead food animals, especially houseflies.</li> <li>– Frequency of water changes: every 2 weeks   1 x/ month.</li> <li>– Type of water (rainwater, tap water, RO water, etc.): 100% stagnant tap water   50% reverse osmosis (RO) water:50% tap water.</li> </ul> |
| Number or percentage of offspring that become adults or sexually mature   | 10%   ca. 80%.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Age/size at sexual maturity                                               | ♂♂: 23–24 mm, ♀♀: 25–26 mm (n=1).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Indicators for reaching sexual maturity                                   | ovaries/vasa deferentia   ♂♂: calls, ♀♀: eggs in ovary.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Sex ratio of the offspring (♂♂:♀♀)                                        | not specified (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Evidence of deformities or diseases                                       | not specified   none.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Mortality of larvae up to metamorphosis                                   | high (> 75%)   high.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Mortality in the first months/years of life                               | mortality of larvae up to metamorphosis (< 25%; 25–50%; > 50–75%; > 75%) or estimated: high/low: not specified   few.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Routine testing for amphibian diseases and parasites                      | no (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Quarantine (type                                                          | no   yes, for 3 months.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |

and extent)

|                                                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|-----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| General characteristics, difficulties with keeping and breeding | inefficient larval rearing   long development time.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Frequency of private breeding and reproduction in zoos          | Assessment of the frequency of husbandry: very rare (n=1). Personal assessment of the difficulty of husbandry: difficult   not easy: high rate of fungal infection of the eggs and relatively few larvae reach metamorphosis.                                                                                                                                                                                                                                                                                                                                                                                               |
| Reproduction in captivity up to F2 generation                   | yes (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Commercial breeding                                             | no (n=2).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Interviews/ Surveys/ Consultations                              | Two participants took part in the survey on <i>V. antisthenesi</i> , both private owners. Based on their own knowledge and the latest literature, both participants were very certain that the species had been correctly identified. Both husbandries labelled the animals kept as wild-caught. The duration of husbandry was four and eight years, both husbandries ended in 2005 and 2009. Both keepers stated that they were endeavouring to breed offspring, which was achieved one year after the start of husbandry in each case. The frequency of offspring was stated to be around ten times or 5–6 clutches/year. |



Fig. 60: *Vitreorana* spp., reproduction

- a *V. antisthenesi*, amplexus (K.-H. Jungfer)
- b *V. antisthenesi*, pair with eggs (K.-H. Jungfer)
- c *V. parvula*, pair (A. Kwet)
- f *V. parvula*, egg guarding (A. Kwet).

## Hylidae

### *Agalychnis lemur* (Boulenger, 1882)

| Species                 | Original description | Common name     | Common name in-ternational    | Known in the trade |
|-------------------------|----------------------|-----------------|-------------------------------|--------------------|
| <i>Agalychnis lemur</i> | (Boulenger, 1882)    | Lemur Leaf Frog | Lemur-Laubfrosch, Lemurfrosch | Yes                |



Fig. 61: *Agalychnis lemur* (all photos by T. Eisenberg)

- a Colouration during the day
- b adult male at night, photo taken at Guayacán, near Siquirres, Costa Rica
- c adult with beginning night coloration, photo taken at Guayacán, near Siquirres, Costa Rica
- d camouflage.

### Morphology and Taxonomy

Medium-sized green tree frog (metachrosis: dorsal surfaces pale to apple green during the day, reddish, lavender or orange-brown in various shades at night, sometimes or in phases with dark red spots and dots), dorsal skin texture smooth, belly creamy white, flanks yellow to orange, forearm dark yellow on top, ventral skin granular, front and rear thigh surfaces orange, fingers with small discs, elbow fold weakly pronounced, running from the elbow to the tip of finger IV, toes without interdigital membranes (at most a slightly pronounced interdigital membrane between toes III and IV), toe V with slight outer edge, tarsal fold absent, occasionally a single tiny tubercle on the heel, adult ♂♂ with single, barely extensible inner median subgular vocal sac with two elongated, paired vocal slits and a brownish, non-spiny nuptial pad at the base of each thumb, iris silvery-white (daytime) or grey (active) with peripheral thin black ring, pupil vertically slit-shaped, SVL ♂♂ 30–41 mm, ♀♀ 39–53 mm, head as



broad as long, eyes large and bulging, lower eyelid without reticular structure, mouth region short and blunt in dorsal view, vertically sloping in profile, tympanic membrane clearly pronounced and moderately large (approx. half the diameter of the eye). Skin peptides with antibacterial effect and against tumour growth and diabetes mellitus have been described. *A. lemur* differs from the other green tree frogs of Costa Rica by a vertical pupil and the absence of interdigital membranes (Duellman 2001, Savage 2002, Kubicki 2004, Leenders 2016, AmphibiaWeb 2024).

### Distribution and Habitat

The species occurs in Costa Rica, Panama and Colombia. It was once widespread on the Caribbean side from near Tilarán, Guanacaste Province, Costa Rica, to western Panama; the isolated records on the Pacific side are from north-west Costa Rica and from south-west, central and extreme eastern Panama in the Darién region, where it extends slightly across the border into Colombia (440–1,600 m asl). Habitat on slopes in humid lowland and montane primary and secondary forests, but always close to rivers. It occurs up to the canopy, from where the calls can be heard (Costa Rica Red List Assessment Workshop September 2019). *A. lemur* is a nocturnal tree frog that is active almost all year round. It sleeps on the undersides of leaves during the day and only becomes active after dark. It rarely jumps, but usually climbs slowly on leaves or branches with its thin, barely muscled extremities (similar to the slow nocturnal locomotion of Malagasy lemurs). The frog approaches its prey slowly and pounces on it from a distance of around 50–60 mm, while continuing to hold on to branches and leaves with its feet. Specimens from Costa Rica are said to be somewhat smaller than those from Panama (Duellman 2001, Savage 2002, Solís et al. 2008).

### Conservation Status and Main Threats

CITES Appendix II since 2023 (Cop19 Proposal 35). The following *Agalychnis* species are now listed on CITES Appendix II: *Agalychnis annae*, *A. callidryas*, *A. lemur* [with a zero export quota for wild-caught specimens per year for commercial purposes], *A. moreletii*, *A. saltator*, *A. spurrelli*, *A. taylori* (listed in Species+ as a subspecies of *A. callidryas*) and *A. terranova*.

The issuance of export permits for all wildlife specimens harvested from the wild (W) for commercial purposes (T) has been suspended in Panama.

EU Council Regulation (EC) No. 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

### IUCN Red List Status

CR (Critically Endangered A2ace, assessed 09 September 2019).

## Threats

The species was once considered quite common in Costa Rica, but most subpopulations disappeared in the late 1980s and early 1990s. As of 2019, the species is certainly only reported from a few areas in Costa Rica: Fila Asunción, 15 km southwest of Limón in Veraguas (an abandoned farm), in a wooded area near Parque Nacional Barbilla, near Siquirres in Limón province (B. Kubicki & S. Salazar pers. comm. September 2019 [all pers. comm. cited in IUCN SSC Amphibian Specialist Group 2020]) and from La Alegría in Guayacán in the province of Limón (García-Rodríguez et al. 2012). The species has been reported from another area in Costa Rica: Cedral, near Miramar, however this record remains unconfirmed (F. Bolaños pers. comm. September 2019). Fila Asunción is the only place known to harbour a large reproducing population (Costa Rica Red List Assessment Workshop September 2019). In 2003, the species was deliberately reintroduced to a historical site in Siquirres. To this end, approx. 75 tadpoles were introduced from another site approx. 30 km away (linear distance). The species is now colonising other neighbouring properties, all of which are within its historical range (B. Kubicki pers. comm. September 2019). All other previously known Costa Rican subpopulations are considered to have disappeared, including those in Monteverde, San Ramón, Parque Nacional Braulio Carrillo and Parque Nacional Tapantí. The species has not recovered in large parts of its range and has not been recorded in the Cordillera Central or the Cordillera de Tilarán in recent years (Costa Rica Red List Assessment Workshop September 2019). In Panama, the species used to be quite common at lower altitudes, but the sharp decline has reduced its range to a few locations in western Panama (Hertz et al. 2012) and isolated records from central Panama. In the Reserva Forestal Fortuna, Chiriquí, a significant decline was noted (no records from this site since 1999) and in El Copé, Coclé, populations of the species have declined since 2004, although the species continued to occur there in very low numbers (Lips et al. 2006). In Colombia, the species is either very rare, very difficult to detect or the population is very small (G.F. Medina-Rangel pers. comm. February 2019). During surveys between 2012 and 2016 in Unguía, Chocó, only two individuals were sighted during an expedition in July 2014. The status of the Colombian subpopulations remains unknown. Overall, it is assumed that the population has been decimated due to a combination of a continuing decline in the extent and quality of the habitat and disease. It is likely that the remaining population has suffered a decline of 80–95% since 1998 (26 years/three generations) due to the disappearance of the western and central Panamanian populations, probably due to chytridiomycosis (Lips et al. 2006, Hertz et al. 2012, Gratwicke et al. 2016). However, studies by Woodhams et al. (2006) found that this species was one of the most resistant to infection among the species studied, possibly explaining its continued persistence at lower numbers. Ranavirus is another potential threat as infected individuals have been documented in Siquirres; however, the impact of this virus remains unknown (S. Whitfield & H. Zumbado-Ulate pers. comm. September 2019). General habitat loss and fragmentation remains a threat throughout the species' range, and this is particularly true in Costa Rica, where deforestation by squatters threatens the Fila Asunción occurrence, one of the few confirmed remaining subpopulations in the country. Another subpopulation in Siquirres is currently under the protection of a private landowner; however, should ownership change in the future, the security of this subpopulation could be jeopardised (Costa Rica Red List Workshop September 2019). The other historical sites in Costa Rica have been deforested for agriculture and livestock (Costa Rica Red List Workshop September 2019). Deforestation and illegal mining are the main threats in the area where the species was recorded in Colombia (G.F. Medina-Rangel pers. comm. February 2019).

About 37% of the estimated range of this species is within protected areas (Urbina-Cardona & Loyola 2008). Within Costa Rica, the former range included several national parks and other protected areas; however, none of the currently remaining subpopulations are located in national parks, but in private areas and an indigenous reserve (G. Chaves pers. comm. 2007, 2019). The placement of water barrels in the forest has successfully attracted this species to breed (B. Kubicki pers. comm. August 2010). It occurs in at least six Panamanian protected areas and is considered a high priority species for conservation in Panama's National Amphibian Conservation Action Plan (ANAM 2011). In 2001, two successful captive breeding programmes began: 1) the Atlanta Botanical Garden, which has since transferred individuals to 19 US zoos that continue breeding in the USA (Gratwicke et al. 2016) and 2) the Manchester Museum, which has transferred some specimens to Bristol Zoo and Norden's Ark to safeguard populations (M. O'Donnell pers. comm. September 2019). Ongoing monitoring is taking place for the two remaining subpopulations in Costa Rica (G. Chaves pers. comm. September 2019). A partial ex situ population of this species is kept at the El Valle Amphibian Conservation Centre in Panama (Gratwicke et al. 2016).

Improved habitat protection is required for the remaining subpopulations in Costa Rica (Costa Rica Red List Workshop September 2019). The causes of declines at several historical sites have been evaluated (H. Zumbado-Ulate & J. Rodríguez pers. comm. September 2019), and reintroductions to sites with suitable habitat should be considered (V. Acosta pers. comm. September 2019).

The species is available in the international pet trade, presumably from captive breeding. It is not known whether individuals are still being collected from the wild (Costa Rica Red List Workshop September 2019, IUCN SSC Amphibian Specialist Group 2020). In Germany, both animals from the Manchester Museum's breeding programme and farm-bred individuals from Canada (Understory Enterprises) have been available in recent years; both breeding lines are supposed to come from the same source from Brian Kubicki's Costa Rican Amphibian Research Centre in Guayacán, near Siquirres, Costa Rica (T. Eisenberg, unpublished data).

## Reproduction

| Topic                       | Details on the reproduction of <i>Agalychnis lemur</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|-----------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters | adult ♂♂ smaller than ♀♀, calls of ♂♂ from single subgular vocal sac.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Sexual maturity             | sexual maturity (adult size) is given as one year. However, the ♂♂ already show nuptial excrescences from the seventh month during the reproductive period (Kubicki 2004, Eisenberg & Kaesling 2012).                                                                                                                                                                                                                                                                                                                                                                     |
| Calls                       | the advertisement calls consist of a very short 'tick' or 'chick' that is repeated every 25 seconds and emitted from the top of the leaf (call length 190–200 ms, 39–41 pulses/s, dominant frequency 800–3,100 Hz). The species is territorial and emits an encounter call of 2–4 pulses when another ♂ is nearby. A release call can also be produced. The ♂♂ are aggressive in defence of their territory, with resident ♂♂ clutching intruding ♂♂ and unresponsive ♀♀ and attempting to push them off the perch (Jungfer & Weygoldt 1994, Savage 2002, Leenders 2016). |
| Mating and spawning         | as with other members of the genus, <i>A. lemur</i> also sticks its clutches to leaves hanging above the water. The eggs are usually laid on the upper and lower leaf surfaces or branches above small ponds, swamps, slow-flowing streams or temporary bodies of water, and after hatching the larvae complete further development until metamorphosis in the body of water below the oviposition site. Hatching takes place 7–14 days                                                                                                                                   |

|                                                   |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | after fertilisation. The embryos are light green and fall into the water or are washed there by rain (Savage 2002, Gomez-Mestre et al. 2008, Leenders 2016).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Reproductive season                               | the breeding season is concentrated in the rainy months between April and July (Savage 2002, Gomez-Mestre et al. 2008).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Eggs/clutch, clutches/year                        | in captivity, clutches consisted of 15–30 green to cream-coloured eggs; at Río Blanco, Limón, Costa Rica, clutches laid in the field consisted of 22.5 $\pm$ 2.1 eggs (n=4). The ♀♀ can produce 1–3 clutches in one night or lay clutches on different nights. The egg masses are laid in one or two layers, with clutches 7.1 $\pm$ 0.3 mm thick (van Eijsden 1977, Jungfer & Weygoldt 1994, Savage 2002, Gomez-Mestre et al. 2008).                                                                                                                                                                                                                                                                     |
| Size of eggs and larvae at hatching               | The eggs have a diameter of 3.0–3.5 mm and are found in gelatinous shells with a diameter of 5–6 mm (Savage 2002, Gomez-Mestre et al. 2008).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Development time from egg laying to metamorphosis | Metamorphosis takes place 69–98 days after fertilisation, when the first green pigment develops. Metamorphosed animals also show metachrosis (colour change between day and night), but they lack the orange or yellow flank colouration, size of metamorphs 25–27 mm (Savage 2002).                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Details on the larvae:                            | Moderately large tadpole, with the larvae reaching a total length of about 42 mm at Gosner stage 30 (Gosner 1960). The body is ovoid, with a moderately large tail with reduced caudal fins and a pointed tip. The eyes are dorsolateral and directed backwards. Spiraculum lateroventral on the left side, cloaca on the right side. Oral disc small, maxillary and mandibular sheath toothed and 2/3 rows of denticles, A2 with slight median gap, 2–3 rows of oral papillae laterally and ventrally. Body colour greyish purple, later olive brown, belly creamy yellow to pink, tail musculature with dark spots, iris golden. The larvae ingest grated algae or filter at the surface (Savage 2002). |

## Husbandry and Captive Breeding B/C

For *Agalychnis lemur*, there is an EAZA studbook (ESB) for frogs kept in zoos, which has been maintained by Kristofer Forsater in Nordens Ark (Sweden) since 2024 (EAZA 2024).

The ex-situ breeding of *A. lemur* has been successfully carried out in human care for many years in Europe, but also, for example, at the Atlanta Botanical Garden, where a conservation breeding project for the species exists and *A. lemur* is regularly presented as a flagship species for amphibians threatened with extinction. In Panama, the species is being bred at the El Valle Amphibian Conservation Center as part of an ex-situ breeding programme.

Since 2018, the species has been kept and bred by zoos and private individuals as part of Citizen Conservation; 9 private owners with 52 animals are currently involved in this breeding programme, for which the author provided the founder population (Eisenberg 2019).

| Topic                                                                                                        | Data from the surveys on the husbandry of <i>Agalychnis lemur</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|--------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Husbandry requirements and husbandry conditions of adults and juvenile frogs, technical and time expenditure | Spacious rainforest terrariums with daytime temperatures of 24–26°C and cooling to 18–20°C at night are suitable for the husbandry of <i>A. lemur</i> . The relative humidity should be more than 70% during the day, rising to almost 100% at night. The author uses well-ventilated containers measuring 60 x 60 x 100 cm (L x W x H) as terrarium sizes. In heated living rooms, one or two fluorescent lamps or LED light bars are usually sufficient for lighting. In winter, one 35 W full-spectrum lamp with UV component (Lucky Reptile BrightSun) is switched on for each tank on an hourly basis. In the local summer months, higher temperatures are also tolerated, but these should not prevail for long periods and should be accompanied by sufficient humidity. After spraying, however, the frogs must not sit permanently in the wet; as a rule of thumb, the leaves should be dried again after about two hours during the day. Our own observations in the species' habitat at the Costa Rican Amphibian Research Center ( <a href="https://cramphibian.com">https://cramphibian.com</a> ) near Guayacán, Costa Rica, also revealed temperatures of 29°C at certain |

points. Lemur tree frogs were found there at night at forest ponds and also slept near them during the day on the underside of shaded leaves. This frog species should therefore also be offered sufficiently large leafy plants (e.g. various *Philodendron* spp. and *Monstera* spp.) as with the larger *Agalychnis* species.

Depending on the size of the tadpoles, the young frogs have a SVL of 19–27 mm when they complete metamorphosis. The small frogs feed for the first time after two to three days, once the rest of their tail has been completely absorbed. They initially cope with micro crickets, bean beetles, pea aphids and large fruit flies in their diet, and are subsequently fed additional small crickets and crickets. The feeder insects must be well nourished and should be dusted with a well-adhering mineral-vitamin supplement before each feeding. The climatic conditions in the rearing terrarium are identical to those of the parent animals. The number of juveniles per container should not be too large in order to avoid overstocking, poor hygiene conditions and the resulting losses. It is easier to monitor and ensure feed intake in smaller rearing terrariums (Jungfer & Weygoldt 1994, Proy 2000, Eisenberg 2003b, 2004b, 2006, 2019, Eisenberg & Kaesling 2012).

#### **The analyses of the surveys yielded the following information:**

Eleven participants took part in the survey, including one zoo, one commercial breeder and nine private owners. All participants were very certain that the species had been correctly identified, although the species identification was usually carried out by the breeder, in collaboration with other specialists or based on their own expertise or the latest literature. With the exception of two sources, one of which received its animals as imported Canadian so-called ‘farm-breds’, all the animals kept were labelled as captive-bred, and one was not specified. Two breeders have been keeping their animals continuously since 2003 and 2004, two others since 2014 and 2015, and the others have been keeping their animals since 2019–2021. Four keepers have not yet been successful with offspring, although all keepers indicated basic breeding ambitions. Two of these husbandries suffered total losses, one lacked a ♀ to breed, and in one fairly young husbandry, breeding has not yet taken place. For the other breeders, breeding success usually occurred within one to three years of starting husbandry. Where breeding was already established, it was recurring or even regular ( $n=7$  [2–3 times per year,  $n=2$ ; annually or almost annually,  $n=2$ ; regularly,  $n=1$  and twice in total,  $n=1$ ]). Three of the seven breeders stated that they had managed regular breeding at least up to the F2 generation, group size and sex ratio varied – depending on the container size – between smaller (0.3 | 2.0 | 2.1 | 2.2 | 2.3) and larger (2.4 | 6.2 | 3.2.3 | 5.4 | 5.5) groups, once there was no indication.

Information on specific questions relating to husbandry and breeding was provided as follows:

Housing conditions (breeding animals):

- Air and water temperature: during the day: 18–29°C, at night: 18–23°C, water: 21–25°C. While very low temperatures were consistently reported in some husbandries, where only 20–22°C were reached even during the day ( $n=2$ ), more keepers utilised the upper range (23–29°C) ( $n=9$ ). This was not relevant for the breeding success, just as husbandry with night temperatures above 22°C did not appear to have any influence on the success of the offspring. The water sections were not heated separately.
- Humidity (rel.%): Ranges of 50–70 ( $n=3$ ) as well as > 70–100 ( $n=7$ ; once not specified) were reported. Higher values were sometimes achieved at night and during irrigation, without the drier husbandries having any influence on reproductive success.
- Lighting/illumination technique/day-night cycle: The lighting duration mostly corresponded to a 12 h day-night cycle ( $n=9$ , 1x 9 h and 1x 14 h). When light sources were specified, LED light bars ( $n=5$ ) were predominantly used (multiple answers possible), followed by fluorescent lamps ( $n=2$ ) and additionally full spectrum lamps ( $n=3$ ) on an hourly basis. Lamps with a UV component ( $n=5$ ) were used in about half of the husbandries; a need for UV light for breeding could not be deduced.
- Container size (length x width x height in cm): Mostly terrariums with edge lengths up to 60 cm were in use ( $n=6$ ), the remaining husbandries used larger containers in



- which at least one of the edge lengths was between 80–140 cm (n=5). Even in the smaller dimensions (45 x 45 x 60 cm), the species could be successfully bred.
- Proportion of water part in the total area (%): 0–100 (often as a moat, with irrigation the entire floor area can be flooded), sometimes the water part consisted of a bowl (n=3) or an artificial rivulet (n=1).
  - Substrate: either organic: river gravel (n=3), Xaxim or cork plates, partly covered with leaves and moss (n=3) or no substrate (n=7; multiple answers possible), in some cases better hygiene without substrate was explicitly mentioned.
  - Furnishing/planting: *Philodendron* (n=11), as well as other tropical plants such as anthuriums, *Monstera* spp., vanilla, bromeliads (*Neoregelia* sp.), various other vines, mosses and ferns, all of which grow epiphytically on cork, coconut, tree fern or Hygrolon® gauze.
  - Water depth (cm): 0–5 (n=5) | 6–10 (n=3) | 50 (n=1) | not specified (n=2).
  - Number of animals per container: 2–10.
  - Food/feeding intervals: crickets, bean beetles, *Drosophila* were named as feeder animals/every night (n=1) | 2 x/ week (n=7) | 3 x/ week (n=7; multiple answers possible) | daily feeding of juvenile frogs (n=2).
  - Supplementation (minerals/vitamins): yes (n=10) | no (n=1; animals died) | not specified (n=4), the following products were also used: Repashy Calcium plus, Repashy Supervit, Repashy Vit A, Korvimin ZVT, Herpetal Amphib.
  - Aggression between several ♂♂ or ♀♀: temporary during the breeding season between ♂♂ (n=6) or no aggression (n=5).

|                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
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| Life expectancy (years)   | 11 (n=1)   8 (n=2)   approx. 6 (n=1)   more than 4 (n=1)   not specified (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Triggers for reproduction | <p>The breeding of this endangered frog species is of particular importance. Only well-fed animals that have undergone a preparatory dry period for cycle control and thus spawning should be used for breeding. To stimulate the animals, cover the ventilation areas with glass panes to a minimum so that the humidity rises almost to the saturation point. An aquarium heater and a pond pump are placed in the bottom tray of the terrarium and the entire bottom section is flooded to a height of around 10–15 cm. A perforated plastic tube can be connected to the pond pump via an aquarium hose, which is attached to the cover pane from the inside using suction cups. This internal water circuit simulates the rainy season, ideally when the air pressure outside is low. Pairs usually come together in amplexus in the first night. The breeding group can also be transferred to a specially set up 'rain chamber' terrarium in which breeding experiments are carried out exclusively. The irrigation can be switched on one to two hours before nightfall and then left to rain for a further two hours. The covered ventilation openings keep the interior moist during the second half of the night. The pairs usually spawn in the following nights on leaves hanging above the water surface. In various cases, clutches have also been found on bare side glass panes and those covered with cork or Xaxim. The eggs are glued to the leaves after the pair has spent a few minutes in temperate water of 25°C. This usually takes place in the second half of the night. If spawning has not taken place, the breeding attempts are cancelled after a few days. Separation of the sexes occurs automatically when the drier housing conditions are restored. Even if experienced breeding animals sometimes spawn spontaneously under the specified conditions, young animals which just reached sexual maturity often cannot be induced to lay eggs even by intensive irrigation, despite mating clutches. In their natural habitat, the temperature often drops by several degrees after heavy rainfall, and this cooling apparently triggers ovulation, i.e. the maturation of the yolk-rich follicles on the ovaries. The best way to achieve this is to expose the well-fed breeding animals to a cooling period of 17–19°C for 3–7 days. This can be simulated by placing the breeding group in a small aquarium with a low water level and several <i>Philodendron</i> vines as a perch in an unheated room. The animals do not become active at night at these low temperatures, but rest in a sleeping position the whole time. After this pre-stimulation, which should only be employed if animals did not lay eggs</p> |

spontaneously in previous breeding attempts, the animals are now watered very intensively. You can even – if you first fill the rain chamber with cold water and then switch on the control heater – continuously simulate this rise in temperature. After one or two nights of irrigation with 25°C warm water, the ♂♂ call and the animals, which are now in the amplexus, mate and lay their eggs by sticking them to leaves in balls of clear jelly. During the breeding season, ♂♂ lemur tree frogs can display territorial and aggressive behaviour towards each other, but also towards ♀♀ that are not ready to spawn, in which lower-ranking animals are clasped or pushed away. If this behaviour persists, stressed animals should be moved if necessary or only one ♂ per breeding group should be kept from the start. However, the latter can have a negative effect on mutual stimulation of the ♂♂ (Jungfer & Weygoldt 1994, Proy 2000, Eisenberg 2003b, 2004b, 2006, 2019, Eisenberg & Kaesling 2012).

Information from the breeder survey:

Triggers (stimuli) for reproduction (e.g. changes in temperature and/or humidity or other environmental variables, technical devices, animal care activities): Cooling period of 2–7 days at 17–19°C, then cold sprinkling, then sprinkling for up to five days at 22–25°C (n=4) | preceded by drier husbandry without sprinkling for approx. four weeks (water source available!), generous feeding, followed by sprinkling (n=1) | preceded by drier husbandry, then more frequent spraying in the presence of a low pressure area outside (n=1) | heavy sprinkling in the rain chamber (n=1) | not specified (n=4).

First offspring (CB) in the year: 2004 (n=1) | 2006 (n=1) | 2015 (n=1) | 2018 (n=1) | 2022 (n=2) | 2023 (n=1) | not specified (n=4).

Frequency of breeding since then (number of clutches): regularly (n=1) | (almost) annually (n=2) | twice in total (n=1) | 2–3 x year (n=2) | not specified (n=5).

Where are the eggs laid (leaves/panes/objects)? Leaves (n=3) | usually leaves, rarely panes, outside of flower pots or walls (n=4) | not specified (n=4).

On which substrate are the eggs laid (plant species, moss, stones) and where exactly (top, bottom or tip of leaf)? *Philodendron*, *Monstera* spp.; underside of leaves (n=3) | both sides (n=2) | not specified (n=6).

What is the structure of the clutch? Single eggs, simple layer (monolayer), complex clutch, other (how?): complex form after swelling of the clutch, can hang down from the leaf (n=6) | monolayer (n=1) | not specified (n=4).

Number of clutches per ♀ in one oviposition: 1 (n=3) | 1–3 (n=3) | not specified (n=5).

Number of clutches/♀/year (min.–max.): 0–2 (n=2) | 2–3 (n=3) | 2–4 (n=1) | not specified (n=5).

Number of eggs/clutch (min.–max.): 5–20 | 8–30 | 10–20 | 10–23 | 10–30 | 10–50 | 10–52 (for 17 clutches, mean 18.8; n=1 each) | not specified (n=4).

|                                                                        |                                                                                                                                                            |
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| Number of fertilised eggs per clutch (min.–max.)                       | 80–100% (n=1)   0–100% (n=1)   0–100% (average from 11 clutches: 68,1%; n=1)   10–100% (n=1)   10–23 eggs (n=1)   nearly none (n=1)   not specified (n=5). |
| Number of embryos hatched per clutch (min.–max.)                       | 80–100% (n=1)   50–80% (n=1)   0–53 (from 11 clutches; n=1)   4–15 (n=1)   7–23 (n=1)   22 (n=1)   0–55 (n=1)   not specified (n=4).                       |
| Hatching rate (number of hatched larvae/ number of eggs)               | 0–95,6% (average from 11 clutches: 39,5%; n=1)   50–75% (n=1)   73% (n=1)   > 75% (n=4)   not specified (n=4).                                             |
| Size of the juvenile frogs just after metamorphosis (min.–max.; in mm) | 10–15 (n=1)   12–15 (n=1)   15–20 (n=3)   15–25 (n=1)   not specified (n=5).                                                                               |
| Number of meta-                                                        | 0–50 (n=1)   10–50 (n=1)   13 (n=1)   35 (n=1)   50–100 (n=1)   28–153 (n=1)   not specified (n=5).                                                        |

| morphosed juvenile frogs per year                                         |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
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| Number of rearing losses up to the 3 <sup>rd</sup> month                  | < 5% (n=4)   0–10% (n=1)   0–30% (n=1)   not specified (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Husbandry conditions (larvae) / Technical requirements for larval rearing | <p>clutch incubation and tadpole rearing are similarly unproblematic as described for the larger members of the genus. Depending on whether the leaf with the clutch has been cut off or not, rearing is successful under uniform conditions both with the parents and in a separate aquarium. Separate rearing offers several advantages, e.g. there are no longer any parents present that could cause fungal infections or cause the clutch to fall into the water by running over it. Furthermore, the transmission of undetected parasites from the parents to the offspring can be prevented quite effectively in this way. However, it is not uncommon for a developing clutch of eggs to remain undetected in the terrarium of the breeding animals and for larvae to suddenly appear in the water section. The clutches are incubated until the larvae hatch in a small aquarium with a low water level and a bubble stone (air diffuser). The leaf and clutch can be attached to the outside of a halved plastic bottle a few centimetres above the water surface using a cloth peg or incubated horizontally in a petri dish with a little water around it. The air temperature should be approx. 24°C and humidity should be high. If the clutches fall into the water after being laid, the eggs will not develop. If they are fertilised, the spawn clumps deposited on the leaf show development after two to three days. At this time, the embryo in each egg can be recognised as an initially rod-shaped structure. Unfertilised clutches and individual unfertilised eggs within a spawning clump show no development as incubation progresses – in these, fungal infestation (saprolegnia) can often be detected, the yolk settles and the jelly becomes cloudy. Although immediately neighbouring eggs sometimes continue to develop without any problems, it is safer to remove such fungal eggs with a large-lumen straw or a biopsy punch. The application of antifungal agents to the clutch is usually unsuccessful because the fungus is more likely to be the result of a previously dead embryo. The tadpoles developing in the clutch initially still have clearly visible external gills that lie against the inside of the egg membranes and with which the larva absorbs the oxygen diffused into the egg. After hatching, however, they regress very quickly and respiration subsequently functions initially via internal gills, then increasingly via the developing lungs.</p> <p>Three ♀♀ laid five clutches totalling 58 eggs in one night, the majority of which hatched after eight days. The fastest development at a water temperature of 24–25°C took only 70 days. The number of eggs per clutch varied at the author's husbandry between 10 and 52, they were laid in one to three clutches of one pair within one night. Other authors describe a development of the larvae in the egg over 7–14 days, the young frogs reached metamorphosis after 69–98 days with a length of 21.5–24 mm. As soon as the tadpoles have front legs, they stop feeding until the tail is completely absorbed and the remodelling of the mouth region is complete. Even at this stage, they emerge from the water on vertical surfaces, so the tadpole pools must be covered. During metamorphosis, the young <i>A. lemur</i> already show greenish colouration. In the aquarium, the losses are low if there is sufficient water volume, quality and feeding (Jungfer &amp; Weygoldt 1994, Proy 2000, Eisenberg 2003b, 2004b, 2006, 2019, Eisenberg &amp; Kaesling 2012).</p> <p>Information from the breeder survey</p> <p>Total length of newly hatched larvae (in mm): estimated 4–5 (n=3)   10 (n=2)   10–13 (n=1)   not specified (n=5).</p> <p>Duration of the larval period (oviposition to metamorphosis; min.–max. [in months]): 1–1.5 (n=1)   1.5–2 (n=4)   usually 2–4 (metamorphosis between first and last larva; n=1)   3–10 (n=1)   not specified (n=4).</p> <p>Special conditions and requirements for larval rearing (including technology and daily time requirements; enumerations): very simple in glass aquaria without substrate, daily time requirement of 10 minutes, tank with aeration pump and bubble stone,</p> |

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|                                                                         | <p>heater, tempered tap water approx. 24°C, daily feeding with fish food, sporadically with salad and vegetables, weekly water change, daily partial water change and offering good quality food are essential, but the species is generally easy to keep, after growth at least 1 l water/tadpole, addition of sea almond tree leaves or tadpole tea to the water (tannins stabilise the water quality), depending on the number of larvae daily 20–60 minutes time requirement, calcium addition to the water   not specified (n=4).</p> <p>– Water temperature (in°C): around 24   approx. 24 during the day, 22 at night   25   23–25 (n=1 each)   20–29 (n=2)   not specified (n=4).</p> <p>– Lighting/type/day-night cycle: Daylight (n=4)   9 h lighting (n=1)   12 h lighting (n=1)   50 W LED strip (12 h) and daylight (n=1)   not specified (n=4).</p> <p>– Container size (length x width x height in cm): 25 x 30 x 20   45 x 30 x 15   60 x 30 x 30   40 litres per 30 larvae   30 x 22 x 17   20 x 50 x 10   50 x 13 x 29 (n=1 each)   not specified (n=4).</p> <p>– Substrate/furnishing/planting: no furnishing/planting (n=5)   oak and beech leaves (n=1)   Java moss and floating aquatic plants, sea almond tree leaves (n=1)   not specified (n=4).</p> <p>– Water depth (in cm): 7–10   10   12   18   25 (n=1 each)   20 (n=2)   not specified (n=4).</p> <p>– Number of animals per container: 10   40 litres of water per 20–30 larvae (n=1 each)   20 (n=2)   up to 50 (n=3)   not specified (n=4).</p> <p>– Filter (type, capacity): mechanical filter only at night to remove food residues (n=1)   no filter (n=3)   airlift sponge filter (n=3)   not specified (n=4).</p> <p>– Tap water with a few alder cones (n=2)   none (n=4)   hardness of tap water approx. 12 °dH (n=1)   daily partial water changes (n=1)   not specified (n=4).</p> <p>– Food of the larvae: Fish flake food (n=3)   red mosquito larvae (n=1)   dried water fleas (n=1)   Viparbaby food and mixture of spirulina, flower pollen, fish food and nettle powder (n=1)   varied food, consisting of chokeberry powder, moringa powder, nettle powder, fish flakes, Pleco tablets/wafers, calcium powder, spirulina powder, all mixed (n=1)   TetraMin, Discus food, spirulina tabs (n=1)   Repashy Super Green (n=1)   not specified (n=4).</p> <p>– Frequency of water changes: daily (n=1)   daily ⅓ to ½ (n=1)   every 2<sup>nd</sup> day 50% (n=1)   weekly (n=3)   partial water change (⅓) once every fortnight (n=1)   not specified (n=4).</p> <p>– Type of water (rainwater, tap water, RO water, etc.): Tap water (n=6)   RO water with minerals (n=1)   not specified (n=4).</p> |
| Number or percentage of offspring that become adults or sexually mature | No information, since the juveniles had been passed on to other keepers (n=1)   70–100 (n=1)   > 90% (n=3)   not specified (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Age/size at sexual maturity                                             | ♂♂ 30 mm; ♀♀ 35–40 mm (n=3)   approx. 1 year for ♂♂, 1–2 years for ♀♀ (n=1)   approx. 1.5 years for ♂♂, nearly 2 years for ♀♀ (n=1)   not specified (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Indicators for reaching sexual maturity                                 | calling and nuptial excrescences of ♂♂ and the larger habitus of ♀♀ (n=2)   call of ♂♂, amplexus (n=1)   call of ♂♂, stagnant growth, sexual dimorphism (n=1)   call of ♂♂, eggs recognisable in the abdomen of ♀♀ (n=1)   not specified (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Sex ratio of the offspring                                              | unknown (n=1)   50/50 (♂♂:♀♀; n=3)   60/40 (♂♂:♀♀; n=1)   not specified (n=6).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Evidence of deformities or diseases                                     | no evidence (n=3)   no malformations, but high susceptibility to parasites, especially helminths ( <i>Strongyloides</i> sp.; n=2)   larval losses presumably due to fungal or bacterial infection; chytrid fungus negative (n=1)   two tadpoles with delayed development, died before metamorphosis (n=1)   not specified (n=4).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Mortality of larvae                                                     | < 5% (n=2)   low mortality (n=1)   < 25% (n=1)   10–50% (n=1)   0–100% (n=1)   very                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |

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| up to metamorphosis                                             | high (n=1)   not specified (n=4).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Mortality in the first months/years of life after metamorphosis | none (n=1)   < 5% (n=3)   0–10% (n=1)   0–30% (n=1)   not specified (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Routine testing for amphibian diseases and parasites            | no (n=3)   parasites 4 x annually, other amphibian diseases only on receipt (n=1)   regular microscopic faecal examinations (n=2)   occasional microscopic faecal examinations (n=1)   faecal check twice for each new group and at least 2 <i>Bd</i> tests (n=1)   daily check for abnormalities (n=1)   not specified (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Quarantine (type and extent)                                    | no new arrivals to date (n=1)   separate quarantine for a fortnight (n=1)   three weeks (n=1)   at least four weeks (n=4)   at least four to six months <sup>18</sup> according to Eisenberg (2003a, 2004a; n=1)   not specified (n=3).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| General characteristics, difficulties with keeping and breeding | Breeding attempts in rain chamber led to amplexus, but not to spawning, temperature previously brought to < 20°C, presumably spawn formation was not yet far enough advanced in the ♀, further breeding attempts are pending (n=1)   the first attempt at larval rearing was unfortunately not successful, the larvae all died one after the other (n=1)   perhaps the tank size should be adjusted to the number of frogs to ensure better food intake. According to this keeper's impression, food animals were difficult to find if the tank was too large. It was also recommended that bean beetles are very suitable as an introductory food so that the frogs can then be familiarised with other food animals such as banded crickets or house crickets (n=1)   not specified (n=7). |
| Frequency of private breeding and reproduction in zoos          | (relatively, very) rare (n=5)   often kept, but not often bred. I think a lot of people do not try to breed the frogs or lose them because they don't clean the terrarium often enough (n=1)   not specified (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Reproduction in captivity up to F2 generation                   | yes (n=3)   no (n=3)   not specified (n=5).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Commercial breeding                                             | yes (n=1)   no (n=10).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Interviews/ Surveys/ Consultations                              | 176 people were contacted and reminded; additionally, as a mailing list to the DGHT AG Anuren and as a survey in the Instagram group 'Glass Frog Breeding COOP' (3,600 members) and WhatsApp group 'Dendrobates Germany' (201 members): 11 responses on this species (UK, Italy, Belgium, Czech Republic, n=1 each, Germany, n=7, including participants in the <i>A. lemur</i> breeding programme of Citizen Conservation, n=5).                                                                                                                                                                                                                                                                                                                                                            |

<sup>18</sup> Small, sterile terrariums (e.g. 30 x 60 x 20 cm) with front and lid wire gauze ventilation and climbing plants (*Philodendron* spp.) without substrate are suitable for this purpose. A moat with overflow serves as a water reservoir. The quarantine should last at least eight weeks and up to six months. During this time, PCR tests are carried out for *Batrachochytrium dendrobatidis*, *Batrachochytrium salamandrivorans*, *Ranavirus*, *Chlamydia* and *Brucella* as well as coproscopic tests for parasites (T. Eisenberg, unpublished data).





Fig. 62: Captive breeding of *Agalychnis lemur* (all photos by T. Eisenberg)

- a terrarium system
- b frontside view of a breeding terrarium
- c 'false' amplexus between two males
- d two clutches of eggs. Note a few unfertilized eggs per clutch (white)
- e recently hatched larvae
- f tadpoles with developing hindlegs
- g metamorphling
- h adult Lemur Leaf frogs (male left, females centre and right).

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**Tobias Eisenberg (15.08.2024)**



## Caudata

## Salamandridae

*Laotriton laoensis* (Stuart & Papenfuss, 2002)

| Species                   | Original description       | Common name     | Common name international | Known in the trade |
|---------------------------|----------------------------|-----------------|---------------------------|--------------------|
| <i>Laotriton laoensis</i> | (Stuart & Papenfuss, 2002) | Laos warty newt | Laos-Warzenmolch          | yes                |



Fig. 63: *Laotriton laoensis* (all photos P. Bachhausen)

- a adult ♀
- b ♂ underbelly marking
- c Juveniles 3 months after metamorphosis
- d Eggs in series, oviposition between long-leaved foliage. Leaf removed on one side
- e F2 offspring at the beginning of metamorphosis
- f Eggs, development status approx. 2 weeks after oviposition.

## Morphology and Taxonomy

*Laotriton* (Dubois & Raffaëlli 2009) is a monotypic genus, which since 2009 has distinguished the Lao newt as the only representative of the genus morphologically (Stuart & Papenfuss 2002) and molecularly (Zhang et al. 2008) from the genus *Paramesotriton*. In 2002, the species was described as *Paramesotriton laoensis*. It is a very large newt with a total length of 170–190 mm. The ♀♀ reach up to 230 mm (Bachhausen 2007), about half of which is accounted for by the tail. The tail of the ♀♀ is relatively longer than that of the ♂♂. The body appears strong overall. The head is broad and blunt. The back has two warty lateral bars and a medial bar. The ground colour is black. Along the three dorsal ridges, in the area of the parotoids, on the top of the head and on the forelegs the animals show a characteristic colouring in mostly intense sulphur yellow (sometimes also brownish or slightly orange). The yellow markings vary from individual to individual and can be used as a distinguishing feature in adults. Sometimes the yellow can cover the entire dorsal surface. On the head, the parotoids are clearly visible and also yellow. The belly is black with large, bright orange irregularly arranged spots. The first third of the lower edge of the tail and the cloaca are also orange-red. The dorsal skin has numerous additional tubercles in addition to the warty ridges, which are weaker on the flanks and absent on the belly. The sexual dimorphism is particularly pronounced during the reproductive period. The ♂♂ then show a silvery-blue band on the sides of the tail, which consists of numerous spots. The silver-blue markings fade during the rest of the period, but are still recognisable as grey markings. Besides the longer tail, the ♀ also shows a somewhat elongated cloaca, while that of the ♂ is flat hemispherical. The ♀ cloaca protrudes conically up to about 10 mm during the spawning season. The iris of the eye of *L. laoensis* is completely black. The juveniles already show distinct yellow/orange dorsal lines during metamorphosis. The spotting of the ventral markings develops in the first months after metamorphosis.

## Distribution and Habitat

Terra typica: Laos, Saysamboun Special Zone, in pools of the Houay Sang Kat stream (18° 52'49 N 103° 06' 32 E; 1160 m asl) at the foot of Phou Sang Kat Mountain, Xieng Khouang province. Other occurrences have been found in Houay Pa Tin and in Phoukhoudt province of Xieng Khouang near Ban Nyot Phae in the north of the country at an altitude of 1,450–1,500 m (Bachhausen & Espallargas 2008). Overall, the occurrence areas are small, covering an area of only 556 km<sup>2</sup> according to current data (Raffaelli 2007).

*L. laoensis* is a specialised flowing water inhabitant that occurs in slow-flowing 1–4 m wide streams around 1,500 m. These are relatively cool (16–20°C) and sometimes hardly shaded. The streams form some scours. The water temperature in August was 19 °C. (Bachhausen & Espallargas 2008). The watercourses have many small waterfalls and are described as being devoid of vegetation, although they do have some riparian vegetation hanging down into the water. Their bottom is covered with sand, boulders and larger rocks. The adults are mainly found in the deep scours (sometimes more than 1.5 m) where the current decreases. After metamorphosis, the juveniles first go ashore, but move no more than a few metres away from the shore. Individuals of the genus *Laotriton* are not territorial, in contrast to the representatives of the closely related genus *Paramesotriton*. They are also diurnal in the habitat. No intraspecific aggression has been observed so far (Raffaelli 2007).



## Conservation Status and Main Threats

CITES Appendix II since 2022 (CoP19 Proposal 36) with a zero annual export quota for wild-caught animals for commercial purposes.

EU Council Regulation (EC) No 338/97: Annex B.

In Germany specially protected under Article 7 (2) No 13 BNatSchG.

Classified as Category I in the Lao National Law for the Protection of Wildlife and Waters since 2008, i.e., catching for trade has been completely banned since then.

## IUCN Red List Status

EN (Endangered B1ab(iii,v), assessed October 16, 2013).

## Threats

The main threat to this species, despite legal protection measures, is capture for the international pet trade, medicinal use and local consumption (Phimmachak et al. 2012; Rowley & Stuart 2014). As the newts are diurnal and conspicuously brightly coloured on the back and live on the bottom of shallow and clear waters, they can be collected there quickly, easily and in large numbers – especially during the breeding season (Stuart & Papenfuss 2002, Phimmachak et al. 2012). It is quite possible to collect all sexually mature specimens within a few days at one site, which is why they have sometimes even been sold as ‘hundreds’ of specimens or by the kilo (S. Phimmachak & B. L. Stuart pers. obs. mid-October 2013). New roads being built within the known range of the species are making it easier to reach more water bodies and also to transport captured animals away quickly. Habitat loss and alteration are also a threat to the species. Although these newts are likely to be able to adapt to minor man-made habitat changes, they suffer from severe changes in water quality or flow in streams, and from extensive burning of grasslands near streams, i.e., the habitat of juveniles (Phimmachak et al. 2012).

## Reproduction

| Topic                               | Details on the reproduction of <i>Laotriton laoensis</i>                                                                                                                                   |
|-------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Secondary sexual characters         | During the mating season clear sex differences: ♂♂ have stronger lateral edges and higher tail fringe than ♀♀. ♂♂ have a swollen cloaca and a silvery-white iridescent stripe on the tail. |
| Reproduction                        | Oviparous, internal fertilization.                                                                                                                                                         |
| Sexual maturity                     | In captivity ♂♂ 3–4 years, ♀♀ 4–5 years, probably longer in the natural habitat.                                                                                                           |
| Mating and spawning                 | Individually, or preferably in small series, between long leaves of underwater vegetation.                                                                                                 |
| Reproductive season                 | In winter at water temperatures of 16–18°C.                                                                                                                                                |
| Eggs/clutch, clutches/year          | About 100–300 eggs/year.                                                                                                                                                                   |
| Size of eggs and larvae at hatching | Eggs have an inner diameter of about 2.5–3 mm; with jelly capsule of 3.5 * 5 mm. Hatch size approx. 1.2–1.5 cm total length.                                                               |
| Development duration                | 4–5 weeks at 18–20°C. Time to metamorphosis 3–6 months, depending on husbandry conditions.                                                                                                 |

|                           |                                                                                                                                                                           |
|---------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| tion egg to metamorphosis |                                                                                                                                                                           |
| Sex determination         | Initially not possible with juveniles, still very difficult with semi-adults. During the mating season, however, very easy, otherwise well possible on closer inspection. |
| Sperm storage             | Not known.                                                                                                                                                                |

## Husbandry and Captive Breeding **B/B**

| Topic                                                           | Data for <i>Laotriton laoensis</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|-----------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Trigger for reproduction                                        | For reproduction, a temperature drop to 15–16°C is necessary in late autumn. A renewed rise in temperature triggers egg laying from 16–18°C.                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Husbandry requirements                                          | Aquatic husbandry with seasonally adapted temperatures between 15 and 25°C. Aquarium size: from 100 x 40 cm, water depth: 30–50 cm.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| General characteristics, difficulties with keeping and breeding | <p>Adults can be kept as pairs or in groups in sufficiently large aquaria (minimum dimensions approximately 100 x 40 x 40 cm). Several hiding places, and at least a small terrestrial part, are required.</p> <p>Plants with long-leaved structures or comparable plastic strips must be offered for egg-laying.</p> <p>Regular, generous water changes and refilling with cooler water will help to make them ready to mate.</p> <p>Newly introduced animals to the stock could be carriers of the salamander fungus Bsal. They should be tested for this when they are taken over and when they are rehomed.</p> |
| Care of the young, technical and time effort                    | <p>The eggs should be removed from the container of the parents, as they eat both eggs and larvae of their own species.</p> <p>Very hygienic conditions are required for rearing the larvae; this is done at temperatures of approx. 19°C. The rearing of freshly metamorphosed animals also requires the greatest attention to hygiene and the provision of different humidity ranges.</p>                                                                                                                                                                                                                         |
| Life expectancy                                                 | As the species has only been known since 2002, its life expectancy can only be estimated. It is probably over 30 years. Successfully reproducing animals with an age of at least 23 years are known.                                                                                                                                                                                                                                                                                                                                                                                                                |
| Frequency of private breeding and reproduction in zoos          | <p>Few private breeders – since 2007 regular offspring; up to the F3 generation.</p> <p>Has also been kept and bred in some zoos, the first breeding in a zoo was probably in 2016, in Newquay (Graf et al. 2024).</p>                                                                                                                                                                                                                                                                                                                                                                                              |
| Breeding difficulty evaluation                                  | Problem-free with experienced breeders. High standard of hygiene required for larvae and rearing of juveniles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Mortality in the first years of life                            | Low in optimal husbandry conditions, but high losses in suboptimal conditions!                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| F2 generation bred in captivity                                 | Repeated breeding successes up to F3 generation are documented (Bachhausen 2017).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Commercial breeding/ranching                                    | No commercial breeder known in the EU.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| Interviews/ Surveys/ Consultations                              | 16 private breeders.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |

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**Paul Bachhausen (14.10.2023).**

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## Acronyms and Abbreviations

| Acronym/<br>Abbreviation | Explanation                                                                                                                                                                                                                                                                                                                                                                                     |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| a                        | Annum (year, years)                                                                                                                                                                                                                                                                                                                                                                             |
| asl                      | Above sea level                                                                                                                                                                                                                                                                                                                                                                                 |
| BArtSchV                 | In German: Bundesartenschutzverordnung. Federal Species Protection Regulations                                                                                                                                                                                                                                                                                                                  |
| BfN                      | Bundesamt für Naturschutz, German Federal Agency for Nature Conservation                                                                                                                                                                                                                                                                                                                        |
| BGBI                     | Bundesgesetzblatt, Federal Law Gazette                                                                                                                                                                                                                                                                                                                                                          |
| BMEL                     | Federal Ministry of Food and Agriculture [Bundesministerium für Ernährung und Landwirtschaft], editor of the guideline 'Mindestanforderungen an die Haltung von Reptilien'                                                                                                                                                                                                                      |
| BMUV                     | Bundesministerium für Umwelt, Naturschutz, nukleare Sicherheit und Verbraucherschutz, Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection                                                                                                                                                                                                         |
| BNatschG                 | In German: Bundesnaturschutzgesetz. Federal Nature Conservation Act in the version promulgated on 06 August 2009 (Federal Law Gazette [Bundesgesetzblatt] I page 2542)                                                                                                                                                                                                                          |
| CB                       | 'Captive Bred', an animal that was born or hatched in captivity                                                                                                                                                                                                                                                                                                                                 |
| CL                       | Carapacial length, length of the chelonian shell measured in straight line                                                                                                                                                                                                                                                                                                                      |
| DGHT                     | Deutsche Gesellschaft für Herpetologie und Terrarienkunde, German Society for Herpetology and Terrarium Science                                                                                                                                                                                                                                                                                 |
| EAZA                     | European Association of Zoos and Aquaria                                                                                                                                                                                                                                                                                                                                                        |
| F1, F2                   | First or second offspring generation (= filial generation)                                                                                                                                                                                                                                                                                                                                      |
| IUCN                     | International Union for Conservation of Nature                                                                                                                                                                                                                                                                                                                                                  |
| CB                       | 'Captive Bred', an animal that was born or hatched in captivity                                                                                                                                                                                                                                                                                                                                 |
| s.l./s.str               | Sensu lato/sensu stricto. Sensu is used in the taxonomy of living creatures to specify which circumscription of a given taxon is meant, where more than one circumscription can be defined. Sensu lato ('in the broad sense') used when referring to more than one valid taxon, sensu stricto ('in the strict sense') refers to the one taxon out of a taxon group, mostly to the nominate form |
| SD                       | Sex determination – TSD: Temperature dependent sex determination/GSD: Genetic sex determination                                                                                                                                                                                                                                                                                                 |
| SVL                      | Snout-Vent Length                                                                                                                                                                                                                                                                                                                                                                               |
| TL                       | Total Length                                                                                                                                                                                                                                                                                                                                                                                    |
| VDA                      | Verband Deutscher Vereine für Aquarien- und Terrarienkunde                                                                                                                                                                                                                                                                                                                                      |

## Relevant CITES Source Codes

| CITES Source Code | Explanation                                                                                                                                                                                                                      |
|-------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| C                 | ‘Captive bred’ (UNEP-WCMC 2024): Animals bred in captivity in accordance with Resolution Conf. 10.16 (Rev.), as well as parts and derivatives thereof. This labeling should not get mixed up with the German term NZ (Nachzucht) |
| F                 | ‘Captive born’: Specimens born or hatched in controlled environment, but do not meet the requirements for ‘C’ (see above) according to CITES Res. Conf. 10.16                                                                    |
| I                 | Confiscated or seized specimens                                                                                                                                                                                                  |
| O                 | Pre-convention; the specimen was obtained before the CITES listing of the species                                                                                                                                                |
| R                 | ‘Ranched’; eggs, larvae or juveniles that were taken from the wild and were raised under controlled captive conditions. Usually, some part of the raised adults is released back to the habitat                                  |
| W                 | Wild caught animal                                                                                                                                                                                                               |

## Glossary

| Keyword               | Explanation                                                                                                                                                                                                                 |
|-----------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| ♂; ♂♂                 | One male; several males                                                                                                                                                                                                     |
| ♀; ♀♀                 | One female; several females                                                                                                                                                                                                 |
| 1,2,3                 | Group composition; first position: number of ♂♂, second position: number of ♀♀, third position: number of juveniles of unknown sex                                                                                          |
| Adult                 | Full grown resp. sexually mature specimen(s)                                                                                                                                                                                |
| aestivation           | Prolonged torpor through hot and dry seasons                                                                                                                                                                                |
| Allochthonous species | Alien, non-native, species which had been introduced by humans.                                                                                                                                                             |
| allopatric            | Biological populations that have become geographically isolated from each other.                                                                                                                                            |
| amplexus              | A form of copulation, found chiefly in amphibians, in which the ♂ grasps the ♀ with his front legs as part of the mating process.                                                                                           |
| animal pole           | Egg development: The animale pole of the egg consists of rapidly dividing cells (hence the name: ‘alive, animalistic’), see also vegetative pole.                                                                           |
| anterolateral         | Located in front and sideways.                                                                                                                                                                                              |
| antivenin, anti-venom | Specific treatment for envenomation. It is composed of antibodies and used to treat certain venomous bites and stings.                                                                                                      |
| aquatic               | Living in water (semi-aquatic: spending parts of their time or life-cycle in water).                                                                                                                                        |
| arboricolous          | Arboreal; living in trees.                                                                                                                                                                                                  |
| arciferal             | Arciferal refers to a morphology of the pectoral girdle of frogs. For comparative anatomy see Hildebrand & Goslow (2001).                                                                                                   |
| areola                | Central plate of the shield in tortoises, the remainder of the hatchling’s first shield. The growth rings are deposited around this areola.                                                                                 |
| areolate              | With small raised warts.                                                                                                                                                                                                    |
| autochthonous species | An autochthonous, or a native, species is indigenous to a given region or ecosystem if its presence in that region is the result of only local natural evolution (though often popularized as ‘with no human intervention). |

| Keyword                 | Explanation                                                                                                                                                                                                                                                                                                                                                                                                           |
|-------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| autopsy                 | An autopsy or post-mortem examination is a surgical procedure that consists of a thorough examination of a corpse by dissection to determine the cause, mode and manner of death or to evaluate any disease or injury that may be present for research or educational purposes.                                                                                                                                       |
| Biopsy punch            | Tool for precise removal of small samples – here: for removing individual non-developing eggs from a frog egg clutch.                                                                                                                                                                                                                                                                                                 |
| biotope preference      | Preference for a certain habitat (and environmental conditions).                                                                                                                                                                                                                                                                                                                                                      |
| blackworm               | The name blackworm is given to at least three distinct <i>Lumbriculus</i> species that are identical in appearance and were once considered a single species.                                                                                                                                                                                                                                                         |
| bloodworm               | The larvae of a non-biting midge (Family Chironomidae) containing hemoglobin.                                                                                                                                                                                                                                                                                                                                         |
| brumation               | Winter dormancy of reptiles and amphibians                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Bsal</i> , <i>Bd</i> | <i>Batrachochytrium salamandrivorans</i> ( <i>Bsal</i> ) is a pathogenic chytrid fungus that infects amphibian species, <i>Batrachochytrium dendrobatidis</i> is a fungus that causes the disease chytridiomycosis in amphibians. In order to prevent further spread, if possible, it is essential to follow the measures described in the two Citizen Conservation/DGHT (2020) documents when handling live animals. |
| Canthal crest           | ‘Muzzle edge’, the more or less angular ridge from the anterior border of the eye to the nostril.                                                                                                                                                                                                                                                                                                                     |
| captive breeding        | (Continuous) reproduction of a species in captivity.                                                                                                                                                                                                                                                                                                                                                                  |
| carapace                | Dorsal part of the shell of turtles and tortoises.                                                                                                                                                                                                                                                                                                                                                                    |
| carnivorous             | is an animal whose food and energy requirements derive mainly or solely from animal products through hunting or carrion-eating.                                                                                                                                                                                                                                                                                       |
| chagrinised             | Leather-like grained, with fine, closely spaced raised and recessed areas on the surface.                                                                                                                                                                                                                                                                                                                             |
| Chaparral               | A sclerophyllous vegetation that is tolerant of seasonal drought. It consists of small trees, woody grasses and oleose, xerophytic shrubs.                                                                                                                                                                                                                                                                            |
| chorioallantois         | The chorioallantois is a highly vascularised membrane found in the eggs of certain amniotes such as birds and reptiles. It is used for the exchange of gases (oxygen and carbon dioxide), the transport of calcium from the eggshell to the embryo and the absorption of water and electrolytes.                                                                                                                      |

| Keyword            | Explanation                                                                                                                                                                                                                                                                                                                                          |
|--------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| chromatophore      | ‘Colour’ cells in the skin which contain pigments or reflecting structures.                                                                                                                                                                                                                                                                          |
| Chytridiomycosis   | Chytridiomycosis is a fungal disease (mycosis) in amphibians. It is caused by the chytrid fungi <i>Batrachochytrium dendrobatidis</i> and <i>Batrachochytrium salamandrivorans</i> .                                                                                                                                                                 |
| clade              | A group of organisms that are monophyletic – that is, composed of a common ancestor and all its lineal descendants.                                                                                                                                                                                                                                  |
| cloaca             | A cloaca is the posterior orifice that serves as the only opening for the digestive, reproductive, and urinary tracts of many vertebrate animals (all amphibians and reptiles). The opening at the vent.                                                                                                                                             |
| CONABIO            | Comisión Nacional para el Conocimiento y Uso de la Biodiversidad of Mexico. Responsible, for example, for maintaining the list of invasive species.                                                                                                                                                                                                  |
| conspecific        | Belonging to the same species.                                                                                                                                                                                                                                                                                                                       |
| coralline          | The origin of this material is corals.                                                                                                                                                                                                                                                                                                               |
| costal node        | Distinctly protruding, often deviantly colored, glandular elevations on the ribs of certain newt species.                                                                                                                                                                                                                                            |
| Crista medialis    | Inner bone ridge on the humerus of some glass frogs.                                                                                                                                                                                                                                                                                                 |
| cryptic species    | Different species that look very similar externally and were therefore initially classified as a single species.                                                                                                                                                                                                                                     |
| delayed hatching   | The fully developed hatchling remains in the egg until an external stimulus (increased humidity, increased temperature) triggers the hatching process.                                                                                                                                                                                               |
| denticles          | Small tooth or bristle-like structures. Dental feature: serrations on the teeth of dinosaurs, lizards, sharks and mammals.                                                                                                                                                                                                                           |
| distal             | lying further away from the centre of the body (opposite: proximal).                                                                                                                                                                                                                                                                                 |
| dominant frequency | The dominant frequency describes the frequency at which the main energy of the call [in frogs] lies. It is dependent on the temperature. The dominance frequency is typical of the species and can, under comparable recording conditions, contribute to the identification of the species as a taxonomic characteristic (Durate-Marín et al. 2023). |
| dorsal             | Anatomical term of location referring to the back or upper side of an organism.                                                                                                                                                                                                                                                                      |
| dorsoanterior      | Anterior part of the dorsal side of the animal.                                                                                                                                                                                                                                                                                                      |
| emarginate         | with a notched tip.                                                                                                                                                                                                                                                                                                                                  |



| Keyword                            | Explanation                                                                                                                                                                                                                      |
|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| embryonic diapause                 | Developmental arrest, frequently directly after laying, when the conditions are not yet optimal for development, e. g. due to low oxygen content in the soil.                                                                    |
| endoscopy                          | The endoscopy procedure uses an endoscope to examine the interior of a hollow organ or cavity of the body with the help of an optical probe head.                                                                                |
| epiphyte                           | An epiphyte is an organism that grows on the surface of a plant and derives its moisture and nutrients from the air and rain or from debris accumulating around it.                                                              |
| Epiweb                             | Synthetic plant substrate made from 70% recycled plastic.                                                                                                                                                                        |
| exo-occipital                      | Bone besides the great foramen.                                                                                                                                                                                                  |
| fibula                             | One of the two bones in the lower leg, alongside the tibia.                                                                                                                                                                      |
| Firebrat                           | <i>Thermobia domestica</i> , a primitive insect used as food for small amphibians and reptiles.                                                                                                                                  |
| follicle                           | An ovarian follicle is a roughly spheroid cellular aggregation set found in the ovaries. The term is often used for eggs in the oviducts prior to shelling.                                                                      |
| Frontline®                         | Treatment agent for snake mites <i>Ophionyssus natricis</i> . Active substance is Fipronil; discuss treatment with a vet or experienced keepers.                                                                                 |
| gestation                          | Pregnancy (for truly live-bearing species)/Gravidity. Period from fertilization to birth/egg laying.                                                                                                                             |
| Glycosaminoglycans                 | Abbreviated to GAG: polysaccharides form the basic substance for connective tissue (tendons, joint cartilage and capsules), as they can bind water and are therefore particularly elastic.                                       |
| gonads                             | Internal sexual organs.                                                                                                                                                                                                          |
| gulars, gular scales, gular scutes | Scales in the central or throat region of lizards and snakes, in chelonians the gular(s) are the most anterior part of the plastron. Some chelonians have paired gular scutes, while others have a single undivided gular scute. |
| gular fold                         | A granular fold found on the ventral throat, located immediately in front of the forelegs, in lizards (Iguanidae) and some other reptiles.                                                                                       |
| gut loading                        | Food animals are often fed with special vitamin- and mineral-rich foods, with the intention of passing those nutrients to the animal for which the prey animal is intended.                                                      |
| halo                               | Coloured ring, blurring towards the outside.                                                                                                                                                                                     |

| Keyword          | Explanation                                                                                                                                                                                                                                                                                                             |
|------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| hatchling        | Freshly hatched juvenile reptile.                                                                                                                                                                                                                                                                                       |
| hemipenis        | A hemipenis (plural hemipenes) is one of a pair of intromittent sexual organ of ♂ squamates (snakes, lizards).                                                                                                                                                                                                          |
| hepatic          | Located near the liver, influenced by the liver.                                                                                                                                                                                                                                                                        |
| herbivore        | An herbivore is an animal anatomically and physiologically adapted to eating plant material.                                                                                                                                                                                                                            |
| heterospecific   | Two individuals are heterospecific if they are considered to belong to different biological species.                                                                                                                                                                                                                    |
| hibernation      | The term is often incorrectly used for reptiles that actually only go into brumation (see above).                                                                                                                                                                                                                       |
| holotypus        | A single (museum) specimen that has already been determined as the name-bearing type when a species or subspecies was established.                                                                                                                                                                                      |
| humeral spine    | Osseous hooks on the upper arm of ♂ frogs, which can be used in combat fights.                                                                                                                                                                                                                                          |
| humidity         | Short for: Relative atmospheric humidity. It is important for the incubation of reptile eggs.                                                                                                                                                                                                                           |
| incertae sedis   | A term used for a taxonomic group where its broader relationships are unknown or undefined.                                                                                                                                                                                                                             |
| incubation media | For captive breeding reptile eggs are often incubated in special incubators, and buried in incubation media to provide a constant humidity. Popular industrially produced incubation media are vermiculite, perlite, seramis or orchid chips, or simply sand, sometimes mixed with peat or soil (see also Köhler 2004). |
| infralabialia    | Scales on the lower jaw.                                                                                                                                                                                                                                                                                                |
| intercalaria     | Rows of smaller scales between the rows of large tail scales in lizards.                                                                                                                                                                                                                                                |
| interorbital     | Between the eye cavities.                                                                                                                                                                                                                                                                                               |
| invasive species | In nature conservation, this term is used for alien species that have undesirable effects on other species, biotic communities or biotopes. For example, invasive species compete with native species for habitat and resources and may even displace them.                                                             |
| iridophores      | Chromatophores that reflect light using plates of crystalline chemochromes made from guanine. When illuminated they generate iridescent colours because of the constructive interference of light.                                                                                                                      |
| Jacobson's organ | The vomeronasal organ or Jacobson's organ, is the paired auxiliary olfactory sense organ located just above the roof of the mouth.                                                                                                                                                                                      |

| Keyword          | Explanation                                                                                                                                                                                                                                                                                                  |
|------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Keratodont       | A tooth-like structure, composed of keratin, which is observed in anuran tadpoles.                                                                                                                                                                                                                           |
| KUDA             | Photo reference number in the University of Kansas Digital Archive (KUDA).                                                                                                                                                                                                                                   |
| lecithotrophy    | A form of development in which the embryo receives no nutrition other than the yolk originally contained within its egg. Some reptile species give birth to live offspring, which were not provided with nutrients via a placenta but via the egg yolk. Offspring hatches out of the permeable egg at birth. |
| loreal region    | The region between the eyes and nostrils.                                                                                                                                                                                                                                                                    |
| LTRF             | Labial tooth row formula.                                                                                                                                                                                                                                                                                    |
| Marginals        | The rim shields of the carapace of turtles.                                                                                                                                                                                                                                                                  |
| maxilla          | In vertebrates the upper bone of the jaw.                                                                                                                                                                                                                                                                    |
| mechanoreceptor  | Sensory receptor that responds to mechanical pressure or distortion.                                                                                                                                                                                                                                         |
| median           | In the middle.                                                                                                                                                                                                                                                                                               |
| melanophores     | Chromatophores containing black pigment.                                                                                                                                                                                                                                                                     |
| metacarpal bones | The bones that form the intermediate part of the hand between the fingers and the wrist. For comparative anatomy see Hildebrand & Goslow (2001).                                                                                                                                                             |
| metachrosis      | Physiological colour change, e.g. in chameleons or frogs.                                                                                                                                                                                                                                                    |
| metamorphosis    | The young amphibians generally undergo metamorphosis from larva with gills to an adult air-breathing form with lungs. A metamorph of an amphibian is an animal which has undergone metamorphosis.                                                                                                            |
| microbiome       | The entirety of microorganisms that live on and in an animal.                                                                                                                                                                                                                                                |
| mimesis          | The resemblance or similarity of an animal species to a feature of its natural surroundings, developed in order to gain some advantage from predators.                                                                                                                                                       |
| monophyletic     | Monophyly is the condition of a taxonomic grouping being a clade. Monophyletic groups are typically characterised by shared derived characteristics (synapomorphies), which distinguish organisms in the clade from other organisms, see Wägele (2005) for the basic principles.                             |
| monotypic        | A monotypic taxon is a taxonomic group (taxon) that contains only one immediately subordinate taxon.                                                                                                                                                                                                         |

| Keyword          | Explanation                                                                                                                                                                                                                                                                                                                                                                  |
|------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| morphogenesis    | Development in the egg to the fully formed hatchling.                                                                                                                                                                                                                                                                                                                        |
| morphometrics    | Quantitative analysis. Morphometrics can be used to quantify a trait of evolutionary significance.                                                                                                                                                                                                                                                                           |
| mosquito larvae  | Larvae and pupae of different mosquito (Culicidae) genera, often called 'wigglers' make a good food source for water-living amphibians as well as for small reptiles that take food from the water. If feeding them alive be sure to use them up quickly, before they turn into adult mosquitoes. Many terrarium animals also feed on them when frozen and carefully thawed. |
| myotome          | A myotome is the group of muscles that a single spinal nerve innervates.                                                                                                                                                                                                                                                                                                     |
| necrosis         | A form of cell injury which results in the premature death of cells in living tissue by autolysis.                                                                                                                                                                                                                                                                           |
| neoteny          | The retention of larval traits in sexually mature individuals, as sometimes seen in newts and salamanders.                                                                                                                                                                                                                                                                   |
| Neozoa           | Neozoa are animal species that do not occur here naturally, but have only come to us as a result of human influence. They are therefore alien or non-native species – sometimes they are inaccurately referred to as 'exotic' or 'alien' species.                                                                                                                            |
| neurotoxic       | Neurotoxicity is a form of toxicity in which a biological, chemical, or physical agent produces an adverse effect on the structure or function of the central and/or peripheral nervous system.                                                                                                                                                                              |
| nuchal           | In the neck region. Nuchal scute: At the anterior of the tortoise or turtle shell there may be a single nuchal scute.                                                                                                                                                                                                                                                        |
| ocelli           | Eye spots.                                                                                                                                                                                                                                                                                                                                                                   |
| odontophores     | Tooth-bearing projections in the jaw.                                                                                                                                                                                                                                                                                                                                        |
| oedema           | Or edema, also known as fluid retention, dropsy, hydrops and swelling, is the build-up of fluid in the body's tissue.                                                                                                                                                                                                                                                        |
| olfactory        | The sense of smell, or olfaction, is the special sense through which smells (or odors) are perceived.                                                                                                                                                                                                                                                                        |
| omnivorous       | Including both animal and vegetable tissue in the diet.                                                                                                                                                                                                                                                                                                                      |
| omphalopla-centa | A type of yolk sac placenta unique to viviparous skinks and other viviparous squamates.                                                                                                                                                                                                                                                                                      |

| Keyword                  | Explanation                                                                                                                                                                                                                                                                                                                                                             |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| oomycetes                | The oomycetes are also often referred to as water molds, although the water-preferring nature which led to that name is not true of most species, which are terrestrial pathogens.                                                                                                                                                                                      |
| orchid chips             | Styrofoam chips as an addition to orchid potting soil. Often used as an incubation medium for reptile eggs.                                                                                                                                                                                                                                                             |
| osteoderm                | Osteoderms are bony deposits forming scales, plates, or other structures based in the skin.                                                                                                                                                                                                                                                                             |
| oviparous, ovoviviparous | Laying eggs. In ovoviviparous species the eggs develop within the mother's body, and the eggs hatch directly at, or shortly after, laying.                                                                                                                                                                                                                              |
| Oxytocine                | A peptide hormone and neuropeptide normally produced in the hypothalamus. In veterinary medicine Oxytocine preparations are sometimes used for the induction of laying in egg bound reptiles.                                                                                                                                                                           |
| palmitoleic acid         | An omega-7 fatty acid, contained in food insects (for example house crickets) if these have previously been gut-loaded.                                                                                                                                                                                                                                                 |
| papillae                 | Wart-like protrusions on the skin or mucous membrane. Can be a diagnostic feature for determining the species of tadpoles.                                                                                                                                                                                                                                              |
| paraspecific             | A polyvalent snakebite antivenin that includes a paraspecific antibody that protects against bites from this and other closely related snake species.                                                                                                                                                                                                                   |
| parotoids                | The parotoid gland is an external skin gland on the back, neck, and shoulder of salamanders. In frogs and toads, the similar glands should be called parotoids, and the often-used term 'parotid glands' should be restricted to the salivary glands of mammals (Tyler et al. 2001).                                                                                    |
| paravertebral scales     | Scales besides of the vertebral column.                                                                                                                                                                                                                                                                                                                                 |
| parietal eye             | Also known as a third eye or pineal eye, is a part of the epithalamus present in some species of fish, amphibians and reptiles.                                                                                                                                                                                                                                         |
| pelvic patch             | pelvic area specialised for fluid absorption                                                                                                                                                                                                                                                                                                                            |
| pericardium              | The pericardium is a tough fibroelastic sac which covers the heart.                                                                                                                                                                                                                                                                                                     |
| peritoneum               | The serous membrane forming the lining of the abdominal cavity. The colouration of the peritoneum (clear or iridescent white) is an important distinguishing feature in anurans. The parietal P. lines the entire inside of the abdominal wall, the visceral or gastrintestinal P. surrounds the intestines, the pericardial P. the heart and the hepatic P. the liver. |



| Keyword                           | Explanation                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|-----------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Perlite                           | An amorphous volcanic glass, that has a relatively high water content, typically formed by the hydration of obsidian. Often used as an incubation substrate.                                                                                                                                                                                                                                                                                                                                                                                                                          |
| phalanges                         | The bones that make up the fingers of the hand and the toes of the foot.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| pholidosis                        | The layout or disposition of the scales of reptiles.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| PIMVS                             | Abbreviation for 'Predios e Instalaciones que Manejan Vida Silvestre'. Exhibition or breeding centres in Mexico that mostly keep and often breed and sell native animal species, but also non-native species.                                                                                                                                                                                                                                                                                                                                                                         |
| pivotal temperature               | Also called pivotal temperature: In reptiles with temperature-dependent sex determination this is the constant incubation temperature yielding a 1:1 hatchling gender ratio. In many chelonians a higher incubation temperature will yield more ♀♀ than ♂♂ hatchlings, while in many geckos and in most crocodiles and alligators the reverse is true.                                                                                                                                                                                                                                |
| plastron                          | Ventral part of the turtle shell.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| polygynous mating                 | One ♂ mates with several ♀♀.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| postorbital scale                 | A scale behind the eye.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| prepollex                         | An additional phalange or rudiment of a phalange on the inner (preaxial) side of the thumb. For comparative anatomy see Hildebrand & Goslow (2001). Prepollicular spine: Bone spine on the prepollex.                                                                                                                                                                                                                                                                                                                                                                                 |
| presacral                         | Lying in front of the sacrum. The sacrum lies in the lower part of the spine. It consists of five fused vertebrae.                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| prevomer                          | One of the palatine bones, see also Vomer                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| pressure immobilization technique | The pressure immobilization technique is a first aid treatment used for treating spider bites, snake bites, or bee, wasp and ant stings in allergic individuals, blue ringed Octopus stings, cone shell stings, etc. The object of pressure immobilization is to contain venom within a bitten limb and prevent it from moving through the lymphatic system to the vital organs. This therapy has two components: pressure to prevent lymphatic drainage, and immobilization of the bitten limb to prevent the pumping action of the skeletal muscles. This method is not undisputed. |
| probing                           | Probing a snake or lizard involves inserting a thin metal rod (called a snake probe) into the vent (cloacal opening) for sexing.                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| probiotics                        | Live bacterial cultures that can help to stabilise the intestinal flora again after antibiotic or protozoa treatment or worming – they are also recommended for acclimatising wild-caught animals or for animals                                                                                                                                                                                                                                                                                                                                                                      |

| Keyword            | Explanation                                                                                                                                                                                                                                                                                                                                                                                                                                |
|--------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                    | stressed for other reasons. There are now also some preparations specifically for reptiles. For amphibians, special solutions containing bacteria can help to prevent skin diseases.                                                                                                                                                                                                                                                       |
| procoagulant       | Promoting blood clotting (coagulation).                                                                                                                                                                                                                                                                                                                                                                                                    |
| proximal           | Located closer to the centre of the body (opposite: distal).                                                                                                                                                                                                                                                                                                                                                                               |
| psammophilic       | An organism that prefers or thrives in sandy soils or areas.                                                                                                                                                                                                                                                                                                                                                                               |
| pterygoid          | A bone of the palate of many vertebrates.                                                                                                                                                                                                                                                                                                                                                                                                  |
| pygal              | Posterior bone plate of the carapace in turtles, above the tail.                                                                                                                                                                                                                                                                                                                                                                           |
| pyramiding         | Pyramiding is a shell deformity of captive tortoises, in which the shell grows unevenly resulting in a pyramid shape underlying each scute. Factors which may contribute to pyramiding include inadequate water supply; the consumption of excessive animal or vegetable protein; inadequate calcium, UVB and/or vitamin D3; poor nutrition, see also in Stärk et al. (2019).                                                              |
| quadrate           | The quadrate bone forms the upper part of the jaw joint.                                                                                                                                                                                                                                                                                                                                                                                   |
| quadratojugal bone | A paired skull bone of the anurans that is connected to the upper jaw bone.                                                                                                                                                                                                                                                                                                                                                                |
| radius             | The radius or radial bone is one of the two large bones of the forearm, the other being the ulna.                                                                                                                                                                                                                                                                                                                                          |
| <i>Ranavirus</i>   | <i>Ranaviruses</i> can infect many vertebrate classes including fish, amphibians and reptiles, but for the most part, research has been focused on non-reptilian hosts, amphibians in particular. More recently, reports of ranaviral infections of reptiles are increasing. To prevent further spread, it is essential to follow the measures described in the two Citizen Conservation/DGHT (2020) documents when handling live animals. |
| rearing            | To care for juvenile animals under captive conditions until they reach maturity (rearing cannot be equated with captive breeding; see there)                                                                                                                                                                                                                                                                                               |
| retractile         | Capable of being drawn back or in.                                                                                                                                                                                                                                                                                                                                                                                                         |
| revalidated        | A genus or species name has been declared valid again.                                                                                                                                                                                                                                                                                                                                                                                     |
| ritualized fight   | ‘Tournament’ or ‘comment’ fight between ♂♂ in which the risk of injury to the competitors is relatively low.                                                                                                                                                                                                                                                                                                                               |
| rostral scale      | The median scale on the tip of the snout that borders the mouth opening.                                                                                                                                                                                                                                                                                                                                                                   |

| Keyword                            | Explanation                                                                                                                                                                                                                                                                                                                              |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| rudiment                           | In biology, a rudiment is a feature that has become partially or completely non-functional during phylogenetic development, but is still present.                                                                                                                                                                                        |
| sacrum                             | The sacrum is a large bone at the base of the spine that forms by the fusing of the sacral vertebrae.                                                                                                                                                                                                                                    |
| saxicolous                         | Living on rocks.                                                                                                                                                                                                                                                                                                                         |
| SEMARNAT                           | Secretaría de Medio Ambiente y Recursos Naturales in Mexico. Responsible, among other things, for the licensing and control of breeding operations and the authorisation of imports and exports of protected species.                                                                                                                    |
| Seramis                            | Clay granules used for potting plants, also a popular reptile egg incubation medium.                                                                                                                                                                                                                                                     |
| sexual dichromatism                | Special form of sexual dimorphism where coloration of sexes is different                                                                                                                                                                                                                                                                 |
| solitary                           | an animal that does not live with others in its species, ♂ and ♀ meet only for mating.                                                                                                                                                                                                                                                   |
| species group, species complex     | A group of closely related organisms that are so similar in appearance that the boundaries between them are often unclear.                                                                                                                                                                                                               |
| spermatophore                      | A capsule or mass containing spermatozoa created by ♂♂ of many salamanders, which is transferred in entirety to the ♀'s ovipore during reproduction.                                                                                                                                                                                     |
| sperm storage/amphigonia retardata | 'Amphigonia retardata' is a term synonymous with 'delayed fertilization' involving the storage of viable sperm by a ♀. More specifically, it may be defined as the union of egg and sperm after the ♂ gametes have been retained in the genital tract for a considerable period after copulation. It occurs in testudines and squamates. |
| spiculum                           | Latin for 'small spike', plural spicules, spiny skin structures in frogs.                                                                                                                                                                                                                                                                |
| spiraculum                         | The spiraculum of frog amphibians is an unpaired gill opening on the ventral side or left side of the body of tadpoles.                                                                                                                                                                                                                  |
| squamates                          | Squamata is the largest order of reptiles, comprising lizards and snakes, which are known as squamates or scaled reptiles.                                                                                                                                                                                                               |
| striae                             | Some salamanders are characterized by dense tubercles on the lateral trunk that form continuous nodule like warts, with thin transverse striae present between these warts.                                                                                                                                                              |
| subacuminate                       | Rather pointed.                                                                                                                                                                                                                                                                                                                          |

| Keyword                    | Explanation                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| subadult                   | Half grown. The term is sometimes used for young animals where the secondary sexual characters are already discernible.                                                                                                                                                                                                                                                                                                                                                                                                              |
| subgular                   | On the underside of the throat.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| sublabialia                | Scales on the lower lip.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| superciliary scales        | The scales directly above the eye, much like eyebrows.                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| supplementa-<br>tion       | Adding of vitamins and minerals to the food. Insects, for example, are dusted with a vitamin/mineral powder to upgrade the nutritional value. See also 'gut loading'.                                                                                                                                                                                                                                                                                                                                                                |
| suprakera-<br>tostoma      | Upper beak, upper area of the mouth opening with keratinised edges.                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| supramarginalia            | Additional marginal scutes above the actual marginalia, on the side of the carapace in turtles of the genus <i>Macrochelys</i> .                                                                                                                                                                                                                                                                                                                                                                                                     |
| sympatric                  | The species existing in the same geographic area.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| syntopy                    | Syntopy is a special case of sympatry. It means the joint occurrence of two species in the same habitat at the same time.                                                                                                                                                                                                                                                                                                                                                                                                            |
| taxon                      | A group of one or more populations of an organism or organisms seen by taxonomists to form a unit. Plural: Taxa                                                                                                                                                                                                                                                                                                                                                                                                                      |
| taxonomy                   | Taxonomy is the practice and science of categorization or classification                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| terra typica               | the area from which the type of a species originates. A terra typica restricta is designated when the nomenclature has to be refined and the originally given type localities are unclear.                                                                                                                                                                                                                                                                                                                                           |
| threshold tem-<br>perature | In species with temperature-dependent sex determination (TSD), 50% ♂♂ and 50% ♀♀ hatchlings hatch from eggs that are constantly incubated at this temperature. In turtles, incubation temperatures above this generally result in more ♀♀, while in crocodiles and geckos they result in more ♂♂ hatchlings. A special feature of turtles is TSD type II (in the Chelydridae): they have two threshold temperatures, whereby incubation temperatures below the lower threshold temperature again lead to predominantly ♀ hatchlings. |
| tibia                      | One of the two bones in the lower leg, alongside the fibula.                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| trigger                    | Stimulation.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| truncated                  | Shortened, blunted, cut off. Used here e.g. for the shape of the snout or the toe discs of glass frogs. Contrast: Rounded.                                                                                                                                                                                                                                                                                                                                                                                                           |
| tubercle                   | Any round nodule, small eminence, or warty outgrowth of the skin.                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |

| Keyword               | Explanation                                                                                                                                                                                                                                                                                                                                 |
|-----------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Tubifex</i>        | <i>Tubifex</i> worms are often used as a live food for amphibians during their aquatic phase. They may come from polluted water bodies, and they may be infected with various diseases. This risk can be partially solved by keeping the worms under brisk running water until they have voided the contents of their digestive systems.    |
| tympanum              | Eardrum.                                                                                                                                                                                                                                                                                                                                    |
| type specimen         | Individual in biological nomenclature that serves to define the features of a particular taxon.                                                                                                                                                                                                                                             |
| type locality         | The place where a type specimen was found.                                                                                                                                                                                                                                                                                                  |
| ulna                  | The ulna or ulnar bone is one of the two large bones of the forearm, the other being the radius.                                                                                                                                                                                                                                            |
| UMA                   | Abbreviation for 'Unidad de Manejo' for the conservation of wild animals in Mexico. Only native animal and plant species are kept here. There are extensive UMAs, which do not restrict the animals' freedom of movement on their property, and intensive UMAs, which keep the animals in outdoor enclosures and sometimes also breed them. |
| valid                 | In taxonomy: Current scientific name of a genus/species.                                                                                                                                                                                                                                                                                    |
| vegetative pole       | Egg development: The 'side' of the vegetative pole of the fertilised egg, which develops much more slowly than the animal pole.                                                                                                                                                                                                             |
| ventral               | Anatomical term of location referring to the abdominal or lower side of an organism.                                                                                                                                                                                                                                                        |
| Vermiculite           | Vermiculite is a sheet silicate of varied composition, and a proven and popular medium for the incubation of reptile eggs.                                                                                                                                                                                                                  |
| viscera               | Abdominal entrails.                                                                                                                                                                                                                                                                                                                         |
| viviparous            | Live bearing.                                                                                                                                                                                                                                                                                                                               |
| vomer, vomerine teeth | The vomer is one of the bones in the roof of the mouth. In urodeles it carries teeth, and their morphology and arrangement can be used as a distinguishing character for species identification.                                                                                                                                            |
| Wolffian duct         | Mesonephric duct, in vertebrates and humans the primary ureter, excretory duct of the prostate and kidneys, in ♂♂ also of the sperm.                                                                                                                                                                                                        |
| whiteworms            | Mostly <i>Enchytraeus albidus</i> and <i>Enchytraeus buchholzi</i> – these small oligochaete worms can be easily cultured as food for urodele larvae.                                                                                                                                                                                       |
| zoochory              | Plant seed dispersal by animals.                                                                                                                                                                                                                                                                                                            |
| <i>Zophobas</i>       | <i>Zophobas morio</i> is a darkling beetle (Tenebrionidae) whose larvae are robust mealworms sold as food for pets.                                                                                                                                                                                                                         |



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