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Cover: Development in the tadpole of *Agalychnis hulli* from Ecuador.
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A growth model for *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) from the Rio Negro predicts growth of individuals from the Xingu River, Brazil

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Abstract

A growth model for *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) from the Rio Negro predicts growth of individuals from the Xingu River, Brazil. Patterns of growth of crocodilians vary geographically within the same species, so models developed in one area may not predict size-age relationships in others. We used recapture data for three females and six males of *Paleosuchus trigonatus* from the Belo Monte hydroelectric dam area on the Xingu River to validate a growth model developed on a tributary of the Rio Negro. Individuals were recaptured between two and 10 years after marking (2012–2022). The data indicate that the monomolecular (von Bertalanffy by length) model is adequate to model growth of intermediate size animals. Recapture of one female after eight years indicates that the Rio Negro model can be used to model growth with accuracy for individuals from the Xingu River.

Keywords: Brazilian Amazonia, Growth, Hydroelectric dam, Schneider's dwarf caiman.

Resumo

Um modelo de crescimento de *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) do Rio Negro prevê o crescimento de indivíduos do rio Xingu, Brasil. Os padrões de crescimento dos crocodilianos variam geograficamente dentro da mesma espécie, de modo que os modelos desenvolvidos em uma área não preveem relações tamanho-idade em outras. Usamos dados de recaptura de três fêmeas e seis machos de *Paleosuchus trigonatus* da área da hidrelétrica de Belo Monte no rio Xingu para validar um modelo de crescimento desenvolvido em um afluente do rio Negro. Os jacarés foram recapturados entre dois e dez anos após a marcação (2012–2022). Os dados indicam que o modelo monomolecular (von Bertalanffy por comprimento) é adequado para modelar

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o crescimento de animais de tamanho intermediário, e a recaptura de uma fêmea após oito anos indica que o modelo Rio Negro pode ser usado para modelar o crescimento com razoável precisão para indivíduos do Rio Xingu.

Palavras-chave: Amazônia brasileira, Crescimento, Jacaré-coroa, Usina hidrelétrica.

Introduction

Paleosuchus trigonatus (Schneider, 1801) is a small species of crocodilian that reaches a maximum total length of about 2.3 m (Medem 1981, Campos *et al.* 2020), and is mainly encountered in Amazonian rainforest streams (Figure 1). Magnusson and Lima (1991) recorded a slower growth rate for *P. trigonatus* in Reserva Adolpho Ducke, a terra-firme area in central Amazonia, than those of other species of crocodilians. That study was based mainly on the growth of very large and very small individuals, and the authors had to assume a monomolecular model for the growth curve. One long-term recapture of an individual indicated that the equations reported in the original study can be used to predict the growth of individuals with accuracy (Magnusson *et al.* 1997). That individual was recaptured in the same study site in which the equations were developed, and it is not known whether they can be used in other areas with different ecological conditions.

Size-age relationships of crocodilians have generally been based on the relationship between growth rate and length of individuals (e.g. Magnusson and Sanaiotti 1995, Dalrymple 1996, Saalfeld *et al.* 2008, Campos *et al.* 2013) using sigmoidal growth models (Andrews 1982). Crocodilian mark-recapture studies often lack data on adults (Abercrombie 1992), but the study by Magnusson and Lima (1991) lacked information on intermediate-sized animals, which are necessary to determine the form of the growth curve.

Validation of growth models requires recapture of known-age animals after long periods, which has been done for some economically important species, such as *Alligator mississippiensis* Daudin, 1801 (Rootes *et al.* 1991, Wilkinson and Rhodes 1997, Wilkinson *et al.* 2016), and authors have reported differences in growth rates due to both environmental conditions and density-dependent processes (Abercrombie 1989, Da Silveira *et al.* 2013).

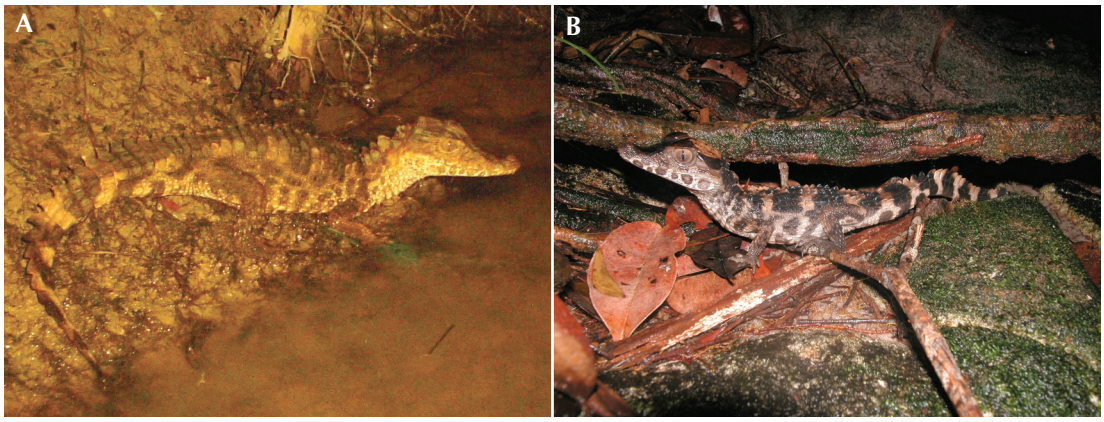

Figure 1. (**A**) Individual of *Paleosuchus trigonatus* in the Jaciparaná River, a tributary of the Madeira River, Rondônia state, northern Brazil. Photo: Zilca Campos. (**B**) Hatchling of *P. trigonatus* in the igarapé, Negro River, Amazonas state, northern Brazil. Photo: William E. Magnusson.

The study by Magnusson and Lima (1991) was undertaken in black-water streams that drain to the Rio Negro, in the Reserva Adolpho Ducke. The area was relatively undisturbed and the streams were under closed-canopy rainforest. In contrast, the Xingu River (Figure 2) has clear water and the Belo Monte dam has resulted in many areas of closed-canopy rainforest being replaced by open-water habitats (Campos *et al.* 2021). In this study, we used long-term mark-recapture data for *P. trigonatus* from the area around the Belo Monte Dam to determine whether growth of individuals in this area can be modeled by equations derived near the Rio Negro, 900 km distant. Size-age relationships of crocodilians show large differences among individuals (Eaton and Link 2011), locations, and species (Da Silveira *et al.* 2013). Whether estimated values can be considered to have sufficient precision depends on the question and whether age is being estimated from size or size is being estimated from age (Magnusson 2012). Deviations from models are presented so that researchers can draw their own conclusions.

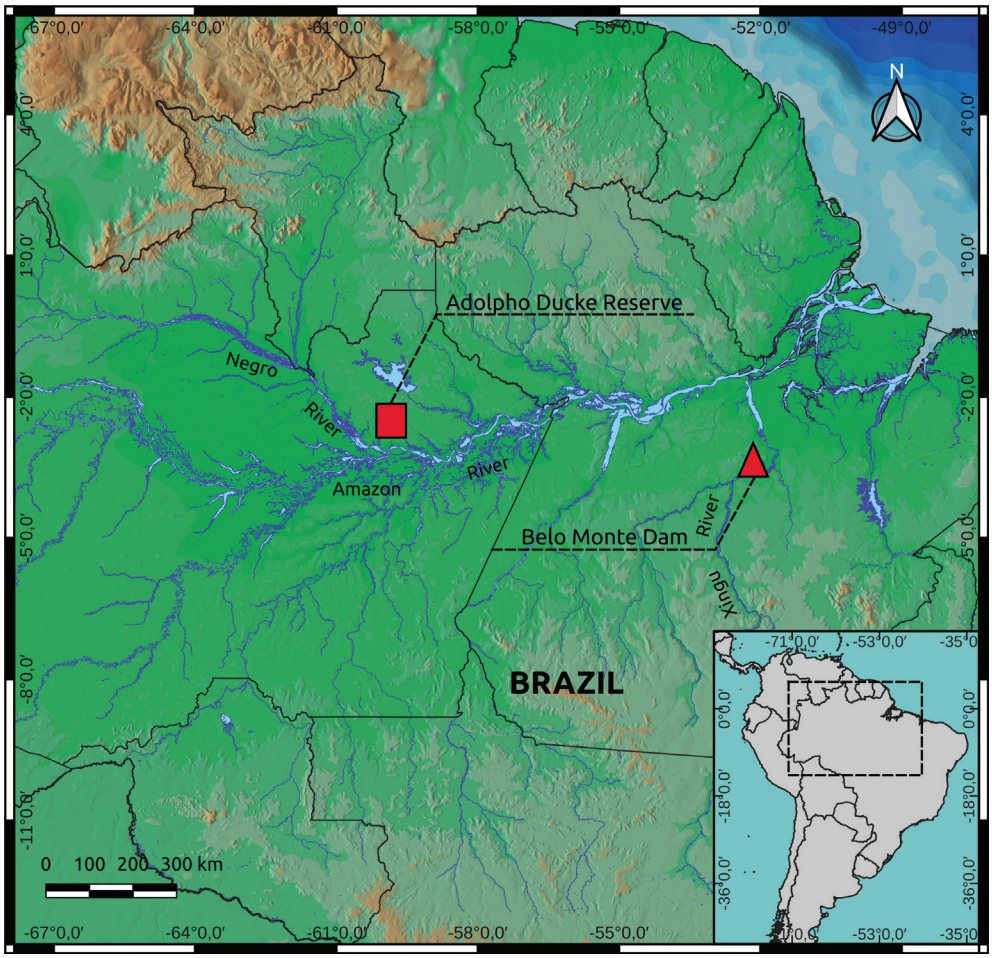

Figure 2. Two study areas in the Amazon region of Brazil: Reserva Adolpho Ducke in the Negro River (red square), and Belo Monte Dam in the Xingu River (red triangle).

Materials and Methods

We applied the growth equation derived by Magnusson and Lima (1991) for male [growth rate in cm per day (GR) = 0.02812 - 0.00035 * snout–vent length (SVL) in cm] and female (GR = 0.03946 - 0.00058*SVL) *P. trigonatus* captured around the reservoir of the Belo Monte Hydroelectric dam (Table 1) to determine how well they could predict growth of individuals from this area. In Magnusson and Lima (1991; Fig. 1), GR was erroneously given as mm per day. In the Xingu River, between 2012 and 2022, we captured and marked 300 individuals of *P. trigonatus* (hatchlings, juveniles, and adults) with numbered plastic tags, aluminum tags, and combination of tail-scute clips. Snout–vent length was measured with a graduated tape (limit of reading 1 mm) and sex identified by inspection of the cloaca at recapture.

Growth rates were estimated as the differences in SVL between captures divided by the intervals between captures. The growth-rate-on-size relationship uses mean sizes of individuals during the growth interval, and we used arithmetic means, as in Magnusson and Lima (1991). Observed data for animals from the Xingu for the size-age relationship were calculated by estimating the age at first capture based on size at first capture from the sex-specific equations given by Magnusson and Lima (1991). We then added this to the interval between captures to estimate age at recapture. Ages (A) were estimated from the equation $A = -1/r*\ln[(S_m-S_o)/(S_m-S)]$ given by Webb *et al.* (1983), where r is the slope of the growth-rate-on-size relationship, S_m = mean asymptotic SVL (68 cm for females and 80 cm for males), S_o = SVL at hatching (12 cm for both sexes), and S = present SVL. Obviously, the expected values from the equation cannot be used to validate the equation, so the usefulness of the data depends on the relative duration of the observed interval to the total age estimate. Only one female was captured at such a small size (14 cm, estimated age 2 months) that the interval

Table 1. The snout–vent length before (SVL_1 cm), after (SVL_2 cm) and mean (SVL_mean) of *Paleosuchus trigonatus* recaptured in the UHE Belo Monte region. DAYS is the interval between capture and recapture. INIT_AGE_EST is the age at first capture estimated from the relationship based on animals captured near the Rio Negro (see methods). TIME is the period between capture and recapture.

SVL_1 (cm)	SVL_2 (cm)	RATE_CM_DAY	DAYS	DATE_1	DATE_2	SEX	INIT_AGE_EST (years)	TIME (years)	SVL_MEAN (cm)
45.7	76.0	0.0120	2597	07 Feb 2014	29 Mar 2021	Male	3.23	7.12	60.85
14.0	61.0	0.0160	2920	14 Feb 2014	16 Feb 2022	Female	0.17	8.00	37.50
54.0	67.0	0.0051	2562	03 Sep 2012	10 Sep 2019	Male	4.54	7.02	60.50
41.0	45.0	0.0090	447	18 Jul 2014	05 Oct 2015	Male	2.63	1.22	43.00
44.5	55.8	0.0250	457	18 Jul 2013	20 Oct 2014	Female	4.10	1.25	50.15
39.0	54.0	0.0154	970	19 Jun 2012	13 Apr 2014	Male	2.39	2.66	46.50
45.7	79.0	0.0111	2997	07 Feb 2014	24 Apr 2022	Male	3.23	8.21	62.35
71.5	81.0	0.0031	3024	10 Jul 2013	24 Oct 21	Female	9.37	8.28	76.25
71.5	89.0	0.0052	3376	23/1/2013	24/4/2022	Male	9.82	9.25	80.25

between first and last captures (8 years) can be considered a known age. For this reason, the validation points on the size-age graph are proportional to the ratio of the known interval to the total estimated age. Larger symbols carry more independent information.

Results

Six male and three female *P. trigonatus* were recaptured after periods of between 447 and 3376 days. The data for intermediate-sized animals were consistent with the linear, decreasing, monomolecular model for both males and females, though one female recaptured after 457 days had a growth rate double that predicted by the model (Figure 3).

In general, the estimated ages were well predicted by the model (Figure 4), though the model tended to underestimate ages of larger males and females. The only known-age (to within a few months) female had an estimated age (9.8 years) close to her known age (about 8.1 years).

Discussion

Relationships between size and growth rate, and hence size and age, for crocodilians show large scatter (Da Silveira *et al.* 2013). If the variation is temporal within individuals, models of means will generally predict size-age relationships reasonably well (Magnusson 2012). If individuals differ systematically in size-specific growth rates, models of means will be very imprecise for individuals (Eaton and Link 2011), and the form of the growth model could vary among areas.

We lack repeated recaptures for intermediate-size *P. trigonatus* from any area, except for one individual from near the Rio Negro (Magnuson and Lima 1991). Long-term recaptures of intermediate-sized *P. trigonatus* are rare, because juveniles usually disperse long distances (Magnusson and Lima 1991). The data indicate that the monomolecular (linear, decreasing)

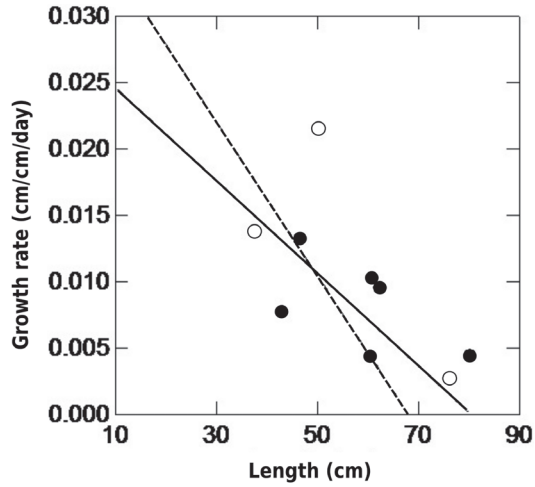

Figure 3. Growth rates of male (filled circles) and female (open circles) *Paleosuchus trigonatus* from the region of the Belo Monte Dam on the Xingu River. The lines are the relationships (males solid line, females dashed line) predicted for animals from the region of the Rio Negro.

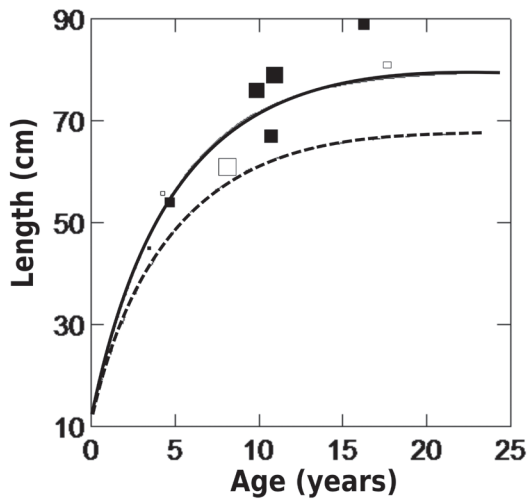

Figure 4. Estimated relationships between age and length for male (solid squares) and female (open squares) *Paleosuchus trigonatus* from the region around the Belo Monte Dam on the Xingu River. Sizes of symbols are proportional to the estimated age based on the interval between captures. The lines are the relationships (males solid line, females dashed line) predicted for animals from the region of the Negro River.

model of growth rate on size derived for individuals from closed-canopy forest near the Rio Negro can be applied to individuals from the Xingu River, and that estimates for individuals based on the reconstituted size-age relationship are at least as precise as those published for other Amazonian species (Da Silveira *et al.* 2013).

The great cost of mark-recapture studies of crocodilians carried out over their life spans (many decades) means that it is unlikely that results from longitudinal studies of individuals will be available for most species of crocodilians in the near future, especially for species such as *P. trigonatus* that are neither endangered nor have commercial value. The models for the Rio Negro tended to underestimate lengths of females and large males at a given age for individuals from the Xingu River. The growth-rate on size relationships indicate that the estimated growth rates are reasonable, but there is reason to believe that the asymptotic sizes differ between the two areas. Fifteen females and seven males captured near the Xingu River had snout-vent lengths larger than the mean for the Rio Negro study, and larger individuals have been reported from other areas (Medem 1981). Estimates based on size-age relationships will always be imprecise for large individuals, but better estimates of asymptotic size in each area may reduce bias, and these are probably easier to obtain in the medium term than multiple recaptures of medium- and large-size individuals.

Because it is unlikely that data for large numbers of animals will be available from any individual study, it is important that researchers make their data available so that the accumulated information is accessible. Also, studies with repeated captures of individuals will allow evaluation of whether individual growth rates tend to be parallel to the mean growth curve or oscillate around it. Without more data, speculation about possible differences among sites is still unwarranted, but the limited data from several areas do support the contention that, despite being of small size, the species takes several decades to reach maturity (Magnusson and Lima 1991), similar to the pattern seen in larger crocodilians.

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An assessment of the herpetofauna of the Oriental Sweetgum forests in southwestern Anatolia, Turkey

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Abstract

An assessment of the herpetofauna of the Oriental Sweetgum forests in southwestern Anatolia, Turkey. Oriental Sweetgum (*Liquidambar orientalis*) is a threatened tree species restricted to Rhodes Island (Greece) and southern Anatolia (Turkey), best known for its rare riparian forests. These small patches of forests are severely fragmented and scattered, and are rarely found in southwestern Turkey. Based on field sampling and data compilation, we performed an assessment of the herpetofauna in these forests in southwestern Turkey during the spring of 2019 and 2021. Sampling was carried out using a line-transect method in 13 forests with various habitats, resulting in data at the community and population levels. Sixteen families, including 26 amphibian and reptile species (four anurans, four turtles, nine lizards, and nine snakes), were recorded from these unique forests, based on 1440 individuals. Twenty-two species were recorded for the first time from these forests; in addition, *Emys orbicularis* and *Elaphe sauromates* were recorded for the first time from the region. Richness in the forest patches, habitat use by the recorded species, and interspecific interactions are discussed to explain the conspicuous patterns observed in the species distributions. The unique distribution pattern of *Phoenicolacerta laevis* among the existing forest patches represents the most prominent finding, with implications for a recent introduction. The fossorial species *Xerotyphlops vermicularis, Blanus strauchi,* and *Eryx jaculus* are unlikely to occur in the Oriental Sweetgum forest due to annual flooding. The data obtained during this study will be transferred to the Oriental Sweetgum forest conservation action plan (2019–2024) as part of the biodiversity monitoring tools for use in the long-term conservation of these forests.

Keywords: Amphibians, *Liquidambar orientalis*, Reptiles, Riparian forests.

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Resumo

Uma avaliação da herpetofauna das florestas orientais de "Sweetgum" no sudoeste da Anatólia, Turquia. O "Oriental Sweetgum" (*Liquidambar orientalis*) é uma espécie de árvore ameaçada, restrita à Ilha de Rodes (Grécia) e ao sul da Anatólia (Turquia), mais conhecida por suas raras florestas ripárias. Essas pequenas manchas de floresta são severamente fragmentadas e dispersas e raramente são encontradas no sudoeste da Turquia. Com base em amostragem de campo e compilação de dados, fizemos uma avaliação da herpetofauna nessas florestas no sudoeste da Turquia durante a primavera de 2019 e 2021. A amostragem foi realizada pelo método de transecto de linha em 13 florestas com vários habitats, resultando em dados nos níveis de comunidade e população. Dezesseis famílias, incluindo 26 espécies de anfíbios e répteis (quatro anuros, quatro tartarugas, nove lagartos e nove serpentes), foram registradas nessas florestas únicas, com base em 1440 indivíduos. Vinte e duas espécies foram registradas pela primeira vez nessas florestas; além disso, *Emys orbicularis* e *Elaphe sauromates* foram registradas pela primeira vez na região. A riqueza nas manchas florestais, o uso do habitat pelas espécies registradas e as interações interespecíficas são discutidas para explicar os padrões conspícuos observados nas distribuições das espécies. O padrão único de distribuição da *Phoenicolacerta laevis* entre os fragmentos florestais existentes representa a descoberta mais proeminente, com implicações para uma introdução recente. É improvável que as espécies fossórias *Xerotyphlops vermicularis, Blanus strauchi* e *Eryx jaculus* ocorram nesse tipo florestal devido à inundação anual. Os dados obtidos durante este estudo serão usados no plano de ação de conservação da floresta "Oriental Sweetgum" (2019-2024) como parte das ferramentas de monitoramento da biodiversidade para uso na conservação dessas florestas a longo prazo.

Palavras-chave: Anfíbios, Florestas ripárias, *Liquidambar orientalis*, Répteis.

Introduction

The tertiary relict Oriental Sweetgum (*Liquidambar orientalis* Mill.) is an endangered endemic tree species of southwestern Anatolia (Turkey) and Rhodes Island (Greece) (Akman *et al.* 1992, Kurt 2008, Kavak and Wilson 2018). It occurs in groups in small groves or on riverbanks throughout its distribution (Ürker and Çobanoğlu 2017). These gallery forests form a unique flooded riparian forest, included in the EUNIS Habitat Classification System under "G1.39 - *Liquidambar orientalis* woods" in "G1.3 - Mediterranean riparian woodland."

The riparian forests formed by the Oriental Sweetgum occur naturally in southwestern Anatolia and partly in the nearby Rhodes Island (Greece). Often seen at low altitudes favoring rich, deep, moist soils, such as banks or marshlands (Kurt 2008, Küçükala *et al.* 2010, Caudullo *et al.* 2017), these forests are typically densely vegetated and located in coastal areas with little relief (Kaya and Alan 2003, Ürker and Yalçın 2011, Kavak and Wilson 2018). The forests are severely fragmented because of anthropogenic impacts, mainly urbanization and transformation to farmlands. Historical records indicate a land cover of 6312 ha in 1949, whereas today, approximately 2000 ha of forests remain, represented by isolated, small patches (Caudullo *et al.* 2017, Özkil *et al.* 2017). Oriental Sweetgum has been classified as Endangered (EN-A2c) on the IUCN Red List (Kavak and Wilson 2018), and EUFORGEN has listed it as protected on the European Continent (Kaya and Alan 2003).

The uniqueness and threatened situation of these forests necessitate immediate conservation actions; however, the biodiversity within these forests has been neglected until recently. The herpetofauna has been no exception; no faunistic report of amphibians or reptiles in these forests exists in the literature, although some records of the herpetofauna in the general vicinity are available Kasparek (1990) compiled records of

three amphibian and 21 reptile species from the Köyceğiz basin, particularly in the Dalyan region. Baran *et al.* (1994) and Kumlutaş *et al.* (2015) published inventories based on field surveys for the specially protected areas (SPAs) of Köyceğiz-Dalyan and Fethiye-Göcek. They reported five amphibians and 24 reptiles, and six amphibians and 20 reptiles, respectively. Ilgaz *et al.* (2016) found *Bufotes sitibundus* (Pallas, 1771), *Phoenicolacerta laevis* (Gray, 1838), and *Ophisops elegans* Ménétries, 1832 in a sweetgum forest patch in Dalaman. To our knowledge, no other publications refer to these forests or to the region.

Herein, we summarize our findings based on field studies and data compilation, focusing on the herpetofauna of Oriental Sweetgum forests and associated habitats at the community and population levels.

Materials and Methods

Oriental Sweetgum forests show remarkably variable habitat diversity based on the areal size, isolation, fragmentation, and nature of origin (Ürker and İlemin 2019, Ürker and Benzeyen 2020) as summarized in Appendix I. This study has been carried out by collecting or compiling data from 13 major Oriental Sweetgum forest patches in Muğla Province on the southwestern Anatolian coast of Turkey (Appendix I, Figures 1 and 2).

Data collection was carried out by a line-transect method using hypothetical straight lines that ran through the core or peripheral regions of each forest patch. In large and intact patches, transects were selected to sample the core regions at least 50 m away from the forest border at the closest point, whereas in small and fragmented patches, we did not implement this rule. In addition, ecotones between forests and the associated biotopes were sampled by peripheral transects, selected 10 to 20 m from the border, outside the forests. Associated biotopes were citrus and pomegranate orchards or grassland, all characterized by a more open

Figure 1. Some views of the Oriental Sweetgum forests. (**A**) Karabatak, (**B**) Hisarönü, and (**C**) Kızılyaka.

Figure 2. Map of the study area: (**A**) Turkey in the world map (©Worldmap 2022); (**B**) Native and isolated populations of the Oriental Sweetgum forests (Caudullo *et al.* 2017); (**C**) Study locations denoted with red pins (Google Earth 2022).

canopy or a lower vegetation height than the Oriental Sweetgum forests. Two separate techniques were used across the transects: pitfall trap surveys were conducted, or one observer proceeded by walking and recording observed specimens.

Sampling with pitfall traps was conducted in the five larger forest patches (>100 ha in surface area), namely Dalaman, Kavakarası, Karabatak, Toparlar, and Kızılyaka. Twelve to 15 cylindrical plastic container (dived 15 cm under surface), 9 × 12 cm^2, were deployed per transect at 10 m intervals. As a result, 255 pitfall traps were used in five forest patches between 22 April 2019 and 14 June 2019. Fifteen transects were used to sample the core, and six transects were used to sample the peripheral parts of these forests. Specimens collected were identified in the field, recorded, and set free immediately if thriving otherwise transferred to the laboratory and stored as museum specimens in the zoological collection of the Department of Biology at Erzincan Binali Yıldırım University.

Transect walks were used to sample the areas during the day (McDiarmid *et al.* 2012). All forest patches except those in Fethiye were sampled with at least one transect walk per patch on 20–26 May 2021. The identity and abundance of every herptile species observed was recorded. During transect walks, individuals fleeing or foraging were recorded by direct observation; rocks, logs, or other organic material were turned for the fossorial species as well. Transect walks were dedicated mainly to the core parts of the forests; nevertheless, forest edges were also sampled, particularly in fragmented patches. Catching, handling, or collecting for identification was not necessary and was avoided.

Another source of data input was gathering observation records from professional field personnel, mainly by photos captured in the field or records collected during routine fieldwork in these forests from various projects since 2018. All data from the Fethiye forest comes from such records.

Chorotypic classification of the species using the Oriental Sweetgum forests was used to assess the uniqueness of the fauna, based on global chorotypes defined by Vigna-Taglianti *et al.* (1999). The conservation status of herpetofaunal species is also reported based on IUCN Red List (Ver.2021.3), Annexes of CITES (UNEP-WCMC 2013), and Annexes of Bern Convention (2021; Council of Europe).

Results

Twenty-six species belonging to four orders and 16 families were recorded in the Oriental Sweetgum forests and the associated habitats, based on 1440 individuals (Table 1). The number of individuals observed in these forest patches varied (Appendix I). The species list is composed of Anura [Bufonidae (2 spp.), Ranidae (1), Hylidae (1)], Testudines [Geoemydidae (1), Emydidae (1), Testudinata (1), Trionychidae (1)], Sauria [Gekkonidae (1), Agamidae (1), Chamaeleonidae (1), Lacertidae (4), Anguidae (1), Scincidae (1)], and Serpentes [Colubridae (6), Natricidae (2), Viperidae (1)] (Figure 3). Taxonomic status, conservation categories (IUCN, Bern, and CITES), and global chorotypes are given in Table 1. The dominant anuran species observed in the Oriental Sweetgum forests was the Water frog, *Pelophylax bedriagae* (Camerano, 1882). The Common toad, [*Bufo bufo* (Linnaeus, 1758)], the Green toad (*Bufotes sitibundus*), and the Oriental tree frog (*Hyla orientalis* Bedriaga, 1890) are three other amphibian species frequently recorded from the Oriental Sweetgum forests and associated habitats. For turtles, *Mauremys rivulata* (Valenciennes, 1833) was the most frequently and abundantly observed species, while *Trionyx triunguis* (Forskål, 1775) was represented as a singleton found dead in Kersele. *Phoenicolacerta laevis* and *Lacerta diplochondrodes* Wettstein, 1952 were two dominant, mutually exclusive lizard species with conspicuous and distinct distribution patterns in these forests. *Phoenicolacerta laevis* was represented by well-established populations in the four southeastern forests

Figure 3. Some amphibian and reptilian species from the study locations: (**A**) *Pelophylax bedriagae;* (**B**) *Mauremys rivulata;* (**C**) *Testudo graeca;* (**D**) *Laudakia stellio;* (**E**) *Chamaeleo chamaeleon;* (**F**) *Anatololacerta pelasgiana;* (**G**) *Phoenicolacerta laevis;* (**H**) *Natrix tessellate;* and (**I**) *Montivipera xanthina.*

(namely the Dalaman, Kavakarası, Eskiköyceğiz, and Zeytinalanı), whereas *Lacerta diplochondrodes* showed a higher frequency with records from nine forest patches, establishing higher abundances in the northeast (in Karabatak and Toparlar). Among snakes, *Platyceps najadum* (Eichwald, 1831), *Dolichophis jugularis* (Linnaeus, 1758), *Natrix natrix* (Linnaeus, 1758), and *Natrix tessellata* (Laurenti, 1768) were the most abundant and frequently observed species, whereas the rest of the species were rarely recorded.

The abundance and species richness varied between 3–239 and 1–14, respectively. In the larger patches Dalaman, Kavakarası, Karabatak, Toparlar, and Kızılyaka, where the sampling effort was greatest, richness varied between 8–14 species (Appendix I). No endemic herptile species were found in these forests. *Emys orbicularis* (Linnaeus, 1758) was identified as "Near Threatened" while *Testudo graeca* Linnaeus, 1758 and *T. triunguis* (Forskål, 1775) were classified as "Vulnerable" in the IUCN red list. *Bufotes sitibundus, Hyla orientalis, Mauremys rivulata, Anatololacerta pelasgiana* (Mertens, 1959), and *Lacerta diplochondrodes* have not been listed yet, whereas the remaining 18 species are listed as "Least Concern." According to Bern criteria, 14 species were listed in Bern's Appendix II (as strictly protected species), and 12 species were classified in Bern's Appendix III (as protected species). *Chamaeleo chamaeleon* (Linnaeus, 1758), *T. graeca,* and *T. triunguis* were listed in CITES' Appendix II, whereas the rest of the species were not listed.

The herpetofauna from the Oriental Sweetgum forests belong to nine global chorotypes (Table 1). The dominant global chorotypes are Turano-Mediterranean (eight species, 31%) and East Mediterranean (seven species, 26%). Turano-Europeo-Mediterranean is represented by three species (11%); both Southwest Asiatic and Mediterranean were represented by two species (8%). Single (4%) species global chorotypes for the study area were listed as European, Europeo-Mediterranean, Centralasiatic-European, and Centralasiatic-Europeo-Mediterranean.

Discussion

Prior to our work, no comprehensive study had focused on the Oriental Sweetgum forests. The pioneering authors Kasparek (1990) and Baran *et al.* (1994) studied Köyceğiz and Dalyan, and Kumlutaş *et al.* (2015) focused on the Fethiye region. Given that Köyceğiz, Dalyan, and Fethiye include the majority of the remaining sweetgum forest patches in Anatolia, previous studies included these forests as a significant component. These authors apparently did not visit or recognize Oriental Sweetgum forests as a unique habitat, except that Baran *et al.* (1994) provided a single record of the water frog *Pelophylax bedriagae* from a forest patch near Toparlar. The contribution of Ilgaz *et al.* (2016) is the second and last record referring to this unique ecosystem, noting the lizard *P. laevis* as the most significant finding. *Pelophylax bedriagae* and *Phoenicolacerta laevis* were the two most abundant species in our inventory, so it is not surprising that they were the first recorded species from these forests.

Pelophylax bedriagae is common in swamps with vegetation throughout western Anatolia (Dufresnes 2019). The occurrence of *Phoenicolacerta laevis* is interesting because it is not common in southwestern Anatolia; this species shows a rather continuous distribution between Hatay, western Syria, and north of Israel (Bischoff and Schmidtler 1999). Other records from Anatolia are scattered throughout the Mediterranean coast, corresponding to 11 isolated populations, including this study (Karış and Göçmen 2014, Ilgaz *et al.* 2016). These populations may be remnants of recent introductions (Bischoff and Schmidtler 1999, Karış and Göçmen 2014), but there is no supporting evidence for this. Tamar *et al.* (2015) showed that the Anatolian populations of *P. laevis* are genetically indistinct, including one of the isolated populations from Turkey (Anamur). Tarkhnishvili *et al.* (2017) discovered an isolated population from Georgia at the Black Sea coast, revealing its origin as an introduction possibly

Table 1. General information on the amphibian and reptilian species found in the Oriental Sweetgum forests. Total abundance: number of recorded individuals of a species. Name of Forest: F, Fethiye; D, Dalaman; O, Okçular; KA, Kavakarası; EK, Eski Köyceğiz; Z, Zeytinalanı; KB, Karabatak; T, Toparlar; HA, Hamitköy; KE, Kersele; KI, Kızılkaya; C, Çetibeli; HI, Hisarönü.

Order/Family	Species	IUCN (Ver.2021.3)	Bern	CITES	Global Chorotype	Total Abundance	Name of Forest Patches
ANURA							
Bufonidae	*Bufo bufo* (Linnaeus, 1758)	LC	III	-	European	184	F, Z, KB, T, KI
	Bufotes sitibundus (Pallas, 1771)	Not Listed	III	-	Turano-Europeo-Mediterranean	9	F, T
Ranidae	*Pelophylax bedriagae* (Camerano, 1882)	LC	III	-	Turano-Europeo-Mediterranean	586	D, KA, EK, Z, KB, T, KE, KI, C, HI
Hylidae	*Hyla orientalis* Bedriaga, 1890	Not Listed	III	-	Europeo-Mediterranean	12	Z, KB, KE, KI, HI
TESTUDINES							
Geoemydidae	*Mauremys rivulata* (Valenciennes, 1833)	Not Listed	III	-	Turano-Mediterranean	70	KA, KB, T, KE, KI, C, HI
Emydidae	*Emys orbicularis* (Linnaeus, 1758)	NT	II	-	Turano-Europeo-Mediterranean	5	D, KB
Testudinidae	*Testudo graeca* Linnaeus, 1758	VU	II	II	Turano-Mediterranean	43	D, KA, KB, T, KE, KI, C, HI
Trionychidae	*Trionyx triunguis* (Forskål, 1775)	VU	II	II	Southwest Asiatic	1	KE
SQUAMATA							
Agamidae	*Laudakia stellio* (Linnaeus, 1758)	LC	II	-	East Mediterranean	53	D, EK, T, C
Anguidae	*Pseudopus apodus* (Pallas, 1775)	LC	II	-	Turano-Mediterranean	2	T, HA
Chamaeleonidae	*Chamaeleo chamaeleon* (Linnaeus, 1758)	LC	II	II	Mediterranean	2	F, EK

Table 1. *Continued.*

Order/Family	Species	IUCN (Ver.2021.3)	Bern	CITES	Global Chorotype	Total Abundance	Name of Forest Patches
Gekkonidae	*Hemidactylus turcicus* (Linnaeus, 1758)	LC	III	-	Mediterranean	2	D, Z
Lacertidae	*Anatololacerta pelasgiana* (Mertens, 1959)	Not Listed	III	-	East Mediterranean	8	T, KE
	Ophisops elegans Ménétries, 1832	LC	II	-	East Mediterranean	12	KE, KI
	Phoenicolacerta laevis (Gray, 1838)	LC	III	-	East Mediterranean	302	D, KA, EK, Z
	Lacerta diplochondrodes Wettstein, 1952	Not Listed	III	-	East Mediterranean	103	D, O, KA, KB, T, HA, KI, C, HI
Scincidae	*Ablepharus kitaibelii* Bibron and Bory St.-Vincent, 1833	LC	II	-	East Mediterranean	2	KA, T
Colubridae	*Dolichophis caspius* (Gmelin, 1789)	LC	III	-	Turano-Mediterranean	2	KB, T
	Dolichophis jugularis (Linnaeus, 1758)	LC	II	-	Southwest Asiatic	6	KB, T, KE
	Platyceps najadum (Eichwald, 1831)	LC	II	-	Turano-Mediterranean	5	D, KA, EK, KE, KI
	Elaphe sauromates (Pallas, 1811)	LC	II	-	Turano-Mediterranean	1	KA
	Hemorrhois nummifer (Reuss, 1834)	LC	III	-	Turano-Mediterranean	1	KI
	Telescopus fallax Fleischmann, 1831	LC	II	-	Turano-Mediterranean	1	KA
Natricidae	*Natrix natrix* (Linnaeus, 1758)	LC	III	-	Centralasiatic-Europeo-Mediterranean	14	EK, KB, KE, C, HI
	Natrix tessellata (Laurenti, 1768)	LC	II	-	Centralasiatic-European	10	F, KA, KB, T, KE, KI
Viperidae	*Montivipera xanthina* (Gray, 1949)	LC	II	-	East Mediterranean	1	HI

from Mersin, Turkey. The current literature does not explain the scattered distribution pattern on the Mediterranean coast of Turkey. Introductions due to transport by historical trading activities may explain the pattern, but more data are needed.

The distribution of *Phoenicolacerta laevis* is non-continuous within the Oriental Sweetgum forests. The forest fragment at Zeytinalanı represents the northernmost limit of this species, and the populations attain high densities in the three larger southern patches: Dalaman, Kavakarası, and Eskiköyceğiz, whereas they are absent in the northern forests. The region where this species occurs is located between two ancient trading ports, which correspond to the primary seaway connections with Egypt (Africa). The ancient port of Kaunos City, located a few kilometers west of the modern town of Dalyan, dates back to the 10th century B.C. and was one of the most important sea connections between Anatolia (and from here to Europe), Africa, the Indian Peninsula, and the Arabic Peninsula (Öğün 1971, Marek and Beck 2006, Türe 2011) (Figure 2). The relatively recent port in Sarsala is located west of the Dalaman River and was built in 1905 for grain shipment from the Dalaman and Ortaca plains to Egypt (Mikhail 1992) (Figure 2). The fact that the southern forest patches harboring *P. laevis* are located between two historically significant trading nodes might be used to confirm a historical introduction event.

Phoenicolacerta laevis is absent in the Karabatak forest, a large patch physically connected with Zeytinalanı, where the species occurs. *P. laevis* can establish high densities in these forests, possibly because it is well adapted to the riparian forest habitat. The small number of individuals recorded in Zeytinalanı might indicate that this species is barely thriving in this small, narrow, fragmented patch. A lower affinity of this lizard to peripheral habitats around the sweetgum forests is evident in the extensively sampled Kavakarası forest as well. This forest is one of the largest and most fragmented patches due to transformation to orchards, mainly citrus or pomegranate. In comparison, *P. laevis* was represented by 30 and six individuals in core and peripheral parts, respectively (Figure 4). This observation indicates a clear preference for intact forest habitat by this lizard species, partly explaining why the Zeytinalanı forest is unsuitable for dispersion and the species could not colonize the Karabatak forest.

The Green lizard *Lacerta diplochondrodes* is the most abundant lizard species in the Oriental Sweetgum forests. It is common in western Anatolia, where it is associated with dense vegetation, explaining its occurrence in these forests. However, even though it was recorded in nine of the 13 forest patches and five of the six large forests throughout the Oriental Sweetgum forests, it attained the highest abundances in the forests around the Köyceğiz city center, namely in Karabatak and Toparlar. In contrast, it is rare or absent in southern patches dominated by *P. laevis,* suggesting that these two species are mutually exclusive (Figure 5). Large populations of *L. diplochondrodes* might be another factor limiting the distribution of *P. laevis* because of competitive exclusion or predation, in addition to its strict habitat preference.

Laudakia stellio (Linnaeus, 1758) is another abundant species but was mainly recorded from peripheral habitats such as large openings in the forest. Likewise, *Anatololacerta pelasgiana*, *Ophisops elegans,* and *Ablepharus kitaibelii* Bibron and Bory St.-Vincent, 1833 were recorded from the peripheral or small, fragmented habitats with edge effects. Evidently, these species rely on habitat structure different from the core sweetgum forests. The amphibian species *Bufo bufo* and *Hyla orientalis* were frequently recorded from both core and peripheral habitats, but their low abundances make it challenging to interpret their reliance on the Oriental Sweetgum forest. The infrequently recorded species *Bufotes sitibundus, Hemidactylus turcicus* (Linneaus, 1758), *Chamaeleo chamaeleon,* and *Pseudopus apodus* (Pallas, 1775) were represented mainly as singletons or doubletons in our inventory,

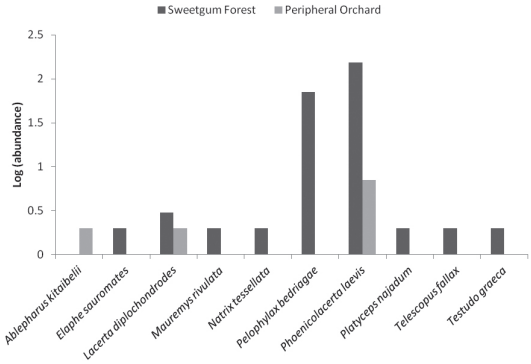

Figure 4. Log transformed abundances measured in the Oriental Sweetgum forest patch and the peripheral habitats from Kavakarası.

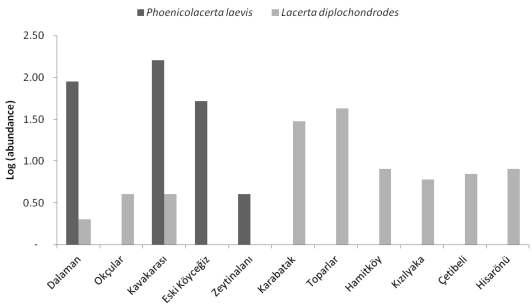

Figure 5. Log transformed abundances measured in the Oriental Sweetgum forest patches for *Phoenicolacerta laevis* and *Lacerta diplochondrodes;* forests sorted in the south to north direction.

implying that their occurrences are coincidental in the sweetgum forests.

Snakes are the most secretive group among herptiles, making it much more challenging to interpret their ecology or the number of species during our study. Our inventory is biased toward diurnal and conspicuous species, whereas nocturnal species such as geckos or cryptic species such as snakes are likely not well represented. *Platyceps najadum, Dolichophis jugularis* (Linnaesu, 1758), *Dolichophis caspius* (Gmelin, 1789), *Natrix tessellata,* and *N. natrix* are well represented in our inventory, indicating their preference for the Oriental Sweetgum forests and possibly explained by the high abundances of prey and availability of suitable habitat. The occurrence of *P. najadum* and *D. jugularis* in a densely vegetated riparian forest habitat is unusual, considering the preference of these species for dry, rocky habitats with low vegetation (Geniez 2018). The availability of lizard prey in high abundances, including *P. laevis* and *L. diplochondrodes,* might explain this phenomenon. The rest of the species were rarely represented in the inventory, indicating the necessity of further sampling.

Among turtles, *Mauremys rivulata* and *Testudo graeca* were the most common species inhabiting aquatic and terrestrial microhabitats in the forests, respectively. *E. orbicularis* appeared as a rare species in our inventory, with records from two of the larger forest patches in Dalaman and Karabatak. Our record of *Trionyx triunguis* is based on an individual found dead in the Kersele forest patch, located at the shore of the lake Köyceğiz. Some of the coastal forest patches, namely Kersele and Karabatak, are flooded annually by the lake during the rainy seasons. The soft-shelled turtle *T. triunguis* is a common species in the lake, but it is unknown whether or how it uses the Oriental Sweetgum forest during the submerged or terrestrial periods.

The dataset we produced enabled comparisons with historical records from the study area. Ilgaz *et al.* (2016) recorded *Bufotes sitibundus* and *Ophisops elegans* as sympatric species with *P. laevis,* referencing the Oriental Sweetgum forest. The abundance of these two species throughout the Mediterranean coast confirms this record. Our data suggest that those records must be either coincidental or due to sampling in peripheral habitats. Our data from the Dalaman forests contained neither of the species in natural forest or in land recently converted into forest, and even if they occurred elsewhere, they were not associated with the Oriental Sweetgum forest, as explained above. We disagree with the emphasis on sympatry in Ilgaz *et al.* (2016). Some other herptile species previously recorded from the region were not found in our inventory.

The fossorial species *Xerotyphlops vermicularis* (Merrem, 1820), *Blanus strauchi* (Bedriaga, 1884), and *Eryx jaculus* (Linnaeus, 1758) are unlikely to occur in the Oriental Sweetgum forest biotope because of annual flooding. *Lyciasalamandra fazilae* (Başoğlu and Atatür, 1974) is another species recorded in the vicinity of dense forests, but our efforts to observe this species in the sweetgum forests were fruitless. These forests do not resemble the typical *Lyciasalamandra* habitat structure because they lack rocky limestone outcrops. Similarly, *Pelobates syriacus* Boettger, 1889, a species that depends on sandy or muddy clay soils with little vegetation, was not recorded from the densely vegetated Oriental Sweetgum forest biotope. The dense vegetation structure of these forests probably acts as a filter for basking reptile species such as *Heremites auratus* (Linnaeus, 1758) and other lizard species that seem to prefer peripheral habitats. For snakes, it is impossible to presume that the species list is complete with so few records; we strongly encourage new projects that sample snakes in this habitat. Finally, we recorded *Emys orbicularis* and *Elaphe sauromates* (Pallas, 1811) for the first time from the region.

We also compared the five large patches sampled by pitfall traps and transect walks. The highest richness (14) was observed in Toparlar, probably because of a considerable amount of non-forested biotopes, which yielded records of species that prefer peripheral habitats. Kavakarası forest had similar habitat but had fewer species (10); this area lacked two toad and two lizard species found in Toparlar. Large intact patches from Dalaman, Karabatak, and Kızılyaka had similar richness with similar composition regardless of whether they consisted of plantations or natural forest. They differed from the fragmented patches mentioned above mainly due to the exclusion of species that prefer peripheral habitats.

The data obtained in this study will be transferred to the Oriental Sweetgum forests conservation action plan (2019–2024) and will be used as practical biodiversity monitoring tools for the long-term conservation of these forests. Due to the annual flooding of the Oriental Sweetgum forests, conservation of this habitat is crucial for hydrophilic reptiles and amphibians such as *Emys orbicularis, Mauremys rivulata, Natrix natrix, N. tessellata, Bufo bufo* and *Bufotes sitibundus.* Finally, the origin of *Phoenicolacerta laevis* in the Oriental Sweetgum forests should be investigated to determine whether it is a relict of a historical retraction or an invader originating from a recent introduction.

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Appendix I. *Study locations and their habitats.*

Locations	Habitat isolation	Habitat fragmentation (fragmentation rate)	Size (ha) and origin	UTM 35 S		Species Richness	Total Abundance
				East	North		
1. Fethiye	Semi-isolated; connection with the sea; moderate interruption with the settlements, agricultural areas, roads, etc	Low fragmented (10–40%)	Riparian forest patch (100–200 ha); converge with a large water body such as a sea; with many permanent water supplies.	684915	4061839	4	4
2. Dalaman	Isolated; no connection with the sea, lake or forest; high interruption with the settlements, agricultural areas, roads, etc.	Non-fragmented (0–10%)	Plantation (100–200 ha); semi-natural, semi-artificial habitat reclaimed by means of intensive planting of sweetgum saplings, following significant degradation.	660955	4073572	8	150
3. Okçular	Isolated; no connection with the sea, lake or forest; high interruption with the settlements, agricultural areas, roads, etc.	Low fragmented (10–40%)	Small grove areas (10–30 ha); located in a rural area with a permanent water supply.	648802	4078017	1	3
4. Kavakarası	Semi-isolated; connection with the lake and forest; moderate interruption with the settlements, agricultural areas, roads, etc.	Highly fragmented (40–100%)	Riparian forest patches (> 200 ha); converge with a large water body such as a lake; with many permanent water supplies.	652364	4085155	10	239
5. Eski Köyceğiz	Semi-isolated; connection with the lake; moderate interruption with the settlements, agricultural areas, roads, etc.	Non-fragmented (0–10%)	Small grove area (10–30 ha); located in a bay and a rural area; with or without a permanent water supply.	654084	4088965	6	92
6. Zeytinalanı	Semi-isolated; connection with the lake; moderate interruption with the settlements, agricultural areas, roads, etc.	Non-fragmented (0–10%)	Small grove area (10–30 ha); located in a bay and a rural area; with or without a permanent water supply.	654045	4090386	6	6
7. Karabatak (Köyceğiz)	Semi-isolated; connection with the lake; moderate interruption with the settlements, agricultural areas etc.	Low fragmented (10–40%)	Riparian forest patches (> 200 ha); converge with a large water body such as a lake; with many permanent water supplies.	651301	4091238	11	203
8. Toparlar	Semi-isolated; connection with the lake and the forest; moderate interruption with the settlements, agricultural areas, roads, etc.	Highly fragmented (40–100%)	Riparian forest patches (> 200 ha); converge with a large water body such as a lake; with many permanent water supplies.	648141	4093443	14	177

Appendix I. *Continued.*

Locations	Habitat isolation	Habitat fragmentation (fragmentation rate)	Size (ha) and origin	UTM 35 S		Species Richness	Total Abundance
				East	North		
9. Hamitköy	Isolated; no connection with the sea, lake or forest; high interruption with the settlements, agricultural areas, roads, etc.	Non-fragmented (0–10%)	Small grove (10–30 ha); inside a rural area	643427	4090668	2	8
10. Kersele	Non-isolated; connection with the lake and the forest; no interruption with the settlements, agricultural areas, roads, etc.	Non-fragmented (0–10%)	Small grove areas (10–30 ha); located in a bay; with a permanent water supply.	642422	4085661	11	140
11. Kızılyaka	Semi-isolated; connection with the forest; moderate interruption with the agricultural areas, roads, etc.	Low fragmented (10–40%)	Plantation area (> 200 ha); semi-natural, semi-artificial habitat reclaimed by means of intensive planting of sweetgum saplings	629704	4096772	10	208
12. Çetibeli	Semi-isolated; connection with the sea and forest; moderate interruption with the settlements, agricultural areas, roads, etc.	Low fragmented (10–40%)	Small grove area (10–30 ha); located in a rural area with a permanent water supply.	614241	4092415	6	37
13. Hisarönü	Semi-isolated; connection with the sea and forest; moderate interruption with the agricultural areas, roads, etc.	Low fragmented (10–40%)	Small grove area (10–30 ha); located in a rural area with a permanent water supply.	602184	4077347	7	173

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Description of the tadpole of *Agalychnis hulli* (Anura: Hylidae)

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Abstract

Description of the tadpole of *Agalychnis hulli* (Anura: Hylidae). The collection of larval specimens from Amazonian Ecuador allows for the scientific description of the tadpole of *Agalychnis hulli*. The tadpole is unusual among Phyllomedusinae and its external morphology appears more similar to species of *Hylomantis* than other species of *Agalychnis,* suggesting the species may well represent an important evolutionary link between these genera. The tadpole, which to date has remained undescribed, can be distinguished from all other *Agalychnis* tadpoles in having an oral disc (i) that is directed anteroventrally and extends to more than half the width of the body, (ii) which is modified into a short funnel-shaped structure, (iii) and surrounded by a single row of marginal papillae.

Keywords: Amphibia, Larvae, Morphology, Phyllomedusinae.

Resumen

Descripción del renacuajo de *Agalychnis hulli* (Anura: Hylidae). Se recolectaron larvas en la Amazonia Ecuatoriana, las cuales permiten la descripción científica del renacuajo de *Agalychnis hulli.* El renacuajo es inusual entre los Phyllomedusinae y su morfología externa es más similar a las especies de *Hylomantis* que a otras especies de *Agalychnis,* lo que sugiere que la especie bien puede representar un vínculo evolutivo importante entre estos géneros. El renacuajo, que hasta la fecha no ha sido descrito, se puede distinguir de todos los demás renacuajos de *Agalychnis* por tener un disco oral (i) que se dirige anteroventralmente y se extiende a más de la mitad del ancho del cuerpo, (ii) que se modifica en una estructura corta en forma de embudo, (iii) y que está rodeado por una sola fila de papilas marginales.

Palabras clave: Amphibia, Larva, Morfología, Phyllomedusinae.

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Resumo

Descrição do girino de *Agalychnis hulli* (Anura: Hylidae). A coleta de espécimes larvais da Amazônia equatoriana permitem a descrição científica do girino de *Agalychnis hulli*. O girino é incomum entre os Phyllomedusinae e sua morfologia externa parece mais similar à das espécies de *Hylomantis* do que a de outras espécies de *Agalychnis*, sugerindo que essa espécie podem representar um importante elo evolutivo entre estes gêneros. O girino, que até hoje não havia sido descrito, pode ser distinguido de todos os outros girinos de *Agalychnis* por apresentar um disco oral (i) dirigido anteroventralmente e estendendos-e para mais da metade da largura do corpo, (ii) modificado em uma estrutura curta em forma de funil, e (iii) rodeado por uma única fileira de papilas marginais.

Palavras-chave: Anfíbios, Larvas, Morfologia, Phyllomedusinae.

Introduction

Agalychnis hulli (Duellman and Mendelson, 1995) is a small to medium sized hylid, originally described from a specimen collected at a small forest pond in the Province of Loreto, Amazonian Peru (Frost 2022). The species was originally placed in the *Phyllomedusa buckleyi* group (Cannatella 1980), subsequently in the *Hylomantis buckleyi* group (Faivovich *et al.* 2005), and later moved to *Agalychnis* Cope, 1864 without further assignment to a particular species group (Faivovich *et al.* 2010). Although it is not a common frog, unlike other *Agalychnis* species it is known to occur in the rainforest lowlands (200–997 m a.s.l.) of the Amazonian region of northeastern Peru and Ecuador; in the latter in Sucumbíos, Orellana, Napo, Pastaza, Morona Santiago, and Zamora Chinchipe provinces (Vigle 2008, Beirne and Whitworth 2011, Ron and Read 2019). The species is easily distinguished from other phyllomedusines from these areas in having coarsely granular skin on both its dorsal and ventral surfaces. The species' reproduction is characteristic of phyllomedusines, where eggs are laid on leaves overhanging temporary ponds into which the developing tadpoles drop upon hatching. All tadpoles currently described (10 species, including this description) that belong to species of the genus *Agalychnis* (14 species) are characterized in having mouthparts of typical suspension feeding phyllomedusines, whereas the mouthparts of *Hylomantis* tadpoles (two species) are modified into short funnel-shaped structures considered to resemble an intermediate morphological condition to those of *Phasmahyla* Cruz, 1991, which have mouthparts modified into an anterodorsal funnel-shaped structure (Pimenta *et al*. 2007). However, to date nothing has been published on *A. hulli* tadpole morphology. Herein we describe the external morphology and mouthparts of the tadpole of *Agalychnis hulli*, which distinctly differ from the tadpoles of other species of *Agalychnis*.

Materials and Methods

Measurements and remarks of ontogenetic changes are based on six tadpoles (MM.D.1299.1, MM.D.1299.2, MM.D.1299.3, MM.D.1299.4, CJ 11821, CJ 4741a) ranging from stages 26 to 44 (Gosner 1960). One of them (CJ 4741a) was field-collected and five were first generation descendent tadpoles born under laboratory conditions at the Centro Jambatu de Investigación y Conservación de Anfibios, Ecuador (CJ).

The description is based on a tadpole specimen (CJ 4741a) at Stage 36, which was collected with others from a pond close to Río Pucayacu, Reserva Otoyacu, (01°22'16.4" S, 77°51'23.4" W; 922 m a.s.l.), Provincia Pastaza, Ecuador, on 12 June 2016 by Elicio E. Tapia, Nadine Dupérré and Anabelle Tapia-Dupérré. The pond was approximately 40 m long × 20 m wide × 80 cm deep and located close to the

river. The pond was artificially modified by the obstruction of a creek due to a road construction, and the marginal vegetation was secondary, with 15–20 m high trees and many bushes surrounding it. The tadpoles were collected at the margins of the pond and transported to CJ to be raised to adulthood.

A resulting female specimen (CJ4741) was successfully raised to adulthood at CJ and maintained in laboratory with adult males from the same series, and also with a wild male collected at Comunidad Yarentaro (01°03'01.3" S, 76°11'37.5" W; 244 m a.s.l.), Parque Nacional Yasuní, Provincia Orellana, Ecuador, by Morley Read and Yerka Sagredo-Nuñez, which had been found perched on a branch 30 cm above ground near a small pond around a petroleum platform on 09 August 2021. The reproducing pair at CJ were not observed while in amplexus or when egg laying so we could not identify if the male in question was from Pucayacu or Yasuní. Therefore, the laboratory-bred tadpoles produced, including five specimens the details of which are incorporated in the measurements and remarks on ontogeny section, were first generation descendants of the Pucayacu female (CJ 4741), and either a male from the same series or the male from Yasuní.

The group of 25 descendant tadpoles was reared within a plastic container measuring 35.5 cm long × 27.5 cm wide, containing water 13.5 cm deep (12 L). They were kept in the lab at temperatures varying from 19°C (at night) to 24°C (during the day). Tadpoles were fed with a mix of *Taraxacum officinale* and Zoo Med's Aquatic Frog Food. A minimum number of specimens (4: MM.D.1299.1, MM.D.1299.2, MM.D.1299.3, MM.D.1299.4) were preserved in formalin (10%).

Two live specimens (the original CJ 4741a) and a descendant (CJ 11821) were reared to adulthood in the laboratory affording the documentation of ontogenetic variation. Adult specimens were identified as *Agalychnis hulli* and distinguished from *Agalychnis buckleyi* (Boulenger, 1882) by having coarsely granular skin on the dorsum (minutely granular skin on the dorsum) and by lacking a small calcar (present). Thus, our specific allocation of the tadpoles described herein is based on the adult similarity of the Reserva Otoyacu population to *A. hulli* from the type locality at Teniente López, Provincia Loreto, Peru. Both localities are at about 240 km airline distance.

Museum acronyms used in the text are MM for Manchester Museum, University of Manchester, and CJ for Centro Jambatu de Investigación y Conservación de Anfibios, Ecuador. Terminology and measurements follow Altig and McDiarmid (1999) and Pimenta *et al.* (2007). Abbreviations used are as follows: TL (total length); BL (body length); TAL (tail length); MTH (maximum tail height); TMH (tail muscle height); TMW (tail muscle width); IND (internarial distance: straight line distance between the inner margins of the nostrils); IOD (interorbital distance: straight line distance between the inner margins of the eyes); BH (greatest body height); BW (greatest body width); ED (eye diameter: horizontal diameter of the eye in lateral view); ODW (oral disc width: greatest horizontal width of the oral disc in front view); LTRF (Labial Tooth Row Formula): A1; A2 (anterior tooth rows); P1, P2 and P3 (posterior tooth rows): DFH (dorsal fin height: greatest height of dorsal fin); VFH (ventral fin height: greatest height of ventral fin); END (eye–nostril distance: straight line distance between the anterior margin of nostril and the tip of snout). The measurements (in mm) were taken using a calipers (to the nearest 0.01 mm) and through the use of a Zeiss stereomicroscope.

Results

Tadpole Description (CJ 4741a), Stage 36 (Figures 1 and 2)

Body shape: Ovoid in dorsal view and slightly triangular in lateral view, about equal in height and width, highest and widest at the midpoint of the body (Figure 1). Body length: 30.4% of the total length (BL = 10.5

mm; TL = 34.5 mm). Snout shape: Rounded in dorsal view and sub-elliptical in lateral view. Eyes: large, located immediately above the midline of the body, directed laterally (ED = 1. 9 mm) representing 25.7% of the interorbital distance and 14.7% of the body length, visible from below. Nostrils: small, ovoid, dorsolaterally positioned, with external openings directed anterolaterally, situated closer to snout than eyes (IND = 2.1 mm representing approximately 28.4% of the interorbital distance). Spiracle: ventral, opening scallop shaped, flap-like, transparent, directed backwards, located mid-body on the left side near the transversal midline, 1.4 mm long, widest towards the opening (1.5 mm wide). Ventral surface with silver covering: internal organs including intestinal tube not visible through the ventral and lateral surfaces of the body: Anal tube: short, dextral, right wall attached to the ventral fin, opening posteroventrally. Tail: tail and body of about equal height. Caudal musculature well developed, slender, becoming progressively thinner caudally. Myosepta and caudal vein defined until about the first half of the tail. Dorsal fin considerably lower than ventral fin (DFH = 1.5 mm, VFH = 2.5 mm), weakly arched, does not extend onto the body, origins anterior third of the tail. Ventral fin approximately 66.7% deeper than the dorsal, weakly arched distally, origins posterior quarter of the body, widest point at approximately midpoint, corresponding with dorsal; both tail fins graduate to a distal point. Caudal tip ends in long flagellum. For measurements see Table 1.

Table 1. Morphometric measurements (in mm) of the tadpole of *Agalychnis hulli* during ontogeny. Developmental stages are according to Gosner (1960).

Specimen number	**MM.D1299.1**	**CJ4741a**	**MM.D.1299.2 CJ11821**	**MM.D.1299.3 MM.D.1299.4 CJ11821**	**CJ4741a**
Stage	26 (*N* = 1)	36 (*N* = 1)	41(*N* = 2)	43 (*N* = 3)	44 (*N* = 1)
Total length	34.5	43.9	52.0–55.0	42.7–56.0	43.4
Body length	10.5	12.9	16.0–16.2	16.3–17.6	22.0
Body width	5.1	6.8	9.0–10.5	8.8–9.7	-
Body height	5.3	6.4	8.0–11.5	4.8–7.2	8.0
Tail length	24.0	31.0	35.8–39.0	26.4–39.0	21.4
Tail muscle height	3.6	4.3	6.0–7.1	3.9–5.2	5.6
Dorsal fin height	-	1.5	1.6	1.6	-
Ventral fin height	2.0	2.5	3.2	2.6	-
Snout–nostril distance	1.3	1.7	2.2–2.4	1.8–2.0	-
Internarial distance	2.0	2.1	2.4–2.6	3.0–3.1	-
Eye–nostril distance	2.2	3.5	3.9–4.0	3.4–3.5	3.8
Eye diameter	1.5	1.9	2.5–2.6	2.6–3.0	3.6
Interorbital distance	4.8	7.4	7.0–8.2	7.9–8.2	-
Oral disc width	2.1	3.7	4.1	3.4–4.2	-
Anal tube length	1.4	2.4	3.0	-	-

Mouthparts

The oral disc is positioned and directed anteroventrally, the outer edge of the labium forming a short funnel-shaped structure, excepting a median dorsal gap in the upper labium being a continuation of the snout (Figure 2A). Except for the median dorsal gap, the labium is bordered by one continuous uniserial row of about 80–100 small conical-shaped marginal papillae along the outer edge, and the inner surfaces have a uniform scattering of papillae which are indiscreet, barely breaking the otherwise smooth surface (being clearly visible within the translucent labium when lit from beneath) (Figure 2B).

The oral disc is large (ODW = 3.7 mm) representing 53.5% of the body width, having a small median emargination in the lower labium. There are two anterior and three posterior rows of teeth; LTRF is 2(2)/3(1). Teeth on the first anterior row (A1) form a broad arch and are smaller in size than in the second anterior row (A2), which is interrupted medially; the anterior rows are longer than the first (P1), second (P2), and third (P3) posterior rows, which reduce in length sequentially; the first posterior row (P1) has a small medial gap, the second (P2) and third (P3) rows are complete. Upper and lower jaw sheaths are robust, heavily pigmented, and both bear fine serrations; upper jaw sheath medially convex; moderately long lateral processes; lower jaw sheath V-shaped (Figure 2A).

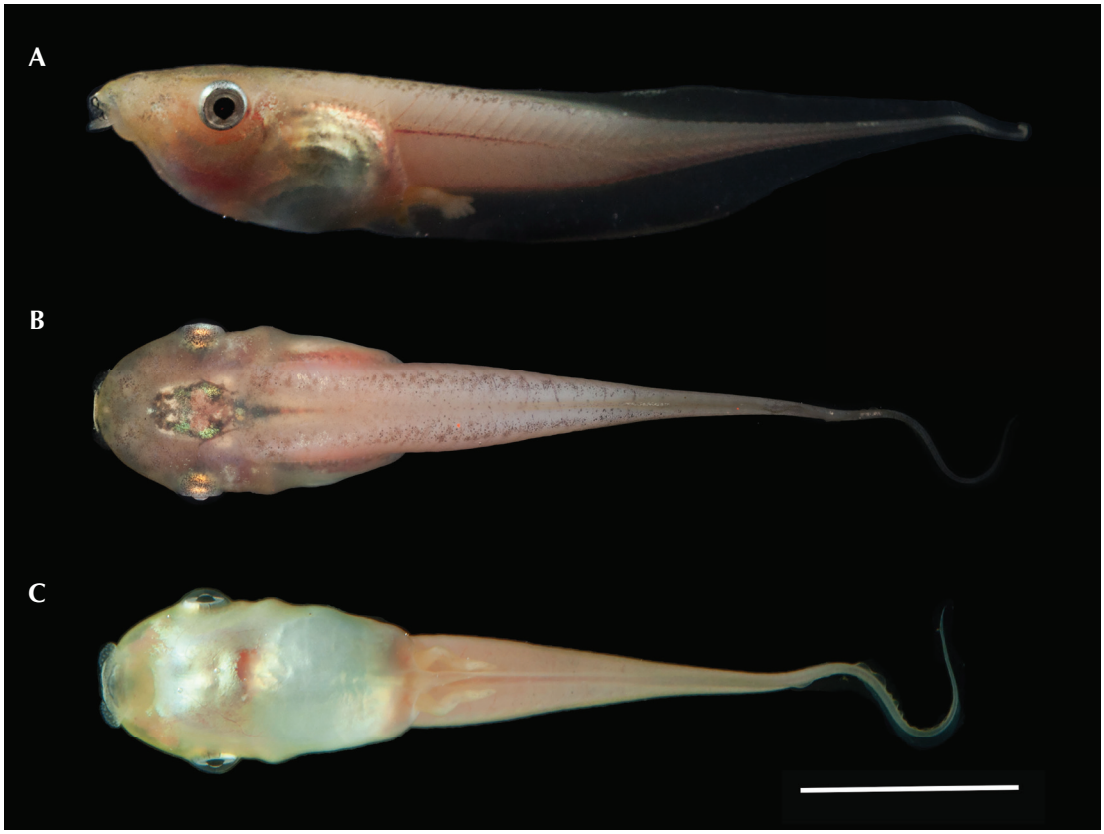

Figure 1. Tadpole of *A. hulli* (CJ 4741a) Stage 36 in lateral (**A**), dorsal (**B**), and ventral (**C**) views. Scale bar 1 cm.

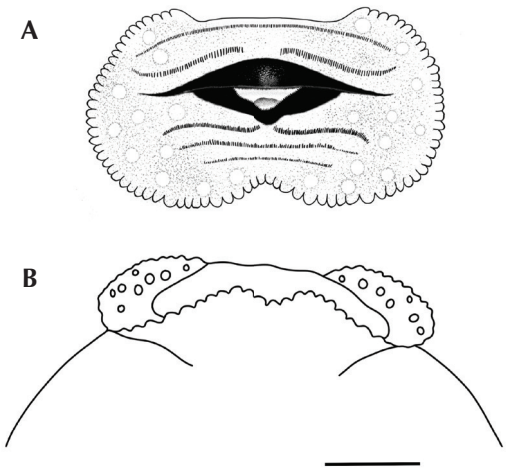

Figure 2. Mouthparts of the tadpole of *A. hulli* (CJ 4741a) Stage 36: (**A**) Oral disc; (**B**) detail of funnel-shaped labia. Scale bar 1 mm.

Coloration

In life.—Background color of body at Stage 36 flesh-pink, having fine dark brown speckling on the dorsal surfaces of the body, extending along caudal musculature at the anterior of the tail. Tail musculature flesh pink, caudal vein dark red until about the first half of the tail. Dorsal and ventral fins transparent. Ventral surface of body silver. Silver covering to internal organs; thus, organs are not visible through the ventral and lateral surfaces of the body. Chondrocranial elements visible dorsally, dark metallic-brown polygon-shaped. Iris silver-grey, periphery with fine silver reticulations. Limb buds and anal tube follow coloration of the body.

In preservative.—Background coloration of body and tail musculature becomes whitish-cream; dorsal surfaces of body and anterior of tail with greyish speckling. Intestinal mass dark grey, clearly visible through lateral and left ventral body walls; caudal vein black until about the first half of the tail. Spiracle, dorsal and ventral fins remain translucent. Iris black. Oral disc and papillae translucent-white, oral surfaces of upper and lower jaw sheaths black.

Ontogenetic Changes

At stages 25–26 the distance between the nostrils and the eye are of about equal width, whereas from Stage 26 the distance between the eye and nostril increases considerably compared to that between each nostril. Throughout development the bilateral myotonic muscle masses and the caudal vein in the tail musculature remain clearly defined. At Stage 36 the pupil has developed an elliptical shape, the spiracle opening is evident although not prominent, and a shallow groove from the posterior edge of the nostril to the eye is observed. Between stages 36–41 a notable increase in the growth of the ventral fin height is seen compared with that of the dorsal fin. This, and growth in the musculature, result in a notable overall change in tail height compared to tail length from about 26.8% at Stage 36 to about 30.6% at Stage 41. From Stage 41, with the onset of metamorphosis, the spiracle and the anal tube disappear, the tail begins to shrink and the nostrils become defined. The overall tail muscle height reduces but the caudal vein remains prominent, the eye to nostril distance starts to decrease, the anterior limbs appear, and fine dorsal granulations seen in the adult also begin to appear. The nostrils become more pronounced, although the shallow groove between the nostril and the eye remains minimal, and a small notch appears at the bottom of the pupil in respect of initiating the pupils' vertical development. One specimen in Stage 44 (CJ 4741a) which emerged during the final stages of metamorphosis showed an TL (total length) of 43.4 mm, including its partially absorbed tail (Figure 3).

Discussion

Faivovich *et al.* (2010) considered it reasonable to assume that a close relationship existed between *Agalychnis hulli* and *A. buckleyi*. This

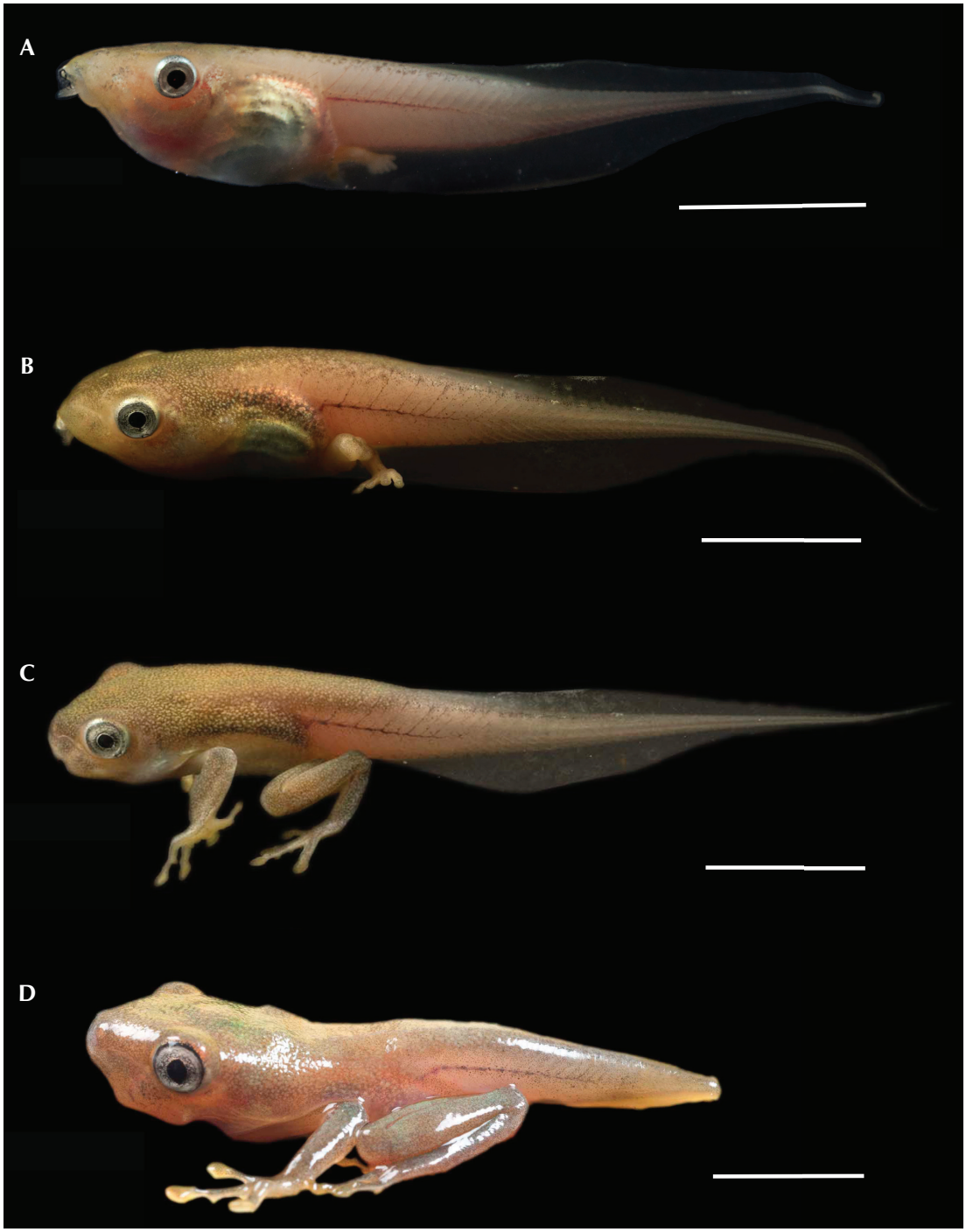

Figure 3. Development in the tadpole of *A. hulli* (CJ 11821) to metamorphosis. Scale bar 1 cm. Stages: (**A**) 36, (**B**) 40, (**C**) 42, (**D**) 43. Photos: Steven Guevara Salvador.

assumption was based on anatomical similarities in adult specimens. Both do look similar and both have an amount of tuberculated skin: *A. hulli* has extensive granulated skin, coarsely granular skin on the dorsum (Duellman and Mendelson 1995); *A. buckleyi* has minutely granular skin on the dorsum (Cannatella 1980). As such, *A. hulli* was placed with *A. buckleyi* within the genus *Agalychnis,* along with all other members that had previously been hypothesized as belonging in *Hylomantis* (Faivovich *et al.* 2010). However, the tadpole described herein differs from the tadpole of *A. buckleyi* (characters in parentheses) described and illustrated by Cannatella (1980) from Río Azuela and Río Salado, Provincia Napo, Ecuador, by having an oral disc being modified into an anteroventrally directed short funnel-shaped structure (not funnel-shaped) and a single row of marginal labial papillae (2–3 rows). These two features of *A. hulli* are unusual within Phyllomedusinae. The funnel-shaped oral disc is however more similar to that seen in both members of the genus *Hylomantis* from Brazil: being most similar to *Hylomantis aspera* Peters, 1873, and to a lesser extent *Hylomantis granulosa* (Cruz 1989). At Stage 36 the mouth of the tadpole of *A. hulli* is large, representing more than half the width of the tadpole, whereas in all other *Agalychnis* tadpoles the mouth lacks the funnel-shape and is thus considerably smaller. The single row of marginal labial papillae possessed by the tadpole of *A. hulli* is a further characteristic seen in *Hylomantis* and not found in any other *Agalychnis* species.

Interestingly, when Pimenta *et al.* (2007) evaluated the oral disc characteristic in the closely related species to *Hylomantis aspera* and *H. granulosa* they considered the distinct anteroventrally directed oral disc (funnel shaped and 50%+ the width of the tadpole) reflected such a distinct morphological character that it could well present a synapomorphy for *Hylomantis*. Although the tadpoles of *H. aspera, H. granulosa,* and *A. hulli* are morphologically similar in this way, we acknowledge that the two species in *Hylomantis* have a wide geographical separation from *A. hulli* (Duellman *et al.* 2016) and there is also the possibility that a resemblance to each other could be due to homoplasy, possibly through these species occurring and reproducing in temporary ponds inside or at forest edges which have a substrate of dead leaves. Nonetheless, according to the molecular phylogenetic analysis of Faivovich *et al*. (2010), *Agalychnis hulli* (from Ahuano, Provincia Napo, Ecuador) is the sister taxon of *Hylomantis aspera* + *H. granulosa* from northeastern Brazil. So, the two tadpole features previously mentioned supports the molecular topology hypothesized by Faivovich *et al.* (2010), and the inclusion of *A. hulli* within *Hylomantis.* However, we refrain of doing the latter generic change given that genetic data are needed from the hypothetically closely related taxa (*A. buckleyi*, *Agalychnis danieli* Ruiz-Carranza, Hernández-Camacho, and Rueda-Almonacid, 1988*, Agalychnis medinae* Funkhouser, 1962*,* and *Agalychnis psilopygion* Cannatella, 1980) before the phylogenetic relationships can be clarified for a suitable classification. It is clear that further molecular work is required in order to clarify some of the hypothesized phylogenetic relationships within the *Agalychnini* (sensu Dubois *et al*. 2021), particularly between *Hylomantis* and those species previously referred to as belonging to the '*buckleyi* group' that are currently placed within *Agalychnis.*

Additionally, the phylogenetic hypothesis of Faivovich *et al*. (2010) indicate that *Hylomantis* (sensu Duellman *et al.* 2016) probably represents an early divergence event in the ancestral lineage that also gave rise to *Agalychnis.* Thus, the mouth feature in *A. hulli* could well be a retained ancestral characteristic, which contrasts with those of other *Agalychnis* species, including *A. buckleyi, Agalychnis lemur* Boulenger, 1882, and *A. psilopygion,* which all have several rows of marginal papillae (Cannatella 1980) and typical oral discs associated with the suspension-feeding tadpoles of most other phyllomedusines (Pimenta *et al.* 2007).

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Sexual dimorphism, female fertility, and diet of *Physalaemus feioi* (Anura: Leptodactylidae) from southeastern Brazil

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Abstract

Sexual dimorphism, female fertility, and diet of *Physalaemus feioi* (Anura: Leptodactylidae) from southeastern Brazil. *Physalaemus feioi* is a South American frog endemic to the Brazilian Atlantic Forest that occurs in the states of Minas Gerais and São Paulo. We evaluated sexual dimorphism, female fertility, and diet of *P. feioi* from two locations in the state of Minas Gerais, including the type locality of the species. We collected 73 individuals (16 adult females and 57 adult males). The number of oocytes of *P. feioi* ($\bar{x}$ = 1385 ± 498.13) was higher than in other species of the genus, such as *P. maculiventris, P. signifer, P. cuvieri,* and *P. ephippifer,* but it resembles that of *P. centralis, P. kroyeri,* and *P. marmoratus*. The prey items with the highest index of importance were Coleoptera (IIR = 24.26) and Formicidae (IIR = 16.46). We found no sex differences regarding the number of ingested prey and the volume of the stomach contents. In summary, *Physalaemus feioi* was similar to other species of the genus regarding sexual dimorphism, fecundity, and feeding habits.

Keywords: Amphibia, Atlantic Forest, Morphology, Natural history, Trophic ecology.

Resumo

Dimorfismo sexual, fertilidade de fêmeas e dieta de *Physalaemus feioi* (Anura: Leptodactylidae) do sudeste do Brasil. *Physalaemus feioi* é uma rã da América do Sul, endêmica da Mata Atlântica, registrada nos estados de Minas Gerais e São Paulo. Avaliamos o dimorfismo sexual, a fertilidade nas fêmeas e dieta dessa espécie em duas localidades do estado de Minas Gerais, incluindo a localidade-tipo da espécie. Coletamos 73 indivíduos (16 fêmeas adultas e 57 machos adultos) por meio de busca

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ativa. O número de oócitos encontrados para *P. feioi* ($\bar{x}$ = 1385 ± 498,13) foi alto quando comparado com outras espécies do gênero como *P. maculiventris*, *P. signifer*, *P. cuvieri* e *P. ephippifer* mas este semelha o número de oócitos de *P. centralis*, *P. kroyeri* e *P. marmoratus*. As presas com maior índice de importância foram Coleoptera (IIR = 24,26) e Formicidae (IIR = 16,46). Não houve diferenças entre machos e fêmeas quanto ao número de presas ingeridas e nem o volume do conteúdo estomacal. Em resumo, *Physalaemus feioi* teve semelhanças com outras espécies do gênero em relação ao dimorfismo sexual, fecundidade e hábitos alimentares.

Palavras-chave: Amphibia, Ecologia trófica, História natural, Mata Atlântica, Morfologia.

Introduction

Physalaemus Fitzinger, 1826 is a genus of small to medium frogs that occur in South America (Cassini *et al.* 2010, Brasileiro and Haddad 2015, Frost 2021, Leal *et al.* 2021). It was divided into seven groups, based on morphometric, morphological, osteological, and adult patterns (Nascimento *et al.* 2005), but without defined phylogenetic relationships. More recently, Lourenço *et al.* (2015) proposed a phylogeny based on nuclear and mitochondrial DNA sequences and recognized two clades: the *P. signifer* and the *P. cuvieri* clades. The latter is composed of five species groups (Lourenço *et al.* 2015), one of which is the *P. olfersii* group, which includes *P. feioi* Cassini, Cruz, and Caramaschi, 2010 together with six other species. Species within this group occur in southeastern and southern states of Brazil (Espírito Santo, Rio de Janeiro, Paraná, Santa Catarina, São Paulo, and Minas Gerais; Nascimento *et al.* 2005, Lourenço *et al.* 2015). *Physalaemus feioi* inhabits the Atlantic Forest of the Serra da Mantiqueira in São Paulo and Minas Gerais states (Figure 1), and is common in gallery forests, around ponds and along creeks and rivulets (Cassini *et al.* 2010, Silva *et al.* 2011, Moura *et al.* 2015). Some aspects of the reproductive biology of the species are known for populations in Piedade de Caratinga (Minas Gerais state), where males vocalize in late spring and summer months (October–February) and females spawn within the same seasons but in a more restricted temporal window (October–December: Silva *et al.* 2011), Like other species in the genus, individuals construct floating foam nests, sometimes communally, as described for individuals from the type locality (Lacerda *et al.* 2009).

Figure 1. Amplexus of *Physalaemus feioi* from Eugenópolis, Minas Gerais state, southeastern Brazil.

Ecological features such as skin patterns and advertisement calls are well known and used in diagnoses of the species (Cassini *et al.* 2010). Other than these features, only phenology and tadpole descriptions are available (Silva *et al.* 2011, Fraga *et al.* 2022). In order to understand the role of a species in an ecosystem, it is necessary to know the diet and trophic connections (Ceron *et al.* 2022a). Data on the natural history and biology of organisms are fundamental to understand the intrinsic characteristics of each species (Stearns 1992), and how ecological and environmental forces

determine their occupation of a given space, including phenology and abiotic factors (Afonso and Eterovick 2007, Schalk and Saenz 2016). Reproductive strategies and investment are essential in determining the conservation status of a species (IUCN 2021). Among these aspects, key characteristics include sexual dimorphism, female fertility, and diet (Vitt and Caldwell 2001). Our objective is to investigate (1) reproductive features, including as sexual dimorphism and female fertility, and (2) the diet of *Physalaemus feioi* from two loctions in Minas Gerais, including the type locality.

Materials and Methods

Data Collection

We collected specimens at night during November and December 2010 by actively searching vocalization and spawning sites (Heyer *et al.* 1994). Four researchers worked four hours per day and collected 26 individuals of *P. feioi* from the type locality, Viçosa municipality (20°45'27.5" S, 42°51'38.7" W, 700 m a.s.l., Datum WGS84), and 47 individuals in Eugenópolis municipality (21º06'06" S, 42º10'59" W, 660 m a.s.l., Datum WGS84). Both areas are in Minas Gerais state, southeastern Brazil, and are separated by a straight-line distance of 66 km. The climate of the region is humid mesothermic, with dry winters (Alvares *et al.* 2013). The type locality has a dam partially surrounded by grass and a secondary semi-deciduous seasonal forest fragment. In Eugenópolis, the collection site is similar and contains a dam bordered by pasture and by a secondary semi-deciduous seasonal forest fragment.

Individuals were killed two hours after collection by application of xylocaine in the ventral region of the body and fixed in 10% formalin. After three days, samples were washed and preserved in 70% Ethanol. We sexed individuals using external sexual characters (e.g., vocal sac and vocal cleft in males) and by dissecting individuals and analyzing their gonads. All individuals were classified as reproductive adults.

Thirteen variables were measure for each specimen using a 0.01 mm precision digital caliper: snout–vent length (SVL), head length (HL), head width (HW), eye diameter (ED), interorbital distance (IOD), upper eyelid width (UEW), eye–nostril distance (END), nostril–snout distance (NSD), internarial distance (IND), hand length (HAL), thigh length (TL), shank length (SL), and foot length, including the tarsus (FL) (Cassini *et al.* 2010).

Oocyte masses of each female were removed and weighed using a Scientech SA 210 scale with an accuracy of 0.0001 g. We weighed ten oocytes per female and calculated an average weight per female in order to estimate the total number of oocytes in each mass.

Stomachs of all individuals were removed, and their contents were identified to Order and counted, with exception of the insect larvae, which were not identified. Using a stereomicroscope with a millimeter eyepiece and Image Pro Plus software (Media-Cybernetics 2002), the width and length of each intact item were measured.

Specimens were deposited in the Museu de Zoologia João Moojen (MZUFV) of the Universidade Federal de Viçosa, Viçosa municipality, Minas Gerais state, Brazil (Eugenópolis samples: MZUFV 10781–10782, 10796–10801, 10803–10807, 10824–10857; Viçosa samples: MZUFV 10808–10822, 10856–10857, 10966–10976).

Data Analysis

Principal Component Analysis (PCA) was used to test for morphometric sexual dimorphism in *P. feioi*. Once PCA identified the three most explanatory axes (PC1, PC2, and PC3) and a Kruscal-Wallis test was used to test for normality, we performed a MANOVA using the results as response variable and sex as factor. In order to test if bigger females had more oocytes, we ran a liner regression using the female body size (SVL) against the number of oocytes.

To describe the diet of *P. feioi* and determinate the importance of each prey item, we used the Pinkas *et al.* (1971) importance index (IRI = %F*(%N+%V), which uses the frequency of occurrence percentage (F%), the numeric percentage (N%) and the volumetric percentage. The prey volume was estimated using the formula for a spheroid (Magnusson *et al.* 2003, Garda *et al.* 2006, Santana and Juncá 2007): $V = 4/3\pi(\text{length}/2)(\text{width}/2)^2$. We did not consider samples with empty stomachs (N = 9) in the diet analyses.

Sex differences in diet were assessed using generalized linear models (GLM) with prey number and total prey volume as variables. Response variables were submitted to residue analysis to verify their error distribution (Crawley 2012). All statistical analyzes were done in the R (R Core Team 2022) program with the Vegan package version 2.3-5 (Oksanen *et al.* 2015).

Results

Sexual Dimorphism

We collected 73 individuals, 16 females with mature oocytes externally evident and 57 males. Females were significantly larger than males (F = 49.15, p < 0.001). Other variables used for sex discrimination (including SVL) were larger in females: snout–vent length (males: $\bar{x}$ = 25.55 ± 1.12 mm; females: $\bar{x}$ = 28.58 ± 1.21 mm), shank length (males: $\bar{x}$ = 12.45 ± 0.56 mm; females: $\bar{x}$ = 14.33 ± 1.51 mm) and foot length including tarsus (males: $\bar{x}$ = 17.91 ± 1.03 mm; females: $\bar{x}$ = 19.46 ± 0.79 mm) (Table 1). The PCA indicated that 86% of the variance was explained by the three first components (PC1 = 67%, PC2 = 12% and PC3 = 7%), mainly PC1 (Figure 2).

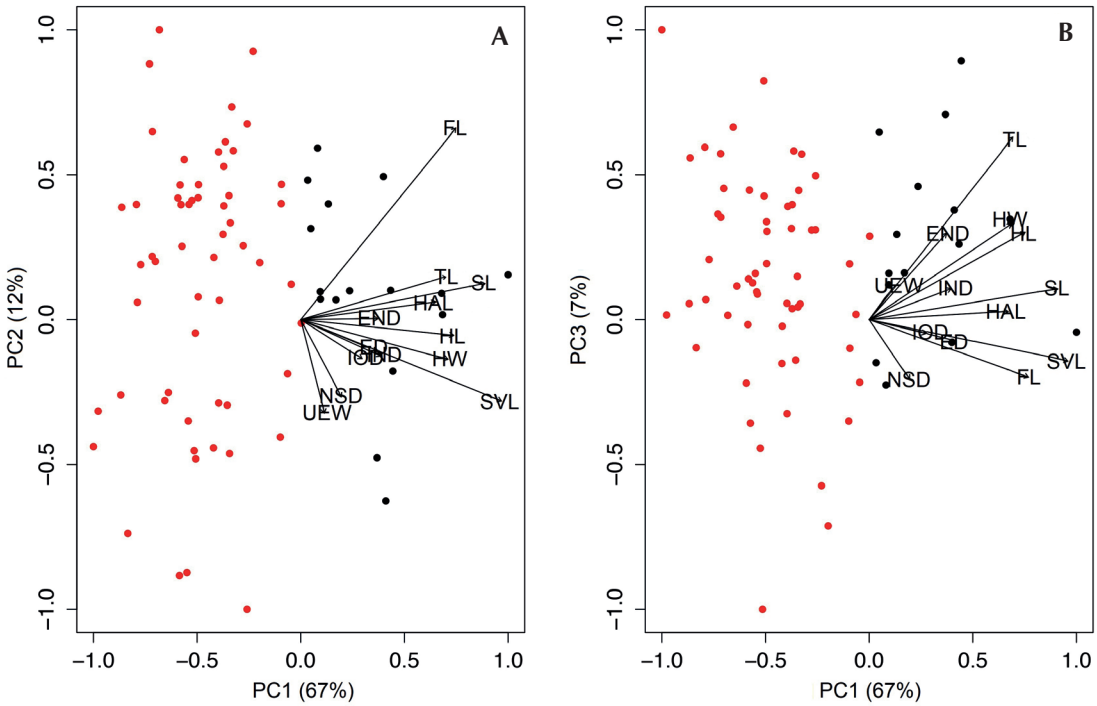

Figure 2. Principal Components Analysis for 13 morphometric characters from adult males (red) and females (black) of *Physalaemus feioi*. Projection of PC1 and PC2 (**A**), and projection of PC1 and PC3 (**B**).

Table 1. Morphometric variation of *Physalaemus feioi* from Eugenópolis and Viçosa (Minas Gerais state, Brazil). Values are in mm as mean ± SD (range). Snout–vent length (SVL), head length (HL), head width (HW), eye diameter (ED), interorbital distance (IOD), upper eyelid width (UEW), eye–nostril distance (END), nostril–snout distance (NSD), internarial distance (IND) hand length (HAL), thigh length (TL), shank length (SL), foot length including tarsus (FL).

Body measurements	Males (*N* = 57)	Females (*N* = 16)
SVL	25.55 ± 1.12 (23.30–27.92)	28.58 ± 1.21 (27.10–31.34)
HL	6.96 ± 0.43 (5.90–7.79)	7.98 ± 0.50 (6.65–8.60)
HW	6.88 ± 0.45 (5.66–7.67)	7.80 ± 0.49 (6.80–8.71)
ED	2.27 ± 0.28 (1.75–2.85)	2.47 ± 0.29 (2.12–3.17)
IOD	2.89 ± 0.30 (2.26–3.52)	3.09 ± 0.32 (2.52–3.69)
UEW	2.00 ± .0.31 (1.23–3.22)	2.11 ± 0.24 (1.64–2.40)
END	2.56 ± 0.30 (1.55–3.20)	2.84 ± 0.27 (2.52–3.36)
NSD	1.33 ± 0.20 (1.01–1.88)	1.42 ± 0.10 (1.26–1.62)
IND	2.01 ± 0.20 (1.59–2.41)	2.25 ± 0.25 (1.77–2.57)
HAL	7.01 ± 0.40 (6.18–7.89)	7.72 ± 0.33 (7.07–8.12)
TL	11.42 ± 0.68 (9.75–12.69)	12.70 ± 0.67 (11.28–13.73)
SL	12.45 ± 0.56 (10.84–13.47)	14.33 ± 1.51 (13.34–14.72)

Female Fertility

Of the 16 females, eight had developed oviducts and two of these were found in amplexus. The estimated number of oocytes for each female ranged from 585 to 2170 ($\bar{x}$ = 1,385 ± 498.13; N = 16). We found a positive relationship between SVL and weight (df = 14, F = 16.47, R^2 = 0.5078, p < 0.01; Figure 3A). We did not find a significant relationship between the SVL of females and the number of oocytes (df = 14, F = 1.9, R^2 = 0.056, p = 0.19; Figure 3B).

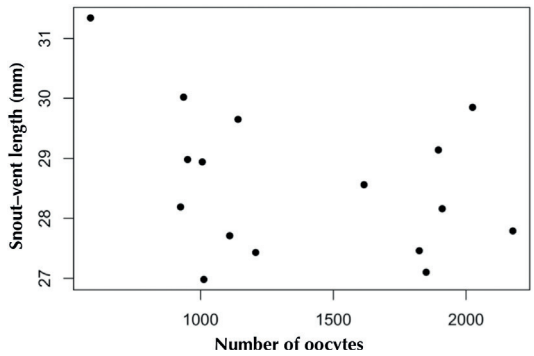

Figure 3. Relationship between size (SVL) and the number of oocytes of *Physalaemus feioi*.

Diet

Nine individuals (four males and five females) had empty stomachs. The diet was composed mostly of adult and larval insects but also of spiders and snails. We found 279 individual items in 11 prey categories (Table 2). The most numerous categories of prey in the diet of *P. feioi* were Coleoptera (IRI = 36.37), Formicidae (IRI = 26.77) and unidentified insect larvae (IRI = 17.99). Hymenopterans other than ants and orthopterans occurred only in the Eugenópolis samples, whereas snails were found only in samples from Viçosa. Insect larvae represented the largest volume (39.59%),

Table 2. Diet of *Physalaemus feioi* from Eugenópolis and Viçosa (Minas Gerais state, Brazil). The category "Other" represents remains of arthropods and unidentified material. Number of stomachs containing each category (F); Number of prey; V = volume of prey (mm³). Items with IRI > 10 represented with *.

Prey Category	F	%F	*N*	%*N*	V	%V	IRI
Arachnida							
Araneae	8	6.96	8	2.85	4.4	3.56	4.46
Insecta							
Coleoptera	42	36.52	129	45.91	32.96	26.69	36.37*
Hemiptera	5	4.35	6	2.14	6.7	5.43	3.97
Hymenoptera (Formicidae)	36	31.30	76	27.05	27.11	21.95	26.77*
Hymenoptera (non-Formicidae)	3	2.61	3	1.07	0.46	0.37	1.35
Isoptera	3	2.61	35	12.46	0.16	0.13	5.06
Orthoptera	2	1.74	2	0.71	1.43	1.16	1.20
Unidentified larvae	10	8.70	16	5.69	48.89	39.59	17.99*
Gastropoda	1	0.87	1	0.36	1.3	1.05	0.76
Undetermined	5	4.35	5	1.78	0.08	0.06	2.06

followed by beetles (26.69%) and ants (21.95%). The numeric frequencies were represented by adult beetles (129 individuals: 45.91%), followed by ants (76 individuals: 27.05%), and termites (35 individuals: 12.46%). Similarly, the first two categories of the occurrence frequencies were adult beetles (36.52%) and ants (31.30%), followed by unidentified insect larvae (2.70%). No significant differences were found between the sexes ($F_{1.59}$ = 0.19, p = 0.66). We did not find differences in sexes in the number of prey ingested (males: $\bar{x}$ = 4.39 ± 3.43; females: $\bar{x}$ = 6.10 ± 9.90) or the total prey volume (males: $\bar{x}$ = 2.11 ± 4.53 mm³; females: $\bar{x}$ = 1.46 ± 1.50 mm³).

Discussion

The mean number of oocytes in females of *P. feioi* ($\bar{x}$ = 1385 ± 498.13) was large compared to the numbers recorded for other species of *Physalaemus*: *P. maculiventris* (129 eggs; Heyer *et al.* 1990), *P. signifer* (273 eggs; Wogel *et al.* 2002), and *P. cuvieri* (474 eggs; Barreto and Andrade 1995). The mean number of oocytes of *P. feioi* resembled that of *P. kroyeri* (1332 eggs), which has a similar average size (30.2 mm) (Gally and Zina 2013). The number of oocytes in *P. feioi* was smaller than *P. centralis* (1872 eggs), a species with a larger female average size (34.5 mm) (Brasileiro and Martins 2006). It is common to find a positive relationship between the number of eggs and SVL of female anurans, such as in *Leptodactylus natalensis* (Ferreira *et al.* 2007), *P. centralis* (Brasileiro and Martins 2006), and *P. signifer* (Wogel *et al.* 2002). However, this relationship was not found for *P. feioi*, indicating that there may be no relationship between the physical status of females of *P. feioi* and the number of oocytes produced.

Although data on prey availability is an important factor in anuran diets (Ceron *et al.* 2022b), *Physalaemus feioi* is an arthropod feeder, as are most anurans. We found numerous prey categories, even mollusks, in the diet of this species, indicating that it is not a diet specialist (e.g., feeding exclusively on ants). Instead, individuals utilize an abundance of certain

categories in their diet (beetles and ants), particularly those that are abundant in leaf litter in Neotropical environments (Lavelle 1996, Barberena-Arias and Aide 2003, Marinoni and Ganho 2003). Termites and insect larvae were second in the composition of the diet. Other species in the genus [*P. cuvieri* (Santos *et al.* 2004, Silva and Rossa-Feres 2010), *P.* cf. *cicada* (Santana and Juncá 2007), *P. ephippifer* (Rodrigues and Santos-Costa 2014), *P. biligonigerus* and *P. gracilis* (Oliveira *et al.* 2015), and *P. nattereri* (Silva and Rossa-Feres 2010)] had diets similar to theat of *P. feioi*, as did other anurans that feed in leaf litter microhabitats: *Leptodactylus natalensis* (Ferreira *et al.* 2007), *Pristimantis labiosus* (Gutiérrez-Cárdenas *et al.* 2016), *Crossodactylus* spp. and *Hylodes* spp. (Almeida-Gomes *et al.* 2007, Caldart *et al.* 2012). The diet of *P. feioi* differs from several species from Argentina, including *P. albonotatus* from Santa Fe (Falico *et al.* 2012), *P. biligonigeros* from a soybean field in Cordoba (Attademo *et al.* 2007), and *P. santafecinus* from a population near Corrientes (Duré 1998).

Previews reports found sex differences in the numerical and volumetric proportions of the diet and relative importance of the categories of prey consumed by *Leptodactylus fuscus* and *L. mystacinus* (De-Carvalho *et al.* 2008), species with sexual dimorphism. Diets of males and females of *P. feioi* were similar, both qualitatively (categories of prey) and quantitatively (IRI, number of prey ingested, total prey volume), despite the sexual dimorphism detected in body size. A possible cause for the similarity observed might be the spatial distribution of individuals at the collection sites, as both males and females were observed and collected in the same microenvironments (e.g., leaf litter, in the water, on fallen logs in the water). Similarities between diets of males and females have also been observed for other species of anurans, including *Lithobates catesbeianus, Physalaemus nattereri, P. cuvieri, P. ephippifer, Leptodactylus podicipinus,* and *Eleutherodactylus planirostris* (Ferreira *et al.* 2007, Silva *et al.* 2009, Silva and Rossa-Feres 2010, Rodrigues and Santos-Costa 2014).

Our results indicate that *Physalaemus feioi* was similar to other congeneric species in relation to sexual dimorphism, fertility, and diet. Studies that focus on aspects of natural history aid in understanding key requirements affecting conservation strategies for anurans.

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Vocalizations, morphological variation, and morphometry of *Pristimantis gutturalis* (Anura: Strabomantidae)

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Abstract

Vocalizations, morphological variation, and morphometry of *Pristimantis gutturalis* (Anura: Strabomantidae). *Pristimantis gutturalis* is a species of the *P. conspicillatus* group described from French Guiana, with distribution so far restricted to the eastern Guiana Shield. Some aspects of this species are yet understudied, including its vocal repertoire which is unknown to date. Although in its original description it was properly characterized with regard to morphology, the description of its coloration in life consisted of brief remarks based on field notes on two females only. Moreover, little morphometric data were presented in its description, with detailed measurements provided for the holotype (a female) only. Subsequent studies have only briefly addressed this species and have not presented significant new data on it. In order to improve the knowledge on *P. gutturalis*, based on data from the state of Amapá, northern Brazil, in the present study we describe for the first time the advertisement and territorial calls of this species, assess its morphological and chromatic variation, provide detailed morphometric data on males and one female, and briefly comment on its natural history. Additionally, we compare the advertisement call of *P. gutturalis* with calls of other species of the *P. conspicillatus* group, and make some remarks on the acoustics of this group.

Keywords: Advertisement call, Bioacoustics, Eastern Guiana Shield, Phenotypic variation, *Pristimantis conspicillatus* group, Taxonomy, Territorial call.

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Resumo

Vocalizações, variação morfológica e morfometria de *Pristimantis gutturalis* (Anura: Strabomantidae). *Pristimantis gutturalis* é uma espécie do grupo de *P. conspicillatus* descrita da Guiana Francesa, com distribuição restrita ao Escudo da Guiana oriental. Alguns aspectos dessa espécie são ainda pouco estudados, incluindo seu repertório vocal que é desconhecido até o momento. Embora na sua descrição original ela tenha sido devidamente caracterizada no que diz respeito à morfologia, a descrição de sua coloração em vida consistiu de breves observações baseadas em notas de campo sobre duas fêmeas apenas. Além disso, poucos dados morfométricos foram apresentados na sua descrição, com medidas detalhadas fornecidas apenas para o holótipo (uma fêmea). Estudos subsequentes apenas abordaram brevemente essa espécie e não apresentaram novos dados significativos sobre ela. A fim de melhorar o conhecimento sobre *P. gutturalis*, com base em dados provenientes do estado do Amapá, norte do Brasil, no presente estudo nós descrevemos pela primeira vez os cantos de anúncio e territorial dessa espécie, avaliamos sua variação morfológica e cromática, fornecemos dados morfométricos detalhados sobre machos e uma fêmea, e brevemente comentamos sobre sua história natural. Além disso, nós comparamos o canto de anúncio de *P. gutturalis* com os cantos de outras espécies do grupo de *P. conspicillatus* e fazemos algumas observações sobre a acústica desse grupo.

Palavras-chave: Bioacústica, Canto de anúncio, Canto territorial, Escudo da Guiana Oriental, Grupo de *Pristimantis conspicillatus*, Taxonomia, Variação fenotípica.

Introduction

Pristimantis Jiménez de la Espada, 1870 is a highly diverse group of direct-developing frogs, composed of 591 species widely distributed in the Neotropics (Frost 2022). Although the genus encompasses 13 species groups, most of its species remain unassigned to any group to date (*sensu* Padial *et al*. 2014, González-Durán *et al*. 2017, Zumel *et al*. 2021). Among these species groups, the *P. conspicillatus* group (*sensu* Padial *et al.* 2014) is the largest with 42 species, ranging from Costa Rica to the eastern Guiana Shield and southern Bolivia, and extending to Amazon, Cerrado, and Atlantic Forest regions in Brazil (Padial *et al.* 2014, 2016, Oliveira *et al.* 2017, 2020, Acevedo *et al.* 2020, Taucce *et al.* 2020, Roberto *et al.* 2022).

Despite this great diversity, the acoustic knowledge on the *Pristimantis conspicillatus* group is still deficient, since only 24 of its species have their advertisement calls described. One of the members of this group whose vocalization remains unknown is *Pristimantis gutturalis* (Hoogmoed, Lynch, and Lescure, 1977), a species described from French Guiana and restricted to the eastern Guiana Shield, occurring in southeastern Suriname, French Guiana, and in the Brazilian state of Amapá (Hoogmoed *et al.* 1977, Lescure and Marty 2000, Ouboter and Jairam 2012, Frost 2022). In its original description, the characterization of its coloration in life was brief, consisting of few remarks based on field notes on two females only (Hoogmoed *et al.* 1977). Moreover, its morphometry was poorly described, with detailed measurements provided for the holotype (a female) only (Hoogmoed *et al.* 1977).

Although *Pristimantis gutturalis* has been addressed in two works subsequent to its description (Lescure and Marty 2000, Ouboter and Jairam 2012), these studies provided only brief accounts that did not present significant new data, and hence some important aspects of this species still remain understudied. Aiming to contribute to the knowledge on *P. gutturalis,* based on data collected in the state of Amapá, northern Brazil, herein we describe for the first time its advertisement and territorial calls, assess its morphological and chromatic variation,

provide morphometric measurements for ten males and one female, and briefly comment on aspects related to its natural history. In addition, we provide comprehensive comparisons between the advertisement call of *P. gutturalis* and calls of other species of the *P. conspicillatus* group, and make remarks on the acoustics of this group.

Materials and Methods

Study Area and Data Collection

We carried out fieldwork in the state of Amapá, northern Brazil, on March 2018 at the Cancão Municipal Natural Park, in the municipality of Serra do Navio [00°54'54.70" N, 52°00'25.20" W, 139 m a.s.l.; ca. 372 km straight line away from the type locality of *Pristimantis gutturalis* (Lower Matarony River, French Guiana)]; and in two adjacent sites (ca. 400 km straight line away from the species type locality) located ca. 300 m from the south bank of the Araguari River, in the municipality of Porto Grande, on 04 and 09 March 2022 (site 1: 00°44'13.20" N, 51°30'0.82" W, 87 m a.s.l.), and on 11 March 2022 (site 2: 00°44'2.70" N, 51°29'54.03"W, 101 m a.s.l.). We obtained vocalizations only in Porto Grande, using a RØDE NTG1 microphone connected to a Tascam DR-100 digital recorder (site 1; sampling rates of 44.1 and 96.0 kHz; 16 bits resolution), and a CSR YOGA HT-81 microphone connected to a Zoom H1N digital recorder (site 2; sampling rate of 96.0 kHz; 16 bits resolution). See Appendix I for further details on recordings. We collected three adult males (CECC 1116, 3250, 3305) and one adult female (CECC 1959) from Serra do Navio, and seven adult males from Porto Grande (CECC 3795–96, 3811–15). We euthanized specimens with 5% lidocaine, fixed them in 10% formalin, and preserved them in 70% ethanol. We deposited specimens in the Herpetological Collection of the Universidade Federal do Amapá (CECC), and deposited recordings in this same collection as well as and in the Fonoteca Neotropical Jacques Vielliard (FNJV).

Acoustic Analyses

We recorded two types of calls, and classified them based on their particular functions associated to the social context involved, following Toledo *et al.* (2015) and Köhler *et al.* (2017). We classified one of these call types as the advertisement call, since it consisted of a conspicuous vocalization continuously emitted by all males. We classified the other type as the territorial call, since it was less frequent than the advertisement call and was not emitted by all individuals, being observed that males emitted this call type when there were many conspecifics calling nearby. Prior to analyses, we applied 400 Hz high-pass and 6000 Hz low-pass filters to the recordings in Raven Pro 1.5 software (K. Lisa Yang Center for Conservation Bioacoustics 2022) to remove background noises. After this step, we normalized (peak -1.0 dB) recordings that presented low amplitude level using Audacity v. 2.2.2 software (Audacity Team 2021). Then, we analyzed calls in Raven under the following settings: window size = 512 samples; 3 dB filter bandwidth = 124 or 270 Hz; window type = Hann; overlap = 80.1% (locked); hop size = 1.06 or 2.31 ms; DFT size = 512 samples; grid spacing = 86.1 or 188 Hz. Terminology and definitions of call traits essentially followed Köhler *et al.* (2017). We obtained dominant, maximum, and minimum frequency values through the "Peak Frequency", "Frequency 95%", and "Frequency 5%" functions, respectively (see Charif *et al.* 2010). We calculated note rate as "number of notes within a call - 1/duration between the onset of the first note to duration the onset of the last note of the call". We produced call figures in R platform v.3.6.2 (R Core Team 2021) using seewave v.2.1.6 (Sueur *et al.* 2008) and tuneR v.1.3.3 (Ligges *et al.* 2018) packages with the following settings: window = Hanning; overlap = 85%; FFT = 512; a relative amplitude scale of 46 dB [indicated by colors, with red being the maximum amplitude (i.e. 0 dB)] was used to produce spectrograms.

Morphological Examination

We examined all collected specimens (10 adult males and one adult female). We assessed morphological and chromatic variation through comparisons with previous descriptions (Hoogmoed *et al.* 1977, Lescure and Marty 2000, Ouboter and Jairam 2012). In the Morphological variation subsection (Results section) we omitted traits that did not differ from previous descriptions, and also included traits that were not previously reported. Terminology and definitions of the morphological and chromatic traits described herein followed Duellman and Lehr (2009). We identified specimens as males by the presence of vocal sac, nuptial pads, and emission of advertisement calls, with the exception of the specimen CECC 1959 which we identified as female by its considerably larger size, lack of vocal sac, and absence of vocalizations.

Morphometric Measurements

Based on Padial *et al.* (2016), we measured the following traits in all collected individuals: snout–vent length (SVL), head length (HL, from posterior margin of lower jaw to tip of snout), head width (HW, at level of rictus), eye length (EL, measured horizontally); eye to nostril distance (EN), internarial distance (IND), eye-eye distance (EE), tympanic membrane height (TYH), tympanic membrane length (TYL), arm length (FA, from posterior margin of thenar tubercle to elbow), tibia length (TL), thigh length (TH, from vent to knee), and foot length (FL, from proximal border of inner metatarsal tubercle to tip of fourth toe). Additionally, following Watters *et al.* (2016) we measured the snout–nostril length (SN) and the snout length (SL). We took all measurements with a digital caliper (0.01 mm precision). Following the argument of Padial *et al.* (2016) that the measurement accuracy of both interorbital distance and upper eyelid width is greatly influenced by preservation conditions, we did not include these two traits. In this sense, we noticed minute fixation artifacts that could affect the accuracy of the measurement of the width of the discs of fingers III and IV, and of toe IV, and for this reason we did not include these three traits neither.

Results

Specimen Identification

Based on comparisons with the species original description (Hoogmoed *et al.* 1977), we identified our specimens as *Pristimantis gutturalis* since they have the following diagnostic traits: (1) a distinct white median longitudinal stripe on the throat, (2) four darker bars on the upper lip and continued on the lower lip (i.e. labial bars), being two originated from the lower margin of the eye, one from the nostril, and one from the region between eye and nostril, (3) cranial crests absent, (4) plain (i.e. uniform) color pattern on the posterior surfaces of thighs, (5) presence of a dark supratympanic stripe, (6) chest and anterior part of belly mottled, and the rest of the belly immaculate, (7) darker, oblique cross-bands on the upper surface of limbs, (8) finger I > finger II, (9) no webbing between fingers and toes, (10) fingers and toes lacking lateral fringes, (11) tarsal fold absent, (12) tympanum large, with both tympanic annulus and tympanic membrane distinct, (13) weak supratympanic fold, obscuring the upper edge of the tympanum, (14) canthus rostralis distinct, rounded, posteriorly convex and anteriorly concave, (15) traces of dorsolateral folds, (16) discoidal fold present, (17) skin on dorsum finely shagreen, with larger pustules interspersed, (18) skin of throat, belly and ventral surfaces of limbs smooth, with the exception of the proximoventral portion of thighs which is areolate.

Call Descriptions

Advertisement call.—The advertisement call of *Pristimantis gutturalis* (N = 11 males, 196 calls analyzed, 223 notes analyzed) (Figure 1A–

C) may be composed of one (*N* = 173 calls), two (*N* = 19 calls), or three (*N* = 4 calls) notes. Calls last 54 ± 39 ms (24–324 ms) and are spaced from each other by intervals of 850 ± 490 ms (150–2700 ms). Notes last 33 ± 4 ms (24–50 ms) and have pulsatile structure (*sensu* Köhler *et al.* 2017), so that pulse units cannot be properly counted or measured. The note structure may vary, with some notes being highly pulsatile (Figure 1B), whereas others are somewhat less pulsatile so that some amplitude peaks may be slightly noticeable (Figure 1C). In calls composed of two or three notes, these notes are spaced from each other by short intervals of 99 ± 1 ms (76–122 ms), being emitted at rates of 7.7 ± 0.3 notes/s (7.2–7.9 notes/s). Notes always have two emphasized frequency bands not harmonically related to each other [hereinafter referred to as the first (FFB) and the second (SFB) frequency bands]. A third frequency band located above the SFB may be present in some notes, but it has much less energy than the other bands (see Figure 1A). The FFB peaks at 1698 ± 76 Hz (1378–2250 Hz), the SFB peaks at 2864 ± 181 Hz (2498–3359 Hz), and the third frequency band, when present, peaks at 4108 ± 295 Hz (3750–5426 Hz). The dominant frequency of the notes can correspond to either the FFB or the SFB: it corresponded only to the FFB in one individual, only to the SFB in eight individuals, and it alternated its correspondence between FFB and SFB along the vocalizations of two individuals. The minimum frequency of the notes is at 1572 ± 105 Hz (1378–2438 Hz), and the maximum frequency is at 3262 ± 186 Hz (3000–3962 Hz). See Appendix II for a compilation of the main advertisement call traits reported to date for species of the *P. conspicillatus* group.

Territorial call.—The territorial call of *Pristimantis gutturalis* (*N* = 9 males, 95 calls analyzed) (Figure 2A–C) is audibly different from the advertisement call, has lower amplitude level than this latter, and is structurally highly variable, encompassing the three main structural patterns described next.

Pattern 1 (*N* = 7 males, 52 calls) (Figure 2A): a call comprising 2.6 ± 0.3 (2–4) fused highly pulsatile notes, with total duration of 83 ± 10 ms (48–142 ms) and spaced from other territorial calls by intervals of 318 ± 240 ms (15–778 ms). Spectrally, it usually has two emphasized bands in which the dominant frequency can alternate [*N* = 45 calls; FFB peaking at 1730 ± 112 Hz (1464–1875 Hz), and SFB at 2746 ± 118 Hz (2412–3188 Hz); a weak third band may be present too], but the energy may also be irregularly distributed over its bandwidth [*N* = 7 calls; dominant frequency at 2590 ± 332 Hz (1723–2813 Hz)]. Its minimum frequency is at 1776 ± 334 Hz (1313–2250 Hz), and its maximum frequency is at 3258 ± 176 Hz (3000–3750 Hz).

Pattern 2 (*N* = 7 males; 43 calls) (Figure 2B): a call consisting of a single highly pulsatile note with duration of 79 ± 10 ms (35–132 ms), spaced from other territorial calls by intervals 366 ± 133 ms (123–1890 ms). The energy is usually irregularly distributed over its bandwidth [*N* = 35 calls; dominant frequency at 2749 ± 51 Hz (2625–2813 Hz)], but it may also have two emphasized bands in which the dominant frequency can alternate [*N* = 8 calls; FFB peaking at 1571 ± 232 Hz (1313–1875 Hz), and SFB at 2683 ± 164 Hz (2498–2813 Hz); a weak third band may be present too]. Its minimum frequency is at 1965 ± 318 Hz (1464–2438 Hz), and its maximum frequency is at 3128 ± 168 Hz (2813–3445 Hz).

Pattern 3 (1 male; *N* = 3 calls) (Figure 2C): a call consisting of a single note that is pulsatile in its initial or final half, while its other half is pulsed. It has duration of 49 ± 13 ms (40–64 ms) and is spaced from other territorial calls by intervals of 155 ± 177 ms (30–280 ms). Spectrally, it may have two emphasized bands in which the dominant frequency can alternate [*N* = 2 calls; FFB at 1594 ± 183 Hz (1464–1723 Hz), and SFB at 2627 ± 305 Hz (2412–2842 Hz)], or the energy may be irregularly distributed over its bandwidth (*N* = 1 call; dominant frequency at 2498 Hz). Its minimum

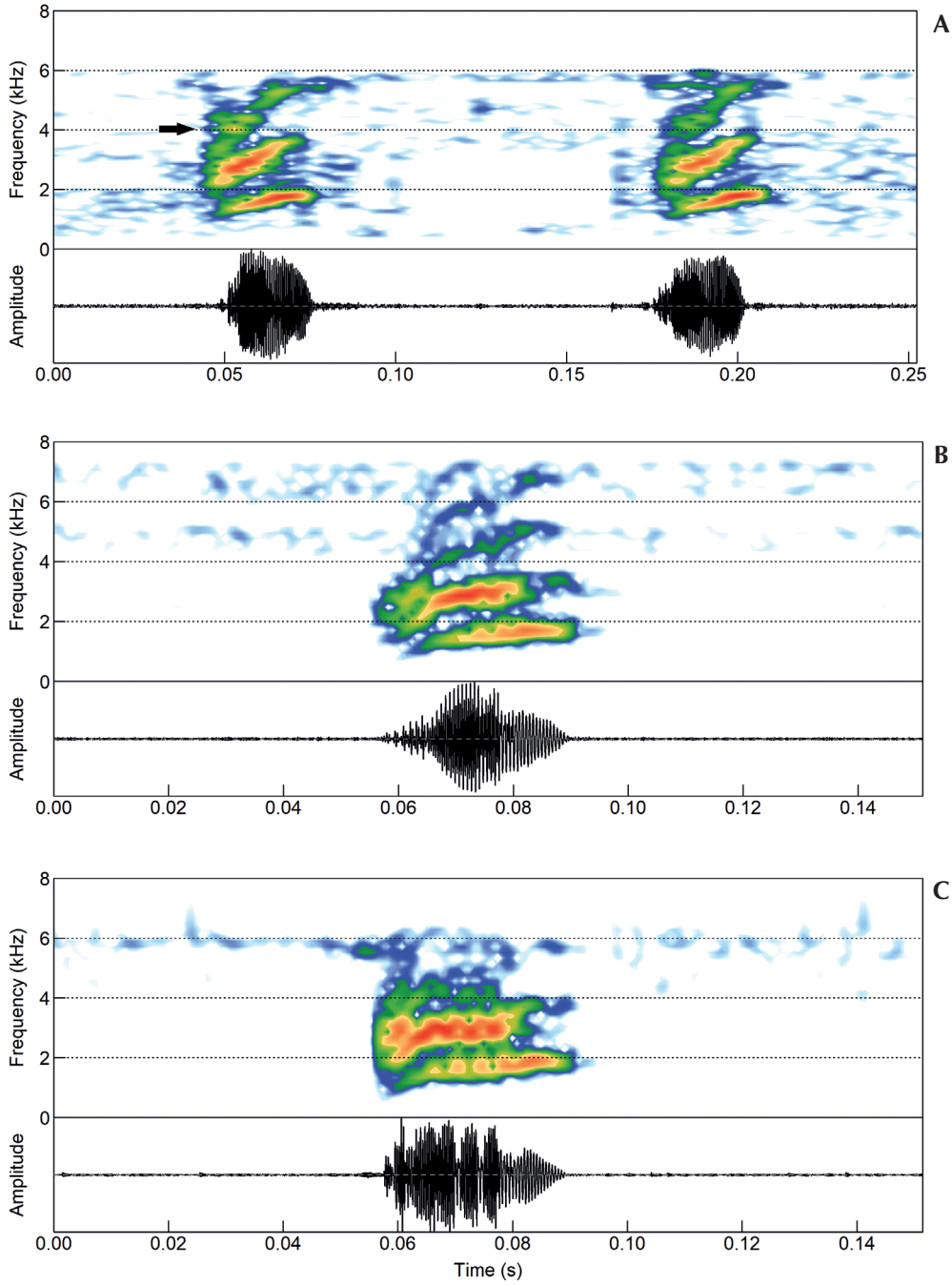

Figure 1. Audiospectrograms (top) and respective oscillograms (bottom) depicting the advertisement call of *Pristimantis gutturalis*. (**A**) Advertisement call composed of two notes (black arrow indicates the weak third band). (**B–C**) Advertisement calls composed of a single note each; notice that the note in C is somewhat less pulsatile than the one in B. Recording labels: (A) FNJV59100 (B) FNJV59093; (C) FNJV59101.

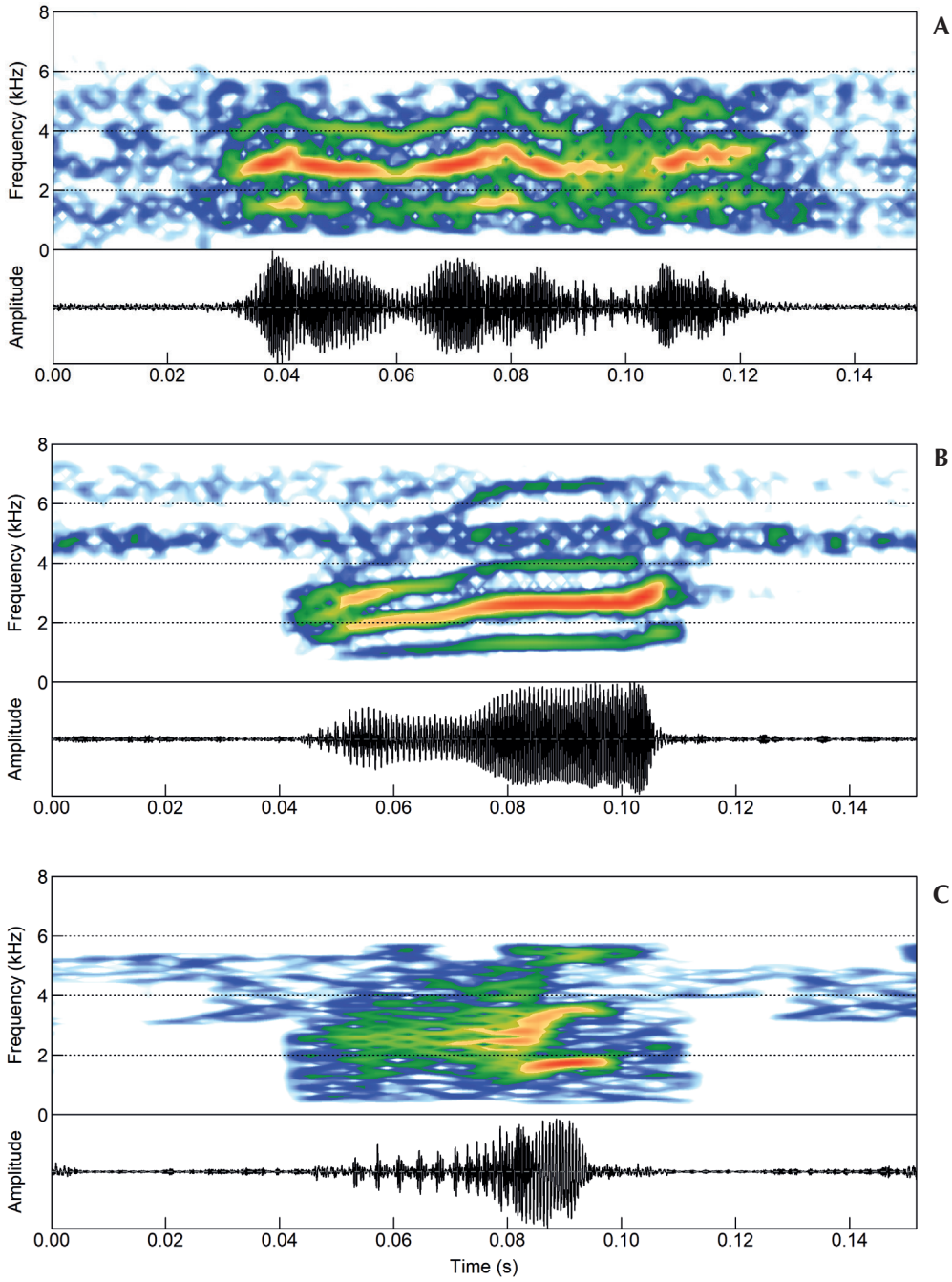

Figure 2. Audiospectrograms (top) and respective oscillograms (bottom) depicting the territorial call of *Pristimantis gutturalis*. (**A**) Territorial call composed of 3 fused pulsatile notes (pattern 1). (**B**) Territorial call composed of a single pulsatile note (pattern 2). (**C**) Territorial call composed of a note that is pulsed in its initial half and pulsatile in its final half (pattern 3). Recording labels: (A) FNJV59094; (B) FNJV59101; (C) FNJV59099.

frequency is at 1579 ± 217 Hz (1378–1809 Hz), and its maximum frequency is at 3359 ± 86 Hz (3273–3445 Hz).

The same individual may emit more than one territorial call pattern. There was no specific emission pattern of territorial calls, with these being emitted before, after, or between advertisement calls, between an advertisement call and another territorial call, or even in a sequence of territorial calls.

Morphological Variation

External morphology.—There is little variation in the external morphology. Dorsal skin is coarsely shagreen bearing interspersed pustules, which are mostly on the upper eyelid and snout regions. Relative length of fingers: III > IV > I > II. A variation was observed regarding toes III and V, with these toes having equal sizes in some specimens, and with the toe V being slightly longer in other specimens. Relative length of toes: IV > V ≥ III > II > I. Moreover, all specimens have ulnar tubercles, and all males have double, poorly developed nuptial pad (features not previously reported).

Coloration in life.—There is great variation in dorsal coloration within our sample (Figure 3) and in comparison to the previous descriptions (which state that the dorsum varies among greyish brown, brown, dark brown, and reddish brown, having red, white or black markings, and a blackish W-shaped mark on the scapular region followed by one or two chevrons; Hoogmoed *et al.* 1977, Lescure and Marty 2000, Ouboter and Jairam 2012). A specimen (CECC 3811; Figure 3A) showed an unusual dorsal pattern, consisting of a large dark brown blotch covering the entire dorsum, extending from the interorbital region to the cloacal region, and also covering the dorsal surface of thighs and shanks; the anterodorsal surface of its head stood out in contrast to the rest of its dorsum by being light beige. Another specimen (CECC 3812; Figure 3B) showed a white median longitudinal stripe over its dorsum, extending from the tip of the snout to the cloacal region. One specimen (CECC 3305; Figure 3C) presented bright orange blotches on its back and anterodorsal surface of its head. The other specimens showed small variations among themselves regarding the dorsal pattern, but within the variation range previously reported (Figure 3D–F). The dark labial bars may be more (Figure 3C–E) or less (Figure 3A–B, F) conspicuous. Iris coloration may be golden with the upper half brighter and the lower half darker (Figure 3 A–B, D, F), or entirely silver (Figure 3C, E). There is a median horizontal broad dark-reddish streak in the iris of all specimens. Tympanum coloration varies between shades of brown, being its upper portion somewhat darker. Flank coloration varies from creamish to brown, and may present some darker speckles, spots, or blotches. Belly coloration varies from creamish white to creamish yellow (Figure 4). Some specimens had reddish pigmentation on the proximoventral portion of thighs (Figure 4A–E). In all individuals, the areas adjacent/lateral to the white stripe on the throat have a darker pigmentation that varies in intensity (i.e. may be more or less pigmented). In most specimens the white stripe on the throat was delimited only by this dark pigmentation laterally spread (Figure 4B–C, F), but in some specimens conspicuous dark longitudinal bars bordering this white stripe on both sides could be distinguished (Figure 4A, D–E). The dark mottling on the chest and anterior part of the belly may be more or less conspicuous (Figure 4).

Coloration in preservative.—Brown blotches on the back became lighter or turned grayish brown. The orange blotches on the back and anterodorsal surface of the head of the individual CECC 3305 became light brown. The dorsal surfaces of limbs vary among creamish yellow, dark brown, and light brown, and the oblique cross-bands or spots became less evident. The dark supratympanic stripe may partially or completely fade. The white median longitudinal stripe on the throat became less conspicuous.

Figure 3. Dorsolateral views of some living adult males of *Pristimantis gutturalis* examined herein, depicting their chromatic variation. (**A**) CECC 3811; SVL 24.5 mm. (**B**) CECC 3812; SVL 22.0 mm. (**C**) CECC 3305; SVL 26.4 mm. (**D**) CECC 3796; SVL 25.1 mm. (**E**) CECC 3815; SVL 24.8 mm. (**F**) CECC 3795; SVL 21.1 mm. Photographs by Carlos Eduardo Costa-Campos.

Figure 4. Ventral views of some living adult males of *Pristimantis gutturalis* examined herein, depicting their chromatic variation. (**A**) CECC 3305; SVL 26.4 mm. (**B**) CECC 3796; SVL 25.1 mm. (**C**) CECC 3812; SVL 22.0 mm. (**D**) CECC 3814; SVL 25.0 mm. (**E**) CECC 3815; SVL 24.8 mm. (**F**) CECC 3795; SVL 21.1 mm. Photographs by Carlos Eduardo Costa-Campos.

Morphometry

Morphometric traits (in mm) of each specimen are provided in Table 1. Male SVL ranges from 21.1 to 26.4 mm, and the SVL of the female (CECC 1959) is of 39.9 mm. Male body proportions: TL 51–59% of SVL, FL 38–46% of SVL, HL 91–99% of HW, EN 107–133% of EL, EL 29–38% of HW, TYL 75–100% of TYH. Compared to males, the body proportions of the female did not differ much: TL 44% of SVL, FL 37% of SVL, HL 92% of HW, EN 104% of EL, EL 40% of HW, TYL 91% of TYH.

Natural History

At both studied localities we found specimens of *Pristimantis gutturalis* within the *terra-firme* rainforest, which is characterized by emergent trees and closed canopy. Males vocalized during the rainy season after 18:00 h, perched on branches and trunks ca. 60–150 cm above the ground, in a nearly vertical position with the head oriented toward the ground. In previous fieldwork carried out during the dry season, we found specimens of this species foraging in the leaf litter by morning and perched on branches and trunks close to the ground by night, but they were not vocally active. Syntopic anuran species at the Cancão Municipal Natural Park were *Allobates femoralis* (Boulenger, 1884), *Ameerega pulchripecta* (Silverstone, 1976), *Anomaloglossus baeobatrachus* (Boistel and de Massary, 1999), *Dendrobates tinctorius* (Cuvier, 1797), *Osteocephalus oophagus* Jungfer and Schiesari, 1995, *P. chiastonotus, P. inguinalis* (Parker, 1940), *P. ockendeni* (Boulenger, 1912), *P. zeuctotylus*, *Ranitomeya amazonica* (Schulte, 1999), *Rhinella castaneotica* (Caldwell, 1991), and *Rhinella lescurei* Fouquet, Gaucher, Blanc and Vélez-Rodriguez, 2007. Syntopic anuran species at the municipality of Porto Grande were *Adenomera andreae* (Müller, 1923), *Ameerega pulchripecta, P. chiastonotus, Rhinella castaneotica, Leptodactylus stenodema* Jiménez de la Espada, 1875, and *Osteocephalus oophagus*.

Discussion

Acoustic Comparisons With Species of the Pristimantis conspicillatus *Group*

The advertisement call traits described here for *Pristimantis gutturalis* allow distinguishing it from all members of the *P. conspicillatus* group whose calls have been described. By having 1–3 notes, the call of *P. gutturalis* differs from those of *P. charlottevillensis, P. chiastonotus, P. iiap, P. paulodutrai, P. rupicola, P. skydmainos* (1 note; Rodríguez 1994, Kaiser *et al.* 1995, Flores and Rodríguez 1997, Heyer and Carvalho 2000, Lescure and Marty 2000, Padial *et al.* 2016, Taucce *et al.* 2020), *P. incertus, P. latro, P. pictus, P. ventrigranulosus, P. vilarsi,* and *P. zeuctotylus* (combined range of 4–8 notes; Kaiser *et al.* 1995, Lescure and Marty 2000, Heyer and Barrio-Amorós 2009, Maciel *et al.* 2012, Oliveira *et al.* 2017, 2020). As its notes last 24–50 ms, the call of *P. gutturalis* differs from the calls of *P. vilarsi* (note duration of 3–21 ms; Heyer and Barrio-Amorós 2009), *P. achatinus* ("kree" notes; see Lynch and Myers 1983), *P. chiastonotus, P. iiap, P. samaipatae,* and *P. skydmainos* (combined range of note duration of 59–450 ms; Lynch and Myers 1983, Rodríguez 1994, Márquez *et al.* 1995, Flores and Rodríguez 1997, Köhler 2000, Lescure and Marty 2000, Padial and De la Riva 2009, Padial *et al.* 2016). The note rate of the call of *P. gutturalis* (7.2–7.9 notes/s) differentiates it from *P. buccinator, P. peruvianus* (combined range of note rate of 1.0–1.6 notes/s; Rodríguez 1994, Duellman 2005), *P. dundeei, P. koehleri, P. ventrigranulosus,* and *P. vilarsi* (combined range of note rate of 11.8–20.7 notes/s; Heyer and Muñoz 1999, Heyer and Barrio-Amorós 2009, Padial and De la Riva 2009, Maciel *et al.* 2012, Giaretta *et al.* 2018). The intervals between the notes of the call of *P. gutturalis* (76–122 ms) are shorter than the interval between notes of the calls of *P. buccinator* and *P. peruvianus* (combined range of inter-note interval of 180–779 ms; Rodríguez 1994), and longer than those of the calls of *P.*

Table 1. Measurements of morphometric traits (mm) and body proportions (ratios) of specimens (10 males and one female) of *Pristimantis gutturalis* from the municipalities of Serra do Navio (CECC 1116, 1959, 3250, 3305) and Porto Grande (CECC 3795–96, 3811–15), both in the state of Amapá, Brazil. Values of the "Overall" column are given as mean ± SD (minimum–maximum). [1] Female. [2] Values taken from Hoogmoed *et al.* 1977.

	CECC 1116	CECC 3250	CECC 3305	CECC 3795	CECC 3796	CECC 3811	CECC 3812	CECC 3813	CECC 3814	CECC 3815	Overall (males)	CECC 1959[1]	Holotype[1,2]
SVL	23.3	21.1	26.4	21.1	25.1	24.5	22.0	22.8	25.0	24.8	23.6 ± 1.8 (21.1–26.4)	39.9	30.4
HL	6.7	7.1	8.6	6.6	8.1	7.7	6.9	7.7	7.5	7.7	7.5 ± 0.6 (6.6–8.6)	10.9	11.6
HW	7.2	7.3	9.3	7.0	8.9	7.8	7.1	7.9	8.0	7.9	7.8 ± 0.8 (7.0–9.3)	11.8	9.9
EL	2.5	2.7	3.2	2.0	2.7	2.6	2.7	2.7	2.7	2.7	2.7 ± 0.3 (2.0–3.2)	4.7	3.9–4.1
EN	2.9	2.9	3.6	2.3	3.0	3.4	2.9	2.9	3.0	3.6	3.1 ± 0.4 (2.3–3.6)	4.9	4.1–4.3
IND	0.9	1.0	1.0	0.9	1.0	1.0	1.0	0.9	0.9	0.9	0.95 ± 0.05 (0.9–1.0)	2.0	-
EE	4.1	2.9	4.6	3.1	3.6	3.9	3.8	3.7	3.5	4.0	3.7 ± 0.5 (2.9–4.6)	6.3	-
SN	0.4	0.7	0.5	0.3	0.4	0.5	0.5	0.6	0.4	0.5	0.5 ± 0.1 (0.3–0.7)	1.1	1.6
SL	3.6	3.5	4.3	3.5	4.0	4.1	3.5	3.5	3.9	4.1	3.8 ± 0.3 (3.5–4.3)	5.9	5.9–6.1
TYH	1.3	1.2	1.3	1.1	1.1	1.3	1.2	1.2	1.1	0.8	1.2 ± 0.2 (0.8–1.3)	2.2	-
TYL	1.0	1.0	1.2	0.9	0.9	1.0	1.0	0.9	0.9	0.8	1.0 ± 0.1 (0.8–1.2)	2	1.8
FA	4.5	4.0	3.6	3.4	5.0	4.4	3.6	5.1	5.1	6.9	4.6 ± 1.0 (3.4–6.9)	9.2	-
TL	13.2	12.4	15.6	11.7	13.0	13.4	11.8	12.4	12.8	12.9	12.9 ± 1.1 (11.7–15.6)	17.6	17.3
TH	10.9	9.9	12.3	9.8	10.9	10.8	10.0	10.9	10.6	10.9	10.7 ± 0.7 (9.8–12.3)	15.8	-
FL	9.8	9.7	10.9	8.6	10.1	9.7	9.2	9.9	10.3	9.5	9.8 ± 0.6 (8.6–10.9)	14.9	-
TL/SVL	0.57	0.59	0.59	0.55	0.52	0.55	0.54	0.54	0.51	0.52	0.55 ± 0.03 (0.51–0.59)	0.44	-
FL/SVL	0.42	0.46	0.41	0.41	0.40	0.40	0.42	0.43	0.41	0.38	0.41 ± 0.02 (0.38–0.46)	0.37	-
HL/HW	0.93	0.97	0.92	0.94	0.91	0.99	0.97	0.97	0.94	0.97	0.95 ± 0.03 (0.91–0.99)	0.92	-
EN/EL	1.16	1.07	1.13	1.15	1.11	1.31	1.07	1.07	1.11	1.33	1.15 ± 0.09 (1.07–1.33)	1.04	-
EL/HW	0.35	0.37	0.34	0.29	0.30	0.33	0.38	0.34	0.34	0.34	0.34 ± 0.03 (0.29–0.38)	0.40	-
TYL/TYH	0.77	0.83	0.92	0.82	0.82	0.77	0.83	0.75	0.82	1.00	0.83 ± 0.08 (0.75–1.00)	0.91	-

achatinus ("ribit" call; see Lynch and Myers 1983) and *P. incertus* (combined range of inter-note interval of 10–50 ms; Lynch and Myers 1983, Kaiser *et al.* 1995). Since the call of *P. gutturalis* is composed of pulsatile notes (i.e. pulses cannot be distinguished), it differs from the calls of *P. buccinator, P. charlottevillensis, P. fenestratus, P. giorgii, P. iiap, P. koehleri, P. latro, P. moa, P. paulodutrai, P. peruvianus, P. pictus, P. pluvian, P. relictus, P. samaipatae, P. ventrigranulosus* [notes composed of 2–23 pulses (combined range); Rodríguez 1994, Kaiser *et al.* 1995, Heyer and Carvalho 2000, Köhler 2000, Padial and De la Riva 2009, Maciel *et al.* 2012, Padial *et al.* 2016, Oliveira *et al.* 2017, 2020, Roberto *et al.* 2022], *P. ramagii, P. vilarsi* (notes described as pulsed; Heyer and Barrio-Amorós 2009, Oitaven *et al.* 2017), *P. rupicola* (notes may be either pulsed or unpulsed; Taucce *et al.* 2020), and *P. skydmainos* (notes are unpulsed; Rodríguez 1994, Flores and Rodríguez 1997). By having its first emphasized frequency band at 1378–2250 Hz, the call of *P. gutturalis* differentiates from the calls of *P. incertus* (first band at 3000 Hz; Kaiser *et al.* 1995) and *P. rupicola* (first band at 2410–3490 Hz; Taucce *et al.* 2020). By having its second emphasized frequency band at 2498–3359 Hz, the call of *P. gutturalis* differentiates from the calls of *P. buccinator, P. charlottevillensis, P. dundeei, P. incertus, P. paulodutrai, P. pluvian, P. relictus, P. rupicola, P. skydmainos, P. ventrigranulosus,* and *P. vilarsi* [second band at 3375–6000 Hz (combined range); Rodríguez 1994, Kaiser *et al.* 1995, Flores and Rodríguez 1997, Heyer and Muñoz 1999, Heyer and Carvalho 2000, Maciel *et al.* 2012, Giaretta *et al.* 2018, Oliveira *et al.* 2020, Taucce *et al.* 2020, Roberto *et al.* 2022]. By its lower value of maximum frequency (3000–3962 Hz), the call of *P. gutturalis* differs from the call of *P. dundeei* (maximum frequency of 4125–5250 Hz; Giaretta *et al.* 2018). The call of *P. gutturalis* further distinguishes from the call of *P. charlottevillensis* by not having a harmonic structure (up to three harmonics in *P. charlottevillensis;* Kaiser *et al.* 1995). For a compilation of the main call traits reported for species of the *P. conspicillatus* group, see Appendix II.

Remarks on the Acoustics of the Pristimantis conspicillatus *Group*

The low note rate reported for *P. achatinus* [0.2–0.4 notes/s ("kree" notes); Lynch and Myers 1983] and *P. relictus* (0.5–2.2 notes/s; Roberto *et al.* 2022) does not seem to be correct in view of the short inter-note intervals that can be noticed in their respective call figures (see Figure 8 in Lynch and Myers 1983; Figure 3 in Roberto *et al.* 2022). The strikingly low values of the first frequency band reported by Rodríguez (1994) (therein referred to as fundamental frequency) for *P. fenestratus* [190 Hz (172–207 Hz)] and *P. peruvianus* [260 Hz (234–280 Hz)] are probably incorrect, and may be due to the limited technology available at the time for call recordings and analyses. The presence of more than one emphasized frequency band in the notes of the advertisement call was found to be a common feature among the species of the *P. conspicillatus* group. Although this feature was not described for *P. chiastonotus, P. zeuctotylus,* and *P. ramagii,* it is possible to notice in the spectrogram figures of the first two (Figure 5 in Lynch and Hoogmoed 1977; p. 367 in Lescure and Marty 2000) and of the latter (Figure 1 in Oitaven *et al.* 2017) that at least two emphasized bands are present. Given the wide range of the dominant frequency reported for *P. fenestratus* (1710–3591 Hz; Padial and De la Riva 2009), *P. giorgii* (1660–4142 Hz; Oliveira *et al.* 2020), and *P. ramagii* (2217–4898 Hz; Oitaven *et al.* 2017), and considering the call figures provided in these studies, it can be inferred that, as in *P. gutturalis,* the dominant frequency alternated its correspondence between the emphasized bands in the calls of these species. As demonstrated herein, these frequency bands may be useful for the acoustic distinction among species of the *P. conspicillatus* group, and therefore we highlight the importance of providing values for each band separately when describing calls of species of this group.

Aggressive vocalizations have been also reported for two other members of the *Pristimantis conspicillatus* group. Lynch and Myers (1983) described "chirp" notes for *P. achatinus* and attributed to them a territorial function. As these "chirps" were mainly emitted during a physical male combat (see Lynch and Myers 1983), we argue that they would actually be better classified as fighting calls (*sensu* Toledo *et al.* 2015). Oitaven *et al.* (2017) described the territorial call of *P. ramagii*, and stated that this vocalization differs from the advertisement call, and is rarely emitted and by a few individuals only. Likewise, the territorial call of *P. gutturalis* was not emitted by all vocally active males and was less frequent than the advertisement call. Although without following a specific emission pattern, territorial calls were emitted when there were many individuals actively calling relatively close to each other (ca. 80–100 cm). This call type showed great variation regarding both temporal and spectral structures (see Figure 2). Modifications in traits of aggressive vocalizations may be directly related to aspects of the social context (e.g. Schwartz 1989; Reichert and Gerhardt 2013, Brasileiro *et al*. 2021), but in-depth behavioral studies are needed to elucidate the specific factors associated to the variation reported here.

Morphology and Morphometry

In the original description of *Pristimantis gutturalis* its coloration in life was briefly described based on field notes on two females only (Hoogmoed *et al*. 1977), and subsequent accounts on this species (Lescure and Marty 2000, Ouboter and Jairam 2012) did not bring substantial new data. Herein we comprehensively assessed its morphological and chromatic variation, and showed that despite little morphological variation, this species has a high chromatic variation, especially with regard to its dorsal pattern (see Figure 3). Although Hoogmoed *et al*. (1977) included the "*Dorsum greyish brown with a blackish W-shaped mark on the scapular region, followed by one or two chevrons*" in the diagnosis section of *P. gutturalis,* we advocate that this trait should not be used to diagnose this species in view of the striking variation in dorsal coloration demonstrated herein.

Hoogmoed *et al*. (1977) described morphometric traits only for the holotype of the species (a female), and provided some body proportions (ratios) for the type series. However, the sample sizes provided in their table of proportions do not exactly match the number of individuals informed as part of the type series (e.g. the ratios tympanum/eye length and tibia/SVL, were allegedly to be based on 4 males and 16 females, but the type series actually comprises only 19 individuals, being 2 males, 8 females, and 9 juveniles). In the diagnosis section the authors reported an SVL of 19.0–20.3 mm for young males and of 17.9–40.9 mm for females, but made it explicit that only one adult female was known. The only subsequent morphometric information provided for this species merely stated that it reaches a maximum size of ca. 41 mm (Lescure and Marty 2000, Ouboter and Jairam 2012). Given these inconsistencies and the paucity of data on the morphometry of this species, herein we provided a thorough morphometric characterization of 10 males and one female of *P. gutturalis*. Examined males are considerably smaller than the examined female, and this latter is also larger than the female holotype (Table 1).

Conclusions

We described the advertisement and territorial calls of *Pristimantis gutturalis,* assessed its morphological and chromatic variation, and described its morphometry. We commented on the acoustics of the *P. conspicillatus* group, and showed that the advertisement call of *P. gutturalis* can be distinguished from calls of all species in this group. We found great chromatic variation, especially with regard to the dorsal pattern, thus contradicting the species description by demonstrating that the dorsal pattern should not be considered as diagnostic. Data presented here

contribute to a better understanding on the vocal repertoire and phenotypic variation of *P. gutturalis,* and may help in future identifications of new populations of this species. Since studies have pointed to a potential cryptic diversity within the *Pristimantis conspicillatus* group (e.g., Oliveira *et al.* 2017, Trevisan *et al.* 2020), providing detailed taxonomic data is crucial to establish clear species boundaries, and thus support future studies in unveiling hidden diversity.

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Appendix I. *Recordings (.wav) analyzed in the present study and associated metadata. All recordings were made in the municipality of Porto Grande, state of Amapá, Brazil (see Material and Methods section for coordinates of Site 1 and Site 2). Abbreviation of the recording equipment (recorder / microphone): TRN (Tascam DR-100 / RØDE NTG1); ZYH (Zoom H1N / YOGA HT-81).*

Recording label	Locality	Time	Date	Air temperature (°C)	Recording equipment	Voucher CECC
FNJV59093	Site 1	18:47	09 March 2022	24.8	TRN	3796
FNJV59094	Site 1	17:22	09 March 2022	24.6	TRN	3795
FNJV59095	Site 1	17:46	04 March 2022	-	TRN	-
FNJV59096	Site 1	17:57	04 March 2022	-	TRN	-
FNJV59097	Site 1	18:28	04 March 2022	-	TRN	-
FNJV59098	Site 1	18:33	04 March 2022	-	TRN	-
FNJV59099	Site 1	18:44	04 March 2022	-	TRN	-
FNJV59100	Site 1	18:55	04 March 2022	24.4	TRN	3814
FNJV59101	Site 2	17:53	11 March 2022	24.8	TRN	3813
FNJV59102	Site 2	18:16	11 March 2022	-	ZYH	-
FNJV59103	Site 2	18:34	11 March 2022	-	ZYH	-
FNJV59104	Site 2	19:02	11 March 2022	-	ZYH	-

Appendix II. *Summary of main advertisement call traits reported to date for the species of the* Pristimantis conspicillatus *group. Data reported herein for* P. gutturalis *are in bold. Values are given as mean ± SD (minimum–maximum). N = calls analyzed/notes analyzed/individuals.* [*] *Considering notes within a call;* [a] *"Kree notes".* [b] *"Ribit call".* [c] *"Bleep notes".* [d] *Originally given as notes/min, but herein converted.* [e] *Middle note duration.* [f] *Last note interval.* [g] *See Discussion section.* [h] *"...a series of quickly repeated whistle-like notes...".* [i] *As* Eleutherodactylus terraebolivaris. [j] *As* Eleutherodactylus ramagii. [k] *As* Eleutherodactylus fenestratus. [l] *As* Eleutherodactylus *sp.*

Species	Call duration (ms)	Notes/ call	Note duration (ms)	Note rate (notes/s)[*]	Inter-note interval (ms)[*]	Peak of the FFB (Hz)	Peak of the SFB (Hz)	Dominant frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	References
P. achatinus[a] (*N* = -/36/2)	-	(1–6)?	320 (150–450)	(0.2–0.4)	170 (70–350)?	1500 or 1600 (1300–1800)	3100 (3000–3400)	= SFB	-	-	Lynch and Myers 1983
P. achatinus[b] (*N* = 20/-/5)	150 (130–180)	2	-	-	30 (10–50)	-	-	(2400–3300)?	-	-	Lynch and Myers 1983
P. achatinus[c] (*N* = -/-/5)	-	-	-	-	-	-	-	-	-	-	Lynch and Myers 1983
P. buccinator (*N* = 6/-/-)	-	(1–6)	(50–66)	1.6[d]	618 (403–779)	(1846–2131)?	3595 (3564–3630)	= SFB	-	-	Rodríguez 1994
P. charlottevillensis (*N* = -/13/-)	51 (43–68)	1	51 (43–68)	-	-	2000	4000	= SFB	-	-	Kaiser *et al.* 1995
P. chiastonotus (*N* = -/-/-)	74	1	74	-	-	-	-	2620–3450[g]	-	-	Lescure and Marty 2000
P. dundeei (*N* = 2/-/2)	(290–530)	(5–8)	(20?–50)	(13.7–14.7)	-	(2067–2153)	(3692–3875)	= SFB	-	-	Heyer and Muñoz 1999
P. dundeei (*N* = -/-/1)	55 (470–642)	10.5 (9–12)	34 (33–34)[e]	18.9 (18.7–19.2)	32 (30–34)[f]	2023 (2006–2039)	4125 (4125–4125)	= SFB	2156 (2062–2250)	5063 (4875–5250)	Giaretta *et al.* 2018
P. dundeei (*N* = -/-/5)	266 ± 74 (136–314)	4.6 ± 1.0 (2–6)	43 ± 3 (40–47)[e]	17.7 ± 1.7 (16.2–20.7)	36 ± 5 (31–41)[f]	1901 ± 79 (1818–2012)	3656 ± 210 (3375–3937)	= SFB	1934 ± 169 (1750–2203)	4375 ± 145 (4125–4500)	Giaretta *et al.* 2018
P. fenestratus (*N* = 3/-/-)	-	3 (1–3)	45	-	(73–84)	190 (172–207)?	3100 (2896–3450)	= SFB	-	-	Rodríguez 1994
P. fenestratus (*N* = 10/-/2)	(160–360)	(2–3)	(50–90)	(7.6–9.1)	-	(1720–2067)	(3531–3617)	= SFB	-	-	Heyer and Muñoz 1999
P. fenestratus (*N* = -/2/1)	75	1	75	-	-	-	-	3270	1300?	5000?	Köhler 2000
P. fenestratus (*N* = 22/55/6)	265 ± 82 (157–458)	2.6 ± 0.6 (2–4)	63 ± 11 (50–91)	10.1 ± 1.5 (7.7–12.7)	-	1747 ± 158 (1542–2048)	-	3086 ± 581 (1710–3591)[g]	-	-	Padial and De la Riva 2009

Appendix II. *Continued.*

Species	Call duration (ms)	Notes/ call	Note duration (ms)	Note rate (notes/s)[*]	Inter-note interval (ms)[*]	Peak of the FFB (Hz)	Peak of the SFB (Hz)	Dominant frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	References
P. giorgii (*N* = 13/42/7)	171 ± 78 (131–278)	(3–4)	40 ± 12 (17–74)	-	-	1512 ± 259 (663–1872)	-	3007 ± 511 (1660–4142)[g]	-	-	Oliveira *et al.* 2020
P. gutturalis **(*N* = 196/223/11)**	**54 ± 39 (24–324)**	**1.2 ± 0.3 (1–3)**	**33 ± 4 (24–50)**	**7.7 ± 0.3 (7.2–7.9)**	**99 ± 1 (76–122)**	**1698 ± 76 (1378–2250)**	**2864 ± 181 (2498–3359)**	**= FFB or SFB**	**1572 ± 105 (1378–2438)**	**3262 ± 186 (3000–3962)**	**Present study**
P. iiap (*N* = -/30/3)	75 (63–84)	1	75 (63–84)	-	-	1857 (1739–2129)	3690 (3136–4010)	= SFB	-	-	Padial *et al.* 2016
P. incertus (*N* = 10/-/-)	138 (128–160)	4	19 (11–26)	-	26 (15–32)	3000	6000	= FFB	-	-	Kaiser *et al.* 1995[i]
P. koehleri (*N* = 21/119/6)	421 ± 160 (173–644)	5.7 ± 1 (3–8)	36 ± 7 (20–54)	14.1 ± 1.8 (11.8–17.3)	-	1854 ± 72 (1732–1971)	3662 ± 129 (3245–3971)	= SFB	-	-	Padial and De la Riva 2009
P. latro (*N* = 7/49/6)	455 ± 69 (402–581)	7	40 ± 5 (31–46)	-	-	1381 ± 36 (1342–1449)	3069 ± 254 (2636–3272)	= SFB	-	-	Oliveira *et al.* 2017
P. moa (*N* = 20/75/6)	294 ± 48 (212–380)	4.3 ± 0.6 (3–5)	45 ± 9 (23–64)	-	-	1510 ± 111 (1321–1660)	3118 ± 159 (2657–3400)	= SFB	-	-	Oliveira *et al.* 2020
P. paulodutrai (*N* = -/10/1)	(27–32)	1	(27–32)	-	-	(2150–2330)	(3540–3970)	= SFB	1500?	4960?	Heyer and Carvalho 2000[j]
P. peruvianus (*N* = 7/-/-)	-	2 (1–5)	30	-	185 (180–380)	260 (234–280)?	3070 (2812–3140)	= SFB	-	-	Rodríguez 1994
P. peruvianus (*N* = -/-/-)	-	>1[h]	150	1.0[d]	-	1300?	1600?	-	-	-	Duellman 2005
P. pictus (*N* = 15/56/4)	235 ± 21 (216–302)	(4–5)	26 ± 4 (17–33)	-	-	1677 ± 113 (1406–1915)	2889 ± 160 (2487–3272)	= SFB	-	-	Oliveira *et al.* 2020
P. pluvian (*N* = 8/16/3)	152 ± 8 (141–165)	2	56 ± 7 (47–73)	-	-	1852 ± 92 (1618–1936)	3645 ± 248 (3484–4312)	= SFB	-	-	Oliveira *et al.* 2020
P. ramagii (*N* = 138/-/9)	151 ± 52 (73–245)	2.6 ± 0.7 (1–4)	36 ± 8 (19–69)	-	-	-	-	3942 ± 491 (2217–4898)[g]	-	-	Oitaven *et al.* 2017
P. relictus (*N* = 181/150/3)	60 ± 80 (20–660)	1.9 ± 1.2 (1–8)	30 ± 10 (20–50)	1.4 ± 0.8 (0.5–2.2)	-	2033 ± 55 (1895–2153)	3923 ± 126 (3618–4221)	= SFB	-	-	Roberto *et al.* 2022

Appendix II. *Continued.*

Species	Call duration (ms)	Notes/ call	Note duration (ms)	Note rate (notes/s)[x]	Inter-note interval (ms)[x]	Peak of the FFB (Hz)	Peak of the SFB (Hz)	Dominant frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	References
P. rupicola (*N* = -/168/15)	31 ± 19 (11–86)	1	31 ± 19 (11–86)	-	-	3010 ± 0230 (2410–3490)	5850 ± 500 (4000–6900)	= FFB	-	-	Taucce *et al.* 2020
P. samaipatae (*N* = 3/-/-)	-	2?	(66–100)	6.0 ± 0.6 (5.7–6.6)[d]	-	(1575–1797)	(3009–3352)	= SFB	-	-	Márquez *et al.* 1995[k]
P. samaipatae (*N* = 3/-/1)	228 ± 3 (225–231)	2	83 ± 66 (73–90)	-	-	-	-	3180	1200?	6800?	Köhler 2000
P. samaipatae (*N* = 98/160/12)	292 ± 168 (82–1062)	2 ± 0.2 (1–3)	89 ± 16 (59–141)	8.5 ± 2.1 (2.7–14.9)	-	1705 ± 64 (1535–1834)	3327 ± 176 (2922–3853)	= SFB	-	-	Padial and De la Riva 2009
P. skydmainos (*N* = -/4/-)	60	1	60	-	-	-	-	4430 (4424–4500)	-	-	Rodríguez 1994[l]
P. skydmainos (*N* = -/6?/1?)	60	1	60	-	-	2120	4240	= SFB	-	-	Flores and Rodríguez 1997
P. ventrigranulosus (*N* = 22/108/3)	289 ± 60 (202−411)	4.9 ± 0.8 (4−7)	44 ± 9 (24−74)	17.1 ± 1.1 (15.6−19.8)	-	3386 ± 314 (2127–3652)	4021 ± 270 (3452–4335)	= SFB	-	-	Maciel *et al.* 2012
P. vilarsi (*N* = -/1/1)	521	8	9 ± 6 (3–21)	14	-	(1959–2256)	(3799–4284)	= SFB	-	-	Heyer and Barrio-Amorós 2009
P. zeuctotylus (*N* = -/-/-)	489	4	45	-	-	-	-	(2140–3250)[g]	-	-	Lescure and Marty 2000

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Reproductive notes and larval development of *Macrogenioglottus alipioi* (Anura: Odontophrynidae) from the northern Atlantic forest

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Abstract

Reproductive notes and larval development of *Macrogenioglottus alipioi* (Anura: Odontophrynidae) from the northern Atlantic forest. The neotropical monotypic genus *Macrogenioglottus,* described to enclose *M. alipioi,* is a forest leaf litter frog with a wide geographic distribution in eastern Brazil, despite being considered a rare species. Herein, we present some reproductive data of this species from a population of the north of the São Francisco River, Northeastern Brazil. We present information on the amplexus, egg clutch, advertisement, and release calls, along with a description of its larval development. Adults were observed only after heavy and continuous rains, in a temporary pond located inside the forest. Males call in chorus at the edge of the pond. The advertisement call consists of a pulsatile single note, with no substantial variation in relation to the other population of the species, but which promptly differs this genus from the remaining Odontophrynidae. The amplexus is axillary. One female deposited 298 pigmented eggs in a plastic bag. The tadpole reaches its larger size at Stage 39, being the largest tadpole within the family. At the end of metamorphosis, the froglet snout–vent length is equivalent to tadpole total length at stage 26–27, indicating substantial postmetamorphic growth until adulthood. Data on body size of males and females are also provided. The uniqueness of some larval traits and mainly on some call attributes supports the systematic distinction of *Macrogenioglottus*.

Keywords: Call, Egg clutch, Morphology, Ontogeny, Reproduction, Tadpole.

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Resumo

Notas reprodutivas e desenvolvimento larval de *Macrogenioglottus alipioi* (Anura: Odontophrynidae) no norte da Mata Atlântica. *Macrogenioglottus alipioi* é uma espécie rara, alocada em um gênero monotípico, habitante da serapilheira de florestas da região Neotropical, com ampla distribuição no leste do Brasil. Apresentamos alguns dados reprodutivos dessa espécie, a partir de uma população encontrada ao norte do rio São Francisco, no nordeste brasileiro. Incluímos informações a respeito do amplexo, desova, cantos de anúncio e de soltura, em conjunto com a descrição do seu desenvolvimento larval. Indivíduos adultos foram observados apenas após chuvas fortes e contínuas, em poça temporária no interior da mata. Machos cantam em coro na margem da poça. O canto de anúncio consiste em uma única nota pulsátil sem diferenças significativas das demais populações da espécie, mas que prontamente difere *Macrogenioglottus* dos demais Odontophrynidae. O amplexo é do tipo axilar. Uma fêmea depositou 298 ovos pigmentados em um saco plástico. O girino adquire o seu maior tamanho do estágio 39, sendo o maior girino dentre aqueles das demais espécies na família. No final da metamorfose o comprimento rostro–cloacal juvenil é equivalente ao comprimento total do girino em estágio 26–27, indicando um crescimento posmetamórfico substancial até atingir a idade adulta. Também fornecemos dados dos tamanhos dos machos e fêmeas. A peculiaridade de alguns caracteres larvais e, principalmente, de alguns atributos do canto, corrobora a distinção sistemática de *Macrogenioglottus*.

Palavras-chave: Canto, Desova, Girino, Morfologia, Ontogenia, Reprodução.

Introduction

Amphibians are the tetrapods with the greatest reproductive diversity documented so far (Duellman 1985, Wells 2007, Crump 2015). Regarding anurans specifically, one conspicuous characteristics of their reproductive behavior concerns the acoustic intraspecific communication. Bioacoustic data have been largely applied in taxonomic evaluation of anuran species with wide geographical distribution, corroborating their current taxonomic status (Mângia *et al.* 2019) or revealing an important cryptic diversity (Fouquet *et al.* 2014, Ron *et al.* 2018, Lopes *et al.* 2020). In fact, most of the anuran calls have primarily reproductive functions (see Toledo *et al.* 2015 for a revision). The most common example here is the advertisement call, usually emitted by males to attract co-specific females during the breeding season (Wells 2007, Toledo *et al.* 2015, Kohler *et al.* 2017), being used for species delimitation in taxonomy due to its role in pre-zygotic isolation (Kohler *et al.* 2017, Carvalho *et al.* 2020). However, there are other types of less documented calls that can be emitted in social contexts and can permeate anuran reproduction, as well as the release calls, which can be produced by both males and non-receptive females when grabbed by another male (Duellman and Trueb 1994, Toledo *et al.* 2015). Just like the advertisement calls, release calls have been useful to differ between close related species (Castellano *et al.* 2002, Grenat and Martino 2013).

Another striking reproductive aspect of anurans is the presence of a distinctive larval phase during its life cycle (Wassersug 1975, Harris 1999). The larval phase reaches a crucial point during the transition to adulthood through metamorphosis. Anuran postembryonic ontogeny encompasses three processes: (1) the development and disappearance of larval structures, (2) the remodeling of larval structures into adult structures, and (3) the development and differentiation of adult structures (Fabrezi *et al.* 2012). New information on this subject is important general developmental patterns, understand ontogenetic diversity and clarify questions about systematic relationships (e.g., Hall *et al.* 1997, Fabrezi *et al.* 2012, Barrionuevo 2018). Thus, developmental changes need to be

well documented and go beyond the information available on standardized ontogenetic tables (e.g., Taylor and Kollros 1946, Gosner 1960), which despite being very useful for different comparative purposes and being well suited for many species, may not take into account interspecific variations (most of them heterochronic processes) that may have played important roles on frog diversification (Chuliver and Fabrezi 2019, Mongin and Carvalho-e-Silva 2013, Silva *et al.* 2018, Cordioli *et al.* 2019).

The neotropical monotypic genus *Macrogenioglottus* Carvalho, 1946 belongs to the family Odontophrynidae (sensu Pyron and Wiens 2011); it is the sister taxon of *Odontophrynus* Reinhardt and Lütken, 1862, and together they are the sister clade of *Proceratophrys* Miranda-Ribeiro, 1920 (Amaro *et al.* 2009, Pyron and Wiens 2011, Martino *et al.* 2019). The genus was described to include *M. alipioi*, a forest leaf litter frog with wide geographic distribution in eastern Brazil, despite being considered a rare species (Toledo *et al.* 2014). *Macrogenioglottus alipioi* occurs in regions of Atlantic Forest from Pernambuco state, in the northeast region, to São Paulo state, in the southeast region (Haddad *et al.* 2013, Frost 2022). The species shows the reproductive mode 2 or 3 (Abravaya and Jackson 1978, sensu Nunes-de-Almeida *et al.* 2021) and its tadpoles are Type IV according to Orton's (1953) classification (Figure 1).

There are some reports on the biology and natural history of *Macrogenioglottus alipioi* (such as tadpole morphology, mating behavior, call and karyotype) that come from populations of the southeastern region of Brazil (Abravaya and Jackson 1978, Silva *et al.* 2003), in the southern limit of its distribution. There are also data about the tadpole from the extreme north distribution, in the area north of the São Francisco River (Lisboa *et al.* 2011, Dubeux *et al.* 2020); and recently, Mira-Mendes *et al.* (2020) published the calls and morphometric data from populations close to and from the type locality (Ilhéus, Bahia state), south of the São Francisco River. In order to know additional aspects of the population from the northern part of its distribution that may help to establish a more complete scenario of the taxonomic status of the genus and its relationships with the other members of the family Odontophrynidae, we present new reproductive data, including egg clutch, advertisement and release calls, and data on its larval development, from a population of *M. alipioi* in the north of the São Francisco River, northeastern Brazil.

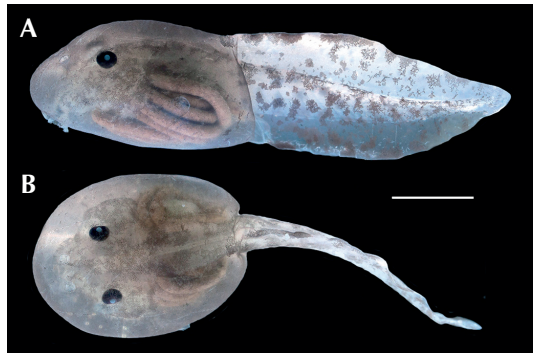

Figure 1. Tadpole of *Macrogenioglottus alipioi* (MHNUFAL 13952) at Stage 26 from Mata do Catolé, Maceió, Alagoas state, northeastern Brazil. (**A**) Lateral and (**B**) dorsal views (scale bar = 5 mm). Photo by Marcos Dubeux.

Materials and Methods

We conducted field surveys at Mata do Catolé (09°35' S, 35°49' W; datum WGS84, 47 m a.s.l.), an Atlantic Rain Forest fragment located at the Environmental Protection Area of Catolé and Fernão Velho, in Alagoas state, northeastern Brazil. In this area, vegetation type is ombrophilous and the regional climate varies from humid to sub-humid, with a rainy season (March–August) and a dry season (September–February). The mean annual rainfall varies from 1500 to 2000 mm, and temperature varies from 23 to 25°C (Assis 2000).

Reproductive observations were made during visual encounter surveys (VES; Heyer *et al.* 1994) at night, in a temporary pond on 12 July and 21 August 2011 (17:30–23:00 h). After heavy rains

at night (21:00–22:00 h, air temperature = 20.8–20.9°C, relative air humidity = 100%), we recorded vocalizations of four males of *Macrogenioglottus alipioi* on 12 July 2011 (one collected, MHNUFAL 10942, SVL = 82.2 mm) at the edge of ponds, using a digital recorder Sony PCM-D50R (sampling rate of 44.1 kHz and resolution of 16 bits) coupled to a unidirectional microphone Sennheiser ME66/K6. The microphone was positioned about one meter from calling males. Vocalizations were classified as advertisement call according to the social context of the observed individuals (Toledo *et al.* 2015). To obtain the release calls, a false amplexus was simulated on one male using the thumb and the forefinger to push him until the emission of calls.

A total of 200 advertisement calls (50 calls per male) and 50 release calls (one male) were analyzed in Raven Pro 1.5 (Bioacoustics Research Program 2014) with the following settings: window type Hann, DFT size 256 samples and overlap 90%. The following temporal and spectral parameters were analyzed: call duration (s), interval intercall (s), call rate (calculated per minute, call/min), dominant frequency (Hz), and minimum and maximum frequency (Hz). The dominant frequency was obtained through the Peak Frequency function, minimum and maximum frequencies through Frequency 5% and Frequency 95%, respectively. Acoustic terminology and analysis follow Köhler *et al.* (2017). Sound figures were produced with Seewave package, version 1.7.3 (Sueur *et al.* 2008), in R 3.1.0 (R Core Team 2018), with the following settings: window Hann, DFT size 1024 samples and overlap 90%. We also included information about snout–vent length (SVL) of females (N = 2) and males (N = 10) from this locality and from Murici Ecological Station (09°12' S, 35°52' W, datum WGS84; 593 m a.s.l.), municipality of Murici, also in Alagoas State, to assess sexual dimorphism. Specimens are deposited in the herpetological collection of the Museu de História Natural, Universidade Federal de Alagoas (MHNUFAL; Appendix I), Brazil. The snout–vent length of females and males was measured with calipers to the nearest 0.1 mm.

One amplectant pair was collected (MHNUFAL 10940–41) and placed in a plastic bag where the female spawned. We count the total number of eggs in the spawn (MHNUFAL 10982), measuring their maximum diameter (without considering the gelatinous layers) using an ocular micrometer installed on a Coleman NSZ 405 stereomicroscope.

We collected 78 tadpoles between May 2008 and August 2011 (Appendix I). All tadpoles came from the same pond, being posteriorly fixed and preserved in 10% formalin. Average rainfall and temperature data were similar over three of the four years along the collection period. In addition, to reduce a hypothetical bias of the environmental conditions of successive years on the development/growth of the tadpoles, we analyzed specimens from the same developmental stages collected in different years to take into account possible variations. Species identification was made by direct comparison with samples from the same locality used by Lisboa *et al.* (2011) in the description of the larvae. We selected specimens to address all stages of development (sensu Gosner 1960), from the emergence of the spiracle (Stage 25) to complete atrophy of the tail (Stage 45), and then we grouped them following the developmental periods of Etkin (1968): premetamorphosis, prometamorphosis and metamorphosis. Morphometric variations were recorded through 16 measurements, six from Altig and McDiarmid (1999): body length (BL), maximum tail height (MTH), tail length (TaL), tail muscle height (TMH), tail muscle width (TMW), and total length (TL); eight from Lavilla and Scrocchi (1986): eye diameter (ED), eye–nostril distance (END), intranarial distance (InD), intraorbital distance (IoD), maximum body height (MBH), maximum body width (MBW), oral disc width (ODW, taken with the oral disc partially opened), and snout–nostril distance (SND); and two from Grosjean (2005): dorsal fin height (DFH) and

ventral fin height (VFH). Most of the measurements were taken using an ocular micrometer installed on a Coleman® NSZ 405 stereomicroscope, except for TL, BL, MBH, and MBW which were measured with calipers (0.1 mm accuracy). The terminology of external morphology follows Altig and McDiarmid (1999). Data are presented as mean ± standard deviation ($\bar{x}$ ± SD).

Results

Observations on Reproduction

Males and females of *Macrogenioglottus alipioi* were only observed after heavy and continuous rains, in a temporary pond inside the forest. Males were found calling in chorus at the edge of the pond (Figure 2A) where they were separated from each other by at least 3 m. Calling activity began after sunset (17:30 h) and continued during the night. We observed three mating events around 21:00 h, all of them occurring in the leaf litter near the pond, and about 1 m apart from each other. The amplexus is axillary (Figure 2B). In one occasion, we separated an amplectant pair and left them 1 m apart from each other. The male began to call immediately, the same female moved towards him, and the amplexus restarted.

Snout–vent length of females were 93.5 and 101.1 mm (N = 2) and SVL of males ranged from 77.7–90.8 mm (84.3 ± 4.1 mm, N = 10).

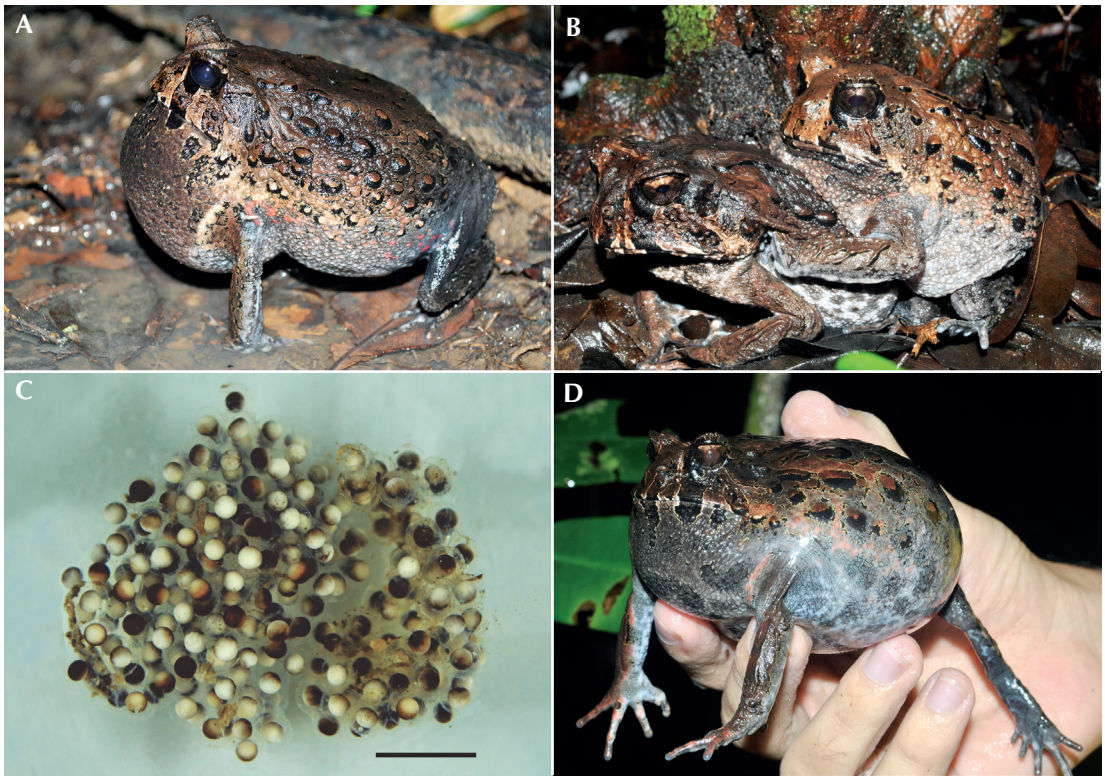

Figure 2. Breeding activity of *Macrogenioglottus alipioi* from Mata do Catolé, Maceió, Alagoas state, northeastern Brazil. (**A**) Male calling on the leaf litter, (**B**) couple in amplexus, (**C**) egg clutch (scale bar = 10 mm), and (**D**) manipulation of a male to emit the release call.

Spawning.—The spawn contained 298 eggs, free or slightly adhered to one another by a gelatinous mass. The eggs had a diameter between 1.8 and 2.6 mm (2.2 ± 0.1 mm, N = 298) and were pigmented in the animal pole, with color ranging from light to dark brown (Figure 2C).

Advertisement call.—The advertisement call (Figure 3A–B) of *Macrogenioglottus alipioi* consists of a pulsatile single note that lasts 0.3–0.6 s (0.4 ± 0.07 s), with intervals between calls varying from 0.3–5.5 s (0.9 ± 0.6 s). Call repetition rate was of 10.3–98.3 calls/min (53.9 ± 18.3 calls/min), dominant frequency ranged from 344.5–430.7 Hz (390.4 ± 43.1 Hz), maximum frequency 430.7–516.8 Hz (492.1 ± 39 Hz) and minimum frequency was 258.4 Hz.

Release call.—The release call (Figure 3C–D) was emitted sporadically by one male during handling (Figure 2D). The call consists of one single low-frequency note, as the advertisement call, but with a shorter duration (0.3 ± 0.02 s) and higher call repetition rate (23.5–77.6 calls/min, 57.6 ± 12.2 calls/min). Inter-call interval ranged from 0.5–2.3 s (0.8 ± 0.4 s), with a dominant frequency of 430.7 Hz. Maximum frequency 775.2–1292.0 Hz (902.7 ± 89.1 Hz) and minimum frequency was 344.5 Hz.

Larval Development

Premetamorphosis (stages 25–35; Figure 4A–D).—This phase is characterized mainly by body and tail growth and early development of the hind limbs. The tadpoles have an ovoid body in dorsal view (MBW/BL 0.6–0.9, 0.71 ± 0.07, N = 46) and depressed laterally (MBH/MBW 0.6–0.8, 0.7 ± 0.06, N = 46). At Stage 25, the mouthparts are already formed, with the typical labial tooth row formula (LTRF) 2(2)/3(1), a single row of marginal papillae and one or two rows of submarginal papillae on the lower labium; the pigmentation of the jaw sheaths is more restricted to the distal margin, which gradually increases as the larva grows until become fully pigmented at about Stage 32 (Figure 5A–B). At Stage 25, the gills are already completely covered by the operculum; there are remnants of the yolk sac, which disappears in the next Stage, and the lateral spiracle is present on the middle third of the body, with the inner wall free, longer than the external wall. At Stage 33, the stylopodium and zeugopodium begin to differentiate. Coloration in preservative: at Stage 25, the body is translucent with two groups of melanophores visible, the first one is filiform in shape, located on the dorsal and lateral integument; the second group is stellate, visible on the connective tissue that covers the chondrocranium and viscera, also forming speckles on the caudal musculature and fins. From Stage 26 to Stage 30 these melanophores become more numerous, with those of the first group also arising ventrally and around the nostrils, and those of the second group forming dark spots on the tail. At Stage 27, there are also small subepidermal whitish punctuated chromatophores on the eyes and dorsum, but more easily seen on the viscera. From Stage 31 the filiform melanophores become denser, interlaced, leaving the tadpole with a dark brown coloration. Light brown stellate spots begin to appear on limb bud at Stage 29. At Stage 28, the lateral line system become apparent.

Prometamorphosis (stages 36–40; Figure 4E).—Along this phase the body is still growing, following the limb development and the beginning of metamorphosis. The body shape does not change (MBW/BL 0.7–0.8, 0.7 ± 0.04, N = 15). At Stage 36, the forelimbs are visualized by transparency inside the gill chambers; as they develop, press the overlying skin. At Stage 38, a slight depression appears around each nostril, the spiracle inner wall becomes smaller than the external one, and the nasolacrimal duct begins to appear in some individuals as a shallow groove from the

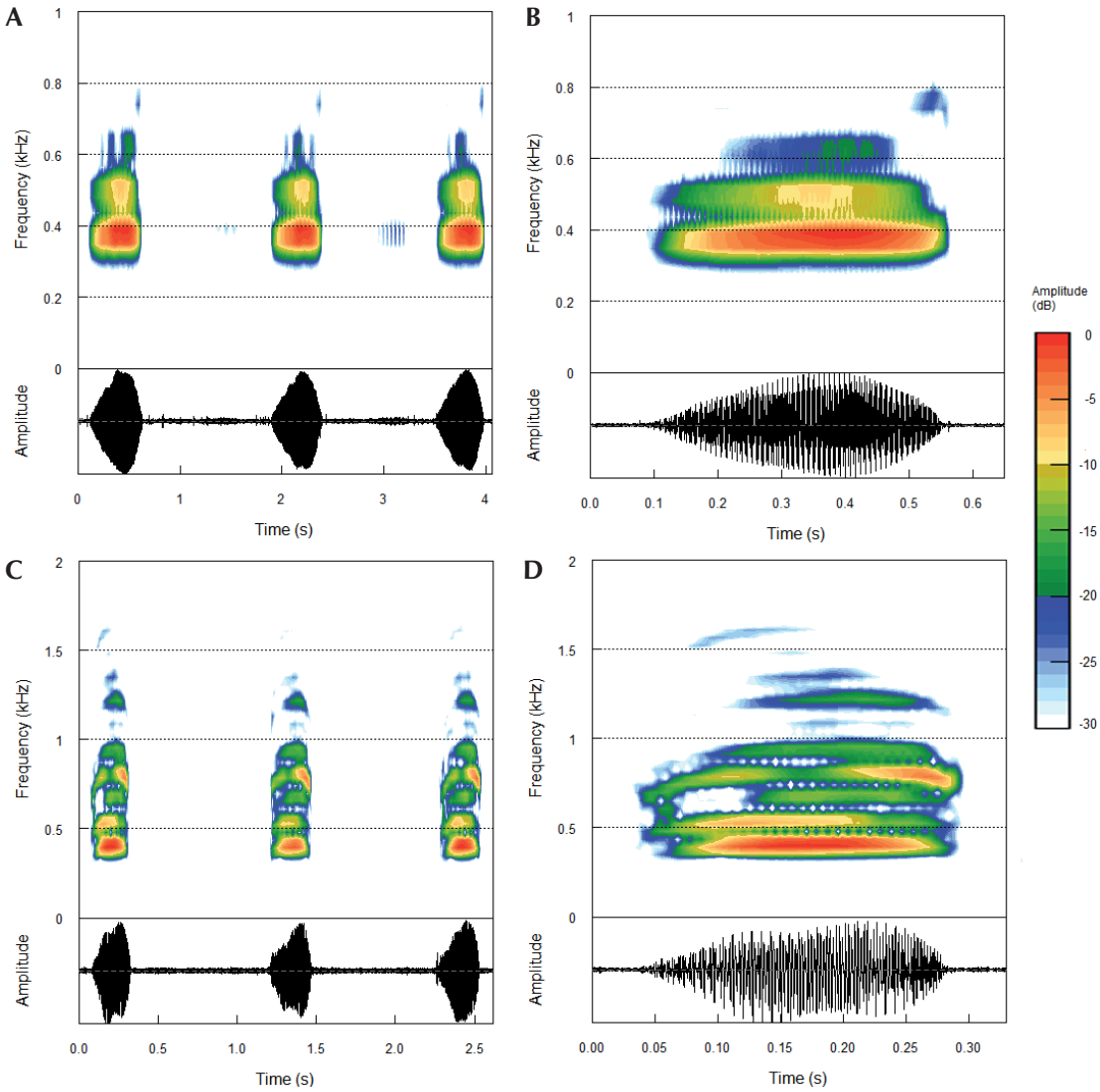

Figure 3. Calls of *Macrogenioglottus alipioi* from Mata do Catolé, Maceió, Alagoas state, northeastern Brazil. (**A**) Series of three advertisement calls (MHNUFAL 10942); (**B**) detail of an advertisement call; (**C**) series of three release calls (specimen not collected); and (**D**) detail of a release call. In all figures, spectogram above and oscillogram below.

anterior region of the eye to the nostrils. At Stage 39, the tadpole acquires its larger size (TL = 69.9 mm, N = 1; Figures 4E and 6A), decreasing progressively in the following stages. The eye–nostril distance begins to decrease gradually (Figure 6B), and the relative size of the eyes starts to increase gradually in relation to the body size. At Stage 40, the

snout–nostril distance also starts to decrease, but in a more abrupt way than the other measures (Figure 6B). Coloration in preservative: from Stage 39 the filiform melanophores form irregular spots on the dorsum. At Stage 38, the brown stellate spots of the limb bud become darker, forming agglomerations. At the following Stage, the pattern of spots on the phalanges begins to differentiate, highlighting the subarticular regions and external metatarsal tubercle.

Metamorphosis (stages 41–46; Figure 4F–I).—This last phase is characterized by an abrupt decrease in size, mostly due to the decrease of tail length, and loss of most larval characters. This overall larval reduction is directly reflect in the continuous reduction of eye-nostril and snout–nostril distances, and in the increase of the intracolular distance in relation to body width (eyes will be positioned laterally), shaping the future adult head (Figure 6B–C). At Stage 41, the tadpole body acquires a more oval shape, with the central dorsal region more prominent, although the bodily relationship almost does not change (MBW/BL = 0.7, N = 4). In the region where the forelimbs will emerge the skin becomes thinner and lighter. The upper and lower eyelids appear (Figure 5E–F). The nostrils aperture become narrower. In the oral disc, labial teeth in A1, A2, P1, and P2 rows becomes progressively vestigial; the P3 row begins to degenerate; the upper jaw acquires a more frontal position while the lower jaw exhibits broken parts (Figure 5C); the mouth is getting bigger (oral disc width/body width ratio increases; Figure 6C). The vent tube degenerates, remaining some remnant connected to the ventral fin, but which disappears completely in the following stages. The caudal fins begin to decrease in height. The skin becomes thicker, tubercles appear on the dorsum, on the eyelids and in the inner region of the thighs (next to the cloaca). There are also small elevations (tubercles or warts) that are darker in the interocular region, along the medial region of the dorsum, and laterally behind the eyes (resembling the adult pattern). At Stage 42, the head begins to differentiate, becoming wider than the rest of the body. The eyelids and eyelid tubercles become more evident (Figure 5F–H). The mouth position becomes gradually more anterior, remaining only a few marginal papillae laterally on the upper lip; there are no more vestiges of the labial teeth and jaws (Figure 5D). In some individuals, the tongue is already visible. The lateral line system disappears. The spiracle and the jaw sheaths have disappeared, and the caudal fins begin to decrease in height. The forelimbs have already emerged, and the ruptured opercular membrane is still visible. At Stage 43, the larva begins to take on the adult appearance, the tubercles are more evident, the *cantus rostralis* are already visible, and the eyes are more extrinsic, with the pupil acquiring an angular shape. The nostrils are positioned more dorsofrontally and there is no record of the larval oral apparatus in the mouth. The caudal fins are atrophied in advanced state, along with the caudal musculature (Figure 5I–K), resulting in an abrupt decrease in the larval total length (37.6 ± 2.2 mm, ranging from 29.6–49.0 mm, N = 5, Figure 6A). The epidermis is much thicker, with the interocular tubercles blackened; the intestines can no longer be seen by transparency. At stages 44–45, there is already an adult configuration (Figure 4I), the eyes are positioned laterally, the nasal cartilage forms a protrusion where the nostrils open, the tail is reduced to a bud (Figure 5L), and the total length is equivalent to that of the tadpoles in Stage 25–26 (17.9 and 18.6 mm, N = 2). Coloration in preservative: body dark brown, with darker spots surrounding the tubercles; belly with a whitish appearance, with light brown spots.

A summary of the main events of postembryonic external development is shown in Table 1, and the morphological measurements of the larvae in Appendix II.

Table 1. Summary of the main external larval developmental features of *Macrogenioglottus alipioi*. Stages are according to Gosner (1960).

Stage	*N*	Main external developmental features	Total length ($\bar{x}$ ± SD) (mm)
25	5	Mouthparts fully formed, pigmentation of the jaw sheaths restricted to the distal margin; no trace of the yolk sac; spiracle with inner wall free and longer than the external wall; body translucent with filiform and star-shaped melanophores.	14.4 ± 1.4
26	5	Jaw sheaths fully formed; hind limb appears as a small bud (L < ½ D); chromatophores more numerous, grouping and forming spots on body and tail, nostrils with pigmented margins.	25.3 ± 1.9
27	5	Hind limb bud slightly longer than half its diameter (L ≥ ½ D); whitish chromatophores on dorsum, eyeballs and viscera; abdomen iridescent.	26.9 ± 5.3
28	4	Lateral line system visible; chromatophores in high density; hind limb bud slightly longer than its diameter (L ≥ D).	33.7 ± 6.1
29	2	Hind limbs longer than one and a half times its diameter (L > 1 ½ D) and with rare light brown punctuations.	39.7 ± 4.6
30	4	Hind limb bud with a length equivalent to twice its diameter (L = 2D).	35.5 ± 2.5
31	5	Submarginal papillae close to emarginations of the oral disc in some individuals; hind limb bud paddle shaped (autopodium with indentations); larva with coloration dark brown due to higher density of chromatophores.	41.9 ± 2.7
32	3	Beginning of indentation between toes IV and V; larva darker, punctuation on limbs forming spots similar to those of the tail.	49.5 ± 1.1
33	4	Beginning of indentation between toes III and IV (estilopodium and zeugopodium differentiated).	45.6 ± 2.7
34	4	Beginning of indentation between toes II and III.	48.4 ± 7.8
35	5	Beginning of indentation between toes I and II.	49.9 ± 7.1
36	2	Visualization of the forelimbs within the branchial chambers; separation of toes III and V.	58.8 ± 1.2
37	4	All five toes separated.	53.9 ± 8.4
38	3	Emergence of a depression around each nostril; spiracle with inner wall longer than the external wall; emergence of the nasolacrimal duct and the spot pattern on the phalanges.	59.8 ± 10.5
39	1	Appearance of subarticular patches and on external metatarsal tubercle; filiform chromatophores agglomerated forming spots on dorsum; hind limbs almost entirely covered by spots.	69.9
40	5	Forelimb larger and clearly visible ventrolaterally within the branchial chamber; appearance of metatarsal tubercles.	65.1 ± 11.3
41	4	Body ovoid, dorsum with medial region prominent; eyes directed laterally, appearance of the upper and lower eyelids; forelimb form a lateral bulge under the skin; advanced degeneration of the mouthparts; disappearance of vent tube; appearance skin tubercles.	61.7 ± 7.3

Table 1. *Continued.*

Stage	*N*	Main external developmental features	Total length ($\bar{x}$ ± SD) (mm)
42	5	Disappearance of lateral line system; head differentiation; disclosure of the tuberculous pattern of adult skin; mouth commissure does not reach the anterior limits of the nostrils; disappearance of spiracle; emergence of forelimbs; decrease of caudal fins; skin thicker, appearance of the tongue.	41.7 ± 3.1
43	5	*Cantus rostralis* evident; skin tubercles more evident; nostrils dorsofrontal; mouth commissure reaches the anterior limits of the eyes; tail and fins in an advanced state of atrophy; skin thicker and darker.	37.5 ± 7.0
44	1	Acquisition of adult form, tail remains as a stub; dark spots surround the tubercles; mouth commissure below the eye.	18.6
45	1	Mouth commissure exceeding the posterior limits of the eye; skin darker.	17.9

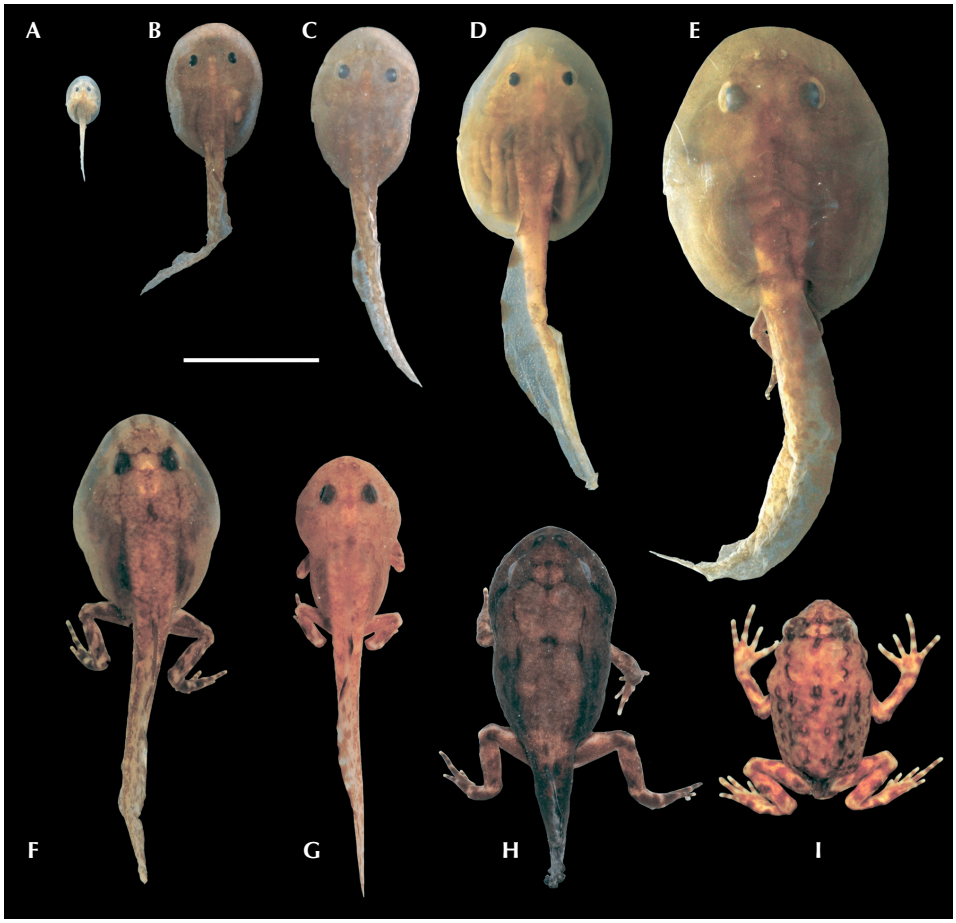

Figure 4. Representative series of *Macrogenioglottus alipioi* development. (**A**) Stage 25, (**B**) Stage 29, (**C**) Stage 32, (**D**) Stage 35, (**E**) Stage 39, (**F**) Stage 41, (**G**) Stage 42, (**H**) Stage 43, and (**I**) Stage 45 (scale bar = 20 mm).

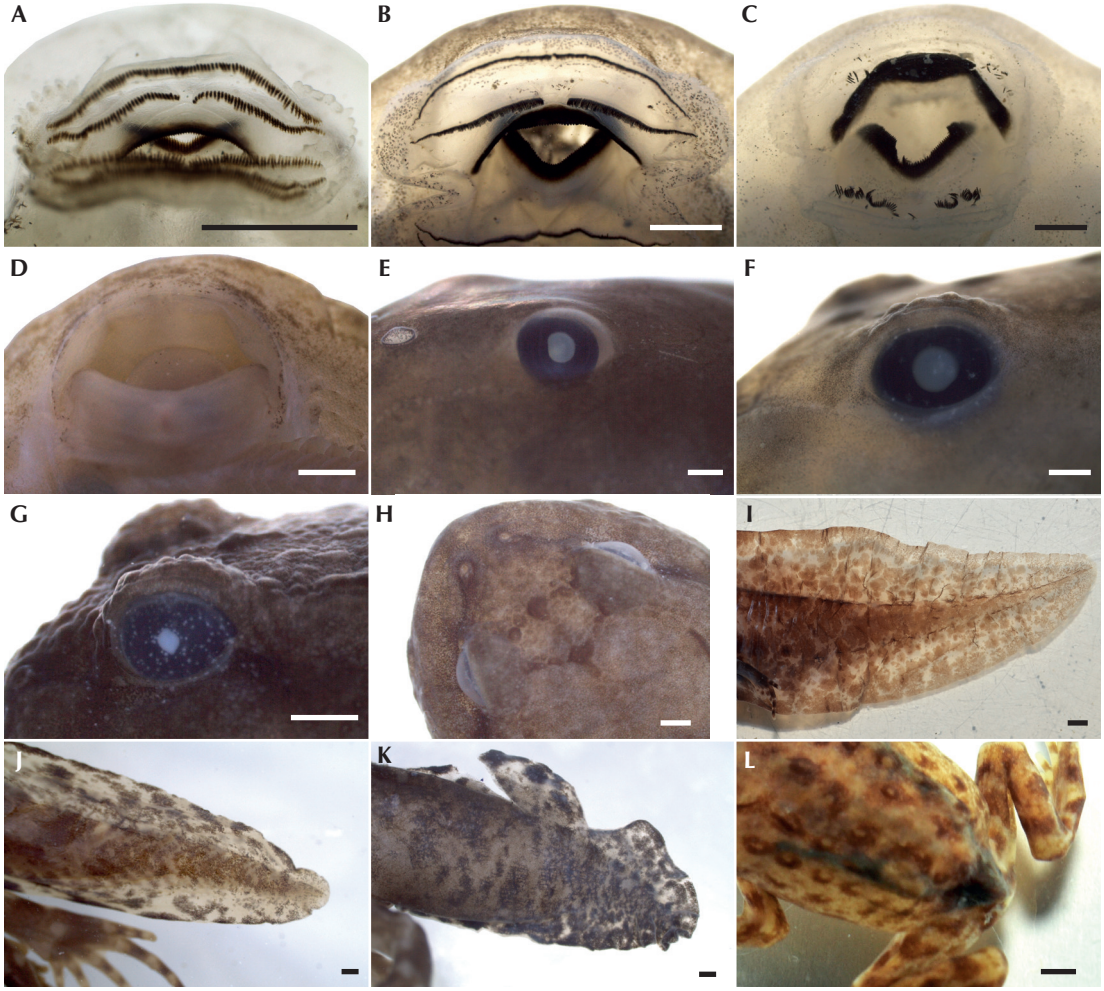

Figure 5. Changes in external morphology during larval development of *Magrogenioglottus alipioi*. (A–D) Mouth transformations in ventral view: (**A**) Stage 25, (**B**) Stage 32, (**C**) Stage 41, and (**D**) Stage 42. (E–G) Transformations in the region of the eyes in lateral view: (**E**) Stage 32 (**F**) Stage 42, and (**G**) Stage 43. (**H**) Region of the eyes and nostrils in dorsal view at Stage 43. (I–K) Tail transformation in lateral view: (**I**) Stage 40, (**J**) Stage 42, (**K**) Stage 43. (**L**) Posterior region of the froglet in dorsal view (Stage 45; scale bar = 1 mm).

Discussion

Reproductive Observations

Abravaya and Jackson (1978) and Mira-Mendes *et al.* (2020) observed reproductive activity of *Macrogenioglottus alipioi* from Santa Teresa (Espírito Santo state) and Uruçuca (Bahia state), respectively, and reported that individuals breed only after heavy rains in ponds. Herein, we corroborated this observation, adding the information that the activity occurs usually in the middle of the rainy season, and suggesting that the temporal reproductive pattern of *M. alipioi* is explosive (sensu Wells 1977), similar to almost all species in the family Odontophrynidae (e.g.,

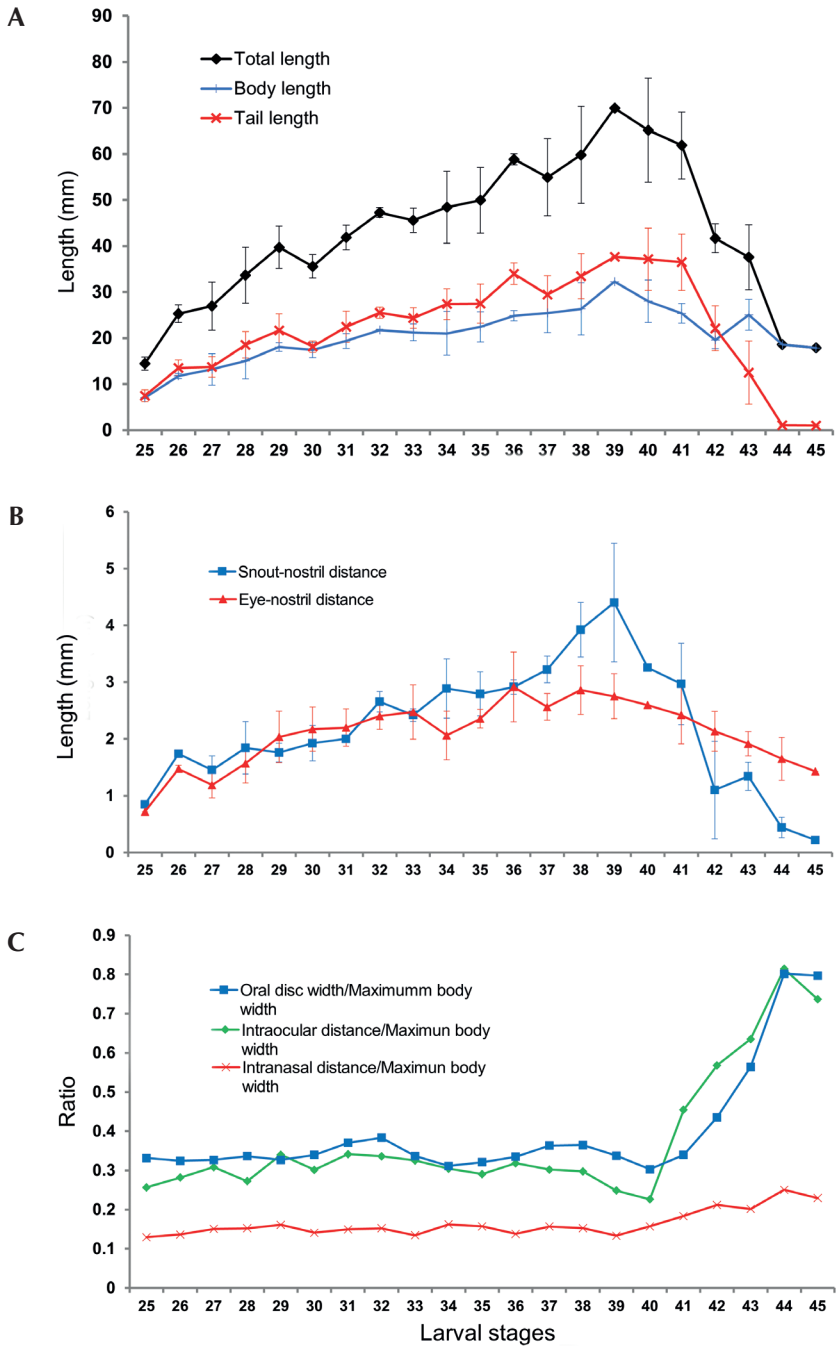

Figure 6. Some morphometric and ratios values of *Macrogenioglottus alipioi* during larval development from stages 25 to 45. (**A**) Mean and standard deviation values of body, tail, and total length; (**B**) mean and standard deviation values of snout–nostril distance and eye–nostril distance; and (**C**) ratio of oral disc width, intraocular distance, and intranasal distance in relation to maximum body width.

Santos *et al.* 2008, Araújo *et al.* 2009, Godinho *et al.* 2013, Valdez and Maneyro 2016, Malagoli *et al.* 2016), which could explain why this species is rarely seen in the field.

Abravaya and Jackson (1978) reported a gravid female of *Macrogenioglottus alipioi* with about 3650 eggs in their ovaries. The authors also stated that the numbers of eggs oviposited on each oviposition event although not determined, would be small, probably less than 20 eggs, an unrealistic hypothesis for a large species with free-living tadpoles (see Crump 1974, Prado and Haddad 2005). Hartmann *et al.* (2010) found 2900 eggs in a *M. alipioi* clutch from Picinguaba (São Paulo state, southeastern Brazil). Our collected spawning from an amplectant pair containing 298 eggs must be considered with caution once it was obtained inside a plastic bag (an artificial situation). Nonetheless, clutch size can vary considerably between females from the same population (Lemckert and Shine 1993, Prado and Haddad 2005) due to numerous factors, such as environmental conditions and female nutritional status (Ryser 1989, Jørgensen 1992).

Sexual dimorphism in snout–vent length occurs in most species of *Odontophrynus* (see references in Mira-Mendes *et al.* 2020) and *Proceratophrys* (Boquimpani-Freitas *et al.* 2002, Giaretta *et al.* 2008, Santana *et al.* 2010, Ávila *et al.* 2011, Nunes *et al.* 2015). Hartmann *et al.* (2010) found significant sexual dimorphism in SVL of *Macrogenioglottus alipioi* from São Paulo state, with females bigger than males. On the other hand, Mira-Mendes *et al.* (2020) did not observe significant differences in the SVL in a sample of *M. alipioi* from Bahia state (although the authors found sexual differences in the head and hind limb size), Despite we found that females of *M. alipioi* are bigger than males, we could not test the existence of sexual dimorphism in our population because our small female sample ($N = 2$), nevertheless the data suggest that sexual dimorphism is a peculiar feature in the genus.

The advertisement call traits of *Macrogenioglottus alipioi* provided here are similar to those described by Mira-Mendes *et al.* (2020) for a population from Bahia state with only the dominant frequency range slightly higher in our sample (430.7–516.8 Hz here, against 344.5–430.7 Hz from the Bahia sample). Although geographic variation in advertisement call of anurans was demonstrated in conspecific population of several species (e.g., Castellano *et al.* 2000, Pröhl *et al.* 2007, Baraquet *et al.* 2015), we could not determine if this is the case here with only these data. Conversely, the pulsatile character of the note emitted by *M. alipioi* promptly distinguishes *Macrogenioglottus* from the pulsed note found in *Odontoprynus* and *Proceratophrys* species (Nascimento *et al.* 2019 and references therein, Magalhães *et al.* 2020, Mira-Mendes *et al.* 2020 and references therein, Simões *et al.* 2020, Rosset *et al.* 2021, Santana *et al.* 2021, Moroti *et al.* 2022). The release call was also similar to that described by Mira-Mendes *et al.* (2020), with the spectral and temporal parameters overlap (dominant frequency 387.60–559.90 Hz against 430.7 Hz in our sample and duration of the call of 0.032–0.314 s against 0.2–0.3 s in our sample) also suggesting that they belong to the same nominal taxon.

Larval Development

When Abravaya and Jackson (1978) described the larval external morphology of *Macrogenioglottus alipioi,* they made only a brief comparison with some species of *Odontophrynus*. In addition, Lisboa *et al.* (2011) reported some differences in relation to the population studied by Abravaya and Jackson but did not discuss it in the context of the family Odontophrynidae. Ten of the 11 species of *Odontophrynus* have their larvae described (Nascimento *et al.* 2013 and references therein, González *et al.* 2014, Menegucci *et al.* 2016, Costa *et al.* 2017, Rocha *et al.* 2017, Santos *et al.* 2017a, Moroti *et al.* 2022). In *Proceratophrys,* on the other hand, for 21 of the 42 known species the larvae have been described (Provete *et al.*

2017 and references therein, Santos *et al.* 2017b, Dias *et al.* 2018, 2019).

The odontophrynid tadpoles have a slightly depressive and ovoid body in dorsal view. The average total length ranges from 33 mm in *Proceratophrys* (stages 34–38), 54 mm in *Odontophrynus* (stages 36–38), and up to 58 mm in *Macrogenioglottus* (Stage 35). *Macrogenioglottus* also presented a much more robust body than the other genera (i.e., larger body size, for example, in relation to the length of the eyes and the oral disc). The nostrils of *Macrogenioglottus* are circular while in *Odontophrynus* they may also be oval/elliptical (with a small cutaneous extension on its medial margin in *O. occidentalis* (Berg, 1896), *O. lavillai* Cei, 1985, *O. maisuma* Rosset, 2008, and *O. monachus* Caramaschi and Napoli, 2012; Lavilla and Srocchi 1991; Grenat *et al.* 2009, Gonzaléz *et al.* 2014 Menegucci *et al.* 2016); in some *Proceratophrys* species it also can be reniform [e.g., *P. appendiculata* (Günther, 1873), *P. bigibbosa* (Peters, 1872), *P. dibernardoi* Brandão, Caramaschi, Vaz-Silva, and Campos, 2013, and *P. renalis;* Nascimento *et al.* 2010, Dias *et al.* 2014, 2018, Santos *et al.* 2017a]. The oral disc is usually surrounded by a single row of marginal papillae (a double row in the lower or lateral labium can be observed in *O. maisuma,* and *O. occidentalis;* Cei 1987, Borteiro *et al.* 2010). The labial tooth row formula is 2(2)/3(1), but may occur 2/3(1) [e.g., *O. carvalhoi*, *P. appendiculata, P. izecksohni* Dias, Amaro, Carvalho-e-Silva, and Rodrigues, 2013, and *P. tupinamba* Prado and Pombal, 2008; Caramaschi 1979, Fatorelli *et al.* 2010, Dias *et al.* 2014) with individual variations, 2(2)/3, 2/3(1), and 2/3 in *O. americanus* (Duméril and Bibron, 1841) and *O. maisuma;* Fernández and Fernández 1921, Echeverría and Montanelli 1992 (1995), Borteiro *et al.* 2010].

The knowledge about external postembryonic development is virtually absent in the family Odontophrynidae, with information only for *Odontophrynus cordobae* Martino and Sinsch, 2002 (Grenat *et al.* 2011). In general, the development phases of *O. cordobae* are quite similar to those of *M. alipioi*. However, some important events seem to occur later in *O. corbobae*. For example, at Stage 25, *M. alipioi* has the mouthparts already fully formed while in *O. cordobae* only the jaws sheaths and the first two tooth rows are present. The tadpole acquires its larger size at Stage 39 in *M. alipioi*, while in *O. cordobae* it occurs later at Stage 41. Lastly, the major modifications of metamorphosis occur at Stage 43 in *O. cordobae*, while in *M. alipioi* they occur at stages 41–42. Before assuming that these differences reflect interspecific variation, we must consider that the larval series used by Grenat *et al.* (2011) came from captive bred specimens and were reared in an artificial environment, which may influence the time of development of the species in comparison to natural population (see Sheil *et al.* 2014).

In most tadpoles, the larval growth that occurs until the onset of metamorphosis follows exponentially on a sigmoid curve (Di Cerbo and Biancardi 2010). This phase corresponds to a period of maximum growth and minimum development (Altig and McDiarmid 1999, Grosjean 2005). In *Macrogenioglotttus alipioi* this phase of almost gradual somatic growth occurs until Stage 39, where the larva reaches the maximum total length. In *O. cordobae*, as said before, this peak occurs a little later at Stage 41. In the majority of anuran species this peak occurs between these two stages [e.g., *Bokermanohyla circundata* (Cope, 1871) - Mongin and Carvalho-e-Silva 2013; *Phasmahyla cruzi* Carvalho-e-Silva, Silva, and Carvalho-e-Silva, 2009 - Costa *et al.* 2010; *P. guttata* (Lutz, 1924) - Costa and Carvalho-e-Silva 2008; *Physalaemus biligonigerus* (Cope, 1861) - Chuliver and Fabrezi, 2019], but we can find species that this event take place earlier [e.g., *Chiasmocleis lacrimae* Peloso, Sturaro, Forlani, Gaucher, Motta, and Wheeler, 2014, Stage 38; Cordioli *et al.* 2019; *Dermatonotus muelleri* (Boettger, 1885), Stage 37; Fabrezi *et al.* 2012; and *Megaelosia goeldii* (Baumann, 1912), Stage 38; Silva *et al.* 2018].

At Stage 25 the mouthparts of *M. alipioi* is already fully formed, as the labial tooth rows reached their definitive number, like most species with a 2/3 tooth row pattern (Gosner and Black 1954, Sedra and Michael 1961, Tubbs *et al.* 1993, Gómez *et al.* 2016). Although the pigmentation of the jaw sheaths is still limited to their edges, they are completed at the next Stage. The first sign of degeneration of larval mouthparts is the loss of labial teeth. In *Dryophytes chrysoscelis* (Cope, 1880), Thibaudeau and Altig (1988) noted that the loss of labial teeth seems to occur haphazardly in all rows; however, in this species the P3 row is absent well before other rows, exactly the last labial teeth row to arise in early postembryonic development. These findings suggested the disappearance could occur in the reverse order of appearance. Our results for *M. alipioi* were not in agreement with this suggestion, since P3 was at the beginning of degeneration when there were only traces of A1, A2, P1 and P2.

Downie *et al.* (2004) found two patterns of tail loss during metamorphosis of ten anuran species: (1) during the first day, the tail reduction is dramatic (to less than 60% of the maximum), then slower over the final stages; and (2) the tail remains at over 80% of its full length for the first day after forelimb emergence, with variable rates of reduction thereafter. In all these cases, tail retention during the early part of metamorphosis was associated with remaining in the water and rapid tail loss with early emergence from the water. Despite the absence of data on developmental time, *Macrogenioglottus alipioi* seems to fit on the first pattern, from Stage 40 there is an abrupt decrease in total length, mainly due to tail atrophy, although body length also decreases during this period. The species left the water soon after forelimb emergence. At the end of the metamorphosis, the snout–vent length is equivalent to the tadpole total length at stages 26–27 (~18 mm) which indicates that substantial post-metamorphic growth until adulthood will occur (~70–100 mm).

The emergence of the forelimbs is usually pointed to as the initial event of the metamorphic climax (Etkin 1936, Gosner 1960). However, according to Hall *et al.* (1997), the abrupt decrease in tail and body sizes may indicate the onset of the metamorphic climax if it occurs clearly before the emergence of the forelimbs. In *Macrogenioglottus alipioi,* the reduction in size of the tadpoles, which starts at Stage 40, was the event that preceded all typical changes of the beginning of metamorphic climax, suggesting the initial sign of metamorphosis, similarly to what occurs in *Odontophrynus cordobae* (Grenat *et al.* 2011) and quite different from other species, such as *Dermatonotus muelleri,* in which body size increases until the emergence of the forelimbs (Fabrezi *et al.* 2012). These facts indicate that the initial event and the sequence of changes are variable among anurans (Fabrezi *et al.* 2012) and corroborate the model proposed by Smith-Gill and Berven (1979), which suggests that larval growth and development are decoupled events.

Macrogenioglottus has an interesting taxonomic history. This genus has been already included in its own family (Macrogenioglottidae; Reig 1972) and has been also considered a junior synonym of *Odontophrynus* (Lynch 1971). Despite the scarcity of data on larval development in Odontophrynidae, the peculiarity of some larval traits, such as the larger size and robustness of the larva at similar developmental stages, and mainly on call characteristic, as the nature pulsatile of the note, pointed out herein supports the taxonomic distinction of *Macrogenioglottus* evidenced previously by molecular data (Amaro *et al.* 2009, Pyron and Wiens 2011, Teixeira-Junior *et al.* 2012).

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Appendix I. *Specimens examined of* Macrogenioglottus alipioi *from norteastern Brazil. Localities (Alagoas state): MC, Mata do Catolé, Maceió; EEM, Estação Ecológica de Murici, Murici.*

MHNUFAL No.	Stage	*N*	Locality	MHNUFAL No.	Stage	*N*	Locality
10982	clutch	-	MC	8432	36	1	MC
9343	25	4	MC	9059	36	1	MC
11276	25	1	MC	10166	36	1	MC
11276	26	1	MC	10987	37	3	MC
11084	26	4	MC	11049	37	1	MC
10165	27	2	MC	11038	38	2	MC
9343	27	1	MC	10165	38	1	MC
11084	27	1	MC	11049	39	1	MC
10811	27	1	MC	11049	40	3	MC
10811	28	1	MC	10985	40	1	MC
9059	28	1	MC	3784	40	1	MC
11276	28	2	MC	10811	41	4	MC
8435	29	1	MC	8430	42	1	MC
10811	29	1	MC	9788	42	4	MC
10166	30	1	MC	10166	43	2	MC
10811	30	3	MC	10985	43	1	MC
10811	31	3	MC	9059	43	2	MC
10166	31	2	MC	2771	44	1	MC
9059	32	1	MC	2770	45	1	MC
10987	32	2	MC	10940	adult male	-	MC
8430	33	1	MC	10941	adult female	-	MC
10165	33	1	MC	8165	adult male	-	MC
10987	33	1	MC	8166	adult male	-	MC
10811	33	1	MC	4948	adult male	-	MC
10811	34	1	MC	5493	adult male	-	MC
8430	34	1	MC	5494	adult male	-	MC
10166	34	1	MC	10942	adult male	-	MC
8432	34	1	MC	5483	adult male	-	MC
9345	34	1	MC	12074	adult female	-	EEM
8433	35	1	MC	12075	adult male	-	EEM
11038	35	1	MC	12076	adult male	-	EEM
8432	35	3	MC				

Appendix II. *Measurements (in mm) of* Macrogenioglottus alipioi *tadpoles. Data presented as mean ± SD. Stages are according to Gosner (1960).*

Measurements	**Stage 25 (*N* = 5)**	**Stage 26 (*N* = 5)**	**Stage 27 (*N* = 5)**	**Stage 28 (*N* = 4)**	**Stage 29 (*N* = 2)**	**Stage 30 (*N* = 4)**	**Stage 31 (*N* = 5)**	**Stage 32 (*N* = 3)**	**Stage 33 (*N* = 4)**	**Stage 34 (*N* = 4)**	**Stage 35 (*N* = 5)**
Total length	14.4 ± 1.4	25.3 ± 1.9	26.9 ± 5.3	33.7 ± 6.1	39.7 ± 4.6	35.5 ± 2.5	41.9 ± 2.7	49.5 ± 1.1	45.6 ± 2.7	48.4 ± 7.8	49.9 ± 7.1
Body length	7.0 ± 0.2	11.8 ± 0.6	13.2 ± 3.4	15.1 ± 3.9	18.1 ± 0.9	19.2 ± 1.7	19.4 ± 1.6	22.4 ± 0.2	21.2 ± 1.8	21.0 ± 4.7	22.4 ± 3.2
Tail length	7.5 ± 1.3	13.5 ± 1.7	13.7 ± 2.2	18.5 ± 2.9	21.6 ± 3.6	16.3 ± 1.2	22.5 ± 3.4	27.1 ± 1.2	24.3 ± 2.2	274 ± 3.4	27.5 ± 4.2
Tail muscle height	1.7 ± 0.1	2.7 ± 0.2	3.3 ± 0.6	3.8 ± 0.8	4.7 ± 0.5	5.0 ± 0.3	5.6 ± 0.3	5.3 ± 0.3	5.4 ± 0.8	5.1 ± 1.0	6.0 ± 0.5
Maximum tail height	4.4 ± 0.2	7.2 ± 0.5	7.7 ± 1.8	8.3 ± 1.9	10.3 ± 1.2	10.4 ± 1.2	10.6 ± 0.4	10.7 ± 2.1	10.6 ± 0.7	11.8 ± 1.3	11.8 ± 2.8
Maximun body height	3.9 ± 0.2	7.4 ± 0.8	7.6 ± 1.6	8.2 ± 2.3	10.6 ± 0.6	10.6 ± 1.0	9.9 ± 1.3	10.6 ± 0.9	10.2 ± 1.9	10.6 ± 3.8	11.8 ± 2.1
Maximum dorsal fin height	1.8 ± 0.1	2.7 ± 0.2	2.7 ± 0.8	3.1 ± 0.6	4.1 ± 0.5	3.9 ± 0.4	4.5 ± 0.4	4.6 ± 0.9	4.6 ± 0.8	5.1 ± 0.8	4.7 ± 1.8
Maximum ventral fin height	1.3 ± 0.1	2.1 ± 0.1	2.1 ± 0.7	2.4 ± ±**0.7**	3.1 ± 0.1	3.0 ± 0.4	3.4 ± 0.4	3.6 ± 0.6	3.4 ± 0.6	3.5 ± 0.8	3.3 ± 1.4
Snout–nostril distance	0.8 ± 0.0	1.7 ± 0.2	1.4 ± 0.5	1.8 ± 0.2	1.8 ± 0.3	1.9 ± 0.1	2.0 ± 0.2	3.0 ± 0.1	2.4 ± 0.5	2.9 ± 0.4	2.8 ± 0.1
Eye–nostril distance	0.7 ± 0.1	1.5 ± 0.2	1.2 ± 0.3	1.6 ± 0.4	2.0 ± 0.4	2.2 ± 0.3	2.2 ± 0.2	2.3 ± 0.5	2.5 ± 0.4	2.1 ± 0.2	2.3 ± 0.6
Eye diameter	0.8 ± 0.1	1.3 ± 0.1	1.4 ± 0.4	1.7 ± 0.4	2.0 ± 0.2	1.8 ± 0.1	1.9 ± 0.2	2.5 ± 0.1	2.0 ± 0.3	2.4 ± 0.5	2.5 ± 0.3
Intranarial distance	0.7 ± 0.0	1.0 ± 0.1	1.4 ± 0.3	1.0 ± 0.2	1.5 ± 0.2	1.5 ± 0.1	1.6 ± 0.1	1.8 ± 0.3	1.6 ± 0.1	1.8 ± 0.8	1.6 ± 0.4
Intraocular distance	1.6 ± 0.1	2.8 ± 0.3	2.9 ± 0.6	3.0 ± 0.9	4.3 ± 0.5	3.9 ± 0.7	4.4 ± 0.4	5.0 ± 0.6	4.8 ± 0.6	4.6 ± 1.4	4.6 ± 1.3
Tail muscle width	1.0 ± 0.1	1.8 ± 0.2	2.3 ± 0.3	2.6 ± 0.5	3.4 ± 0.1	3.5 ± 0.5	3.7 ± 0.1	4.6 ± 0.6	4.0 ± 0.4	4.1 ± 0.6	4.4 ± 0.4
Maximun body width	6.2 ± 0.3	9.8 ± 0.7	9.5 ± 2.0	11.2 ± 2.4	12.6 ± 1.6	12.9 ± 1.9	12.9 ± 0.8	14.3 ± 0.6	14.7 ± 1.4	15.1 ± 4.5	15.8 ± 3.2
Oral disc width	2.1 ± 0.2	3.1 ± 0.2	3.1 ± 0.9	3.8 ± 1.0	4.1 ± 0.4	4.3 ± 0.3	4.8 ± 0.4	6.4 ± 0.3	4.9 ± 0.4	4.7 ± 0.4	5.0 ± 0.5

Appendix II. *Continued.*

Measurements	Stage 36 (*N* = 2)	Stage 37 (*N* = 4)	Stage 38 (*N* = 3)	Stage 39 (*N* = 1)	Stage 40 (*N* = 5)	Stage 41 (*N* = 4)	Stage 42 (*N* = 5)	Stage 43 (*N* = 5)	Stage 44 (*N* = 1)	Stage 45 (*N* = 1)
Total length	58.8 ± 1.2	53.9 ± 8.4	59.8 ± 10.5	69.9	65.1 ± 11.3	61.7 ± 7.3	41.7 ± 3.1	37.5 ± 7.0	18.6	17.9
Body length	24.9 ± 1.1	25.6 ± 4.3	26.3 ± 5.7	32.3	28.0 ± 4.6	25.4 ± 2.2	19.6 ± 1.8	25.0 ± 3.4	18.6	17.9
Tail length	34.0 ± 2.3	28.3 ± 4.1	33.5 ± 4.9	37.7	37.1 ± 6.7	36.5 ± 6.1	22.1 ± 4.9	12.5 ± 6.8	1.1	1.0
Tail muscle height	6.0 ± 0.4	5.8 ± 0.9	6.5 ± 1.3	8.1	6.8 ± 1.2	5.9 ± 0.7	4.5 ± 0.4	5.8 ± 1.0	-	-
Maximum tail height	13.1 ± 1.3	11.8 ± 2.8	15.1 ± 4.8	18.1	15.8 ± 2.3	13.4 ± 0.8	7.1 ± 1.3	7.1 ± 2.1	-	-
Maximun body height	12.2 ± 0.9	13.5 ± 3.4	12.7 ± 3.9	19.6	14.6 ± 3.6	12.5 ± 1.4	8.2 ± 1.0	9.4 ± 1.3	7.3	6.0
Maximum dorsal fin height	5.9 ± 0.3	5.2 ± 1.5	6.7 ± 1.8	7.9	7.2 ± 1.0	6.1 ± 0.5	2.8 ± 0.5	1.6 ± 1.1	-	-
Maximum ventral fin height	3.7 ± 0.5	3.6 ± 0.7	3.7 ± 0.7	6.5	4.8 ± 0.9	4.3 ± 0.4	1.6 ± 0.4	0.9 ± 0.6	-	-
Snout–nostril distance	2.9 ± 0.2	3.3 ± 0.5	3.9 ± 1.0	4.4	3.2 ± 0.7	3.0 ± 0.9	1.1 ± 0.2	1.3 ± 0.2	0.4	0.2
Eye–nostril distance	2.9 ± 0.2	2.5 ± 0.4	2.9 ± 0.4	2.7	2.6 ± 0.5	2.4 ± 0.3	2.1 ± 0.2	1.9 ± 0.3	1.7	1.4
Eye diameter	2.3 ± 0.0	2.8 ± 0.5	2.8 ± 0.5	3.3	3.2 ± 0.4	3.3 ± 0.0	2.4 ± 0.2	2.5 ± 0.5	2.2	2.1
Intranarial distance	1.9 ± 0.1	1.8 ± 0.2	2.0 ± 0.2	2.3	1.8 ± 0.4	1.7 ± 0.2	1.3 ± 0.1	1.6 ± 0.2	1.5	1.1
Intraocular distance	5.3 ± 0.2	5.2 ± 1.3	5.5 ± 1.9	6.2	4.6 ± 1.0	8.1 ± 0.1	6.4 ± 0.2	7.9 ± 0.7	7.1	6.7
Tail muscle width	4.1 ± 0.3	4.4 ± 0.7	5.4 ± 1.3	6.5	5.9 ± 1.0	5.0 ± 0.4	3.9 ± 0.4	5.2 ± 0.9	-	-
Maximun body width	16.7 ± 1.2	17.5 ± 3.4	18.5 ± 3.9	24.7	20.6 ± 4.2	18.0 ± 1.7	11.3 ± 1.4	12.4 ± 1.6	8.8	9.1
Oral disc width	5.6 ± 0.1	6.5 ± 1.0	6.7 ± 1.1	8.3	6.3 ± 1.3	6.1 ± 0.6	4.9 ± 0.5	7.0 ± 1.8	7.0	7.3

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Short Communication

Ecological observations of *Chiropterotriton chiropterus* (Caudata: Plethodontidae), an endangered salamander from Mexico

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Keywords: Canopy cover, Conservation, Environmental characteristics, Montane cloud forests, Periods of activity.

Palavras-chave: Características ambientais, Cobertura do dossel, Conservação, Florestas de neblina, Habitat, Períodos de atividade.

Chiropterotriton chiropterus (Cope, 1863) is a species of plethodontid salamander, endemic to Mexico, listed as Critically Endangered by the IUCN (Parra-Olea *et al.* 2008, 2020, IUCN 2021) and under special protection by national regulation NOM-059 (SEMARNAT 2010). Its known distribution extends from the municipality of Huatusco in northeast Veracruz, the type locality, southward to the northern part of the Sierra Madre de Oaxaca, with a reported elevational range of 1400 to 2170 m a.s.l. (Parra-Olea *et al.* 2020). In Oaxaca, there are currently 79 records of *C. chiropterus* observed between 1958 and 2020 (Parra-Olea *et al.* 2020, GBIF 2022) although available ecological information for the species is scarce. Habitat loss, emerging diseases, land use change, and the deterioration of its microhabitat due to the removal of bromeliads for cultural purposes have been proposed as its main threats (IUCN 2021).

We report ecological data for six new records of *C. chiropterus* from the community of "La Esperanza" in the municipality of Santiago Comaltepec (17°37'41.88" N, 96°22'5.88" W, Datum WGS84), in the physiographic subprovince of the Sierra Madre de Oaxaca (Ortiz-Pérez *et al.* 2004). This locality is within the cultural region of La Chinantla, considered to be one of the most complex in Mexico, mainly due to its orography, diversity of climates, and types of ecosystems including the montane cloud forest that stands out for its biodiversity and endemism (Gual-Díaz and Rendón-Correa 2014,

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Simón-Salvador *et al.* 2021, Tobar-Suárez *et al.* 2021). Temperatures at the site vary from 21.6°C to 28.2°C with an average rainfall of 10.5 mm to 211 mm per month during the dry season (December to May). During the wet season, temperatures vary from 11.9°C to 19.1°C with an average rainfall of 201 mm to 481 mm per month (June to November) (Prediction of Worldwide Energy Resources 2022). All reported organisms were found active at night during the dry season (Table 1). The sex and age were determined according to size and presence or absence of mental glands (Petranka 1998).

We observed the first specimen (Id1), an adult male (Figure 1A), near a permanent stream (17°35'25" N, 96°23'33" W; Datum WGS84). It was on a leaf of *Palicourea padifolia* (Humb. & Bonpl. ex Roem. and Schult.) C.M. Taylor and Lorence a native herbaceous plant at a height of 1 m from the ground and at a distance of 80 cm from the water. The stream had the following characteristics: riverbed, 70 m long and 1.76 m wide, obtained with a flexometer (Truper TFC-50), and speed of the water, 0.7 m/s, measured with a digital flowatch (JDC Electronics) (Figure 1B).

The second specimen, an active juvenile at the same stream (Id2), was observed moving on the leaf of a fern *Diplazium* sp. Sw. at a height of 40 cm from the ground (Figure 1C). It was found at 1.20 m from the highway (17°35'25" N, 96°23'33" W, Datum WGS84) (Figure 1D). At another stream (17°35'20" N, 96°23'45" W, Datum WGS84) we observed two more juvenile specimens (Id3 and Id4) and two adults (Id5 and Id6). The first juvenile (Id3) was on a native herbaceous plant, *Miconia* sp. Ruiz and Pav., at a height of 35 cm from the ground and 86 cm from the stream. The second juvenile (Id4) was on a leaf of a fern *Diplazium* sp. above the stream at 1 m from the water. The first adult was a female (Id5) positioned on a mossy log above the stream at a height of 35 cm from the water. Finally, the second adult was a male (Id6) found climbing the stem of a leaf of *Miconia* sp. above the stream at a height of 1.5 m from the water.

Table 1. Environmental and morphometric data for the six individuals of *Chiropterotriton chiropterus* found in La Esperanza. Relative Humidity (RH), Dew Point (DP), Barometric Pressure (BARO), and vapor pressure deficit (VPD) are listed along with other environmental variables.

Individual	Life stage/ Sex	Date	Time	Elevation (m a.s.l.)	Mass (g)	SVL (mm)	Tail length (mm)	Total length (mm)	Body temperature (°C)	Substrate temperature (°C)	Ambient temperature (°C)	RH (%)	DP (°C)	BARO (InHg)	Wind speed (m/s)	Canopy cover (%)	VPD (kPa)
Id1	Adult male	17 Feb 2022	20:50	1890	1.0	32.0	31.0	63.0	11.6	11.8	11.9	82.5	9.6	23.8	0.4	93.0	24.53
Id2	Juvenile	18 Feb 2022	22:15	1825	0.3	24.0	20.0	44.0	9.8	10.0	10.6	86.7	9.4	24.0	0.3	87.4	17.44
Id3	Juvenile	30 Apr 2022	23:36	1986	0.5	27.0	24.4	51.4	13.8	13.6	15.6	81.8	12.5	23.8	0.3	96.2	33.08
Id4	Juvenile	30 Apr 2022	23:46	1988	0.9	28.8	30.0	58.8	12.8	12.6	18.0	71.7	12.5	23.8	0	95.9	58.41
Id5	Adult female	01 May 2022	00:05	2027	1.9	32.8	40.0	72.8	12.6	12.5	18.8	71.7	12.5	23.8	0	97.0	39.67
Id6	Adult male	01 May 2022	01:20	2026	2.3	41.0	51.0	92.0	14.3	14.2	20.7	74.0	15.0	23.7	0.1	97.8	36.45

Figure 1. (**A**) Adult male of *Chiropterotriton chiropterus* perching on a plant (*Palicourea padifolia*) over a perennial stream. (**B**) Perennial stream in the community of La Esperanza, Oaxaca**.** (**C**) Juvenile of *Chiropterotriton chiropterus* climbing on a plant (*Miconia* sp.) near the highway. (**D**) Federal highway 175 that crosses through La Esperanza, Oaxaca. Photographs by Carlos A. Flores (A and B) and Medardo Arreortua (C and D).

The environmental characteristics recorded on the site at the time of each encounter were: environmental temperature (TEMP), relative humidity (RH), dew point (DP), barometric pressure (BARO), and wind speed. Measurements of these variables were taken using a portable meteorological meter (Kestrel 3500 Pocket weather meters). Canopy cover data were taken using a concave mirror densiometer (Lemmon 1956), and the vapor pressure deficit was calculated using the formula VPD = [(100 - HR).SVP] / 1000, where SVP is saturated vapor pressure (Ludwig 1945).

From these observations we conclude the following: (1) canopy cover plays an important role for this species. All individuals in this study were found at sites with 87% or greater canopy cover. Tree composition influences the presence of salamanders because it provides them with favorable microclimates to take refuge and feed (McEntire 2016, Aguilar-López *et al.* 2017). (2) As expected, as the dry season advances, the drying capacity of the air increases as reflected in the VPD measurements. This variable may influence the salamanders' use of microhabitat and thus periods of activity because plethodontid salamanders depend exclusively on moisture in their skin for gas exchange (Gatz *et al.* 1975, Feder and Londos 1984). We observed more salamanders near the water on the driest nights (high values of VPD). Despite the high values of VPD, resistance to dehydration of this species may increase in high-temperature conditions (Table 1), which has been observed in other species of plethodontids (Riddell and Sears 2015). (3) Although this species has been associated with bromeliads (McEntire 2016, Parra-Olea *et al.* 2020), we found all individuals on top of leaves, branches, or trunks not higher than 0.76 m above the ground. Only one individual (Id2) was away from water. However, this site had the highest percentage of humidity, the lowest temperature, and the lowest VPD values in relation to the sites where the other five individuals were found close to water (Table 1). These observations suggest that periods of activity of this species seem to correlate with low-temperature nights, when they are active for some hours before retreating to their shelters in the canopy and bromeliads to escape adverse conditions during the day (Ruano-Fajardo *et al.* 2014, Riddell and Sears 2015, McEntire 2016).

Currently, montane cloud forests are one of the most threatened ecosystems worldwide, mainly due to deforestation, climate change, and land use change (Toledo-Aceves *et al.* 2011). The physiographic subprovince of the Sierra Madre de Oaxaca has some of the best-preserved areas of montane cloud forest in Mexico, although logging for different purposes is still a frequent threat in some areas (Gual-Díaz and Rendón-Correa 2014). Communal efforts to protect montane cloud forests play a major role in the conservation of optimal habitat for native herpetofauna (Simón-Salvador *et al.* 2021, Tobar-Suárez *et al.* 2021). The community of La Esperanza conserves 4421 ha of mostly montane cloud forest by the Indigenous and Community Conservation Areas (ICCA's) modality (CONANP 2020). This conservation measure protects the existence of areas where many endemic amphibians find the necessary resources for their survival, such as perennial streams, connected habitats, forests with good canopy cover, and favorable undergrowth conditions. However, La Esperanza is crossed by a federal highway that runs from Oaxaca City to Tuxtepec (Figure 1D). We have observed people that use this highway extracting herbaceous plants from the roadside, dumping garbage in the forest and streams, and abandoning domestic animals like cats and dogs which become feral, threatening small vertebrates like the herpetofauna. These activities pose notable threats to the native amphibians of La Esperanza and must be addressed to support the admirable conservation efforts of the community.

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Short Communication

Ocular anomalies in two species of *Osteocephalus* (Anura: Hylidae) from the Amazonian region of northern Brazil

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Palavras-chave: Amphibia, Dados Deficientes, Heterocromia, Neotrópicos, Olho preto.

Anomalies may affect anurans during their initial phase of development, as well as by extrinsic factors that alter organs or structures that were formed correctly (Meteyer 2000, Henle *et al.* 2017a), such as exposure to chemical pollutants or UV-radiation (Lannoo 2009, Agostini *et al.* 2013), parasitic or virulent infections (Kiesecker 2002), and attacks thwarted by predators (Borges *et al.* 2019); in some cases, these factors may interact (Toledo and Ribeiro 2010, Bionda *et al.* 2012, Henle *et al.* 2017a). In wild populations not exposed to external contaminants, the occurrence of anomalies typically does not exceed 5% (Ouellet 2000, Blaustein and Johnson 2003). Studies around the world indicate that limb anomalies are prevalent in anuran populations (e.g., Henle *et al.* 2017a, b, Pedroso-Santos *et al.* 2020, Souza *et al.* 2021). In Brazil, for instance, a recent review of anuran anomalies showed that the majority of records is anecdotal, and their consequences on individual survival and reproduction, as well as on larger population processes, are underestimated (Souza *et al.* 2021). Despite this, anecdotal observations related to anomalies in poorly known species add relevant information for future ecological studies. This condition may affect survival and ultimately increase our knowledge of this phenotypic variation.

Regarding the nomenclature of anuran anomalies, Henle *et al.* (2017b) argued that the terms "malformations" and "deformities" may be outdated because many studies erroneously use these terms to detail whether they are external or osteological. Therefore, the term "anomalies" has been most frequently used to designate such non-typical phenotypes in a generalized way (Henle *et al.* 2017a, b). To specifically designate anomalies occurring in the eye, several terms have been used in the

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literature, such as black-eyedness, heterochromia, perforated eye, opacity of the eye, and microphthalmia (see Ingle 1976, Toledo and Ribeiro 2010, Pedroso-Santos *et al.* 2020, Souza *et al.* 2021). All of these terms can be placed under the general term of ocular anomaly.

In this paper, we report cases of black-eyedness and heterochromia (according to Henle *et al.* 2017b) in the arboreal hylids *Osteocephalus* sp. and *O. oophagus* Jungfer and Schiesari, 1995, respectively, from a well-preserved forested area in the eastern Amazonian rainforest. Field observations were made within at the Reserva Extrativista Municipal Beija-Flor Brilho de Fogo (REMBFBF) (0.7918° N, 51.9783° W), municipality of Pedra Branca do Amapari, Amapá state, Brazil. This area is characterized by dense forest with sandy and clayey soil, which has a high degree of acidity and low fertility (Drummond *et al.* 2008, Lima 2008). Both species are known to occur in this area and are easily distinguished from the other co-occurring congeneric species (Faivovich *et al.* 2005, Dewynter *et al.* 2016).

The first observation was made on 17 October 2020 at about 19:30 h. An individual of *Osteocephalus* sp. was found perched on a branch approximately 1.50 m above a bank of the Água Fria River (0.7918° N, 51.9784° W; Datum WGS84; 110 m a.s.l.). We noticed that its left eye had an abnormal color, and apparently its left eyeball was enlarged (Figure 1A); following Henle *et al.* (2017b), this condition is known as "black-eyedness." It is a normal phenotype in some anuran species (e.g., dendrobatids) [e.g., caused by the lack of iridophores, a reduction of xanthophores, and a predominance of melanophores (Dubois 1976)]. We observed an unusual behavior that might be related to this ocular anomaly. When a researcher standing behind the frog perched on a branch moved a hand parallel to the left side of the frog (with the normal eye), it tended to change its position. When this movement was done on the right, with the black eye, the individual did not react, suggesting some degree of loss of vision. The absence of vision or low vision in anurans may be detrimental, possibly causing an inability to perceive potential predators. This individual of *Osteocephalus* sp. was collected and deposited in the Herpetological Collection of the Universidade Federal do Amapá (CECCAMPOS 3594).

The second observation occurred on 25 March 2022 at about 11:30 h. We found an individual of *O. oophagus* perched on a branch approximately 1 m above the ground (0.7955° N, 52.2602° W; Datum WGS84; 190 m a.s.l.). This individual had different iris colors in each eye. The right eye was gray with black rays, whereas the left eye was the usual gold with black rays (Figure 1B). According to Henle *et al.* (2017b), this condition is referred to as heterochromia. Heterochromia may be related to genetic factors in animals (Bond 1913), and this anomaly is characterized by the difference in pigmentation between the eyes. Only one eye has the typical pigmentation of the species, but both eyes have normal characteristics such as iris size and rays (Henle *et al.* 2017b).

Our reports are anecdotal but add information about the natural history and phenotypic variation of these two species of *Osteocephalus.* Cases of ocular anomalies are rarely described in the literature (e.g., Ramalho *et al.* 2017, Sousa and Costa-Campos 2017, Brassaloti and Bertoluci 2018, Mônico *et al.* 2019, Pedroso-Santos *et al.* 2020, Souza *et al.* 2021), and to our knowledge, no reports in the literature associate black-eyedness with blindness. Black-eyedness in anurans is related to habitat disruption (e.g., Guerra and Aráoz 2016, Gurushankara *et al.* 2007). However, our observations come from a well-preserved forested area, in which there are no reports of anomalies in animals or of environment degradation. Although ocular anomalies have been described in non-contaminated habitats (e.g., Eaton *et al.* 2004, Ramalho *et al.* 2017), their causes are not fully understood. Further studies on the origins of anomalies and their consequences are needed. We encourage researchers to describe ocular anomalies in future studies of anurans.

Figure 1. Specimens of *Osteocephalus* with ocular anomalies at the Reserva Extrativista Municipal Beija-Flor Brilho de Fogo, municipality of Pedra Branca do Amapari, Amapá state, Brazil. **(A)** Black-eyedness in *Osteocephalus* sp. (CECCAMPOS 3594), and **(B)** heterochromia in *O. oophagus.*

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Short Communication

Xanthism in the Leaf-frog *Phyllomedusa vaillantii* (Anura: Hylidae)

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Keywords: Amphibians, Chromatic abnormality, Eastern Amazon, Neotropics, Phyllomedusinae.

Palavras-chave: Amazônia Oriental, Anfíbios, Anormalidade cromática, Neotrópicos, Phyllomedusinae.

Different colors and patterns play an important role in the life history of anurans. Cryptic colors may help camouflage prey, whereas aposematic colors may alert potential predators to avoid individuals (Pedroso-Santos *et al.* 2022). Color anomalies are characterized by pigmentation abnormalities that are restricted to all or partof an animal's body. These anomalies are rare in most cases, especially in natural populations (Hoffman and Blouin 2000). Color anomalies have been observed in fishes (Lara-Mendoza and Guerra-Jiménez 2020), anurans (Pereira and Santos 2012, Tavares-Pinheiro *et al.* 2020), lizards (Sanches *et al.* 2019), snakes (Mendonça *et al.* 2020), birds (Camacho *et al.* 2022), and mammals (Talamoni *et al.* 2017). Among the most commonly recognized types of color anomalies are albinism, flavism, leucism, melanism, piebaldism, axanthism, and xanthism (Henle *et al.* 2017). Xanthism is a chromatic abnormality characterized by the predominant production of the purine base xanthine, an organic compound that gives the organism a yellowish coloration (Henle *et al.* 2017). In this study, xanthism is reported for the subfamily Phyllomedusinae for the first time.

Phyllomedusinae is a subfamily whose representatives are commonly known as monkey, leaf, or green frogs. *Phyllomedusa* Wagler, 1830 is widely distributed in the Neotropics and is the

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most speciose genus in the subfamily. (Frost 2022). *Phyllomedusa vaillantii* Boulenger, 1882, popularly known as White-lined Leaf Frog or the White-lined Monkey Frog, is a medium-sized nocturnal tree frog found in all Amazonian countries: French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil (Frost 2022). In the Amazon region of Brazil, it is found around temporary ponds in forested areas (Lima *et al.* 2012). Little variation in coloration has been observed within and between populations throughout Amazonia (e.g., Duellman 2005, Lima *et al.* 2012, Ouboter and Jairam 2012). In life, adults of *P. vaillantii* have a dorsal pattern that is uniform dark green with a sawtooth dorsolateral line of tubercles extending from behind the eye to the midbody, and a ventral surface that is pale grayish-orange with a white or cream spot on the chest (Duellman 1974, Lima *et al.* 2012, Smith *et al.* 2019).

We found an adult male *P. vaillantii* during a nocturnal search for amphibians and reptiles in primary forest near the right margin of the stream Água Fria in Reserva Extrativista Municipal Beija-Flor Brilho de Fogo, municipality of Pedra Branca do Amapari, state of Amapá, in eastern Amazonia. The individual (snout–vent length 54.4 mm) was collected by APF at the beginning of the rainy season on 24 March 2022, at 08:27 h, calling 1.45 m above ground on leaves in riparian vegetation (00°47'43.8" S, 52°15'36.4" W; 190 m a.s.l.). Sympatric amphibians included the hylids *Phyllomedusa bicolor* (Boddaert, 1772), *Callimedusa tomopterna* (Cope, 1868), *Boana geographica* (Spix, 1824), and *Dendropsophus* gr. *microcephalus.*

The individual collected was almost entirely yellow, including the head and limbs. The flanks and anterior parts of the hindlimbs were orange to red, and only the eyes, venter, anterior parts of the forelimbs, fingers, and adhesive discs were normal in coloration (see Figure 1 for a comparison between a normal-colored and a xanthic individual of *P. vaillantii*). The specimen was killed with lidocaine, fixed in 10% formalin, and preserved in 70% ethanol. It was deposited in the Herpetological Collection of Universidade Federal do Amapá, Macapá, Brazil. Its catalogue number is CECC 3819.

To our knowledge, our record of xanthism in *P. vaillantii* is the first reported case in anurans from the Neotropics, as well as for the genus *Phyllomedusa.* We hope our study will inspire future investigations on the frequency and possible causes of these unusual pigmentations, including whether these anomalies may affect survivorship and reproduction.

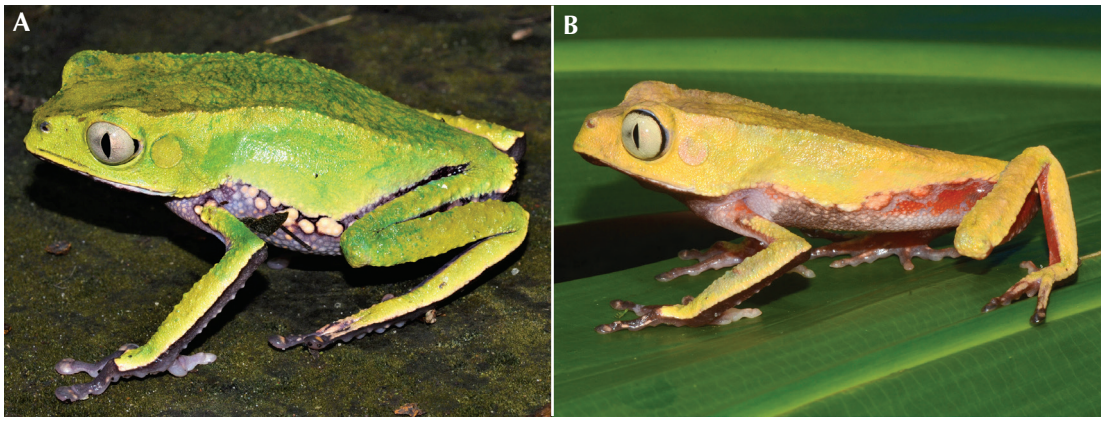

Figure 1. Comparative dorsolateral views of *Phyllomedusa vaillantii.* (**A**) Normal individual and (**B**) xanthic individual from Eastern Amazonia (CECC 3819).

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Short Communication

Cannibalism in *Telmatobius rubigo* (Anura: Telmatobiidae) and comments on seasonal variation of diet

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Keywords: Aquatic Andean Frog, Cannibalism, Central Andean Puna, Diet overlap, Stomach flushing, Threatened species.

Palabras claves: Canibalismo, Especie amenazada, Lavado de estómago, Puna Andina Central, Rana Acuática Andina, Sobreposición de dieta.

Palavras-chave: Canibalismo, Espécie ameaçada, Lavagem estomacal, Puna Andina Central, Rã-aquática-andina, Sobreposição de dieta.

The knowledge on natural history of the Aquatic Andean Frogs of the genus *Telmatobius* was increased in the last decade (Catenazzi *et al*. 2013, Lobos *et al.* 2016, 2018, Brunetti *et al.* 2017, Acosta *et al.* 2020, Gastón 2022, Sáez *et al.* 2022), particularly about feeding habits, diet and trophic ecology (Barrionuevo 2016, Watson *et al.* 2017, Lobos *et al.* 2018, 2021, Akmentins and Gastón 2020, Muñoz-Saravia *et al.* 2020, Abdenur-A *et al.* 2022). One shared characteristic of most *Telmatobius* species is that these frogs inhabit high-altitude Andean lotic and lentic aquatic systems, characterized by their simplified food webs (Lujan *et al.* 2013). Precise information on feeding habits could have direct and indirect implications for conserving one of the world's most threatened amphibian taxa (IUCN 2022).

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Telmatobius rubigo Barrionuevo and Baldo, 2009 is a fully aquatic frog inhabiting lotic endorheic systems between 3500 to 4300 m a.s.l. in the harsh arid environment of Central Andean Puna ecoregion of Jujuy province in northwestern Argentina (Barrionuevo and Abdala 2018, Gastón 2022). The Laguna de Los Pozuelos' Rusted Frog was assessed as vulnerable in the IUCN red list because it is threatened by the introduction of exotic predatory fishes (rainbow trout), mining, and poor water management (IUCN 2022).

In the present study, we report a case of cannibalism in *T. rubigo* and analyze the seasonal variation of the diet. Finally, we discussed the implications of our registers for the ecology and conservation of this threatened aquatic Andean frog.

Frog surveys were carried out once per month in August, September, and November 2021 in the locality of Santa Catalina, Argentina (21°56'58.2" S, 66°02'21.6" W; 3802 m a.s.l.), in

coincidence with the breeding events of the species during the dry season (Gastón 2022). The methodology indicated by Akmentins and Gastón (2020) was followed. Briefly, individuals were located by active search by visual encounter survey (Crump and Scott 1994) and captured manually, immediately then the stomach contents were obtained *in situ* by stomach flushing (Solé *et al.* 2005). Each frog was sexed and measured its snout–vent length (SVL) with a digital dial caliper (Mitutoyo Absolute Digimatic) to the nearest 0.1 mm and weighed with a portable digital scale (OHAUS) to the nearest 0.1 g. After stomach flushing, the individuals were returned to the same capture site.

The stomach contents were analyzed under a stereomicroscope and were identified as the lower taxonomic category as possible. For each item (prey category), number (*N*), volume (V), and occurrences (*F*) were calculated in percentage values. The volume for intact prey items was calculated according to the formula used by Dunham (1983) for a prolate spheroid: $V = 4\pi/3(\text{prey length}/2)(\text{prey width}/2)^2$.

For comparison of seasonal variation of the diet of *T. rubigo*, the data on stomach contents obtained in the same locality during the wet season from January to March 2020 (Akmentins and Gastón 2020) were used. The importance value of main dietary items for pooled stomachs was calculated with the *Ip* index of Biavati *et al.* (2004). The trophic niche breadth in dry and wet seasons was estimated using Levin's standardized index (Krebs 1989), and breadth niche values were interpreted according to Novakowski *et al.* (2008) as high (> 0.6), intermediate (0.4 to 0.6), or low (< 0.4). The degree of diet overlap between seasons was determined with the Morisita-Horn Index (Horn 1966) and values greater than 0.60 were considered significant diet overlap (Zaret and Rand 1971).

A total of 32 diet samples from both seasons were analyzed, representing acceptable prey sampled completeness for the species (Akmentins and Gastón 2020). For the dry season, 17 diet samples were obtained from three females and 15 males. Females had a SVL of 52.3 ± 3.8 mm (mean ± SD) and weighed 14.9 ± 2.6 g (mean ± SD). Males had a SVL of 46.8 ± 2.5 mm and weighed 10.3 ± 1.9 g. In the pooled stomach contents were found 149 prey items and a mean number of preys per stomach of 8.7 ± 4.7. For the wet season, 15 diet samples obtained from five females and 10 males were analyzed. Females had a SVL of 51.7 ± 8.9 mm and weighed 11.5 ± 7.4 g. Males had a SVL of 51.1 ± 5.1 mm and weighed 12.2 ± 4.7 g. In the pooled stomach contents were found 71 prey items and a mean number of preys per stomach of 4.7 ± 5.7.

Two cases of anurophagy were detected in the dry season. One tadpole of *T. rubigo* in a Gosner (1960) stage circa 30 was preyed on by an adult female (SVL 55.08 mm; weight 15.6 g) (Figure 1), and one undetermined tadpole was preyed on by an adult male (SVL 46.43 mm; weight 10.36 g). The confirmation of the cannibalism event was made based on external characteristics of the preyed tadpole (Figure 1), such as mouth position, oral disc, and arrangement of lateral line neuromasts (Barrionuevo and Baldo 2009). These characteristics of the tadpole of *T. rubigo* differ from other tadpoles of sympatric species as *Rhinella altiperuviana* (Gallardo, 1961), *Boana riojana* (Koslowsky, 1895), and *Pleurodema cinereum* (Cope, 1878) (pers. obs.).

Cannibalism and anurophagy were reported for other *Telmatobius* species (Allen 1922, Valencia *et al.* 1982, Wiens 1993, Barrionuevo 2015, Muñoz-Saravia *et al*. 2020, Abdebur-A *et al.* 2022). One of the suggested causes for cannibalism in aquatic anurans is the high concentration of several cohorts in small water bodies (Barrionuevo 2015, Measey *et al.* 2015, Muñoz-Saravia *et al.* 2020). *Telmatobius rubigo* inhabits and breeds in shallow waters (Gastón 2022), although anurophagy and cannibalism were not observed in an extensive survey during the wet season (Akmentins and Gastón 2020). We suggest that this behavior occurs particularly during the dry season when the water deficit is

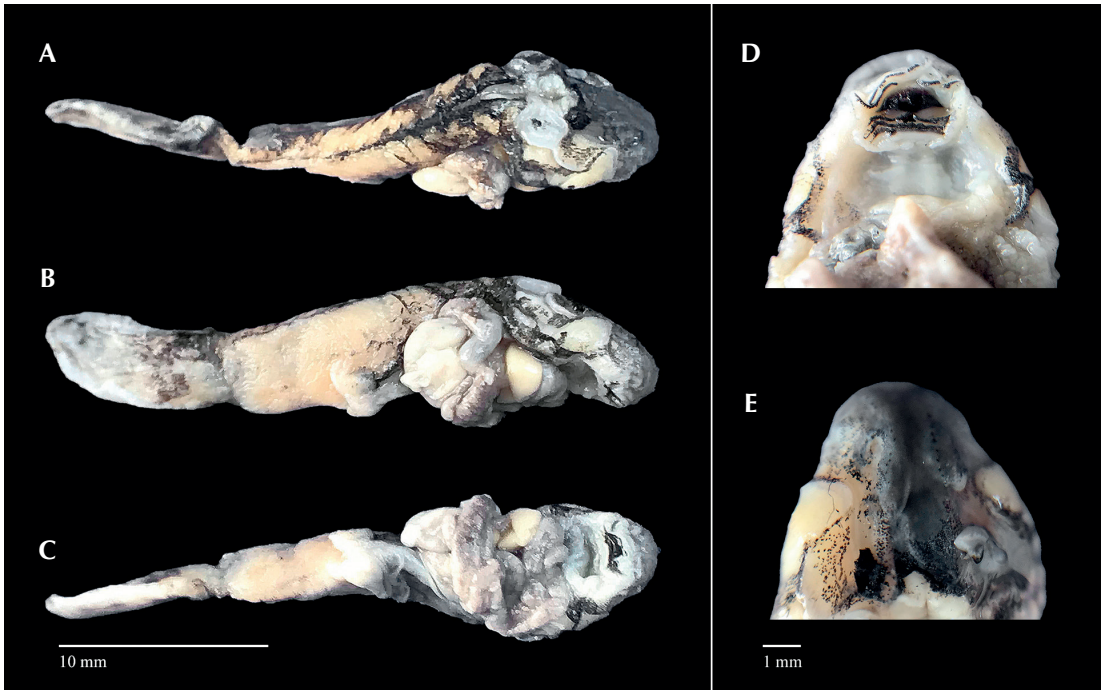

Figure 1. Detail of the stomach content of a female *Telmatobius rubigo* (SVL 55.08 mm; weight 15.6 g) with a cannibalism event of a tadpole in stage circa 30. (**A**) Dorsal, (**B**) lateral, and (**C**) ventral view; (**D**) oral disc detail; (**E**) lateral line neuromast detail.

more pronounced in the Central Andean Puna ecoregion (Garreaud *et al.* 2003, Santamans *et al.* 2021). It will be interesting to evaluate if extreme climate events associated with the global climate crisis (Urrutia and Vuille 2009) and the sustained trend of reduction of water bodies area reported in the region (Casagranda *et al.* 2019) could increase the frequency of the cannibalism in Aquatic Andean Frogs.

The trophic niche of *T. rubigo* in the dry season was mainly based on aquatic prey, with the anecdotic occurrence of one spider as an allochthonous (terrestrial) item (Table 1). In the wet season, *T. rubigo* consumed a wider range of prey that frequently includes allochthonous such as earthworms, adult dragonflies, and ants (Table 1). There is a noticeable variation in the importance of main consumed items, with increased relevance of amphipod shrimps, coleopteran larvae, backswimmers (Notonectidae), and larvae and pupae of dipterans in the dry season (Table 1). This resulted in a narrower trophic niche of *T. rubigo* in the dry season with intermediate and non-significant diet overlaps between dry and wet seasons (Table 1). This result contrasts with the Chilean Altiplano species of *Telmatobius,* that have no or slight variation in its diet between wet and dry seasons (Lobos *et al.* 2018, 2021). This shift in food preferences could be related to a change in the environmental offer of allochthonous and aquatic prey items during the summer months in the Central Andean Puna ecoregion. However, a study on prey availability throughout the year in consecutive seasons is needed to confirm it.

Table 1. Summary of the identified prey items consumed by *Telmatobius rubigo* during dry and wet seasons, with the percentages of number (*N*), volume (V, in mm^3), frequency of occurrence (F), and dietary importance value index (*Ip*). The development stages of the insect prey items are in parentheses. Categories with *Ip*-values above 10% are in bold. The two last rows show Levin's standardized index of trophic niche breadth for dry and wet seasons, and the Morisita-Horn index of seasonal diet overlap. *Allochthonous prey items.

Prey item	**Dry season (*N* = 17)**				**Wet season (*N* = 15)**			
	N (%)	F (%)	V (%)	*Ip*	*N* (%)	F (%)	V (%)	*Ip*
Oligachaeta*	-	-	-	-	11.27	26.67	72.93	**36.96**
Ostracoda	1.34	11.76	0.03	4.38	1.41	6.67	0.02	2.70
Amphipoda	27.52	76.47	21.58	**41.86**	19.72	40.00	7.70	**22.47**
Araneae*	0.67	5.88	1.69	2.75	-	-	-	-
Odonata (nymph)	0.67	5.88	0.42	2.33	-	-	-	-
Odonata (adult)*	-	-	-	-	1.41	6.67	6.01	4.70
Ephemeroptera (nymph)	-	-	-	-	1.41	6.67	0.08	2.72
Diptera (larvae/pupae)	26.17	70.59	5.59	**34.12**	14.08	40.00	0.75	**18.28**
Coleoptera (larvae)	13.42	70.59	33.22	**39.08**	16.90	40.00	6.49	**21.13**
Coleoptera (adult)	1.34	11.76	0.11	4.40	29.58	40.00	5.53	**25.04**
Hemiptera	27.52	64.71	17.28	**36.50**	-	-	-	-
Formicidae*	-	-	-	-	4.23	20.00	0.48	8.24
Anura	1.34	11.76	20.08	**11.06**	-	-	-	-
Levin's standardized index	0.39				0.53			
Morisita-Horn index	0.55							

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Short Communication

Filling distribution gap on *Sibon annulatus* and *S. ayerbeorum* (Serpentes: Dipsadidae) in Colombia

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Palabras claves: Bosque húmedo, Chocó, Morfología, Neotropico, Registros de distribución, Serpientes.

Palavras-chave: Chocó, Floresta tropical, Morfologia, Neotrópicos, Registros de distribuição, Serpentes.

The genus *Sibon* Fitzinger, 1826 comprises 17 species distributed from central Mexico to Brazil (Uetz and Hošek 2022). Some members present a variety of contrasting coloration pattern of rings or blotches that mimics coral snakes or arboreal pitvipers respectively (Solórzano 2002, Campbell and Lamar 2004). These color patterns are consistent taxonomically and used to define three species groups (sensu Peters 1960): (i) regularly blotched or banded pattern (*S. annulatus* group), (ii) ocellate pattern (*S. argus* group), and (iii) irregular small blotches, spots, or stippling, all combining to produce a highly disruptive pattern (*S. nebulatus* group). Despite high diversity in Central America (14 species), only five species inhabit South America: *Sibon dunni* Peters, 1957 (endemic to Ecuador), *S. nebulatus* (Linnaeus, 1758) (widespread from Mexico to Brazil), *S. annulatus* (Günther, 1872) (Moreno-Arias 2010, Meneses-Pelayo *et al.* 2016), the recently described species *S. bevridgelyi* Arteaga, Salazar-Valenzuela, Mebert, Peñafiel, Aguiar, Sánchez-Nivicela, Pyron, Colston, Cisneros-Heredia, Yánez-Muñoz, Venegas, Guayasamin and Torres-Carvajal, 2018, and *S. ayerbeorum* Vera-Pérez, 2019.

Among the South American species, *Sibon annulatus* and *S. ayerbeorum* are mainly distributed in the lowlands of the Chocoan region between Colombia and Ecuador. The taxonomic history of *S. annulatus* has been dynamic; it was synonymized with *S. dimidiatus* (Günther, 1872), because of poor definition and the lack of available material for comparisons (Wilson and Myer 1985, Kofron 1990). However, Savage and McDiarmid (1992) later recognized *S. annulatus*

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as a unique species based on comprehensive sampling. Moreno-Arias (2010) provided the first record of *S. annulatus* from Colombia and South America, from Alto de la Paz, San Martin, Cesar (7.9562° N, 73.3480° W; 1,402 m a.s.l.). Subsequently, Meneses-Pelayo *et al.* (2016) updated its distribution in Colombia based on three newly collected specimens from San José del Palmar, Chocó (4.9684° N, 76.2277° W; 1,500 m a.s.l.); El Afirmado, Pie de Pato, Chocó (5.6419° N, 77.0755° W; 320 m a.s.l.); Serranía de los Yariguies, La Colorada, San Vicente de Chucurí, Santander (6.7925° N, 73.4795° W; 1,420 m a.s.l.). They also defined the species' distribution limits in Colombia and Ecuador based on literature records, but without detailed information (Meneses-Pelayo *et al.* 2016). This species may be differentiated from most of its congeners other than *S. dimidiatus* by having (i) dorsal bands extending across the venter and (ii) penultimate supralabial not contacting the orbit. *Sibon annulatus* differs from *S. dimidiatus* (characteristics in parenthesis) by having (i) two postmentals, partially fused or reduced to a single small scale (single large postmental) and (ii) ventral scales 161–192 (187–200) (Savage and McDiarmid 1992, Köhler *et al.* 2010, Lotzkat *et al.* 2012).

S*ibon ayerbeorum* was recently described based on four specimens (Vera-Pérez, 2019) collected from La Playa and La Cueva sites in Parque Nacional Natural Munchique, Cauca, Colombia (2.771000° N, 76.980167° W; 1,135 m a.s.l.). Later, a fifth specimen was collected at Parcela Permanente de Investigación Biológica, Chocó, Colombia (5.360° N, 76.646° W; 96 m a.s.l.) by Echevarría-Rentería and Medina-Rangel (2021), a distance of 282 km from the type locality. This species is distinguished from all other *Sibon* species, except from *S. argus* (Cope, 1875) and *S. longifrenis* (Stejneger, 1909), by having (i) ocellated coloration pattern; (ii) dorsal scale rows 15-15/17-15; (iii) preocular absent; (iv) six supralabial, with the penultimate supralabial in contact with the eye; (v) first pair of infralabial generally in contact behind symphysial. But differs from *S. argus* and *S. longifrenis* by having (i) fewer ventral scales, 155 and 136–140 in males and females respectively (*S. argus:* 181–201 in males and 186–192 in females; *S. longifrenis:* 166–173 in males and 147–168 in females); (ii) fewer subcaudal scales, 93 and 78–79 in males and females respectively (*S. argus:* 112–121 in males and 186–192 in females; *S. longifrenis:* 95–106 in males and 80–101 in females); (iii) non-protuberant eyes (protuberant in *S. argus*); (iv) postmental scale absent (can be absent or present in *S. longifrenis*) (Vera-Pérez 2019).

Herein, we fill the distribution gap of *S. annulatus* and *S. ayerbeorum* in the Colombian Chocoan lowlands based on specimens that were found in sympatry at El Salto, Buenaventura, Valle del Cauca (3.855785° N, 76.782063° W; 756 m a.s.l.: Figures 1 and 2). Additionally, we summarize the records of *S. annulatus* from Ecuador.

An uncollected juvenile of *S. annulatus* (Figure 2A) was found on a shrub at 23:00 h on 29 October 2014. We identified it by absence of contact between orbit and large penultimate supralabial (Figure 3A), postmental scales two (Figure 3A), ventral scales 168, dorsal scale rows 15-15-15 (Table 1), and coloration pattern (Figure 2A): consisting of 58 black irregular bands, extending to the venter, giving the impression of zigzag black blocks; these bands contrast with ground colour that is red middorsally, yellow laterally and pale yellow-cream ventrolaterally; eyes red with subelliptical black pupil.

An adult *S. ayerbeorum* (IMCN:REP:215, Museo de Ciencias Naturales Federico Carlos Lehmann Valencia; Figure 2B) was collected from a Pteridophyta leaf at 01:00 h on 07 January 2015. We identified it by the contact between orbit and large supralabial scale (Figure 3B), absence of postmental scales (Figure 3B); first pair of supralabials not in contact behind the symphysial; ventral scales 149; dorsal scale rows 14-15-15 (Table 1); coloration pattern (Figure 2B) consisting of yellowish-brown dorsal

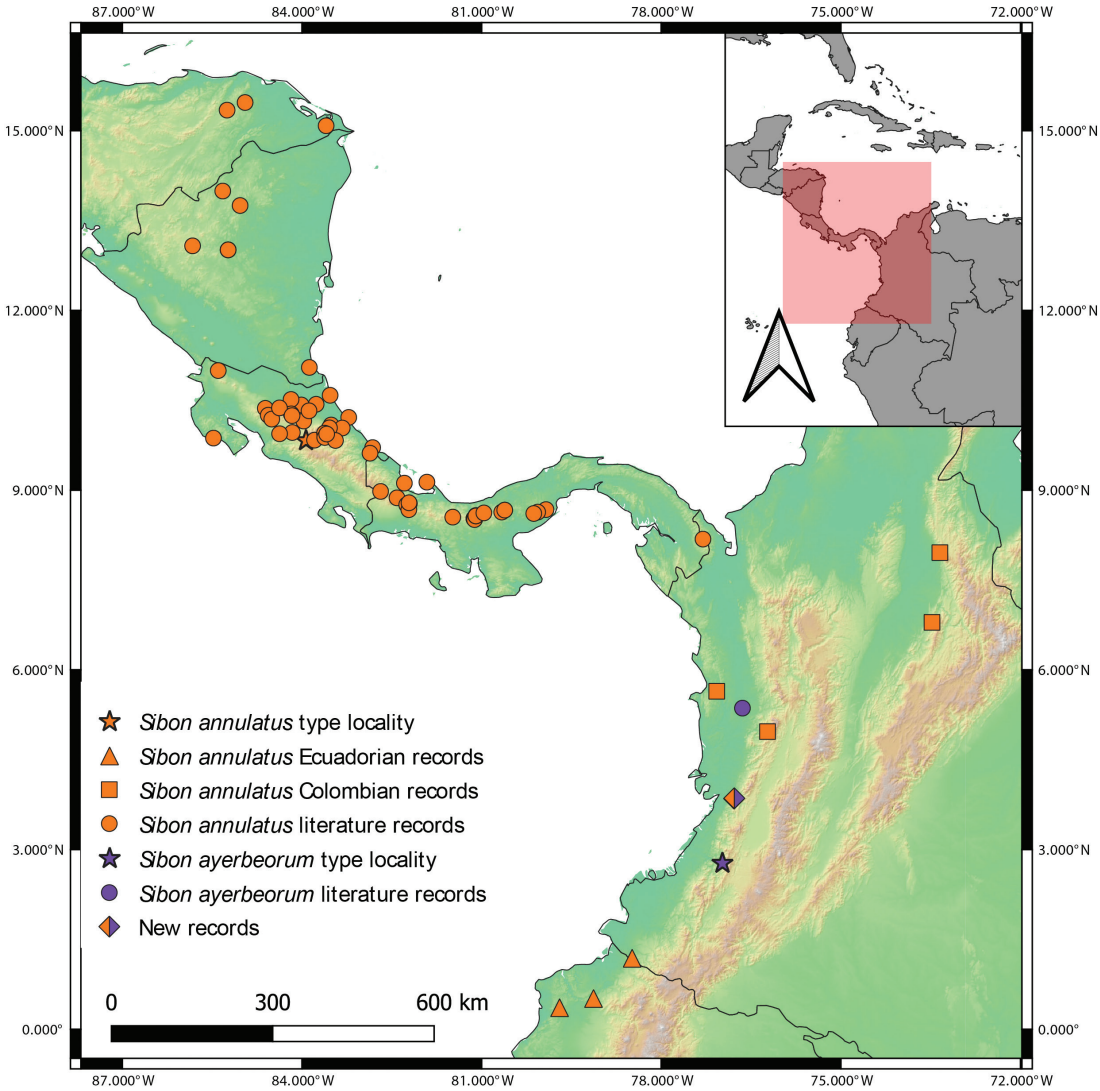

Figure 1. Distribution map of *Sibon annulatus* (orange), *S. ayerbeorum* (purple) and the new record of both species. All records are provided in Appendix I.

background with several irregular ocelli in paravertebral and lateral region bordered with reddish-brown with dark brown extending to the edge of the ventral scales, Black lateral blotches in contact on the anterior and middle part of the body, creating a narrow lateral black stripe; some ocelli on the tail are connected laterally; the ventral pattern consists of alternating yellow and black blotches, similar to a chess-board; eyes brown with yellow mottling, pupil black.

Ecuadorian specimens of *S. annulatus* initially recorded by Yánez-Muñoz *et al.*

Table 1. Scutellation counts of new Colombia specimens of *Sibon annulatus* and *S. ayerbeorum*. Left-right variation is indicated by a slash.

	Sibon annulatus (unvouchered)	***Sibon ayerbeorum*** (IMCN:REP:215)
Total length (mm)	288	371
Ventrals	168	149
Subcaudals	105	93
Dorsal scale rows	15-15-15	14-15-15
Postmentals	2	0
Postoculars	2/2	2/2
Anterior temporals	2/2	1/1
Posterior temporals	2/3	2/2
Supralabials	7/8	7/8
Infralabials	7/7	6/6
Supraoculars	1/1	1/1
Preoculars	0/0	0/0
Contact eye-penultimate supralabilal	No	Yes
Anal	Entire	Entire

(2009) at Tobar Donoso, Carchi province (unvouchered: 1.184507° N, 78.488011° W; 120 m a.s.l.), exhibit similarity in coloration (Yánez-Muñoz *et al.* 2009: see their Anexo I) and lepidosis to the specimens recorded in Colombia (Meneses-Pelayo *et al.* 2016; this study). A second specimen (unvouchered) was reported as *Sibon* sp. (Figure 2C) at the Bilsa Biological Station (0.3591° N, 79.7005° W; Figure 1), Esmeraldas province by Ortega-Andrade *et al.* (2010: page 126, Figure 9B). A third specimen (MZUTI 3034) was recorded in Reserva Itapoa, Esmeralda province (0.51307° N, 79.13401° W; Figure 1) by Arteaga *et al.* (2018: Figure 2A). These two last specimens had similar scutelation (ventral scales 197; dorsal scale rows 15-15-14; two post-ocular scales; 5-6 supralabial scales in contact with the orbit; eight infralabial scales) and coloration pattern (42 dark bands separated by paler interspaces) with the new specimen, but differ from our new specimen in color (red with yellow tonalities and black bands vs reddish brown with green and brown bands). We believe that this difference is due to ontogenic changes documented in several species of the family [*Atractus* Wagler, 1828 (Passos *et al.* 2010a, b, c), *Dipsas* Laurenti, 1768 (Harvey *et al.* 2008, Barros *et al.* 2012), *Oxyrhopus* Wagler, 1830 (Lynch, 2009), *Sibon* (Lotzkat *et al*., 2012)]. Although Arteaga (2020) compiled the records from Ecuador without providing source information (museum/collection specimens, observation or literature), we accept that his identifications and distribution records are valid. However, we did not include them here due to the lack of specimen location information.

During the course of the examination of the *S. ayerbeorum* specimen, the contact of the first infralabial scales behind the symphysial was difficult to determine. It seems that there is more

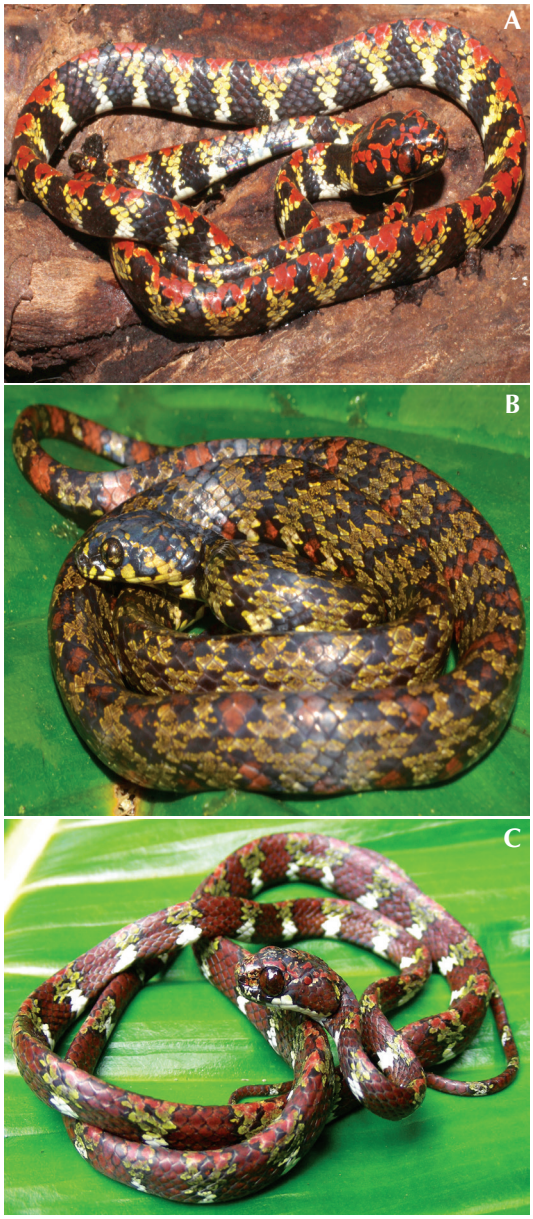

Figure 2. Color in life of (**A**) *Sibon annulatus* from El Salto, Buenaventura, Colombia (photo by OH); (**B**) *S. ayerbeorum* IMCN:REP:215 from El Salto, Buenaventura, Colombia (photo by AFJ); (**C**) *S. annulatus* from the Bilsa Biological Station, Esmeraldas, Ecuador (photo by Julieta Bermingham).

variation than the expected "generally in contact". In our new specimen and one paratype (MHNUC-He-Se-000660; Vera-Pérez, 2019: Figure 2B) both infralabials are separated by the chinshield and mental, whereas in the holotype (MHNUC-He-Se-000659; Vera-Pérez, 2019: Figure 2A) and Chocó specimen (COLZOOCH-H 1173; Echevarría-Rentería and Medina-Rangel 2021; Figure 2C) they are in contact. The absence of contact led to the possibility that the specimen could be *S. longifrenis,* because this species has no contact between the first infralabials, absence/presence of tiny postmental scale, and the lower counts of ventral and subcaudal scales resemble the count of our new specimen. However, the differences between these two species are not completely clear, and we hypothesize that they are sister species due to morphological similarities. To distinguish between the two species, we proposed the use of the postmental scale condition (absent in *S. ayerbeorum* and present in *S. longifrenis*) rather than contact between the first infralabials to diagnose them. Savage and McDiarmid (1992) stated for *S. longifrenis* "*almost always with single small postmental (absent in one specimen)*", meaning that of their nine examined specimens from Costa Rica and Panama postmental scales were absent in only one. This may indicate that the different specimen was actually *S. ayerbeorum.* For this reason, a further study including the *S. longifrenis* specimens from Central America is needed to confirm or reject our observations and improve the variation and differences between both species.

Until new evidence (molecular and hemipenial data) is provided, we allocate these Chocoan specimens to *S. annulatus* and *S. ayerbeorum,* based on scale counts and coloration pattern. These records fill a gap in the known distribution of *S. annulatus* at 150 km south and 600 km north from the closest records in Colombia and Ecuador respectively. The new record of *S. ayerbeorum* is 121 km north from the type locality and 167 km south of the record provided by Echavarría-Rentería *et al.* (2021).

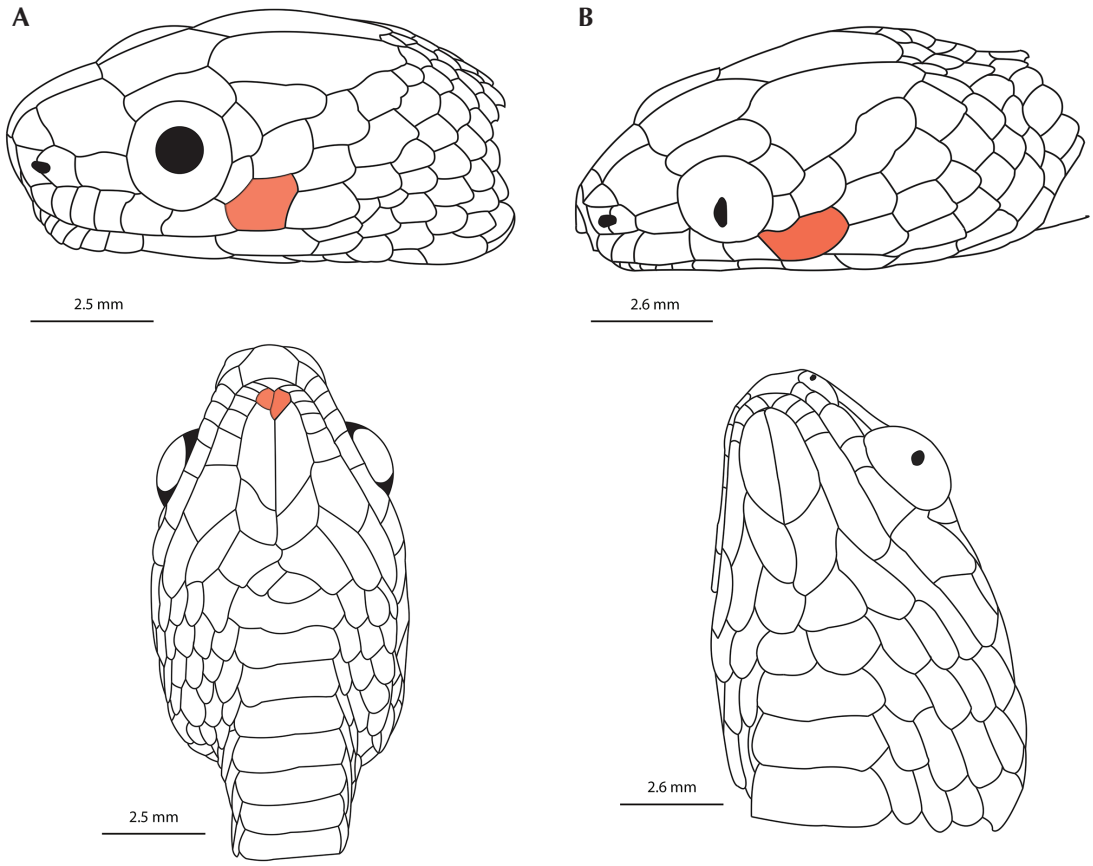

Figure 3. Illustration of lateral and ventral view of head in (**A**) *Sibon annulatus* and (**B**) *S. ayerbeorum* from El Salto (Buenaventura, Colombia). The large supralabial and the postmental scales are shown in red.

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Appendix I. *Records of* Sibon annulatus *and* S. ayerbeorum.

Longitude	Latitude	Record type
-83.935635	9.826328	*Sibon annulatus* - Type locality
-83.53333333	10.5833333	*Sibon annulatus* - Literature record
-83.76666667	10.4333333	*Sibon annulatus* - Literature record
-83.22277778	10.2138889	*Sibon annulatus* - Literature record
-83.610943	9.920028	*Sibon annulatus* - Literature record
-82.822926	9.710193	*Sibon annulatus* - Literature record
-84.015	10.421946	Sibon annulatus - Literature record
-83.516668	10.087367	*Sibon annulatus* - Literature record
-83.973629	10.153257	*Sibon annulatus* - Literature record
-84.185638	10.513241	*Sibon annulatus* - Literature record
-83.330986	10.037173	*Sibon annulatus* - Literature record
-85.40195	10.99637	*Sibon annulatus* - Literature record
-82.86666667	9.6166667	*Sibon annulatus* - Literature record
-84.615769	10.365485	*Sibon annulatus* - Literature record
-84.566667	10.250492	*Sibon annulatus* - Literature record
-83.793066	9.834581	*Sibon annulatus* - Literature record
-83.5445	10.0396	*Sibon annulatus* - Literature record
-84.50787	10.18564	*Sibon annulatus* - Literature record
-83.626236	9.951882	*Sibon annulatus* - Literature record
-84.182416	10.273189	*Sibon annulatus* - Literature record
-85.481384	9.868858	*Sibon annulatus* - Literature record
-83.88573	10.324289	*Sibon annulatus* - Literature record
-84.164143	9.962061	*Sibon annulatus* - Literature record
-83.622876	9.879236	*Sibon annulatus* - Literature record
-83.443688	9.829227	*Sibon annulatus* - Literature record
-83.590692	9.936801	*Sibon annulatus* - Literature record
-84.377457	9.94134	*Sibon annulatus* - Literature record
-84.379357	10.372805	*Sibon annulatus* - Literature record
-84.169232	10.243636	*Sibon annulatus* - Literature record
-83.6	15.0833	*Sibon annulatus* - Literature record
-85.254026	15.34399	*Sibon annulatus* - Literature record
-84.95332778	15.4710528	*Sibon annulatus* - Literature record
-85.83038889	13.0783611	*Sibon annulatus* - Literature record
-85.0367	13.7517	*Sibon annulatus* - Literature record
-85.3267	13.9933	*Sibon annulatus* - Literature record
-85.2366	13.0114	*Sibon annulatus* - Literature record

Appendix I. *Continued.*

Longitude	Latitude	Record type
-85.23656	13.01139	*Sibon annulatus* - Literature record
-83.88011	11.04856	*Sibon annulatus* - Literature record
-85.23655556	13.0113889	*Sibon annulatus* - Literature record
-80.61666667	8.6666667	*Sibon annulatus* - Literature record
-80.66666667	8.6333333	*Sibon annulatus* - Literature record
-82.6901	8.9785	*Sibon annulatus* - Literature record
-82.4159	8.8714	*Sibon annulatus* - Literature record
-82.2092	8.7776	*Sibon annulatus* - Literature record
-82.2543	8.7553	*Sibon annulatus* - Literature record
-82.2185	8.6739	*Sibon annulatus* - Literature record
-82.2155	8.7891	*Sibon annulatus* - Literature record
-81.4847	8.5494	*Sibon annulatus* - Literature record
-81.1328	8.5249	*Sibon annulatus* - Literature record
-81.1193	8.5146	*Sibon annulatus* - Literature record
-81.121	8.5082	*Sibon annulatus* - Literature record
-81.0989	8.569	*Sibon annulatus* - Literature record
-81.0971	8.577	*Sibon annulatus* - Literature record
-81.0989	8.569	*Sibon annulatus* - Literature record
-79.92755556	8.6750278	*Sibon annulatus* - Literature record
-80.0666	8.6333	*Sibon annulatus* - Literature record
-80.61666667	8.6666667	*Sibon annulatus* - Literature record
-82.292758	9.116576	*Sibon annulatus* - Literature record
-80.131693	8.609784	*Sibon annulatus* - Literature record
-81.916667	9.133333	*Sibon annulatus* - Literature record
-80.965002	8.619461	*Sibon annulatus* - Literature record
-77.305385	8.182102	*Sibon annulatus* - Literature record
-73.479595	6.792548	*Sibon annulatus* - Colombia record
-73.348031	7.956254	*Sibon annulatus* - Colombia record
-77.0755	5.64194	*Sibon annulatus* - Colombia record
-76.227597	4.968406	*Sibon annulatus* - Colombia record
-79.70055556	0.3591667	*Sibon annulatus* - Ecuador record
-78.488011	1.184507	*Sibon annulatus* - Ecuador record
-79.13401	0.51307	*Sibon annulatus* - Ecuador record
-76.980167	2.771	*Sibon ayerbeorum* - Type locality
-76.646	5.36	*Sibon ayerbeorum* - Record
-76.782063	3.855785	New records

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Short Communication

New record size, increased distribution range, and threat category reassessment proposal for *Tropidophis morenoi* (Serpentes: Tropidophiidae)

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Keywords: Central Cuba, Cuban dwarf boa, Extent of occurrence, IUCN, Threat category, Trope Zebra.

Palavras-chave: Boa-cubana-anã, Categoria de ameaça, Cuba central, Extensão de ocorrência, IUCN.

The Zebra Trope, *Tropidophis morenoi* Hedges, Garrido and Díaz, 2001, is one of 17 currently recognized species of Cuban dwarf boa (Díaz and Cádiz 2020), with a north central Cuba distribution (Henderson and Powell 2009, Rodríguez-Schettino *et al.* 2013; Figure 1A). This snake was previously placed in the *T. maculatus* species group by Hedges (2002), but Díaz and Cádiz (2020) transferred it to the *T. pardalis* species group. It is not well represented in museum collections and was described on the basis of two specimens (CZACC 4.5492-93) from Dolinas de Cueva de Humboldt, Caguanes, Sancti Spíritus province (Hedges *et al.* 2001). A third specimen (CZACC 4.12052) was reported from the type locality, which was a size record for species (Domínguez *et al.* 2006). Later, Domínguez and Parada (2009) reported new localities for this species including Loma de Cunagua, Bolivia municipality and Alevinaje, Morón municipality, both from Ciego de Ávila province; and Coco Key from Sabana-Camagüey archipelago (specimens CIEC 66-67; CIEC 150, respectively). That provided the first records for Ciego Ávila province on the main island and Sabana-Camagüey archipelago, extending the distribution range 75.6 km E from the type locality at Caguanes. With that addition, Coco Key was shown to harbor the highest number of *Tropidophis* species among Cuban keys (Domínguez and Parada 2009, Rodríguez-Schettino *et al.* 2013). Additionally, a specimen (MNHNCu 5088) from Jobo Rosado, Jatibonico municipality, Sancti Spíritus province was reported by Díaz and Cádiz (2020), extending the distribution range 17.4 km SW from Caguanes.

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According to Tolson and Henderson (1993), despite the large number of species of *Tropidophis* in Cuba, many are known from few specimens, and their distributions are poorly understood. In the last decade, the reports of distribution records for several Cuban dwarf boas have increased (e.g. Fong and Armas 2011, Torres *et al.* 2013, 2016, Díaz *et al.* 2014, Iturriaga and Olcha 2015, Cajigas *et al.* 2018, Rodríguez-Cabrera *et al.* 2020, 2021, Rodríguez-Cabrera and Teruel, 2022). The addition of new localities increases our knowledge about natural history and fills gaps in records from field observations that allow for the implementation of management and conservation programs (Torres *et al.* 2013, Díaz *et al.* 2014, Tanaka *et al.* 2018). We herein report new locality records and morphological data of *T. morenoi,* and we propose to reassess its conservation status.

During a field expedition to Caguanes National Park, in the north of Central Cuba, on 22 August 2017, a speleological group visited Cueva del Abono (22°22'46.429" N, 78°58'56.744" W) in Judas´ hill, Yaguajay municipality, Sancti Spíritus province. The group found two specimens of *T. morenoi,* but only one, a male, was captured (Figure 1B). Each individual was resting on a rock at the entrance to the cave. The captured specimen was identified by Michel Domínguez and deposited in the Institute of Ecology and Systematics, Havana Cuba (CZACC 4.13169). This locality is approximately 15.2 km airline E from the type locality. The cave is located within semideciduous forest on limestone (Figure 1C), in a mountain system formed by three small adjacent kartsic hills with a maximum height of 33.4 m a.s.l., an area of 0.5 km^2, and a distance of 1.5 km from the coastline. In the past, this area was dedicated to growing sugar cane, but is now used for grazing and agriculture, and there is also abundant secondary vegetation. We took the linear measurements and meristic characters of the collected male specimen and it represents a new size record, with 429 mm snout–vent length (SVL), and 479 mm total length (TL). The previous record was 359 mm SVL and 416 mm TL for an adult female, (Domínguez *et al.* 2006). The morphological data on the specimens are in Table 1.

A field expedition by biologists from the Coastal Ecosystems Research Center (CIEC) in April 2012 collected an adult male in the city of Morón (22°06'34.025" N, 78°37'38.213" W), Morón municipality and a pregnant female in the elevations of Punta Alegre (22°14'40.227" N, 78°47'27.958" W), Chambas municipality, both from Ciego Ávila province. The latter locality is completely covered by sicklebush *Dichrostachys cinerea* (L.) Wight and Arn. (Fabaceae) presently. The first specimen was deposited in the herpetological collection of CIEC (CIEC 55) (Figure 2A), and the last one was kept in captivity for two weeks until it had three offspring. The mother was later released at its point of capture and the offspring were kept in captivity for a month. They were fed frogs of the genus *Eleutherodactylus* and small *Anolis sagrei* Duméril and Bibron, 1837. Later, they were euthanized and deposited in the herpetological collection of the CIEC (CIEC 78-80) (Figure 2B). On another field expedition, a third specimen was sighted at El Coy (22°18'47.830" N, 78°40'20.280" W), Isla de Turiguanó, Morón municipality, Ciego de Ávila province. This locality is lowland with mangroves and swamp forests. These reports represent one and three new geographic records of *T. morenoi* for Sancti Spíritus and Ciego de Ávila provinces, respectively, and increase the number of localities within its distribution range (Díaz and Cádiz 2020).

Table 1 summarizes the linear measurements and morphological characters of *T. morenoi* specimens deposited in the herpetological collections of IES and CIEC. All individuals were similar to one another; and the morphological characteristics agree in general with the description of the holotype and paratype (Hedges *et al.* 2001), although there are some small variations. The specimen CIEC 55 measures 258 mm SVL and tail length 39 mm; its dorsal scale rows formula is very different,

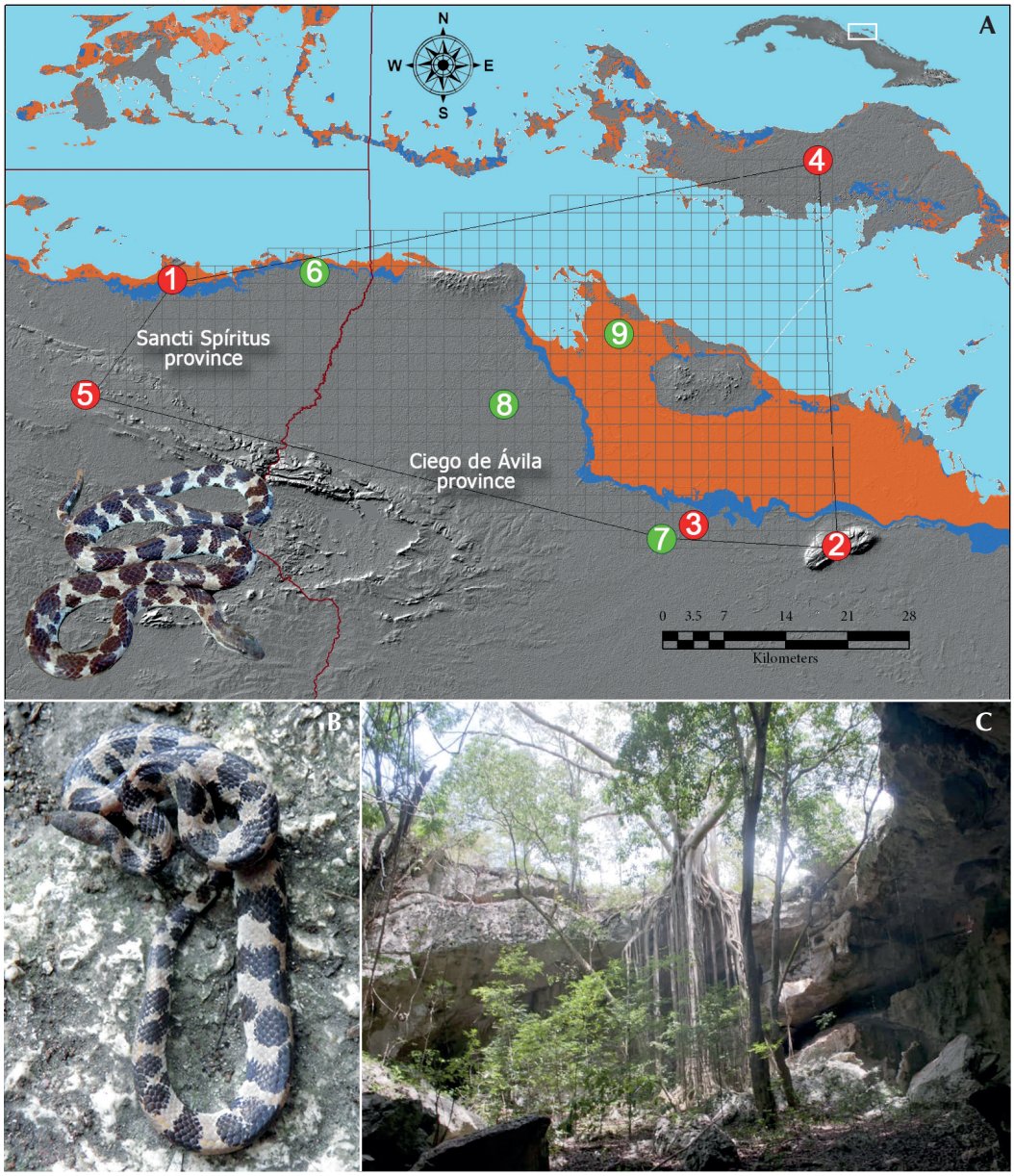

Figure 1. (**A**) Previous and new records (red and green circles, respectively): (1) Cueva de Humboldt, Cayo Caguanes, Sancti Spíritus province; (2) Loma de Cunagua, Ciego de Ávila province; (3) Alevinaje, Ciego de Ávila province; (4) Coco Key, Sabana-Camagüey archipelago; (5) Jobo Rosado, Sancti Spíritus province; (6) Cueva del Abono, Judas´hill, Caguanes, Sancti Spíritus province; (7) city of Morón, Ciego de Ávila province; (8) Punta Alegre, Ciego de Ávila province; (9) El Coy, Isla de Turiguanó, Ciego de Ávila province. Area of extent of occurrence, and modeling of potentially lost areas by 2050 (orange zone) and 2100 (blue zone) of *T. morenoi*. Photo: Dariel López. (**B**) Adult male Zebra Trope (*Tropidophis morenoi*, CZACC 4.13169) photo by ARL. (**C**) Area under a sinkhole with associated vegetation in Cueva del Abono, Judas' hill, Yaguajay municipality, Sancti Spíritus province. Photo: Raudel del Llano.

Figure 2. (**A**) Adult male of Zebra Trope, *Tropidophis morenoi,* (CIEC 55), (**B**) and three juvenile specimens (CIEC 78-80). Photos by EM.

because the anterior and middle counts of scale rows are less than in the type series and specimens CZACC 4.12052 and CZACC 4.13169. The ventral scale count ranges from 190 to 199, although the specimen CZACC 4.13169 has the lowest count with 187 scales. Subcaudal scale counts are between 41 and 44, although specimens CZACC 4.12052 and CIEC 55 have the lowest counts with 38 and 37, respectively. The specimen CZACC 4.13169 has nine supralabials and 10 infralabials on each side, the remainder of specimens have 10 supralabials and 11 infralabials. All specimens exhibit very similar ground and dorsal color pattern, and rows of spots. CIEC 78 and 80 have the fewest body spots. The tail tip is whitish yellow, light beige, tan or yellowish tan.

The addition of new locality records for *T. morenoi* increases the area of occupancy (AOO) by 36 km^2, from the 16 km^2 given by Rodríguez-Schettino (2012). The known and new localities cover an extent of occurrence of 1530 km^2 by means of the minimum convex polygon (Fig 1A). The nine localities where this species occurs can be assigned to five threat-based locations according to the topographic features of landscape and main known threats (Figure1 A). Location 1: Jobo Rosado, is a Managed-Resources Protected Area, located in the mountainous system of Meneses-Cueto´s Mountain Range and belongs to the Special Regions of Sustainable Development of Bamburanao-Turquino (CNAP 2013). The main threats are logging, excessive ecological tourism, agriculture, livestock and expansion of human settlements (González *et al.* 2015). Location 2: is Judas´ hill, Caguanes National Park and Isla de Turiguanó. These localities are situated in lowlands, with mangroves and swampy areas, very close to the north coast of Sancti Spíritus and Ciego de Ávila provinces. The main threats are livestock, agriculture, and expansion of human settlements. Location 3: Cunagua hill is a mountain range with a surface area of 24.2 km^2

Table 1. Main linear measures and meristic characters of specimens of *Tropidophis morenoi* of herpetological collections from Institute of Ecology and Systematics (CZACC) and Coastal Ecosystems Research Center (CIEC). * Linear measurements and meristic data of specimen CZACC 4.12052 not available, the body anterior third is damaged. ** Data of specimens CIEC 78-80 not available.

Characters	Holotype	Paratype	CZACC 4. 12052	CZACC 4. 13169	CIEC 55	CIEC 78	CIEC 79	CIEC 80
Sex	Female	Female	Female	Male	Male	Juvenile	Juvenile	Juvenile
Snout–vent lenght	295	285	359	429	258	116	122	107
Tail lenght	42	44	57	50	39	20	13	20
Total lenght	337	329	416	479	297	136	135	127
Head width	7.2	6.4	*	7.6	6.6	4.1	4.0	4.3
Neck width	5.2	4.2	*	4.9	4.8	2.5	2.3	2.3
Head width/Neck width	1.38	1.52	*	1.56	1.38	1.64	1.74	1.87
Eye width/Head width	0.24	0.27	*	0.25	0.14	0.17	0.20	0.19
Dorsal scale rows formula	23-23-17	23-23-17	21-23-17	21-23-16	20-20-17	**	**	**
Ventral scales	198	199	*	187	195	191	195	190
Subcaudal scales	42	44	38	41	37	43	41	43
Supralabials	10i/10d	10i/10d	*	9i/9d	10i/10d	10i/10d	10i/10d	10i/10d
Scales in contact with eye	4--5	4--6	*	8i/8d	7i/7d	7i/7d	7i/7d	7i/7d
Infralabials	11i/11d	11i/11d	*	10i/10d	11i/11d	11i/11d	11i/11d	11i/11d
Preoculars	1i/1d	1i/1d	*	1i/1d	1i/1d	1i/1d	1i/1d	1i/1d
Postoculars	3i/3d	3i/2d	*	3i/3d	3i/3d	3i/3d	3i/3d	3i/3d
Ground color	Whitish beige	Whitish beige	Tan	Whitish beige	Beige	Beige	Beige	Beige
Dorsal pattern	Narrow bands	Narrow bands	Narrow bands	Narrow bands	Narrow bands	Narrow bands	Narrow bands	Narrow bands
Ventral pattern	Spots	Spots	Spots	Spots	Spots	Spots	Spots	Spots
Spot rows	6	6	6	6	6	6	6	6
Body spots	38i/39d	38i/38d	35i/38d	31i/30d	34i/33d	31i/32d	33i/33d	31i/31d
Tail spots	4i/5d	8i/6d	5i/4d	5i/5d	6i/6d	5i/5d	6i/6d	5i/6d
Tail tip	Whitish yellow	Whitish yellow	Tan	Yellowish tan	Light beige	Yellowish tan	Yellowish tan	Yellowish tan

and a height of 321 m a.s.l., located 14 km SE airline from La Laguna de la Leche, inland of Ciego de Ávila province and bordered by lowlands (Nerey-Contreras *et al.* 2014). It is a Faunal Refuge Protected Area that is affected by forest fires, felling of remaining forests for grazing and sugar cane cultivation, and expansion of human settlements (Lima-Moreno *et al.* 2019). Location 4: The city of Morón, Alevinaje and Punta Alegre are located in the plain area of inland of Ciego Ávila province, and suffer the greatest anthropic disturbances from aquaculture, agriculture, grazing, gypsum mining and human construction. Location 5: Coco Key is located in Sabana-Camagüey archipelago, 15 km from the main island. The main threat to this locality is tourism and fragmentation of semideciduous forest patches from construction of two main roads and various buildings.

All Cuban dwarf boas are included in appendix II of CITES (UNEP-WCMC 2021), and also in the appendix I of resolution 160/2011 of Minister of Science, Technology and Environment of Cuba. They are found in 29.4% of protected areas of the National System of Protected Areas of Cuba (Rodríguez-Schettino *et al.* 2015). In the Red Book of Vertebrates of Cuba (González-Alonso *et al.* 2012), *T. morenoi* was one of 11 threatened species of *Tropidophis* included, with an AOO of 16 km^2 and unknown population size. The main threats were anthropic activities and sea-level rise; therefore, it was assessed as Critically Endangered by Rodríguez-Schettino (2012). Meanwhile, Fong (2021) listed this species as Vulnerable on the IUCN Red List, due to its restricted range, in three locations with these main threats: agricultural activities, tourism development and continuing decline in the extent and quality of existing habitat. According to the IUCN criteria (IUCN Standards and Petitions Committee 2019), we believe that *T. morenoi* could be reclassified as Endangered (EN) under criterion B.1, and the subcriterion a (number of locations $\leq$ 5) and biii (continuing decline in quality of habitat); contrary to proposals of Rodríguez-Schettino (2012) in the Red Book of Vertebrates of Cuba, and Fong (2021) for IUCN. We suggest that the conservation status of the species and EOO be reassessed by IUCN appropriately.

We reviewed the management plans of Ciego de Ávila province, and the habitat loss and fragmentation are more serious for those localities outside of jurisdiction of National System of Protected Areas of Cuba (Lima-Moreno *et al.* 2019). Despite the level of disturbance in some areas, the records of *T. morenoi* from localities such as the city of Morón and Alevinaje provide hope for the conservation of this species, and highlight the resilience that the dwarf boas show in disturbed areas (e.g. Torres *et al.* 2013, Díaz *et al.* 2014, Rodríguez-Cabrera *et al.* 2021). Fong (2021), also mentioned that the collection of specimens for the illegal pet trade is another threat for *T. morenoi*. Although there are currently no species of Cuban dwarf boa cited on pet trade lists (Altherr *et al.* 2019), the surveillance and measures implemented by the Cuban authorities need to be stricter to prevent any illegal trading. Finally, we predict by future projections that for 2050 and 2100, 24% (371 km^2) and 29% (447 km^2) of the total EOO of *T. morenoi* will be lost, respectively, in areas very close to the coast (Figure 1A). Therefore, the sea-level rise should be considered as a potential threat to those populations in the lowlands near the north coast of Sancti Spíritus and Ciego de Ávila provinces. The situation is similar for *Tropidophis celiae* Hedges, Estrada and Diaz, 1999, a species with a restricted distributional range, very close to the north coast of western Cuba (Rodríguez-Cabrera and Teruel 2022). According to Iturralde-Vinent and Serrano (2015), there are many localities prone to coastal flooding due to sea-level rise in the Cuban archipelago, and the implementation of measures to face this threat are necessary. In summary, comprehensive species extinction risk assessments are necessary to provide an appropriate threat category and implement species-specific conservation programs; especially for this species of dwarf boa, for which there is currently no management plan (Fong 2021).

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INSTRUCTIONS TO AUTHORS

General Information. *Phyllomedusa* publishes articles dealing with the entire field of herpetology. The journal also maintains sections for Short Communications and Book Reviews. Manuscripts are considered on the conditions that they: (1) have not been published elsewhere; (2) are not under consideration for publication, in whole or in part, in another journal or book; and (3) are submitted by the authors in the format and style of *Phyllomedusa* and in accordance with the specifications included in the Instructions to Authors. Manuscripts should be submitted as a single Microsoft Word document via e-mail. High-quality color images are accepted. Manuscripts must be written in English with appropriate abstracts in alternate languages. If English is not your primary language, arrange to have your manuscript reviewed for English usage before you submit it. Direct any questions about manuscript submission to the primary editor. Publication in *Phyllomedusa,* including color images, is free of charge.

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✓ **More than two authors in a journal series:**

Hero, J.-M., W. E. Magnusson, C. F. D. Rocha, and C. P. Catterall. 2001. Antipredator defenses influence the distribution of amphibian prey species in the central Amazon rain forest. *Biotropica 33:* 131–141.

✓ **Chapter in an edited volume:**

Hedges, S. B. 1999. Distribution patterns of amphibians in the West Indies. Pp. 211–254 *in* W. E. Duellman (ed.), *Patterns of Distribution of Amphibians. A Global Perpective.* Baltimore and London. The Johns Hopkins University Press.

✓ **Unpublished thesis or dissertation:**

Verdade, V. K. 2001. Revisão das espécies de *Colostethus* Cope, 1866 da Mata Atlântica (Anura, Dendrobatidae). Unpublished M.Sc. Dissertation. Universidade de São Paulo, Brazil.

✓ **Book:**

McDiarmid R. W. and R. Altig (eds.). 1999. *Tadpoles. The Biology of Anuran Larvae.* Chicago and London. The University of Chicago Press. 633 pp.

✓ **Material from the World Wide Web:**

Frost, D. R. (ed.). 2010. Amphibian Species of the World: an Online Reference. Version 5.4 (8 April 2010). Electronic Database accessible at http: // research.amnh.org/vz/herpetology/amphibia/American Museum of Natural History, New York, USA. Captured on 22 August 2010.

✓ **Software:**

Maddison, W. P. and D. R. Madison. 2010. Mesquite. A Modular System for Evolutionary Analysis. Version 2.73. URL: http://mesquiteproject.org

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Jaime Bertoluci
Editor-in-Chief

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