



Harlequin frog tadpoles—comparative buccopharyngeal morphology in the gastromyzophorous tadpoles of the genus *Atelopus* (Amphibia, Anura, Bufonidae), with discussion on the phylogenetic and evolutionary implication of characters

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Abstract

The Neotropical genus *Atelopus* is the most diverse genus of bufonids comprising 99 species. Tadpoles of these frogs are readily distinguished based on the presence of a belly sucker, used by them to stay attached to rocks in fast-flowing streams. Despite their intriguing biology, information about their anatomy is scarce and many morphological systems are unknown. We describe the buccopharyngeal cavity of five *Atelopus* species. The *Atelopus* buccopharyngeal cavity is characterized by (1) presence of a pendulum-like papillae in the prenarial arena, (2) presence of a glandular zone in the prenarial arena, (3) narial vacuities, (4) conical median ridge, (5) absence of buccal roof arena papillae, (6) absence of buccal roof pustulations, (7) single pair of infralabial papillae, (8) absence of lingual papillae, and (9) absence of pustulations in the buccal floor. We propose that characters 1, 2, and 3 are new synapomorphies for the genus. We also propose that the presence of a single pair of infralabial papillae is a synapomorphy for bufonid. Finally, we discuss the convergent evolution of gastromyzophorous and suctorial tadpoles withing anurans.

Keywords *Atelopus balios* · *A. carrikeri* · *A. nahumae* · *A. nanay* · *A. subornatus* · Systematics

Introduction

The Neotropical genus *Atelopus* currently comprises 99 recognized species—the most diverse genus of bufonids, and several other species have been identified and are awaiting a formal description. At least 131 species (Lötters et al. 2023) are distributed in Central and South Americas, from Costa Rica to Bolivia, along the Andes, Amazonia, and Guiana Shield, from the sea level to elevations up to 3.600 m.a.s.l. (Frost 2023). Contrasting with its large diversity, *Atelopus*

is one of the most threatened amphibian genera; the last 30 years witnessed an unprecedented populational decline and many species are considered to be extinct (La Marca et al. 2005; Stuart et al. 2008; Wake and Vredenburg 2008; Lötters et al. 2023).

These diurnal, slow-moving frogs are frequently found in association with fast-flowing streams (Lötters 1996). They are popularly known as harlequin frogs due to the bright coloration of many species (Fig. 1a). Also, several species are known to possess tetrodotoxin (TTX) in their skin (Daly et al. 1994; Mebs et al. 1995; Yotsu-Yamashita and Takei 2010), and other compounds have also been reported in *Atelopus* species (see Pearson and Tarvin 2022). *Atelopus* frogs are characterized by their heads longer than broader, bearing a long, acuminate snout (McDiarmid 1971; Peters 1973), interdigital webbing well-developed, and by a reduction in size of the first digit that is often associated with the reduction in the number of phalanges (McDiarmid 1971; Lynch 1993; Fig. 1a). The middle ear is lacking in most species (McDiarmid 1971; Cannatella 1981; Lötters et al. 2011; Pereyra et al. 2016), although *Atelopus* may hear high

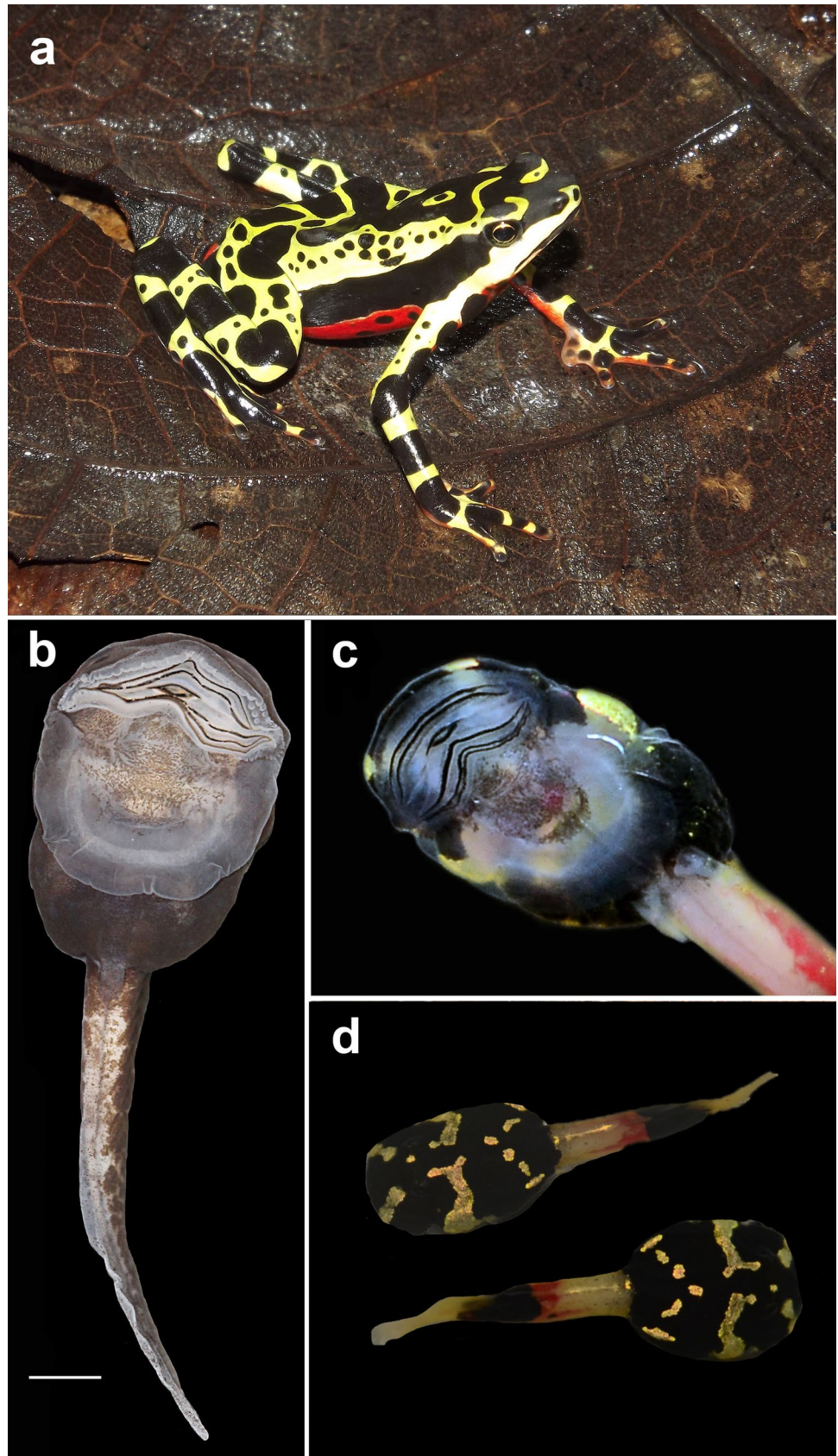
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Fig. 1 Characteristics of *Atelopus*. In life (**a**, **c**, **d**), some adults (*Atelopus* sp.) and larvae (*Atelopus subornatus*) have bright coloration. Tadpoles of *Atelopus* are characterized by the presence of a belly sucker (**b**), used by these larvae to attach on rocks. Scale bar = 10 mm



frequencies, above 1500 Hz, a unique feature among bufonids (Womack et al. 2018).

During breeding season, amplexant pairs can be found in streams in which strings of eggs are laid submerged, beneath rocks and vegetation (Lynch 1986; Lötters 1996; Karraker et al. 2006). The harlequin frog tadpoles may also have bright colors, are gastromyzophorous (Fig. 1), and adapted to live in fast-flowing waters (Altig and Johnston 1989), in which they use their abdominal sucker to attach to rocks (Starrett 1967; Duellman and Lynch 1969; Lynch 1986; Lötters 1996). Tadpoles of 30 species have been described so far (Table 1), but aspects of their internal morphology are restricted to the cranial anatomy of *A. tricolor* (Lavilla and de Sá 2001; Haas 2003). Herein, we describe for the first time the buccopharyngeal morphology for five *Atelopus* species (*A. balios*, *A. carrikeri*, *A. nahumae*, *A. nanay*, and *A.*

subornatus) and discuss the evolutionary and phylogenetic implications of our findings for the systematics of bufonids.

Material and methods

Buccopharyngeal morphology assessment

We studied the buccopharyngeal morphology in the tadpoles of five species of *Atelopus*. This material is housed at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá, Colombia, herpetological collection of the Universidad del Magdalena (CBUMAG), Santa Marta, Colombia, and Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador. Developmental stages are according to Gosner (1960). Additional bufonids were examined for comparison purposes; we also examined other suctorial and/or gastromyzophorous tadpoles to understand the evolution of buccopharyngeal cavity in these guilds. The complete list of examined material and developmental stages is in the [Appendix](#).

Tadpoles of *Atelopus balios* and *A. nanay* used in the present study are part of the lots used in the tadpoles' original descriptions: Coloma and Lötters (1996) and Coloma (2002), respectively. Tadpoles of *A. carrikeri* were collected in the same locality as those used in the original description (Rueda-Solano et al. 2015; see also Pérez-Gonzalez et al. 2020). Tadpoles of *A. nahumae* and *A. subornatus* were identified by comparisons with the original descriptions (Lynch 1986; Enciso-Calle et al. 2017; Pérez-Gonzalez et al. 2020) and by comparisons with fresh collected tadpoles of both species (M.A. personal observation).

Two tadpoles per species were dissected according to Wassersug (1976) to expose the buccopharyngeal cavity and stained with methylene blue solution. After inspection under the stereoscopic microscope, one individual per species was submitted to a protocol for scanning electron microscopy (SEM) as follows: (1) samples were washed in distilled water, (2) put in ethanol 25% for 2 h, (3) put in ethanol 70% for 24 h, (4) put in ethanol 100%: 2 baths of 15 min, 20 min prior to the critical point, (5) critical point dried in carbon dioxide, (6) mounted in the stubs with double face carbon tape, and (7) covered with a thin layer gold. Terminology for buccopharyngeal cavity follows Wassersug (1976, 1980) and Dias et al. (2018a).

Phylogenetic relationships and character optimization

The monophyly of *Atelopus* is well supported by molecular and phenotypical evidence (e.g., McDiarmid 1971; Lötters et al. 2011; Jetz and Pyron 2018). Unfortunately, of the five species studied by us, only *A. nanay* was included in

Table 1 Described tadpoles of *Atelopus*

Species	Reference
<i>Atelopus balios</i>	Coloma and Lötters (1996)
<i>Atelopus carbonerensis</i>	Mijares-Urrutia and La Marca (2005)
<i>Atelopus carrikeri</i>	Rueda-Solano et al. (2015)
<i>Atelopus certus</i>	Duellman and Lynch (1969)
<i>Atelopus cruciger</i>	Mebs (1980)
<i>Atelopus ebenoides</i>	Lynch and Suárez-Mayorga (2011)
<i>Atelopus elegans</i>	Marcillo-Lara et al. (2020)
<i>Atelopus exiguus</i>	Coloma et al. (2000)
<i>Atelopus flavescens</i>	Lescure (1981)
<i>Atelopus franciscanus</i>	Boistel et al. (2005)
<i>Atelopus hoogmoedi</i>	Gawor et al. (2012); Lötters et al. (2022)
<i>Atelopus ignescens</i>	Duellman and Lynch (1969)
<i>Atelopus laetissimus</i>	Pérez-Gonzalez et al. (2020)
<i>Atelopus manauensis</i>	Gascon (1989)
<i>Atelopus mindoensis</i>	Lötters (2001)
<i>Atelopus mittermeieri</i>	Acosta-Galvis et al. (2006)
<i>Atelopus mucubajiensis</i>	Mijares-Urrutia and La Marca (2005)
<i>Atelopus nahumae</i>	Pérez-Gonzalez et al. (2020)
<i>Atelopus nanay</i>	Coloma (2002)
<i>Atelopus palmatus</i>	Marcillo-Lara et al. (2020)
<i>Atelopus peruensis</i>	Gray and Cannatella (1985)
<i>Atelopus pulcher</i>	Lötters et al. (2002)
<i>Atelopus sorianoii</i>	Mijares-Urrutia and La Marca (2005)
<i>Atelopus</i> sp. aff. <i>spumarius</i> (Puyo, Ecuador)	Duellman and Lynch (1969)
<i>Atelopus spumarius</i>	Rodríguez and Duellman (1994)
<i>Atelopus subornatus</i>	Lynch 1986; Enciso-Calle et al. (2017)
<i>Atelopus tamaense</i>	Mijares-Urrutia and La Marca (2005)
<i>Atelopus tricolor</i>	Lavilla et al. (1997)
<i>Atelopus varius</i>	Starrett (1967); Savage (2002)
<i>Atelopus zeteki</i>	Lindquist and Hetherington (1998)

a phylogenetic analysis. Given that the monophyly of the genus is supported, and some characters are invariable within the five species (see “Results”), we discuss the evolution of characters regarding *Atelopus* and other bufonids and treat apomorphic character states as putative synapomorphies for the genus.

We selected taxa for comparison based on Jetz and Pyron’s (2018) phylogenetic hypothesis that has a dense taxonomic sampling. We personally examined representatives of 11 bufonid genera and complemented our dataset with literature information (e.g., Viertel 1982; Müller 2019). The larva of *Frostius erythropthalmus* is not known, but data is available for *F. pernambucensis* (Dubeux et al. 2023), and we assumed the monophyly of *Frostius* and the sister relationship between *F. erythropthalmus* and *F. pernambucensis* for optimization purposes. We included representatives of Odontophrynidae larvae, the sister group of Bufonidae in Jetz and Pyron’s (2018) hypothesis, as outgroups. The complete list of examined material and references used is listed in the Appendix.

We propose nine transformation series (Hennig 1966; Grant and Kluge 2004) to account for the variation of the buccopharyngeal morphology in the larvae of *Atelopus* in comparison with other bufonids. The character matrix was built and edited in Mesquite V. 3.70 (Maddison and Maddison 2021) (Supporting Information), and character optimization was performed in T.N.T. v. 1.5 (Goloboff and Catalano 2016). There is no information for several bufonid genera, but we opt to include them in our optimization to

demonstrate which parts of the bufonids tree of life require more studies on larval morphology.

Results

Buccopharyngeal morphology

The buccopharyngeal morphology of the five species is quite similar. A single, condensed, description is provided and differences noted when present.

Buccal roof (Figs. 2a, 4a, 5a, 6a, 7a) triangular Prenarial arena semi-elliptical, with a pendulum-like papilla (Fig. 3a) and several secretory pits (Fig. 3b, c; absent in *A. subornatus*); these pits are located immediately posterior to the upper jaw sheath and before the pendulum-like papilla, covering the entire width of that region. The pits are rounded, and a secretion residue can be observed in several pits (Fig. 3c). Internal nares elliptical, transversally oriented; posterior valve free, lacking marginal projection. Vacuities (Fig. 3d, e) present, circumscribed by margins of inner nares, presenting ciliated cells (Fig. 3f). Postnarial arena diamond-shaped, two conical, tall postnarial papillae; first pair shorter than second pair. Lateral ridge papillae short, triangular, bifurcated (not bifurcated in *A. carrikeri*). Median ridge low, conical (bifurcated in *A. carrikeri*), papilla-like. Buccal roof arena poorly defined, completely lacking papillae or pustulation.

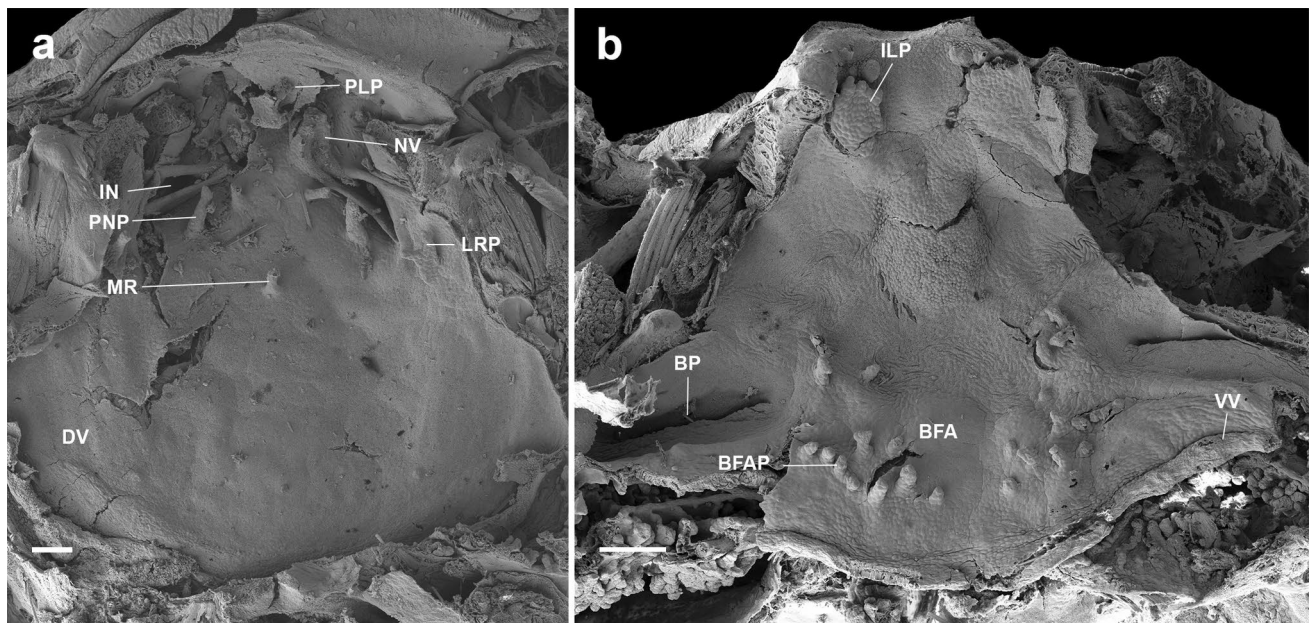


Fig. 2 Buccal roof (a) and floor (b) of the tadpole of *Atelopus balios* (QCAZ 2670) at stage 34. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; ILP,

infralabial papillae; IN, internal nares; LRP, lateral ridge papilla; MR, median ridge; NV, narial vacuities; PLP, pendulum-like papillae; PNP, postnarial papillae; VV, ventral velum. Scale bar = 100 μ m

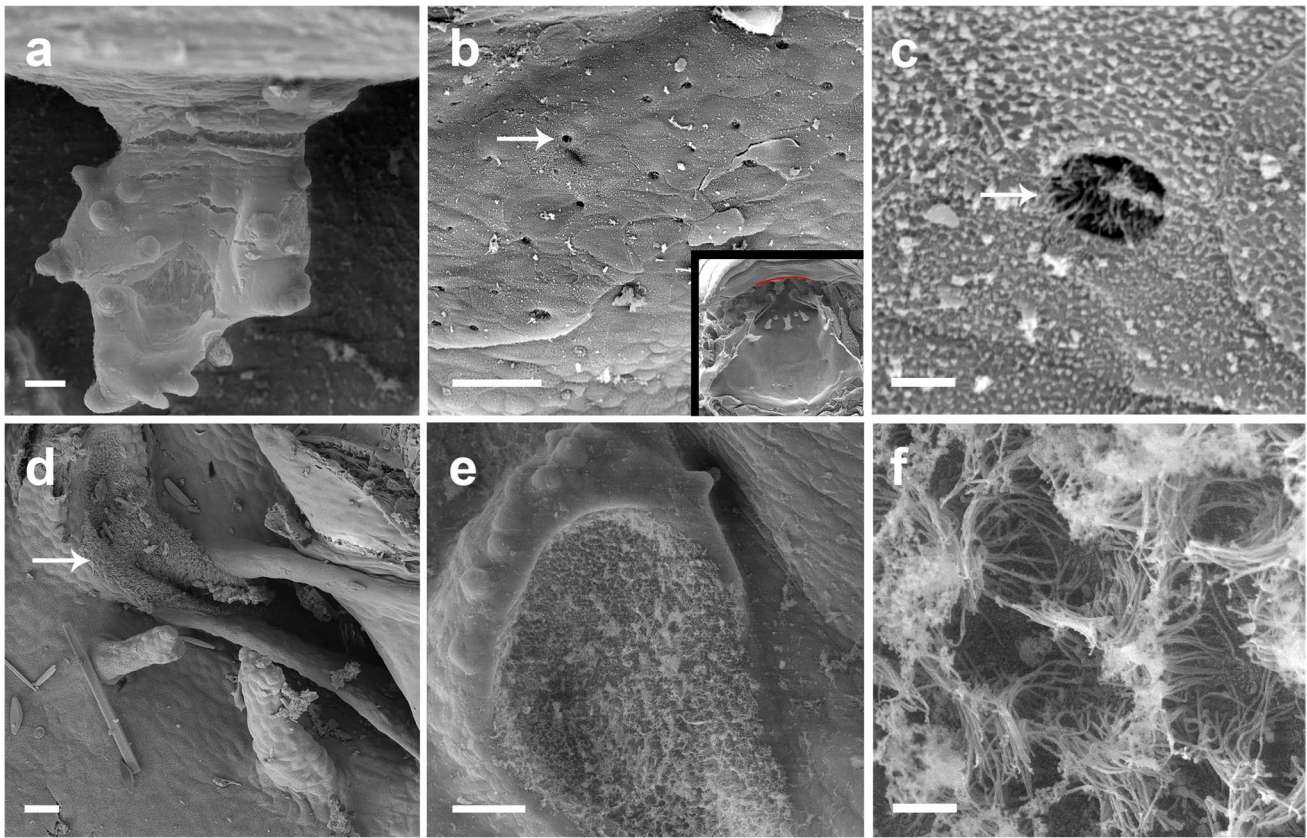


Fig. 3 Anatomical details of the pendulum-like papilla in the pre-narial arena (**a**), of the glandular zone (**b**, **c**), of the narial vacuities (**d**, **e**) with its ciliated epithelium (**f**) in the larvae of *Atelopus carrikeri* (CBUMAG 0892) at stage 35. Inset in (**c**) showing in red the area

in the buccal roof where the secretory pits can be found. Character states, when present, are identical in the other studied species. Scale bars = 50 μm (**a**, **d**, **e**), 20 μm (**b**), and 2 μm (**c**, **f**)

Dorsal velum medially discontinued, devoid of papillae or projections, arch-shaped.

Buccal floor (Figs. 2b, 4b, 5b, 6b, and 7b) triangular Single pair of flat, wide, infralabial papillae; tip crenulated. Lingual bud poorly defined; lingual papillae absent. Buccal floor arena bell-shaped; buccal floor arena papillae present (10–11 in *A. balios*; 10–12 in *A. carrikeri*; 13–14 in *A. nahumae*; 9–11 in *A. nanay*; 7–8 in *A. subornatus*). Buccal floor arena lacking pustulations. Prepocket papillae and pustulation absent. Buccal pockets deep, wide, oblique slit-shaped. Ventral velum present; spicular support inconspicuous; medial notch absent; marginal projections present; secretory pits poorly developed; secretory ridges present. Branchial basket triangular, short, poorly developed, wider than long. Three filter cavities, well-defined, partially covered by ventral velum.

Evolution of characters

Character 1: pre-narial arena, pendulum-like papilla: absent (0), present (1)

The pre-narial arena is the area between the internal nares and the mouth opening (Wassersug 1976). Several structures have been reported in that region in different anuran larvae, such as crests, ridges, and pustulations, among others (e.g., Wassersug 1980; Vera Candiotti 2007; Nascimento et al. 2013; Dias et al. 2018a, b). *Atelopus* larvae have a pendulum-like papillae (state 1; Fig. 3a).

Taxonomic distribution and optimization The presence of a pendulum-like papillae was invariable in the five studied *Atelopus* species and also present in *Frostius pernambucensis* larvae; current optimization of this character (Fig. 8a)

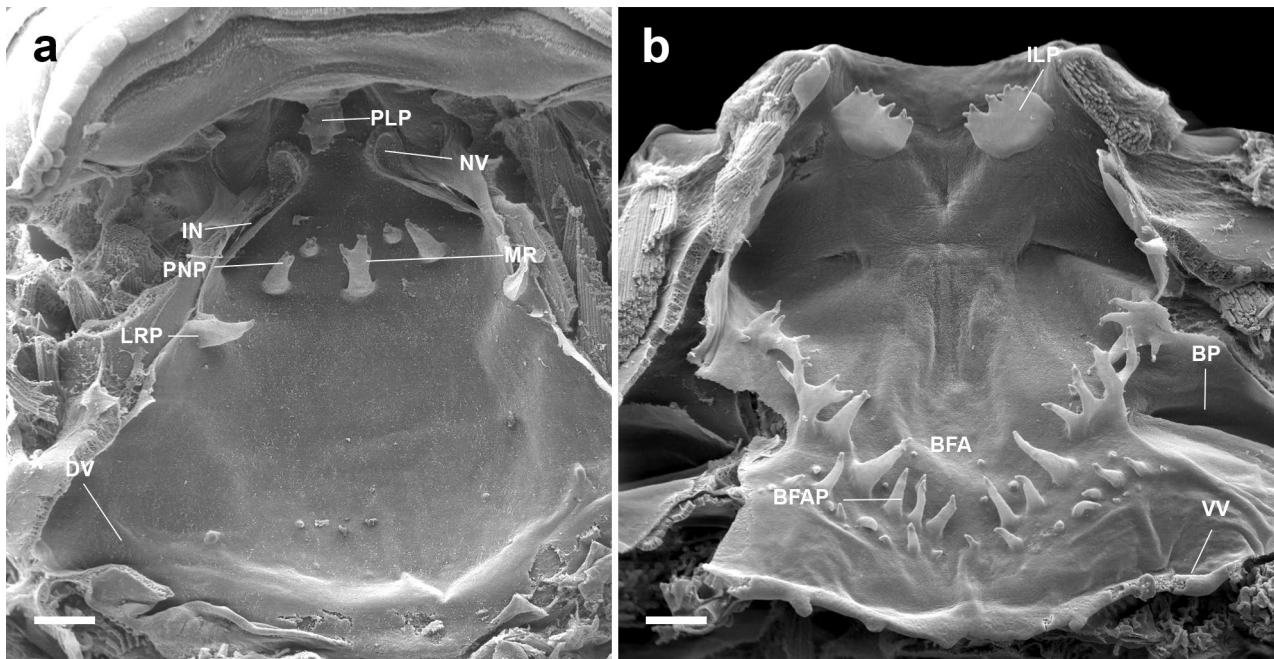


Fig. 4 Buccal roof (a) and floor (b) of the tadpole of *Atelopus carikeri* (CBUMAG 0892) at stage 35. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; ILP,

infralabial papillae; IN, internal nares; LRP, lateral ridge papilla; MR, median ridge; NV, naria vacuities; PLP, pendulum-like papillae; PNP, postnarial papillae; VV, ventral velum. Scale bar = 100 μ m

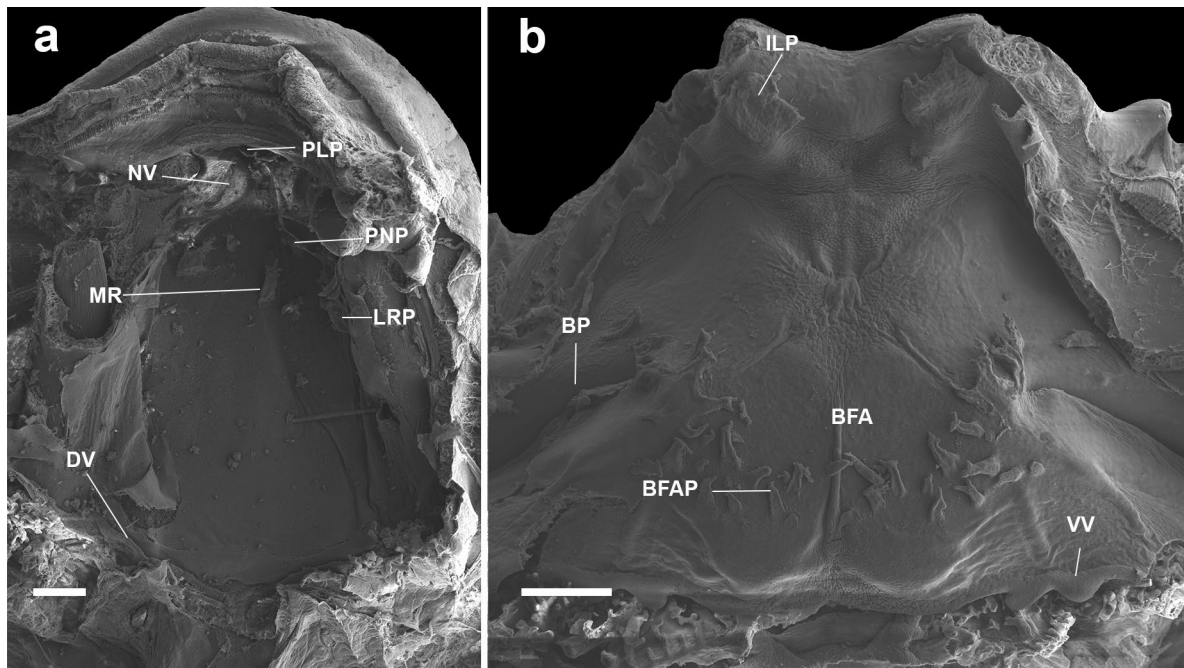


Fig. 5 Buccal roof (a) and floor (b) of the tadpole of *Atelopus nahumae* (ICN 33202) at stage 29. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; ILP,

infralabial papillae; IN, internal nares; LRP, lateral ridge papilla; MR, median ridge; NV, naria vacuities; PLP, pendulum-like papillae; PNP, postnarial papillae; VV, ventral velum. Scale bar = 100 μ m

suggests it as a synapomorphy of *Atelopus*. Additionally, similar papilla was observed in the suctional tadpoles of *Ansonia* and *Werneria* (Fig. 9), but the absence of data for their

close related taxa (*Ansonia*: *Pelophryne* and *Ghatophryne*; *Werneria*: *Nectophryne*, *Didynapius*, and *Nimbaphrynoides*) renders the optimization ambiguous within these lineages.

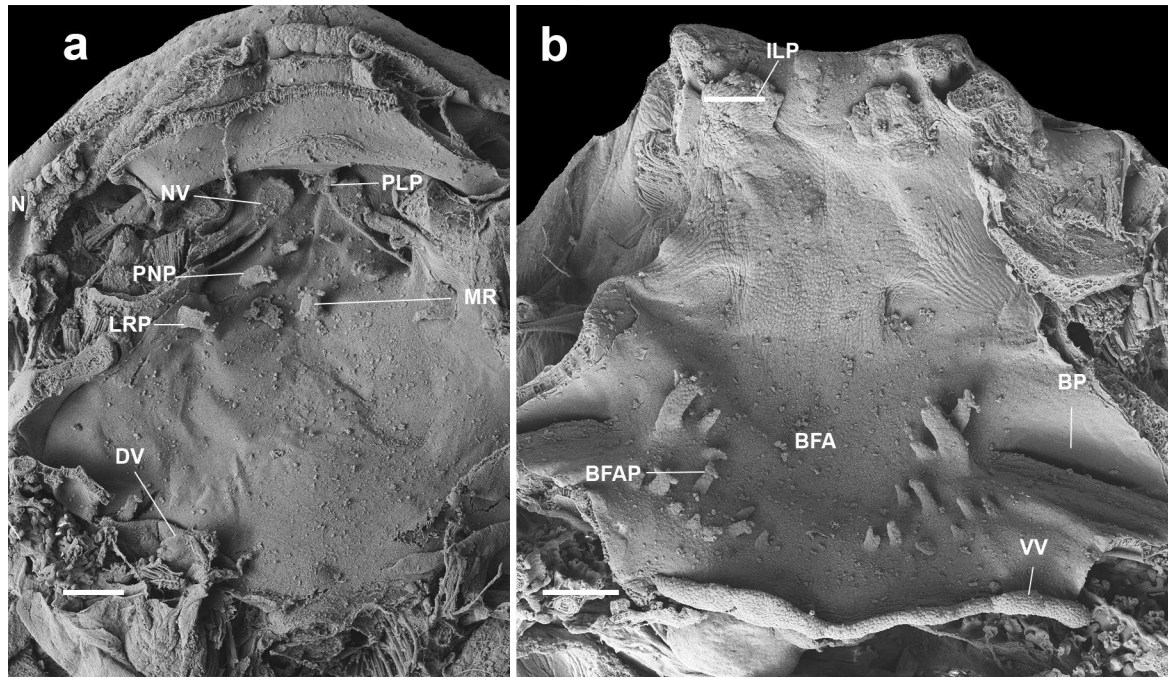


Fig. 6 Buccal roof (a) and floor (b) of the tadpole of *Atelopus nanay* (QCAZ 3672) at stage 27. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; ILP,

infralabial papillae; IN, internal nares; LRP, lateral ridge papilla; MR, median ridge; NV, naria vacuities; PLP, pendulum-like papillae; PNP, postnarial papillae; VV, ventral velum. Scale bar = 100 µm

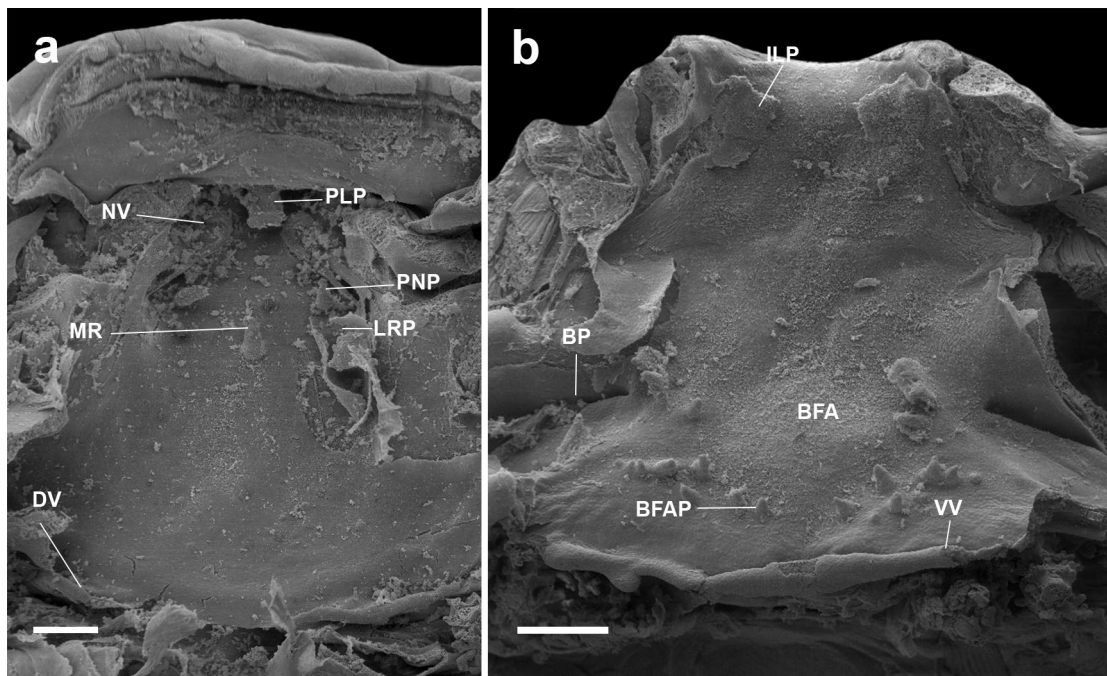


Fig. 7 Buccal roof (a) and floor (b) of the tadpole of *Atelopus subornatus* (ICN 31435) at stage 32. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; ILP,

infralabial papillae; IN, internal nares; LRP, lateral ridge papilla; MR, median ridge; NV, naria vacuities; PLP, pendulum-like papillae; PNP, postnarial papillae; VV, ventral velum. Scale bar = 100 µm

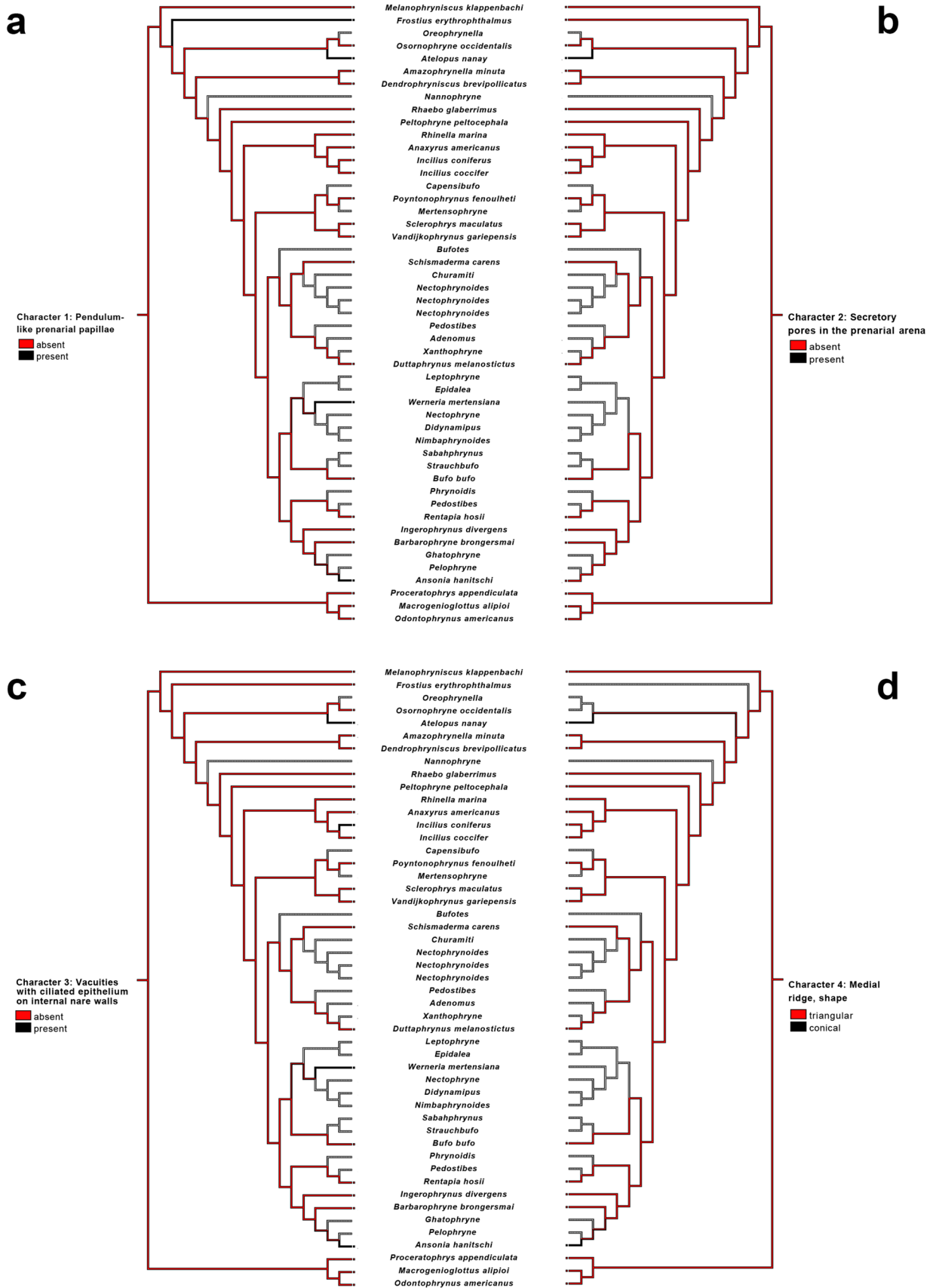


Fig. 8 Parsimonious optimization of characters 1 (a), 2 (b), 3 (c), and 4 (d). Gray represents unknown condition

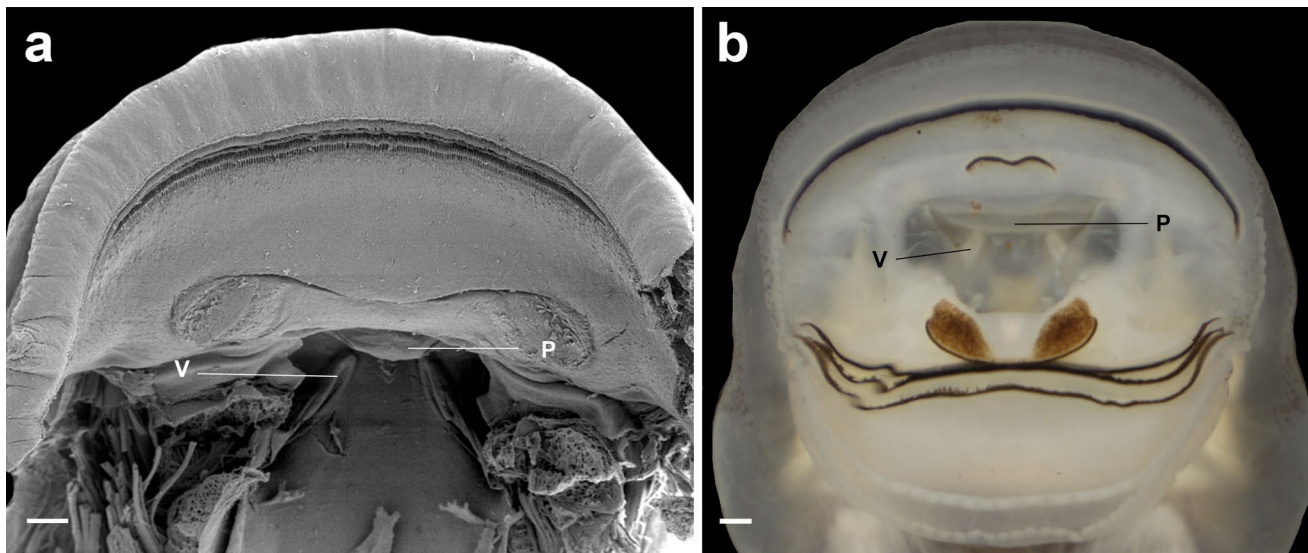


Fig. 9 Presence of a pendulum-like papillae and of narial vacuities in the bufonid larvae of *Ansonia hanitschi* (ZMH A08803; stage 29) and *Werneria mertensiana* (ZMB 79695; stage 30). Scale bars = 200 μ m

Character 2: prenarial arena, glandular zone: absent (0), present (1)

In the species of *Atelopus*, a large portion of the prenarial arena is covered with small pits (Fig. 3b), very similar to secretory pits of the ventral velum of other tadpoles. These pits are rounded, deep, being secreted. The function of these pits in such peculiar region is unknown.

Taxonomic distribution and optimization Character state 1 was observed only in *Atelopus* (except in *A. subornatus*), and we suggest it as a new synapomorphy for the genus (Fig. 8b). As far as we know, it has not been reported in any other anuran larvae.

Character 3: vacuities circumscribed by margins of inner nares: absent (0), present (1)

Van Eeden (1951:9) found what he called “a band of ciliated epithelium” in *Ascaphus truei* and suggested that the cilia could have some role in the feeding mechanism proposed by Noble (1927). Wassersug (1980) described this “*cul de sac*” feature in other taxa and suggested that it may have a chemosensory function. Later, vacuities have been reported in several taxa, particularly in Cophomantinae (e.g., Kolenc et al. 2008), Leptodactylidae (e.g., Nascimento et al. 2021), Centrolenidae (e.g., Rada et al. 2019; Dias et al. 2020), and in tadpoles of the *Scinax perpusillus* species group (e.g., Dias and Pie 2021).

Taxonomic distribution and optimization We observed the presence of vacuities in all the five *Atelopus* examined, which suggested it as another synapomorphy for the genus (Fig. 8c). We also observed the presence of vacuities in *Ansonia* and *Werneria* (Fig. 9); however, as discussed above (see character 1), the lack of data precludes a non-ambiguous optimization of this character state in those clades.

Character 4: median ridge, shape: triangular (0), conical (1), trapezoidal (2); unordered

The median ridge marks the end of the postnarial arena. It is a feature highly variable among tadpoles. According to Wassersug (1980), due to its central location, the median ridge may play a role in splitting the respiratory current into right and left ones. The shape of the median ridge has been used as a character in the systematics of several groups; for instance, Dias et al. (2019a) suggested a trapezoidal median ridge as a synapomorphy for the *Proceratophrys bigibbosa* species group. Within examined taxa, three different morphologies were observed for the median ridge: triangular (state 0), as in most of bufonids, conical, as in *Atelopus* and *Ansonia* (state 1), and trapezoidal (state 2) in some outgroup taxa (e.g., *Odontophrynus*).

Taxonomic distribution and optimization Conical median ridge was present in all *Atelopus* examined and also in *Ansonia*. The absence of median ridge in *Osornophryne* (inapplicable) and the lack of data for *Oreophrynella* render

the optimization of this character ambiguous (Fig. 8d). It is likely that *Oreophrynella* will also lack a median ridge due to its endotrophic development—see Wassersug and Duellman (1984) for discussion of buccopharyngeal cavity in endotrophic and direct-developer frogs—which will prevent the optimization of this character in the future as well.

Character 5: buccal roof arena papillae: absent (0), present (1)

The buccal roof arena papillae are usually conical, with one or few bifurcated papillae (Wassersug 1976). Some authors (e.g., Wassersug 1980) suggested that these papillae may contribute to the sorting of food particles in the mouth. These papillae delimitate the buccal roof arena and may be very abundant, as in *Hylodes* (e.g., Montesinos et al. 2022), or completely absent, as in *Atelopus*, which renders the buccal roof arena also absent.

Taxonomic distribution and optimization The optimization of this character is complex (Fig. 10A); we found the buccal roof arena papillae absent in all examined *Atelopus*, plus in the endotrophic larvae *Frostius pernambucensis*, in the direct developer tadpole-like *Osornophryne occidentalis*, in *Amazophrynella minuta*, and in *Ansonia*. The optimization of this character is ambiguous in all mentioned taxa. The presence of buccal roof papillae in *Dendrophryniscus brevipollicatus* and the absence of data for *Nannophryne* make the optimization of this character difficult at the base of Bufonidae except *Melanophryniscus*.

Character 6: buccal roof pustulations: absent (0), present (1)

In many anuran taxa, both buccal floor and roof are covered with a field of rounded pustulation. The function of these structures is unknown, but its abundancy seems to be correlated with benthic, lotic species (e.g., Vera Candiotti 2007; Dias et al. 2014). The reduction or absence of pustulations has been reported in endotrophic (e.g., Wassersug and Duellman 1984; Wassersug and Heyer 1988), fossorial (e.g., Wassersug 1980; Rada et al. 2019; Dias et al. 2020), macrophagous (e.g., Wassersug 1980; Vera Candiotti et al. 2004; Vera Candiotti 2005; Dias et al. 2019b), oophagous (e.g., Vera Candiotti et al. 2021), and suctorial (e.g., Wassersug and Heyer 1988) tadpoles. In all examined *Atelopus*, there was no pustulation in the buccal roof.

Taxonomic distribution and optimization The absence of pustulations followed the exact same pattern as that of the absence of buccal roof arena papillae, being absent in *Ansonia*, *Amazophrynella minuta*, *Frostius pernambucensis*, *Osornophryne occidentalis*, and *Schismaderma carens*.

Thus, the optimization of this character is highly ambiguous (Fig. 10b).

Character 7: number of infralabial papillae: 2 (0), 4 (1)

The infralabial papillae are the first papillae observed in the buccal floor; they are positioned right after the mouth's opening and can vary in number, size, and shape—there may be a single pair as in *Cycloramphus stejnegeri* (Wassersug and Heyer 1983) or up to 12 in tadpoles of *Heleophryne natalensis* (Wassersug and Heyer 1988); they can be conical (e.g., Vera Candiotti 2007) or branched (e.g., Dias et al. 2019a). Wassersug (1980) hypothesized that these papillae play an important role selecting food particles that will enter in the buccal cavity of tadpoles.

Taxonomic distribution and optimization *Atelopus* as well as all other bufonids present only a single pair (two papillae) of infralabial papillae, contrasting with the two pairs (four) of papillae in Odontophrynidae. Thus, the presence of two infralabial papillae is a synapomorphy for Bufonidae (Fig. 10c).

Character 8: lingual papillae: absent (0), present (1)

Lingual papillae are located in the tongue anlage (Wassersug 1976) and are likely to have gustatory function (Hammerman and Thomas 1967). Lingual papillae are present in most frogs, although absent by definition in the aglossal pipids and in several other lineages.

Taxonomic distribution and optimization *Atelopus* larvae lack lingual papillae (state 0). The same condition was observed in *Frostius* and *Osornophryne*. Given the presence of lingual papillae in *Melanophryniscus* and other bufonids, the optimization of this character was ambiguous (Fig. 10d).

Character 9: buccal floor pustulations: absent (0), present (1)

Pustulations are commonly present in the buccal floor of tadpoles (e.g., Vera Candiotti 2007; Nascimento et al. 2013; Dias et al. 2014) and have rarely been reported absent (e.g., *Ascaphus truei*; Wassersug 1980).

Taxonomic distribution and optimization Pustulations on the buccal floor were absent in all examined *Atelopus*. Also, *Frostius*, *Osornophryne*, *Amazophrynella*, and *Dendrophryniscus* lacked these pustulations, rendering its absence a synapomorphy for all bufonids minus *Melanophryniscus* (Fig. 11). Pustulations were also absent in *Ansonia* and *Schismaderma carens*.

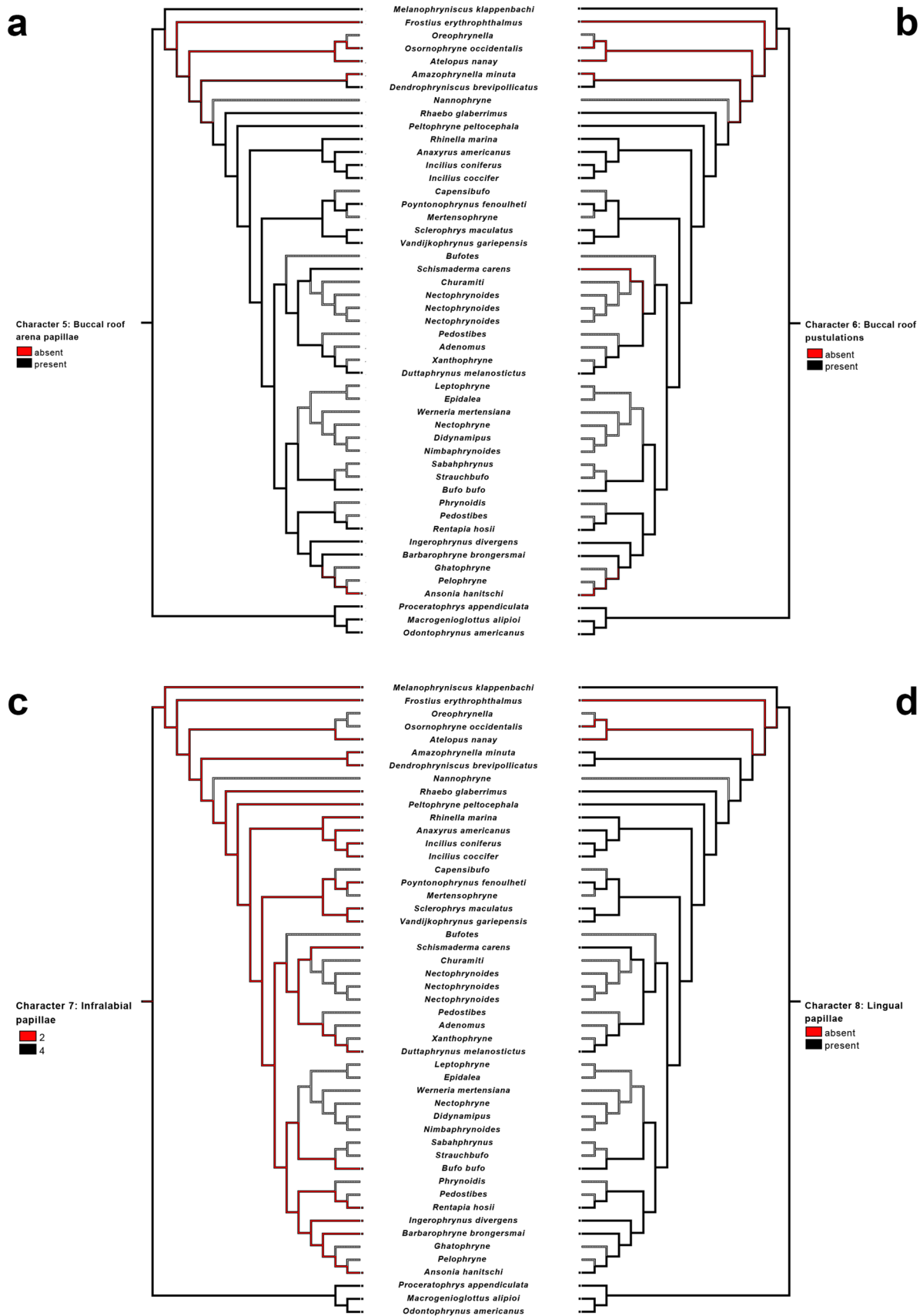
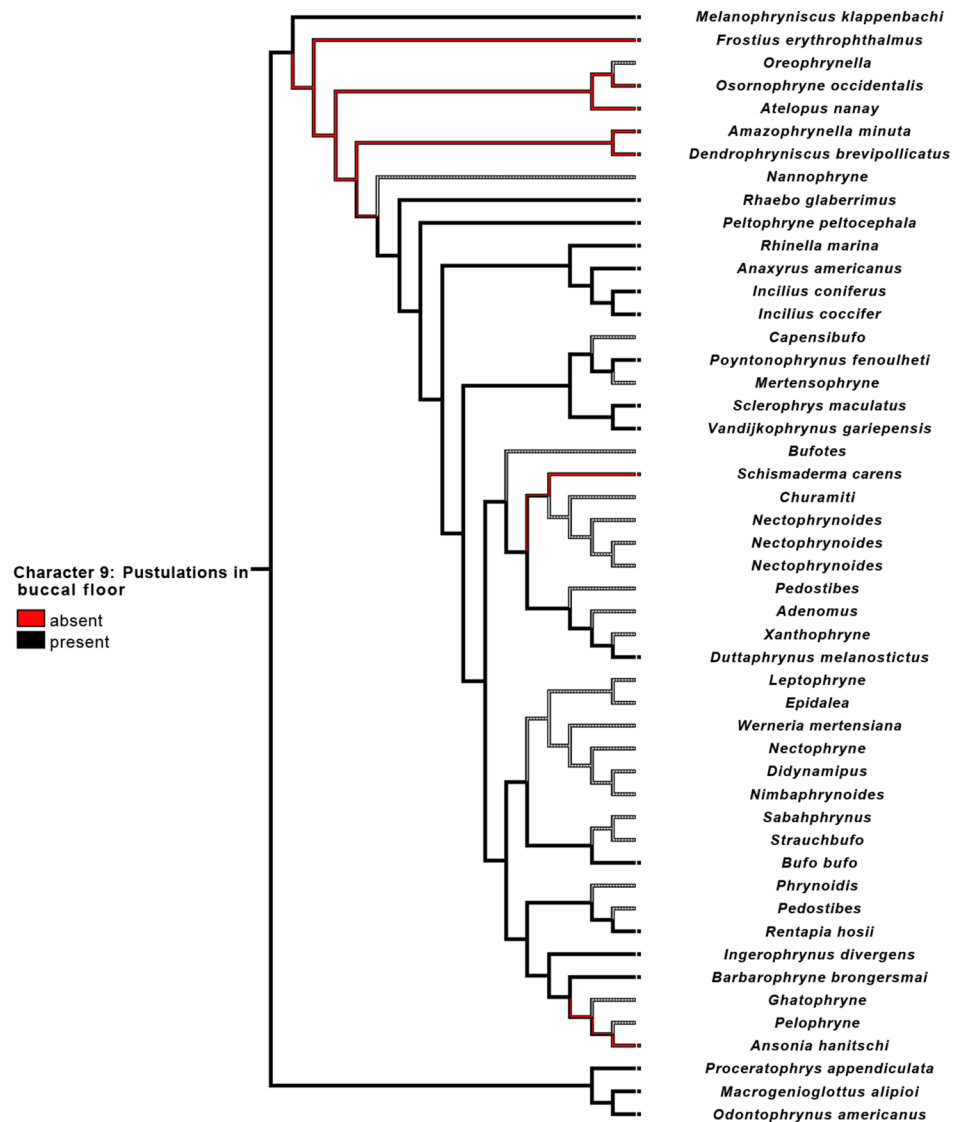


Fig. 10 Parsimonious optimization of characters 5 (a), 6 (b), 7 (c), and 8 (d). Gray represents unknown condition

Fig. 11 Parsimonious optimization of character 9. Gray represents unknown condition



Discussion

Larval morphology and the systematics of bufonids

Atelopus have a distinctive larva within bufonids; their abdominal sucker, wide oral disc, and color pattern (e.g., Duellman and Lynch 1969; Lötters 1996; Pérez-González et al. 2020) make these tadpoles easily distinguished from other bufonids. The comparative analysis of the buccopharyngeal cavity of *Atelopus* revealed a series of new unique, intriguing character states in these tadpoles. The *Atelopus* buccopharyngeal cavity is characterized by (1) presence of a pendulum-like papillae in the prenarial arena, (2) presence of a glandular zone in the prenarial arena, (3) narial vacuities, (4) conical median ridge, (5) absence of buccal roof arena papillae, (6) absence of buccal roof pustulations, (7) single pair of infralabial papillae, (8) absence

of lingual papillae, and (9) absence of pustulations in the buccal floor. We propose that characters 1, 2, and 3 are new synapomorphies for the genus *Atelopus*.

The prenarial arena of tadpoles is characterized by the presence of several features, ranging from pustulations to crests (e.g., Vera Candioti 2007). These features play an important role in the feeding mechanism of tadpoles; for instance, it has been hypothesized that the presence of an inverted V structure in the prenarial arena of umbelliform tadpoles' interlocks with the infralabial papillae to prevent large food particles from entering the mouth (Wassersug 1980; Dias et al. 2018b, 2021). The presence of a large, pendulum-like papillae in the larvae of *Atelopus* is very intriguing; a similar feature is rare among anurans. We speculate two putative functions to it: (1) such large papilla would prevent large particles of reaching the vacuities' area; (2) it could deviate the water flow to the vacuities. It is important to note that vacuities possibly have a

chemosensory function (Wassersug 1980), and both diverting water towards them, as well as preventing them from being obstructed by large particles, seem possible explanations for the presence of this pendulum-like papillae. Nevertheless, further studies are required to test our hypotheses. Interesting to note that a similar, although narrower, feature was described in the prenarial arena of *Rhinella quechua* (Aguayo et al. 2009), another gastromyzophorous bufonid.

The posterior region of buccal floor is usually marked by secretory tissue in most anurans (Kenny 1969; Wassersug 1980)—secretory tissue, however, may be present in other regions, as in the buccal floor of *Rhacophorus vampyrus* (Vera Candioti et al. 2021). Usually, secretory cells are organized in pits and ridges (Wassersug and Rosenberg 1979). Many authors agree with the hypothesis that the secretory pits, through the production of mucus strands, may aid in food entrapment (de Jongh 1968; Kenny 1969; Wassersug 1976, 1980; Wassersug and Rosenberg 1979). Although experimental studies testing this hypothesis are lacking, the anatomy and topographical distribution of the secretory pits provide some support to that view. We observed secretory pits in the prenarial arena the *Atelopus* tadpoles examined, except in *A. subornatus* that phenotypically resembles the secretory pits of the velum of anuran larvae. The function of these pits is unknown and, as far as we know, this character state has never been reported for other anurans. Further studies are required to understand the biological meaning of these pits, notwithstanding, and we propose their presence in the prenarial arena as a synapomorphy for the genus *Atelopus*.

Vacuities were originally described in *Ascaphus* tadpoles (van Eeden 1951) and since then reported in few taxa (e.g., Wassersug 1980; d'Heursel and Haddad 2007; Magalhães et al. 2015; Pezzuti et al. 2015; Dias and Pie 2021). Kolenc et al. (2008) suggested that the presence of vacuities was a synapomorphy for the Cophomantini tribe. Dias et al. (2020; see also Rada et al. 2019) observed this feature in several centrolenids, suggesting its presence as a synapomorphy for glass frogs. However, as more researchers pay attention to this structure, more reports emerge. For instance, recently, Nascimento et al. (2021) reported the presence of vacuities in tadpoles of *Lithodytes lineatus* and in several species of the *Leptodactylus pentadactylus* species group; Dias and Pie (2021) reported them in the larvae of *S. v-signatus* and suggested it as synapomorphy for the *S. perpusillus* species group. These findings suggest that vacuities are more widely distributed within anurans than previously imagined. We observed vacuities in all examined *Atelopus* and also in other unrelated bufonids, such as *Ansonia*, *Incilius*, and *Werneria*. Current optimization suggests that the presence of vacuities in *Atelopus* is a synapomorphy. We also predict that, as more taxa are examined, the presence of vacuities will also optimize as a synapomorphies for *Ansonia* and *Werneria*.

The median ridge is highly variable among anuran larvae (e.g., Wassersug 1980; Vera Candioti 2007; Dias et al. 2019a, 2021), but conical median ridge is particularly rare. It has been reported in few taxa, such as the suctorial *Heleophryne natalensis* (Wassersug and Heyer 1988), and was present in all *Atelopus* examined, although with ambiguous optimization regarding bufonids.

Lack of pustulations and papillae in the buccal floor and roof is not common in anurans and often associated with endotrophic development (Wassersug and Duellman 1984; Romero-Carvajal et al. 2023). Nevertheless, feeding tadpoles may also present a reduction or lack these features, as in the case of oophagous (e.g., Vera Candioti et al. 2021) and macrophagous (e.g., Dias et al. 2019b, 2023) tadpoles. The diet of *Atelopus* larvae is poorly unknown—as that of most species (Altig et al. 2007)—but some elements of their anatomy may suggest some degree of macrophagy; the secretory tissues involved in filtering particles are reduced, they lack several papillae and pustulation, lingual papillae are absent, and the presence shortened intestines (PHD, personal observation). In captivity, the larvae of *Atelopus flavescens* were reported to feed on algae (Gawor et al. 2012), but fish food was also supplemented. Both captivity and field observation as well as detail study of trophic ecology are necessary to better understand what these tadpoles eat.

We observed a single pair of infralabial papillae in *Atelopus* larvae. This condition differs of that observed in tadpoles of Odontophrynidae that usually present two pairs of infralabial papillae (e.g., Nascimento et al. 2013; Dias 2020). Tadpoles of other closely related lineages, such as centrolenids and leptodactylids, also present two pairs of infralabial papillae, (e.g., Wassersug and Heyer 1988; Vera Candioti et al. 2007; Rada et al. 2019; Dias et al. 2020; Nascimento et al. 2020). Dubeux et al. (2023) suggested that the presence of two infralabial papillae could represent a synapomorphy of Bufonidae, and we provide additional evidence for that hypothesis.

Lingual papillae are also present in most anuran larvae, with some few exceptions (e.g., micohylids and several Dendropsophini; Vera Candioti 2007; Dias et al. 2023). All *Atelopus* lack lingual papillae, as well as the endotrophic larvae of *Frostius* (Dubeux et al. 2023) and the direct developer *Osornophryne* (Romero-Carvajal et al. 2023). The optimization of this character state is ambiguous, but it is interesting noting that absence of it in *Frostius* and in *Osornophryne* is probably related to endotrophic development, while *Atelopus* retained a plesiomorphic state or lost those papillae independently is an interesting evo-devo question.

Convergent evolution in gastromyzophorous and suctorial tadpoles

Convergent evolution is the independent evolution of homoplastic character states in different lineages, usually

in association with similar selective pressures (Losos et al. 1998; Losos 2011). Gastromyzophorous tadpoles evolve independently at least eight times in anurans, although highly concentrated in two clades, bufonids and ranids, with one instance in hylids. Gastromyzophorous tadpoles have been reported in *Amolops*, *Huia*, *Meristogenys*, *Sumaterana*, *Wijayarana*, and *Rana sauteri*—(e.g. Kuramoto et al. 1984; Arifin et al. 2021); in three species of the *Rhinella veraguensis* group (*R. chrysophora*, *R. quechua*, and *R. veraguensis*), in *Sabahphrynus maculatus*, in *Adenomus kandianus*, and in *Bufo aspinius* (Rao and Yang 1994; Matsui et al. 2007; Aguayo et al. 2009; Meegaskumbura et al. 2015); finally, the hylid *Phyllodytes gyrinaethes* is also gastromyzophorous (Peixoto et al. 2003; Vera Candioti et al. 2017).

Notwithstanding, the development of a belly sucker was not the only solution provided by natural selection to enable tadpoles to adhere to the substrate in fast-flowing waters; suctorial tadpoles also evolved in several lineages (Fig. 12), such as *Ansonia*, *Nasikabatrachus*, *Odontobatrachus*, and many hylids. Gastromyzophorous and suctorial tadpoles, in general, have convergent phenotypic traits, such as enlarged oral discs, depressed bodies with extended and broad snouts, robust and well-keratinized jaw sheaths, strong tails with reduced tail fins, dorsal eyes (Fig. 13), and

several modifications in the musculoskeletal system (Gan et al. 2015; Vera Candioti et al. in press).

The buccopharyngeal cavity of gastromyzophorous and suctorial tadpoles also evolved convergently. The buccopharyngeal cavity has been described for few taxa: *Amietia ruwenzorica* (Viertel et al. 2012) *Ansonia longidigita*, *Ansonia hanitschi*, *Ansonia minuta* (Inger 1985; Haas and Das 2008), *Ascaphus truei* (Wassersug 1980), *Heleophryne natalensis* (Wassersug and Heyer 1988), *Huia cavitympanum*, *Meristogenys phaeomerus*, *Meristogenys poecilus*, *Meristogenys kinabaluensis* (Inger 1985), *Nasikabatrachus sahyadrensis* (Raj et al. 2012), and *Rhinella quechua* (Aguayo et al. 2009).

A different combination of the characters described here for *Atelopos* is present in several of these species (Table 2; Fig. 13). For instance, the presence of a developed element in the prenarial arena is almost invariable within gastromyzophorous and suctorial larvae; similarly, vacuities are present in the many of taxa, suggesting an adaptive value in these traits. Unfortunately, for many of these characters, there are no robust hypotheses about their function and how they might increase fitness in torrent environments is still obscure.

Nevertheless, the fact that some species described as suctorial (e.g., *Amietia ruwenzorica*) differ phenotypically from

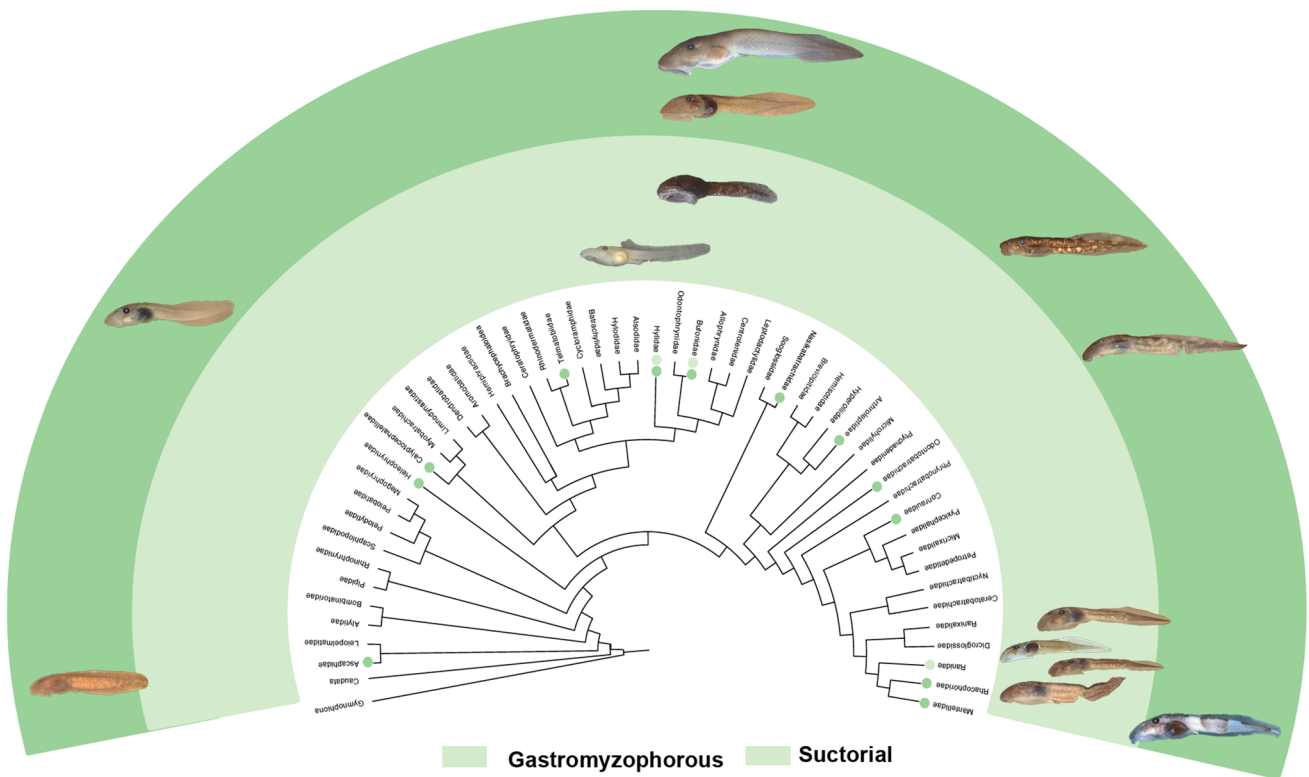


Fig. 12 Gastromyzophorous and suctorial larvae evolved independently several times within anurans. The phylogenetic hypothesis of Jetz and Pyron (2018) showing the families in which these tadpoles have evolved

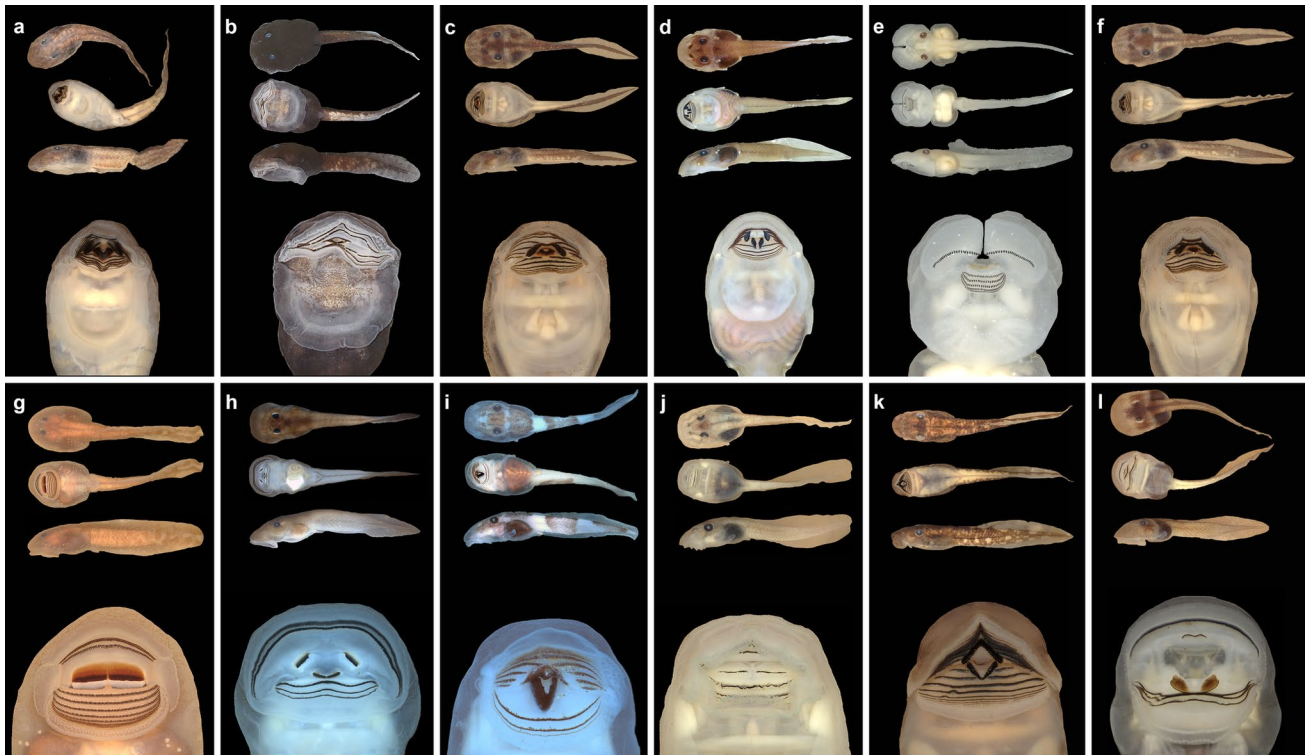


Fig. 13 Morphology of gastromyzophorous (a–f) and suctorial (g–l) tadpoles. Dorsal views and details of the oral disc; dorsal, ventral, and lateral views and detail of the oral disc of *Amolops creminobatus* (a), *Atelopus subornatus* (b), *Mesristogenys jerboa* (c), *Huia cavi-*

tympanum (d) *Phyllodytes gyrinaethes* (e), *Sumaterana dabulescens* (f), *Ascaphus truei* (g), *Ansonia hanitschi* (h), *Boophis schubae* (i), *Heleophryne hewitti* (j), *Astylosternus robustus* (k), and *Werneria mertensiana* (l)

Table 2 Comparative buccopharyngeal morphology among gastromyzophorous and suctorial larvae

Taxa/character	Prenarial arena element	Narial vacuities	Median ridge	Papillae buccal roof	Lingual papillae	Reference
<i>Amietia</i>	Present	Absent	Triangular	Abundant	Present	Viertel et al. (2012)
<i>Ansonia</i>	Present	Present	Conical	Absent	Absent	Inger (1985); Haas and Das (2008); this study
<i>Ascaphus</i>	Absent	Present	Absent	Absent	Present	Wassersug (1980); this study
<i>Astylosternus</i>	Absent	Absent	Absent	Reduced	Absent	This study
<i>Atelopus</i>	Present	Present	Conical	Absent	Absent	This study
<i>Boophis</i>	Present	Present	Conical	Absent	Absent	This study
<i>Corythomantis</i>	Present	Present	Triangular	Reduced	Present	Oliveira et al. (2017)
<i>Heleophryne</i>	Present	Present	Conical	Absent	Present	Wassersug and Heyer (1988)
<i>Hyloscirtus</i>	Present	Present	Conical	Reduced	Present	Aguilar et al. (2007)
<i>Huia</i>	Absent	Absent				Inger (1985)
<i>Megastomatohyla</i>	Present	?	Conical	Reduced	Absent	Wassersug (1980)
<i>Meristogenys</i>	Absent	Present	Conical	Reduced	Absent	Inger (1985); this study
<i>Nasikabatrachus</i>	Present	Absent				Raj et al. (2012)
<i>Odontobatrachus</i>	Absent	Present	Absent	Reduced	Absent	This study
<i>Rhinella</i>	Present	Absent	Present	Reduced	Absent	Aguayo et al. (2009)
<i>Telmatobius</i>	Absent	Absent	Triangular	Abundant	Present	Aguilar et al. (2007)

that pattern (see Viertel et al. 2012), resembling rheophilous larvae (e.g., Montesinos et al. 2022, 2023), suggests that internal morphology characters should also be included in the studies of ecomorphological guilds of anurans. Moreover, it also suggests that the current structure of ecomorphological guilds might hide ecological, functional, and morphological diversity.

Conclusion and remarks

The buccopharyngeal cavity provided additional information to understand the taxonomy and the evolution of *Atelopus*. Our study can be added to the growing list of studies about larval morphology of previously poorly known groups in the last 20 years; one important conclusion from those studies is that as more species are investigated, novel and astonishing new morphologies are discovered (e.g., Haas et al. 2006, 2014; Grosjean et al. 2011; Rowley et al. 2012; Vera Candioti et al. 2017, 2021; Dias 2020; Dias et al. 2023). Also, tadpoles have been proven excellent model organism to study evolutionary phenomena; for instance, convergent evolution has been constantly reported in tadpoles of different lineages (e.g., Rada et al. 2019; Grosjean and Preininger 2020) demonstrating how they can be used to better understand the independent evolution of similar phenotypes. This highlights the importance of training new generations of morphologists and evolutionary biologists interested in tadpoles.

Appendix. Examined material

All the material used in the present study is housed at American Museum of Natural History (AMNH), Amphibians' Collection, Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Eugenio Izecksohn, deposited at Universidade Federal Rural do Rio de Janeiro (EI), Herpetological Collection of the Universidad del Magdalena (CBUMAG), Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ), Museu de História Natural, Universidade Federal de Alagoas (MUFAL), Universidad de Costa Rica (UCR), University of Michigan Museum of Zoology (UMMZ), Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Zoological Museum Hamburg (ZMH), Zoologisches Museum Berlin (ZMB), and Zoologische Staatssammlung München (ZSM).

Taxa	Buccopharyngeal cavity
<i>Amazophrynella minuta</i>	ICN 54915
<i>Anaxyrus americanus</i>	UMMZ 139255
<i>Ansonia hanitschi</i>	ZMH A08803

<i>Atelopus balios</i>	QCAZ 2670
<i>Atelopus carrikeri</i>	CBUMAG 0892
<i>Atelopus nahumae</i>	ICN 33202
<i>Atelopus nanay</i>	QCAZ 3672
<i>Atelopus subornatus</i>	ICN 31435
<i>Barbarophryne brongersmai</i>	ZMH 12162
<i>Bufo bufo</i>	Viertel 1982
<i>Dendrophryniscus brevipollicatus</i>	UNIRIO 3394
<i>Duttaphrynus melanostictus</i>	ZMH 13591
<i>Frostius pernambucensis</i>	EI 7253
<i>Incilius coniferus</i>	UCR 18999
<i>Ingerophrynus divergens</i>	Inger 1985
<i>Melanophryniscus klappenbachi</i>	Baldo et al. 2014
<i>Osornophryne occidentalis</i>	Romero-Carvajal et al. 2023
<i>Peltophryne peltoccephala</i>	AMNH 38451
<i>Poyntonophrynus fenoulheti</i>	Lambris 1994
<i>Rentapia hosii</i>	Inger 1985
<i>Rhaebo glaberrimus</i>	ICN 49629
<i>Rhinella marina</i>	ICN 53853
<i>Schismaderma carens</i>	Lambris 1994; Viertel and Channing 2017
<i>Sclerophrys maculatus</i>	ZMH 11955
<i>Vandijkophrynus garipeensis</i>	Lambris 1994
<i>Werneria mertensiana</i>	ZMB 79695
Other taxa	
<i>Amolops cremnobatus</i>	ZFMK 95596
<i>Ascaphus truei</i>	ZFMK 44444
<i>Astylosternus robustus</i>	ZMB 82040
<i>Boophis schubae</i>	ZSM 817–2004
<i>Heleophryne hewitti</i>	ZMB 74986
<i>Huia cavitympanum</i>	ZMH13441
<i>Macrogenioglottus alipioi</i>	MUFAL 10811
<i>Meristogenys jerboa</i>	ZMH10164
<i>Odontobatrachus fouta</i>	ZMB 88109
<i>Odontophrynus cultripes</i>	UFMG 937
<i>Phyllodytes gyrinaethes</i>	MUFAL
<i>Proceratophrys appendiculata</i>	UNIRIO 4036
<i>Sumaterana dabulescens</i>	ZMH12654
<i>Werneria mertensiana</i>	ZMB 79695

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Declarations

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References

- Acosta-Galvis A, Rueda-Amonacid J, Velásquez-Alvarez AA, Sánchez-Pacheco SJ, Peña-Prieto J (2006) Descubrimiento de una nueva especie de *Atelopus* (Bufonidae) Para Colombia: ¿Una luz de esperanza o el ocaso de los sapos arlequines? *Rev Acad Colomb Cienc* 20:271–290
- Aguayo R, Lavilla EO, Vera Candiotti MF, Camacho T (2009) Living in fast-flowing water: morphology of the gastromyzophorous tadpole of the bufonid *Rhinella quechua* (R. veraguensis group). *J Morph* 270:1431–1442. <https://doi.org/10.1002/jmor.10768>
- Aguilar C, Siu-Ting K, Venegas P (2007) The rheophilous tadpole of *Telmatobius atahualpai* Wiens, 1993 (Anura: Ceratophryidae). *S Am J Herpetology* 2:165–174
- Altig R, Johnston GF (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetol Monogr* 3:81. <https://doi.org/10.2307/1466987>
- Altig R, Whiles MT, Taylor CL (2007) What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshwater Biol* 52:386–395. <https://doi.org/10.1111/j.1365-2427.2006.01694.x>
- Arifin U, Chan KO, Smart U, Hertwig ST, Smith EN, Iskandar DT, Haas A (2021) Revisiting the phylogenetic predicament of the genus *Huia* (Amphibia: Ranidae) using molecular data and tadpole morphology. *Zool Linn Soc* 193:673–699. <https://doi.org/10.1093/zoolinnean/zlaa158>
- Baldo D, Candiotti FV, Haad B, Kolenc F, Borteiro C, Pereyra MO, Zank C, Colombo P, Bornschein M, Sisa FN, Brusquetti F, Contes CE, Nogueira-Costa P, Almeida-Santos P, Pie MR (2014) Comparative morphology of pond, stream and phytotelm-dwelling tadpoles of the South American Redbelly Toads (Anura: Bufonidae: Melanophryniscus). *Biol J Linn Soc* 112(3):417–441
- Boistel R, Grosjean S, Lötters S (2005) Tadpole of *Atelopus franciscus* from French Guyana, with comments on other larvae of the genus (Anura: Bufonidae). *J Herpetol* 39:148–153. [https://doi.org/10.1670/0022-1511\(2005\)039\[0147:TOAFFF\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2005)039[0147:TOAFFF]2.0.CO;2)
- Cannatella DC (1981) A new *Atelopus* from Ecuador and Colombia. *J Herpetol* 15:133–138. <https://doi.org/10.2307/1563371>
- Coloma LA (2002) Two new species of *Atelopus* (Anura: Bufonidae) from Ecuador. *Herpetologica* 58:229–252. [https://doi.org/10.1655/0018-0831\(2002\)058\[0229:TNSOAA\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2002)058[0229:TNSOAA]2.0.CO;2)
- Coloma LA, Lötters S (1996) The tadpole of *Atelopus balios* (Anura: Bufonidae) from the pacific lowlands of Ecuador. *Herpetologica* 52:66–70
- Coloma LA, Lötters S, Salas AW (2000) Taxonomy of the *Atelopus ignescens* complex (Anura: Bufonidae): designation of a neotype of *Atelopus ignescens* and recognition of *Atelopus exiguous*. *Herpetologica* 56:303–324
- d'Heursel A, Haddad CFB (2007) Anatomy of the oral cavity of hyliid larvae from the genera *Aplastodiscus*, *Bokermannohyla*, and *Hypsiboas* (Amphibia, Anura): description and systematic implications. *J Herpetol* 41:458–468. [https://doi.org/10.1670/0022-1511\(2007\)41\[458:AOTOCO\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2007)41[458:AOTOCO]2.0.CO;2)
- Daly JW, Gusovsky F, Myers CW, Yotsu-Yamashita M, Yasumoto T (1994) First occurrence of tetrodotoxin in a dendrobatid frog (*Colostethus inguinalis*), with further reports for the bufonid genus *Atelopus*. *Toxicol* 32:279–285. [https://doi.org/10.1016/0041-0101\(94\)90081-7](https://doi.org/10.1016/0041-0101(94)90081-7)
- de Jongh HJ (1968) Functional morphology of the jaw apparatus of larval and metamorphosing *Rana Temporaria* L. *Neth J Zool* 18:1–133. <https://doi.org/10.1163/002829668X00072>
- Dias PHS (2020) The remarkable larval anatomy of *Proceratophrys minuta* Napoli, Cruz, Abreu and Del-Grande, 2011 (Amphibia: Anura: Odontophrynidae). *J Morphol* 281:1086–1097
- Dias PHS, Pie MR (2021) Buccopharyngeal morphology of the tadpoles of *Scinax v-signatus*, with comments on larval characters of the *S. perpusillus* species group (Amphibia: Anura: Hyliidae). *Zootaxa* 4964:195–200. <https://doi.org/10.11646/zootaxa.4964.1.12>
- Dias PHS, Carvalho-e-Silva AMPT, Carvalho-e-Silva SP (2014) The tadpole of *Proceratophrys izecksohni* (Amphibia: Anura: Odontophrynidae). *Zoolgia* 31:181–194. <https://doi.org/10.1590/S1984-46702014000200010>
- Dias PHS, Brandão AP, Grant T (2018a) The buccopharyngeal morphology of the tadpole of *Ameerega flavopicta* (Anura: Dendrobatidae: Colostethinae), with a redescription of its external morphology. *Herpetologica* 74:323–328. <https://doi.org/10.1655/Herpetologica-D-17-00055.1>
- Dias PHS, Mongin-Aquino M, Candiotti FV, Carvalho-e-Silva AMPT, Baêta (2018b) Internal larval morphology of two species of shining leaf frogs (Anura: Phyllomedusidae: *Phasmahyla*). *S Am J Herpetol* 13:44–53. <https://doi.org/10.2994/SAJH-D-16-00055.1>
- Dias PHS, Araujo-Vieira K, Santos RF, Both C (2019a) Review of the internal larval anatomy of the *Proceratophrys bigibbosa* species group (Anura: Odontophrynidae), with description of the tadpole of *P. brauni* Kwet and Faivovich, 2001. *Copeia* 107:417–429. <https://doi.org/10.1643/CH-18-138>
- Dias PHS, Araujo-Vieira K, Carvalho-e-Silva AMPT, Orrico VGD (2019b) Larval anatomy of *Dendropsophus decipiens* (A. Lutz 1925) (Anura: Hylidae: Dendropsophini) with considerations to larvae of this genus. *PLoS One* 14:e0219716. <https://doi.org/10.1371/journal.pone.0219716>
- Dias PHS, Anganoy-Criollo M, Rada M, Grant T (2020) Comparative larval buccopharyngeal morphology of two glass frog species (Anura: Centrolenidae: *Vitreorana*). *Zool Anz* 289:118–122. <https://doi.org/10.1016/j.jcz.2020.10.007>
- Dias PHS, Anganoy-Criollo M, Rada M, Grant T (2021) The tadpoles of the funnel-mouthed dendrobatids (Anura: Dendrobatidae: Colostethinae: *Silverstoneia*): external morphology, musculoskeletal anatomy, buccopharyngeal cavity, and new synapomorphies. *J Zool Syst Evol Res* 59:691–717. <https://doi.org/10.1111/jzs.12455>

- Dias PHS, Marcondes BC, Pezzuti TL, Vera Candiotti F, Araújo-Vieira K, Prodocimo MM, Silva HR, Orrico VGD, Haas A (2023) The missing piece of the puzzle: larval morphology of *Xenohyla truncata* (Anura: Hylidae: Dendropsophini) and its implication to the evolution of Dendropsophini tadpoles. *Zoomorphology* 142:111–126. <https://doi.org/10.1007/s00435-022-00575-3>
- Dubeux MJM, Nascimento FAC, Dias PHS (2023) Larval morphology of *Frostius pernambucensis* (Anura): contribution of larval characters for the systematics of the family Bufonidae and evolution of endotrophic tadpoles. *Zoomorphology*. <https://doi.org/10.1007/s00435-023-00623-6>
- Duellman WE, Lynch JD (1969) Descriptions of *Atelopus* tadpoles and their relevance to atelopodid classification. *Herpetologica* 25:231–240
- Enciso-Calle MP, Viuche-Lozano A, Anganoy-Criollo M, Bernal HH (2017) Rediscovery of *Atelopus subornatus* Werner, 1899 (Anura: Bufonidae), with a redescription of the tadpole. *Zootaxa* 4344:160–162. <https://doi.org/10.11646/zootaxa.4344.1.7>
- Frost DR (2023) Amphibian species of the world: an online reference. Version 6.1 (Accessed at August 10, 2023). Electronic database accessible at <https://amphibiansoftheworld.amnh.org/index.php>
- Gan LL, Hertwig S, Das I, Haas A (2015) The anatomy and structural connectivity of the abdominal sucker in the tadpoles of *Huia cavitympanum*, with comparisons to *Meristogenys jerboa* (Lissamphibia: Anura: Ranidae). *J Zool Syst Evol Res* 54:46–59. <https://doi.org/10.1111/jzs.12113>
- Gascon C (1989) The tadpole of *Atelopus pulcher* Boulenger (Anura, Bufonidae) from Manaus, Amazonas. *Rev Bras Zool* 6:235–239. <https://doi.org/10.1590/S0101-81751989000200007>
- Gawor A, Rauhaus A, Karbe D, der Straeten V, Lötters S, Ziegler T (2012) Is there a chance for conservation breeding? Ex situ management, reproduction, and early life stages of the Harlequin toad *Atelopus flavescens* Duméril & Bibron, 1841 (Amphibia: Anura: Bufonidae). *Amphib Reptil Cons* 5:29–44
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 2016:1–18. <https://doi.org/10.1111/cla.12160>
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 5:183–190
- Grant T, Kluge AG (2004) Transformation series as an ideographic character concept. *Cladistics* 20:23–31. <https://doi.org/10.1111/j.1096-0031.2004.00003.x>
- Gray P, Cannatella DC (1985) A new species of *Atelopus* (Anura, Bufonidae) from the Andes of northern Perú. *Copeia* 1985:910. <https://doi.org/10.2307/1445241>
- Grosjean S, Preininger D (2020) Description of two Staurois tadpoles from Borneo, *Staurois parvus* and *Staurois tuberilinguis* (Anura: Ranidae). *Zootaxa* 4896:523–534. <https://doi.org/10.11646/zootaxa.4896.4.4>
- Grosjean S, Straus A, Glos J, Randrianiaina RD, Ohler A, Vences M (2011) Morphological and ecological uniformity in the funnel-mouthed tadpoles of Malagasy litter frogs, subgenus *Chonomantis*. *Zool J Linn Soc* 162:149–183. <https://doi.org/10.1111/j.1096-3642.2010.00667.x>
- Haas A (2003) Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* 19:23–89
- Haas A, Das I (2008) Larval identities of *Ansonia hanitschi* Inger, 1960 (Amphibia: Bufonidae) and *Polypedates colletti* (Boulenger, 1890) (Amphibia: Rhacophoridae) from East Malaysia (Borneo). *Salamandra* 44:85–100
- Haas A, Hertwig S, Das I (2006) Extreme tadpoles: the morphology of the fossorial megophryid larva, *Leptobranchella mjobergi*. *Zoology* 109:26–42. <https://doi.org/10.1016/j.zool.2005.09.008>
- Haas A, Pohlmeier J, McLeod DS, Kleinteich T, Hertwig ST, Das I, Buchloz DR (2014) (2014) Extreme tadpoles II: the highly derived larval anatomy of *Occidozyga baluensis* (Boulenger, 1896), an obligate carnivorous tadpole. *Zoomorphology* 133:321–342. <https://doi.org/10.1007/s00435-014-0226-7>
- Hammerman DL, Thomas RF (1967) Lingual premetamorphic papillae as larval taste structures in frogs. *Nature* 215:98–99. <https://doi.org/10.1038/215098a0>
- Hennig W (1966) *Phylogenetic systematics*. University of Illinois Press, Chicago, IL
- Inger RF (1985) Tadpoles of the forested regions of Borneo. *Fieldiana* 26:1–89. <https://doi.org/10.5962/bhl.title.3403>
- Jetz W, Pyron RA (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat Ecol Evol* 2:850–858. <https://doi.org/10.1038/s41559-018-0515-5>
- Karraker NE, Richards CL, Ross HL (2006) Reproductive ecology of *Atelopus zeteki* and comparisons to other members of the genus. *Herpetol Rev* 37:284–288
- Kenny JS (1969) The amphibia of Trinidad. *St Fauna Curaçao Caribbean Islands* 29:1–78
- Kolenc F, Borteiro C, Alcalde L, Baldo D, Cardozo D, Faivovich J (2008) Comparative larval morphology of eight species of *Hypsiboas* Wagler (Amphibia, Anura, Hylidae) from Argentina and Uruguay, with a review of the larvae of this genus. *Zootaxa* 1927:1–66. <https://doi.org/10.11646/zootaxa.1927.1.1>
- Kuramoto M, Wang CS, Yü HT (1984) Breeding, larval morphology and experimental hybridization of Taiwanese brown frogs, *Rana longicrus* and *R. sauteri*. *J Herpetol* 18:387–395. <https://doi.org/10.2307/1564101>
- La Marca E, Lips KR, Lötters S, Puschendorf R, Ibáñez R, Rueda-Almonocid VR, Schulte R, Marty C, Castro F, Manzaniilla-Puppo J, Gacía-Pérez JE, Bolaños F, Chaves G, Pounds JA, Toral E, Young BE (2005) Catastrophic population declines and extinctions in neotropical harlequin frogs (Bufonidae: *Atelopus*). *Biotropica* 37:190–201. <https://doi.org/10.1111/j.1744-7429.2005.00026.x>
- Lambris AJL (1994) Laryngeal and buccopharyngeal morphology of some South African Bufonidae: new data sets for anuran taxonomy. *Ann Natal Mus* 35:261–307
- Lavilla EO, de Sá RO (2001) Chondrocranium and visceral skeleton of *Atelopus tricolor* and *Atelophryniscus chrysophorus* (Anura, Bufonidae). *Amphibia-Reptilia* 22:167–177. <https://doi.org/10.1163/15685380152030391>
- Lavilla EO, de Sá RO, de La Riva I (1997) Description of the tadpole of *Atelopus tricolor*. *J Herpetol* 31:121–124. <https://doi.org/10.2307/1565340>
- Lescure J (1981) Contribution à l'étude des Amphibiens de Guyane française IX. Le têtard gastromyzophore d'*Atelopus flavescens* Duméril et Bibron (Anura, Bufonidae). *Amphibia-Reptilia* 2:209–215
- Lindquist J (1981) Contribution à l'étude des Amphibiens de Guyane française IX. Le têtard gastromyzophore d'*Atelopus flavescens* DUMÉRIL et BIBRON (Anura, Bufonidae). *Amphibia-Reptilia* 2:209–215. <https://doi.org/10.1163/156853881X00032>
- Lindquist ED, Hetherington TE (1998) Tadpoles and juveniles of the Panamanian golden frog, *Atelopus zeteki* (Bufonidae), with information on development of coloration and patterning. *Herpetologica* 54:370–376
- Losos JB (2011) Convergence, adaptation, and constraint. *Evolution* 65:1827–1840. <https://doi.org/10.1111/j.1558-5646.2011.01289.x>
- Losos JB, Jackman TR, Larson A, Queiroz K, Rodríguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–2118. <https://doi.org/10.1126/science.279.5359.2115>
- Lötters S (1996) The Neotropical toad genus *Atelopus*: Checklist, biology, distribution. Glaw Verlags, Köln, M. Vences & F

- Lötters S (2001) Tadpole of *Atelopus mindoensis* Peters (Anura, Bufonidae) from Northwestern Ecuador. *Copeia* 2001:276–278. [https://doi.org/10.1643/0045-8511\(2001\)001\[0276:TOAMPA\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2001)001[0276:TOAMPA]2.0.CO;2)
- Lötters S, Haas W, Schick S, Böhme W (2002) On the systematics of the harlequin frogs (Amphibia: Bufonidae: *Atelopus*) from Amazonia. II: Redescription of *Atelopus pulcher* (Boulenger, 1882) from the eastern Andean versant in Peru. *Salamandra* 38:165–184
- Lötters S, Van der Meijden A, Coloma LA, Boistel R, Cloetens P, Ernst R, Lehr E, Veit M (2011) Assessing the molecular phylogeny of a near extinct group of vertebrates: the Neotropical harlequin frogs (Bufonidae; *Atelopus*). *Syst Biodivers* 9:45–57. <https://doi.org/10.1080/14772000.2011.557403>
- Lötters S, Plewnia A, Hönig A, Jung A, Laudor J, Ziegler T (2022) The gastromyzophorous tadpole of the pink harlequin frog from Suriname with comments on the taxonomy of Guianan Clade *Atelopus* (Amphibia, Bufonidae). *Zootaxa* 5087:591–598. <https://doi.org/10.11646/zootaxa.5087.4.7>
- Lötters S et al (2023) The amphibian extinction crisis is still an emergency. <https://doi.org/10.21203/rs.3.rs-2711241/v1>
- Lynch JD (1986) Notes on the reproductive biology of *Atelopus subornatus*. *J Herpetol* 20:126–129. <https://doi.org/10.2307/1564145>
- Lynch JD (1993) A new harlequin frog from Cordillera Oriental of Colombia. *Alytes* 11:77–87
- Lynch JD, Suárez-Mayorga AM (2011) Clave ilustrada de los renacuajos en las tierras bajas al oriente de los Andes, con énfasis en Hylidae. *Caldasia* 33:235–270
- Maddison WP, Maddison DR (2021) Mesquite: a modular system for evolutionary analysis. Version 3.70. Available at <http://www.mesquiteproject.org>
- Magalhães FDM, Mercês EDA, Santana DJ, Juncá FA, Napoli MF, Garda AA (2015) The tadpole of *Bokermannohyla flavopicta* Leite, Pezzuti and Garcia, 2012 and oral cavity anatomy of the tadpole of *B. oxente* Lugli and Haddad, 2006 (Anura: Hylidae). *S Am J Herpetol* 10:211–218. <https://doi.org/10.2994/SAJH-D-15-00017.1>
- Marcillo-Lara A, Coloma LA, Álvarez-Solas S, Terneus E (2020) The gastromyzophorous tadpoles of *Atelopus elegans* and *A. palmatus* (Anura: Bufonidae), with comments on oral and suction structures. *Neotrop Biodivers* 6:1–13. <https://doi.org/10.1080/23766808.2019.1709378>
- Matsui M, Yambun P, Sudin A (2007) Taxonomic relationships of *Ansonia anotis* Inger, Tan, and Yambun, 2001 and *Pedostibes maculatus* (Mocquard, 1890), with a description of a new genus (Amphibia, Bufonidae). *Zool Res* 24:1159–1166
- McDiarmid RW (1971) Comparative morphology and evolution of frogs of the neotropical genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*. *Bull Los Angeles County Mus Nat Hist* 12:1–66
- Mebs D (1980) Zur Fortpflanzung von *Atelopus cruciger* (Amphibia: Salientia: Bufonidae). *Salamandra* 16:65–81
- Mebs D, Yotsu-Yamashita M, Yasumoto T, Lötters S, Schlüter A (1995) Further report of the occurrence of tetrodotoxin in *Atelopus* species (family: Bufonidae). *Toxicon* 33:246–249. [https://doi.org/10.1016/0041-0101\(94\)00149-3](https://doi.org/10.1016/0041-0101(94)00149-3)
- Meegaskumbura M, Senevirathne G, Wijayathilaka N, Jayawardena B, Bandara C, Manamendra-Arachchi K, Pethiyagoda R (2015) The Sri Lankan torrent toads (Bufonidae: Adenominae: *Adenomus*): species boundaries assessed using multiple criteria. *Zootaxa* 3911:245–261
- Mijares-Urrutia A, La Marca E (2005) Los renacuajos de cuatro especies de *Atelopus* (Anura: Bufonidae) de los Andes de Venezuela. *Croizatia* 6:33–47
- Montesinos R, Carvalho ALG, Silva HR, Anganoy-Criollo M, Dias PHS (2022) The tadpole of *Hyloides perere* Silva & Benmaman 2008 (Anura: Hylodidae). *Zootaxa* 5219:388–396. <https://doi.org/10.11646/zootaxa.5219.4.6>
- Montesinos R, Carvalho ALG, Dias PHS (2023) The tadpole of *Hyloides amnicola* Pombal, Feio & Haddad 2002 (Anura: Hylodidae): external morphology and buccopharyngeal anatomy. *Zootaxa* 5380:395–400. <https://doi.org/10.11646/zootaxa.5380.4.8>
- Müller H (2019) Description of the tadpole of the critically endangered Ethiopian toad *Aliphrynoides osgoodi* (Amphibia: Anura: Bufonidae). *J Herpetol* 53:218–223. <https://doi.org/10.1670/19-047>
- Nascimento FAC, Mott T, Langone JA, Davis CA, de Sá RO (2013) The genus *Odontophrynus* (Anura: Odontophrynidae): a larval perspective. *Zootaxa* 3700:140–158. <https://doi.org/10.11646/zootaxa.3700.1.5>
- Nascimento FAC, de Sá RO, Garcia PCA (2021) Larval anatomy of monotypic painted ant nest frogs *Lithodytes lineatus* reveals putative homoplasies with the *Leptodactylus pentadactylus* group (Anura: Leptodactylidae). *Zool Anz* 290:135–147. <https://doi.org/10.1016/j.jcz.2020.12.003>
- Nascimento FAC, de Sá RO, Garcia PCA (2020) Larval anatomy of monotypic painted ant nest frogs *Lithodytes lineatus* reveals putative homoplasies with the *Leptodactylus pentadactylus* group (Anura: Leptodactylidae). *Zool Anz* 290:135–147
- Noble GK (1927) The value of life history data in the study of the evolution of the Amphibia. *Ann New York Acad Sci* 30:31–128. <https://doi.org/10.1111/j.1749-6632.1927.tb55359.x>
- Oliveira MIRR, Weber LN, de Sá RO, Ferreira JS, Libório AEC, Takazone AMG (2017) Chondrocranium and internal oral morphology of the tadpole of *Corythomantis greeningi* (Anura: Hylidae). *Phyllomedusa* 16:71–80
- Pearson KC, Tarvin RD (2022) A review of chemical defense in harlequin toads (Bufonidae: *Atelopus*). *Toxicon* X 13:100092
- Peixoto OL, Caramaschi U, Freire EMX (2003) Two new species of *Phyllodytes* (Anura: Hylidae) from the state of Alagoas, north-eastern Brazil. *Herpetologica* 59:235–246. [https://doi.org/10.1655/0018-0831\(2003\)059\[0235:TNSOPA\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2003)059[0235:TNSOPA]2.0.CO;2)
- Pereyra MO, Womack MC, Barrionuevo JS, Blotto BL, Baldo D, Targino M, Ospina-Sarria JJ, Guayasamin JM, Coloma LA, Hoke KL, Grant T, Faivovich J (2016) The complex evolutionary history of the tympanic middle ear in frogs and toads (Anura). *Sci Rep* 6:1–9. <https://doi.org/10.1038/srep34130>
- Pérez-Gonzalez JL, Pérez-Gonzalez JL, Rada M, Vargas-Salinas F, Rueda-Solano LA, Rueda-Solano LA (2020) The tadpoles of two *Atelopus* species (Anura: Bufonidae) from the Sierra Nevada de Santa Marta, Colombia, with notes on their ecology and comments on the morphology of *Atelopus* larvae. *S Am J Herpetol* 2020:47–62. <https://doi.org/10.2994/SAJH-D-17-00093.1>
- Peters J (1973) The frog genus *Atelopus* in Ecuador (Anura: Bufonidae). *Smithson Contrib Zool* 145:1–49
- Pezzuti TL, Santos MTT, Martins SV, Leite FSF, Garcia PCA, Faivovich J (2015) The tadpoles of two species of the *Bokermannohyla circumdata* group (Hylidae, Cophomantini). *Zootaxa* 4048:151–173. <https://doi.org/10.11646/zootaxa.4048.2.1>
- Rada M, Dias PHS, Pérez-Gonzalez JL, Anganoy-Criollo M, Rueda-Solano LA, Pinto-E MA, Quintero LM, Vargas-Salinas F, Grant T (2019) The poverty of adult morphology: bioacoustics, genetics, and internal tadpole morphology reveal a new species of glassfrog (Anura: Centrolenidae: *Ikakogi*) from the Sierra Nevada de Santa Marta, Colombia. *PlosOne* 14:e0215349. <https://doi.org/10.1371/journal.pone.0215349>
- Raj P, Vasudevan K, Deepak V, Sharma R, Singh S, Aggarwal RK, Dutta SK (2012) Larval morphology and ontogeny of *Nasikabatrachus sahyadrensis* Biju & Bossuyt, 2003 (Anura,

- Nasikabatrachidae) from Western Ghats, India. *Zootaxa* 3510:65–76
- Rao D, Yang D (1994) The study of early development and evolution of *Torrentophryne aspinia*. *Zool Res* 15:142–157
- Rodriguez LO, Duellman WE (1994) Guide to the frogs of the Iquitos Region, Amazonian Peru. *Univ Kansas Nat Hist Mus* 22:1–113
- Romero-Carvajal A, Negrete L, Salazar-Nicholls MJ, Vizuete K, Debut A, Dias PH, Vera CF (2023) Direct development or endotrophic tadpole? Morphological aspects of the early ontogeny of the plump toad *Osornophryne occidentalis* (Anura: Bufonidae). *J Morphol* 284:e21582
- Rowley JKL, Tran DTA, Le DTT, Hoang HD, Altig R (2012) The strangest tadpole: the oophagous, tree-hole dwelling tadpole of *Rhacophorus vampyrus* (Anura: Rhacophoridae) from Vietnam. *J Nat Hist* 46:2969–2978. <https://doi.org/10.1080/00222933.2012.732622>
- Rueda-Solano LA, Vargas-Salinas F, Rivera-Correa M (2015) The highland tadpole of the harlequin frog *Atelopus carrikeri* (Anura: Bufonidae) with an analysis of its microhabitat preferences. *Salamandra* 51:25–32
- Savage JM (2002) The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas. University of Chicago Press
- Starrett P (1967) Observations on the life history of frogs of the family Atelopodidae. *Herpetologica* 23:195–204
- Stuart SN, Hoffmann M, Chanson J, Cox NA, Berridge RJ, Young BE (2008) Globally threatened amphibian species. Lynx Edicions, Barcelona, Spain; IUCN, Gland, Switzerland; and Conservation International, Arlington, Virginia, USA
- Van Eeden JA (1951) The development of the chondrocranium of *Ascaphus truei* Stejneger with special reference to the relations of the palatoquadrate to the neurocranium. *Acta Zool* 32:41–176. <https://doi.org/10.1111/j.1463-6395.1951.tb00359.x>
- Vera Candiotti MFV (2005) Morphology and feeding in tadpoles of *Ceratophrys cranwelli* (Anura: Leptodactylidae). *Acta Zool* 86:1–11. <https://doi.org/10.1111/j.0001-7272.2005.00178.x>
- Vera Candiotti MFV (2007) Anatomy of anuran tadpoles from lentic water bodies: systematic relevance and correlation with feeding habits. *Zootaxa* 1600:1–175. <https://doi.org/10.11646/zootaxa.1600.1.1>
- Vera Candiotti MFV, Lavilla EO, Echeverría DD (2004) Feeding mechanisms in two treefrogs, *Hyla nana* and *Scinax nasicus* (Anura: Hylidae). *J Morphol* 261:206–224. <https://doi.org/10.1002/jmor.10239>
- Vera Candiotti M, Brusquetti F, Netto F (2007) Morphological characterization of *Leptodactylus elenae* tadpoles (Anura: Leptodactylidae: *L. fuscus* group), from central Paraguay. *Zootaxa* 1435:1–17. <https://doi.org/10.11646/zootaxa.1435.1.1>
- Vera Candiotti F, Haas A, Altig R, Peixoto O (2017) Cranial anatomy of the amazing bromeliad tadpoles of *Phyllodytes gyrinaethes* (Hylidae: Lophohylini), with comments about other gastromyzophorous larvae. *Zoomorphol* 136:61–73. <https://doi.org/10.1007/s00435-016-0334-7>
- Vera Candiotti MFV, Dias PHS, Rowley JLL, Hertwig S, Haas A, Altig R (2021) Anatomical features of the phytotelma dwelling, egg-eating, fanged tadpoles of *Rhacophorus vampyrus* (Anura: Rhacophoridae). *J Morphol* 282:769–778. <https://doi.org/10.1002/jmor.21348>
- Vera Candiotti F, Dias PHS, Haas A (in press) Chapter 8: musculo-skeletal system. In Viertel, B. (ed.) *Anuran Larvae*. Chimaira, Frankfurt am Main
- Viertel B (1982) The oral cavities of central European anuran larvae (Amphibia). Morphology, ontogenesis and generic diagnosis. *Amphibia-Reptilia* 3:327–360. <https://doi.org/10.1163/156853882X00059>
- Viertel B, Channing A (2017) The larva of *Schismaderma carens* (Smith, 1849) (Anura: Bufonidae) - a redescription. *Alytes* 33:38–46
- Viertel B, Veith M, Schick S, Channing A, Kogoolo S, Baeza-Urrea O, Sinsch U, Lötters S (2012) The stream-dwelling larva of the Ruwenzori River Frog, *Amietia ruwenzorica*, its buccal cavity and pathology of chytridiomycosis. *Zootaxa* 3400:43–57. <https://doi.org/10.11646/zootaxa.3400.1.3>
- Wake DB, Vredenburg VT (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc Natl Acad Sci USA* 105:11466–11473. <https://doi.org/10.1073/pnas.0801921105>
- Wassersug RJ (1976) Oral morphology of anuran larvae: terminology and general description. *Occ Pap Mus Nat Hist Kansas Univ* 48:1–23
- Wassersug RJ (1980) Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and ecological considerations. *Univ Kansas Publ Museum Nat Hist* 68:1–146. <https://doi.org/10.5962/bhl.title.16230>
- Wassersug RJ, Duellman WE (1984) Oral structures and their development in egg-brooding hylid frog embryos and larvae: evolutionary and ecological implications. *J Morphol* 182:1–37. <https://doi.org/10.1002/jmor.1051820102>
- Wassersug RJ, Heyer WR (1983) Morphological correlates of subaerial existence in leptodactylid tadpoles associated with flowing water. *Can J Zool* 61:761–769. <https://doi.org/10.1139/z83-101>
- Wassersug RJ, Heyer WR (1988) A survey of internal oral features of Leptodactyloid larvae (Amphibia: Anura). *Contrib Zool* 457:1–99. <https://doi.org/10.5479/si.00810282.457>
- Wassersug RJ, Rosenberg K (1979) Surface anatomy of branchial food traps of tadpoles: a comparative study. *J Morphol* 159:393–425. <https://doi.org/10.1002/jmor.1051590307>
- Womack MC, Christensen J, Hoke KL (2018) Sensitive high-frequency hearing in earless and partially eared harlequin frogs (*Atelopus*). *J Exp Biol* 221: jeb169664. <https://doi.org/10.1242/jeb.169664>
- Yotsu-Yamashita, Takei E (2010) First report on toxins in the Panamanian toads *Atelopus limosus*, *A. glyphus* and *A. certus*. *Toxicon* 55:153–156. <https://doi.org/10.1016/j.toxicon.2009.07.003>

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