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The Buccopharyngeal Morphology of the Tadpole of *Ameerega flavopicta* (Anura: Dendrobatidae: Colostethinae), with a Redescription of its External Morphology

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ABSTRACT: We describe the buccopharyngeal morphology of the dendrobatid poison frog *Ameerega flavopicta*—the first such description for the genus—and discuss diagnostic characters and variation of buccopharyngeal morphology within Dendrobatoidea. We also redescribe the external larval morphology of this species, and compare it with all known tadpoles of the genus. The buccopharyngeal morphology of *A. flavopicta* most closely resembles that of *Hyloxalus* species and appears to be the result of convergent evolution. Larval *A. flavopicta* can be readily distinguished from congeners by the absence of a medial notch in the arch-shaped upper jaw sheaths and the medial interruption of the first posterior tooth row.

Key words: Dendrobatoidea; Internal oral morphology; Larval morphology

THE DENDROBATID genus *Ameerega* currently comprises 31 species that, together with its sister group *Leucostethus*, forms an exclusively cis-Andean radiation (Grant et al. 2017) distributed in the Cerrado, the Atlantic Forest, and Amazonia and the adjacent flanks of the Andes (Frost 2018). The clade is delimited by several phenotypic synapomorphies, including granular dorsal skin, Finger IV of adult males with weak preaxial swelling, and a pale proximal calf spot, among others (Grant et al. 2017). Although several recent studies have contributed substantially to the understanding of this diverse clade (e.g., Grant et al. 2006, 2017; Twomey and Brown 2008; Brown and Twomey 2009), the tadpoles of *Ameerega* remain poorly known. External morphology has been described for only 14 species (Wyman 1859; Cope 1887; Lescure 1976; Silverstone 1976; Lamotte and Lescure 1977; Myers and Daly 1979; Rodríguez and Myers 1993; Haddad and Martins 1994; Rodríguez and Duellman 1994; Lötters et al. 1997; Duellman 2005; Twomey and Brown 2008; Poelman et al. 2010), and no aspect of their internal anatomy has been described.

Ameerega flavopicta is a small to medium-sized (21.4–30.5 mm snout–vent length; Haddad and Martins 1994) poison frog that mainly inhabits the Cerrado biome, from the northeastern Maranhão to northeastern São Paulo states in Brazil (Martins and Giarretta 2012). This diurnal, brightly colored species breeds in montane streams (Haddad and Martins 1994) or rocky pools (Costa et al. 2006). Males call from rock cervices (Haddad and Martins 1994), low vegetation (Magrini et al. 2010), or even termite nests (Lima and Eterovick 2013). Females lay terrestrial clutches of up to 31 eggs under large rocks, and males transport 11–21 tadpoles to rocky pools or temporary trenches where tadpoles complete their development (Toledo et al. 2004; Costa et al. 2006; Lima and Eterovick 2013). Advertisement calls of nominal *A. flavopicta* vary extensively (Haddad and Martins 1994; Costa et al. 2006; Magrini et al. 2010; Martins and Giarretta 2012; Lima and Eterovick 2013), suggesting that this taxon might comprise more than one species.

Several studies have reported data on the larval morphology of *Ameerega flavopicta* (Costa et al. 2006; Haddad and Martins 1994; Grant et al. 2006). Nevertheless, those studies did not examine internal anatomy and included only limited information on external morphology. For instance, character states of the oral disc, spiracle wall, vent tube morphology, and lateral line stitches, among others, are lacking. Herein, we provide the first description of buccopharyngeal anatomy for any species of *Ameerega* and a detailed redescription of the free-living tadpole of *A. flavopicta*, and we compare our observations with all available descriptions of *Ameerega* larvae.

MATERIALS AND METHODS

Terminology and measurements follow Altig and McDiar-mid (1999) and Altig (2007): total length (TL), body length (BL), tail length (TAL), body width (BW), body height (BH), tail height (TH), nostril to snout distance (NSD), eye to snout distance (ESD), interorbital distance (IOD), eye to nostril distance (END), internarial distance (IND), oral disc width (ODW), and eye diameter (ED). Terminology for lateral line system characters follows Schlosser (2002). Tadpole staging follows Gosner (1960). Regarding the upper jaw sheath morphology, we followed Sanchez (2013). We measured specimens with a digital caliper (± 0.1 mm). Descriptive statistics are given in mm as mean \pm 1 SD, and range. Description of the color in life is based on the photograph of a live tadpole provided by Martins and Sazima (1989).

To study buccopharyngeal morphology, we dissected two tadpoles according to Wassersug (1976) and stained the oral features with methylene blue. We then submitted one of the dissected and stained tadpoles to the protocol of Alcalde and Blotto (2006) for scanning electron microscopy analysis. Terminology follows Wassersug (1976, 1980), with exception of the postnarial papillae, which we considered to be just those elements immediately posterior to the caudal border of the internal nares; we used the term “postnarial arena papillae” for other elements in that area. We made all comparisons with available descriptions (Table 1) or direct comparison with additional material (Appendix).

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TABLE 1.—Available descriptions for tadpoles of *Ameerega* species.

Species	Reference
<i>A. altamazonica</i>	Twomey and Brown 2008
<i>A. bilinguis</i>	Poelman et al. 2010
<i>A. braccata</i>	Cope 1887; Haddad and Martins 1994
<i>A. flavopicta</i>	Haddad and Martins 1994; Costa et al. 2006; this study
<i>A. hahneli</i>	Haddad and Martins 1994; Rodríguez and Duellman 1994; Duellman 2005; Menin et al. 2017
<i>A. macero</i>	Rodríguez and Myers 1993
<i>A. parvula</i>	Poelman et al. 2010
<i>A. petersi</i>	Silverstone 1976
<i>A. picta</i>	Lescure 1976; Silverstone 1976; Haddad and Martins 1994; Duellman 2005; Schulze et al. 2015
<i>A. rubriventris</i>	Lötters et al. 1997
<i>A. silverstonei</i>	Silverstone 1976; Myers and Daly 1979
<i>A. smaragdina</i>	Silverstone 1976
<i>A. trivittata</i>	Wyman 1859; Silverstone 1976; Rodríguez and Duellman 1994

Institutional acronyms follow Sabaj (2016). For species that we were unable to examine personally, data were taken from published descriptions and illustrations, as follows: *A. altamazonica* (Twomey and Brown 2008), *A. braccata* (Haddad and Martins 1994), *A. flavopicta* from Goiás state (Costa et al. 2006), and *A. rubriventris* (Lötters et al. 1997).

RESULTS

External Morphology ($n = 10$, Stages 34–35, Figs. 1–3)

In dorsal view, body elliptical, snout rounded; in lateral view, body oval, depressed (BW/BH = 1.16–1.32), snout rounded (Fig. 1). Eyes dorsal, medium-size (ED/BL = 0.07–0.09), directed anterolaterally. Nares elliptical, located dorsally, directed laterally; nares with marginal rim smooth, projected, and lacking fleshy projection on sagittal margin (Fig. 2A). Nares closer to snout than eyes (NSD/END = 0.62–0.82); internarial distance ca. twice eye diameter (ED/IND = 0.38–0.57). Internarial distance 57% of interorbital distance.



FIG. 1.—The tadpole of *Ameerega flavopicta* (ZUEC 1574, Gosner Stage 34) in lateral (A), dorsal (B), and ventral (C) views. Scale bar = 10 mm. A color version of this figure is available online.

Spiracle sinistral, tubular, lateral, located ventral to midline of body, directed posterolaterad in dorsal view, dorsad at angle of 30–45° in lateral view; inner wall present, fused to body proximally and medially, free distally, longer than external wall; opening round, smaller than spiracle width (Fig. 2B). Lateral line stitches present but inconspicuous, forming supraorbital, infraorbital, and preopercular rami. Intestinal tube coiled, switchback laterally dislocated to the left body wall. Vent tube dextral, tubular, positioned at level of ventral fin, right margin shorter than left, opening elliptical, parallel in lateral view (Fig. 1A). Tail long (TAL/TL = 0.55–0.61); caudal muscles not reaching acute tip; dorsal fin arched, originating on body's posterior third, ventral fin arched; dorsal fin slightly higher than ventral fin. Myotomes V-shaped, arranged in serial blocks; maximum tail height 17% of total length.

Oral disc (Fig. 3) anteroventral, laterally emarginated, bordered by single row of conical, alternating marginal papillae; upper lip with large diastema; oral disc width 30% of body width; submarginal papillae absent. Labial tooth row formula 2(2)/3(1); A1 and A2 length subequal; A2 gap large; P1 and P2 length subequal, longer than P3. Jaw sheaths present, serrate, strongly keratinized over ca. 50% of area; upper jaw sheath arch-shaped; medial notch on upper jaw lacking, lower jaw sheath V-shaped. Labial tooth long, well-developed, and multicuspid; head and body with no distinct separation (Fig. 3B).

Measurements.—TL 27.3 ± 0.6 (26.2–28.0); BL 10.5 ± 0.4 (10.1–11.2); TAL 16.1 ± 0.4 (15.5–16.7); BW 6.8 ± 0.3 (6.5–7.2); BH 5.4 ± 0.3 (5.0–6.0); TH 4.8 ± 0.4 (4.4–5.4); NSD 1.3 ± 0.1 (1.1–1.4); ESD 2.9 ± 0.1 (2.7–3.1); IOD 3.3 ± 0.2 (3.1–3.7); END 1.7 ± 0.1 (1.4–1.9); IND 1.9 ± 0.1 (1.8–2.0); ODW 2.2 ± 0.1 (2.0–2.4); ED 0.9 ± 0.1 (0.7–1.1).

Color in life.—Dorsum dark brown, becoming darker laterally. Ventrolaterally yellowish orange. Venter with silver iridophores. Tail yellowish red. Brown blotches scattered on the tail, dorsal fin, and terminal portion of the ventral fin. Gold eyes.

Color in preservative.—Dorsum dark brown; lateral stripes on the middorsum gray; posterior dorsum tan on account of the coloration of the digestive tract. Middorsal body muscles light tan. Ventrally translucent, whitish gray anteriorly and light brown posteriorly because of the digestive tract. Tail cream color, fading gradually toward tip. Dorsal and ventral fins translucent. Brown blotches scattered through the tail and dorsal fin.

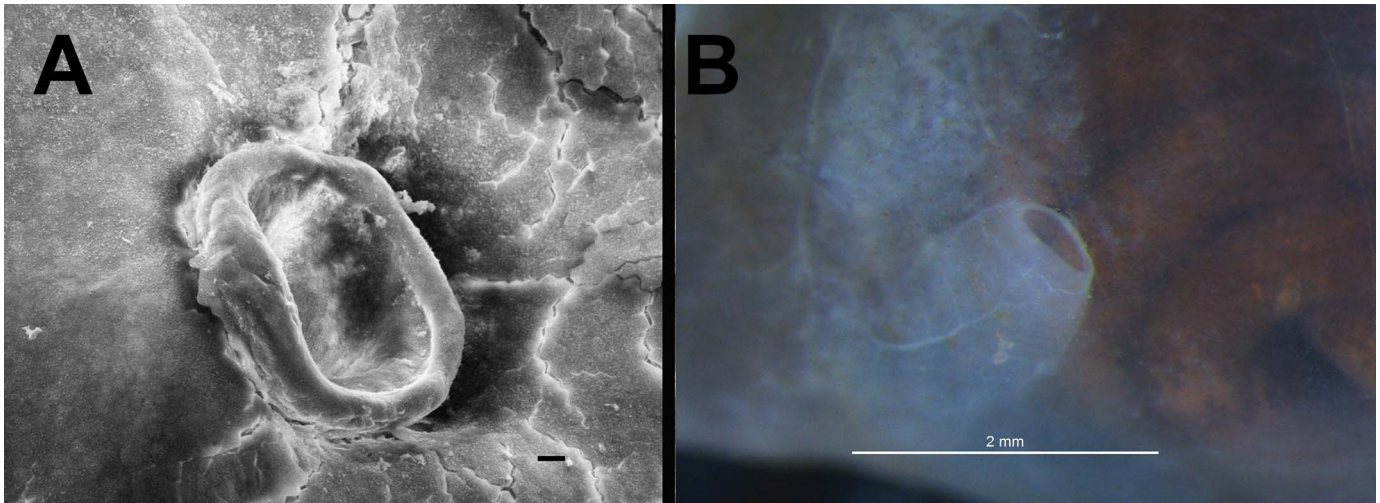


FIG. 2.—Details of the larval nostril (A) and spiracle (B) of *Ameerega flavopicta* (ZUEC 1574, Gosner Stage 34). Scale bar in (A) = 20 μ m. Anterior is to the left in both images. A color version of this figure is available online.

Buccopharyngeal Morphology

Buccal floor triangular (Fig. 4A) with three pairs of infralabial papillae; first and second (from medial to lateral) pairs conical; third pair flap-like. Lingual bud elliptical, bearing single pair of conical lingual papillae. Buccal floor arena U-shaped, delimited by 17 papillae on each side, devoid of pustulations; posteriorly, delimited by two rows (4–5) of conical papillae. Pustulations and prepocket papillae absent. Buccal pocket oriented transversely. Glandular zone poorly developed with no spicular support. Ventral velum arch-shaped, irregular margin, and small, rounded terminal projections (double at the branchial septa II and III). Branchial basket triangular, three well-developed filter cavities. Branchial plates with 4–5 filter rows. Medial notch present; glottis partially exposed.

Buccal roof triangular (Fig. 4B). Prenarial arena cylindrical, arch-shaped crest present. Internal nares elliptical, oriented transversely; anterior border with four to five conical pustulations; posterior margin with well-developed valve. Two pairs of conical postnarial papillae present; anterior pair taller than posterior; pustulations on apex of first pair, absent on second pair. Postnarial arena rectangular

with single pair of small papillae anterior to median ridge and one pair of pustulation. Median ridge conical, tall, and narrow. Lateral ridge papillae flap-like, trifurcate, with pustulations. Buccal roof arena U-shaped, delimited laterally by five conical papillae, possesses few pustulations. Lateral roof papillae present, in a single row of 4–5 papillae. Glandular zone well-developed, secretory pits evident. Dorsal velum V-shaped, interrupted medially.

Comparison with Other *Ameerega* spp.

Tadpoles of *Ameerega flavopicta* are the most easily identifiable of the genus (Table 2) because the upper jaw sheath lacks medial notch (all other species of the genus, except Peruvian specimens of *A. trivittata*, present a medial notch on the upper jaw) and interruption of the first posterior tooth row (also present in Peruvian population of *A. hahneli*). The anteroventral position of the mouth differentiates *A. flavopicta* from *A. bilinguis*, *A. braccata*, *A. hahneli*, *A. macero*, *A. parvula*, *A. pulchripecta*, *A. smaragdina*, and *A. trivittata* (mouth ventral). The alternating marginal papillae differentiate *A. flavopicta* from *A.*

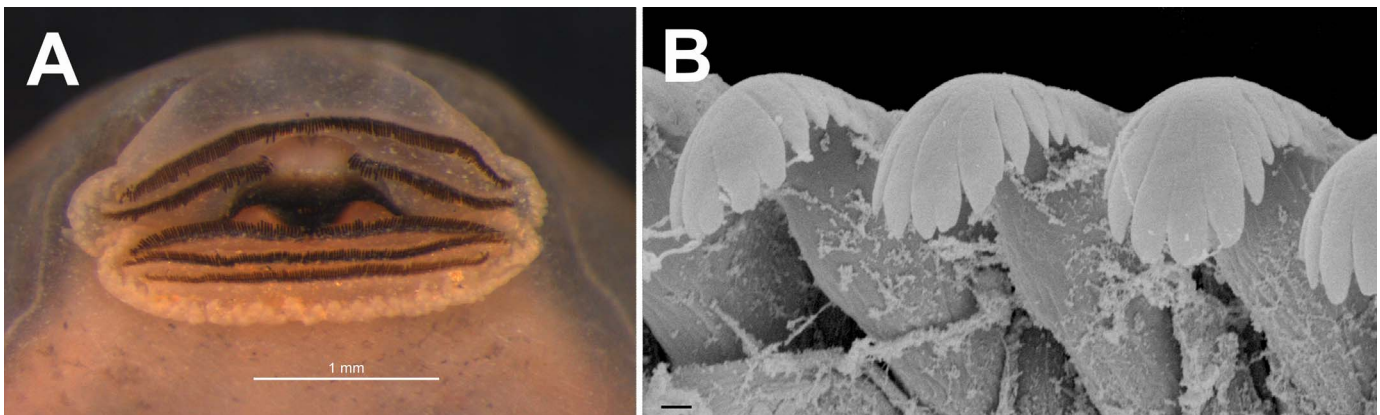


FIG. 3.—Details of the larval oral disc (A) and teeth (B) of *Ameerega flavopicta* (ZUEC 1574, Gosner Stage 34). In panel (B), anterior is to the top and scale bar = 0.001 mm. A color version of this figure is available online.

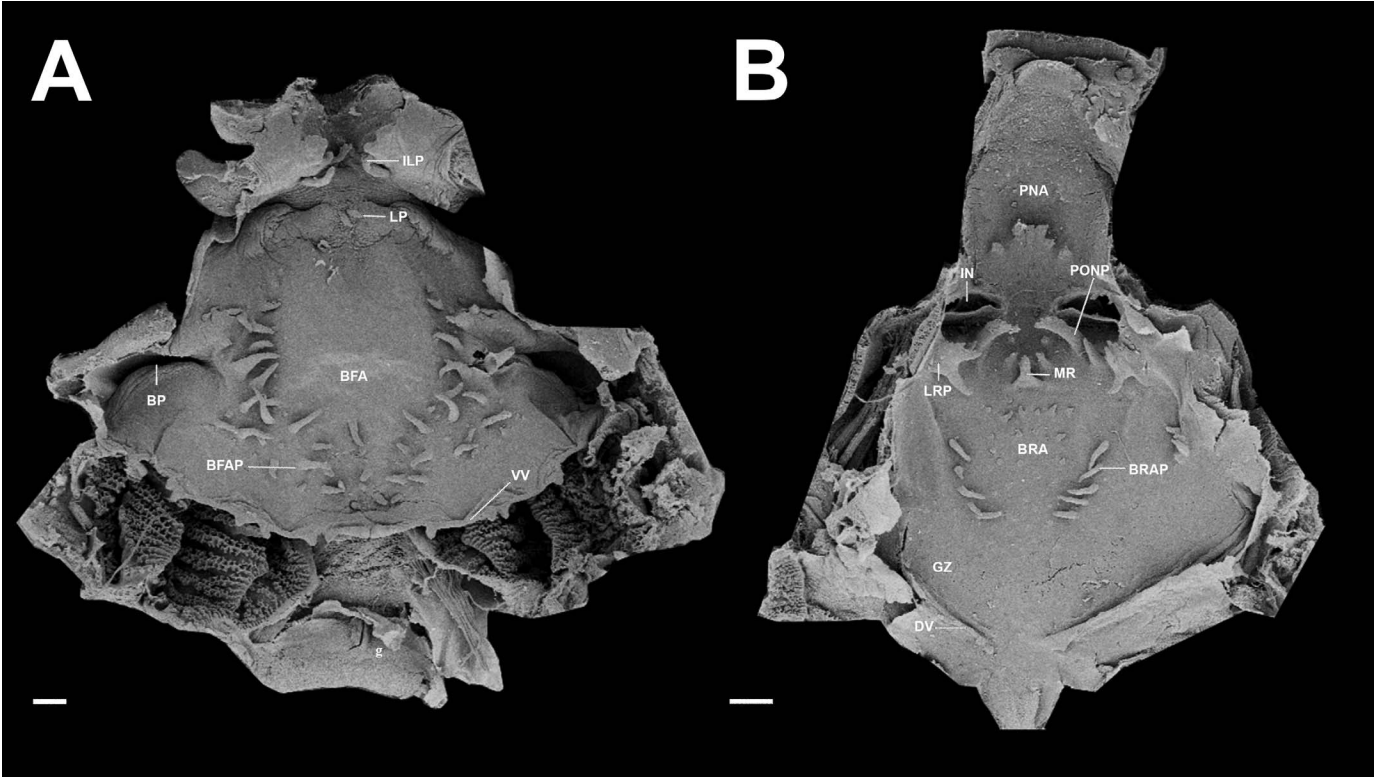


FIG. 4.—Buccopharyngeal morphology of larval *Ameerega flavopicta* (ZUEC 1574, Gosner Stage 34). Buccal floor (A) and buccal roof (B). BFA = buccal floor arena; BFAP = buccal floor arena papillae; BP = buccal pocket; BRA = buccal roof arena; BRAP = buccal roof arena papillae; DV = dorsal velum; g = glottis; GZ = glandular zone; ILP = infralabial papillae; IN = internal nares; LP = lingual papillae; LRP = lateral ridge papillae; MR = median ridge; PNA = prenarial arena; PONP = postnarial papillae; VV = ventral velum. Anterior is to the top in both images; scale bars = 200 μm.

bassleri, *A. hahneli*, *A. parvula*, *A. petersi*, *A. picta*, and *A. smaragdina*.

The oval body in lateral view differentiates *Ameerega flavopicta* from the tadpoles of *A. altamazonica*, *A. bilinguis*, *A. hahneli*, *A. macero*, *A. pulchripecta*, *A. smaragdina*, and *A. trivittata* (body cylindrical in lateral view). The tubular spiracle differentiates *A. flavopicta* from *A. altamazonica*, *A. hahneli*, *A. silverstonei*, and *A. trivittata* (conical spiracle). The distally free spiracle (clearly free distal edge) differentiates *A. flavopicta* from *A. bassleri*, *A. petersi*, *A. silverstonei*, *A. smaragdina*, and *A. trivittata* (only the edge is free;

free portion of the spiracle not forming a tube) and Peruvian specimens of *A. hahneli* (completely fused to body; no distinction of the inner wall of the spiracle free).

The absence of a medial fleshy projection on the nares differentiates *Ameerega flavopicta* from *A. bassleri*, *A. bilinguis*, and some populations of *A. hahneli*, and *A. trivittata* (present). The origin of the dorsal fin at the posterior third of the body differentiates *A. flavopicta* from *A. bilinguis*, *A. hahneli*, *A. macero*, *A. parvula*, *A. petersi*, and *A. smaragdina* (at body/tail junction). The fully fused

TABLE 2.—Comparisons among tadpoles of *Ameerega* species. Abbreviations for spiracle morphology: BF = border free; DF = distally free.

Species	Trait							
	Upper jaw	Gap in P1	Mouth	Body in lateral view	Spiracle	Fleshy projection	Dorsal fin	Vent tube
<i>A. altamazonica</i>	W-shaped	Absent	Anteroventral	Cylindrical	Conical/-	?	Bod/tail	?
<i>A. bassleri</i>	W-shaped	Absent	Anteroventral	Oval	Tubular/BF	Present	Posterior 1/3	Fully fused
<i>A. bilinguis</i>	W-shaped	Absent	Ventral	Cylindrical	Tubular/DF	Present	Tail	Free distally
<i>A. bracatta</i>	W-shaped	Absent	Ventral	Oval	Tubular/-	?	Tail?	?
<i>A. flavopicta</i>	Arch-shaped	Present	Anteroventral	Oval	Tubular/DF	Absent	Posterior 1/3	Fully fused
<i>A. hahneli</i>	W-shaped	Absent	Ventral	Cylindrical	Conical/DF	Present	Tail	Fully fused
<i>A. macero</i>	W-shaped	Absent	Ventral	Cylindrical	Tubular/DF	Absent	Bod/tail	Fully fused
<i>A. parvula</i>	W-shaped	Absent	Ventral	Oval	Tubular/DF	Absent	Tail	Free distally
<i>A. petersi</i>	W-shaped	Absent	Anteroventral	Oval	Tubular/BF	Absent	Bod/tail	Fully fused
<i>A. picta</i>	W-shaped	Absent	Anteroventral	Oval	Tubular/DF	Absent	Posterior 1/3	Fully fused
<i>A. pulchripecta</i>	W-shaped	Absent	Ventral	Cylindrical	?	?	Tail	?
<i>A. rubriventris</i>	W-shaped	Absent	Anteroventral	Oval	Tubular/DF	?	Posterior 1/3	?
<i>A. silverstonei</i>	W-shaped	Absent	Anteroventral	Oval	Conical/BF	Absent	Posterior 1/3	Fully fused
<i>A. smaragdina</i>	W-shaped	Absent	Ventral	Cylindrical	Tubular/BF	Absent	Bod/tail	Fully fused
<i>A. trivittata</i>	W-shaped	Absent	Ventral	Cylindrical	Conical/DF	Present	Posterior 1/3	Fully fused

vent tube differentiates it from *A. bilinguis* and *A. parvula* (distally free).

Ameerega flavopicta can be further distinguished from *A. hahneli* by having dorsal eyes (lateral), marginal papillae on the lateral portion of the upper lip (absent), and the second superior and the second and third tooth ridges on the mouth (absent). The presence of keratodonts might differentiate from some populations of *A. hahneli* (labial tooth row formula varies from 0/0, 1/1, to 1/2 in *A. hahneli*; see also Menin et al. 2017).

The larvae of *Ameerega flavopicta* studied herein can be distinguished from those of Caldas Novas, Goiás, by the dorsal fin originating on the posterior third of the body (body/tail junction), presenting the nostril closer to the snout than to the eyes (equidistant), the conical marginal papillae (rounded), and lacking submarginal papillae (present).

DISCUSSION

Costa et al. (2006) described *Ameerega flavopicta* tadpoles from Caldas Novas, Goiás state, Brazil. They found that their tadpole differed from those described by Haddad and Martins (1994) in the origin of the dorsal fins, reporting this trait to occur at the body/tail junction instead of the posterior third of body. Although we were unable to locate the tadpoles examined by Haddad and Martins (1994), our additional tadpoles from the same locality (Jaboticatubas, Minas Gerais state, Brazil, ~60 km from the type locality) are consistent with the illustration of this character state (Haddad and Martins 1994). Nevertheless, it is interesting to note that the dorsal fin of the tadpoles from Caldas is shallower at its origin than in Minas Gerais specimens.

Costa et al. (2006) also described the presence of submarginal papillae on the lateral portion of the lower lips. Among the species of Dendrobatoidea for which descriptions of tadpoles are available, submarginal papillae are known to occur only in the funnel-mouthed species of the genus *Silverstoneia* and in *Hyloxalus edwardsi* (Lynch 1982; Grant and Myers 2013). Costa et al. (2006) did not provide illustrations of the oral disc and we did not examine their specimens, so we cannot confirm or refute the presence of submarginal papillae. If corroborated, this would be an interesting autapomorphy that strengthens the hypothesis that *A. flavopicta* comprises more than one species. We stress, however, that submarginal papillae are rare in dart-poison frogs (Grant et al. 2006) and have been reported only in the genus *Silverstoneia* (e.g., Dunn 1924; Grant and Myers 2013) and in *Hyloxalus edwardsi* (Lynch 1982).

Data on buccopharyngeal anatomy are restricted to the descriptions of *Hyloxalus subpunctatus* and *Silverstoneia nubicola* (Wassersug 1980) and scanning electron micrographs of a specimen reported as *H. whymperi* by Wassersug and Heyer (1988; species identity doubtful, and voucher number and locality not given [Coloma 1995]; also, see Grant et al. 2017). Excluding the highly modified tadpole of *S. nubicola*, other dendrobatoid larvae (*Ameerega flavopicta* and *H. subpunctatus*) share a set of character states in their oral cavity: (1) a transverse ridge formed by series of pustulations in the prenarial arena, (2) a long postnarial papilla, (3) a lateral ridge of papilla that is branched, (4) three pairs of infralabial papillae, (5) one pair of lingual papillae, (6) marginal projections on the ventral velum, and

(7) presence of lateral roof papillae. Nevertheless, *A. flavopicta* can be distinguished from those species on the basis of the papilla-like median ridge lacking projections, transverse orientation of buccal pockets, a more exposed glottis, and arenas with fewer pustulations. Additional data on both the internal anatomy and external morphology of dendrobatoid larvae are required to test hypotheses about the evolutionary sequence and biological significance of larval characters, and to understand the evolution of dendrobatoid larval diversity.

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RESUMO: Nós fornecemos uma redescritção da morfologia externa dos girinos de *Ameerega flavopicta* e descrevemos sua morfologia bucofaríngea—a primeira para o gênero. Também comparamos nossos dados com todos os girinos conhecidos para o gênero e discutimos alguns caracteres diagnósticos e a variação da morfologia bucofaríngea em Dendrobatoidea. Os girinos de *A. flavopicta* podem ser prontamente diferenciados de seus congêneros pela lamina mandibular superior lisa e em forma de arco e pela presença de uma interrupção na primeira fileira posterior de dentes. Alguns caracteres da anatomia oral interna são compartilhados com girinos de *Hyloxalus* e podem ser o fruto de evolução convergente.

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APPENDIX

Specimens Examined

- Ameerega bassleri*.—**Peru**: San Martín: San Martín: MUSM 22595, 22795. San Juan de Pacayaza: MUSM 6283.
- Ameerega bilinguis*.—**Ecuador**: Orellana: Parque Nacional Yasuní: QCAZ 32198.
- Ameerega flavopicta*.—**Brazil**: Minas Gerais: Jaboticatubas: ZUEC 15166, 15168, 15170, 15174.
- Ameerega hahneli*.—**Colombia**: Amazonas: Leticia: ICN 53105. **Peru**: Panguana: Puerto Inca: MUSM 26937.
- Ameerega macero*.—**Peru**: Madre de Dios: Parque Nacional del Manu, Cocha Cashu Biological Station: AMNH 133207.
- Ameerega parvula*.—**Ecuador**: Napo: Cerca de San Pedro, Río Arajuno: QCAZ 32918.
- Ameerega petersi*.—**Peru**: Panguana: Puerto Inca: MUSM 29102. Panguana: Yuyapichis: MUSM 24692.
- Ameerega picta*.—**Bolivia**: Santa Cruz: CFBH 39896.
- Ameerega pulchripeetra*.—**Brazil**: Amapá: Serra do Navio: AMNH 137289.
- Ameerega silverstonei*.—**Peru**: Huánuco: Cordillera Azul, NE Tingo María: AMNH 94795.
- Ameerega smaragdina*.—**Peru**: Pasco: Iscozasin Valley: LACM 64436.
- Ameerega trivittata*.—**Brazil**: Pará: MPEG: 22375, 22377–8, 22412. **Colombia**: Amazonas: Leticia: ICN 53107, 55113. **Peru**: San Martín: San Martín: MUSM 17796.