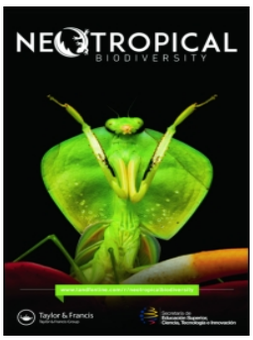

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The gastromyzophorous tadpoles of Atelopus elegans and A. palmatus (Anura: Bufonidae), with comments on oral and suction structures

Alejandro Marcillo-Lara[a,b], Luis A. Coloma[b], Sara Álvarez-Solas[c] and Esteban Terneus[d]

[a]Escuela de Biología Aplicada, Universidad Internacional del Ecuador, Quito, Ecuador; [b]Centro Jambatu de Investigación y Conservación de Anfibios, San Rafael, Quito, Ecuador; [c]Universidad Regional Amazónica Ikiam, Muyuna, Tena, Ecuador; [d]Escuela de Gestión Ambiental, Universidad Internacional del Ecuador, Quito, Ecuador

ABSTRACT

The tadpoles of the Neotropical genus *Atelopus* are only known for 26 out of 96 species described. Here, we describe the tadpoles of *A. elegans* and *A. palmatus* including ontogenetic information, measurements, and images of individuals in several stages of growth. Both species are compared with their congeners taking into account some relevant features such as the coloration and relative measurements. Our description focuses on the abdominal sucker and mouth by providing scanning electron microscopy images and comparing the suctorial mechanism with other groups of anurans and fish. We also provide an update to knowledge of the abdominal suckers, and information about their lateral line system and the distribution of their lateral line openings. The results show that brown marks over a tan surface and an irregular distribution of marks along the body and tail are unique to *A. elegans*; while a patterned distribution of contrasting marks, and the presence of submarginal papillae are unique to *A. palmatus*. Also, both species show differences in the structures of their teeth. Finally, we conclude that some characters such as coloration, presence or absence of some structures, and relative measurements are useful for identifying the species.

RESUMEN

Los renacuajos del género neotropical *Atelopus* se conocen para solamente 26 de un total de 96 especies descritas. Aquí, describimos los renacuajos de *A. elegans* y *A. palmatus* incluyendo su información ontogénica, mediciones e imágenes de individuos en varias etapas de desarrollo. Ambas especies se comparan con sus congéneres teniendo en cuenta algunas características relevantes como la coloración y las medidas relativas. Nuestra descripción se enfoca en la ventosa abdominal y la boca al proporcionar imágenes de microscopía electrónica de barrido y al comparar el mecanismo de succión con otros grupos de anuros y peces. Además, proveemos una actualización del conocimiento de las ventosas abdominales, e información sobre su sistema de línea lateral y la distribución de los orificios de la línea lateral. Los resultados muestran que las marcas marrones sobre una superficie marrón y una distribución irregular de marcas a lo largo del cuerpo y la cola son exclusivas de *A. elegans*; mientras que una distribución con patrones de marcas contrastantes y la presencia de una papila submarginal son exclusivas de *A. palmatus*. Además, ambas especies muestran diferencias en las estructuras de sus dientes. Finalmente, llegamos a la conclusión de que algunos caracteres como la coloración, presencia o ausencia de algunas estructuras y medidas relativas son útiles para identificar las especies.

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Larvas; ventosa abdominal; ontogenia; Ecuador

Introduction

Atelopus is the largest genus of the bufonids with 96 species described to date [1], and many others awaiting description (e.g. Tapia *et al.* [2]:Table 1). They are distributed in the tropical rainy and cloud forests, and along the paramos of Central and South America [2]. More than 90% of the species is either Endangered, Critically Endangered and/or Possibly extinct, and the rest are either Data Deficient, Non-threatened or not evaluated [2–4]. Their tadpoles belong to the gastromyzophorus ecomorphological guild, which means that they use an abdominal sucker to keep their position in fast and turbulent streams and rivers [5,6]. However, there are some species from the lowlands that also exploit slow running streams [7]. The diversity of *Atelopus* larvae is still poorly known. For example, there exist morphological descriptions for only 26 species: Mijares-Urrutia and La Marca [8] (*A. carbonerensis, A. mucubajiensis, A. sorianoi, A. tamaense*); Rueda et al. [9] (*A. carrikeri*); Duellman and Lynch [10] (*A. certus, A. ignescens, A.* sp. (*spumarius* complex, from Puyo, Ecuador)); Gascon [11] *A.* sp. (*spumarius* complex from Manaus, Brazil [11]; Mebs [12] (*A. cruciger*); Lescure [13] (*A. flavescens*); Boistel et al. [14] (*A. franciscus*); Gawor et al. [15] (*A. hoogmoedi)*; Acosta et al. [16] (*A. mittermeieri*); Gray and Canatella [17] (*A. peruensis*); Lötters et al. [18] (*A. pulcher*); Enciso et al. [19] (*A. subornatus*); Lavilla et al. [20] (*A. tricolor*); Starrett [21] (*A. varius*); Lindquist and Hetherington [22] (*A. zeteki*); Coloma et al. [23] (*A. exiguus*); Lötters [24]

CONTACT Alejandro Marcillo-LARA alejomarcillo@hotmail.com

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Table 1. Measurements (mm) of 14 tadpoles of *Atelopus elegans* CJ 9759. Mean and standard deviation are provided at the first row and below are the ranges.

Stage	N	BL	TAL	TL	IND	IOD	MTH	TMH	TMW
25	3	2.7 ± 0.1	3.8 ± 0.1	6.4 ± 0.2	0.7 ± 0.1	0.9 ± 0.1	1.1 ± 0.1	0.5 ± 0.1	0.4 ± 0.1
		(2.6–2.8)	(3.6–3.9)	(6.2–6.7)	(0.7–0.8)	(0.8–1)	(1–1.2)	(0.4–0.5)	(0.3–0.4)
26	1	2.8	4.1	6.9	0.7	0.9	1.2	0.4	0.3
31	1	4.5	5.3	9.8	1.1	1.4	1.4	0.7	0.5
32	1	4.7	5.9	10.6	1	1.5	1.9	0.8	0.6
33	3	4.9 ± 0.2	5.9 ± 0.3	10.8 ± 0.5	1.1 ± 0.1	1.6 ± 0.1	1.8 ± 0.1	0.9 ± 0.1	0.6 ± 0.1
		(4.6–5.1)	(5.6–6.4)	(10.4–11.5)	(1.1–1.2)	(1.4–1.8)	(1.7–1.8)	(0.7–1)	(0.5–0.6)
34	4	5.4 ± 0.3	6.3 ± 0.3	11.7 ± 0.5	1.1 ± 0.1	1.7 ± 0.1	1.9 ± 0.1	0.9 ± 0.2	0.7 ± 0.1
		(5–5.8)	(5.9–6.6)	(10.9–12.2)	(1.1–1.2)	(1.5–1.8)	(1.8–2)	(0.6–1)	(0.6–0.7)
35	1	5.4	6.6	12	1.3	1.6	1.9	0.7	0.7

Stage, Gosner stages; N, sample size; BL, body length; TAL, tail length; TL, total length; IND, internarial distance; IOD, interorbital distance; MTH, maximum tail height; TMH, tail muscle height; and TMW, tail muscle width.

(*A. mindoensis*); Coloma and Lötters [7] (*A. balios*); Coloma [25] (*A. nanay*)). Six of them are of species of *Atelopus* occurring in Ecuador (*A. balios, A. exiguus, A. ignescens, A. mindoensis, A. nanay*, and *A*. sp. (*spumarius* complex from Puyo, Ecuador)).

The available descriptions show high variability in tadpole morphology, color patterns, and other anatomical characters. Some of these features are also useful to distinguish among species. Unfortunately, many traits still remain unknown. For example, there are not any published scanning electron microscopy (SEM) images of *Atelopus* larvae, and only a mention of SEM used to describe the abdominal sucker of *A. subornatus* and *A*. sp. (*ignescens* complex) (under the name *A. ignescens*) by Kaplan [26].

In Ecuador, the larvae of at least 18 described species of *Atelopus* remain unknown. The finding of a relictual population of *A. palmatus* [27], and the subsequent search for tadpoles by field parties of the Colorado State University and the Saint Louis Zoo resulted in a series of tadpoles, some of which were raised under laboratory conditions until Stage 43. Nonetheless, our allocation of these tadpoles to *Atelopus palmatus* is temptative and based on the fact that this is the only species recorded at this site. Also, the breeding of *A. elegans* under laboratory conditions supplied a series of alive and preserved specimens. Thus, we provide for the first-time descriptions of larvae of *A. elegans* and of *A. palmatus*. *Atelopus elegans* is distributed in the lowlands of the Pacific of Colombia, and between 300 and 1140 m in Ecuador [28]. We exclude from the nominal taxon Atelopus elegans the populations from the Gorgona Island, off the Pacific coast of Colombia, which we consider as a different species, *Atelopus gracilis*, following Barbour [29] and Coloma [30] *Atelopus palmatus* inhabits the humid montane forests of the Amazonian versant of the Andes in provinces of Napo, Pastaza and Tungurahua in Ecuador, between 1150 and 1740 m [31].

Material and methods

The description of *Atelopus elegans* tadpoles is based on a series of 14 tadpoles at stages 25, 26, 31, 32, 33, 34 and 35 (CJ 9759) born under laboratory conditions at CJ. This description is based on an individual at Stage 25 (CJ 9759a), from a series of 14 tadpoles (CJ 9759). This individual was second descendant generation of parents collected at Río Durango (243-m ASL), Durango, Provincia Esmeraldas, Ecuador, on 18 May 2011 by Elicio E. Tapia.

The description of *Atelopus palmatus* tadpoles is based on a series of eight tadpoles at stages 25, 26, 28, 30 and 34 (CJ 2063) collected in the wild. This description is based on an individual at Stage 28 (CJ 2063a), from a series of eight tadpoles (CJ 2063), collected at Río Negro (1618-m ASL), Provincia Tungurahua, Ecuador, on 11 February 2014, by Kim Hoke, Luis A. Coloma, Elicio E. Tapia, Mark Wanner, and Sara Amstrong.

Both series were fixed in 10% formalin. Tadpoles of *Atelopus elegans* were kept in the lab at a mean temperature of 22°C and pH 7. Groups of tadpoles were placed in either glass or plastic tanks about 34-cm long x 25-cm wide x 15-cm deep, with a capacity of 10 L of water. The water entering the container was filtered to prevent the presence of chlorine, arsenic, bacteria, and other harmful agents. Tadpoles were fed three times a week with a paste made of dandelion (*Taraxacum officinale*) spread on porous pieces of building blocks. Tadpoles in several stages of development were preserved in a 10% formalin solution. In order to report ontogenetic changes in development and morphology, all developmental stages (sensu Gosner [32]) that were available were described. Specimens examined are housed at Centro Jambatu de Investigación y Conservación de anfibios (CJ).

Morphology

The terminology of tadpole features follows Altig and Johnston [5], and McDiarmid & Altig [33] for body length (BL), body width (BW), tail length (TAL), total length (TL), internarial distance (IND), interorbital distance (IOD), maximum tail height (MTH), tail muscle height (TMH), tail muscle width (TMW), and mouthparts; moreover, the terminology of suction structures follows Kaplan [26]. Tadpoles staging follows Gosner

Table 2. Measurements (mm) of eight tadpoles of *Atelopus palmatus* CJ 2063. Mean and standard deviation are provided at the first row and below are the ranges.

Stage	N	BL	TAL	TL	IND	IOD	MTH	TMH	TMW
25	2	3.3	4.8 ± 0.3	8.1 ± 0.3	0.8	1.2 ± 0.1	1.4 ± 0.1	0.9 ± 0.2	0.6 ± 0.1
			(4.5–5.1)	(7.8–8.4)		(1.1–1.2)	(1.3–1.4)	(0.7–1)	(0.5–0.6)
26	3	3.4 ± 0.1	5.1 ± 0.5	8.5 ± 0.4	0.9 ± 0.1	1.3 ± 0.2	1.4	0.8 ± 0.1	0.6 ± 0.1
		(3.3–3.4)	(4.7–5.8)	(8.1–9.1)	(0.8–0.9)	(1.1–1.5)		(0.7–1)	(0.6–0.7)
28	1	3.5	4.7	8.2	0.8	1	1.1	0.7	0.6
30	1	4.7	7.2	11.9	1.1	1.6	2	1	1
34	1	5.1	6.6	11,7	1	1.7	1.6	1	0.8

Stage, Gosner stages; N, sample size; BL, body length; TAL, tail length; TL, total length; IND, internarial distance; IOD, interorbital distance; MTH, maximum tail height; TMH, tail muscle height; and TMW, tail muscle width.

[32]. Measurements were taken to the nearest 0.1 mm using an IP67 Absolute Coolant-Proof Caliper, an Olympus SZ61 stereo microscope, and a fiber optic illuminator. Mean, standard deviation, and ranges of the measurements are provided in Tables 1 and 2 (intraspecific comparisons).

Color in life descriptions, ontogeny and metamorphical variation of both species is based on sequential digital photographs.

Comparisons were done among *Atelopus elegans, A. palmatus*, and the 26 species of *Atelopus* described so far.

Electron microscopy

The microstructure of body and mouthparts of one tadpole of *Atelopus elegans* (Stage 25) (CJ 6383) and one of *A. palmatus* (Stage 30) (CJ 2063) was analyzed by scanning electron microscopy (SEM, Jeol JSM 6400, Akishima, Tokyo, Japan) at 20 kV, using the protocol of sample preparation for scanning electron microscopy [34]. The composition of teeth was analyzed from samples prepared as for environmental SEM. We used an integrated-system analysis with an energy dispersive spectrometer (in semiquantitative mode) and wave-length dispersive spectrometer of X-ray coupled with the FEI-Quanta 200 microscopy (Oxford Instruments, Oxford, UK). Identification of elements was made according to a database of internal standards provided by Oxford Instruments with INCA platform software. The description and nomenclature of the abdominal sucker in both species follows Kaplan [26], except that we abbreviate fa for friction area instead of pb.

Results

Description of the tadpole of Atelopus elegans

The following measurements are based on an individual at Stage 25. Total length of 6.2 mm, body length of 2.6 mm, and body width of 1.8 mm. The body is dorsally ovoid and ventrally flattened. The snout is rounded in dorsal view and in profile. The body is constricted at eyes level and at spiracle level. The nostrils diameter is 0.1 mm, at about one-half the distance from eye to the tip of snout; they have circular shape, and an incomplete rim, and they are located dorsolaterally. The eyes are dorsal and directed dorsolaterally; their diameter is 0.5 mm, the interocular distance is 1.0 mm (taken from the medial edges of the corneas). The spiracle is sinistral, originating at 1.62 mm (61%) from the tip of snout to end of body; the diameter of opening is about equal to the length (length taken at the dorsal side) of the free tube, the opening is directed dorsally. The vent tube does not protrude from end of body. The caudal musculature is robust anteriorly and narrows evenly starting at one-third the distance from the end of body to the end of the tail. The tail is rounded. The dorsal fin height is about 40% of the tail height, the TAL is 58% of the TL. The dorsal fin begins at the level of the body, the ventral fin begins posterior to the vent tube. The tail length is 3.6 mm.

The mouth is ventral and surrounded by labia forming complete oral disc that is 1.8 mm wide. There are uniserial marginal papillae dorsally and laterally, and a ventral gap present in most of the posterior lip. The submarginal papillae are absent. The labial tooth row formula is 2/3; the rows are complete with the anterior and posterior tooth rows are equal in length. The jaw sheaths are equal in length, and their inner margins are serrate. The upper beak is slightly concave while the lower beak is slightly V-shaped. The abdominal sucker extends from the posterior labium to about 44% of total length.

SEM micrographs of the mouthparts, abdominal sucker, lateral line canal openings, and teeth are depicted in Figure 2. There are short and long cusped teeth, and some others that are not cusped. They are moderately curved towards the inside of the mouth. The number of cusps is undeterminable, but in accordance with Figure 2 there are between 15 and 20 cusps in each tooth (Figure 2(d–f)).

In the abdominal sucker (Figure 2(a–c)), the friction area (fa), located between the intermediate region (ir) and free edge (fe), is composed by a stripe of protruding and large cells. This stripe is rounded at the posterior part, following the internal outline of the free edge, and becomes wider at the ends. This stripe is composed by 6–7 cells width at the mid-lateral of the stripe; 7–9 cells width at the posterior part of the stripe; and 10–12 cells width at both wider parts (borders). The intermediate

region is located in the inner part of the friction area, following its internal outline, and its posterior part is as wide as the posterior and lateral parts of the free edge. The intermediate region ends posteriorly in two circle-like and wider borders. These borders have a crease from where extends a transverse fold (tf) that connects both borders. Moreover, there is only the left ligament (li) in a border of the intermediate region, and the oral disc has 37 marginal papillae.

The lateral line system is characterized by several lateral line canal openings, following an irregular pattern, concentrated at the snout area, and surrounding the eyes and narines. Moreover, there are a few openings at the external anterior part of the oral disc, and at the anterior borders of the free edge of the abdominal sucker.

Color in preservative

The dorsum and flanks are uniformly tan with brown marks that spread along the body, concentrated at the anterior part of the body, around the nostrils and above the eyes. The tail is tan anteriorly with brown marks and translucent posteriorly with brown staining at the edges of tail musculature. The spiracle is unpigmented. The oral disc and abdominal sucker are translucent; the venter is tan, and the gut is not visible.

Color in life

Based on CJ 9759b at Stage 27. The body is dark tan with black marks and both brown and mustard spots. The black marks are larger than the brown spots, and the brown spots larger than the mustard spots. The mustard spots are accumulated above the eyes where there are neither black flecks nor brown spots. The spiracle only has a few mustard spots at the base. The tail is tan and has mainly brown spots in dorsal view. In lateral view, there are black marks at the anterior part of the tail muscle and black marks only at the edges of the posterior part of the tail muscle. Ventrally, the heart is visible, and some blood vessels are visible around it. The oral disc and abdominal sucker are translucent.

Variation

Based on series CJ 9759b–n (13 tadpoles). Meristic variation of tadpoles (CJ 9759) in stages between 25 and 35 is indicated in Table 1. In advanced stages (e.g., from Stage 30) large submarginal papillae are visible.

Metamorph variation of CJ 919 (not preserved) is shown between Stages 41 and 43 (Figure 1). At Stage 41 it is visible a golden dorsolateral stripe, that becomes well defined and cream at Stage 43. The abdominal sucker is absent, and tail fins decrease in height at Stage 43.

Description of the tadpole of Atelopus palmatus

The following measurements are based on an individual at stage 28. Total length of 8.2 mm, body length of 3.5 mm, and body width of 2.4 mm. The body is dorsally ovoid and ventrally flattened. The snout is rounded in dorsal view and in profile. The body is constricted at eyes level and at spiracle level. The nostrils diameter is 0.1 mm, at about one-third the distance from eye to the tip of snout; they have oval shape, and a complete rim, and they are located dorsolaterally. The eyes are dorsal and directed dorsolaterally; their diameter is 0.4 mm, the interocular distance is 1.0 (taken from the medial edges of the corneas). The spiracle is sinistral, originating at 2.17 mm (62%) from the tip of snout to end of body; the diameter of opening is larger than the length of the fused tube (taken from the middle of the tube), the opening is directed dorsally. The vent tube is slightly protruding. The caudal musculature is robust anteriorly and narrows evenly starting at about one-half the distance from the end of body to the end of the tail. The tail tip is narrowly rounded. The dorsal fin height is about 18.18% of the tail height, the tail length is 57.31% of the TL. The dorsal fin begins at level of vent tube, the ventral fin begins at level of the end of abdominal sucker. The tail length is 4.7 mm.

The mouth is ventral and surrounded by labia forming complete oral disc that is 2.1 mm wide. There are uniserial marginal papillae dorsally and laterally, and a ventral gap present in most of the posterior lip. There are submarginal papillae in each side. The labial tooth row formula is 2/3; the rows are complete, the anterior tooth rows are equal in length; the P3 is slightly smaller than P1 and the P2; the lower jaw sheath is smaller than the upper jaw sheath, and their inner margins are serrate; the upper beak is slightly concave; the lower beak is slightly convex. The abdominal sucker extends from the posterior labium to about 32.9% of total length.

SEM micrographs of the lateral line canal openings, narines, and teeth are depicted in Figure 4. There are long cusped teeth, which are barely curved, aligned in a single row. In accordance with Figure 4, there are between 24 and 26 cusps each tooth (Figure 4(d)). There are several lateral line canal openings, following an irregular pattern, concentrated at the snout area, at the dorsum, surrounded the eyes, and at the dorsolateral and lateral area of the end of body; moreover, there are some little groups surrounded the narines, at the ventrolateral area of the end of body, and at the anterior borders and mid of the free edge

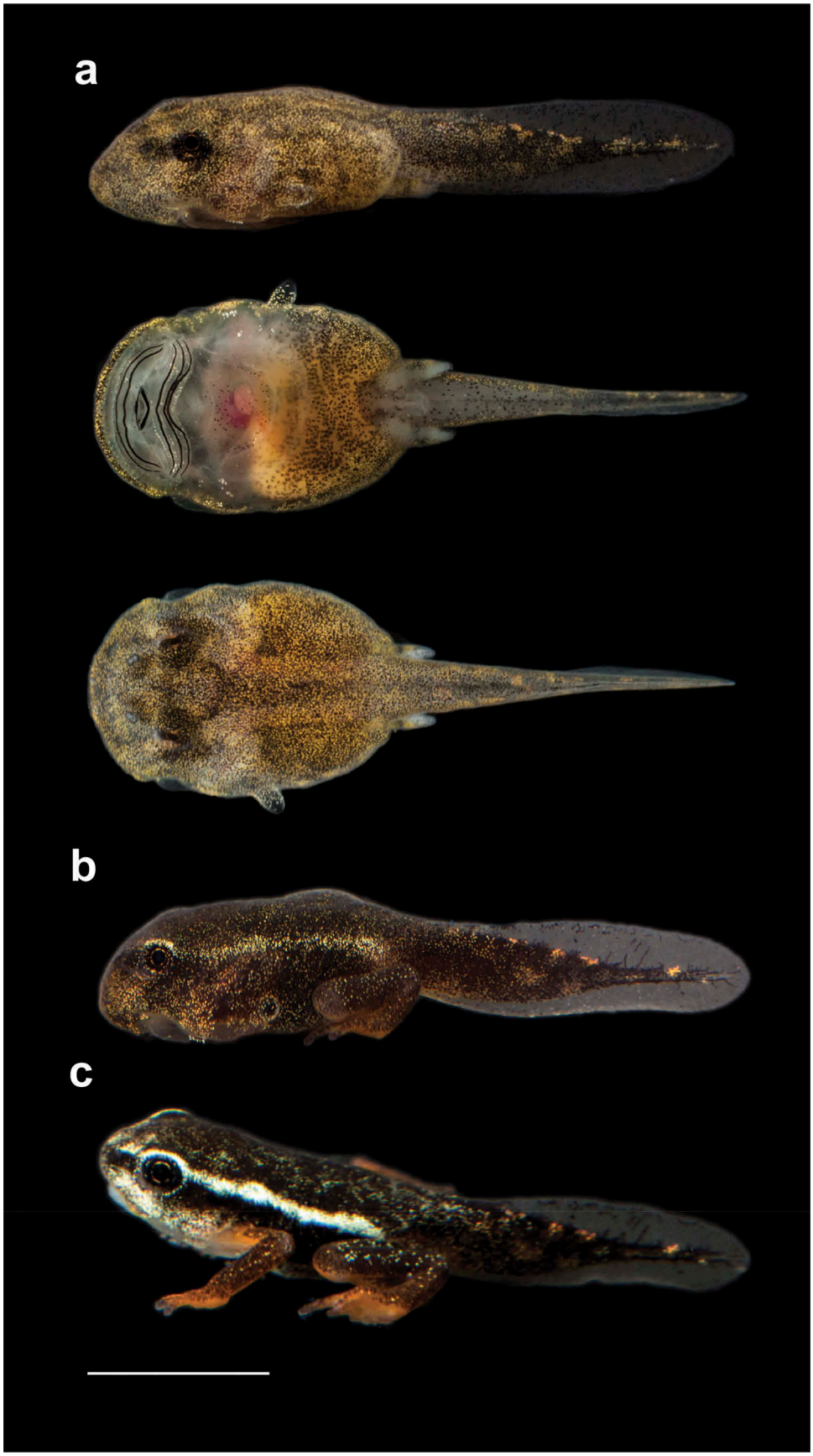

Figure 1. Tadpole and metamorph of *Atelopus elegans* CJ 1220. (a) tadpole (Stage 25); (b) metamorph (Stage 41); (c) metamorph (Stage 43). From Durango, Provincia Esmeraldas, Ecuador. Scale = 5 mm. Photos by LAC.

(Figure 4(a–b)). Furthermore, there is a well-defined stripe of lateral line canal openings from the beginning of tail until the mid-tail, located along the outline of the tail muscle, and one submarginal papillae at the right side of the oral disc, both sorts were seen in unpublished images.

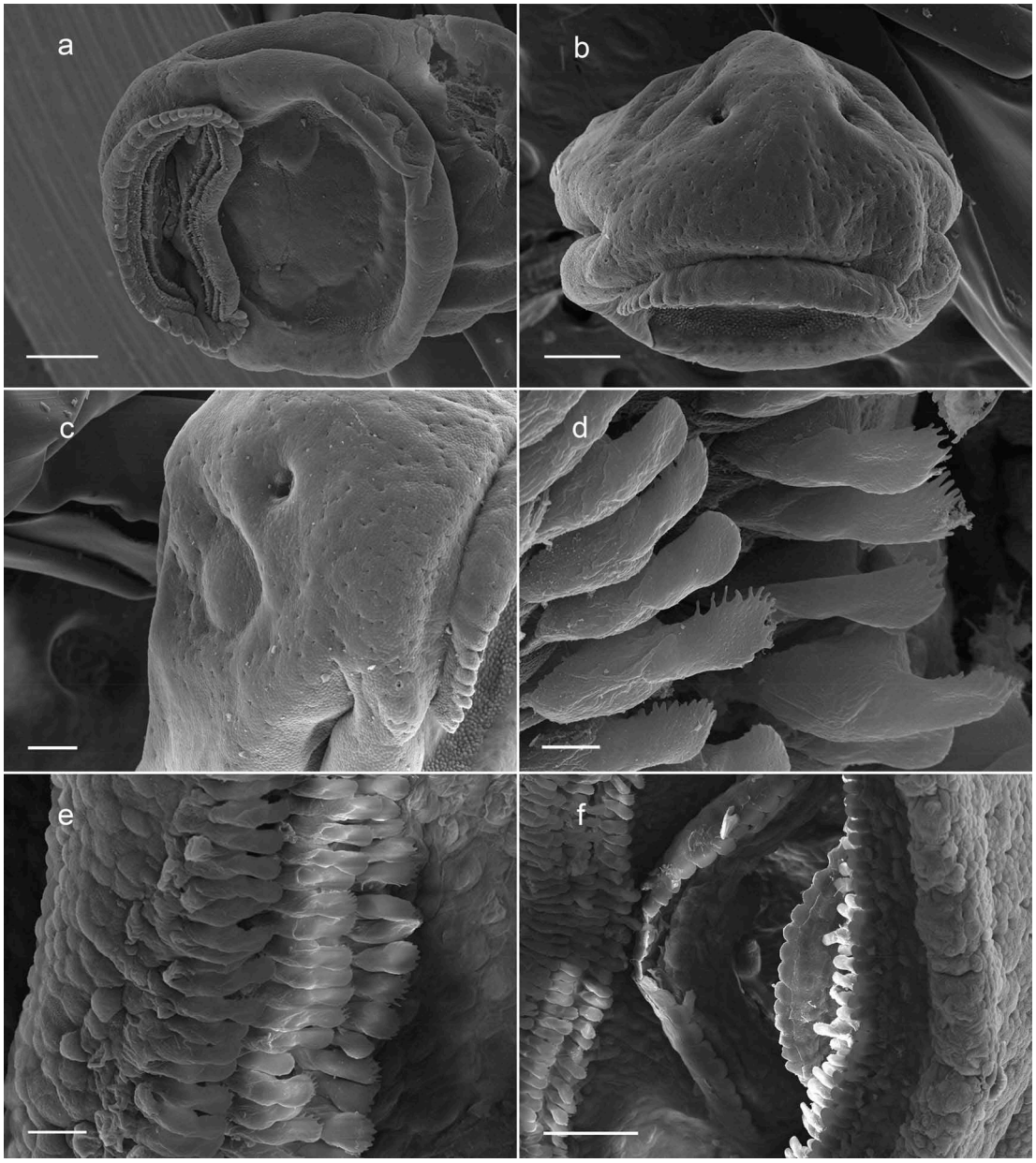

Figure 2. Scanning electron microscope micrographs of a tadpole of *Atelopus elegans* (CJ 6383) at Stage 25. (a) Ventral view, scale = 250 µm; (b) frontal view, scale = 250 µm; (c) lateral side, scale = 150 µm; (d) teeth, scale = 5 µm; (e) posterior (lower) tooth rows, scale = 12.5 µm; (f) Oral disc (mouthparts), scale = 50 µm.

Color in preservative

The dorsum and flanks are tan with colorless areas in the snout, between eyes and spiracles and at the end of body dorsally. There are brown spots along the body, and some of them accumulated forming a stripe above the body. The tail is unpigmented; it is anteriorly with brown spots in dorsal and lateral view. The spiracle is unpigmented. The oral disc is translucent. The abdominal sucker is translucent with few brown spots; the venter is unpigmented, it has brown spots, and the gut is not visible.

Color in life

Based on CJ 1220 at Stage 30. The body is black with cream marks, and both brown and tan spots. One of the marks is at the snout area, two others at the dorsum and flanks and one more at the end of body dorsally. The spiracle is black at the base and translucent at the rest of the tube. The tail is black anteriorly and tan at the rest of the tail. There are black spots at the anterior part of the tail but not at the rest of the tail. The oral disc and abdominal sucker are translucent.

Variation

Based on series CJ 2063b–h (7 tadpoles) collected at the same locality, on Río Negro, Provincia Tungurahua. Meristic variation of tadpoles between stages 25–34 is indicated in Table 2. The individual used for the description is different from others because it has not a protruding spiracle tube unlike to others that have

a protruding spiracle tube, and its opening is directed dorsally unlike others whose opening is directed posterodorsally.

Metamorph variation of CJ 1220 is shown between stages 34–35 and 43 (Figure 3). At Stage 43, the cream flecks at the snout, and between the eyes and spiracle vanish. Moreover, at Stage 43 there are cream stripes dorsolaterally along the body. At Stage 43 the limbs are lightly orange, and the dorsum becomes less dark (cryptic). At stage 30 the tip of tail is narrowly rounded, but at stage 34–35 it becomes rounded.

Discussion

The work presented here brings the number of described tadpoles of *Atelopus* to 28, which represents 27% of the 96 recognized species. The larvae of *Atelopus* possess some traits such as the presence of an abdominal sucker (a putative synapomorphy), a sinistral spiracle, a robust caudal musculature, marginal papillae in the outside of the oral disc, a labial tooth formula of 2/3. The color patterns and pigmentation, the presence or absence of submarginal papillae, and size at different stages are unique characteristics for each species. These characteristics are potentially useful for their identification and differentiation. In Table 3, we include information of six useful variable characters of the 28 species: body color, tail color, pigmentation of the spiracle, presence or absence of submarginal papillae, percentage of the abdominal sucker length in relation to the body length, and percentage of the tail length in relation to the total length.

Comparisons

The body color is very helpful for identifying or gathering species or groups of species in tadpoles of the *Atelopus* genus [7,8]. Some species possess particular color patterns in the dorsum and flanks. Both *A. elegans* and *A. palmatus* have marks in the body, but *A. palmatus* has well-defined marks. The vast majority of tadpoles of *Atelopus* are generally brown or black in a determined range of degrees that goes from cream, tan, brown, grey, dark brown to black (Table 3). A feature that is common in some species of *Atelopus* is the presence of marks or bands in the dorsum and sides of body. These marks are generally located at the snout area, between the spiracle and eyes, and at the end of body. This complete general mark pattern or unless one of these marks are present in *A. balios, A. carbonerensis, A. certus, A. cruciger, A. exiguus, A. flavescens, A. franciscus, A. hoogmoedi, A. laetissimus, A. mittermeieri, A. nanay, A. palmatus, A. pulcher, A. sorianoi, A. subornatus, A. tamaense, A. tricolor*, and *A. zeteki*; the rest of species, including *A. elegans*, have marks, but irregularly distributed, or lack them.

Duellman and Lynch [10] also suggested that tadpoles, which come from high Andean zones, have larger tails and abdominal suckers. This trend applies for some species such as *Atelopus carrikeri* (2350–4800 m), *A. ignescens* (2500–4200 m), *A. nanay* (3600–4100 m), and *A. tamaense* (2950–3200 m) [1,31,32,35,36]. It is possible that larger tails and abdominal suckers provide increased attachment strength. The latter, the suction force (SF), is estimated by the area of suction times the differential pressure ΔP. ΔP is the difference between the atmospheric pressure (AP) and the cup interior pressure (CIP). As AP and ΔP decrease with increasing altitude, a larger area of the abdominal sucker would provide a mechanism for increasing SF. However, it is intriguing that there are some species that live on high Andean zones that do not show increase in their abdominal sucker area. For example, *A. peruensis* which distribution is between 2800 and 4000 m [1], but its relative tail and abdominal sucker length is low, or *A. mucubajiensis* (2300–3500 m) [1] whose relative tail length is high, but its abdominal sucker is small. The *A. elegans* is distributed (300–1140) [1] in the lower montane forest, and show abdominal sucker length relatively large. Meanwhile, *A. palmatus* keeps relatively medium measurements that slightly apply with its distribution (1150–1740). Even though there are some species, which comply with the hypotheses that larger tails and abdominal suckers provide increased attachment strength, the relation between the relative abdominal sucker length and the distribution of each species do not have statistical significance (Pearson correlation; $r^2 = 0.3$). Nonetheless, intraspecific variation in relation to altitudinal range (in species with a broad altitudinal distribution) needs to be studied.

Although there is no information about the purpose of the submarginal papillae in the genus *Atelopus*, the presence or absence of them could become key for defining species. Nonetheless, it is not always an easy task to record its absence given the fact that its presence might vary ontogenetically (e.g., absent at Stage 25 vs present at Stage 30 in *A. elegans*), thus a correct coding of absence of this character needs a sampling of specimens in advanced stages. Generally, in *Atelopus*, the minute submarginal papillae are located beneath the anterior lip, and the prominent ones are located in the lateral region, at the end of the teeth rows. The length of the beaks can be important to define species, for instance, tadpoles of *A. pulcher* (from Tarapoto, Peru) or *Atelopus* sp. (*spumarius* complex, from Manaus Brazil) differ from others by having the upper beak shorter than the lower one. Unfortunately, the information related to beaks is focused on shape. Furthermore, pigmentation of the spiracles could be a feature for classifying and differentiate some species of *Atelopus*. This feature has been shown in some species, every one of them surpass

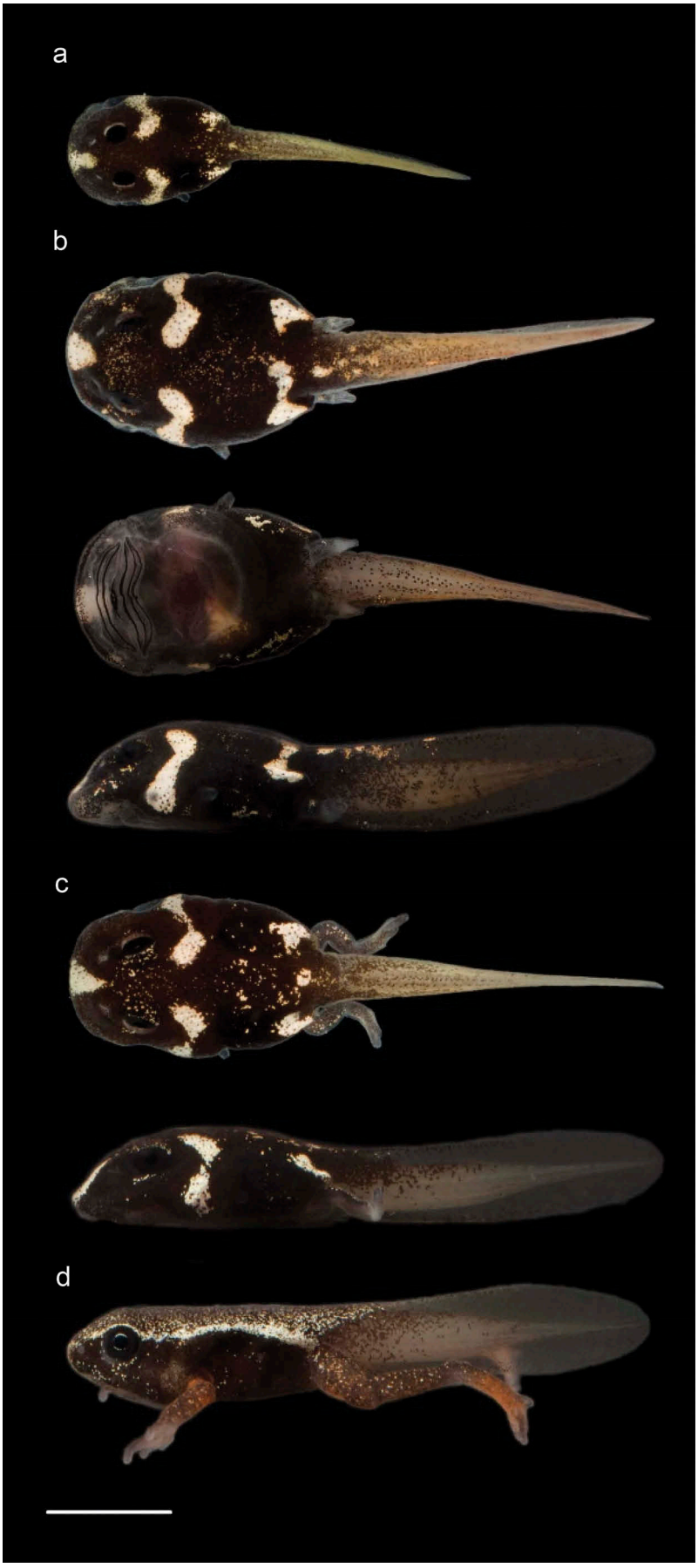

Figure 3. Tadpole and metamorph of *Atelopus palmatus* CJ 1220. (a) tadpole (Stage 25); (b) tadpole (Stage 30); (c) tadpole (Stages 30–35); (d) metamorph (Stage 43). From Las Estancias, Río Negro, Provincia Tungurahua, Ecuador. Scale = 5 mm. Photos by LAC.

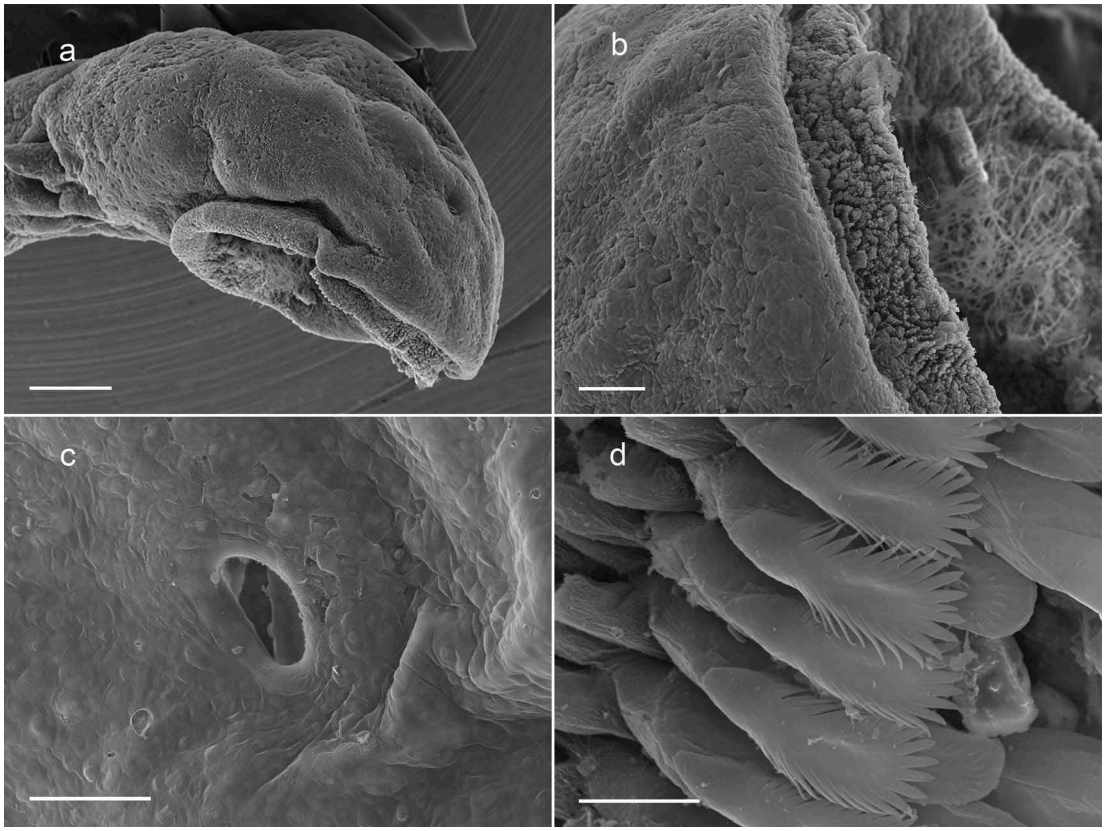

Figure 4. Scanning electron microscope micrographs of a tadpole of *Atelopus palmatus* (CJ 2063) at Stage 30. Ventrolateral view of body, scale = 0.5 µm; (b) Neuromasts of the snout, scale = 150 µm; (c) Narines, scale = 100 µm; (d) Teeth, scale = 10 µm.

2000 m. In other words, species whose distribution lays below 2000 m do not have a pigmented spiracle.

Electronic microscopy

So far there are no available descriptions of the abdominal sucker, based on electronic microscopy, neither in *Atelopus* nor in some other gastromyzophorus species. Kaplan [26] described the anatomy of the abdominal sucker of the genus *Atelopus*, but he did not mention the species. According to him, the friction area is composed of between 10 and 15 protuberances; nevertheless, it is not specified which area of this stripe corresponds to these numbers since this range may correspond to the mid-lateral, posterior, or wider part. Therefore, this range should be considered as a total range, so the total range in *A. elegans* would be 6–12. Moreover, in contrast to the description of Kaplan, that states that there are two ligaments between the borders of the intermediate region, *A. elegans* has only the right one.

Like the abdominal sucker, there are some other traits that have not been described deeply so far in *Atelopus*, for instance the mouthparts. In every description of tadpoles of *Atelopus*, only the general shape and configuration of each structure is described, but there is no information about the structure of each part. The form of teeth is different between both species. While the teeth of *A. elegans* are short-cusped, the [7,10] ones of *A. palmatus* are long cusped, but the curvature of the teeth of *A. palmatus* is stronger than in the *A. elegans* ones. In addition, nostrils variation is clearly seen between *A. elegans* and *A. palmatus*, both in their shape and presence or absence of rim.

According to Lannoo, the generalized lateral line system of tadpoles consists of three main lines each on the trunk and head [37]. Our description of the system in *Atelopus* varies in that the lines in the head follow an irregular pattern, whereas the generalized pattern is visible in the tail.

Analogous sucking organs in other amphibians and fish

Besides the species of *Atelopus*, there are other groups being part of the gastromyzophorous ecomorphological guild such as bufonids (some species of the *Rhinella veraguensis* group) [38], and ranids (genus *Amolops, Huia, Meristogenys*, and *Rana*) [39]. Only few studies have focused on the structure of the abdominal sucker in these groups. For example, Gan et al. [40] presented the detailed structure of the abdominal sucker in *Huia cavitympanum*. This description shows the structures and muscles, also present in the *Atelopus´* abdominal sucker but arranged differently. The gastromyzophorous tadpoles of the genus *Rana*, are different from the other ranids because the edge of the former´s abdominal sucker is not as well defined as the other ranids.

Table 3. Summary of morphological characters found in tadpoles of the genus *Atelopus*.

Species	Tail color	Body color	Pigmentation of spiracle	Submarginal papillae	Percentage of the ASL in relation to the BL	Percentage of the TAL in relation to the TL	Distribution (altitude)
A. balios	Brown with white marks and fin with scattered brown flecks	Brown with pale marks behind eyes, one at mid-body and two at the end of body; and some white marks along the periphery of snout and between spiracle and eyes	No	Present	47.9 *	59.0	200–460 (EC)
A. carbonerensis	Cream	Dark brown with two vertical cream marks between spiracle and eyes and two cream marks below eyes and narines	Yes	Absent	49.3	58.0	2330 (VE)
A. carrikeri	Brown marks	Uniformly brown	Yes	Absent	56.3*	64.0	2350–4800 (C)
A. certus	Cream with brown marks	Dark brown above, white flecks below, and the edge of snout lacking pigment	-	-	45.6	51.4	500–1150 (PA)
A. cruciger	-	Dark with a continuous flank from the posterior part of the spiracle rounded the below part of body	-	Absent	60.3 *	57.7 *	100–2200 (VE)
A. elegans	Tan with brown marks	Tan with brown marks	No	Absent (in early stages)	66.7	58.5	300–1140 (EC, CO)
A. exiguus	Dark brown anteriorly, and unpigmented posteriorly	Dark brown translucent marks below eyes and translucent vertical bands behind eyes	Yes	Absent	52.2 *	60.4	3000–4000 (EC)
A. flavescens	Brown	Brown with some unpigmented areas	No	Present	41 *	62.1	0–300m (GU)
A. franciscus	Dark grey	Dark grey with white and rounded areas behind each eye, and a rectangular area in the snout	No	Present	58.3 *	57.1	5–200 (GU)
A. hoogmoedi	Dark brown with cream marks	Dark brown with a regular pattern of cream marks in front of and behind eyes	-	-	-	59.0	-
A. ignescens	Dark brown	Black	-	-	58.0	62.1	2500–4200 (EC)
A. laetissimus	Light cream with black spots	Uniformly black with translucent border around the snout connected with a vertical mark between spiracle and eyes	No	Present	43.5 *	61.7	1900–2800 (C)
A. mindoensis	One-third dark brown, and the rest tan with brown flecks	Uniformly brownish orange with minute brown spots	No	Absent	45.1 *	60.8	587–1830
A. mittermeieri	White with a black mark at the middle tail and the last part is reticulated	Black with a small unpigmented area between eyes and spiracle	Yes	Absent	37.9	55.4	2525
A. mucubajiensis	Dark brown with brown spots	Dark brown with almost unpigmented areas in the snout, and some marks behind the eyes and anterior to the spiracle and a white vertical line anterior of the spiracle	No	Absent	46.4	61.7	2300–3500
A. nahumae	Light cream with black spots	Black with a horizontal band behind the eyes and two marks between nostrils and snout tip	No	Present	54.8 *	64.4	1900–2800
A. nanay	Two thirds uniformly brown, and the last third white with scattered brown pigment	Uniformly brown	Yes	Present	72.7	60.7	3600–4100
A. palmatus	Unpigmented with brown spots anteriorly	Tan with colorless areas in the snout, between eyes and spiracle and at the end of body	No	Present	51.5	57.7	1150–1740
A. peruensis	Dark	Dark brown with gray mottling	-	-	56.2 *	45.7	2800–4000
A. pulcher	Brown with white marks	Brown with withe marks anterior and posterior to eyes	-	Present	47.7 *	59.6 *	600–900
A. sorianoi	Creamily white	Dorsum and flanks brown and the anterior area mainly white	-	Absent	52.2	63.2	2400–2718

(*Continued*)

Table 3. (Continued).

Species	Tail color	Body color	Pigmentation of spiracle	Submarginal papillae	Percentage of the ASL in relation to the BL	Percentage of the TAL in relation to the TL	Distribution (altitude)
A. sp. (*spumarius* complex from Manaus, Brazil)	Strongly pigmented	Light with scattered pigmentation	-	Absent	54.4 *	54.8 *	-
A. sp. (*spumarius* complex from Puyo, Ecuador)	Presence of vertical cream and black bands	Dark above and laterally with scattered white flecks	-	-	43.5	49.6	-
A. subornatus	Cream anteriorly with dark spots, black in the middle, and translucent posteriorly	Black with two white marks at the snout area, two vertical marks behind eyes and some others at the posterior part	Yes	Present	70.0	59.2	2150–2800
A. tamaense	Dark brown	Brown with some vertical bands behind the eyes without bending in the dorsum	-	Present	73.3	60.0	2950–3200 (VE)
A. tricolor	Dark brown with unpigmented areas	Dark brown with darker dots, unpigmented marks behind eyes	-	Present	-	56.0	1250–2500 (PE)
A. varius	Dark brown	Uniformly dark	-	Absent	48.5 *	55.6 *	16–2000 (PA)
A. zeteki	One third pigmented, and the rest unpigmented	Dark brown with lighter gray areas at the flanks	No	-	48.3 *	52.5	335–1315 (PA)

Asterisks (*) mean information is taken from pictures or illustrations. ASL, abdominal sucker lengt; BL, body length; TAL, tail length; TL, total length; EC, Ecuador; VE, Venezuela; C = Colombia; PA, Panama; GU = Guyane.

Abdominal suckers are common in freshwater environments not only in some species of amphibians but also in some groups of fish such as gobbies, loricariid catfish, and balitorid loaches. These structures fulfill the same function as in tadpoles, helping them to keep their position in high-speed currents [41]. Some gobbids from oceanic islands that live in fast-currents exhibit ventral suckers derived from the fusion of pelvic fins [42,43]. This structure plays the same role as the *Atelopus* tadpoles, but with a different purpose [43]. For instance, the waterfall-climbing gobioid eggs hatch upstream and are swept to the ocean. After a few weeks of development, they come back to streams facing physiological challenges (osmoregulation), strong river currents, and having to climb vertical rocks of waterfalls. This migration intends to find breeding habitats and scape from non-climbing predators [43,44]. Several studies [45,46] suggest that the evolutionary adaptation to fast running water could represent an advantage for the species in terms of reducing predation if compared to those sites with calm water flow due to expansive predator populations. Additionally, the adaptation to fast running waters might have an advantage in the colonization of the headwaters of streams. This would facilitate the process of speciation in aquatic running environments and could play an important role in the occupation of a new niche which has the highest diversity of those species of this genera present [47], increasing the survival probabilities of the species. In terms of bioindication, species that live in fast-flowing environments and with these morphological adaptations are potential indicators of healthy environments.

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No potential conflict of interest was reported by the authors.

ORCID

Alejandro Marcillo-Lara http://orcid.org/0000-0001-9180-5135
Luis A. Coloma http://orcid.org/0000-0003-0158-2455
Sara Álvarez-Solas http://orcid.org/0000-0002-8267-9816

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