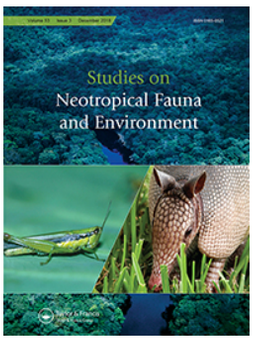

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ORIGINAL ARTICLE

A comparison of tadpoles of two populations of *Leptodactylus plaumanni* (Anura: Leptodactylidae), with a discussion of *Leptodactylus* tadpole morphology

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ABSTRACT

Of the currently known 75 species within the four recognized species groups of *Leptodactylus*, the *L. fuscus* group contains 30 species, of which tadpoles are known for 24, including *L. plaumanni* described based on a population from Argentina. Herein, we describe external and internal oral morphology of *L. plaumanni* tadpoles collected in Brazil and compare with tadpoles from Argentina. In addition, we compare phenetic groups obtained from analysis of larval characters with the currently recognized species groups. The tadpole of *L. plaumanni* from Brazil is identified by: body globular in lateral view, ventral fin forming a wide arc, oral disc lateroventrally emarginate, marginal papillae of oral disc biseriate, more than 10 papillae on each side delimiting the mouth floor, and buccal roof arena trapezoidal. Of the 23 analyzed external morphological characters, only eight were shared by tadpoles from Argentina and Brazil, and they also shared 14 of the 15 internal oral morphological characters. Tadpoles of both populations differ in external morphology and, although such intraspecific differences can be due to plasticity, the hypothesis that these two populations represent different species cannot be dismissed. Phenetic groups obtained using larval characters are consistent with species groups proposed for *Leptodactylus* by phylogenetic analysis, based on adult characters.

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KEYWORDS
Larval morphology; taxonomic groups; internal oral morphology; *Leptodactylus fuscus* group

Introduction

The genus *Leptodactylus* Fitzinger, 1826 consists of 75 species distributed from North to South America and West Indies (de Sá et al. 2014). The included species were originally clustered into four phenetic groups based on morphological and behavioral characters of adults: *L. latrans*, *L. melanonotus*, *L. pentadactylus*, and *L. fuscus* species groups (Heyer 1969a, 1970a, 1978, 1979; Maxson & Heyer 1988). An integrative systematic approach based on molecular (mitochondrial and nuclear markers), morphological, and behavioral characters of adults, corroborated the monophyly of the genus and the phenetic groups proposed (de Sá et al. 2014). More than 80% of the species of *Leptodactylus* were included in their analysis, and their results required the reallocation of just a few species in order to render the four species groups as monophyletic.

The *Leptodactylus fuscus* species group (de Sá et al. 2014) consists of 30 species that range in size from small (SVL = 30.9 mm) to large (SVL = 105.1 mm) and are distinguished from species of the other species groups by lacking interdigital membranes and having nostrils that are adjacent to or in contact with each other along their median edges. The combined species distribution extends from the US state of Texas to Argentina, on both sides of the Andes, and on some islands of the Antilles, with a large number of species concentrated in the southern and eastern regions of the Amazon Basin (Heyer 1978).

Leptodactylus plaumanni is distributed in southern South America from Misiones, Argentina, to the states of Rio Grande do Sul, Santa Catarina and Paraná, in Brazil (de Sá et al. 2014). The tadpole of this species was described based on specimens from Misiones, Argentina (Grosso 2015). Comparing the description of the species

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with tadpoles from Brazilian populations, we noticed extensive discrepancies, such as shape of body in lateral view, total body length, body height, snout shape, dorsal and ventral fin shape and marginal papillae. Herein, we describe the external and internal oral morphology of *L. plaumanni* tadpoles collected in Brazil and compare them to the tadpoles described from Argentina (Grosso 2015). Despite the extensive number of characters employed in the phylogenetic analysis of de Sá et al. (2014), larval morphology was not included. Considering that different life cycle phases can be under the influence of different processes, we thought it of interest to also evaluate the usefulness of larval morphology for understanding relationships among the species of the genus *Leptodactylus*.

Material and methods

Sampling, habitat and identification of L. plaumanni *tadpoles from Brazil*

Brazilian tadpoles of *L. plaumanni* were collected between January 2007 and January 2008, in the municipality of General Carneiro (26°24′S, 51°22′W), State of Paraná, and in the municipalities of Ponte Serrada, Passos Maia and Vargem Bonita, State of Santa Catarina at the boundaries of Parque Nacional das Araucárias (26°47′S, 51°56′W). The two locations are 51 and 137 km, respectively, from Nova Teutônia, the type locality of *L. plaumanni* (Ahl 1936).

Tadpoles were found in *Araucaria* forest associated with natural grasslands ('campos naturais', *sensu* Maack 2002), in four temporary water bodies: one located at the forest edge, two in an area of natural grassland, and one in a pasture. During two years of monthly samplings, adults and tadpoles of only two species of *Leptodactylus* were recorded in all areas sampled: *L. latrans* and *L. plaumanni* (Conte 2010; Conte pers. com. for the municipality of Vargem Bonita). Tadpoles belonging to *L. plaumanni* were identified using a taxonomic key (Gonçalves 2014). For species confirmation, we raised individual tadpoles until they were frogs and could be identified by the following characteristics, which are in agreement with those of *L. plaumanni* (de Sá et al. 2014) (Figure 1):

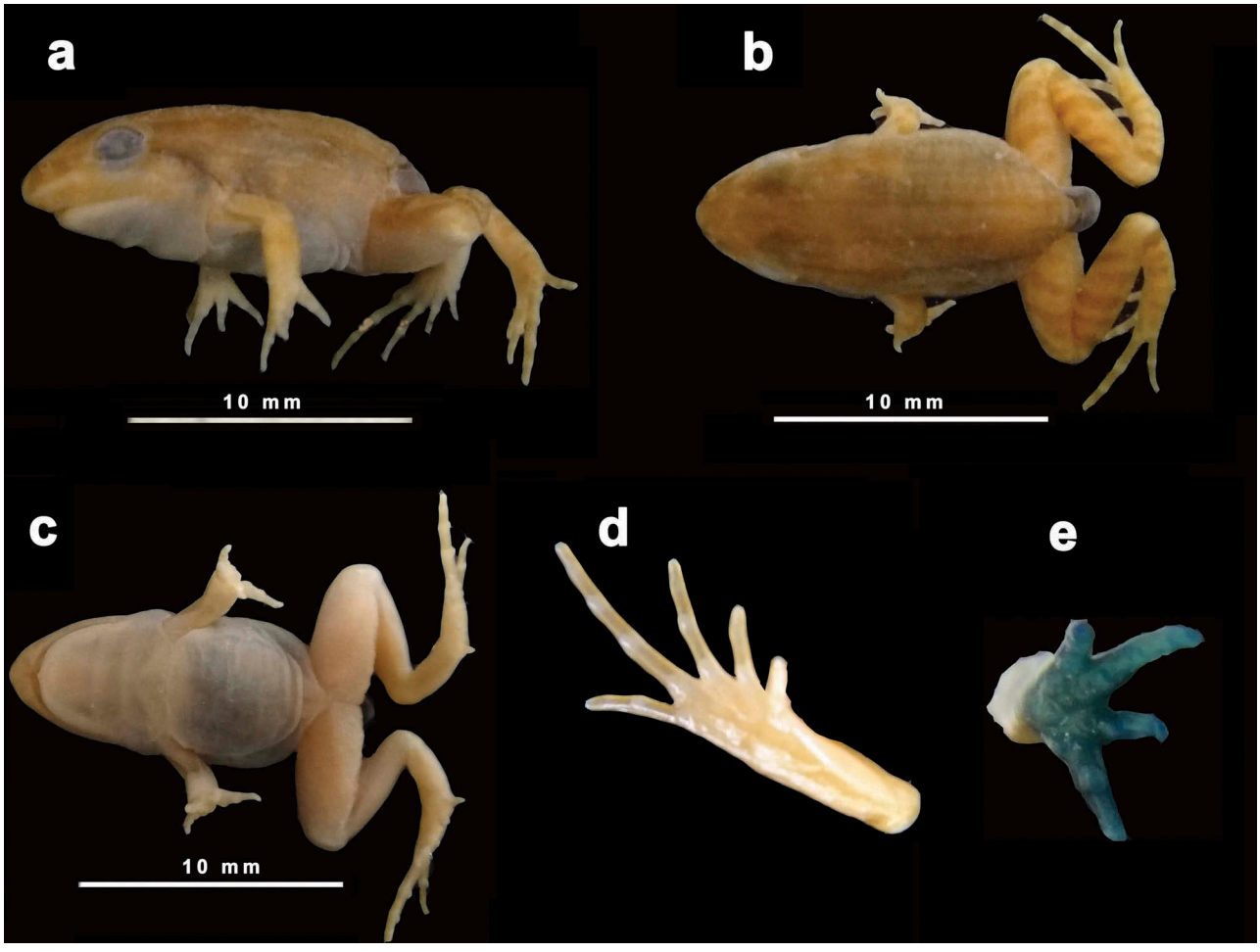

Figure 1. Juvenile specimen of *Leptodactylus plaumanni* from Brazil in (A) lateral view (B) dorsal view and (C) ventral view, and (D) hind limb and (E) forelimb.

male snout calloused, not spatulate; males lacking thumb and chest spines; light upper lip stripe distinct; pair of dorsal folds distinct; pair of dorsolateral folds distinct; pair of lateral folds distinct; posterior of thigh with light stripe; upper shank with narrow longitudinal light stripes; belly uniformly light in color; and toes without lateral fringes. Tadpoles and juvenile frogs are deposited in the Coleção Científica de Anfíbios of the Departamento de Zoologia e Botânica of UNESP de São José do Rio Preto (DZSJRP Amphibia-Tadpoles: 1561.2, 1709.3, 1733.1 and 1713.1). One tadpole of *L. plaumanni* from the Argentinian locality was provided by Dr. Diego Baldo, Laboratory of Evolutionary Genetics, Universidad Nacional de Misiones (LGE: 03379), from which we obtained the photographs presented herein.

Databases and morphological analysis

The description of *Leptodactylus plaumanni* tadpoles from Brazil is based on 16 tadpoles between developmental stages 34 and 38 (*sensu* Gosner 1960). Data were collected and analyzed for 20 morphometric dimensions of external morphology, 12 morphometric proportions calculated from the morphometric dimensions (Table 1), 12 qualitative characters of external morphology (Tables 2, 3).

Morphological characters and measurements were taken under a Leica® MZ16 stereomicroscope (Huston, Texas, US) with an ocular grid, with the exception of total length, body length, and body width, which were measured to the nearest 0.01 mm using a digital calipers. Terminology and measurements followed Altig and McDiarmid (1999), except for internarial and interocular distance, which were measured from the internal margins and not from the centers of those structures. Photographs of tadpoles were obtained with a stereoscopic microscope coupled to a Leica® DFC500 digital camera system and using Leica Application Suite v.40 software. Images were combined to plates using Combine ZP software. The final images were prepared using Adobe Photoshop CS3 Extended v.10.0 image editing software (San Jose, CA, US).

Analysis of the internal oral morphology of *L. plaumanni* tadpoles from Brazil was performed using four tadpoles at stage 37 (*sensu* Gosner 1960) following the protocol presented in Conte et al. (2007). Images were obtained with a Zeiss model Leo 435 VP scanning electronic microscope (Jena, Thuringia, Germany) housed at UNESP, São José do Rio Preto, SP. Terminology for buccal-pharyngeal morphology follows Wassersug (1976).

Table 1. Morphometric proportions of *Leptodactylus plaumanni* tadpoles from Brazil, with classification of ratios. Position of the nostrils and the spiracle were determined relative to the longitudinal axis. BH: body height; BL: body length; BW: body width; DFH: maximum dorsal fin height; ED: eye diameter; SED: snout-eye distance; SH: spiracle height; SL: spiracle length; SND: snout-nostril distance; SOW: spiracle open width; SW: spiracle width; TMH: maximum tail muscle height; TMW: maximum tail muscle width; VFH: maximum ventral fin height.

Measure	Formula	Ratios	Classification
Nostrils size	ED/BL	> 0.03	Large
		< 0.03	Small
		-	Absent
Nostrils position	SND/SED	< 0.4	Next to end of nose/mouth
		> 0.5	Next to eyes
		0.4–0.5	Intermediate
Eye diameter	ED/BW	> 0.12	Large
		< 0.12	Small
Spiracle length	SL/BL	< 0.13	Short
		> 0.13	Long
Spiracle opening position	SH/BL	< 0.69	In middle third of body
		> 0.69	In posterior third of body
Spiracle width	SW/BH	> 0.18	Wide
		< 0.18	Narrow
Spiracle opening width	SOW/SW	> 0.54	Wide
		< 0.54	Narrow
Maximum tail muscle width (dorsal view)	TMW/BL	> 0.20	Wide
		< 0.18	Narrow
		0.18–0.20	Intermediate
Dorsal fin shape		DFH > TMH	Wide arc
		DFH < TMH	Arc
		DFH = TMH	Parallel
Maximum dorsal fin height	DFH/TMH	> 1.0	High
		< 0.89	Low
		0.89–1.0	Intermediate
Ventral fin shape		VFH > TMH	Wide arc
		VFH < TMH	Arc
		VFH = TMH	Parallel
Maximum ventral fin height	VFH/TMH	> 1.0	High
		< 0.89	Low
		0.89–1.0	Intermediate

For comparisons, the external morphology of tadpoles of 27 species of *Leptodactylus* from different localities was analyzed using information available from literature (Heyer 1969b, 1970b; McCranie et al. 1986; Wogel et al. 2000; Langone & de Sá 2005; Bilate et al. 2006; Prado & d'Heursel 2006; Rossa-Feres & Nomura 2006; Borteiro & Kolenc 2007; Vieira et al. 2007; de Sá et al. 2007a, 2007b; Heyer et al. 2010; Menin et al. 2010; Heyer & de Sá 2011; Pezzuti 2011; Magalhães et al. 2013; Grosso 2015) and in the SISBIOTA tadpoles project database (CNPq: 563075/2010–4 and FAPESP: 2010/52321–7; (http://www.bv.fapesp.br/pt/auxilios/30170/girinos-de-anuros-da-mata-atlantica-da-amazonia-do-pantanal-do-cerrado-e-de-zonas-de-transicao-c/). From this last source, we used information of tadpoles of three *Leptodactylus* species: *L. knudseni*, *L. longirostris* and *L. macrosternum*. However, this database is not publicly available until 2020, when all project results will be published.

Table 2. External morphological characters of the body and tail of tadpoles of 27 species of *Leptodactylus*. BR: *Leptodactylus plaumanni* from Brazil; AR: *L. plaumanni* from Argentina.

	Shape in lateral view					Shape of fin	
Species	Body	Snout	Eye position	Direction of spiracle	Position of spiracle in body	Dorsal	Ventral
L. caatingae	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Arc	Parallel
L. cunicularius	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Arc	Arc
L. elenae	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Wide Arc	Arc
L. furnarius	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Arc	Arc
L. fuscus	Globular/depressed	Sloping	Dorsal	Posterodorsal	Middle	Arc	Parallel
L. gracilis	Globular/depressed	Rounded	Dorsolateral	Posterodorsal	Middle	Arc	Arc
L. jolyi	Globular	Sloping	Dorsal	Posterodorsal	Middle	Arc	Arc
L. latinasus	Globular/depressed	Sloping	Dorsolateral	Posterodorsal	Middle	Arc	Parallel
L. longirostris	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Arc	Parallel
L. mystacinus	Globular/depressed	Sloping	Dorsolateral	Posterodorsal	Middle	Wide Arc	Wide Arc
L. notoakitites	Globular/depressed	Sloping	Dorsolateral	Posterodorsal	Middle	Arc	Arc
L. plaumanni (BR)	Globular	Sloping	Dorsal	Posterodorsal	Middle	Wide Arc	Wide Arc
L. plaumanni (AR)	Globular/depressed	Sloping	Dorsal	Posterodorsal	Middle	Arc	Arc
L. poecilochilus	Globular	Sloping	Dorsal	Posterodorsal	Middle	Wide Arc	Wide Arc
L. spixi	Globular/depressed	Sloping	Dorsolateral	Posterodorsal	Posterior end	Arc	Arc
L. melanonotus	Globular	Rounded	Dorsolateral	Posterodorsal	Middle	Wide Arc	Wide Arc
L. podicipinus	Globular/depressed	Sloping	Dorsal	Posterodorsal	Middle	Parallel	Parallel
L. pustulatus	Globular/depressed	Rounded	Dorsolateral	Posterolateral	Middle	Arc	Parallel
L. silvanimbus	Globular	Rounded	Dorsal	Posterolateral	Middle	Arc	Arc
L. insularum	Globular	Rounded	Dorsolateral	Posterodorsal	Posterior end	Wide Arc	Arc
L. macrosternum	Globular/depressed	Rounded	Dorsal	Posterolateral	Anterior end	Arc	Arc
L. latrans	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Parallel	Parallel
L. knudseni	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Parallel	Parallel
L. labyrinthicus	Globular/depressed	Rounded	Dorsal	Posterodorsal	Posterior end	Parallel	Parallel
L. pentadactylus	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Arc	Wide Arc
L. rhodonotus	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Wide Arc	Wide Arc
L. savagei	Globular/depressed	Rounded	Dorsal	Posterodorsal	Middle	Wide Arc	Wide Arc
L. vastus	Globular/depressed	Rounded	Dorsolateral	Posterodorsal	Middle	Arc	Parallel

Table 3. External morphological characters of the oral disc of tadpoles of 27 species of *Leptodactylus*. BR: *Leptodactylus plaumanni* from Brazil; AR: *L. plaumanni* from Argentina.

Species	Type of emargination of oral disc	Marginal papillae	Position of oral disc	Coverage of lower jaw	Dental formula
L. caatingae	Absent	Biseriate	Anteroventral	U	2(2)/3(1)
L. cunicularius	Absent	Uniseriate/alternate	Anteroventral	V	2(2)/3(1)
L. elenae	Lateral	Uniseriate/biseriate	Anteroventral	V	2(2)/3(1)
L. furnarius	Absent	Uniseriate/alternate	Anteroventral	V	2(2)/3(1)
L. fuscus	Absent	Uniseriate	Anteroventral	V	2(2)/3(1)
L. gracilis	Absent	Uniseriate/biseriate	Anteroventral	U	2(2)/3(1)
L. jolyi	Ventrolateral	Uniseriate/alternate	Anteroventral	V	2(2)/3(1)
L. latinasus	Absent	Uniseriate/biseriate	Anteroventral	V	2(2)/3(1)
L. longirostris	Absent	Biseriate	Anteroventral	V	2(2)/3
L. mystacinus	Absent	Uniseriate	Anteroventral	V	2(2)/3(1)
L. notoakitites	Ventral	Uniseriate	Anteroventral	U	2(2)/3
L. plaumanni (BR)	Lateral	Biseriate	Anteroventral	V	2(2)/3(1)
L. plaumanni (AR)	Absent	Uniseriate	Anteroventral	V	2(2)/3(1)
L. poecilochilus	Absent	Uniseriate/biseriate	Anteroventral	V	2(2)/3(1)
L. spixi	Absent	Uniseriate/biseriate	Anteroventral	V	2(2)/3
L. melanonotus	Absent	Biseriate	Anteroventral	U	2(2)/3
L. podicipinus	Ventral	Triseriate/biseriate	Anteroventral	V	2(2)/3
L. pustulatus	Ventrolateral	Uniseriate/biseriate	Anteroventral	U	2(2)/3
L. silvanimbus	Absent	Uniseriate/alternate	Anteroventral	V	2(2)/3
L. insularum	Absent	Uniseriate/biseriate	Anteroventral	V	2/3
L. macrosternum	Ventral	Uniseriate/alternate	Anteroventral	V	2/3
L. latrans	Ventral	Triseriate/biseriate	Anteroventral	U	2/3
L. knudseni	Ventral	Uniseriate	Terminal	U	2(2)/2(1–2)
L. labyrinthicus	Ventral	Uniseriate	Terminal	V	1/2(1)
L. pentadactylus	Ventrolateral	Uniseriate	Terminal	V	1/2(1)
L. rhodonotus	Absent	Uniseriate/alternate	Anteroventral	V	2(2)/3(1) or 2(2)/3
L. savagei	Absent	Uniseriate	Terminal	V	2(2)/3(1)
L. vastus	Absent	Uniseriate/biseriate	Terminal	V	1/2(1)/1/3(1)

Considering the available data, we calculated 11 morphometric proportions (Supplementary online material, Tables S1, S2), and compiled data on 12 characters of external morphology (Tables 2, 3) and 15 characters of internal oral morphology provided by Miranda et al. (2014): number of infralabial papillae; shape of infralabial lateral papillae; number of lingual papillae; shape of the buccal floor arena; number of

pustules in the buccal floor arena; number of papillae (on each side) delimiting the buccal floor arena; size of papillae of buccal floor arena; number of projections on posterior margin of ventral velum (on each side of the glottis); projections of pre-nasal arena; number of post nasal papillae (per side); shape of median ridge; size of lateral ridge of median papillae; shape of lateral papillae of median ridge; shape of the buccal roof arena; number of papillae limiting the buccal roof arena (per side).

Statistical analyses

For phenetic analysis of larval characters of species of the genus *Leptodactylus*, the states of morphological data were transformed into binary data (Supplementary online material, Tables S3, S4), and assembled in a presence/absence matrix in order to perform an ANOSIM similarity analysis. ANOSIM is a non-parametric test that measures the difference between two or more groups using distance metrics, in this case the binary Jaccard similarity index. Distances are converted into 'ranks' and compared within and between groups of species (Clarke 1993; Legendre & Legendre 2012). To illustrate the differences between groups we employed non-metric multidimensional scaling (NMDS) (Clarke & Warwick 1994). The starting point of this analysis is a similarity matrix of the groups being compared; in our case we used the similarity matrices constructed from the morphological and morphometric characteristics using Jaccard similarity. Then, NMDS synthesizes the information from multiple dimensions into just a few that can then be displayed and interpreted. Furthermore, NMDS uses rank orders, and thus is an extremely flexible technique that can accommodate a variety of different kinds of data (Legendre & Legendre 2012). Both ANOSIM and NMDS were performed with the software PAST v. 2.17 (Hammer et al. 2001).

Results

Description of the tadpole of Leptodactylus plaumanni *from Brazil*

Leptodactylus plaumanni (Figures 2, Table 4) has Orton Type IV, exotrophic, lentic, and benthic tadpoles. Body in dorsal view ovoid (69%) or oval/elliptical (31%) (N = 16); in lateral view globular. Snout slightly truncate in dorsal view and sloped in lateral view. Eyes small, positioned dorsally, oriented dorsolaterally. Nostrils small, oval, positioned dorsally (vertical axis), near the tip of snout (longitudinal axis), opening directed dorsolaterally, internal border wide and complete (apophysis absent). Spiracle sinistral, short, wide, cone-shaped, directed posterodorsally; terminal portion of centripetal wall short and free; spiracle opening narrow, positioned medially at middle third of body, directed posterodorsally. Vent tube medial, attached to ventral fin, opening oriented medially. Caudal musculature wide, gradually tapering, reaching end of caudal fin; dorsal fin low, beginning at body-tail junction at an angle of about 58°, contour forming wide arc; ventral fin low, contour forming wide arc; both fins similar in height; tail tip pointed, flagellum absent. Lateral line not conspicuous. Oral disc positioned anteroventrally, emarginated lateroventrally; marginal papillae triangular, in double rows, with wide dorsal gap of about 54% of oral disc width (Figure 2D). Tooth row formula 2(2)/3(1), A-1 and A-2 arc-shaped, A-2 slightly longer than A-1, P-2 and P-1 sub-equal in length, P-3 slightly shorter than P-2. Mandibular and maxillary sheaths large, mandible V-shaped, maxilla M-shaped; serrations of maxilla short with wide base.

Oral internal morphology

Buccal floor

Buccal floor triangular (Figure 3A); four infralabial papillae present; anterior pair cylindrical, positioned on median line with bases fused; posterior pair triangular-shaped, one on each side of buccal floor. Lingual region elliptical, located just posterior to posterior pair of infralabial papillae; four cylindrical lingual papillae present with abruptly tapering apexes, arranged side by side forming a single row; external lingual papillae smaller than central papillae. Mouth floor arena hexagonal, delimited by 11 to 12 cone-shaped elongated papillae on each side; papillae vary in size, apexes oriented toward center of buccal floor arena; approximately 50 pustules concentrated in terminal region of floor arena. Buccal pockets wide, deep, arranged transversely. Ventral velum wide, four projections present on each side of glottis (Figure 3B), approximately two projections located more distant from glottis. Glandular zone not conspicuous, located next to velum projections.

Buccal roof

Buccal roof rectangular; pre-nasal arena trapezoidal, pre-nasal papillae absent (Figure 3C); choanae oval, oriented transversely; post-nasal arena oval, short, narrow, with two triangular post-nasal papillae directed toward the pre-nasal arena; post-nasal arena bound by a triangular median ridge, three papillae of variable sizes present and arranged in row; three papillae arranged in a row immediately posterior to median ridge (Figure 3D) two of four tadpoles possess three

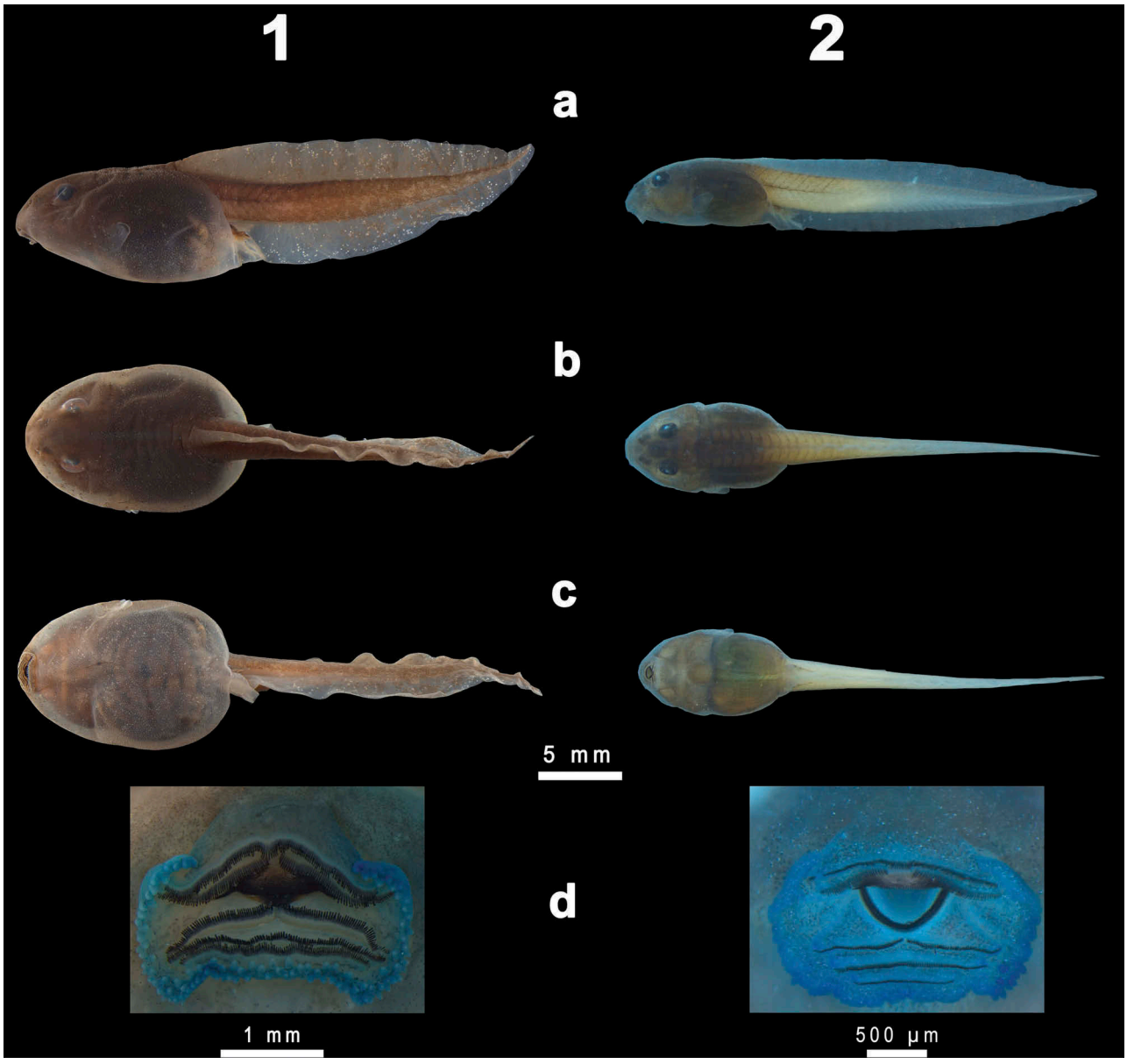

Figure 2. *Leptodactylus plaumanni* tadpoles: (1) specimen from Brazil at stage 37 and (2) specimen from Argentina at stage 37. (A) lateral view; (B) dorsal view; (C) ventral view; (D) oral disc.

papillae arranged in a row (Figure 3D), while papillae posterior to the median ridge are absent in the other two tadpoles; pair of conical papillae present, about same size as postnasal papillae but with wider bases and apexes directed toward median ridge, present in the same direction of median ridge. Roof arena triangular, delimited by eight conical papillae with four grouped on each side, anterior papillae longer than posterior papillae, apexes directed toward arena center; approximately 70 pustules distributed throughout the arena, concentrated centrally and terminally. Dorsal velum narrow, sparse pustules present right posterior of buccal roof arena; glandular area restricted to posterior of dorsal velum.

Coloration in preservative

Ventral region translucent, intestine visible; small dark spots present under epidermis, concentrated in region of intestine posterior to gular region; whitish marks formed by chromatocytes concentrated between gular region and posterior region of intestine; center of gular region opaque and without median spots. Dorsum dark brown, with translucent areas from lateral to the eyes to the snout; notch present in area of spiracle; whitish marks concentrated between eyes and in region of caudal musculature origin, absent or very scattered between eyes and snout. Laterally skin becomes completely translucent; intestine visible despite high

Table 4. Comparison of morphometric measurements (means ± SD, range) of *Leptodactylus plaumanni* tadpoles from Brazil and Argentina.

	Mean ± SD (range)	
Character (mm)	Tadpoles from Brazil (N = 16)	Tadpoles from Argentina (N = 10[a] ; *N = 1, from plate)
Total length	35.00 ± 5.38 (28.10–44.50)	26.03 ± 1.29
Body length	14.13 ± 1.38 (11.75–16.25)	8.87 ± 0.41
Body height	8.63 ± 1.86 (6.25–12.25)	3.9 ± 0.22
Body width	10.56 ± 2.30 (7.88–15.00)	5.4 ± 0.22
Eye diameter	1.11 ± 0.11 (0.91–1.18)	1.12 ± 0.07
Interorbital distance	2.30 ± 0.33 (1.73–2.64)	1.26 ± 0.06
Nostril diameter	0.32 ± 0.05 (0.27–0.36)	0.24 ± 0.05
Internarial distance	1.80 ± 0.15 (1.55–2.09)	1.32 ± 0.10
Tail muscle width*	3.19 ± 0.50 (2.75–4.25)	2.34
Dorsal fin height*	2.61 ± 0.82 (1.75–4.75)	1.71
Ventral fin height*	2.54 ± 0.86 (1.88–4.75)	1.40
Tail muscle height	3.04 ± 0.68 (2.25–4.00)	2.49 ± 0.33
Eye–snout distance*	2.64 ± 0.53 (1.91–3.45)	2.24
Nostril–snout distance*	0.92 ± 0.27 (0.55–1.36)	0.98
Spiracle length*	1.75 ± 0.39 (1.18–2.64)	1.38
Spiracle height*	3.17 ± 0.64 (2.18–4.18)	2.03
Spiracle width*	1.46 ± 0.28 (1.00–1.91)	1.09
Spiracle open width*	0.80 ± 0.19 (0.55–1.27)	0.68
Oral disk width	2.75 ± 0.35 (2.31–3.25)	2.50 ± 0.16
Angle of emergence of dorsal fin (°)	13.08 ± 3.87 (7.10–19.50)	–

[a]Values from Grosso (2015)
*Morphometric dimensions not available in Grosso (2015), but measured based on the plate presented therein.

concentration of whitish marks above translucent spiracle and between spiracle and snout; whitish blotches scattered throughout lateral region of some individuals. Skin of posterior portion of intestine region is translucent and milky in color. Tail musculature brown; black spots present throughout the entire length, concentrated on horizontal septa, forming irregular spots on the posteromost third; color darker brown dorsally at muscle fin junction. Dorsal fin translucent, patterned as musculature with black spots, forming irregular spots posteriorly. Ventral fin colored similarly to dorsal fin, with few spots on anterior half.

Phenetic comparisons

The distribution of external morphological and morphometric characteristics of larvae of species of the genus *Leptodactylus* are, in general, consistent with the currently recognized species groups of *Leptodactylus* (ANOSIM: $R = 0.60$; $p < 0.0001$), with overlap in the tadpole characters of the following species groups of *Leptodactylus: fuscus* and *melanonotus* (Figure 4A). Likewise, characteristics of tadpole internal oral morphology also agree with the clades previously proposed, despite the fewer number of species considered in our analysis (ANOSIM: $R = 0.74$; $p < 0.0001$), with overlaps between the species groups of *fuscus* and *melanonotus*, and of *latrans* and *melanonotus* (Figure 4B).

Discussion

Leptodactylus plaumanni from Brazil: comparison with Argentinean specimens and tadpoles of L. fuscus group

Tadpoles of Brazilian populations of *L. plaumanni* can be best diagnosed by a combination of external morphological and internal oral characteristics. These characters are either exclusive to a species, or shared with a maximum of two other species of the *fuscus* group: (1) body globular in lateral view (shared with *L. jolyi* and *L. poecilochilus*), (2) ventral fin forming wide arc (shared with *L. mystacinus* and *L. poecilochilus*), (3) oral disc emarginated lateroventrally (shared with *L. jolyi*), (4) double marginal papillae of oral disc (shared with *L. longirostris* and *L. caatingae*), (5) more than 10 papillae delimiting each side of the mouth floor arena (shared with *L. plaumanni* from Argentina) and (6) buccal roof arena trapezoidal. The latter is the only character unique to *L. plaumanni* tadpoles from Brazil.

Tadpoles of Brazilian and Argentinean populations of *L. plaumanni* are easily differentiated by external morphology. Of the 23 characters analyzed, about 65% (n = 15) differ between tadpoles form Brazil and Argentina. Nonetheless, assuming that tadpoles from both countries belong to the same species, a greater similarity in external morphology was expected. On the other hand, with respect to the internal oral morphology, all eight buccal floor characters and six of seven buccal roof characters analyzed in Brazilian tadpoles were similar to those of the Argentinean tadpoles, whereas the trapezoidal shape of the buccal roof arena of Brazilian tadpoles differed from the rounded shape (Grosso 2015) in Argentinean tadpoles. In general, tadpoles of the *L. fuscus* group seem to be very similar in their internal oral morphology (Miranda et al. 2014). Thus, the similarity in internal oral morphology between Brazilian and Argentinean populations of *L. plaumanni* tadpoles follows the pattern of the genus.

The remarkable differences that we found in external morphology are not due to a random deviation resulting from a very small sampling size. As the tadpoles from Brazil were collected from a site near the type locality of *L. plaumanni*, they likely reflect the morphology of tadpoles of the population at the type locality. In contrast to this, the tadpoles from Argentina were collected at the type locality of *L. geminus* (Barrio 1973), a species that was later synonymized with *L. plaumanni* on the basis of their vocalizations and adult morphology (Kwet et al.

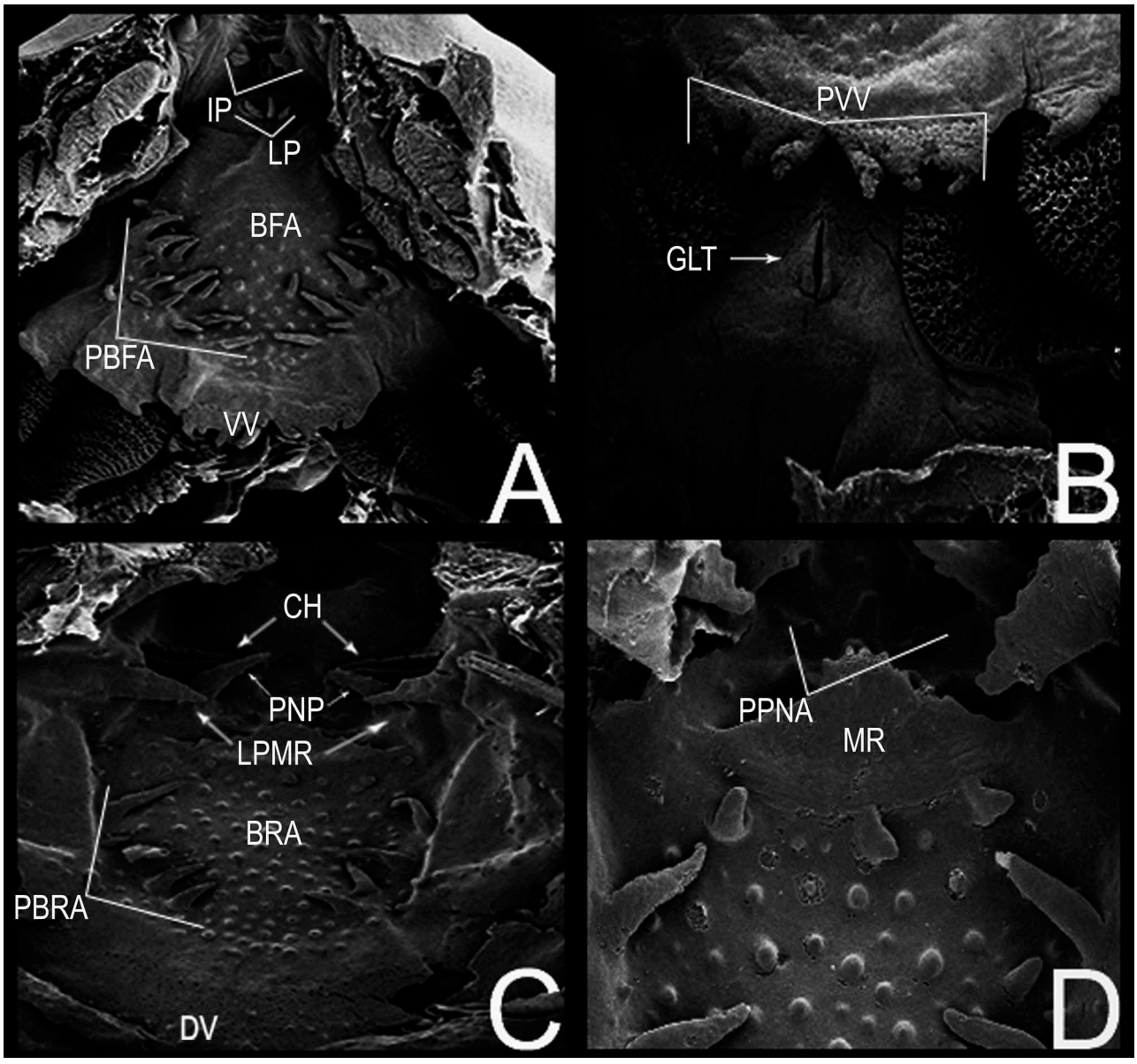

Figure 3. Internal oral morphology of *Leptodactylus plaumanni* tadpole from Brazil: (A) buccal floor; (B) glottis region; (C) buccal roof; and (D) median ridge region, showing papillae arranged in a row in the post nasal region. BFA: buccal floor arena; BRA: buccal roof arena; CH: choanae; DV: dorsal velum; GLT: glottis; IP: infralabial papillae; LP: labial papillae; LPMR: lateral papillae of median ridge; MR: median ridge; PBFA: papillae of buccal floor arena; PBRA: papillae of buccal roof arena; PNP: post nasal papillae; PPNA: papillae of post nasal arena; PVV: projections of ventral velum; VV: ventral velum.

2001). Therefore, our findings call for a taxonomic revision and a genetic analysis of *L. plaumanni* from both type localities involving not only adult morphology, vocalizations and geographic distribution, but also tadpole morphology, to determine if these tadpoles represent two different species.

Comparisons among species groups of Leptodactylus

The 15 tadpoles of the *fuscus* group analyzed are very similar in external morphology (Supplementary online material, Table S3), with overlaps among species of at least 80% involving the following characters: relative body height, body shape in lateral view, relative tail length, relative height of ventral and dorsal fins, shape of lower jaw sheath, tooth row formula, position of spiracle and relative height of tail musculature. A posterodorsally directed spiracle is found in all tadpoles of this group and this feature is also found in half of the species of the *latrans* group, more than 60% of the species of the *melanonotus* group, and all species of the *pentadactylus* group (Supplementary online material, Table S3). Likewise, an

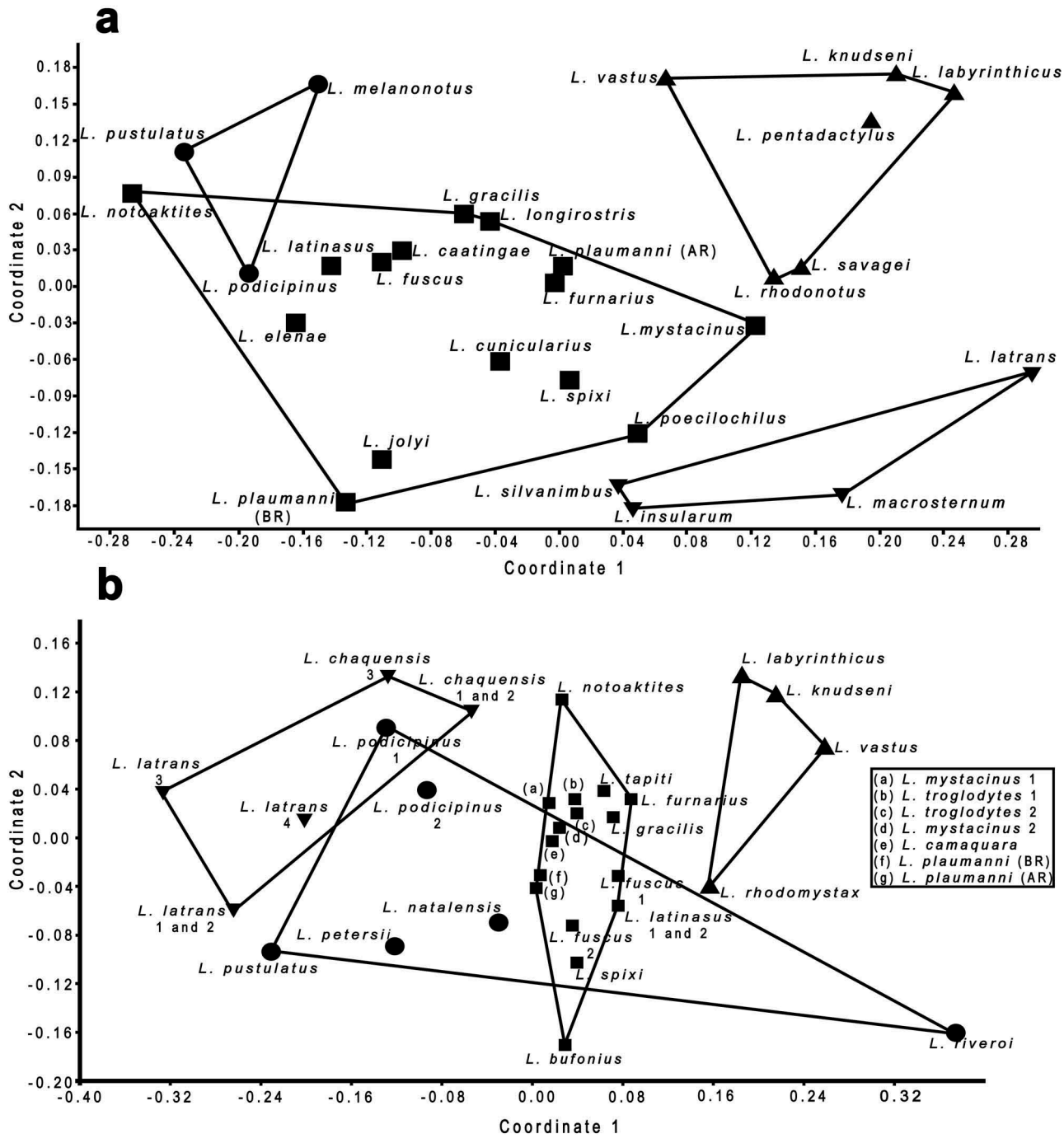

Figure 4. (A) Ordination according to the first two axes of the nonmetric multidimensional scaling analysis (NMDS) of external morphologic characteristics of tadpoles of 27 species of anurans, indicating and linking species according to the clades (species groups) proposed by de Sá et al. (2014): ■: *fuscus* clade; ●: *melanonotus* clade; ▲: *pentadactylus* clade; ▼: *latrans* clade. (B) Ordination according to the first two axes of the nonmetric multidimensional scaling analysis (NMDS) of the internal oral morphological characteristics of tadpoles of 23 species of anurans, indicating and linking species according to the clades (species groups) proposed by de Sá et al. (2014): ■: *fuscus* clade; ●: *melanonotus* clade; ▲: *pentadactylus* clade; ▼: *latrans* clade. Numbers after species names indicates different populations (*sensu* Miranda et al. 2014).

anteroventral oral disc is shared with tadpoles of all species of both the *latrans* and *melanonotus* species groups (Supplementary online material, Table S3).

Considering internal morphology (Supplementary online material, Table S4), overlaps of at least 90% occur among the species of the *fuscus* group for which internal oral morphology is known. These characters are: four Number lingual Papillae (NLP), different sizes of papillae of buccal floor arena (SPB), presence of a post nasal papilla (PNP) on each side,

and up to five projections of ventral velum (PVV). As with the external morphology, internal oral morphological characters are shared with other species of the *fuscus* group, but are not unique to the group. For instance, the presence of four NLP was recorded in 50% of the species of the *pentadactylus* group and in about 43% of the species of the *latrans* group (Supplementary online material, Table S4). Likewise, having up to five PVV was detected in about 83% of the species of the *melanonotus* group (Supplementary online material, Table S4).

All three tadpoles of the *melanonotus* group analyzed possessed: large eyes; body low and wide; a tall and short tail; spiracle insertion at mid-body; tail musculature low; anteroventral oral disc; and tooth row formula of 2(2)/3 (Supplementary online material, Table S3). Internal oral morphology (Supplementary online material, Table S4) varied widely among the species of the *melanonotus* group with only three characteristics occurring in all of the tadpoles: 15–30 pustules in the buccal floor arena; SPB of different sizes; and a triangular buccal floor arena (BFA). In addition to tadpoles of the *melanonotus* group, the presence of 15–30 NPU was also observed in tadpoles of the *fuscus*, *latrans* and *pentadactylus* groups (50, 30 and 25%, respectively).

Tadpoles of the *latrans* group share the following external morphological characteristics: relative height of body and tail intermediate, tail low, snout rounded, ventral fin arc-shaped and oral disc positioned anteroventrally (Supplementary online material, Table S3). Among internal oral morphological characteristics, tadpoles of the *latrans* group share an oval buccal roof arena (BRA), and about 60% possess chela-shaped lateral papillae of median ridge (LMR) chela-shaped (Supplementary online material, Table S4). Although chela-shaped papillae are not present in all tadpoles of this species group, they are unique to this group.

The *pentadactylus* group has a unique characteristic: it is the only species group in which all tadpoles have a globular/depressed body in lateral view, large total size; spiracle short; dorsal fin low and ventral fin parallel and low (Supplementary online material, Table S3). In addition, they have a rounded snout, a low ventral fin and a posterodorsally directed spiracle, although these characteristics are shared with other species groups. Despite the fact that descriptions of tadpoles of the *pentadactylus* group (Heyer 1969b; Rossa-Feres & Nomura 2006; Vieira et al. 2007; Heyer et al. 2010; Menin et al. 2010) have reported anteroventral oral discs, it is clear when analyzing the figures/plates of tadpoles provided in the original descriptions that it is more terminal than ventral, relative to the body, than in other species groups of *Leptodactylus* (with the exception of *L. rhodonotus*). Total length is a characteristic that the *pentadactylus* group shares only with *L. latrans* (Supplementary online material, Table S3). Labial tooth row formula of 1/2(1), 1/3(1) and 2(2)/2 (1–2) appeared in approximately 50%, 16% and 16% of the species of the *pentadactylus* group, respectively, but there is intraspecific variation with 2(2)3/(1) and 2(2)/3 being observed in *L. rhodonotus*, and 1/2(1) or 1/3(1) in *L. vastus* (Supplementary online material, Table S3). The internal oral morphology of the *pentadactylus* group exhibits interesting characteristics (Miranda et al. 2014), including small LRP (a characteristic exclusive of the *pentadactylus* group), which are square-shaped (a feature shared only with *L. furnarius* and *L. tapiti*) (Supplementary online material, Table S4). Among the species examined, 50% and 25% possessed a trapezoidal or circular BFA, respectively (characteristics found only in tadpoles of the *pentadactylus* group) (Supplementary online material, Table S4).

The phenetic analysis of external morphology and internal oral morphology corroborated the species groups proposed by de Sá et al. (2014) using phylogenetic analysis. The overlap found between species of the *latrans* and *melanonotus* groups had been previously recognized, and a larger *latrans-melanonotus* clade was proposed based on a phylogenetic analysis using tadpole chondrocranial characters (Larson & de Sá 1998).

Leptodactylus silvanimbus was considered a basal species within the genus since morphological and molecular analyses failed to provide evidence for its inclusion in any recognized species group (Heyer et al. 2005). Despite this, some authors have tried to allocate this species to some phenetic groups, such as McCranie et al. (1980), who used information from reproductive biology to place *L. silvanimbus* within the *pentadactylus* group. On the basis of larval external morphology (McCranie et al. 1986) and advertisement call (Heyer et al. 1996), the species has also been associated with the *melanonotus* group. Larson and de Sá (1998) demonstrated that *L. silvanimbus* belongs to the *latrans-melanonotus* clade. More recently, using a robust dataset of morphological and molecular characteristics, de Sá et al. (2014) established that *L. silvanimbus* is a member of the *latrans* group. This is corroborated by the present study, which found that six of the 23 tadpole characters analyzed are shared exclusively between *L. silvanimbus* and the *latrans* group, and only one is shared with the *melanonotus* group. Thus, larval morphology supports a close relationship between *L. silvanimbus* and species of the *latrans* group as previously suggested.

Since its description by Heyer and Pyburn (1983), the relationship of *L. riveroi* to established species groups of

the genus has also been unclear. The species has been considered morphologically intermediate between the *latrans* and *melanonotus* groups; however, DNA sequence data and morphological characteristics of the tadpole chondrocranium suggest that *L. riveroi* is related to species of the *melanonotus* group, specifically as the sister species of *L. melanonotus* (de Sá et al. 2014). Unlike *L. silvanimbus*, whose tadpoles are similar to those of the *latrans* group, the tadpoles of *L. riveroi* are very different from those of the species that comprise the *melanonotus* group. The tadpoles of *L. riveroi* lack seven of the 15 character states considered, and share only three character states with at most one tadpole in the *melanonotus* group. Furthermore, when compared to all the other tadpoles studied, this species possesses three unique characteristics: two lingual papillae, pustules as projections in the pre-nasal arena and the absence of papillae delimiting the buccal roof arena.

Some of the descriptions of tadpole internal oral morphology for species of the genus *Leptodactylus* did not report intraspecific variation (Wassersug & Heyer 1988; Prado & d'Heursel 2006; de Sá et al. 2007a). According to Wassersug and Heyer (1988), individuals collected from the same place and at the same time are unlikely to exhibit phenetic differences since there is a good chance that they are siblings. On the other hand, internal oral morphology of tadpoles of different populations of the same species have been found to vary (Miranda et al. 2014), and the further apart the populations, the greater the differences, even when the number of individuals is small (2–4), as observed for populations of *L. fuscus*, *L. podicipinus*, *L. latrans* and *L. chaquensis*.

Some questions cannot be answered using data currently available in the literature for internal oral morphology. For instance, there are no data regarding how internal oral morphology may be associated with habitat. Despite the difficulties involved with analyzing internal oral morphology for a large number of tadpoles, including tadpoles from different localities, it is clear that a greater number of individuals from different populations are needed in order to quantify intraspecific variation.

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Disclosure statement

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Geolocation information

General Carneiro, Paraná, Brazil (point): 26°24′S, 51°22′W, Parque Nacional das Araucárias, Santa Catarina, Brazil (point): 26°47′S, 51°56′W.

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