

Tadpole morphology of *Leptodactylus plaumanni* (Anura: Leptodactylidae), with comments on the phylogenetic significance of larval characters in *Leptodactylus*

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ABSTRACT

In this paper I summarize the morphology of the *Leptodactylus plaumanni* tadpoles, describing the external morphology, buccal cavity, and cranial skeleton and associated muscles. A distinctive combination of traits include the truncated snout in dorsal view, dorsal fin originated anterior to the body-tail junction, submarginal papillae present in some specimens, two slight indentations in the lower lip, ceratobranchial III free from the hypobranchial plate, small ventrolateral projections of the corpus of the suprarostal cartilage, m. subarcualis rectus I with three heads, and m. subarcualis rectus II-IV inserting in ceratobranchial I and connective tissue between branchial processes II and III. The buccal cavity shares the typical features in species of the group, namely four lingual papillae, two pairs of infralabial papillae, two postnarial papillae, and one pair of not branched lateral ridge papillae. Attending to the increasing role of larval characters in phylogenetic analyses, further research is needed to understand the evolution of tadpole morphology in this genus.

Key words: Buccal Cavity; Chondrocranium; Cranial Musculature; *Leptodactylus fuscus* Species Group

RESUMEN

En este trabajo resumo la morfología larval de *Leptodactylus plaumanni*, describiendo su morfología externa, cavidad bucal, esqueleto craneal y músculos asociados. Una combinación distintiva de caracteres incluye el rostro truncado en vista dorsal, aleta dorsal originada anterior a la unión cuerpo-cola, papilas submarginales en algunos especímenes, dos pequeñas escotaduras en el labio inferior, ceratobranchial III no fusionado al hipobranquial, pequeños procesos en el cuerpo y alas del suprarostal, m. subarcualis rectus I con tres haces, y m. subarcualis rectus II-IV inserto en el ceratobranquial I y en tejido conectivo entre los procesos branquiales II y III. La cavidad bucal comparte los rasgos típicos de las especies del grupo, por ejemplo las cuatro papilas linguales, dos pares de papilas infralabiales, dos papilas postnariales, y un par de papilas laterales no ramificadas. Atendiendo al creciente rol de los caracteres larvales en análisis filogenéticos, investigaciones adicionales son necesarias para interpretar la evolución de la morfología larval en este género.

Palabras clave: Cavidad Bucal; Condrocraqueo; Musculatura Craneal; Grupo *Leptodactylus fuscus*.

Introduction

The White Lipped Frog *Leptodactylus plaumanni* (Ahl, 1936) is a medium sized leptodactylid distributed from northeastern Misiones (Argentina) to south Brazil (Santa Catarina, Parana, and Rio Grande do Sul states). It belongs to the *L. fuscus* group (Heyer, 1978), which, as redefined by de Sá

et al. (2014), currently comprises another 30 species including *L. siphax* and *L. laticeps* formerly in the *L. pentadactylus* group.

Larval stages of almost all species in the *Leptodactylus fuscus* group are known, excepting *L. didymus*, *L. laticeps*, *L. labrosus*, *L. poecilochilus*,

L. sertanejo, and *L. ventrimaculatus*, whereas the tadpole of *L. plaumanni* was only described as part of a PhD thesis (Carvalho *et al.*, 2005), still pending a formal description. Conversely, the information about internal features is still limited within the whole genus; data of 11 species of the *L. fuscus* group are available (e.g., Fabrezi and Vera, 1997; Larson and de Sá, 1998; Wassersug and Heyer, 1988; Sandoval, 2004; Alcalde, 2005; Prado and d'Heursel, 2006) and four additional species are included in a recent phylogenetic analysis (Miranda *et al.*, 2014). The present work emphasizes on external morphology, buccal cavity features, and chondrocranial architecture. Results are discussed and interpreted on the light of available data for related species and within the frame of a comprehensive phylogenetic hypothesis for the genus (de Sá *et al.*, 2014).

Materials and methods

A set of 26 larvae of *Leptodactylus plaumanni* was collected in Bernardo de Irigoyen (Misiones, Argentina – 26°11'48"S/ 53°58'54"W). The tadpoles were euthanized in the field with tricaine mesylate, fixed and preserved in 4% formalin, and staged after Gosner table (1960). Voucher specimens are housed at the Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical (CONICET-UNaM; Posadas, Argentina-LGE 3379).

Descriptions were made using a stereomicroscope, and measurements were obtained from 10 tadpoles using a micrometric ocular and following Lavilla (1983) and Altig and McDiarmid (1999): total length (TL), body length (BL), body maximum width (BMW), body width at nares (BWN), body width at eyes (BWE), body maximum height (BMH), tail length (TAL), tail muscle height (TMH), maximum tail height (MTH), nare length (N), extranarial distance (END), internarial distance (IND), eye diameter (E), extraorbital distance (EOD), interorbital distance (IOD), rostro-spiracular distance (RSD), fronto-narial distance (FND), eye-nares distance (EN), oral disc width (OD), and dorsal gap width (DG). Three tadpoles were dissected and prepared for buccal structure examination, exposing the cavity after Wassersug (1976a) technique, and then staining with methylene blue. Two larvae were also prepared for scanning electron microscopy, following a standard dehydration, critical point and metallization protocol (Echeverría, 1995). Specific terminology is that proposed by Wassersug (1976a). For muscu-

loskeletal system features record, eight larvae were double stained for cartilage and bone (Wassersug, 1976b), interrupting the procedure before clearing so those muscles are not digested and can be contrasted with Lugol's solution (Böck and Shear, 1972). Terminology is that used by Larson and de Sá (1998) and Haas (2003).

Results

External Morphology (N=18; St. 34–37; Figs. 1 and 2). Tadpoles have an ovoid, depressed body without constrictions. The snout is truncated in dorsal view, and slightly rounded in lateral view. The nares are dorsolaterally located, ovoid with a raised edge. The eyes are also dorsolateral, visible in dorsal and lateral view. The spiracle is sinistral and located lateral in the posterior half of the body; the spiracle tube extends dorso-posteriorly and attaches to the body wall leaving the end free and an ovoid opening. The proctodeal tube is short, uniformly wide, and medial. The lateral lines are not visible macroscopically at the studied stages. The tail is twice longer than the body and nearly straight. The fins, slightly taller than the body, have their maximum height at the second third. The dorsal fin originates before the body-tail junction and the ventral fin starts after the proctodeal tube; the tail tip is rounded, the tail's muscles reach until the tip and the fins get narrower at that point. The oral disc (Fig. 1C and 2A) is subterminal, not emarginate, and represents almost half of the maximum body width. The upper lip is a continuation of the snout meanwhile the lower lip is separated of the body wall. The disc is oblong with two slight lower indentations at the level of P3 edges (Fig. 2A). It is delimited by a single alternate row of marginal papillae (not seen in the specimen of Figs. 1 and 2), dorsally interrupted by a wide gap that represents 56% of the maximum width of the disc. Two or three submarginal papillae are present at the commissures in some specimens. Labial teeth are arranged in two anterior rows (A1, A2), the second with a wide gap, and three posterior rows decreasing in length from proximal to distal (P1, P2, P3), the first one with a narrow gap, giving a labial tooth row formula (LTRF) 2(2)/3(1); labial tooth density is approximately 100/mm. Individual labial teeth present three regions: a slightly curved, spoon-shaped head with six to eight cusps, an intermediate body, and a broad sheath (Fig. 2B,C). The jaws sheaths are keratinized (as indicated by coloration) and distally serrated (60 serration/



Figure 1. External morphology of *Leptodactylus plaumanni*, Stage 36-37 (A) Lateral view; (B) Dorsal and ventral view of the body, bar = 1mm; (C) Oral disc, bar = 500µm.

mm approx.), the upper one convex and the lower one smaller and V-shaped.

Coloration in preservative. The tadpole presents a dark brown coloration suggested by a spray of spots at dorsal, specially over the mid line. The spots gradually scatter at the laterals rendering the venter almost translucent. The coiled gut and several ventral muscles are seen through the abdominal wall. Caudal muscles are softly pigmented specially in the first half of the tail. Fins are transparent, with some small brown dots dispersed.

Buccal cavity. (N = 4; St. 34-37; Fig. 3). In the buccal roof (Fig. 3A) the prenarial arena is quadrangular and shows two broad, crescent-shaped prenarial ridges medially placed (Fig. 3B). The internal nares are long and transversally arranged; a smooth narial valve is differentiated at the posterior wall, and small prenarial papillae appear at the anterior wall. Two long, finger-like papillae with jagged surface extend medially on the postnarial arena, accompanied by small, sparse pustulations. Lateral ridge papillae are simple, slightly pustulated, shorter and wider than postnarial papillae, and project medially towards the median ridge. The median ridge

is placed slightly posterior to the level of the lateral ridge papillae; it is low and triangular and shows several short projections at the free margin. The U-shaped buccal roof arena is delimited by 4-5 paired conical papillae, the most caudal are larger; about 50 pustulations are scattered on the central region. Groups of 5-6 lateral roof papillae, some often fused at their bases, appear on both sides of the arena. The glandular zone (Fig. 3C) appears as a broad band array, and secretory pits are very large, especially those most distal. The dorsal velum (not shown) is interrupted medially and displays finger-like papillae and pustulations next to the notch.

In the buccal floor (Fig. 3D) there are four infralabial papillae (Fig. 3E): the two anterior are globose, close to each other in the midline, whereas the two posterior are hook-shaped and project medially from the Meckel's cartilages. The tongue anlage has four conical lingual papillae, the two medial being larger and wider, often fused for half their length. The buccal pockets are long and transversely arranged, and show a few short prepocket papillae and pustulations. The V-shaped buccal floor arena is lined by 7-8 paired long, conical papillae, accompanied by

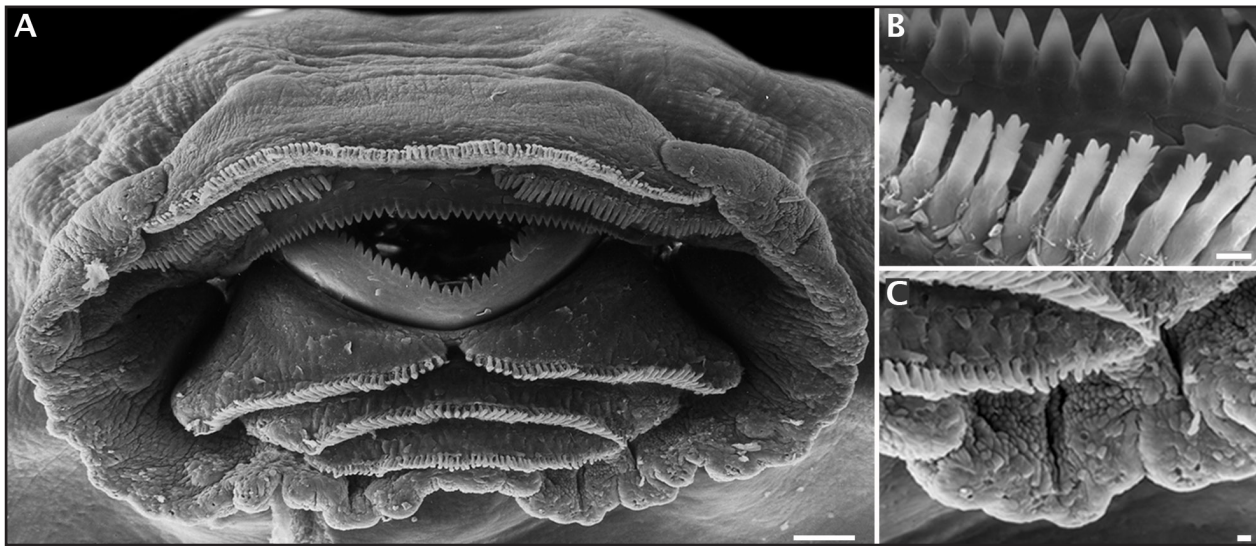


Figure 2. SEM micrographs of the oral disc of *Leptodactylus plaumanni*, Stage 36–37 (A) Oral disc, bar = 100µm; (B) Detail of the labial teeth of P1 and lower jaw sheath; (C) Detail of the marginal papillae, bar = 10µm.

numerous pustulations (more than 50); those papillae at the level of the buccal pocket are the largest and often fused at their bases. A second row of buccal papillae locate caudally following the anterior edge of the ventral velum. The ventral velum is semicircular and supported by the spicules; its margin is smooth and thick, with a marginal projection over each filter plate and a median notch (Fig. 3F) with small projections on each side; large secretory pits are seen at the whole margin of the velum.

Chondrocranium. (N = 8; St. 34–37; Fig. 4). The chondrocranium (Fig. 4A,B) represents almost half the total body length (49%). The maximum width is at the posterior region of the subocular bar near to the ascending process. The suprarostril cartilage (Fig. 4E) shows two stout corpora fused ventromedially forming a U-shaped structure, and two lateral alae. In the corpora, two small, rounded protuberances face to each other from the medial margins, and two smaller processes project from the ventrolateral margin towards the alae (Fig. 4F). The alae are flat and triangular, and fuse dorsally to the corpora; their ventral margins are rounded and exceed each corpus length; three processes are visible on each ala: long, acute posterior dorsal processes, a robust, lower anterior dorsal process, and a small ventral process projecting towards the corpus. A diffuse adrostral tissue mass is visible next to the posterior dorsal process of the ala. The trabecular horns represent almost the fourth part (23%) of the chondrocranium length; they are flat, distally wider, and slightly curved ventrally to articulate with the anterior dorsal process of the suprarostril cartilage.

The lateral trabecular process is absent. The sole nasal structures present at the studied stages is the lamina orbitonasales, visible as two small, triangular projections laterally oriented.

The chondrocranial floor is weakly chondrified at the studied stages; the carotid foramina are visible at the posterior region, caudal to the ascending process attachment, whereas the craniopalatine foramina are not evident in most specimens. The orbital cartilages are not fully developed and they are only visible at the posterior region next to the otic capsules; the optic and oculomotor foramina are well delimited and the trochlear foramen is poorly defined; the prootic foramen is dorsally open in most specimens. The frontoparietal fontanelle remains open at the studied stages, with no tectal structures developed.

The otic capsules (Fig. 4D) are ovoid, representing almost 30% of the chondrocranium length; a thin larval crista parotica is present at each capsule lateral margin, and two processes are differentiated: a long, acute anterolateral process projected toward the subocular bar, and a weak, triangular posterolateral process. The fenestra ovalis is large and ventromedially placed and the operculum is not yet developed; the endolymphatic, perilymphatic inferior and superior, acoustic and jugular foramina are defined.

The palatoquadrate is anteriorly narrow and becomes wider posteriorly, with a smooth, curved lateral margin. The wide and short articular process is easily distinguishable from the muscular process in lateral view. The muscular process is triangular, outwardly curved with a rounded proximal edge;

Table 1. Measurements of external morphology of *Leptodactylus plaumanni* tadpoles (N = 10, St. 34–36). Measurements are given in mm.

	Mean \pm 1 SD	Ratio	Mean \pm 1 SD
Total length (TL)	26.03 \pm 1.29		
Body length (BL)	8.87 \pm 0.41	BL/TL	0.34 \pm 0.01
Body maximum width (BMW)	5.4 \pm 0.22		
Body width at nares (BWN)	2.84 \pm 0.11		
Body width at eyes (BWE)	4.65 \pm 0.19	BWE/BWN	1.64 \pm 0.04
Body maximum height (BMH)	3.9 \pm 0.22	BMH/BWN	0.72 \pm 0.03
Tail length (TAL)	17.16 \pm 1.11	TAL/TL	0.66 \pm 0.01
Tail muscle height (TMH)	2.49 \pm 0.33	TMH/BMH	0.64 \pm 0.07
Maximum tail height (MTH)	4.56 \pm 0.15	MTH/BMH	1.17 \pm 0.05
Nare length (N)	0.24 \pm 0.05	N/BWN	0.083 \pm 0.02
Extranarial distance (EN)	1.8 \pm 0.08		
Internarial distance (IND)	1.32 \pm 0.10	IND/BWN	0.46 \pm 0.04
Eye diameter (E)	1.12 \pm 0.07	E/BWE	0.24 \pm 0.02
Extraorbital distance (EOD)	3.53 \pm 0.10		
Interorbital distance (IOD)	1.26 \pm 0.06	IOD/BWE	0.27 \pm 0.01
Rostro-spiracular distance (RSD)	5.98 \pm 0.31	RSD/BL	0.67 \pm 0.03
Fronto-narial distance (FN)	0.64 \pm 0.08	FND/EN	0.36 \pm 0.05
Eye-nare distance (END)	0.95 \pm 0.08		
Oral disc width (OD)	2.50 \pm 0.16	OD/BMW	0.46 \pm 0.02
Dorsal gap width (DG)	1.32 \pm 0.11	DG/OD	0.53 \pm 0.05

a small process projects laterally from the anterior margin. The palatoquadrate is attached to the neurocranium via three structures: the quadratocranial commissure that shows an acute quadratoethmoid process, the quadratoorbital commissure, and the thin ascending process with a perpendicular, intermediate attachment to the pila antotica. In the lower jaw (Fig. 4F), the Meckel's cartilages have a sigmoid shape and three conspicuous process: the retroarticular process and the dorso- and ventromedial processes. The infrarostrals are small and dorsally curved, proximally narrow and wider near to the articulation with the Meckel's cartilage.

In the hyobranchial skeleton (Fig. 4C), the elongated ceratohyals show four conspicuous processes: a triangular, wide anterior process, a lower, medially curved anterolateral process, a triangular, wide posterior process not in contact with the hypobranchial plate, and finally a broad, robust articular condyle. The ceratohyals are connected medially through the pars reuniens, often scarcely chondrified. The basibranchial is almost as long as the pars reuniens and it is continuous with the hypobranchial plates; a small urobranchial process projects caudally from its posterior region. The basihyal is absent. The

hypobranchial plates are wide and flat, and articulate to each other through one or two connections along the medial margin; they diverge caudally leaving a narrow U-shaped notch. The ceratobranchials are thin, long and curved, excepting the fourth one which is wider, shorter, and fairly flat. All ceratobranchials have numerous lateral projections on their margins. Proximally, the ceratobranchials I, II and IV are continuous to the hypobranchial plate, whereas the ceratobranchial III joins the plate by a narrow ligament. Ceratobranchials are distally joined by terminal commissures, whereas proximal commissures are absent. The spicules I–III are long, curved, and clearly visible; the fourth spicule appears to be incorporated to the distal edge of the hypobranchial plate. Branchial processes I–III are well developed.

Musculature. (Fig. 5). Table 2 shows the list of cranial muscles, detailing insertions sites and some comments.

Discussion

Larval morphology in the *Leptodactylus fuscus* group. The external morphology of larval stages has

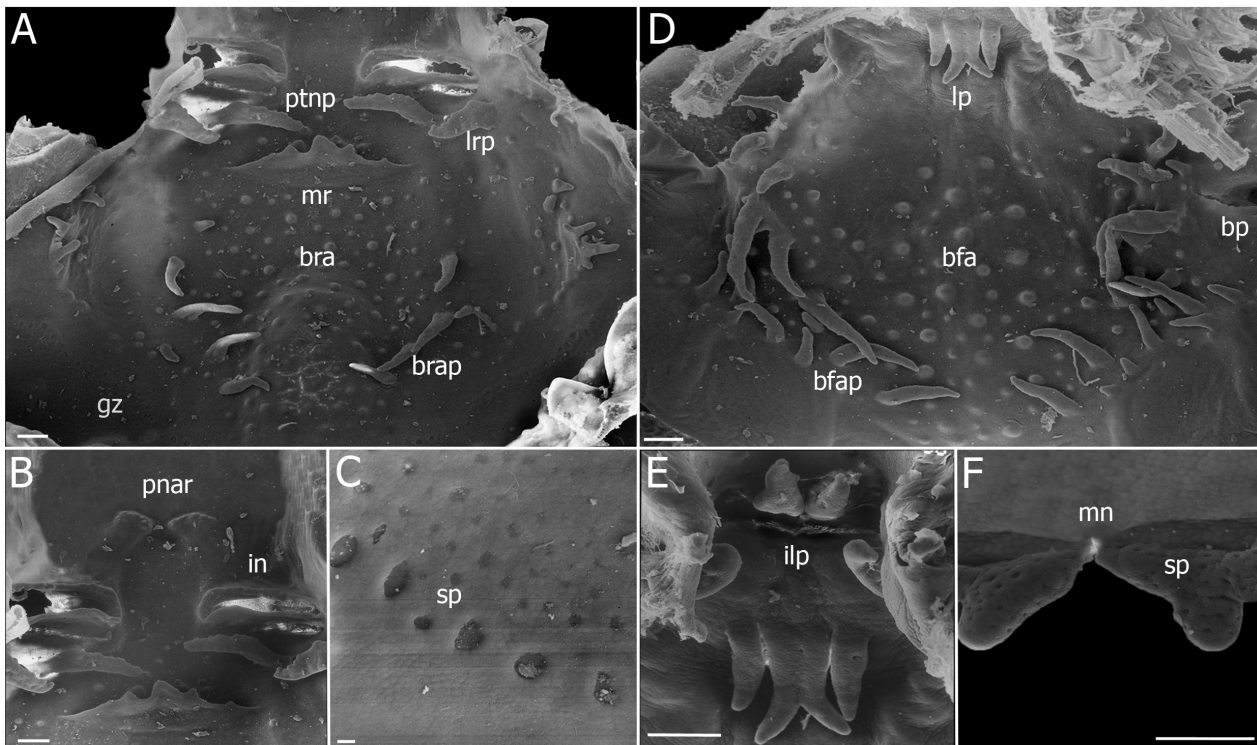


Figure 3. SEM micrographs of the oral cavity of *Leptodactylus plaumanni*, Stage 36–37 (A) Buccal roof; (B) Prenarial arena; (C) Glandular zone next to the dorsal velum; (D) Buccal floor, bar = 100µm; (E) Detail of the infralabial and lingual papillae, bar = 10µm; (F) Medial notch and glandular zone of the ventral velum, bar=100µm. BFA: buccal floor arena, BFAP: buccal floor arena papillae, BP: buccal pocket, BRA: buccal roof arena, BRAP: buccal roof arena papillae, ILP: infralabial papillae, IN: internal nares, MN: medial notch, MR: median ridge, LP: lingual papillae, LRP: lateral ridge papillae, PNAR: prenarial ridge, PTNP: postnarial papillae, SP: secretory pits.

been described (and in many cases redescribed) for 23 species of this group: *L. albilabris*, *L. bufonius*, *L. caatingae*, *L. camaquara*, *L. cunicularis*, *L. cupreus*, *L. elenae*, *L. fragilis*, *L. furnarius*, *L. fuscus*, *L. gracilis*, *L. jolyi*, *L. latinasus*, *L. longirostris*, *L. marambaiae*, *L. mystaceus*, *L. mystacinus*, *L. notoakitites*, *L. poecilochilus*, *L. spixi*, *L. syphax*, *L. tapiti*, and *L. troglodytes* (Fernández and Fernández, 1921; Heyer, 1970; Lescure, 1972; Sazima, 1975; Sazima and Bokermann, 1978; Cei, 1980; Crombie and Heyer, 1983; Cascon and Peixoto, 1985; Solano, 1987; Hero, 1990; Muramatsu and Cruz, 1996; Rossa-Feres and Nomura, 1996; Eterovick and Sazima, 2000; Wogel *et al.*, 2000; Langone and de Sá, 2005; Bilate *et al.*, 2006; Prado and d’Heursel, 2006; Borteiro and Kolenc, 2007; de Sá *et al.*, 2007; Motta *et al.*, 2010; De Medeiros Magalhães *et al.*, 2013). *Leptodactylus plaumanni* tadpoles share several features with most of the previously described larvae, such as the spotted and cryptic coloration, depressed body elliptic in dorsal view, body about 30–40% of the total length, sinistral spiracle, ventromedial vent tube, intestinal assa left sided, straight tail axis, tail muscles reaching the tail tip, and an oral disc with a wide rostral gap and LTRF 2(2)/3(1). Some distinct

traits that could be useful to identify *L. plaumanni* tadpoles are the truncated snout in lateral view (also in *L. camaquara*, *L. cupreus*, *L. fragilis*, *L. latinasus*, and *L. mystaceus*), dorsal eyes (like in *L. elenae*, *L. jolyi*, *L. mystaceus*, *L. syphax*, and *L. tapiti*), dorsal fin originated anterior to the body-tail junction (also in *L. marambaiae* and *L. notoakitites*), labial tooth row P3 shorter than P1 (like in *L. albilabris*, *L. gracilis*, and *L. latinasus*), marginal papillae in a single row (like in *L. marambaiae* and *L. notoakitites*), submarginal papillae present in some specimens (also reported for *L. bufonius* and *L. cupreus*), and two slight indentations in the lower lip (although more pronounced in *L. albilabris*, *L. bufonius*, and *L. mystacinus*). Tadpoles of *L. plaumanni* are very similar to those of *L. gracilis*, a partially sympatric species traditionally reported as a sibling species only distinguishable through advertisement call. However, some variations are registered mainly in the oral disc, with *L. gracilis* larvae having marginal papillae double at commissures (single through the whole margin in *L. plaumanni*), submarginal papillae absent (present in some specimens), lower lip indentation absent (present), snout rounded in lateral view (truncated), and eyes dorsolateral (dorsal). On the

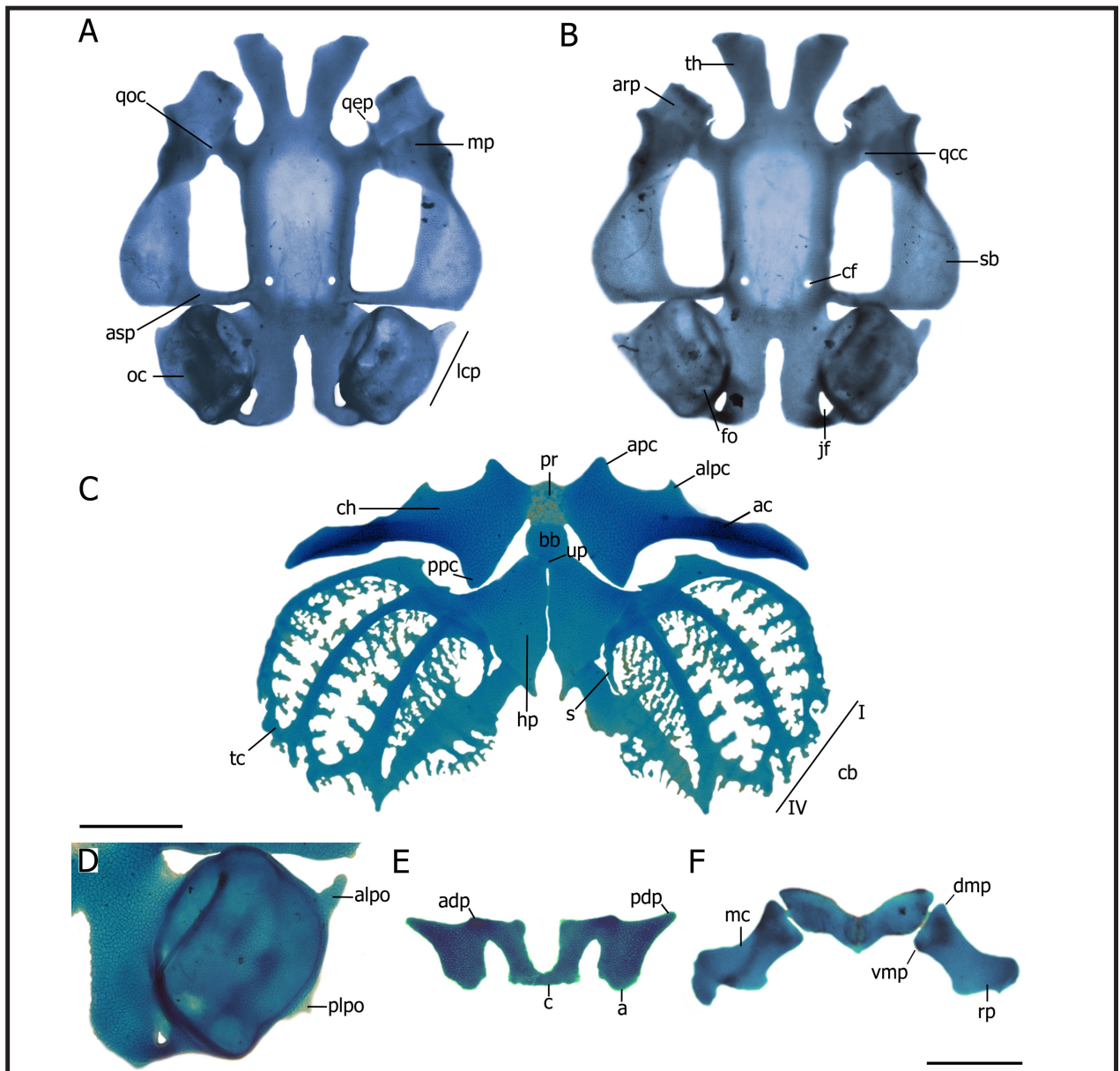


Figure 4. Chondrocranium of *Leptodactylus plaumanni*, Stage 36–37 (A) dorsal view of the neurocranium and palatoquadrate; (B) ventral view of the neurocranium and palatoquadrate; (C) ventral view of the hyobranchial apparatus, bar = 1mm; (D) detail of the larval crista parotica in a dorsal view of the capsule; (E) Detail of the suprarostrals (F) Detail of the lower jaw cartilages, bar = 500 μ m. A: ala of the suprarostrals, AC: articular condyle, ADP: anterior dorsal process of the ala of the suprarostrals, ALPO: anterolateral process of the otic capsule, ALPC: anterolateral process of ceratohyal, APC: anterior process of the ceratohyal, ARP: articular process, ASP: ascending process, BB: basibranchial, C: corpus of the suprarostrals, CB: ceratobranchial, CF: carotid foramen, CH: ceratohyal, DMP: dorsomedial process of the Meckel's cartilage, FO: fenestra ovalis, HP: hypobranchial plate, JF: jugular foramen, LCP: larval crista parotica, MC: Meckel's cartilage, MP: muscular process, OC: otic capsules, PDP: posterior dorsal process of the ala of the suprarostrals, PLPO: posterolateral process of the otic capsule, PPC: posterior process of the ceratohyal, PR: pars reuniens, QCC: quadratoorbital commissure, QEP: quadratoethmoid process, QOC: quadratoorbital commissure, RP: retroarticular process of the Meckel's cartilage, S: spicule, SB: subocular bar, TC: terminal commissure, TH: trabecular horns, UP: urobranchial process, VMP: ventromedial process of the Meckel's cartilage.

other hand, the relationship between *L. plaumanni* and *L. marambaie* is supported by morphology, behavior and molecular data (de Sá *et al.*, 2014) but some larval features are distinctive between them, with *L. marambaie* showing dorsolateral eyes (dorsal in *L. plaumanni*), lateral lines visible (not visible), dorsal fin with the highest point at the second third (almost straight), P1 complete (narrow gap), P3 as

long as P1 (shorter), lower lip indentation absent (present), and submarginal papillae absent (present in some specimens).

Concerning the buccal cavity, the features of 10 species of the group are described to date: *Leptodactylus caatingae*, *L. elenae*, *L. furnarius*, *L. fuscus*, *L. gracilis*, *L. latinasus*, *L. mystacinus*, *L. notoaktites*, and *L. spixi* (Wassersug and Heyer, 1988; Prado and

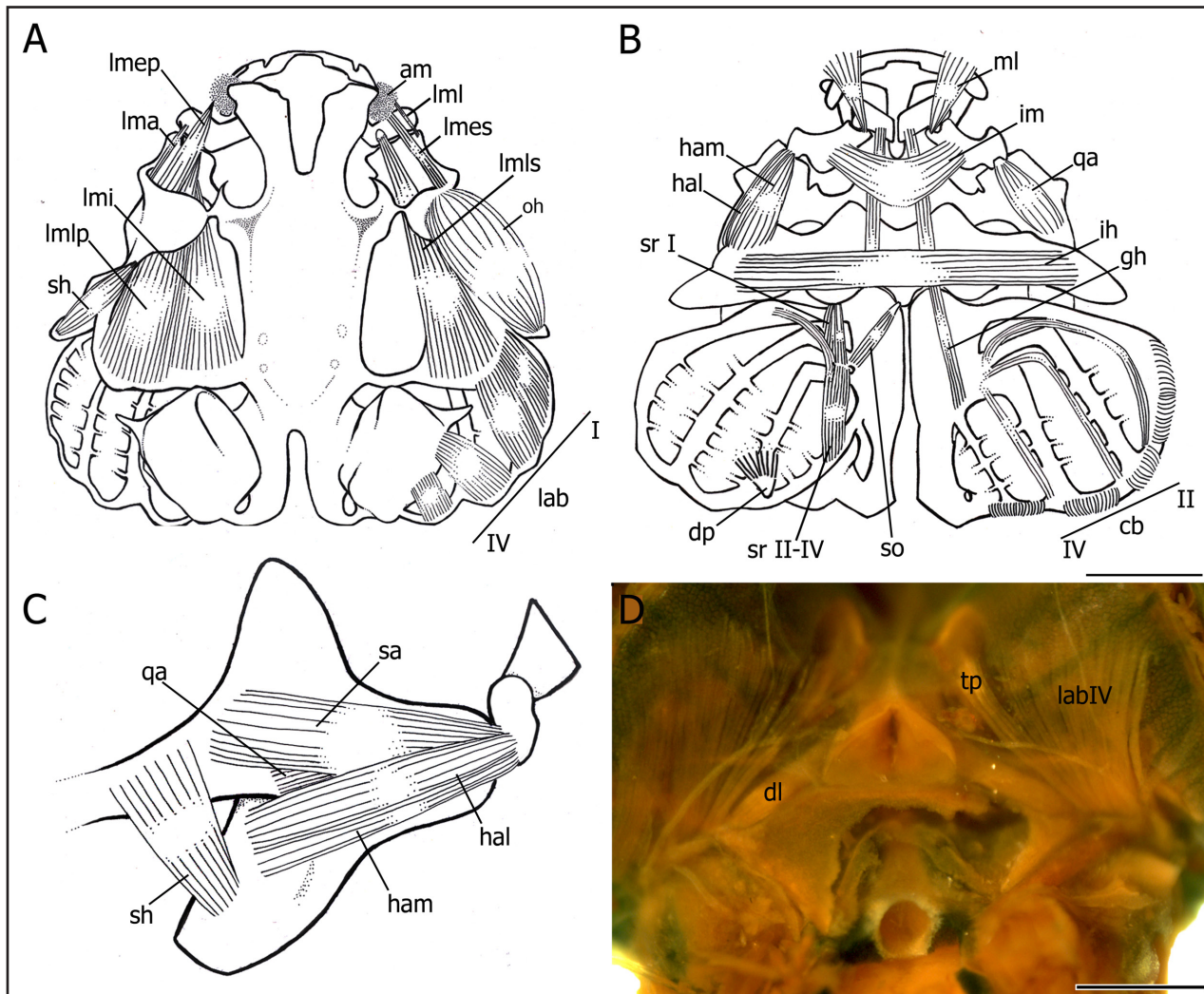


Figure 5. Chondrocranial muscles of *Leptodactylus plaumanni*, Stage 36–37 (A) Dorsal view; (B) Ventral view, bar = 1mm; (C) Detail of the angular muscles; (D) Detail of the glottis and its related muscles, bar = 500µm. AM: adrostral tissue mass, CB: mm. constrictores branchiales, DL: m. dilator laryngis, DP: diaphragmatobranchialis, GH: m. geniohyoideus, HAL: m. hyoangularis lateralis, HAM: m. hyoangularis medialis, IH: m. interhyoideus, IM: m. intermandibularis, LAB: mm. levatorae arcumm branchialium, LMA: m. l. m. articularis, LMEP: m. l. m. externus profundus, LMES: m. l. m. externus superficialis, LMI: m. l. m. internus, LML: m. l. m. lateralis, LMLP: m. l. m. longus profundus, LMLS: m. l. m. longus superficialis, ML: m. mandibulolabialis inferior, OH: m. orbitohyoideus, QA: m. quadratoangularis, SH: m. suspensoriohyoideus, SO: m. subarcualis obliquus, SR I: m. subarcualis rectus I, SR II–IV: m. subarcualis rectus II–IV, TP: m. tympanopharyngeus. NOTE: superficial muscles were removed from the right sides of A and B parts of the lamina. The mm. rectus abdominis, rectus cervicis, interhyoideus posterior and diaphragmatopraecordialis were removed to examine deep layers, and then are not pictured.

d’Heursel, 1996; Sandoval, 2004; Bilate *et al.*, 2006; de Sá *et al.*, 2007; Vera Candiotti, *et al.* 2007; Miranda and Ferreira, 2009; De Medeiros Magalhães *et al.*, 2013). Features of *L. bufonius*, *L. camaquara*, *L. tapiti*, and *L. troglodytes* were not explicitly described but are included in the matrix of larval characters by Miranda *et al.* (2014). Traits in *L. plaumanni* are similar to those of most other species of the group, with four lingual papillae, two pairs of infralabial papillae, two postnarial papillae, one pair of not branched lateral ridge papillae, and ventral velum with median notch and marginal projections. Some inter- and intraspecifically variable features concern

the size and number of papillae and pustulations of the buccal floor and roof arenas, the shape of the median ridge, and the size of the marginal projections of the dorsal and ventral velum.

As regard to skeletal characters, information is available for 11 species of the group: *Leptodactylus albilabris*, *L. bufonius*, *L. caatingae*, *L. elanae*, *L. fuscus*, *L. gracilis*, *L. labrosus*, *L. latinasus*, *L. longirostris*, *L. mystacinus*, and *L. notoaktites* (Sokol, 1981; Fabrezi and Vera, 1997; Larson and de Sá, 1998; Haas, 2003; Vera Candiotti *et al.*, 2007; De Medeiros Magalhães *et al.*, 2013); four more (*L. camaquara*, *L. furnarius*, *L. tapiti*, and *L. troglodytes*) were scored in Miranda

Table 2. Larval musculature of *Leptodactylus plaumanni* (N =6, St. 34–36)

Muscle	Insertion sites	Comments
Levator mandibulae articularis	anteroventral part of the inner surface of the muscular process – Meckel's cartilage	
Levator mandibulae externus profundus	anteroventral part of the inner surface of the muscular process – lateroventral margin of the ala of the suprarostrum	it inserts by a tendon shared with the m. l.m.l. profundus
Levator mandibulae externus superficialis	ventral region of the anterior margin of the muscular process – ala of the suprarostrum	it is scarcely developed; the mandibular branch of the trigeminal nerve runs dorsally to this muscle
Levator mandibulae internus	ventral margin of the ascending process – retroarticular process of the Meckel's cartilage	the insertion is via a long tendon that runs ventral to the tendon of m. l.m.l. profundus
Levator mandibulae lateralis	articular process of the palatoquadrate – dorsolateral edge of the ala of the suprarostrum	
Levator mandibulae longus profundus	subocular bar and ascending process – lateroventral margin of the ala of the suprarostrum	the area of origin is similar to that of the m. l.m. superficialis, the insertion is via a long tendon shared with the m. l.m.e. profundus
Levator mandibulae longus superficialis	posterior margin of the subocular bar – dorsomedial region of Meckel's cartilage	it is well-developed and its insertion is via a wide tendon
Intermandibularis	midventral region of Meckel's cartilage – median aponeurosis	
Mandibulolabialis	ventromedial process of the Meckel's cartilage – lower lip of the oral disc	it is only a single slip, corresponding to m. mandibulolabialis inferior
Hyoangularis lateralis	dorsal surface of the lateral edge of the ceratohyal – retroarticular process of the Meckel's cartilage	
Hyoangularis medialis	dorsal surface of the lateral edge of the ceratohyal – retroarticular process of the Meckel's cartilage	slightly anterior and ventral to the m. hyoangularis lateralis
Quadratoangularis	ventral surface of the muscular process – retroarticular process of the Meckel's cartilage	it is completely covered by the mm. hyoangulares and suspensorioangularis; it inserts on the Meckel's cartilage through a wide and short tendon
Suspensorioangularis	ventral part of the descending margin of the muscular process – retroarticular process of the Meckel's cartilage	fibers occupy approximately the ventral half of the muscular process
Orbitohyoideus	dorsal and anterior margins of the muscular process – lateral edge of the ceratohyal	
Suspensoriohyoideus	posterior part of the descending margin of muscular process and anterior region of the subocular bar – posterior surface of the lateral edge of the ceratohyal	it is almost entirely covered by the m. orbitohyoideus
Interhyoideus	ventral surface of the lateral edge of the ceratohyal – median aponeurosis	
Interhyoideus posterior	fibers loosely disposed in the anterior region of the branchial basket, ventral to the peribranchial chamber	
Diaphragmatopraecordialis	connective tissue near the insertion of the fibers of the m. interhyoideus posterior – connective tissue dorsal to the pericardium, close to the mm. interhyoideus and rectus cervicis	
Levator arcuum branchialium I	posterolateral edge of the subocular bar – ceratobranchial I	very close to m. l.a.b. II
Levator arcuum branchialium II	posterolateral edge of the subocular bar and lateral part of the otic capsule – terminal commissure II	
Levator arcuum branchialium III	lateroventral part of the otic capsule – terminal commissure II	

Levator arcuum branchialium IV	posterolateral part of the otic capsule – ceratobranchial IV	it can be present as two slips very close to each other, varying even intraindividually
Constrictor branchialis II	branchial process II – terminal commissure I	it is disposed on the ceratobranchial I
Constrictor branchialis III	branchial process III – terminal commissure II	it is disposed on the ceratobranchial II
Constrictor branchialis IV	branchial process III – distal edge of the cb III	it is disposed near the ceratobranchial III
Subarcualis rectus I	three slips sharing origin at the lateroventral edge of the posterior process of the ceratohyal – branchial processes I and II (dorsal and medial slips), and branchial process III (ventral slip)	the dorsal and middle slips are no discrete, some fibers attach to branchial process I and some others continue to branchial process II; also, some ventral fibers attach to branchial process II and the connective tissue between ceratobranchials II and III
Subarcualis rectus II-IV	ceratobranchial IV – connective tissue between the proximal regions of ceratobranchias II and III	some fibers diverge distal and slightly lateral to reach ceratobranchial I
Subarcualis obliquus	urobranchial process – branchial process II	
Tympanopharyngeus	posterolateral part of the otic capsule – connective tissue anterior to the glottis	fibers originate very close to the m. l.a.b. IV at the otic capsule and diverge medially
Dilatator laryngis	posterolateral surface of the otic capsule – soft tissue surrounding the glottis	
Constrictor laryngis	sphincter-like in the glottis lips	
Diaphragmatobranchialis	peritoneum – distal edge of the ceratobranchial III	
Geniohyoideus	ventral surface of the infrarostral – ventral side of the hypobranchial plate, at the level of the proximal edge of the ceratobranchial IV	
Rectus abdominis	transverse septum – pelvic girdle	
Rectus cervicis	transverse septum – branchial process III	

et al. (2014) analysis. Shared features between *L. plaumanni* and previously described tadpoles of the group are the ascending process of the palatoquadrate attaching to the neurocranium in an angle of 80°–90°, and the posterior region of the palatoquadrate not surpassing the level of the attachment of that process. Other features are also observed in species of the *L. pentadactylus* group, namely the articular process distinct from the muscular process in lateral view, the wide and narrowly separated suprarostal corpora, and the open branchial process. Some interspecifically variable characters are the adrostral tissue mass (absent in *L. camaquara*, *L. fuscus*, *L. latinasus*, *L. mystacinus*, *L. spixi*, and *L. troglodytes*), and the ventrolateral projections of the corpus and ala of the suprarostal cartilage (which can be alternatively absent or fused to each other). The absence of tectal structures in *L. plaumanni* is unusual in tadpoles of the genus (and in tadpoles in general), and it could be due to poor staining of cartilages or to a late development.

Finally, the musculature is the less studied

system in the *Leptodactylus fuscus* species group, and in anuran tadpoles in general; only six taxa of the group are described: *L. bufonius*, *L. elenae*, *L. fuscus*, *L. gracilis*, *L. latinasus*, and *L. mystacinus*, and outside the group data are restricted to *L. chaquensis*, *L. latrans*, and *L. pentadactylus* (Starrett, 1968; Palavecino, 1997, 2000; Haas, 2003; Alcalde, 2005; Vera Candiotti *et al.*, 2007). Tadpoles of *L. plaumanni* share two distinctive muscular characters with the analyzed species: m. hyoangularis medialis present (except in *L. bufonius*), and m. levator mandibulae externus superficialis inserted at the ala of the suprarostal cartilage. Many others features are variable: the m. submentalis is absent in the analyzed stages of *L. plaumanni*, *L. elenae*, *L. gracilis*, and *L. latinasus*, but it is present in specimens described by Palavecino (2000). The m. subarcualis rectus I has three heads in *L. plaumanni*, like in *L. elenae* and *L. latinasus*, but is depicted with two heads in *L. gracilis*, *L. latinasus*, and species of the *L. latrans* group. In *L. plaumanni* tadpoles, the m. subarcualis obliquus has one head inserted at the branchial process II,

whereas in *L. elenae* and *L. latinasus* fiber muscles reach the ceratobranchial III; the species analyzed by Alcalde (2005) show two heads with close insertions at the ceratobranchials II and III. Finally, in all *Leptodactylus* species the m. subarcualis rectus II-IV is a single slip inserted in the ceratobranchial I; however in *L. plaumanni* it inserts at the connective tissue between the ceratobranchials II and III and only some distal fibers diverge reaching the ceratobranchial I.

Phylogenetic remarks. Larval characters in *Leptodactylus* were traditionally considered phylogenetically not very informative because of their high ecomorphological correlation (Wassersug and Heyer, 1988; Prado and d'Heursel, 2006; de Sá *et al.*, 2014). However, attempts to analyzing them exclusively or as part of larger matrices provide resolved (although often not congruent) relationship hypotheses (Heyer, 1978; Larson and de Sá, 1998; Ponssa, 2008; Miranda *et al.*, 2014). This is in agreement with the increasing role of larval features in phylogenetic analyses of anurans in general (e.g., Haas, 2003; Púgener *et al.*, 2003; Grant *et al.*, 2006; Maglia *et al.*, 2001).

Leptodactylus is recovered as a monophyletic clade in works with different sources of information (e.g., Ponssa, 2008; de Sá *et al.*, 2014). The analysis by Larson and de Sá (1998) on larval chondrocranial characters, although not designed to test the monophyly of the genus, summarizes 12 characters common to the *Leptodactylus* species studied. All are shared by *L. plaumanni* tadpoles here examined, with the exception of the fusion of ceratobranchials to the hypobranchial plate, which in *L. plaumanni* involves ceratobranchials I, II and IV instead of all. These skeletal characters were later integrated with new buccal and chondrocranial characters by Miranda *et al.* (2014), resulting a matrix of 84 larval anatomical characters for 22 *Leptodactylus* species. Fifteen synapomorphies recovered by this analysis include a triangular buccal floor arena, slightly prominent projections on the posterior margin of the ventral velum, reduced postnarial arena, and quadratoorbital commissure present, among others. Although most of these features are indeed observed in *L. plaumanni*, this subject should be taken cautiously because the analysis of Miranda *et al.* (2014) fails to include species of genera historically related to *Leptodactylus*, such as *Adenomera*, *Lithodytes*, *Hydrolaetare* and the actual leiuperines (Bogart, 1974; de Sá *et al.*,

2005; Frost, 2006; Pyron and Wiens, 2011; de Sá *et al.*, 2014). In fact, some of these not included species do show several of the features attributed to *Leptodactylus*. For example, the shape of the buccal floor and postnarial arena are comparable in *Physalaemus* species (as the authors themselves have pointed out), and the quadratoorbital commissure is also present in this related genus (e.g., Fabrezi and Vera, 1997; Alcalde *et al.*, 2006). The inclusion of some of the said taxa could change the phylogenetic relationships among the species analyzed, and which characters are recovered as synapomorphic and at which levels. Additionally, some characters (e.g., width of the ventromedial fusion of the corpus of the suprarostrol, length of the Meckel's cartilage, lateral processes of the ceratobranchials) need to be strictly redefined before scoring further species.

As regards to intrageneric relationships, the groups initially proposed by Heyer (1969) are in general recovered in phylogenetic analyses (e.g., Larson and de Sá, 1998; Ponssa, 2008, Ponssa *et al.*, 2010; de Sá *et al.*, 2014). The relationships among them are somewhat variable, but for instance six larval skeletal synapomorphies (all shared by *L. plaumanni* here examined) are recovered for the clade joining *L. fuscus* and *L. pentadactylus* groups (Larson and de Sá, 1998). Miranda *et al.* (2014) obtain a different topology, with the traditional groups mostly dismembered, and this is suggested by de Sá *et al.* (2014) to be result of a low number of taxa included and a high homoplasy of larval buccal cavity characters.

Finally, as regards to the interspecific relationships within the *Leptodactylus fuscus* group; a small clade of species including *L. plaumanni*, *L. marambaia*, *L. camaquara*, *L. cunicularis*, *L. furnarius*, and *L. tapiti*, is recovered by de Sá *et al.* (2014). The group is characterized by several morphological larval features that give the tadpoles a streamlined aspect, such as the shallow body, proportionately long tail, and low, straight caudal fins, and some of these species were recognized as a morphological divergent group by Langone and de Sá (2005). Sazima and Bokermann (1978) had first suggested that those traits in some of the species could have a correlation with ecological features concerning the structural aspects of the nests and the liberation mechanism of tadpoles. Comprehensive, comparative approaches are required to examine the contribution of ecological features to morphological divergence in this and other distinct clades of the genus.

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