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THE TADPOLE OF *LEPTODACTYLUS ELENAE* (ANURA: LEPTODACTYLIDAE), WITH THE DESCRIPTION OF THE INTERNAL BUCCAL ANATOMY

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Abstract: The external morphology and internal buccal characteristics of *Leptodactylus elenae* tadpoles are described and compared with other *Leptodactylus* species. The external morphology and anatomy of the buccal cavity of *L. elenae* are similar to other *Leptodactylus* in the *fuscus* group and suggest a pond-larval diet. The most variable features among *Leptodactylus* species are the lingual papillae number and the lateral ridge papillae. The latter are small and lack terminal branches in tadpoles of *L. elenae. Leptodactylus* tadpoles exhibit variable morphology, sometimes convergent with other genera in the family. However, it seems that both external larval morphology and internal buccal features support the current groups of *Leptodactylus.*

Key words: *Leptodactylus,* tadpole, external morphology, internal oral anatomy, Pantanal, Brazil

Introduction

Adult and larval traits are important tools to resolve or examine relationships among amphibian taxa (e. g., Eterovick and Sazima, 2000). Larval buccal anatomy has also been used to help understand species relationships (Viertel, 1982; Kaplan and Ramírez-Bautista, 1996; d'Heursel and de Sá, 1999).

The genus *Leptodactylus* belongs to the Neotropical family Leptodactylidae and is one of the most diversified groups in South America (Heyer and Maxson, 1982) with approximately 66 recognized species (Frost, 2004). This genus is traditionally divided into four species groups: *ocellatus, melanonotus, pentadactylus,* and *fuscus* (Heyer, 1969). Frogs of the *Leptodactylus fuscus* group are comprised of about 25 species (Frost, 2004) that deposit eggs in foam nests placed on land, in subterranean chambers constructed by males; exotrophic larvae (*sensu* Thibaudeau and Altig, 1999) in advanced stages are released by floods or rain to lentic or lotic water bodies (Prado *et al.,* 2002).

Tadpoles of some species of the *fuscus* group have already been described (Lescure, 1972; Heyer, 1978; Sazima and Bokermann, 1978) and a review of larval characters was provided by Langone and de Sá (2005); however, tadpoles of several species remain unknown. *Leptodactylus elenae* Heyer, 1978 is a member of the *fuscus* group that is widely distributed in the semi-arid Chaco, cerrado, caatinga, and dry forests from the eastern slopes of Bolivia to Mato Grosso, Brazil, and south through Paraguay to north-central Argentina (Heyer and Heyer, 2002). Here we describe the external morphology and the internal buccal anatomy of *L. elenae* tadpoles and compare them to other *Leptodactylus* species.

Materials and Methods

Tadpoles were collected with a sieve in a temporary rain puddle, on 17 October, 2000, in the south Pantanal, municipality of Corumbá (19°34'S; 57°00'W), Mato Grosso do Sul State, Brazil. Description of external morphology and drawings were based on tadpoles at stages 35-36 (Gosner, 1960). Terminology of external morphological traits and measurements follow Altig and McDiarmid (1999). Measurements of total length, body length, tail length, maximum body height, and maximum body width were made with a digital caliper to the nearest 0.01 mm. The remaining measurements were made under a stereomicroscope Zeiss® Stemi SV11, with an ocular micrometer. Three individuals were dissected for observation of the internal buccal anatomy (stage 33, BL = 8.36 mm, TL = 20.98 mm; stage 36, BL = 8.62 mm, TL = 21.01 mm; stage 39, BL = 9.27 mm, TL = 29.07 mm). Terminology of internal surface features follows Wassersug (1976). Tadpoles were identified based on individuals raised to metamorphosis in the laboratory. Voucher *L. elenae* tadpoles (CFBH 9329) and juveniles (CFBH 8387-8388) are housed at

the Célio F. B. Haddad collection, in the Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil. The tadpole that is illustrated corresponds to CFBH 9330.

Results

Tadpole measurements (mm): Mean ± SD (range) of 10 specimens at Gosner (1960) developmental stage 35-36: total length 21.57 ± 1.30 (19.6-24.1); body length 8.35 ± 0.46 (7.6-9.1); tail length 13.12 ± 0.91 (11.5-14.7); maximum body height 3.80 ± 0.20 (3.5-4.1); maximum body width 4.54 ± 0.31 (4.0-5.0); eye diameter 1.00 ± 0.08 (0.95-1.14); nostril diameter 0.25 ± 0.05 (0.19-0.29); interorbital distance 2.60 ± 0.11 (2.47-2.85); internarial distance 1.34 ± 0.10 (1.24-1.52); nostril-snout distance 0.95 ± 0.10 (0.86-1.14); eye-snout distance 2.52 ± 0.18 (2.28-2.85); maximum tail height 3.75 ± 0.16 (3.52-4.09); maximum dorsal fin height 1.42 ± 0.08 (1.24-1.52); maximum ventral fin height 1.15 ± 0.10 (0.95-1.33); maximum tail muscle width 1.42 ± 0.14 (1.24-1.71); maximum tail muscle height 1.44 ± 0.08 (1.33-1.52). Body length relative to total length 38.7% ± 1.16 (37.4-40.3), eye diameter relative to body length 12.1% ± 0.75 (10.8-13.1).

External morphology: Body ovoid in dorsal view and ovoid/depressed in lateral view (Figs. 1A, B). Snout rounded in dorsal and lateral views. Eyes relatively small and dorsolaterally directed. Nostril small, dorsal, and ovoid, with laterally directed aperture. Spiracle sinistral, long, and narrow, with free distal edge. Centripetal wall of the spiracle tube fused to body wall, spiracular opening directed posterodorsally on the middle of the body. Vent tube long, medial, attached to the ventral fin, with medial directed opening (Fig. 1C). The lateral line system is visible, mainly the middle body line (sensu Lanoo, 1999).

Oral disc ventral (Fig. 1D), laterally emarginated. A single row of marginal papillae (8-10 papillae) is on either side of a wide anterior gap; ventral marginal papillae in double row. Papillae long, simple, and digitiform. Tooth row formula 2(2)/3(1); A-1 and A-2 rows subequal in length, P-1 and P-3 slightly shorter than P-2; A-2 interrupted medially by a gap approximately eight to ten labial teeth wide, P-1 interrupted medially by a gap two to three labial teeth wide; in four tadpoles, mean tooth density per millimeter in row A-2 75.7 ± 10.2 (67-90). Labial teeth dark, slightly curved toward the oral opening. Jaw sheaths heavy, darkly pigmented; upper sheath slightly M-shaped and the lower V-shaped; individual serration triangular.

Caudal muscle robust, higher than dorsal fin along the anterior third of the tail. Dorsal fin low, weakly convex, originating on the posterior third of the body; ventral fin narrower than dorsal fin at the mid portion of tail.

Coloration: Preserved specimens with body uniformly brown; ventrally transparent. Caudal muscle with small brown dots irregularly distributed, sometimes forming a medial line in the first half part of tail. Fins transparent, with slight reticulation formed by blood vessels and with some small brown dots on dorsal and ventral fins. In life, coloration is very similar to that of preserved tadpoles.

Internal buccal anatomy: Buccal floor (Fig. 2A) triangular, wider than long. Two pairs of infralabial papillae of similar size, rectangular, with rugose margins; medial pair on floor of mouth, fused at base, and other pair directly lateral to medial pair. Two rows of small pustulations lie on either side of mouth, anterior to infralabial papillae. Four anteriorly to posteriorly flattened lingual papillae forming a row on tongue anlage. Five buccal floor arena papillae on each side forming an anterior-posterior row, converging towards the midline; papillae long, thin and conical; those near buccal pockets bifurcated. One or two pre-pocket papillae on either side amongst about eight pustulations. Buccal pockets narrow, transverse; not perforated. Free velar surface; conspicuous spicular support. Posterior edge of ventral velum with three long, distinct, posteromedially directed, marginal projections on each side and two short papillae on either side of large median notch.

Buccal roof (Fig. 2B) relatively narrow with a long prenarial area. Large horizontal, rectangular ridge in center of prenarial area and small papilla anterior to ridge. Nares of moderate size, transversely oriented. Anterior narial wall thick and smooth. Posterior wall large with smooth edges. Two large, trapezoid, postnarial papillae located just below nares, pointing medially, with rugose free edges. Median ridge large, wide, semi-circular, with rugose margin. Lateral-ridge papillae large, trapezoid, with rugose medial margin, lateral and slightly anterior to median ridge. Buccal roof arena U-shaped. Four buccal roof arena papillae on each side, long, attenuate and simple. Four lateral roof papillae. Pustulations scattered evenly about buccal roof arena. Glandular zone with distinct anterior margin of secretory pits.

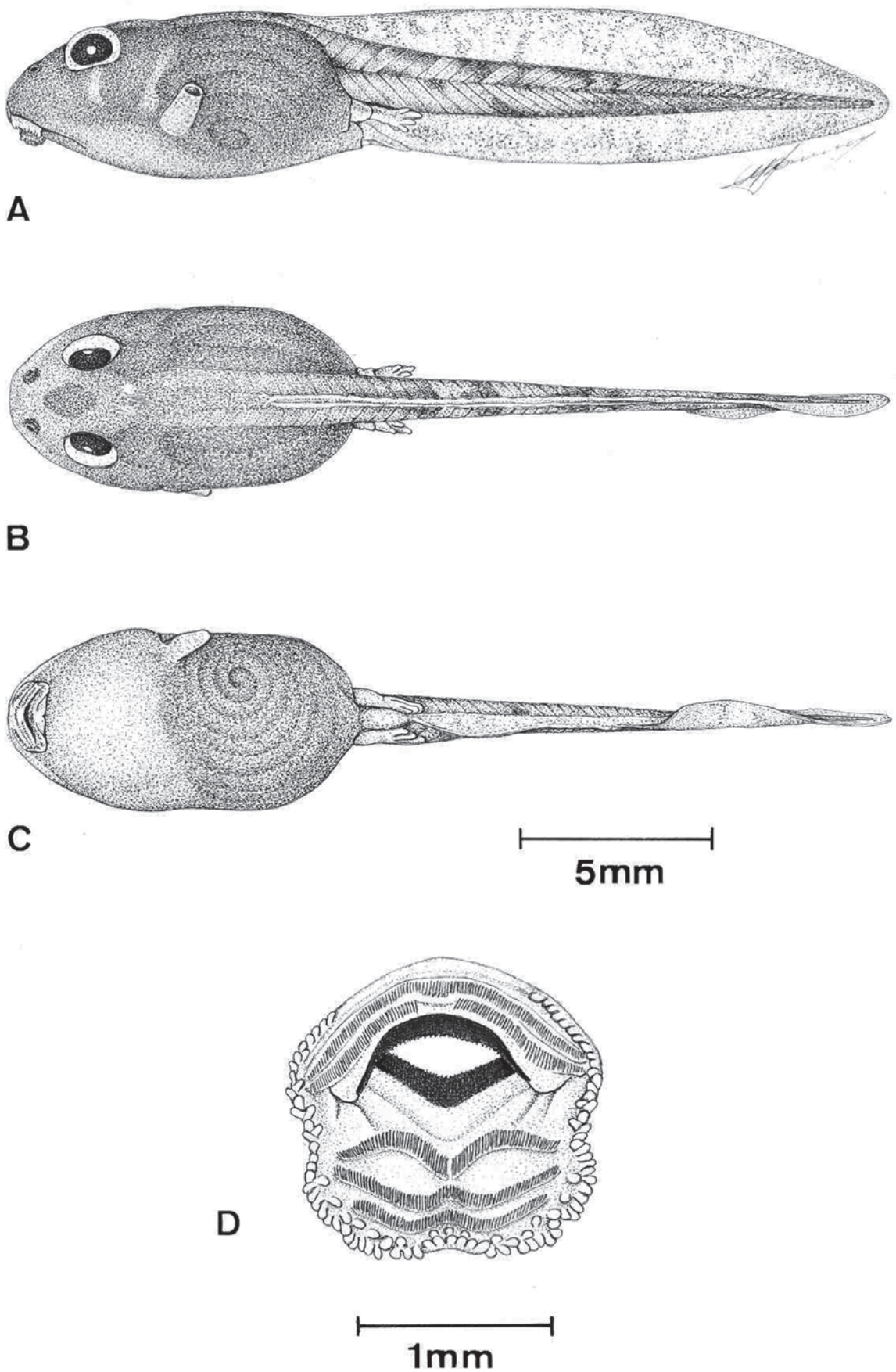

Figure 1: Lateral (A), dorsal (B), and ventral views (C), and the oral disc (D) of *Leptodactylus elenae* tadpole (CFBH 9330) at stage 35 (Gosner, 1960).

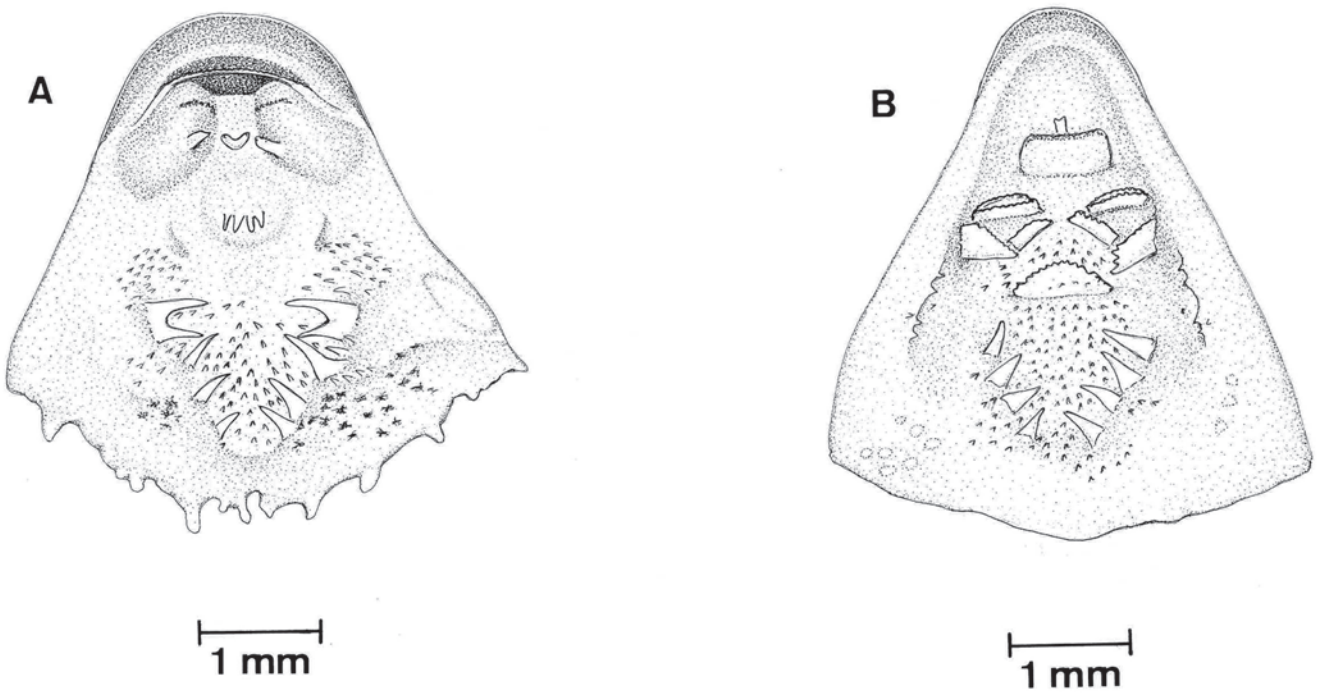

Figure 2: *Leptodactylus elenae* tadpole floor (A) and roof (B) of oral cavity.

Habitat: In the southern Pantanal, Mato Grosso do Sul State, males of *L. elenae* were reported to call during the rainy season (October to March) from the ground in the gallery forest subjected to floods (Prado *et al.,* 2005), or in open areas at the edge of forest formations. Tadpoles were observed in small rain-filled puddles, containing mainly grass as vegetation cover. These tadpoles are primarily benthonic, have cryptic coloration, and do not form aggregates.

Discussion

The external morphology of *L. elenae* tadpoles resembles those of other tadpoles included in the *L. fuscus* group, such as *L. mystaceus* (described as *L. amazonicus* by Heyer, 1978), *L. gracilis* (Langone and de Sá, 2005), *L. mystacinus* (Sazima, 1975; Langone and de Sá, 2005), *L. furnarius,* and *L. cunicularius* (Sazima and Bokermann, 1978). Main features shared by these tadpole species are: body ovoid in lateral view, dorsal eyes and nostrils, oral disc ventral and laterally emarginated, low fins, caudal muscle heavy, brown body coloration, and tooth row formula 2(2)/3(1) (Table 1). Body shape in most tadpoles in the *L. fuscus* group may be related to their benthic life (Sazima, 1975; this study) and caudal shape seems to be adapted to a life inside the foam nest, where these tadpoles may remain for a long period before being carried to water (Heyer, 1969; Prado *et al.,* 2002). As mentioned before by Heyer (1978), and corroborated by Langone and de Sá (2005), external traits in the *L. fuscus* group are not much use for recognizing species.

The structures observed on the buccal floor and roof of *L. elenae* are similar to those found in other species of *Leptodactylus* (Wassersug and Heyer, 1988; Spirandeli-Cruz, 1991) and suggest a pond-larval diet and morphology. The lateral ridge papillae in tadpoles of *L. chaquensis* and *L. ocellatus* (*L. ocellatus* species group) are complex and bifurcated but in *L. elenae, L. fuscus, L. gracilis,* and *L. mystacinus* (*L. fuscus* species group), *L. knudseni* and *L. pentadactylus* (*L. pentadactylus* species group), and *L. podicipinus* (*L. melanonotus* species group; Wassersug and Heyer, 1988, referred to as *L. wagneri;* W. R. Heyer, pers. comm.) they are smaller and lack terminal branches (Wassersug and Heyer, 1988; Spirandeli-Cruz, 1991; this study). The number of papillae on the buccal floor and buccal roof arena also varies among species and in tadpoles of *L. elenae* this number lies within the lower range. The most distinguishing feature between the tadpoles of the different species groups is the number of lingual papillae. As observed in the other species from the *L. fuscus* species group (see Wassersug and Heyer, 1988), tadpoles of *L. elenae* have four lingual papillae. Tadpoles of species in the *L. ocellatus* group

Table 1: Comparison of larval characteristics among the four *Leptodactylus* species groups proposed by Heyer (1969). Traits are based on tadpoles in stages 31-40 (Gosner, 1960). BSLV: body shape in lateral view; BL/TL: body length relative to body length; LLS: lateral line system; TRF: tooth row formula; VMPR: ventral marginal papillae row; S: single; D: double.

Group/Species	Body color	TRF	VMPR	LLS	BSLV	BL/TL(%)	Source
Fuscus							
L. elenae	brown	2(2)/3(1)	D	Yes	ovoid	38.7	this study
L. mystaceus	_	2(2)/3(1)	S	No	ovoid	33-40	Heyer (1978)
L. cunicularius	brown	2(2)/3(1)	D	No	ovoid	33	Sazima & Bokermann (1978)
L. furnarius	brown	2(2)/3(1)	D	No	ovoid	33	Sazima & Bokermann (1978)
L. fuscus	brownish grey	2(2)/3(1)	D	No	ovoid	33	Sazima (1975)
L. gracilis	brown	2(2)/3(1) or 2(2)/3(1,3) or 2(2)/3(1,2)	S/D	No	ovoid	40	Langone & de Sá (2005)
L. mystacinus	brown	2(2)/3(1) or 2(2)/3(2-3)	D	Yes	ovoid	37	Langone & de Sá (2005)
Melanonotus							
L. melanonotus	dark brown	2(2)/3	D	_	ovoid	36	Orton (1951)
L. podicipinus	dark brown	2(1)/3 or 2/3	D	Yes	ovoid	35.4	Vizotto (1967) & C.P.A. C.P.A. Prado unpubl. data
L. silvanimbus	dark brown	2(2)/3	D	_	ovoid	38.7	Heyer, de Sá & Muller (2002)
Ocellatus							
L. chaquensis	dark brown	2/3	D	Yes	ovoid	39	C.P.A. Prado unpubl. data
L. macrosternum	dark brown	2/3	D	Yes	ovoid	40	Vizotto (1967)
Pentadactylus							
L. labyrinthicus	brown	1/2(1) or 1/3(1)	S	Yes	ovoid	20	Vizotto (1967)
L. lithonaetes	brown	2(2)/3 or 2(2)/3(1)	S	_	depressed	28-31	Heyer (1995)
L. rugosus	brown	2(2)/3(1)	S	_	depressed	29.3	Heyer & Thompson (2000)
L. syphax	brown	2(2)/3(1)	D	_	ovoid	38	Eterovick & Sazima (2000)

and *L. pentadactylus* group have three lingual papillae (see Wassersug and Heyer, 1988; Spirandeli-Cruz, 1991) and in the tadpole of *L. podicipinus,* lingual papillae are absent (Wassersug and Heyer, 1988, referred to as *L. wagneri,* W. R. Heyer, pers. comm.). A summary of these characters for *L. elenae* and data for other *Leptodactylus* from the literature are given in Tables 2 and 3.

Based on morphology and behavior of adults, Heyer (1969) proposed four species groups for the genus *Leptodactylus: ocellatus, melanonotus, pentadactylus,* and *fuscus.* At that time, Heyer (1969) mentioned that larvae belonging to different groups were quite generalized. However, since then, many other tadpoles have been described (e.g., Heyer, 1995) and by comparing tadpole external morphology among the four groups of *Leptodactylus,* it is possible to distinguish the groups by external morphology (Table 1). Taking into account the number of species compared herein, tooth row formula tends to be consistent in each group, mainly in the *L. fuscus* group, although interpopulation variation may be observed in some species (Langone and de Sá, 2005). The tooth row formula of *L. silvanimbus* (Heyer, de Sá, and Muller, 2002) and that of *L. rugosus* (Heyer and Thompson, 2000) were erroneously published as being 2(1)/3 and 2(1)/3(1), respectively. Actually, these species have tooth row formulae of 2(2)/3 and 2(2)/3(1), respectively (W. R. Heyer, pers. comm.) and the correct formulae are used in Table 1. The ventral marginal papillae row tends to be double in most *Leptodactylus* species, except in the *pentadactylus* group, where most species exhibit single row. Tadpoles tend to be cryptically colored, except for the *melanonotus* and *ocellatus* groups, where female parental care occurs and tadpoles form dark evident schools (Wells and Bard, 1988; Prado *et al.,* 2000). The lateral line system is not commonly observed in tadpoles of the *L. fuscus* group. However, as pointed out by Langone and de Sá (2005), the lack of information about the lateral line system in most descriptions makes it difficult to compare species concerning this trait.

Although similarities can be observed in the four *Leptodactylus* groups proposed by Heyer (1969), four distinct morphotypes occur concerning external morphology (W. R. Heyer, pers. comm.), which do not always correspond to these groups: (1) the tadpoles of the *L. fuscus* group have very similar morphology, as mentioned above, and this same morphology is also observed in some members of the *L. pentadactylus*

Table 2: Comparison of internal morphology of buccal floor among *Leptodactylus* species. BFA: Buccal Floor Arena.

Group/Species	Infralabial papillae	Lingual papillae	BFA papillae (per side)	Pre-pocket papillae (per side)	Source
Fuscus					
L. elenae	two pairs (medial pair fused)	4	5	1 or 2	this study
L. fuscus	three	4	few	1 or 2	Wassersug and Heyer (1988)
L. gracilis	two pairs (medial pair fused)	4	8-10	1 or 2	Wassersug and Heyer (1988)
L. mystacinus	two pairs (medial pair fused)	4	7-8	absent	Wassersug and Heyer (1988)
Melanonotus					
L. podicipinus	three	absent	10-15	0-3	Wassersug and Heyer (1988)
Ocellatus					
L. chaquensis	two pairs	3	10-15	absent	Wassersug and Heyer (1988)
L. ocellatus	two	3	25-30	absent	Spirandeli-Cruz (1991)
Pentadactylus					
L. knudseni	five	3	10	2 or 3	Wassersug and Heyer (1988)
L. pentadactylus	two pairs (medial pair fused)	3	5-6	absent	Wassersug and Heyer (1988)

Table 3: Comparison of internal morphology of buccal roof among *Leptodactylus* species. BRA: Buccal Roof Arena.

Group/Species	Postnarial papillae	Median ridge	Lateral ridge papillae	Lateral roof papillae (per side)	BRA papillae (per side)	Source
Fuscus						
L. elenae	2	broad, semi-circular	non-branching	4	4	this study
L. fuscus	4	triangular	not very branched	1-4	4-5	Wassersug and Heyer (1988)
L. gracilis	4	broad, triangular	non-branching	1-4	4-5	Wassersug and Heyer (1988)
L. mystacinus	4	broad, triangular	non-branching	1-4	4	Wassersug and Heyer (1988)
Melanonotus						
L. podicipinus	4	triangular	non-branching	1-4	6	Wassersug and Heyer (1988)
Ocellatus						
L. chaquensis	2	triangular	branched	1-4	5-8	Wassersug and Heyer (1988)
L. ocellatus	4	triangular	branched	3-4	13	Spirandeli-Cruz (1991)
Pentadactylus						
L. knudseni	2	broad, triangular	non-branching	1-4	2-3	Wassersug and Heyer (1988)
L. pentadactylus	2	small, rounded	non-branching	1-4	1-2	Wassersug and Heyer (1988)

group, such as *L. rhodonotus* and *L. syphax* (Eterovick and Sazima, 2000); (2) the almost black, socially aggregating tadpoles of the *L. melanonotus* and *L. ocellatus* groups, and the *L. pentadactylus* group member *L. rhodomystax;* (3) the semiterrestrial larvae of *L. lithonaetes* and *L. rugosus* are morphologically much more similar to *Thoropa* and *Cycloramphus* tadpoles than other *Leptodactylus* tadpoles; (4) the facultatively carnivorous tadpoles of the *Leptodactylus pentadactylus* cluster *(L. labyrinthicus, L. flavopictus, L. knudseni)* are more elongate and have small, anteriorly positioned oral disks when compared to other *Leptodactylus* species – this morphology is taken to the extreme in the trophic egg eating tadpoles of *L. pentadactylus* and particularly *L. fallax* (Eterovick and Sazima, 2000; W. R. Heyer, pers. comm.). These observations suggest that, although general morphology exhibits phylogenetic tendencies, there are some traits that might be molded by ecological factors, such as habitat type and food habits. Our data on external morphology as well as on the internal buccal features seem to support the groups proposed by Heyer (1969). However, the description of many other tadpole species of *Leptodactylus,* in addition to molecular data, would be very useful to elucidate the phylogenetic relationships among these groups.

Resumo

A morfologia externa e a anatomia oral interna de girinos de *Leptodactylus elenae* são aqui descritas e comparadas com as de outras espécies do gênero *Leptodactylus.* Tanto a morfologia externa quanto a anatomia da cavidade bucal de *L. elenae* são similares às

de outros *Leptodactylus* do grupo *fuscus* e sugerem um hábito alimentar associado à ambientes lênticos. As características que mais variaram entre as espécies de *Leptodactylus* foram o número de papilas linguais e as terminações das papilas laterais, as quais são menores e não apresentam ramos terminais em girinos de *L. elenae*. Girinos de *Leptodactylus* apresentam morfologias variáveis, algumas vezes convergentes com outros gêneros na família, porém, tanto a morfologia externa quanto a anatomia oral interna parecem suportar os grupos atuais de *Leptodactylus*.

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