

7-9-2007

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Rafael O. de Sá

*University of Richmond*, rdesa@richmond.edu

Reuber Brandão

Lorena Dall'ara Guimarães

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## Recommended Citation

de Sá, Rafael O., Reuber Brandão, and Lorena Dall'ara Guimarães. "Description of the Tadpole of *Leptodactylus pustulatus* Peters, 1870 (Anura: Leptodactylidae)." *Zootaxa* 1523, no. 1 (July 9, 2007): 49-58.

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## Description of the tadpole of *Leptodactylus pustulatus* Peters, 1870 (Anura: Leptodactylidae)

RAFAEL O. DE SÁ<sup>1,4</sup>, REUBER BRANDÃO<sup>2</sup> & LORENA DALL'ARA GUIMARÃES<sup>3</sup>

<sup>1</sup>Department of Biology, University of Richmond, Richmond, VA 23173, USA.

<sup>2</sup>Departamento de Engenharia Florestal - EFL, Universidade de Brasília - UnB, Brasília, DF, Brasil. CEP 70 910-900.

<sup>3</sup>Instituto de Ciências Biológicas, Departamento de Biologia Geral, Laboratório de Comportamento Animal, Universidade Federal de Goiás, Cx. Postal 131, Setor Itatiaia, cep: 7400-970

<sup>4</sup>Corresponding author. E-mail: rdesa@richmond.edu

### Abstract

The external morphology and oral disc of the tadpole of *Leptodactylus pustulatus* Peters, 1870, are described and illustrated for Gosner stage 39. The internal oral anatomy was analyzed with SEM at Gosner stage 36 whereas chondrocranial anatomy is reported for Gosner stage 35. The overall characteristics do not depart from those known for the genus *Leptodactylus* and they particularly agree for those of the *melanonotus* species group. The labial tooth row formula is 2(2)/3. Observations are presented that suggest that *L. pustulatus* engages in larval parental care.

**Key words:** *Leptodactylus pustulatus*, tadpole, SEM oral anatomy, chondrocranium, natural history

### Resumo

São descritas a morfologia externa e o disco oral do girino de *Leptodactylus pustulatus* Peters 1870, no estágio 39 de Gosner. A anatomia oral interna foi analisada ao MEV no estágio 36, enquanto a anatomia do condrocânio é descrita para o estágio 35. As características analisadas não separam a espécie de outras conhecidas do gênero *Leptodactylus* e concordam particularmente com aquelas descritas para espécies do grupo *melanonotus*. A fórmula de fileiras de denticúlos labiais é 2(2)/3. São descritas observações que sugerem que *L. pustulatus* apresenta cuidado parental de girinos.

### Introduction

*Leptodactylus pustulatus* is a species within the *melanonotus* species group; it is distributed throughout central Brazil, associated with the flooded terrains of the Araguaia, Tocantins, Xingu, and Parnaíba Rivers. The species has been reported for the Brazilian States of Goiás, Tocantins, Mato Grosso, Pará, Maranhão, Ceará and Piauí occupying Cerrado environments. Cerrado habitats refer to the Brazilian central highlands that cover approximately 23% of Brazil's surface area, second only to the Amazonian rainforest, and corresponding to the most extensive woodland-savanna in South America.

Since its original description little has been published on the biology of this species and the larval stage has not been reported. Herein we: 1) describe and illustrate the larval external morphology and oral disk, 2) report its internal oral anatomy (based on scanning electron microscopy analysis), 3) describe and illustrate the characteristics of the chondrocranial anatomy, and 4) present field observations on the natural history and parental care of the *Leptodactylus pustulatus*.

## Material and methods

Four tadpoles of *Leptodactylus pustulatus* were collected by R. A. Brandão and B. A. Duar, at Britânia, Goiás, on October 15, 1995 (CHUNB 38508–38511); L. D. Guimarães collected four additional tadpoles at Matrinchã, Goiás, on December 21, 2004 (CHUNB 49611 and CHUNB 49619). The larvae were fixed in 10% commercial grade formalin and staged following Gosner (1960). Species identification is based on two juveniles raised in laboratory in December 1995. The larvae are deposited at the herpetological collection of the University of Brasilia. The larvae were between Gosner stages 35 and 40.

Measurements and terminology follow those of Lavilla and Scrocchi (1986) and Altig and McDiarmid (1999). Measurements were taken with a Mitutoyo digital caliper. Tadpole description and illustration are based on a Gosner stage 39 specimen (CHUNB 49619). One tadpole in Gosner stage 35 was prepared for chondrocranial analysis; methodology and terminology follow those of Larson and de Sá (1998). One tadpole in Gosner stage 36 was dissected for SEM analysis. The specimen was prepared as follows: ultrasonically cleaned for 15 min, fixed in 3–4% solution of glutaraldehyde for 2 h at room temperature (rt), followed by three 15 min washes with 0.1 M phosphate buffer, post fixed for 2 h in a 1% solution of osmium tetroxide rt, three 15 min washes in 0.1 M phosphate buffer were repeated. Subsequently, samples were dehydrated using 15 min changes of the following graded ethanol series: 35%, 50%, 70%, 80%, 95%, and three 100% changes. Specimens were critical point dried in CO<sub>2</sub>, mounted on aluminum stubs and sputter coated with gold/palladium, 22 nanometers thick, using a Hummer VII sputtering system. Internal oral anatomy was examined in a Hitachi S–2300 scanning electron microscope at 15 kV, 20 kV and 25 kV and photographed using Polaroid 55 positive/negative film. Morphological features were recorded using the methodology presented by Wassersug (1976) and Wassersug and Heyer (1988); terminology follows that of de Sá and Langone (2002).

## Results

### Tadpole description

#### External morphology (Stage 39).

Tadpoles of *Leptodactylus pustulatus* are exotrophic, lentic, and benthic guild members (McDiarmid & Altig 1999, guild IIA1). Tadpoles have an oval, elongated, and compressed body, without visible constriction (Fig. 1). Body length represents 37.2% of total length, whereas body width is about 1.3X of body height. The maximum body width is located at the level of the eyes. The snout is rounded in lateral and dorsal view. The eyes are small, rounded, and dorsolaterally positioned, and are visible in dorsal and lateral view. The external nares are about half way between the eyes and the tip of the snout; narial openings are laterodorsal, small, rounded, and show margins marked by lighter coloration, but without a marginal rim. The orbitonasal line is not visible. The lateral line system is distinctly visible as light dots that run caudally from the tip of the snout, pass dorsal to the nares and eyes, run ventrally behind the eye and posteriorly over the dorsal body, and extend into the anterior half of the caudal musculature; lateral line system is also visible in the area above and in front of the spiracle. Tail fins are low; dorsal and ventral fins are about equal in height and nearly parallel to the tail musculature. The dorsal fin originates at the tail and body junction; the ventral fin originates at the posterior ventral terminus of the body and it is hidden by the vent tube. Maximum tail height is about 17% higher than body height, the tail fins slope uniformly and gradually to a rounded tail tip. The main tail axis is eutiurial; the myotomes of the tail musculature are poorly defined, almost indistinguishable in the tail posterior half, and extend to the tip of the tail. The spiracle tube is sinistral, simple, short, and posterolaterally directed; spiracular opening is midlateral and slightly elliptical. The vent tube and vent tube's opening are medial relative to the ventral fin; vent tube opening is circular.

The oral disc is not emarginate and anteroventrally positioned; it corresponds to about 30.8% of the body

width (Fig. 2). A double row of large and rounded marginal papillae are found on the ventral and lateroventral margins of the oral disc, whereas the laterodorsal margins bear a single row of marginal papillae; a large rostral gap occupies most of the upper labium (about 54% of the width of the oral disk); mental gap is absent. No submarginal or intramarginal papillae were found. The labial tooth row formula is 2(2)/3; all labial tooth rows are sub-equal in length; tooth row A-2 is interrupted by a wide gap (about 24% of the length of A-1). Upper and lower jaw sheaths are wide, pigmented in no more than 1/4 of their width, and their edge is serrated.

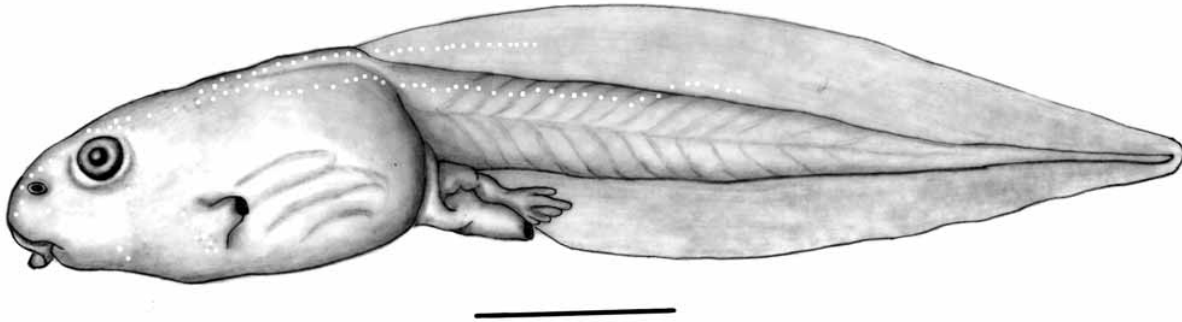


FIGURE 1. Tadpole of *Leptodactylus pustulatus*, Gosner stage 39, CHUNB 49619. Bar = 5 mm.

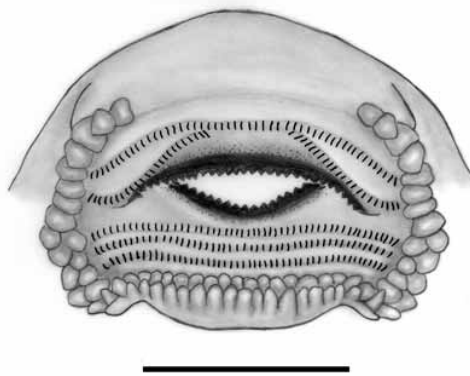


FIGURE 2. Oral disk of *Leptodactylus pustulatus*, Gosner stage 39, CHUNB 49619. Bar = 1 mm.

**Coloration of larvae.** In life, the larvae of *Leptodactylus pustulatus* are overall dark brown, with darker tails. Specimens in 10% formalin are overall black, lighter on the ventral surfaces of body, with intestinal coils slightly visible through the ventrolateral skin of the body. The dorsal and dorsolateral surfaces of the body are homogeneously black, grading continuously to a dark gray on the ventral surfaces. The tail fins and tail musculature are smooth dark gray.

**Measurements of larvae** (in mm, n = 4). Total length  $x = 29.07 \pm 0.91$ ; body length  $x = 10.79 \pm 0.34$ ; body height  $x = 4.54 \pm 0.30$ ; body width  $x = 5.82 \pm 0.25$ ; tail height  $x = 5.98 \pm 0.13$ ; tail length  $x = 18.28 \pm 0.84$ ; eye diameter  $x = 1.32 \pm 0.04$ ; eye-nostril distance  $x = 1.23 \pm 0.13$ ; interorbital distance  $x = 2.35 \pm 0.13$ ; internarial distance  $x = 1.62 \pm 0.09$ ; width of oral disc  $x = 1.99 \pm 0.04$ ; body length/total length  $x = 36.12\%$ ; eye diameter/body length  $x = 12.23\%$ .

#### Internal Oral Anatomy (Stage 36).

**Buccal roof.** The oral roof is overall longer than wide, with a relatively narrow prenarial arena. A broad (width about 25% greater than its height) rectangular ridge with few pustulations is present in the prenarial arena. Two pairs of large, long, pustulated postnarial papillae are found at the anterior tip of the internal nares.

The most anterior pair is almost twice the length of the second pair. Internal nares are narrow, elliptical slits positioned in a 45° angle relative to the main axis of the buccal roof; nares are found posteriorly, in the anterior third of the buccal roof (Fig. 3). Narial walls are thick and the posterior margin of each nare bears papillae, whereas the anterior edge appears smooth; no narial valve was observed. Lateral ridge papillae are absent. A few pustulations are found on the postnarial arena between the internal nares and the median ridge; a pair of simple and short papillae is found immediately in front of the median ridge. The median ridge is overall triangular and has an irregular edge; the height of the median ridge is less than half of its width. Buccal roof arena (BRA) rounded, bounded anteriorly by the median ridge, laterally by numerous elongated and pointed papillae that are mostly arranged in a double row, and posteriorly by a single row of papillae that are slightly shorter than the lateral ones. BRA field densely and evenly scattered with pustulations. Dorsal velum long, curving gradually towards the midline; margin of velum bears papillae. The glandular zone of the velum is wide.



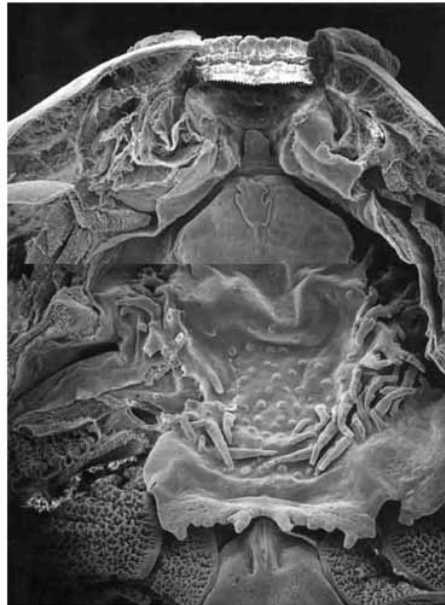
**FIGURE 3.** Buccal roof anatomy of *Leptodactylus pustulatus*, Gosner stage 36.

Buccal floor overall triangular and broad (Fig. 4). One pair of infralabial papillae present. The tongue anlage has a large lingual papilla with irregular margins. Buccal floor arena (BFA) is semicircular and defined by several pairs of long and conical papillae; BFA homogeneously scattered with pustulations. Velar surface free; posterior margin jagged by marginal projections; median notch distinct and secretory pits present. Gill filters of moderate size with an average filter mesh.

### **Chondrocranial Anatomy (Stage 35).**

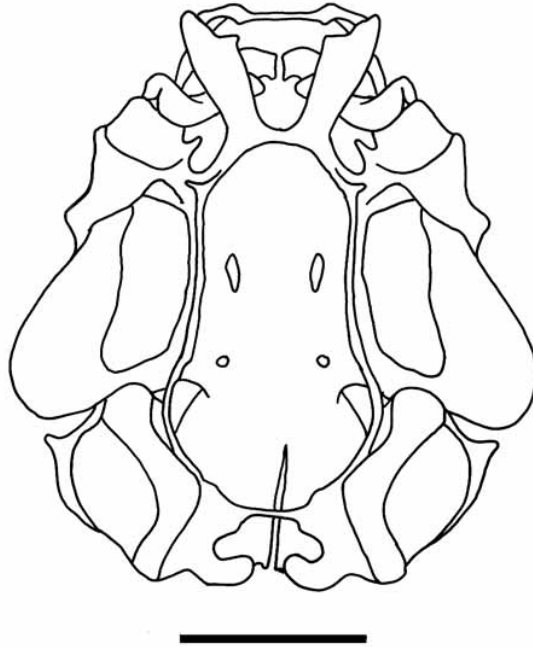
The chondrocranium of *Leptodactylus pustulatus* is about 10% longer than wide (Fig. 5). The suprarostrals consist of thin corpora ventrally fused at the midline, forming a wide U-shaped space between them. The corpora are continuous dorsolaterally with the suprarostrals. The cornua trabeculae are narrow and long, their length represents about 24% of the total chondrocranial length and they diverge in a V-shape fashion. The processus (p.) lateralis trabeculae of the cornua trabeculae is indistinct, whereas the p. quadratoethmoidalis of the commissura quadratocranialis anterior is long and distinctly visible. At stage 35, the basicranial fenestra is closed; two pairs of foramina, f. craniopalatina and f. carotica primaria, are clearly visible. The orbital carti-

lages are well developed and confluent with the otic capsules, forming the lateral wall of the braincase, where the foramen opticum, oculomotorium, and prooticum are visible. Dorsally, the frontoparietal fenestra remains undivided. The otic capsules are ovoid and their length is about 34% of the total chondrocranial length; they possess a narrow crista parotica that bears a distinct, pointed, and overall triangular-shaped p. anterolateralis; no p. posterolateralis was found. Anteriorly, the palatoquadrate connects to the braincase via the commissura quadratocranialis anterior; a p. pseudopterygoideus is absent; posteriorly, the connection to the braincase is through the p. ascendens, with a low attachment. The posterior curvature of the palatoquadrate extends beyond the level of the attachment of the p. ascendens to the braincase. The p. muscularis quadrati is broad and its rounded tip connects to the commissura quadratocranialis anterior by a chondrified commissura quadratoorbitalis. The pars articularis quadrati is broad and short and articulates with a robust and sigmoid-shaped Meckel's cartilage. The infrarostrals connect, but are not fused, ventromedially forming a V-shaped structure. The ceratohyalia of the visceral skeleton are wide and bear two short and pointed processes, the p. anterolateralis and p. anterior hyalis (Fig. 6). The ceratohyalia are connected by a distinct pars reuniens that is continuous with the copula posterior that bears a short and rounded p. urobranchialis. The hypobranchial plates are not fused. The hypobranchial plates possess a distinct, hook-like, p. anterior branchialis. The branchial baskets consist of four well-developed ceratobranchials; ceratobranchials I and IV are broadly continuous with the hypobranchial plates. Ceratobranchials II and III have a closed p. branchialis.

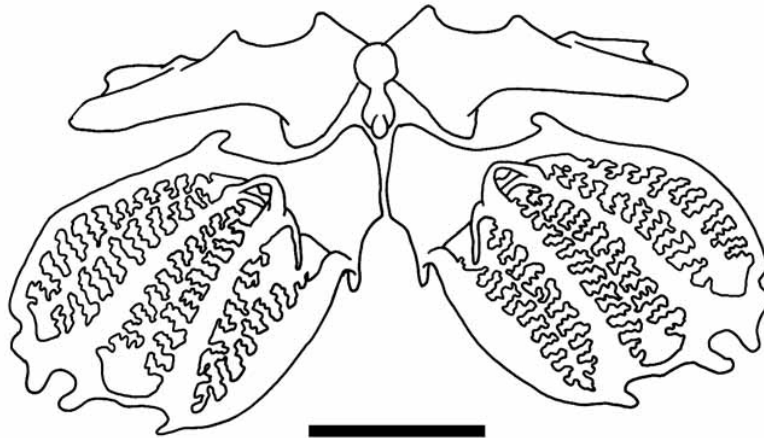


**FIGURE 4.** Buccal floor anatomy of *Leptodactylus pustulatus*, Gosner stage 36.

**Natural history.** The habitat where *Leptodactylus pustulatus* was found corresponds to “veredas” environments, i.e., flooded grasslands and areas of flooded gallery forests (see Ribeiro & Walter 2001 for an account of Cerrado physiognomies). Calling males were more commonly found in lentic habitats, usually large ponds with deeper areas of between 1 and 2 m. Individuals were observed calling close to aquatic plants and dead trunks, sometimes at the deeper areas of the ponds. The most common vegetation in these ponds was “buriti” palms (*Mauritia vinifera*), Cyperaceae, and Poaceae at the edges, and Nymphaeaceae, Araceae, Musaceae, and Pontederiaceae vegetation covered the deeper areas. *Leptodactylus pustulatus* has also been found in small cattle dams and other types of flooded areas (Brandão & Heyer 2005).



**FIGURE 5.** Dorsal view of the chondrocranium of *Leptodactylus pustulatus*, Gosner stage 35, CHUNB 38511. Bar = 1mm



**FIGURE 6.** Ventral view of the hyobranchial apparatus of *Leptodactylus pustulatus*, Gosner stage 35, CHUNB 38511. Bar = 1mm.

Tadpoles collected on October 15, 1995, were found on a pond formed by the damming of a stream by road shaft. The larvae were swimming around a female *Leptodactylus pustulatus* while this was floating on the water surface. When disturbed, the tadpoles congregated above the female and remained still, the female did not show any defensive or aggressive behavior while the tadpoles were collected. The tadpoles exhibited schooling behavior by forming a massive cluster of tadpoles that swam around the female. Recently metamorphosed *L. pustulatus* were caught in pitfall traps in an area of seasonal flooded Cerrado at Palmas, Tocantins State, during the months of November and December 1995. Adults were always found in aquatic environments. The water snake, *Helicops angulatus*, and the wolf fish, *Hoplias* sp., were observed in same habitat of *L. pustulatus*. These species are likely predators of both *Leptodactylus* tadpoles and adults individuals. Other

anurans found along with *L. pustulatus* at Palmas and Britânia were *Leptodactylus podicipinus*, *Pseudis tocantins*, *Lysapsus caraya*, *Hypsiboas punctatus*, and *Hypsiboas raniceps*.

Tadpoles were also collected on December 21, 2004, at 21:00 hs, at Matrinchã, west Goiás State. A female *Leptodactylus pustulatus* was observed attending a group of about 50 tadpoles in a small pond in “vereda” habitat surrounded by cattle pastures; the pond had a sandy substrate and the tadpoles were on the shallow margin of the pond (about 4–5 cm deep). The larvae were swimming around a female *L. pustulatus* that floated on the surface of the pond. During the 1.5 hour of observation, the female grouped and displaced the tadpoles that surrounded her three times; we cannot discard that this behavior may have been triggered by our presence in the pond. The grouping and moving of the larvae to other areas on the edge of the pond was accomplished through movements of the anterior and posterior limbs; these movements appear to the human eye as if the female was “grouping” the larvae. The female had an overall triangular area on the dorsal surface of the head that lacked skin. This injury could be caused by territorial combats or predator attacks, but we did not directly observed this.

## Discussion

The *Leptodactylus melanonotus* species group consists of 16 species (Frost 2007). The larvae of *L. melanonotus* (Orton 1951), *L. podicipinus* (Vizzotto 1967), and *L. silvanimbus* (Heyer *et al.* 2002) have been described. *Leptodactylus pustulatus* has a tooth row formula of 2(2)/3, which seems a common formula for species in the group (Langone & de Sá, 2005), although the reports for *L. podicipinus* differ from this tooth row formula: 2(1)/3 (Vizzotto 1967) and 2/3 (Prado, pers. obs. in Prado & d’Heursel 2006).

The only available data on the internal oral anatomy for species of the *melanonotus* species group is limited to the description of *Leptodactylus podicipinus* (Wassersug & Heyer 1988, as *L. wagneri*; corrected in Heyer, 1994, pg. 120). *Leptodactylus pustulatus* differs from the previously reported species (*L. podicipinus* characteristics in parentheses) by: a) possessing two infralabial papilla (three), b) large and single lingual papillae (absent), c) lack of lateral ridge papillae (present), and d) internal nares in a 45 degrees angle with the main axis of the buccal roof (90 degrees) resulting in the positioned of postnarial papillae on the posterior side at the most anterior tip of the internal nares (postnarial papillae not at the anterior tip of the internal nares).

*Leptodactylus pustulatus* have characteristics that differ from those reported for other species in the genus. In *Leptodactylus* the internal nares are arranged in a 90 degrees angle with the main oral axis, whereas in *L. pustulatus* the nares are arranged in a 45 degrees angle with that axis; related to the different orientation of the internal nares, the postnarial papillae are arranged far forward at the anterior tip of the internal nares. Previous studies have reported the presence of lateral ridge papillae in *Leptodactylus*, but these papillae are absent in *L. pustulatus*. The large and elongated lingual papilla with irregular margins reported herein for *L. pustulatus* is highly unusual and an anonymous reviewer labeled it as “tongue-like” lingual papilla.

Larson and de Sá (1998) previously reported variation in the chondrocranial anatomy of 22 species of *Leptodactylus*; that study included characteristics for four species in the *melanonotus* group, *L. melanonotus*, *L. petersii*, *L. podicipinus*, and *L. validus*. Overall, *L. pustulatus* has the 12 characteristics reported for the genus *Leptodactylus*. Furthermore, *L. pustulatus* possesses the following characteristics that are common among other species in the *melanonotus* species group (Larson & de Sá 1998): 1) narrow and widely separated suprarostrals, 2) a low attachment of the p. ascendens of the palatoquadrate (*sensu* Sokol 1981), 3) a closed p. branchialis of the visceral skeleton, i.e., a cartilaginous bridge connects ceratobranchials II and III), 4) posterior curvature of the palatoquadrate beyond the anterior margin of the otic capsule, and 5) narrow and widely diverging cornua trabeculae.

Our knowledge of the biology of *Leptodactylus pustulatus* is limited to the available description of its advertisement call and natural history observations (Brandão & Heyer 2005) and notes on its habitat and col-



oration (Fenolio *et al.* 2006). Our field observations on the reproductive biology of *L. pustulatus* showed that females remain with their tadpoles, for at least part of their larval development, and that the females actively “group” and “push” the tadpoles around the pond. These behaviors suggest that the species should be added to the anuran species with parental care of the larval stage.

Different levels of parental care, i.e., beyond the construction of a foam nest, has been reported for *Leptodactylus*. The *L. fuscus* species group is characterized by depositing the foam nest in terrestrial chambers, e.g., *L. latinaus* (Gallardo 1958), *L. fallax* (Brooks 1968; Lescure 1979), *L. fuscus* (Lescure 1973); detailed descriptions of the terrestrial nest and nest construction behaviors within the “*fuscus*” species group are those for *L. mystacinus* (Sazima 1975; Giaretta & De Olivera 2006). Descriptions of active defense of the foam nest and the larvae by adults were reported for *L. ocellatus* (Fernández & Fernández 1921; Gallardo 1964); the elaborate parental behavior, communication, and tadpole schooling of this species were further studied by Vaz-Ferreira and Gehrau (1974, 1975, 1986). Similar complex behaviors were reported for *L. insularum* (Wells & Bard 1988; Vaira 1997; Ponssa 2001). Attendance of larvae, but no defensive parental care, was reported for *L. chaquensis* (Prado *et al.* 2000); given the purported close relationship between *L. ocellatus* and *L. chaquensis* it is likely that further field observations would find defensive parental care in the latter species.

Among species in the “*melanonotus*” group, parental care of eggs and larvae has been reported for *L. leptodactyloides* (R. Cocroft & V. Morales, pers. com. in Downie 1996), *L. podicipinus* (Prado *et al.* 2000, 2002; Martins 2001), and *L. validus* (Downie 1996). After leaving the foam nest, the larvae of the above species form schools that are attended by the female until metamorphosis. Furthermore, those studies reported that the female seems to guide and/or push the larvae towards particular microhabitats within the ponds; microhabitats that may enhance survival of the tadpoles e.g., to avoid predation or desiccation, to have optimal developmental temperatures, etc. The observations reported here for *L. pustulatus* are similar to the parental care reported for other species in the “*melanonotus*” group.

The more complex behaviors of tadpole attendance, guidance, and active protection are found in members of the currently defined “*melanonotus*” and “*ocellatus*” species groups. A closer relationship between these two species groups among *Leptodactylus* was originally suggested (Heyer 1969) and more recently supported by larval anatomical characteristics (Larson & de Sá 1998). Lack of a phylogenetic framework for *Leptodactylus* precludes any attempts to decipher the evolution of parental care in the genus.

## Acknowledgments

We thank Guarino Colli and Fernanda Werneck who facilitated our work at the CHUNB and Rogeiro Bastos (UFG), Carolina Canedo, and Thiago Barbosa for their assistance. The manuscript benefited from the comments of two anonymous reviewers. This work was supported by: CAPES (to LDG) and NSF award 0342918 (to RdS and WRH).

## Literature cited

- Altig, R. & McDiarmid, R.W. (1999) Body plan. Development and morphology. In: McDiarmid, R.W. & Altig, R. (Eds.), *Tadpoles - the biology of anuran larvae*. The University of Chicago Press, Chicago, pp. 24-51.
- Brandão, R.A. & Heyer, W.R. (2005) The complex calls of *Leptodactylus pustulatus* (Amphibia, Anura, Leptodactylidae). *Amphibia-Reptilia*, 26, 566-570.
- Brooks, G.R. (1968). Natural history of the West Indian frog *Leptodactylus fallax*. *Virginia Journal of Science*, 19, 176.
- de Sá, R.O. & Langone, J. (2002) The tadpole of *Proceratophrys avelinoi* (Mercadal de Barrio and Barrio, (Anura: Leptodactylidae). *Journal of Herpetology*, 36, 490-494.
- Downie, J.R. (1996) A new example of female parental behaviour in *Leptodactylus validus*, a frog of the leptodactylid 'melanonotus' species group. *Herpetological Journal*, 6, 32-34.

- Fenolio, D., Silva, H.L.R. & Da Silva, N.J. Jr. (2006) *Leptodactylus pustulatus* Peters, 1870 (Amphibia: Leptodactylidae): Notes on habitat, ecology, and color in life. *Herpetological Review*, 37, 140.
- Fernández, K. & Fernández, M. (1921) Sobre la biología y reproducción de algunos batracios argentinos. I. Cystignathidae. *Anales de la Sociedad Científica de Argentina*, 91, 97–140.
- Frost, D.R. (2007) Amphibian Species of the World: an Online Reference. Version 5.0 (1 February 2007). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.php>. American Museum of Natural History, New York, USA.
- Gallardo, J.M. (1958) Observaciones biológicas sobre *Leptodactylus prognathus* Boulenger. *Ciencia e investigación*, 14, 460–465.
- Gallardo, J.M. (1964) Consideraciones sobre *Leptodactylus ocellatus* (L.), (Amphibia, Anura) y especies aliadas. *Physis*, 24, 373–384.
- Giaretta, A.A. & de Olivera, J.C. (2006) *Leptodactylus mystacinus* (Shovel-Nosed Frog). Parental care. *Herpetological Review*, 37, 2, 204–205.
- Gosner, K.L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.
- Heyer, W.R. (1969) The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution*, 23, 421–428.
- Heyer, W.R. (1994) Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology*, 546, 1–124.
- Heyer, W.R., de Sá, R.O. & Muller, S. (2002) *Leptodactylus silvanimbus* (Anura: Leptodactylidae). *Catalogue of American Amphibians and Reptiles*, 743, 1–743.
- Langone, J.A. & de Sá, R.O. (2005) Redescrición de la morfología larval externa de dos especies del grupo de *Leptodactylus fuscus* (Anura, Leptodactylidae). *Phyllomedusa*, 4, 49–59.
- Larson, P. & de Sá, R.O. (1998) Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): its utility in phylogenetic reconstruction. *Journal of Morphology*, 238, 287–305.
- Lavilla, E.O. & Scrocchi, G.J. (1986) Morfometría larval de los géneros de Telmatobinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis*, 44, 39–43.
- Lescure, J. (1973) Contribution a l'étude des amphibiens de Guyane française. II. *Leptodactylus fuscus* (Schneider). Observations écologiques et éthologiques. *Annales du Musée d' Histoire Naturelle de Nice*, 1, 91–100.
- Lescure, J. (1979) Etude taxonomique et éco-éthologiques d'un amphibien des petites Antilles: *Leptodactylus fallax*, Müller, 1926 (Leptodactylidae). *Bulletin du Muséum National d' Histoire naturelle*, 1, 3, 757–774.
- Martins, I.A. (2001) Parental care behaviour in *Leptodactylus podicipinus* (Cope, 1862) (Anura, Leptodactylidae). *Herpetological Journal*, 11, 29–32.
- Orton, G.L. (1951) The tadpole of *Leptodactylus melanonotus* (Hallowell). *Copeia*, 1951, 62–66.
- Ponssa, M.L. (2001) Cuidado parental y comportamiento de cardúmen de larvas en *Leptodactylus insularum* (Anura, Leptodactylidae). *Alytes*, 19, 183–195.
- Prado, C.P. de A. & d'Heursel, A. (2006) The tadpole of *Leptodactylus elenae* (Anura: Leptodactylidae), with the description of the internal buccal anatomy. *South American Journal of Herpetology*, 1, 79–86.
- Prado, C.P. de A., Uetanabaro, M. & Haddad, C.F.B. (2002) Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization toward terrestriality in the genus. *Copeia* 4, 1128–1133.
- Prado, C.P. de A., Uetanabaro, M. & Lopes, F.S. (2000) Reproductive strategies of *Leptodactylus chaquensis* and *L. podicipinus* in the Pantanal, Brazilian. *Journal of Herpetology*, 34, 135–139.
- Ribeiro J.F. & Walter B.M.T. (2001) Fitofisionomias do bioma Cerrado. In: Sano, S.M. & Almeida, S.P. (Eds.), *Cerrado: Ambiente e Flora*. Embrapa, Brasília.
- Sazima, I. (1975) *Habitos reproductivos e fase larvaria de Leptodactylus mystacinus e L. sibilatrix* (Anura, Leptodactylidae). MS Thesis, University of Sao Paulo, Sao Paulo.
- Sokol, O.M. (1981) The larval chondrocranium of *Pelodytes punctatus*, with a review of tadpole chondrocrania. *Journal of Morphology*, 169, 161–183.
- Vaira, M. (1997) *Leptodactylus bolivianus* (NCN). Behavior. *Herpetological Review*, 28, 200.
- Vaz-Ferreira, R. & Gehrau, A. (1974) Protección de la prole en leptodactylidos. *Revista de biología del Uruguay*, 2, 59–62.
- Vaz-Ferreira, R. & Gehrau, A. (1975) Comportamiento epimelético de la rana común, *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae). I. Atención de la cría y actividades alimentarias relacionadas. *Physis (B)*, 34, 1–14.
- Vaz-Ferreira, R. & Gehrau, A. (1986) *Comportamiento de los renacuajos gregarios de Leptodactylus ocellatus*. Catedra de Zoología, Facultad de Humanidades y Ciencias, Universidad de la República, Montevideo, Uruguay, 23 pp.
- Vizzoto, L.D. (1967) *Development of anurans from northwestern So Paulo state*. Ph.D. dissertation, Faculdade de Filosofia Ciências e Letras, So Jos do Rio Preto, Brazil.
- Wassersug, R. J. (1976) Oral morphology of anuran larvae: terminology and general description. *Occasional Papers of*

- the Museum of Natural History, University of Kansas*, 48, 1–23.
- Wassersug, R.J. & Heyer, W.R. (1988) A survey of internal oral features of Leptodactyloid larvae (Amphibia: Anura). *Smithsonian Contributions to Zoology*, 457, 1–99.
- Wells, K.D. & Bard, K.M. (1988) Parental behavior of an aquatic-breeding tropical frog, *Leptodactylus bolivianus*. *Journal of Herpetology*, 22, 361–364.