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Source: South American Journal of Herpetology, 12(1):14-23.

Published By: Brazilian Society of Herpetology

DOI: <http://dx.doi.org/10.2994/SAJH-D-16-00029.1>

URL: <http://www.bioone.org/doi/full/10.2994/SAJH-D-16-00029.1>

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The Tadpole of the Microendemic, Bromeligenous *Crossodactylodes itambe* (Anura, Leptodactylidae) from the Endangered ‘Campo Rupestre’ of Southeastern Brazil, with Additional Comments on Natural History

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Abstract. We describe the external larval morphology of the microendemic leptodactylid frog *Crossodactylodes itambe* from the ‘campo rupestre’ of the Espinhaço Mountain Range in the state of Minas Gerais, Brazil. The species identity of the only previously described *Crossodactylodes* tadpole cannot be confirmed, making this the first description of a tadpole of known taxonomic identity for the genus. The tadpole of *C. itambe* differs from the previously described *Crossodactylodes* tadpole in total length, origin of dorsal fin, development of tail musculature, spiracle position, absence of inner wall of spiracle and shape, and direction of vent tube. Characters such as narrow lateral gaps of marginal papillae and the distinct medial serration on the oral face of the upper jaw are proposed as putative synapomorphies for the genus. Tadpoles of *C. itambe* occur exclusively in the axils of the rupicolous bromeliad *Vriesea medusa*. Observation on the natural history, eggs, and larvae are also reported.

Keywords. Bromeliad; Espinhaço Mountain Range; Larvae; Paratelmatobiinae; Phytotelmata.

Resumo. Nós descrevemos a morfologia larval externa do anuro leptodactilídeo *Crossodactylodes itambe*, uma espécie microendêmica do campo rupestre da Cadeia do Espinhaço do estado de Minas Gerais, Brasil. A determinação da espécie da única larva de *Crossodactylodes* previamente descrita não pode ser confirmada, tornando esta a primeira descrição de um girino do gênero com identidade taxonômica conhecida. O girino de *C. itambe* distingue-se do girino de *Crossodactylodes* previamente descrito pelo tamanho total, origem da nadadeira dorsal, desenvolvimento da musculatura da cauda, posição do espiráculo, ausência de parede interna do espiráculo e forma e direção do tubo ventral. Caracteres como as interrupções laterais estreitas de papilas marginais e o serrilhado medial distinto na face oral da maxila superior são propostos como sinapomorfias putativas para o gênero. Girinos de *C. itambe* são encontrados exclusivamente nas axilas da bromélia rupícola *Vriesea medusa*. Observações sobre história natural, ovos e larvas são fornecidas.

INTRODUCTION

The genus *Crossodactylodes* Cochran, 1938, consist of five described bromeligenous (i.e., all life cycle stages associated with bromeliads) species: *Crossodactylodes pinto* Cochran, 1938; *C. bokermanni* Peixoto, 1982; *C. izecksohni* Peixoto, 1982; *C. septentrionalis* Teixeira Jr., Recoder, Amaro, Damasceno, Cassimiro and Rodrigues, 2013; and *C. itambe* Barata, Santos, Leite and Garcia, 2013. The genus is distributed throughout highland areas of the Atlantic Forest in the states of Rio de Janeiro, Espírito Santo, and Bahia, Brazil (Cochran, 1938; Peixoto, 1982; Teixeira Jr. et al., 2013), and one location in ‘campo rupestre’ (rupesrian grassland, Silveira et al., 2015) of the

Espinhaço Mountain Range in the state of Minas Gerais, Brazil (Barata et al., 2013).

The only known tadpole for the genus is that of a *Crossodactylodes pinto* (Peixoto, 1981) based on specimens from the municipality of Santa Teresa in the state of Espírito Santo, Brazil. Subsequently, two additional species were described from this location (*C. bokermanni* and *C. izecksohni*) and previous reported larvae were assigned to *C. bokermanni* or *C. izecksohni* (Peixoto, 1982). Moreover, significant variation in morphological characters of these tadpoles (e.g., length and shape of the vent tube; Peixoto, 1981), raises the possibility that the analyzed lots might contain both species. Later, an unidentified tadpole specimen from the same locality was used in

a comparative survey of internal oral features of neobatrachian anurans (Wassersug and Heyer, 1988).

Information concerning natural history is especially scarce for species of *Crossodactylodes*, but the limited information available indicates that (1) they are associated with bromeliads on mountaintops (Peixoto, 1981; Peixoto, 1982; Barata et al., 2013; Teixeira Jr. et al., 2013), (2) females lay few large eggs attached to bromeliads (Peixoto, 1995; Barata et al., 2013), and (3) tadpoles complete their development in the water accumulated in leaf axils (Peixoto, 1981). *Crossodactylodes* tadpoles were listed as detritivorous by Peixoto (1981), but their internal oral features suggested a mixture of macrophagy and suspension feeding (Wassersug and Heyer, 1988).

Crossodactylodes itambe is a microendemic species known only from the summit of Itambé within Parque Estadual do Pico do Itambé, municipality of Santo Antônio do Itambé in the state of Minas Gerais, Brazil, and represents the westernmost distribution of the genus (Barata et al., 2013). Herein, we describe the tadpole of this species, which represents the first larval description assuredly attributed to a single species of the genus, and report additional data from natural history observations.

MATERIALS AND METHODS

Tadpole identification

We sequenced a 645 base pairs (bp) fragment of the mitochondrial cytochrome oxidase c subunit I (COI) from one tadpole (lot UFMG 1477; GenBank accession KY362547) and four paratypes of *Crossodactylodes itambe* (UFMG 13376, 13377, 13379, 13381; GenBank accessions KY362548–KY362551, respectively). The primers employed are AnF1 and AnR1 (Lyra et al., 2017). DNA extraction, amplification and sequencing methods follow the protocols described in Blotto et al. (2013). Chromatograms obtained from the automated sequencer were read and assembled using the sequence editing software SeqScape® v 2.6 (Thermo Fisher Scientific, Waltham, MA, USA). Our sampling was complemented with COI sequences from GenBank produced by Fouquet et al. (2013) and Teixeira Jr. et al. (2013), including four specimens of *C. bokermanni* (KF534659.1, KF534658.1, KF534657.1, KF534656.1), five specimens of *C. izecksohni* (KF534655.1, KF534654.1, KF534653.1, KF534652.1, KF534651.1) and one specimen of *C. septentrionalis* (KC603985.1). Complete sequences were aligned in the MEGA7 software' CLUSTALW module under default parameters (Larkin et al., 2007; Kumar et al., 2016). Next, we calculated intraspecific and interspecific pairwise distances in MEGA7 (Kumar et al., 2016).

Study area and morphological examination

Tadpoles of *Crossodactylodes itambe* were collected from rupicolous bromeliads using a collecting aspirator (Silva and Alves-Silva, 2008) at the type locality on the summit of Itambé (18°23'52"S, 43°20'39"W; 1,769–2,063 m above sea level (asl); Datum WGS 84), in Parque Estadual do Pico do Itambé, municipality of Santo Antônio do Itambé, the southeastern part of the Espinhaço Mountain Range in Southeastern Brazil. Collecting took place over four days in November 2012.

Tadpoles were euthanized in 5% lidocaine solution and fixed and preserved in 10% commercial grade formalin. Voucher are housed in the Tadpole Collection of the Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil (voucher numbers UFMG 1477–79). Larval staging follows Gosner (1960). Descriptions of external morphology and proportions were based on five tadpoles in stages 36–39 and measurements were based on 21 specimens in stages 26–39. Terminology and measurements follow Altig and McDiarmid (1999a) for total length (TL), body length (BL), tail length (TAL), maximum tail height (MTH), internarial distance (IND), interorbital distance (IOD), tail muscle height (TMH) and tail muscle width (TMW); Lavilla and Scrocchi (1986) for body height (BH), body width (BW), body width at eye level (BWE), body width at narial level (BWN), snout–spiracular distance (SSD), eye–snout distance (ESD), eye–nostril distance (END), nostril–snout distance (NSD), eye diameter (ED), narial diameter (ND) and oral disc width (ODW); Grosjean (2005) for dorsal fin height (DFH) and ventral fin height (VFH); adapted from Altig and Johnston (1989) for oral disc position (ODP; i.e., angle formed by the tangent of the extended line connecting the superior and inferior lips and the longitudinal plane of the tadpole, characterized as ventral if $0^\circ < x < 30^\circ$ and anteroventral if $31^\circ < x < 80^\circ$; and Pinheiro et al. (2012) for spiracle length (SL), spiracle distal edge height (SDH) and dorsal fin insertion angle (DFiA). All measurements were taken to the nearest 0.1 mm with the aid of ImageTool version 3.0 (Wilcox et al., 1996). To obtain high quality photos we used an adjustable platform to support tadpoles immersed in water (Schacht and McBrayer, 2009). Terminology for egg morphology and ovipositional mode follow Altig and McDiarmid (2007). For morphological comparisons to other *Crossodactylodes* species we used the tadpole description of Peixoto (1981) and, given the impossibility of taxonomic confirmation, refer to this tadpole below as *Crossodactylodes* sp.

Natural history observations

Observations were made in February 2014 and February–May 2015. In February 2014, we surveyed 123 bromeliads during four nights at elevations of

Table 1. Uncorrected pairwise distances among COI sequences of a tadpole from lot UFMG 1477, four paratypes of *Crossodactylodes itambe*, four specimens of *C. bokermanni*, five specimens of *C. izecksohni*, and one specimen of *C. septentrionalis*. Intraspecific distances are highlighted in gray in diagonal, distances from tadpole to other species, and interspecific distances are shown under the diagonal, and standard error estimates are shown above the diagonal. N/C = not calculated, since there is only one individual.

Intraspecific and interspecific p-distances					
	Tadpole	<i>C. itambe</i>	<i>C. bokermanni</i>	<i>C. izecksohni</i>	<i>C. septentrionalis</i>
Tadpole	N/C	0.001	0.014	0.011	0.012
<i>C. itambe</i>	0.002	0.0031 (± 0.0020)	0.014	0.011	0.012
<i>C. bokermanni</i>	0.146	0.144	0.0	0.013	0.014
<i>C. izecksohni</i>	0.115	0.116	0.161	0.0084 (± 0.0029)	0.012
<i>C. septentrionalis</i>	0.129	0.127	0.169	0.146	N/C

1,713–2,063 m asl (the summit). In February–May 2015, the study area was divided in three elevational gradients: low (1,713–1,841 m asl), medium (1,853–1,957 m asl), and high (1,977–2,063 m asl), and we surveyed 48 bromeliads in each gradient for six nights each month.

RESULTS

Tadpole identification

The molecular analysis confirmed the identity of the tadpole as *Crossodactylodes itambe*. The distance between the tadpole and paratypes of *C. itambe* is 0.002 (SE = 0.001), whereas the distances between the tadpole and other species of *Crossodactylodes* vary from 0.115–0.146 (Table 1). Moreover, considering only the COI sequences of tadpole and paratypes of *C. itambe*, there are only three segregating sites in the COI fragment, and we identified four haplotypes, with the haplotype of the tadpole from lot UFMG 1477 being identical to that of the paratype UFMG 13379.

Tadpole description

External morphology

Maximum total length 36.6 mm (at stage 36; Table 2). Body 0.33–0.36 times TL, strongly depressed (BH/BW = 0.49–0.56), elliptical in dorsal view, with

Table 2. Measurements in mm or degrees (ODP and DFIA) of *Crossodactylodes itambe* from Santo Antônio do Itambé (UFMG 1477–79), state of Minas Gerais, Brazil. Data presented as mean ± SD (range). TL: total length; BL: body length; BH: body height; BW: body width; BWE: body width at eye level; BWN: body width at narial level; TAL: tail length; MTH: maximum tail height; TMH: tail muscle height; DFH: dorsal fin height; VFH: ventral fin height; TMW: tail muscle width; SL: spiracle length; SDH: spiracle distal edge height; SSD: snout–spiracular distance; ESD: eye–snout distance; END: eye–nostril distance; NSD: nostril–snout distance; ED: eye diameter; IOD: interorbital distance; ND: narial diameter; IND: internarial distance; ODW: oral disc width; ODP: oral disc position; DFIA: dorsal fin insertion angle.

Measurements	Stage 26–29 (n = 6)	Stage 30–35 (n = 10)	Stage 36–39 (n = 5)
TL	25.9 ± 2.0 (24.1–29.2)	33.2 ± 1.7 (30.3–36.4)	34.6 ± 1.6 (32.5–36.6)
BL	8.8 ± 0.6 (8.2–9.6)	11.1 ± 0.4 (10.5–11.6)	11.7 ± 0.4 (11.2–12.2)
BH	3.5 ± 0.12 (3.2–3.7)	4.3 ± 0.2 (3.9–4.5)	4.5 ± 0.3 (4.1–4.8)
BW	6.5 ± 0.5 (5.8–7.2)	8.1 ± 0.5 (7.1–8.8)	8.3 ± 0.5 (7.6–8.8)
BWE	5.9 ± 0.4 (5.3–6.2)	7.1 ± 0.4 (6.5–7.8)	7.3 ± 0.5 (6.6–7.8)
BWN	4.1 ± 0.3 (3.7–4.5)	5.0 ± 0.5 (4.2–5.9)	5.2 ± 0.3 (4.8–5.6)
TAL	17.1 ± 1.6 (15.4–19.6)	22.1 ± 1.4 (19.6–24.7)	22.9 ± 1.4 (20.8–24.5)
MTH	3.5 ± 0.2 (3.2–3.6)	4.0 ± 0.2 (3.6–4.2)	4.1 ± 0.2 (3.9–4.3)
TMH	1.8 ± 0.1 (1.7–2.0)	2.6 ± 0.2 (2.3–3.0)	2.7 ± 0.3 (2.3–3.0)
DFH	1.2 ± 0.1 (1.1–1.3)	1.3 ± 0.1 (1.2–1.5)	1.4 ± 0.2 (1.3–1.6)
VFH	1.0 ± 0.1 (1.0–1.1)	1.3 ± 0.1 (1.1–1.5)	1.3 ± 0.1 (1.2–1.5)
TMW	2.0 ± 0.2 (1.8–2.3)	2.6 ± 0.2 (2.3–2.9)	2.9 ± 0.3 (2.5–3.1)
SL	0.8 ± 0.01 (0.7–0.9)	1.1 ± 0.2 (0.9–1.5)	1.1 ± 0.2 (1.0–1.3)
SDH	0.8 ± 0.2 (0.6–1.1)	0.9 ± 0.2 (0.7–1.3)	0.9 ± 0.2 (0.8–1.2)
SSD	5.5 ± 0.3 (5.0–5.9)	6.5 ± 0.3 (6.0–6.9)	6.9 ± 0.3 (6.5–7.2)
ESD	2.6 ± 0.1 (2.4–2.8)	3.1 ± 0.2 (2.7–3.3)	3.3 ± 0.1 (3.1–3.5)
END	1.6 ± 0.1 (1.5–1.7)	1.8 ± 0.1 (1.7–2.0)	2.0 ± 0.1 (1.8–2.0)
NSD	1.0 ± 0.1 (1.0–1.2)	1.3 ± 0.1 (1.1–1.4)	1.3 ± 0.1 (1.3–1.5)
ED	0.7 ± 0.1 (0.7–0.8)	0.9 ± 0.1 (0.8–1.1)	0.9 ± 0.1 (0.9–1.0)
IOD	2.5 ± 0.1 (2.3–2.6)	3.1 ± 0.1 (3.0–3.3)	3.3 ± 0.2 (3.0–3.5)
ND	0.3 ± 0.1 (0.2–0.3)	0.3 ± 0.1 (0.3–0.4)	0.3 ± 0.1 (0.3–0.4)
IND	0.9 ± 0.1 (0.8–1.0)	1.4 ± 0.1 (1.1–1.5)	1.4 ± 0.1 (1.3–1.6)
ODW	2.6 ± 0.1 (2.4–2.8)	3.1 ± 0.1 (3.0–3.3)	3.2 ± 0.1 (3.00–3.3)
ODP	18.3 ± 2.4 (14.7–21.3)	18.6 ± 2.1 (15.1–22.1)	16.8 ± 4.2 (12.1–21.3)
DFIA	6.8 ± 1.0 (5.6–8.3)	7.1 ± 1.3 (5.5–9.0)	7.1 ± 1.7 (5.4–9.5)

well-marked lateral constrictions; depressed in lateral view, with ventral contour approximately straight from peribranchial region to abdomen (Fig. 1A–B). Snout semicircular in dorsal view (BWN/BWE = 0.70–0.75) and sloped in lateral view. Eyes 0.12–0.15 times BW, dorsally located (IOD/BWE = 0.40–0.49), dorsolaterally directed. Nostrils elliptical, dorsal, 0.02–0.03 times BL, located closer to snout than to eyes (NSD/ESD = 0.39–0.43), anterolaterally directed and with a continuous and elevated rim, without fleshy projection. Spiracle sinistral, lateroventral (SDH/BH = 0.18–0.24), posteriorly directed, 0.08–0.11 times BL, opening at the middle third of body (SSD/BL = 0.56–0.61); inner wall absent (Fig. 1A). Lateral line system indistinct. Intestinal switchback point located at the center of abdominal region (Fig. 1C). Vent tube

medial, ventrally directed, small, extensively broad, fused to ventral fin and positioned at its margin (Fig. 1C). Oral disc 0.37–0.40 times BW, ventral (ODP = 12.1–21.3°), laterally emarginated; a single row of alternated marginal papillae with a wide dorsal gap and narrow lateral gaps (at the emargination regions); submarginal papillae absent; labial tooth row formula (LTRF) 2(2)/3, A-1=A-2, P-1=P-2>P3; jaw sheaths narrow, finely serrated, with a distinct medial serration on the oral face of the upper jaw, which has elevated surface; upper jaw sheath arc-shaped and lower sheath “V”-shaped (Fig. 1D–E). Tail low (MTH/TAL = 0.16–0.20); musculature robust (TMH/BH = 0.56–0.63), not reaching the broad, rounded tail tip; dorsal fin approximately equal in height to ventral fin (DFH/VFH = 1.03–1.14). Dorsal fin height 0.05–0.08 times TAL,

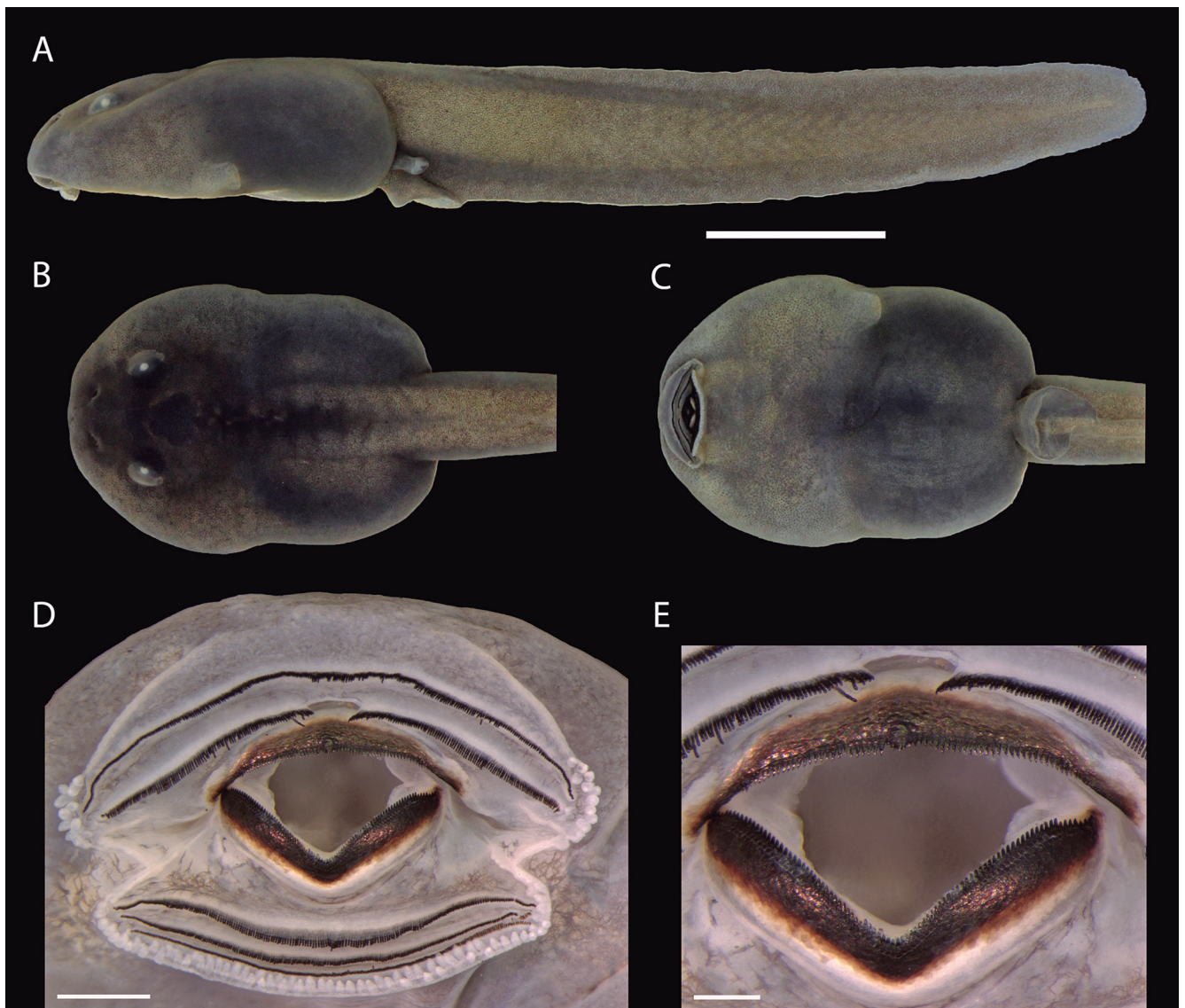


Figure 1. The tadpole of *Crossodactylodes itambe* (lot number: UFMG 1478) in stage 34 (Gosner, 1960). Body and tail shown in (A) lateral, (B) dorsal, and (C) ventral views (scale = 5.0 mm). (D) Oral disc (scale = 0.5 mm). (E) Detail of jaw sheaths showing the distinct medial serration on the oral face of the upper jaw (scale = 0.2 mm).

with slightly convex external margin; emerging on the anterior third of tail with a low slope ($DFiA = 5.4\text{--}9.5^\circ$); maximum height at the posterior third of tail. Ventral fin height 0.05–0.07 times TAL, with slightly convex external margin; originates at level of vent tube.

Coloration

In life, body uniformly dark brown with scattered melanophores; spiracle lightly pigmented; iris uniformly dark brown; caudal musculature light brown with numerous melanophores along its entire length. This pattern is also present on the fins, which are dark brown (Fig. 2A). In preservative, the color is similar to that in life but fades over time. Body and fins become grayish brown, tail musculature yellowish, spiracle whitish, and iris darker (Fig. 1A).

Morphological variation

There is little intrapopulational variation in shape and coloration. Two individuals, stages 34 and 35, have

truncated snouts in dorsal view. Two individuals, stages 30 and 33, have slightly rounded snouts in lateral view. Tadpoles showed some variation in the disposition and number of marginal papillae. Three individuals have small series of marginal papillae aligned posterolaterally and/or in the medial portion of posterior labium. Some have small biseriolate ($n = 2$), or triseriolate sections of marginal papillae posterolaterally ($n = 3$). These variations are apparently unrelated to ontogeny.

Natural history

Tadpoles of *Crossodactylodes itambe* were found exclusively in the rupicolous bromeliad *Vriesea medusa* Versieux, 2008, a species that is endemic to the southeastern part of the Espinhaço Mountain Range but is not restricted to the Itambé massif (Versieux et al., 2010). The bromeliads possess funnel-form rosettes, 55–80 cm diameter and approximately 70 cm high (Versieux, 2008), and usually occur in clusters of 2–5 rosettes in the study

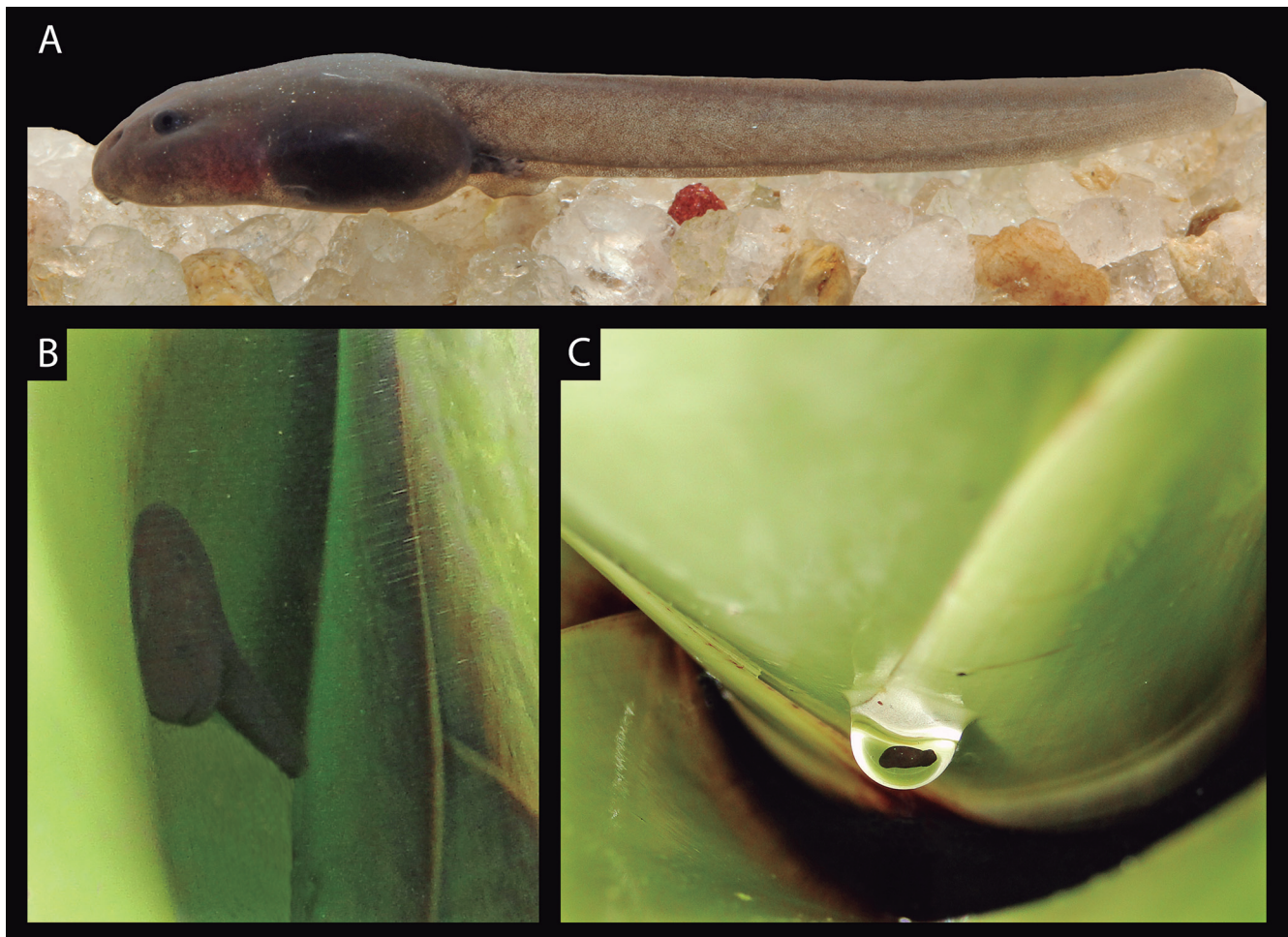


Figure 2. (A) A tadpole of *Crossodactylodes itambe* photographed in life. (B) The resting posture of *C. itambe* tadpole. (C) A single egg of *C. itambe* attached to the abaxial surface of a bromeliad leaf. (Photos: L.O. Drummond).

area. Tadpoles were found inside the axils of lateral leaves of bromeliads (Fig. 2B) where water is retained.

In February 2014, we recorded 34 tadpoles exclusively above 1,895 m, although adults were found at lower elevations. Most tadpoles were found above 1,969 m asl (22 individuals between 1,969–2,063 m asl and 12 individuals between 1,895–1,968 m asl). Surveys in February–May 2015 recorded 470 tadpoles (February, $n = 29$; March, $n = 81$; April, $n = 163$; May, $n = 197$), of which 13 were collected in the lowest elevational gradient, 166 in the mid-level gradient, and 291 at the highest gradient. The lowest elevation at which tadpoles were recorded was 1,769 m asl.

In most cases, more than one tadpole was recorded inside a given bromeliad (maximum of six individuals per bromeliad), but tadpoles never occupied the same leaf axil. Due to difficulties in sampling and observing tadpoles within their axil, we could not determine developmental stages of tadpoles within and between months. Although we conducted surveys during day and night, tadpoles were most easily observed at night. When tadpoles detected us handling or even shining a light on a bromeliad, they usually dove quickly to the bottom of the axils. The normal larval resting posture is with the snout pointing upward (Fig. 2B).

Eggs of *Crossodactylodes itambe* were found as single eggs attached to either the abaxial or adaxial surface of bromeliad leaves slightly above the surface of the water of the axil, positioned singly (Fig. 2C). Eggs are large and dark-pigmented; embryos are uniformly darkly pigmented and surrounded by two visible, tough jelly layers (an inner translucent layer and an outer opaque layer; Fig. 2C). In November 2012, we observed 13 eggs, including two in the same bromeliad but on different leaves, two at different development stages juxtaposed on the same leaf, and nine that were the only egg in the bromeliad. Of these nine eggs, four were found in a same bromeliad cluster, two in another cluster, and three were the sole occupants of their bromeliad cluster. On two occasions, we observed an adult male sitting alongside an egg; in both cases, the male dove quickly into the axil water while being photographed.

Aggregations of adults were found on the same bromeliad and/or cluster as eggs and tadpoles. Such groupings included: (1) one male and one female, six tadpoles and four eggs; (2) one male and one female, five tadpoles and two eggs; (3) one male and one female, four tadpoles and two eggs; (4) one male and one female, one juvenile, two tadpoles and one egg; (5) one male and one female, three juveniles and one tadpole; (6) one male and two females, one juvenile and one egg; (7) two males and two females and four tadpoles; (8) two females and two eggs and (9) one male and one egg. In addition to these groupings, we also recorded 12 observations of one male and one female occupying the same bromeliad with no tadpoles and/or eggs. Amplexant pairs were not observed.

The following species were syntopic with *Crossodactylodes itambe*: *Bokermannohyla alvarengai* (Bokermann, 1956), *Bokermannohyla nanuzae* (Bokermann and Sazima, 1973), *Bokermannohyla saxicola* (Bokermann, 1964), *Hypsiboas botumirim* Caramaschi, Cruz and Nascimento, 2009, *Scinax squalirostris* (Lutz, 1925), *Crossodactylus trachystomus* (Reinhardt and Lutken, 1862), *Rhinella rubescens* (Lutz, 1925), *Thoropa megatympanum* Caramaschii and Sazima, 1984, *Leptodactylus camaquara* Sazima and Bokermann, 1978 and *Physalaemus deimaticus* Sazima and Caramaschii, 1986. However, the only species occupying the same microhabitat as *C. itambe* in the study area (i.e., inside bromeliads) was *B. nanuzae*, but this species was not observed using bromeliads for breeding activity (no records of tadpoles, amplexus, or calling activity).

DISCUSSION

Larvae of *Crossodactylodes* correspond to tadpole Type IV (Orton, 1953), exotrophic, lentic, arboreal—a category that includes bromeligenous tadpoles (McDiarmid and Altig, 1999). The reproductive mode, consisting of eggs and exotrophic tadpoles in water in aerial plants, is reproductive mode 6 (Haddad and Prado, 2005). The only previous tadpole description for *Crossodactylodes* (Peixoto, 1981) cannot be reliably assigned to a single species (Peixoto, 1982). Consequently, the description of the tadpole of *C. itambe* represents the first of known species identity for this genus. The previously described tadpoles (Peixoto, 1981) share several morphological features with the tadpole of *C. itambe*, thereby strengthening the identification of those tadpoles to the generic level. These similarities are: depressed body with lateral constrictions; long tail with rounded tip; LTRF 2(2)/3; presence of narrow lateral gaps of marginal papillae; tail musculature not reaching the tail tip and presence of a distinct medial serration on the oral face of the upper jaw—the last two features were illustrated in Peixoto (1981).

Despite these similarities, the tadpole of *Crossodactylodes itambe* has some striking differences from the tadpole of *Crossodactylodes* sp., including total length 30.3–36.4 mm in *C. itambe* ($n = 10$, stages 30–35; 19 mm in *Crossodactylodes* sp.; $n = 1$, stage 35); dorsal fin emerging on the anterior third of tail (posterior third of body in *Crossodactylodes* sp.); tail musculature robust (narrow in *Crossodactylodes* sp.); spiracle position lateroventral (lateral in *Crossodactylodes* sp.); inner wall of spiracle absent (present in *Crossodactylodes* sp.); vent tube medial, ventrally directed and extensively broad (dextral, posteriorly directed and not broad in *Crossodactylodes* sp.). The last four features are seen in the illustration by Peixoto (1981).

The absence of the inner wall of the spiracle and the peculiar widening and direction of the vent tube are

features exclusive to *Crossodactylodes itambe* among described tadpoles of Leptodactylidae (e.g., Altig and McDiarmid, 1999b; Rossa-Feres and Nomura, 2006; Garcia et al., 2009; Juncá and Lugli, 2009; Kolenc et al., 2009; Provete et al., 2011). The narrow lateral gaps of marginal papillae and the distinct medial serration on the oral face of the upper jaw reported for *Crossodactylodes* sp. and *C. itambe* do not occur in any other described tadpole of Paratelmatobiinae (Cardoso and Haddad, 1990; Giaretta and Castanho, 1990; Pombal and Haddad, 1999; Garcia et al., 2009; Juncá and Lugli, 2009; Domenico et al., 2014) and are, therefore, putative synapomorphies for the genus.

Despite the same amount effort surveying bromeliads at lower elevational gradients, more tadpoles were recorded at higher gradients. Furthermore, few adults were found at lower elevations (i.e., from 1,713–1,841 m asl), but tadpoles were never recorded below 1,769 m asl. This suggests that the species preferentially breeds above 1,977 m. Since bromeliads can also be found at lower elevations (from 1,500 m asl; Versieux, 2008), the optimum area of distribution for *Crossodactylodes itambe* might be related to higher elevations, specifically microclimate and local ecological features, such as bromeliad density (which increases with elevation), which seems essential for species reproduction.

Tadpoles of *Crossodactylodes itambe* are easily found at night using flashlights but are rarely observed during the day. This might be due to their period of activity (which could occur mostly at night when they are expected to move closer to the surface of the water) or their dark coloration and the low luminosity inside bromeliads during the day (making it more difficult for them to be observed). The behavior we observed of tadpoles of *C. itambe* diving towards the bottom of bromeliad axils when disturbed has also been reported for other bromeligenous tadpoles, e.g., *Scinax perpusillus* group (Silva and Alves-Silva, 2008; Lacerda et al., 2012). The use of a collecting aspirator (Silva and Alves-Silva, 2008) allowed sampling of almost the entire contents of bromeliad axils, which made it easier to count individuals than using flashlights. This method enables sampling a greater number of individuals without damaging them or the bromeliads.

The resting posture of tadpoles of *Crossodactylodes itambe*, with the snout pointing upward (Fig. 2B), has also been reported for other arboreal-developing tadpoles (Perret, 1962; Lanoo et al., 1986). The water bodies of bromeliads usually have low levels of dissolved oxygen due to their heterotrophic metabolism (Guimaraes-Souza et al., 2006), which might force tadpoles to surface for oxygen uptake, which their resting posture could facilitate. The long tail with well-developed muscles and low fins may function as a static-postural organ, serving to position the body nearer to the water's surface (Lanoo et al., 1986). The lungs of these tadpoles may also facilitate this

behavior by providing buoyancy, whereas their low fins may minimize oxygen loss due to reduced cutaneous surface area (Lanoo et al., 1986).

The melanic pigmentation found in eggs of *Crossodactylodes itambe* usually occurs in species that inhabit open areas (Altig and McDiarmid, 2007) and probably offers protection from high exposure to solar radiation (Salthe and Duellman, 1973; Bastos et al., 2010). The low number of eggs found in proximity to each other within a bromeliad cluster (< 5) indicates that clutches of *C. itambe* contain just one, or perhaps a few, large isolated eggs. For many anuran assemblages, the number of eggs is negatively correlated with their diameter (Salthe, 1969; Crump, 1974; Hartmann et al., 2010), and species with more specialized reproductive modes usually lay fewer larger eggs (Hartmann et al., 2010). Other bromeliad-breeding species, such as species of *Phyllodytes* and the *Scinax perpusillus* group, lay a small number of eggs (Bokermann, 1966; Giaretta, 1996; Eterovick, 1999; Alves-Silva and Silva, 2009), a reproductive strategy that increases the chance of survival of each descendant. Lower tadpole density decreases competition for food and dissolved oxygen, and also decreases pollution of the small aquatic habitat with larval waste (Alves-Silva and Silva, 2009).

Other strategies adopted by other bromeligenous species to cope with limited resources and favour offspring survival include laying eggs with a large amount of yolk (Krugel and Richter, 1995; Peixoto, 1995; Duellman et al., 2011), or even laying unfertilized trophic eggs to provide food for tadpoles (oophagy; Lanoo et al., 1986; Weygoldt, 1987; Jungfer, 1996; Jungfer and Weygoldt, 1999; Lourenço-de-Moraes et al., 2013). According to Lanoo et al. (1986), this latter strategy is usually accompanied by a morphological adaptation in the number of tooth rows, which is usually reduced to 1/1 or less. The lack of this feature, and the low number of eggs reported for *Crossodactylodes itambe*, provide strong evidence that oophagy does not occur in this species. According to Peixoto (1981), tadpoles of *Crossodactylodes* sp. feed on organic detritus accumulated in the water of bromeliad axils. Based on internal oral features (e.g., reduction of the median ridge and presence of secretory ridges), Wassersug and Heyer (1988) suggested that they have features tending towards macrophagy, while characters related to suspension feeding are also present.

Parental investment in offspring survival in *Crossodactylodes* species might involve changes in ovipositional mode and behavior of adults (see Altig and McDiarmid, 2007). The occurrence of tadpoles of *Crossodactylodes itambe* individually in different axils suggest that adults might choose oviposition sites to decrease competition between tadpoles. Additionally, the occurrence of males near eggs might indicate that they are performing egg-guarding behavior. This may explain the hypertrophied forearms and the spines on the inner surface of the first

finger of males of *C. itambe* (Barata et al., 2013). These features may also be indicative of other intraspecific social interactions, such as breeding site defense. If species of *Crossodactylodes* do indeed perform parental care, it would be consistent with Crump (1996), who states that most anurans that exhibit this behavior are small and have small clutch sizes.

Species of Paratelmatobiinae exhibit a variety of reproductive strategies: *Crossodactylodes* species lay a low number of large eggs in bromeliads (Peixoto, 1995; Barata et al., 2013); *Rupirana* lays clutches with approximately 120 eggs in shallow backwaters or ponds (Juncá and Lugli, 2009); *Paratelmatobius cardosoi* and *P. yepiranga* lay ca. 20 eggs in muddy ponds (Pombal and Haddad, 1999; Garcia et al., 2009); *P. poecilogaster* lays a terrestrial egg mass adhered to humid rocks with approximately 5–13 eggs (Pombal and Haddad, 1999); and *Scythrophrys sawayae* lays clutches with approximately 30 eggs in small, shallow ponds with muddy bottoms formed by the backwaters of streams (Garcia, 1996). Based on this information, Fouquet et al. (2013) suggested that oviposition in bromeliads is a putative synapomorphy of *Crossodactylodes*, which is reinforced by the findings of the present study. In addition, despite the lack of information on the natural history of some species of *Crossodactylodes*, the low number of eggs reported for *C. itambe* and *Crossodactylodes* sp. relative to other Paratelmatobiinae might represent another putative synapomorphy for the genus. Denser sampling of this poorly known genus is needed in order to better understand the distribution of the morphological and natural history characters in *Crossodactylodes*.

ACKNOWLEDGMENTS

We are grateful to Dr. Erik Wild for critically reading the manuscript and two anonymous reviewers for their comments and suggestions that improved the manuscript; Rafael F. Magalhães, Stenio E. Vittorazzi and Luciana B. Lourenço for laboratory assistance. We thank the IEF-MG and the staff of Parque Estadual do Pico do Itambé, especially J.M. Ribeiro for logistical support. This study is part of M.S. Dissertation of MTTTS at Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. MTTTS is supported by a FAPEMIG scholarship. PCAG thanks CNPq for a research productivity fellowship. IMB is supported by PhD scholarships from CAPES, and was granted by MBZ Species Conservation Fund and The Rufford Foundation. We also thank PAN Herpetofauna do Espinhaço (on behalf of H. Bonfin ICMBio/RAN), FAPEMIG/VALE, Funarpeq VIII/2015, and FAPEMIG for financial support. Specimens were collected under collection permits n° 35198-3, IBAMA registration 85162664,

and IEF 108/12. T. Mota provided information about the bromeliads and P.C. Rocha, L.O. Drummond, F. Leal, E.P. Silva, and J.M. Ribeiro provided field assistance.

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