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The tadpoles of two species of the *Bokermannohyla circumdata* group (Hylidae, Cophomantini)

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Abstract

We describe the external morphology and oral cavity of the tadpoles of *Bokermannohyla caramaschii* and *B. diamantina* respectively from the states of Espírito Santo and Bahia, Brazil. Larvae of both species are distinguished from each other by external characters such as body shape, labial tooth-row formula, number of marginal papillae, coloration and internal oral anatomy features. Some of the character states of the tadpoles of *B. caramaschii* and *B. diamantina* that are shared with all other described tadpoles of the *Bokermannohyla circumdata* group, such as the absence/reduction of small flaps with accessory labial teeth laterally in the oral disc, and the absence/reduction of submarginal papillae, may represent morphological synapomorphies of this species group, or at least of some internal clade. The general pattern of brownish coloration with longitudinal stripes on the caudal muscle is also common to most species of the group. We did not find character states of the oral cavity that are exclusively shared by species of the *B. circumdata* group, or by other groups of *Bokermannohyla*.

Key words: Hylinae, *Bokermannohyla caramaschii*, *Bokermannohyla diamantina*, larval external morphology, oral cavity, lateral line system

Resumo

Descrevemos a morfologia externa e cavidade oral dos girinos de *B. caramaschii* e *B. diamantina*, respectivamente dos estados do Espírito Santo e Bahia, Brasil. As larvas de ambas as espécies são diferenciadas entre si por caracteres externos, como formato do corpo, fórmula de fileiras de dentículos labiais, número de papilas marginais, coloração e caracteres de anatomia oral interna. Alguns dos estados de caracteres dos girinos de *B. caramaschii* e *B. diamantina*, que são compartilhados com outros girinos do grupo de *B. circumdata* descritos, como ausência/redução das pequenas abas com dentículos acessórios e de papilas submarginais podem representar sinapomorfias morfológicas deste grupo de espécies, ou ao menos, de algum clado interno. O padrão de coloração dos girinos, amarronzado, com listras longitudinais na musculatura da cauda também é bastante comum na maioria das espécies do grupo. Não encontramos caracteres da cavidade oral exclusivamente compartilhados por espécies do grupo de *B. circumdata*, ou outros grupos de *Bokermannohyla*.

Palavras-chave: Hylinae, *Bokermannohyla caramaschii, Bokermannohyla diamantina*, morfologia larval externa, cavidade oral, sistema de linha lateral

Introduction

The hylid frog genus *Bokermannohyla* Faivovich, Haddad, Garcia, Frost, Campbell & Wheeler, 2005, occurs in the

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Brazilian Atlantic Forest, Cerrado, and Caatinga domains, and currently comprises 32 species (Frost 2015). Faivovich *et al*. (2005, 2009) recognized four species groups in the genus: the *B. circumdata*, *B. claresignata*, *B. martinsi*, and *B. pseudopseudis* groups. Eighteen species are recognized as belonging to the *B. circumdata* group, occurring from southern to northeastern Brazil and predominantly in the Atlantic Forest (Napoli & Juncá 2006; Napoli & Pimenta 2009; Carvalho *et al.* 2012). Some of these species are stream dwellers in forest physiognomies within the Cerrado and Caatinga domains (e.g. Caramaschi *et al.* 2001; Napoli & Juncá 2006; Carvalho *et al.* 2012).

The *Bokermannohyla circumdata* species group is supported mostly by molecular evidence, with simple transverse dark stripes (usually thin) on the posterior surfaces of the thighs being its only putative morphological synapomorphy (Faivovich *et al.* 2005). Other adult morphological characters, such as a single, large, sharp prepollex, males with hypertrophied forearms and brown dorsal surfaces (in life and preserved) have traditionally been recognized as diagnostic features of the group (Heyer 1985; Napoli & Juncá 2006; Napoli & Pimenta 2009), although they are clearly not synapomorphies within *Bokermannohyla* nor Cophomantini. So far, the monophyly of this group has been tested only with restricted taxonomic sampling, leaving the group in need of a more taxonomically comprehensive analysis.

In recent years, the taxonomic richness of *Bokermannohyla* (e.g. Leite *et al.* 2011, 2012; Brandão *et al.* 2012) and information on its biology (e.g. Carvalho *et al.* 2013; Pinheiro *et al.* 2014; Taucce *et al.* 2015) have increased significantly, yet there is no comprehensive treatment of its larval morphology and biology. Only 20 of the 32 species in the genus had their external morphology described; of these, 11 are species of the *B. circumdata* group (Table 2). Despite this reasonable percentage of described tadpoles (ca. 63%), many still lack accurate and complete descriptions of external morphology. Data on the internal anatomy of *Bokermannohyla* larvae are even more scarce, with musculoskeletal morphology remaining undescribed for even a single species, and the oral cavity having been described for only six (Table 3), three of which are in the *B. circumdata* group (D'Heursel & Haddad 2007; Mongin & Carvalho-e-Silva 2013).

Putative larval morphological synapomorphies in Cophomantini have already been suggested for different clades (Faivovich *et al*. 2005; D'Heursel & Haddad 2007; Sánchez 2010). Faivovich *et al*. (2005) suggested the ventral oral disc with complete marginal papillae as a possible larval synapomorphy for the tribe, with these states subsequently transforming in less inclusive groups within the clade. Other larval character states, such as the presence of anteromedial vacuites in the prenarial wall in the roof of the oral cavity, and fleshy projections of variable shape in the inner margin of the nares, also drew attention due their presence in many species of Cophomantini (see Faivovich *et al*. 2005; Kolenc *et al.* 2008; Sánchez 2010). Other putative larval synapomorphies were suggested for some genera and species groups, such as the saccular structure associated with the vent tube in *Hyloscirtus* (Sánchez 2010), complex lateral ridge papillae in *Bokermannohyla*, and an anteroposterior row or ridge in the prenarial arena of the buccal roof in the *B. pseudopseudis* species group (D'Heursel & Haddad 2007). These morphological traits and their evolutionary history are far from being completely understood, mainly due to gaps in the basic information available to date, and the absence of a comprehensive phylogenetic framework.

In this paper, we describe the external morphology and oral cavity of the tadpoles of *B. caramaschii* (Napoli, 2005) and *B. diamantina* Napoli & Juncá, 2006, from the Brazilian states of Espírito Santo and Bahia, respectively. We provide comparisons of these descriptions with the information available on larval morphology for the genus, aiming to provide additional data towards a better understanding of the taxonomic distribution of character states relevant for the study of the phylogenetic relationships of *Bokermannohyla* and Cophomantini.

Material and methods

Specimens are housed in the Tadpole Collection of the Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil. Tadpoles of *B. caramaschii* were collected at the Estação Biológica de Santa Lúcia (type locality; 40°32'16"W, 19°57'55"S, 643 m a.s.l, collected on October 10, 2012—UFMG 1418), and in a forest fragment located about 6 km to the north (40°33'08"W, 19°55'06"S, 831 m a.s.l, collected on November 1, 2012—UFMG 1425); both localities are in the Municipality of Santa Teresa, State of Espírito Santo, Brazil. Tadpoles of *B. diamantina* were collected at Serra do Itobira, Serra do Espinhaço, in the Municipality of Rio de Contas, about 12 km south of the type locality (41°52'53"W, 13°22'32"S, 1688 m a.s.l, collected on December 11,

2010—UFMG 1060), State of Bahia, Brazil. Adults of these species were the only anurans reproducing in the environments where the larvae were found. Furthermore, for both species, the presence in our samples of pre-metamorphic tadpoles already exhibiting the adult color pattern confirmed the species identity of the tadpoles. Tadpoles were killed in 5% lidocaine solution and preserved in 10% formalin.

For *B. caramaschii*, the description of the external morphology and proportions were based on five specimens in stages 35−38 (Gosner 1960; lot UFMG 1418a), and measurements were taken from 16 specimens in stages 29−39 (lots UFMG 1418a,b; UFMG 1425—Table 1). For *B. diamantina*, the description of the external morphology and proportions were based on five tadpoles in stages 36−38 (lot UFMG 1060a), and measurements were taken from 15 specimens in stages 29−38 (UFMG 1060a,b). Throughout the descriptions the ratios between measurements are expressed as ranges.

Measurements and terminology follow Altig & McDiarmid (1999) for total length (TL), body length (BL), tail length (TAL), maximum tail height (MTH), internarial distance (IND), interorbital distance (IOD), tail muscle width (TMW), and tail muscle height (TMH); Lavilla & Scrocchi (1986) for body width (BW), body width at narial level (BWN), body width at eye level (BWE), body height (BH), eye-snout distance (ESD), eye-nostril distance (END), nostril-snout distance (NSD), eye diameter (ED), narial diameter (ND), snout-spiracular distance (SSD), and oral disc width (ODW); Grosjean (2005) for dorsal fin height (DFH) and ventral fin height (VFH). Additional measurements taken were spiracle length (distance between the anterior insertion of the spiracle and its distal margin; SL), and spiracular-venter distance (perpendicular distance between the spiracle distal margin and the ventral surface of the tadpole; SVD). All measurements were taken to the nearest 0.1 mm with the aid of ImageTool version 3.00 (Wilcox *et al.* 1996). To obtain high quality photos we used an adjustable platform to support tadpoles immersed in water (Schacht & McBrayer 2009). Lateral line descriptions and terminology is that of Lannoo (1987).

Two specimens of *B. caramaschii* in stages 35−36 (lot UFMG 1418a), and three of *B. diamantina* in stage 35 (lot UFMG 1060a) were dissected for examination of internal morphology. One individual per species was prepared for scanning electron microscopy (SEM), observed and photographed with a Quanta 200 microscope at Centro de Microscopia da UFMG, Universidade Federal de Minas Gerais. Terminology of oral cavity morphology follows Wassersug (1976). For detailed morphological examination the oral disc, spiracle, narial opening, vent tube, lateral line system, and buccopharyngeal cavities were stained with methylene blue and analyzed using multifocal photographs, which were taken with a Leica M205 stereomicroscope.

Data on morphology of known tadpoles of *Bokermannohyla* were obtained from their original descriptions (Table 2). Characters were reinterpreted to facilitate appropriate comparisons, thus avoiding differences due to methods and terminology. Comparisons related to measurements and proportions from literature were made with caution, because researchers used different methods with varying degrees of accuracy.

Data on tadpoles of *B. alvarengai*, *B. nanuzae,* and *B. saxicola* were also obtained from specimens in the UFMG Tadpole Collection (Lots UFMG 160, 1106, 516, and 229, respectively; details listed in Appendix). Walker *et al*. (2015) recently analyzed tadpoles, vocalizations and adult morphology of *B*. *feioi* (Napoli & Caramaschi 2004) and *B. nanuzae* (Bokermann & Sazima 1973), concluding that the former is a junior synonym of the latter, due to the absence of diagnostic characters. Our comparisons include the distinct populations of *B. nanuzae* (i.e., Serra do Cipó and Serra do Ibitipoca).

Results

Bokermannohyla caramaschii

External morphology. Maximum total length 48.9 mm (at stage 37; Table 1). **Body** depressed (BH/BW = 0.84–0.91), ovoid, or elliptical in dorsal view, 0.29–0.32 times TL; in lateral view, ventral contour slightly convex from peribranchial region to abdomen (Fig. 1A, B). **Snout** rounded in dorsal (BWN/BWE = 0.78–0.82) and lateral views. **Eyes** medium-sized (ED/BWE = 0.19–0.23), dorsally located (IOD/BWE = 0.63–0.73), dorsolaterally directed. **Nostrils** elliptical, medium-sized (ND/BL= 0.029–0.036), dorsally located, dorsolaterally directed, distance to snout 48–52% of eye-snout distance; elevated marginal rim, with well-developed trapezoidal to triangular fleshy projection on the medial margin, irregularly scalloped on lateral margin (Fig. 1E, F). **Spiracle** sinistral, lateral (SVD/BH = 0.46–0.62), posterodorsally directed, short (SL/BL = 0.04–0.07), opening at the

TABLE 1. Measurements (in mm) of tadpoles of *Bokermannohyla caramaschii* from Santa Teresa, State of Espírito Santo (UFMG 1418, 1425), and *Bokermannohyla diamantina* from Rio de Contas, State of Bahia (UFMG 1060), for some groups of Gosner (1960) stages. Data presented as mean ± standard deviation (range). For abbreviations, see text.

	Bokermannohyla caramaschii				*Bokermannohyla diamantina*		
Lot	UFMG 1418			UFMG 1425	UFMG 1060		
Stage (n)	29–33 (6)	35–38 (5)	39 (2)	30–35 (3)	27–30 (5)	33–35 (5)	36–38 (5)
TL	39.3 ± 0.8 (38.4–40)	45.4±2.8 (41.2–48.9)	(47.7–48.4)	46.5±2.2 (44.7–48.9)	41.8±3.0 (37.9–44.9)	43.3±1.3 (41.5–44.9)	43.8±1.3 (42.5–46.1)
BL	13.1±0.3 (12.8–13.6)	13.8±0.9 (12.7–15.1)	(13.4–15.6)	14.3±0.9 (13.6–15.3)	12.9±0.4 (12.4–13.6)	13.3±0.9 (11.6–13.9)	13.8±0.2 (13.4–14.1)
TAL	26.2±1.1 (24.8–27)	31.6±2.1 (28.0–34.2)	(32.7–34.2)	32.2±1.3 (31.1–33.7)	28.9±2.9 (25.2–32.5)	29.9±1.0 (28.8–31.2)	30.0±1.2 (28.8–32.1)
MTH	7.3±0.6 (6.5–8.1)	8.2±0.4 (7.9–8.9)	(8.3–8.6)	8.7±0.8 (7.9–9.5)	8.6±0.4 (8.2–9.3)	8.2±0.1 (8.0–8.5)	8.5±0.5 (7.8–9.4)
DFH	2.4±0.1 (2.3–2.5)	2.6±0.2 (2.3–2.3)	(2.3–2.6)	2.7±0.2 (2.4–2.8)	2.9±0.2 (2.6–3.1)	2.7±0.2 (2.5–3.0)	2.7±0.2 (2.4–3.0)
VFH	1.9±0.1 (1.8–2.1)	2.2±0.1 (2.0–2.4)	(1.9–2.1)	2.2±0.1 (2.0–2.3)	2.2±0.1 (2.0–2.4)	2.2±0.1 (2.0–2.4)	2.2±0.2 (2.0–2.6)
TMH	3.9±0.2 (3.7–4.2)	4.3±0.2 (4.0–4.5)	(4.5–4.5)	4.8±0.6 (4.2–5.4)	4.3±0.2 (4.0–4.6)	4.1±0.1 (3.9–4.3)	4.3±0.2 (4.1–4.6)
BH	6.8±0.3 (6.4–7.1)	7.3±0.7 (6.5–8.3)	(6.5–7.7)	7.9±0.6 (7.2–8.5)	7.5±0.6 (6.5–8.1)	7.7±0.6 (6.6–8.3)	7.7±0.5 (6.7–8.2)
SL	0.9±0.1 (0.8–1)	0.8±0.1 (0.6–0.9)	(0.7–0.9)	1.0±0.1 (0.9–1.0)	0.8±0.1 (0.7–1.0)	0.7±0.1 (0.7–0.9)	0.8±0.1 (0.7–1.0)
SVD	3.7±0.4 (3.2–4.3)	4.3±0.5 (3.8–5.0)	(4.1–4.2)	4.5±0.4 (4.1–4.9)	4.0±0.4 (3.7–4.5)	4.3±0.6 (3.7–5.2)	4.2±0.5 (3.5–5.0)
SSD	7.8±0.5 (7.3–9)	8.0±0.5 (7.3–8.8)	(6.6–9.6)	9.0±0.6 (8.3–9.4)	7.8±0.4 (7.2–8.4)	7.7±0.4 (7.0–8.1)	8.0±0.5 (7.3–8.8)
ED	1.2±0.1 (1.1–1.3)	1.4±0.1 (1.3–1.6)	(1.4–1.8)	1.3±0.2 (1.2–1.6)	1.2±0.1 (1.1–1.3)	1.2±0.1 (1.1–1.4)	1.5±0.0 (1.4–1.5)
BW	7.8±0.2 (7.6–8)	8.5±0.9 (7.2–9.9)	(8.6–9.4)	9.2±0.8 (8.6–10.1)	9.6±0.9 (8.2–10.5)	10.0±0.7 (8.5–10.5)	10.2±0.6 (9.0–10.7)
BWN	4.9±0.2 (4.7–5.1)	5.3±0.4 (4.8–5.6)	(5.0–5.0)	5.5±0.7 (4.8–6.3)	5.0±0.2 (4.7–5.3)	4.9±0.3 (4.7–5.4)	5.2±0.1 (5.0–5.4)
BWE	6.2±0.1 (6.1–6.3)	6.6±0.4 (6.1–7.2)	(6.6–6.9)	7.0±0.6 (6.5–7.7)	6.5±0.3 (6.2–7.0)	6.5±0.2 (6.3–6.7)	6.8±0.3 (6.5–7.2)
TMW	3.5±0.2 (3.2–3.7)	3.8±0.2 (3.6–4.1)	(4.3–6.6)	3.9±0.3 (3.6–4.2)	4.1±0.2 (3.8–4.3)	3.9±0.2 (3.7–4.1)	4.2±0.2 (4.0–4.5)
END	1.8±0.1 (1.7–2.0)	2.0±0.1 (1.8–2.2)	(2.0–2.1)	2.0±0.1 (1.9–2.1)	1.9±0.1 (1.9–2.1)	2.0±0.1 (1.8–2.1)	2.2±0.1 (2.1–2.4)
ESD	3.8±0.0 (3.8–3.8)	3.9±0.3 (3.7–4.4)	(3.4–4.0)	4.0±0.2 (3.8–4.2)	3.9±0.1 (3.8–4.1)	3.9±0.2 (3.6–4.2)	4.3±0.1 (4.1–4.4)
NSD	2.0±0.1 (1.9–2.0)	2.0±0.2 (1.8–2.2)	(1.4–1.9)	2.0±0.1 (1.9–2.1)	1.9±0.1 (1.9–2.1)	2.0±0.2 (1.8–2.2)	2.0±0.1 (2.0–2.2)
ND	0.5±0.0 (0.5–0.5)	0.4±0.0 (0.4–0.5)	(0.4–0.4)	0.4±0.0 (0.4–0.4)	0.4±0.0 (0.4–0.5)	0.42±0.0 (0.3–0.5)	0.4±0.0 (0.3–0.5)
IND	2.4±0.1 (2.2–2.6)	2.6±0.1 (2.4–2.8)	(2.5–2.7)	2.8±0.1 (2.7–2.9)	2.6±0.1 (2.5–2.9)	2.7±0.0 (2.7–2.8)	2.7±0.1 (2.6–2.8)
IOD	4.2±0.1 (4–4.3)	4.4±0.2 (4.0–4.8)	(4.3–4.8)	4.6±0.4 (4.4–5.0)	4.4±0.2 (4.2–4.6)	4.4±0.1 (4.3–4.6)	4.8±0.1 (4.7–4.8)
ODW	2.6±0.2 (2.5–2.9)	2.9±0.1 (2.7–3.1)	(2.7–3.0)	2.8±0.2 (2.6–3.1)	2.8±0.1 (2.6–2.9)	2.9±0.2 (2.6–3.1)	2.9±0.2 (2.7–3.2)

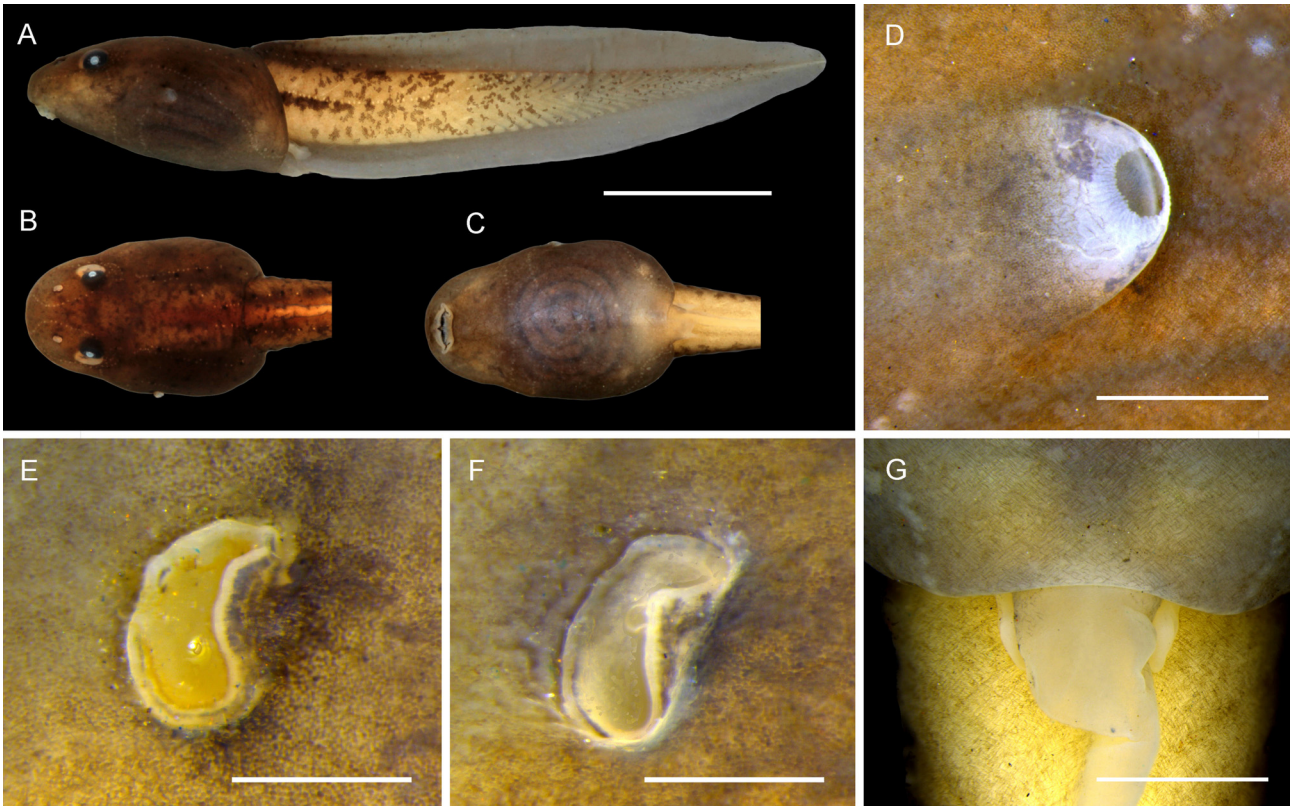

FIGURE 1. *Bokermannohyla caramaschii* (UFMG 1418) at stage 35: (A) lateral, (B) dorsal, and (C) ventral views. Scale bar = 10 mm. Details of (D) spiracular aperture, (E, F) margin of right nostrils with trapezoidal and triangular fleshy projections, respectively. Scale bars = 0.5 mm. (G) vent tube. Scale bar = 2 mm.

middle third of the body (SSD/BL = 0.52–0.61); internal wall fused to the body, with distal portion free and longer than the external wall (Fig. 1D). **Intestinal tube** circularly coiled, switchback point located at center of abdominal region (Fig. 1C). **Vent tube** dextral, posteriorly directed, twice as long as wide (Fig. 1G), fused to the ventral fin and positioned at its ventral margin. **Oral disc** medium-sized (ODW/BW = 0.30–0.38), ventrally positioned, with three posterior emarginations (Fig. 2); 169–178 conical marginal papillae arranged in a single row, with its bases offset throughout the oral disc; narrow anterior gap present (about 0.17 of ODW); submarginal papillae absent; labial tooth row formula (LTRF) 2(2)/4(1), A2>A1, P1=P2>P3>P4; gaps in A-2 and P-1 about 0.2 and 0.08 mm, respectively; tooth density on P1 40–48 teeth/mm; absence of flaps with labial teeth laterally in the oral disc; jaw-sheaths wide, pigmented, finely serrated on the margins (22 to 28 triangular serrations on the upper jaw), upper jaw sheath arc-shaped and lower jaw sheath V-shaped, upper wider than lower. **Tail** low (MTH/TAL = 0.24–0.28); musculature robust (TMH/BH = 0.54–0.62); dorsal fin higher than ventral fin (DFH/VFH = 1.08–1.28); tail tip acute. Dorsal fin low (DFH/TAL = 0.07–0.09) with a slightly convex external margin; emerging at posterior third of the body with a low slope; maximum height at posterior third of tail. Ventral fin low (VFH/TAL = 0.06–0.07), with the external margin almost parallel to the longitudinal axis of the tail musculature; originates at base of tail, concealed by vent tube. **Lateral line system** distinct in life and in preserved specimens (Figs. 3, 4). All lines with transversally oriented stitches composed of two or three neuromasts. Supraorbital line with 15–16 stitches converging anteriorly on head, medial to nares, approaching the infraorbital series of 14–18 stitches. Infraorbital line begins behind eyes, extends anteriorly and is slightly curved in lateral profile (Fig. 3A, B). Posterior infraorbital line consists of a small aggregate series of five to seven stitches with no clear organization. Posterior supraorbital line composed of five stitches located near posterior portion of the supraorbital line. Angular line with 20–25 stitches, extends from below eyes to venter (Fig. 3A). Anterior oral line with 12–15 stitches, extends from lateral region of oral disc and approaches region of angular line, ventrally. Longitudinal oral line with 7–8 stitches, located between anterior region of anterior oral line and angular line**.** Two series of lines extend from mid body posteriorly throughout tail length (Fig. 3B): the first, dorsal line, with 13–15 stitches, located medially, converging before body-tail junction and continuing posteriorly with 22–27 stitches along dorsal fin base, until end of tail (Fig.

3C); the second, middle-body line, with 20–22 stitches located laterally, joins the middle caudal series with 34–40 stitches. Along the approximate first third of tail this middle series projects dorsally reaching the dorsal fin base. A ventral body-line of 40–50 stitches extends anterodorsally from near vent tube forming a semicircle around spiracle, and after a small gap without neuromasts continues posteroventrally until mid abdominal region. A cumulus of neuromasts is present anterolateral to base of vent tube, near ventral line (Fig. 3D).

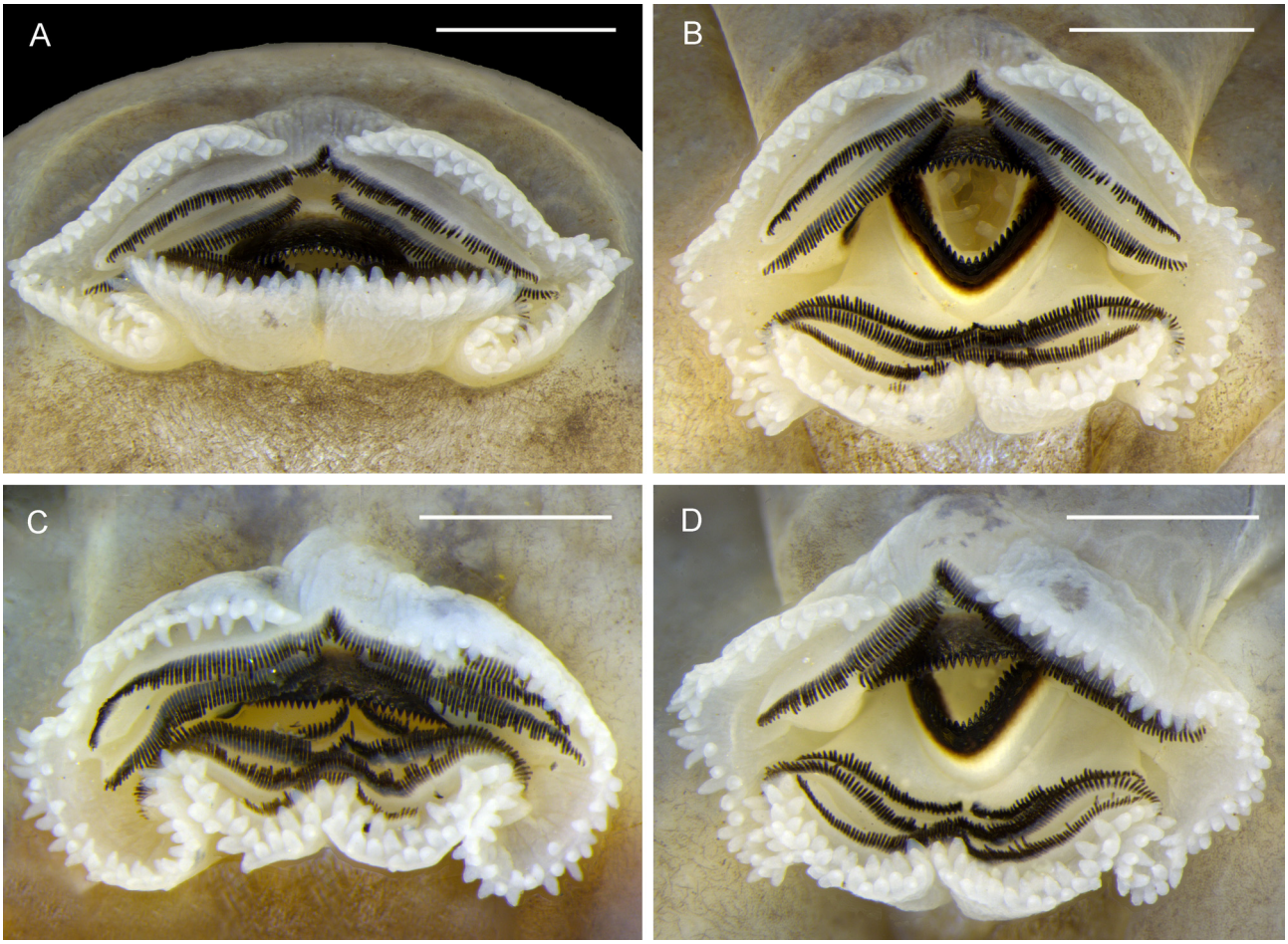

FIGURE 2. Oral discs of *Bokermannohyla caramaschii* (UFMG 1418): a closed (A) and opened (B) typical oral disc of a specimen at stage 37. Note the three posterior emarginations and the reduced P4. (C) Unusual presence of flap with labial teeth anteriorly to A1 in a specimen at stage 34. (D) The less common LTRF 2(2)/3(1) of an individual at stage 29. Scale bars = 1 mm.

Coloration. In life, general pattern reddish to dark brown (Fig. 4A). Body with regularly scattered black spots; distal margin of spiracle lightly pigmented; iris reddish with irregularly scattered golden dots. Tail musculature finely reticulated with melanophores, and with irregular and dispersed dark spots, mainly on its anterior half; a longitudinal dark stripe starting from posterior end of body and extending posteriorly along medial caudal muscle line for first anterior 1/4 of tail; dorsal margin of caudal musculature with an interrupted narrow brown line; dorsal and ventral fins translucent, with irregularly scattered spots mainly on the dorsal fin. Neuromasts golden. In metamorphosing specimens, limbs light brown, with orange spots (Fig. 4B). In 10% formalin, the coloration fades and looses golden dots. Iris looses its golden tones and becomes black.

Variation. Two specimens in stages 29 and 33 have few submarginal papillae (1–2) randomly distributed laterally in the oral disc. Two individuals in stage 39, and one in stage 29, have LTRF 2(2)/3(1) (Fig. 2D). A specimen at stage 34 has a flap of labial teeth anterior to A1 (Fig. 2C). Three specimens have dorsal and ventral fins of the same height. The shape of the fleshy projections on the medial and lateral nostril margins is variable, even within the same specimen (i.e., right/left nostrils). There is no clear pattern of ontogenetic change in these characters.

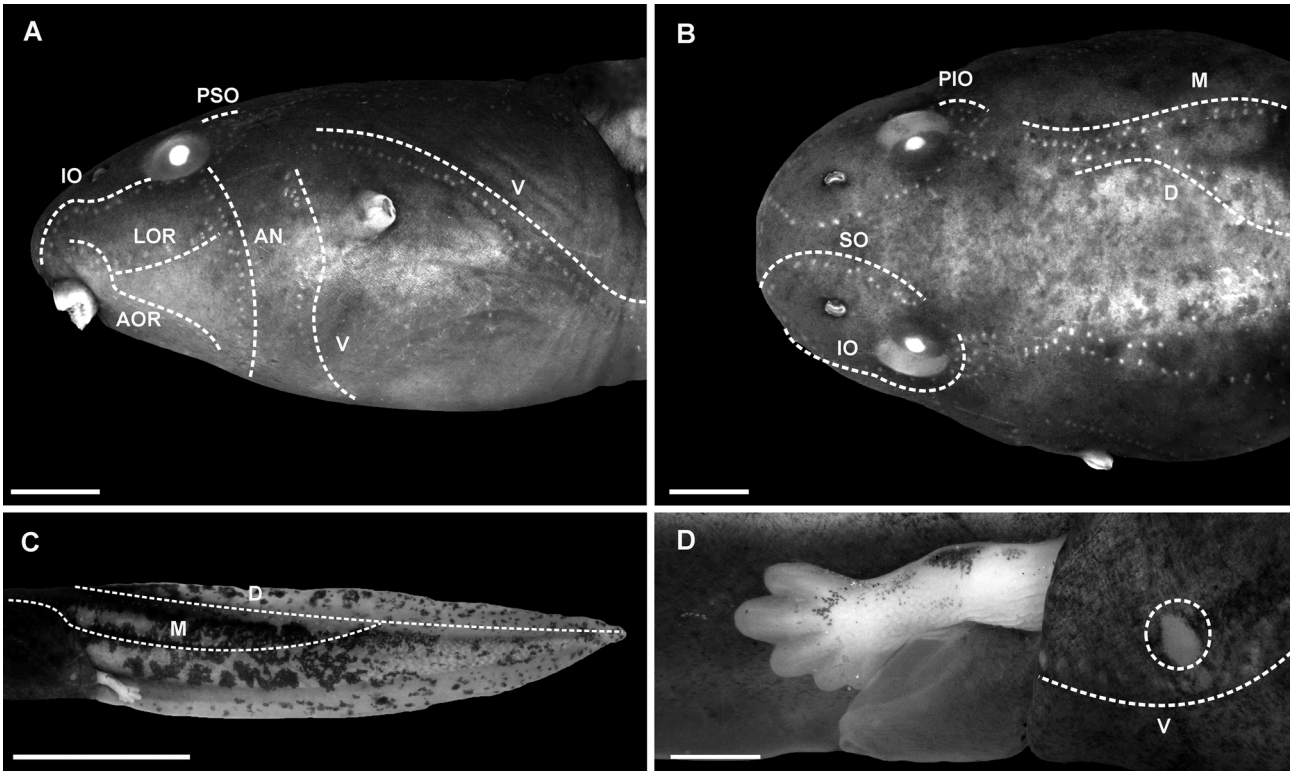

FIGURE 3. The lateral line system of *Bokermannohyla caramaschii* (UFMG 1418) in a stage 36 specimen. (A) Lateral view of body indicating the angular (AN), infraorbital (IO), longitudinal oral (LOR), anterior oral (AOR), posterior supraorbital (PSO), and ventral (V) lines. (B) Dorsal view of body showing the supraorbital (SO), infraorbital (IO), posterior infraorbital (PIO), middle (M), and dorsal (D) lines. Scale bars = 2 mm. (C) Detail of the tail and the distribution of the dorsal (D) and middle (M) lines. Scale bar = 10 mm. (D) Detail of the vent tube region of body showing the ventral line of neuromasts (V) and, encircled, the associated ventrolateral cumulus of neuromasts (N). Scale bar = 1 mm.

Natural history notes. *Bokermannohyla caramaschii* tadpoles were found on the bottom of shallow, slow-flowing muddy swamps associated with backwaters of permanent streams surrounded by semi-deciduous forests. The tadpoles are benthic and more active at night, when they can be found foraging among the sediment. Tadpoles in several developmental stages (including early stages) and froglets (Fig. 4B) were found in the same type of environment at both localities.

Oral cavity morphology. Buccal roof—roof sub-triangular, about 1.2 times longer than wide (Fig. 5A). One to three prenarial arena papillae with undulated margins disposed as transversal ridge along prenarial arena midline. Maximal internal nares length about 33% of Buccal Roof Width (BRW); internarial distance about 8% of BRW. Nares oriented 45° from midline; anterior wall short and thick with irregular margin; posterior wall (narial valves) large, wide and with distinct papillae; narial valves extending forward, covering almost completely the internal nares, but only a small portion of the vacuities. Large elliptical, smoothly concave, and shallow vacuities attached anteromedially to internal nares. Postnarial arena with one or two pairs of papillae distributed in an inverted V-shape, with posterior and external papillae larger than those more anterior and medial; three to five randomly distributed pustulations present. Median ridge trapezoidal to triangular with six to seven blunt, short papillae on anterior surface. One pair of medium-sized lateral ridge papillae with three to four secondary projections. Buccal Roof Arena (BRA) hexagonal with 7–14 short buccal roof arena papillae distributed mainly posterolaterally. In addition, 6–10 digitiform lateral roof papillae on each side. BRA with 288–310 homogeneously distributed pustulations. Secretory pits distinct in glandular zone, mainly posterolaterally in the dorsal velum. Dorsal velum large, discontinuous at midline (gap corresponding to 41% of BRW); irregular, discrete marginal papillae present. **Buccal Floor**—floor triangular, 1.2 times wider than long (Fig. 5B). Three pairs of infralabial papillae; two large hand-like papillae located anteriorly, and one pair of short digitiform papillae posteriorly. Some pustulations present antero-laterally. One pair of tall, digitiform lingual papillae present. Buccal Floor Arena (BFA) triangular, surrounded by 49–52 long, digitiform papillae. These papillae are disposed in two rows, one medially

from anterior region of buccal pockets to median region of BFA, and one extending laterally and more obliquely following the anterior margin of ventral velum, towards the posterior region of BFA; larger papillae located anteriorly; two or three large papillae bifurcated. BFA with 197–210 pustulations, more concentrated posteriorly. Buccal pockets about 6 times wider than high, transversally oriented, deep, its width about 33% of Buccal Floor Width (BFW). Five or six short, conical prepocket papillae on each side. Ventral velum height about 31% of BFW. Posterior margin scalloped, with six distinct peaks over filter cavities; peaks 6% of BFW; median notch depth about 9% of BFW. Secretory pits distinct when stained with methylene blue, more concentrated on posterior margin of ventral velum but absent on median notch region. Glottis large, 20% visible, width about 10% of the BFW; thick and broad lips.

FIGURE 4. A tadpole at stage 37 (A) and a froglet (B) of *Bokermannohyla caramaschii* in life (UFMG 1418).

Bokermannohyla diamantina

External morphology. Maximum total length 46.1 mm (at stage 37; Table 1). **Body** depressed (BH/BW = 0.73–0.77), ovoid in dorsal view, 0.31–0.32 times TL; in lateral view, ventral contour flat in peribranchial region and convex in abdominal region (Fig. 6A, B). **Snout** rounded in dorsal (BWN/BWE = 0.72–0.79) and lateral views. **Eyes** medium-sized (ED/BWE = 0.21–0.22), dorsally located (IOD/BWE = 0.68–0.71), dorsolaterally directed. **Nostrils** elliptical, medium-sized (ND/BL= 0.025–0.036), dorsally located, dorsolaterally directed, distance to snout 47–52% eye-snout distance; elevated marginal rim, with well-developed triangular or small round fleshy projection on the medial margin, irregularly scalloped on lateral margin (Fig. 6E, F). **Spiracle** sinistral, lateral (SVD/BH = 0.47–0.65), posterodorsally directed, short (SL/BL = 0.05–0.07), opening at the middle third of the body (SSD/BL = 0.52–0.60); internal wall fused to the body, with distal portion free and longer than the external wall (Fig. 6D).

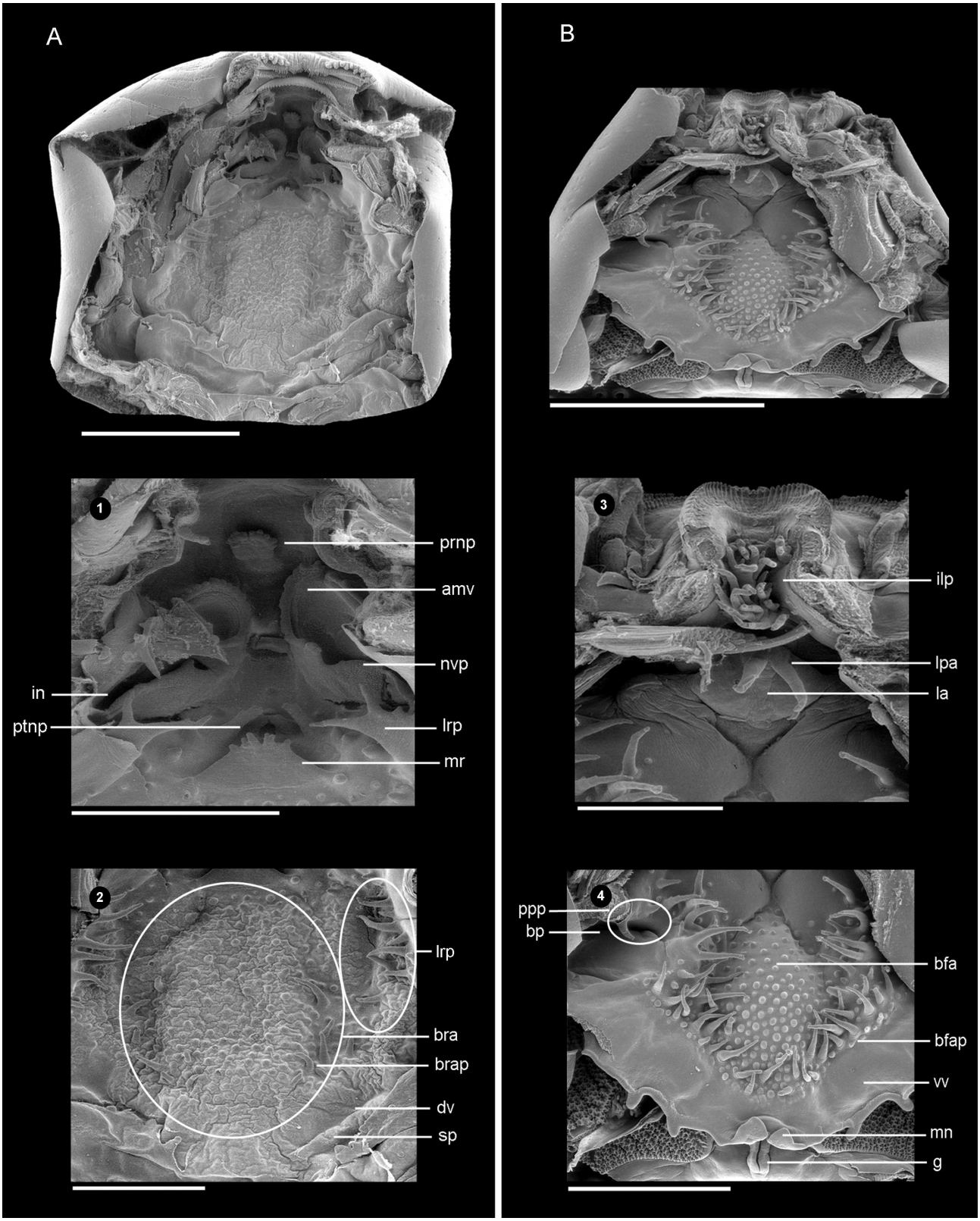

FIGURE 5. SEM micrographs of oral roof (A) and floor (B) of *Bokermannohyla caramaschii* at stage 37 (UFMG 1418). Scale bars = 2 mm. (1) Detail of the anterior region of roof: prenarial arena papillae (prnp); anteromedial vacuity of internal nares (amv); internal nares (in); narial valve projection (nvp); lateral ridge papilla (lrp); median ridge (mr); postnarial papillae (ptnp). (2) Detail of the posterior region of roof: lateral roof papillae (lrp); buccal roof arena (bra); buccal roof arena papillae (brap); dorsal velum (dv); secretory pits (sp). (3) Detail of the anterior region of floor: infralabial papillae (ilp); lingual papillae (lpa); lingual anlage (la). (4) Detail of the posterior region of floor: buccal floor arena (bfa); buccal floor arena papillae (bfap); buccal pocket (bp); prepocket papillae (ppp); vv (ventral velum); median notch (mn); glottis (g). Scale bars = 1 mm.

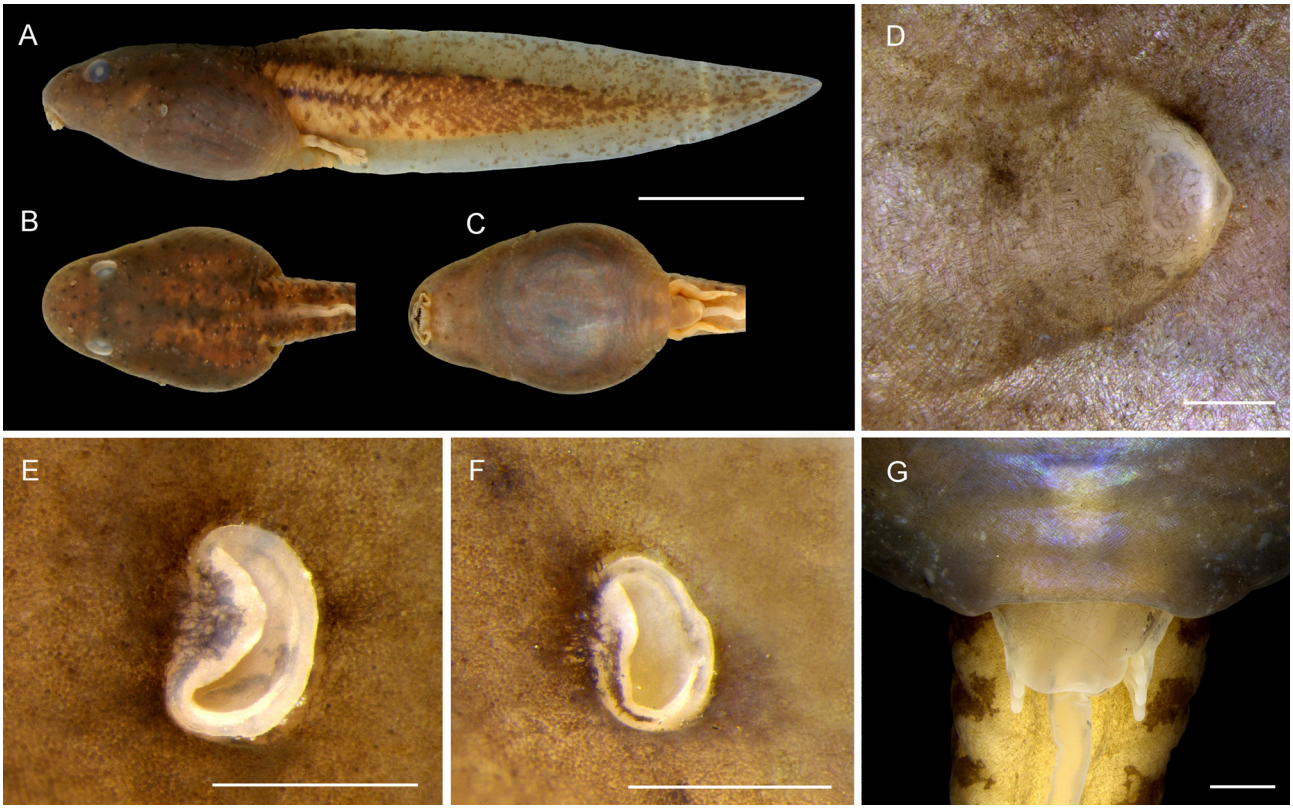

FIGURE 6. *Bokermannohyla diamantina* (UFMG 1060) at stage 37: (A) lateral, (B) dorsal, and (C) ventral views. Scale bar = 10 mm. Details of (D) spiracular aperture, (E, F) margin of left nostril with well-developed triangular and small round fleshy projections, respectively. Scale bars = 0.5 mm. (G) Vent tube of a specimen at stage 35. Scale bar = 1 mm.

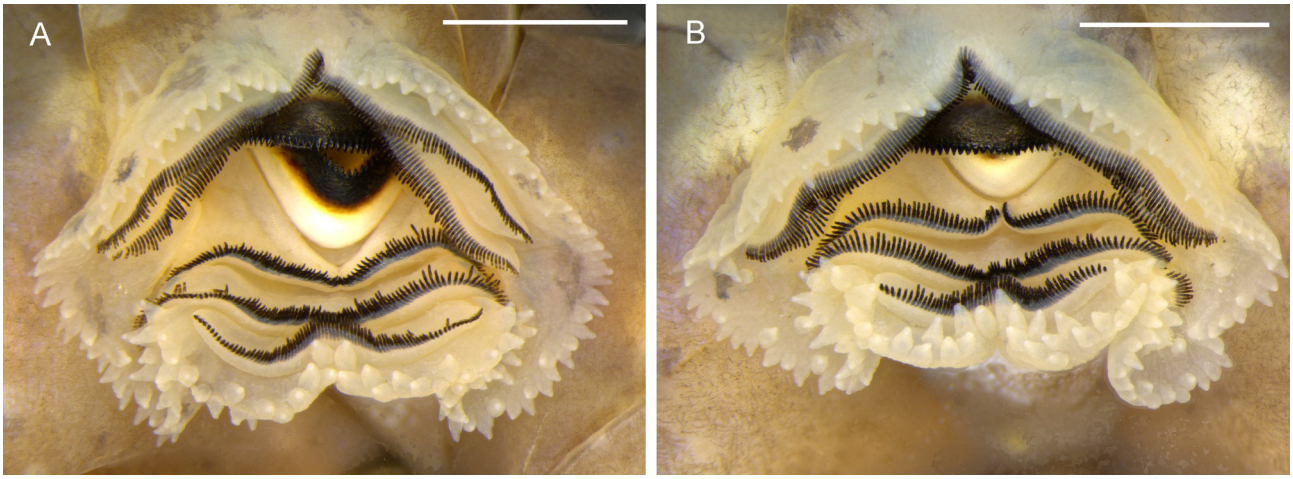

FIGURE 7. Oral disc of *Bokermannohyla diamantina* (UFMG 1060): (A) a typical oral disc of a specimen at stage 37. (B) Presence of few submarginal papillae laterally in the oral disc of a specimen at stage 36. Scale bars = 1 mm.

Intestinal tube circularly coiled, switchback point located at center of abdominal region (Fig. 6C). **Vent tube** dextral, posteriorly directed, slightly wider than long (Fig. 6G), fused to the ventral fin and positioned at its ventral margin. **Oral disc** medium-sized (ODW/BW = 0.25–0.30), ventrally positioned, with three posterior emarginations (Fig. 7); 130-138 conical marginal papillae arranged in a single row, with its bases offset throughout the oral disc; narrow anterior gap present (about 0.15 of ODW); submarginal papillae absent; LTRF 2(2)/3(1), A2=A1, P1=P2>P3; gaps in A-2 and P-1 about 0.3 and 0.02 mm, respectively; tooth density on P1 37–44 teeth/mm; absence of flaps with labial teeth laterally in the oral disc; jaw-sheaths wide, pigmented, finely serrated on the margins (20 to 24 triangular serrations on the upper jaw), upper jaw-sheath arc-shaped and lower jaw sheath V-

shaped, upper wider than lower. **Tail** low (MTH/TAL = 0.27–0.30); musculature robust (TMH/BH = 0.51–0.58); dorsal fin higher than ventral fin (DFH/VFH = 1.26–1.36); tail tip acute. Dorsal fin low (DFH/TAL = 0.09–0.10), with a slightly convex external margin; emerging at posterior third of the body with a low slope; maximum height at posterior third of tail. Ventral fin low (VFH/TAL = 0.07–0.08), with the external margin almost parallel to the longitudinal axis of the tail musculature; originates at base of tail, concealed by vent tube. **Lateral line system** distinct in preserved specimens (Fig. 8). All lines with transversally oriented stitches composed of two or three neuromasts. Supraorbital line with 14–17 stitches converging anteriorly on head, medial to nares, approaching the infraorbital series of 12–14 stitches. Infraorbital line begins behind eyes, extends anteriorly and is slightly curved in lateral profile (Fig. 8A, B). Posterior infraorbital line consists of a small aggregate series of seven to nine stitches with no clear organization. Posterior supraorbital line composed of three stitches located near posterior portion of the supraorbital line. Angular line with 16–20 stitches, extends from below eyes to venter (Fig. 8A). Anterior oral line with 11–12 stitches, extends from lateral region of oral disc and approaches region of angular line, ventrally. Longitudinal oral line with 7–8 stitches, located between anterior region of anterior oral line and angular line. Two series of lines extend from the mid body posteriorly throughout tail length (Fig. 8B): the first, dorsal line, with 16–18 stitches, located medially, converging abruptly before body-tail junction and continuing posteriorly with 10–18 stitches along dorsal fin base, until end of tail (Fig. 8C); the second, middle-body line, with 18–21 stitches located laterally, joins the middle caudal series with 38–40 stitches. Along the approximate first third of tail this middle series projects dorsally reaching the dorsal fin base. A ventral body-line of 45–48 stitches extends anterodorsally from near vent tube forming a semicircle around the spiracle, and after a small gap without neuromasts continues posteroventrally until mid abdominal region. A cumulus of neuromasts is present anterolateral to base of vent tube, near ventral line (Fig. 8D).

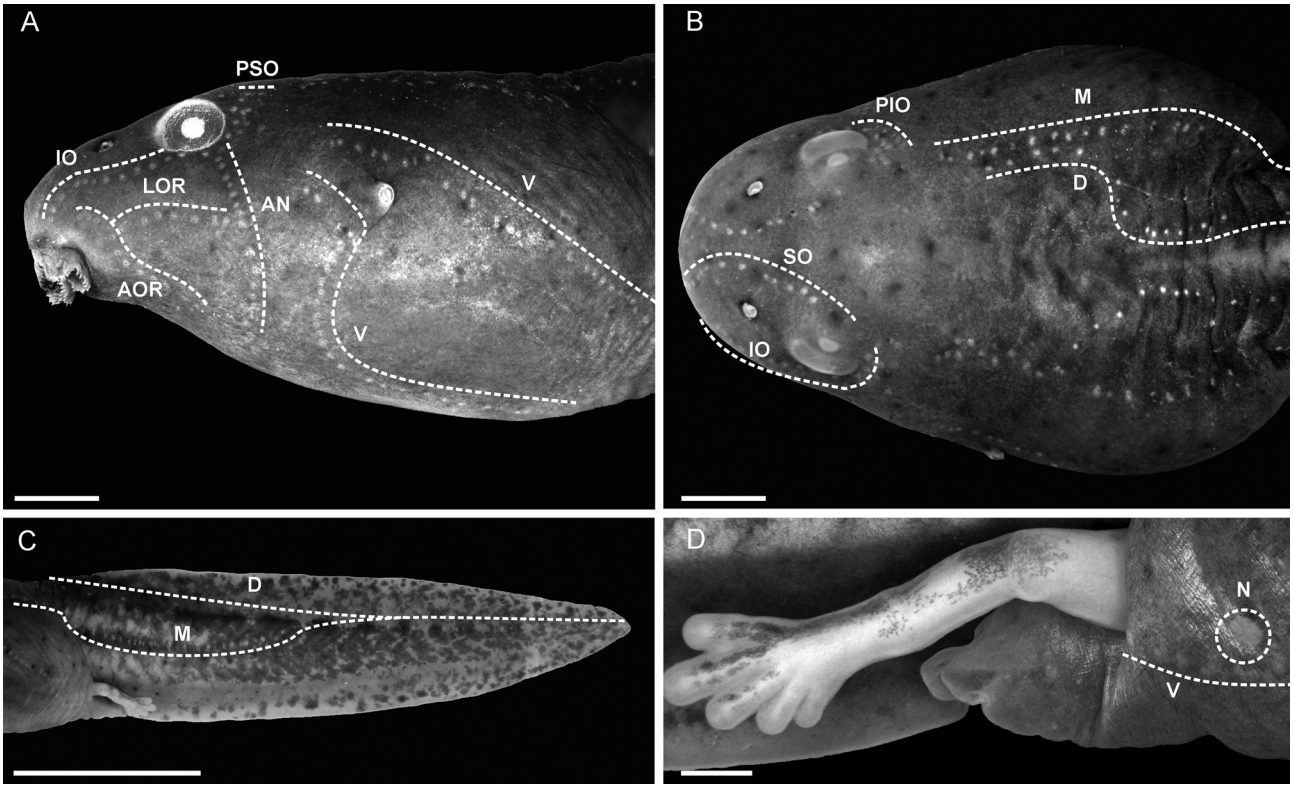

FIGURE 8. The lateral line system of *Bokermannohyla diamantina* (UFMG 1060) in a stage 38 specimen. (A) Lateral view of body indicating the angular (AN), infraorbital (IO), longitudinal oral (LOR), anterior oral (AOR), posterior supraorbital (PSO), and ventral (V) lines. Scale bar = 2 mm. (B) Dorsal view of body showing the supraorbital (SO), infraorbital (IO), posterior infraorbital (PIO), middle (M), and dorsal (D) lines. Scale bar = 2 mm. (C) Detail of the tail and the courses of the dorsal (D) and middle (M) lines. Scale bar = 10 mm. (D) Detail of vent tube region of the body showing the ventral line of neuromasts (V), and, encircled, the associated ventrolateral cumulus of neuromasts (N). Scale bar = 1 mm.

Coloration. In 10% formalin, general pattern uniformly brown (Fig. 6). Body with regularly scattered black spots; distal margin of spiracle lightly pigmented. Tail musculature densely marbled by irregular dark spots mainly on posterior half; a longitudinal dark stripe starting from posterior end of body and extending posteriorly along medial caudal muscle line, for first anterior 1/3 of tail; dorsal margin of caudal musculature with an interrupted or continuous narrow brown line; dorsal and ventral fins densely marbled by irregular spots mainly on anterior portion of dorsal fin.

Variation. Two specimens in stage 29 have an elliptical body in dorsal view. Four specimens in stages 34–36 have few submarginal papillae (1–2) laterally in the oral disc (Fig. 7B). The shape of the fleshy projections on the medial and lateral nostril margins is variable, even within the same specimen (i.e., right/left nostrils). There is no clear pattern of ontogenetic change in these characters.

Natural history notes. Tadpoles of *Bokermannohyla diamantina* are benthic and were found in shallow puddles (lotic environment) associated with water springs of high elevation mountain streams (i.e., 1688 m a.s.l. at Serra do Itobira), in swampy grasslands (open environment), close to narrow gallery forest edges or small islands of arborescent vegetation. Grasslands were covered manly by Graminaceae, Euryocaulaceae, *Xyris* (Xyridaceae), and Apiaceae. These sites are surrounded by *campos rupestres* (rocky fields), a mosaic of habitat types including exposed grasslands, rock surfaces, cerrado, and small forests. Although we only collected tadpoles in the open grassland habitats, calling males were also found in these open areas and their associated forest habitats mainly on the ground or perched on vegetation. Adult calling activity was recorded in December and January at the beginning of the hot and rainy season (other months were not sampled).

Oral cavity morphology. Buccal roof—roof triangular, about 1.1 longer than wide (Fig. 9A). Two or three prenarial arena papillae with undulated margins, irregularly distributed or forming a longitudinal ridge along prenarial arena midline. Maximal internal nares length about 35% of BRW; internarial distance about 10% of BRW. Nares oriented 45º from midline; anterior wall short and thick with irregular margin; posterior wall (narial valves) large, wide and with distinct papillae; narial valves extending forward, covering almost completely the internal nares, and about half of the vacuities. Large elliptical, smoothly concave, and shallow vacuities attached anteromedially to internal nares. Postnarial arena with two or three pairs of papillae distributed in an inverted V-shape, with posterior and external papillae larger than those more anterior and medial; six to ten randomly distributed pustulations present. Median ridge rounded to triangular with three to eight blunt, short papillae on anterior surface. One pair of medium-sized lateral ridge papillae with three to four secondary projections. BRA hexagonal with 13–20 short buccal roof arena papillae distributed mainly posterolaterally. In addition, 8–11 digitiform lateral roof papillae on each side. BRA with 370–430 homogeneously distributed pustulations. Secretory pits distinct in glandular zone, mainly posterolaterally in the dorsal velum. Dorsal velum large, discontinuous at midline (gap corresponding to 28% of BRW); irregular, discrete marginal papillae present. **Buccal Floor**—floor triangular, as wide as long (Fig. 9B). Two pairs of infralabial papillae; one large, hand-like papillae located anteriorly, and one pair of short digitiform papillae posteriorly. One pair of tall, digitiform lingual papillae present. BFA triangular, surrounded by 44–50 long, digitiform papillae. These papillae are disposed in two rows, one medially from anterior region of buccal pockets to median region of BFA, and one extending laterally and more obliquely following the anterior margin of ventral velum, towards the posterior region of BFA; larger papillae located anteriorly; two or three large papillae bi or trifurcated. BFA with 169–195 pustulations, more concentrated posteriorly. Buccal pockets about 8 times wider than high, transversally oriented, deep, width about 25% of BFW. Four to seven conical prepocket papillae on each side; few (2–3) short prepocket papillae lying on the anterior wall of pocket. Ventral velum height about 30% of BFW. Posterior margin scalloped, with eight distinct peaks over filter cavities; peaks 8% of BFW; median notch depth about 7% of BFW. Secretory pits distinct when stained with methylene blue, more concentrated on posterior margin of ventral velum but absent on median notch region. Glottis large, 20% visible, width about 6% of BFW; thick and broad lips.

Discussion

External morphology. Tadpoles of *Bokermannohyla caramaschii* and *B. diamantina* differ in body shape in lateral view (ventral contour in peribranchial region slightly convex in *B. caramaschii* and flat in *B. diamantina*), and a more depressed body in the later. The most common LTRF in *B. caramaschii* is 2(2)/4(1), while in *B. diamantina* it

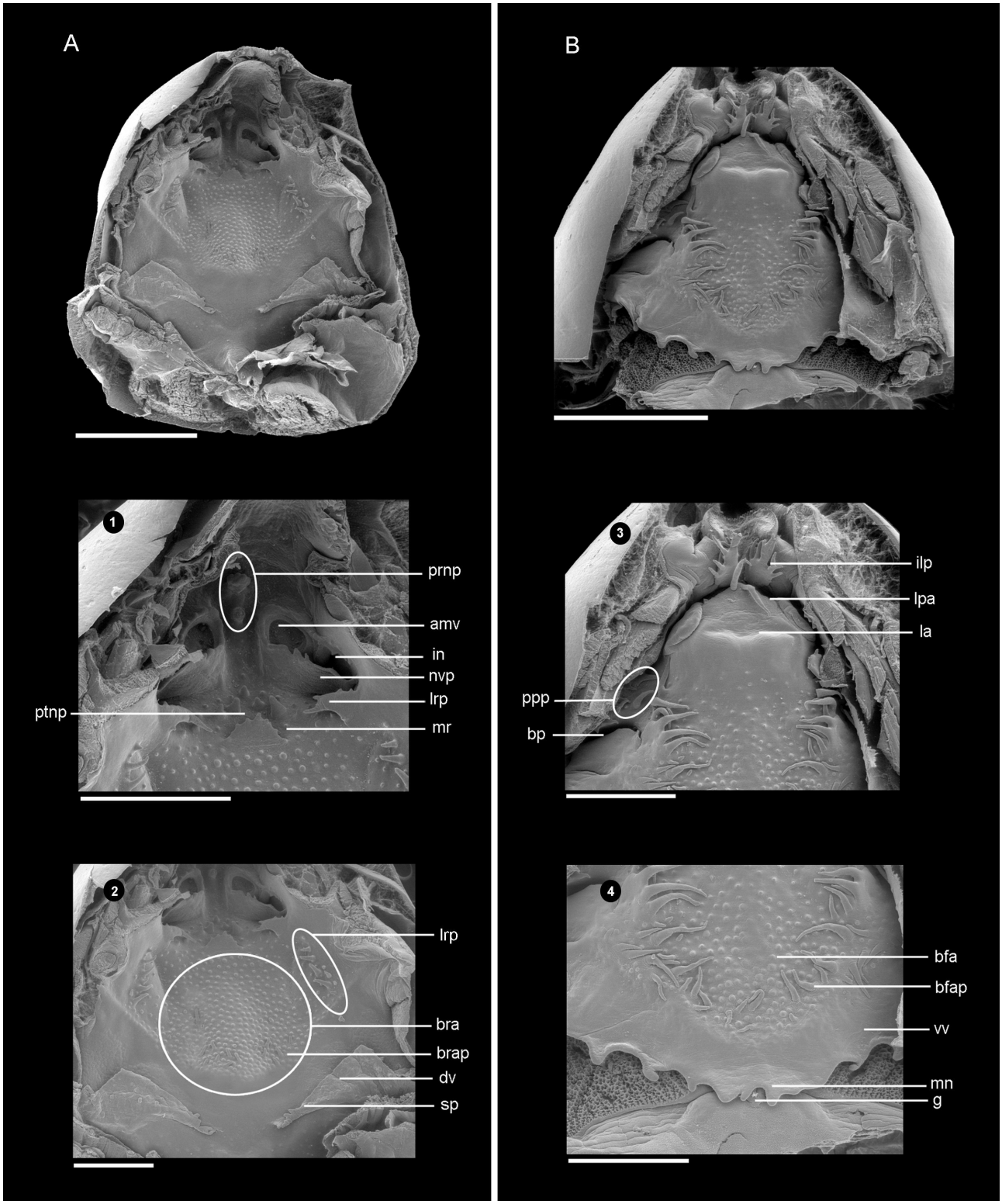

FIGURE 9. SEM micrographs of oral roof (A) and floor (B) of *Bokermannohyla diamantina* at stage 35 (UFMG 1060). Scale bars = 2 mm. (1) Detail of the anterior region of roof: prenarial arena papillae (prnp); anteromedial vacuity of internal nares (amv); internal nares (in); narial valve projection (nvp); lateral ridge papilla (lrp); median ridge (mr); postnarial papillae (ptnp). (2) Detail of the posterior region of roof: lateral roof papillae (lrp); buccal roof arena (bra); buccal roof arena papillae (brap); dorsal velum (dv); secretory pits (sp). (3) Detail of the anterior region of floor: infralabial papillae (ilp); lingual papillae (lpa); lingual anlage (la); buccal pocket (bp); prepocket papillae (ppp). (4) Detail of the posterior region of floor: buccal floor arena (bfa); buccal floor arena papillae (bfap); vv (ventral velum); median notch (mn); glottis (g). Scale bars = 1 mm.

is 2(2)/3(1). The number of marginal papillae surrounding the oral disc is also a reliable character for differentiating tadpoles of *B. caramaschii* from those of *B. diamantina*, with the former having 23% more papillae than the latter. Lastly, the marbled pattern of the tail is distinct in both species.

One of the external character states apparently shared by *Bokermannohyla caramaschii*, *B. diamantina* and the other species of the *Bokermannohyla circumdata* group is the absence of small flaps possessing labial teeth laterally in the oral disc (Table 2). This condition has only rarely been found in *B. nanuzae* from the type locality (Serra do Cipó; two of the 12 individuals analyzed, in stages 32–39—UFMG 516) anteriorly and posteriorly in the oral disc. Although, the taxonomic distribution of these flaps among the seven species of the *B. circumdata* group with undescribed tadpoles needs to be assessed, it seems that their absence could be considered a putative synapomorphy of the group, or at least of some internal clade.

The developmental origin of similar flaps with tooth rows has been reported to be from submarginal papillae in *Hyloscirtus* (Sánchez 2010). In *Bokermannohyla*, the presence of these accessory tooth rows in the *B. pseudopseudis*, *B. claresignata*, and *B. martinsi* groups is frequently accompanied by the presence of submarginal papillae, which suggests that a similar ontogenetic process could be occurring. Moreover, flaps with tooth rows have been recorded in larvae of *Hypsiboas* (Faivovich, 1996; Kolenc *et al.* 2008), and informally cited for *Osteocephalus* (Hylidae: Hylinae: Lophiohylini; Sánchez 2010).

Submarginal papillae also seem to occur rarely in the *Bokermannohyla circumdata* group, except in *B. nanuzae* from Serra do Cipó, for which nine of the 12 individuals analyzed, in stages 32–39 have submarginal papillae (UFMG 516; Walker *et al*. 2015). However, some of the original descriptions are not consistent with the referenced illustrations (e.g. Peixoto 1981; Gaiga *et al.* 2013—Table 2), thereby not allowing comparisons of this character. Sometimes comparisons are rendered difficult also in relation to the presence of a gap in the marginal papillae. Oral discs with complete marginal papillae were reported in the original description of *B. nanuzae* (Bokermann & Sazima 1973—the authors mention the presence of sparse and undeveloped papillae on the medial region of anterior labium) and also for individuals from Serra do Ibitipoca (Napoli & Caramaschi 2004, as *B. feioi*). However, anterior small gaps in the marginal papillae were figured for both populations in Walker *et al*. (2015), and occur in all individuals of the analyzed lots (UFMG 516, 1106). The analysis of the original lots used in descriptions is important in order to know whether polymorphism in the presence/absence of gaps occur in these populations. Hence, almost all known tadpoles of species of the *Bokermannohyla circumdata* group have a dorsal gap in the marginal papillae, with the exception of *B. hylax*, which has the oral disc with complete marginal papillation (Bertoluci *et al.* 2003—Table 2).

The most common LTRFs in species of the *Bokermannohyla circumdata* group vary from 2(2)/3(1) to 2(2)/4(1), and reaching 2(2)/5(1) in *B. carvalhoi* (Peixoto 1981) and *B. nanuzae* (Bokermann & Sazima 1973—Table 2). Variation in LTRF, as reported in *B. caramaschii*, is expected to occur, since it has been documented in many species (Lutz & Orton 1946; Bokermann 1972; Eterovick & Brandão 2001; Bertoluci *et al.* 2003; Lugli & Haddad 2006a; Leite & Eterovick 2010; Mongin & Carvalho-e-Silva 2013; Walker *et al*. 2015). Sánchez (2010) stated that the number of tooth rows and of accessory tooth rows increase with development and size in tadpoles of *Hyloscirtus*. This positive association was also observed in *Myersiohyla neblinaria*, but not in *M. chamaeleo* (Faivovich *et al*. 2013). In *Bokermannohyla*, an ontogenetic pattern of tooth row addition was reported for *B. saxicola* (Eterovick & Brandão 2001), *B. circumdata* (Mongin & Carvalho-e-Silva 2013), and briefly mentioned for *B. pseudopseudis* (Eterovick & Brandão 2001), however, this latter description was based on a series of tadpoles that actually included larvae of *B. pseudopseudis* and *B. sapiranga* (see Brandão *et al.,* 2012), making it necessary to reassess their observations. Variation in the pattern and number of labial tooth rows, and the underlying mechanism of ontogenetic change, remain to be fully explored in *Bokermannohyla*, and other Cophomantini genera.

The fleshy projections of variable shape on the inner margin of the nostrils are a potentially informative character in Cophomantini (Faivovich *et al*. 2005). However, basic information about the presence/absence, shape and variation of these projections are not yet available for *Bokermannohyla* (see Table 2). The fleshy projections in *B. caramaschii* and *B. diamantina* were always present, but exhibited variation in the degree of development and shape, even within the same specimen (i.e., right/left nostrils).

The lateral line system, although apparently conspicuous in many species of Cophomantini (see Kolenc *et al.* 2008; Sánchez 2010; Faivovich *et al.* 2013) is also rarely described for *Bokermannohyla*. It is mentioned for 14 species (Table 2), and briefly described only for *B. itapoty* and *B. oxente* (Lugli & Haddad 2006a,b). While *B.*

caramaschii, *B. diamantina*, and *B. oxente* have ten lines, only seven were reported for *B. itapoty*, with LOR, AOR, and PSO being absent. Furthermore, in *B. itapoty* IO is fused to M (there is a gap between these lines in *B. caramaschii*, *B. diamantina*), and D terminates at the beginning of the muscular tail (D is continuous onto the dorsal fin base in *B. caramaschii*, *B. diamantina*). In all four of these species M projects dorsally to reach the dorsal fin base.

Cumuli of neuromasts on the posterolateral wall of the body are not mentioned for *B. itapoty* and *B. oxente* (Lugli & Haddad 2006 a,b), but are evident in both species described here as well in many other species of *Bokermannohyla* (Table 2), *Hypsiboas* (Kolenc *et al.* 2008), *Aplastodiscus* (Pezzuti *et al*. 2010), and *Hyloscirtus* (Sánchez 2010). The investigation of this character in *Myersiohyla* and in other Hylinae tribes will determine if the presence of cumuli of neuromasts could be considered a putative synapomorphy of Cophomantini, or of a less inclusive clade.

Tadpoles of many species of the *Bokermannohyla circumdata* group, including *B. caramaschii* and *B. diamantina*, resemble each other in having a general coloration pattern of brown with dark longitudinal stripes on the tail muscle (Table 2). Exceptions include a few species with a marbled tail without defined stripes (*B. carvalhoi*, and *B. nanuzae* from Serra do Ibitipoca), and others that are homogeneously colored (*B. ibitipoca*, *B. nanuzae* from Serra do Cipó).

Oral cavity morphology. *Bokermannohyla caramaschii* differs from *B. diamantina* in the pattern of distribution of papillae in the prenarial arena (transversally oriented in the former, and with no ordered disposition or oriented longitudinally in *B. diamantina*), and by the number of pairs of infralabial papillae (three and two, respectively).

Like larvae of all known species of *Bokermannohyla* and other Cophomantini described so far, *B. caramaschii* and *B. diamantina* have large, elliptical, smoothly concave and shallow vacuities attached anteromedially between the internal nares (see Wassersug 1980; D'Heursel & De Sá 1999; D'Heursel & Haddad 2007; Kolenc *et al.* 2008). These structures have been suggested to have a chemoreceptive function (Wassersug, 1980), and their presence has been considered a putative synapomorphy of the tribe (Faivovich *et al*. 2005; D'Heursel & Haddad 2007), pending its study in *Hyloscirtus* and *Myersiohyla*. Furthermore, the shape, and pattern of organization and distribution of the ciliated and secretory epithelia that lie on the bottom of the vacuities seem to be variable among species (TLP, personal observation), and deserves further investigation.

Both species studied here differ from *B. nanuzae* and *B. luctuosa* by having papillae in the prenarial arena (absent in these species—D'Heursel & Haddad 2007—Table 3). In *B. diamantina*, these papillae can be irregularly distributed, as in *B. circumdata* (Mongin & Carvalho-e-Silva 2013), or form a longitudinal ridge along the midline. This state has been reported only for *B. alvarengai*, *B. itapoty*, and *B. saxicola*, and was considered as a putative synapomorphy of the *B. pseudopseudis* group (D'Heursel & Haddad 2007). In *Aplastodiscus* and *Hypsiboas* these papillae are frequently organized in a transverse ridge or randomly distributed in the prenarial arena (D'Heursel & Haddad 2007; Kolenc *et al.* 2008).

D'Heursel & Haddad (2007) highlighted the presence of distinct, complex lateral ridge papillae in five species of *Bokermannohyla* (Table 3). In fact, all species studied at that time differed from other known Cophomantini species by having large, hand-like lateral ridge papillae, with five long, digitiform secondary projections (Table 3). However, *B. caramaschii*, *B. diamantina*, and *B. circumdata* (Mongin & Carvalho-e-Silva 2013) have smaller and narrower lateral ridge papilla with just 3–4 projections, with one or two of them being elongate. These papillae are still larger than those of most *Hypsiboas* and *Aplastodiscus*, which have short, stubby secondary projections (D'Heursel & Haddad 2007; Kolenc *et al.* 2008), but similar to those of other species, which have longer projections (e.g. *Hypsiboas punctatus rubrolineatus*, Kolenc *et al.* 2008; *Aplastodiscus eugenioi*, D'Heursel & Haddad 2007). Therefore, a denser sampling of species of all genera is crucial to understanding the homology of these character states and their distribution among the species of Cophomantini.

As with other tadpoles of *Bokermannohyla*, and some of *Aplastodiscus* (see D'Heursel & Haddad 2007), *B. caramaschii*, *B. diamantina* and *B. circumdata* (Mongin & Carvalho-e-Silva 2013) have postnarial papillae forming an inverted V-shape anterior to the median ridge. However, in these species the posterolateral papillae are larger than those more anterior and medial (in other species of *Bokermannohyla* the anteromedial papillae are larger than those more posterior and lateral). In *Hypsiboas* a variable number of papillae are arranged transversely or form a wide arch between the lateral ridge papillae (D'Heursel & Haddad 2007; Kolenc *et al.* 2008).

TABLE 2. Comparison among external characters of known tadpoles of *Bokermannohyla*. Species groups are those discussed by Faivovich *et al.* (2005, 2009).

	TL mm (Gosner stage)	Predominant LTRF	Dorsal gap on marginal papillae	Small flaps with labial teeth	Submarginal papillae	Fleshy projections on the medial margins of nostrils	Lateral line system/ventrolateral cumuli of neuromasts	Pattern of coloration	References
***Bokermannohyla circumdata* group**									
B. capra	48.7 (34–37)	2(2)/4(1)	Present	Absent	Absent/rarely present	Rounded	Visible/present	Brown with tail stripes	Mercês *et al.* 2012
B. caramaschii	45.4 (35–38)	2(2)/4(1)[1]	Present	Absent	Absent/rarely present	Trapezoidal to triangular	Visible/present	Brown with tail stripes	Present study
B. carvalhoi	47 (31)	2(2)/5(1)	Present	Absent	Absent	Present	Visible/present	Brown with marbled tail	Peixoto 1981
B. circumdata	44 (37)	2(2)/4–3(1)[1]	Present	Absent	Absent/present[3]	Present	Visible/not mentioned	Brown with tail stripes	Peixoto 1981; Mongin & Carvalho-e-Silva 2013
B. diamantina	44 (36–38)	2(2)/3(1)	Present	Absent	Absent/rarely present	Rounded to triangular	Visible/present	Brown with tail stripes	Present study
B. gouveai	47.1 (30–37)	2(2)/3	Present	Absent	Absent	Not mentioned	Not mentioned	Brown with tail stripes	Costa *et al.* 2010
B. hylax	34.2 (37)	2(2)/4(1–2)	Absent	Absent	Absent/rarely present	Not mentioned	Visible/not mentioned	Brown with tail stripes	Bertoluci *et al.* 2003
B. ibitipoca	46.7 (37)	2(2)/4(1)	Present	Absent	Absent/rarely present	Rounded	Visible/not mentioned	Uniformly brown	Magalhães *et al.* 2012
B. lucianae	39.6 (26–28)	2(2)/4(1)	Present	Absent	Absent/rarely present	Not mentioned	Visible/present	Brown with tail stripes	Mercês *et al.* 2015
B. luctuosa	14.9 (25)	2(2)/3(1)	Present	Absent	Absent	Not mentioned	Not visible	Uniformly brown	Pombal & Haddad 1993
B. nanuzae[5]	65.0 (33–34)	2(2)/5(1)[1]	Present[2]	Absent/rarely present[2]	Present/rarely absent[2]	Rounded[2]	Visible/present[2]	Uniformly black	Bokermann & Sazima 1973; Walker *et al.* 2015; UFMG 516

……*continued on the next page*

TABLE 2. (Continued)

	TL mm (Gosner stage)	Predominant LTRF	Dorsal gap on marginal papillae	Small flaps with labial teeth	Submarginal papillae	Fleshy projections on the medial margins of nares	Lateral line system/ventrolateral cumuli of neuromasts	Pattern of coloration	References
B. nanuzae[6]	54 (36)	2(2)/4(1)[1]	Present[2]	Absent	Absent/rarely present	Rounded	Visible/present[2]	Brown with marbled tail	Napoli & Caramaschi 2004; Walker *et al*. 2015; UFMG1106
B. sazimai	60 (27)	2(2)/4(1)	Present	Absent	Absent	Present	Not mentioned	Brown with tail stripes	Cardoso & Andrade 1982
B. vulcaniae	33.6 (26–27)	2(2)/3(1)	Present	Absent	Present[4]	Not mentioned	Not mentioned	Uniformly brown	Gaiga *et al*. 2013
***Bokermannohyla pseudopseudis* group**									
B. alvarengai	53 (40)	2(2)/5(1)	Present	Present[2]	Present[2]	Rounded[2]	Visible/absent[2]	Brown with marbled tail	Sazima & Bokermann 1977; UFMG160
B. ibitiguara	62 (35)	2(2)/4(1)	Present	Not mentioned	Not mentioned	Not mentioned	Not mentioned	Uniformly dark brown	Cardoso 1983
B. itapoty	73.6 (37)	2(2)/6(1)[1]	Absent	Present	Present	Not mentioned	Visible/not mentioned	Brown with marbled tail	Lugli & Haddad 2006a
B. oxente	58.7 (37)	2(2)/5(1)	Present	Present	Present	Not mentioned	Visible/not mentioned	Brown with marbled tail	Lugli & Haddad 2006b
B. pseudopseudis[7]	73.2 (37)	2(2)/6(1)[1]	Absent	Present	Present	Not mentioned	Not mentioned	Brown with marbled tail	Eterovick & Brandão 2001
B. saxicola	65.4 (36)	2(2)–3(3)/ 6– 8(1)	Absent	Present	Present	Rounded[2]	Visible/present	Brown with marbled tail	Eterovick & Brandão 2001; UFMG229

……*continued on the next page*

TABLE 2. (Continued)

	TL mm (Gosner stage)	Predominant LTRF	Dorsal gap on marginal papillae	Small flaps with labial teeth	Submarginal papillae	Fleshy projections on the medial margins of nares	Lateral line system/ventrolateral cumuli of neuromasts	Pattern of coloration	References
***Bokermannohyla claresignata* group**									
B. claresignata	60 (?)	7(7)–9(9)/11–14(1)	Absent	Present	Present	As a distinct papilla	Not mentioned	Dark with marbled tail	Lutz & Orton 1946
B. clepsydra	57 (37)	7(7)–(8)/12–13(1)	Absent	Present	Present	Not mentioned	Not mentioned	Brown with marbled tail	Bokermann 1972
***Bokermannohyla martinsi* group**									
B. martinsi	46.3 (25)	3(3)/5–6(1)	Absent	Present	Present	Present	Visible/present	Uniformly black	Leite & Eterovick 2010

[1] Note that some variation in LTRF was reported in the original descriptions.
[2] Character state reported only through direct examination of specimens when differing from that reported in the original descriptions.
[3] Character state (presence of submarginal papillae) illustrated in Peixoto, 1981, but not reported in Mongin & Carvalho-e-Silva, 2013.
[4] Character state (presence of submarginal papillae) described in text, but not illustrated.
[5] Specimens from Serra do Cipó.
[6] Specimens from Ibitipoca.
[7] The original description (Eterovick & Brandão 2001) was based on a mixed series of *B. pseudopseudis* and *B. sapiranga* (Brandão *et al.* 2012).

TABLE 3. Oral cavity characters of known tadpoles of *Bokermannohyla*. Species groups are those discussed by Faivovich *et al.* (2005, 2009).

	Buccal Roof						Bucal Floor				
	Vacuities anterior to the internal nares	Prenarial arena Row of papillae or ridge	Lateral ridge papillae relative size/Secondary projections	Post narial papillae	BRA papillae	Lateral roof papillae (per side)	Pairs of infralabial papillae	Total number of lingual papillae	Number of BFA papillae (per side)	Number of prepocket papillae	References
***Bokermannohyla circumdata* group**											
B. caramaschii	Present	Transverse	Median sized/3–4 projections	Posterolateral papillae larger than the others	7–14	6–10	3	2	25–26	5–6	Present study
B. circumdata	Present	Irregularly distributed	Median sized/4 projections	Posterolateral papillae larger than the others	Present	8	5	2	24	~6	Mongin & Carvalho-e-Silva 2013
B. diamantina	Present	Irregularly distributed or longitudinal	Median sized/3–4 projections	Posterolateral papillae larger than the others	13–20	8–11	2	2	22–25	4–7	Present study
B. luctuosa	Present	Absent	- /5 projections	Anteromedial papillae larger than the others	6	6	2*	3	20–25	5–7	D'Heursel & Haddad 2007
B. nanuzae	Present	Absent	Large/5 projections	Anteromedial papillae larger than the others	Absent	6	2*	2	20–40	5–7	D'Heursel & Haddad 2007
***Bokermannohyla pseudopseudis* group**											
B. alvarengai	Present	Longitudinal	Large/5 projections	Anteromedial papillae larger than the others	Absent	6	2*	2	~30	5–7	D'Heursel & Haddad 2007
B. itapoty	Present	Longitudinal	Large/5 projections	Anteromedial papillae larger than the others	Absent	6	2*	2	30–40	5–7	D'Heursel & Haddad 2007
B. saxicola	Present	Longitudinal	Large/5 projections	Anteromedial papillae larger than the others	Absent	6	2*	2	20–25	5–7	D'Heursel & Haddad 2007

* All species with at least two pairs of infralabial papillae, but with the exact number not specified in the original description (D'Heursel & Haddad 2007).

In addition to the species studied here, *B. circumdata* and *B. luctuosa* also differ from the other species of the genus by the presence of BRA papillae (absent in the other species; D'Heursel & Haddad 2007; Mongin & Carvalho-e-Silva 2013—Table 3). All studied species of *Bokermannohyla* have at least six lateral roof papillae per side. BRA papillae and lateral roof papillae can be absent in some species of *Hypsiboas* (e.g. *H. caingua*, *H. faber*, *H. raniceps*; Kolenc *et al.* 2008), but numerous in others (e.g. some species of the *Hypsiboas pulchellus* group; Kolenc *et al.* 2008), as well as in *Aplastodiscus* (D'Heursel & Haddad 2007).

The dorsal velum is well developed laterally and reduced in the midline in *B. caramaschii* and *B. diamantina*, as in other species of *Bokermannohyla*, *Aplastodiscus* and some *Hypsiboas* (D'Heursel & Haddad 2007; Kolenc *et al.* 2008). However, many species of *Hypsiboas* have a continuous dorsal velum (Kolenc *et al.* 2008), indicating an informative variation of this character in Cophomantini.

As with most species of the genus, *B. caramaschii* and *B. diamantina* have one pair of tall digitiform lingual papillae (*B. luctuosa* has three lingual papillae; D'Heursel & Haddad 2007). A similar condition seems to occur in most studied species of *Hypsiboas* and *Aplastodiscus*, but sometimes papillae can be shorter (e.g. *Hypsiboas cinerascens*, *A. albofrenatus*, *A. callipygius*, *A. cochranae*; D'Heursel & Haddad 2007), with forked tips (e.g. in the *H. faber* species group; Kolenc *et al.* 2008), or with a variable number of associated pustules (e.g. *H. faber*, *H. pulchellus*; Kolenc *et al.* 2008).

The number of prepocket and BFA papillae are also similar among species of *Bokermannohyla*, ranging from four to seven, and from 20 to 40 per side, respectively. The organization of BFA papillae into a pattern of two divergent lines is similar to that described for many species of *Hypsiboas* (i.e.,V-shaped pattern; Kolenc *et al.* 2008), and *Aplastodiscus* (D'Heursel & Haddad 2007). The number of pairs of infralabial papillae of larvae of *Bokermannohyla* varies from two to five (Table 3). All species have at least one pair of large hand-like papillae with long and digitiform secondary projections located anteriorly, and one short pair of digitiform papillae posteriorly. One or two pairs of infralabial papillae are recorded in species of *Aplastodiscus* and *Hypsiboas*, but the secondary projections are frequently shorter in the latter (D'Heursel & Haddad 2007; Kolenc *et al.* 2008).

Although the generic level relationships in Cophomantini are well established (Faivovich *et al.* 2005, 2013), the internal relationships of some of these genera still require further research. In *Bokermannohyla*, for example, only about 25% of the diversity has been included in phylogenetic analyses (Faivovich *et al.* 2005, 2013). Our data indicates that tadpole external and internal morphology provides informative variation for studying the phylogenetic relationships within *Bokermannohyla* (D'Heursel & Haddad 2007; Leite & Eterovick 2010). However, there is a complex scenario of character distribution in Cophomantini that requires further study. Together with molecular, behavioral, ecological, and adult morphological data, it is evident that larval characters are assuredly relevant in the study of the systematics of Cophomantini and the internal relationships of its genera.

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APPENDIX. Specimens examined.

Bokermannohyla alvarengai. Brazil, state of Minas Gerais, Municipality of Santana do Riacho: UFMG 160, eight specimens in stages 26−37.

Bokermannohyla caramaschii. Brazil, state of Espírito Santo, Municipality of Santa Teresa: UFMG 1418a,b, 13 specimens in stages 29−39; UFMG 1425, three specimens in stages 30−35.

Bokermannohyla diamantina. Brazil, state of Bahia, Municipality of Rio de Contas: UFMG 1060, 15 specimens in stages 27−38.

Bokermannohyla nanuzae. Brazil, state of Minas Gerais, Municipality of Lima Duarte: UFMG 1106, 12 specimens in stages 32−39; Municipality of Santana do Riacho: UFMG 516, 12 specimens in stages 32–39.

Bokermannohyla saxicola. Brazil, state of Minas Gerais, Municipality of Santana do Riacho: UFMG 229, seven specimens in stages 26−32.