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Larval chondrocranial and internal oral morphology of the neotropical treefrog *Boana crepitans* (Wied-Neuwied, 1824; Amphibia, Anura, Hylidae)

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Abstract

We describe the internal oral morphology and chondrocranial anatomy for *Boana crepitans* tadpoles, and compare them with available descriptions for other species in the subfamily Cophomantinae. Among species of the *Boana faber* group, the chondrocranial anatomy has been reported only for one species internal oral morphology and cranial anatomy are similar to other described species of *Boana* and Cophomantinae. *B. crepitans* lacks unique features in the oral cavity and chondrocranium that would distinguish it from other congeneric species. We identify six characters from the internal oral anatomy of tadpoles unique for Cophomantinae. In addition, *Boana* has infralabial papillae projections, buccal floor arena papillae, and lateral ridge papillae projections shorter than those described for *Aplastodiscus* and *Bokermannohyla*.

KEY WORDS

Cophomantinae, internal oral anatomy, SEM, tadpole skeleton

1 | INTRODUCTION

The genus *Boana* Gray, 1825 currently consists of 94 species distributed in Central and South America, from Nicaragua to Argentina, Trinidad, and Tobago (Frost, 2021). This genus belongs to the Cophomantinae Hoffman, 1878 subfamily together with “*Hyla*” *nicefori* (Cochran & Goin, 1970), *Aplastodiscus* Lutz, 1950 (16 sp.), *Bokermannohyla* Faivovich et al., 2005 (30 sp.), *Hyloscirtus* Peters, 1882 (37 sp.), *Myersiohyla* Faivovich et al., 2005 (6 sp.), and a new monospecific genus *Nesorohyla* Pinheiro et al., 2018 (1 sp.).

Boana species are clustered in seven species groups: *Boana albopunctata*, *Boana benitezi*, *Boana faber*, *Boana pellucens*, *Boana pulchella*, *Boana punctata*, and *Boana semilineata* (Faivovich et al., 2005).

The *Boana faber* group consists of eight species: *Boana albomarginata* (Spix, 1824), *Boana crepitans* (Wied-Neuwied, 1824), *Boana exastis* (Caramaschi & Rodrigues, 2003), *B. faber* (Wied-Neuwied, 1820), *Boana lundii* (Burmeister, 1856), *Boana pardalis* (Spix, 1824), *Boana pugnax* (Schmidt, 1857), and *Boana rosenbergi* (Boulenger, 1898).

The larval internal oral morphology of *Boana* (* = *B. faber* species group) has been reported for the following species: *B. albopunctata*, *B. albomarginata**, *B. atlantica*, *B. caingua*, *B. cinerascens*, *B. cordobae*, *B. faber**, *B. geographica*, *B. joaquinii*, *B. leptolineata*, *B. lundii**, *B. polytaenia*, *B. prasina*, *B. pulchella*, *B. punctata*, *B. raniceps*, *B. riojana*, *B. rosenbergi**, *B. rufitela*, and *B. semilineata* (Both et al., 2007; D'Heursel & de Sá, 1999; D'Heursel & Haddad, 2007; Kolenc et al., 2008; Lavilla & Fabrezi, 1987; Luna-Dias et al., 2019;

Nascimento et al., 2009; Spirandeli-Cruz & Gomes, 1991; Vera Candiotti, 2007; Wassersug, 1980).

Although the *Boana* genus is diverse, only around 20% of its tadpoles have their internal oral morphology and chondrocranium described. Among the currently 94 known species of *Boana*, chondrocranial anatomy data are available for only seven species: *B. geographica*, *B. lanciformis*, *B. pulchella*, *B. raniceps*, *B. riojana*, *B. rosenbergi*, and *B. semilineata* (Alcalde & Rosset, 2003; de Sá, 1988; D'Heurzel & de Sá, 1999; Hoyos et al., 2012; Lavilla & Fabrezi, 1987; Vera Candiotti, 2007). However, from the *B. faber* species group, only the chondrocranium of *B. rosenbergi* has been described (Vera Candiotti, 2007).

Boana crepitans was described from Tamburil, Municipality of Condeúbas, State of Bahia, Brazil (Bokermann, 1966). Larval development of *B. crepitans*, from eggs to metamorphosis (including tadpole), was described based on specimens from Venezuela (Donoso-Barros & León-Ochoa, 1972) and the tadpole was described from the Municipality of Feira de Santana, Bahia, Brazil (Casal & Juncá, 2008). As larvae morphology patterns shows an uncoupling of phenotypic evolution across life history phases in comparison with adults (Valero et al., 2017), it is important to understand the overall morphology of tadpoles. Herein, we describe the internal oral morphology and the chondrocranial anatomy of the larvae of *B. crepitans* and compare it with available data for *Boana* as with other species of Cophomantinae.

2 | MATERIAL AND METHODS

Tadpoles were collected at the locality of Riachão, Municipality of Brotas de Macaúbas, Bahia State, Brazil. Tadpoles were reared in the laboratory through metamorphosis and were compared with the available larvae description (Casal & Juncá, 2008). Voucher specimens were preserved in formalin 8% and deposited in the herpetological collection of the Museu de Zoologia da Universidade Federal da Bahia (lot number UFBA10611) and Universidade Federal do Maranhão (lots numbers HUFMA2080–2081).

Tadpole stages were determined following Gosner (1960) using a Leica EZ4 and Leica 10S8APO stereomicroscopes. Morphological descriptions are based on individuals at Stages 30 and 36 ($n = 6$). For analysis of internal oral morphology, four larvae were dissected (following Wassersug, 1976) and prepared for scanning electron microscopy (SEM) as follow: after dissection, samples were washed in sterile water for 15 min, fixed in a 2–3% glutaraldehyde solution for 3–4 h at room temperature, followed by three 15 min washes in 0.1 mol L^{-1} phosphate buffer, postfixed for 2 h in a 1% solution of osmium tetroxide at room temperature, three 15 min washes in 0.1 mol L^{-1} phosphate buffer were repeated. Subsequently, samples were dehydrated using 15 min changes of the following graded ethanol series: 35, 50, 70, 80, 95, and three 100% changes. Specimens were critical point dried in CO_2 , mounted on aluminum stubs and sputter coated with gold and palladium in camera “Denton Vacuum desk III Cold Sputter-Etch Unit.” Photographs were taken using a scanning electron microscope attached to computer with Jeol JSM 6360LV operative system; terminology

follows Wassersug (1976). Measurements and additional observations of the internal oral morphology features were made using an ocular micrometer on a stereoscopic microscope (Leica 10S8APO) following modified protocol of Weber and Caramaschi (2006).

Larval chondrocranial anatomy is described based on two individuals (Stages 30 and 36) that were examined cleared and double-stained, that is, bone and cartilage, specimens using a technique of Taylor and Dyke (1985); terminology follows de Sá (1988) and Haas (1995, 1997). Chondrocranial illustrations were produced in Photoshop CS5 from photographs obtained using a stereomicroscope microscope (Leica DFC295) with the image analyzer software Leica Application Suite 4.0.0.

3 | RESULTS

3.1 | Internal oral morphology

3.1.1 | Buccal floor

Overall broadly triangular, slightly wider than long (Figure 1, Table 1). The prelingual area bears pustules anteriorly and posteriorly has a pair of distinct and hand-shaped infrabial papillae with broad bases that extend medially from the lateral walls of the mouth. The tongue rudiment is elliptical and carries a pair of short and cylindrical lingual papillae with bifurcated distal tips and several pustules. The buccal floor arena (BFA) is overall circular; laterally and posteriorly bounded by about 20 conical papillae on each side. The BFA papillae are arranged in two rows. An anterior row that begins at the posterolateral corners of the tongue rudiment and overall forms a semicircle. Most of the papillae of this row are single, elongated, and cone-shaped. However, posterolateral and on each side of this row and at the level of the buccal pockets, there is a broad base papilla with a branched apex into 3–4 distal projections. Behind this row, there is a second and irregular row of papillae. The anterior and posterior thirds of the BFA are devoid of papillae and pustules over its surface. The buccal pockets are large and shallow; 5–7 prepocket papillae, with interspaced pustules, are found anterior to the buccal pockets, the prepocket papillae are shorter than the BFA papillae. The ventral velum is broad, smooth, and has a narrow glandular margin with secretory pits and four marginal projections. The glottis is not exposed.

3.1.2 | Buccal roof

Overall triangular, a low V-shaped ridge is located medially in the pre-narial region along with a few papillae and pustules. The choanae are large, ovoid, and obliquely oriented. The anterior wall is densely papillated whereas the posterior wall is smooth. Large extensions of the posterior walls form the narial valves; anteromedial vacuities present.

The distance between the internal nares is about 24% of the buccal roof length. There are about 10 conical postnarial papillae, some with bifurcated apices, aligned and forming a transverse row anterior

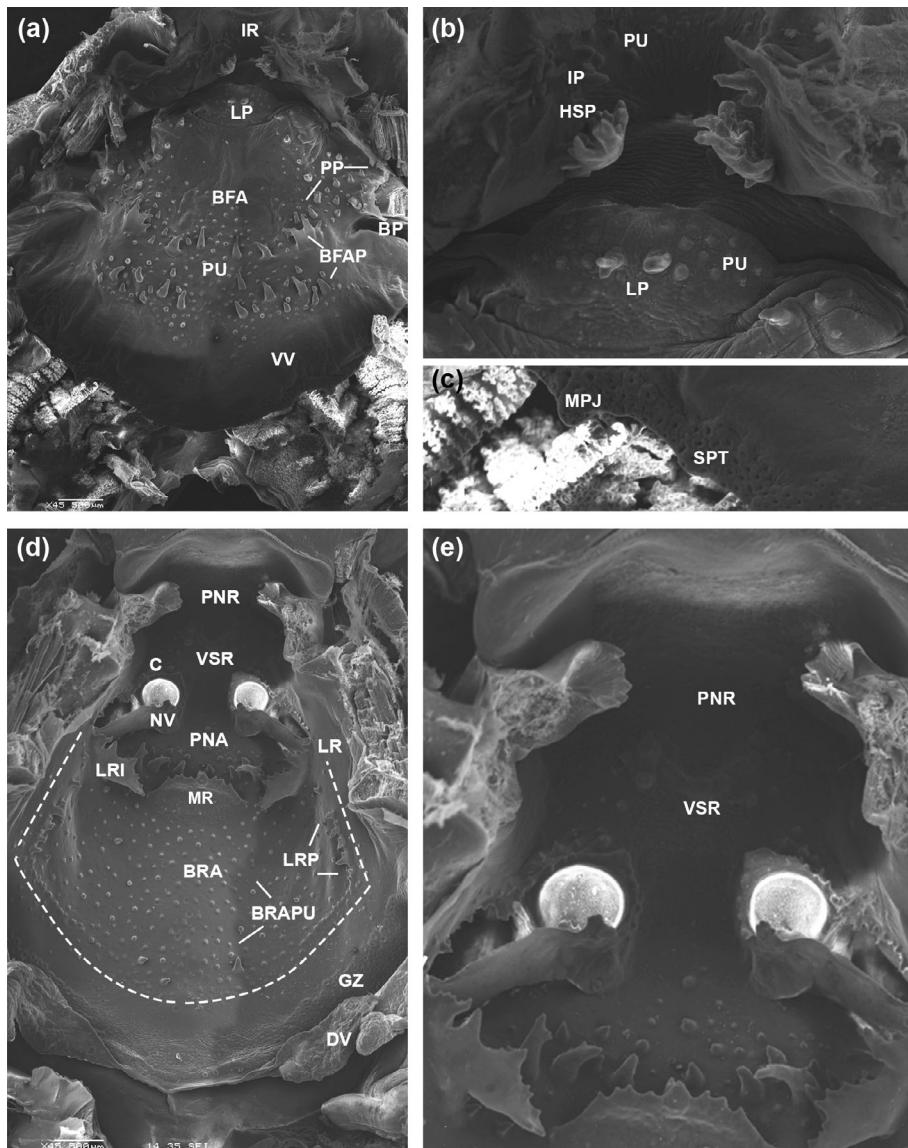


FIGURE 1 *Boana crepitans*, the internal oral morphology of the tadpole. (a) General aspect of the buccal floor, (b) details of the infralabial region and lingual region, (c) velar margin with secretory pits, (d) general aspect of the buccal roof and aligned papillae on the lateral edge (dashed line), (e) details of the prenarial, postnarial, choanae, median ridge, and lateral ridge papillae. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; BRA, buccal roof arena; BRAPU, buccal roof arena pustules; DV, dorsal velum; GZ, glandular zone; HSP, hand-shaped papillae; IP, infralabial papillae; IR, infralabial region; LP, lingual papillae; LR, lateral ridge; LRI, lateral ridge papilla; LRP, lateral roof papillae; MPJ, marginal projections of the ventral velum; MR, median ridge; NV, narial valve; PNA, postnarial arena; PNR, prenarial region; PP, prepocket papillae; PU, pustules; SPT, secretory pits of the ventral velum; VSR, V-shaped ridge; VV, ventral velum. Specimens at Stages 30 and 36

to the median ridge; the postnarial area is scattered with pustules. The median ridge is semicircular and low, bearing a low serrated edge. The lateral ridge papillae are overall triangular, long, and projecting from a broad base. These papillae have smooth surfaces and their anterior margins bear deep notches as well as long and short projections. A row of lateral roof papillae is found on each side of the BRA; these papillae are small and continuing with a row of short and closely placed papillae that denote the posterolateral boundaries of the BRA. The BRA is evenly scattered with pustules. Posteriorly, there is a broad glandular zone with distinct secretory pits that extend onto a narrow dorsal velum.

3.2 | Chondrocranial anatomy

The chondrocranium is oval shaped and longer than wide (Figure 2, Table 2). The suprarostral cartilages consist of two elements, the *pars corporis* and *pars alaris* that are ventrally separated from each other and

fused dorsally near the point of articulation with the *cornua trabeculae*. The *cornua trabeculae* are large, corresponding to about 24% of the chondrocranial length; they are broader in their anterior half. In dorsal view, the space between the *cornua trabeculae* is a narrow U-shape.

3.2.1 | Braincase

A large and undivided *frontoparietal fenestra* is present at Stages 30 and 36. Anteriorly bounded by the *planum ethmoidale*, laterally by the *taenia tecti marginalis*, and posteriorly by the *tectum synoticum*. The *cartilago orbitalis* is well developed, forms the lateral walls of the braincase, and it is pierced by three foramina: *f. opticum*, *f. oculomotorium*, and *f. trochlearis*. The floor of the braincase is poorly chondrified, medially there is a broad *fenestra basicranialis*; laterally, the *foramen caroticum primarium* is rounded whereas the *f. craniopalatinum* is ovoid. The notochordal notch is long; posteriorly broad and anteriorly narrow.

TABLE 1 Summary of some character states for internal oral anatomy of *Boana* larvae

Species	Infralabial papillae pairs	Lingual papillae	Buccal floor arena rows of papillae	Buccal floor arena papillae on each side	Prepocket papillae	Postnarial papillae	Lateral roof papillae presence	Lateral roof papillae rows
<i>Boana crepitans</i>	1	2	2	20	5–7	10	+	2
<i>Boana albopunctata</i>	2	2	1	10–15	Not mentioned	Not mentioned	–	Not mentioned
<i>Boana albomarginata</i>	1	2	1	<10	Not mentioned	Not mentioned	+	1
<i>Boana atlantica</i>	2	4	0	Not mentioned	Not mentioned	Not mentioned	+	Not mentioned
<i>Boana caingua</i>	1	2	2	5–7	24	6	+	0
<i>Boana cinerascens</i>	1	2	1	<10	5–7	10–20	+	1
<i>Boana cordobae</i>	1	2	2	25	44	8	–	Not mentioned
<i>Boana faber</i>	2	2	2	38	18	19	+	0
<i>Boana geographica</i>	1	2	Not mentioned	10–15	10	6–10	+	2–3
<i>Boana joaquinii</i>	1	2	0	12–25	10–15	10–20	+	1
<i>Boana leptolineata</i>	1	2	2	Not mentioned	Not mentioned	Not mentioned	+	2
<i>Boana lundii</i>	2	4	0	25	Not mentioned	Not mentioned	+	Not mentioned
<i>Boana polytaenia</i>	2	2	Not mentioned	11–30	Not mentioned	8–10	+	1
<i>Boana prasina</i>	2	2	0	10–15	Not mentioned	Not mentioned	+	Not mentioned
<i>Boana pulchella</i>	1	2	2	22/63–83	16/6–8	6/11–20	+	1
<i>Boana punctata</i>	1	2	0	44	32	18	–	Not mentioned
<i>Boana raniceps</i>	2	2	2	24	20	12	–	Not mentioned
<i>Boana riojana</i>	2	2	2	64	14	18	–	Not mentioned
<i>Boana rosenbergi</i>	3	2	2	12	Not mentioned	4	–	Not mentioned
<i>Boana rufitela</i>	1	Not mentioned	1	18/15–25	Not mentioned	6–8	–	Not mentioned
<i>Boana semilineata</i>	1	2	Not mentioned	10–15	10	6–10	+	3–4

3.2.2 | Otooccipital region

Round otic capsules occupy approximately 27% of the chondrocranial length. They are dorsally connected by the *tectum synoticum*. The *crista parotica* is present laterally and the *processus anterolateralis* of the otic capsules is well developed and extends ventrally, toward the palatoquadrate, but do not contact with it. A large *fenestra ovalis* is found on the lateroventral wall of the otic capsule.

3.2.3 | Palatoquadrate

This element lies just below, parallel, and attaching to the braincase by the *commissura quadratocranialis anterior* and the *processus ascendens quadrati*. The *processus ascendens quadrati* has a low attachment (Sokol, 1981) to the braincase. The *processus muscularis quadrati* is tall, broad, has a rounded apex, and inclined toward the chondrocranial midline. A *commissura quadroorbitalis* is absent; a distinct *processus antorbillaris* projects from the anterior side of the braincase but does not fuse to the tip of *processus muscularis quadrati*. The *pars articularis quadrati* has a well-developed *processus quadratoethmoidalis*. The *fenestra subocularis* is large and oval, ventrally bounded by a broad

arcus subocularis with a distinct convex outer margin. The *processus pseudopterygoideus* and *processus oticus* larval are absent.

3.2.4 | Lower jaws

The *cartilago Meckeli* is sigmoid and articulate with the *pars articularis quadrati*. The *cartilago infrarostrales* are short, robust, and connected medially by the *commissura intermandibularis*.

3.2.5 | Hyobranchial apparatus

The ceratohyals have four well-developed processes. *Processus anterior hyalis*, *processus anterolateralis hyalis* and *processus posterior hyalis* are large and triangular; *processus lateralis hyalis* is elongated.

The ceratohyals are joined by the *pars reunions*. The *copula anterior* is broad and slender whereas the *copula posterior* is overall rectangular with a small and truncated *processus urobranchialis*. The *plana hypobranchiale* are broad and in contact with each other medially. The *ceratobranchialia* are long with lateral projections and continuous with the *plana hypobranchiale*. Three well-developed *spicula* are observed

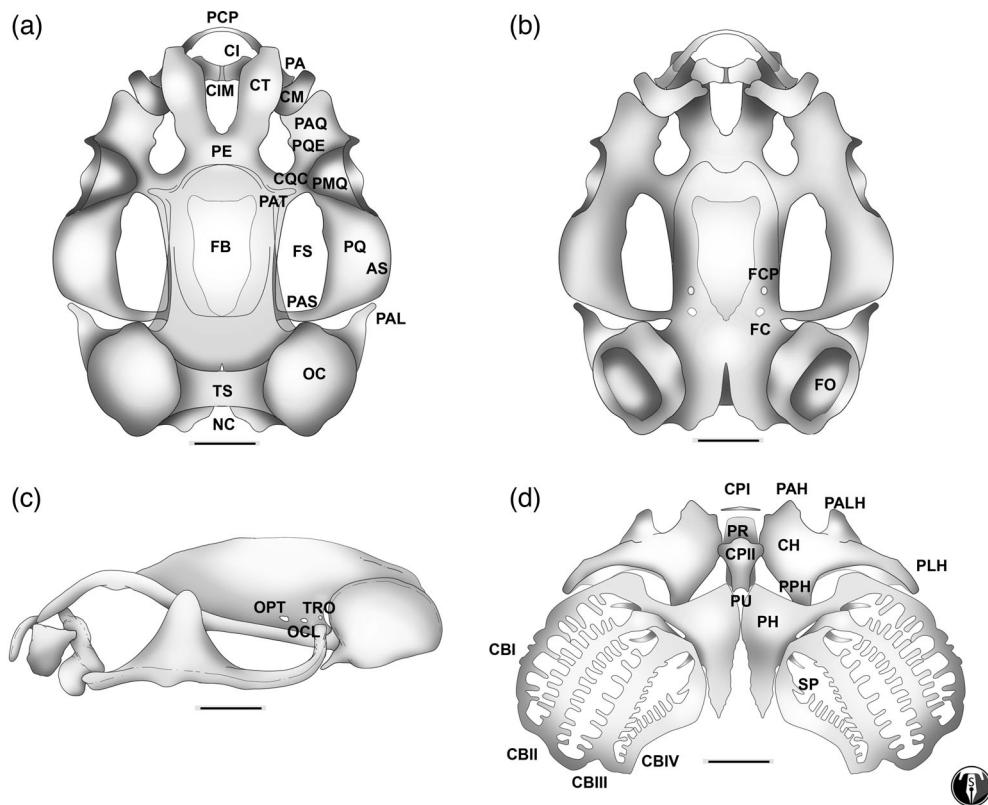


FIGURE 2 *Boana crepitans*, the chondrocranium and hyobranchial apparatus of tadpoles at Stages 30 and 36. (scale bar = 1 mm). (a) Dorsal view, (b) ventral view, (c) lateral view, (d) Hyobranchial apparatus. AS, arcus subocularis; CB (I, II, III, IV), ceratobranchial; CH, ceratohyal; CI, cartilages infrarostrales; CIM, commissura intramandibularis; CM, cartilago Meckeli; CPI, copula anterior; CPII, copula posterior; CQC, commissura quadratocranialis anterior; CT, cornua trabeculae; FB, fenestra basicranialis; FC, foramen caroticum primarium; FCP, foramen craniopalatinum; FO, fenestra ovalis; FS, fenestra subocularis; NC, notochord; OC, otic capsule; OCL, foramen oculomotorium; OPT, foramen opticum; PA, pars alaris; PAH, processus anterior hyalis; PAL, processus anterolateralis of the otic capsule; PALH, processus anterolateralis hyalis; PAQ, pars articularis quadrati; PAS, processus ascendens quadrati; PAT, processus antorbitalis; PCP, pars corporis; PE, planum ethmoidale; PH, planum hypobranchiale; PLH, processus lateralis hyalis; PMQ, processus muscularis quadrati; PPH, processus posterior hyalis; PQ, palatoquadrate; PQE, processus quadratoethmoidalis; PR, pars reuniens; PU, processus urobranchialis; SP, spicula; TRO, foramen trochlearis; TS, tectum synoticum

between the *ceratobranchia* and the fourth one is small. The *processus branchialis* is absent.

4 | DISCUSSION

4.1 | Internal oral morphology

Oral cavity in *Boana crepitans* is similar to other species of *Boana* as well as other Cophomantinae (Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007; D'Heursel & Haddad, 2007; Vera Candioti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015; this work). *Boana crepitans* lacks unique features in the oral cavity that would allow its distinction from other congeneric species. However, based on the literature review, we identified six internal oral morphology characteristics for Cophomantinae: (1) presence of at least a pair of large infrabuccal papillae with secondary projections, (2) a pair of lingual papillae, (3) 8–40 BFA papillae on

each side, (4) narial vacuities present, (5) a row of papillae or ridge on the prenarial arena, and (6) presence of lateral roof papillae. We consider these as purported synapomorphies for the subfamily; however, information on additional species in the genus is needed to verify them.

The buccal floor of *Boana*, *Aplastodiscus*, and *Bokermannohyla* have at least one pair of large infrabuccal papillae with secondary projections. Most *Boana* species have papillae with short projections (i.e., *B. albopunctata*, *B. albomarginata*, *B. cinerascens*, *B. crepitans*, *B. faber*, *B. geographica*, *B. joaquinii*, *B. lundii*, *B. rufitela*, *B. riojana*, and *B. semilineata*). Whereas *Boana caingua*, *B. prasina*, *Aplastodiscus* and *Bokermannohyla* species have digitiform projections (Wassersug, 1980; Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007; D'Heursel & Haddad, 2007; Vera Candioti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015; this work).

Cophomantinae have two lingual papillae; however, *Bokermannohyla luctuosa* has three and *B. atlantica* and *B. lundii* have four (Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007;

TABLE 2 Summary of some character states for chondrocranium and hyobranchial apparatus of *Boana* larvae

Species	<i>Boana crepitans</i>	<i>Boana geographica</i>	<i>Boana lanciformis</i>	<i>Boana pulchella</i>	<i>Boana raniceps</i>	<i>Boana rosenbergi</i>	<i>Boana semilineata</i>
Cornua trabeculae divergence	U-shaped	V-shaped	U-shaped	Not mentioned	Not mentioned	Not mentioned	V-shaped
Fenestra basicranialis presence	+	+	—	—	+	+	+
Foramen craniopalatinum	+	+	+	—	—	+	Not mentioned
Palatoquadrate/braincase connections	2	2	2	3	2	3	2
Processus oticus	—	Not mentioned	Not mentioned	Not mentioned	Absent	Present	Not mentioned
Processus branchialis	—	+	Not mentioned	Not mentioned	+	Not mentioned	+
Taenia tecti medialis	—	Not mentioned	+	—	+	+	Not mentioned
Taenia tecti transversalis	—	Not mentioned	+	—	+	—	Not mentioned

D'Heursel & Haddad, 2007; Vera Candiotti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015; this work). BFA papillae in *Boana* are shorter and range from 8 to 25 on each side (Wassersug, 1980; D'Heursel & de Sá, 1999; D'Heursel & Haddad, 2007; Vera Candiotti, 2007; Kolenc et al., 2008; this work). More numerous and longer BFA papillae were reported in *Aplastodiscus* (15–30 on each side, D'Heursel & Haddad, 2007) and *Bokermannohyla* (15–40 on each side, Spirandeli-Cruz & Gomes, 1991; D'Heursel & Haddad, 2007; Magalhães et al., 2015; Mongin & Carvalho-e-Silva, 2013; Pezzuti et al., 2015).

Narial vacuities are present in all reported Cophomantinae (Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007; D'Heursel & Haddad, 2007; Vera Candiotti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015; this work). Nasal vacuities were first reported in *B. rufitela* (=*Hyla rufitela*, Wassersug, 1980) and, subsequently, this structure in *B. crepitans* corroborates the hypothesis that this feature is a synapomorphy of Cophomantinae (Faivovich et al., 2005). However, the internal oral morphology has not been reported for any of *Colomascirtus*, *Hyloscirtus*, or *Myersiophyla*.

Prenarial arena typically possesses groups of papillae or ridges transversally arranged in *Boana* (*B. albopunctata*, *B. albomarginata*, *B. caingua*, *B. cinerascens*, *B. cordobae*, *B. crepitans*, *B. faber*, *B. geographica*, *B. joaquinii*, *B. leptolineata*, *B. lundii*, *B. prasina*, *B. pulchella*, *B. punctata*, *B. raniceps*, *B. rosenbergi*, *B. rufitela*, and *B. semilineata*), *Aplastodiscus* (*A. alboprenatus*, *A. eugenioi*, *A. callipygius*, *A. cochranae*, *A. peruviridis*), and *Bokermannohyla* (*B. caramaschi*, *B. flavopicta*, and *B. oxente* (Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007; D'Heursel & Haddad, 2007; Vera Candiotti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; Pezzuti et al., 2015; Magalhães et al., 2015; in this work)). Overall, three median-ridge shapes have been reported for Cophomantinae: semicircular/rounded, pentagonal, and triangular; always with undulations, pustules, or projections on its free margin (Spirandeli-Cruz & Gomes, 1991; D'Heursel & de Sá, 1999; Both et al., 2007; D'Heursel & Haddad, 2007; Vera Candiotti, 2007; Kolenc et al., 2008; Nascimento et al., 2009; this work). The postnarial arena

in *B. cordobae*, *B. pulchella*, *B. raniceps* (D'Heursel & Haddad, 2007; Kolenc et al., 2008), *B. lundii*, and *B. rufitela* (D'Heursel & Haddad, 2007; Wassersug, 1980) possess papillae arranged forming an inverted “V,” a pattern also found in *Aplastodiscus* (D'Heursel & Haddad, 2007) and *Bokermannohyla* (D'Heursel & Haddad, 2007; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015).

Lateral ridge papillae in *Boana* frequently have short projections on their edge (D'Heursel & Haddad, 2007; Kolenc et al., 2008; in this work), but in *B. rosenbergi*, the margin is postulated (Vera Candiotti, 2007) and in *B. riojana*, *B. raniceps*, and *Bokermannohyla*, these projections are digitiform (D'Heursel & Haddad, 2007; Kolenc et al., 2008; Magalhães et al., 2015; Mongin & Carvalho-e-Silva, 2013; Pezzuti et al., 2015).

BRA papillae are absent in many *Boana*, except *B. cordobae*, *B. leptolineata*, *B. riojana*, *B. pulchella*, and *B. prasina* (Both et al., 2007; D'Heursel & Haddad, 2007; Kolenc et al., 2008) that have short papillae delimiting the BRA, including *B. punctata*, which presents no more than two papillae (Kolenc et al., 2008). Some Cophomantinae have lateral roof papillae (D'Heursel & Haddad, 2007; Mongin & Carvalho-e-Silva, 2013; Magalhães et al., 2015; Pezzuti et al., 2015; this work) but these papillae are absent in *B. albopunctata*, *B. albomarginata*, *B. cinerascens*, *B. cordobae*, *B. punctata*, *B. raniceps*, and *B. riojana* (Alcalde & Rosset, 2003; D'Heursel & Haddad, 2007; Kolenc et al., 2008).

4.2 | Chondrocranial anatomy

Chondrocranial descriptions are scarce for Cophomantinae. The chondrocranium is similar among described *Boana*. The *pars corporis* and *pars alaris* are dorsally articulated in *Boana* and other Cophomantinae (de Sá, 1988; D'Heursel & de Sá, 1999; Alcalde & Rosset, 2003; Vera Candiotti, 2007; Hoyos et al., 2012). In *Boana raniceps*, the connection between the *pars corporis* and *pars alaris* with the *cornua trabeculae* is a syndesmotic connection (Alcalde & Rosset, 2003). The divergence of the *cornua trabeculae* in *Boana geographica* and *B. semilineata* is “V-shaped” whereas in *B. crepitans* and *B. lanciformis* is “U-shaped”

(de Sá, 1988; D'Heursel & de Sá, 1999; Vera Candiotti, 2007; this work). The palatoquadrate in *B. crepitans*, *B. geographica*, *B. lanciformis*, *B. pulchella*, *B. raniceps*, *B. rosenbergi*, and *B. semilineata* is attached to the braincase through two connections: the *commissura quadratocranialis anterior* and the *processus ascendens quadrati* (Lavilla & Fabrezi, 1987; de Sá, 1988; D'Heursel & de Sá, 1999; Alcalde & Rosset, 2003; Vera Candiotti, 2007; Hoyos et al., 2012).

Boana crepitans, *B. pulchella*, *B. raniceps*, and *B. rosenbergi* have a *processus ascendens quadrati* that is attached perpendicularly to the braincase whereas in *B. geographica* and *B. semilineata* it is attached obliquely (Lavilla & Fabrezi, 1987; de Sá, 1988; D'Heursel & de Sá, 1999; Alcalde & Rosset, 2003; Vera Candiotti, 2007; Hoyos et al., 2012). In *B. crepitans* and *B. lanciformis*, the *processus ascendens* connects the palatoquadrate to the braincase in the anterior area to the otic capsule, low attachment sensu Sokol, 1981 (de Sá, 1988, this work). The *foramina craniopalatina* are identifiable on the braincase floor in *B. crepitans* and *B. geographica* at Stage 30, but not in *B. semilineata* (D'Heursel & de Sá, 1999; this work).

A crista parotica has been reported for *B. crepitans*, *B. geographica*, *B. lanciformis*, *B. pulchella*, *B. semilineata*, and *B. raniceps* (D'Heursel & de Sá, 1999; de Sá, 1988; Lavilla & Fabrezi, 1987; Alcalde & Rosset, 2003; this work). The *processus anterolateralis* is very large and acute in *Boana crepitans*, *B. geographica*, *B. lanciformis*, *B. pulchella*, *B. raniceps*, *B. rosenbergi*, and *B. semilineata* (Lavilla & Fabrezi, 1987; de Sá, 1988; D'Heursel & de Sá, 1999; Vera Candiotti, 2007; this work). The *processus anterolateralis* is not continuous but contact with the posterior edge of the palatoquadrate by a tiny fibrous ligament; this may correspond to otic ligament described (state "1" of character 66, Haas, 2003).

The *hyobranchial apparatus*, in all *Boana* has three well-developed *spicula* and the fourth one is scarcely visible (Lavilla & Fabrezi, 1987; de Sá, 1988; D'Heursel & de Sá, 1999; Vera Candiotti, 2007; this work).

Our comparisons of the internal oral morphology and chondrocranial anatomy of *Boana crepitans* with the limited available data for the larvae of other species of *Boana* showed overall similarity on these larval traits. However, given the scarcity of data on the chondrocranial anatomy for species of the *B. faber* group, precludes highlighting characteristics for this clade and highlights the need for further studies of the larval anatomy on this group.

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AUTHOR CONTRIBUTIONS

Marianna Rodrigues de Oliveira: Conceptualization; formal analysis; investigation; methodology; project administration; writing-original draft. **Luiz Weber:** Methodology; resources; supervision; writing-

original draft. **Johnny Ferreira:** Conceptualization; investigation; writing-review & editing. **Anna Coimbra Libório:** Conceptualization; investigation; methodology. **André uimaraes Takazone:** Investigation; methodology; writing-original draft. **Rafael de Sá:** Conceptualization; methodology; writing-original draft; writing-review & editing.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study

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