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# Chondrocranium and internal oral morphology of the tadpole of *Corythomantis greeningi* (Anura: Hylidae)

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## Abstract

**Chondrocranium and internal oral morphology of the tadpole of *Corythomantis greeningi* (Anura: Hylidae).** *Corythomantis greeningi* is a casque-headed frog that occurs in xeric and sub-humid regions of northeastern Brazil. Individuals are often found on rocks on banks of temporary streams or in ponds upon “lajedos”. Suctorial tadpoles are often found clasping to the rocks in the streams so as not to be dragged by the current; therefore, they have modified external and internal morphology. Here, we describe the internal oral anatomy and the chondrocranium of the tadpole of *C. greeningi* and compare it to the available descriptions of Lophyohylineae and other suctorial tadpoles. The internal oral morphology in *C. greeningi* resembles pond-dwelling casque-headed frogs, although it has been found in temporary lotic environments. *Corythomantis greeningi* has unusual chondrocranial morphology relative to that of other described Lophyohylineae, including marked differences at the *cornua trabeculae* and *palatoquadrate*. Apparently, the chondrocranial morphology is related to its ecomorphology, because it is structurally more similar to other suctorial tadpoles that inhabit lotic environments than to phylogenetically related species such as *Trachycephalus typhonius* and *Phyllodytes gyrinaethes*.

**Keywords:** Casque-headed Frog, cranial morphology, Lophyohylineae, oral cavity.

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## Resumo

**Morfologia do condrocânio e da cavidade oral do girino de *Corythomantis greeningi* (Anura: Hylidae).** *Corythomantis greeningi* é uma perereca-de-cabeça-ossificada que ocorre em regiões xéricas e sub-úmidas do nordeste do Brasil. Frequentemente os indivíduos são encontrados sobre as rochas às margens de riachos temporários ou em acúmulos de água nos “lajedos”. Girinos suctoriais muitas vezes são encontrados aderidos às rochas dos riachos para não serem carreados pelas correntes e por isso, apresentam morfologia externa e interna muito particulares. Aqui, descrevemos a anatomia oral interna e o condrocânio do girino de *C. greeningi* e comparamos com as descrições disponíveis de representantes da subfamília Lophyohylineae e outros girinos suctoriais. A morfologia oral interna em *C. greeningi* assemelha-se aos girinos dos demais sapos de cabeça ossificada que se desenvolvem em poça, apesar deste ter sido encontrado em ambiente temporário lótico. *Corythomantis greeningi* tem uma morfologia condrocranial particular em relação aos outros Lophyohylineae descritos, apresentando marcadas diferenças nos *cornua trabeculae* e *palatoquadrate*. Aparentemente, a morfologia do condrocânio está mais relacionada a aspectos ecomorfológicos, pois é estruturalmente mais semelhante a outros girinos suctoriais que habitam ambientes lóticos do que com espécies filogeneticamente mais próximas, como *Trachycephalus typhonius* and *Phyllodytes gyrinaethes*.

**Palavras-chave:** cavidade oral, Lophyohylineae, morfologia craniana, perereca-de-cabeça-ossificada.

## Introduction

The neotropical genus *Corythomantis* Boulenger, 1896 currently comprises two species, *C. galeata* Pombal, Menezes, Fontes, Nunes, Rocha, and Van Sluys, 2012 and *C. greeningi* Boulenger, 1896. These species occur in northeastern Brazil, and the genus is currently placed in the subfamily Lophyohylineae Miranda-Ribeiro, 1926, along with 11 other genera. Most members of this clade are known as casque-headed frogs: *Aparasphenodon*, *Argenteohyla*, *Dryaderces*, *Itapotihyla*, *Nyctimantis*, *Osteocephalus*, *Osteopilus*, *Phyllodytes*, *Phytotriades*, *Tepuihyla*, and *Trachycephalus* (Duellman *et al.* 2016, Frost 2017).

*Corythomantis greeningi* is distributed throughout Atlantic Forest and Caatinga morphoclimatic domains, in xeric and sub-humid regions of northeastern Brazil (Frost 2017). Individuals usually are found on vegetation, including in bromeliads, and frequently in rock outcrops near temporary streams (Juncá *et al.* 2008, IUCN 2017).

The tadpole morphology of *C. greeningi* corresponds to typical morphology for suctorial

larvae inhabiting benthic fast-water habitats. According to McDiarmid and Altig (1999), suctorial tadpoles are often found clasping rocks in streams so as not to be dragged by the current and therefore have modified external and internal morphology. Juncá *et al.* (2008) described and illustrated the external morphology of the larvae based on specimens from Serra São José and Lages, state of Bahia, Brazil. However, the internal oral anatomy and chondrocranial morphology is not known. We describe the internal oral anatomy using scanning electron microscopy (SEM) and chondrocranial morphology of *C. greeningi* and compare them with available descriptions for other casque-headed treefrogs and suctorial tadpoles.

## Materials and Methods

Tadpoles were collected at Fazenda Água Doce (12°11'46,84" S, 44°57'9,59" W), Municipality of Barreiras, Bahia state, Brazil. This population inhabits an area of seasonal forest in the Cerrado biome, predominant at this locality. Species identification was made by comparing the larvae with the available description in Juncá *et al.*

(2008) and by raising larvae in the laboratory through metamorphosis. Voucher specimens were preserved in 8% formalin and deposited in the herpetological collection of the Museu de Zoologia da Universidade Federal da Bahia (UFBA10612) and Universidade Federal do Maranhão (HUFMA2083–2085).

Tadpole stages were determined following Gosner (1960) using Leica EZ4 and Leica 10S8APO stereomicroscopes. Morphological descriptions are based on individuals at Stage 33 and 35 ( $N = 9$ ). Dissections for internal oral morphology followed Wassersug (1976). Internal oral anatomy was photographed using scanning electron microscopy (SEM). Specimens for SEM were dissected, washed 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 M phosphate buffer, post fixed for 2 h in a 1% solution of osmium tetroxide at room temperature, and followed by another three 15 min washes in 0.1 M phosphate buffer. 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  $\text{CO}_2$ , mounted on aluminum stubs and sputter coated with gold and palladium in camera Denton Vacuum desk III Cold sputter-Etch Unit. Features of dorsal and ventral internal oral anatomy were examined and photographed using a scanning electron microscope attached to a computer with Jeol JSM 6360LV operating system. Internal oral anatomy terminology follows Wassersug (1976). Measurements and observation of the oral morphology features were made using an ocular micrometer under a stereoscopic microscope (Leica 10S8APO).

Specimens for chondrocranial morphology were bleached and double-stained for bone and cartilage using the technique of Taylor and van Dyke (1985); terminology follows De Sá (1988) and Haas (1995, 1997). Chondrocranial illustrations were produced in Photoshop CS5 from photographs obtained under a stereomicroscope with the image analyzer.

## Results

### *Internal Oral Morphology (Figure 1) (N = 5, Stages 33 and 35)*

The buccal floor is overall triangular; anteriorly, two pairs of infralabial papillae are present. The posterior pair is larger and hand-shaped with papillae along the edge. The lingual bud has one pair of lingual papillae. The buccal pockets are large and shallow, obliquely arranged, and have a few prepocket papillae and pustules. The buccal floor arena (BFA) is diamond-shaped, with 8–10 conical papillae on each side. A larger and bifurcated papilla is found on each side, closer to the buccal pocket; the buccal floor is scattered with pustulations except in the central area. The ventral velum is long, and has two marginal projections on each side of a well-marked median notch. The velar margin has secretory pits, and the glottis is distinct and exposed.

The buccal roof is overall triangular and concave. The prenarial arena bears a Y-shaped ridge and some pustulations. The nares are wide, obliquely oriented in transverse plane, and have high posterior margins forming a narial vacuities. The postnarial arena has five to six conical papillae and some pustulations. The median ridge is overall semicircular, sometimes appearing trapezoid in shape, and the free edge is slightly serrated. The lateral ridge papillae are triangular, with irregular edges. The buccal roof is densely pustulated, but lacks papillae delimiting the buccal roof arena (BRA). About three small lateral roof papillae are found aligned on each side. The glandular zone has distinct secretory pits. The dorsal velum is wide laterally and has a glandular folded edge.

### *Chondrocranial Morphology (Figure 2) (N = 4, Stages 33 and 35)*

The chondrocranium is oval-shaped and slightly longer than wide. The suprarostrals cartilages consist of two elements: *pars corporis*

and *pars alaris*. These elements are proximally fused at the point of articulation with the *cornua trabeculae* and are distally separated by a notch. The *pars alaris* has a short *processus anterior dorsalis* and a rounded and acute *processus posterior dorsalis*. The *cornua trabeculae* are robust, short, and have a broad distal edge a V-shaped divergence and with a U-shaped notch in dorsal view; the *processus lateralis trabeculae* is absent.

**Braincase.**—The anterior wall of the braincase is formed by a broad *planum ethmoidale*: dorsolaterally and posteriorly it is delimited by the *taenia tecti marginalis* and the *tectum synoticum* respectively, defining a large and undivided frontoparietal fontanelle. The *cartilago orbitalis* is poorly chondrified (e.g. lightly stained) and the *foramen opticum*, *f. trochlearis*, and *f. oculomotorium* are not visible. Medially, the braincase floor is poorly chondrified and has a broad *fenestra basicranialis*; the *foramen caroticum primarium* and *f. craniopalatinum* are visible and ovoid-shaped.

**Palatoquadrate.**—This long cartilage, with smooth margins, attaches to the braincase through three connections: the *commissura quadratocranialis anterior*, the *processus ascendens* and the larval *processus oticus*. The *processus articularis quadrati* is short and wide and the *commissura quadratocranialis anterior* is about twice as broad as the *processus articularis quadrati*. The *fenestra subocularis* is overall ovoid, and is longer than wide. The *arcus subocularis* has an irregular external edge and is posteriorly narrower. The *processus muscularis quadrati* inclines toward the braincase; the *processus quadratoethmoidalis* and the *commissura quadratoorbitalis* are absent. The *processus ascendens* is short and has a low attachment to braincase.

**Otooccipital region.**—The otic capsules are overall quadrangular and overlie the *processus ascendens*; they represent about 25% of the

chondrocranial length and are dorsally connected by the *tectum synoticum* that forms the dorsal edge of the *foramen magnum*. The *processus anterolateralis* reaches the posterior curvature of the palatoquadrate and a larval *processus oticus* is formed. The *fenestra ovalis* is moderate in size.

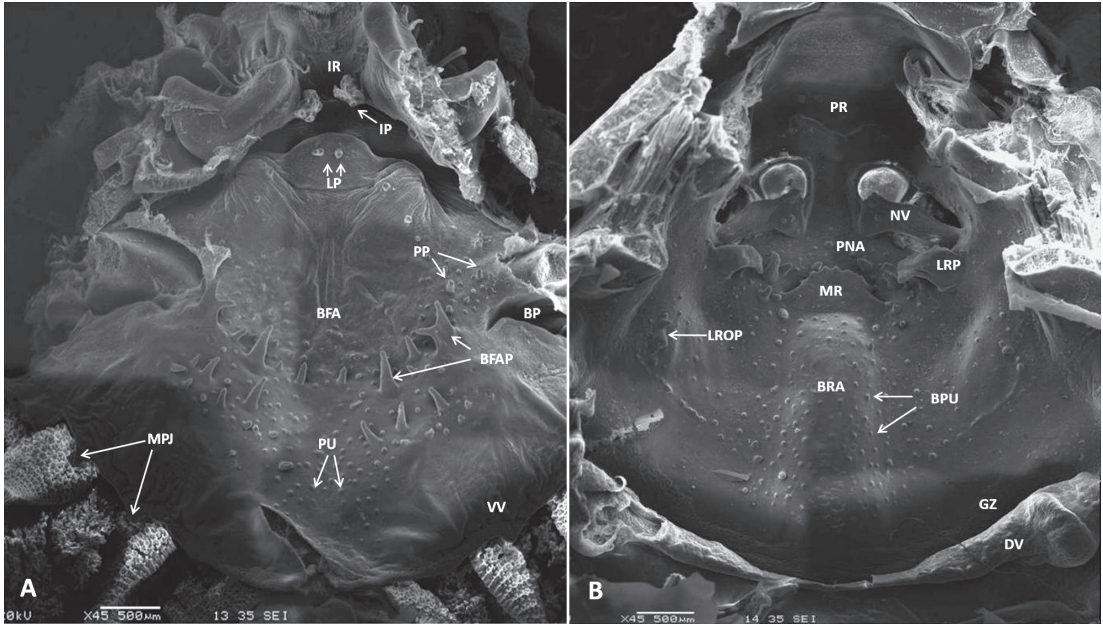
**Lower jaws.**—The *cartilago Meckeli* are sigmoid and articulate with the *pars articularis quadrati*. The *cartilago infrarostrales* are short, robust, and connected medially by the *commissura intermandibularis*.

**Hyobranchial apparatus.**—The *copula anterior* is short and the *copula posterior* is rectangular and has a small and truncated *processus urobranchialis*. The ceratohyals bear well-developed *processus anterior hyalis*, *processus anterolateralis hyalis*, *processus lateralis hyalis*, and *processus posterior hyalis*. The ceratohyals are joined by the *pars reuniens*. The *condylus articularis* is short. The hypobranchial plates are well-developed, medially connected by the *commissura inter-hyal*; *ceratobranchialia I-V* are long, thin, and distally connected through the *commissurae terminales I-III* and proximally by *commissura proximalis I-II*; spicule I, II and III are well-developed, but spicule IV is very small and scarcely visible.

## Discussion

Available information on the internal anatomy of Lophyohylineae larvae is currently limited. Among the 83 described species, the internal oral morphology has been reported in *Aparasphenodon brunoi* Miranda-Ribeiro, 1920 (Wogel *et al.* 2006), *Argenteohyla siemersi* (Mertens, 1937) (Cajade *et al.* 2010), *Osteopilus ocellatus* (Linnaeus, 1758) (= *O. brunneus* Trueb and Tyle, 1974) and *O. septentrionalis* (Duméril and Bibron, 1841) (Lannoo *et al.* 1987), *Osteocephalus oofhagus* Jungfer and Schiesari, 1995 and *O. taurinus* Steindachner, 1862 (Schiesari *et al.* 1996), *Phyllodytes brevirostris*





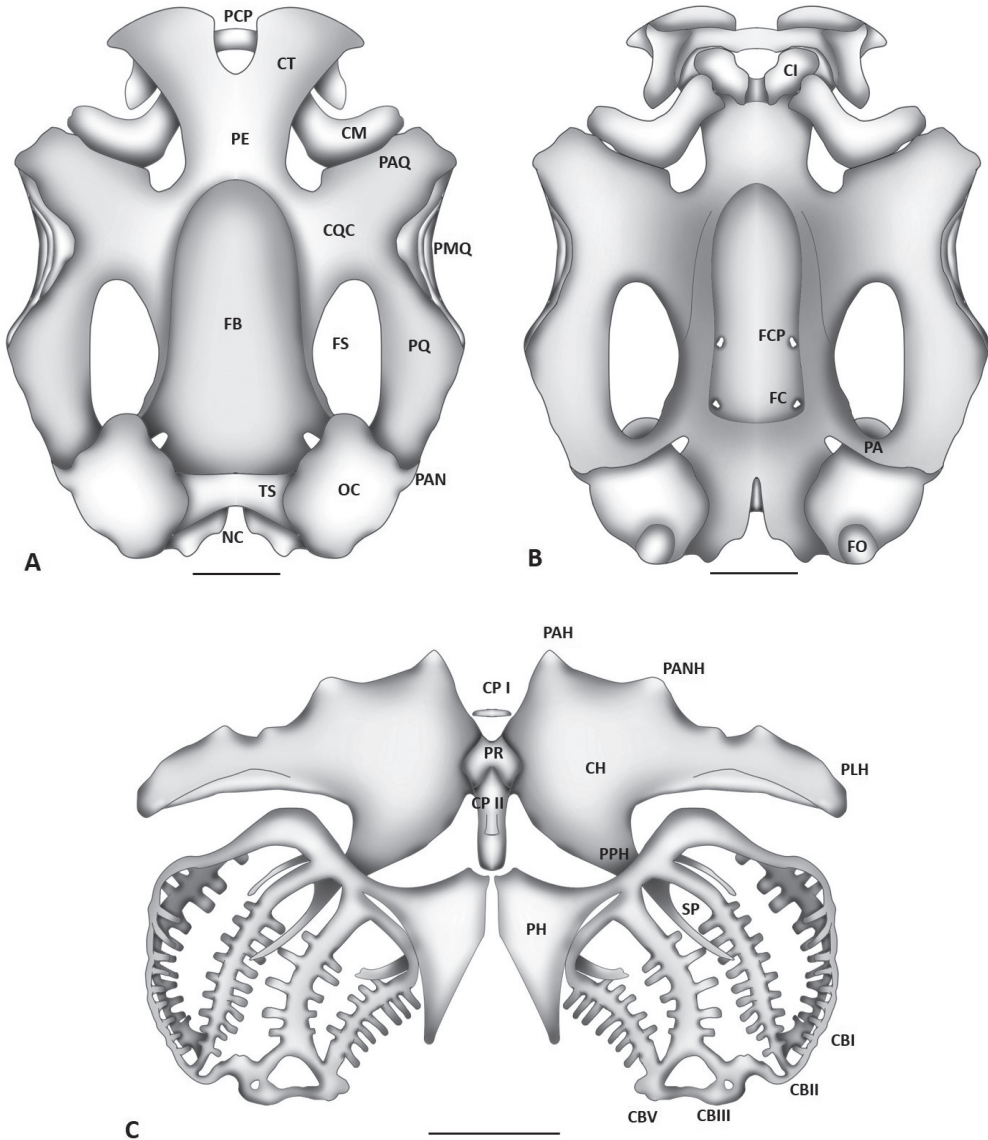
**Figure 1.** Internal oral morphology of *Corythomantis greeningi* tadpoles. (A) Buccal floor and (B) buccal roof. (IR) infralabial region, (IP) infralabial papillae, (LP) lingual papillae, (PU) pustulations, (BFA) buccal floor arena, (BFAP) buccal floor arena papillae, (PP) prepocket papillae, (BP) buccal pocket, (VV) ventral velum, (MPJ) projections and (SPT) secretory pits, (BPU) buccal roof arena pustulations, (BRA) buccal roof arena, (PR) prenarial region; (NV) narial valve, (PNA) postnarial arena, (MR) median ridge, (LR) lateral ridge, (BRA) buccal roof arena, (LROP) lateral roof papillae, (GZ) glandular zone, (DV) dorsal velum. Specimens at Stage 35.

Peixoto and Cruz, 1988 (Vieira *et al.* 2009), *P. wuchereri* (Peters, 1873) (Magalhães *et al.* 2015a), *Trachycephalus atlas* Bokermann, 1966 (Barreto *et al.* 2015), *T. cunauaru* Gordo, Toledo, Suárez, Kawashita-Ribeiro, Ávila, Morais, and Nunes, 2013 (Grillitsch 1992), *T. resinifictrix* (Goeldi, 1907) (Schiesari *et al.* 1996), and *T. typhonius* (Linnaeus, 1758) (Schiesari *et al.* 1996, Fabrezi and Vera 1997), representing only 14% of the species. Cajade *et al.* (2010) provided valuable comparisons of the internal oral morphology of the available Lophyohyline tadpoles. Chondrocranial morphology has been reported only for *Aparasphenodon bruno*i (Da Silva 1994), *Phyllodytes gyrinaethes* Peixoto, Caramaschi, and Freire, 2003 (Vera-Candiotti *et al.* 2017), *T. resinifictrix*

(some features by Haas 2003) and *T. typhonius* (Fabrezi and Vera 1997).

Tadpoles of Lophyohyline display different ecomorphological types, from the most generalized pond-dwelling species (e.g. many *Trachycephalus*) to those highly specialized forms such as arboreal bromeliad-dwelling types (e.g. *Osteocephalus*, *Osteopilus* and *Phyllodytes*), gastromyzophorous forms (e.g. *P. gyrinaethes*), and suctorial types such as *Corythomantis greeningi* (McDiarmid and Altig 1999).

*Corythomantis greeningi* reproduces in temporary shallow rivers, which mainly form during the rainy season across wide bare stones locally named “lagedos”. In this environment, males call among rock crevices and tadpoles can be observed in small ponds along the drying



**Figure 2.** Chondrocranial morphology of *Corythomantis greeningi* tadpoles. (A) Chondrocranium in dorsal view; (B) Chondrocranium in ventral view; (C) hyobranchial apparatus. (scale bar = 2 mm). (Pcp) pars corporis, (CI) cartilagine infrastralis, (CT) cornua trabeculae, (CM) cartilago Meckeli, (PE) planum ethmoidale, (PAQ) pars articularis quadrati, (PMQ) processus muscularis quadrati, (CQC) commissura quadratocranialis anterior, (FS) fenestra subocularis, (PQ) palatoquadrate; (PA) processus ascendens quadrati; (OC) otic capsule; (TS) tectum synoticum; (PAN) processus anterolateralis; (FB) fenestra basicranialis; (fcp) foramen craniopalatinum; (FC) foramen caroticum primarium; (NC) notochordal canal; (FO) fenestra ovalis (CPI) copula anterior, (PR) pars reuniens, (CP II) copula posterior, (CH) ceratohyal, (PAH) processus anterior hyalis, (PANH) processus anterolateralis hyalis, (PLH) processus lateralis hyalis, (PPH) processus posterior hyalis, (PH) planum hypobranchiale, (sp) spicula, (CB I, II, III, IV) Ceratobranchial, (TS) tectum synoticum. Specimens at Stage 35.

river bed, in lotic waters, or, frequently, clasping on the rocky river bed (Juncá *et al.* 2008). Suctorial anuran larvae are highly specialized for living in fast-flowing waters, using their oral discs as adhesive organs to attach to the substrate (Haas and Richards 1998).

The internal oral morphology in *C. greeningi* resembles pond-dwelling casque-headed frogs (Cajade *et al.* 2010), although it has been found in temporary lotic environments. Casque-headed frog tadpoles from lentic and lotic environments have more complex and specialized internal oral features when compared to the overall reduction observed within arboreal tree-hole-dwelling and bromeliad-dwelling casque-headed frog larvae (Cajade *et al.* 2010). Within the buccal floor, the infralabial region frequently has a variable number of short papillae or pustules anteriorly to one or two pairs of broad based and large papillae with branching edges. An exception is *Osteopilus ocellatus* (= *O. brunneus*), in which the infralabial region is free from papillae and pustules (Lannoo *et al.* 1987), and is usually associated with the first filter to select the particles that will be captured for food (Wassersug 1980).

The central area of the buccal floor arena (BFA) is always bare, with papillae and pustules found on the lateral and lower regions. The BFA papillae are often conical or digitiform; typically, there is a large papilla with a broad base or two or more fused papillae near the buccal pocket (Lannoo *et al.* 1987, Schiesari *et al.* 1996, Wogel *et al.* 2006, Cajade *et al.* 2010; this work).

The prenarial arena possess pustules or small papillae that fuse to form ridges with variable shapes (e.g. “Y”, “U”, “T” or irregular shaped). The choanae are wide and vary in orientation in relation to the median line (e.g., 10°, 25°, 45°, and 90°). The nasal vacuities observed in *C. greeningi* are unique, and not described for other Lophyohylineae species. These structures were first reported in *Boana rufitela* (Fouquette, 1961) (= *Hyla rufitela*; Wassersug 1980), suggested as chemoreceptors and considered a putative synapomorphy for the subfamily Cophomantinae,

which includes the genera *Aplastodiscus*, *Bokermannohyla*, *Colomascirtus*, *Hyloscirtus*, *Boana* and *Myersiophyla* (Faivovich *et al.* 2005, Duellman *et al.* 2016). Cophomantinae and Lophyohylineae are closely related according to Duellman *et al.* (2016). Similar to *C. greeningi*, some Cophomantinae are found in lotic environments, such as temporary streams (e.g. Mongin and Carvalho-e-Silva 2013, Magalhães *et al.* 2015b).

Most Lophyohylineae tadpoles have densely scattered pustules on the buccal roof arena and 3–6 papillae may be found in some species (these papillae are absent in *C. greeningi*); these tadpoles commonly have short lateral roof papillae but these are variable in number among species (Lannoo *et al.* 1987, Schiesari *et al.* 1996, Wogel *et al.* 2006, Cajade *et al.* 2010; this work). *Osteopilus septentrionalis* lacks pustules and lateral roof papillae (Lannoo *et al.* 1987). Some Cophomantinae have lateral roof papillae (D ‘Heursel and Haddad 2007, Mongin and Carvalho-e-Silva 2013, Magalhães *et al.* 2015b, Pezzuti *et al.* 2015).

The lack of descriptions of the chondrocranium in Lophyohylineae limits the taxonomic comparisons presented here with more closely related species. Some available descriptions are brief and do not contain illustrations. The chondrocranium of *Aparasphenodon brunoi* is briefly described by Da Silva (1994), but is not figured. *Trachycephalus resinifictrix* was not fully described by Haas (2003), and only a few characters were discussed.

*Corythomantis greeningi* has a different chondrocranial morphology relative to other described Lophyohylineae; marked differences occur in the *cornua trabeculae* and *palatoquadrate*. *Corythomantis greeningi* differs from *Trachycephalus typhonius* in *cornua trabeculae* size (larger in *C. greeningi*), shape and distal edge of the *cornua trabeculae* (“V” shaped and with a broad distal edge in *C. greeningi*), *processus articularis quadrati* and *commissura quadratocranialis* width (very broad in *C. greeningi*) and *processus muscularis quadrati*

width (wider in *C. greeningi*). *Corythomantis greeningi* and *Trachycephalus typhonius* have the parotic crista and larval *processus oticus* (Fabrezi and Vera 1997; this work), but these structures are absent in *Phyllodytes gyrinaethes* (Vera-Candiotti et al. 2017).

The external and chondrocranial morphology of the tadpole of *Corythomantis greeningi* is more similar to other tadpoles that clasp onto substrate and inhabit lotic environments, such as Pelodyadinae Günther, 1858 *Ranoidea dayi* (Günther, 1897) (= *Nyctimystes dayi*), *R. nannotis* (Andersson, 1916) (= *Litoria nannotis*) and Mantellidae Laurent, 1946 *Boophis* sp. (Haas and Richards 1998). Tadpoles of these species are characterized by a dorsoventrally flattened body, thick tail muscle, tail fin originating posterior to the tail-body junction, undivided tooth rows, and a large, ventrally located oral disc with an uninterrupted outer row of oral papillae (Haas and Richards 1998). Some of these features are described for *C. greeningi* in Juncá et al. (2008).


According to Haas and Richards (1998) suctorial tadpoles evolved several times independently in Anura and share various features regardless of their phylogenetic position. Among these features are the *cornua trabeculae* that are expanded anteriorly and sometimes fused, robust lower jaws, greatest width of the skull at the level of the jaw articulation (not in *C. greeningi*), upper jaw cartilages partially or fully fused, *palatoquadrate* robust and connected to the skull by a wide *commissura quadratocranialis anterior*, *processus oticus*, *processus basalis* (in some species), and *processus ascendens* (vestigial or absent in some species). The external and internal morphology of the tadpole of *Phyllodytes gyrinaethes* recently described by Vera-Candiotti et al. (2017) is highly modified, with marked restructuring of the oral region, *palatoquadrate*, and branchial baskets, features considered unique among known tadpoles.

The chondrocranial morphology of *Corythomantis greeningi* apparently is related to its ecomorphology, because it is structurally more

similar to other tadpoles that inhabit lotic environments and clasp onto the substrate (e.g. Clasping, Adherent and Suctorial) (McDiarmid and Altig 1999) than to closely related species such as *Trachycephalus typhonius* (Fabrezi and Vera 1997) and *P. gyrinaethes* (Vera-Candiotti et al. 2017).

The data presented in this work corroborate in part the phylogenetic tree for Lophyohylineae proposed by Duellman et al. (2016) because of the similarity between the internal oral morphology of the tadpoles of *C. greeningi* and those of pond-dwelling casque-headed frogs, such as many species of *Trachycephalus*. However, our data do not corroborate many aspects of the external and chondrocranial morphology, which correlates better with ecomorphology than with phylogeny.

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