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Research paper

Comparative larval buccopharyngeal morphology of two glass frog species (Anura: Centrolenidae: *Vitreorana*)

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ABSTRACT

Centrolenidae is a monophyletic group of Neotropical tree frogs. Centrolenid tadpoles usually lack pigmentation on their bodies, presenting reddish coloration in life, and are fossorial. Several phenotypic characters have been associated with fossoriality, but data on larval morphology is scarce. Herein, we describe the buccopharyngeal morphology of two *Vitreorana* tadpoles and identify putative synapomorphies for the family, including 1) the presence of vacuities on the buccal roof arena; 2) the nares being oriented longitudinally; 3) the presence of a conical median ridge at the end of the postnarial arena; and 4) the posterior–most pair of postnarial papilla being aligned in row with the median ridge.

1. Introduction

Centrolenidae is a monophyletic group of tree frogs that currently comprises 156 species (Frost 2020) found throughout Central and South America, from southern Mexico to northern Argentina (Frost 2020). Centrolenids are commonly known as glass frogs due to their transparent ventral skin, leaving some or all internal organs visible (Cisneros-Heredia & McDiarmid 2007; Guayasamin et al. 2009; 2020; Rada et al. 2017). These small frogs are also known for their complex breeding biology that, in most cases, involves male combat, courtship, and maternal or paternal care (Delia et al. 2017a). Eggs are laid on leaves or rocks outside of water, and, after hatching, the tadpoles drop into the water to complete their development (Altig & McDiarmid 2007; Delia et al. 2014 2017b).

Glass frog tadpoles develop in fast-flowing streams (Ruiz-Carranza & Lynch 1991a), burrowing into the substrate (Altig & Johnston 1989; Mijares-Urrutia 1990; Rada et al. 2007) where they feed on the microbiota (Verbug et al. 2007). Externally, they are characterized by an elongate, depressed body, reduced eyes and oral disc, robust caudal muscles, shallow tail fins, and depressed, truncate snouts (Hoffman 2010; Rada et al. 2019). Similarly, like the adults, most centrolenid tadpoles are devoid of skin pigmentation (but see Rada et al. 2007), being almost translucent; interestingly, in life, they are usually reddish as a result of the extensive blood flow through the densely vascularized integument (Hoffman 2010; Ospina-Sarria et al. 2011; Rada et al. 2019).

The peculiar phenotype associated with their fossorial habits makes glass frogs tadpoles unique among Neotropical anurans; however, their morphology and ecology are poorly studied (Hoffman 2010). To date, only 37 tadpoles have been described (Rada et al. 2019), corresponding to less than 25% of the known species diversity. The lack of knowledge of their internal morphology is even more striking: buccopharyngeal morphology has only been described for *Hyalinobatrachium fleischmanni* (Boettger 1893), *Ikakogi ispacue* Rada et al. 2019, and *Ikakogi tayrona* (Ruiz-Carranza & Lynch 1991b) (Wassersug 1980; Rada et al. 2019), and larval muscles and chondrocranial morphology have only been described for *Cochranella granulosa* (Taylor, 1949) (Haas 2003) and the two species of *Ikakogi* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada, and Vilà, 2009 (Rada et al., 2019).

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The lack of data contrasts with the highly variable phenotype of centrolenid tadpoles that can be highly informative for the taxonomy, phylogeny, and ecology of the family. For example, Rada et al. (2019) studied the tadpoles of *Ikakogi* and described several new characters, including new musculo-skeletal character-states never reported for any other anuran larvae (e.g. an additional slip of the levator arcuum branchialium III on the dorsal surface of the otic capsule). Similarly, larval characters were pivotal for the recognition of *I. ispacue*, the second species of the genus.

The dearth of information on larvae is exemplified by *Vitreorana* Guayasamin et al., 2009. The genus currently comprises 10 species found throughout the Amazonian and Guyana Basins from Colombia to French Guiana and from Venezuela to the Atlantic forest in Brazil (Frost 2020). They are characterized by the presence of white hepatic peritonea (partially covering liver in *Vitreorana ritae* (Lutz 1952); see Guayasamin et al. 2009). Although tadpoles of half the species have been described, including *Vitreorana castroviejoi* (Ayarzagüena & Señaris, 1997) (Señaris & Ayarzagüena, 2005), *Vitreorana eurygnatha* (Lutz, 1925) (Heyer, 1985), *Vitreorana helenae* (Ayarzagüena 1992) (Señaris & Ayarzagüena, 2005), *V. ritae* (Menin et al., 2009), and *Vitreorana uranoscopa* (Müller, 1924) (Heyer 1985), most were in early developmental stages, and no aspects of their internal morphology are known. In the present study, we compare the buccopharyngeal anatomy of *V. eurygnatha* and *V. uranoscopa*—*V. eurygnatha* is distributed in the highlands of southeastern Brazil, from Bahia to Santa Catarina states, Brazil, and *V. uranoscopa* can be found from Minas Gerais to Rio Grande do Sul states in Brazil, but also in northeastern Argentina (Frosts 2020)— and comment on its value for the systematic of the family.

2. Materials and methods

All material used in the descriptions is housed at the Museu de Zoologia da Universidade de São Paulo (MZUSP) under catalog numbers MZUSP 80034 (*V. eurygnatha*; collected Senador Vergueiro, Campo de fruticulture de Bocaina, SP, Brazil) and MZUSP 59946 (*V. uranoscopa*; collected in Teresópolis, RJ, Brazil), and preserved in formalin solution. Tadpoles were identified by comparison with the published descriptions (Heyer 1985); we examined all the characters proposed by Heyer (1985:14–16) as diagnostic (e.g. snout length, mouth position, marginal and submarginal papillae arrangement). Tadpole staging follows Gosner (1960).

Two individuals per species (stages 34–36) were dissected according to Wassersug (1976) to expose the buccopharyngeal cavity. One individual per species (stage 36 for *V. eurygnatha* and 34 for *V. uranoscopa*) was submitted to the protocol of Alcalde and Blotto (2006) for scanning electron microscopy (SEM). Descriptive terminology follows Wassersug (1976, 1980), with additions by Dias et al. (2018a) and Rada et al. (2019).

We compared our results to data available in the literature (Wassersug 1980). Additionally, we directly observed the buccopharyngeal morphology of two *Ikakogi* species for comparison, housed at the Colección herpetológica de la Universidad del Magdalena, Santa Marta, Colombia (CBUMAG:ANF 01016, *I. ispacue*, stage 28) and the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN 58308, *I. tayrona*, stage 29).

3. Results

3.1. *Vitreorana eurygnatha*

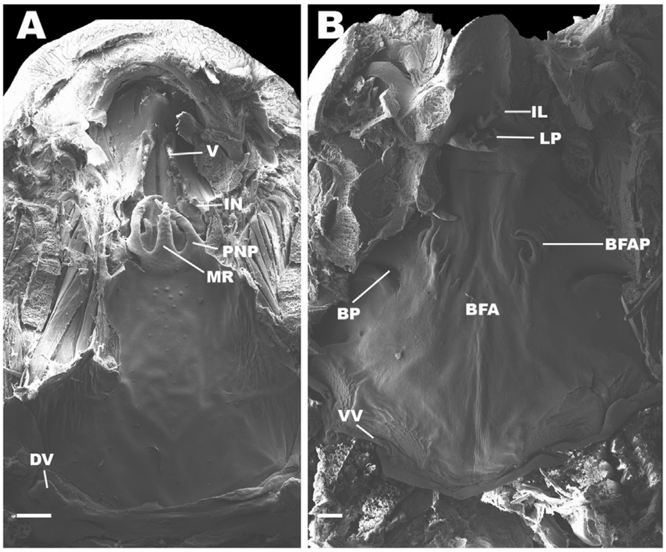

Fig. 1. Buccopharyngeal morphology of *Vitreorana eurygnatha* (MZUSP 80034; stage 36). Buccal roof (A) and buccal floor (B). BFA, buccal floor arena; BFAP, buccal floor arena papilla; BP, buccal pocket; DV, dorsal velum; IL, infralabial papilla; IN, internal nares; LP, lingual papilla; MR, median ridge; PNP, postnarial papilla; V, vacuities; VV, ventral velum. Scale bar = 200 μm.

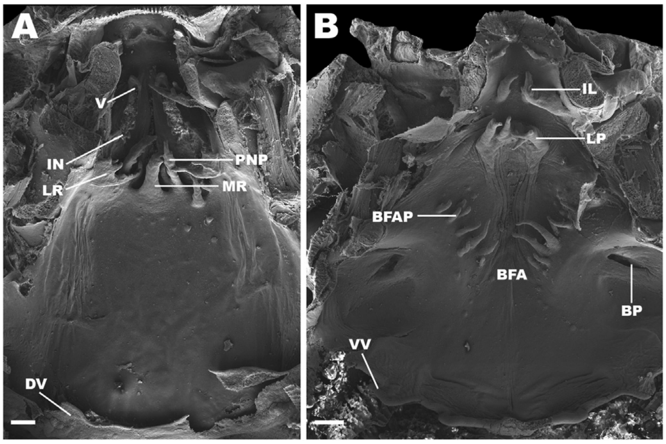

Fig. 2. Buccopharyngeal morphology of *Vitreorana uranoscopa* (MZUSP 59946; stage 34). Buccal roof (A) and buccal floor (B). BFA, buccal floor arena; BFAP, buccal floor arena papilla; BP, buccal pocket; DV, dorsal velum; IL, infralabial papilla; IN, internal nares; LP, lingual papilla; LR, lateral ridge papillae; MR, median ridge; PNP, postnarial papilla; V, vacuities; VV, ventral velum. Scale bar = 200 μm.

Buccal roof (Fig. 1A) elongate, elliptical, longer than wide, with most structures concentrated anteriorly. Prenarial arena (Fig. 3A) semi-elliptical with inverted arch-shaped dermal crest covered with pustulations. Internal nares elliptical (Fig. 3A), oriented longitudinal to main body axis; anterior margin with prenarial papillae; posterior margin forming a narial valve with papillate margin. Vacuities present, circumscribed by margins of inner nares, presenting ciliated cells (Fig. 3A). Postnarial papillae present, conical, arranged in series of two; second postnarial papillae tallest, bearing few pustulations, located lateral to median ridge. Median ridge conical, tall. Lateral ridge papilla present, simple, long, triangular, with small pustulations. Buccal roof arena absent, lacking papillae; few ($n = 9$) small, rounded pustulation posterior to median ridge. Dorsal velum arched, devoid of papillae, medially continuous. Glandular zone inconspicuous.

Buccal floor (Fig. 1B) wider posteriorly than anteriorly, with most structures concentrated anteriorly. Infralabial papillae present in two pairs; central pair shorter, conical, bearing postulation; lateral pair large, tall, located on Meckel's cartilage, wider on the

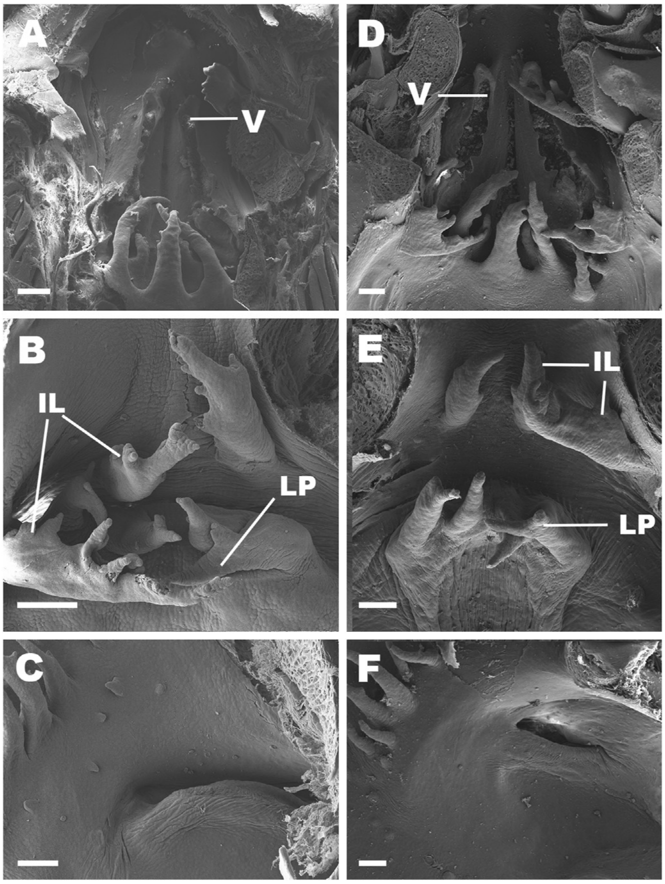

Fig. 3. Buccopharyngeal morphology of *Vitreorana eurygnatha* (A, B, and C) and *V. uranoscopa* (D, E, and F). Details of the prenarial arena, internal nares, vacuities, V, and median ridge (A and B), infralabial, IL and lingual papillae, LP (C and D), and buccal pocket (E and F). Scale bar = 100 μm.

base, bearing pustulations (Fig. 3B). Dermal crest present, small, at the base of lower jaw sheath. Tongue anlage inconspicuous, bearing four conical, tall, lingual papillae (Fig. 3B). Prepocket papillae present. Buccal pocket well marked, slit shaped; circularly perforated (Fig. 3C). Buccal floor arena U-shaped, reduced, restricted to the small area of the buccal floor; devoid of pustulations; ten (five each side) lateral buccal floor arena papillae conical, tall, investing the central arena. Glandular zone well evident; spicular support evident. Ventral velum with marginal projection and discrete medial notch; ventral surface with glandular pores.

3.2. *Vitreorana uranoscopa*

Buccal roof (Fig. 2A) elongate, elliptical, longer than wide, with most structures concentrated anteriorly. Prenarial arena (Fig. 3D) semi-elliptical with inverted arch-shaped dermal crest covered with pustulations. Internal nares elliptical, oriented vertically, longitudinal to main body axis; anterior margin with prenarial papillae; posterior margin forming a narial valve with papillate margin (Fig. 3D). Vacuities present, circumscribed by margins of inner nares, presenting ciliated cells (Fig. 3D). Postnarial papillae present, conical, arranged in series of two; second postnarial papillae tallest, bearing few pustulations, located laterally to median ridge. Median ridge conical, tall (Fig. 3B). Lateral ridge papilla present, trifurcated, long, triangular, with small pustulations; two conical papillae present below lateral ridge papillae on one side (single individual). Buccal roof arena absent, lacking papillae; few ($n = 5$) pustulations posterior to the median ridge. Dorsal velum arched, devoid of papillae, medially continuous. Glandular zone inconspicuous.

Buccal floor (Fig. 2B) wider posteriorly than anteriorly, with most structures concentrated anteriorly. Infralabial papillae present in two pairs; central pair shorter, conical, bearing postulation; lateral pair large, tall, located on Meckel's cartilage, wider on the base, bearing pustulations (Fig. 3E). Dermal crest present, small, at the base of lower jaw sheath. Tongue anlage inconspicuous, bearing four conical, tall, lingual papillae. Prepocket papillae absent. Buccal pocket poorly evident superficially; elliptically perforated (Fig. 3F). Buccal floor arena U-shaped, reduced, restricted to the small area of the buccal floor; with few pustulations (4–6 on each side); 8–9 lateral buccal floor arena papillae conical, tall, investing central arena. Glandular zone well evident; spicular support evident. Ventral velum with marginal projection and discrete medial notch; ventral surface with glandular pores.

3.3. Comparison of the two species

The buccopharyngeal morphology of *V. eurygnatha* and *V. uranoscopa* is highly similar but exhibits a few differences. The tadpoles of *V. eurygnatha* can be differentiated from those of *V. uranoscopa* by the simple, conical lateral ridge papilla (trifurcated in *V. uranoscopa*), absence of crests at the mouth opening (present), and smaller number of buccal floor arena papillae (5 on each side in *V. eurygnatha*; 8–9 in *V. uranoscopa*).

4. Discussion

Comparing the buccopharyngeal morphology of *V. eurygnatha* and *V. uranoscopa* of *I. ispacue*, *I. tayrona*, and *H. fleischmanni* (Wassersug 1980) reveals that all centrolenid tadpoles for which buccal morphology is described share a set of character-states: 1) elongate buccal cavity; 2) with most structures concentrated anteriorly; 3) two pairs of infralabial papillae; 4) four lingual papillae; 5) presence of narial vacuities; 6) nares oriented longitudinally; 7) conical median ridge, 8) posteriormost pair of postnarial papilla aligned in row with median ridge; and 9) few pustulations (<7) and papillae (<10) on both floor and roof.

The evolutionary history of most of these features is clouded by the lack of data at a broader scale—both within Centrolenidae and among its closely related lineages, especially Allophrynidae, for which tadpoles are unknown—to determine character polarity. Some character-states seem to be plesiomorphic in Centrolenidae, such as the number of infralabial and lingual papillae; two pairs of infralabial papillae and four lingual papillae have also been reported in tadpoles of several Leptodactylidae (e.g. Wassersug & Heyer 1988; de Sá et al. 2007; Vera Candioti et al. 2007; Provete et al. 2012; Magalhães et al. 2013), the sister taxa of Allophrynidae + Centrolenidae (e.g. Frost et al. 2006; Guayasamin et al. 2009; Pyron & Wiens 2011; Jetz & Pyron 2018).

Nevertheless, other characters appear to be synapomorphic for centrolenids. The vacuities around the anterior margin of internal nares are very rare among anurans. This character-state was first described by van Eeden (1951) for the tadpoles of *Ascaphus truei* Stejneger, 1899. Later, Wassersug (1980) confirmed the presence of this structure in *A. truei* and also reported for *Boana rufitela* (Fouquette, 1961) and *H. fleischmanni*. Since then, this character has been reported in several species of Cophomantinae (e.g. d'Heursel & Haddad 2007; Magalhães et al. 2015; Pezzuti et al. 2015)—suggested as a synapomorphy for that subfamily (Kolenc et al. 2008)—but not in other anuran lineages. The presence of vacuities in the distantly related species *H. fleischmanni* (Wasssersug 1980), *I. ispacue*, *I. tayrona* (Rada et al., 2019, Fig. 4), and both *Vitreorana*

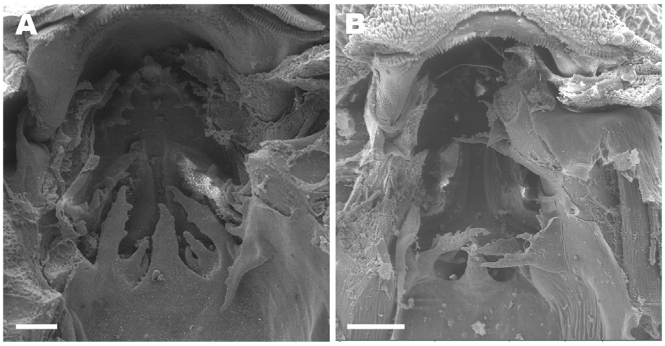

Fig. 4. Buccopharyngeal morphology and details of the prenarial arena, internal nares, and median ridge of *Ikakogi ispacue* (A) and *I. tayrona* (B), stages 28 and 29, respectively. Scale bar = 100 μm.

studied here suggests that this character might be a synapomorphy of the family. Additional studies on other centrolenids, as well as on the tadpoles of *Allophryne* Gaige, 1926 (currently unknown), are necessary to test this hypothesis.

Additionally, the longitudinal orientation of the internal nares (Figs. 1–4) is very uncommon among Neotropical anurans. In most anurans, the nares are oriented transversely (e.g. *Phasmahyla guttata*; Dias et al., 2018b) or slightly transversely, with a small angle relative to the longitudinal body axis (e.g. *Dendropsophus decipiens* (Lutz, 1925); Dias et al., 2019). Given the phylogenetic disparity among the described species of centrolenids, the longitudinal orientation of the nares in all of them and its absence in all potential sister groups (e.g. Wassersug & Heyer 1988; de Sá et al. 2007) lead us to propose it as a putative synapomorphy of the family. Moreover, it is interesting to note that a similar condition has been described in the fossorial larva of *Leptobrachella mjobergi* (Inger, 1985), suggesting a possible functional relationship between fossoriality and narial morphology.

Another interesting characteristic found in glass frog tadpoles is a conical median ridge. The median ridge marks the end of the postnarial arena and has been hypothesized to divide the respiratory current into right and left channels (Wassersug 1980). It is a highly variable feature among species, but it is usually triangular or trapezoidal (e.g. Wassersug 1980; Inger 1985; Vera Candioti 2007; Nascimento et al. 2013; Baldo et al. 2014; Dias 2018). The conical condition is unique to centrolenids and occurs in all described species of the family, being another putative synapomorphy for Centrolenidae.

Although centrolenids differ in the number of postnarial papillae, one in *H. fleischmanni*, two in *Vitreorana* (this study), and three in *Ikakogi* (Rada et al., 2019), the posteriormost pair of postnarial papillae is aligned in a row with the median ridge. To our knowledge, this arrangement has never been reported in any other tadpole. An alternative interpretation for this unusual morphology, given its topographical relationships, would be a portioning of the medial ridge into three elements. Our choice in considering these papillae as postnarial papillae is based on the fact that postnarial have been reported in several anuran families (e.g. Wassersug 1980; Wassersug & Heyer 1988; Dias 2020), but a tripartite median ridge has not. We hypothesize that the unusual position of the postnarial papillae in line with the median ridge would be the result of the elongation of the buccal roof. Additionally, given the occurrence of this character-state in *Ikakogi*, *Hyalinobatrachium*, and *Vitreorana*, we suggest it as a synapomorphy for the family.

Finally, our results corroborate Rada et al. (2019) hypothesis that the arrangement of the buccopharyngeal elements was modified as a result of the elongation of the body. For example, the buccal floor arena is reduced, being restricted to a narrow area of the buccal floor and leaving a wide, elongated area between the end of the buccal floor arena and the ventral velum. The same condition is observed in the larvae of *Ikakogi* (Rada et al., 2019) and *Hyalinobatrachium* (Wassersug, 1980). Further investigation is necessary to understand the developmental mechanism and functional implications of buccopharyngeal elongation.

Larval morphology is an exciting area of research. As more species are studied, new characters are consistently described (e.g. Rowley et al. 2012; Peixoto et al. 2003; Haas et al. 2014; Vera Candioti et al. 2017). Unfortunately, data are lacking for most anuran lineages, like Centrolenidae. Rada et al. (2019) demonstrated the value of larval morphology for the systematics of the family, and our results also support their findings. Further studies on internal larval morphology will undoubtedly reveal new characters and shed more light on the evolution of these highly modified tadpoles.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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