Living in Fast-Flowing Water: Morphology of the Gastromyzophorous Tadpole of the Bufonid *Rhinella quechua* (*R. veraguensis* Group)

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ABSTRACT   We describe the bufonid gastromyzophorous tadpoles of *Rhinella quechua* from montane forest streams in Bolivia. Specimens were cleared and stained, and the external morphology, buccopharyngeal structures, and the musculoskeletal system were studied. These tadpoles show a combination of some traits common in *Rhinella* larvae (e.g., emarginate oral disc with large ventral gap in the marginal papillae, labial tooth row formula 2/3, prenarial ridge, two infralabial papillae, quadratoorbital commissure present, larval otic process absent, mm. mandibulolabialis superior, interhyoideus posterior, and diaphragmatopraecordialis absent, m. subarcualis rectus I composed of three slips), some traits apparently exclusive for the described species of the *R. veraguensis* group (e.g., second anterior labial tooth row complete, lingual papillae absent, adrostral cartilages present), and some traits that are shared with other gastromyzophorous tadpoles (e.g., enlarged oral disc, short and wide articular process of the palatoquadrate, several muscles inserting on the abdominal sucker). In the context of the substantial taxonomic and nomenclatural changes that the former genus *Bufo* has undergone, and despite the conspicuous morphological differences related to the presence of an abdominal sucker, the larval morphology of *R. quechua* supports including it in the genus *Rhinella* and placing it close to species of the *R. veraguensis* assemblage. J. Morphol. 270:1431–1442, 2009.   © 2009 Wiley-Liss, Inc.

KEY WORDS: rheophilous tadpoles; external morphology; musculoskeletal system; buccopharyngeal cavity; ecomorphology

INTRODUCTION

Tadpoles of many anuran species inhabit flowing water systems. McDiarmid and Altig (1999) and Hoff et al. (1999) summarized seven ecomorphological guilds that occur only in or around lotic environments (i.e., clasping, adherent, suctorial, gastromyzophorous, fossorial, psammonic, and semiterrestrial). A variety of morphological features evolved adapting the tadpoles to live in flowing water. These include oral disc adhesion in clasping, adherent, and suctorial forms (e.g., *Boophis*, *Duellmanohyla*, *Mantidactylus*, *Ascaphus*, *Heleo-*

phryne, and *Hyloscirtus*), oral disc plus abdominal sucker adhesion in gastromyzophorous forms (e.g., *Atelopus*, *Amolops*, and *Meristogenys*), or slender, depressed, vermiform bodies associated with specific behaviors of hiding, burrowing, burying, or tail flipping in fossorial, psammonic, and semiterrestrial forms (e.g., some centrolenids, *Leptobrachella mjobergi*, *Otophryne pyburni*, *Cycloramphus*, and *Thoropa*). Gastromyzophorous tadpoles occur in the Ranidae (*Amolops*, *Huia*, *Meristogenys*, *Rana sauteri*; Matsui et al., 2006; Ngo et al., 2006; Stuart, 2008) and Bufonidae (*Atelopus*, *Rhinella*, *Sabahphrynus maculatus*, "*Bufo*" *pageoti*; Starrett, 1967; Cadle and Altig, 1991; Rao and Yang, 1994; Matsui et al., 2007).

Following the works by Frost et al. (2006), Pramuk (2006), and Chaparro et al. (2007), the genus *Bufo* has undergone a substantial taxonomic and nomenclatural rearrangement, and the name *Rhinella* was resurrected for most South American species. The genus *Rhinella* currently comprises 77 taxa distributed from southern North America to southern South America. Within *Rhinella*, the *R. veraguensis* group was proposed by Duellman and Schulte (1992) based on the external morphology and osteology. Pramuk and Lehr (2005) presented an analysis in which gastromyzophorous

Fig. 1. *Rhinella quechua* Stage 36. Tadpole. **A**: Dorsal view; **B**: ventral view; **C**: lateral view. Scale bar = 1 mm.

larvae of *R. chrysophora* (formerly *Atelophryniscus chrysophorus*) appear as the sister taxon of *R. veraguensis*, and this clade, in turn groups with other species of the *R. veraguensis* group. Later analyses of combined molecular and morphological data (Pramuk, 2006; Chaparro et al., 2007) showed a nonmonophyletic condition for the group. Currently, 14 taxa are tentatively assigned to this species assemblage: *R. amboroensis*, *R. arborescandens*, *R. chavin*, *R. chrysophora*, *R. fissipes*, *R. inca*, *R. justinianoi*, *R. manu*, *R. multiverrucosa*, *R. nesiotes*, *R. quechua*, *R. rumbolli*, *R. tacana,* and *R. veraguensis* (Frost, 2009). Only two of these species have been described to have gastromyzophorous larvae: *R. veraguensis* (Cadle and Altig, 1991) and *R. chrysophora* (McCranie et al., 1989).

Rhinella quechua (Gallardo, 1961) inhabits forest streams in the eastern versants of the Bolivian Andes between 1900 and 2600 m a.s.l. Tadpoles can be found in fast and turbulent water, and they aggregate in groups of about 40 individuals, usually clinging to rocks or lying on the bottom. Here, we provide a description of the gastromyzophorous tadpoles of this species, including external morphology, buccopharyngeal structures, and the musculoskeletal system. These data are compared with morphological data of species in the *R. veraguensis* group, other species in the genus *Rhinella*, and gastromyzophorous larvae of other bufonid and nonrelated ranid genera.

MATERIALS AND METHODS
Specimens

Thirty five tadpoles of *R. quechua* were collected from the Río Huayramayu, Sehuencas, Carrasco National Park, Cochabamba, 17°56′S, 65°29′W, on July 2007. The lot is deposited at Colección de Vertebrados del Centro de Biodiversidad y Genética, Cochabamba, Bolivia (CBG 1502). Thirty tadpoles were euthanized with clove oil and then fixed in 10% buffered formalin shortly after collection; five tadpoles were reared in the laboratory to verify species identification.

External Morphology

Tadpoles were staged as Gosner Stages 31–37 (Gosner, 1960). The oral apparatus was described according to the terminology of Altig (2007). Measurements were taken with dial calipers (nearest 0.1 mm) according to Lavilla and Scrocchi (1986) and Altig and McDiarmid (1999). We measured total length (TL), body length (BL), body maximum width (BMW), body width at plane of nostrils (BWN), body width at plane of eyes (BWE), body maximum height (BMH), tail length (TaL), tail fin height (FH), tail musculature height (TaMH), sucker length (SL), sucker width (SW), nostril major axis (N), eye diameter (E), rostro-spiracular distance (RS, taken from snout tip to the posterior edge of the spiracular tube), fronto-narial distance (FN, from the snout tip to the anterior edge of nostrils), eye–nostril distance (EN, from the posterior edge of nares to the anterior edge of eyes), internarial distance (IN, taken between the external edges of narial opening), interocular distance (IO, distance between interior edges of eyes), oral disc width (OD), dorsal gap length (DG), and ventral gap length (VG).

Internal Morphology

Eight specimens at Gosner Stage 31 were selected for anatomical studies. Buccopharyngeal cavity features were recorded

TABLE 1. Larval measurements of Rhinella quechua, Stages 31–37 (N = 30)

Measurement	Mean	SD	Ratio	Mean	SD
Body length (BL)	9.69	0.73			
Total length (TL)	26.83	2.50	BL/TL	0.36	0.29
Body maximum height (BMH)	4.94	0.39			
Body maximum width (BMW)	6.87	0.56	BMH/BMW	0.41	0.03
Body width at plane of eyes (BWE)	6.13	0.44			
Body width at plane of nostrils (BWN)	4.88	0.34	BWE/BWN	1.26	0.06
Tail length (TaL)	17.14	1.83	TaL/TL	0.64	0.01
Fin height (FH)	4.07	0.44	FH/BMH	1.45	0.10
Tail muscle height (TaMH)	2.81	0.37	TaMH/BMH	0.58	0.08
Sucker length (SL)	7.11	0.51	SL/BL	0.73	0.03
Sucker width (SW)	6.07	0.50	SW/BMW	0.89	0.05
Nostril (N)	0.48	0.12	N/BWN	0.10	0.02
Eye (E)	1.37	0.14	E/BWE	0.22	0.02
Rostro-spiracular distance (RS)	7.53	0.57	RS/BL	0.78	0.03
Fronto-narial distance (FN)	2.31	0.19			
Eye-nostril distance (EN)	0.87	0.12	FN/EN	2.71	0.34
Internarial distance (IN)	1.66	0.17	IN/BWN	0.34	0.03
Interocular distance (IO)	2.45	0.41	IO/BWE	0.40	0.05
Oral disc width (OD)	4.33	0.48	OD/BMW	0.63	0.07
Dorsal gap width (DG)	3.57	0.40	DG/BMW	0.83	0.05
Ventral gap width (VG)	2.66	0.35	VG/BMW	0.62	0.08

Measurements are in millimeter.

after staining of structures with methylene blue (Wassersug, 1976a). For skeletal studies, samples were cleared and stained according to Wassersug's protocol (1976b). To visualize the musculature, this procedure was interrupted before the immersion in glycerol; Lugol's solution was used to improve the contrast between orange muscles and blue cartilages (Böck and Shear, 1972). The terminology followed for buccal and musculoskeletal descriptions was proposed by Wassersug (1976a) and Haas (2003), respectively.

RESULTS
External Morphology

Tadpoles at Stages 31–37 average at 26.8 ± 2.5 mm in total length and have a dorsoventrally flattened body (Fig. 1 and Table 1). The body length is about 40% of total length; in dorsal view, the body shape is elliptical and the maximum width occurs at the base of the spiracular tube. A constriction is present at the plane of the nostrils, and a slight indentation occurs in the deeper pigmented tissues at the plane of the distal margin of the eyes. The snout is truncated in dorsal view and rounded in lateral view. Ventrally, the large abdominal sucker is quadrangular, almost as wide as the body, and it extends to the plane of the spiracular opening; it is bounded anteriorly by the oral disc, and the lateral and posterior edges remain free from the body as a raised, bulbous rim.

The dorsolateral nostrils are small, elliptical, and closer to the eyes than to the tip of the snout; they are situated in a slight depression and have a fringed edge. The eyes are small and dorsolateral. With high magnification, the pineal organ is visible as a small protuberance between the eyes. The lateral line system is not evident. The spiracle is single, sinistral, short, and located ventrolaterally at the beginning of the posterior third of the body,

it is fused for almost its entire length to the body wall and the opening is circular. The vent tube varies from cylindrical to conical; it is two times longer than wide, and attaches to the margin of the ventral fin base. The opening is circular and dextral.

The tail is long and taller than the body height. The dorsal fin begins at the body–tail junction and the beginning of the ventral fin is concealed by the vent tube. The tail axis is straight, and the well-developed musculature becomes gradually lower toward the tip. The tail tip is rounded.

The oral disc (Fig. 2) is well developed, not visible in dorsal view, triangular, and emarginate; its maximum width is about 63% of the body width. One row of marginal papillae bordering its lateral regions is absent at the emarginations. There is a large dorsal gap of about 83% of the oral disc width; the ventral gap is about 62% of the oral disc width. All marginal papillae are about the same size and are simple and conical, and a few submarginal papillae occur on the upper and lower
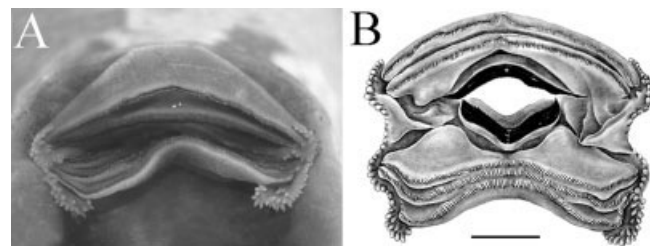

Fig. 2. *Rhinella quechua* Stage 31. **A**: Microphotography of the oral disc, frontal view, resting position; **B**: Camera lucida drawing of the oral disc, frontal view, open. Scale bar = 1 mm.
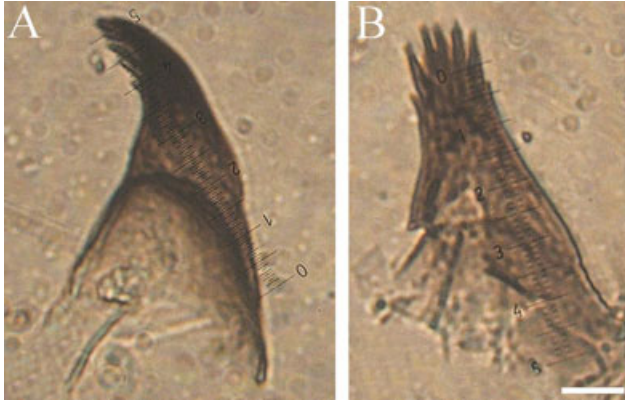
Fig. 3.   *Rhinella quechua* Stage 31. Microphotographies of the labial teeth. **A**: Lateral view; **B**: frontal view. Note the short, wide tooth head with long, acute cusps almost aligning at the tooth tip. Scale bar = 0.01 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

labia and the commissural region. The upper jaw sheath is large, curved, weakly keratinized (based on the color of the structure) and weakly serrated; the lower jaw sheath is V-shaped, weakly keratinized, and serrated. Labial teeth are arranged in a labial tooth row formula 2/3, with all rows about equal in length. Individual labial teeth are short and slightly curved (Fig. 3). The head of the teeth is short and wide and shows 7–10 long, acute cusps oriented toward the tooth tip almost reaching the same level. The body is poorly defined, and the sheath is broad and longer than the head.

The dorsum and flanks of the tadpole are uniformly black to dark grayish. The venter is dark and the abdominal sucker is peripherally unpigmented, with some scattered melanophores in the center. The attachments of the mm. intermandibularis and the posterior walls of the pericardium and branchial chambers can be seen through the transparent tissue at the anterior and posterior thirds of the sucker. The spiracle is transparent with a few melanophores scattered on the base. The vent is also often clear with a few scattered melanophores. The dorsum of the tail musculature is darkly pigmented and shows an unpigmented stripe along the entire length of the ventral edge. The dorsal fin is pigmented with scattered melanophores, and the ventral fin is translucent except for a few small melanophores on the distal part.

Buccal Cavity

On the buccal roof (Fig. 4A), the prenarial arena has a tall, narrow ridge oriented caudally. The large choanae are arranged obliquely at an angle of 42° from the transverse line. The anterior margin has small prenarial papillae, and the narial valve is visible. The two medial postnarial papillae are large and slightly bifid, and the lateral ones are small and conical. Some pustulations appear between the

internal nares and these papillae. The lateral ridge papillae are flat, short, and well developed, with 3–4 acute tips. The median ridge is narrow and tall with a pustulate tip. The buccal roof arena is not well defined, and only 1–2 pairs of buccal roof arena papillae occur on the posterolateral region; in the central and posterior regions, several pustulations are scattered unevenly. The glandular zone is not evident at the magnification we used, and the dorsal velum is short with a gently undulating margin.

On the buccal floor (Fig. 4B), posterior to the lower jaw, there are two rows of transversely arranged pustulations on each side of the midline. The two infralabial papillae are flap-like, flat, and wide, with 4–5 round tips oriented anteriorly. There are no lingual papillae. The buccal floor arena is rounded and delimited on both sides by 14–16 pairs of tall, conical buccal floor arena papillae; the papillae nearest the buccal pockets are the largest. Several pustulations and low papillae are scattered among the main papillae. Groups of 6–8 papillae, some that are often joined at their bases, diverge laterally along the anterior margin of the buccal pockets. Finally, several low, conical papillae delimit the anterior edge of the ventral velum. The buccal pockets are elongated and arranged transversely. The ventral velum is semicircular and supported by spicules; three marginal projections appear on each side over each filter plate. The median notch is absent, and secretory pits occur on the edge of the velum.

Chondrocranium and Hyobranchial Skeleton

At Stage 31, the chondrocranium is almost as wide as long, dorsoventrally flattened, mostly open
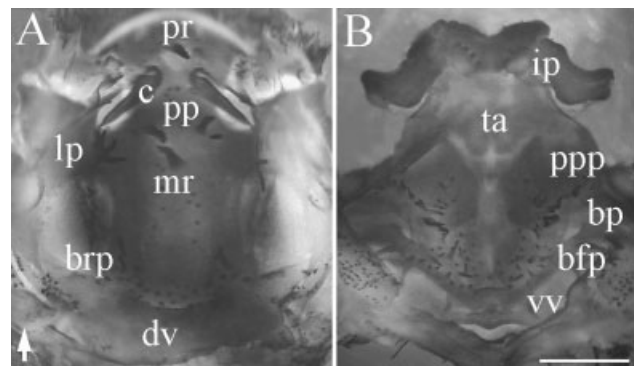

Fig. 4.   *Rhinella quechua* Stage 31. Microphotographies of the buccopharyngeal cavity (methylene blue staining). **A**: Buccal roof; **B**: buccal floor. The arrow in the lower left corner indicates rostral region. bfp, buccal floor arena papillae; bp, buccal pocket; brp, buccal roof arena papillae; c, choana; dv, dorsal velum; ip, infralabial papillae; lp, lateral ridge papillae; mr, median ridge; pr, prenarial ridge; ppp, prepocket papillae; pp, postnarial papillae; ta, tongue anlage; vv, ventral velum. Most features resemble those of other species of *Rhinella*; however, note the flap-like infralabial papillae and the absence of lingual papillae on the tongue anlage, possibly diagnostic characters for the *R. veraguensis* group. Scale bar = 1 mm.

dorsally, and heavily chondrified (Fig. 5A). Each suprarostral cartilage (Fig. 5B) has two corpora fused medially to form a single, U-shaped element separated from the pars alaris by a thin band of connective tissue. The pars alaris on each side is perpendicular to the pars corporis, and the entire suprarostral is perpendicular to the longitudinal axis of the chondrocranium. Close to the posterior tips of the suprarostral cartilage, adrostral cartilages are visible as two diffuse areas of chondrification. The trabecular horns (Fig. 5A) are about 17% of the chondrocranial length and are independent from each other along their length; they are ventrally curved throughout their length, and the anterior margins are scarcely expanded in

Fig. 5. *Rhinella quechua* Stage 31. Microphotographies of the chondrocranium (clearing and alcian blue staining). **A**: Chondrocranium, dorsal view. The arrow in the lower left corner indicates rostral region. **B**: Details of the suprarostral cartilage, frontal view. **C**: Details of the lower jaw, ventral view. ac, adrostral; ap, articular process; asp, ascending process; ic, infrarostral; ltp, lateral trabecular process; mc, Meckel's cartilage; mp, muscular process; ns, nasal septum; oc, otic capsule; qcc, quadratocranial commissure; qep, quadratoethmoid process; qoc, quadratoorbital commissure; sa, suprarostral ala; sb, subocular bar; sc, suprarostral corpus; sr, suprarostral; th, trabecular horn; ts, tectum synoticum; ttm, taenia tecti marginalis; ttme, taenia tecti medialis; ttt, taenia tecti transversalis. Several features resemble those of pond-type tadpoles of *Rhinella*, but some characters are apparently exclusive of species of the *R. veraguensis* group and shared with other rheophilous tadpoles, e.g., the adrostral cartilages and the short and wide articular process of the palatoquadrate. Scale bars = 1 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

relation to the basal width. A small projection on the ventral and outer margin of each horn represents the lateral trabecular process. In the ethmoid region, there is a short nasal septum and a thin tectum nasi that delimits an oval foramen olfatorius on each side. The lamina orbitonasalis is not yet developed at Stage 31, and there are no differentiated structures for the insertion of the outer meninges.

From a lateral view (not shown), the orbital cartilages are low with an irregular dorsal margin and are well chondrified up to the level of the insertion of the suspensorium; beyond that point almost no chondrification exists. The very well-defined foramina are visible on the posterior ends of the cartilage (foramen opticum and foramen oculomotorium). The foramen prooticum is visible and almost open dorsally because of the incomplete development of the taenia tecti marginalis. The center of the basicranial floor is occupied by a large fenestra basicranialis that is covered by a sheet of irregularly chondrified tissue. The foramina carotica primaria and craniopalatina are visible as thin, long, and irregular openings at the posterolateral edges of the fenestra, and they are separated from each other by a narrow band of cartilage.

The otic capsules (Fig. 5A) are flat and they appear as rhomboidal, irregular structures that correspond to about 27% of chondrocranial length. The fenestra ovalis occurs ventrally and the operculum is not yet developed. The otic capsules are fused to the basicranial floor; they connect to each other dorsally by a thin but strongly chondrified tectum synoticum. A well-developed taenia tecti medialis arises from the middle of the tectum synoticum and ends in the middle of a thin, chondrified taenia tecti transversalis that extends between the posterior ends of the orbital cartilages. The taeniae tecti marginales are weakly chondrified, and the crista parotica and the larval otic process are absent.

The ascending process of the palatoquadrate (Fig. 5A) is continuous with the posterior tip of the subocular bar. It is oriented anteriorly and forms an angle of about 55° with the main chondrocranial axis. It fuses with the trabeculae cranii below the foramen oculomotorium to form a low suspensorium attachment. The subocular bar has almost the same width along its length, and its posterior tip extends back to about the anterior 1/3 of the otic capsules. The fenestra subocularis extends for about 28% of the chondrocranial length. The anterior end of the palatoquadrate has a distinct and robust articular process, which articulates with the Meckel's cartilage. The muscular process is low and triangular. The quadratocranial commissure bears a sharp and triangular quadratoethmoid process. The quadratoorbitalis commissure extends between the tip of the muscular process
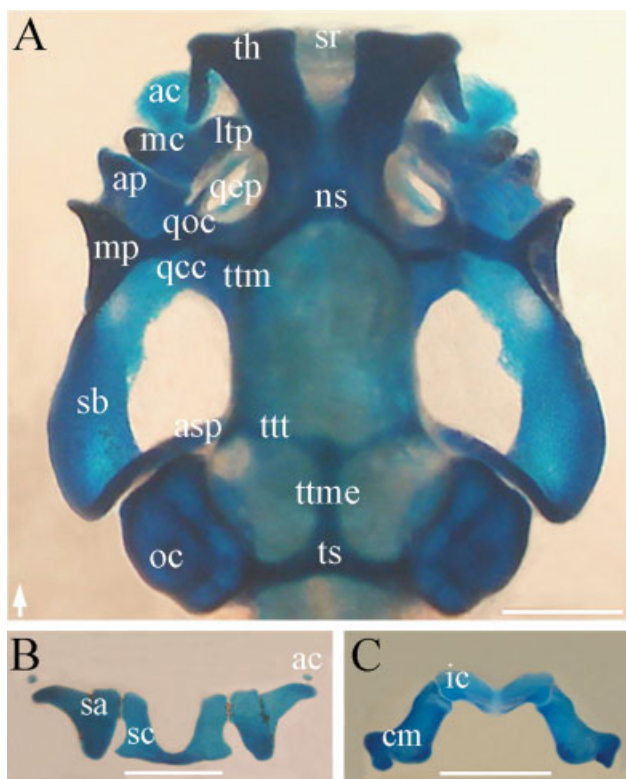
and the base of the quadratoethmoid process. The pseudopterygoid process is absent.

In the lower jaw (Fig. 5C), Meckel's cartilages are wide and curved. The proximal edge is rounded and bears a rounded retroarticular process that articulates with the anterior tip of the articular process of the palatoquadrate. The anterior tip has ventromedial and dorsomedial processes. The intramandibular commissure is formed by a weakly chondrified ligament and extends from the medial process of Meckel's cartilage to the respective infrarostral cartilage. The infrarostral cartilages are paired, curved, and connected medially through a relatively wide and weakly chondrified symphysis.

In the hyobranchial skeleton (Fig. 6A), a thin, wide, and well-chondrified basihyal is present. The ceratohyals are strongly chondrified and bear the typical five processes (anterior, anterolateral, lateral, and posterior processes, and the articular condyle), with the anterior process being the most prominent. The pars reuniens is less chondrified than the quadrangular and massive basibranchial; the urobranchial process is not evident. The hypobranchial plates are well chondrified and fused medially along the entire inner margin. The four pairs of ceratobranchials are well developed and
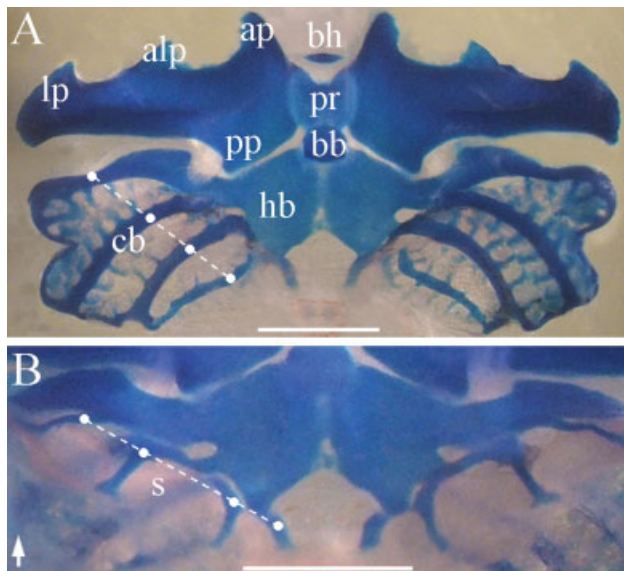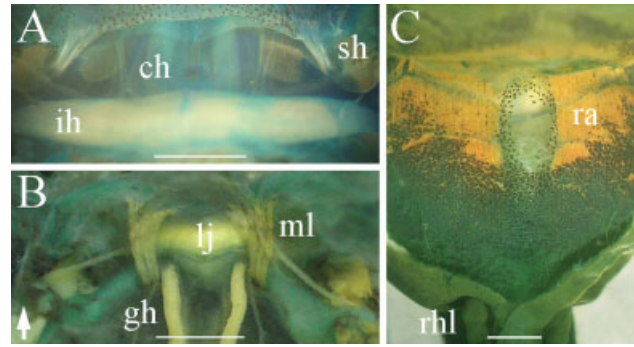

Fig. 7. *Rhinella quechua* Stage 31. Microphotographies of the abdominal sucker configuration, ventral view; ventral skin has been lifted to show underlying structures. **A**: Details of subhyoideus ligament (alcian blue staining). **B**: Details of m. mandibulolabialis inserting on the sucker anterior margin (alcian blue and Lugol's solution staining). **C**: Details of m. rectus abdominis inserting on the sucker posterior margin (alcian blue and Lugol's solution staining). The arrow in the lower left corner indicates rostral region. ch, ceratohyal; gh, geniohyoideus; ih, interhyoideus; lj, lower jaw sheath; ml, mandibulolabialis; ra, rectus abdominis; rhl, right hindlimb; sh, subhyoideus ligament. Scale bars = 1 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

have lateral projections. Ceratobranchials I–III are continuous with the hypobranchial plate, while the fourth ceratobranchial is joined to the third by a secondary bridge. The ceratobranchials are connected posteriorly by well-developed terminal commissures; dorsally, four long, curved spicules are present (Fig. 6B).

Five ligaments extend between skeletal structures and the dorsal tissue of the abdominal sucker. The paired subhyoideus ligaments are thick and fan shaped and extend between the lateral margin of the ceratohyal anterolateral process and the mediolateral region of the sucker (Fig. 7A). The paired subquadrate ligaments are scarcely developed and extend between the palatoquadrate articular process and the anterolateral region of the sucker. The fifth element, the submaxillary ligament, is very thin and extends between a region ventral to the infrarostral cartilages and the central region of the abdominal sucker. Also, the posterior walls of the pericardium and branchial chambers are attached dorsally to the posterior third of the sucker.

Fig. 6. *Rhinella quechua* Stage 31. Microphotographies of the hyobranchial skeleton (clearing and alcian blue staining). **A**: Hyobranchial skeleton, ventral view. **B**: Detail of the spicules, dorsal view. The arrow in the lower left corner indicates rostral region. ap, anterior process; alp, anterolateral process; bh, basihyal; pr, pars reuniens; bb, basibranchial; hb, hypobranchial plate; pp, posterior process; lp, lateral process; cb, ceratobranchials; s, spicules. Several features resemble those of pond-type tadpoles of *Rhinella*, but some characters are apparently exclusive of species of the *R. veraguensis* group and shared with other rheophilous tadpoles, e.g., the large ceratohyals and the ceratobranchial area smaller than in generalized species. Scale bars = 1 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Musculature

R. quechua cranial muscles are similar to those of other *Rhinella* tadpoles described elsewhere (see Discussion section). Special features include different insertion sites of some mandibular, branchial, and spinal muscles. The m. intermandibularis extends between the anterior margin of Meckel's cartilage and a median aponeurosis; additionally, some fibers attach to the abdominal sucker anterior margin. The m. mandibulolabialis runs
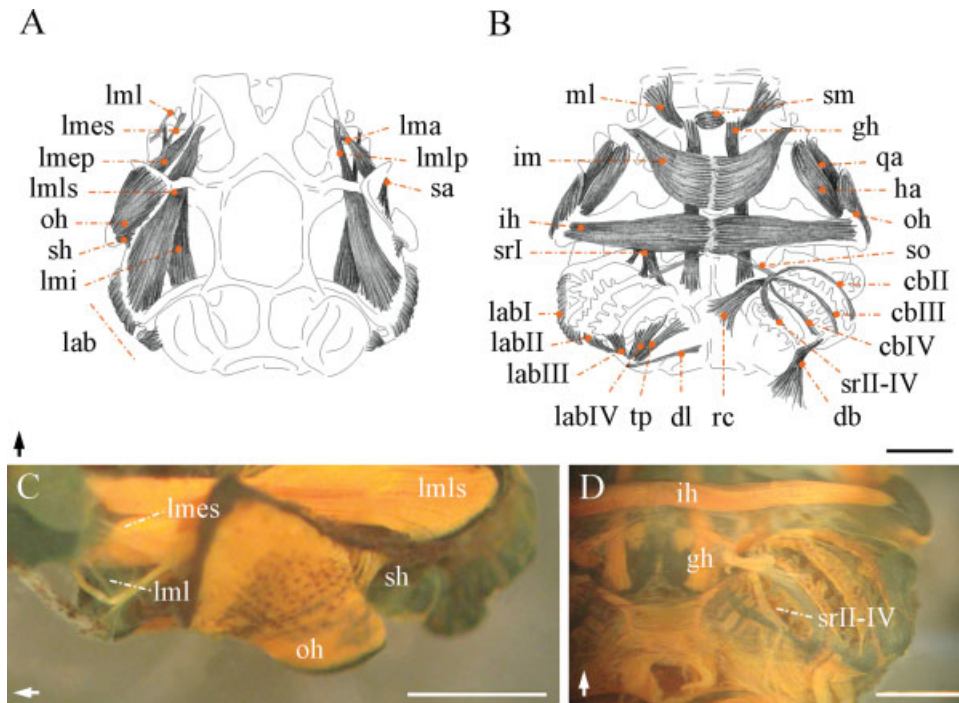
Fig. 8. *Rhinella quechua* Stage 31. Camera lucida drawings of the musculature. **A**: Dorsal view; **B**: ventral view; **C**: micropho-tography of mandibular muscles, dorsolateral view (alcian blue and Lugol's solution staining); **D**: microphotography of branchial muscles, ventral view (alcian blue and Lugol's solution staining). Arrows in lower left corners indicate rostral region. cb(II-IV), con-strictor branchialis (II-IV); db, diaphragmatobranchialis; dl, dilatator laryngis; gh, geniohyoideus; ha, hyoangularis; ih, interhyoi-deus; im, intermandibularis; lab(I-IV), levator arcuum branchialium (I-IV); lma, levator mandibulae articularis; lmep, levator man-dibulae externus profundus; lmes, levator mandibulae externus superficialis; lmi, levator mandibulae internus; lml, levator mandi-bulae lateralis; lmlp, levator mandibulae longus profundus; lmls, levator mandibulae longus superficialis; ml, mandibulolabialis; oh, orbitohyoideus; qa, quadratoangularis; rc, rectus cervicis; sa, suspensorioangularis; sh, suspensoriohyoideus; sm, submentalis; so, subarcualis obliquus; sr(I-IV), subarcualis rectus (I-IV); tp, tympanopharyngeus. Note the mm. levator arcuum branchialium IV and tympanopharyngeus distinguishable from one another, and the constrictor branchialis-like configuration of the m. subarcualis rectus II-IV, both distinctive features of this species. Scale bars = 1 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

between the ventromedial edge of Meckel's carti-lage and the connective tissue between the oral disc and the abdominal sucker. A small m. sub-mentalis appears between the ventral surfaces of the infrarostrals. The mm. levator mandibulae externus superficialis and l. m. lateralis are very thin, formed of scarce fibers, and insert on the adrostral cartilages. Among branchial muscles, the m. levator arcuum branchialium IV runs between the posterolateral surface of the otic capsule and the medial margin of the ceratobranchial IV. The fibers of the m. tympanopharyngeus originate near the m. l. a. b. IV, and then anteromedially diverge to insert on connective tissue anterior and lateral to the glottis. The m. subarcualis rectus II–IV extends between the ceratobranchial IV and the branchial process II, and some fibers are continu-ous with those of the m. constrictor branchialis II. Finally, the mm. diaphragmatobranchialis, and two spinal muscles, the mm. rectus cervicis and rectus abdominis, insert on the medial region and posterior margins of the abdominal sucker. Muscu-lar configurations in *R. quechua* tadpoles are sum-marized in Figures 7B,C and 8, and Supporting In-formation S-Table 1.

DISCUSSION

Most *Rhinella* tadpoles inhabit benthic lentic environments and have a generalized morphology associated with pond-type larvae. Apart from *R. quechua*, two species in the *R. veraguensis* group have gastromyzophorous larvae: *R. chrysophora* (McCranie et al., 1989) and *R. veraguensis* (Cadle and Altig, 1991). Tadpoles of *R. quechua* can be distinguished from them by several features of the oral disc, the abdominal sucker, and the tail (Table 2). With respect to other external traits, tadpoles of this group are very similar. In spite of the obvious differences resulting from morphological modifications in a gastromyzophorous tadpole, sev-eral features typical of *Rhinella* are evident in gas-tromyzophorous forms of *R. quechua*, *R. veraguen-sis*, and *R. chrysophora*. The ventral gap in the marginal papillae is almost universally present in *Rhinella* (except for *R. scitula*; Caramaschi and

TABLE 2. Comparison between larvae of the Rhinella veraguensis group

	Rhinella quechua (this study)	*Rhinella veraguensis* (Cadle and Altig, 1991)	*Rhinella chrysophora* (McCranie et al., 1989; Lavilla and De Sá, 2001)
External morphology			
Papillar margin of the oral disc	With dorsal and ventral gaps, and emargination without papillae; ventral gap $\cong$62% oral disc width	With dorsal and ventral gaps, with emargination apparently with papillae; ventral gap $\cong$70% oral disc width	With dorsal and ventral gaps, apparently with emargination with papillae; ventral gap $\cong$32% oral disc width
Submarginal papillae	Few or lacking	Several, on upper and lower lips	Several, on upper lip
Abdominal sucker	$\cong$74% body length	$\cong$41% body length	$\cong$75% body length
Vent tube	Dextral	Dextral	Medial
Tail coloration	Laterally dark and dorsally without marks or spots	Laterally dark and dorsally with large, nonpigmented spots	Brown with pale tan bands or spots
Dorsal fin shape	Regularly curved	Slightly arched and deepest at about midpoint of tail	Slightly arched and deepest at about midpoint of tail
Chondrocranium and hyobrachial skeleton			
General aspect	Width = Length	—	Width > Length
Suprarostral	Independent corpus and alae	—	Fused corpus and alae
Adrostrals	Diffuse chondrification	—	Well defined, elliptical
Trabecular horn-suprarostral articulation	Straight, smooth	—	Two notches
Trabecular horn length	Short (17%)	—	Long (25%)
Trabecular horn extreme/base	Slightly wider (1.5)	—	Very wider (2)
Septum and tectum nasi	Developed	—	Not developed
Orbital cartilages	Whole chondrified	—	Chondrified only on the posterior extreme
Taenia tectum medialis	Complete	—	Incomplete
Taenia tectum transversalis	Present	—	Absent
Subocular bar	Reaches 1/3 of the otic capsule	—	Reaches the caudal extreme of the otic capsule
Ceratobranchials	Four pairs	—	Three pairs
Ceratobranchials/hypobranchial plate	I–III fused to the plate	—	I fused to the plate
Urobranchial process	Absent	—	Present

Niemeyer, 2003), it also occurs in gastromyzophorous larvae of *Atelopus* and *Sabahphrynus* (e.g., Duellman and Lynch, 1969; Inger, 1992; Inger et al., 2001; Boistel et al., 2005), and it has been proposed as a synapomorphy of Bufonidae (Haas 2003; Frost et al., 2006). The number of labial tooth rows seems to follow the same pattern, and the presence of 2/3 rows, common in *Rhinella* and other bufonids, also characterizes gastromyzophorous larvae. However, unlike most *Rhinella*, which have a divided A2 tooth row, a complete A2 is present in the three sucker-bearing tadpoles (McCranie et al., 1989; Cadle and Altig, 1991), and it is a trait shared with other gastromyzophorous bufonids, *Atelopus* and *Sabahphrynus*. An enlarged oral disc with a 2/3 LTRF is also present in *R. rumbolli* (*R. veraguensis* group; FVC unpublished data). The shape of individual labial teeth also differs from those described for other *Rhinella* (e.g., Fiorito de López and Echeverría, 1984, 1989; Echeverría, 1998; Vera Candioti, 2007); they are curved, with thick, short and wide heads, broad and long sheaths, and a characteristic pattern of cusps (Vera Candioti and Altig, unpublished data).

In the buccal cavity, *R. quechua* tadpoles share the presence of a prenarial ridge and two infralabial papillae with other congeneric species (Fiorito de López and Echeverría, 1989; Fabrezi and Vera, 1997; Ulloa Kreisel, 2003; Vera Candioti, 2007). Conspicuous differences include the poorly defined buccal roof arena, the flap-like infralabial papillae, and the absence of lingual papillae; although this latter trait is also found in *R. veraguensis*, and possibly diagnostic for this species group (Cadle and Altig, 1991).

The cranial skeleton of *R. quechua* has several peculiar differences with those of *R. chrysophora* described by Lavilla and De Sá (2001), particularly in the suprarostral cartilages, ethmoid region, palatoquadrates, and hyobranchial skeleton (Table 2). On the other hand, the skeleton has several traits similar to those of *Rhinella* species with pond-type tadpoles (e.g., *R. arenarum*, *R. spinulosa*, *R. marina*, *R. schneideri*). These include a suprarostral with a single corpus and differentiated, dorsally fused alae; the presence of a quadratoorbital commissure, quadratoethmoid process and lateral process of trabecular horns, and the absence of a larval otic process are some common characters (Fabrezi and Vera, 1997; Haas 2003; Vera Candioti, 2007).

Larval musculature studies for the Bufonidae are uncommon, but several genera (following Frost et al., 2006; Chaparro et al., 2007) are represented

(e.g., *Amietophrynus*, *Anaxyrus*, *Ansonia*, *Atelopus*, *Brachycephalus*, *Bufo*, *Crepidophryne*, *Duttaphrynus*, *Epidalea*, *Incilius*, *Melanophryniscus*, *Oreophrynella*, *Pedostibes*, *Peltophryne*, *Pseudepidalea*, *Rhaebo*, and *Rhinella*; Sedra, 1950; Starrett, 1968; Carr and Altig, 1991; Haas, 2001, 2003; Vera Candioti, 2007). *R. quechua* tadpoles share with *R. arenarum*, *R. spinulosa*, and *R. marina*, a m. mandibulolabialis composed of a single slip, mm. levator mandibulae externus superficialis, l. m. e. profundus, and l. m. lateralis present, m. subarcualis rectus I with three slips, and mm. interhyoideus posterior and diaphragmatopraecordialis absent (Haas, 2003; Vera Candioti, 2007). In *R. quechua*, the mm. levator arcuum branchialium IV and tympanopharyngeus are very thin but distinguishable from one another, whereas in other species, these muscles cannot be distinguished. Also, in most bufonids, the mm. subarcualis rectus II–IV has a thin, divergent slip invading the branchial septum IV (Haas, 2003; Vera Candioti, 2007), whereas in *R. quechua*, the entire muscle has a disposition similar to that of mm. constrictores branchiales by inserting distally on the medial margin of the ceratobranchial IV. In contrast to the gastromyzophorous tadpoles of *Atelopus varius* (Starrett, 1968) and *A. tricolor* (Haas, 2003), *R. quechua* has the mm. l. m. lateralis and suspensoriohyoideus present. Several muscular characters of *Rhinella* are maintained at the family level (e.g., configuration of the mm. mandibulolabialis and subarcualis rectus I; Sedra, 1950; Starrett, 1968; Carr and Altig, 1991; Haas, 2001, 2003), and the absence of the m. diaphragmatopraecordialis and the configuration of the m. subarcualis rectus II–IV have been proposed as synapomorphies of Bufonidae (Frost et al., 2006).

From an ecomorphological point of view, the ecological mode of *R. quechua* and other lotic tadpoles correlates with convergent patterns in their morphology. Tadpoles from mountain streams typically have several characters associated with life in fast-flowing systems, such as the robust and depressed body, strong tail musculature, and low tail fins. An abdominal sucker has evolved convergently in several species of Bufonidae and Ranidae, and its external characteristics vary taxonomically [e.g., relative size, presence of medial and lateral prominences (*Amolops*), and bands of keratinized tissue (*Meristogenys*, *Huia*); Noble, 1929; Inger, 1966, 1985; Inger and Gritis, 1983; Nodzenski and Inger, 1990; Liu et al., 2000; Shimada et al., 2007] and ecologically (e.g., *Atelopus* spp. from highlands with larger suckers; Duellman and Lynch, 1969). These taxa in general share an enlarged oral disc and numerous and often complete labial tooth rows and marginal papillae (e.g., *Ansonia*, *Ascaphus*, *Hyloscirtus*, *Isthmohyla*, *Plectrohyla*, *Rhacophorus*, *Staurois*; Inger, 1954, 1960, 1966, 1985, 1992; Altig and Johnston, 1989; Cadle

and Altig, 1991; Lötters et al., 2005; Matsui et al., 2005). Besides the general configuration of the oral disc, the pattern of labial tooth cusps (long, terminal, almost aligned at the tooth tip) probably increases tooth contact and working surface, which might have functional consequences during substrate adhesion. Short, curved, broad-based labial teeth with characteristic cusp patterns can be observed in other lotic larvae (e.g., *Atelopus*, *Ascaphus*, *Huia*, *Meristogenys*; Inger, 1985; Altig and Johnston, 1989; Vera Candioti and Altig, unpublished data).

The absence of lingual papillae (Cadle and Altig, 1991) is a specific buccal trait that is different from that of other *Rhinella* species but possibly maintained within the *R. veraguensis* group. Other rheophilous tadpoles have a variable number of lingual papillae, thus there appears no strict relationship to the microhabitat. Several lotic tadpoles have oral structures that seal the mouth during suction, e.g., dense buccal roof and floor arena papillae, and thick ventral vela (Wassersug, 1980). However, except for the large, flap-like infralabial papillae, the other buccal papillae are not particularly well developed in *R. quechua*, and the buccal cavity does not differ much from that of the pond-type *Rhinella*, despite their major differences in their ecology.

Lavilla and De Sá (2001) commented on the skeletal features of the tadpoles of *R. chrysophora* and *A. tricolor* and compared them with those of suctorial larvae described by Haas and Richards (1998). Overall, the skeleton of the gastromyzophorous larvae appears less robust than that of suctorial species. These authors suggested that the weaker condition of the chondrocranium of the gastromyzophorous tadpoles could be compensated by the action of the abdominal sucker. This would also be the case with some oral features that are not as developed in *R. quechua* as in those taxa that employ only the oral disc for substrate adhesion. Besides these differences, several skeletal features seen in *Rhinella* tadpoles occur in other rheophilous tadpoles. The presence of adrostral cartilages (apparently exclusive of *R. veraguensis* group), short and wide articular process, and a palatoquadrate arranged parallel or divergent from the chondrocranium longitudinal axis can be observed in the larvae of *Atelopus*, *Boophis*, *Heleophryne*, *Hyloscirtus*, *Litoria*, and *Telmatobius*, (Noble, 1929; Lavilla and De la Riva, 1993; Haas and Richards, 1998; Lavilla and De Sá, 2001; Aguilar et al., 2007). These features are correlated with the relatively wider oral disc. These lotic larvae often show a higher in-lever arm proportion in the hyobranchial skeleton, smaller ceratobranchial area (in *R. chrysophora* and *A. tricolor*, the ceratobranchial IV is so reduced so as to be detected only by histological examination), and larger ceratohyal area than those of generalized species (Wassersug and Hoff, 1979; Lavilla and De la Riva, 1993; Haas

and Richards, 1998; Aguilar et al., 2007). Preliminary observations in *R. quechua* reveal similar results (in-lever arm proportion = 0.38; ceratobranchial area = 0.44; ceratohyal area = 0.40). Finally, the ligaments joining the chondrocranium and hyobranchial skeleton with the soft tissue of the abdominal sucker in *Rhinella* are the same as those described by Noble (1929) in *Amolops ricketti*.

The mechanism of adhesion to the substrate in several types of tadpoles that inhabit fast-flowing streams is effected through the oral disc. This mechanism includes a close adhesion of the oral disc to the substrate, and a buccal pump mechanism that creates negative pressure within the buccal cavity (e.g., Gradwell, 1971, 1973, 1975). Muscles involved in these functions (e.g., mm. mandibulolabialis, orbitohyoideus) are often more developed than in generalized tadpoles (Satel and Wassersug, 1981; Carr and Altig, 1991). In gastromyzophorous tadpoles, the abdominal sucker provides a suction force in addition to that of the oral disc and the buccal pump. The functioning of the sucker is independent from the buccal pump, which would explain the average development of buccal pump muscles in *R. quechua* (interhyoideus/orbitohyoideus volume $\cong 0.5$). Muscular array of the abdominal sucker of *R. quechua* tadpoles resembles that described for *R. veraguensis*, and species of *Atelopus* and *Amolops* (Noble, 1929; Cadle and Altig, 1991; Kaplan, 1997), and includes several muscles that in generalized tadpoles are related to feeding or breathing. In *Rhinella* tadpoles, these muscles are the mm. diaphragmatobranchialis, rectus cervicis, rectus abdominis, and some fibers of the mm. mandibulolabialis and intermandibularis. In *Atelopus*, these muscles include m. intermandibularis, m. rectus abdominis, and fibers of the m. orbitohyoideus, abdominal mm. transversus, and obliquus externus. In the ranid *Amolops*, the muscles are mm. interhyoideus (anterior and posterior slips), diaphragmatopraecordialis, rectus cervicis, and rectus abdominis. The fact that these muscles are not the same in both groups of gastromyzophorous species highlights the phylogenetic component constraining the ecological convergence (recall mm. interhyoideus posterior and diaphragmatopraecordialis are absent in bufonids studied).

Noble (1929) described the functioning of the sucker of *A. ricketti* as consisting essentially of a contraction of the ventral musculature which, assisted by ligaments, would lift the ventral skin and form a vacuum within the rim, provided that the mouth was held next to the substrate. Conversely, on the basis of the small size and the peripheral, angled insertion of the muscles on the sucker of *Atelopus*, Kaplan (1997) suggested that suction in these tadpoles would be passive, with a role of ligaments but without the involvement of the musculature. A friction mechanism, as suggested by the presence of a friction area with minuscule protuberances, would provide the *Atelopus* tadpoles a better grip on substrates with texture. In *R. quechua*, at least the well developed and centrally inserted mm. rectus cervicis may assist the ligaments to raise the central region of sucker. The remaining peripheral muscles may help to press the rim against the substrate (especially the well-developed m. rectus abdominis with its orientation parallel to the sucker plane) or alternatively, as suggested by Kaplan (1997), to detach the sucker from it. The complete set of muscles (some inserted both on the oral disc and the abdominal sucker) and ligaments attached to the underlying skeleton would act as a coordinated oral disc-buccal pump-sucker system that strongly adhere the tadpole to the substrate. Among other lotic environment species, suctorial tadpoles of *Ascaphus*, *Boophis*, *Heleophryne*, *Hyloscirtus*, *Hypsiboas*, *Litoria*, and fossorial tadpoles of *L. mjobergi* have a well-developed mm. rectus abdominis (in *Leptobrachella*, the m. rectus cervicis also) that extend far anteriorly (level of palatoquadrates or Meckel's cartilages) and possibly flex the body on the vertebral column, pull the body close to the substrate, and even assist in lower jaw abduction (Noble, 1929; Gradwell, 1973; Haas and Richards, 1998; Haas et al., 2006). *Telmatobius* larvae also have a m. rectus abdominis inserting anteriorly (level of palatoquadrate articular process), but the function in these rather lentic tadpoles remains unclear (Vera Candioti, 2008). Finally, in *Leptobrachella* larvae, the m. diaphragmatobranchialis appears to be recruited for the locomotor function as well, probably intervening in body movements during burrowing (Haas et al., 2006).

Further research in several fields concerning gastromyzophorous tadpoles is still pending. For instance, the development of the abdominal sucker needs to be revisited. Apparently, this structure appears at Stages 23–25 as a small shallow depression that becomes deeper as the margins rise (Mebs, 1980; Kuramoto et al. 1984), but the statement that it is derived from the adhesive glands (Peters, 1964; Rao and Yang, 1994) seems developmentally very unlikely. It is intriguing that gastromyzophorous tadpoles are known to occur only in the Bufonidae and Ranidae. Comparative developmental and functional studies on tadpoles of *Cycloramphus* and *Thoropa* (Cycloramphidae; Wassersug and Heyer, 1983; Hoff et al., 1999) could assess that their flattened and expanded venters could be a morphological precursor to an abdominal sucker. The biomechanical and ecological aspects such as feeding behavior, microhabitat selection, substrate preference, and water flow speed tolerance of gastromyzophorous and other lotic larvae are also yet to be explored. Lastly, Barrionuevo et al. (2008) reported the first occurrence

of *Batrachochytrium dendrobatidis* in amphibians of Bolivia based on *R. quechua* tadpoles. This study can serve as a baseline for future applied studies and conservation work with this species.

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