

Independent Evolution of Suction Feeding in Neobatrachia: Feeding Mechanisms in Two Species of *Telmatobius* (Anura:Telmatobiidae)

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ABSTRACT

The most common feeding mechanism among aquatic vertebrates as fishes, turtles, and salamanders is inertial suction. However, among the more than 6,400 species of anurans, suction feeding occurs only in pipids. Pipidae is a small basal lineage relative to Neobatrachia, an enormous clade that contains about 96% of extant anurans. The Andean neobatrachian frogs of the genus *Telmatobius* include strictly aquatic and semiaquatic species. Diet analyses indicate that some species of *Telmatobius* feed on strictly aquatic prey, but until now their feeding mechanisms have been unknown. Herein, the feeding mechanisms in two species of *Telmatobius*, that represent the two predominant modes of life in the genus, are explored. The semiaquatic *T. oxycephalus* and the fully aquatic *T. rubigo* are studied using high-speed cinematography and standard anatomical techniques to provide a qualitative approach to feeding behavior and a detailed morphological description of the mouth, tongue, hyoid and related muscles. *T. oxycephalus* uses similar mechanisms of aquatic prey capture as do the vast majority of anurans that are capable of forage in water, whereas the fully aquatic *T. rubigo* is an inertial suction feeder. This is the first report of an objective record of this unique feeding behavior in a Neobatrachian. Several morphological characters seem to be related with this function and are convergent with those of pipids. Anat Rec, 00:000–000, 2015. © 2015 Wiley Periodicals, Inc.

Key words: tongue morphology; hyoid apparatus; muscles; feeding behavior; suction feeding; *Telmatobius*; Anura

This article includes AR WOW Videos. Video 1 can be viewed at <http://bcove.me/no1jo2kc>, Video 2 can be viewed at <http://bcove.me/2jj8uwbn>, Video 3 can be viewed at <http://bcove.me/0l499mz8>, Video 4 can be viewed at <http://bcove.me/a6npaavu>, Video 5 can be viewed at <http://bcove.me/jq3zgdh>.

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INTRODUCTION

Suction feeding is the most common way aquatic vertebrates capture their prey, and occurs in fishes, turtles, salamanders, and in a small group of basal anurans, the pipids (Sokol, 1969; Lauder, 1985; Deban and Wake, 2000; Carreño and Nishikawa, 2010). Vertebrates share the same basic mechanism of suction feeding, which involves generating a drop in intraoral pressure and propelling water into the mouth with the prey. Rapid expansion of the bucco-pharyngeal cavity decreases intraoral pressure. A suction force that is strong enough to maintain the position of the prey relative to the predator during the lunge (rather than pushing it away) is called compensatory suction (Van Damme and Aerts, 1997). For the predator to seize the prey, compensatory suction must be accompanied by scooping, ram feeding, or jaw prehension. Inertial suction occurs when the suction force alone is sufficient to move the prey toward the mouth (Van Damme and Aerts, 1997), in which case, the use of forelimbs or jaw prehension is unnecessary.

During the evolution of Tetrapoda there was a transition from aquatic suction feeding, commonplace in fishes, to other mechanisms to capture terrestrial prey. The muscular tongue of tetrapods has played a central role in this transition. Many groups of salamanders are suction feeders (e.g. Amphiumidae, Cryptobranchidae, Proteidae, Salamandridae, and Sirenidae; Deban, 2003), whereas other groups have evolved striking terrestrial specializations such as the ballistic tongue in Plethodontidae (e.g. Deban et al., 1997),

Unlike salamanders, anurans with more than 6,400 species, mostly feed on land and use their tongues for prey capture. There are at least three basic mechanisms of tongue use in frogs and toads: mechanical pulling, and inertial and hydrostatic elongation (Nishikawa, 2000). Although most anurans are terrestrial feeders, some forage in water (e.g. *Bombina*, *Lepidobatrachus*, *Calyptocephalella*; O'Reilly et al., 2002). These species catch their prey by forearm scooping, ram feeding, jaw prehension, or a combination thereof. The only anurans where suction feeding has been described are the pipids, fully aquatic frogs that lack a tongue. Pipidae is basal to the clade Neobatrachia that contains about 96% of extant frogs (Fig. 1; Frost et al., 2006; Pyron and Wiens 2011). *Xenopus* and *Pipa* may use their forearms to scoop prey in compensatory suction (Avila and Frye, 1977; Gray, Reilly and Nishikawa, 1997; O'Reilly et al., 2002), but *Hymenochirus* and *Pseudhymenochirus* catch their prey solely by inertial suction (Sokol, 1969; Carreño and Nishikawa, 2010). Robinson and Cappo (1989) mentioned that *Litoria platycephala* (as *Cyclorana platycephala*) sucks its prey aided by its hands, but no additional information was provided. At present the occurrence of suction feeding was not described in any member of Neobatrachia.

The Genus *Telmatobius*

The neobatrachian frogs of the genus *Telmatobius* live in Andean streams and lakes from Ecuador to Argentina. At present, 63 species have been described (Frost, 2015). The cloud forest and inter-Andean valleys species are, in general, semiaquatic. These species can be found both inside and outside the streams (Vellard, 1951;

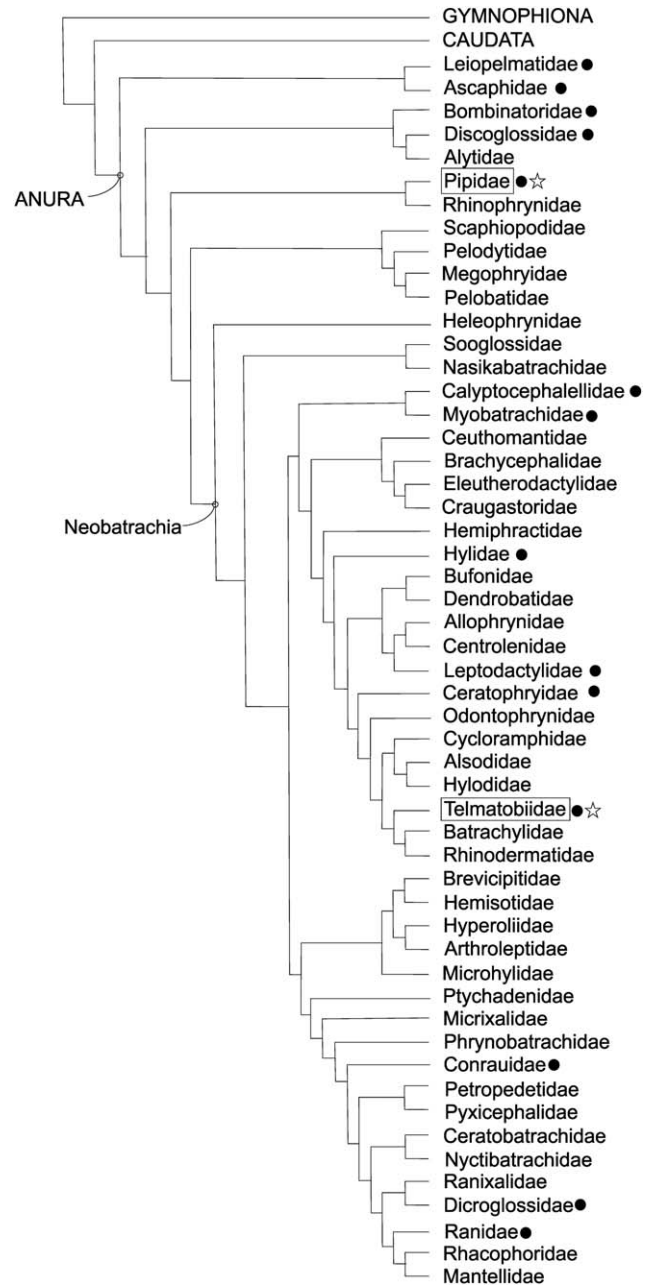


Fig. 1. A simplified version of Pyron and Wiens (2011) phylogenetic tree showing all anuran families and the clade Neobatrachia. The terminals marked with dots correspond to families with at least one water foraging member; the star shows the occurrence of suction feeding behavior (references in the text). The position of Pipidae and Telmatobiidae in this tree is highlighted in a square.

Laurent, 1970, 1973; De la Riva, 1994), and their diet consists of terrestrial or aquatic prey (Lavilla, 1984; Wiens, 1993). On the other hand, the high Andean or Puna species are exclusively aquatic (De la Riva, 2005; Vellard, 1951; Parker, 1940). They are found always in the water and the evidence from stomach contents indicates that these species feed exclusively on aquatic prey (Allen, 1922; Formas et al., 2005). Indeed, some high Andean species of *Telmatobius* live exclusively in great

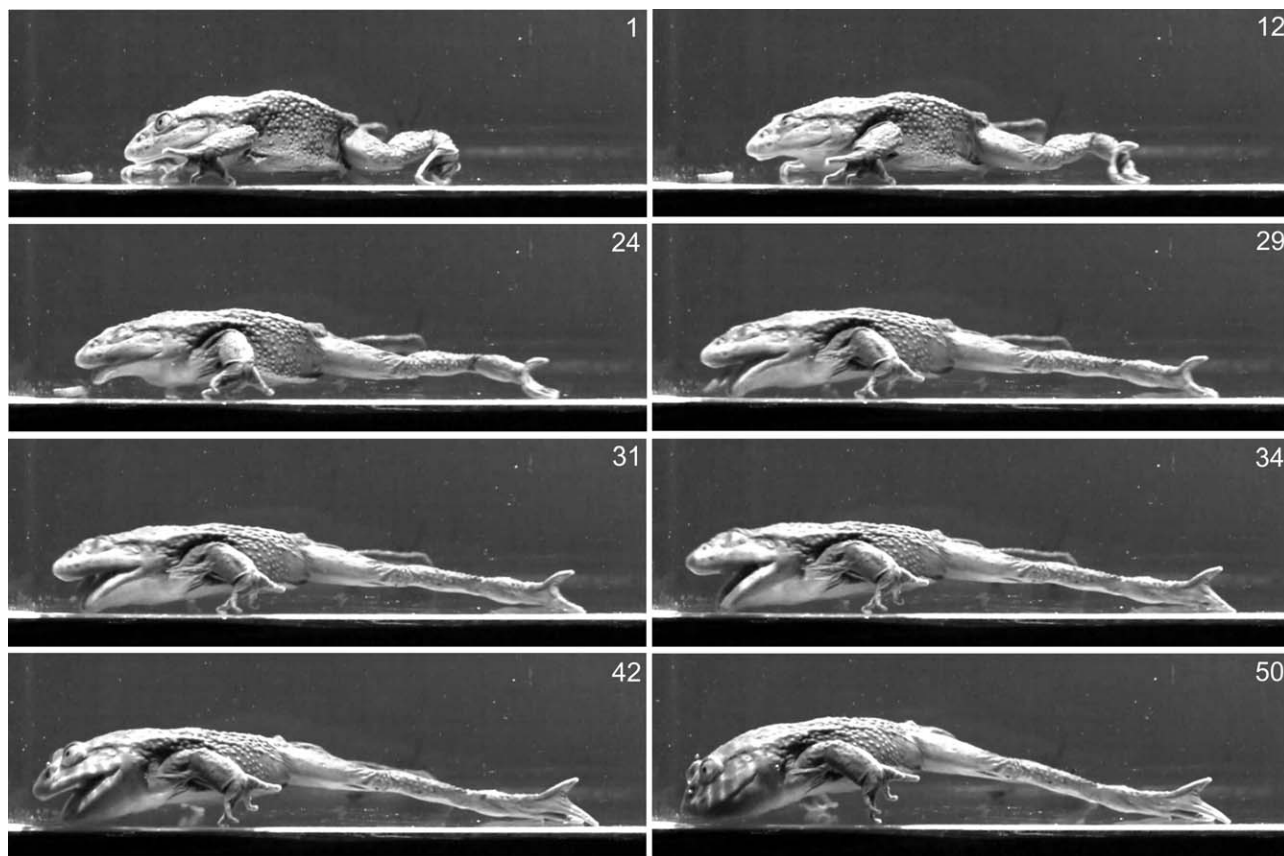


Fig. 2. Selected frames from high-speed video recordings (480 frames/sec) of *Telmatobius rubigo* capturing a mealworm underwater. The frames were numbered from the initiation of the feeding cycle (just before the frog lunges at the prey) to the end (after the prey is completely engulfed). See Video 1: http://bcove.me/F2_no1jo2kc, Video 2: <http://bcove.me/2jj8uwbn>, and Video 3: <http://bcove.me/0l499mz8>.

Andean lakes that never abandon (e.g. *T. culeus* from Titicaca Lake or *T. macrostomus* from Junín Lake; Gorman, 1876; Barbour and Noble, 1920; Vellard, 1951), taking the aquatic mode of life to an extreme.

Telmatobius rubigo and *T. oxycephalus* are distributed in northwestern Argentina. *Telmatobius rubigo* is a fully aquatic member of the genus inhabiting streams in the Puna highland plateau at an altitude around 4,000 m. In the field, the individuals of *T. rubigo* are always found under water. The semiaquatic *Telmatobius oxycephalus* inhabit streams in forest and inter-Andean valley from 1,400 to 3,000 m and the frogs are found both inside water and in the immediately margins of the streams. In a partial phylogenetic analysis of Bolivian *Telmatobius* based on sequences of mtDNA, De la Riva et al. (2010) proposed three phylogenetic groups within the genus. These groups show an interesting distribution pattern with different morphological and behavioral characters associated to each group. Although *T. rubigo* and *T. oxycephalus* have not been included in previous phylogenetic hypotheses, several characters suggest that they may represent two of the three different evolutionary lines within the genus (Barrionuevo, 2013).

Although the evidence from diet indicates that species of *Telmatobius* feed on aquatic prey (Allen, 1922; Formas

et al., 2005), no direct observations of the frogs during feeding have been reported. The only exception is a comment in Gray et al. (1997), indicating that members of *Telmatobius* use their forehands for prey capture. Unfortunately these authors did not specify the species observed or if the captures were recorded in water or in land. The knowledge on morphology of the feeding apparatus in *Telmatobius* is scarce, with the exception of Regal and Gans (1976) that compare the tongue and its muscles on a broad sample of anurans including comments on *Telmatobius marmoratus*. More recently, Fabrezi and Lobo (2009) included comments on hyoid and tongue muscles of *T. oxycephalus* in the context of a study of hyoglossal apparatus of *Lepidobatrachus*.

With the intent to improve the knowledge on evolution of aquatic habits in Telmatobiidae, this study analyzes functional and morphological aspects of feeding mechanisms in two species of *Telmatobius* representing the two predominant modes of life in the genus. Therefore, the goals of this study are (i) to characterize qualitatively the underwater feeding behavior of *Telmatobius rubigo*, a fully aquatic species, and *T. oxycephalus*, a semiaquatic member of the genus, by using high-speed cinematography, and (ii) to analyze in detail the morphology of the feeding apparatus (mouth, tongue, hyoid, and related muscles) of both species.

MATERIALS AND METHODS

For the observation of prey capture, three adult specimens of the fully aquatic *Telmatobius rubigo* and three adult specimens of the semiaquatic *T. oxycephalus* were housed in aquaria at room temperature (approximately 20–23°C) and fed live earthworms, crickets, mealworms, fish and tadpoles of *Hypsiboas* sp. Frogs were placed in a separate filming tank for feeding trials. Aquatic feeding behavior was videotaped with Sony NEX-FS700UK Super 35 Camcorder at a rate of 480 frames/sec with natural illumination. Feeding sequences of the two species were analyzed frame by frame to describe qualitatively the feeding behavior. The initial position of the prey item was marked on the video screen and movement of the prey item relative to a stationary reference point was observed. Inertial suction was only thought to occur if bucco-pharyngeal expansion generated a rearward flow that accelerated the prey toward the mouth relative to a stationary reference point.

For the morphological analysis, museum specimens of *Telmatobius rubigo* and *T. oxycephalus* were studied. To examine musculature and provide contrast between muscles and cartilaginous elements of hyoid, cartilage was stained with Alcian Blue as described by Wassersug (1976) but interrupting the process at his point. In this way, bone was not stained and soft tissues were not cleared. To examine osteology, the protocol of Wassersug (1976) was finished, that is, specimens were cleared and double-stained with Alizarin Red S (for bone) and Alcian Blue (for cartilage). Specimens are housed in Fundación Miguel Lillo Herpetological Collection (FML) and the National Herpetological Collection of Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). *Telmatobius oxycephalus* FML 03836-I (adult female, cleared and stained -CS-), 3836-II, and 3836-III (adult males, CS); FML 2867-I, 2867-II (adult males, CS), 2867-III, and 2867-IV (adult females, CS); FML SB 016, 555, MACN 39082 (adult females, stained -S-), FML 019 (adult male, CS), 556 (adult male, S). *Telmatobius rubigo* FML 20829 (adult male, CS); MACN 41671 (adult male, S), 41673 (adult female, S), 41661, 41668 (adult females), 41679, 41682 (adult males).

RESULTS

Feeding Behavior

The underwater feeding pattern in *Telmatobius rubigo* includes movements of the body (approach and/or lunge), jaws (opening and closing), and buccal floor (retraction-depression and protraction-elevation). The prey-capture sequence begins when the frog approaches the prey (Fig. 2, SVideo 1: <http://bcove.me/noljo2kc>, Video 2: <http://bcove.me/2jj8uwbn>, and Video 3: <http://bcove.me/01499mz8>). A lunge, powered by extension of the hind limbs, often is initiated before the mouth is opened. The mouth is opened when the frog is close to the prey; the gape angle does not exceed 45°. This small gape is limited to the anterior part of

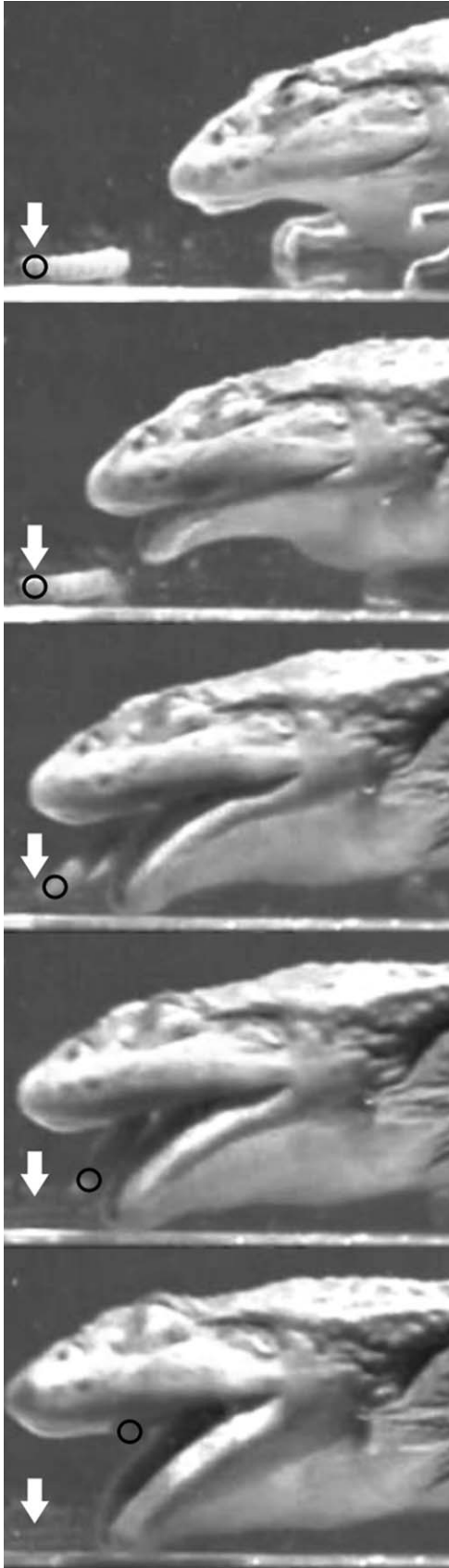


Fig. 3. A close view of *Telmatobius rubigo* during prey capture by inertial suction. The arrow is in a fixed position and the mealworm is marked by an open circle. It is evident the movement of the prey toward the mouth without the use of forelimbs.

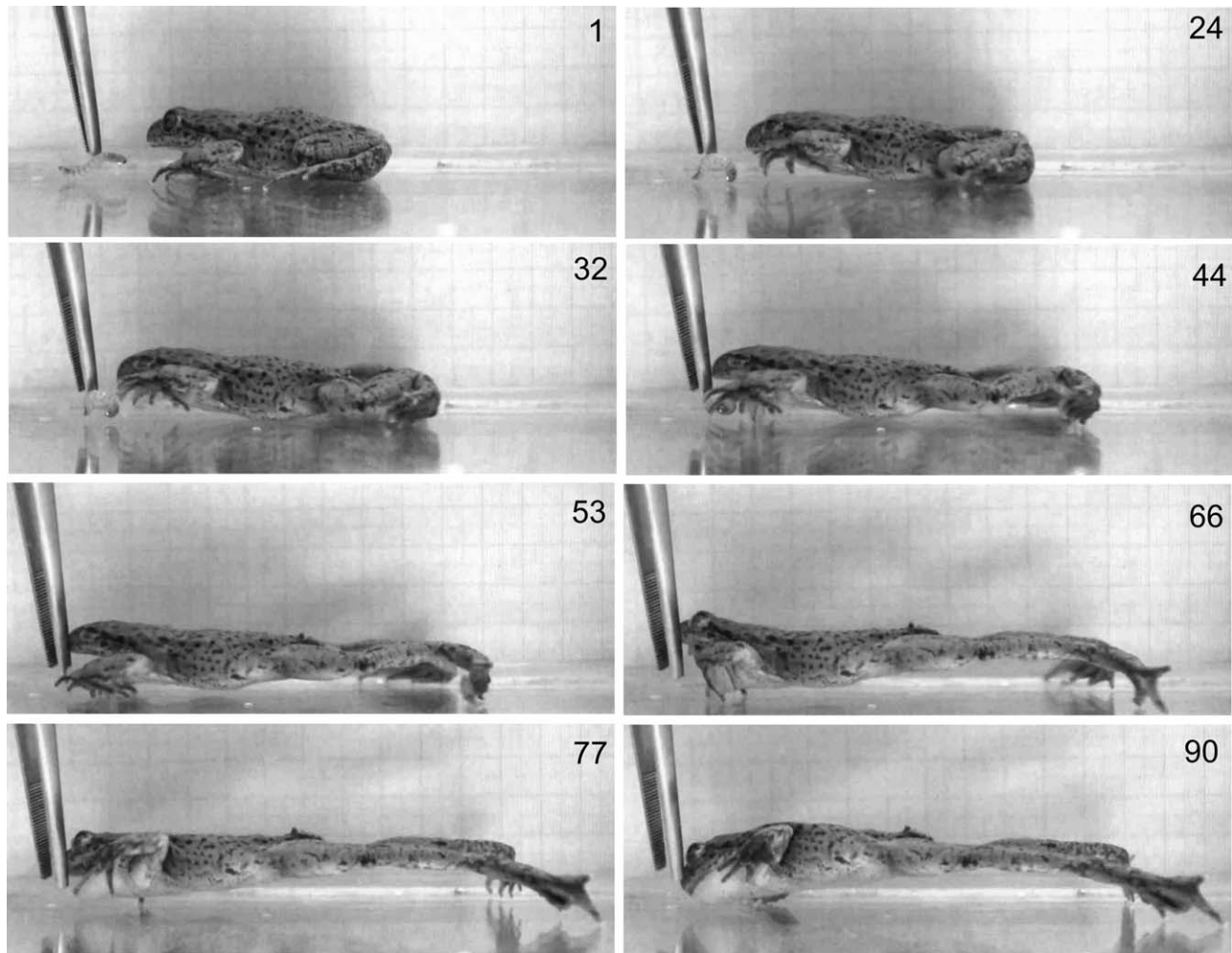


Fig. 4. Selected frames from high-speed video recordings (480 frames/sec) of *Telmatobius oxycephalus* capturing a mealworm underwater. The frames were numbered from the initiation of the feeding cycle (just before the frog lunges at the prey) to the end (after the prey is completely engulfed). See Video 4: <http://F4bcove.me/a6npaavu>.

the mouth, whereas the lateral sides of the mouth remain closed or barely opened. The lower jaw bending and the depression of the buccal floor are evident. Immediately after mouth opening, the prey moved toward the frog (in an earth-bound frame of reference) and the forelimbs are not involved in the ingestion (inertial suction feeding, Fig. 3). In fact, *Telmatobius rubigo* was never observed using forelimbs for prey capture; during feeding, the forelimbs remain on the substrate. Although *T. rubigo* did not use its forelimbs to catch prey, it has been observed that it is capable of some manual dexterity when the prey is not completely engulfed. In that case *T. rubigo* can use the dorsal side of its hands to accommodate the prey. Once the prey is engulfed, the mouth closes as the buccal floor is raised and water is expelled from the anterior part of the mouth. This is evidenced by air bubbles that appear as water is expelled.

The underwater feeding pattern in *Telmatobius oxycephalus* includes movements of the body (approach and/or

lunge), jaws (opening and closing), and forelimbs (extension and scooping). The prey-capture sequence begins when the frog approaches the prey (Fig. 4, Video 4: <http://bcove.me/a6npaavu>). The mouth is opened when the frog is close to the prey, and the gape angle is around 90°. This striking wide gape is radically different from that of *T. rubigo*. Lower jaw bending is not evident. As the mouth opens, the frog extends its forelimbs forward to scoop the prey into the mouth with the dorsal side of its hands. During the feeding cycle, depression of the buccal floor was less evident than in *T. rubigo*. The forelimbs obstruct the direct observation of the profile of the frog during feeding. However, in one of the trials, the prey was pressed against the tank wall and the frog could not extend its forelimbs; in this sequence, the absence of buccal floor depression was evident. After engulfing the prey, the frog closes its mouth; the mouth can be open again to manipulate the prey by pushing it with the forelimbs. In land, *T. oxycephalus* was observed to use its round and short tongue (Video 5: <http://bcove.me/jq3zgdwh>). As its

TABLE 1. Major morphological differences between *Telmatobius rubigo* and *T. oxycephalus* in relation to hyoid apparatus, tongue, lower jaw, and mouth configuration

	<i>Telmatobius rubigo</i>	<i>Telmatobius oxycephalus</i>
Hyoid apparatus		
Hyoid plate	Broad, mineralized	Narrow, cartilaginous
Hyoglossal sinus	Shallow, at the level of the anterolateral processes	Deep, posterior to the level of the anterolateral processes
Ossification of posteromedial processes	Extending to the plate and to the base of the posterolateral processes	Not extending to the plate and posterolateral processes
m. sternohyoideus	Bulky, two slips	Less bulky, one slip
m. sternohyoideus insertion	Broad insertion on the plate	Narrow insertion on the plate
Tongue		
General aspect of tongue	Small and flat	Larger and thicker
Attachment to the buccal floor	Around 90°	Around 70°
m. hyoglossus	Thin, not completely fused to each other	Bulky, indistinguishable to each other
m. hyoglossus insertion	Superficial, not entering the tongue, reaching far anteriorly	Deep, entering the tongue, not reaching far anteriorly
m. genioglossus	Superficial, the interdigitation with m. hyoglossus fibers is evident	Deep, the interdigitation with m. hyoglossus fibers less evident
m. depressor		
m. depressor general aspect	Bulky	Thin
m. depressor anterior slip origin	Annulus tympanicus, otic ramus sq, epimysium	Mainly epimysium, some fibers from tympanic annulus and otic ramus of sq
m. depressor posterior slip	Its origin reaching posteriorly the level of the m. obliquus externus; covers entirely the m dorsalis scapulae and the m latissimus dorsi	Its origin not extending as far posteriorly as in <i>T. rubigo</i> ; covers only the anterior half of the m. dorsalis scapulae
length and orientation of posterior slip fibers	Longer and more horizontally oriented	Shorter and more vertically oriented
otic ramus sq	More developed	Less developed
Mouth and labial configuration		
Labial lobes	Present	Absent
Angle of gape	Around 45°	Around 90°
Teeth	Pedicellate, nonocuspoid, fanglike	Pedicellate, nonocuspoid, fanglike
Lower jaw in lateral view	High	Low
Lower jaw at the level of the symphysis	Lower in relation to the rest of the lower jaw	As low as the rest of the lower jaw

tongue cannot extend too farther, the frog needs to lunge over the prey to get closer to catch the prey with the tongue.

Morphology of the Feeding Apparatus

The major differences found between *Telmatobius rubigo* and *T. oxycephalus* in relation to the hyoid apparatus and related muscles, tongue, lower jaw, and labial configuration are summarized in Table 1.

Hyoid apparatus and related muscles. The hyoid of adult anurans typically consist in a broad cartilaginous plate that bears 4 pairs of processes. The anterior hyalia are slender cartilaginous processes that, in most anurans, connect the hyoid with the otic capsules. Usually, there are three other pairs of processes that arise from the lateral and posterior margins of the plate—the anterolateral, the posterolateral, and the posteromedial processes. In most anurans, just posteromedial processes ossify. The hyoid plate of *Telmatobius rubigo* is broad, with the anteromedial margin of the hyoglossal sinus lying at about the level of the anteromedial processes (Fig. 5). Ossification of the posteromedial processes reaches the level of the base of the posterolateral processes. In addition, the central and anterolateral regions of the plate are heavily mineralized. The hyoid plate in

T. oxycephalus is narrower than in *T. rubigo* and the medial margin of the hyoglossal sinus lies well posterior to the level of the anteromedial processes. The hyoid plate is completely cartilaginous and the ossification of the posteromedial processes is not reaching the base of the posterolateral processes.

As in other anurans, in *Telmatobius* there are hyoid protractors (the m. geniohyoideus) and hyoid retractors (the m. sternohyoideus), as well as hyoid levators (the m. petrohyoideus) and depressors (the m. omohyoideus). The m. sternohyoideus originates from the sternum (but some fibers are in continuity with m. rectus abdominis) and inserts in the ventral surface of the hyoid plate. The hyoid muscles of *T. rubigo* and *T. oxycephalus* differ primarily in relation to the morphology and insertion of the m. sternohyoideus.

In *T. rubigo*, the m. sternohyoideus is massive, and it is formed by two slips: a deep slip and a superficial slip. The deep or dorsal slip inserts along the posterior border of the hyoid plate near the bases of the posterolateral and posteromedial processes. The superficial or ventral slip inserts on the anterior part of the hyoid plate at the base of hyale and the anterolateral process, almost reaching the medial line of the hyoid plate. In *T. rubigo*, the area of the hyoid plate where the m. sternohyoideus inserts is heavily mineralized. In *T. oxycephalus*, the m. sternohyoideus is single and less massive than in

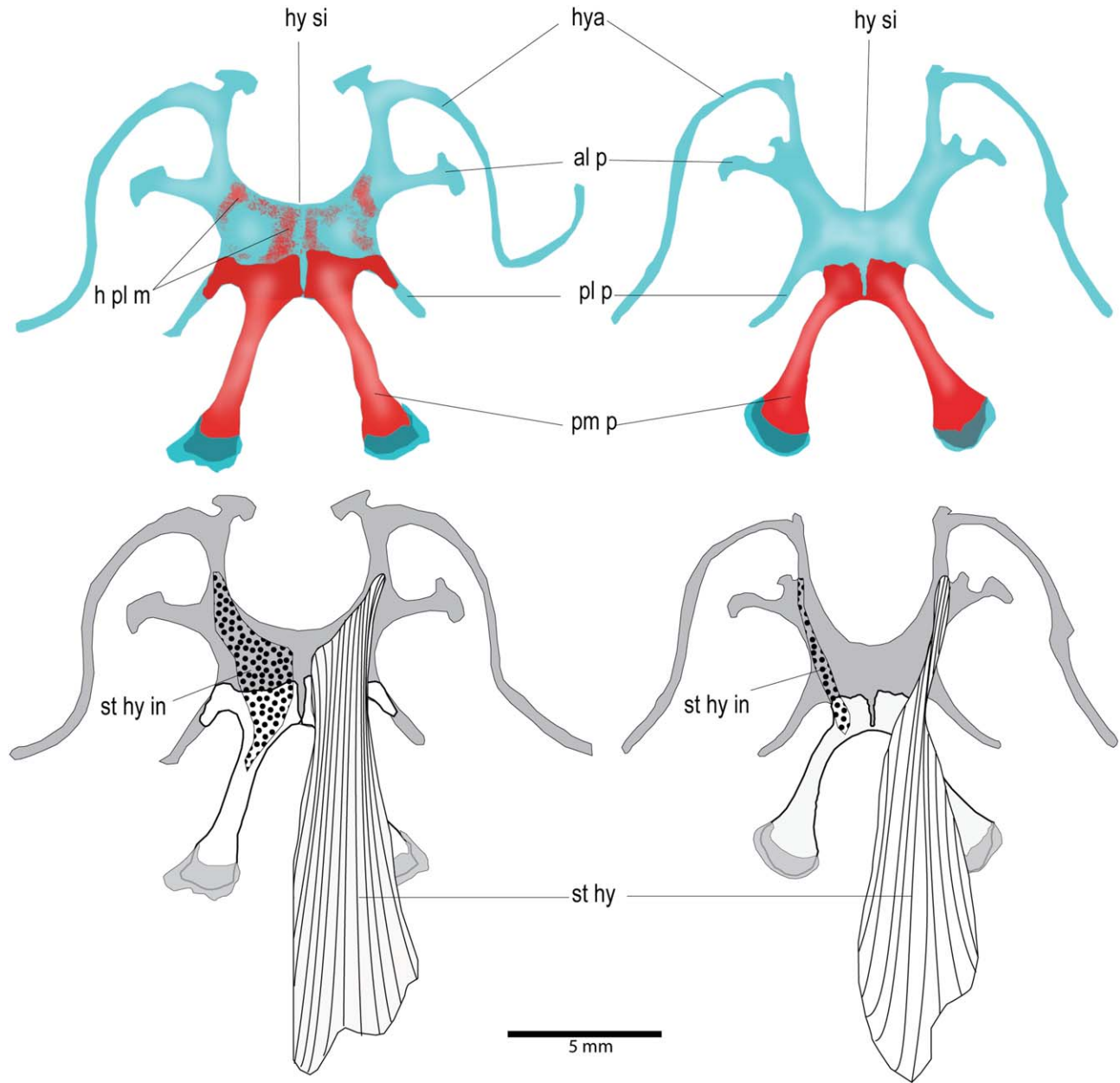


Fig. 5. Hyoid apparatus and the m. sternohyoideus and its insertion area in the hyoid plate of *Telmatobius rubigo* (upper and lower left) and *T. oxycephalus* (upper and lower right). In *T. rubigo*, it is evident the broader insertion area of *M. sternohyoideus*. Note the mineralized hyoid plate and the invasion of the ossification of the posteromedial processes into the more wide and robust plate of *T. rubigo*. In con-

trast, the larger hyoglossal sinus in *T. oxycephalus* is associated with a more developed hyoglossal musculature and tongue. Abbreviations: al p (anterolateral process), h pl m (hyoid plate mineralizations), hy si (hyoglossal sinus), hya (hyalia), pl p (posterolateral process), pm p (posteromedial process), st hy (m. sternohyoideus), st hy in (m. sternohyoideus insertion area).

T. rubigo. This muscle inserts along the lateral margin of the hyoid plate, near the base of the hyale and the base of the anterolateral, posterolateral and posteromedial processes. The area of insertion is smaller than in *T. rubigo*, and the hyoid plate is not mineralized.

Tongue and related muscles. *Telmatobius rubigo* has a small and flat tongue (Fig. 6A,C) that is attached to the buccal floor approximately to 90% of

its extension, with only the posterior margin free. In contrast, the tongue of *T. oxycephalus* is better developed, thicker and it is also attached to the buccal floor (Fig. 6B,D) but approximately to 70% of its total length, and the posterior and posterolateral margins are free.

The tongue of anurans is composed of two muscles (Figs. 7 and 8)—the m. genioglossus (protracting the tongue) and the m. hyoglossus (retracting the tongue). The paired m. hyoglossus originates from the

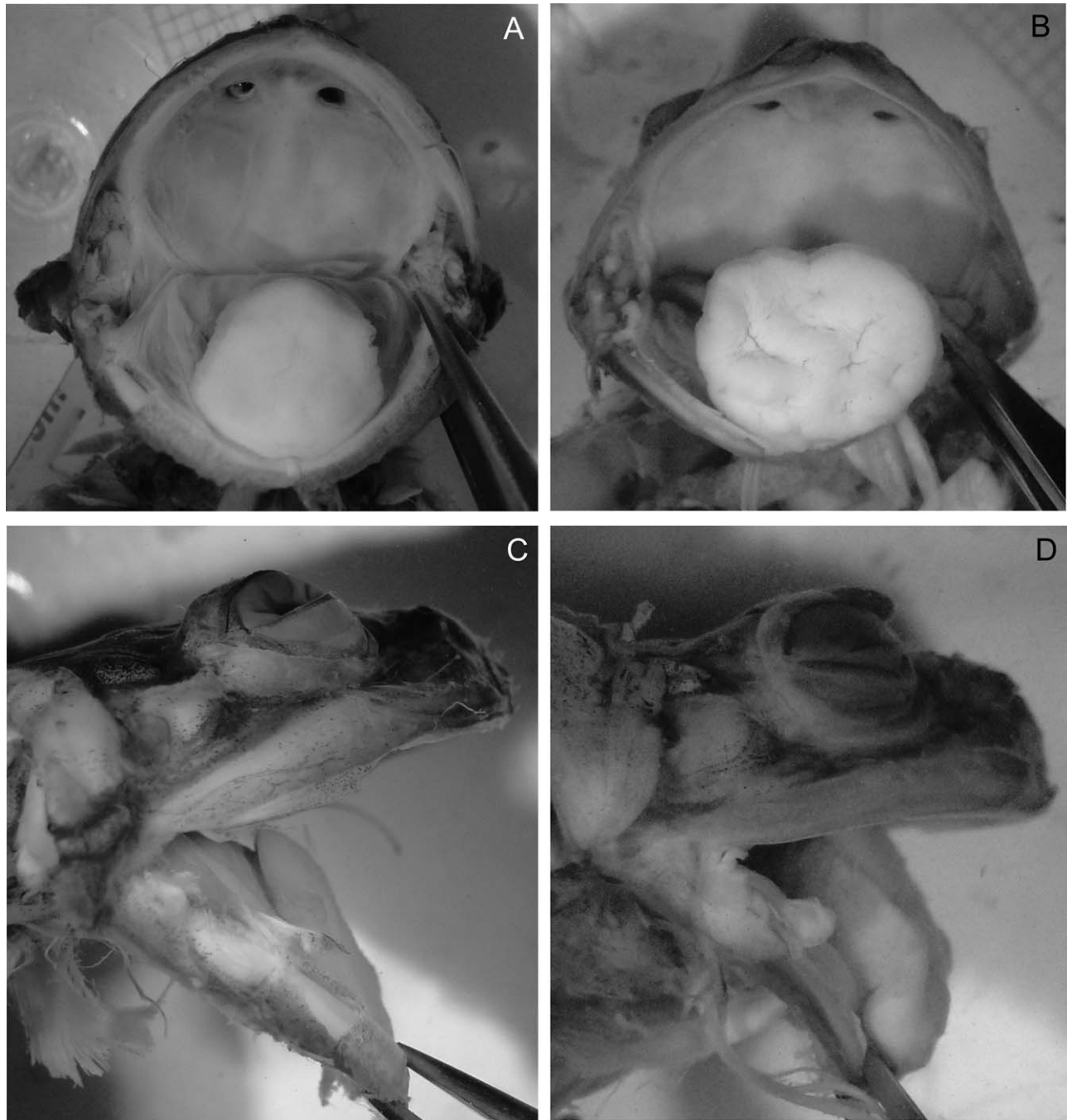


Fig. 6. Frontal (A,B) and lateral view (C,D) of the tongue of *Telmatobius rubigo* (A,C) and *T. oxycephalus* (B,D). Note the less muscular tongue in *T. rubigo*. In this species, the tongue has a more extensive attachment to the buccal floor than in *T. oxycephalus*.

posteromedial process of hyoid and the anterior fibers enter the tongue. In *T. rubigo*, the m. hyoglossus is not massive, and the contralateral muscles are not completely fused to each other; the anterior fibers of the m. hyoglossus insert superficially in the tongue and divides in segments that interdigitated with the m. genioglossus. The ventralmost fibers of m. hyoglossus insert to the anterior part of the tongue (Fig. 8). In *T. oxycephalus*,

the paired hyoglossus muscles are massive and fused to one another (Fig. 8); the anterior fibers enter the tongue and their anterior segments are not evident as in *T. rubigo*. In both species, only the interdigitating element of the m. genioglossus is present. This muscle originates from the mandibular symphysis and radiate posterolaterally to enter the tongue. The interdigitation of the posterior fibers of the m. genioglossus is more

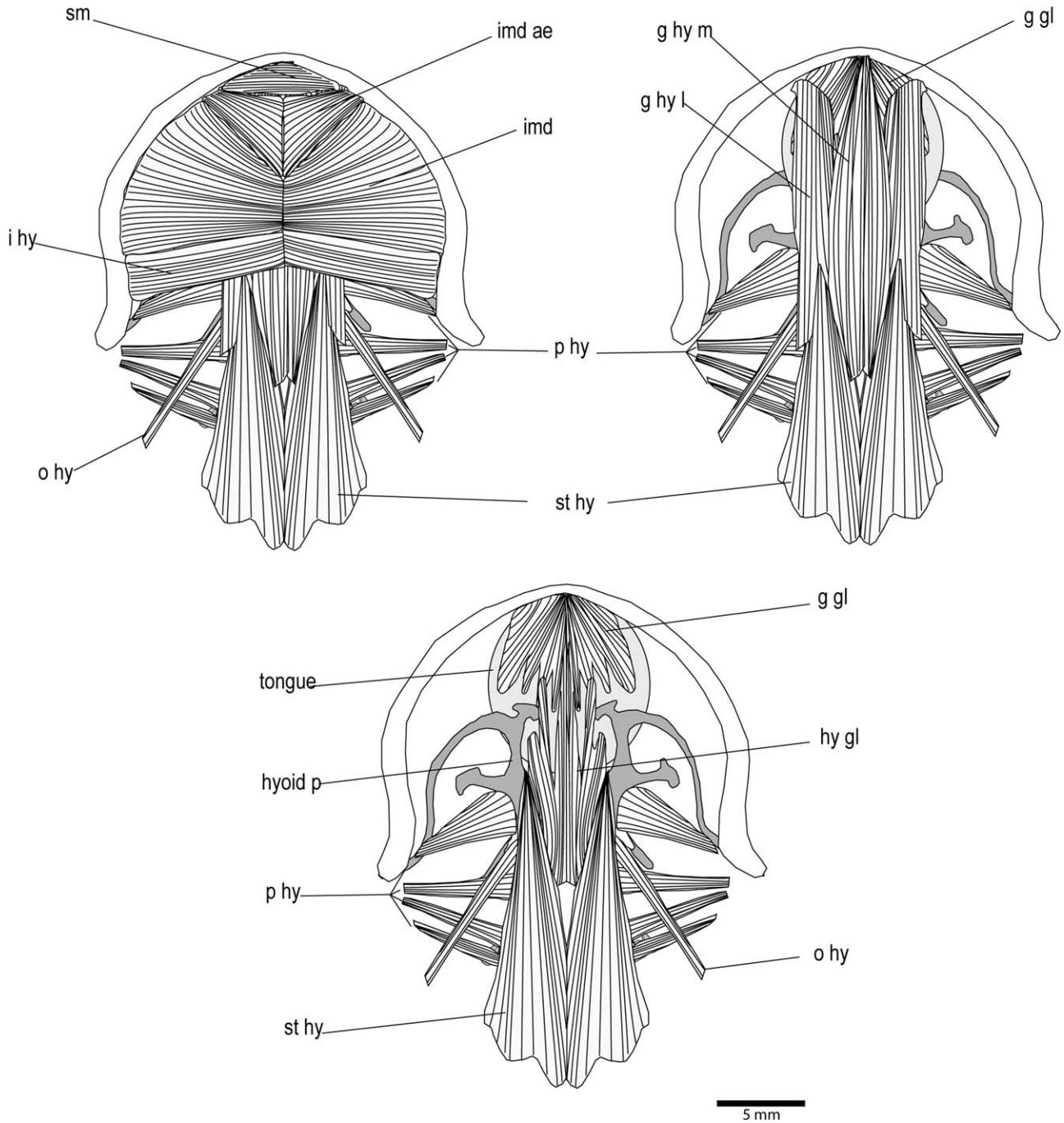


Fig. 7. Submandibular, hyoid, and tongue muscles in *Telmatobius rubigo*. In the upper left figure the skin and the pectoral girdles have been removed to reveal the submandibular muscles. In the upper right figure, the submandibular muscles have been removed; the geniohyoid muscles are evident. In the lower-center figure, the geniohyoid muscles have been removed to expose the tongue muscles.

Abbreviations: g gl (m. genioglossus), g hy l (m. geniohyodeus lateralis), g hy m (m. geniohyodeus medialis), hy gl (m. hyoglossus), hyoid p (m. hyoid plate), i hy (m. interhyoideus), imd (m. intermandibularis), imd ae (m. intermandibularis, apical element), o hy (m. omohyoideus), p hy (m. petrohyoideus), sm (m. submentalis), st hy (m. sternohyoideus).

superficial and evident in *T. rubigo*, than in *T. oxycephalus*, where the posterior fibers enter the larger tongue. The ventral element of the m. genioglossus is absent in both species.

Jaw and submandibular muscles. The jaw muscles consist, basically, of one set of muscles to open the mouth (depressor) and several sets of muscles to close it (levators).

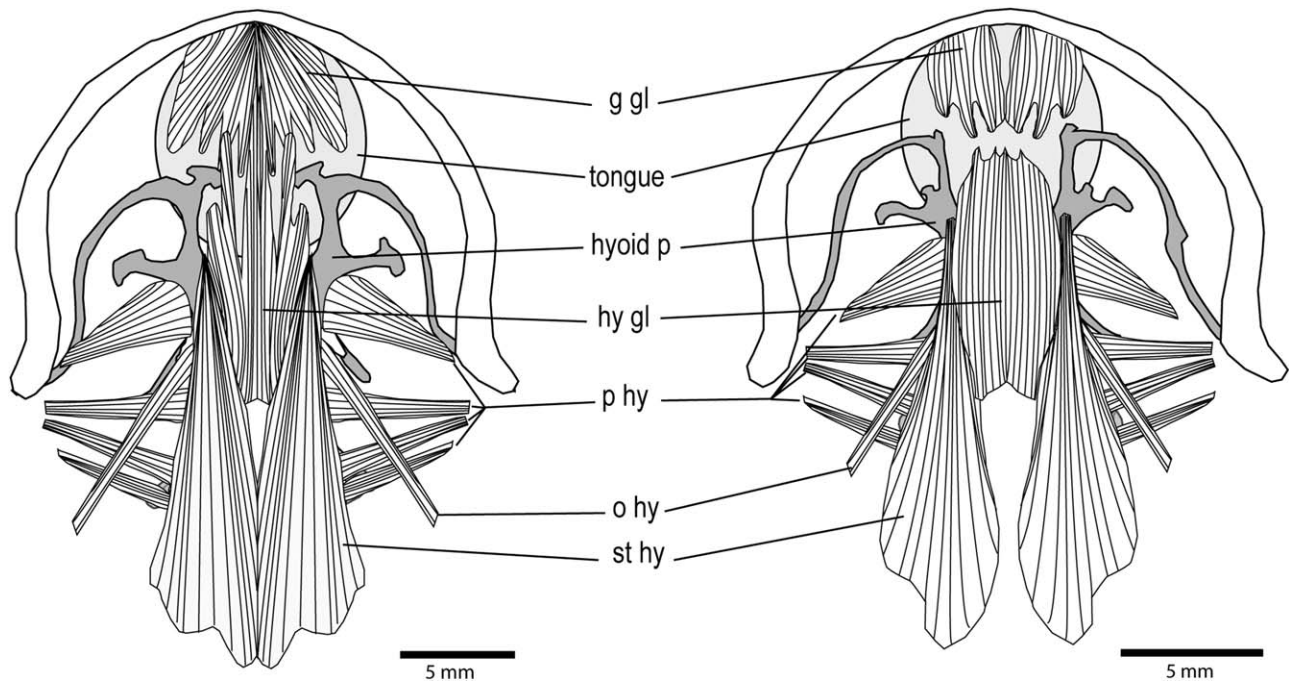


Fig. 8. Hyoid and tongue muscles in *Telmatobius rubigo* (left), and *T. oxycephalus* (right). The more striking differences between these species consist in the development and insertion of the hyoglossus. In *T. rubigo*, it is less developed and inserts more anteriorly and superficially than in *T. oxycephalus*. See Figure 7 for abbreviations.

In *Telmatobius rubigo*, the m. depressor mandibulae is composed of anterior and posterior parts (Fig. 9). The anterior slip originates from the annulus tympanicus, otic ramus of squamosal and the epimysium of the lateral edge of m. levator mandibulae posterior longus. This slip is bulky and inserts on the articular process of the lower jaw. The posterior slip originates from the dorsal fascia; it is thick and triangular, and almost entirely covers the m. dorsalis scapulae and the m. latissimus dorsi. The most posterior fibers originate at the level of m. obliquus externus. Like the anterior slip, the posterior inserts on the articular process of lower jaw. In *T. oxycephalus*, the anterior part of the m. depressor mandibulae is less bulky than in *T. rubigo*. It originates mostly from the epimysium of the lateral edge of m. levator mandibulae posterior longus, although some fibers originate in tympanic annulus and in the otic ramus of squamosal (Fig. 9). The posterior slip does not extend as far posteriorly as in *T. rubigo*; it covers only the anterior half of the m. dorsalis scapulae (Fig. 9).

The difference in the origins of the posterior slip of depressor mandibulae between the two species implies differences in the orientation and length of the muscle. In *T. rubigo*, the posterior fibers are longer and are more horizontally oriented than in *T. oxycephalus*. In contrast, the depressor mandibulae of *T. oxycephalus* is sheet-like and notably thinner than in *T. rubigo*.

The otic ramus of squamosal, one of the points of origin of the anterior slip of m. depressor mandibulae, is longer and more robust in *T. rubigo* than in *T. oxycephalus*.

Among the five levators generally present in adult anurans, two are larger than the rest and originate in

the dorsal region of the skull. These are the m. levator mandibulae longus (m. l. m. longus), which originates from the prootic, and the m. l. m. internus, which originates from the frontoparietals. These muscles, together with the m. l. m. articularis, which originates from the ventral ramus of squamosal, form the group of levators that insert in the medial side of the lower jaw. The m. l. m. externus originates from the zygomatic ramus of squamosal, whereas the m. l. m. lateralis originates from the quadratojugal and adjacent palatoquadrate region. Both muscles insert along the lateral side of the lower jaw. No obvious differences are apparent in the levators of *T. rubigo* and *T. oxycephalus* but some differences are found in the bones where some levators originate. One of these is the zygomatic ramus of squamosal (where m. l. m. externus originates). This ramus is better developed in *T. rubigo* than in *T. oxycephalus*. Additionally, in *T. rubigo*, the frontoparietals are fused to each other posteriorly, coinciding with the region where the m. l. m. internus originates, whereas in *T. oxycephalus* the frontoparietals are not fused or have a variable degree of fusion.

Both species of *Telmatobius* have a similar submandibular musculature, with three sets of muscles (Fig. 7). The m. submentalis traverses the anterior ends of the mandibles; it bends the mandibles during feeding and closes the nares by lifting the mentomeckelian bones upward (Gans and Pyles, 1983; Wolff, Lee and Anderson, 2004). Despite the degree to which *T. rubigo* can flex the mandible, there seem to be no significant differences in the submandibular musculature of the two species. The m. intermandibularis arises from the lingual surface of the lower jaw and inserts on a median raphe. This

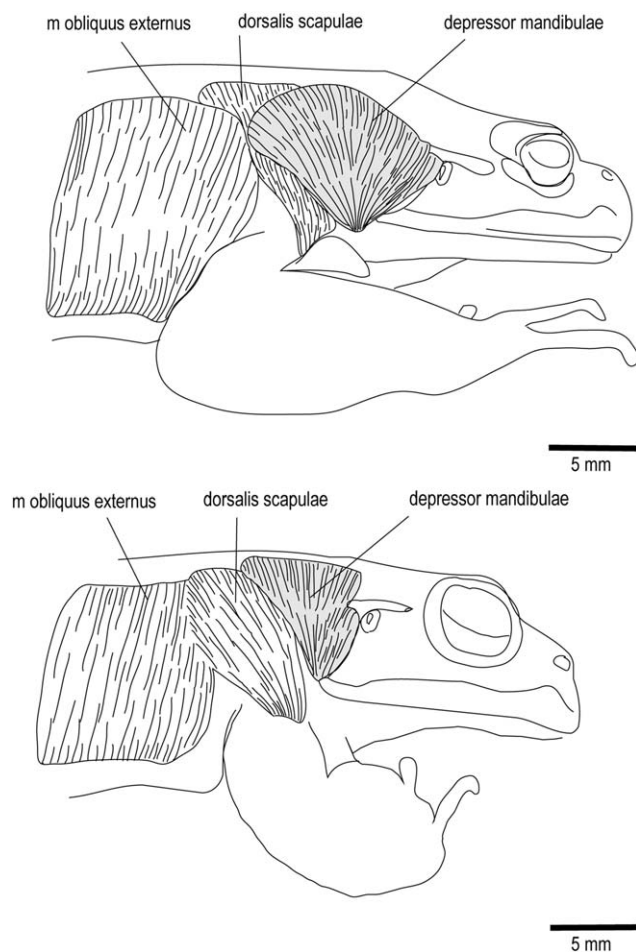


Fig. 9. Lateral view of depressor mandibulae muscle in *Telmatobius rubigo* (top) and *T. oxycephalus* (bottom). The more posterior point of origin of the depressor covering the m. dorsalis scapula and in contact with the m. obliquus externus in *T. rubigo* is evident.

muscle is composed of a supplementary apical element and a posterior principal element. The m. interhyoideus arises from the hyalia and also insert on a median raphe.

The mouth: Labial and lower jaw configuration. The upper lip of *Telmatobius rubigo* is well developed; it overhangs and covers the lower lip along the lateral margins of the mandible (Fig. 10A). The upper lip does not overlap the lower lip at the anterior part of the mouth, thereby creating a notch in the upper lip above the mandibular symphysis (Fig. 10C). This labial configuration is obvious when forceps are used to open the frog's mouth (Fig. 10E): when the mouth begins to open, the gape is restricted only to the anterior part. *Telmatobius rubigo* has a lower jaw remarkably high in lateral profile (Fig. 11B). The height of lower jaw diminishes markedly toward the medial symphysis (Fig. 11B') matching the notch in the upper lip (see above).

In *T. oxycephalus*, the upper lip does not overhang the lower lip (Fig. 10B); thus, a medial notch in the upper lip is absent (Fig. 10D,F) and when the mouth begins to

open, the gape is evident alongside the entire mouth. The lower jaw has a uniform height in lateral view (Fig. 11A,A') that is notable lower than in *T. rubigo*.

Both species have well-developed pedicellate, monocuspid, and fanglike teeth that are embedded in the labial mucosa of the upper jaw.

DISCUSSION

The occurrence of suction feeding in a neobatrachian frog is described herein for the first time along with associated morphological characters. This way of feeding, recorded in the fully aquatic *Telmatobius rubigo*, was not observed in the semiaquatic *Telmatobius oxycephalus*, although this species can capture prey underwater very efficiently. Preliminary data on stomach contents (Barrionuevo, unpublished data) support anecdotal information of the main habits of these species. The most abundant prey found in the stomach of wild caught individuals of *T. rubigo* ($n=4$) consisted on aquatic Diptera larvae (Ephydriidae) that constitute more than 90% of the total prey; the rest consist on aquatic crustaceans (*Hyaella*), and in less quantity aquatic Trichoptera larvae. The terrestrial preys were insignificant and probably accidental. The stomach content of wild caught *T. oxycephalus* ($n=6$) show that the main prey are the terrestrial isopod crustaceans (Oniscidea) that live in the humid borders of the streams.

There is a wide taxonomic spectrum of anurans that, like *Telmatobius oxycephalus*, can feed in water but are not suction feeders. This spectrum, ranging from basal anurans to neobatrachians, includes at least one member of the following families (Fig. 1): Leiopelmatidae (Stephenson and Stephenson, 1957), Ascaphidae (Metter, 1964); Bombinatoridae, Calyptocephallidae and Discoglossidae (O'Reilly et al., 2002), Pipidae (Sokol, 1969; Carreño and Nishikawa 2010), Myobatrachidae (Ingram, 1989), Hylidae (Hylinae, Solé and Miranda, 2006; Pelodyadinae, Robinson and Cappo, 1989; Tyler, 1989), Lepidodactylidae (Da Silva et al., 2009), Ceratophryidae (Hulse, 1978, O'Reilly et al., 2002), Telmatobiidae (this work), Conrauidae (Sabater-Pi, 1985), Dicroglossidae (Hirschfeld and Rödel, 2011), Ranidae (Wu et al., 2005). Members of the basal clades, as *Ascaphus*, *Leiopelma*, and *Bombina* have a round tongue, broadly attached to the buccal floor (Horton, 1982). Despite the limited protractability of the tongue, these anurans are capable of capture prey on land by mechanical pulling (Nishikawa, 2000). The aquatic ceratophryid *Lepidobatrachus* has a much-reduced tongue (Fabrezi and Lobo, 2009) and it can prey on aquatic and terrestrial animals (Hulse, 1978) by using forelimbs and jaw prehension (O'Reilly et al., 2002). The aquatic hylid *Pseudis cardosoi* feeds on both aquatic and terrestrial prey, and during aquatic captures, has been observed to use the forelimbs (Solé and Miranda, 2006). Two hylids of the Pelodyadinae subfamily, *Litoria dahlia* and *L. platycephala*, feed underwater. Robinson and Cappo (1989) described their prey capture mechanisms and mentioned that *L. platycephala* sucks its prey, but the use of hands is involved. Although these authors did not discuss this point, this could be a case of compensatory suction as described for *Xenopus* and *Pipa*, and is deserving of further study. Opportunistic frogs, like *Lithobates catesbeianus* and *Leptodactylus latrans*, can capture aquatic prey such as

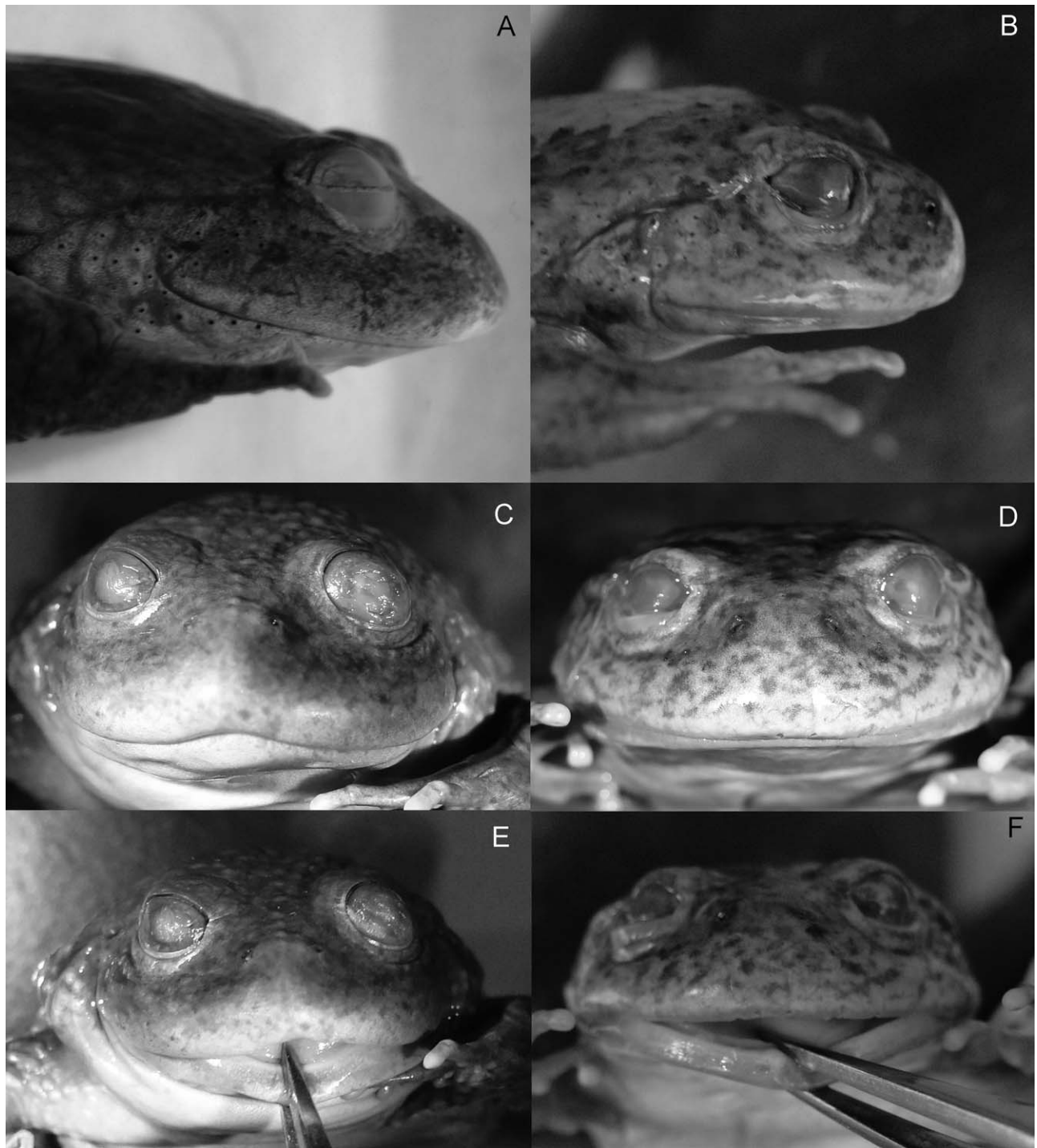


Fig. 10. Lateral and frontal views of the mouth and the lips of *Telmatobius rubigo* (A, C, E) and *T. oxycephalus* (B, D, F). In E and F, the mouth was opened with forceps to show the shape of the gape when the mouth begins to open.

tadpoles or fish (Wu et al., 2005; Da Silva et al., 2009; Solé et al., 2009). These species have a well-developed, protractable tongue specialized for capturing prey on land by inertial elongation (Nishikawa, 2000), but apparently they manage to perform aquatic captures also.

O'Reilly et al. (2002) described the use of jaws and forearm scooping for aquatic captures in *Lithobates catesbeianus*.

A morphological overview of such a diverse array of anurans, ranging from frequent to occasional aquatic

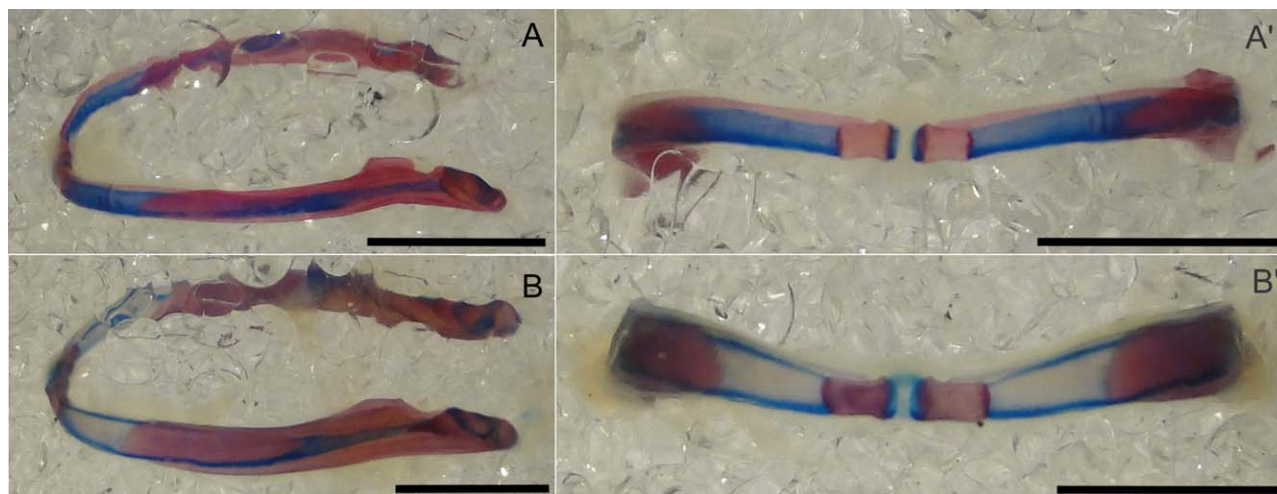


Fig. 11. Lateral (A, B) and frontal (A', B') view of the lower jaw of *Telmatobius oxycephalus* (A, A') and *T. rubigo* (B, B'). Note the higher lower jaw of *T. rubigo* (B) decreasing abruptly at the level of the symphysis (B'). By contrast, in *T. oxycephalus* the mandible is low (A) but uniform, even at the level of the symphysis (A'). Bar = 5 mm.

feeders, does not reveal obvious morphological specializations for the capture of prey in water. In contrast, suction feeding has been associated with several morphological characters (Deban and Wake, 2000): (1) reinforcement of hyoid apparatus via mineralization or ossification of cartilage (Özeti and Wake, 1969; Deban and Wake, 2000; Nishikawa 2000; Deban, 2003); (2) loss or reduction of tongue; and (3) presence of labial lobes to occlude the gape laterally. Additionally, Dean (2003) stated that the absence of teeth is related to suction feeding, but he did not elaborate this hypothesis. All of these features characterize the suction feeders *Hymenochirus* and *Pseudhymenochirus* and some of them are present in *Pipa* and *Xenopus* (lack of tongue, strong hyoid apparatus).

Hyoid Apparatus and Related Muscles

Typically, the hyoid plate in anurans consists in a cartilaginous, flexible, and lightly built structure (Trewavas, 1933; Trueb, 1973), and its ossification is rare. The hyoid in the suctorial pipids *Hymenochirus* and *Pseudhymenochirus* (Sokol, 1969; Cannatella and Trueb, 1988) is massive and heavily ossified, forming a rigid frame to the attachment of the muscles that depress the buccal floor. In *Telmatobius rubigo*, the hyoid plate is wider and mineralized unlike the slender and completely cartilaginous hyoid plate of *T. oxycephalus*. Additionally, the ossification of posteromedial processes advances over the plate and posterolateral processes in *T. rubigo* but not in *T. oxycephalus*. Although this relation is suggestive, the relation of morphology of hyoid plate and feeding in anurans seems to be more complex. The reinforcement of hyoid plate is not exclusive of suction feeders. Several basal anurans (e.g. *Bombina*, *Barbourula*, *Ascaphus*) have a ventral ossification known as parahyoid bone (Cannatella, 1985). Among neobatrachians, a dorsal dermal ossification is present in *Lepidobatrachus* (Fabrezi, 2006; Fabrezi and Lobo, 2009). Interestingly, a common feature among these species with ossified hyoids is that

they have simple or reduced tongues with limited protractability. If we assume that during the inertial elongation of the tongue (typical and well exemplified in Bufonidae or Ranidae) the flexibility of hyoid is necessary, there may be functional constraints that preclude its mineralization or ossification. By contrast, in species with a reduced tongue, the hyoid is liberated from these constraints. Hypothetically, this scenario may constitute a prerequisite of subsequent and more efficient reinforcement to fulfill the requirements of suction feeding, which have precisely, the opposite constraints.

The hyoid plate is retracted by the m. sternohyoideus (de Jongh and Gans, 1969; Martin and Gans, 1972), which, at the same time, depresses the buccal floor and causes the fall of intraoral pressure. The mineralized areas of the hyoid plate in *T. rubigo* coincide with the insertion area of the m. sternohyoideus; this may indicate that these regions are bearing major loads during the depression of the hyoid plate. In *T. rubigo* this muscle is more massive and has a broader insertion in the hyoid plate than in *T. oxycephalus*. Additionally, in *T. rubigo* the m. sternohyoideus has two slips (a feature shared with Ceratophryinae; Fabrezi and Lobo, 2009), whereas in *T. oxycephalus* has one component (Fabrezi and Lobo, 2009). The robustness of the m. sternohyoideus in *T. rubigo* may be associated with the need for more traction force for the rapid depression of buccal floor.

Tongue Morphology and Function

A protractile, sticky tongue seems to be ineffective in the dense aquatic environment (Regal and Gans, 1976; Bramble and Wake, 1985). Among amphibians, the reduction or loss of the tongue is well known in pipids (Horton, 1982; Cannatella and Trueb, 1988) and suctorial salamanders (Özeti and Wake, 1969). The size of the tongue may affect suction feeding performance. A smaller tongue occupies less space in the buccal cavity, thereby allowing an increase in intraoral volume during

buccal expansion and increasing negative pressure to move water more rapidly into the mouth (Bramble and Wake, 1985). Additionally, it has been suggested that a smaller tongue may reduce the turbulence of flow water into the mouth (Bramble and Wake, 1985; Miller and Larsen, 1989). Regal and Gans (1976) mentioned that tongue muscles in *Telmatobius marmoratus* are relatively simple, with a level of organization similar to that of basal anurans such as *Bombina*. Although in *Telmatobius*, in general, the tongue is simple and it is attached largely to the buccal floor, there is variation in tongue development within the genus (Barrionuevo, pers. obs.). *Telmatobius rubigo* has a reduced, less muscular tongue that is more attached to the buccal floor than does *T. oxycephalus*. The tongue muscles encompass these external differences: (i) the anterior fibers of m. hyoglossus and posterior fibers of the m. genioglossus are more superficial, making its interdigitation evident, and (ii) each m. hyoglossus are in contact but failed to fused to each other in *T. rubigo*, whereas in *T. oxycephalus*, (i) the m. hyoglossus and m. genioglossus insert deeper in the larger tongue making its interdigitation not evident, and (ii) the more robust m. hyoglossus are fused to each other. The pattern found in *T. rubigo* is similar to the condition described in *Lepidobatrachus*, whose tongue is reduced as well as its related muscles (Fabrezi and Lobo, 2009). A common feature in both species of *Telmatobius* is the absence of the ventral element of the m. genioglossus. This element is also absent in *Lepidobatrachus* and *Pseudis* (Fabrezi and Lobo, 2009) as well as in basal anurans with simple tongues (e.g. *Ascaphus*, *Rheobatrachus*, *Pelobates*; Horton, 1982). However, Fabrezi and Lobo (2009) briefly mentioned that the ventral element of the m. genioglossus is present in *T. oxycephalus* but they did not provide any images or more details about this muscle. This element, described in species with a highly protrusible tongue (Horton, 1982), is clearly absent in the specimens of *T. oxycephalus* analyzed. Its lack in *Telmatobius* is consistent with the absence of this muscle in other species with limited tongue protraction. This is not the only difference in relation to the description of Fabrezi and Lobo (2009). These authors reported the absence of the m. omohyoideus in *T. oxycephalus*, but the examination of the specimens included here showed that this element is present.

Functional Morphology of the Jaw and Associated Muscles

Previously to the depression of the buccal floor, the normal sequence of suction feeding commences with the rapid opening of the mouth. However, the mouth must be opened in an environment almost 800 times denser than air, which constitutes a functional challenge. The main muscle involved in mouth opening is the m. depressor mandibulae. In *Telmatobius rubigo* this muscle originates more posteriorly (resulting in longer fibers) and it is more robust than in *T. oxycephalus*. This could be associated with a faster and stronger action. Curiously, the same pattern has been described comparing aquatic and terrestrial turtles. Aquatic species have depressor that originates more posteriorly than the terrestrial ones (Schumacher, 1973; Lemell et al. 2000). Although this morphological pattern is suggestive, its functional significances must to be explore.

Mouth Configuration and Feeding Behavior

In addition to the features of the hyoid and tongue, labial lobes or oral flaps have been associated with suction feeding (Deban and Wake 2000; Deban and Marks 2002). These lobes preclude a lateral gape in the jaws, and thus, restrict the movement of water into the mouth, improving the power of suction. Labial lobes occur in all suctorial salamanders (Deban and Wake 2000; Deban and Marks 2002), but in anurans, they have only been mentioned for *Hymenochirus* (O'Reilly et al. 2002). In other pipids as *Pipa* and *Xenopus*, the labial lobes are absent (Measey, 1998). Carreño and Nishikawa (2010) demonstrated that members of these genera can generate an intraoral pressure drop; however, in the absence of labial lobes, water flow cannot be focused. Thus, the frogs could not generate enough suctorial force to suck in prey, and must use the forelimbs to scoop up prey. In *T. rubigo* the upper lips are overhanging laterally the lower lips and a notched is formed in the front of the mouth. This configuration seems to generate a lateral occlusion of the jaws when the mouth begins to open. This occlusion may control the movement of water in the mouth and generate more localized water flow forces. This trait can act as the labial lobes described in suctorial salamanders or *Hymenochirus*. Besides the lips configuration present in *T. rubigo*, lower jaw morphology, that is high posteriorly and low anteriorly, also contributes to the reduction of gape. This set of characters constitutes a key acquisition that parallels *Hymenochirus* and suctorial salamanders. By contrast, *T. oxycephalus* lacks those traits and show an impressive wide gape during feeding (Figs. 4 and 10).

Phylogenetic and Evolutionary Implications

The constraints of suction feeding seem to be strong, given the observed convergent morphological traits present not only in pipids and salamanders, but even in turtles (Bramble and Wake, 1985). In salamanders, suction feeding evolved independently in several lineages (Deban, 2003), and it is noteworthy that this mode of feeding is not widespread among anurans, especially if we consider that several species of anurans from a wide taxonomic spectrum forage in water (Fig. 1). O'Reilly et al. (2002) hypothesized that the absence of suction feeding in anuran larvae has constrained the evolution of this type of feeding mechanism in adults. This hypothesis is based on the fact that salamanders that feed underwater by suction as adults have a suction feeding larva. This is also the case of *Hymenochirus*, whose tiny tadpole uses suction for catching small prey (Deban and Olson, 2002). The case of *Hymenochirus* is exceptional because the vast majority of anuran larvae are predominantly suspension feeders. This hypothesis has been challenged by the finding that adult *Pipa* and *Xenopus*, both with suspension feeding larvae, are capable of suction (Carreño and Nishikawa, 2010). This is also the case in *Telmatobius*. All known *Telmatobius* tadpoles are suspension feeders (e.g. Aguilar and Pacheco, 2005; Vera Candiotti, 2008; Barrionuevo and Baldo 2009a), including the tadpole of *T. rubigo* (Barrionuevo and Baldo, 2009b).

We lack a comprehensive phylogeny of *Telmatobius*; however, De la Riva, et al. (2010) and Sáez et al. (2014) provided phylogenetic hypotheses of Bolivian and

Chilean species based on mitochondrial sequences (16S and cyt b). In these hypotheses several clades were recovered and an interesting pattern arises in relation to species habits and habitats. The basal *T. verrucosus* species group consists predominantly in semiaquatic middle altitude species, inhabiting fast flowing streams from forest and subparamo. One of the two derived groups, the *T. bolivianus* species group consist in aquatic and semiaquatic species inhabiting mid altitude streams at forest and dry inter-Andean valleys. The other derived group, the *T. marmoratus* species group, consists in fully aquatic species living in highland streams of Altiplano and Puna. Based on several morphological characters (Barrionuevo and Baldo, 2009b; Barrionuevo, 2013), *T. oxycephalus* could be related with the *T. bolivianus* species group, whereas *T. rubigo* could be related to the *T. marmoratus* species group (De la Riva et al, 2010). The remarkable morphological similarity of *T. rubigo* with the species of the *T. marmoratus* clade (e.g. *T. marmoratus*, *T. huayra*, *T. hintoni*) suggests that these species could capture their aquatic prey by suction. If this holds true, this type of feeding seems to have evolved in this clade in relation to the fully aquatic habits adopted by these frogs in the context of the colonization of the high Andean range, a harsh environment for anurans with a terrestrial mode of life.

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