

Chondrocranium, cranial muscles and buccopharyngeal morphology on tadpoles of the controversial leptodactylid frog *Limnomedusa macroglossa* (Anura: Leptodactylidae)

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Abstract. The present paper provides original data on the chondrocranium, cranial muscles, oral disc and buccopharyngeal morphology of *Limnomedusa macroglossa*. We found that the cranial muscles and the buccopharyngeal papillation are not useful to relate *Limnomedusa* either to telmatobiine or leptodactyline genera. There are two chondrocranial characters (presence of a long processus pseudopterygoideus and sindesmotic connection of the partes alares and partes corpora of the cartilago suprarostralis) that relate *Limnomedusa* to the telmatobiine genera more than to any other genus within Leptodactylidae. Additionally, the processus pseudopterygoideus of *Limnomedusa* is fused to the basi crani, a character state only known for some telmatobiine genera such as *Alsodes* and *Telmatobius*.

Introduction

The monotypic *Limnomedusa* is a medium-sized leptodactylid genus that inhabits rocky streams in southern Brazil, Uruguay, and north-eastern Argentina (Barrio, 1971; Gudynas and Gehrau, 1981). The position of *Limnomedusa* within Leptodactylidae has been historically controversial, having been considered either as Leptodactylinae or Telmatobiinae. Lynch (1971) and Heyer (1975) placed *Limnomedusa* within Leptodactylinae on the basis of characters from adult external morphology, adult myology, life history data, and osteology. Barrio (1971) and Barrio and Rinaldi de Chieri (1971), based upon the presence of a karyotype $2n = 26$ suggested the inclusion of *Limnomedusa macroglossa* either within the Elosiinae (now considered within Cycloramphinae) or Telmatobiinae (Laurent, 1986). Later, Lynch (1978) re-analyzed some telmatobiine genera collectively known as "Lower Telmatobiines"

and, employing primarily osteological characters, grouped *Limnomedusa* with them. Lanzone and Prigioni (1985) studied the oviposition of *Limnomedusa macroglossa* and considered data of previous authors to support the proposal of Lynch (1978). Other authors, without presenting new data, have assigned *Limnomedusa* either to the Leptodactylinae (Cei, 1980; Frost, 1985; Laurent, 1986; Lavilla and Cei, 2001) or the Telmatobiinae (Lavilla, 1988).

The present paper provides original data on the chondrocranium, cranial muscles, oral disc and buccopharyngeal morphology of *Limnomedusa macroglossa* in order to: 1) compare with previously published data for other leptodactylid tadpoles (mainly Telmatobiinae and Leptodactylinae), and 2) assess the previous views relative to the subfamilial position of *Limnomedusa*.

Materials and methods

On 12 January 1994, a complete developmental series of *Limnomedusa macroglossa* ($n = 49$; stages 25 – froglets) was collected by J. Faivovich at Salto del Río Kozac, INTA San Antonio, Dpto. General Belgrano, Misiones province, Argentina. The examined material was deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Tadpoles were fixed after capture in 10% buffered formalin and then staged using the table of Gosner (1960). Four tadpoles (stages 36 and 38, MACN 34996) were stained following the technique of Taylor and

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Van Dyke (1985). The procedure was interrupted before the clearing stage for muscular observation; afterward the specimens were cleared for chondrocranium description. For scanning electronic microscope (SEM) examination of buccopharyngeal morphology and keratinized structures of the oral disc, one tadpole (stage 31) was: 1) put in ethanol 30%: 3 15-minute baths; 2) put in ethanol 50%: one week; 3) cut according to Wassersug (1980); 4) put in ethanol 70%: 3 15-minute baths; 5) put in ethanol 100%: 15 minutes prior to the critical point; 6) critical point dried in carbon dioxide using amyl acetate as an intermediate liquid; and finally 7) mounted on a double-face Carbon tape and sputter coated with gold-palladium 400 Å thick using a Model Ion Sputter Fine Coat JFC-1100 (Jeol System). Features of oral internal anatomy were examined under a Jsm-T100 scanning electron microscope at 5-15 kV and the photographs were taken using an Ilford camera. The buccopharyngeal morphology of an additional tadpole (stage 36) was also examined under a stereomicroscope. All observations, measurements and drawings of the chondrocranium and cranial muscles were made using a Reichert Wien stereomicroscope equipped with measurement accessories (to the nearest 0.1 mm) and camera lucida.

Terminology follows D'Heursel and de Sá (1999) and Haas (1995) for chondrocranium descriptions, Alcalde and Rosset (2003) for chondrocranial measurements, Haas (2001) for mandibular musculature, Haas and Richards (1998) and Haas (2003) for branchial and hyoid musculature, Schlosser and Roth (1995) for musculature innervation, and Wassersug (1980) for buccopharyngeal morphology. To compare our data with those of other leptodactylids, we follow the family scheme in five subfamilies (*Ceratophryinae*, *Cycloramphinae*, *Eleutherodactylinae*, *Leptodactylinae*, and *Telmatobiinae*) as in Frost (2004), who follows Laurent (1986).

Results

Oral disc and buccopharyngeal morphology (figs. 1-3)

The keratinized structures of the oral disc are the jaw sheaths and five keratodont rows, two anterior and three posterior, making the tooth row formula 1(2)/3(1). There are no morphological differences between the keratodonts of different rows. They are spatulated and slightly curved towards the mouth opening. Each keratodont bears approximately 12 distal serrations at its free distal end (fig. 1A). The well-developed jaw sheaths are completely keratinized and their free margins possess conical indentations (fig. 1B).

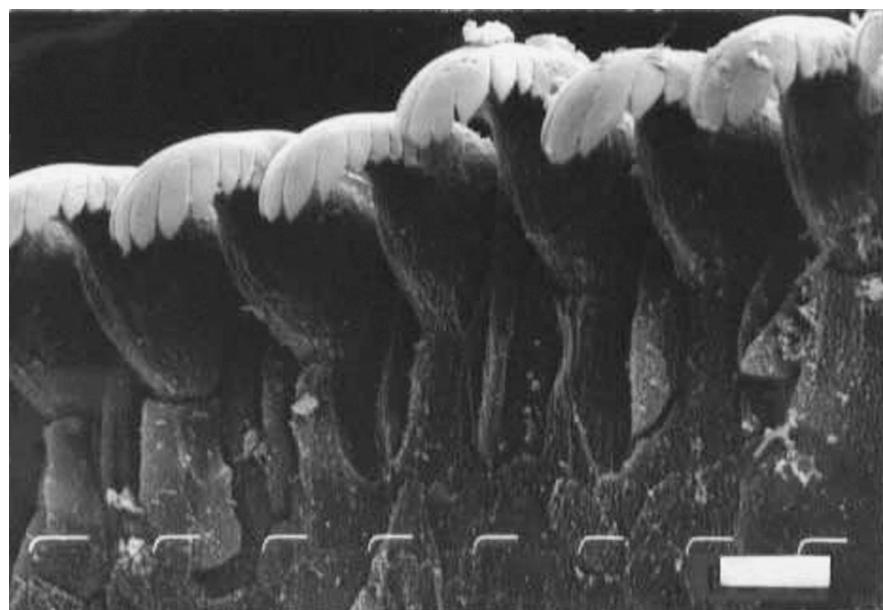
The buccal roof (fig. 2A) lacks infrarostral papillae. The prenarial arena bears an arch of eight robust and short papillae. The postnarial arena possesses two lateral lines of three serrated papillae placed anteriorly to each lateral ridge, two medial lines of seven serrated papillae placed anterior to the lateral margins of the median ridge, and a central cluster of about eight pustulations placed just anterior to the median ridge (fig. 3A, B). The papillae of the lateral line become larger from the posteriormost (smallest) to the anterior one (tallest) (fig. 3A, B). The papillae of the medial line increase in size from the anteriormost (smallest) to the most posterior papilla (tallest). The well-developed median ridge is triangular and serrated. The lateral ridges have four serrated papillae, arranged from smallest (anterior) to tallest (posterior) (fig. 3A, B). There are over 70 central pustulations and approximately 30 long and conical papillae arranged in a U-shaped pattern on the buccal roof arena. There is an arch of about 60 postulations and numerous secretory pits placed posteriorly to the buccal roof arena.

The buccal floor (fig. 2B) possesses four long and serrated lingual papillae. There is no infrabial papilla in the buccal floor. There are 20 long and conical papillae, and few pustules on the preocket arena. The buccal floor arena has approximately 60 long and conical papillae, and about 30 pustules. The ventral velum has serrated posterior margins and bears secretory pits.

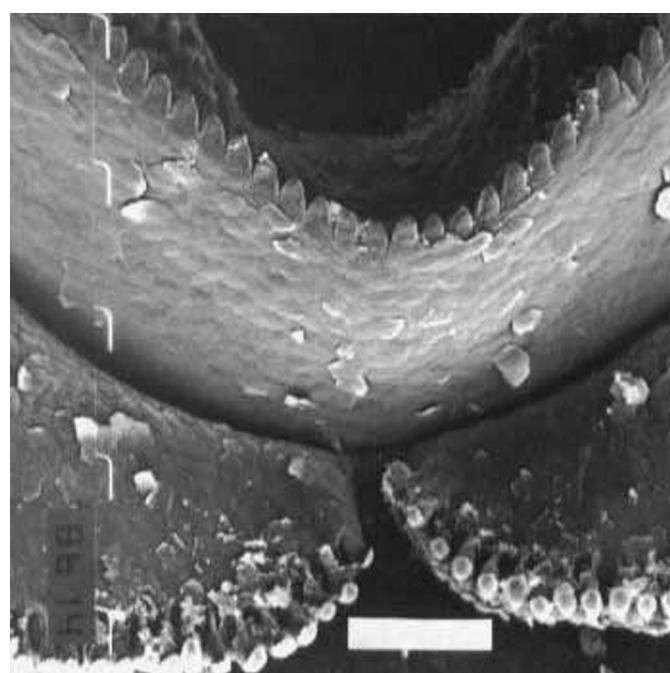
Chondrocranium (fig. 4)

The neurocranium is almost square-shaped (Width/Length = 0.92-0.94) with its greatest width at the level of the processus ascendens.

The upper horny beak is supported by a paired cartilago suprarostralis (fig. 4C). Both partes corporis of this cartilage are distally fused and there are no cartilaginous connections between the pars alaris and the pars corporis. The pars alaris has a well-developed processus posterior dorsalis and bears a small and rounded processus anterior dorsalis in the point of articulation with the pars corporis and the cornu tra-



(A)



(B)

Figure 1. Scanning electronic microscope photographs of the keratodonts of the first rostral row (A), and of the infrarostrodont (B) of *Limnomedusa macroglossa* at stage 31. Scale bars: 10 μm (A) and 100 μm (B).

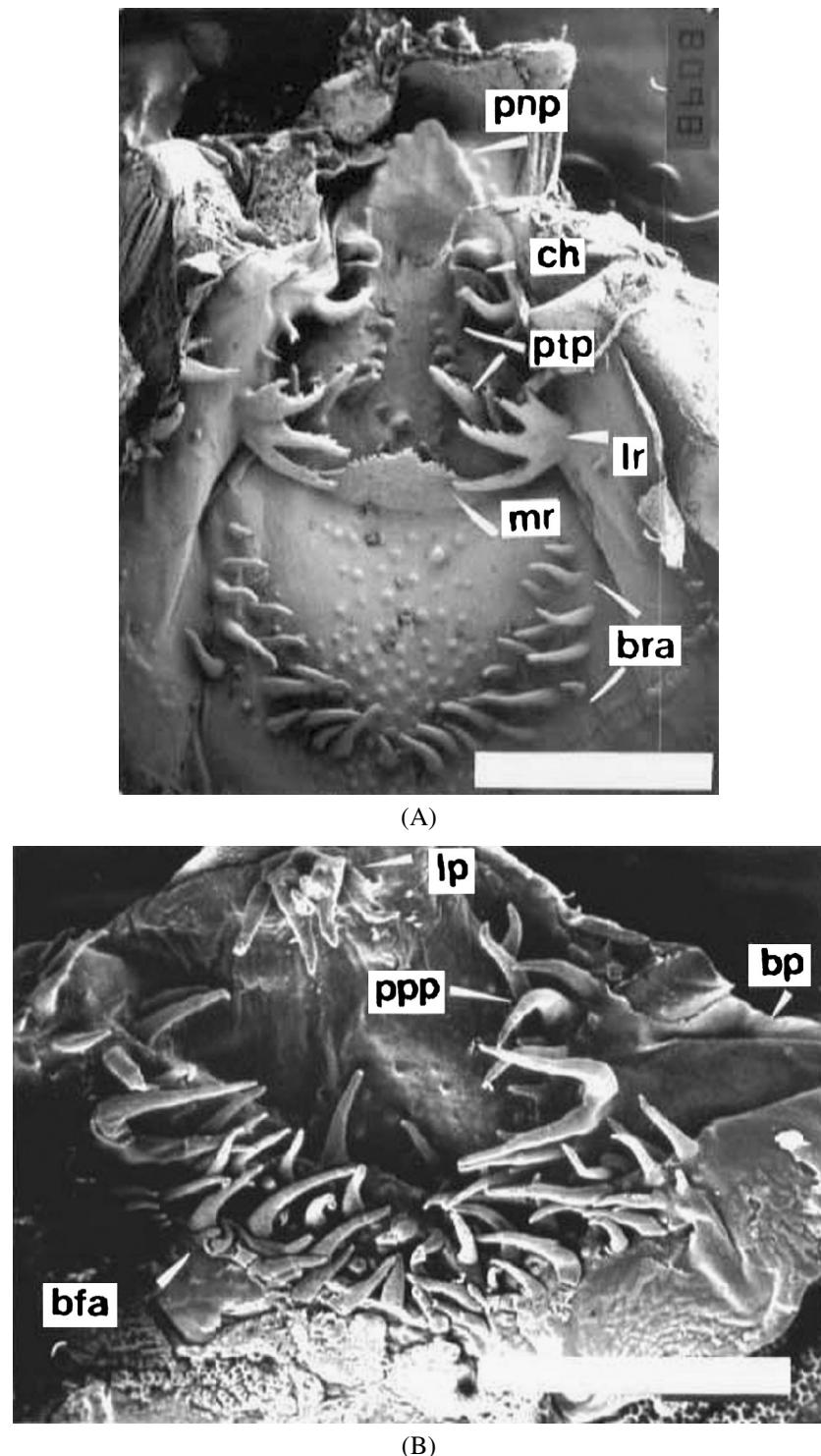


Figure 2. Scanning electronic microscope photographs of the buccal roof (A) and the buccal floor (B) papillation of *Limnomedusa macroglossa* at stage 31. Scale bars: 1000 μm . Legends: bfa, buccal floor arena; bp, buccal pocket; bra, buccal roof arena; ch, choana; lp, lingual papilla; lr, lateral ridge; mr, median ridge; pnp, prenarial papillae; ppp, prepocket papillae; ptp, postnarial papillae.

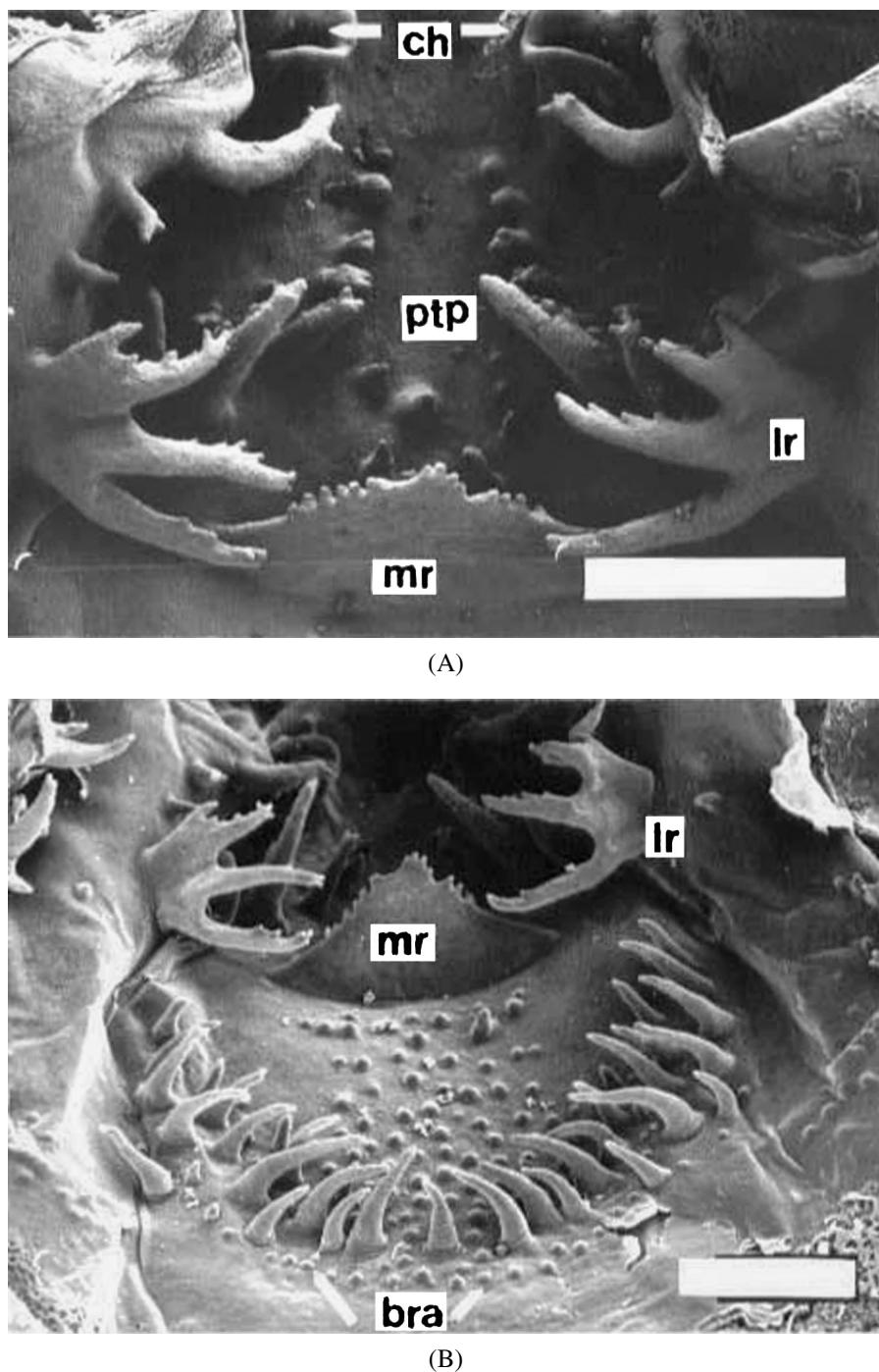


Figure 3. Detailed scanning electronic photographs of the buccal roof arena (A) and the anterior buccal roof (B) papillation of *Limnomedusa macroglossa* at stage 31. Scale bars: 50 μm (A) and 500 μm (B). Legends are as in Figure 2.

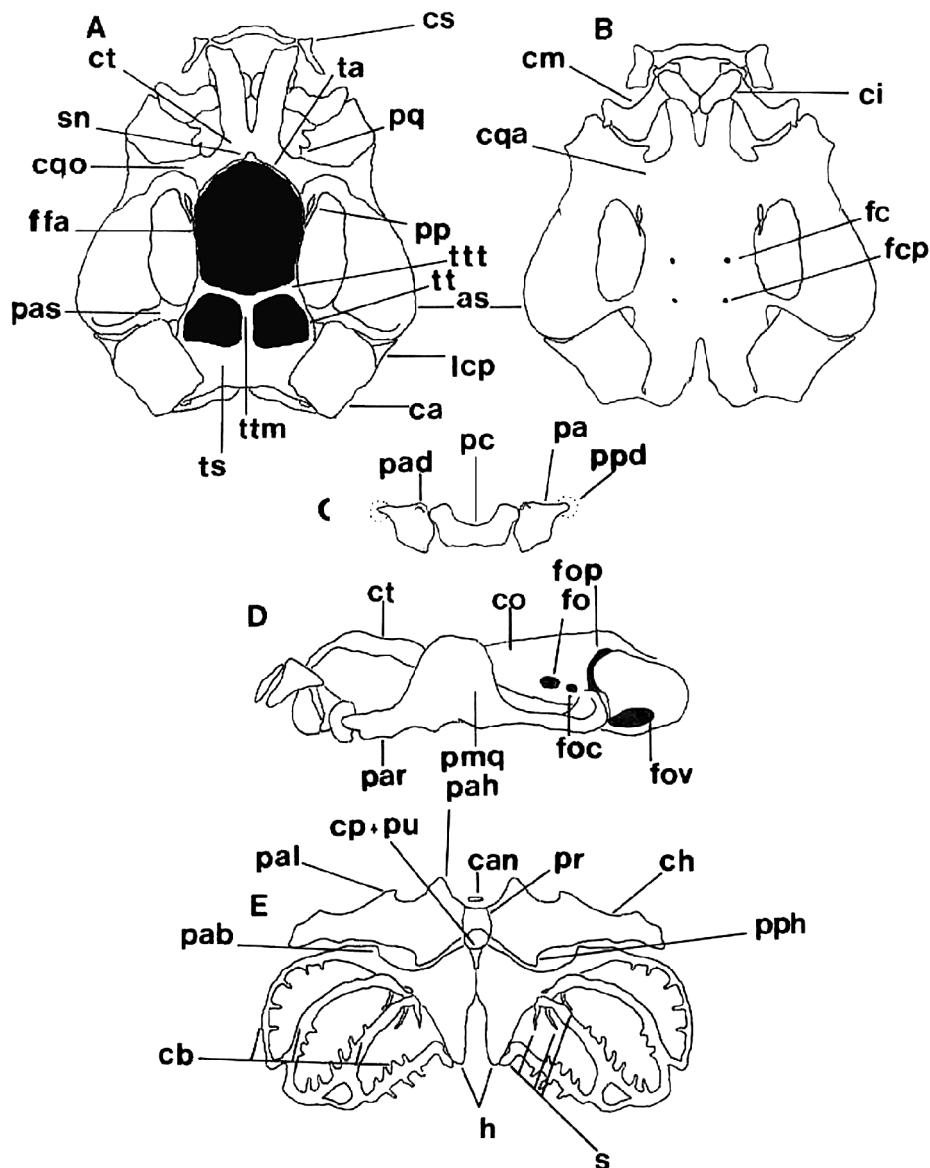


Figure 4. Chondrocranium of *Limnomedusa macroglossa* at stage 36 (MACN 34996). **A.** Dorsal, **B.** ventral, and **D.** lateral views of the neurocranium and mandibular arch. **C.** Frontal view of the cartilago supraorostralis. **E.** Ventral view of the hyobranchial apparatus. Dark areas represent cranial fenestrations. Scale bar: 1 mm. Legends: as, arcus subocularis; ca, capsula auditiva; can, copula anterior; cb, ceratobrachiales; ch, ceratohyale; ci, cartilago infrarostrale; cm, cartilago meckeli; co, cartilago orbitale; cp, copula posterior; cqa, commissura quadrato-cranialis anterior; cqa, commissura quadrato-orbitalis; cs, cartilago supraorostralis; ct, cornu trabeculae; fc, foramen craneopalatinum; fcp, foramen caroticum primarium; ffa, fenestra frontoparietalis anterior; fo, foramen opticum; foc, foramen oculomotorium; fop, foramen prooticum; fov, fenestra ovalis; h, hypobranchiales; lcp, larval crista parotica; pa, pars alaris; pab, processus anterior branchialis; pad, processus anterior dorsalis; pah, processus anterior hyalis; pal, processus anterolateralis hyalis; par, processus articulatus; pas, processus ascendens; pc, pars corporis; pmq, processus muscularis quadrati; pp, processus pseudopterygoideus; ppd, processus posterior dorsalis and adrostral tissue mass; pph, processus posterior hyalis; pq, processus quadrato-ethmoidalis; pi, pars reunions; pu, processus urobranchialis; s, spicula; sn, septum nasi; ta, tectum anterius; ts, tectum synoticum; tt, taenia tecti marginalis; ttm, taenia tecti marginalis; ttt, taenia tecti transversalis.

beculae. Adrostrals are represented by a tissue mass containing a small cartilaginous nucleus placed just posterior to the processus posterior dorsalis of the pars alaris.

The cornua trabeculae account for about 16-19% of the chondrocranial length. Their anterior free ends are oblique; they are uniformly wide throughout their length and bear a small and triangular processus lateralis, and diverge anterolaterally from the planum ethmoidale (fig. 4A). Their distal ends curve ventrally and expand slightly anteriorly to articulate sindesmotically with the cartilago suprarostral is (fig. 4D).

The nasal structures are represented by a septum nasi placed dorsad to the planum ethmoidale (fig. 4A). The basi cranii is pierced by the foramen caroticum primarium and the foramen craneopalatinum (fig. 4B).

The well-developed cartilagines orbitales are pierced by the opticum, oculomotor, and prooticum foramina (fig. 4D).

The fontanella frontoparietalis is divided in both anterior and posterior parts by the taenia tecti transversalis (fig. 4A). The anterior part, or fontanella frontalis, is delimited anteriorly by the tectum anterior, laterally by the dorsum of the cartilagines orbitales, and posteriorly by the taenia tecti transversalis. The posterior fontanella is divided into two left and right fontanellas parietales by the taenia tecti medi alis. Their margins are formed anteriorly by the taenia tecti transversalis, laterally by the taenia tecti marginalis and the otic capsule, and posteriorly by the tectum synoticum.

The capsula auditivae are sub-quadrangular (Width/Length = 0.82-0.94). The larval crista parotica possesses a well-developed triangular processus anterolateralis. This process is ventrally overlapped to the palatoquadrate, but without establishing a cartilaginous connection (fig. 4D). The large fenestra ovalis lacks an operculum (fig. 4D).

The upper jaw is formed by the palatoquadrate, which runs laterally to the neurocranium and joins the basi cranii via the commissura

quadrato-cranialis anterior and the processus ascendens. The commissura quadrato-cranialis anterior bears three processes: the processus quadrato-ethmoidalis anteriorly, the long processus pseudopterygoideus (*sensu* Haas, 2003) posteriorly, and the commissura quadrato-orbitalis dorsally (fig. 4A, B). The processus quadrato-ethmoidalis receives the ligamentum quadrato-ethmoidale from the cornua trabeculae. The processus pseudopterygoideus receives the ligamentum tectum inferius and fuses distally to the basi cranii (fig. 4A, B). The commissura quadrato-orbitalis represents the complete chondrification of the ligamentum tectum superius. This commissura projects from the dorsum of the processus muscularis quadrati towards the commissura quadrato-cranialis anterior.

The arcus subocularis possesses a posterodorsal fossa in which both muscles levatorae mandibulae longus originate (fig. 4A).

The processus ascendens joins the pila antotica at the level of the foramen oculomotor (intermediate union, fig. 4D). The processus ascendens is at right angles to the trabecula cranii (fig. 4A). The larval processus oticus is absent.

The lower jaw comprises the sigmoid-shaped cartilagines meckeli and the rod-like cartilagines infrarostrales (fig. 4B). The cartilago meckeli possesses three processes, the retroarticularis, dorsomedialis, and ventromedialis processes. The processus retroarticularis articulates with the pars articularis quadrati. The processus dorsomedialis and the processus ventromedialis articulate with the cartilago infrarostralis by the commissura intramandibularis. The cartilagines infrarostrales connect ventromedially by an elastic symphysis.

The hyobranchial apparatus (fig. 4E) possesses both ceratohyalia joined medially by a poorly defined pars reuniens. The small, rod-like and transversely oriented copula anterior lies anterior to the pars reuniens. The copula posterior is continuous to the pars reuniens and bears a short and blunt processus urobranchialis.

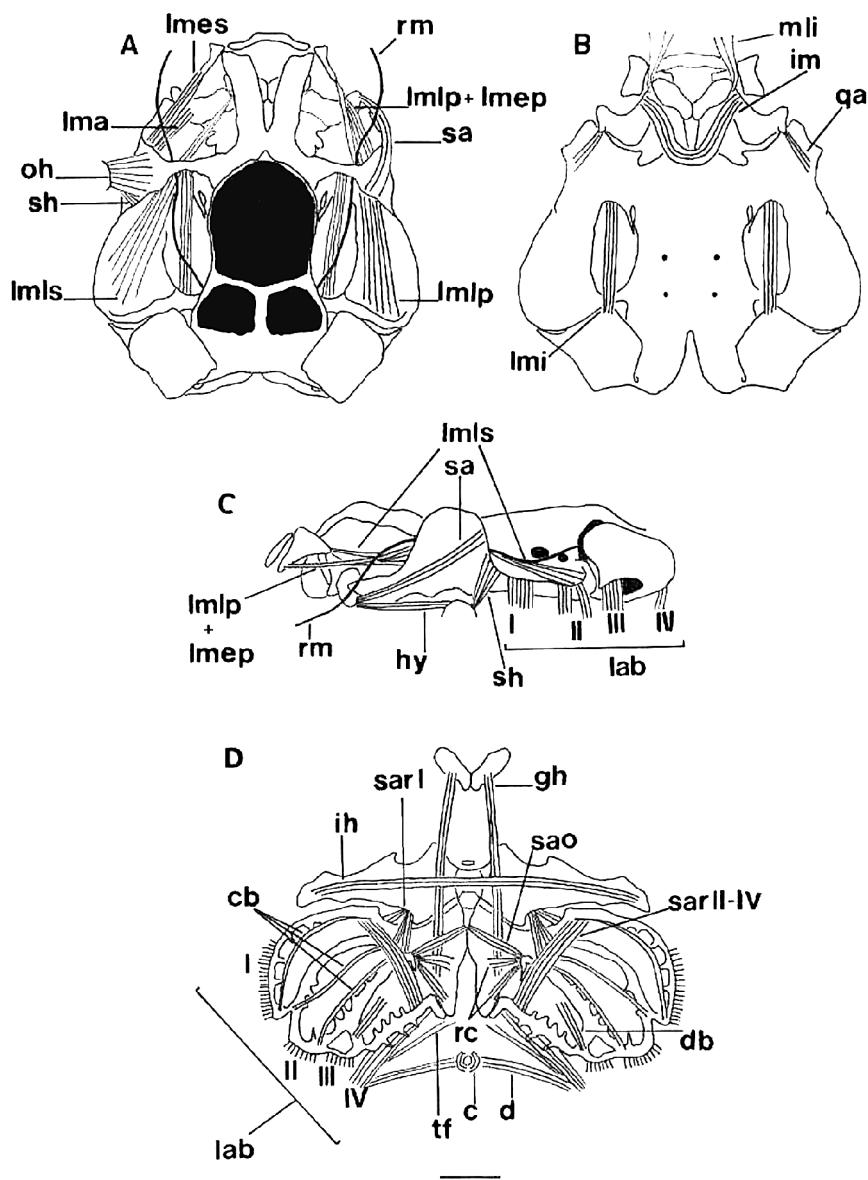


Figure 5. Cranial muscles of *Limnomedusa macroglossa* at stage 36 (MACN 34996). **A.** Dorsal, **B.** ventral, and **C.** lateral views of muscles related to neurocranium and mandibular arch. **D.** Ventral view of muscles related to hiobranchium and mandibular arch. In **A.**, mm. levator mandibulae externus profundus and levator mandibulae longus profundus (left side), levator mandibulae articularis, levator mandibulae externus superficialis, levator mandibulae longus superficialis, orbitohyoideus and suspensoriohyoideus (right side), were removed. In **C.**, levator mandibulae externus superficialis and orbitohyoideus, were removed. In **D.**, the superficial mm. diaphragmatopraecordialis and interhyoideus posterior, were removed. Dark areas represent cranial fenestrations. Scale bar: 1 mm. Legends: c, constrictor laryngis; cb, constrictor branchiales II, III and IV; d, dilatator laryngis; db, diaphragmatobranchialis; gh, geniohyoideus; hy, hyoangularis lateralis; ih, interhyoideus; im, intermandibularis; lab I, levator arcum branchialium I; lab II, levator arcum branchialium II; lab III, levator arcum branchialium III; lab IV, levator arcum branchialium IV; lma, levator mandibulae articularis; lme, levator mandibulae externus profundus; lmes, levator mandibulae externus superficialis; lmi, levator mandibulae internus; lmp, levator mandibulae longus profundus; lmls, levator mandibulae longus superficialis; mli, mandibulolabialis inferior; oh, orbitohyoideus; qa, quadratoangularis; rc, rectus cervicis; rm, ramus mandibularis of trigeminus nerve; sa, suspensorioangularis; sao, subarcualis obliquus II; sar I, subarcualis rectus I; sar II-IV, subarcualis rectus II-IV; sh, suspensoriohyoideus; tf, tympanopharyngeus.

Table 1. Origin and insertion of the mandibular and hyobranchial muscles of *Limnomedusa macroglossa*.

Muscle	Origin	Insertion
Nervus trigeminus (cranial nerve V), mandibular musculature		
Levator mandibulae internus	Ventral side of capsula auditiva and processus ascendens	Cartilago meckeli
Levator mandibulae longus superficialis	Posterolateral fossa of the arcus subocularis	Processus dorsomedialis of cartilago meckeli
Levator mandibulae longus profundus	Posterolateral fossa of the arcus subocularis completely obscured by the m. l. m. l. superficialis	Laterally to the pars alaris by a common tendon with the m. l. m. e. profundus
Levator mandibulae externus profundus	Medial face of processus muscularis quadrati	Pars alaris by a common tendon with the m. l. m. l. profundus
Levator mandibulae externus superficialis	Processus muscularis quadrati	Processus posterior dorsalis of pars alaris
Levator mandibulae articularis	Processus muscularis quadrati, ventral to m. l. m. e. profundus	Cartilago meckeli
Levator mandibulae lateralis	Absent at the studied stages	
Submentalis	Absent at the studied stages	
Intermandibularis	Cartilago meckeli	Median raphe
Mandibulolabialis inferior	Cartilago meckeli	Ventral area of the oral disc
Mandibulolabialis superior	Absent	
Nervus facialis (cranial nerve VII), hyoid musculature		
Suspensoriohyoideus	Processus muscularis quadrati and arcus subocularis	Ceratohyale's distal end
Suspensorioangularis	Posterolateral margin of processus muscularis quadrati obscured by the m. orbitohyoideus.	Processus retroarticularis of cartilago meckeli
Quadratoangularis	Palatoquadrate ventral face at level of the processus muscularis quadrati	Processus retroarticularis of cartilago meckeli
Hyoangularis lateralis	Lateral to ceratohyale's processus articularis	Processus retroarticularis of cartilago meckeli
Hyoangularis medialis	Absent	
Interhyoideus	Ceratohyale's distal ends	Median raphe
Interhyoideus posterior	Composed by a tiny sheet of lax fibers below the branchial chamber	
Diaphragmatopraecordialis	M. interhyoideus posterior	Peritoneal wall
Nervus glossopharyngeus (cranial nerve IX), branchial musculature		
Levator arcuum branchialium I	Arcus subocularis just posterior to m. suspensoriohyoideus	Commissura terminalis of ceratobranchiale I
Subarcualis rectus I	The dorsal head originates at the ceratobranchiale I. Both ventral heads originate on ceratobranchiale II	Ceratohyale's posterior wall
Constrictor branchialis I	Absent	

The hypobranchiales are separated in the midline by a large posterior sinus. The ceratobranchiales bear well-developed rays, lack commissura proximales, and are distally joined by the commissura terminalis. The spicula are well developed, specially the fourth. The first ceratobranchiale is continuous with the hypo-

branchiale. The remaining ceratobranchiales are free from the hypobranchiale.

Cranial musculature (fig. 5)

The details about the origin and insertion of each muscle are in Table 1. The ramus mandibularis of the nervus trigeminus runs laterally to all muscles levatorae mandibulae.

Table 1. (Continued).

Muscle	Origin	Insertion
Nervus vagus (cranial nerve X), branchial musculature		
Constrictor branchialis II	Base of ceratobranchiale I	Commissura terminalis I-II
Constrictor branchialis III	Base of ceratobranchiale II	Commissura terminalis II-III
Constrictor branchialis IV	Base of ceratobranchiale III	Distal end of ceratobranchiale III
Diaphragmatobranchialis	Peritoneal wall lateral to m. rectus cervicis	Distal end of ceratobranchiale III
Levator arcuum branchialium II	Arcus subocularis posterior to m. l. a. branchialium I	Commissura terminalis of ceratobranchiales II and III
Levator arcuum branchialium III	Anterolateral wall of capsula auditiva	Distal end of ceratobranchiale III
Levator arcuum branchialium IV	Posteroventral wall of the capsula auditiva	Ceratobranchiale IV
Subarcualis obliquus II	By one head between ceratobranchiales II and III	Processus urobranchialis
Subarcualis rectus II-IV	Ceratobranchiale IV	Ceratobranchiale I
Tympanopharyngeus	M. levator arcuum branchialium IV	Pericardium
Dilatator laryngis	Posteroventral wall of capsula auditiva	Lateral sides of larynx
Constrictor laryngis	Forms an annulus surrounding the larynx	
Transversus ventralis IV	Absent	
Nervus hypoglossus (spinal nerve II), hypobranchial musculature		
Geniohyoideus	Hypobranchiale at level of ceratobranchiale IV	Cartilago infarostrale
Rectus cervicis	By two heads on the peritoneal wall	Base of ceratobranchiales II and III

Discussion

The comparison of our results with the keratinized structures of the oral disc, buccopharyngeal papillation, chondrocranium, and cranial muscles reported for other leptodactylid larvae (see Table 2) indicates that: 1) internal and external oral features, and cranial muscles morphology do not provide any conclusive information to relate *Limnomedusa* to other leptodactylid genera; 2) two chondrocranial characters ally *Limnomedusa* to the telmatobiine genera. These characters are the presence of a long processus pseudopterygoideus (as defined by Haas, 2003), and the syndesmotic connection of the partes alares and partes corpora of the cartilago suprarostralis. *Eupsophus calcaratus* is the only genus of Telmatobiinae which possesses a short processus pseudopterygoideus and a cartilaginous connection between the partes corpora and the partes alares of the cartilago suprarostralis (Vera Candioti et al., 2005). This departure from the pattern of the known Telmatobi-

inae genera could be related to the endotrophic-nidicolous development mode of this species.

The long processus pseudopterygoideus also occurs in some hylids (*Pseudis* spp., *Gastrotheca* spp. and *Hyla annectans*), ranids (*Pyxicephalus adspersus*) and other leptodactylids (*Odontophrynus*) (Fabrezi and Lavilla, 1992; Hass, 1996, 1999, 2003). According to the phylogenetic hypothesis of Haas (2003) this character state is clearly homoplastic, having arisen at least three times within the Neobatrachia.

In light of the lack of evidence for the monophony of Telmatobiinae, we cannot consider the presence of a long processus pseudopterygoideus as a synapomorphy of this group. However, the telmatobiine genera for which chondrocranial descriptions are available (*Alsodes*, *Caudiverbera* and *Telmatobius*) possess this character state (except *Eupsophus calcaratus*). *Limnomedusa* and *Odontophrynus* are the other leptodactylid genera that possess a long processus pseudopterygoideus. *Limnomedusa* has been assigned either within Leptodactylinae

Table 2. Leptodactylid genera employed for chondrocranial (1), cranial muscles (2), and buccopharyngeal (3) comparisons.**Subfamily Telmatobiinae**

- Alsodes*^{1, 3} (Wassersug and Heyer, 1988; Lavilla, 1992; Echeverría et al., 2001; Formas and Brieva, 2004)
*Atelognathus*³ (Wassersug and Heyer, 1988)
*Batrachyla*³ (Brieva Vasquez, 1988; Wassersug and Heyer, 1988)
Caudiverbera^{1, 3} (Reinbach, 1939; Wassersug and Heyer, 1988)
*Hylorina*³ (Wassersug and Heyer, 1988)
Eupsophus^{1, 2, 3} (Vera Candioti et al., 2005)
Telmatobius^{1, 2, 3} (Wassersug and Heyer, 1988; Fabrezi and Lavilla, 1993; Palavecino, 1999)

Subfamily Leptodactylinae

- Adenomera*³ (Wassersug and Heyer, 1988)
*Edalorhina*² (Starret, 1968)
Leptodactylus^{1, 2, 3} (Starret, 1968; Sokol, 1981; Wassersug and Heyer, 1988; Fabrezi and Vera, 1997; Palavecino, 1997; Larson and de Sá, 1998; Palavecino, 2000, 2002; Haas, 2003)
Physalaemus^{1, 2, 3} (Starret, 1968; Wassersug and Heyer, 1988; Fabrezi and Vera, 1997; Larson and de Sá, 1998; Palavecino, 2000, 2002; Haas, 2003)
Pleurodema^{1, 2, 3} (Wassersug and Heyer, 1988; Fabrezi and Vera, 1997; Palavecino 2000, 2002; Haas, 2003)
*Pseudopaludicola*³ (Wassersug and Heyer, 1988)

Subfamily Ceratophryinae

- Ceratophrys*^{1, 2, 3} (Wassersug and Heyer, 1988; Lavilla and Fabrezi, 1992; Wild, 1997; Palavecino, 1999; Haas, 2003)
*Chacophrys*¹ (Wild, 1999)
Lepidobatrachus^{1, 2, 3} (Ruibal and Thomas, 1988; Wassersug and Heyer, 1988; Lavilla and Fabrezi, 1992; Palavecino, 1999; Haas, 2003)
Odontophrynus^{1, 2, 3} (Wassersug and Heyer, 1988; Fabrezi and Vera, 1997; Palavecino, 1999; Haas, 2003)
*Proceratophrys*³ (Wassersug and Heyer, 1988)

Subfamily Cycloramphinae

- Crossodactyloides*³ (Wassersug and Heyer, 1988)
Crossodactylus^{1, 2, 3} (Wassersug and Heyer, 1988; Larson and de Sá, 1998; Haas, 2003)
Cycloramphus^{1, 3} (Wassersug and Heyer, 1988; Lavilla, 1991)
Hylocles^{1, 2, 3} (Wassersug and Heyer, 1988; Haas, 2003)
*Paratelmatoibius*³ (Wassersug and Heyer, 1988)

Subfamily Eleutherodactylinae

- Eleutherodactylus*^{1, 2, 3} (Wassersug and Heyer, 1988; Hanken et al., 1992; Cannatella, 1999; Haas, 2001)

(Lynch, 1971; Heyer, 1975) or Telmatobiinae (Lynch, 1978). *Odontophrynus* has been placed either within Telmatobiinae (Lynch, 1971) or Ceratophryinae (Heyer, 1975). The absence of a long processus pseudopterygoideus in both Ceratophryinae (Ruibal and Thomas, 1988; Wild, 1997, 1999) and Leptodactylinae (Larson and de Sá, 1998; Haas, 2003) suggests a relationship of *Limnomedusa* and *Odontophrynus* with the telmatobiine genera mentioned above.

Some telmatobiine genera are unique in having the processus pseudopterygoideus and the basi cranii fused to some degree. The processus pseudopterygoideus and the basi cranii are partially fused in *Telmatobius* spp. and *Alsodes*

barrio (Lavilla, 1992; Fabrezi and Lavilla, 1993), a condition reported herein for *Limnomedusa*. Although Formas and Brieva (2004) did not report the processus pseudopterygoideus for *Alsodes vanzolinii* and *A. verrucosus*, the complete fusion of this process to the basi cranii may be inferred from the figures in that paper (see Formas and Brieva, 2004, fig. 4 A, B, pp. 158). The fusion of the processus pseudopterygoideus to the basi cranii is interesting since Lavilla (1988) found that the presence of an intramarginal row of papillae in the oral disc is a character shared by *Alsodes*, *Limnomedusa*, *Telmatobufo*, and some species of *Telmatobius*. The processus pseudopterygoideus is not fused to

the basi cranii in other genera of Telmatobiinae such as *Caudiverbera* (Reinbach, 1939), *Batrachyla* and *Hylorina* (Alcalde, pers. obs.)

The other character state shared by *Limnomedusa* and the telmatobiine genera is the absence of cartilaginous connection between the partes alares and the partes corpora of the cartilago suprarostralis (except *Eupsophus calcarius*). This character state is widespread in the Neobatrachia outside Leptodactylidae (Lavilla and Fabrezi, 1987; Fabrezi and Lavilla, 1992; de Sá and Hill, 1998; D'Heursel and de Sá, 1999). Within this family it only occurs in Telmatobiinae (Reinbach, 1939; Lavilla, 1992; Fabrezi and Lavilla, 1993; Formas and Brieva, 2004) and in one species of Leptodactylinae (*Physalaemus cuquii*) (Fabrezi and Vera, 1997).

Conclusions

The cranial muscles and the buccopharyngeal papillation are not useful to relate *Limnomedusa* either to telmatobiine or leptodactyline genera. Two chondrocranial characters (presence of a long processus pseudopterygoideus and sindesmotically connected partes alares and partes corpora of the cartilago suprarostralis) ally *Limnomedusa* to the telmatobiine genera more than to any other genera within Leptodactylidae. Within Telmatobiinae, a processus pseudopterygoideus fused to the basi cranii is present only in *Alsodes*, *Limnomedusa*, and *Telmatobius*.

Acknowledgements. We want to thank J. Faivovich and J. Wiens for their critical comments on the manuscript. This paper is the scientific contribution Nº 774 of the Instituto de Limnología "Dr. R.A. Ringuelet". L. Alcalde acknowledges UNLP for financial support (Doctoral Scholarship 2004).

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