

Morphology of premetamorphic larvae of *Lysapsus limellus* (Anura: Pseudinae)

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Abstract. The chondrocranium, visceral skeleton, mandibular, hyoid and hyobranchial musculature, buccal apparatus and buccopharyngeal cavity of premetamorphic larvae of *Lysapsus limellus* from Santa Fe, Argentina are described. The cartilaginous skeleton corresponds in general terms to that of a typical pond type tadpole. Some characteristic features are the flat triangular projection of the arcus subocularis quadrati, the scarce development of the cartilagine orbitales, the presence of the processus pseudopterygoideus and quadratoethmoidalis, the open fenestra basicranialis, and the presence of a reticulating cartilaginous connection between the spicula III, IV and the plana hypobranchialia. Regarding muscles, the most salient characters are the configuration of the m. levator mandibulae lateralis, with nasal insertion, and the presence of a discontinuous m. subarcualis rectus II-IV. The oral disc and buccal cavity show features that indicate a generalist-mesophagous diet, for example the presence of jaw sheaths, rows of keratodonts, filter structures on the buccal floor and roof, and a glandular epithelium in the ventral velum.

Introduction

For a long time, diverse systematic studies were unable to elucidate the phylogenetic relationships of pseudids (Duellman and Trueb, 1985; Ford and Cannatella, 1993; Manzano, 1996). This group has been classified as either a clade among leptodactylid frogs, a family of frogs (Pseudidae, related to hylids), or a subgroup of hylids (Savage and de Carvalho, 1953). Recently Duellman (2001) included them within the Hylidae, as subfamily Pseudinae. All these analyses took into account mostly adult and only a few larval characters. Haas (2003) found synapomorphic characters in larvae of the two *Pseudis* species (*P. paradoxa* and *P. minuta*) and grouped them together with Pelodyadinae, Hylinae and Phyllomedusinae in a monophyletic clade.

Several authors have studied pseudines larval morphology. Lavilla and De Sá (1999) describe the chondrocranium of *Pseudis minuta*, and they mention Parker (1882) and Ridewood (1898), who studied it in *P. paradoxa*. Haas (2003) studied chondrocranium,

muscles and some buccal characters in these two species. *Lysapsus limellus*, the third pseudine found in Argentina, has not been studied in depth before. In fact, previous literature on larval morphology only includes the original description of the tadpole (Kehr and Basso, 1990).

This paper affords new data on morphological characters of *Lysapsus limellus* tadpoles, thus adding to available information on pseudines.

Materials and methods

Fifteen specimens of *Lysapsus limellus* (Gosner stages 31-35) were collected in a temporary pool in Ciudad Universitaria, Paraje El Pozo, Santa Fe Province, during January 2000. Larvae were fixed with 10% formalin (1 part of commercial concentrated formalin in 9 parts of water; equal to 4% formaldehyde). Five specimens were cleared and stained following Wassersug (1976a) protocol, to study the chondrocranium and visceral skeleton. For the study of the mandibular, hyoid and hyobranchial musculature, five specimens were prepared according to the same protocol, but interrupting the procedure before immersion in glycerol (Lavilla and Fabrezi, pers. comm.). The specimens were then colored with lugol solution, to enhance the contrast between blue cartilages and brown-reddish muscles (Bock and Shear, 1972). Finally, the buccal apparatus and buccopharyngeal cavity of five different specimens were exposed and stained with methylene blue, following Wassersug (1976b). Dissections and drawings were made using a stereomicroscope equipped with a camera lucida.

The terminology employed for description of cartilaginous skeleton follows that of Haas and Richards (1998). The nomenclature for muscles follows Sedra (1951) and recent modifications by Haas (2001). Characterization of oral disc morphology, keratinized structures and buccopharyngeal cavity follows Altig and McDiarmid (1999), Van Dijk (1966, as cited in Echeverría, 1992) and Viertel (1982).

As the studied tadpoles were highly modified after each analysis, intact individuals from the same original series were preserved as voucher specimens. They are housed at the Herpetological Collection of Fundación Miguel Lillo, under the number FML: 13257.

Results

Chondrocranium and hyobranchial apparatus (figs. 1-2)

Descriptions were made from stage 35 tadpoles. The chondrocranium represents 63% of the snout-vent length. The maximum width is at the level of the arcus subocularis.

The cartilago labialis superior has a simple pars corporis with a dorsal V-shaped indentation, and it is fused to the partes alares. The partes alares can still be distinguished and bear a processus dorsalis posterior and a processus dorsalis anterior (fig. 1D).

The cornua trabeculae correspond approximately to 24% of the total length of the chondrocranium. They are strongly chondrified and they are continuous with the trabeculae cranii posteriorly. They are wider in the anterior region, with a slightly prominent external portion of the margin. They articulate with the cartilago labialis superior by means of a thickened surface which corresponds to a similar surface in the pars alaris. The processus lateralis is not conspicuous (fig. 1A).

The cartilagine orbitales are incomplete in stage 35, only represented by a posterior chondrification (pila metoptica, according to Lavilla and De Sá, 1999). Teniae tecti

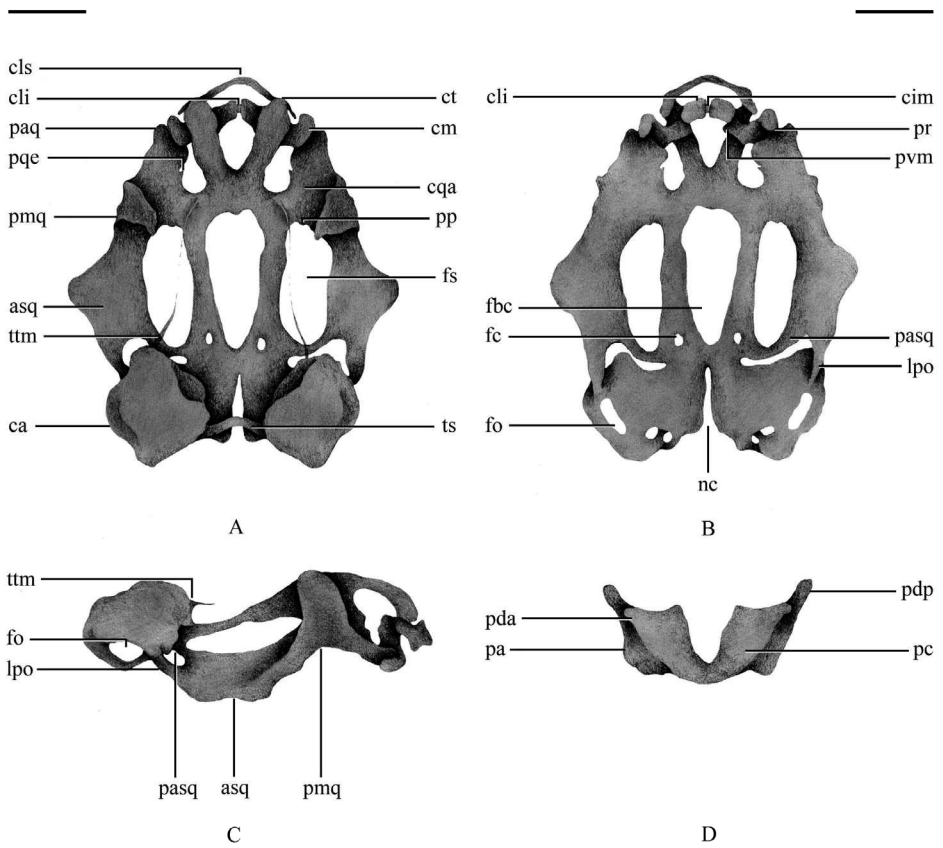


Figure 1. *Lysapsus limellus* stage 34-35. Chondrocranium. A. Dorsal view. B. Ventral view. C. Lateral view. D. Detail of cartilago labialis superior, frontal view. Scale bar = 1 mm. Legends: asq, arcus subocularis quadrati; ca, capsula auditiva; cim, commissura intramandibularis; cli, cartilago labialis inferior; cls, cartilago labialis superior; cm, cartilago meckeli; cqa, commissura quadratocranialis anterior; ct, cornu trabeculae; fbc, fenestra basicranialis; fc, foramen caroticum; fo, fenestra ovalis; fs, fenestra subocularis; lpo, larval processus oticus; nc, notochordal canal; pa, pars alaris; paq, pars articularis quadrati; pasq, processus ascendens quadrati; pc, pars corporis; pda, processus dorsalis anterior; pdp, processus dorsalis posterior; pmq, processus muscularis quadrati; pp, processus pseudopterygoideus; pqe, processus quadratoethmoidalis; pr, processus retroarticularis; pvm, processus ventromedialis; ts, tectum synoticum; ttm, taenia tecti marginalis.

marginales are insinuated in the posterolateral region of what would be the fenestra frontoparietalis. The ethmoidal plate, septum nasi and tectum nasi are not yet developed.

The capsulae auditivae are quadrangular and take up about 29% of the total length of the chondrocranium; they are joined by the tectum synoticum. The fenestra ovalis is visible from a ventral and lateral view and its dimensions reach 41% of the whole capsula.

The floor of the cranial cavity is not completely chondrified. The center is occupied by a basicranial fenestra that probably includes the foramina craniopalatina. The foramina

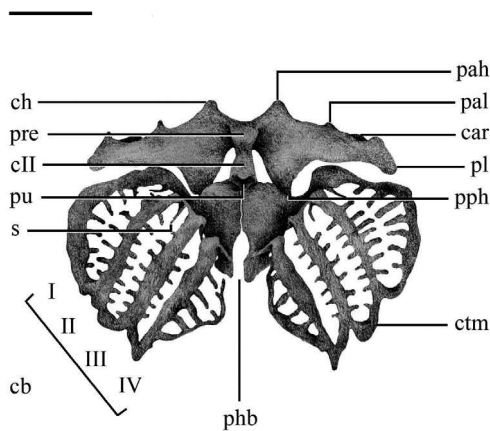


Figure 2. *Lysapsus limellus* stage 34-35. Hyobranchial apparatus, ventral view. Scale bar = 1 mm. Legends: car, condylus articularis; cb(I-IV), ceratohyal; ch, ceratohyal; ctm, commissura terminalis; cII, copula II; pah, processus anterior hyalis; pal, processus anterolateralis; phb, planum hypobranchiale; pl, processus lateralis; pph, processus posterior hyalis; pre, pars reuniens; pu, processus urobranchialis; s, spiculum.

carotica are visible at the posterolateral edges of the fenestra. In the posterior border of the cranial floor is the notochordal canal, which penetrates around 1/6 of the total length of the chondrocranium.

The palatoquadrate has a thin pars articularis quadrati, a high, triangular and medially curved processus muscularis quadrati, and an arcus subocularis that widens posteriorly forming a flat triangular projection. There are three points of articulation with the neurocranium: first, the commissura quadratocranialis anterior, with a well developed processus quadratoethmoidalis and an insinuated processus pseudopterygoideus, second, the processus ascendens, which attaches to the neurocranium floor, and finally the larval processus oticus (fig. 1C).

The lower jaw is formed by the cartilagine meckeli and the cartilagine labiales inferiores, connected by a chondrified commissura intermandibularis. The cartilagine meckeli are sigmoid and have a conspicuous processus retroarticularis, ventromedialis and a short process located in the middle region of the internal margin. The short, oblongated and curve cartilagine labiales inferiores are connected via the commissura intramandibularis (fig. 1B).

The hyobranchial apparatus consists of paired ceratohyalia and the branchial basket (fig. 2). The ceratohyalia are thick and elongated cartilages, with four processes, processus anterior hyalis, anterolateralis, lateralis and posterior hyalis, and the condylus articularis. The ceratohyalia articulate medially with each other via the pars reuniens. Copula I is absent and copula II is longer than the pars reuniens and bears a short, round-tipped processus urobranchialis (17% of the total length of the copula).

In the branchial basket, paired plana hypobranchialia are continuous with the copula II. From each planum arise four ceratobranchialia with numerous lateral projections. Ceratobranchialia are bridged distally by the commissurae terminales. The ceratobranchiale I is fully fused with the planum hypobranchiale, and the three remaining ones have connective tissue attachments. The ceratobranchialia II and III are jointed by a conspicuous processus branchialis. Dorsally there exist two thin well defined spicula, which correspond to ceratobranchialia I and II. The third and the fourth one form a flat, quadrangular and poorly chondrified plate that is continuous with the planum hypobranchiale.

Musculature (figs. 3-5)

Descriptions have been made on the basis of five specimens at stages 34 and 35. Table 1 shows each muscle, its origin and insertion.

Regarding the muscle complex of the levatores mandibulae, one peculiar feature is the presence of both the levator mandibulae externus superficialis and profundus, and the location of the ramus mandibularis of the trigeminus nerve dorsally to both. A second feature is the occurrence of the m. levator mandibulae lateralis, which extends between the nasal sac and the pars articularis quadrati (fig. 3).

The m. mandibulolabialis originates in the posterior region of the cartilago meckeli. It borders the latter posteriorly and then appears ventrally. Its two slips, mandibulolabialis inferior and superior, insert in the lower and upper papillar margin respectively (fig. 4).

An unusual feature in the hyobranchial group is the configuration of the mm. subarcuales recti. The m. subarcualis rectus I has three heads. They originate in the lateral base of the processus posterior hyalis; two of them insert on the proximal part of the ceratobranchiale I and the third one on the processus branchialis between ceratobranchialia II and III. The m. subarcualis rectus II-IV is subdivided into two parts: the anterior part has two slips and extends between the proximal region of the ceratobranchiale I and the processus branchialis; the posterior part originates on the processus branchialis and inserts on the proximal region of the ceratobranchiale IV (fig. 4).

Buccal apparatus and buccopharyngeal cavity (figs. 6-7)

The larvae described belong to stages 31 and 35. Kehr and Basso (1990) previously characterized the buccal apparatus of this species. The relaxed oral disc has the shape of an inverted triangle lacking lateral folds. As mentioned by Kehr and Basso, it has a terminal location and its length represents 23% of the snout-vent length. It is lined by a single or double row of marginal papillae, accompanied by smaller submarginal papillae located in the lateral region. The marginal papillation is interrupted forming a wide rostral gap (fig. 6). The jaw sheaths (suprarostrodont and infrarostrodont) are finely serrated and less than 50% keratinized. The keratodonts are disposed in five rows, arranged in the labial tooth row formula (1)(1-1)/(3). The P3 is the shortest one, with a length of approximately 1/3 of A1.

Table 1. Musculature of *Lysapsus limellus* stages 34 and 35.

Muscle	Origin	Insertion
Mandibulolabialis	two slips; posterior region of cartilago meckeli	lower and upper papillar margin
Intermandibularis	ventromedial region of cartilago meckeli	aponeurosis media
Levator mandibulae longus superficialis	lateral and posterior margin of arcus subocularis quadrati and part of processus ascendens quadrati	dorsomedial region of cartilago meckeli
Levator mandibulae longus profundus	lateral and posterior margin of arcus subocularis quadrati and part of processus ascendens quadrati	pars alaris of cartilago labialis superior
Levator mandibulae lateralis	anterolateral part of pars articularis quadrati	nasal sac
Levator mandibulae externus superficialis	anterior margin of processus muscularis quadrati	ligamentum mandibulo-suprarostrale
Levator mandibulae externus profundus	medial inferior surface of processus muscularis quadrati	pars alaris of cartilago labialis superior
Levator mandibulae articularis	inferior part of medial surface of processus muscularis quadrati	processus retroarticularis of cartilago meckeli
Suspensoriohyoideus	posterior descendent margin of processus muscularis quadrati	posterior surface of the lateral side of ceratohyal
Orbitohyoideus	anterior and superior margin of processus muscularis quadrati	lateral side of ceratohyal
Suspensorioangularis	descendent margin of processus muscularis quadrati	processus retroarticularis of cartilago meckeli
Quadratoangularis	ventral anterior surface of palatoquadrate	processus retroarticularis of cartilago meckeli
Hyoangularis	dorsal lateral surface of ceratohyal	processus retroarticularis of cartilago meckeli
Interhyoideus	oblique crest on the ventral face of ceratohyal	aponeurosis media
Geniohyoideus	posterior ventral surface of cartilago labialis inferior	planum hypobranchiale of branchial basket
Levator arcuum branchialium I	lateral margin of arcus subocularis quadrati	ceratobranchiale I
Levator arcuum branchialium II	processus oticus	commissura terminalis I
Levator arcuum branchialium III	lateral part of capsula auditiva	commissura terminalis II
Levator arcuum branchialium IV	posterolateral part of capsula auditiva	commissura terminalis III and ceratobranchiale IV
Constrictor branchialis II	processus branchialis	commissura terminalis I
Constrictor branchialis III	processus branchialis	commissura terminalis II
Constrictor branchialis IV	proximal part of ceratobranchiale III	commissura terminalis III
Subarcualis rectus I	three slips, processus posterior hyalis	two slips insert in the proximal part of ceratobranchiale I, the third one on the processus branchialis
Subarcualis rectus II-IV		
anterior part	ceratobranchiale I	processus branchialis
posterior part	processus branchialis	ventral proximal part of ceratobranchiale IV
Subarcualis obliquus	processus urobranchialis	processus branchialis

Table 1. (Continued).

Muscle	Origin	Insertion
Tympanopharyngeus	ceratobranchiale IV	tympanic region of capsula auditiva
Diaphragmatobranchialis	peritoneum	distal part of ceratobranchiale III
Rectus cervicis	peritoneum	processus branchialis III

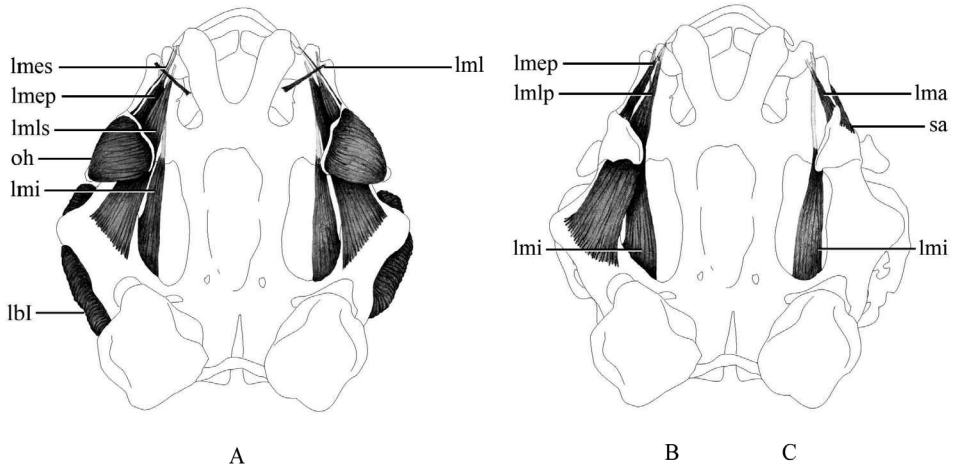
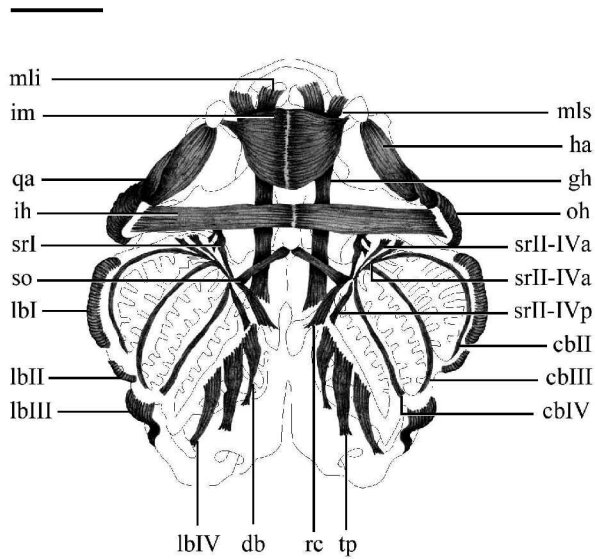


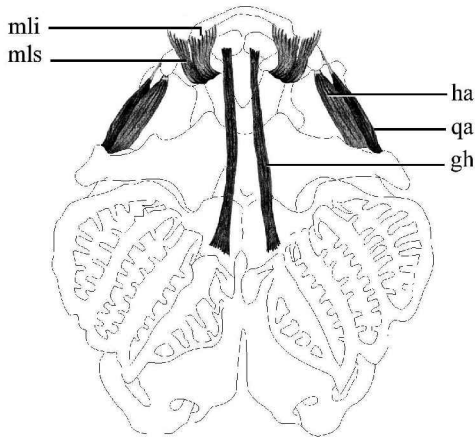
Figure 3. *Lysapsus limellus* stage 35. Musculature. Dorsal view. A. Superficial plane. B. Middle plane. C. Deep plane. Scale bar = 1 mm. Legends: lbi, levator arcum branchialium I; lma, levator mandibulae articularis; lmep, levator mandibulae externus profundus; lmes, levator mandibulae externus superficialis; lmi, levator mandibulae internus; lml, levator mandibulae lateralis; lmlp, levator mandibulae longus profundus; lmls, levator mandibulae longus superficialis; oh, orbitohyoideus; sa, suspensorioangularis.

The roof of the buccal cavity (fig. 7A) is not pigmented. The prenarial arena contains a group of scarce central pustules. The internal nares are transversely oriented. They are oblong, with projections in the anterior margin and a well developed nasal valve. The postnarial arena contains two pairs of conical papillae and central pustules. The median ridge is trapezoidal with an irregular free margin with slight projections. The lateral ridge papillae are paired, simple and the tallest of the buccal papillae. The buccal roof arena has two pairs of short conical papillae and a few uniformly distributed pustules.

The buccal floor (fig. 7B) is triangular and pigmented, with chromatophores scattered in the floor arena, from lingual anlage to ventral velum. The orobranchial cavity shows groups of pustules, which are transversely aligned in more than one row on both sides of the middle axis. Posteriorly there are a pair of short and bifurcated papillae and two short conical papillae. Converging toward the middle axis, there is a pair of hand-like infralabial papillae, which do not overlap one another. The tongue anlage has a couple of



A



B

Figure 4. *Lysapsus limellus* stage 35. Musculature. Ventral view. A. Superficial plane. B. Deep plane. Scale bar = 1 mm. Legends: cb(II-IV), constrictor branchialis; db, diaphragmatobranchialis; gh, geniohyoideus; ha, hyoangularis; ih, interhyoideus; im, intermandibularis; lb(I-IV), levator arcuum branchialium; mli, mandibulolabialis inferior; mls, mandibulolabialis superior; oh, orbitohyoideus; qa, quadratoangularis; rc, rectus cervicis; so, subarcualis obliquus; srl, subarcualis rectus I; srII-IV(a-p), subarcualis rectus II-IV (anterior part — posterior part); tp, tympanopharyngeus.

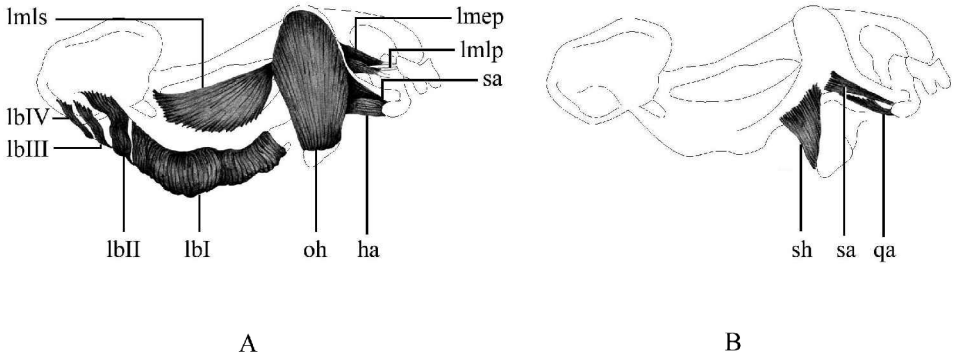


Figure 5. *Lysapsus limellus* stage 35. Musculature. Lateral view. A. Superficial plane. B. Deep plane. Scale bar = 1 mm. Legends: ha, hyoangularis; lb(I-IV), levator arcuum branchialium; lmep, levator mandibulae externus profundus; lmlp, levator mandibulae longus profundus; lmls, levator mandibulae longus superficialis; oh, orbitohyoideus; qa, quadratoangularis; sa, suspensorioangularis; sh, suspensoriohyoideus.

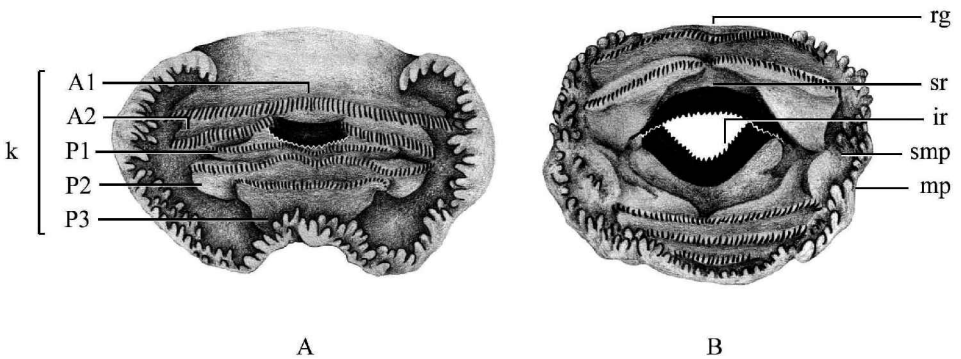
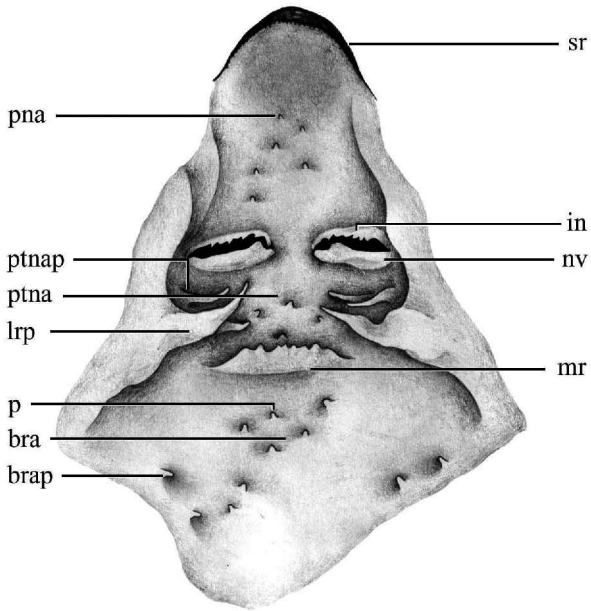
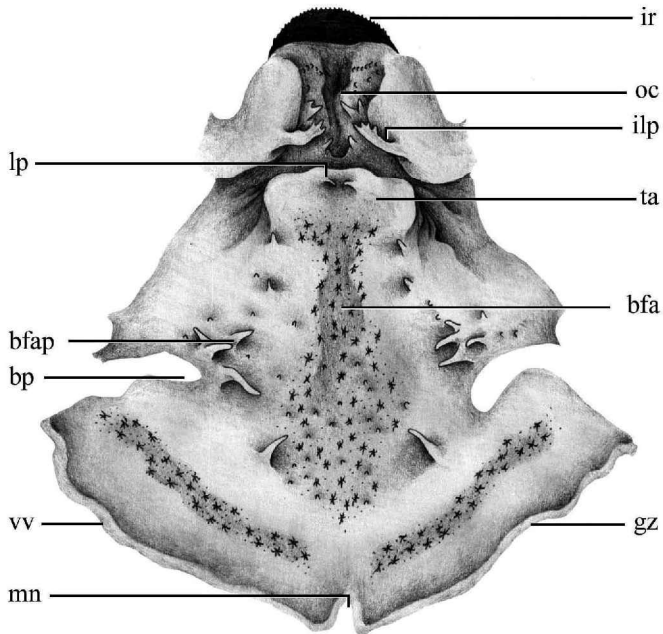


Figure 6. *Lysapsus limellus* stage 31. Oral disc. A. Relaxed. B. Open. Scale bar = 1 mm. Legends: ir, infrarostrodont; k, keratodonts; mp, marginal papillae; rg, rostral gap; smp, submarginal papillae; sr, suprarostrodont.

conical lingual papillae. Seven pairs of symmetrically arranged buccal floor arena papillae delimit the buccal floor arena. The two anterior pairs are the smallest ones. They are located behind the tongue anlage and are aligned anteroposteriorly. The following four pairs are situated at the level of buccal pockets, and the last pair is located posteriorly. A few pustules are distributed between these buccal floor papillae. The buccal pockets are deep and transversely oriented and show one or two pustules situated laterally with respect



A



B

to the buccal floor arena papillae. The ventral velum is semicircular and has gentle marginal projections and a conspicuous V inverted-shaped median notch. As mentioned above, the anterior edge shows a narrow band of chromatophores. On the free margin of the velum, as well as in the zone immediately adjacent to it, there is a conspicuous glandular epithelium.

Discussion

Lavilla and De Sá (1999) discuss the presence of chondrocranial characters of *Pseudis minuta* which had not been reported before, or not frequently found in other anuran larvae. They mention, for example, the variable patterns of cephalic chondrifications, the articular surfaces in the cartilago labialis superior, the scarce development of the cartilagine orbitales in the studied stages, the low attachment between the processus ascendens and the floor of the neurocranium, the expansion of the middle and posterior region of the arcus subocularis, the development of the larval processus oticus, the position of the processus muscularis quadrati, the presence of processus quadratoetmoidalis and pseudopterygoideus, and the structure of the spicula of the hyobranchial skeleton. These authors compare these features to those of *P. paradoxa*, and most of them coincide.

Lysapsus limellus larvae share with *Pseudis* species most of the listed characters. In the cases where *P. minuta* and *P. paradoxa* differ, *L. limellus* resembles *P. minuta*. For example, in the absence of septum nasi, the open fenestra basicranialis and the inconspicuous processus lateralis of the cornua trabeculae (table 2).

Haas (2003) studied larval musculature in *Pseudis* species. He mentioned two synapomorphies, the nasal sac insertion of the m. levator mandibulae lateralis and a distinct gap in the m. subarcualis rectus II-IV. *Lysapsus limellus* shows both features, the only difference being the presence of two slips in the anterior part of the m. subarcualis rectus II-IV. According to Haas (2003), these are unique features among the species he analyzed. Interestingly, *Hyla nana* and *Hyla microcephala* tadpoles have the same configuration of the m. levator mandibulae lateralis and a very similar m. subarcualis rectus II-IV (Haas, 1996; pers. obs.). In these two species, the anterior part of the m. subarcualis rectus II-IV originates in soft tissue next to the lateral side of ceratobranchiale I, and some fibers are continuous with those of the m. constrictor branchialis IV, at the level of the processus branchialis III. The posterior part includes fibers stemming from the processus branchialis III and fibers of the anterior part, both bundles inserting on the ceratobranchiale IV. The

Figure 7. *Lysapsus limellus* stage 31. A. Buccal roof. B. Buccal floor. Scale bar = 1 mm. Legends: bfa, buccal floor arena; bfap, buccal floor arena papillae; bp, buccal pocket; bra, buccal roof arena; brap, buccal roof arena papillae; gz, glandular zone; in, internal nares; ilp, infralabial papillae; ir, infrarostrodont; lrp, lateral ridge papillae; mn, median notch; mr, median ridge; nv, nasal valve; oc, orobranchial cavity; p, pustule; pna, prenarial arena; ptna, postnarial arena; ptnap, postnarial arena papillae; sr, suprarostrodont; ta, tongue anlage; vv, ventral velum.

Table 2. Comparison among chondrocrania of pseudines.

Character	<i>Pseudis paradoxa</i> (Parker, 1882; Ridewood, 1898; Haas, 2003)	<i>Pseudis minuta</i> (Lavilla and De Sá, 1999; Haas, 2003)	<i>Lysapsus limellus</i> (Present study)
Articular surfaces between cartilago labialis superior and cornua trabeculae	present	present	present
Septum nasi	developed?	not developed at St. 35	not developed at St. 35
Cartilaginee orbitales	with scarce development	with scarce development	with scarce development
Processus ascendens quadrati	attached to the floor of the neurocranium	attached to the floor of the neurocranium	attached to the floor of the neurocranium
Fenestra basicranialis	closed in early stages	open	open
Arcus subocularis quadrati	with a flat triangular projection	with a flat triangular projection	with a flat triangular projection
Processus pseudopterygoideus	present; well developed	present	present
Processus quadratoethmoidalis	present	present	present
Processus lateralis of cornu trabeculae	present; in contact with processus pseudopterygoideus	present; not conspicuous	present; not conspicuous
Reticulating cartilaginous connections between spicula III and IV	present; fused to planum hypobranchiale	present; fused to planum hypobranchiale	present; fused to planum hypobranchiale

presence of these unusual characters outside the subfamily Pseudinae raises new questions on the phylogenetic relationships among the genera of Hylidae.

In contrast with the m. subarcualis rectus II-IV, m. subarcualis rectus I in *Lysapsus limellus* does not diverge from the general pattern of three heads present in most hylids (Haas, 1997, 2003).

The relation of the ramus mandibularis of the trigeminal nerve with the mm. levator mandibulae externus superficialis and profundus varies among anuran larvae. There are three possibilities: external (dorsal to both muscles), internal (ventral) and “in between” position (Haas, 2001). *Lysapsus limellus* resembles hylids such as *Litoria* spp., *Hyla* spp. and *Scinax* spp., since the V_3 is dorsal respect to these muscles. However, among hylids this character has little diagnostic importance, since the location of V_3 can be variable even among closely related species (e.g. within genera: Haas, 1996, 2001; Haas and Richards, 1998).

The remaining musculature does not differ from the other pseudines and from other patterns described for generalized pond-type larvae (Cannatella, 1999).

For the analysis of the buccal apparatus and buccopharyngeal cavity, information is scarce. The only previous study is that of De Sá and Lavilla (1997) on *Pseudis minuta*. As regard this species, there appear some differences. The oral disc shows keratodonts arranged in a different labial tooth row formula. In general terms the buccal roof has fewer filter structures than in *P. minuta*, for example, less prenarial papillae and BRA pustules. In the buccal floor also, papillation is reduced in *L. limellus* compared to *P. minuta* (infralabial papillae: 2 vs. 4; lingual papillae: 2 vs. 3; BFA papillae: 7 pairs vs. 12 pairs).

Lysapsus limellus tadpoles present morphological traits that suggest a microphagous-generalist diet. The mechanical features of the cartilagine ceratohyalia (lateral portion of the ceratohyal much smaller than medial portion) and associated musculature (comparable development of the levator and depressor muscles of the buccal floor) coincide with the findings of Wassersug and Hoff (1979) regarding larvae with this type of feeding. Furthermore, the buccal apparatus, the various groups of papillae and other sieving structures, the secretory pits, and the large branchial basket that supplies a large supporting area for the gill filters, allow larvae to obtain and hold small particles. Lajmanovich (1998) describes the feeding habits of this species, and reports a diet consisting mainly of diatoms and chlorophytes. These data confirm the assumptions made on the basis of anatomic features.

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