

## Internal features of larvae belonging to two species of *Pseudopaludicola* (Anura: Leiuperinae)

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**Abstract.** We described the buccal cavity, chondrocranium, and cranial muscles in tadpoles of two species of *Pseudopaludicola*: *P. boliviana* (*P. pusilla* species group) and *P. falcipes*. The two species share states of only three relevant and informative characters: (1) absence of m. levator mandibularis lateralis, (2) absence of m. levator mandibularis externus superficialis at advanced premetamorphic stages, and (3) presence of long lateral arena papillae of both the roof and floor of the buccal cavity. The larvae of *P. falcipes* is diagnosed by (states of *P. boliviana* between parentheses): (1) three lingual papillae (four), (2) one-two pairs of short and blunt infralabial papillae (single pair of multifid papillae), (3) low median ridge (tall), (4) distal connection between pars corpora and pars alaris of the cartilago suprarostalis present (absent), and (5) m. subarcualis rectus II-IV inserted at ceratobranchiale I (ceratobranchiale II insertion). The combination of a processus pseudoptyergoideus together with proximal and distal connections on the cartilago suprarostalis occurs in most species of *Pleurodema* as well. Absence of m. levator mandibularis lateralis is also known for *Physalaemus fernandezae* and absence of m. levator mandibularis externus superficialis at advanced stages of development (Stage 39 onward) is shared with *Edalorhina perezii* and *Pleurodema diplolister*.

**Keywords:** buccal features, chondrocranium, muscles, *Pseudopaludicola boliviana*, *P. falcipes*, tadpoles.

The small toad-like frogs of the Neotropical genus *Pseudopaludicola* comprise seventeen species that are distributed along the eastern slopes of the Andes from northern Colombia to Argentina (Andrade and Carvalho, 2013; Frost, 2013). Lynch (1989) recognized a monophyletic group of *Pseudopaludicola pusilla* based on the presence of T-shaped terminal phalanges. Lobo (1995) supported the monophyly of the genus and of the *Pseudopaludicola pusilla* group, rendering the “*Pseudopaludicola falcipes* group” (*sensu* Lynch, 1989) a non-monophyletic assemblage.

*Pseudopaludicola* was traditionally considered the sister genus of *Physalaemus* within the paraphyletic family “Leptodactylidae” (see discussion in Lobo, 1995). More recently, the DNA-based phylogenetic analysis of Frost et

al. (2006) recovered *Pseudopaludicola* nested within the monophyletic Leptodactylidae. At the same time, Grant et al. (2006) found *Pseudopaludicola* to be sister to all other genera in the monophyletic Leiuperidae, a family resurrected by the authors in order to accommodate the genera *Edalorhina*, *Engystomops*, *Physalaemus*, *Pleurodema*, and *Pseudopaludicola*. Correa et al. (2006) recovered a clade formed by *Pseudopaludicola* and *Physalaemus*, with no further comments on the systematics of this clade. Although not specifically focusing on the Leiuperidae, Faivovich et al. (2012) obtain a topology that places *Pseudopaludicola* outside this group. Finally, the extensive molecular phylogeny by Pyron and Wiens (2011) has shown leiuperids as a subfamily within Leptodactylidae, being *Pseudopaludicola* the most basal Leiuperinae genus.

External descriptions of larvae are available for four species of *Pseudopaludicola* (Lobo, 1991; Pereira and Nascimento, 2004; Kehr and Schaefer, 2005; Laufer and Barreneche, 2008). In addition, a few external characters have been commented for some of the species of the group for which complete larval descriptions are ab-

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sent (Giaretta and Facure, 2009; Toledo, 2010; Lynch and Suárez Mayorga, 2011). On the contrary, internal features remain so far mostly unknown: features of the buccal cavity were described for only one unassigned species of *Pseudopaludicola* (Wassersug and Heyer, 1988) and chondrocranial and cranial muscles have actually never been assessed in this genus. Therefore, the present work provides the first cranial description for *Pseudopaludicola* larvae based on individuals of *P. falcipes* and *P. boliviana*, and also a first characterization of the larvae of the genus according to chondrocrania, cranial muscles and buccal cavity features of these species.

Larvae of both species are held at the Museo de La Plata (Buenos Aires, Argentina). Both species were collected in Argentina. Larvae of *P. boliviana* were collected near the Río Pilcomayo National Park in the province of Formosa (specimens MLP.A-5380) and in the province of Corrientes (specimens MLP.A-5455). Larvae of *P. falcipes* were collected in Atalaya, Magdalena, in the province of Buenos Aires (specimens MLP.A-4775). Species assignment was made using the descriptions of Laufer and Barreneche (2008) for *P. falcipes*, Kehr and Schaefer (2005) for *P. boliviana*, and also by rearing some of the larvae (MLP.A-5456) until metamorphosis. Larvae were staged following Gosner (1960) and then prepared for: (1) cranium analysis according to Taylor and Van Dyke (1985); (2) muscle observation by stopping the process before clearing; and (3) analysis by scanning electronic microscope (SEM) photographs of buccal cavity features according to Alcalde and Blotto (2006).

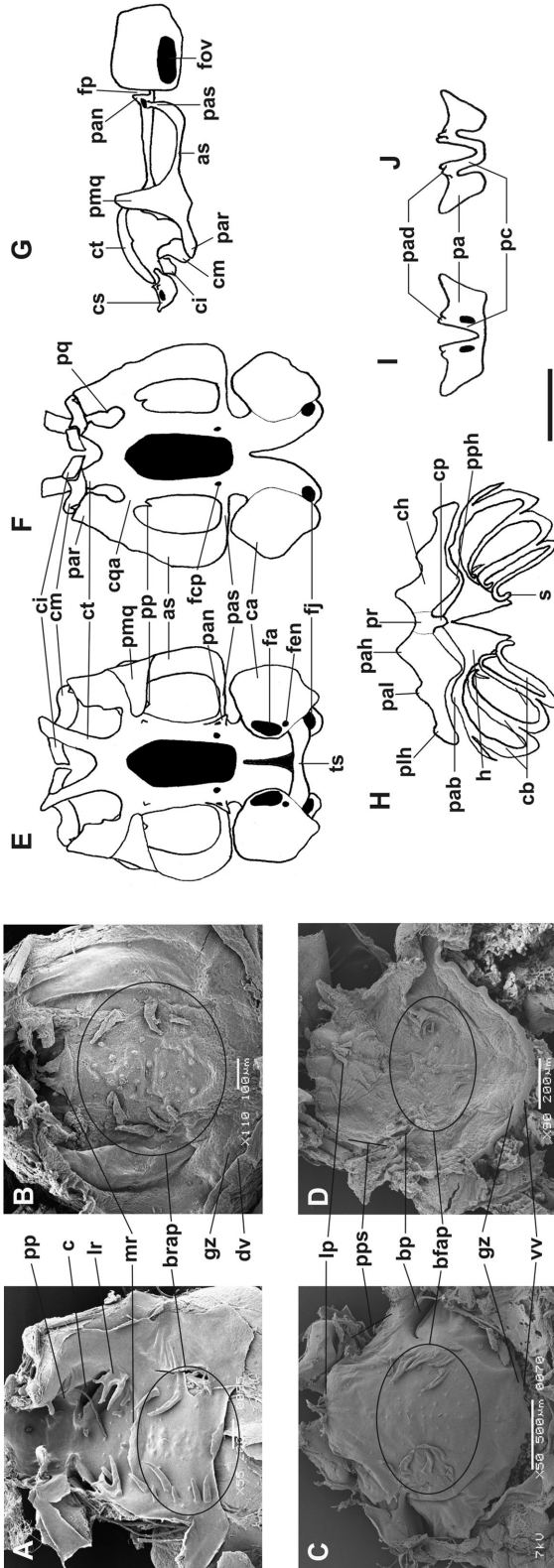
Two Stage 36 and two Stage 39 tadpoles of *P. falcipes* (MLP.A-3836) and five Stage 32 (MLP.A-5381) and two Stages 38 and 40 (MLP.A-5455, 5457) larvae of *P. boliviana* were prepared for chondrocranial and cranial muscles descriptions. Two Stage 39 larvae of *P. falcipes* and two Stage 32 larvae of *P. boliviana* were used for SEM analyses of buccal cavity features. In addition, SEM preparations were complemented with examinations of two Stage 39 and one Stage 37 larvae of *P. falcipes* (MLP.A-5382) and one Stage 32 larva of *P. boliviana* (MLP.A-5383) that were dissected and studied under a stereomicroscope.

The terminology used here follows d'Heursel and de Sá (1999) and Haas (1995) for chondrocranium (except the term fenestra hypophyseos that follows de Beer, 1937), Haas (2003) for cranial muscles, Schlosser and Roth (1995) for muscular innervation, and Wassersug (1980) for buccal cavity features. In the following, the two species are presented simultaneously, and differences between species are opportunely signaled.

**Buccal cavity.** Both species have prenarial arena bearing a pair of transversely arranged

small pustules, and postnarial arena with a central patch of few randomly distributed low papillae and pustules. There is a pair of long conical papillae placed just in front of the lateral ridge papillae. The median ridge is low, wide, and serrated in *P. falcipes* (fig. 1A), whereas the median ridge of *P. boliviana* bears one pair of triangular projections (fig. 1B). The forked lateral ridge papillae of *P. falcipes* are taller than the median ridge. *Pseudopaludicola boliviana* differs by having three-forked lateral ridge papillae as tall as the median ridge. Both species are characterized by a buccal roof arena with no more than 20-30 pustules flanked by 5-6 pairs of rostro-caudally aligned very long and conical papillae. Dorsal velum and secretory pits are present in both species.

The oral cavity of *Pseudopaludicola falcipes* is flanked by one (commonly) or two pairs of short and blunt infralabial papillae, being the anterior (when present) slightly larger than the posterior. We were unable to verify if the single pair condition corresponds either to the most anterior pair only or to fusion of both pairs forming a large papilla (see fig. 1A). *Pseudopaludicola boliviana* always has a single, wide and very well-developed multifid infralabial papillae (accidentally removed from photos of fig. 1B, D). The lingual anlage of *P. falcipes* projects three long lingual papillae, the central one (simple) and usually slightly longer than the lateral ones (forked) (fig. 1C). *Pseudopaludicola boliviana* has four conical and tall lingual papillae (fig. 1D). Both species have a single pair of short conical papillae surrounded by few small papillae and a smooth surface on the prepocket arena (see fig. 1A, B, although difficult to appreciate). Buccal floor arena scattered with no more than 30 pustules, flanked by four pairs of rostro-caudally aligned long conical papillae and some short papillae. *Pseudopaludicola boliviana* differs by having 2-3 pairs of rostrocaudally aligned papillae. Both species present a serrated ventral velum with abundant secretory pits and no median notch.



**Figure 1.** (A-D) SEM photographs of the buccal roof (A) and floor (C) of a Stage 39 larva of *Pseudopaludicola falciptes*, and of the buccal roof (B) and floor (D) of a Stage 32 larva of *P. boliviana*. The chondrocranium of *Pseudopaludicola falciptes* at Stage 36: (E) Dorsal, (F) ventral, and (G) lateral views of the neurocranium and mandibular arch; (H) ventral view of the hyobranchial apparatus; (I) and (J) represent frontal views of the cartilago suprarostalis of *P. falciptes* and *P. boliviana*, respectively. The cartilago suprarostalis was removed from (E) and (F). Dark areas represent cranial fenestrations. Abbreviations (A-D): bfap: buccal floor arena papillae, bp: buccal pocket, brap: buccal roof arena papillae, c: choana, dv: dorsal velum, gz: glandular zone, lr: lateral ridge, mr: median ridge, pp: postmarial papillae, pps: preopocket smooth surface, vv: ventral velum. Abbreviations (E-J): as: arecus subocularis, ca: capsula auditiva, cb: ceratohyale, ci: cartilago infrastrale, cm: cartilago meckeli, cp: copula posterior and processus urobranchialis, cqa: commissura quadrato-cranialis anterior, cs: cartilago suprastralis, ct: cornu trabeculae, fa: fenestra ovalis, fca: foramen caroticum secundarium, fcp: foramen caroticum primarium, fen: endolymphatic foramen, fj: foramen jugulare, fov: fenestra ovalis, fp: fissura prootica, h: hypobranchiale, h: hypobranchiale, pa: pars alaris, pab: processus anterior branchialis, pad: processus anterior dorsalis, pah: processus anterolateralis hyalis, pal: pila antotica, par: processus articularis quadrati, pas: processus ascendens, pc: processus lateralis hyalis, pmq: processus muscularis quadrati, pp: processus pseudopterygoideus, pph: processus posterior hyalis, pr: pars reuniens, s: spicula, ts: tectum synoticum. Scale bars (A-D) as shown; scale bars (E-H) = 1 mm; I-J are not to scale.

*Chondrocranium.* The neurocranium is rectangular (width/length = 0.78-0.82) and depressed (height/width = 0.18), with the greatest width at the level of the arcus subocularis. The partes corpora of the cartilago suprarostalis are medially joined by a distal bridge. The pars alaris of the cartilago suprarostalis joins the pars corpora by proximal and distal connections in *P. falcipes*. *Pseudopaludicola boliviana* has the proximal connection only (fig. 1I-J). The cornua trabeculae comprise 24-25% of the chondrocranial length, are uniformly wide, and bear a well-developed processus lateralis trabeculae. In all studied stages, the cranium is roofed by the tectum synoticum only, and the lateral walls (cartilagine orbitales) are widely open, but pila metoptica and pila antotica are present (fig. 1E-G). Similarly, the basis cranii is opened by a wide fenestra hypophyseos and pierced by the foramina carotica primaria (fig. 1E-F). The capsulae auditivae represent about 33-35% of the neurocranial length, lateral projections are absent, and are dorsally independent from the processus ascendens. The medial walls of the capsulae auditivae are pierced by the acoustic and the endolymphatic foramina (fig. 1E) whereas the posterior walls are opened by the superior perilymphatic foramina. The operculum is not chondrified at the stages studied.

The palatoquadrate bears the normal set of features of most anuran larvae: processus articularis quadrati, processus muscularis quadrati, commissura quadrato-cranialis anterior, processus quadrato-ethmoidalis, and processus ascendens. In addition to these features, a short processus pseudopterygoideus is present only in *P. falcipes*. The commissura quadrato-orbitalis and the larval processus oticus are absent in both species. The processus ascendens joins the pila antotica by an intermediate connection (fig. 1E-G).

The lower jaw is segmented into the cartilagine meckeli and cartilagine infrarostrales. The processus retroarticularis of the cartilago meckeli is short and articulates with the processus articularis quadrati. The cartilago meck-

eli has the ventromedialis and dorsomedialis processes to articulate with the cartilagine infrarostrales (fig. 1E-G).

The hyobranchial apparatus lacks copula I in both species. The ceratohyalia of both species bear the normal set of processes of most anuran larvae: processus anterior hyalis, processus anterolateralis hyalis, processus lateralis hyalis and processus posterior hyalis. Both ceratohyalia are medially joined by a rectangle-shaped pars reuniens. The copula II bears a short processus urobranchialis. In both species the ceratobranchiale I is continuous to the planum hypobranchiale whereas ceratobranchiales II-III-IV are joined by ligaments (fig. 1H). The commissurae proximales are absent in all ceratobranchiales, the processus branchiales of ceratobranchiales II and III are not fused. All spiculae are well developed. No ossifications centers were observed at the studied stages.

*Cranial muscles.* The supplementary material provides a list of the main features of the cranial muscles for *P. falcipes*. The ramus mandibularis of the trigeminus nerve runs laterally to all muscles of the levatorae mandibulae group. The only variation between the species is in the insertion of m. subarcualis rectus II-IV, which inserts on ceratobranchiale II in *P. falcipes* and on ceratobranchiale I in *P. boliviana*.

The current lack of data for some species of Leiuperinae (e.g., *Pleurodema somuncurensis*) and the fragmentary knowledge for some genera (e.g., *Edalorhina*) limit the present discussion to a detailed comparison of the characters published for the genera *Edalorhina*, *Engystomops*, *Physalaemus*, and *Pleurodema* (see below). The internal oral morphology of *Physalaemus* species is discussed on the basis of the information presented in recent studies on the larvae of this genus (Ruggeri and Weber, 2012; Provete et al., 2012). Similarly, information on buccal features of other leiuperids was taken from studies by Wassersug and Heyer (1988) and Barrasso et al. (2012), and references cited therein.

Wassersug and Heyer (1988) described the buccal cavity of one unassigned species of *Pseudopaludicola* from Minas Gerais (Brazil). The external features of this *Pseudopaludicola* sp. match with the larval descriptions of *P. mineira* and *P. serrana*. Unfortunately, the larval descriptions of two recently described species from Minas Gerais remain unknown. Therefore, the buccal cavity of the unassigned species of Wassersug and Heyer (1988) could not be assigned to any of them. The large rostro-caudally aligned lateral arena papillae present at both the roof and floor of the buccal cavity, and the presence of a trapezoid median ridge are buccal character states shared by the two species of *Pseudopaludicola* studied by us and that described by Wassersug and Heyer (1988). Other buccal features that we found potentially informative within leiuperids are: (1) number of infralabial papillae (varies from one to six pairs); (2) number of lingual papillae (varies from one to five pairs); (3) buccal floor arena (from poorly defined to having  $\geq 5$  papillae per side); (4) median ridge shape (semicircular, triangular, trapezoid); (5) median ridge surface (simple, pustulated, irregular or serrated, with projections); (6) prenarial arena (with or without papillae, or forming crest); (7) lateral ridge papillae (simple, forked, three-forked, tetra-forked, six-forked). Interestingly, *Engystomops pustulosus* and *E. petersi* are very consistent in their buccal features. These species share the same states for the seven buccal cavity characters mentioned above. Finally, all species of *Pleurodema* share the same states for buccal characters 1 and 3: presence of two pairs of infralabial papillae and, buccal floor arena presenting  $\geq 5$  papillae per side.

The chondrocranial and cranial muscle features of *Pseudopaludicola* species are compared in the following to data published for other leiuperids, such as *Edalorhina*, *Engystomops*, *Physalaemus*, and *Pleurodema* (Starrett, 1968; Fabrezi and Vera, 1997; Larson and de Sá, 1998; Palavecino, 2000; Haas, 2003; Alcalde, Natale and Cajade, 2006; Prado, 2006; Vera Candioti,

2007; Provete et al., 2011; Barrasso et al., 2012; Provete et al., 2012). We found that the processus pseudopterygoideus is present in *Pseudopaludicola falcipes*, *Physalaemus nattereri*, *P. marmoratus* and all *Pleurodema* species that have been studied so far, but is absent in *Engystomops* and the remainder *Physalaemus*. Similarly, a distal connection between the pars alaris and pars corporis of the cartilago suprarostralis is present in the *Pseudopaludicola falcipes* examined and all *Pleurodema*, but is absent in *Pseudopaludicola boliviana* and all *Physalaemus*. Interestingly, the chondrocranial characters mentioned above seem to divide *Pseudopaludicola* into two groups, with *P. boliviana* more similar to *Physalaemus* and *Engystomops*, and *P. falcipes* more similar to *Pleurodema*. Because the chondrocranium of leiuperids is poorly known, since described in less than 5% of the species, we are unable to discuss in detail about chondrocranial characters within the group of interest in this study.

The hyomandibular muscles are known for *Pleurodema bufoninum*, *P. thaul* (Barrasso et al., 2012), *P. diplolister* (only mandibular muscles; Starrett, 1968), *P. borellii*, *P. cinereum*, *P. tucumanum* (Palavecino, 2000), *P. kriegi* (Haas, 2003), *Physalaemus fernandezae* (Alcalde, Natale and Cajade, 2006), *P. biligonigerus*, *P. cuqui* (Palavecino, 2000), *P. santafecinus* (Vera Candioti, 2007), *Edalorhina perezii*, *Engystomops pustulosus* (Starrett, 1968), and the two *Pseudopaludicola* species studied here. The branchial muscles are known for few species: *Physalaemus fernandezae* (Alcalde, Natale and Cajade, 2006), *P. santafecinus* (Vera Candioti, 2007), *Pleurodema kriegi* (Haas, 2003), *P. bufoninum*, *P. thaul* (Barrasso et al., 2012), and the *Pseudopaludicola* studied here. Considering these descriptions, the two *Pseudopaludicola* species studied here and *Physalaemus fernandezae* share the absence of m. levator mandibular lateralis at advances stages of the premetamorphic development. Similarly, the m. levator mandibularis externus superficialis is absent at advances developmental stages (39)

of *Pseudopaludicola boliviana* and *P. falcipes* (this study), and of *Edalorhina perezi* and *Pleurodema diplolister*. This muscle is invariably present since early stages in *Engystomops pustulosus*, most *Physalaemus* species, and almost all *Pleurodema* species (except *P. diplolister*). Therefore, all the above discussed features are useful to diagnose the two studied species of *Pseudopaludicola*, *P. boliviana* and *P. falcipes*.

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