



## Different pathways are involved in the early development of the transient oral apparatus in anuran tadpoles (Anura: Leiuperidae)

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Received 28 March 2011; revised 12 May 2011; accepted for publication 12 May 2011

The oral apparatus of anuran tadpoles is a unique structure composed of soft and keratinized parts surrounding the mouth. Among the many variations, a common oral apparatus involves a dorsal gap in the marginal papillae, keratinized jaw sheaths, and two upper and three lower rows of labial teeth. In Leiuperidae, besides this generalized morphology, four configurations are distinguished by the arrangement of the lower marginal papillae and the number of lower tooth rows. Study of the early oral ontogeny in 12 species representing these five configurations shows variations in the development of the lower marginal papillae and the third lower labial tooth row. Similar configurations may result from similar pathways (e.g. *Physalaemus cuvieri* group and *Pseudopaludicola falcipes*) or different pathways (e.g. generalized oral discs of *Pleurodema* and *Physalaemus*). Different oral configurations may result from overlapping trajectories ending at different stages (e.g. *Physalaemus riograndensis* and *Ph. biligonigerus*) or different trajectories (e.g. *Ph. henselii* and *Ph. gracilis*). Further studies are needed to interpret the role that heterochrony has played in evolutionary change within this family. The unsuspected variation occurring in this transient structure highlights its evolutionary potential and might be insightful in studies of anuran phylogenies that are largely based on adult characters. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 104, 330–345.

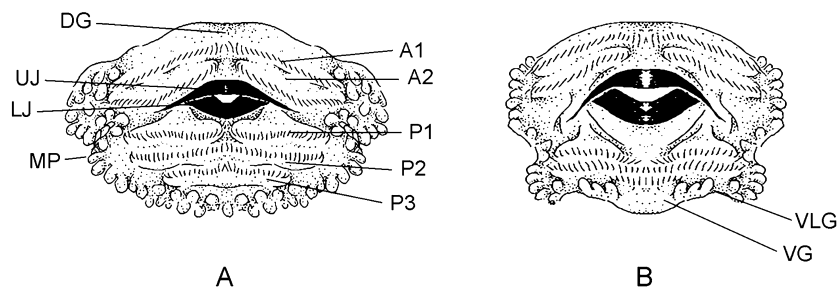
**ADDITIONAL KEYWORDS:** generalized oral apparatus – labial tooth rows – *Physalaemus* – *Pleurodema* – *Pseudopaludicola* – ventral gap – ventrolateral gaps.

### INTRODUCTION

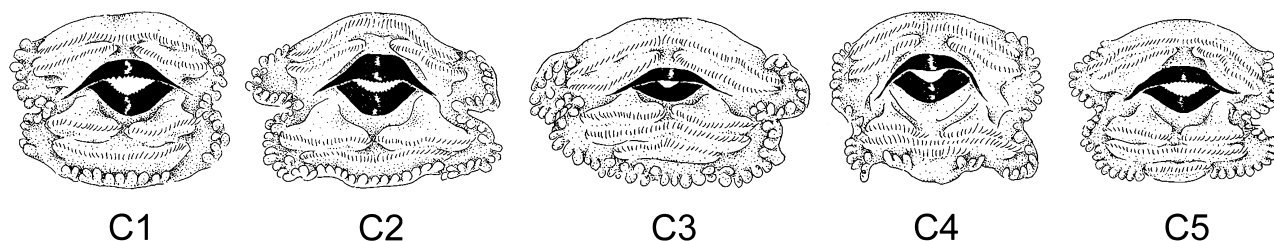
The oral apparatus (oral disc) of anuran tadpoles is a unique, complex structure composed of soft and keratinized parts surrounding the mouth (Altig, 2006). Soft parts include the upper and lower labia with transverse tooth ridges and marginal and submarginal papillae; keratinized parts include jaw sheaths

that cover the supra- and infrarostral cartilages, labial teeth that are positioned on the crests of the tooth ridges, and occasional keratinized zones adjacent to the jaw sheaths (Kolenc, Borteiro & Tedros, 2003; Altig, 2007). Among the many variations in oral structures (e.g. Wassersug, 1980; Donnelly, De Sá & Guyer, 1990; Vera Candiotti, 2007; Vera Candiotti & Altig, 2010), a common, generalized oral apparatus involves a dorsal gap in the marginal papillae, keratinized jaw sheaths, and two upper and three lower rows of labial teeth (Fig. 1A).

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**Figure 1.** Schematic views of the oral apparatus of anuran tadpoles. A, generalized oral apparatus with a dorsal gap in the marginal papillae and five tooth rows. B, oral apparatus of *Physalaemus cuqui* with gaps in the lower marginal papillae. A1, first anterior (upper) tooth row; A2, second anterior tooth row; DG, dorsal gap in marginal papillae; LJ, lower jaw sheath; MP, marginal papillae; P1, first posterior (lower) tooth row; P2, second posterior tooth row; P3, third posterior tooth row; UJ, upper jaw sheath; VG, ventral gap in marginal papillae; VLG, ventrolateral gap in marginal papillae.



**Figure 2.** Five configurations of the oral discs of leiuperid tadpoles: C1, labial tooth row formula 2/2, dorsal and ventrolateral gaps in marginal papillae; C2, LTRF 2/2, dorsal gap; C3, LTRF 2/3, dorsal gap; C4, LTRF 2/3, dorsal, ventrolateral, and ventral gaps; C5, LTRF 2/3, dorsal and ventral gaps.

The development of the oral apparatus of relatively few tadpoles have been studied (e.g. Cusimano-Carollo, Fangone & Reverbei, 1962; Cusimano-Carollo, 1963, 1969, 1972; Pyburn, 1967; Agarwal & Niazi, 1980; Thibaudeau & Altig, 1988; Nodzinski & Inger, 1990; Khan & Mufti, 1994; Altig & McDiarmid, 1999; Zaracho, Céspedes & Álvarez, 2003). Most studies concerning species with keratinized mouthparts have involved taxa with oral apparatuses similar to the generalized oral disc (e.g. Fiorito de López & Echeverría, 1984; Marinelli *et al.*, 1985; Marinelli & Vagnetti, 1988; Tubbs *et al.*, 1993). Studies generally agree on a common pattern in the sequence of appearance of mouthparts during embryogenesis (Thibaudeau & Altig, 1988). However, because of biases in the species that have been studied and the enormous variation in oral configurations of tadpoles, a wider sampling is desirable to provide new information on homologies and developmental patterns and timing of the structures involved.

Here we address oral disc development in 12 species of three genera in the family Leiuperidae. This family ranges from southern Mexico to southern Argentina, and the small benthic tadpoles live in still water. The family was resurrected by Grant *et al.* (2006) to include the genera *Edalorhina*, *Engystomops*, *Eupemphix*, *Physalaemus*, *Pleurodema*,

*Pseudopaludicola*, and *Somuncuria*. However, conflicting results were obtained in other phylogenetic analyses (Frost *et al.*, 2006; Lourenço *et al.*, 2008) so that the relationships of these taxa with the other Leptodactyliformes (*sensu* Frost *et al.*, 2006) should be reassessed. We chose this group because it shows remarkable variation in the oral apparatuses of even closely related species, in some cases also involving characters that are not present in the generalized larval oral discs (Fig. 1B). The larval oral apparatus has been described for 29 of the 42 species of *Physalaemus*, and five different oral configurations that consider the number of anterior and posterior tooth rows (i.e. labial tooth row formula, LTRF) and the marginal papillae can be recognized: C1, LTRF 2/2, dorsal and ventrolateral gaps in the marginal papillae; C2, LTRF 2/2, dorsal gap; C3, LTRF 2/3, dorsal gap (i.e. the generalized configuration mentioned above); C4, LTRF 2/3, dorsal, ventrolateral, and ventral gap; and C5, LTRF 2/3, dorsal and ventral gaps. In the genus *Pleurodema*, oral configurations C2 and C3 have been described. In the genus *Pseudopaludicola*, C1, C2, C4, and C5 are present along with some intraspecific variation. Figure 2 depicts the morphologies described and Supporting Information Table S1 summarizes the oral configurations of leiuperid tadpoles that have been described.

The goals of our study were (1) to compare the early ontogenies of the oral apparatuses in tadpoles of three leiuperid genera with different oral configurations, (2) to study interspecific variation in order to identify specific and shared patterns through comparisons with other taxa, and (3) to consider possible implications of heterochronic development in leiuperid evolution among genera and intrageneric groups. Without having a proper phylogenetic hypothesis and any data on the genetic control of oral formation, we hope that such a comparative study provides better understanding of the evolution of oral structures in this group.

## MATERIAL AND METHODS

Early development of the oral apparatus was studied in developmental series of *Physalaemus biligonigerus*, *Ph. cuqui*, *Ph. cuvieri*, *Ph. fernandezae*, *Ph. gracilis*, *Ph. henselii*, *Ph. riograndensis*, *Ph. santafecinus*, *Pleurodema bibroni*, *Pl. borellii*, *Pl. cf. guayapae*, and *Pseudopaludicola falcipes*. Eggs were collected from amplexant pairs or clutches from several breeding places in Argentina and Uruguay throughout several reproductive seasons (supporting Table S1). Embryos were raised in containers with tap water, at ambient room temperatures and a natural light cycle. Specimens were killed every 6–8 h, preserved in 10% formalin and prepared for observation with a stereomicroscope. Staining with methylene blue provided increased contrast of soft parts (Wassersug, 1976). A subset of 6–13 embryos that showed important morphological changes in the oral apparatus of each species was prepared for observation with scanning electron microscopy. Our work emphasized morphological patterns of development through stages; the consideration of time as a variable is beyond the scope of this presentation and it would have required a different methodological approach (e.g. Chipman *et al.*, 2000). We used the developmental stages of Gosner (1960) as a standard to compare events during oral disc development in the studied species. We recorded developmental events between the differentiation of upper and lower labia (about Gosner stage 20) and the formation of the entire oral apparatus at about the appearance of hind limb buds (stage 25/28). Oral disc terminology follows that of Altig (2007).

## RESULTS

We summarize the oral ontogeny of each species (stages 21–28; see the supporting Table S2 for additional details). The primary interspecific differences relate to the development of the posterior labial tooth rows and the arrangement of marginal papillae on the lower labium.

*PHYSALAEMUS* (EIGHT SPECIES: *PH. BILIGONIGERUS*, *PH. CUQUI*, *PH. CUVIERI*, *PH. FERNANDEZAE*, *PH. GRACILIS*, *PH. HENSELII*, *PH. RIOGRANDENSIS*, AND *PH. SANTAPECINUS*)

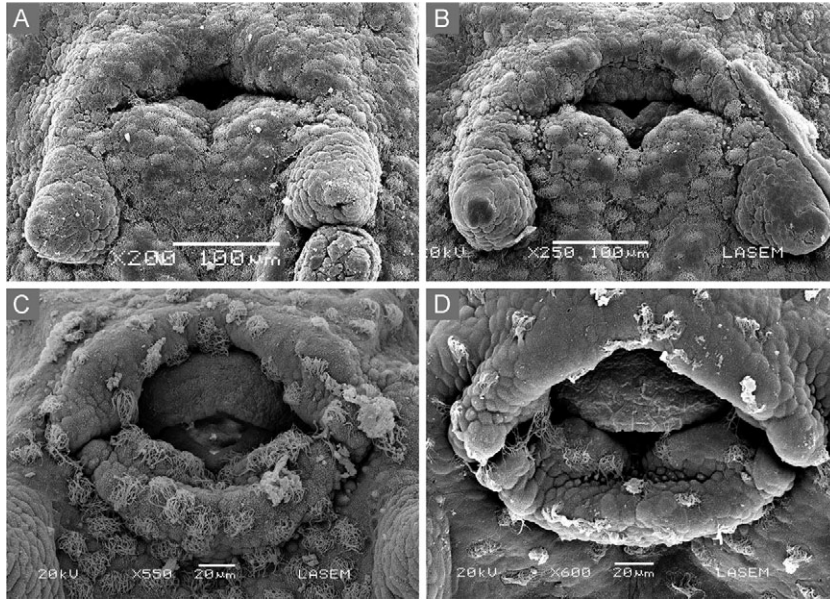
Tadpoles of *Physalaemus* share the first stages of oral disc development, including the formation of the jaw sheaths, labial tooth rows A1, A2, P1, and P2, and the marginal papillae on the lateral margins of the upper and lower labia. At about Gosner stage 21 the upper and lower labia are outlined; the upper labium is narrow and arc-shaped, and the lower labium has a deep medial groove; the edge of the lower jaw sheath becomes noticeable (Fig. 3A). At about stage 22 the upper jaw sheath develops and the medial groove in the lower labium is deeper, corresponding to the gap in row P1 (Fig. 3B). Next (about stage 23), the extremes of the upper labium (corresponding to tooth ridge for row A1) become more prominent; the lower labium shows a transverse ridge that lengthens in a medial-to-lateral direction and forms the non-divided P2 tooth ridge. Marginal papillae progressively appear from this stage, and their differentiation is initially evident at the lateral margins of the labia (Fig. 3C). After stage 23, the oral disc has a longer P2 and more papillae are visible laterally; on the upper labium, row A2 appears as two short sections posterior to the lateral ends of the A1 tooth ridge (Fig. 3D). At about stage 24, the lower labium has two well-defined tooth ridges and a distinctive, prominent ventromedial region where typical features of each taxa will form. From this stage, two different developmental trajectories can be identified (summarized in Fig. 4):

1. In *Physalaemus riograndensis* (Fig. 5), development continues with the progressive appearance of labial teeth in rows A1, P1, and P2, and with the formation of a single central papilla on the ventromedial region of the lower labium (Fig. 5B). At about stage 26, some labial teeth appear on row A2, and progressive development of papillae in the lower labium from the lateral ends and the centre leaves two ventrolateral gaps (Fig. 5C, D).

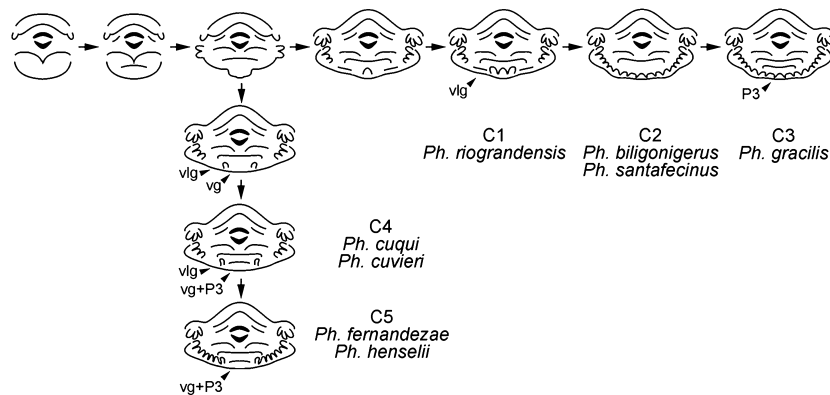
*Physalaemus biligonigerus* and *Ph. santafecinus* (Fig. 6) develop similarly as above, but unlike *Ph. riograndensis*, the marginal papillae on the lower labium become complete by stages 25–26. The development of *Ph. santafecinus* is slightly slower (with regard to external gill development) than that of *Ph. biligonigerus*, and specimens at stage 26 still have ventrolateral gaps (Fig. 6D).

In specimens of *Physalaemus gracilis* (Fig. 7) older than stage 24, papillae develop in the ventromedial





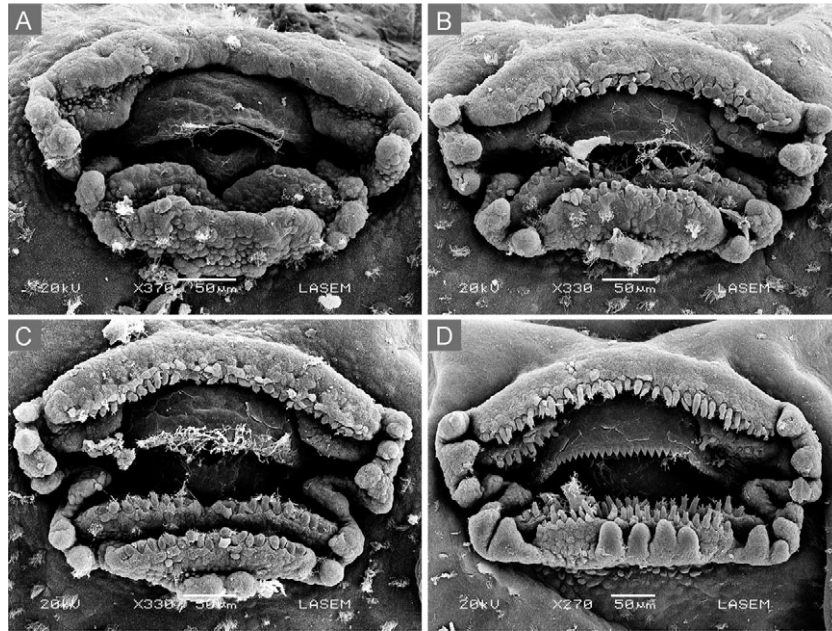
**Figure 3.** Oral ontogeny in *Physalaemus* tadpoles; first stages shared by the studied species. A, *Ph. biligonigerus* stage 21. B, *Ph. biligonigerus* stage 22. C, *Ph. santafecinus* stage 23. D, *Ph. santafecinus* stage > 23.



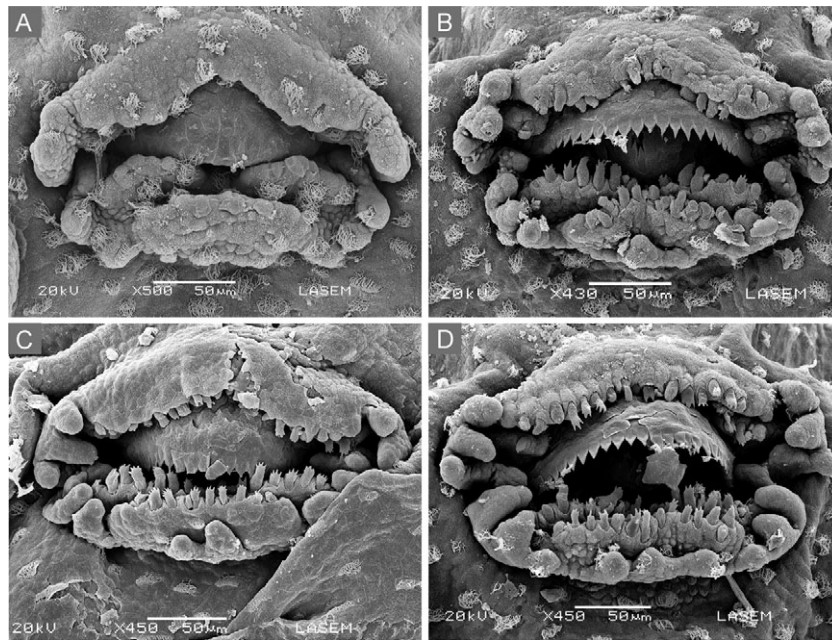
**Figure 4.** Oral ontogeny in *Physalaemus* tadpoles; schematic representation of two alternative trajectories of oral disc development. The formation of the jaw sheaths, labial tooth rows A1, A2, P1, and P2, and marginal papillae on the lateral margins of the upper and lower labia occur in a similar way in all the studied species. Later, two different developmental trajectories are identified. (1) A single central papilla on the ventromedial region of the lower labium appears, and progressive development of papillae in the lower labium from the lateral ends and the centre leaves two ventrolateral gaps (C1); ventrolateral gaps close (C2); a third labial tooth row develops (C3). (2) Two large papillae develop at the edges of the middle part of the lower labium, and labial teeth appear between them to form a short row P3 (C4); ventrolateral gaps close (C5). P3, third lower tooth row; VG, ventral gap in marginal papillae; VLG, ventrolateral gap.

region but seemingly they do not appear in a strict numerical progression like in the other species (Fig. 7B). The rapid filling of the ventrolateral gaps results in early completion of the marginal papillae (stage < 25; Fig. 7C). At about stage 25, the third tooth ridge appears as a series of small bumps (Fig. 7D), and by stage 26 a short, well-defined row P3 has newly emerged labial teeth (Fig. 7E). Row P3 persists as a shorter tooth row in the definitive oral disc (Fig. 7F).

2. *Physalaemus cuvieri* (Fig. 8) and *Ph. cuqui* (Fig. 9) follow a different developmental trajectory; as stage 25 approaches, two large papillae appear at the edges of the middle part of the lower labium with a small ventral gap between them (Fig. 8C). This part of the labium widens and flexes anteriorly; labial teeth appear between the large papillae to form a short row P3 (Fig. 8D). In *Ph. cuqui*, the labial teeth of row P3 develop slightly earlier, by stage 25 (Fig. 9).



**Figure 5.** Oral ontogeny of *Physalaemus riograndensis* tadpoles: C1, ventrolateral gaps in marginal papillae never close. A, stage 25. B, stage > 25. C, stage < 26. D, stage 26.



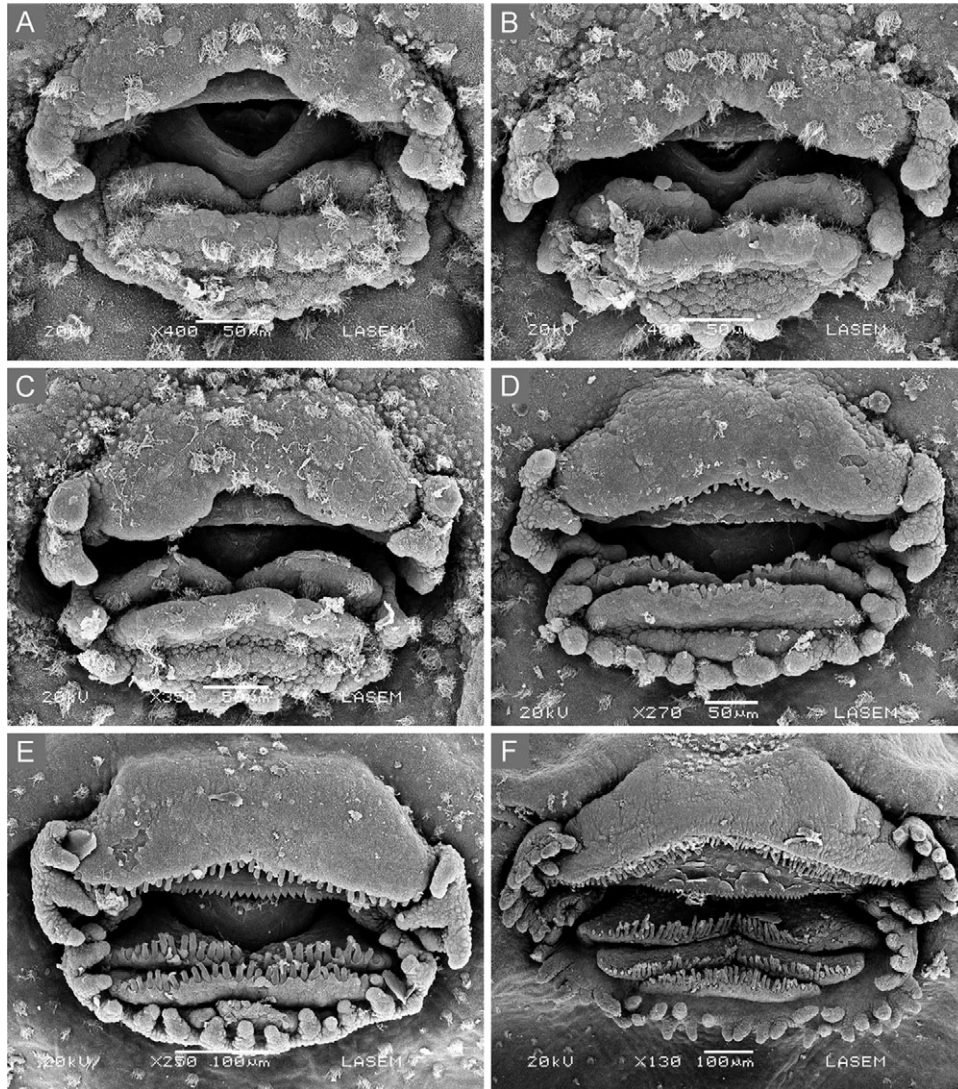
**Figure 6.** Oral ontogeny of *Physalaemus santafecinus* tadpoles: C2, ventrolateral gaps in marginal papillae close after Gosner stage 26. A, stage < 24. B, stage < 25. C, stage 25. D, stage 26.

*Physalaemus fernandezae* and *Ph. henselii* (Fig. 10) pass through these developmental stages in a similar way, but they surpass *Ph. cuvieri* and *Ph. cuqui* in that marginal papillae fill the ventrolateral gaps by stage 26 (Fig. 10C).

*PLEURODEMA* (THREE SPECIES: *PL. BIBRONI*,  
*PL. BORELLII*, AND *PL. CF. GUAYAPAE*)

Development of the oral disc in species of the genus *Pleurodema* (Figs 11, 12) differs in several aspects

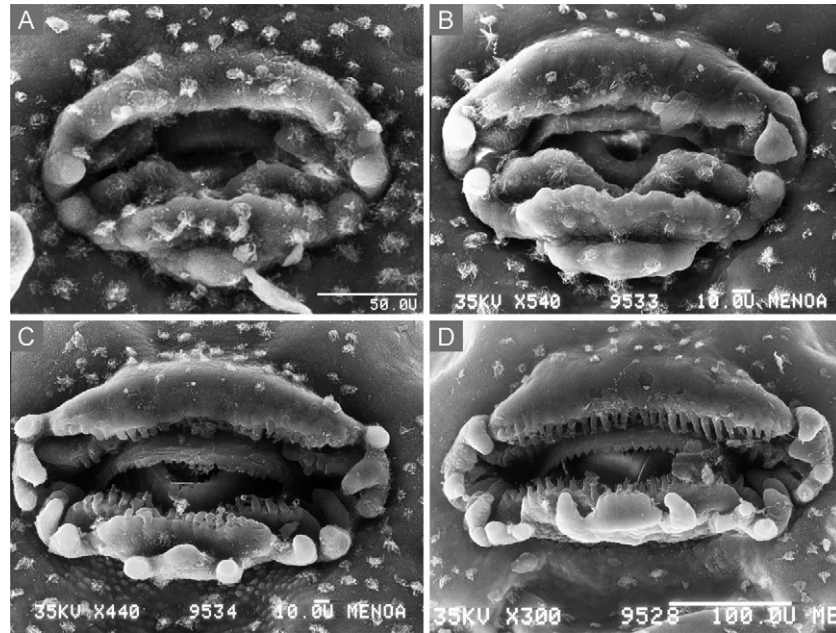




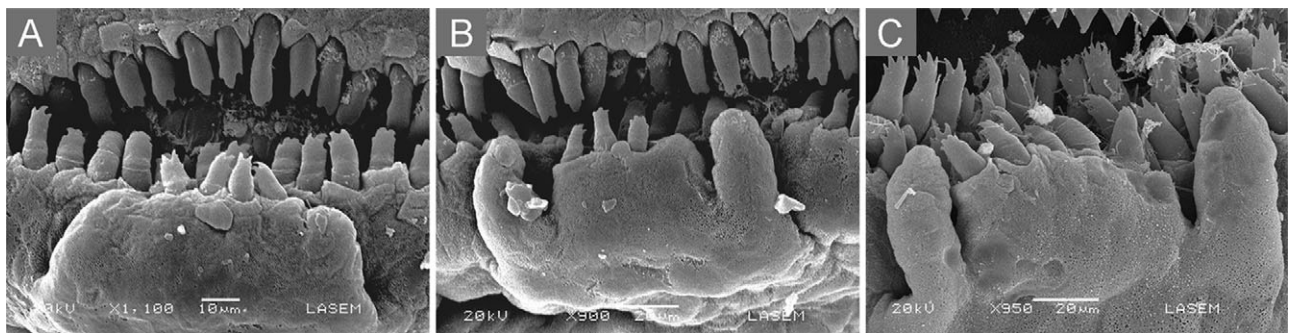
**Figure 7.** Oral ontogeny of *Physalaemus gracilis* tadpoles: C3, a third labial tooth row appears and ventrolateral gaps in marginal papillae close after Gosner stage 25. A, stage < 24. B, stage > 24. C, stage < 25. D, stage 25. E, stage 26. F, stage 29.

from what was observed for *Physalaemus*, and the development of some structures is relatively slower. The tooth ridges for rows P1 and P2 appear almost simultaneously because they are part of a common ridge that later splits into two structures (Figs 11D, 12C). Labial teeth also emerge simultaneously on the tooth ridges for rows P1 and P2. Also, formation of the marginal papillae on the lower labium occurs from the lateral ends and develop medially from both sides (Fig. 11D–F, 12C–F). After this stage, oral disc development follows two trajectories:

1. In *Pleurodema cf. guayanae*, the marginal papillae are fully formed by stage 25 (Fig. 11F), and labial teeth begin to appear at stage 26; at stage 27, teeth still do not have their larval morphology (Fig. 11G).
2. *Pleurodema bibroni* (Fig. 12) and *Pl. borellii* develop the tooth ridge for row P3. In *Pl. bibroni* the formation of the marginal papillae is not complete until this ridge is fairly evident and bears teeth; in most specimens this occurs considerably later than stage 26 in tadpoles about twice as large as at stage 25. Also, the length of row P3 in *Pl. bibroni* never reaches that of the other lower labial tooth rows. Conversely, the definitive oral disc (bearing teeth with definitive morphology) is produced at stage 25 in *Pl. borellii*. It is interesting to note that most morphological changes in the oral disc of *Pl. bibroni* occur very rapidly at about Gosner stage 25 (i.e. simultaneously to the spiracle development; see Fig. 12).



**Figure 8.** Oral ontogeny of *Physalaemus cuvieri* tadpoles: C4, a short third labial tooth row appears in the ventromedial region of the lower labium and ventrolateral gaps in marginal papillae never close. A, stage > 23. B, stage < 24. C, stage 25. D, stage 26.



**Figure 9.** Oral disc of *Physalaemus cuqui*: C4, details of the development of the third labial tooth row. A, stage 25. B, stage > 25. C, stage 27.

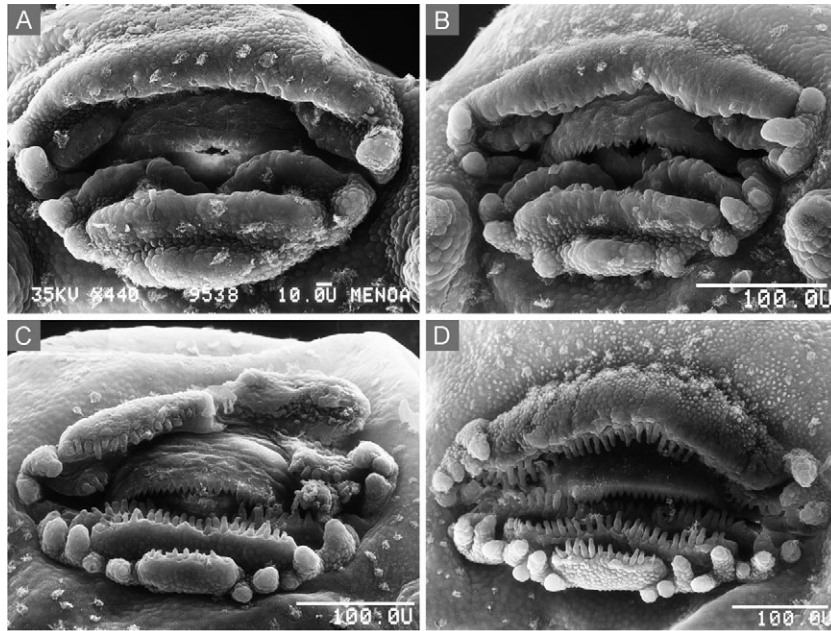
#### *PSEUDOPALUDICOLA* (ONE SPECIES: *PS. FALCIPES*)

The first stages of oral disc development in *Pseudopaludicola falcipes* are similar to those of *Physalaemus cuqui* and *Ph. cuvieri* of the *Ph. cuvieri* species group. Formation of the upper and lower labia, jaw sheaths, labial tooth rows A1, A2, P1, and P2, and lateral marginal papillae occurs in a comparable way between stages 21 and 24 (Fig. 13A, B). After stage 24, the ventromedial part of the lower labium region becomes more prominent and wide (Fig. 13C, D). Two lateral bumps will differentiate as marginal papillae (Fig. 13E) and the central region develops either as a tooth ridge with labial teeth or as marginal papillae that eventually support teeth

(Fig. 13F, G). This variation implies that the ventral gap is not always present in premetamorphic larvae, as we confirmed while observing several additional series of tadpoles of this species.

In all these leiuiperid species, the face of the disc and the surface surrounding the mouth of embryos are characterized by ciliated epidermal cells that progressively regress by about Gosner stage 26. Ciliated cells are less dense and persist for a shorter period in *Pseudopaludicola falcipes* than in the remaining species. In all species, the jaw sheaths have acute serrations (Fig. 14A). We found two different configurations of labial teeth in *Physalaemus*: teeth with a marked body and head with numerous, marginal cusps (in species with C3 and C5; Fig. 14B, C), and





**Figure 10.** Oral ontogeny of *Physalaemus henselii* tadpoles: C5, a short third labial tooth row appears in the ventromedial region of the lower labium and ventrolateral gaps in marginal papillae close after Gosner stage 26. A, stage < 25. B, stage 25. C, stage 26. D, stage > 26.

teeth with a short head that is scarcely distinguishable from the body and a few long, distal cusps (in species with C1, C2, and C4; Fig. 14D–F). In species of *Pleurodema* we also observed two different configurations of labial teeth that differed in developmental timing. Teeth of *Pl. cf. guayanae* are short, with distal cusps short or absent, and as late as stage 27 they still do not achieve their larval morphology (Fig. 14G). In *Pl. bibroni* and *Pl. borellii* definitive teeth appear before stage 26 and have a slightly longer head with numerous marginal cusps (Fig. 14H). The labial teeth in *Pseudopaludicola falcipes* have the same morphology as those of tadpoles in the *Physalaemus cuvieri* species group (i.e. head and body scarcely marked, and few long, distal cusps; Fig. 14I). Finally, larval adhesive (cement) glands develop in all species as two separated, conical structures that lie posterolateral to the mouth (e.g. Fig. 12A–E). They appear earlier than stage 17 and regress by stages 25–28.

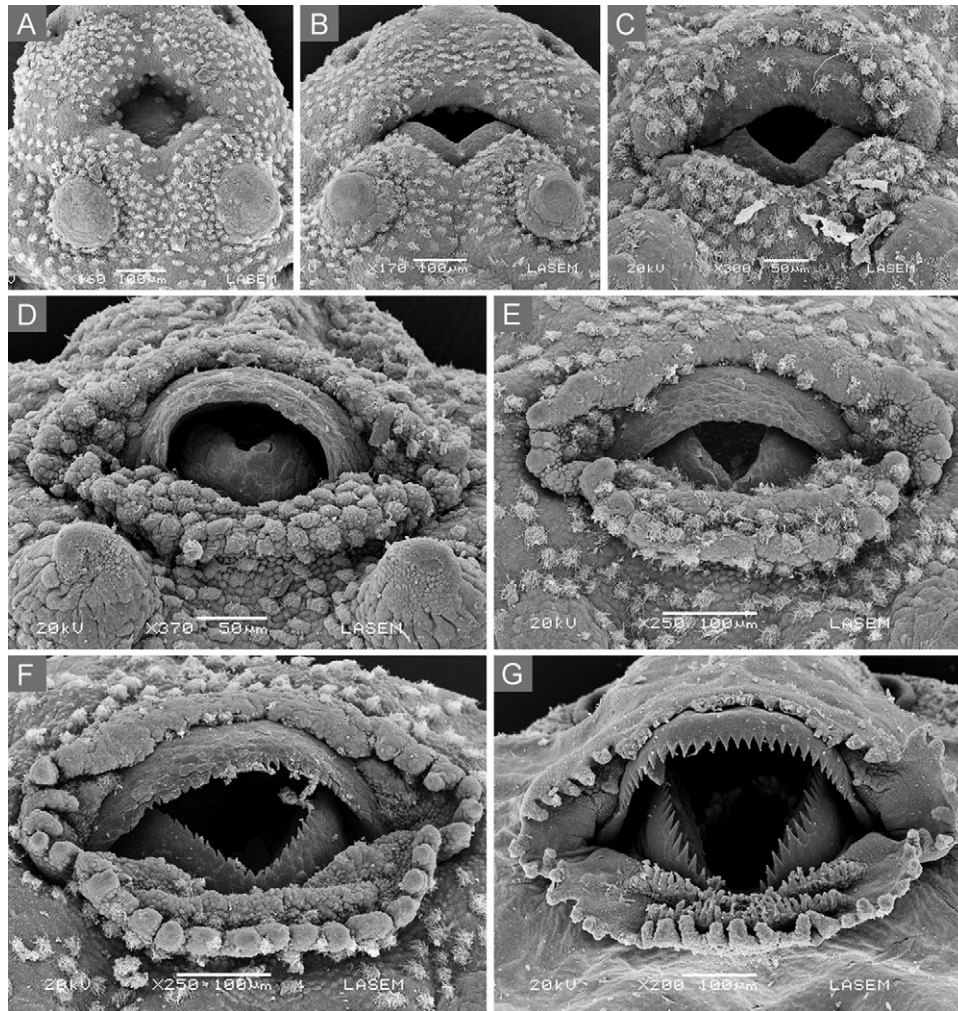
## DISCUSSION

In leuperids, variations in larval oral apparatuses are accompanied by variations in their ontogenetic patterns. These variations are interesting from at least two interrelated perspectives. From a developmental approach, the unsuspected, wide variation that occurs in an early, transient structure that disappears at metamorphosis is of interest because of

the early mechanisms causing it and the high evolutionary potential. From a systematic approach, shared and divergent trajectories might indicate phylogenetic relationships in a group of species where other character sources are not conclusive.

Within the first approach, the study by Thibaudeau & Altig (1988) on the oral ontogeny of six anuran species identified a sequential development of the mouthparts that produce the generalized oral disc: stomodeum, jaw sheaths, marginal papillae, tooth ridges A1, P2, P1, A2, and P3, and finally submarginal papillae. Labial teeth develop slightly later but in the same sequence as the tooth ridges and in a medial-to-lateral progression on each ridge (Tubbs *et al.*, 1993). The sequence of development in several other species described differs in some events, such as the time of appearance of row A2 (e.g. Sedra & Michael, 1961; Hall, Larsen & Fitzner, 1997). In species of *Physalaemus* and *Pseudopaludicola*, the formation of the first two lower tooth ridges differs from what is described above: the prominent lower labium with a medial groove corresponds to the tooth ridge for row P1, and P2 develops as a transverse ridge that lengthens in a medial-to-lateral direction. This early formation of P1 is accompanied by the appearance of the first labial teeth on that ridge. Conversely, in *Pleurodema* tadpoles, tooth ridges for rows P1 and P2 are formed almost simultaneously, from a common ridge that soon divides into two sections.

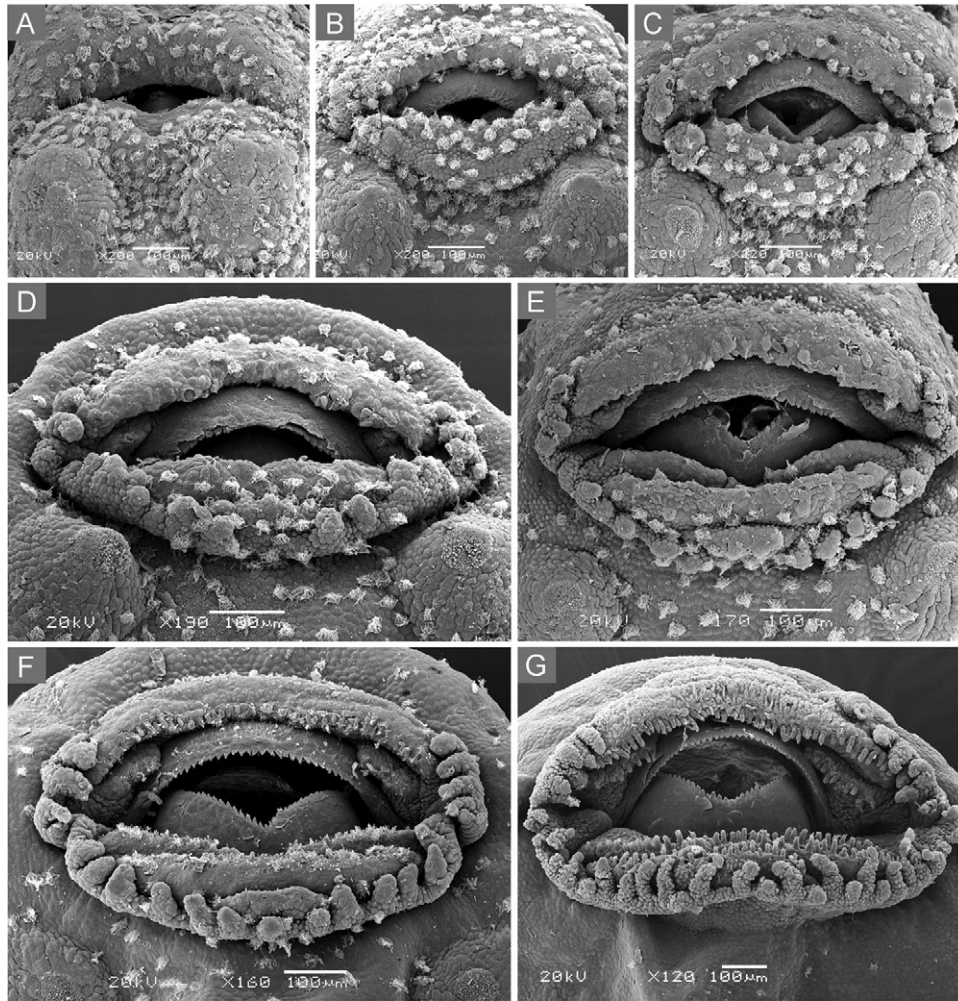




**Figure 11.** Oral ontogeny of *Pleurodema* cf. *guayapae* tadpoles: C2, marginal papillae develop only from lateral regions of the oral disc. A, stage 20. B, stage 21. C, stage > 21. D, stage 23. E, stage > 23. F, stage < 25. G, stage 27.

Two characters during leiperid development are worthy of further note: the marginal papillae of the lower labium and labial tooth row P3. Marginal papillae of the lower labium appear in two alternative ways: (1) from the lateral portions of the disc margin, progressing in a medial direction; and (2) from the lateral and medial portions of the disc margin, progressing in both medial and lateral directions. The first case produces a ventral gap that is transient during the development of *Pleurodema*. The second case results in two different oral configurations. In one of them, papillae of the ventromedial portion of the disc appear at the very centre, so that a ventral gap is never present, and two ventrolateral gaps persist until progressive development fills them. This possibly occurs in all species of *Physalaemus* with oral configurations C1, C2, and C3 (see supporting Table S1, Fig. 4). Alternatively, ventromedial marginal papillae first appear

on the extremes of a prominent, undifferentiated region and delimit a short ventral gap that will persist during development; as in the latter case, ventrolateral gaps are present until the ventromedial and lateral marginal papillae fill them in some taxa. This is probably the case of all *Physalaemus* species with oral configuration C4 and C5 (see supporting Table S1; Fig. 4). In the only species of *Pseudopaludicola* that we studied, the marginal papillae are formed in this latter way, but in some specimens a region delimited by the two first ventromedial papillae may develop more papillae that bear labial teeth and form a short row P3. Two other oral disc configurations have been unequivocally described for *Pseudopaludicola* (i.e. C1 and C2; supporting Table S1); in both cases, whether papillae of the ventromedial region are formed as in C1 and C2 of *Physalaemus* (i.e. progressively from the centre) or as an alternative state in the trajectory to



**Figure 12.** Oral ontogeny of *Pleurodema bibroni* tadpoles: C3, marginal papillae develop only from lateral regions of the oral disc and a third labial tooth row appears. A, stage 22. B, stage < 25. C, stage < 25. D, stage < 25. E, stage 25. F, stage > 25. G, stage 26.

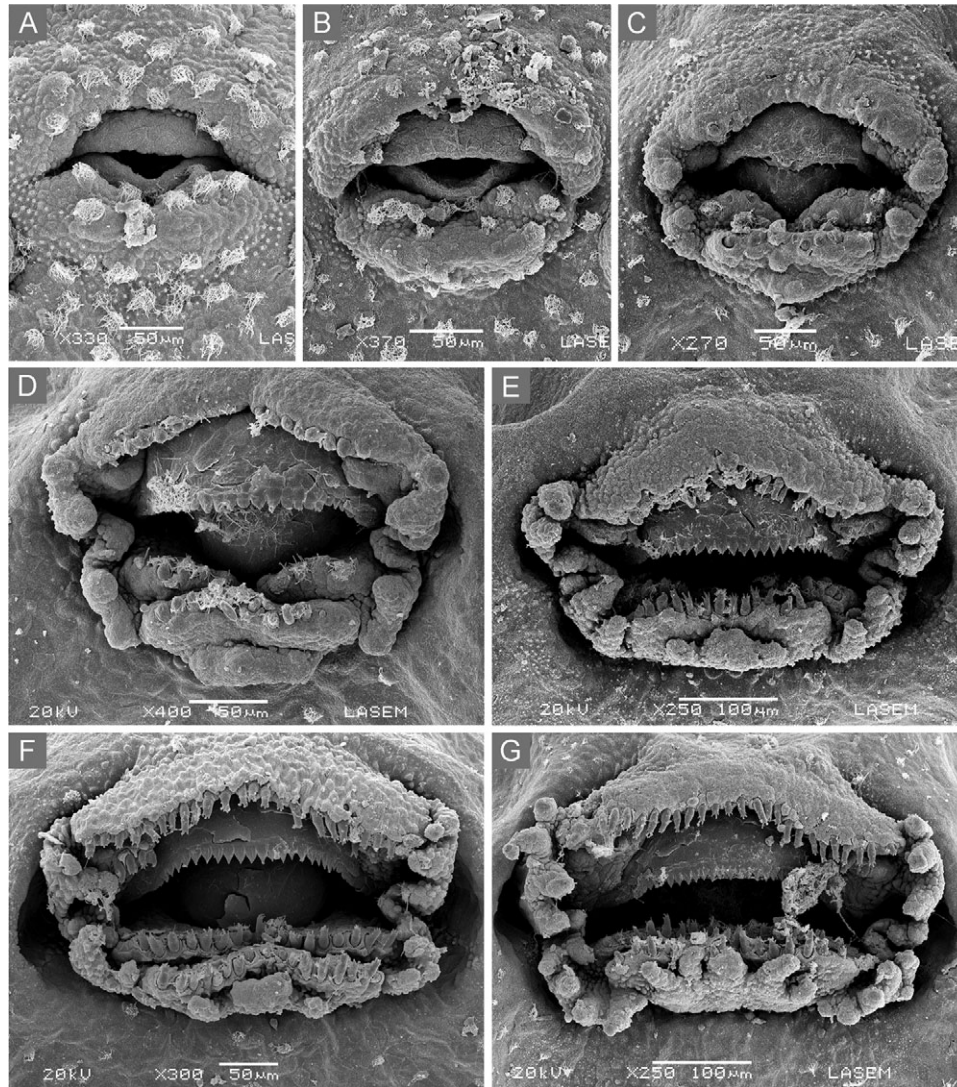
C4 and C5 (i.e. instead of differentiating labial teeth, papillae fill the ventral gap) is unknown.

Labial tooth row P3, which appears in tadpoles of several species of Leiuperidae (see supporting Table S1) may be short or long. A short row P3 develops in the ventromedial region of the disc in *Physalaemus cuqui*, *Ph. cuvieri*, *Ph. fernandezae*, *Ph. henselii*, and *Pseudopaludicola falcipes*, after this region is delimited by a pair of marginal papillae; for that reason it always coexists with a ventral gap of about the same length (Fig. 4). The long row P3 occurring in *Physalaemus gracilis* develops after completion of the marginal papillae and never coexists with a ventral gap (Fig. 4). In *Pleurodema*, row P3 of some species is about half the length of the other posterior rows (i.e. *Pl. bibroni*, *Pl. diplolister*, and *Pl. kriegi*; Kolenc *et al.*, 2009). Whether short or long, row P3 in this case always develops within the

tract of the marginal papillae that progress from the lateral portions of the disc margin, and thus it briefly coexists with a ventral gap of variable length that is usually completed later during development.

The developmental trajectories described help to explain some cases of intraspecific variation. For example, in *Physalaemus marmoratus* (Nomura, Rossa-Feres & Prado, 2003), *Ph. riograndensis* (Prigioni & García, 2002; Borteiro & Kolenc, 2007) and *Pseudopaludicola ternetzi* (Lobo, 1991; Pereira & Nascimento, 2004), oral configurations C1 and C2 were described; this can be interpreted as indicating that in some specimens oral ontogeny proceeds to a subsequent stage and the ventrolateral gaps fill with marginal papillae, as suggested by Borteiro & Kolenc (2007). This would also explain the oral configuration C5 mentioned by Cei (1980) for *Ps. falcipes*, although subsequent observations of several additional series





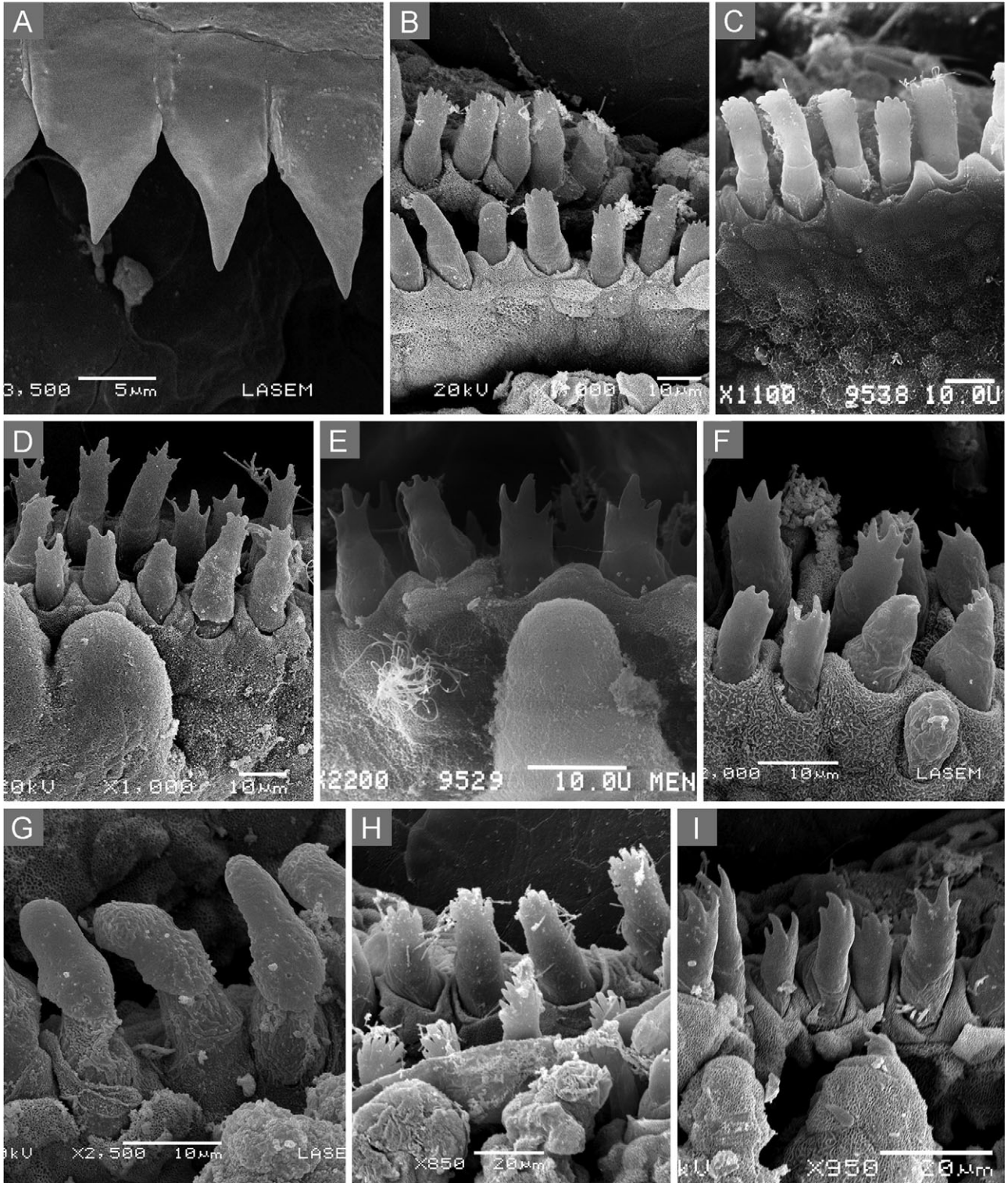
**Figure 13.** Oral ontogeny of *Pseudopaludicola falcipes* tadpoles: C4, a third labial tooth row develops in the ventromedial region, as a third tooth ridge (as in F) or alternatively, labial teeth develop on ventromedial papillae (as in G). A, stage 23. B, stage < 25. C, stage 25. D, stage > 25. E, stage 26. F, stage 26. G, stage 26.

of tadpoles did not find this pattern. In *Ph. centralis* (Rossa-Feres & Nomura, 2006; Giaretta & Facure, 2009) and *Ps. aff. canga* (Giaretta & Facure, 2009), oral configurations C1 and C4 were described; this may be because the ventromedial region of the marginal papillae differentiates as either papillae or labial teeth. The oral disc tissue is considered multipotent for papillae or labial tooth formation (e.g. Altig, 2006), and accessory tooth rows that occur in several species (Altig & McDiarmid, 1999) may develop from marginal papillae (Sánchez, 2010). A short ventral gap is described in specimens of *Pleurodema kriegi*, *Pl. bufoninum*, *Pl. thaul*, *Pl. marmoratum*, and *Somuncuria* (reviewed by Kolenc *et al.*, 2009), and this condition may be caused by

arrested development of the marginal papillae that was never completed in some of these tadpoles.

The observed variation in labial tooth morphology is consistent with the developmental schemes proposed. The species of *Pleurodema* with three lower labial tooth rows (C3) and the species of *Physalaemus* at the end of both ontogenetic trajectories (i.e. species with C3 and C5) have labial teeth with long, curved heads with numerous marginal cusps. Conversely, in the species of *Pleurodema* with only two lower labial tooth rows (C2), the remaining species of *Physalaemus*, and the single studied species of *Pseudopaludicola* (all with C1, C2, and C4), the less complex labial teeth have a short head and few distal cusps. An association between labial teeth with





**Figure 14.** Jaw sheaths and labial teeth of leiuiperid tadpoles. A, *Physalaemus santafecinus* upper jaw sheath at stage <25. B, *Ph. gracilis* labial teeth at stage 26. C, *Ph. henselii* labial teeth at stage 30. D, *Ph. riograndensis* labial teeth at stage 26. E, *Ph. cuvieri* labial teeth at stage 26. F, *Ph. santafecinus* labial teeth at stage 26. G, *Pleurodema cf. guayapae* labial teeth at stage 27. H, *Pl. bibroni* labial teeth at stage 26. I, *Pseudopaludicola falcipes* labial teeth at stage 26.



simpler morphology and fewer labial tooth rows has also been noted in several unrelated taxa (Vera Candiotti & Altig, 2010).

Heterochronic changes of developmental trajectories are likely common mechanisms of modification and diversity. In anuran tadpoles, a remarkable variation in timing and sequence of early events has been documented (Chipman *et al.*, 2000; Chipman, 2002), and with regard to the oral apparatus, there is some evidence suggesting that ontogenetic patterns of gains and losses of oral structures are mimicked in phylogeny (Altig, 2006). From the present study it is evident that different oral configurations in some leiuperid tadpoles can be obtained via either prolongation or truncation of overlapping developmental trajectories, resulting in pera- or paedomorphic oral discs. For instance, patterns C3 and C5 of *Physalaemus* are advanced stages of alternative developmental trajectories, and species with such morphologies reach their patterns via the C1, C2, and C4 configurations, respectively; in turn, these latter configurations are definitive stages of larvae of other species groups. Likewise, the configurations C2 and C3 of *Pleurodema* are part of a common ontogenetic trajectory that apparently becomes interrupted at different stages in the two species groups of the genus. The absence of a phylogenetic hypothesis including species with the various oral configurations exhibited in this genus does not allow for a proper analysis of the direction of the morphological change in oral disc arrangement, and hence interpretation of the heterochronic patterns involved. On the other hand, developmental trajectories of the oral apparatus may diverge early in embryonic stages of related taxa, in agreement with recent embryological studies at high taxonomic levels (Richardson *et al.*, 1997). Additionally, although the larval oral configurations in some leiuperids are similar, the developmental trajectories leading to them sometimes differ. The C3 pattern of *Physalaemus* is not achieved in the same way as the C3 pattern of *Pleurodema*. In other words, the oral configuration C3, which we refer to as 'the generalized oral apparatus', is the morphological outcome of at least two different pathways in this group. Also, the C2 of *Physalaemus* is not achieved in the same way as the C2 of *Pleurodema*, and the C4 of *Pseudopaludicola* may not develop exactly as the C4 of *Physalaemus*.

Variations in developmental trajectories may be discussed within a phylogenetic context. The available phylogenetic hypotheses involving the three genera studied herein differ in their topologies. *Pseudopaludicola*, first suggested to be related to *Physalaemus* (e.g. Cannatella & Duellman, 1984; Lynch, 1989), is recovered in the most recent hypotheses as the sister taxa of a clade including

*Pleurodema* and *Physalaemus* (e.g. Frost *et al.*, 2006; Grant *et al.*, 2006) or as sister taxa of *Leptodactylus*, with the Leiuperidae family being polyphyletic (Lourenço *et al.*, 2008). Further developmental studies and a more inclusive phylogeny will help to elucidate the nature of the resemblance between larval morphology and ontogeny of *Physalaemus* and *Pseudopaludicola* mentioned earlier. The remaining leiuperid genera have larvae with oral configuration C3 (see supporting Table S1), but whether this is obtained through a developmental sequence like that of *Physalaemus* or *Pleurodema* (i.e. with or without ventrolateral gaps) is still unknown. Outside the Leiuperidae, a configuration C3 is also the most frequent among anuran tadpoles (Altig & Johnston, 1989). In most of the species this is in fact achieved as in *Pleurodema* (e.g. Thibaudeau & Altig, 1988; Hall *et al.*, 1997; our personal observations). This is also the case with most bufonids (the basal family of Agastrophrynia, the sister group of Leiuperidae; Grant *et al.*, 2006); although the process is interrupted, marginal papillae never form medially and thus a ventral gap persists (e.g. Limbaugh & Volpe, 1957; Bonacci *et al.*, 2008; our personal observations). Nevertheless, the lack of further developmental studies and a comprehensive phylogeny of the Leiuperidae precludes making hypotheses whether this generalized C3 is the plesiomorphic configuration for the family.

Oral developmental patterns are also relevant to interpret relationships within Leiuperidae. Recently, Nascimento, Caramaschi & Cruz (2005) proposed taxonomic changes, including a rearrangement of the species groups of *Physalaemus* recognized by Lynch (1970). Their work has been deeply criticized (Funk *et al.*, 2007), and characters from several systems such as adult and larval morphology, cytogenetics, ecology, and biogeography suggest different relationships among species (e.g. Barrio, 1964a, 1965; Lobo, 1996; Alcalde, Natale & Cajade, 2006; Kolenc *et al.*, 2006; Borteiro & Kolenc, 2007; Tomatis *et al.*, 2009). Developmental patterns of the oral disc also contradict the species grouping by Nascimento *et al.* (2005). For example, in the *Ph. albifrons* group (supporting Table S1), *Ph. biligonigerus*, *Ph. santafecinus*, and probably also *Ph. marmoratus* share a developmental pathway that produces oral configuration C2 (Fig. 4). The larval oral disc of *Ph. albifrons* (Oliveira, Weber & Ruggeri, 2010) differs considerably from this configuration (*contra* the interpretation of the authors), and the oral disc is almost identical to that of the tadpoles of the *Ph. cuvieri* group (C4). On the other hand, *Ph. riograndensis* was considered a member of the *Ph. cuvieri* group (Lynch, 1970) and later reassigned to the *Ph. henselii* group (Nascimento *et al.*, 2005). The oral disc ontogeny of *Ph. riograndensis*

(C1) follows those of *Ph. biligonigerus* and *Ph. san- tafecinus*; neither the early development nor the definitive larval morphology of the oral apparatus of this species (Borteiro & Kolenc, 2007) supports its inclusion in the *Ph. henselii* group, otherwise characterized by configuration C5.

Within *Pleurodema*, some intrageneric relationships that were recognized on the basis of adult characters are supported by larval oral morphology and ontogeny, such that species with only two lower labial tooth rows are always grouped in phylogenetic hypothesis available (the *Pl. nebulosum* group, C2; Barrio, 1964b; Duellman & Veloso, 1977).

Knowledge of the diversity of the genus *Pseudopaludicola* has increased notably (e.g. Giarretta & Facure, 2009; Toledo, 2010; Toledo *et al.*, 2010) since the last phylogenetic hypothesis presented by Lobo (1995). The lack of ontogenetic studies in the vast majority of species and the variations in the oral discs of known taxa highlight the necessity of further comparative studies. The *Ps. falcipes* group (Lynch, 1989) includes species with at least three oral disc configurations. On the other hand, in the *Ps. pusilla* group the tadpoles of only two species have been described, and the oral disc in one of them, *Ps. boliviana*, is curiously quite different (the only leiuperid tadpole having a combination of two lower labial tooth rows and a ventral gap in the marginal papillae; Kehr & Schaefer, 2005; supporting Table S1).

Morphological features of larval anurans have been used for systematics studies (e.g. Haas, 2003). The present study of a group with controversial taxonomy like the Leiuperidae is a good example of the potentially informative variation underlying the oral disc development of tadpoles. Oral disc development in other unrelated taxa, especially genera that include species exhibiting similar variations, such as *Lithobates* (Ranidae; e.g. Moler, 1985), *Crinia*, *Geocrinia* (Myobatrachidae; e.g. Doughty, Anstis & Price, 2009; Anstis, 2010), and *Boophis* (Mantellidae; e.g. Randrianiaina *et al.*, 2009), requires detailed ontogenetic studies. The mechanisms of oral disc development, although conserved in several lineages, seem to be plastic enough to allow the occasional occurrence of developmental trajectories that are typical of other taxa (e.g. ventrolateral gaps form occasionally in *Hyla chrysoscelis*; Thibaudeau & Altig, 1988). Also, environmental factors such as temperature are known to influence the development of mouthparts (e.g. Bresler, 1954; Trubetskaya, 2006); a detailed understanding of how different temperatures and temperature variations affect the extent and timing of oral development is needed. These facts support the relevance of larval characters in taxonomic studies, and the mapping of them on phylogenetic analyses should be interpreted in the context of their developmental processes.

## ACKNOWLEDGEMENTS

We are indebted to D. Barrasso for providing the ontogenetic series of *Physalaemus fernandezae*. We thank CONICET, Instituto de Herpetología – Fundación Miguel Lillo, and the following funds: PICT 2007 01485 and PICT 2007 02202 (ANPCyT), PIP 1112008010 2422 (CONICET), CIUNT-G430 (UNT). C.B. and F.K. acknowledge Agencia Nacional de Investigación e Innovación (ANII). Finally, we also thank LASEM (UNSA) and LAMENOA (UNT) for their help with scanning electron microscopy.

## REFERENCES

- Agarwal SK, Niazi IA. 1980.** Development of the mouthparts in the tadpoles of *Rana tigrina* (Daud.). *Proceedings of the Indian Academy of Sciences* **89**: 127–131.
- Alcalde L, Natale GS, Cajade R. 2006.** The tadpole of *Physalaemus fernandezae* (Anura: Leptodactylidae). *Herpetological Journal* **16**: 203–211.
- Altig R. 2006.** Discussions of the origin and evolution of the oral apparatus of anuran tadpoles. *Acta Herpetologica* **2**: 95–105.
- Altig R. 2007.** A primer for the morphology of anuran tadpoles. *Herpetological Conservation and Biology* **2**: 71–74.
- Altig R, Johnston GF. 1989.** Guilds of anuran larvae: relationships among developmental modes, morphologies and habits. *Herpetological Monographs* **3**: 81–109.
- Altig R, McDiarmid RW. 1999.** Body plan: development and morphology. In: McDiarmid RW, Altig R, eds. *Tadpoles. The biology of anuran larvae*. Chicago, IL: University of Chicago Press, 24–51.
- Anstis M. 2010.** A comparative study of divergent embryonic and larval development in the Australian frog genus *Geocrinia* (Anura: Myobatrachidae). *Records of the Western Australian Museum* **25**: 399–440.
- Barrio A. 1964a.** Relaciones morfológicas, eto-ecológicas y zoogeográficas entre *Physalaemus henseli* (Peters) y *P. fernandezae* (Müller) (Anura, Leptodactylidae). *Acta Zoologica Lilloana* **20**: 284–305.
- Barrio A. 1964b.** Especies crípticas del género *Pleurodema* que conviven en una misma área, identificadas por el canto nupcial (Anura, Leptodactylidae). *Physis* **24**: 471–489.
- Barrio A. 1965.** El género *Physalaemus* (Anura, Leptodactylidae) en la Argentina. *Physis* **25**: 421–448.
- Bonacci A, Brunelli E, Sperone E, Tripepi S. 2008.** The oral apparatus of tadpoles of *Rana dalmatina*, *Bombina variegata*, *Bufo bufo*, and *Bufo viridis*. *Zoologischer Anzeiger* **247**: 47–54.
- Borteiro C, Kolenc F. 2007.** Redescription of the tadpoles of three species of frogs from Uruguay (Amphibia: Anura: Leiuperidae and Leptodactylidae), with notes on natural history. *Zootaxa* **1638**: 1–20.
- Bresler J. 1954.** The development of labial teeth in salientian larvae in relation to temperature. *Copeia* **1954**: 207–211.
- Cannatella DC, Duellman WE. 1984.** Leptodactylid frogs of the *Physalaemus pustulosus* group. *Copeia* **1984**: 902–921.



- Cei JM. 1980.** Amphibians of Argentina. *Monitore Zoologico Italiano, Monografia* **2**: 1–609.
- Chipman AD. 2002.** Variation, plasticity and modularity in anuran development. *Zoology* **105**: 97–104.
- Chipman AD, Haas A, Tchernov E, Khaner O. 2000.** Variation in anuran embryogenesis: differences in sequence and timing of early developmental events. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* **288**: 352–365.
- Cusimano-Carollo T. 1963.** Investigation on the ability of the neural folds to induce a mouth in the *Discoglossus pictus* embryo. *Acta Embryologiae et Morphologiae Experimentalis* **6**: 158–168.
- Cusimano-Carollo T. 1969.** Phenomena of induction by the transverse neural folds during the formation of the mouth in *Discoglossus pictus*. *Acta Embryologiae Experimentalis* **1969**: 97–110.
- Cusimano-Carollo T. 1972.** The mechanism of the formation of the larval mouth in *Discoglossus pictus*. *Acta Embryologiae Experimentalis* **1972**: 289–332.
- Cusimano-Carollo T, Fangone A, Reverbei G. 1962.** On the origin of the larval mouth in the anurans. *Acta Embryologiae et Morphologiae Experimentalis* **5**: 82–103.
- Donnelly MA, De Sá RO, Guyer C. 1990.** Description of the tadpoles of *Gastrophryne pictiventris* and *Nelsonophryne aterrima* (Anura: Microhylidae), with a review of morphological variation in free-swimming microhylid larvae. *American Museum Novitates* **2976**: 1–19.
- Doughty P, Anstis M, Price LC. 2009.** A new species of *Crinia* (Anura: Myobatrachidae) from the high rainfall zone of the northwest Kimberley, Western Australia. *Records of the Western Australian Museum* **25**: 127–144.
- Duellman WE, Veloso A. 1977.** Phylogeny of *Pleurodema* (Anura, Leptodactylidae). A biogeographic model. *Occasional Papers of the Museum of Natural History, University of Kansas* **64**: 1–46.
- Fiorito de López LE, Echeverría DD. 1984.** Morfogénesis de los dientes larvales y pico córneo de *Bufo arenarum* (Anura: Bufonidae). *Revista del Museo Argentino de Ciencias Naturales, Zoología* **13**: 573–578.
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, De Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC. 2006.** The amphibian tree of life. *Bulletin of the American Museum of Natural History* **297**: 1–370.
- Funk WC, Caldwell JP, Peden CE, Padial JM, De la Riva I, Cannatella DC. 2007.** Tests of biogeographic hypotheses for diversification in the Amazonian forest frog, *Physalaemus petersi*. *Molecular Phylogenetics and Evolution* **44**: 825–837.
- Giarretta AA, Facure KG. 2009.** Habitat, egg-laying behaviour, eggs and tadpoles of four sympatric species of *Pseudopaludicola* (Anura, Leiuperidae). *Journal of Natural History* **43**: 995–1009.
- Gosner KL. 1960.** A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**: 183–190.
- Grant T, Frost DR, Caldwell JP, Gagliardo R, Haddad CFB, Kok PJR, Means BD, Noonan BPSW, Wheeler WC. 2006.** Phylogenetic systematics of dart-poison frogs and their relatives (Anura: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History* **299**: 1–262.
- Haas A. 2003.** Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* **19**: 23–89.
- Hall JA, Larsen JH Jr, Fitzner RE. 1997.** Postembryonic ontogeny of the Spadefoot toad, *Scaphiopus intermontanus* (Anura: Pelobatidae): external morphology. *Herpetological Monographs* **11**: 124–178.
- Kehr AI, Schaefer EF. 2005.** Description of the tadpole of *Pseudopaludicola boliviana* (Anura: Leptodactylidae). *Herpetological Review* **36**: 250–252.
- Khan MS, Mufti SA. 1994.** Oral disc morphology of amphibian tadpole and its functional correlates. *Pakistan Journal of Zoology* **26**: 25–30.
- Kolenc F, Borteiro C, Baldo D, Ferraro DP, Prigioni CM. 2009.** The tadpoles and advertisement calls of *Pleurodema bibroni* Tschudi and *Pleurodema kriegi* (Müller), with notes on their geographic distribution and conservation status (Amphibia, Anura, Leiuperidae). *Zootaxa* **1969**: 1–35.
- Kolenc F, Borteiro C, Tedros M. 2003.** La larva de *Hyla uruguayana* Schmit, 1944 (Anura: Hylidae), con comentarios sobre su biología en Uruguay y su status taxonómico. *Cuadernos de Herpetología* **17**: 87–100.
- Kolenc F, Borteiro C, Tedros M, Núñez D, Maneyro R. 2006.** The tadpole of *Physalaemus henselii* (Peters) (Anura: Leiuperidae). *Zootaxa* **1360**: 41–50.
- Limbaugh BA, Volpe EP. 1957.** Early development of the Gulf Coast toad *Bufo valliceps* Wiegmann. *American Museum Novitates* **1842**: 1–32.
- Lobo F. 1991.** Descripción de la larva de *Pseudopaludicola mystacalis* (Anura: Leptodactylidae). *Boletín de la Asociación Herpetológica Argentina* **7**: 22–24.
- Lobo F. 1995.** Análisis filogenético del género *Pseudopaludicola*. *Cuadernos de Herpetología* **9**: 21–43.
- Lobo F. 1996.** Nuevas observaciones sobre la osteología del género *Physalaemus* (Anura, Leptodactylidae). *Acta Zoologica Lilloana* **43**: 317–326.
- Lourenço LB, Bacci-Júnior M, Martins VG, Recco-Pimentel SM, Haddad CFB. 2008.** Molecular phylogeny and karyotype differentiation in *Paratelmatobius* and *Scythrops* (Anura, Leptodactylidae). *Genetica* **132**: 255–266.
- Lynch JD. 1970.** Systematic status of the American leptodactylid frog genera *Engystomops*, *Eupemphix* and *Physalaemus*. *Copeia* **1970**: 488–496.
- Lynch JD. 1989.** A review of the leptodactylid frogs of the genus *Pseudopaludicola* in northern South America. *Copeia* **1989**: 577–588.
- Marinelli M, Tei S, Vagnetti D, Sensi P. 1985.** SEM observation on the development and the regression of the oral disc of *Bufo vulgaris* larva. *Acta Embryologiae et Morphologiae Experimentalis* **6**: 31–39.
- Marinelli M, Vagnetti D. 1988.** Morphology of the oral disc of *Bufo bufo* (Salientia: Bufonidae) tadpoles. *Journal of Morphology* **195**: 71–81.
- Moler PE. 1985.** A new species of frog (Ranidae: *Rana*) from northwestern Florida. *Copeia* **1985**: 379–385.

- Nascimento LB, Caramaschi U, Cruz CAG. 2005.** Taxonomic review of the species groups of the genus *Physalaemus* Fitzinger, 1826 with revalidation of the genera *Engystomops* Jiménez-de-la-Espada, 1872 and *Eupemphix* Steindachner, 1863 (Amphibia, Anura Leptodactylidae). *Arquivos do Museu Nacional, Rio de Janeiro* **63**: 297–320.
- Nodzinski E, Inger RF. 1990.** Uncoupling of related structural changes in metamorphosing torrent-dwelling tadpoles. *Copeia* **1990**: 1047–1054.
- Nomura F, Rossa-Feres DC, Prado VHM. 2003.** The tadpole of *Physalaemus fuscomaculatus* (Anura: Leptodactylidae), with a description of internal oral morphology. *Zootaxa* **370**: 1–8.
- Oliveira MIRR, Weber LN, Ruggeri J. 2010.** The tadpole of *Physalaemus albifrons* (Spix, 1824) (Anura, Leiuperidae). *South American Journal of Herpetology* **5**: 249–254.
- Pereira EG, Nascimento LB. 2004.** Descrição da vocalização e do girino de *Pseudopaludicola mineira* Lobo, 1994, com notas sobre morfologia de adultos (Amphibia, Anura, Leptodactylidae). *Arquivos do Museu Nacional, Rio de Janeiro* **62**: 233–240.
- Prigioni CM, García JE. 2002.** Descripción de la larva de *Physalaemus riograndensis* Milstead, 1960 (Anura: Leptodactylidae). *Acta Zoológica Platense* **5**: 1–5.
- Pyburn WF. 1967.** Breeding and larval development of the hylid frog *Phrynohyas spilomma* in southern Veracruz, Mexico. *Herpetologica* **23**: 184–194.
- Randrianiaina RD, Navarro Antúnez R, Canitz J, Forth F, Lemme I, Rodríguez B, Rinas H, Thänert R, Tröger P, Westphal N, Willim A, Wollenberg KC, Strauß A, Vences M. 2009.** Vogue or adaptive character? A tadpole's goatee helps to distinguish two cryptic treefrog species of the genus *Boophis*. *Herpetology Notes* **2**: 165–173.
- Richardson MK, Hanken J, Gooneratne ML, Pieau C, Raynaud A, Selwood L, Wright GM. 1997.** There is no highly conserved embryonic stage in the vertebrates: implications for current theories of evolution and development. *Anatomy and Embryology* **196**: 91–106.
- Rossa-Feres DC, Nomura F. 2006.** Characterization and taxonomic key for tadpoles (Amphibia, Anura) from the northwestern region of São Paulo State, Brazil. *Biota Neotropica* **6**: 1–26.
- Sánchez DA. 2010.** Larval development and synapomorphies for species groups of *Hyloscirtus* Peters, 1882 (Anura: Hylidae: Cophomantini). *Copeia* **2010**: 351–363.
- Sedra SN, Michael MI. 1961.** Normal table of the Egyptian toad, *Bufo regularis* Reuss, with an addendum on the standardization of the stages considered in previous publications. *Ceskoslovenska Morfologie* **9**: 333–351.
- Thibaudeau DG, Altig R. 1988.** Sequence of ontogenetic development and atrophy of the oral apparatus of six anuran tadpoles. *Journal of Morphology* **197**: 63–69.
- Toledo F. 2010.** Description of a new species of *Pseudopaludicola* Miranda-Ribeiro, 1926 from the state of São Paulo, southeastern Brazil (Anura, Leiuperidae). *Zootaxa* **2681**: 47–56.
- Toledo LF, Siqueira S, Duarte TC, Veiga-Menoncello ACP, Recco-Pimental SM, Haddad CFB. 2010.** Description of a new species of *Pseudopaludicola* Miranda-Ribeiro, 1926 from the state of São Paulo, southeastern Brazil (Anura, Leiuperidae). *Zootaxa* **2496**: 38–48.
- Tomatis C, Baldo D, Kolenc F, Borteiro C. 2009.** Chromosomal variation in the species of the *Physalaemus henselii* Group (Anura: Leiuperidae). *Journal of Herpetology* **43**: 555–560.
- Trubetskaya EA. 2006.** Anomalies of mouthparts in *Rana arvalis* Nilss tadpoles and ecological conditions providing for their emergence. *Russian Journal of Ecology* **37**: 193–199.
- Tubbs LOE, Stevens R, Wells M, Altig R. 1993.** Ontogeny of the oral apparatus of *Bufo americanus*. *Amphibia-Reptilia* **14**: 333–340.
- Vera Candiotti MF. 2007.** Anatomy of anuran tadpoles from lentic water bodies: systematic relevance and correlation with feeding habits. *Zootaxa* **1600**: 1–175.
- Vera Candiotti MF, Altig R. 2010.** A survey of shape variation in keratinized labial teeth of anuran larvae as related to phylogeny and ecology. *Biological Journal of the Linnean Society* **101**: 609–625.
- Wassersug RJ. 1976.** Oral morphology of anuran larvae: terminology and general description. *Occasional Papers of the Museum of Natural History, University of Kansas* **48**: 1–23.
- Wassersug RJ. 1980.** Internal oral features of larvae from eight anuran families. Functional, systematics, evolutionary and ecological considerations. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* **65**: 1–146.
- Zaracho VH, Céspedes JA, Álvarez BB. 2003.** Descripción de caracteres morfológicos en larvas prometamórficas de *Physalaemus biligonigerus* (Anura, Leptodactylidae). *Facena* **19**: 123–134.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Leiuperid tadpoles described (number of species described/total number of species), species groups, and oral disc configurations.

**Table S2.** Most relevant changes in morphological pattern during oral disc development in 12 species of Leiuperidae.

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