THE TADPOLE OF PHYSALAEMUS FERNANDEZAE (ANURA: LEPTODACTYLIDAE)

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This paper describes the external and buccopharyngeal morphology, chondrocranium and cranial muscles in tadpoles of Physalaemus fernandezae. The data are compared with those for other species of Physalaemus to improve the diagnosis of the “species group” within the genus. Species of the “P. biligonigerus” group have four infralabial papillae, two semicircular arches of pustulations in a V-shaped pattern on the prenarial arena, 6–8 conical papillae and 40–60 pustulations on the buccal roof arena, four postnarial papillae, a semicircular median ridge, claw-shaped lateral ridges and larval crista parotica with a poorly-developed anterior process. Species of the “P. pustulosus” group possess four infralabial papillae (shared with the P. biligonigerus group), tooth row formula 2(2)/3, four lingual papillae, two postnarial papillae, twelve conical papillae and 16–20 pustulations on the buccal roof arena, short lateral ridges with rough concave margins and larval crista parotica with a well-developed anterior process and reduced posterior process. Species of the “P. cuvieri” group present two infralabial papillae, three pustulations and two serrated papillae on the prenarial arena, five pustulations and two serrated papillae on the postnarial arena, four long and bifid papillae and more than 60 pustulations on the buccal roof arena, and lack larval crista parotica. In species of the “P. signiferus” group both medial and lateral mental gaps are absent, and the tooth row formula is 2(2)/3(1).

Key words: amphibian, larvae, frog, morphology, musculature

INTRODUCTION

The neotropical genus Physalaemus comprises a group of small toad-like leptodactylid frogs distributed from Mexico to northern Argentina (Frost, 2004). Following Lynch (1970), four species groups of Physalaemus are currently recognized: the P. cuvieri, P. biligonigerus, P. pustulosus and P. signiferus groups.

At present, anuran tadpole morphology is receiving increasing attention in phylogenetic analyses (Larson & de Sá, 1998; Faivovich, 2002; Haas, 2003). Of the 48 species of Physalaemus (Caramaschi et al., 2003; Cruz & Pimenta, 2004; Frost, 2004; Haddad & Sazima, 2004; Ron et al., 2004, 2005), the tadpoles of only 20 have been described (Nomura et al., 2003; Pimenta et al., 2005). The buccopharyngeal morphology, chondrocranium and cranial muscles of Physalaemus larvae remain poorly known (Larson & de Sá, 1998; Palavecino, 2000; Nomura et al., 2003).

Physalaemus fernandezae belongs to the “P. cuvieri” group and inhabits flooded grasslands in northeastern Argentina and southwestern Uruguay (Langone, 1994). Several studies have been carried out concerning the mating call, natural history and adult morphology of this species (Gallardo, 1963; Barrio, 1964, 1965; Lobo, 1992) but a detailed description of its tadpole is not available. Gallardo (1963), Barrio (1964), Cei (1980) and Langone (1994) give some information about total length and general aspects of the oral disc.

The aim of this paper is to describe the external and buccopharyngeal morphology, chondrocranium and cranial muscles of Physalaemus fernandezae tadpoles in the context of the other Physalaemus species. This information will be used to improve the diagnosis of the Physalaemus species group, which so far has been based only on adult characters.

MATERIALS AND METHODS

Between May and July 2001, we collected tadpoles of Physalaemus fernandezae at Punta Lara (Buenos Aires province, Argentina). Some of them (n=13) were fixed after capture in 10% buffered formalin and then staged using Gosner’s (1960) table. The material examined is deposited in the amphibian collection of the Museo de La Plata (MLP). The remaining tadpoles were reared until metamorphosis to corroborate the species identification. Seven tadpoles were employed for oral disc and external morphology descriptions (stages 32, 35, 36, 37 and 38, MLP 3333). Two stage 35 (MLP 3334) and three stage 40 (MLP 3335) specimens were stained following the technique of Taylor & Van Dyke (1985). The process was interrupted before clearing; tadpoles were dissected for observation of muscles and then cleared for chondrocranium description. One tadpole (stage 39) was dehydrated in a graded ethanol series (30%; three 15-minute baths; 50%; a week; 70%; three 15-minute baths; 100%; 15 minutes prior to the critical point) for scanning electronic microscope examination of the buccopharyngeal morphology and keratinized structures of the oral disc. The tadpole was sectioned according to Wassersug (1980) and critical point dried.
in carbon dioxide using amyl acetate as intermediate liq-
uid, mounted on a double-face Carbon tape and
sputter-coated with 400 Å thick gold-palladium using a
Model Ion Sputter Fine Coat JFC-1100 (Jeol System).
Photographs were taken using a Jsm-T100 scanning
electron microscope at 5-15 kV equipped with an Ilford
camera. The buccopharyngeal morphology of a stage 35
tadpole was also examined under a stereomicroscope.
Observations, measurements and drawings referring to
external morphology, chondrocranium and cranial mus-
cles were made under a Reichert Wien
stereomicroscope with measuring equipment (accurate
to the nearest 0.1 mm) and camera lucida.
Terminology follows D’Heursel & de Sá (1999) and
Haas (1995) for chondrocranium structures, Alcalde &
Rosset (2003) for chondrocranial measurements, Haas
(2001) for mandibular musculature, Haas & Richards
(1998) and Haas (2003) for branchial and hyoid muscu-
lature, Schlosser & Roth (1995) for muscular
innervation, Wassersug (1980) for buccopharyngeal
morphology, Van Dijk (1966) and Lavilla (1983) for
external morphology, Johnston & Altig (1986) for oral
disc morphology and Altig & Johnston (1989) for tad-
pole ecomorphological types.

RESULTS

EXTERNAL MORPHOLOGY

The following description is based on seven speci-
mens at developmental stages 32–38. External
morphology is illustrated in Fig. 1. Measurements are in
mm (arithmetic mean ± 95% confidence limits). Per-
centages were calculated based on the maximum and
minimum values of each variable.
Type IV, exotrophic, lentic and benthic tadpoles.
Size small, total length 26.84 mm (±1.92), body length
(8.73±0.84) one-third of total length; body shape oval,
body length 50–60% of body height (4.96±0.60), and
body width (5.23±0.32) 80–100% of body height, with-
out constrictions between head and trunk; snout
rounded in dorsal and lateral profile; eyes relatively

FIG. 1. External morphology of the tadpole of Physalaemus fernandezae at stage 38 (MLPA 3333). A) Lateral view; B) ventral view of the vent tube; C) oral disc. Scale bars=1 mm.

FIG. 2. Scanning electron microscope photographs of the keratodonts of the first mental row (A) and of the third left marginal papilla bearing small keratodonts (B) of Physalaemus fernandezae at stage 39. Scale bars 10 μm.
(5.86±0.26) 63–71% of body length. Vent tube length (2.08±0.75) 14–29% of body length; vent opening medial. Tail length (15.79±1.57) 59–63% of total length, tail height at the base of the tail (2.74±0.36) 55–56% of body height, caudal musculature width at the base of the tail 2.51±0.27; myotomes clearly visible, the posteriormost ones not reaching the end of the tail.

Oral disc sub-terminal, not visible dorsally; oral disc width 1.91±0.14, disc small, about 36–38% of maximum body width; disc with angular constrictions; an irregular double row of triangular and rounded marginal papillae in lateral regions; small mental gap present (0.43±0.11); with medium-sized rostral gap (1.16±0.08), about 61% of oral disc width; intramarginal papillae absent; tooth row formula 2(2)/3(1), rostroodonts well developed and keratinized, margins serrated (Fig. 1C); keratodonts spatulated and serrated (Fig. 2A). One specimen bears small keratodonts on the marginal papillae (Fig. 2B).

In life, dorsum and lateral body sides uniformly greyish, darker dorsally than laterally; ventral region grey, peribranchial zone paler than abdominal region, abdomen rich in guanophores producing silvery and golden sheens; fins scantily pigmented, transparent, and dotted with few irregular rows of melanophores; caudal musculature darker with melanophores arranged more densely than on fins. In preservative, creamy white tail with few isolated brown spots more abundant in the hypaxial musculature. Body darker than tail, dorsally dark-brown, ventrally pale brown. Intestinal mass visible through transparency.
**Buccopharyngeal morphology.** The buccal floor (Fig. 3A) possesses two short and rounded infralabial papillae (not visible in Fig. 3A), and one triangular lingual papilla. The buccal floor area has more than 60 pustulations and six large and serrated papillae (Fig. 3A). There are 12 short and conical papillae (sometimes serrated) and few pustulations on the prepocket arena. The ventral velum presents secretory pits.

The buccal roof (Fig. 3B) possesses two trifid infraorostral papillae (not visible in Fig. 3B). Prenarial arena with three pustulations and two long and trifid papillae. The postnarial arena presents three central pustulations and two lateral and serrated papillae placed anteriorly to the median ridge, and one small pustulation anterior to each lateral ridge. The well-developed median ridge is subcircular and serrated. The lateral ridges are rectangular and serrated. There are more than 60 central pustulations, and four long and bifid papillae on the buccal roof arena.

**Chondrocranium.** Neurocranium almost rectangular (width/length=0.86) and depressed (height/width=0.4), with greatest width at level of the arcus subocularis. Medial corpora of the cartilago suprarostralis connected by a distal bridge (Fig. 4D). Lateral partes alares and partes corpora joined by a proximal connection. Well-developed processus posterior dorssalis. Cornua trabeculae forming about 19% of chondrocranial length, uniformly wide, with well-developed processus lateralis. The cranion is roofed only between the capsula auditivae by the tectum synoticum. Lateral walls (cartilagines orbitales) formed by the pila ethmoidea (sensu de Beer, 1985), pila preoptica, pila metoptica and pila antotica (Fig. 4C). Basi cranii closed and pierced by the foramina carotica primaria and cranio-palatina (Fig. 4B). Capsulae auditivae subshperical representing about 38% of the chondrocranial length; dorsally coupled with the processus ascendens and lacking larval crista parotica. Medial walls of the capsula auditivae pierced by the acoustic and the endolimphatic foramina. No inferior perilimphatic foramen at the studied stages. Superior perilimphatic foramen opening in the posterior wall of the capsula auditiva, just in front of the jugular foramen. Operculum not chondrified.

Palatoquadrate with processus articularis quadrati, processus muscularis quadrati, commissura quadrocranialis anterior, processus quadro-ethmoidalis and processus ascendens, but lacking commissura quadro-orbitae, processus pseudoterygoideus and larval processus oticus. No lateral projections on the margins of the arcus subocularis, and processus ascendens joined to pila antotica by an intermediate union (Fig. 4C).

Lower jaw consisting of cartilago meckeli and cartilagines infraorostrales. Processus retroarticularis of cartilago meckeli short and articulating with processus articularis quadrati. Both processus ventromedialis and dorsomedialis of the cartilago meckeli articulating with the cartilagines infraorostrales by the sindesmotic commissura intramandibularis (Fig. 4B).

Copula I absent. All ceratohyale processes are well developed, except the very short processus anterolateralis hylais. Ceratohyalia medially joined by a rectangle-shaped pars reuniens. Copula II bearing a short processus urobranchialis. Ceratobranchiale I continuous with the hypobranchiale; the remaining ceratobranchiales sindesmotically joined to the hypobranchiale (Fig. 4E). Ceratobranchiales III and IV
TABLE 1. Origin and insertion of each mandibular and hyobranchial muscle on tadpoles of *Physalaemus fernandezae*.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
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<tr>
<td><strong>NERVUS TRIGEMINUS (CRANIAL NERVE V), MANDIBULAR MUSCULATURE</strong></td>
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<tr>
<td>Levator mandibulae internus</td>
<td>Processus ascendens</td>
<td>Cartilago meckeli</td>
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<tr>
<td>Levator mandibulae longus superficialis</td>
<td>Arcus subocularis</td>
<td>Cartilago meckeli</td>
</tr>
<tr>
<td>Levator mandibulae longus profundus</td>
<td>Arcus subocularis</td>
<td>Both muscles insert together in the pars alaris by a common tendon.</td>
</tr>
<tr>
<td>Levator mandibulae externus profundus</td>
<td>Processus muscularis quadrati</td>
<td>Pars alaris</td>
</tr>
<tr>
<td>Levator mandibulae externus superficialis</td>
<td>Processus muscularis quadrati</td>
<td>Cartilago meckeli</td>
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<tr>
<td>Levator mandibulae lateralis</td>
<td>Absent at the studied stages</td>
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<tr>
<td>Submentalis</td>
<td>Absent at the studied stages</td>
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<tr>
<td>Intermandibularis</td>
<td>Cartilago meckeli</td>
<td>Median raphe</td>
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<tr>
<td>Mandibulolabialis inferior</td>
<td>Cartilago meckeli</td>
<td>Oral disc</td>
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<tr>
<td>Mandibulolabialis superior</td>
<td>Absent</td>
<td></td>
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<tr>
<td><strong>NERVUS FACIALIS, (CRANIAL NERVE VII), HYOID MUSCULATURE</strong></td>
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<tr>
<td>Suspensoriohyoideus</td>
<td>Processus muscularis quadrati and arcus subocularis</td>
<td>Ceratohyale</td>
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<tr>
<td>Suspensorioangularis</td>
<td>Processus muscularis quadrati</td>
<td>Cartilago meckeli</td>
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<tr>
<td>Quadraangularis</td>
<td>Anterior and ventral on the palatoquadrate</td>
<td>Cartilago meckeli</td>
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<tr>
<td>Hyoangularis lateralis</td>
<td>Ceratohyale</td>
<td>Cartilago meckeli</td>
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<tr>
<td>Hyoangularis medialis</td>
<td>Absent</td>
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<tr>
<td>Interhyoideus</td>
<td>Ceratohyale</td>
<td>Median raphe</td>
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<tr>
<td>Interhyoideus posterior</td>
<td>These muscles were not found under dissections, but they may be observable in histological sections</td>
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<tr>
<td>Diaphragmatopraecordialis</td>
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<tr>
<td><strong>NERVUS GLOSSOPHARYNGEUS (CRANIAL NERVE IX), BRANCHIAL MUSCULATURE</strong></td>
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<tr>
<td>Levator arcuum branchialium I</td>
<td>Arcus subocularis</td>
<td>Commissura terminalis I</td>
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<tr>
<td>Subarcualis rectus I</td>
<td>The dorsal head on ceratobranchiale I</td>
<td>Ceratohyale</td>
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<td></td>
<td>The ventral heads on ceratobranchiales II and III</td>
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<tr>
<td>Constrictor branchialis I</td>
<td>Absent</td>
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<td><strong>NERVUS VAGUS (CRANIAL NERVE X), BRANCHIAL MUSCULATURE</strong></td>
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<tr>
<td>Constrictor branchialis II</td>
<td>Ceratobranchiale I</td>
<td>Commissura terminalis I</td>
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<tr>
<td>Constrictor branchialis III</td>
<td>Ceratobranchiale II</td>
<td>Commissura terminalis II</td>
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<tr>
<td>Constrictor branchialis IV</td>
<td>Ceratobranchiale III</td>
<td>Commissura terminalis III</td>
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<tr>
<td>Diaphragmatobranchialis</td>
<td>Peritoneal wall</td>
<td>Ceratobranchiale III</td>
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<tr>
<td>Levator arcuum branchialium II</td>
<td>Arcus subocularis</td>
<td>Commissura terminalis II</td>
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<tr>
<td>Levator arcuum branchialium III</td>
<td>Capsula auditiva</td>
<td>Commissura terminalis III</td>
</tr>
<tr>
<td>Levator arcuum branchialium IV</td>
<td>Capsula auditiva</td>
<td>Ceratobranchiale IV</td>
</tr>
<tr>
<td>Subarcualis obliquus II</td>
<td>Between ceratobranchiales II and III</td>
<td>Processus urobranchialis</td>
</tr>
<tr>
<td>Subarcualis rectus II-IV</td>
<td>Ceratobranchiale IV</td>
<td>Ceratobranchiale II</td>
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<tr>
<td>Tymanopaphryngeus</td>
<td>M. levator arcuum branchialium IV</td>
<td>Pericardium</td>
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<tr>
<td>Dilatator laryngis</td>
<td>Capsula auditiva</td>
<td>Larynx</td>
</tr>
<tr>
<td>Constrictor laryngis</td>
<td>Forms an annulus rounding the larynx</td>
<td></td>
</tr>
<tr>
<td>Transversus ventralis IV</td>
<td>Absent</td>
<td></td>
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<tr>
<td><strong>NERVUS HYPOGLOSSUS (SPINAL NERVE II), HIPOBRANCHIAL MUSCULATURE</strong></td>
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<tr>
<td>Geniohyoideus</td>
<td>Hypobranchiale</td>
<td>Cartilago infarostrale</td>
</tr>
<tr>
<td>Rectus cervicis</td>
<td>Peritoneal wall</td>
<td>Ceratobranchiales II and III</td>
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</table>
joined by a commissura proximalis. Processus branchiales not closed. All spiculae well developed.

**Ossifications.** The paraphenoid is the only bone present at the studied stages.

**Cranial muscles.** The cranial muscle pattern of Physalaemus fernandezae's tadpoles is shown in Figure 5. Table 1 provides details about the origin and insertion of each muscle. The ramus mandibularis of the nervus trigeminus runs laterally to all muscles levatorae mandibulae.

**DISCUSSION**

External tadpole morphology has been described for four species of the “Physalaemus biligonigerus” group: Physalaemus biligonigerus (Féandez & Féandez, 1921; Cei, 1980), P. fuscomaculatus (Nomura et al., 2003), P. nattereri (Vizzoto, 1967; Cei, 1980) and P. santafecinus (Perotti & Céspedes, 1999); nine of the “P. cuvieri” group: P. aguirrei (Pimenta & Cruz, 2004), P. albonotatus (Kehr et al., 2004), P. centralis (Rossa-Feres & Jim, 1993), P. cuqui (Perotti, 1997), P. cuvieri (Bokermann, 1962; Cei, 1980; Heyer et al., 1990), P. enesefae (Duellman, 1997), P. gracilis (Langone, 1989), P. henselii (Barrio, 1964; Cei, 1980) and P. riograndensis (Prigioni & Garcia, 2001); three of the “P. pustulosus” group: P. coloradorum (Cannatella & Duellman, 1984), P. peteri (Duellman, 1978) and P. pustulosus (Breden, 1946); and five of the “P. signiferus” group: P. atlanticus (Haddad & Saizima, 2004), P. bokermannii (Cardoso & Haddad, 1985), P. camacan (Pimenta et al., 2005), P. maculiventris (Bokermann, 1963) and P. spiniger (Haddad & Pombal, 1998). The tadpole of Physalaemus rupestris is also known but does not belong to any of the four species groups (Nascimento et al., 2001).

We compared these tadpoles’ descriptions with the tadpole of Physalaemus fernandezae in order to obtain a characterization of the known larvae of Physalaemus. In light of the present knowledge, Physalaemus larvae are small (total length=14.8–31.5 mm), possess medium-sized tail (43–68% of total length), ovoid body, rounded snout, dorsolateral eyes, dorsal fin higher than ventral fin and sub-terminal emarginated oral disc with rostral gap.

Some features of the larvae of Physalaemus, such as the vent tube opening, the mental gap, the marginal papillae row and the tooth row formula, are highly variable and do not exhibit unique states for each of the species groups proposed by Lynch (1970). The vent tube of most larvae is positioned medially, but its opening may be medial (P. atlanticus, P. bokermannii, P. camacan, P. fernandezae, P. rupestris, P. spiniger) or dextral (P. albonotatus, P. cuqui, P. fuscomaculatus, P. maculiventris, P. nattereri). The vent opening of P. centralis may be medial, dextral or sinistral within the same population. Previous authors have not made a clear difference between the position of the vent tube and the vent opening for other species. In them, the vent tube position (or the vent opening?) should be dextral (P. biligonigerus, P. cuvieri, P. gracilis, P. riograndensis, P. santafecinus) or sinistral (P. enesefae).

The marginal papillae is present as a single row in tadpoles of most species of Physalaemus (P. albonotatus, P. biligonigerus, P. bokermannii, P. centralis, P. cuqui, P. cuvieri, P. fuscomaculatus, P. maculiventris, P. nattereri, P. peteri, P. pustulosus, P. riograndensis, P. rupestris). In other species, the marginal papillae row may be ventrally double and laterally single (P. atlanticus, P. spiniger), completely double (P. gracilis), ventrally single and double at some areas of the lateral region (P. fernandezae), ventrally single and double at the infra-angular areas (the internal rows of P. fuscomaculatus and P. santafecinus were described as intramarginal papillae by Perotti & Céspedes, 1999, and Nomura et al., 2003), ventrally and laterally single but double or triple at the lateral folds (P. coloradorum), or laterally single but double or triple at mental region (P. camacan).

In anuran tadpoles, the marginal papillae row may be incomplete for lacking either the anterior (rostral gap) or posterior papillae (mental gap – here identified as medial mental gap). Some species of Physalaemus have two ventrolateral gaps on each side of the oral disc, here identified as lateral mental gaps. According to these types of mental gaps, larvae of Physalaemus may possess four oral disc configurations: (1) medial mental gap present and lateral mental gaps absent (P. fernandezae, P. henselii); (2) both medial and lateral mental gaps present (P. albonotatus, P. cuqui); (3) both mental gaps absent (P. atlanticus, P. biligonigerus, P. bokermannii, P. camacan, P. coloradorum, P. enesefae, P. gracilis, P. maculiventris, P. nattereri, P. peteri, P. pustulosus, P. riograndensis, P. rupestris, P. santafecinus, P. spiniger); and (4) only lateral mental gaps present (P. centralis). Physalaemus fuscomaculatus is unique in having configurations 3 and 4 within a single population. Contradictory information has been published about this character state for P. cuvieri. This species was described as possessing configurations 1 (Bokermann, 1962) and 4 (Heyer et al., 1990).

There are seven tooth row formulae in Physalaemus: 2(2)/3(1) (P. albonotatus, P. atlanticus, P. bokermannii, P. camacan, P. cuqui, P. fernandezae, P. gracilis, P. maculiventris, P. nattereri, P. spiniger); 2(2)/2(1) (P. fuscomaculatus, P. riograndensis, P. santafecinus); 2/3(1) (P. cuvieri, P. henselii); 2(1)/3 (P. enesefae); 2(2)/3 (P. coloradorum, P. peteri, P. pustulosus), or 2(2)/3(1-2) (P. rupestris). The tooth row formula 2(2)/3 is unique to the species assembled in the “P. pustulosus” species group.

The buccopharyngeal papillae has been described for Physalaemus biligonigerus, P. fuscomaculatus, P. nattereri, and P. santafecinus (“P. biligonigerus” group), P. peteri and P. pustulosus (“P. pustulosus” group) (Wassersug & Heyer, 1988; Spirandeli-Cruz,
“Species group” | Species | Lingual papillae | Prepocket papillae | Buccal floor arena |
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<tr>
<td>“Physalaemus biligonigerus” group</td>
<td><em>P. biligonigerus</em> (Perotti &amp; Céspedez, 1999)</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td><em>P. santafecinus</em> (Perotti &amp; Céspedez, 1999)</td>
<td>X</td>
<td>X</td>
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<tr>
<td></td>
<td><em>P. fuscomaculatus</em> (Nomura et al., 2003)</td>
<td>X</td>
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<td><em>P. nattereri</em> (Spirandeli-Cruz, 1991)</td>
<td>X</td>
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<tr>
<td>“P. pustulosus” group</td>
<td><em>P. petersi</em> (Wassersug &amp; Heyer, 1988)</td>
<td>data unknown</td>
<td>X</td>
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<td><em>P. pustulosus</em> (Wassersug &amp; Heyer, 1988)</td>
<td>X</td>
<td></td>
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<tr>
<td>“P. cuvieri” group</td>
<td><em>P. fernandezeae</em></td>
<td>X</td>
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The chondrocranium is known for *Physalaemus cuqui* (“P. cuvieri” group), *P. biligonigerus* (“P. biligonigerus” group), and *P. pustulosus* (“P. pustulosus” group) (Fabrezi & Vera, 1997; Larson & de Sá, 1998; Haas, 2003). Comparisons among these species and *P. fernandezeae* allow a preliminary recognition of the following chondrocranial patterns within the genus: (1) the larval crista parotica is absent (“P. cuvieri” group), represented by a poorly developed anterior process (“*P. biligonigerus*” group), or possesses a well developed anterior process and a very reduced posterior process (“*P. pustulosus*” group); (2) closed commissura quadrato-orbitalis (*P. biligonigerus, P. cuqui and P. pustulosus*), or open (*P. fernandezeae*); and (3) the processus anterolateralis hyalis of the ceratohyale may be reduced (*P. fernandezeae*) or well developed (*P. cuqui, P. biligonigerus*). Larson & de Sá (1998) did not report this character for *Physalaemus pustulosus*.

The larval cranial musculature has been described for *Physalaemus cuqui* (“P. cuvieri” group), *P. biligonigerus* (“P. biligonigerus” group) and *P. pustulosus* (“P. pustulosus” group) (Starrett, 1968; Palavecino, 2000; Haas, 2003). The only difference among these species is that the muscle levator mandibulae lateralis is absent at advanced developmental stages in *P. fernandezeae*, but it is present from stage 31 in the remaining species (Palavecino, 2000).

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