The tadpole of *Proceratophrys izecksohni* (Amphibia: Anura: Odontophrynidae)

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ABSTRACT. We describe the external morphology of the tadpole of *Proceratophrys izecksohni* Dias, Amaro, Carvalho-e-Silva & Rodrigues, 2013, its internal oral features, and chondrocranial anatomy, based on specimens collected at the type locality. The tadpole has short and oval body, spiracle with inner wall fused to the body, and oral formula 2/3(1). The oral cavity of *P. izecksohni* is typical of stream-dwelling tadpoles, with several papillae and pustulations. The chondrocranium is longer than wide and the suprarostal corpora are free ventromedially. The palatoquadrate has a well-developed processus pseudopterygoideus. We also compare the tadpole of *P. izecksohni* with tadpoles of other species of the genus, emphasizing the usage of larval morphology to assist in the systematic of the genus.

KEY WORDS. Chondrocranium; description; internal oral morphology; *Proceratophrys appendiculata* complex; systematics.


Species without palpebral appendages are assigned to the *Proceratophrys bigibbosa* and *P. cristiceps* species groups. Species of the *Proceratophrys cristiceps* group occur in open and dry environments of Cerrado and Caatinga. They are characterized by the absence of post-ocular swellings (Giaretta et al. 2000, Cruz et al. 2012, Godinho et al. 2013). The thirteen species included in the group are: *P. aridas* Cruz, Nunes & Juncã, 2012; *P. bagnoi*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. branti*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. caramaschii* Cruz, Nunes & Juncã, 2012; *P. carranca* Godinho, Moura, Lacerda & Feio, 2013; *P. concavitympanum* Giaretta, Bernarde & Kokubum, 2000; *P. cristiceps* (Müller, 1883); *P. cururu* Eterovick & Sazima, 1998; *P. dibernardoi*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. godaya* (Miranda-Ribeiro, 1937); *P. huntingtoni* Ávila, Pansonato & Strüssmann, 2012; *P. moratoi* (Jim & Caramaschi, 1980); *P. rotundipalpebra*, Martins & Giaretta, 2013; *P. strussmannae* Ávila, Kawashita-Ribeiro & Morais, 2011; and *P. vielliardi* Martins & Giaretta, 2011.

*Proceratophrys bigibbosa* group is found in southern and southeastern Brazil, Argentina, and Paraguay. The species in this group are characterized by a blunt and short snout, by the presence of a post-ocular swelling, and a large marginal row of tubercles on the eyelid (Kwet & Faivovich 2001). Currently four species are assigned to the group: *P. avelinoi* Mercadal de Barrio & Barrio, 1993; *P. bigibbosa* (Peters, 1872); *P. brauni* Kwet & Faivovich, 2001; and *P. palustris* Giaretta & Sazima, 1993.

Species with a long and single palpebral appendage are placed in the *Proceratophrys appendiculata* and *P. boiei* groups (Izecksohn et al. 1998, Prado & Pombal 2008, Cruz & Napoli 2010, Dias et al. 2013a). The species of the *P. boiei* group occur primarily in the Atlantic Forest, from Paraíba to Santa Catarina states (Prado & Pombal 2008); *P. boiei* (Wied-Neweuid, 1824); *P. pavioti* Cruz, Prado & Izecksohn, 2005; and *P. renalis* (Miranda-Ribeiro, 1920).

*Proceratophrys appendiculata* species group is found only in Atlantic Forest, from Bahia to Santa Catarina states (Izecksohn et al. 1998, Cruz & Napoli 2010, Dias et al. 2013a). The ten included species, listed below, are characterized by the presence of a triangular rostral appendage: *P. appendiculata* (Günther, 1873); *P. belzebul* Dias, Amaro, Carvalho-e-Silva & Rodrigues, 2013; *P. izecksohni* Dias, Amaro, Carvalho-e-Silva & Rodrigues, 2013; *P. laticeps* Izecksohn & Peixoto, 1981; *P. melanopogon* (Miranda-Ribeiro, 1926); *P. moehringi* Weygoldt & Peixoto, 1985; *P. phyllostomus* Izecksohn, Cruz & Peixoto, 1998; *P. sancturitae* Cruz & Napoli, 2010; *P. subguttata* Izecksohn, Cruz & Peixoto, 1998; and *P. tupinamba* Prado & Pombal, 2008.

In addition, *Proceratophrys schirchi* (Miranda-Ribeiro, 1937), *P. rondonae* Prado & Pombal, 2008 (which have a short single multi-cuspidate palpebral appendage) (Prado & Pombal...
2008, Napoli et al. 2011) and P. minuta Napoli, Cruz, Abreu & Del-Grande, 2011 and P. roducta Teixeira, Amaro, Recoder, Dal Vechio & Rodrigues, 2012 (which has a series of small appendages on the eyelid) are not associated with any species group.

The classification of Proceratophrys into species groups has been used due the morphological similarity among adults. In stipe of the practical utility of these groups, recent molecular analysis has not recovered them as monophyletic units (Amaro et al. 2009, Teixeira et al. 2012, Dias et al. 2013a).

Larval morphology and bioacoustic data have not been used in assessing evolutionary relationships within the genus (Dias et al. 2013b,c). Larval morphology, however, has been successfully used in taxonomic and phylogenetic studies (Larson & de Sá 1998, Maglia et al. 2001, Haas 2003, Pugnner et al. 2003, Grant et al. 2006, Candidoti 2008) and seems to be a very useful tool in the classification of Odontophrynidae frogs (Dias et al. 2013b, Nascimento et al. 2013). Nevertheless, the absence of data on larval morphology, especially on internal morphology, limits the use of such characters in broader analyses.

Within Proceratophrys, only 15 species have their tadpoles described (Fattorelli et al. 2010, Nascimento et al. 2010, Napoli et al. 2011, Provent et al. 2013). The internal oral morphology is known for eight species (Wassersug & Heyer 1988, de Sá & Langone 2002, Vieira et al. 2007, Nascimento et al. 2010, Provent et al. 2013), and chondrocranial data for five species (Dias et al. 2013b). Herein we provide a description of the tadpole of Proceratophrys izecksohni including the internal oral features and chondrocranial morphology.

Proceratophrys izecksohni is a small to medium sized species (SVL 32.1-54.1 mm in males) occurring in the southeastern portion of the state of Rio de Janeiro (Dias et al. 2013a). It can be found ca 200 m above sea level, at least in its type locality – Reserva Rio das Pedras, Mangaratiba municipality (Carvalho-e-Silva et al. 2008).

MATERIAL AND METHODS

Tadpoles were collected at the type locality Reserva Rio das Pedras, municipality of Mangaratiba, Rio de Janeiro state Brazil (22°59’29”S, 44°06’01”W, ca. 200 m above sea level). Voucher specimens are deposited in the Amphibians Collection of the Laboratório de Biossistemática de Anfíbios of Universidade Federal do Estado do Rio de Janeiro (UNIRIO). The tadpole illustration provided herein is based on a specimen on Gosner stage 33 (UNIRIO 4218). The internal oral morphology and bioacoustic data for five species (Dias et al. 2013a). The description of the chondrocranium was based on 19 tadpoles between Gosner stages 30-39 cleared and double stained following Dias et al. 2013b; illustration is based on a specimen on Gosner stage 33 (UNIRIO 4010-B). Chondrocranial terminology follows Larson & de Sá (1998) and Haas (2003).


RESULTS

Description of the tadpole (stage 35-36 n = 10) (Figs 1-9, Table I)

Tadpole with an oval body and a rounded snout (Figs 1-4); height of body representing 14.4% of the total length. The eyes are in a latero-dorsal position, separated by a distance approximately twice the eye’s diameter. The nostrils are reniform and positioned on the dorsal side, separated by approximately 1.5 times the diameter of an eye; eye diameter representing 15% of the body width and 7.2% of body length. Internarial distance about 74.2% of interorbital distance; eye to nostril distance corresponding to 33% of eye to snout distance; eye to snout distance corresponding to 20% of body length and 7.4% of total length. The lateral line system is not distinguished nor in living or fixed tadpoles.

The mouth is ventral and has a dermal fringe on its contour; presence of a single row of sub-marginal papillae on the lower labium, bearing two folds; keratinized denticles in two upper series and three lower series, with the first lower series being interrupted [2/3(1)]; A-1 = A-2, P-1 = P-2>P-3 (Fig. 5); upper jaw large than lower jaw; jaws serrated; upper jaw arch shaped and lower jaw “V” shaped. Oral disc width corresponding to 27.2% of body width.

Spiracle sinistrally, short, slightly prominent posterodorsal, inner wall fused to the body, and opercular opening slightly tilted upwards. The cloacal tube is short, with a wide opening turned toward the right side.

ZOOLOGIA 31 (2): 181–194, April, 2014
Tail muscles distinct ending in a rounded tip; the tail length represents 63.2% of the total length, with its height slightly greater than the height of the body (TH/BH 98.2%). Dorsal fin originates on the posterior third of the body. Maximum tail height (at its medial portion) representing 15.2% of total length; dorsal and ventral fins about the same height; they slightly decrease in height, ending in rounded tip.

Color in life. Dorsum of a light brown color (fawn color), covered with small darker brown spots, giving a granite-like appearance. A small brown spot is found between the eyes (amber color). The overall coloration of the lateral portion of the body is similar to that described for the dorsum. Ventral skin is translucent, with a brownish tone owing to the gut’s content. The iris has a golden color (clay color). At the end of the body there are two very clear small round spots (cream color). Two other small spots of the same color can be seen, one on the dorsum, parallel to the spots at the end of the body and another near the top of the tail fin (Figs 6-9). Light brown spots are also found. There is an overall silver coloration on the lateral side of the fins (pearl gray). The tail is pale with a pinkish color in muscles due to the circulatory system; it has four small dark brown stripes (hair brown).

Color of the tadpole in preservative. Translucent skin, central and tail areas of a pale yellow coloration (cream color), with small spaced spots of a dark brown tone (tawny).

**Internal oral morphology (Fig. 10-11)**

Buccal roof (BF). The buccal roof is triangular in shape. It is longer than wider; its width corresponding to 45% of the buccal roof length. The prenarial arena is trapezoidal in shape, possessing six to twelve pustulations; it also bears a reduced transverse triangular ridge. The internal nares are elliptical and placed transversally to the main axis, forming a 60° angle. There are four to five postnarial papillae on each side of the postnarial arena, oriented parallel to the nares; the narial velve is well

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Table I. Measurements of *Proceratophrys izecksohni* larvae. Measurements for the illustrated tadpole (UNIRIO 4010, stage 35) with mean ± standard deviation (SD) are provided below as well as the range among the tadpoles used in the description (n = 10, stages 35-36).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Drawn tadpole</th>
<th>Mean ± SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length</td>
<td>33.0</td>
<td>32.5 ± 1.3</td>
<td>(29.9-33.4)</td>
</tr>
<tr>
<td>Body length</td>
<td>13.0</td>
<td>11.7 ± 1.0</td>
<td>(10.4-13.5)</td>
</tr>
<tr>
<td>Tail length</td>
<td>20.2</td>
<td>20.5 ± 0.3</td>
<td>(20.2-21.0)</td>
</tr>
<tr>
<td>Body width</td>
<td>9.4</td>
<td>7.2 ± 1.5</td>
<td>(5.8-9.8)</td>
</tr>
<tr>
<td>Body height</td>
<td>6.5</td>
<td>4.6 ± 1.0</td>
<td>(3.4-6.6)</td>
</tr>
<tr>
<td>Tail height</td>
<td>5.3</td>
<td>4.9 ± 0.7</td>
<td>(4.1-6.1)</td>
</tr>
<tr>
<td>Nostril to snout distance</td>
<td>1.8</td>
<td>1.4 ± 0.2</td>
<td>(1.2-1.8)</td>
</tr>
<tr>
<td>Eye to snout distance</td>
<td>2.6</td>
<td>2.4 ± 0.3</td>
<td>(2.1-2.9)</td>
</tr>
<tr>
<td>Interorbital distance</td>
<td>2.5</td>
<td>2.3 ± 0.1</td>
<td>(2.2-2.6)</td>
</tr>
<tr>
<td>Eye to nostril distance</td>
<td>1.1</td>
<td>1.0 ± 0.08</td>
<td>(0.8-1.1)</td>
</tr>
<tr>
<td>Internarial distance</td>
<td>1.4</td>
<td>1.6 ± 0.1</td>
<td>(1.4-1.8)</td>
</tr>
<tr>
<td>Oral disc width</td>
<td>2.1</td>
<td>2.3 ± 0.1</td>
<td>(1.9-2.8)</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>1.0</td>
<td>1.09 ± 0.1</td>
<td>(0.9-1.2)</td>
</tr>
</tbody>
</table>
developed. The postnarial papillae are conical in shape and orientated toward the postnarial arena; the surface of each papillae is covered by pustulations. The postnarial arena is triangular in shape and has a thick lateral ridge papilla, which is divided into five conical projections covered by pustulations; the two most anterior projections are longer than the others. The median ridge is low and triangular, with six to nine short papillae around it. The buccal roof arena is an inverted “U”. It is laterally delimited by 14 to 18 approximately uniform conical papillae on each side, which face the center of the buccal roof arena. The buccal roof arena is densely covered with pustulations (over 300). Also, about 10-12 papillae are located on the posterior third of the postulation area of the buccal roof arena interspersed with the pustulations. Posteromedially, the buccal roof arena is delimitate by 10 to 13 conical papillae with varied sizes near the velum, which is smooth.

Buccal floor (BF). The buccal floor is ovoid in shape. It has four infralabial papillae, a medial pair and two lateral. The medial ones are hand-shaped, covered with pustulations, unequal in size. The lateral papillae are short and multi-branched, covered with pustulations. The lingual bud is elliptic and possesses two pairs of lingual papillae. The lingual papillae are parallel to infralabial papillae; they are hand-shaped, bifurcated, with pustulations on their surface. The buccal floor arena (BFA) is triangular, delimited by approximately 75 conical papillae; apices of papillae point to the center of buccal floor arena.

Figures 6-9. Living specimens of *Proceratophrys izecksohni*: (6) UNIRIO 4216 stage 25; (7) specimen in its natural habitat; (8) specimen raised in laboratory stage (45); (9) froglet UNIRIO 4218.
The buccal floor arena is also covered with pustulations (over 350). The buccal pockets are shallow. The ventral vellum presents irregular edge.

**Chondrocranial morphology (stage 33, UNIRIO 4010-B) (Figs 12-16)**

Until stage 33 the chondrocranium is entirely cartilaginous; by stage 34 the paraphenoid begins to ossify and at stage 35 the frontoparietals and the exoccipitals are visible. The chondrocranium is longer than wide; its greatest width (at the level of the palatoquadrate) is approximately 80% and its greatest height (at the level of the processus muscularis) is about 25% of its length.

**Neurocranium**

Ethmoidal region. The upper jaw sheets are supported by the paired suprarostral cartilages. The suprarostral (Fig. 15) consists of a central corpus and lateral alae. These elements are dorally fused. The corpora are free on its medial region; they are thin, sub rectangular shaped; in frontal view it shows a “V”. The lateral alae are wide, flattened, and rectangular in shape, with rounded ventral surface. Each ala curves posteriorly from its point of fusion with the corpora. The posterodorsal margin of each ala possesses a well-developed processus posterior dorsalis. The cornua trabeculare articulate with the suprarostral at the point of junction of the corpora and the alae.

The cornua trabeculare originate from the planum trabeculare anticum and represent 40% of the chondrocranium length. They diverge forming a “V” and are curved ventrally. They are uniform along their extension. The planum trabeculare anticum is continuous with the planum ethmoidale that forms the anterior wall of the braincase. At the point of confluence of the cornua trabeculare, the septum nasi is visible as a small strip of cartilage.

Orbitotemporal region. The fenestra basicranialis is closed by a thin sheet of cartilage, the planum intertrabeculare, which also closes the central area of the cranial floor. The chondrocranial floor is pierced by two pairs of foramina. The anterior, smaller pair is the foramina cranioptica, and the posterior, larger pair is the foramina carotica primaria.

The lateral walls of the braincase are formed by the orbital cartilages, which are posteriorly connected to the otic capsule. This connection forms the dorsal margin of the foramen prooticum, a large foramen located between the anterior edge of the otic capsule and the posterior margin of the orbital cartilage. Other two foramina are visible in the orbital cartilage: the foramen opticum and the foramen oculomotorium.

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Figures 12-16. Chondrocranium of *Proceratophrys izecksohni* (UNIRIO 4010), Gosner stage 33: (12) dorsal; (13) ventral; (14) lateral views; (15) suprarostral cartilage; (16) hyobranchial apparatus. (cb I-IV) Ceratobranchials I-IV, (ch) ceratohyal, (cq) commissura quadratoorbitalis, (cqa) commissura quadratocranialis anterior, (ct) cornua trabeculae, (fcp) foramen caroticum primarium, (fcrp) foramen craniopalatinum, (fo) foramen opticum, (fom) foramen oculomotorium, (fov) fenestra ovalis, (fpo) foramen prooticum, (hp) hyobranchial plate, (i) infrarostral cartilage, (mc) Meckel cartilage, (oc) otic capsule, (pah) processus anterior hyalis, (pal) processus anterolateralis hyalis, (paq) pars articularis quadrati, (pas) processus ascendens, (pm) processus muscularis, (pp) processus pseudopterygoideus, (pph) processus posterior hyalis, (pq) palatoquadrate, (pr) pars reuniens, (s) spicules, (sa) suprarostral alae, (sc) suprarostral corpus, (sn) septum nasi, (ts) tectum synoticum. Scale bars = 0.5 mm.
The frontoparietal fontanelle is large and ovoid in shape; its width represents 50% of its length. This fontanelle represents 50% of the chondrocranial length. Laterally, it is bordered by the taenia tecti marginales, anteriorly by the planum ethmoidale, and posteriorly by the tectum synoticum.

Otoocipital region. The otic capsules are rhomboid in shape and represent about 25% of the chondrocranial length. In dorsal view, it bears a distinct anterolateral triangular projection, the larval crista parotica. The tectum synoticum bridges the two otic capsules and forms the dorsal roof of the foramen magnum. Each arcus occipitalis is continuous with the tectum synoticum dorsally and with the planum basale ventrally, forming the foramen magnum and the foramen jugulare. The foramen perilymphaticum is found laterally to the foramen jugulare.

**Visceral components**

**Palatoquadrate.** In dorsal view the palatoquadrate is C shaped, wider in its medial region. Posteriorly it connects to the braincase through the processus ascenden, a thin rod-like cartilage. The processus ascenden attaches just posterior of the oculomotorium foramen (intermediate condition *sensu* Sorol 1981). The processus ascenden is almost perpendicular to the main axis of the chondrocranium, forming an angle of 90°.

Anteriorly the palatoquadrate connects to the commissura quadratocranialis anterior. The commissura quadratocranialis anterior extends between the palatoquadrate, at the level just posterior to the pars articularis quadrtati, and the floor of the neurocranium. The anterior margin of the commissura bears a triangular process, the processus quadratoethmoidalis. A triangular-shaped processus pseudopterygoideus is present on the posterior margin of the commissura quadratocranialis.

Each palatoquadrate bears two distinct processes: the processus muscularis quadrtati and the pars articularis quadrtati. The broad and flat processus muscularis quadrati extend dorsally from the lateral edges from the palatoquadrate at the level posterior to the pars articularis quadrati. The edges of the processus muscularis quadrati curves to attach the processus antorbitalis forming the commissura quadratoorbitalis.

Below the processus muscularis and ventrolaterally on the palatoquadrate there is a process, the facies articularis hyalis that serves as the point of articulation of the ceratohyal to the palatoquadrate. This feature is partially formed by the hyoquadrate process, a ventral enlargement of the palatoquadrate. The pars articularis quadrati, the anterior tip of the palatoquadrate, articulates with the posterior margins of the Meckel’s cartilage.

Meckel’s cartilage and cartilage labialis inferior. Together with the infrarostral cartilages, the Meckel’s cartilage forms the mandible. Meckel’s cartilage is sigmoid shaped and represents 20% of the chondrocranial length. It is wider on its posterior edge, narrowing towards the rostral portion. Meckel’s cartilage is oriented almost perpendicular to the main axis of the chondrocranium, positioned ventrally to the cornua trabeculae. Rostrally, it articulates to the cartilage labialis inferior and posteriorly with the pars articularis quadrati trough the processus retroarticularis.

The paired infrarostral cartilages provide support for the lower horny beak. They are almost rectangular. They are bounded by connective tissue, and slightly curved towards main chondrocranial axis, forming a ”V” shape structure in ventral view.

**Hyobranchial apparatus.** The ceratohyalia are wide, flat, and subtriangular shaped cartilages; they are dorsally twisted to articulate with the facies articularis of the palatoquadrate. Each ceratohyal bears two distinct processes: the processus anterior hyalis and the processus anterolateralis hyalis. Both processes are almost triangular in shape. Additionally, they possess a well-developed triangular processes posterior hyalis.

The ceratohyalia are bounded together by the pars reuniens, which bears a developed processus urobranchialis. The plana hypobranchiales are wide sheets of cartilage that serve as the point of attachment of the ceratohyals.

The branchial basket has four ceratobranchials that are distally continuous via the commissurae terminales. Proximally, ceratobranchial I attaches to the planum hypobranchiale by a wide strip of cartilage. Ceratobranchials I, II and III bear a dorsally projecting spiculum near their point of attachment to the planum hypobranchiale.

**Natural History.** Adults and tadpoles were found at least 200 m above sea level in a dense, undisturbed, forest. Tadpoles occur in moderately deep rocky stream with sandy bottom. This is also true of a closely related species *P. appendiculata* (Peixoto & Cruz 1980, Dias & Carvalho-e-Silva 2012). The tadpoles of *P. izecksohnii* are bentonic and cryptic with the sand (Fig. 7); at the first sign of disturbance of the water, the tadpoles swim down the rocks or bury in the debris. They were found together with tadpoles of *Hylodes asper* (Müller, 1924), *Hylodes phylloides* (Heyer & Cocroft, 1986), and *Phasmaphyla cruzi* Carvalho-e-Silva, Siva & Carvalho-e-Silva, 2009.

**Comparisons with other tadpoles**

Data for species in comparison are given in parenthesis; major morphological variation is summarized in the Tables II-IV.

External morphology. The tadpole of *Proceratophrys izecksohnii* can be promptly differentiated from tadpoles of the following groups by having the second row of denticles without interruption (second row of denticles interrupted in the species enumerated below): *P. bigibbosa* [P. avelinoi (de Sá & Langone 2002), *P. palistris* (Giaretta & Sazima 1993)], *P. cristiceps* groups (*P. concavitympanum* (Giaretta et al. 2000), *P. cristiceps* (Veiga et al. 2007), *P. cururu* (Etievicz & Sazima 1998), *P. moratoi* (Rossa-Feres & Jim 1996]) and *P. boiei* (*P. izecksohnii* et al. 1979), *P. renalis* (Nascimento et al. 2010)], as well as of *P. laticeps* (*Peixoto et al. 1981), *P. melanopogon* (Provete et al. 2013), *P. moehringi* (Weygoldt & Peixoto 1985), *P. schirchi* (*Peixoto et al. 1984) and *P. minuta* (Napoli et al. 2011). *Proceratophrys izecksohnii* tadpoles also differ from the tadpoles of *P. boiei*, *P. concavitympanum*, *P. cristiceps*, *P. cururu*, *P.
Table II. Variation of the described tadpoles of *Proceratophrys* (measurements in millimeters). (DL) Developmental stage (Gosner 1960), (n) number of examined specimens, (TL) total length, (BL) body length, (TAL) tail length, (BW) body width, (BH) body height, (TH) tail height, (NSD) nostril to snout distance, (ESD) eye to snout distance, (IOD) interorbital distance, (END) eye to nostril distance, (IND) internarial distance, (ODW) oral disc width, (ED) eye diameter.

| Species          | DL (n) | TL   | BL   | TAL  | BW   | BH   | TH   | NSD  | ESD  | IOD  | IND  | END  | ED   | ODW  | Reference                  |
|------------------|--------|------|------|------|------|------|------|------|------|------|------|------|------|-----------------------------|
| *P. appendiculata* | 35-36 (n = 12) | 32.70 | 13.10 | 21.10 | 7.80 | 6.10 | 6.00 | 1.60 | 3.00 | 2.30 | 1.65 | 1.00 | 1.10 | 2.10 | This study                  |
| *P. avelinoi*    | 36 (n = 4) | 32.60 | 12.20 | –     | 7.90 | 6.50 | –    | 1.10 | –    | 2.60 | 1.60 | 1.10 | 1.10 | 2.20 | DE SA & LANGONE (2002)      |
| *P. boiei*       | 34 (n = 7) | 31.00 | 12.00 | –     | 8.00 | 6.00 | –    | –    | –    | –    | –    | –    | 1.00 | –              | IKECKSOHN et al. (1979)    |
| *P. concavitypanum* | 36 (n = 2) | 50.10 | 16.90 | 30.60 | 12.00 | 9.80 | 9.50 | –    | 4.60 | 2.10 | 2.10 | –    | 2.10 | 9.00 | GIARETTA et al. (2000)      |
| *P. cristiceps*  | 39 (n = 20) | 30.31 | 12.45 | 19.44 | 7.15 | 5.51 | 6.10 | –    | 1.94 | 1.91 | 1.09 | 0.99 | 1.89 | 2.58 | VIEIRA et al. (2007)        |
| *P. cururu*      | 38 (n = 2) | 39.50 | –     | –     | –    | –    | –    | –    | –    | –    | –    | –    | –    | –              | ETEROVICK & SAZIMA (1998) |
| *P. izecksohni*  | 35-36 (n = 10) | 32.50 | 11.70 | 20.50 | 7.20 | 4.60 | 4.90 | –    | 2.40 | 2.30 | 1.60 | –    | 1.00 | –              | IKECKSOHN et al. (1979)    |
| *P. laticeps*    | 36 (n = ?) | 31.00 | 11.00 | –     | 7.00 | 5.00 | –    | –    | 2.50 | 1.50 | 1.50 | –    | 1.00 | –              | PEIXOTO et al. (1981)      |
| *P. melanopogon* | 34 (n = 2) | 27.63 | 12.71 | 14.92 | 8.91 | 6.80 | 7.30 | 1.34 | 2.93 | 2.19 | 1.66 | –    | 1.13 | 2.95 | PREVEE et al. (2013)        |
| *P. minuta*      | 36 (n = 2) | 35.70 | 14.30 | 21.40 | 10.00 | 7.00 | 7.50 | 2.90 | 4.00 | 4.00 | 1.70 | 1.10 | 1.30 | 3.30 | NAPO et al. (2011)          |
| *P. moehringi*   | 29 (n = 7) | 23.60 | 8.50  | –     | 4.60 | 4.00 | 3.00 | –    | 2.00 | 1.00 | 1.10 | –    | –    | –              | WEGOLDT & PEIXOTO (1985)   |
| *P. moratoi*     | 37 (n = 9) | 31.70 | 13.30 | 18.30 | 7.40 | 6.80 | 7.30 | 1.34 | 2.93 | 2.19 | 1.66 | –    | 1.13 | 2.95 | NASCIMENTO et al. (2010)    |
| *P. palustris*   | 35 (n = 5) | 33.00 | 13.30 | 19.70 | 9.00 | 6.90 | 6.50 | 1.80 | –    | 2.80 | 1.60 | 1.00 | 1.40 | 2.90 | NASCIMENTO et al. (2010)    |
| *P. renalis*     | 34 (n = 7) | 31.00 | 11.70 | –     | 8.00 | 6.30 | –    | –    | 3.20 | –    | –    | –    | 1.20 | –              | PEIXOTO et al. (1984)      |
| *P. schirchi*    | 25-28 (n = 8) | 22.70 | 8.30  | 16.80 | 4.30 | 4.30 | 3.50 | 0.90 | 1.70 | 2.30 | 1.30 | 0.60 | 0.60 | 1.80 | FATORELLI et al. (2010)     |

Table III. Morphological variation of *Proceratophrys* species. Characteristics followed by an * were inferred from the illustrations, which can be found in correspondent reference. The # refers to observations of NASCIMENTO et al. (2010) for *P. boiei* from Camanducaia, Minas Gerais state, Brazil.

<table>
<thead>
<tr>
<th>Species/Structure</th>
<th>Nostril shape</th>
<th>Spiracle</th>
<th>Origin of dorsal fin</th>
<th>Tip of the tail</th>
<th>Labium emargination</th>
<th>Oral formula</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. appendiculata</em></td>
<td>reniform</td>
<td>fused to the body</td>
<td>posterior third of the body</td>
<td>rounded</td>
<td>two folds</td>
<td>2/3(1)</td>
<td>Present study</td>
</tr>
<tr>
<td><em>P. avelinoi</em></td>
<td>rounded</td>
<td>–</td>
<td>junction body/tail</td>
<td>rounded</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>DE SA &amp; LANGONE (2002)</td>
</tr>
<tr>
<td><em>P. boiei</em></td>
<td>reniform</td>
<td>free#</td>
<td>posterior third of the body</td>
<td>rounded</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>IKECKSOHN et al. (1979)</td>
</tr>
<tr>
<td><em>P. concavitypanum</em></td>
<td>rounded</td>
<td>free*</td>
<td>posterior third of the body</td>
<td>acute</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>GIARETTA et al. (2000)</td>
</tr>
<tr>
<td><em>P. cristiceps</em></td>
<td>rounded</td>
<td>fused to the body</td>
<td>posterior third of the body</td>
<td>rounded</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>VIEIRA et al. (2007)</td>
</tr>
<tr>
<td><em>P. cururu</em></td>
<td>–</td>
<td>–</td>
<td>posterior third of the body</td>
<td>acute*</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>ETEROVICK &amp; SAZIMA (1998)</td>
</tr>
<tr>
<td><em>P. izecksohni</em></td>
<td>reniform</td>
<td>fused to the body</td>
<td>posterior third of the body</td>
<td>rounded</td>
<td>two folds</td>
<td>2/3(1)</td>
<td>Present study</td>
</tr>
<tr>
<td><em>P. laticeps</em></td>
<td>reniform</td>
<td>–</td>
<td>posterior third of the body</td>
<td>acute</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>PEIXOTO et al. (1981)</td>
</tr>
<tr>
<td><em>P. melanopogon</em></td>
<td>oval</td>
<td>free</td>
<td>posterior third of the body</td>
<td>rounded</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>PREVEE et al. (2013)</td>
</tr>
<tr>
<td><em>P. minuta</em></td>
<td>reniform</td>
<td>free</td>
<td>junction body/tail</td>
<td>rounded</td>
<td>none</td>
<td>2(2)/3(1)</td>
<td>NAPO et al. (2011)</td>
</tr>
<tr>
<td><em>P. moehringi</em></td>
<td>rounded</td>
<td>–</td>
<td>junction body/tail</td>
<td>rounded</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>WEGOLDT &amp; PEIXOTO (1985)</td>
</tr>
<tr>
<td><em>P. moratoi</em></td>
<td>rounded</td>
<td>fused to the body</td>
<td>junction body/tail</td>
<td>acute</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>ROSSA-FERES &amp; JM (1996)</td>
</tr>
<tr>
<td><em>P. palustris</em></td>
<td>reniform</td>
<td>free</td>
<td>posterior third of the body</td>
<td>acute</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>GIARETTA &amp; SAZIMA (1993)</td>
</tr>
<tr>
<td><em>P. renalis</em></td>
<td>reniform</td>
<td>–</td>
<td>posterior third of the body</td>
<td>acute</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>NASCIMENTO et al. (2010)</td>
</tr>
<tr>
<td><em>P. schirchi</em></td>
<td>reniform</td>
<td>fused to the body*</td>
<td>posterior third of the body</td>
<td>acute</td>
<td>two folds</td>
<td>2(2)/3(1)</td>
<td>PEIXOTO et al. (1984)</td>
</tr>
<tr>
<td><em>P. tupinamba</em></td>
<td>rounded</td>
<td>fused to the body</td>
<td>junction body/tail</td>
<td>acute</td>
<td>two folds</td>
<td>2/3(1)</td>
<td>FATORELLI et al. (2010)</td>
</tr>
</tbody>
</table>
Table IV. Major variation on internal oral features of *Proceratophrys* larvae. Buccal floor (BF); buccal floor arena (BFA), buccal roof (BR), buccal roof arena (BRA), infralabial papillae (IL), lingual papillae (LP), postnarial arena (PONA). Characteristics followed by an * were inferred from the illustrations, which can be found in correspondent reference.

<table>
<thead>
<tr>
<th>Species</th>
<th>BR shape</th>
<th>PONA papillae</th>
<th>BRA shape</th>
<th>BRA papillae</th>
<th>BRA pustulations</th>
<th>BF shape</th>
<th>IL papillae</th>
<th>LP papillae</th>
<th>BFA shape</th>
<th>BFA papillae</th>
<th>BFA pustulations</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. appendiculata</em></td>
<td>triangular</td>
<td>5 to 10</td>
<td>inverted U</td>
<td>30-36</td>
<td>230</td>
<td>ovoid</td>
<td>4</td>
<td>4</td>
<td>triangular</td>
<td>30-50</td>
<td>270-320</td>
<td>Present study</td>
</tr>
<tr>
<td><em>P. cururu</em></td>
<td>hexagonal</td>
<td>12</td>
<td>elliptical</td>
<td>28</td>
<td>80-90</td>
<td>elipsoid</td>
<td>2</td>
<td>4</td>
<td>hexagonal</td>
<td>50</td>
<td>40</td>
<td>PROVETE et al. (2013)</td>
</tr>
<tr>
<td><em>P. izecksohni</em></td>
<td>triangular</td>
<td>4</td>
<td>to 10</td>
<td>14 to 18</td>
<td>about 360</td>
<td>ovoid</td>
<td>4</td>
<td>4</td>
<td>triangular</td>
<td>75</td>
<td>about 370</td>
<td>Present study</td>
</tr>
<tr>
<td><em>P. melanopogon</em></td>
<td>trapezoid</td>
<td>10 to 12</td>
<td>quadrate</td>
<td>14 to 30</td>
<td>100-200</td>
<td>triangular</td>
<td>4</td>
<td>5</td>
<td>rounded</td>
<td>50</td>
<td>180</td>
<td>PROVETE et al. (2013)</td>
</tr>
<tr>
<td><em>P. moratoi</em></td>
<td>rectangular</td>
<td>6</td>
<td>rounded</td>
<td>15</td>
<td>40-50</td>
<td>triangular</td>
<td>2</td>
<td>4</td>
<td>diamond</td>
<td>40-50</td>
<td>50</td>
<td>PROVETE et al. (2013)</td>
</tr>
</tbody>
</table>

The tadpole of *Proceratophrys izecksohni* is a putative synapomorphy for this clade. The evolutionary transition of the oral formula 2(2)/3(1) to 2/3 is a potential synapomorphy that remained unknown before. However, adult morphology, advertisement call, and breeding behavior support this relationship with the appendiculata clade (Das et al. 2013a).
izecksohni and 50 papillae in P. boiei), the presence of 4-5 papillae in the prenarial arena (a single papilla) and by the inverted U buccal roof arena (U-shaped).

*Proceratophrys izecksohni* tadpoles differs from those of *P. cristiceps* (Viria et al. 2007) by the ovoid buccal floor (circular), by having four lingual papillae (three), by the larger number of papillae in the buccal floor arena (about 75 papillae in *P. izecksohni* and 28-34 papillae in *P. cristiceps*), by the presence of papillae on the posterior part of postnatal area of the buccal floor arena (30-40 papillae homogeneously spread in the buccal floor arena), by the larger number of papillae in the median ridge (6-9 in *P. izecksohni* and 4-5 in *P. cristiceps*), and by presenting about 10-12 papillae located on the posterior part of the postnatal area of the buccal roof arena (20-30 papillae well distributed on the postnatal area of buccal roof in *P. cristiceps*).

*Proceratophrys izecksohni* larvae differ from those of *P. renalis* (Nascimento et al. 2010) by two pairs of infralabial papillae (single pair), two pairs of lingual papillae (three pairs), an overall triangular buccal roof (circular), by the presence of pustulations on the postnatal area (pustulations absent), “U” shaped buccal roof area (circular), triangular buccal floor area (“U” shaped), larger number of papillae surrounding the buccal floor area, i.e., approximately 75 (42-46), posterior part of buccal floor area only with papillae (papillae spread within postnatal buccal floor).

*Proceratophrys izecksohni* tadpoles differ from those of *P. avelinii* (de Sá & Langone 2002) by triangular buccal roof (semi-circular), triangular buccal floor area (“U” shaped), and by the 8-10 postnatal papillae (5-6).

Larvae of *Proceratophrys izecksohni* differ from those of *P. cururu* (Provête et al. 2013) by the triangular buccal roof (hexagonal), by the angle of the nares (60° in *P. izecksohni* and 45° in *P. cururu*), by the U-shaped buccal roof (elliptical), by the smaller number of buccal roof area papillae (14-18 in *P. izecksohni* and 28 in *P. cururu*), by a greater number of pustulations in the buccal roof area (360 in *P. izecksohni* and 80-90 in *P. cururu*), by the ovoid buccal floor shape (ellipsoid), by having four infralabial papillae (two), by the triangular shaped buccal floor area (hexagonal), by the absence of papillae in the center of the buccal floor area (10 present), by the greater number of buccal floor area papillae (75 in *P. izecksohni* and 50 in *P. cururu*) and by the greater number of pustulations in the buccal floor area (370 in *P. izecksohni* and 40 in *P. cururu*).

It differs from the tadpoles of *P. moratoi* (Provête et al. 2013) by the triangular buccal roof (rectangular), by the larger number of pustulations in the prenarial arena (6-12 in *P. izecksohni* and 3 in *P. moratoi*), by the angle of the nares (60° in *P. izecksohni* and 30° in *P. moratoi*), by the larger number of postnatal papillae (8-10 in *P. izecksohni* and 6 in *P. moratoi*), by the smaller number of lateral ridge (a single papilla in *P. izecksohni* and two rows of papillae in *P. moratoi*), by the inverted U buccal roof area (rounded), by the larger number of pustulations in buccal roof (360 in *P. izecksohni* and 40-50 in *P. moratoi*), by the ovoid buccal floor (triangular), by the triangular buccal floor area (diamond shaped), by the larger number of buccal floor papillae (75 in *P. izecksohni* and 40-50 in *P. moratoi*), and by the larger number of pustulations in the buccal floor area (about 370 in *P. izecksohni* and 50 in *P. moratoi*).

The tadpoles of *Proceratophrys izecksohni* can be distinguished from those of *P. melanopogon* (Provête et al. 2013) by the shape of the buccal roof (triangular in *P. izecksohni* and trapezoid in *P. melanopogon*), by the larger number of pustulations in the prenarial arena (6-12 in *P. izecksohni* and two in *P. melanopogon*), by the ovoid buccal floor (triangular), by having four lingual papillae (five), by triangular buccal floor area (rounded), by the larger number of papillae in the buccal floor area (75 in *P. izecksohni* and 50 in *P. melanopogon*), and by the larger number of pustulations in the buccal floor area (about 370 in *P. izecksohni* and 180 in *P. melanopogon*).

The internal oral morphology of the tadpoles of *P. izecksohni* seems very similar to that of *P. appendiculata*. We found as the major distinction between them the larger number of papillae delimiting the buccal floor area (75 in *P. izecksohni* and 30-50 in *P. appendiculata*), the smaller number of papillae in the buccal roof area (14-18 in *P. izecksohni* and 30-36 in *P. appendiculata*), the larger number of pustulations in the buccal roof area (360 in *P. izecksohni* and 230 in *P. appendiculata*) and in the buccal floor area (370 in *P. izecksohni* and 270-320 in *P. appendiculata*). Our observations for *P. appendiculata* differ in some points from that made by Wasserburg & Heyer (1988); this is probably due to the sample size – Wasserburg & Heyer (1988) observed only one specimen also collected in Teresópolis municipality, Rio de Janeiro state, while in this work nine specimens were analyzed.

Chondrocranium morphology. The tadpoles of *P. izecksohni* differs from those of *P. appendiculata*, *P. cristiceps*, *P. laticeps*, *P. tupinamba* and *P. boiei* from Rio de Janeiro state (Dias et al. 2013b) by the morphology of the suprarosstral cartilage. The central elements – the corpora – are not fused ventromedi ally (fused in those species). The tadpole of *P. izecksohni* also differs from those of *P. boiei* from Minas Gerais state by not presenting either the taenia tecti transversals or mediales (present), and by not ventrally free superosstral corpus from the alae joined ventrally (joined); from the tadpoles of *P. boiei* from Paraná state by the morphology of the ventral surface of the hypobranchial plate (smooth in *P. izecksohni* and acute in *P. boiei*).

The tadpoles of *Proceratophrys izecksohni* also differ from the tadpoles of *P. cristiceps* by a thinner palatoquadrate (broader), by a less developed processus muscularis (robust), by a broader ethmoidal region (reduced), by a longer cornua trabeculae (reduced) and by the morphology of the supra rostral cartilages, which has the corpora and alae almost completely fused in *P. cristiceps* and are fused just dorsally in *P. izecksohni*.

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DISCUSSION

Proceratophrys tadpoles – taxonomy, phylogeny, and perspectives

Previous studies have suggested that the tadpoles of Proceratophrys possess a highly conserved morphology. For instance, de Sá & Langone (2002) enumerated the following set of external characteristics as representative for the genus: 1) oval body; 2) low caudal fins; 3) ventral mouth; 4) sinistral spiracle with midlateral opening; 5) dextral vent tube’s opening; 6) labial tooth row formula 2(2)/3(1) or 2/3(1); 7) oral disk emarginated and with two folds of the posterior labium; 8) single row of marginal papillae with a large rostral gap; and 9) serrated, keratinized jaw sheaths.

The internal oral morphology also seems to be conserved, with several papillae and pustulations in the buccal roof and floor arenas, hand-like lateral ridge papillae. Wassersug & Hély (1988) – classified Proceratophrys within other stream-dwelling species – classification corroborated by other studies (de Sá & Langone 2002, Vieira et al. 2007, Nascimento et al. 2010, Provete et al. 2013, present study). The morphology of the chondrocranium also proved to be very conservative, at least within species that possess a long and unique palpebral appendage (Dias et al. 2013b).

Several other morphological traits (e.g., tail tips, nostril shape, folds on the lower labium) vary considerably among the known tadpoles (Provete et al. 2013). The absence of data for more than 50% of the species limits our understanding of the variation in this genus. Moreover, several characteristics reported as variable have been constantly inferred from rudimentary descriptions (Izemann et al. 1979, Peixoto et al. 1984, Weygoldt & Peixoto 1985) or from illustrations (some illustrations are particularly questionable). Sanchez (2013), analyzing tadpoles from Dendrobatoidea Cope, pointed out that coding data from illustrations can be problematic, once the interpretations of the illustrator might not be congruent with the actual morphology of the animal, as well as the interpretation of the reader.

Another problem is that the distribution of some morphological traits among tadpoles are not consistent with available phylogenies (Amaro et al. 2009, Prado & Pombal 2008) and by the peculiar morphology of the frontoparietal bones, which extends toward the esquamous and perspectives like bony plates (Izemann et al. 2005).

The second step is the standardization of the terminology from the observed morphological features and a survey of internal morphological data. Including the results of the present study, the internal oral morphology is known from only nine species (Table IV), chondrocranium for only six species (Dias et al. 2013b, present study), and the myology is completely unknown – in other words, our knowledge of the internal aspects of these animals is restricted to less than 30% of the species of the genus.

Proceratophrys appendiculata complex vs P. appendiculata clade

Izemann et al. (1998) defined a species complex within Proceratophrys in which all members presented a single, long, unicuspitate palpebral appendage, and a rostral fleshy appendage. They included the following species in this complex: Proceratophrys appendiculata, P. laticeps, P. melanopogon, P. moehringi, P. phyllostomus, and P. subguttata. Subsequently, P. tupinamba, P. sanctaritae, and P. belzebul were added to it.

Although supported by the overall adult morphology, molecular data indicates that the P. appendiculata complex is not monophyletic. In the phylogenies referred to below, P. laticeps is frequently recovered as the sister species of the clade P. cururu – P. renalis (Amaro et al. 2009, Teixeira et al. 2012); or all species are inserted in a broad clade composed of P. cururu, P. renalis, P. moratoi, P. concavitympanum, P. boiei and P. goyana (Dias et al. 2013a). Prado & Pombal (2011), however, argued that P. laticeps is sister to the clade P. renalis – P. boiei. The other species (from which tissue sample is available) form a well supported clade composed of P. izecksohni, P. tupinamba, P. appendiculata and P. belzebul; the sister group of this clade is composed by several evolutionary lineages associated with P. melanopogon (Dias et al. 2013a). The phylogenetic position of P. moehringi, P. phyllostomus, P. subguttata and P. sanctaritae was never accessed.

The larval morphology provides support for a P. appendiculata clade, composed of P. izecksohni, P. tupinamba and P. appendiculata and P. belzebul. The oral formula 2/3(1) is known from all those species (with exception of P. belzebul, whose tadpoles are unknown). It might represent a putative synapomorphy for this clade (Fig. 17). The internal oral morphology and the morphology of the chondrocranium of P. appendiculata and P. izecksohni (Dias et al. 2013b, present study) reinforce the close relationships between them.

The chondrocranium morphology of P. laticeps resembles that of P. appendiculata and P. izecksohni (Dias et al. 2013b; this study), but the external morphological features of the tadpoles, such as tail tips and the oral formula do not fit with that clade. This is expected, once the adult of P. laticeps differs from P. izecksohni, P. tupinamba, P. appendiculata and P. belzebul by the absence of a peculiar cutaneous crest (Izemann et al. 1998, Prado & Pombal 2008) and by the peculiar morphology of the frontoparietal bones, which extends toward the esquamosal like bony plates (Izemann et al. 2005).
Adults of *P. moehringi* are extremely similar to those of *P. izecksohni*, *P. tupinamba*, *P. appendixculata*, and *P. belzebul* (IZECKSOHN et al. 1998, PRADO & POMBAL 2008, DIAS et al. 2013a). Moreover, the advertisement call of *P. moehringi* is more similar to that of *P. appendixculata* – even more than that of *P. melanopogon* – and both species share several behavioral traits, such as calling from under large rocks and during all day (WEYGOLDT & PEIXOTO 1985, DIAS et al. 2013c). However, the oral formula of *P. moehringi* tadpole is 2(2)/3(1) and specimens present a rounded nostril.

The internal morphology of the tadpole of *P. moehringi* is unknown. Furthermore, this species is sympatric with several other *Proceratophrys* species, such as *P. boiei*, *P. laticeps*, *P. paviotii*, and *P. schirchi* (PRADO & POMBAL 2008), some of which are morphologically similar to *P. moehringi*. The tadpole described by WEYGOLDT & PEIXOTO (1985) might not correspond to this species.

The corroboration of the existence of a monophyletic *P. appendixculata* clade might be attested with the survey of new data, specifically with the descriptions of the tadpoles of *P. phyllostomus*, *P. subguttata*, and *P. sanctariae* and tissues from DNA analysis. New samples of tadpoles of *P. moehringi* are necessary.

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