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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 suprarostral corpora are free ventromedially. The palatoquadrate has a well developed processus pseudopterygoideus. We also compare the tadpole of *P. izecksohni* with tadpoles those 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.

The Neotropical genus *Proceratophrys* Miranda-Ribeiro, 1920 currently consist of 36 species distributed in Brazil, Argentina, and Paraguay (Frost 2014). The species of *Proceratophrys* have been clustered in species groups or complexes based on overall morphological similarity (Lynch 1971, Izecksohn *et al*. 1998, Giaretta *et al*. 2000, Kwet & Faivovich 2001, Prado & Pombal 2008).

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. aridus* Cruz, Nunes & Juncá, 2012; *P. bagnoi*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. branti*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. caramaschii* Cruz, Nunes & Juncá, 2012; *P. carranca* Godinho, Moura, Lacerda & Feio, 2013; *P. concavitympanum* Giareta, Bernarde & Kokubum, 2000; *P. cristiceps* (Müller, 1883); *P. cururu* Eterovick & Sazima, 1998; *P. dibernardoi*, Brandão, Caramaschi, Vaz-Lima & Campos, 2013; *P. goyana* (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-Neuwied, 1824); *P. paviotii* 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. sanctaritae* 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. redacta* 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 bioacustic 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, Hass 2003, Púgener *et al.* 2003, Grant *et al.* 2006, Candioti 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 (Fatorelli *et al.* 2010, Nascimento *et al.* 2010, Napoli *et al.* 2011, Provete *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, Provete *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 sate 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 (1960) stage 36, deposited with the catalog number UNIRIO 4010.

The following dimensions of ten tadpoles (stages 35-36) were measured according to Altig & McDiamird (1999) and Altig (2007): total length (TL), body length (BL), tail length (TAL), body width (BW), body height (BH), tail height (TH), nostril to snout distance (NSD), eye to snout distance (ESD), interorbital distance (IOD), eye to nostril distance (END), internarial distance (IND), oral disc width (ODW) and eye diameter (ED). Colors patterns are standardized according with Smithe's (1975) catalog. Developmental stages were determined following Gosner's (1960) staging table. Some individuals were raised through metamorphosis to confirm species identifications (UNIRIO 4218). *Proceratophrys izecksohni* is not sympatric with any other *Proceratophrys* species in Mangaratiba municipality.

For analysis of the internal oral morphology, six tadpoles (Gosner 34-35) were dissected according with Wassersug (1976) and the oral features were stained with methylene blue solution. Terminology follows Wassersug (1976, 1980) and Wassersug & Heyer (1988). We also analyzed the internal oral features of eight tadpoles (Gosner stages 35-36) of a close related species, *P. appendiculata*, collected in its type locality, Serra dos Órgãos (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).

Material examined (given in lots). *Proceratophrys izecksohni*. Brazil, *Rio de Janeiro*: Mangaratiba (Reserva Rio das Pedras), UNIRIO 368, 4010, 4203, 4216. *Proceratophrys appendiculata*. Brazil, *Rio de Janeiro*: Teresópolis (Parque Nacional da Serra dos Órgãos), UNIRIO 2676, 3592, 3852, 4027, 4030, 4036.

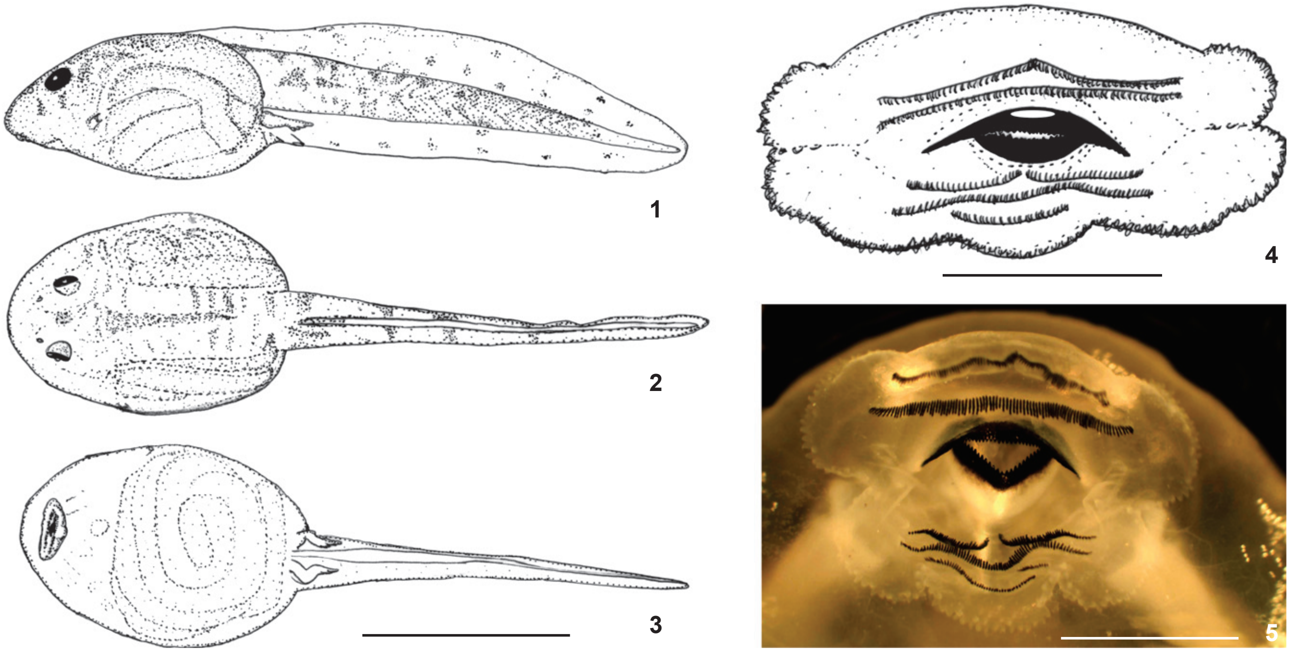
RESULTS

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; keratizned 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 sinistral, 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.



Figures 1-5. Tadpole of *Proceratophrys izecksohni*, UNIRIO 4010, stage 36: (1) dorsal; (2) lateral; (3) ventral views; (4) oral disc morphology; (5) detail of the oral disc – oral formula 2/3(1). Scale bars: 1-3 = 10.0 mm, 4-5 = 1.0 mm.

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).

	Drawn tadpole	Mean ± SD	Range
Total length	33.0	32.5 ± 1.3	(29.9-33.4)
Body length	13.0	11.7 ± 1.0	(10.4-13.5)
Tail length	20.2	20.5 ± 0.3	(20.2-21.0)
Body width	9.4	7.2 ± 1.5	(5.8-9.8)
Body height	6.5	4.6 ± 1.0	(3.4-6.6)
Tail height	5.3	4.9 ± 0.7	(41-6.1)
Nostril to snout distance	1.8	1.4 ± 0.2	(1.2-1.8)
Eye to snout distance	2.6	2.4 ± 0.3	(2.1-2.9)
Interorbital distance	2.5	2.3 ± 0.1	(2.2-2.6)
Eye to nostril distance	1.1	1.0 ± 0.08	(0.8-1.1)
Internarial distance	1.4	1.6 ± 0.1	(1.4-1.8)
Oral disc width	2.1	2.3 ± 0.1	(1.9-2.8)
Eye diameter	1.0	1.09 ± 0.1	(0.9-1.2)

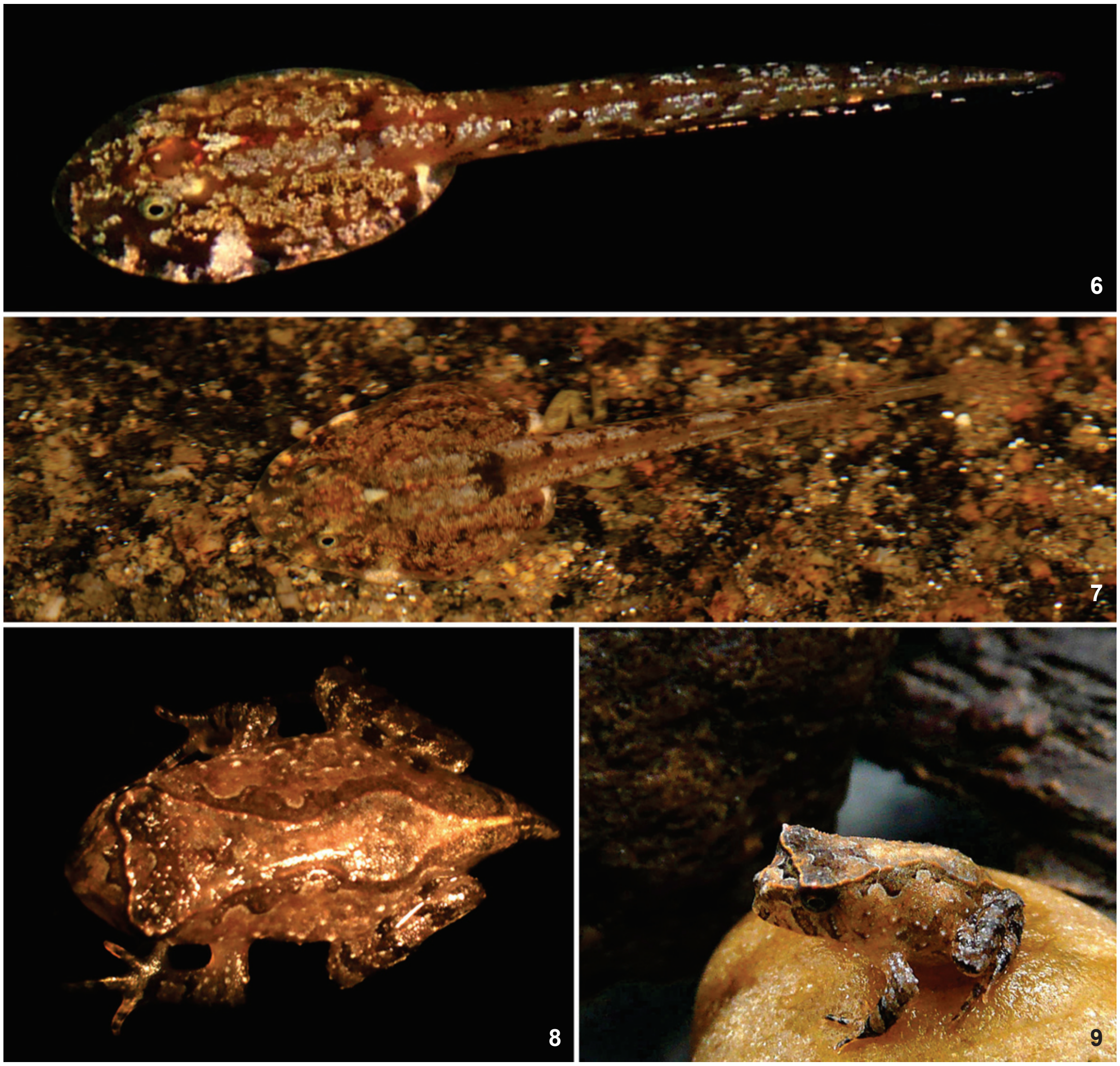
Tail muscles distinct ending in a rounded tip; the tail length represents 63.2% of the total length, with its height slightly greater than the height of the body (TH/BH 98.2%). Dorsal fin originates on the posterior third of the body. Maximum tail height (at its medial portion) representing 15.2% of 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)

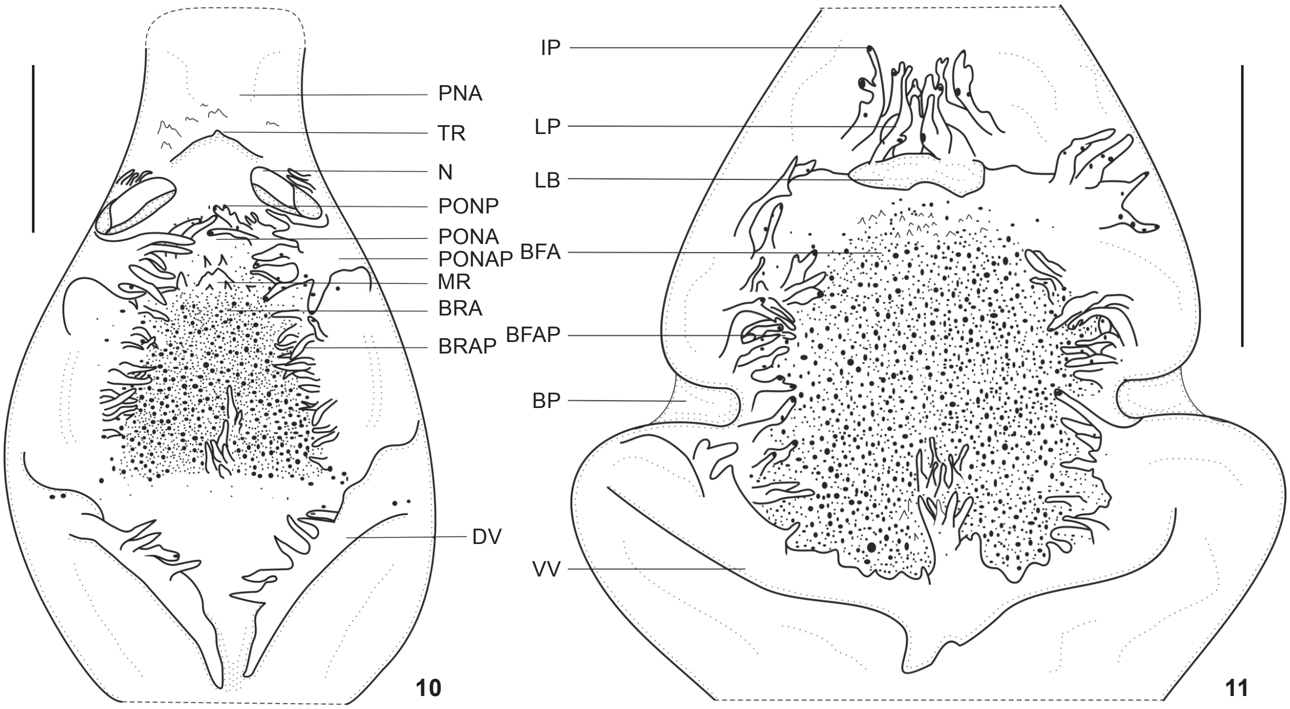
Buccal roof (BF). The buccal roof is triangular in shape. It is longer than wider; its width corresponding to 45% of the buccal roof length. The prenarial arena is trapezoidal in shape, possessing six to twelve pustulations; it also bears a reduced transverse triangular ridge. The internal nares are 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



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.

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 delimitated 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 vellum, 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 posses 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, delimitated by approximately 75 conical papillae; apices of papillae point to the center of buccal floor arena.



Figures 10-11. Internal oral features of *Proceratophrys izecksohni*: (10) buccal roof; (11) buccal floor. (BFA) Buccal floor arena, (BFAP) buccal floor arena papillae, (BP) buccal pocket, (BRA) buccal roof arena, (BRAP) buccal roof arena papillae, (DV) dorsal vellum, (IP) infralabial papillae, (LB) lingual bud, (LP) lingual papillae, (MR) median ridge, (N) nare, (PNA) prenarial arena, (PONA) postnarial arena, (PONAP) postnarial arena papillae, (PONP) postnarial papillae, (TR) transverse ridge, (VV) ventral vellum. Scale bars = 1.5 mm.

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 parasphenoid 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.

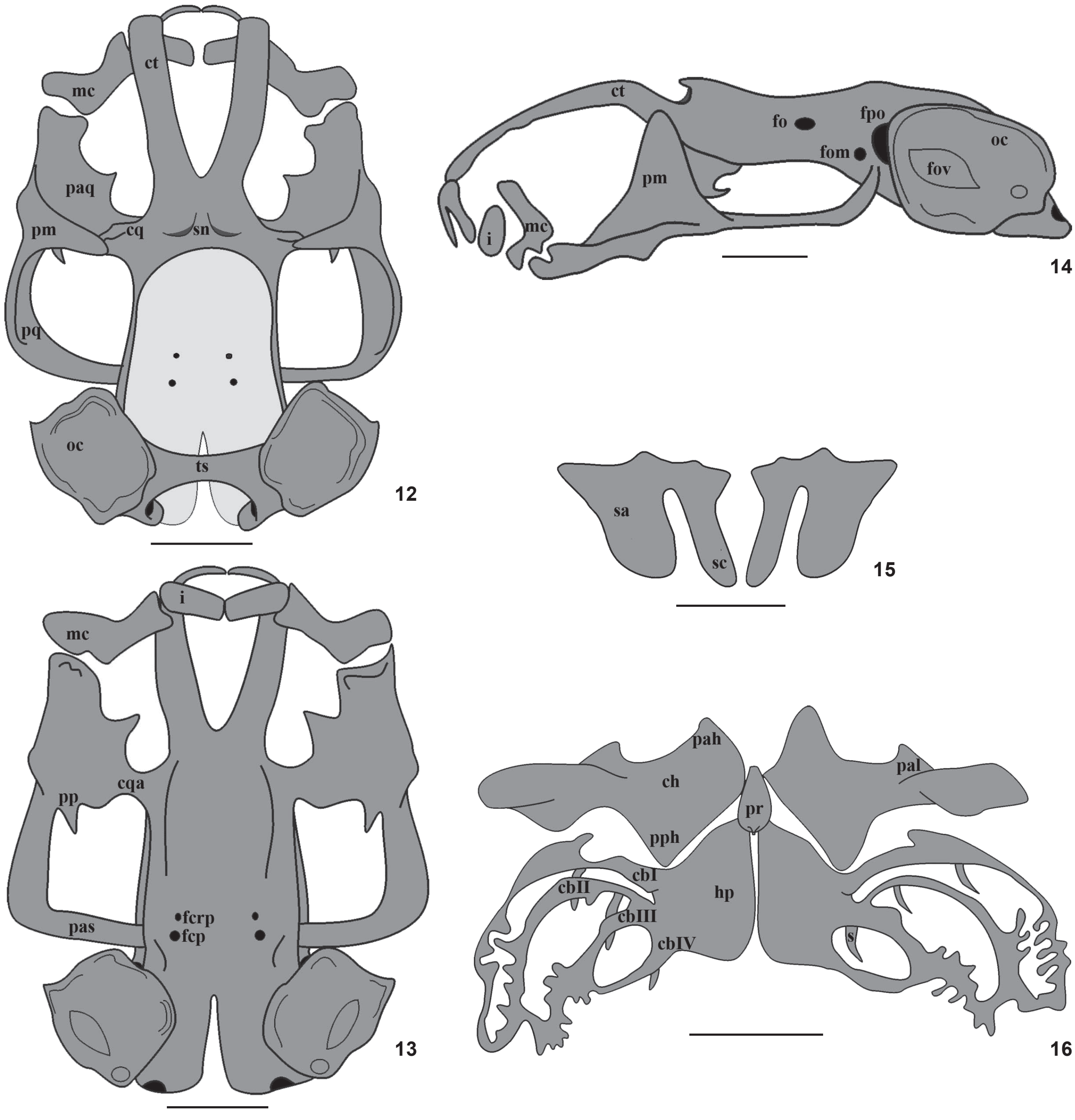
Neurocranium

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 dorsally 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 trabeculae articulate with the suprarostral at the point of junction of the corpora and the alae.

The cornua trabeculae originate from the planum trabeculare anticum and represent 40% o 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 trabeculae, 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 craniopalatina, 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.



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) hipobranchial plate, (i) infrarostral caratilage, (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 chondrocranium 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 represents about 25% of the chondrocranium 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 ascendens, a thin rod-like cartilage. The processus ascendens attaches just posterior of the oculomotorium foramen (intermediate condition *sensu* Sokol 1981). The processus ascendens is almost perpendicular to the main axis of the chondrocranium, forming an angle of 90°.

Anteriorly the palatoquadrate connects to the braincase through the commissura quadratocranialis anterior. The commissura quadratocranialis anterior extends between the palatoquadrate, at the level just posterior to the pars articularis quadrati, 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 quadrati and the pars articularis quadrati. 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 processus 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 ceratobranchials.

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. izecksohni* are benthonic 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 phyllodes* (Heyer & Cocroft, 1986), and *Phasmahyla 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 *P. izecksohni* can be promptly differentiated from tadpoles of the following groups of 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. palustris* (Giareta & Sazima 1993)], *P. cristiceps* groups [*P. concavitympanum* (Giaretta *et al.* 2000), *P. cristiceps* (Vieira *et al.* 2007), *P. cururu* (Eterovick & Sazima 1998), *P. moratoi* (Rossa-Feres & Jim 1996)] and *P. boiei* [*P. boiei* (Izecksohn *et al.* 1979), *P. renalis* (Nascimento *et al.* 2010)], as well 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 izecksohni* 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 Sá & Langone (2002)
P. boiei	34 (n = ?)	31.00	12.00	–	8.00	6.00	–	–	–	–	–	–	1.00	–	Izecksohn *et al.* (1979)
P. concavitympanum	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	1.40	2.40	2.30	1.60	1.00	1.10	2.30	Present study
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	Provete *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	Napoli **et al.** (2011)
P. moehringi	29 (n = ?)	23.60	8.50	–	4.60	4.00	3.00	–	2.00	1.00	1.10	–	–	–	Weygoldt & Peixoto (1985)
P. moratoi	37 (n = 9)	31.70	13.30	18.30	7.40	6.30	–	–	1.90	1.54	1.50	0.70	1.70	–	Rossa-Feres & Jim (1996)
P. palustris	37 (n = 1)	36.00	14.00	–	9.40	7.70	–	–	1.10	2.00	2.00	–	1.60	–	Giaretta & Sazima (1993)
P. renalis	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. schirchi	34 (n = ?)	31.00	11.70	–	8.00	6.30	–	–	3.20	–	–	–	1.20	–	Peixoto *et al.* (1984)
P. tupinamba	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.

Sepcies/Structure	Nostril shape	Spiracle	Origin of dorsal fin	Tip of the tail	Labium emargination	Oral formula	Reference
P. appendiculata	reniform	fused to the body	posterior third of the body	rounded	two folds	2/3(1)	Present study
P. avelinoi	rounded	–	junction body/tail	rounded	two folds	2(2)/3(1)	de Sá & Langone (2002)
P. boiei	reniform	free#	posterior third of the body	rounded	none	2(2)/3(1)	Izecksohn *et al.* (1979)
P. convavitympanum	rounded	free*	posterior third of the body	acute	none	2(2)/3(1)	Giaretta *et al.* (2000)
P. cristiceps	rounded	fused to the body	posterior third of the body	rounded	none	2(2)/3(1)	Vieira *et al.* (2007)
P. cururu	–	–	posterior third of the body	acute*	none	2(2)/3(1)	Eterovick & Sazima (1998)
P. izecksohni	reniform	fused to the body	posterior third of the body	rounded	two folds	2/3(1)	Present study
P. laticeps	reniform	–	posterior third of the body	acute	two folds	2(2)/3(1)	Peixoto *et al.* (1981)
P. melanopogon	oval	free	posterior third of the body	rounded	none	2(2)/3(1)	Provete *et al.* (2013)
P. minuta	reniform	free	junction body/tail	rounded	none	2(2)/3(1)	Napoli *et al.* (2011)
P. moehringi	rounded	–	–	rounded	two folds	2(2)/3(1)	Weygoldt & Peixoto (1985)
P. moratoi	rounded	fused to the body	junction body/tail	rounded	none	2(2)/3(1)	Rossa-Feres & Jim (1996)
P. palustris	–	fused to the body	junction body/tail	acute	two folds	2(2)/3(1)	Giaretta & Sazima (1993)
P. renalis	reniform	free	posterior third of the body	acute	two folds	2(2)/3(1)	Nascimento *et al.* (2010)
P. schirchi	reniform	fused to the body*	posterior third of the body	acute	two folds	2(2)/3(1)	Peixoto *et al.* (1984)
P. tupinamba	rounded	fused to the body	junction body/tail	acute	two folds	2/3(1)	Fatorelli *et al.* (2010)

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.

Sepcies	BR shape	PONA papillae	BRA shape	BRA papillae	BRA pustulations	BF shape	IL papillae	LP papillae	BFA shape	BFA papillae	BFA pustulations	Reference
P. appendiculata	triangular	5 to 10	inverted U	30-36	230	ovoid	4	4	triangular	30-50	270-320	Present study
P. avelinoi	semi-circular	5 to 6	rounded	30	–	triangular	4	4	U-shaped	20-25	–	DE SÁ & LANGONE (2002)
P. boiei	ovoid*	–	U-shaped	30	–	triangular*	2	4	oval	50	–	WASSERSUG & HEYER (1988)
P. cristiceps	triangular	4	semi-circular	18-20	–	circular	4	3	triangular	28-34	–	VIEIRA *et al.* (2007)
P. cururu	hexagonal	12	eliptical	28	80-90	elipsoid	2	4	hexagonal	50	40	PROVETE *et al.* (2013)
P. izecksohni	triangular	8 to 10	inverted U	14 to 18	about 360	ovoid	4	4	triangular	75	about 370	Present study
P. melanopogon	trapezoid	10 to 12	quadrate	14 to 30	100-200	triangular	4	5	rounded	50	180	PROVETE *et al.* (2013)
P. moratoi	rectangular	6	rounded	15	40-50	triangular	2	4	diamond	40-50	50	PROVETE *et al.* (2013)
P. renalis	circular	5	circular	24	–	triangular	2	6	U-shaped	42-46	–	NASCIMENTO *et al.* (2010)

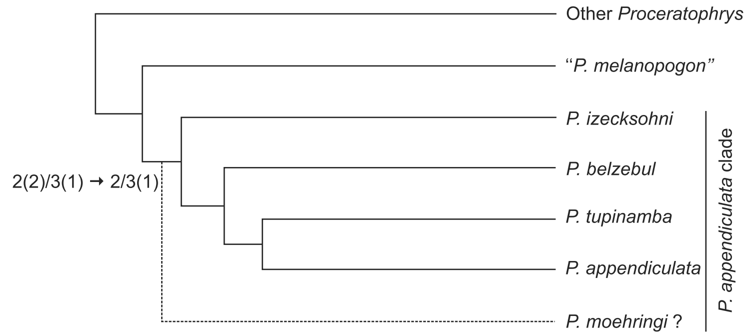


Figure17. Hypothesis of phylogenetic relationships within *Proceratophrys* (DIAS *et al.* 2013a). The evolutionary transition of the oral formula 2(2)/3(1) to 2/3(1) is a putative synapomorphy for this clade. The phylogenetic position of *P. moehringi* (dotted line) had remained unknown before. However, adult morphology, advertisement call and breeding behavior suggest a close relationship with *P. appendiculata* (DIAS *et al.* 2013a,c).

melanopogon, *P. minuta*, and *P. moratoi* by presenting two folds in the margin of the lower labium (no folds). Additionally, *P. izecksohni* tadpoles can be distinguished from the tadpoles of *P. concavitympanum*, *P. cururu*, *P. laticeps*, *P. palustris*, *P. renalis*, *P. schirchi*, and *P. tupinamba* (FATORELLI *et al.* 2010) by a rounded tail tip (acute in those species). The posterodorsal orientation of the spiracle distinguishes the tadpole of *P. izecksohni* from those of *P. cristiceps* and *P. cururu* (spiracle oriented dorsally). The reniform-shaped nostrils also set the tadpole of *P. izecksohni* apart from the tadpoles of *P. avelinoi*, *P. concavitympanum*, *P. cristiceps*, *P. moehringi*, *P. moratoi*, *P. palustris P. tupinamba* (rounded) and *P. melanopogon* (oval). *Proceratophrys izecksohni* tadpoles differ from the tadpoles of *P. concavitympanum*, *P. melanopogon*, *P. minuta* and *P. renalis* by presenting the inner wall of the spiracle fused to the body wall (free); from the tadpoles of *P. avelinoi*, *P. minuta*, *P. moratoi*, *P. palustris* and *P. tupinamba* by having the tail fins originating on the posterior third of the body (tail fins originated at the tail/body junction).

Proceratophrys izecksohni tadpoles can be distinguished from the tadpoles of *Proceratophrys tupinamba* by presenting a pair of cream dots in the lateral portion of the body (absent) and several silvered areas along the body (uniform brown coloration of the body) and by having submarginal papillae in the oral disc (absent).

From the tadpole of *P. appendiculata*, *P. izecksohni* tadpoles can be distinguished by presenting a lower body height in relation to total length (BH/TL 14% in *P. izecksohni* and 19% in *P. appendiculata*), by the lower tail height in relation to total length (TH/TL 15% in *P. izecksohni* and 19% in *P. appendiculata*), by the larger internarial distance in relation to interorbital distance (IND/IOD 74% in *P. izecksohni* and 72% in *P. appendiculata*), by the smallest eye to nostril distance in relation to body length (END/BL 7.5% in *P. izecksohni* and 9% in *P. appendiculata*), by the smallest body width in relation to total length (BW/TL 24% in *P. izecksohni* and 22% in *P. appendiculata*) and by the overall coloration; tail with silver dots (silver dots absent) and a single cream dot on the dorsum (absent).

Internal oral morphology. The internal oral features of *P. izecksohni* tadpoles differ from those of of *P. boiei* (WASSERSUG & HEYER 1988) by the larger number of papillae in the buccal floor arena (about 75 papillae in *P.*

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* (Vieira *et al*. 2007) by the ovoid buccal floor (circular), by having four lingual papillae (three), by the larger number o papillae in the buccal floor arena (about 75 papillae in *P. izecksohni* and 28-34 papillae in *P. cristiceps*), by the presence of papillae only on the posterior part of postulation 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 postulation area of the buccal roof arena (20-30 papillae well distributed on the postulation 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 postnarial arena (pustulations absent), "U" shaped buccal roof arena (circular), triangular buccal floor arena ("U" shaped), larger number of papillae surrounding the buccal floor arena, i.e., approximately 75 (42-46), posterior part of buccal floor arena only with papillae (papillae spread within postulation buccal floor).

Proceratophrys izecksohni tadpoles differ from those of *P. avelinoi* (de Sá & Langone 2002) by triangular buccal roof (semicircular), triangular buccal floor arena ("U" shaped), and by the 8-10 postnarial papillae (5-6).

Larvae of *Proceratophrys izecksohni* differ from those of *P. cururu* (Provete *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 arena papillae (14-18 in *P izecksohni* and 28 in *P. cururu*), by a greater number of pustulations in the buccal roof arena (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 arena (hexagonal), by the absence of papillae in the center of the buccal floor arena (10 present), by the greater number of buccal floor arena papillae (75 in *P. izecksohni* and 50 in *P. cururu*) and by the greater number of pustulations in the buccal floor arena (370 in *P. izecksohni* and 40 in *P. cururu*).

It differs from the tadpoles of *P. moratoi* (Provete *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 postnarial 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 arena (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 arena (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 arena (about 370 in *P. izecksohni* and 50 in *P. moratoi*).

The tadpoles of *Proceratophrys izecksohni* can be distinguished from those of *P. melanopogon* (Provete *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 inverted U shaped buccal roof arena (quadrate), by the larger number of pustulations in the buccal roof arena (about 360 in *P. izecksohni* and 100-200 in *P. melanopogon*), by the ovoid buccal floor (triangular), by having four lingual papillae (five), by triangular buccal floor arena (rounded), by the larger number of papillae in the buccal floor arena (75 in *P. izecksohni* and 50 in *P. melanopogon*), and by the larger number of pustulations in the buccal floor arena (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. appendiculta*. We found as the major distinction between them the larger number of papillae delimitating the buccal floor arena (75 in *P. izecksohni* and 30-50 in *P. appendiculata*), the smaller number of papillae in the buccal roof arena (14-18 in *P. izecksohni* and 30-36 in *P. appendiculata*), the larger number of pustulations in the buccal roof arena (360 in *P. izecksohni* and 230 in *P. appendiculata*) and in the buccal floor arena (370 in *P. izecksohni* and 270-320 in *P. appendiculata*). Our observations for *P. appendiculata* differ in some points from that made by Wassersug & Heyer (1988); this is probably due to the sample size – Wassersug & 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 suprarostral cartilage. The central elements – the corpora – are not fused ventromedially (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 for not ventrally free suprarostral 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*.

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 & Heyer (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 (Izecksohn *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, Pyron & Wiens 2011, Teixeira *et al*. 2012, Dias *et al*. 2013a), but rather with phenetic groups (Dias *et al*. 2013b). A solution to this problem is the incorporation of multiple sources of evidence (i.e., internal and external morphological data, from adults and tadpoles, DNA sequences, behavioral and bioacoustics) in a broad and extensive phylogenetic reconstruction.

A first step to recover such phylogenies, leastwise in relation to larval morphology, would be a broad sampling of specimens, especially from unknown and from rare tadpoles – most tadpoles have been described based on one or few specimens (e.g., Peixoto *et al*. 1981, 1984, Weygoldt & Peixoto 1985, Giaretta & Sazima 1993, Eterovick & Sazima 1998, Giaretta *et al*. 2000, de Sá & Langone 2002). New samples are rare in herpetological collections.

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

Izecksohn *et al*. (1998) defined a species complex within *Proceratophrys* in which all members presented a single, long, unicuspidate 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*, *P. belzebul* and *P. izecksohni* 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). Pyron & Wiens (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. phyllostumus*, *P. subguttata* and *P. sanctaritae* was never accessed.

The larval morphology provides support for a *P. appendiculata* clade, composed of *P. izecksohni*, *P. tupinamba*, *P. appendiculata* and *P. belzebul*. The oral formula 2/3(1) is known from all those species (with exception of *P. belzebul*, whose tadpoles is 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 preocular cutaneous crest (Izecksohn *et al*. 1998, Prado & Pombal 2008) and by the peculiar morphology of the frontoparietal bones, which extends toward the esquamosals like bony plates (Izecksohn *et al*. 2005).

Adults of *P. moehringi* are extremely similar to those of *P. izecksohni*, *P. tupinamba*, *P. appendiculata*, 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. appendiculata* – 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 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. appendiculata* clade might be attested with the survey of new data, specifically with the descriptions of the tadpoles of *P. phyllostomus*, *P. subguttata*, and *P. sanctaritae* and tissues from DNA analysis. New samples of tadpoles of *P. moehringi* are necessary.

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