Zootaxa 3682 (2): 277–304
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3682.2.5
http://zoobank.org/urn:lsid:zoobank.org:pub:DCB6EF07-50FC-4AE1-A64E-849ADC24AA0B

Two new species of *Proceratophrys* Miranda-Ribeiro, 1920 (Anura; Odontophrynidae) from the Atlantic forest, with taxonomic remarks on the genus

PEDRO HENRIQUE DOS SANTOS DIAS[1,2,4], RENATA CECÍLIA AMARO[3], ANA MARIA PAULINO TELLES DE CARVALHO-E-SILVA[2]& MIGUEL TREFAUT RODRIGUES[3]

[1]*Universidade Federal do Rio de Janeiro, Instituto de Biologia, Av. Brigadeiro Trompowsky, s/nº. CCS.Bl. A. Ilha do Fundão, CEP 21941-590, Rio de Janeiro, RJ, Brazil*

[2]*Universidade Federal do Estado do Rio de Janeiro, Departamento de Zoologia, Laboratório de Biossistemática de Anfíbios, Av. Pasteur, n° 458, Urca,CEP 22290-240 Rio de Janeiro, RJ, Brazil*

[3]*Universidade de São Paulo, Departamento de Zoologia, Instituto de Biociências,Rua do Matão n° 101, CEP 05508-090, São Paulo, SP, Brazil*

[4]*Corresponding author. E-mail: pedrodiasherpeto@gmail.com*

Abstract

We describe two new species of *Proceratophrys* allied to the *P. appendiculata* species complex by the presence of single and long palpebral appendages and a triangular rostral appendage. *Proceratophrys izecksohni* **sp. nov.** is characterized by having small to medium size (SVL 32.1–54.2 mm in males), elongated hindlimbs (thigh length plus tibia length corresponding to more than 90% of snout-vent length), a broad head (head width corresponding to 55% of the snout-vent length), and by the light brown gular region and a cream colored ventral surface with scattered brown dots. *Proceratophrys belzebul* **sp.nov.** is characterized by its medium size (SVL 40.5–51.3 mm in males), by the absence of contact between the nasals bones and between the nasals and frontoparietals, by a very reduced iliac projection, by having frontoparietal bones very depressed and broad rostrally, by the smooth surface of the squamosal and nasal, by shallow, inconspicuous ventral pits on the maxillae, and by the females presenting the gular region dark brown. The two new species were previously confused with *P. appendiculata* for which we provide a new diagnosis. A molecular analysis based on mitochondrial and nuclear genes recovers a monophyletic *Proceratophrys* with high support, and the two new species in a clade with *P. appendiculata* and *P. tupinamba*. The data also reinforce the idea that the species groups presently admitted to the genus are not monophyletic.

Key words: *Proceratophrys izecksohni* sp.nov.; *Proceratophrys belzebul* sp.nov.; *Proceratophrys appendiculata*; taxonomy

Resumo

Descrevemos duas novas espécies de *Proceratophrys* associadas ao complexo de *Proceratophrys appendiculata* pela presença de apêndices palpebrais longos e de um apêndice rostral triangular. *Proceratoprhys izecksohni* **sp.nov.** é caracterizada por apresentar porte pequeno a médio (CRC 32,1–54,2 mm nos machos), membros longos (comprimento da coxa somado ao comprimento da tíbia correspondendo a mais do que 90% do comprimento rostro-cloacal), cabeça larga (largura da cabeça representando 55% do comprimento rostro-cloacal), e coloração marrom clara na região gular e creme na região ventral, com manchas marrons espalhadas. *Proceratophrys belzebul* **sp.nov.** é caracterizada pelo porte médio (CRC 40,5–51,3 mm nos machos), pela ausência de contato entre os ossos nasais e entre estes e os frontoparietais, pela projeção reduzida do ílio, por apresentar os frontoparietais deprimidos e alargados rostralmente, pela superfície lisa dos esquamosais e nasais, pelas fossetas maxilares pouco desenvolvidas e pelas fêmeas apresentarem a região gular marrom escuro. As duas novas espécies eram previamente confundidas com *P. appendiculata* para a qual fornecemos uma nova diagnose. Uma análise molecular

Accepted by M. Vences: 23 May 2013; published: 27 Jun. 2013

baseada em genes mitocondriais e nucleares recuperou o gênero *Proceratophrys* como monofilético, com altos valores de suporte e as duas espécies novas em um clado juntamente com *P. appendiculata* e *P. tupinamba*. Os dados também reforçam a ideia de que os grupos de espécies atualmente aceitos para o gênero não são monofiléticos.

Introduction

The Neotropical genus *Proceratophrys* Miranda-Ribeiro, 1920 currently comprises 29 species distributed in Argentina, Brazil, and Paraguay (Ávila *et al*. 2012; Cruz *et al*. 2012; Frost 2013). These species are commonly grouped within phenetic groups or species complexes based on external morphological similarity (Izecksohn *et al*. 1998; Giaretta *et al*. 2000; Kwet & Faivovich 2001; Prado & Pombal 2008) despite molecular data indicate the non monophyletism of these groups (Amaro *et al.* 2009; Teixeira *et al*. 2012).

Species without palpebral appendages are assigned to the *Proceratophrys bigibbosa* and *P. cristiceps* species groups. Species of *P. bigibbosa* group are found in south and southeastern Brazil, Argentina and Paraguay. They are characterized by a blunt and short snout, by the presence of post-ocular swellings and by having a large marginal row of tubercles in the eyelid (Kwet & Faivovich 2001). Currently four species are assigned to the group: *P. avelinoi* Mercadal de Barrio and Barrio 1993; *P. bigibbosa* (Peters 1872); *P. brauni* Kwet and Faivovich 2001; and *P. palustris* Giaretta and Sazima 1993.

Species of the *Proceratophrys cristiceps* group are typically found in open and dry environments of Cerrado and Caatinga. They are characterized by the absence of post-ocular swellings (Giaretta, Bernarde & Kokubum 2000; Cruz *et al*. 2012). The nine species that compose the group are: *P. aridus* Cruz, Nunes and Juncá 2012; *P. caramaschii* Cruz, Nunes and Juncá 2012; *P. concavitympanum* Giaretta, Bernarde and Kokubum 2000; *P. cristiceps* (Müller 1883); *P. cururu* Eterovick and Sazima 1998; *P. goyana* (Miranda-Ribeiro 1937); *P. huntingtoni* Ávila, Pansonato and Strüssmann 2012; *P. moratoi* (Jim and Caramaschi 1980); *P. strussmannae* Ávila, Kawashita-Ribeiro and Morais 2011; and *P. vielliardi* Martins and Giaretta 2011.

Species presenting a long and single palpebral appendage are assembled in the species complexes of *Proceratophrys boiei* and *P. appendiculata* (Izecksohn *et al.* 1998; Prado & Pombal 2008; Cruz & Napoli 2010). The species of the *P. boiei* group occur primarily in Atlantic Forest, from Paraiba to Santa Catarina states (Prado & Pombal 2008): *P. boiei* (Wied-Neuwied 1824); *P. paviotii* Cruz, Prado and Izecksohn 2005; and *P. renalis* (Miranda-Ribeiro 1920).

The *Proceratophrys appendiculata* species complex is found only in the Atlantic Forest, from Bahia to Santa Catarina states (Izecksohn *et al.* 1998; Cruz & Napoli 2010). These species are characterized by the presence of a triangular rostral appendage and assembles eight species: *P. appendiculata* (Günther 1873); *P. laticeps* Izecksohn and Peixoto 1981; *P. melanopogon* (Miranda-Ribeiro 1926); *P. moehringi* Weygoldt and Peixoto 1985; *P. phyllostomus* Izecksohn, Cruz and Peixoto 1998; *P. sanctaritae* Cruz and Napoli 2010; *P. subguttata* Izecksohn, Cruz and Peixoto 1998; and, *P. tupinamba* Prado and Pombal 2008.

Besides the species cited above, *Proceratophrys schirchi* (Miranda-Ribeiro 1937), *P. rondonae* Prado and Pombal 2008 that presents a short single multi-cuspidate palpebral appendage (Prado & Pombal 2008; Cruz & Napoli 2010; Napoli *et al.* 2011) and *P. minuta* Napoli, Cruz, Abreu and Del-Grande 2011 which has a series of small appendages on the eyelid had never been associated with any of the previous groups. However, recently molecular evidence (Teixeira *et al*. 2012) suggests that the newly described *Proceratophrys redacta* Teixeira, Amaro, Recoder, Dal Vechio and Rodrigues 2012 is the sister group of *P. minuta* and that this clade clusters to a clade assembling *P. cristiceps* and *P. schirchi*. This last paper also showed that the monophyly of most of the presently admitted species groups of *Proceratophrys* was not recovered.

Herein we present morphological and molecular evidences to recognize two cryptic new species of *Proceratophrys* from the Atlantic Forest previously assigned as *P. appendiculata*. We describe these new species and provide a new diagnosis for *P. appendiculata*.

Material and methods

Morphological assessment. Museum acronyms of specimens used in the description or examined for comparisons are: Laboratório de Biossistemática de Anfíbios, Universidade Federal do Estado do Rio de Janeiro (**UNIRIO)**, Zoological collection of Universidade Federal do Rio de Janeiro **(ZUFRJ)**, Eugenio Izecksohn personal collection, allocated in Universidade Federal Rural do Rio de Janeiro **(EI)**, Herpetological collection of Museu Nacional **(MNRJ)**, Célio F.B. Haddad collection **(CFBH)**, allocated in Universidade Estadual Paulista, Municipality of Rio Claro, State of São Paulo, and Laboratório de Herpetologia da Universidade de São Paulo **(MTR)** to be deposited at Museu de Zoologia, Universidade de São Paulo (MZUSP).

Measurements of adults specimens follow Duellman (1970) adapted: snout-vent length (SVL), head length (HL), head width (HW), thigh length (THL), tibia length (TIL), tarsus length (TRL), foot length (FL), humerus length (HUL), forearm length (FAL), hand length (HAL), interorbital distance (IOD), eye-nostril distance (END), eye-snout distance (ESD), internarial distance (IND), nostril-snout distance (NSD) and eye diameter (ED). Head width and length were taken from the corner of the mouth. The specimens were measured with a 0.01mm-accurate digital caliper.

Morphometric characters were tested in relation to their normality and homocedasticity using the tests of Kolmogrov-Smirnov and Levene respectively. Homocedastic characters were used in discriminating analysis performed in Statistica7.0 (StarSoft, Inc.). Three Operational Taxonomic Units (OTUs; Heyer 2005) (*n* = 36 males) were grouped based on molecular and osteological data (OTU 1, *n*=5; OTU 2, *n*=6; OTU 3, *n*=4). We performed a canonical discriminant analysis (CDA) to study multivariate patterns. The separation of *a priori* formed groups was made by maximizing the variation between-groups in relation to that within-group (Reis 1988).

Colors of specimens were standardized according to Smithe's catalog (1975). Osteological features were observed in cleared and stained specimens. We used double-staining with Alizarin red and Alcian Blue, following an adapted protocol of Taylor and Van Dyke (1985). Specimens were considered adults when they reach half of the size of the largest specimen of each OTU following Prado and Pombal (2008) criteria. Previous cleared and stained specimens examined were considered adults in function of the ossifications of the carpals (see Bumbury & Maglia, 2006).

The terminology for morphological structures follows Prado and Pombal (2008). The observations used for comparison with the different species that compose the genus are in accordance with Prado and Pombal (2008), Cruz and Napoli (2010), Martins and Giaretta (2011), Ávila *et al.* (2011, 2012), Napoli *et al.* (2011), Cruz *et al*. (2012) and Teixeira *et al*. (2012).

Molecular data. Partial sequences of three mitochondrial (16S, 12S and cyt*b*) and two nuclear (Rag-1 and Rhodopsin) genes were obtained for 28 individuals of *Proceratophrys appendiculata* complex (Appendix 1). We also included sequences of *P. avelinoi*, *P. bigibbosa*, *P. boiei*, *P. concavitympanum*, *P. cristiceps*, *P. cururu*, *P. goyana*, *P. laticeps*, *P. moratoi*, *P. renalis*, *P. schirchi*, *Odontophrynus americanus* (Duméril and Bibron 1841); *O. carvalhoi* Savage and Cei 1965; *O. cultripes* Reinhardt and Lütken 1862; *Macrogenioglottus alipioi* Carvalho 1946; *Cycloramphus acangatan* Verdade and Rodrigues 2008; and *Thoropa taophora* (Miranda-Ribeiro 1923) from Amaro *et al.* (2009) and Teixeira *et al*. (2012), resulting in a matrix with 48 terminals and 2291 base pairs (bp) (534 bp from 16S, 401bp from 12S, 595bp from cyt*b*, 428 bp from Rag-1 and 331 bp from Rhodopsin).

Total genomic DNA was extracted from liver and muscle according to Fetzner (1999) and amplification was carried using standard PCR protocols with primers 16SAR and 16SBR (Palumbi 1996) for amplification of 16S, primers 12SA and 12SB (Palumbi 1996) for 12S, primers CB1, CB3, LGL765 and H15149 for cyt*b* (Kocher *et al*. 1989; Bickham *et al*. 1995; Palumbi 1996), primers R1GFF and R1GFR (Faivovich *et al.* 2005) for Rag-1 and primers Rhod1A, Rhod1C and Rhod1D (Bossuyt & Milinkovitch 2000) for rhodopsin. The PCR cycle protocol consisted of one initial cycle of 94 °C for 5 min followed by 35 cycles of 94 °C for 40 sec, 48-60 °C for 40 sec, 72 °C for 40 sec and the products were directly purified with Exonuclease I and Shrimp Alkaline Phosphatase (USB or Fermentas). Automated sequencing was carried out using BigDye Terminator v3.1 Cycle Sequencing kit (Applied Biosystems), followed by analysis on ABI Prism 310, 3700 or 3170 Genetic Analyzer Sequencers (Applied Biosystems) according to the manufacturer's instructions. Sequences were edited and initially aligned in CodonCode Aligner (CodonCode Corporation).

Different modes of inference were used in phylogenetic analyses: Bayesian analysis (BA) implemented in MrBayes 3.0b4 (Ronquist & Huelsenbeck 2003) and Maximum Likelihood (ML) in RAxML 7.3.2 (Stamatakis

2006) available on Cipres Science Gateway (Miller, Pfeiffer & Schwartz 2010**).** Two independent Bayesian analyses were performed for each partition, with a random starting tree, four incrementally heated Markov chains, and 20,000,000 generations, with trees sampled every 1,000 generations to estimate likelihood and sequence evolution parameters. For Bayesian analyses, the best-fit model of nucleotide substitution for each data partition was selected in MrModeltest v.2.2 (Nylander 2004) using the Akaike information criterion (AIC) and we used a separate model for each gene (GTR +I +G for 16S, 12S and rhodopsin; HKY+I+G for cyt*b* and Rag-1). Stationarity for each run was detected by plotting the likelihood scores of the trees against generation time, and the topology, posterior probability values, and branch lengths inferences were estimated after discarding 25% of the initial trees of each run as burn-in samples. Nodes with posterior probability ≥ 95% on a 50% majority rule consensus tree from both runs were considered significant support for a given clade. Maximum likelihood (ML) bootstrapping (1,000 replicates) was performed in RAxML 7.3.2. The majority 50% consensus trees saved with posterior probabilities and bootstrap values on the nodes were visualized using FigTree 1.4.0 (http://tree.bio.ed.ac.uk/). Uncorrected genetic distances (*p* distances) were calculated using PAUP* 4.0b10 (Swofford 2003) for 16S and Rag-1 fragments. Relationships among haplotypes of each dataset were explored using median joining networks (Bandelt *et al*. 1999) obtained in NETWORK 4.5.1.6 (http://www.fluxus–engineering.com).

Results

Morphometric data

We found pronounced morphometric variation in specimens attributed to *Proceratophrys appendiculata* (Fig.1). The three OTUs were separated along the axis CD1, with a small overlapping of the OTU 1 (specimens from the Serra dos Órgãos, Rio de Janeiro state) with the OTU 2 (specimens from the southeastern coast of Rio de Janeiro state). The OTU 3 represented by specimens of São Paulo state formed a well defined cluster. The OTU 2 also presents some tendency of separation of the other two OTUs in the axis CD2, but with some overlapping.
CD 1 and CD2 represent 74.3% and 25.7% of the amount of variations observed in the sample respectively. Such variation is due to head, tarsus and humerus lengths, distances between eye and nostril, nostril and snout, internarial distance and eye diameter values. The standardized coefficients of the canonical axis are summarized in Table 1.

TABLE 1. Standardized coefficients (CD) from canonical discriminant analysis (CDA; Fig.1) for seven morphometric characters (which passed the tests of normality and homoscedasticity) from adult males of three Operational Taxonomic Units (OTUs) related to *Proceratophrys appendiculata*. Abbreviations are defined in the text.

Characters	CD1	CD2
HL	-0,527104	0,428907
TRL	1,20856	-0,46306
HUL	-0,52705	-0,011038
END	-0,28383	0,546484
IND	0,794485	0,581344
NSD	-0,31927	0,049762
ED	0,119438	-0,005230
Eigenvalues	2,616439	0,903395
Cumulative proportion	0,743342	1,000000

Taxonomic account

Generic identification. All specimens studied are assigned to the genus *Proceratophrys* by lacking nuptial pads on thumb, body without enlarged glands, toes not webbed or fringed laterally, supernumerary tubercles present on hands and feet, dorsal surfaces of fingers and toes wrinkled, zygomatic ramus of squamosal bone in sutural contact with maxilla and cervical cotylar arrangement type II of Lynch (1971) (cotyles closely approximated). Specimens were associated to *Proceratophrys appendiculata* species complex by the presence of a long, uni-cuspidate palpebral appendages and a triangular rostral appendage. All three species differs from *P. aridus*, *P. avelinoi*, *P. bigibbosa*, *P. brauni*, *P. caramaschii*, *P. concavitympanum*, *P. cristiceps*, *P. cururu*, *P. goyana*, *P. huntingtoni*, *P. minuta*, *P. moratoi*, *P. palustris*, *P. redacta*, *P. schirchi*, *P. strussmannae*, and *P. vielliardi* by the presence of a single elongate palpebral appendage (absent). From *P. rondonae* by presenting an uni-cuspidate palpebral appendage (palpebral appendage multi-cuspidate). And from *P. boiei*, *P. paviotii* and *P. renalis* it differs by presenting a rostral appendage (absent).

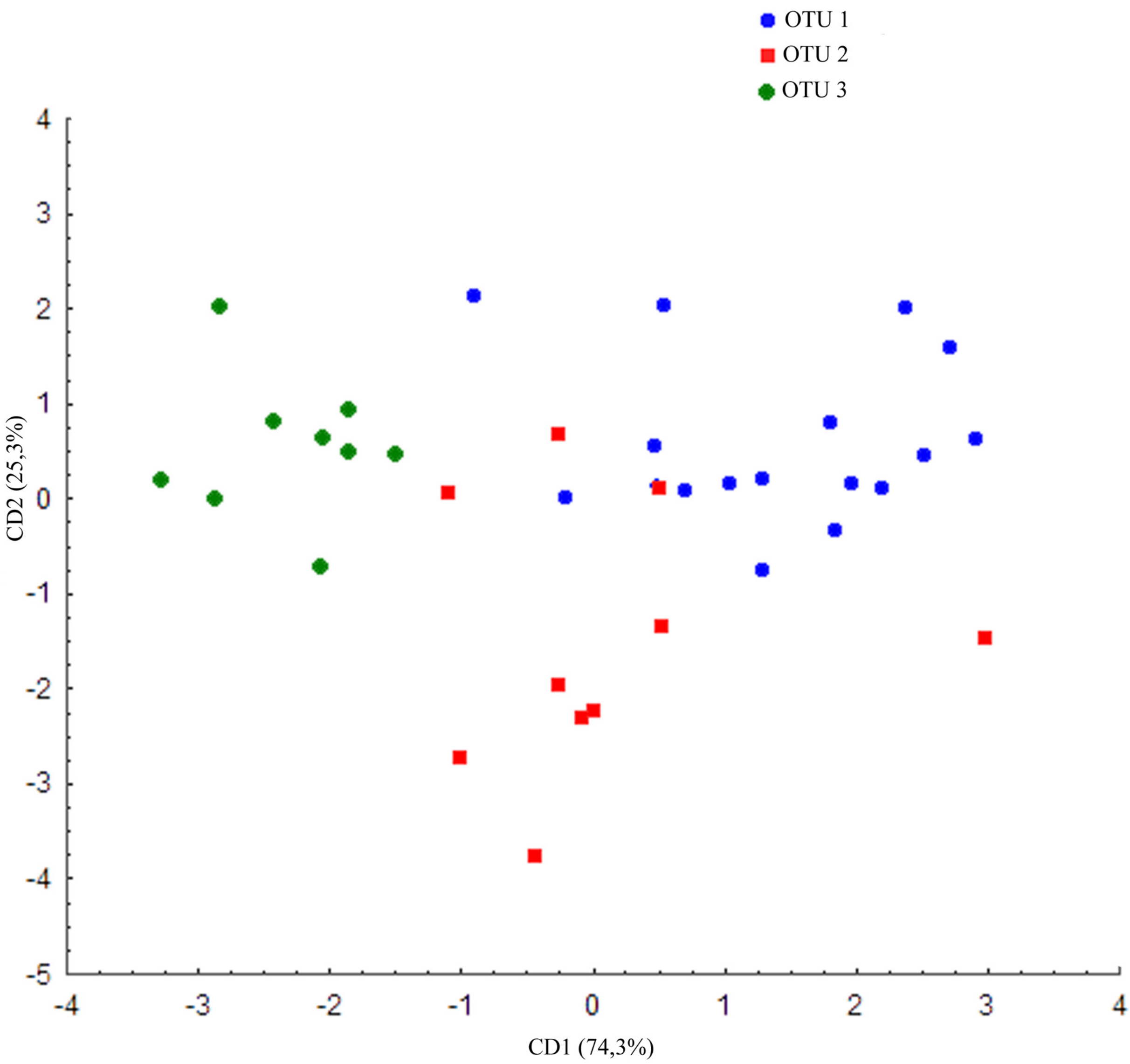

FIGURE 1. Plots of individual scores resulted from canonical discriminant analysis (CDA) of morphometric data from three Operational Taxonomic Units (OTUs) of *Proceratophrys appendiculata* adult males in the space of the first and second canonical axes.

Proceratophrys izecksohni sp. nov.

(Figs. 2–3)

Etymology. The specific epithet is a patronym given in honor of Eugenio Izecksohn, a herpetologist who greatly contributed to the current knowledge of Brazilian frog fauna, particularly to the genus *Proceratophrys*.

Holotype: UNIRIO 739, adult male collected in Reserva Rio das Pedras (RERP), Mangaratiba municipality, Rio de Janeiro state (22°59'29''S, 44°06'01''W ca. 200 meters above sea level) on 06 July, 1999 by A.M.P.T. Carvalho-e-Silva, S.P. Carvalho-e-Silva, L. Americo, G.R. Silva and J.A. Chaves (Figs. 2A and 3).

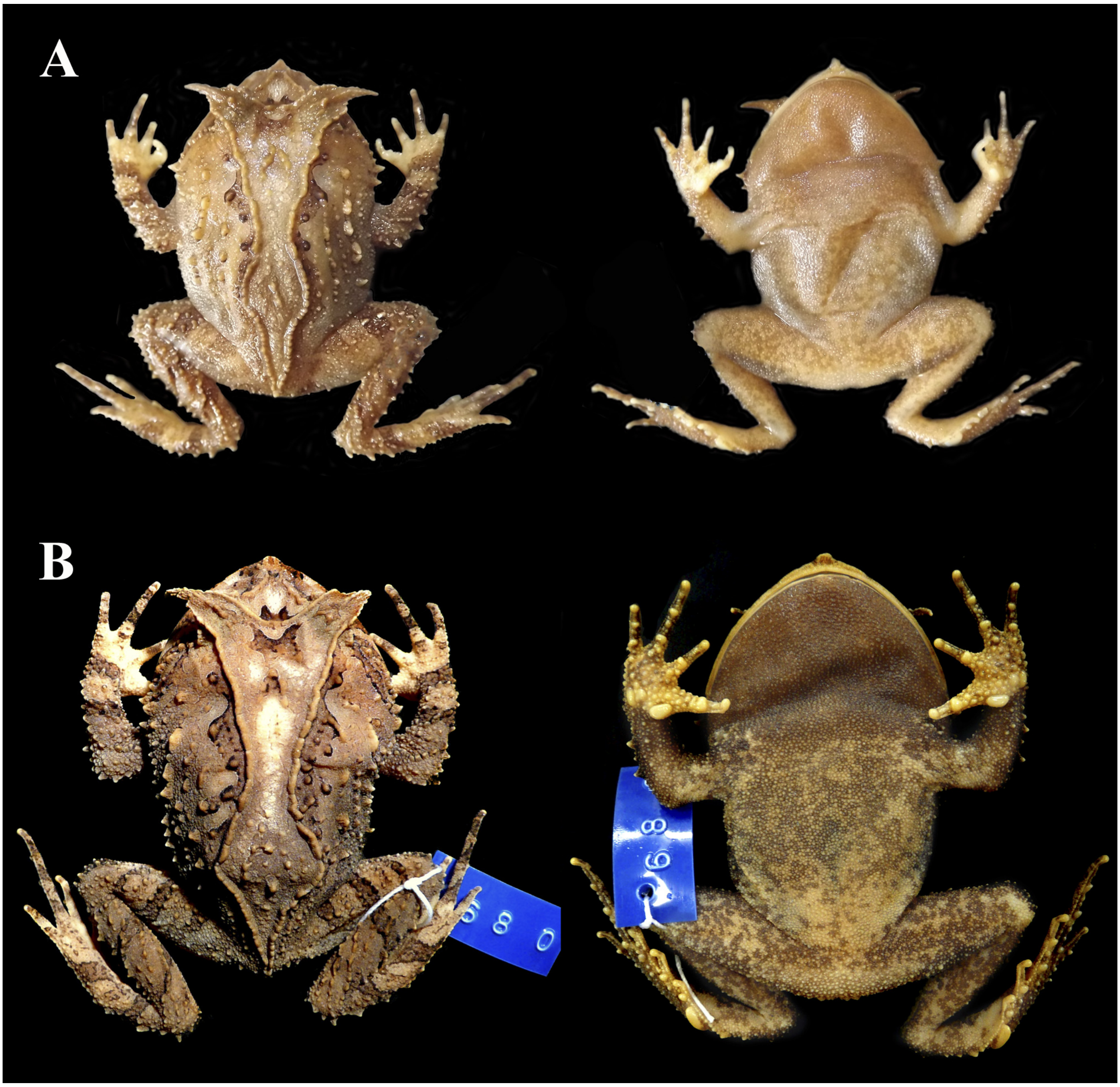

FIGURE 2. Dorsal (left) and ventral (right) views of the holotype of *Proceratophrys izecksohni* **sp.nov.** (UNIRIO 739; SVL 32.1 mm) (A); and dorsal (left) and ventral (right) views of the female of *Proceratophrys izecksohni* **sp.nov.** (UNIRIO 680; SVL 49.6 mm) (B).

Paratopotypes: **Adult males -** UNIRIO 623 (04 October, 1999), UNIRIO 731 (06 December, 1999) by A.M.P.T. Carvalho-e-Silva, S.P. Carvalho-e-Silva, L. Americo, G.R. Silva and J.A. Chaves, UNIRIO 1218 (cleared and stained) (06 January, 2001) by A.M.P.T. Carvalho-e-Silva and S.P. Carvalho-e-Silva, UNIRIO 2095 (cleared and stained) (01 October, 2004), MNRJ 40713 (November, 2005) by V. Borges Jr. **Adult females—**UNIRIO 680 (06 July, 1999) (Fig. 2B) by G.R. Silva and J.A. Chaves, UNIRIO 1117 (27 October, 2000) by A.M.P.T. Carvalho-e-Silva, S.P. Carvalho-e-Silva, L. Americo, G.R. Silva and J.A. Chaves, UNIRIO 2847 (08 September, 2007) by A.M.P.T. Carvalho-e-Silva, S.P. Carvalho-e-Silva, L.A. Cordioli, P.A. Valadares and T.S. Soares.

Other paratypes: *Angra dos Reis municipality, Rio de Janeiro state*: **Adult -** MNRJ 2000 (18 March and 11 May, 1948) (cleared and stained) by Carvalho and Berla. **Adult female -** MNRJ 34016 (without collecting date, although determined in 2007) by H.R. Silva and I. Fichberg.

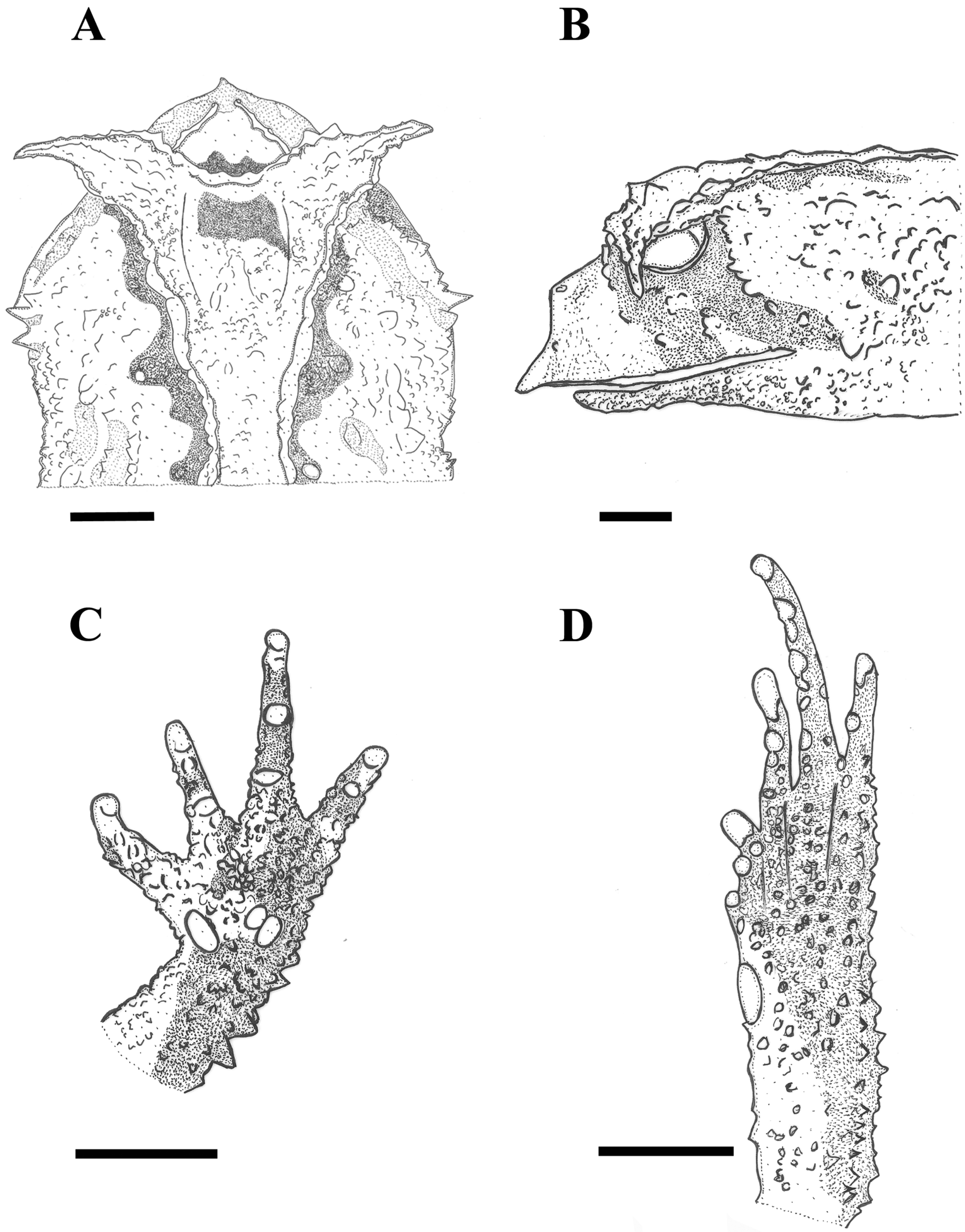

FIGURE 3. Dorsal (A) and lateral (B) views of the head; hand (C); and foot (D) of the holotype of *Proceratophrys izecksohni* **sp.nov.** (UNIRIO 739; SVL 32.1 mm). Scale bar = 3.5 mm.

Itaguaí, municipality, Rio de Janeiro state: **Adult females -** EI 9030-9031 (24 April, 1974) by O.F. Fraga and C.A.G. Cruz.

Paraty municipality, Rio de Janeiro state: **Adult males -** EI 9034 (7 April, 1979) by S.P. Carvalho-e-Silva, E. Izecksohn and C.A.G. Cruz, MNRJ 64586, (11 November, 2010) by C.C. Ciqueira, M.C. Kiefer and V.A. Menezes, ZUFRJ 405 (06-07 April, 1979) by S.P. Carvalho-e-Silva, E. Izecksohn, C.A.G. Cruz and O.L. Peixoto. **Adult females -** MNRJ 1367 (November/December, 1941), MNRJ 10535 (November or December, 1946), MNRJ 10537, (September or December, 1946), MNRJ 10539 (September or December, 1946) by A.L. Carvalho and B. Lutz, MNRJ 64584-64585 (11 November, 2010) by C.C. Ciqueira, M.C. Kiefer and V.A. Menezes.

Diagnosis. The species is characterized by: 1) small to medium size (SVL 32.1–54.1 mm in males and 30.4–50.0 mm in females); 2) broad head, dorso-ventrally depressed (HW/SVL 54%); 3) thigh length plus tibia length corresponding to more than 90% of SVL); 4) gular region light brown; 5) ventral surface cream with scattered brown dots; 6) contact between nasal bones in their rostral extremities (Fig.4); 7) wide contact between nasal and frontoparietal bones in their posterior extremities (Fig.4); 8) iliac projection corresponding to more than 50% of ilium diameter.

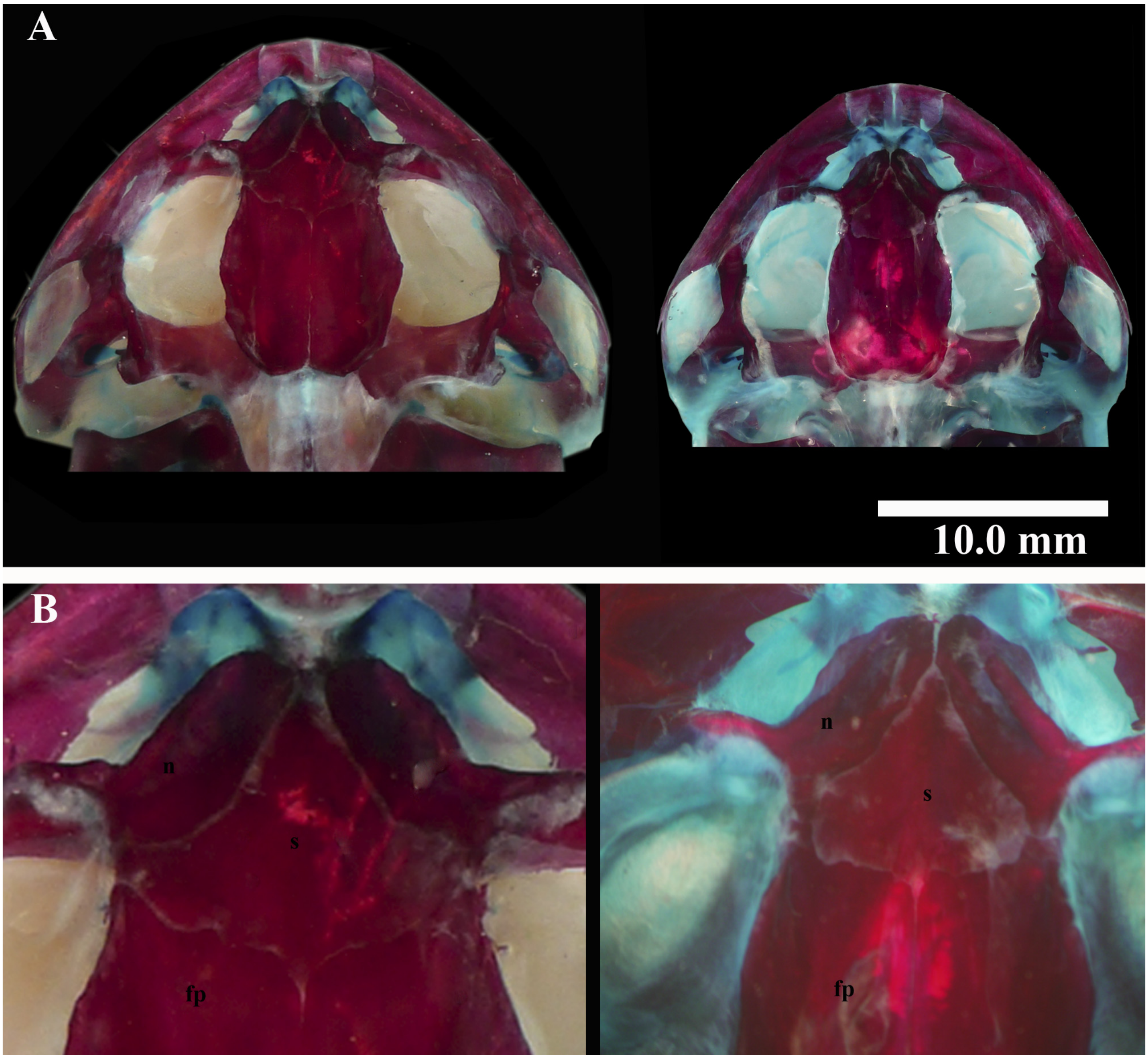

FIGURE 4. Dorsal view of the cranium of *Proceratophrys appendiculata* (left—UNIRIO 2063) Teresópolis, RJ, and *Proceratophrys izecksohni* **sp.nov.** (right—paratype, UNIRIO 2095) from Mangaratiba, RJ (A). Detail of nasal bones in *Proceratophrys appendiculata* (left) showing absence of contact between them and with frontoparietal and and the opposite condition observed in *Proceratophrys izecksohni* **sp.nov.** (right). fp, frontoparietal; n, nasal; s, sphenethmoid.

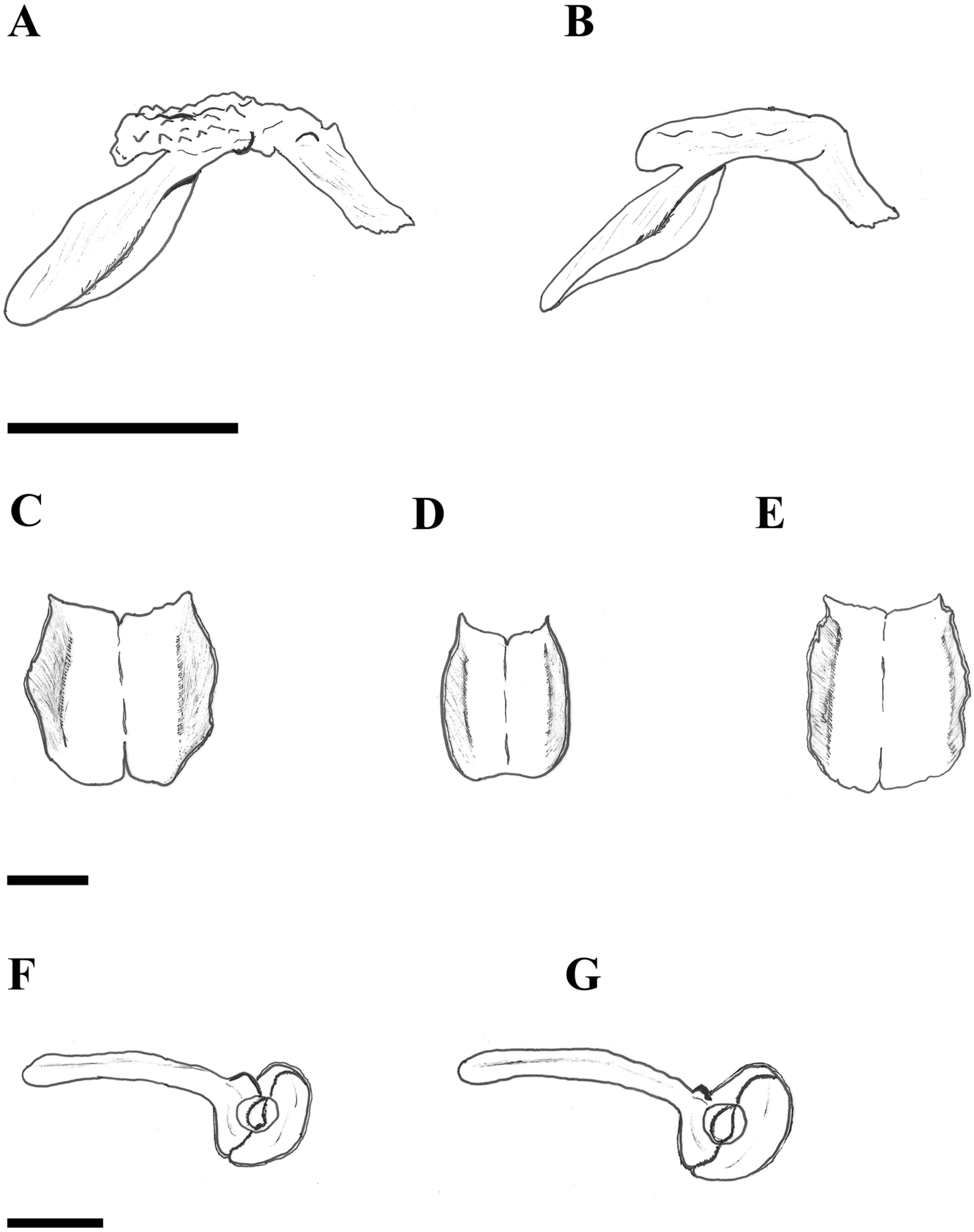

FIGURE 5. Osteological features of *Proceratophrys* species. Squamosal bone of *Proceratophrys appendiculata*, with tubercles and crests (A) and *Proceratophrys izecksohni* **sp.nov.** with smooth surface (morphology also representative of *Proceratophrys belzebul* **sp.nov.** (B); frontoparietal bones morphology for *Proceratophrys appendiculata* (C), *Proceratophrys izecksohni* **sp.nov.** (D), and *Proceratophrys belzebul* **sp.nov.** (E); ilium of *Proceratophrys appendiculata* (F) and *Proceratophrys belzebul* **sp.nov.** with a small projection, representing less than 30% of ilium diameter (G). Scale bar = 10.0 mm.

Comparisons with other species (data for species in comparison are given in parenthesis; biometric comparisons only between males). *Proceratophrys izecksohni* differs from *P. laticeps*, *P. melanopogon*, *P. phyllostomus* and *P. subguttata* by presenting a preocular cutaneous crest (preocular cutaneous absent). From *P. moehringi* by the presence of a well developed rostral appendage in adults (rostral appendage absent or vestigial). It differs from *P. sanctaritae* by presenting a larger head length in relation to head width (HL/HW 90% in *P. izecksohni* [87–91%] and 80% in *P. sanctaritae* [78–83%]), by having longer hindlimbs (THL+TIL/SVL 93% in *P. izecksohni* [90–99%] and 83% in *P. sanctaritae* [80-84%]). It differs from *P. tupinamba* and *P. appendiculata* by presenting nasal bones widely in contact with the frontoparietal bones in their posterior extremities (nasals do not contact frontoparietals) and by presenting the nasal bones contacting each other rostrally (nasals do not contact each other) (Fig.4). It also differs from *P. tupinamba* by the smaller size (SVL 32.1–54.2 in *P. izecksohni* and SVL 52.6–63.4 in *P. tupinamba*), by presenting a smaller eye diameter in relation to the head length (*P. izecksohni*, 18%; *P. tupinamba,* 25%), by the smaller foot size in relation to snout vent length (FL/SVL 48% in *P. izecksohni* [47–48%] and 59% in *P. tupinamba* [63–67%]); by having a more prominent iliac projection (corresponding to more than 50% of ilium diameter in *P. izecksohni* and less than 40% in *P. tupinamba*); from *P. appendiculata* by the smaller size (SVL 32.1–54.2 mm in *P. izecksohni* and SVL 43.1–58.0 mm in *P. appendiculata*), by the longer hindlimbs (THL+TIL/SVL 93% in *P. izecksohni* [90-99%] and 89% in *P. appendiculata* [89.5–90%]); by the texture of the squamosal bones (smooth in *P. izecksohni* and rough, with tubercles and crests in *P. appendiculata*) (Fig.5A and B); by presenting shallow maxillary pits (moderately deep in *P. izecksohni* and very deep in *P. appendiculata*); and by the shape of frontoparietal bones (almost uniform along their extension in *P. izecksohni* and broader medially in *P. appendiculata*) (Fig.5C and D).

FIGURE 6. Living specimens of *Proceratophrys izecksohni* **sp.nov.** from Mangaratiba, RJ (A); *Proceratophrys belzebul* **sp.nov.** from Ubatuba, SP (B); *Proceratophrys appendiculata* from Teresópolis, RJ (C); and *Proceratophrys tupinamba* from Ilha Grande, Angra dos Reis, RJ (D).

Description of holotype (Figs. 2A and 3)**.** Adult male with 32.14 mm of snout vent length; head slightly rounded, wider than long; head length representing 94.2% of head width; nostrils elliptical, separated by a distance of approximately half of the eye diameter; snout short; distance of eye to snout corresponding to 21.1% of head length; eye to nostril distance approximately 21.3% of the head length; eyes lateral with a diameter equivalent to 22.2% of the head length; a single and long palpebral appendage; pre-ocular crest present, continuous with the palpebral appendage; canthal crest present and well developed; row of tubercles ranging from the posterior corner of the eye to angle of jaw; vomerine teeth present; tongue cordiform, free posteriorly; frontoparietal crests poorly developed, with its outer margins parallels; region between frontoparietal crests slightly depressed; interocular ridge present and concave; tympanum not clearly defined; arm and forearm robust; forearms covered by conical tubercles; median outer metacarpal tubercles rounded and slightly prominent elliptical distal outer metacarpal tubercles; inner metacarpal tubercle elliptical; finger lengths IV ≈ II< I < III; fingers not webbed; legs elongate, with tibia longer than tight; tibia length plus thigh length corresponding to 93.4% of SVL; foot length approximately equal to thigh length; foot length representing 48.9% of snout vent length; outer metatarsal tubercle absent; inner metatarsal tubercle elliptical, poorly developed; toe lengths I<II≈V<III<IV; toes poorly webbed; rough skin, covered by tubercles which are more evident on the limbs, and triangular tubercles in the flank area; ocular-dorsal ridge continuous with palpebral appendages, reaching the dorsal extreme of urostyle, with spear shape.

Holotype Dimensions (mm): SVL: 32.1; HL: 15.9; HW: 16.9; THL: 14.2 TIL: 15.7; TRL: 7.5; FL: 15.7; HUL: 7.8; FAL: 8.1; HAL: 9.4; IOD: 6.5; END: 3.4; ESD: 6.85; IND: 1.5; NSD: 3.8 and ED: 3.5.

Color in life (names in parentheses from Smithe's catalog) (Fig.6A)**.** Dark brown color on the dorsum (Dark Grayish Brown); region between the oculo-dorsal ridges with brighter areas of a light brown color (Buff); anterior and posterior limbs color's similar to the dorsum, with light brown transversal stripes (Dark Drab); ventral surface of the body light brown (Clay color) with spaced darker spots more concentrated in the gular region (Dusky Brown); head with a black stain in the shape of an "M" between the canthal crests; dark brown iris (Cinnamon); tubercles of the ocular-dorsal ridge slightly lighter than the color of the dorsum (Raw umber).

Color in preservative. The color has fainted in preservative (70% ethanol), with the presence of transversal stripes on the limbs becoming more visible.

Variation. There is a variation in the hue of the dorsum, with some individuals darker than others. Measurements data are given in the Tables 2 and 3 for males and females respectively.

Geographical distribution. The new species is known from the municipalities of Angra dos Reis, Itaguaí, Mangaratiba and Paraty in Rio de Janeiro state, Brazil (Fig.7).

TABLE 2. Descriptive statistics of the measurements (mm) of adult males of *Proceratophrys izecksohni* **sp.nov.**, *Proceratophrys belzebul* **sp.nov.**, and *Proceratophrys appendiculata*. n, number of specimens; SD, standard deviation. Other abbreviations are defined in the text.

	P. izecksohni **sp.nov.** (n=9)	*P. belzebul* **sp.nov.** (n=10)	*P. appendiculata* (n=17)
SVL	40.5±7.4 (32.1–54.1)	48.0±3.9 (40.5–53.5)	52.8±4.7 (43.1–58.0)
HW	22.0±4.6 (17.9–28.3)	26.0±2.0 (23.0–28.4)	27.8±3.5 (17.2–33.6)
HL	20.0±3.6 (15.6–25.8)	23.4±2.0 (20.1–26.2)	25.0±3.3 (17.1–31.4)
THL	18.4±4.1 (14.3–26.7)	21.0±2.6 (17.8–24.5)	23.6±2.1 (19.1–26.2)
TIL	19.0±4.4 (14.3–27.0)	21.0±3.3 (18.2–22.4)	23.2±1.8 (19.6–25.8)
TRL	8.3±1.1 (7.0–10.7)	6.7±1.0 (5.8–9.1)	10.4±1.1 (7.3–12.2)
FL	19.4±4.0 (15.0–26.0)	23.0±2.1 (18.6–25.7)	24.7±1.6 (22.0–27.0)
HUL	9.4±2.3 (7.1–13.5)	10.7±1.8 (7.5–13.2)	12.2±1.6 (9.7–14.3)
FAL	9.6±2.4 (7.0–13.2)	10.6±1.0 (8.5–12.0)	12.0±1.2 (9.2–14.3)
HAL	11.6±2.3 (8.9–14.8)	14.0±1.2 (12.2–15.7)	14.6±1.1 (12.5–16.6)
IOD	8.5±1.3 (6.5–10.4)	10.1±0.7 (8.8–11.4)	10.6±0.7 (9.1–11.5)
END	4.3±0.7 (3.3–5.3)	4.7±0.3 (4.3–5.3)	5.00±0.5 (4.3–6.5)
ESD	9.8±3.9 (6.8–14.7)	10.2±0.8 (9.1–13.0)	11.0±1.1 (8.4–12.8)
IND	2.2±0.4 (1.6–2.8)	2.5±0.2 (2.1–3.0)	3.1±0.3 (2.3–3.8)
ED	3.5±0.5 (2.7–4.6)	3.9±0.3 (3.4–4.3)	4.3±0.5 (3.1–5.0)
NSD	5.0±0.9 (3.8–6.6)	5.4±0.6 (4.3–6.4)	5.8±0.9 (4.2–7.2)

TABLE 3. Descriptive statistics of the measurements (mm) of adult females of *Proceratophrys izecksohni* **sp.nov.**, *Proceratophrys belzebul* **sp.nov.**, and *Proceratophrys appendiculata*. n, number of specimens; SD, standard deviation. Other abbreviations are defined in the text.

	P. izecksohni **sp.nov.** (n=12)	*P. belzebul* **sp.nov.** (n=12)	*P. appendiculata* (n=7)
SVL	37.4±7.5 (30.4–50.0)	51.4±9.4 (34.6–62.0)	53.4±9.5 (39.5–61.8)
HW	20.4±4.5 (16.0–28.6)	27.26±6.6 (16.7–35.5)	27.0±4.9 (20.2–32.5)
HL	18.3±3.5 (14.6–25.1)	25.0±4.2 (17.0–30.7)	25.1±3.7 (19.5–29.0)
THL	16.5±3.5 (13.1–23.9)	22.1±4.2 (14.5–28.0)	23.7±4.0 (17.5–28.3)
TIL	17.3±3.5 (13.0–23.0)	23.0±4.3 (14.8–28.8)	23.0±3.6 (17.6–26.0)
TRL	7.8±2.0 (5.0–11.2)	7.7±1.9 (4.7–11.3)	10.4±2.7 (6.0–13.1)
FL	18.5±3.7 (14.5–24.5)	24.4±5.0 (15.1–30.0)	23.8±3.1 (19.1–28.1)
HUL	9.1±2.1 (6.4–12.3)	12.02.1 (8.4–16.0)	12.0±2.5 (8.4–14.4)
FAL	8.7±1.7 (6.3–11.8)	11.1±2.1 (8.1-13.5)	11.4±1.8 (8.6–13.0)
HAL	11.0±2.1 (8.6–14.1)	14.7±3.0 (9.1–18.0)	15.7±5.1 (10.9–26.7)
IOD	8.0±1.7 (5.5–10.4)	10.8±1.7 (8.0–13.2)	11.1±2.3 (8.04–12.0)
END	4.0±0.6 (2.7–4.7)	5.5±0.7 (4.1–6.9)	5.0±0.8 (3.6–6.0)
ESD	8.0±2.1 (3.1–11.1)	11.3±2.1 (7.6–14.4)	11.0±1.6 (8.7–13.0)
IND	2.2±0.5 (1.7–3.7)	2.8±0.7 (1.7–3.7)	3.2±0.7 (2.4–4.7)
ED	3.2±0.4 (2.3–4.0)	3.8±0.4 (3.0–4.5)	3.8±0.5 (2.9–4.5)
NSD	4.4±1.1 (3.0–6.7)	6.1±1.3 (3.7–8.0)	6.1±0.8 (4.9–7.0)

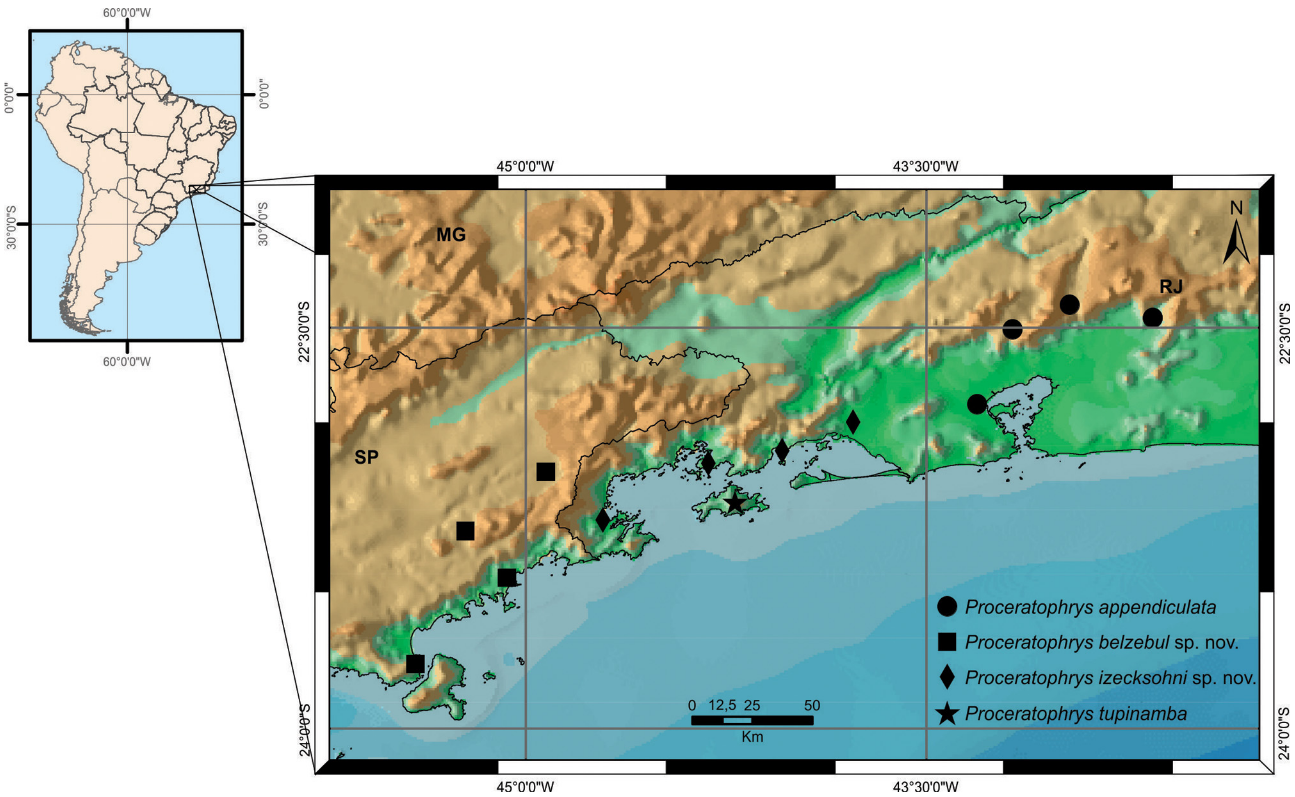

FIGURE 7. Geographic distribution of *Proceratophrys appendiculata* (circles); *Proceratophrys izecksohni* ***sp.nov.*** (diamonds); *Proceratophrys belzebul* ***sp.nov.*** (squares); and *Proceratophrys tupinamba* (star).

***Proceratophrys belzebul* sp.nov.**
(Figs.8–9)

Etymology. The specific epithet is an invariable noun in apposition and makes allusion to horn-like palpebral appendages and the dark color of the specimens. *Baal Zebub* is a Semitic deity that was worshiped in the Philistine—the prince of demons. *Belzebul* is one of the numerous variants of the latinized *Beelzebub*.

Holotype: CFBH 16283, adult male collected in Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, São Luis do Paraitinga municipality (23º20'S, 45º03') São Paulo state on 14 March, 2005 by L.O.M. Giasson (Figs.8A and 9).

Paratopotypes: Adult males—CFBH 5819 (21 January, 2003) (cleared and stained), CFBH 11302 (23 February, 2006) by L.M.O. Giasson, CFBH 14813 (19 December, 2006) (cleared and stained) by L.M.O. Giasson, C.P.A. Prado, O.G. Araújo and F. Zara. **Adult females—**CFBH 8410 (14 April, 2004), CFBH, 8411 (14 April, 2004) (Fig. 8B), CFBH 8062 (12 January, 2005), CFBH 10792 (24 January, 2006) by L.M.O. Giasson.

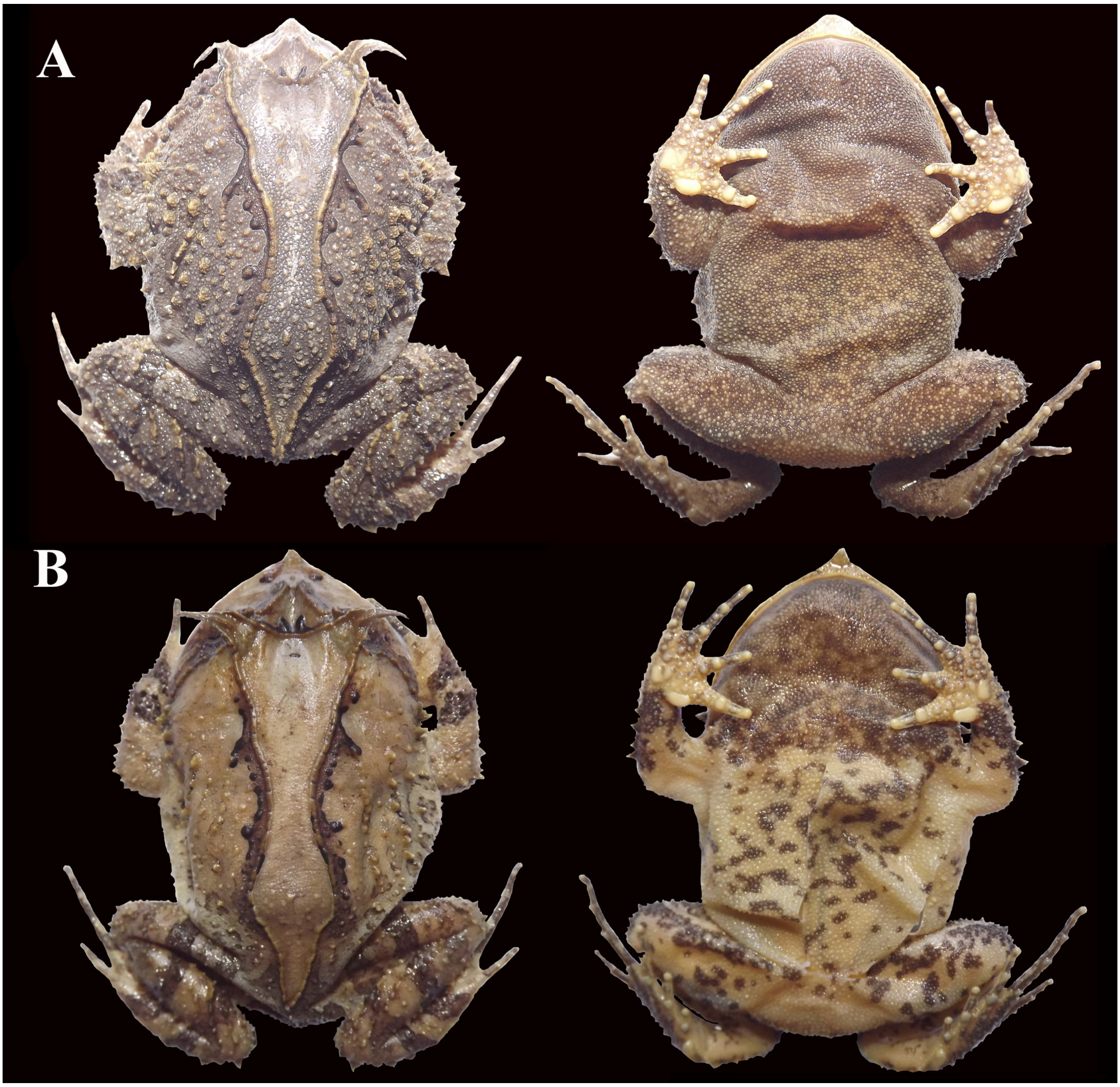

FIGURE 8. Dorsal (left) and ventral (right) views of the holotype of *Proceratophrys belzebul* **sp.nov.** (CFBH 16283; SVL 56.6 mm) (A); and dorsal (left) and ventral (right) views of the female of *Proceratophrys belzebul* **sp.nov.** (CFBH 8411; SVL 60.6 mm) (B).

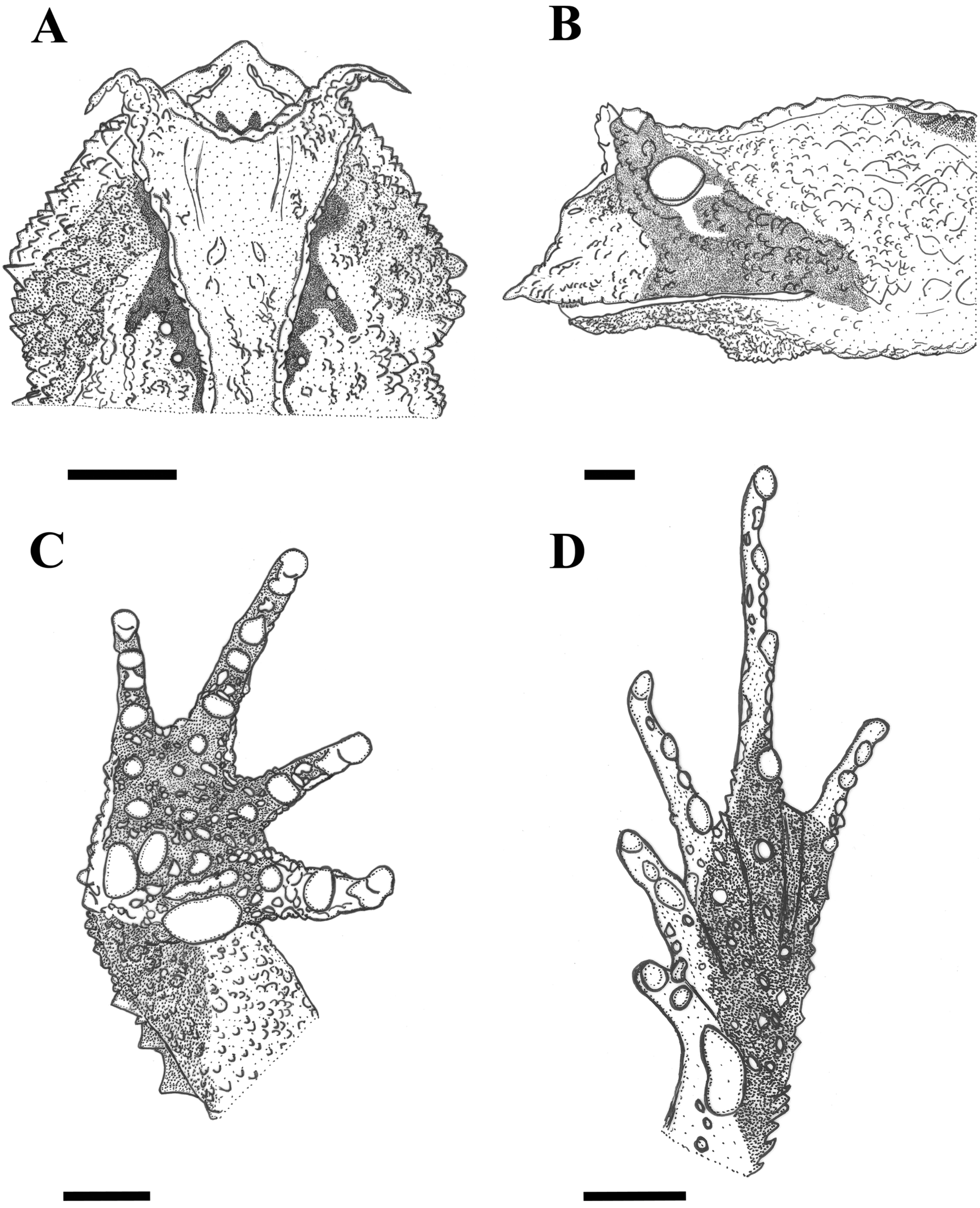

FIGURE 9. Dorsal (A) and lateral (B) views of the head; hand (C); and foot (D) of the holotype of *Proceratophrys izecksohni* **sp.nov.** (CFBH 16283; SVL 56.6 mm). Scale bar = 3,5 mm.

Other paratypes: *Cunha municipality*: **Adult males—**CFBH 29681 (01 February, 2005) (cleared and stained), CFBH 29682 (01 February, 2005) by D. Picinini. **Adult females—**CFBH 10751 (01 March, 2005), CFBH 10752 (01 March, 2005) by D. Seale, CFBH 29680 (01 February, 2005), CFBH 29684 (01 February, 2005), CFBH 29685 (01 February, 2005) by D. Picinini.

São Sebastião municipality: **Adult males—**CFBH 12110 (February, 2005) by M. Martins, MTR 9456 (May, 2000) by G. Skuk and D. Pavan.

Ubatuba municipality: **Adult male—**CFBH 5660 (15 October, 2002) (cleared and stained) by P.A. Hartmann. **Adult females—**CFBH 5414 (20 September, 2002), CFBH 21941 (09 January, 2009) by C.F.B.H. and S.F. Reis.

Diagnosis. The species is characterized by: 1) medium size (SVL 40.5–53.5 mm in males and 34.6–62.0 mm in females); 2) nasal bones broadly separated in their medial region; 3) nasal bone broadly separated from frontoparietal in their posterior region; 4) small iliac projection (iliac projection representing less than 30% of ilium diameter) (Fig.5F and G); 5) frontoparietal bones very depressed and broad rostrally (Fig.5E); 6) nasal and squamosal bones with smooth surface (without or with very reduced swellings and tubercles); 7) maxillary pits very reduced, almost vestigial; 8) female presenting the gular region dark brown (Fig. 8B).

Comparisons with other species (Data for species in comparison are given in parenthesis; biometric comparisons only between males). *Proceratophrys belzebul* differs from *P. laticeps*, *P. melanopogon*, *P. phyllostomus* and *P. subgutatta* by presenting a preocular cutaneous crest (preocular cutaneous absent). From *P. moehringi* by the presence of a well developed rostral appendage in adults (rostral appendage absent or vestigial). It differs from *P. sanctaritae* by the color of ventral surface of the body (predominantly cream with gular region black in *P. sanctaritae* and light brown with scattered dark dots all over the belly in *P. belzebul*), by the largest head in relation to snout-vent length (HL/SVL 49% in *P. belzebul* [47.3–50%] and 45% in *P. sanctaritae* [44–47%]) and in relation to head width (HL/HW 90% in *P. belzebul* [87–92%] and 80% in *P. sanctaritae* [78–83%]). It differs from *P. tupinamba* by the smaller size (SVL 40.5–53.5 mm in *P. belzebul* and SVL 52.6–63.4 in *P. tupinamba*), by the smaller eye diameter (ED/HL 16.2% in *P. belzebul* [16–17%] and 23% in *P. tupinamba* [24–24.2%]) and by the smaller foot (FL/SVL 48% in *P. belzebul* [46–48%] and 59% in *P. tupinamba* [63-67%]). It differs from *P. appendiculata* by the smaller size (SVL 40.5–53.5 mm in *P. belzebul* and 43.1–58.0 in *P. appendiculata*), by presenting the surface of the squamosal bones smooth, without or with very reduced projections and tubercles (surface of the squamosal covered with projections) (Fig. 5A and B), by presenting the outer margins of frontoparietals expanded rostrally (frontoparietal outer margins curved and medially expanded) (Fig. 5C and E), by having a small iliac projection (iliac projection representing less than 30% of ilium diameter in *P. belzebul* and more the 45% in *P. appendiculata*) (Fig. 5F and G), by presenting the nasal surface smoother (nasal with furrow and projections), by the deepness of ventral slits of maxillae (poorly deep in *P. belzebul* and very deep and evident in *P. appendiculata*), and by the presence of dark brown color in female's gular region (gular region of the same coloration of ventral surface in females). It differs from *P. izecksohni* by the smaller distance between eye and nostril (END/HL 21% in *P. belzebul* [19–21.3%] and 22% in *P. izecksohni* [21–23%]), by the smaller eye diameter (ED/HL16% in *P. belzebul* [16.4–17%] and 18% in *P. izecksohni* [17.3–18%]), by the smaller hindlimbs (THL+TIL/SVL 87.5% in *P. belzebul* [88–89%] and 93% in *P. izecksohni* [90–99%]), by having a smaller iliac projection (iliac projection representing approximately 28% in *P. belzebul* and more than 50% of ilium diameter in *P. izecksohni*), and by the shape of frontoparietal bones (broader rostrally in *P. belzebul* and almost uniform along their extension in *P. izecksohni*) (Fig. 5D and E).

Description of the holotype (Figs. 8A and 9)**.** Adult male with 56.6 mm of snout vent length; head elliptical, with much narrowed snout, wider than long; head length presenting 86.6% of head width; elliptical nostril, separated by a distance of approximately 80% of the eye diameter; distance of eye to snout corresponding to 45% of head length; eye to nostril distance of approximately 20.1% of the head length; eyes lateral, with a diameter equivalent to 14.3% of the head length; a single and long palpebral appendage; pre-ocular crest present, continuous with the palpebral appendage; canthal crest present and well developed; row of tubercles ranging from the posterior corner of the eye to angle of jaw; vomerine teeth present; tongue cordiform, free posteriorly; frontoparietal crests poorly developed, with parallel outer margins; region between frontoparietal crests slightly depressed, with its rostral portion deeper than the posterior; frontoparietals slightly wider on its rostral portion; interocular ridge present and concave; tympanum not clearly defined; arm and forearm robust; arm stout, very close to the body; metacarpal tubercles poorly developed; median outer metacarpal tubercles rounded and something like elliptical distal outer metacarpal tubercles; inner metacarpal tubercle elliptical; finger lengths IV ≈ II < I < III; fingers not webbed; tibia longer than tight; tibia length plus thigh length corresponding to 86.6% of SVL; foot longer than thigh and tibia; foot length represents 47.7% of snout vent length; outer metatarsal tubercle absent; inner metatarsal tubercle elliptical, well developed; toe lengths I<II<V<III<IV; very rough skin, covered by tubercles, well developed all over the body; ocular-dorsal ridge continuous with palpebral appendages, reaching the dorsal extreme of urostyle, with spear shape.

Holotype Dimensions (mm): SVL: 56.6; HL: 24.6; HW: 28.4; THL: 22.0 TIL: 21.9; TRL: 6.3; FL: 24.1; HUL: 10.7; FAL: 10.9; HAL: 14.6; IOD: 10.2; END: 5.3; ESD: 11.3; IND: 2.3; NSD: 6.3 and ED: 3.5.

Color in preservative (names in parentheses from Smithe's catalog). All dorsal and ventral surface of the body dark brown (Dark grayish). Darker (Dark brown) strips flanking the ocular-dorsal ridge and in the arms and legs. The gular region possesses the same dark coloration as the dorsum and ventral surface, both in males and females.

Variation. Specimens are congruent with respect to morphological characters. Some specimens (CFBH 11302; 29685) presented a black (Raw umber) mask-like pattern. Ventral surface also show some degree of variation, with specimens without brown dots presenting a completely uniform cream color, with exception of the gular region. Measurements data are given in the Tables 2 and 3 for males and females respectively.

Geographical distribution. The new species is known from the municipalities of Cunha, São Sebastião, São Luis do Paraitinga, and Ubatuba in São Paulo state, Brazil (Fig. 7).

Proceratophrys appendiculata **(Günther, 1873)**
(Fig. 10)

Holotype. BMNH 027, adult male, without collecting date (Fig. 10). Unfortunately the holotype could not be examined by us, because it could not be found in the collection of British Museum of Natural History (Mark Wilkinson and Barry Clarke, personal communication). Günther's (1873) description stated that specimen was purchased and it is from Brazil, but it could not be ascertained exactly from where. Boulenger (1882) redescribed the holotype housed at the British Museum, and no additional information about the locality was quoted. Nevertheless, the osteological data provided by Boulenger (1882) and Prado and Pombal (2008) compared to those retrieved from the cleared specimens examined indicate its probable origin. In the holotype (Fig. 10), as in specimens from Serra dos Órgãos (Fig. 5C), the outer margins of the frontoparietal bones are curved, and poorly developed, whereas in other species examined they are almost parallel and well developed, giving a characteristic shape to this bone. Thus, we propose that the type was collected somewhere at the Serra dos Órgãos.

Our finds also corroborate the taxonomic position of other taxa as junior synonym of *Proceratophrys appendiculata* such as *P. cafferi* (=*Ceratophrys cafferi*; Camerano, 1879) collected in Serra dos Órgãos and *P. unicolor* (= *Stombus appendiculatus* var. *unicolor*; Miranda-Ribeiro, 1926) collected in Japuíba, Cachoeiras de Macacu municipality, Rio de Janeiro state.

Diagnosis. The species is characterized by: 1) medium size (SVL 43.1–58.0 mm in males and 39.5–61.8 mm in females); 2) rounded head; 3) rounded snout in dorsal view; 4) frontoparietal crests slightly accentuated; 5) nasal bones do not contact each other (Fig. 4); 6) nasals do not contact the frontoparietal; 7) outer margin of frontoparietal bones curved and expanded medially (Fig. 5C); 8) squamosal bones with tubercles and crests (Fig. 5A); 9) maxillary pits very deep; 10) humerus very robust.

Comparisons with other species (Data for species in comparison are given in parenthesis; biometric comparisons only between males). *Proceratophrys appendiculata* differs from *P. laticeps*, *P. melanopogon*, *P. phyllostomus* and *P. subgutatta* for presenting a preocular cutaneous crest (preocular cutaneous absent). From *P. moehringi* by the presence of a well developed rostral appendage in adults (rostral appendage absent or vestigial). It differs from *P. sanctaritae* by the larger size (SVL 43.1–58.0 in *P. appendiculata* and 38.4–45.5 in *P. sanctaritae*), and by the longer hindlimbs (THL+TIL/SVL 89% in *P. appendiculata* [89–90%] and 83% in *P. sanctaritae* [80–84%]). It differs from *P. tupinamba* by the smaller eye diameter in relation to head length (ED/HL 16% in *P. appendiculata* [16–18%] and 23% in *P. tupinamba* [24–24.6%]) and by the smaller foot length (FL/SVL 47% in *P. appendiculata* [46–51%] and 59% in *P. tupinamba* [63–67%]). It also differs from *P. izecksohni* and *P. belzebul* by its robust humerus (humerus diameter representing approximately 55% of the greatest humerus width in *P. appendiculata* and less than 50% in *P. izecksohni* and *P. belzebul*).

Redescription of holotype. For redescription and further data on the holotype see Prado and Pombal (2008).

Geographical distribution. The species is known from the municipalities of Duque de Caxias, Cachoeiras de Macacu, Petrópolis, and Teresópolis in Rio de Janeiro state, Brazil (Fig. 7).

Conservation. Recent researches conduced with *Proceratophrys appendiculata* in the Serra dos Órgãos demonstrate some abnormalities in the tadpole's development (Dias & Carvalho-e-Silva 2012). These findings become more relevant now that the geographic distribution of the species is reduced. As Dias & Carvalho-e-Silva (2012) attest, more investigations on this population are needed.

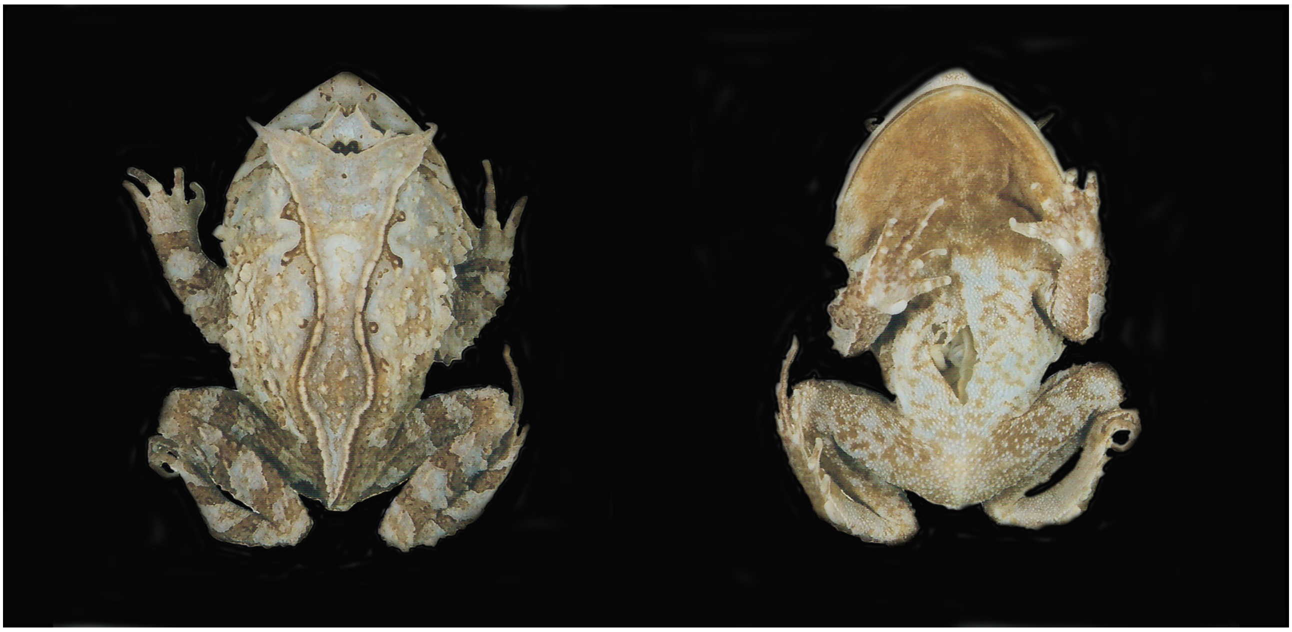

FIGURE 10. Dorsal (left) and ventral (right) views of the holotype of *Proceratophrys appendiculata* (BMNH 027; SVL 50.0 mm).

Molecular data

Our analysis recovered a monophyletic *Proceratophrys* with high support, however none of the traditional phenetic assemblages of the genus were recovered as monophyletic, except for the *P. bigibbosa* group represented by *P. avelinoi* and *P. bigibbosa* (Fig. 11). Three major lineages were recovered: one containing *P. cristiceps*, *P. minuta*, *P. redacta* and *P. schirchi*, sister group of remaining species; other composed by *P. avelinoi* and *P. bigibbosa*, and a third lineage that includes the remaining species of the genus.

In this third lineage a clade comprising *Proceratophrys appendiculata*, *P. tupinamba*, *P. izecksohni* and *P. belzebul* was recovered. In this clade *P. izecksohni* is the sister group of all other species, *P. appendiculata* clusters with *P. tupinamba* and both are sister to *P. belzebul*. These relationships were recovered both in analysis of only mitochondrial genes (Fig. 12A), as well in combined dataset (Fig. 11). When only nuclear dataset is analyzed, all lineages are recovered as single clade (Fig. 12B), but haplotype network of Rag-1 marker showed no sharing of haplotypes among the four lineages (Fig. 12C), as the mitochondrial dataset (data not shown).

Proceratophrys laticeps (included in *appendiculata* complex) is included in a clade with low support comprising species from Atlantic Forest (*P. boiei*, *P. renalis*, and *P. cururu*), and from Cerrado (*P. goyana*, *P. concavitympanum*, and *P. moratoi*). *Proceratophrys melanopogon*, which possesses palpebral and rostral appendages, is recovered as sister of the former clades in BA, but in ML analysis its monophyly was not recovered, with individuals from Santos, Bertioga and São Sebastião (SP) recovered as sister to a clade composed by *P. appendiculata*, *P. belzebul*, *P. izecksohni*, *P. tupinamba* and the remaining *P. melanopogon* individuals. It is interesting to note that *P. melanopogon* is highly structured, and may represent a complex of cryptic species as also indicated after preliminary morphometric analysis from Mângia, Santana & Feio (2011).

Uncorrected *p* distances among *Proceratophrys* species ranged from 1 to 11% for 16S and 1 to 5% for Rag-1 (Table 3). Distances of 16S among *P. appendiculata*, *P. belzebul* and *P. tupinamba* were lower (1–2%) than to *P. izecksohni* (3–4%), but differences among the sequences of each species were not shared.

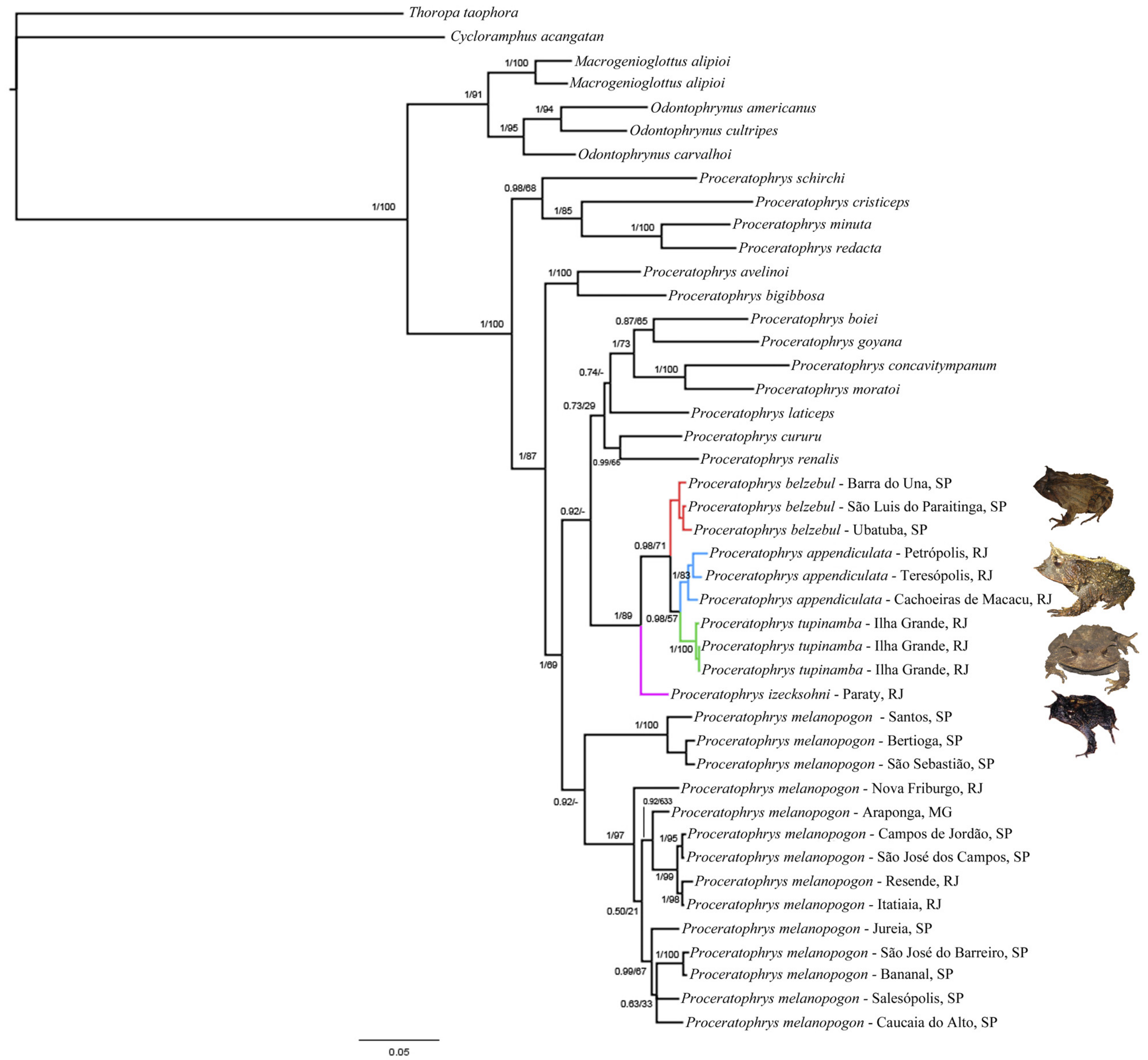

FIGURE 11. Bayesian tree topology obtained from the combined molecular data set (16S, 12S, cyt*b,* Rag-1 and rhodopsin); Figure shows the 50% majority-rule consensus phylogram. Posterior probability and ML bootstrap values are shown above the branches.

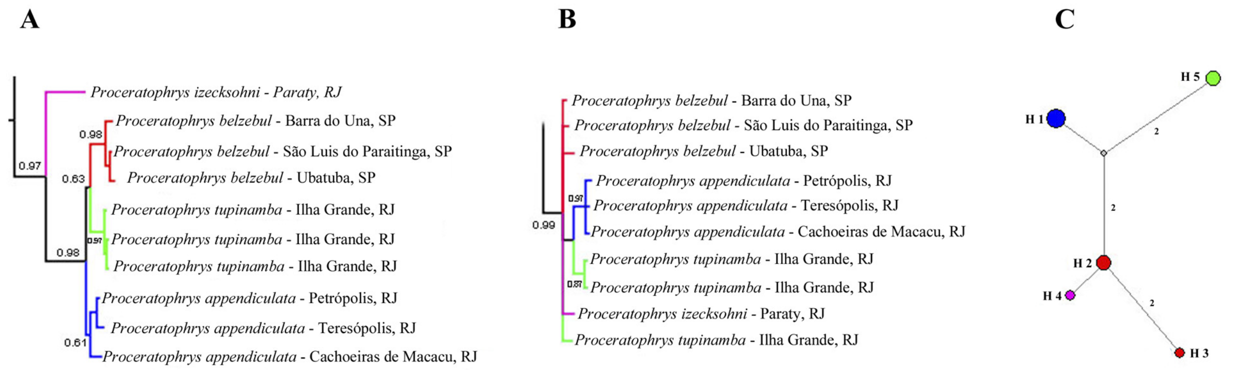

FIGURE 12. Bayesian tree topology obtained from (A) mitochondrial (16s, 12S and cyt *b*) and (B) nuclear (Rag-1 and rhodopsin) datasets of *P. appendiculata* species complex. C) Haplotype network of Rag-1. H1=haplotype of individuals of *P. appendiculata* from Teresópolis, Petrópolis and Cachoeiras de Macacu, RJ; H2=*P. belzebul* individuals from Barra do Una and São Luis do Paraitinga, SP; H3= *P. belzebul* from Ubatuba, SP; H4=*P. izecksohni* from Paraty, RJ; H5= 3 individuals of *P. tupinamba* from Ilha Grande, RJ.

TABLE 4. Uncorrected *p* distances among species of *Proceratophrys* of mitochondrial genes 16S (diagonal below) and Rag-1 (diagonal above).

Taxons	1	2	3	4	5	6	7	8	9	10	11	12
1) *P. avelinoi*		0.01	0.03	0.03	0.05	0.02	0.03	0.01	0.02	0.02	0.03	0.04
2) *P. bigibbosa*	0.04		0.02	0.02	0.05	0.02	0.03	0.02	0.02	0.03	0.04	0.04
3) *P. boiei*	0.07	0.07		0.02	0.04	0.02	0.02	0.02	0.01	0.03	0.04	0.04
4) *P. concavitympanum*	0.07	0.07	0.08		0.04	0.03	0.02	0.02	0.01	0.02	0.03	0.04
5) *P. cristiceps*	0.08	0.09	0.10	0.09		0.05	0.04	0.04	0.04	0.04	0.05	0.04
6) *P. cururu*	0.05	0.04	0.06	0.08	0.09		0.02	0.02	0.02	0.01	0.04	0.04
7) *P. goyana*	0.05	0.05	0.05	0.07	0.09	0.04		0.02	0.01	0.03	0.04	0.04
8) *P. laticeps*	0.04	0.04	0.05	0.07	0.08	0.03	0.04		0.01	0.01	0.03	0.03
9) *P. moratoi*	0.07	0.08	0.07	0.06	0.08	0.07	0.07	0.06		0.02	0.03	0.03
10) *P. renalis*	0.06	0.06	0.06	0.08	0.09	0.03	0.05	0.03	0.08		0.04	0.03
11) *P. schirchi*	0.07	0.07	0.08	0.09	0.07	0.07	0.08	0.06	0.08	0.08		0.05
12) *P. minuta*	0.08	0.06	0.09	0.10	0.06	0.08	0.08	0.08	0.10	0.09	0.07	
13) *P. redacta*	0.08	0.06	0.10	0.09	0.08	0.09	0.09	0.08	0.11	0.09	0.08	0.04
14) *P. melanopogon* Santos SP	0.07	0.07	0.08	0.10	0.10	0.06	0.06	0.06	0.09	0.08	0.09	0.10
15) *P. melanopogon* Caucaia SP	0.04	0.04	0.07	0.07	0.08	0.04	0.05	0.03	0.07	0.05	0.07	0.08
16) *P. melanopogon* E.B. Boracéia SP	0.04	0.04	0.07	0.07	0.07	0.03	0.05	0.03	0.06	0.05	0.06	0.07
17) *P. melanopogon* Jureia SP	0.05	0.05	0.07	0.08	0.08	0.03	0.05	0.03	0.07	0.05	0.07	0.08
18) *P. melanopogon* S. José dos Campos SP	0.04	0.04	0.06	0.07	0.08	0.03	0.05	0.02	0.06	0.04	0.06	0.07
19) *P. melanopogon* Araponga MG	0.05	0.04	0.06	0.07	0.07	0.03	0.05	0.03	0.06	0.05	0.06	0.07
20) *P. melanopogon* Bertioga SP	0.06	0.06	0.07	0.08	0.08	0.05	0.05	0.05	0.07	0.06	0.08	0.08
21) *P. melanopogon* Nova Friburgo RJ	0.05	0.04	0.06	0.07	0.08	0.03	0.05	0.02	0.06	0.05	0.07	0.08
22) *P. melanopogon* Itatiaia RJ	0.05	0.04	0.06	0.07	0.08	0.03	0.05	0.02	0.06	0.05	0.07	0.07
23) *P. melanopogon* E.E. Bananal SP	0.05	0.05	0.07	0.08	0.08	0.04	0.05	0.03	0.07	0.05	0.07	0.08
24) *P. melanopogon* Campos do Jordão SP	0.04	0.04	0.06	0.07	0.08	0.03	0.05	0.02	0.06	0.04	0.06	0.07
25) *P. melanopogon* São Sebastião SP	0.05	0.05	0.06	0.08	0.08	0.05	0.04	0.04	0.07	0.06	0.07	0.08
26) *P. melanopogon* S. José do Barreiro SP	0.05	0.05	0.07	0.08	0.08	0.04	0.05	0.03	0.07	0.05	0.07	0.08
27) *P. melanopogon* Resende RJ	0.05	0.04	0.06	0.07	0.08	0.03	0.05	0.02	0.06	0.05	0.07	0.07
28) *P. appendiculata* Teresopolis RJ	0.05	0.04	0.05	0.06	0.07	0.04	0.04	0.03	0.06	0.04	0.06	0.07
29) *P. appendiculata* Petropolis RJ	0.05	0.05	0.05	0.06	0.07	0.04	0.05	0.03	0.05	0.04	0.06	0.07
30) *P. appendiculata* Cachoeiras de Macacu RJ	0.05	0.04	0.06	0.06	0.07	0.03	0.04	0.03	0.06	0.04	0.06	0.07
31) *P. belzebul* Barra do Una SP	0.06	0.06	0.07	0.08	0.09	0.05	0.06	0.04	0.08	0.06	0.08	0.09
32) *P. belzebul* S. Luis do Paraitinga SP	0.05	0.05	0.06	0.07	0.07	0.04	0.05	0.03	0.06	0.05	0.07	0.07
33) *P. belzebul* Ubatuba SP	0.05	0.05	0.06	0.06	0.08	0.04	0.05	0.04	0.06	0.05	0.07	0.07
34) *P. izecksohni* Paraty RJ	0.04	0.04	0.06	0.07	0.07	0.03	0.05	0.03	0.06	0.05	0.06	0.07
35) *P. tupinamba*	0.05	0.04	0.06	0.06	0.07	0.04	0.04	0.03	0.06	0.04	0.07	0.07
36) *P. tupinamba*	0.05	0.04	0.06	0.06	0.07	0.04	0.04	0.03	0.06	0.04	0.07	0.07
37) *P. tupinamba*	0.05	0.04	0.06	0.06	0.07	0.04	0.04	0.03	0.06	0.04	0.07	0.07

……continued on the next page

TABLE 4. (Continued)

Taxons	13	14	15	16	17	18	19	20	21	22	23	24
1) *P. avelinoi*	0.04	0.02	0.02	-	0.02	0.02	0.02	0.02	0.02	0.02	0.02	-
2) *P. bigibbosa*	0.04	0.02	0.02	-	0.02	0.02	0.03	0.02	0.03	0.02	0.02	-
3) *P. boiei*	0.03	0.02	0.02	-	0.02	0.03	0.03	0.03	0.03	0.03	0.03	-
4) *P. concavitympanum*	0.03	0.03	0.03	-	0.03	0.03	0.04	0.03	0.03	0.03	0.03	-
5) *P. cristiceps*	0.04	0.05	0.05	-	0.04	0.05	0.05	0.05	0.04	0.05	0.05	-
6) *P. cururu*	0.04	0.02	0.02	-	0.02	0.02	0.03	0.02	0.02	0.02	0.02	-
7) *P. goyana*	0.04	0.02	0.03	-	0.02	0.03	0.03	0.03	0.03	0.03	0.03	-
8) *P. laticeps*	0.03	0.01	0.01	-	0.01	0.02	0.02	0.01	0.02	0.02	0.02	-
9) *P. moratoi*	0.03	0.02	0.02	-	0.02	0.03	0.03	0.02	0.03	0.03	0.03	-
10) *P. renalis*	0.03	0.02	0.02	-	0.02	0.03	0.03	0.03	0.02	0.03	0.03	-
11) *P. schirchi*	0.04	0.04	0.03	-	0.03	0.03	0.03	0.03	0.03	0.03	0.04	-
12) *P. minuta*	0.02	0.04	0.04	-	0.04	0.05	0.04	0.04	0.04	0.05	0.04	-
13) *P. redacta*		0.04	0.04	-	0.04	0.04	0.04	0.04	0.04	0.04	0.04	-
14) *P. melanopogon* Santos SP	0.11		0.02	-	0.02	0.02	0.02	0.02	0.02	0.02	0.02	-
15) *P. melanopogon* Caucaia SP	0.08	0.06		-	0.00	0.01	0.01	0.02	0.01	0.01	0.01	-
16) *P. melanopogon* E.B. Boracéia SP	0.08	0.05	0.01		-	-	-	-	-	-	-	-
17) *P. melanopogon* Jureia SP	0.08	0.06	0.02	0.02		0.01	0.01	0.02	0.01	0.01	0.01	-
18) *P. melanopogon* S. José dos Campos SP	0.08	0.05	0.02	0.01	0.02		0.01	0.02	0.01	0.00	0.01	-
19) *P. melanopogon* Araponga MG	0.08	0.05	0.02	0.01	0.02	0.01		0.03	0.01	0.01	0.02	-
20) *P. melanopogon* Bertioga SP	0.09	0.02	0.04	0.04	0.04	0.04	0.04		0.03	0.02	0.03	-
21) *P. melanopogon* Nova Friburgo RJ	0.08	0.05	0.02	0.01	0.02	0.00	0.01	0.04		0.01	0.01	-
22) *P. melanopogon* Itatiaia RJ	0.08	0.05	0.02	0.01	0.02	0.00	0.01	0.03	0.00		0.01	-
23) *P. melanopogon* E.E. Bananal SP	0.08	0.06	0.01	0.01	0.02	0.01	0.02	0.04	0.02	0.02		-
24) *P. melanopogon* Campos do Jordão SP	0.08	0.05	0.02	0.01	0.02	0.00	0.01	0.04	0.00	0.00	0.01	-
25) *P. melanopogon* São Sebastião SP	0.09	0.02	0.04	0.03	0.04	0.03	0.03	0.00	0.03	0.03	0.04	0.03
26) *P. melanopogon* S. José do Barreiro SP	0.08	0.05	0.01	0.01	0.02	0.01	0.02	0.04	0.02	0.02	0.00	0.01
27) *P. melanopogon* Resende RJ	0.07	0.05	0.02	0.01	0.02	0.00	0.01	0.03	0.00	0.00	0.02	0.00
28) *P. appendiculata* Teresopolis RJ	0.08	0.07	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	0.05	0.04
29) *P. appendiculata* Petropolis RJ	0.08	0.07	0.05	0.04	0.05	0.03	0.04	0.05	0.04	0.04	0.05	0.03
30) *P. appendiculata* Cachoeiras de Macacu RJ	0.07	0.06	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.04	0.04	0.04
31) *P. belzebul* Barra do Una SP	0.10	0.07	0.06	0.05	0.06	0.05	0.05	0.07	0.05	0.05	0.06	0.05
32) *P. belzebul* S. Luis do Paraitinga SP	0.08	0.07	0.05	0.04	0.05	0.03	0.04	0.05	0.04	0.04	0.05	0.03
33) *P. belzebul* Ubatuba SP	0.08	0.07	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	0.05	0.04
34) *P. izecksohni* Paraty RJ	0.07	0.05	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01
35) *P. tupinamba*	0.08	0.07	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	0.05	0.04
36) *P. tupinamba*	0.08	0.07	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	0.05	0.04
37) *P. tupinamba*	0.08	0.07	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	0.05	0.04

……continued on the next page

TABLE 4. (Continued)

Taxons	25	26	27	28	29	30	31	32	33	34	35	36
1) *P. avelinoi*	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.02	0.02
2) *P. bigibbosa*	0.02	0.02	0.02	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.02	0.02
3) *P. boiei*	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03
4) *P. concavitympanum*	0.03	0.03	0.04	0.03	0.03	0.03	0.02	0.02	0.02	0.03	0.03	0.03
5) *P. cristiceps*	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04
6) *P. cururu*	0.02	0.02	0.02	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02
7) *P. goyana*	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
8) *P. laticeps*	0.01	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.01	0.01
9) *P. moratoi*	0.02	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
10) *P. renalis*	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.02	0.02
11) *P. schirchi*	0.03	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.03	0.03
12) *P. minuta*	0.04	0.04	0.05	0.04	0.04	0.04	0.03	0.03	0.03	0.04	0.04	0.04
13) *P. redacta*	0.04	0.04	0.04	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.02	0.02
14) *P. melanopogon* Santos SP	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
15) *P. melanopogon* Caucaia SP	0.02	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.01	0.01
16) *P. melanopogon* E.B. Boracéia SP	-	-	-	-	-	-	-	-	-	-	-	
17) *P. melanopogon* Jureia SP	0.02	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.02	0.01	0.01	0.01
18) *P. melanopogon* S. José dos Campos SP	0.02	0.01	0.00	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
19) *P. melanopogon* Araponga MG	0.03	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
20) *P. melanopogon* Bertioga SP	0.00	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.02	0.02
21) *P. melanopogon* Nova Friburgo RJ	0.03	0.01	0.01	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02
22) *P. melanopogon* Itatiaia RJ	0.02	0.01	0.00	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
23) *P. melanopogon* E.E. Bananal SP	0.03	0.00	0.01	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02
24) *P. melanopogon* Campos do Jordão SP	-	-	-	-	-	-	-	-	-	-	-	-
25) *P. melanopogon* São Sebastião SP		0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.02	0.02
26) *P. melanopogon* S. José do Barreiro SP	0.03		0.01	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02
27) *P. melanopogon* Resende RJ	0.03	0.02		0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.02	0.02
28) *P. appendiculata* Teresopolis RJ	0.05	0.05	0.04		0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
29) *P. appendiculata* Petropolis RJ	0.05	0.05	0.04	0.01		0.00	0.01	0.01	0.01	0.01	0.01	0.01
30) *P. appendiculata* Cachoeiras de Macacu RJ	0.05	0.04	0.04	0.01	0.01		0.01	0.01	0.01	0.01	0.01	0.01
31) *P. belzebul* Barra do Una SP	0.06	0.06	0.05	0.02	0.02	0.02		0.00	0.01	0.01	0.01	0.01
32) *P. belzebul* S. Luis do Paraitinga SP	0.05	0.05	0.04	0.01	0.01	0.01	0.01		0.01	0.01	0.01	0.01
33) *P. belzebul* Ubatuba SP	0.05	0.05	0.04	0.01	0.01	0.01	0.01	0.00		0.01	0.02	0.02
34) *P. izecksohni* Paraty RJ	0.03	0.01	0.01	0.04	0.03	0.03	0.04	0.03	0.04		0.01	0.01
35) *P. tupinamba*	0.05	0.05	0.04	0.01	0.01	0.01	0.02	0.01	0.01	0.03		0.00
36) *P. tupinamba*	0.05	0.05	0.04	0.01	0.01	0.01	0.02	0.01	0.01	0.03	0.00	
37) *P. tupinamba*	0.05	0.05	0.04	0.01	0.01	0.01	0.02	0.01	0.01	0.03	0.00	0.00

Discussion

The genus *Proceratophrys* have been shown more diverse than previously thought—ten new species were described in the last five years (Prado & Pombal 2008; Cruz & Napoli 2010; Ávila *et al.* 2011, 2012; Martins & Giaretta 2011; Napoli *et al.* 2011; Cruz *et al*. 2012; Teixeira *et al*. 2012). Despite these efforts, the taxonomic position of many species still remains doubtful. Osteological, morphometric and molecular analysis led us to recognize three species under the name *Proceratophrys appendiculata*.

Based on the topology recovered in our molecular analysis, we could propose two different scenarios: 1) all lineages belong to a single species (*P. appendiculata*) and *P. tupinamba* should be synonymized to *P. appendiculata*; or 2) individuals from São Paulo state and from Paraty, Rio de Janeiro state are species closed related to *P. appendiculata* and should be described. In addition to reciprocal monophyly in mitochondrial genes, the lineages also have different haplotypes in the nuclear gene Rag-1 which could indicate a probable lack of gene flow among the lineages. As also additional lines of evidence are concordant, i.e., osteological and morphometric differences among the lineages, the second scenario was favored and we described *Proceratophrys izecksohni* and *P. belzebul*.

Despite the extensive revision made by Prado and Pombal (2008) for the species with palpebral appendages, some populations associated with the *Proceratophrys appendiculata* complex, as those from Serra dos Órgãos and São Paulo state lacked a detailed analysis of their osteological features. The cranial osteology of the specimens of these areas proved to be very similar to that described by Prado and Pombal (2008) for *P. tupinamba*, with individuals having no contact between the nasal bones, or between nasal and frontoparietal bones.

However, morphometric differences, characters from external morphology and other osteological features, like the prominence of the iliac projection, the deepness of the maxillary pits, the smoothness of squamosal and nasal bones, proved to be diagnostic, and, associated with molecular data allowed us to describe *Proceratophrys belzebul*.

Together with the insular species *Proceratophrys tupinamba*, the three species analyzed here present a very interesting subject to evolutionary and biogeographical studies (Miranda & Dias 2012). Contrarily to expected from geographical evidence, our molecular analysis recovered a sister relationship between *P. appendiculata* and *P. tupinamba*. Considering the oscillations of sea level during the Quaternary affecting this part of the coast (Mahiques *et al*. 2010.), and their geographic proximity it was much more reasonable to admit a sister relationship between *P. tupinamba*, apparently isolated at Ilha Grande with *P. izecksohni* which occurs on the adjacent mainland. This intriguing puzzle reveals how far we are to understand the diversification of these species and the biogeography of the Brazilian Atlantic Forest. Molecular evidences indicate that the region between southeastern of Rio de Janeiro and northeast of São Paulo state is an important zone of phylogeographic break associated with early Pliocene or late Pleistocene (Grazziotin *et al.* 2006; Martins *et al*. 2011; Amaro *et al.* 2012), as well of intense tectonic activity (Saadi 1993; Riccomini *et al*. 2010).

The level of genetic divergence among these close related species could indicate that the differentiation of lineages occurred recently when compared to *P. boiei* lineages (Amaro *et al*. 2012), but additional data are necessary to test this hypothesis. Despite the low values of genetic distances between *Proceratophrys appendiculata*, *P. belzebul* and *P. tupinamba* our data set provides support to recognize them as separated evolutionary lineages (Wiley 1978), both by congruence and accumulation of different sources of data. Each of them represents a clade recovered by both the likelihood and the Bayesian analysis, and they do not share haplotypes in Rag-1. They also can be distinguished by osteological and morphometric characters, some of them autapomorphic, *e.g.* frontoparietal shape, texture of the surface of squamosal, maxillary pits and robustness of the humerus, foot length, among others (see species descriptions and comparisons).

Besides, differences between the tadpoles of *Proceratophrys appendiculata* and *P. tupinamba* are remarkable—to date it was observed on morphometric analysis and especially on color pattern studies (Peixoto & Cruz 1981; Fatorelli *et al*. 2010; P.H.S. Dias personal observation). All those differences, associated to geographical distribution—*Proceratophrys tupinamba* is an endemic insular species and *P. appendiculata* and *P. belzebul* are disjunctly distributed, with *P. izecksohni* standing between then—provide strong evidences to consider those lineages as valid taxonomic species despite the low genetic distance among them.

As noted by Martins and Giaretta (2011) for Brazilian savannahs, our findings suggest that the real diversity of the genus *Proceratophrys* in the Atlantic forest is still underestimated. Integrative taxonomic approaches (Padial *et al.* 2010) for other species of the genus might contribute to our knowledge of the evolutionary history of South America.

Acknowledgements

We thank Sergio P. de Carvalho e Silva for his suggestions during this work; we would like to thank José. P. Pombal Jr., Eugenio Izecksohn, Célio F.B. Haddad, Hussam Zaher and Oswaldo L. Peixoto for the access to the collections; we thank Nadya Pupin for her assistance with the borrowing of CFBH specimens. We thank Gustavo M. Prado for gently conceding the picture of the holotype of *Proceratophrys appendiculata* and Célio F.B. Haddad and Pedro Fatorelli for providing pictures of living specimens of *P. belzebul* and *P. tupinamba* respectively; we thank Mark Wilkinson and Barry Clarke for they efforts in finding the holotype of *P. appendiculata*; we are very thankful to Fabio Hepp for his assistance with statistical analysis; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the fellowship conceded to P.H.S. Dias; Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support to M.T. Rodrigues and R.C. Amaro , and IBAMA/RAN for the collection permits (number 13256-1).We thank the following persons for their invaluable help in the field, collecting specimens or sending tissues: D. Baldo; A.C. Carnaval; J. Cassimiro; F. Dal Vechio; M. Dixo; S. Favorito; R. Fernandes; T. Grant; J.M. Ghellere; C.F.B. Haddad; F.S.F. Leite; A.C. Leonel; D.T. Pavan; J.P. Pombal Jr; R.S. Recoder; D. Santana; J.W. Silva; G. Skuk; M. Teixeira Jr; V.K. Verdade; D. Vrcibradic and H. Zaher and; and Sabrina Baroni for technical assistance. Finally, we are very thankful to Dr. Miguel Vences and an anonymous reviewer for their helpful and valuable comments and suggestions on the earlier version of this contribution.

References

Amaro, R.C., Pavan, D. & Rodrigues, M.T. (2009) On the generic identity of *Odontophrynus moratoi* Jim & Caramaschi, 1980 (Anura; Cycloramphidae). *Zootaxa*, 2071, 61–68.

Amaro, R.C., Carnaval, A.C.Q., Yonenaga-Yassuda, Y. & Rodrigues, M.T. (2012) Demographic process in montane Atlantic rainforest: Molecular and cytogenetic evidence from the endemic frog *Proceratophrys boiei*. *Molecualar Phylogenetics and Evolution*, 62, 880–888.
http://dx.doi.org/10.1016/j.ympev.2011.11.004

Ávila, R.W., Kawashita-Ribeiro, R.A. & Morais, D.H. (2011) A new species of *Proceratophrys* (Anura: Cycloramphidae) from western Brazil. *Zootaxa*, 2890, 20–28.

Ávila, R.W., Pansonato, A. & Strüssmann, C. (2012) A new species of *Proceratophrys* (Anura; Cycloramphidae) from Midwestern Brazil. *Journal of Herpetology*, 46(4), 446–472.
http://dx.doi.org/10.1670/11-038

Bandelt, H.J., Forster, P. & Röhl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, 16, 37–48.
http://dx.doi.org/10.1093/oxfordjournals.molbev.a026036

Bickham, J.W., Wood, C.C. & Patton, J.C. (1995) Biogeographic implications of Cytochrome *b* sequences and allozymes in sockeye (*Oncorhynchusnerka*). *Journal of Heredity*, 86, 140–144.

Bossuyt, F., & Milinkovitch, M.C. (2000). Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences USA*, 97, 6585–6590.

Boulenger, G.A. (1882) *Catalog of the Batrachia Salientia S. Ecaudata in the Collection of the British Museum*. Second Edition. British Museum, London.

Bumbury, B. & Maglia, A.M. (2006) Skeletal development of the Mexican spadefoot, *Spea multiplicata* (Anura: Paleobatidae). *Journal of Morphology*, 267, 803–821.
http://dx.doi.org/10.1002/jmor.10441

Camerano, L. (1879) Anfibii anuri esistenti nelle collezioni del R. Museo Zoológico. *Atti Della Reale Academia delleScienze di Torino, Classe di ScienzeFisiche e Matematiche*, 14, 866–898.

Carvalho, A.L. (1946) Um novo gênero de ceratofridídieo do sudeste baiano. *Boletim do Museu Nacional. Nova Serie Zoologia*, 73, 1–18.

Cruz, C.A.G. & Napoli, M.F. (2010) A new species of smooth horned frog, genus *Proceratophrys* Miranda-Ribeiro (Amphibia: Anura: Cycloramphidae), from the Atlantic Rain Forest eastern Bahia, Brazil. *Zootaxa*, 1660, 57–67.

Cruz, C.A.G., Prado, G.M.& Izecksohn, E. (2005) A new species of *Proceratophrys* Miranda-Ribeiro, 1920 from Southeastern Brazil (Amphibia, Anura, Leptodactylidae). *Arquivos do Museu Nacional*, 63, 289–295.

Cruz, C.A.G., Nunes, I. & Juncá, F.A. (2012) Redescription of *Proceratophrys cristiceps* (Müller, 1883) (Amphibia, Anura, Cycloramphidae), with description of two new species without eyelid appendages from northeastern Brazil. *South America Journal of Herpetology*, 7, 110–122.
http://dx.doi.org/10.2994/057.007.0201

Dias, P.H.S. & Carvalho-e-Silva, A.M.P.T. (2012) Records of abnormalities in *Proceratophrys appendiculata* (Günther, 1873) (Anura; Cycloramphydae; Alsodinae). *Herpetology Notes*, 5, 197–199.

Duellman, W.E. (1970) The Hylidae frogs of Middle America. *Monography of American Museum of Natural History, University of Kansas*, 1, 1–80.

Duméril, A.M.C. & Bibron, G. (1841) *Erpétologie Genérale ou Histoire Naturelle Complète des Reptiles*. Librarie Encyclopedique de Roret.

Eterovick, P. & Sazima, I. (1998) New species of *Proceratophrys* (Anura: Leptodactylidae) from southeastern Brazil. *Copeia*, 159–164.

Faivovich, J., Haddad, C.F., Garcia, P.C., Frost, D.R., Campbell, J.A. & Wheeler, W.C. (2005) Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, 294, 1–240.
http://dx.doi.org/10.1206/0003-0090(2005)294[0001:SROTFF]2.0.CO;2

Fatorelli, P., Costa, P.N., Laia, R.C., Almeida-Santos, M., Van Sluys, M. & Rocha, C.F.D. (2010) Description, microhabitat and temporal distribution of the tadpole of *Proceratophrys tupinamba* Prado and Pombal, 2008. *Zootaxa*, 1684, 57–62.

Fetzner, J.W. (1999) Extracting high-quality DNA from shed reptile skins: A simplified method. *Biotechniques*, 26, 1052–1054.

Frost, D.R. (2013). Amphibian Species of the World: an Online Reference. Version 5.6 (9 January 2013). Electronic Database available from: http://research.amnh.org/herpetology/amphibia/index.html (Accessed 26 June 2013) American Museum of Natural History, New York, USA.

Giaretta, A.A., Bernarde, P.S. & Kokubum, M.N.C. (2000) A new species of *Proceratophrys* (Anura: Leptodactylidae) from the Amazon Rain Forest. *Journal of Herpetology*, 34, 173–178.
http://dx.doi.org/10.2307/1565412

Giaretta, A.A. & Sazima, I. (1993) Nova espécie de *Proceratophrys* Mir. Rib. do Sul de Minas Gerais, Brasil (Amphibia, Anura, Leptodactylidae). *RevistaBrasileira de Biologia*, 53, 13–19.

Grazziotin, F.G., Monzel, M., Echeverrigaray, S. & Bonatto, S.L. (2006) Phylogeography of the *Bothrops jararaca* complex (Serpentes: Viperidae): past fragmentation and island colonization in the Brazilian Atlantic Forest. *Molecular Ecology*, 15, 3969–3982.
http://dx.doi.org/10.1111/j.1365-294X.2006.03057.x

Günther, A.C.L.G. (1873) Contribution to our knowledge of *Ceratophrys* and *Megalophrys*. *Annals and Magazine of Natural History*, 11, 417–419.

Heyer, W.R. (2005) Variation and taxonomic classification of the large species of *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. *Arquivos de Zoologia*, 37, 269–348.

Izecksohn, E. & Peixoto, O.L. (1981) Nova espécie de *Proceratophrys*, da hiléia Bahiana, Brasil (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia*, 41, 19–24.

Izecksohn, E., Cruz, C.A.G. & Peixoto, O.L. (1998) Sobre *Proceratophrys appendiculata* e algumas espécies afins (Amphibia: Anura: Leptodactylidae). *Revista da Universidade Rural, Série Ciências da Vida*, 20, 37–54.

Jim, J. & Caramaschi, U. (1980) Uma nova espécie de *Odontophrynus* da região de Botucatu, São Paulo, Brasil (Amphibia, Anura). *Revista Brasileira de Biologia*, 40, 357–360.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X., & Wison, A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the Natural Academy of Sciences of the United States of America*, 86, 6196–6200.

Kwet, A. & Faivovich, J. (2001) *Proceratophrys bigibbosa* species group (Anura, Leptodactylidae), with description of a new species. *Copeia*, 2001, 203–215.
http://dx.doi.org/10.1643/0045-8511(2001)001[0203:PBSGAL]2.0.CO;2

Lynch, J.D. (1971) Evolutionary relationships, osteology, and zoogeography of Leptodactyloid frogs. *Miscellaneous Publications of the University of Kansas Museum of Natural History*, 53, 1–238.
http://dx.doi.org/10.2307/1442765

Mahiques, M.M., Sousa, S.H.M., Furtado, .V., Tessler, M.G., Toledo, F.A.L., Burone, L., Figueira, R.C.L., Klein, D.A., Martins, C.C. & Alves, D.P.V. (2010) The southeastern Brazilian shelf: general characteristics, Quaternary evolution and sediment distribution. *Brazilian Journal of Oceanography*, 58, 25–34.

Mângia, S., Santana, D.J. &Feio, R.N. (2011). Análise morfométrica e morfológica em populações de *Proceratophrysmelanopogon* (Miranda-Ribeiro, 1926). In: *IX Congresso Latinoamericano de Herpetologia*, 2011, Curitiba.

Martins, F.M., Gifalli-Iughetti,C., Koiffman, C.P. & Harris, E.E. (2011) Coalescent analysis of mtDNA indicates Pleistocene divergence among three species of howler monkey (*Alouatta* spp.) and population subdivision within Atlantic Costal Forest species, *A. guariba*. *Primates*, 52, 77–87.
http://dx.doi.org/10.1007/s10329-010-0226-2

Martins, L.B. & Giaretta, A.A. (2011) A new species of *Proceratophrys* Miranda-Ribeiro (Amphibia: Anura: Cycloramphidae) from central Brazil. *Zootaxa*, 2880, 41–50.

Mercadal de Barrio, I.T. & Barrio, A. (1993) Una nueva especie de *Proceratophrys* (Leptodactylidae) del nordeste de Argentina. *Amphibia-Reptilia*, 14, 13–18.
http://dx.doi.org/10.1163/156853893X00156

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In:* Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1–8.

Miranda, G.S. & Dias, P.H.S. (2012) Biogeografia de vicariância: histórico e perspectivas da disciplina que lançou um novo olhar sobre a diversidade na Terra. *Filosofia e História da Biologia*, 7, 215–240.

Miranda-Ribeiro, A. (1920) Algumas considerações sobre o gênero *Ceratophrys* e suas espécies. *Revista do Museu Paulista*, 12, 291–304.

Miranda-Ribeiro, A. (1923) Os hylodideos do Museu Paulista. *Revista do Museu Paulista*, 13, 825–846 (3–24).

Miranda-Ribeiro, A. (1926) Notas para servirem ao estudo dos Gymnobatrachios (Anura) brasileiros. *Arquivos do Museu Nacional*, 42, 389–418.

Miranda-Ribeiro, A. (1937) Especies novas do gênero *Stombus* da serie de appendices oculares reduzidos. *O Campo*, 1937, 24.

Müller, F. (1883) *DritterNachtrag. Katalog der herpetologischenSammlung des Basler Museums*. J.G. Bauer, Basel.

Napoli, M.F., Cruz, C.A.G., Abreu, R.O. & Del-Grande, M.L. (2011) A new species of *Proceratophrys* Miranda-Ribeiro (Amphibia: Anura: Cycloramphidae) from the ChapadaDiamantina, State of Bahia, northeastern Brazil. *Zootaxa*, 3133, 37–49.

Nylander, J.A.A. (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre: Uppsala University.

Padial, J.M., Miralles, A., De La Riva, I. &Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7, 2–14.
http://dx.doi.org/10.1186/1742-9994-7-16

Palumbi, S.R. (1996) Nucleic acids II: The Polymerase Chain Reaction. *In:*Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.) *Molecular Systematics*. Sinauer, Sunderland, MA, pp. 205–247.

Peixoto, O.L. & Cruz, C.A.G. (1981) Notas sobre o girino de *Proceratophrys appendiculata* (Günther, 1873) (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia*, 41, 553–555.

Peters, W.C.H. (1872) Über die von Spix in Brasilien gesammelten Batrachier des Königl. NaturalienkabinetzuMünichen. *Monatsberichte de Königlichen Preussische Akademie des Wissenschaften Zu Berlin*, 1872, 196–227.

Prado, G.M & Pombal, J.P. (2008) Espécies de *Proceratophrys* Miranda-Ribeiro, 1920 com apêndices palpebrais (Anura; Cycloramphidae). *Arquivos de Zoologia*, 39, 1–85.

Reinhardt, J. & Lütken, C. (1862 "1861") Bidrag til Kundskab om Brasiliens Padder og Krybdyr. *Videnskabelige Meddelelser fra den naturistoriske Forening i Kjobenhavn*, 1861, 143–242, pls. 3–6.

Reis, S.F. (1988) Morfometria e estatística multivariada em biologia evolutiva. *Revista Brasileira de Zoologia*, 5, 571–580.
http://dx.doi.org/10.1590/S0101-81751988000400005

Riccomini, C., Grohmann, C.H., Sant'Anna, L.G., Hiruma, S.T., (2010) A captura dascabeceiras do Rio Tietê pelo Rio Paraíba do Sul. In: Modenesi-Gauttieri, M.C.,Bartorelli, A., Mantesso-Neto, V., Carneiro, C.D.R., Lisboa, M.B.A.L. (Eds.), A Obrade Aziz NacibAb'Sáber. Becca, São Paulo, pp. 157–169.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
http://dx.doi.org/10.1093/bioinformatics/btg180

Saadi, A. (1993). Neotectônica da plataforma brasileira: esboço e interpretações preliminares. *Geonomos*, 1, 1–15.

Savage, J.M. & Cei, J.M. (1965) A reviewe of the leptodactylid frog genus *Odontophrynus*. *Herpetologica*, 21, 178–195.

Smithe, F.B. (1975) *Naturalist's Color Guide*. American Museum of Natural History, New York.

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
http://dx.doi.org/10.1093/bioinformatics/btl446

Swofford, D.L. (2003) PAUP* - Phylogenetic Analysis Using Parsimony (*and Other Methods) v. 4b10. Sinauer Associates, Sunderland, Massachusetts.

Taylor, W. & Van Dyke, G. (1985) Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.

Teixeira, M., Amaro, R.C., Recoder, R.S., Dal Vechio, F. & Rodrigues, M.T. (2012) A new dwarf species of *Proceratophrys* Miranda-Ribeiro, 1920 (Anura, Cycloramphidae) from highlands of Chapada Diamantina, Bahia, Brazil. *Zootaxa*, 3551, 25–42.

Verdade, V.K. & Rodrigues, M.T. (2003) A new species of *Cycloramphus* (Anura, Leptodactylidae) from the Atlantic Forest, Brazil. *Herpetologica*, 59, 513–518.
http://dx.doi.org/10.1655/02-78

Weygoldt, P. &Peixoto, O.L. (1985) A new species of horned toad (*Proceratophrys*) from Espírito Santo Brazil (Amphibia: Anura: Salientia: Lepodactylidae). *Senckenbergiana Biologica*, 66, 1–8.

Wied-Neuwied, M.P (1824) Verzeichnis der Amphibien welche in zweiten Bande der Naturgeschichte Brasiliens von Prinz Max von Neuwied warden beschreiben Werden. *Isis von Oken*, 14, 661–673.

Wiley, E.O. (1978) The evolutionary species concept reconsidered. *Systematic Zoology*, 27, 17–26.
http://dx.doi.org/10.2307/2412809

Additional examined material

Proceratophrys izecksohni sp.nov.

Mangaratiba municipality, Rio de Janeiro state –**Juveniles: UNIRIO** 410, 438, 456, 724, 748, 1107 (cleared and stained), 1315 (cleared and stained), 1348, 2067, 2636, 4010, 4195, 4203, 4218, 2634.

Paraty municipality, Rio de Janeiro state –**Juveniles: MNRJ** 678, 7507-12; **CFBH** 1321.Cleared and stained individual without sex determination: **MNRJ** 2037.

Proceratophrys belzebul sp.nov.

Cunha municipality, São Paulo state—**Juveniles: CFBH** 29683.

São Luiz do Paraitinga municipality, São Paulo state—**Juveniles: CFBH** 5820, 6489, 9887.

Ubatuba municipality, São Paulo state—**Juveniles: CFBH** 3949, 4324, 13049.

Proceratophrys appendiculata

Duque de Caxias municipality, Rio de Janeiro state—**Adult male: MNRJ** 61203 (x-Ray). **Adult female: MNRJ** 49715.

Cachoeiras de Macacu municipality, Rio de Janeiro state—**Adult male: UNIRIO** 4618 (cleared and stained), **MNRJ** 0298.

Petrópolis municipality, Rio de Janeiro state—**Adult female: MNRJ** 37291.

Teresópolis municipality, Rio de Janeiro state—**Adult males: UNIRIO** 148, 1999 (cleared and stained), 2063 (cleared and stained), 2542, 4471-73, 4494; **ZUFRJ** 3835, 6188, 8970, 1023, 11414; **MNRJ** 34497. **Adult females: UNIRIO** 2543; **ZUFRJ** 8971; **MNRJ** 39094, 43733, 53936. **Juveniles: UNIRIO** 710, 1519 (cleared and stained), 1543, 2522 (cleared and stained); **CFBH** 22018.

Proceratophrys tupinamba

Ilha Grande, Angra dos Reis municipality, Rio de Janeiro state—**Adult males: MNRJ** 18282 (Holotype), 25102 (cleared and stained) (Paratype), 25103 (cleared and stained) (Paratype), 54541 (Paratype).

Proceratophrys moheringi

Santa Teresa municipality, Espirito Santo state—**Adult male: MNRJ** 46804.

Proceratophrys melanopogon

Itatiaia municipality, Rio de Janeiro state—**Adult males: UNIRIO** 1327, 1471.

Nova Friburgo municipality, Rio de Janeiro state—**Adult female: MNRJ** 51761 (x-Ray).

Santa Rita de Jacutinga municipality, Minas Gerais state—**Adult male: UNIRIO** 1353.

APPENDIX 1. Species, voucher numbers and localities of individuals sampled in this study. Voucher abbreviations are AF (Laboratório de Citogenética de Vertebrados, Instituto de Biociências, Universidade de São Paulo, Brazil), JC (field number of José Cassimiro, Universidade de São Paulo, Brazil), FSFL (Field numberof Felipe Sá Fortes Leite, Pontifícia Universidade Católica de Minas Gerais, Brazil), CFBH (Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil), DB (Diego Baldo, Universidad Nacional de Misiones, Argentina), MNRJ (Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil), MZUSP (Museu de Zoologia, Universidade de São Paulo, Brazil), TG (Taran Grant, Universidade de São Paulo, Brazil), UNIRIO (Universidade Federal do Estado do Rio de Janeiro, Brazil), ZUFRJ (Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil), MZUFV (Museu de Zoologia João Moojen, Universidade Federal de Viçosa, Brazil). *only tissue sample from tissue collection of Universidade Estadual Paulista, Rio Claro, São Paulo.

Species	Voucher number	Locality	GenBank accession number				
			cyt *b*	16S	Rag-1	12S	Rhod
Cycloramphus acangatan	AF 1605	Caucaia do Alto, Cotia, SP	FJ685663	FJ685683	FJ685703	KF214096	KF214198
Macrogenioglottus alipioi	AF 919	Serra do Teimoso, Jussari, BA	FJ685664	FJ685684	FJ685704	KF214097	KF214199
	AF 1607	Caucaia do Alto, Cotia, SP	FJ685665	FJ685685	FJ685705	KF214098	KF214200
Odontophrynus americanus	AF 665	Poços de Caldas, MG	FJ685666	FJ685686	FJ685706	KF214099	KF214201
O. carvalhoi	JC 1224	Mucugê, BA	FJ685667	FJ685687	FJ685707	KF214100	KF214202
O. cultripes	FSFL 875	Varginha, MG	FJ685668	FJ685688	FJ685708	KF214101	KF214203
Proceratophrys appendiculata	MNRJ 37291	Petropolis, RJ	-	KF214152	KF214188	KF214129	KF214230
	MNRJ 53936	Teresopolis, RJ	KF214172	KF214151	KF214189	KF214130	KF214231
	MNRJ 54759	Cachoeiras de Macacu, RJ	KF214173	KF214153	KF214190	KF214131	KF214232
P. avelinoi	DB 1246	Misiones, Argentina	FJ685671	FJ685691	FJ685711	KF214102	KF214204
P. belzebul	MTR 9456	Barra do Una, São Sebastião, SP	KF214174	KF214154	KF214191	KF214132	KF214233
	28*	Picinguaba, Ubatuba, SP	-	KF214156	KF214193	KF214134	KF214234
	CFBH 8062	São Luis do Paraitinga, SP	KF214175	KF214155	KF214192	KF214133	-
P. bigibbosa	DB 2313	Misiones, Argentina	FJ685673	FJ685693	FJ685713	KF214103	KF214205
P. boiei	AF 1587	Serra da Cantareira, São Paulo, SP	FJ685672	FJ685692	FJ685712	KF214104	KF214206
P. concavitympanum	AF 1094	Usina Hidrelétrica de Lajeado, Palmas, TO	FJ685674	FJ685694	FJ685714	KF214105	KF214207
P. cristiceps	AF 887	Parque Nacional da Serra das Confusões, PI	FJ685675	FJ685695	FJ685715	KF214106	KF214208
P. cururu	FSFL 580	Cardeal Mota, MG	FJ685676	FJ685696	FJ685716	KF214107	KF214209
P. goyana	AF 1188	Petrolina de Goiás, GO	FJ685677	FJ685697	FJ685717	KF214108	KF214210
P. izecksohni	MNRJ64584	Paraty, RJ	-	KF214157	KF214194	KF214135	KF214235
P. laticeps	AF 1900	Reserva Natural da Vale do Rio Doce, Linhares, ES	FJ685678	FJ685698	FJ685718	KF214109	KF214211

……*continued on the next page*

APPENDIX 1. (Continued)

Species	Voucher number	Locality	GenBank accession number				
			cyt *b*	16S	Rag-1	12S	Rhod
P. melanopogon	CFBH 5755	Maringá, Itatiaia, RJ	FJ685679	FJ685699	FJ685719	KF214119	KF214221
	AF 1446*	Santos, SP	JX987065	JX987066	JX987067	KF214115	KF214217
	AF 1606	Caucaia do Alto, Cotia, SP	KF214161	KF214139	KF214179	KF214116	KF214218
	AF 1741	Estação Biológica de Boracéia, Salesópolis, SP	KF214162	KF214140	-	KF214117	KF214219
	AF 2145	Jureia, SP	KF214163	KF214141	KF214180	KF214118	KF214220
	CFBH 6294	São José dos Campos, SP	KF214164	KF214142	KF214181	KF214120	KF214239
	MZUFV 10139	Araponga, MG	-	KF214143	KF214182	KF214121	KF214222
	AF 1988	Bertioga, SP	KF214165	KF214144	KF214183	KF214122	KF214223
	MNRJ 51360	Nova Friburgo, RJ	KF214166	KF214145	KF214184	KF214123	KF214224
	MZUSP 131930	Estação Ecológica do Bananal, Bananal, SP	KF214167	KF214146	KF214185	KF214124	KF214225
	MZUSP 135186	Campos do Jordão, SP	KF214168	KF214147	-	KF214125	KF214226
	MZUSP 135333	São Sebastião, SP	KF214169	KF214148	FJ685710	KF214126	KF214227
	TG 3295	Serra da Bocaina, São José do Barreiro, SP	KF214170	KF214149	KF214186	KF214127	KF214228
	UNIRIO 4603	Resende, RJ	KF214171	KF214150	KF214187	KF214128	KF214229
P. minuta	AF 2008	Miguel Calmon, BA	JX982961	JX982965	JX982969	KF214113	KF214215
P. moratoi	CFBH 6515	Itirapina, SP	FJ685669	FJ685689	FJ685709	KF214110	KF214212
P. redacta	MTR 22579	Morro do Chapéu, BA	JX982963	JX982966	JX982971	KF214114	KF214216
P. renalis	ZUFRJ 8682	Brejo Madre de Deus, PE	FJ685680	FJ685700	FJ685720	KF214111	KF214213
P. schirchi	371*	São Lourenço, Santa Teresa, ES	FJ685681	FJ685701	FJ685721	KF214112	KF214214
P. tupinamba	MNRJ 54541	Ilha Grande, RJ	KF214176	KF214158	KF214195	KF214136	KF214236
	MTR 15449	Ilha Grande, RJ	KF214177	KF214159	KF214196	KF214137	KF214237
	MTR 15452	Ilha Grande, RJ	KF214178	KF214160	-	KF214138	KF214238
Thoropa taophora	AF 1434	Santos, SP	FJ685662	FJ685682	FJ685702	KF214095	KF214197