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# A New Species of *Proceratophrys* (Amphibia: Anura: Odontophrynidae) from the Araripe Plateau, Ceará State, Northeastern Brazil

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Abstract: Natural rain forest enclaves in northeastern Brazil (called Brejos de Altitude) are present in isolated areas surrounded by the semiarid Caatinga biome. Among these montane areas, the Araripe Plateau in Ceará state harbors Caatinga, Cerrado, and Atlantic Forest remnants and is considered a priority area for biodiversity conservation. Herein, we describe a new species of *Proceratophrys* (Amphibia: Anura: Odontophrynidae; Horned Frogs) endemic to the Araripe Plateau. Based on nuclear and mitochondrial DNA sequences, we show that this new species is related to the Amazonian species *P. concavitympanum* but can be diagnosed based on the row of tubercles on the forearm and by the number, size, and disposition of tubercles on the dorsal region. It is also widely disjunct, known only from the mesic forests of the Araripe Plateau, 2400 km away from the type locality of *P. concavitympanum*. The new species depends on streams for reproduction and is currently known from an area that is severely impacted by deforestation and diversion of local streams for agriculture and recreation. Considering the many threatened species occurring in the same region, there is a need for future studies to quantify the new species' full distribution and evaluate population trends to correctly assess its conservation status.

**Key words:** Brejos de Altitude; Caatinga biome; Horned Frogs; Phylogeny; Pleistocene

The Caatinga biome is a semiarid region in northeastern Brazil characterized by high solar radiation, low relative humidity, limited cloud cover, and low and unpredictable rainfall (Prado 2003). Plant and animal species occurring in the Caatinga are well adapted to arid conditions (Brazão et al. 1992). During Pleistocene climatic cycles, the Amazon and Atlantic forests expanded and contracted repeatedly, establishing intermittent connections across the diagonal of open formations (Cerrado, Caatinga, and Chaco) that cut across South America from southwest to northeast (Por 1992; Ledo and Colli 2017). Such connections likely enabled faunal exchanges between these biomes, a hypothesis that has been corroborated by phylogenetic and phylogeographic studies of different vertebrate groups (Ledo and Colli 2017). During glacial periods, forested environments are thought to have contracted, whereas dry areas expanded (Costa 2003; Werneck et al. 2011; Batalha-Filho et al. 2014; Gehara et al. 2017). Rain forest enclaves (called Brejos de Altitude in northeastern Brazil) presently occur in isolated areas surrounded by semiarid Caatinga vegetation (Ab'Sáber 1977). Such remnants persist on the slopes and on tops of high-altitude areas such as the Baturité, Borborema, Ibiapaba, and Araripe plateaus in northeastern Brazil because lower temperatures and orographic rains allow the maintenance of mesic habitats (Andrade-Lima 1982).

Because such rain forest enclaves were isolated during the Pleistocene, vicariance is posited to have promoted high speciation rates in these areas (Werneck et al. 2011). Indeed, several endemic amphibians (e.g., *Rhinella casconi*, *Adelophryne baturitensis*, *A. maranguapensis*) and squamates (e.g., *Atractus ronnie*, *Leposoma baturitensis*, *Placosoma limaverdorum*) are associated with these high-altitude regions (Hoogmoed et al. 1994; Rodrigues and Borges 1997; Loebmann et al. 2009; Roberto et al. 2014; Borges-Nojosa et al. 2016; Roberto and Loebmann 2016). Among these montane areas in northeastern Brazil, the Araripe Plateau harbors fragments of Caatinga, Cerrado, and Atlantic Forest and is considered a priority area for biodiversity conservation (MMA 2007; Camardelli and Napoli 2012).

Currently, the genus *Proceratophrys* (Amphibia: Anura: Odontophrynidae; Horned Frogs) comprises 40 recognized species organized into four morphological, nonmonophyletic groups: the *P. bigibbosa* and *P. cristiceps* species groups and the *P. boiei* and *P. appendiculata* species complexes (Izecksohn et al. 1998; Giaretta et al. 2000; Kwet and Faivovich 2001; Prado and Pombal 2008). The *P. cristiceps* species group (sensu Giaretta et al. 2000) includes 15 species and is characterized by the absence of rostral and palpebral appendages or postocular elevations. Species of this group are mainly associated with seasonally open habitats in Brazilian Cerrado and Caatinga biomes (sensu Ab'Sáber 1977), with *P. cristiceps* (Müller 1883), *P. cururu* Eterovick and Sazima 1998, *P. goyana* (Miranda-Ribeiro 1937), and *P. concavitympanum* occurring in the Amazon region (Giaretta et al. 2000). Later, *P. moratoi* (Jim and Caramaschi 1980) from the Cerrado was placed in the *P. cristiceps* group (Amaro et al. 2009). All species recently described and

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allocated in this group are distributed in open areas of the Cerrado and Caatinga biomes: *Proceratophrys strussmannae* Ávila, Kawashita-Ribeiro and Morais 2011; *P. vielliardi* Martins and Giaretta 2011; *P. huntingtoni* Ávila, Pansonato and Strüssmann 2012; *P. carranca* Godinho, Moura, Lacerda and Feio 2013; *P. rotundipalpebra* Martins and Giaretta 2013; *P. bagnoi* Brandão, Caramaschi, Vaz-Silva and Campos 2013; *P. branti* Brandão, Caramaschi, Vaz-Silva and Campos 2013; and *P. dibernardoi* Brandão, Caramaschi, Vaz-Silva and Campos 2013 occur in the Cerrado biome (Ávila et al. 2011, 2012; Martins and Giaretta 2011, 2013; Brandão et al. 2013; Godinho et al. 2013); and *P. caramaschii* Cruz, Nunes and Juncá 2012 and *P. aridus* Cruz, Nunes and Juncá 2012 are distributed in the Caatinga biome (Cruz et al. 2012).

During several field expeditions to the Araripe Plateau, we collected 14 specimens of a species belonging to the genus *Proceratophrys*. Herein, we described the populations from this region as a new species belonging to the *P. cristiceps* species group related to the Amazonian species, *P. concavitympanum*. It is diagnosable by several morphological features in combination as well as by genealogical exclusivity. Current data indicate the new species has a very small range and is likely of great conservation concern.

## Materials and Methods

### Study Area

The Araripe Plateau spans the border between Ceará and Pernambuco states and separates the São Francisco and Mid-Northeastern Caatinga ecoregions (Rosa et al. 2003). The formation has a maximum elevation ranging from 900 to 1000 m above sea level (a.s.l.). Cerrado-like savannas characterize the vegetation on the top of the plateau, whereas humid forests occur along the slopes and Caatinga vegetation is found in the lowland surrounding areas. The humid forests along the slopes of the Araripe Plateau are about 200 km long and mostly composed of trees 8–15 m tall (Girão and Souto 2005; Claudino-Sales and Lira 2011). The region has two marked seasons: dry from May to November (rainfall, <60 mm) and rainy from December to April (mean rainfall, 1033 mm). The mean annual temperature is 25.7°C (Girão and Souto 2005; Linhares et al. 2010). The area is situated within the sustainable use Environment Protected Area of Chapada do Araripe.

### Morphological Assessment

Specimens used in the description, and examined for comparisons (Appendix), are housed in the following collections: Coleção Herpetológica da Universidade Federal do Rio Grande do Norte (UFRN), Coleção Herpetológica da Universidade Federal de Pernambuco (CHUFPE), Museu de Zoologia da Universidade Federal da Bahia (MZUFBA), Coleção Zoológica da Universidade Federal de Mato Grosso (UFMT), Coleção Célio F. B. Haddad, Universidade Estadual Paulista (CFBH), Museu de Zoologia Prof. Adão José Cardoso, Universidade Estadual de Campinas (ZUEC), Museu de Zoologia da Universidade Estadual de Feira de Santana (MZFS), Coleção Herpetológica da Universidade Federal de Minas Gerais (CHUFMG), Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais (MCNAM), Museu Nacional do Rio de Janeiro, Universidade Federal do Rio de Janeiro (MNRJ), and Coleção de Herpetologia da Universidade Regional do Cariri (URCA-H).

We follow the terminology for morphological characters of Cruz and Napoli (2010), Teixeira et al. (2012), Brandão et al. (2013), and Mângia et al. (2014). We followed Prado and Pombal (2008) in taking measurements of 11 adult specimens (8 males, 3 females) by using a digital caliper (±0.01 mm): snout–vent length (SVL), head length (HL), head width (HW), distance from the interocular crest to the tip of snout (DICS), internarial distance (IND), eye–nostril distance (END), eye diameter (ED), upper eyelid width (UEW), interorbital distance (IOD), thigh length (THL), tibia length (TL), foot plus tarsus length (FL), and forearm and hand length (FHL). We determined the sex of each individual by the presence of vocal slits in males and their absence in females. To avoid including juveniles in our analyses, we only used specimens whose SVLs were 50% or larger than the largest specimen recorded for each sex (Prado and Pombal 2008).

### Vocalizations

We recorded the advertisement calls of two males (URCA83 and URCA84, total of 31 calls) at Mata do Clube Recreativo Grangeiro (7°16′49′′S, 39°26′22′′W; 720 m a.s.l.; in all cases, datum = WGS84), Crato Municipality, Ceará state, on 22 October 2011 (air temperature, 24°C) by using a Marantz PMD 660 tape recorder coupled to a Yoga EM 9600 directional microphone. We also recorded the advertisement call of three males (individuals not collected, total of 89 calls) at Sítio Caianas (7°16′36′′S, 39°26′42′′W), Crato Municipality, Ceará state, on 13 January 2008 (air temperature not available) by using a Sony TCM 5000 EV tape recorder coupled to a Sennheiser ME 66 directional microphone. We digitalized the recordings at 44.1 kHz, with a resolution of 16 bits. We analyzed calls in Raven Pro v1.5 for Mac (Bioacoustics Research Program 2012) and constructed audio spectrograms in R using the package 'seewave' (Sueur et al. 2008) with the following parameters: FFT window width = 256, frame = 100, overlap = 75, and flat top filter. We analyzed several acoustic parameters typically evaluated in anuran taxonomy studies (e.g., Brasileiro et al. 2008; Mângia et al. 2014): call duration, pulse number per call, pulse number per second, and dominant frequency. Terminology of call descriptions follows Köhler et al. (2017), and values are reported as means ± 1 SD. Comparative data for other species were obtained from the literature (see Santana et al. 2010; Nunes et al. 2016; Table 1).

### Molecular Data

We sequenced fragments of 16S ribosomal RNA mitochondrial gene from 5 individuals of the new species, 10 *P. cristiceps*, and 1 *P. concavitympanum*. For the nuclear gene rhodopsin, we sequenced five individuals of the new species, three of *P. cristiceps*, and one of *P. concavitympanum* (Table 2). We extracted genomic DNA from muscle samples, liver samples, or both by using the phenol–chloroform protocol of Sambrook et al. (1989). For 16S, we used the 16Sa/16Sb primer pair of Palumbi et al. (2002), following polymerase chain reaction (PCR) conditions described by Costa el al. (2016). For rhodopsin, we used primers Rhod1A and

TABLE 1.—Acoustic parameters of the advertisement calls of species from the *Proceratophrys cristiceps* group. Values are presented as mean ± 1 SD (range).

| Species | Duration (s) | Notes/call | Pulses/call | Pulses/s | Dominant frequency (Hz) | Location[a] | Source |
|---|---|---|---|---|---|---|---|
| *P. ararype* sp. nov. 3 males, 120 calls | 0.498 ± 0.06 (0.374–0.648) | 1 | 49.4 ± 6.6 (38–65) | 99 ± 1.5 (95.7–102.7) | 1167.2 ± 76.8 (1033.6–1378.1) | Crato, CE | This study |
| *P. caramaschii* 3 males, 45 calls | 0.570 ± 0.01 (0.410–0.740) | 1 | 45 ± 9.2 (33–59) | 80.0 ± 0.9 (78.6–81.8) | 860 or 1030 | Planalto de Ibiapaba, CE | Nunes et al. 2016 |
| *P. carranca* 1 male, 76 calls | 0.107 ± 0.04 (0.045–0.191) | 1–10 | 12.2 ± 3.9 (5–21) | 111.1–109.9 | 1178.0 ± 65.5 (1033.6–1378.1) | Buritizeiro, MG | Godinho et al. 2013 |
| *P. concavitympanum* 3 males, 33 calls | 0.367 ± 0.06 (0.230–0.500) | 1 | 38.7 ± 7.4 (23–51) | 106.3 ± 3.1 (100–112.3) | 948.2 ± 66.7 (851.0–1116.4) | Aripuanã, MT | Santana et al. 2010 |
| *P. concavitympanum* 1 male, 13 calls | 0.278 ± 0.04 (0.178–0.326) | 1 | 30.9 ± 4.8 (19–37) | 110.9 ± 5.2 (100.7–119.3) | 819.2 ± 62.2 (754.3–874.5) | Espigão do Oeste, RO | Santana et al. 2010 |
| *P. cristiceps* 2 males, 29 calls | 0.660 ± 0.05 (0.520–0.790) | 1 | 57.5 ± 6.0 (46–69) | 89.5 ± 1.2 (87.4–91.9) | 940 ± 20 (900–990) | Feira de Santana, BA | Nunes and Juncá 2006 |
| *P. cururu* | 0.600–1.000 | 1 | 40 | 45 | 900 (600–1000) | Serra do Cipó, MG | Eterovick and Sazima 1998 |
| *P. goyana* 12 males, 8–45 calls/male | 0.104 ± 0.15 (0.071–0.195) | 1–34 | 99.3 ± 4.4 (83.3–120.5) | 10.2 ± 1.4 (7–18) | 1005.9 ± 28.4 (937.3–1125.0) | Chapada dos Veadeiros, GO | Martins and Giaretta 2013 |
| *P. huntingtoni* 2 males, 103 calls | 0.270 ± 0.01 (0.200–0.320) | 1 | 21.3 ± 1.2 (19.0–25.0) | 78–95 | 1250.2 ± 49.9 (1095.0–1344.5) | Chapada dos Guimarães, MT | Ávila et al. 2012 |
| *P. moratoi* 4 males, 126 calls | 0.245 ± 0.03 (0.185–0.307) | 1 | 20.5 ± 2.5 (15–26) | 81–85 | 1343.0 ± 73.7 (1174–1444) | Itirapina, SP | Brasileiro et al. 2008 |
| *P. moratoi* 2 males, 59 calls | 0.207 ± 0.02 (0.146–0.238) | 1 | 17.5 ± 1.5 (12–20) | 82–84 | 1348.7–86.6 (1153–1420) | Botucatu, SP | Brasileiro et al. 2008 |
| *P. moratoi* 2 males, 44 calls | 0.232 ± 0.02 (0.181–0.268) | 1 | 19 ± 3.0 (14–23) | 77–86 | 1440 ± 50 (1406–1594) | Ituiutaba, MG | Martins and Giaretta 2012 |
| *P. moratoi* 7 males, 148 calls | 0.253 ± 0.04 (0.179–0.335) | 1 | 19 ± 2.0 (14–23) | 69–78 | 1327 ± 108 (1219–1464) | Uberlândia, MG | Martins and Giaretta 2012 |
| *P. rotundipalpebra* 17 males, 8–45 calls/male | 0.093 ± 0.04 (0.050–0.200) | 1–24 | 9.3 ± 1.7 (5–19) | 101.0 ± 8.9 (78.1–130.4) | 1287 ± 54.4 (1125.0–1453.1) | Chapada dos Veadeiros, GO | Martins and Giaretta 2013 |
| *P. vielliardi* 4 males, 35 calls | 0.059 ± 0.08 | 3–20 | 6.4 ± 0.9 (4–9) | 107.7 ± 6.2 (95.6–118.8) | 1133.8 ± 93.3 (1022.0–1291.0) | Caldas Novas, GO | Martins and Giaretta 2011 |

[a] CE = Ceará; MG = Minas Gerais; MT = Mato Grosso; RO = Rondônia; BA= Bahia; GO = Goiás; SP = São Paulo.

Table 2.—Voucher numbers, municipalities, and GenBank accession numbers for 16S and rhodopsin genes of specimens included in the molecular analyses.

| Species | Municipality, state | Voucher | GenBank accession no. | | Reference |
|---|---|---|---|---|---|
| | | | Rhodopsin | 16S | |
| *Proceratophrys ararype* sp. nov. | Crato, Ceará | CHUFPE156 | MF953403 | KX858852 | This study |
| *Proceratophrys ararype* sp. nov. | Crato, Ceará | CHUFPE152 | MF953405 | KX858854 | This study |
| *Proceratophrys ararype* sp. nov. | Crato, Ceará | CHUFPE160 | MF953404 | KX858853 | This study |
| *Proceratophrys ararype* sp. nov. | Crato, Ceará | AAGARDA2736 | MF953409 | KX855986 | This study |
| *Proceratophrys ararype* sp. nov. | Crato, Ceará | AAGARDA2741 | MF953412 | KX855987 | This study |
| *Proceratophrys concavitympanum* | Aripuanã, Mato Grosso | FMT-A 11698 | MF953406 | KX858855 | This study |
| *Proceratophrys concavitympanum* | Palmas, Tocantins | MTR7884 | KF214207 | FJ685694 | Amaro et al. 2009 |
| *Proceratophrys moratoi* | Itirapina, São Paulo | CFBH6515 | KF214213 | FJ685689 | Amaro et al. 2009 |
| *Proceratophrys tupinamba* | Ilha Grande, Rio de Janeiro | MNRJ54541 | KF214236 | KF214158 | Dias et al. 2013 |
| *Proceratophrys goyana* | Petrolina de Goiás, Goiás | AF1188 | KF214210 | FJ685697 | Amaro et al. 2009 |
| *Proceratophrys mantiqueira* | Araponga, Minas Gerais | MZUFV10139 | KF214222 | KF214143 | Dias et al. 2013 |
| *Proceratophrys avelinoi* | Misiones, Argentina | DB1246 | KF214204 | FJ685691 | Amaro et al. 2009 |
| *Proceratophrys laticeps* | Linhares, Espírito Santo | MTR12156 | KF214211 | FJ685698 | Amaro et al. 2009 |
| *Proceratophrys boiei* | São Paulo, São Paulo | AF1587 | KF214206 | FJ685693 | Amaro et al. 2009 |
| *Proceratophrys itamari* | Campos do Jordão, São Paulo | MZUSP135186 | KF214226 | KF214147 | Dias et al. 2013 |
| *Proceratophrys izecksohni* | Paraty, Rio de Janeiro | MNRJ64584 | KF214235 | KF214157 | Dias et al. 2013 |
| *Proceratophrys belzebul* | São Sebastião, São Paulo | MTR9456 | KF214233 | KF214233 | Dias et al. 2013 |
| *Proceratophrys melanopogon* | São José do Barreiro, São Paulo | TG3295 | KF214228 | KF214149 | Dias et al. 2013 |
| *Proceratophrys pombali* | Bertioga, São Paulo | AF1988 | KF214223 | KF214148 | Dias et al. 2013 |
| *Proceratophrys cururu* | Cardeal Mota, Minas Gerais | FSFL580 | KF214209 | FJ685696 | Amaro et al. 2009 |
| *Proceratophrys appendiculata* | São Sebastião, São Paulo | MNRJ53936 | KF214231 | FJ685690 | Amaro et al. 2009 |
| *Proceratophrys bigibbosa* | Misiones, Argentina | DB2313 | KF214205 | FJ685692 | Amaro et al. 2009 |
| *Proceratophrys renalis* | Brejo da Madre de Deus, Pernambuco | ZUFRJ8682 | KF214213 | FJ685700 | Amaro et al. 2009 |
| *Proceratophrys schirchi* | Santa Tereza, Espírito Santo | 371 | KF214214 | FJ685701 | Amaro et al. 2009 |
| *Proceratophrys cristiceps* | Macaíba, Rio Grande do Norte | AAGARDA1754 | MF953407 | KX855989 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | AAGARDA2739 | MF953410 | KX855993 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | AAGARDA2735 | MF953408 | KX855990 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | AAGARDA2738 | —[a] | MF953399 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | GRCOLLI21987 | MF953413 | MF953400 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | GRCOLLI22131 | MF953414 | MF953401 | This study |
| *Proceratophrys cristiceps* | Crato, Ceará | GRCOLLI22955 | — | MF953402 | This study |
| *Proceratophrys minuta* | Miguel Calmon, Bahia | MZUSP146499 | KF214215 | JX982965 | Teixeira et al. 2012 |
| *Proceratophrys redacta* | Morro do Chapéu, Bahia | MZUSP150266 | KF214216 | JX982967 | Teixeira et al. 2012 |
| *Odontophrynus americanus* | Poços de Caldas, Minas Gerais | AF665 | KF214201 | FJ685686 | Amaro et al. 2009 |
| *Macrogenioglottus alipioi* | Jussari, Bahia | AF919 | KF214199 | FJ685684 | Amaro et al. 2009 |
| *Cycloramphus acangatan* | Cotia, São Paulo | AF1605 | KF214198 | FJ685683 | Amaro et al. 2009 |

[a] The dashes represent molecular marker not sequenced.

Rhod1C of Bossuyt and Milinkovitch (2000). PCR reactions consisted of 1× buffer, dNTP at 0.2 mM, each primer at 0.2 μM, $MgCl_2$ at 2 mM, 1 μL of Taq polymerase, and 2 μL of template DNA, in a total reaction volume of 25 μL. We used the following PCR cycling program: 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 59°C for 1 min, and 72°C for 1 min, and concluding with a 5-min extension at 72°C. We purified PCR products with ethanol/sodium acetate and sequenced them on an ABI 3730XL DNA analyzer (Applied Biosystems). Resulting sequences were edited and aligned using Geneious v.9.1.2 with the MUSCLE algorithm using default parameters (Edgar 2004). The final dataset was 453 base pairs (bp) for 16S and 350 bp for rhodopsin. We deposited our sequences in GenBank (Table 2).

For phylogenetic analyses, we included 16S and rhodopsin sequences from 21 species of *Proceratophrys* available in GenBank, along with *Macrogenioglottus alipioi*, *Odontophrynus americanus*, and *Cycloramphus acangatan* as outgroups (Table 2). To determine the most probable pair of alleles for rhodopsin, we used the PHASE algorithm (Stephens et al. 2001) implemented in DNASP v.5.10 (Librado and Rozas 2009) using default options. We also determined the model of nucleotide substitution for each gene with jModelTest (Darriba et al. 2012) using the Akaike Information Criterion. The best-fit models were GTR+I+G for 16S and K80+I+G for rhodopsin.

First, we performed a Bayesian phylogenetic analysis of 16S by using BEAST v.1.8 (Drummond et al. 2012) for 30 million generations, sampling every 1000 steps by using a Yule Process tree prior. We checked for stationarity by visually inspecting trace plots and ensuring that all values for effective sample size (ESS) were above 200 in Tracer v.1.5 (Rambaut and Drummond 2007). To infer the timing of speciation events within *Proceratophrys* we constructed a species tree in *BEAST using both mitochondrial (16S) and nuclear (rhodopsin) genes in BEAST v1.8 (Drummond et al. 2012). Because of the lack of fossil calibrations for this group, we used a general anuran 16S mutation rate of 0.0028 per lineage per million years (Lemmon et al. 2007; Lymberakis et al. 2007). We ran 250 million generations, sampling every 10,000 generations. We determined stationarity and ensured that all ESS values were >200 by using Tracer. The first 10% of sampled genealogies were discarded as burn-in, and the maximum clade credibility tree with median node ages was calculated with TreeAnnotator v.1.8 (Drummond et al. 2012). We calculated sequence divergence (uncorrected *p*-distance) among species/individuals by using MEGA v.6.06 (Tamura et al. 2013).

FIG. 1.—*Proceratophrys ararype* (holotype, adult female, CHUFPE 156, snout–vent length = 44.3 mm): (a) dorsal and (b) ventral views. Photos by B.F. Santos. A color version of this figure is available online.

## SPECIES DESCRIPTION

*Proceratophrys* ***ararype*** sp. nov.
(Figs. 1–3)

*Proceratophrys cristiceps* Ribeiro et al. 2012
*Proceratophrys aridus* Ferreira-Silva et al. 2016 (in part)

**Holotype.**—CHUFPE 156, adult female, collected at Mata do Clube Recreativo Grangeiro, Crato Municipality, Ceará state (7°16′49″S, 39°26′22″W; 720 m a.s.l.), on 14 December 2014, by P.M.S. Nunes, M.P.L. Castro, K.M. Kameoka, and M.C. Guarnieri.

**Paratopotypes.**—CHUFPE 160, CHUFPE 161 (adult males), CHUFPE 152 (juvenile) collected with the holotype, CHUFPE 226 and CHUFPE 227 (juvenile) collected on May 2015 by P.M.S. Nunes, A.V.A. Mello, M.P.L. Castro, A.N. Cabral, A.R.M. Gonzaga, and M.C. Guarnieri. URCA83–84 (adult males) collected on 22 October 2011, by R.W. Ávila. URCA-H 1030 (adult female) and URCA-H 1031–34 (adult males) collected on 13 December 2011, by S.C. Ribeiro.

**Paratypes.**—AAGARDA 2736, AAGARDA 2741 (adult males) collected at Clube Serrano Atlético Cratense, Crato Municipality, Ceará state (7°16′10″S, 39°27′35″W; 740 m a.s.l.), on May 2011, by D.J. Santana and A.A. Garda. URCA-H 114 (adult female) collected at Nascente, Chapada do Araripe, Crato Municipality, Ceará state, on 1 May 2008, by S.C. Ribeiro; URCA-H 4028–29 (adult males) collected at Nascente, Chapada do Araripe, Crato Municipality, Ceará state, on 1 January 2009.

**Diagnosis.**—The new species can be distinguished using the following combination of traits: (1) medium size (males, 38.4–42.2 mm; females, 51.7–57.0 mm); (2) snout rounded in dorsal and ventral views, obtuse and slightly vertical in profile; (3) presence of short, fused, but not pointed, warts on upper eyelid border (L 1, 2/5, 3; R 1, 2/5, 2); (4) one row of small and pointed tubercles on the forearm; (5) dorsal region with pointed tubercles on the head, arms, legs, and presacral region; the flanks, sacral-urostyle region, and coccyx end with shorter and fewer tubercles than the rest of the dorsal region; (6) ventral region cream with dark-brown mottling on the gular region, chest, and belly; (7) advertisement call consisting of a multipulsed note of 0.498 ± 0.06 s in duration (0.374–0.648 s), 49.4 ± 6.6 pulses/call (38–65), 99 ± 1.5 pulses/s (95.7–102.7), and dominant frequency of 1167.2 ± 76.8 Hz (1033.6–1378.1 Hz).

**Comparison with other species.**—*Proceratophrys ararype* differs from *P. appendiculata*, *P. belzebul*, *P. boiei*, *P. gladius*, *P. itamari*, *P. izecksohni*, *P. laticeps*, *P. mantiqueira*, *P. melanopogon*, *P. moheringi*, *P. paviotii*, *P. phyllostomus*, *P. pombali*, *P. renalis*, *P. rondonae*, *P. sanctaritae*, *P. subguttata*, and *P. tupinamba* by the absence of single unicuspidate palpebral and rostral appendages (present in those species; single, short and multicuspidate in *P. rondonae*). In addition, *P. ararype* can be distinguished from *P. appendiculata*, *P. gladius*, *P. itamari*, *P. izecksohni*,

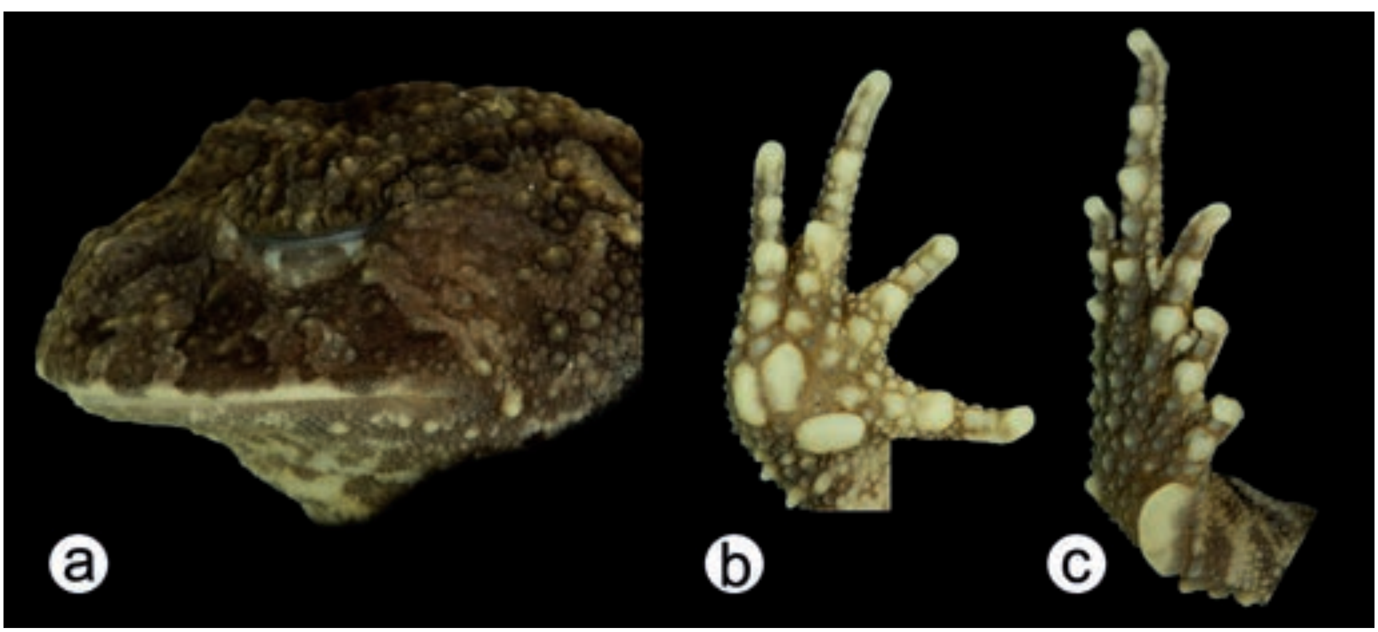

FIG. 2.—*Proceratophrys ararype* (holotype, adult female, CHUFPE 156, snout–vent length = 44.3 mm): (a) lateral view of the head; ventral views of (b) hand and (c) foot. Photos by B.F. Santos. A color version of this figure is available online.


Fig. 3.—Live specimens of *Proceratophrys ararype* from Crato Municipality, Ceará state, Brazil: (a) adult female (holotype, CHUFPE 156) from Mata do Clube Recreativo Grangeiro, and (b) male calling at Sítio Caianas. Photos by P.M.S. Nunes (a), I.J. Roberto (b). A color version of this figure is available online.

*P. laticeps*, *P. mantiqueira*, *P. melanopogon*, *P. moheringi*, *P. phyllostomus*, *P. pombali*, *P. sanctaritae*, *P. subguttata*, and *P. tupinamba* by lacking a rostral appendage (present in those species). *Proceratophrys ararype* differs from *P. avelinoi*, *P. bigibbosa*, *P. brauni*, and *P. palustris* by lacking postocular swellings (present in these species). *Proceratophrys ararype* has short, fused, and not pointed warts on upper eyelid border (fused with small points in *P. goyana*, *P. strussmannae*, *P. carranca*, *P. branti*, and *P. concavitympanum*; small, rounded, and not fused in *P. cururu* and *P. rotundipalpebra*; slightly fused without appendage in *P. huntingtoni*, *P. vielliardi*, and *P. moratoi*; conical and pointed in *P. bagnoi*; enlarged, pointed, and with the largest tubercle in the middle more projected than lateral tubercles in *P. minuta*; small and rounded in *P. redacta*; multiple short and pointed expansions in *P. schirchi*). From *P. bagnoi*, *P. concavitympanum*, *P. dibernardoi*, and *P. goyana*, *P. ararype* differs by the presence of a single row of tubercles on the forearm (two rows in *P. bagnoi*, *P. concavitypanum*, and *P. dibernardoi*; tubercles not organized in rows in *P. goyana*). From *P. concavitympanum*, *P. ararype* also differs by the number, size, and disposition of tubercles on the dorsal region: tubercles more concentrated on the head, arms, legs, and presacral constriction; less concentrated and smaller tubercles on the flanks, sacral-urostyle, and coccyx regions (tubercles uniformly distributed on the dorsal region with no variation in size in *P. concavitympanum*).

A cream-colored ventral region with dark-brown mottling on the gular region, chest, and belly distinguishes *P. ararype* from *P. aridus*, *P. branti*, *P. caramaschii*, *P. carranca*, *P. cristiceps*, *P. redacta*, and *P. strussmannae* (dark spots in *P. branti* and *P. carranca*, light-brown dots on the gular region and chest, or ventral surface cream in *P. aridus*, *P. caramaschii*, and *P. cristiceps*; gular region blackish, scattered small, dark-brown dots on the chest in *P. redacta* and on the chest and belly in *P. strussmannae*).

*Proceratophrys ararype* can be distinguished from sympatric *P. cristiceps* by advertisement call with higher number of pulses per second (95.7–102.7 in *P. ararype* vs. 87.4–91.9 in *P. cristiceps*) and higher dominant frequency (1033.6–1378.1 Hz in *P. ararype* vs. 900–990 Hz in *P. cristiceps*). *Proceratophrys ararype* also differs from *P. caramaschii* by higher number of pulses per second (78.6–81.8 in *P. caramaschii*). Advertisement call also distinguishes *P. ararype* from *P. huntingtoni* and *P. moratoi* by longer duration (0.374–0.648 s in *P. ararype* vs. 0.200–0.320 s in *P. huntingtoni* and 0.179–0.335 s in *P. moratoi*), higher number of pulses per call (38–65 in *P. ararype* vs. 19–25 in *P. huntingtoni* and 12–26 in *P. moratoi*), and higher number of pulses per second (78–95 in *P. huntingtoni* and 69–86 in *P. moratoi*).

**Description of the holotype.**—Head wider than long, head length 46% of SVL, snout rounded in dorsal and ventral views, obtuse and slightly vertical in profile; nares elliptical and prominent, canthal crests marked, prominent and covered by small tubercles; no preocular crests; eyes directed anterolaterally, eye diameter 22% of head length and 92% of the palpebral appendage; eyelid with short and fused warts, five warts on the left eyelid and four on the right (L 1, 2/5, 3; R 1, 2/5, 2), with one larger and more prominent; presence of one row of tubercles on the eyelid; indistinct tympanum; vomerine teeth in two short rows between the choannae; frontoparietal crests well developed; region between frontoparietal crests shallow; interocular ridge of warts organized in a row, markedly curved; ocular-dorsal ridge of warts complete from the eyes to the coccyx region; two parallel rows of warts on the suprascapular region. Dorsal surface, including flanks, arms and legs, with various warts of different sizes and shapes, one row of close and pointed forearm tubercles, reaching the hands; ventral surfaces, except hands and feet, covered by numerous small, rounded, uniform warts. Finger lengths IV < II < I < III (Fig. 2b); interdigital webbing absent; inner metacarpal tubercle large and elliptical; outer metacarpal divided in two parts, the internal oval and the external elliptical; scarce small rounded supernumerary tubercles; subarticular tubercles large, rounded, but grooved anteriorly and posteriorly. Thigh length longer than tibia length, the sum of thigh and

TABLE 3.—Morphometric measurements (mm) for paratype specimens of *Proceratophrys ararype* sp. nov. from Ceará state, Brazil. Values are presented as mean ± 1 SD (range).

| | *Proceratophrys ararype* | |
|---|---|---|
| Measurement(mm)[a] | Males ($n$ = 8) | Females ($n$ = 3) |
| SVL | 38.7 ± 2.6 (35.6–42.2) | 54.1 ± 4.1 (51.3–57.0) |
| HW | 16.6 ± 1.4 (15.1–19.0) | 24.3 ± 1.9 (23.0–25.6) |
| HL | 11.7 ± 1.3 (10.5–13.9) | 16.7 ± 0.9 (16.1–17.3) |
| DICS | 8.1 ± 1.1 (7.9–10.3) | 11.8 ± 0.5 (11.5–12.2) |
| IND | 2.6 ± 0.6 (2.1–3.7) | 3.6 ± 0.8 (3.0–4.1) |
| END | 3.6 ± 0.2 (3.3–3.9) | 4.4 ± 0.1 (4.4–4.5) |
| ED | 5.4 ± 0.5 (4.7–6.0) | 5.6 ± 0.8 (5.0–6.2) |
| UEW | 4.9 ± 0.4 (4.2–5.2) | 6.6 ± 1.1 (5.8–7.4) |
| IOD | 3.0 ± 0.2 (2.8–3.3) | 4.0 ± 0.1 (3.9–4.0) |
| THL | 14.7 ± 1.4 (13.1–16.9) | 20.7 ± 2.1 (19.2–22.2) |
| TL | 14.5 ± 1.1 (12.8–15.4) | 20.3 ± 2.2 (18.7–21.8) |
| FL | 22.4 ± 1.3 (21.0–24.0) | 30.7 ± 2.9 (28.7–32.8) |
| FHL | 19.4 ± 1.2 (18.1–21.3) | 25.0 ± 0.5 (24.6–25.4) |

[a] SVL = snout–vent length; HL = head length; HW = head width; DICS = distance from the interocular crest to the tip of snout; IND = internarial distance; END = eye–nostril distance; ED = eye diameter; UEW = upper eyelid width; IOD = interorbital distance; THL = thigh length; TL = tibia length; FL = foot plus tarsus length; FHL = forearm and hand length (FHL).

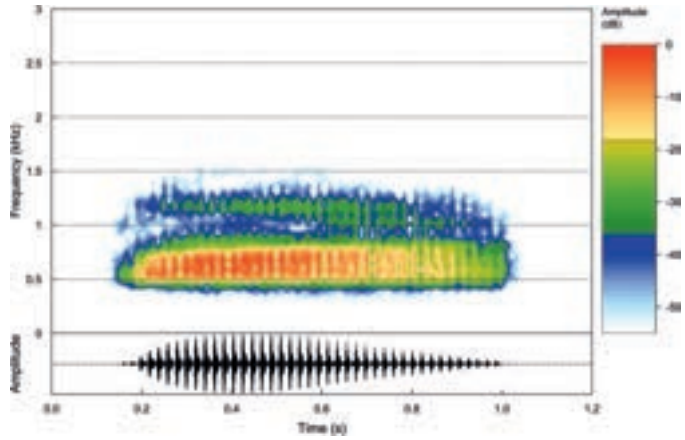


FIG. 4.—Advertisement call of male *Proceratophrys ararype* (URCA-H 84, snout–vent length 35.3 mm; air temperature, 24°C): (top) oscillogram and (bottom) audiospectogram of a single call. A color version of this figure is available online.

tibia lengths 79% of SVL; toe lengths I < II < V < III < IV; inner metatarsal tubercle large, elliptical, spatulated; outer metatarsal tubercle small, rounded; scarce small rounded supernumerary tubercles; subarticular tubercles large, nearly rounded, grooved anteriorly and posteriorly.

**Measurements of the holotype (mm).**—SVL, 44.3; HL, 20.6; HW, 13.0; DICS, 10.4; IND, 2.6; END, 4.2; ED, 4.5; UEW, 4.9; IOD, 2.9; THL, 18.8; TL, 16.2; FL, 24.8; FHL, 23.2.

**Color in life of the holotype.**—Based on photographs of the holotype (Fig. 3a). Dorsal background gray, maculated with variegate brown and dark-brown pattern, resembling dead leaves. Area delimited by the ocular-dorsal ridge of warts light brown, bordered along the external sides by a dark-brown band with four wave-like blotches on each side. Two brown bands from the eye to the upper lip. From two to three transverse dark-gray bars on fingers and toes.

**Color in preservative of the holotype.**—Dorsal background color dark gray. Area delimited by the ocular-dorsal ridge of warts light gray, bordered along external sides by a black band with four wave-like blotches on each side. Two dark-gray bands from the eye to the upper lip. From two to three transverse dark-gray bars on the fingers and toes. Ventral surface background color cream with mottling dark brown in the gular region, chest, and belly (Fig. 1b).

**Variation.**—Some individuals do not have a complete ocular-dorsal ridge of warts (CHUFPE 161, adult male; CHUFPE 227, juvenile). One individual (CHUFPE 227, juvenile) has a cream dorsal background color. The measurements of the type series are provided in Table 3.

**Advertisement call.**—Based on the 120 calls from the three males recorded, the advertisement call of *P. ararype* consists of a pulsed note (Fig. 4) with a duration of 0.498 ± 0.06 s (0.374–0.648 s), emitted sporadically with 49.4 ± 6.6 pulses/call (38–65), 99 ± 1.5 pulses/s (95.7–102.7 pulses/s), and a dominant frequency of 1167.2 ± 76.8 Hz (1033.6–1378.1 Hz).

**Geographic distribution.**—*Proceratophrys ararype* sp. nov. is known from the type locality at Mata do Clube Recreativo Grangeiro, from Clube Serrano Atlético Cratense, and from Sítio Caianas, Crato Municipality, Ceará state, Brazil (Fig. 5). We collected and analyzed *Proceratophrys* populations throughout northeastern Brazil, comparing specimens morphologically ($n$ = 358) and molecularly ($n$ = 109). With 51 localities analyzed, including several other Brejos de Altitude, *P. ararype* only occurs in Chapada do Araripe, within an area of 3100 km$^2$ (Appendix; Fig. S1).

**Etymology.**—The Araripe Plateau spans the borders of Ceará, Pernambuco and Piauí states. "Araripe," from the ancient tupi, *ararype*, means "on the *Araras* River" (*arara*, arara + *'y*, river + *pe*, on the; *Arara* means Macaw in Tupi and in vernacular Portuguese). Because the new species is known only from the Araripe region, we name it after this area. The specific epithet *ararype* is treated as a noun in apposition.

**Environment and habitat.**—The holotype and paratopotypes were collected in a forest remnant on the slopes of the Araripe Plateau, within the limits of a recreational club (Clube Grangeiro). The area has suffered significant anthropogenic modification, including the planting of exotic trees (such as coconut, *Cocus nucifera*) and the use of trails for hiking. Palm trees (Arecaceae) cover most of the area and the local drainage is composed of several permanent streams that emerge from springs on the slopes of Chapada do Araripe. Many of these streams and rivulets are partially or fully diverted for local water supply, presenting a problem for *P. ararype*, which uses lotic environments for reproduction. Ferreira-Silva et al. (2016) reported reproductive activity of *P. ararype* (as *P. aridus*) from September to December. Some specimens (CHUFPE 152, 156, 160, and 161) were collected in December 2014, from 2000 to 2200 h. Males were calling along a permanent stream with males of other species (*Physalaemus cuvieri*, *Adenomera* sp., and *Dendropsophus minutus*). The specimens collected in May 2015 (CHUFPE 226 and 227) were collected in pitfall traps. We also recorded the species in Sítio Caianas, located on the slopes of Chapada do Araripe. There, the primary habitat is humid forest, where male *P. ararype* were found calling in the leaf litter along streams (10–50 cm from the stream edge). Other species found calling contemporaneously were *Physalaemus cuvieri, Adenomera* sp., and *Scinax* gr. *ruber*.

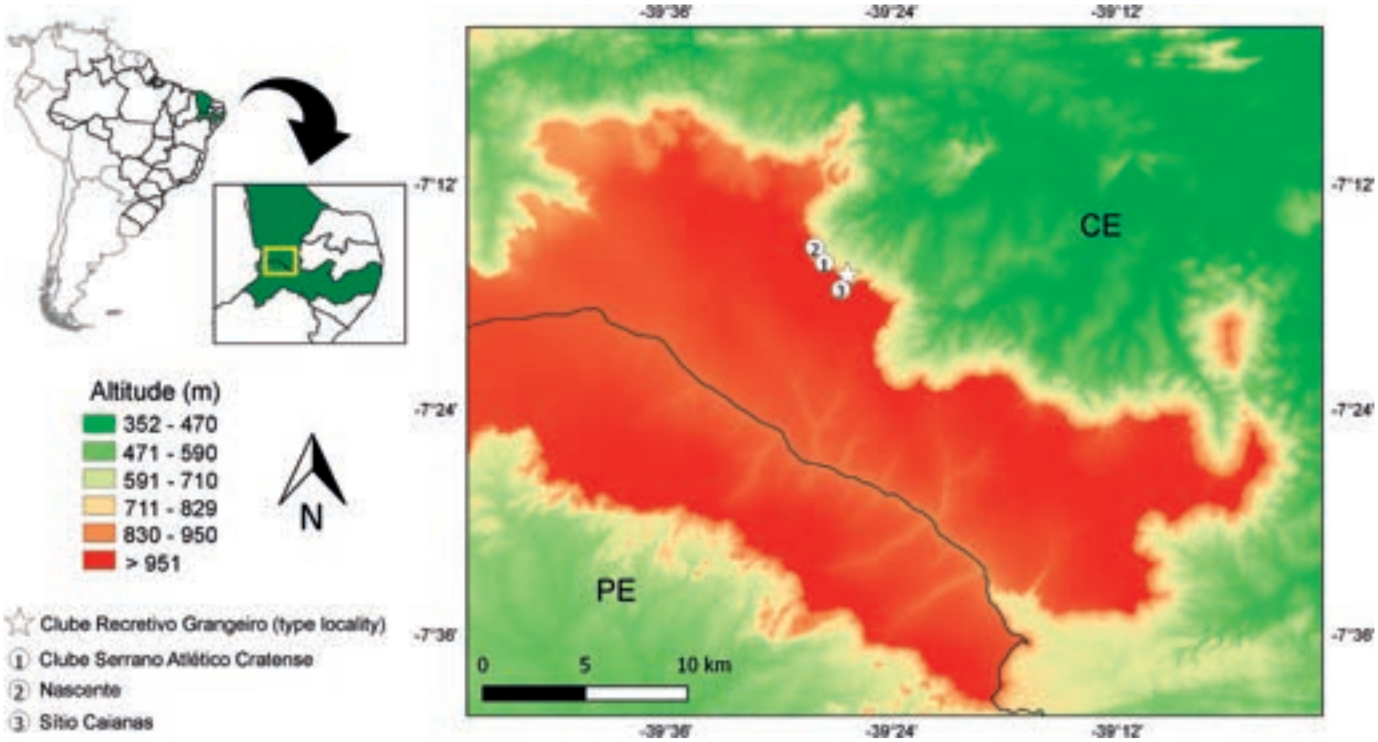


Fig. 5.—Location of the study area within Ceará (CE) and Pernambuco (PE) states (shaded areas within inset) of northeastern Brazil (upper left), and elevation map of the Araripe Plateau showing sampling locations where *Proceratophrys ararype* was collected. A color version of this figure is available online.

**Molecular phylogeny and genetic divergence of the new species.**—Our 16S mtDNA gene tree (Fig. 6) confirmed that *Proceratophrys cristiceps* also occurs in the Araripe Plateau region, sympatrically with *P. ararype*. However, these species belong to different lineages within *P.*. Sequence divergence between *P. ararype* and *P. cristiceps* for 16S is about 8%; and 4% between *P. ararype* and *P. concavitympanum* from Aripuanã Municipality, Mato Grosso state (Table 4).

The species tree (Fig. 7), based on Bayesian analysis of the 16S and rhodopsin genes, recovered *P. ararype* as the sister taxon of *P. concavitympanum* from Palmas Municipality, Tocantins state, Brazil (Posterior Probability [PP] = 0.96). *Proceratophrys concavitympanum* from Aripuanã Municipality, Mato Grosso state, Brazil, forms a well-supported clade with the two previous species (PP = 098). Divergence between *P. ararype* and *P. concavitympanum* from Palmas occurred in the Pleistocene (Fig. 7). The large confidence intervals on node ages preclude any other meaningful assertions on the history of speciation in *Proceratophrys*.

## Discussion

Relictual species occurring in natural rainforest enclaves in northeastern Brazil (e.g., Brejos de Altitude) support historical connections between these remnants and the Amazon and Atlantic Forests (Ledo and Colli 2017). For example, phylogenetic and comparative studies recovered *Adelophryne baturitensis*, *A. maranguapensis*, and *Rhinella casconi* more closely related to forest congeners than congeners from open formations (Fouquet et al. 2012; Roberto and Loebmann 2016). Likewise, some snake species reinforce past connections between Chapada do Araripe and the Amazon Forest, including *Anilius scytale*, *Bothrops* aff. *atrox*, and *Drymoluber dichrous* (Ribeiro et al. 2012; Roberto and Loebmann 2016). The same pattern was recovered for *P. ararype*, which is sister to the Amazonian *P. concavitympanum*, indicating that Araripe forest enclaves were once previously connected with the Amazon.

*Proceratophrys ararype* diverged from *P. concavitympanum* during the Pleistocene, probably as a result of forest expansions and contractions resulting from climatic cycles (Por 1992). Many forest-restricted species occur in montane areas of Ceará state and likely originated from ancestors from the Amazon Forest, Atlantic Forest, or both (Roberto and Loebmann 2016). Therefore, we hypothesize that *P. concavitympanum* was likely more widespread in the past and one population became isolated in forest remnants around the Araripe Plateau as forests contracted in response to cold climates during the Pleistocene. This population remained surrounded by the semiarid Caatinga vegetation, leading to divergence in isolation from *P. concavitympanum*. This raises the possibility that other such microendemic relatives of *P. concavitympanum* might exist in similar forest fragments outside the Amazon.

We confirmed that *P. cristiceps* occurs sympatrically with *P. ararype* in the Araripe Plateau region. Previous work considered *P. cristiceps* to occur in the Caatinga and in the humid forested slopes of the Araripe Plateau (Roberto and Loebmann 2016). However, *P. cristiceps* seems to be restricted to the Cerradão phytophysiognomy (mesic deciduous foliage tropical forest; Bezerra et al. 2003) on top of the

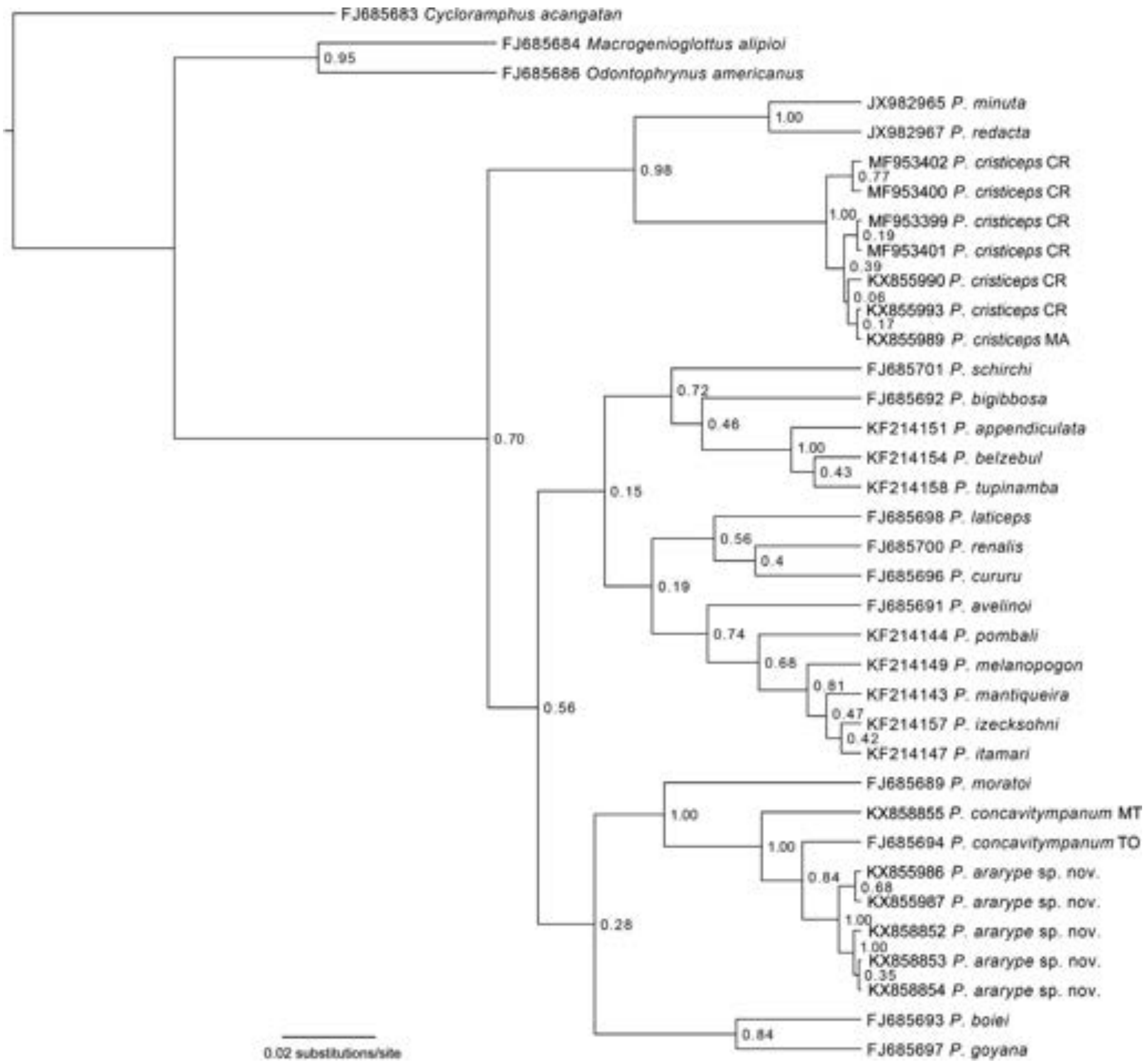


FIG. 6.—Gene tree for genus *Proceratophrys* inferred from Bayesian analysis of the 16S mitochondrial gene fragment. Values adjacent to branch nodes indicate posterior probabilities. Scale bar represents number of substitutions per site.

Araripe Plateau and to the Caatinga at lower elevation areas, whereas *P. ararype* is restricted to the humid forests.

The phylogenetic diversity within *P. concavitympanum* is still likely underestimated. The first phylogenetic tree constructed for the genus *Proceratophrys* used a sample from Palmas Municipality (Tocantins state, Brazil) to represent *P. concavitympanum* (Amaro et al. 2009). In our study, we included a sample from Aripuanã Municipality, Mato Grosso state (see Fig. 6), a municipality that is much closer (straight-line distance, 200 vs. 1400 km) to the type locality of *P. concavitympanum* and within the same Amazon area of endemism (Silva and Oren 1996; Garda et al. 2010). Based on morphology, genetic and geographic distances, area of endemism (within the Rondônia area of endemism), and previous morphological and acoustic analyses (Santana et al. 2010), we consider the population of Aripuanã, Mato Grosso as typical *P. concavitympanum*. Hence, our results indicate that the taxonomic status of the population of *Proceratophrys* from Palmas needs further evaluation.

Superficially, a picture of the specimen sequenced from this locality resembles more *P. concavitympanum* than *P. ararype*, but a larger sample is needed to unequivocally establish the taxonomic status of the population from Palmas. Additional cryptic diversity within the *P. concavitympanum* complex will likely result from including samples from other Amazon areas of endemism. These areas are delimited by large rivers, such as the rivers separating Tocantins and Aripuanã populations (Tapajós and Xingu

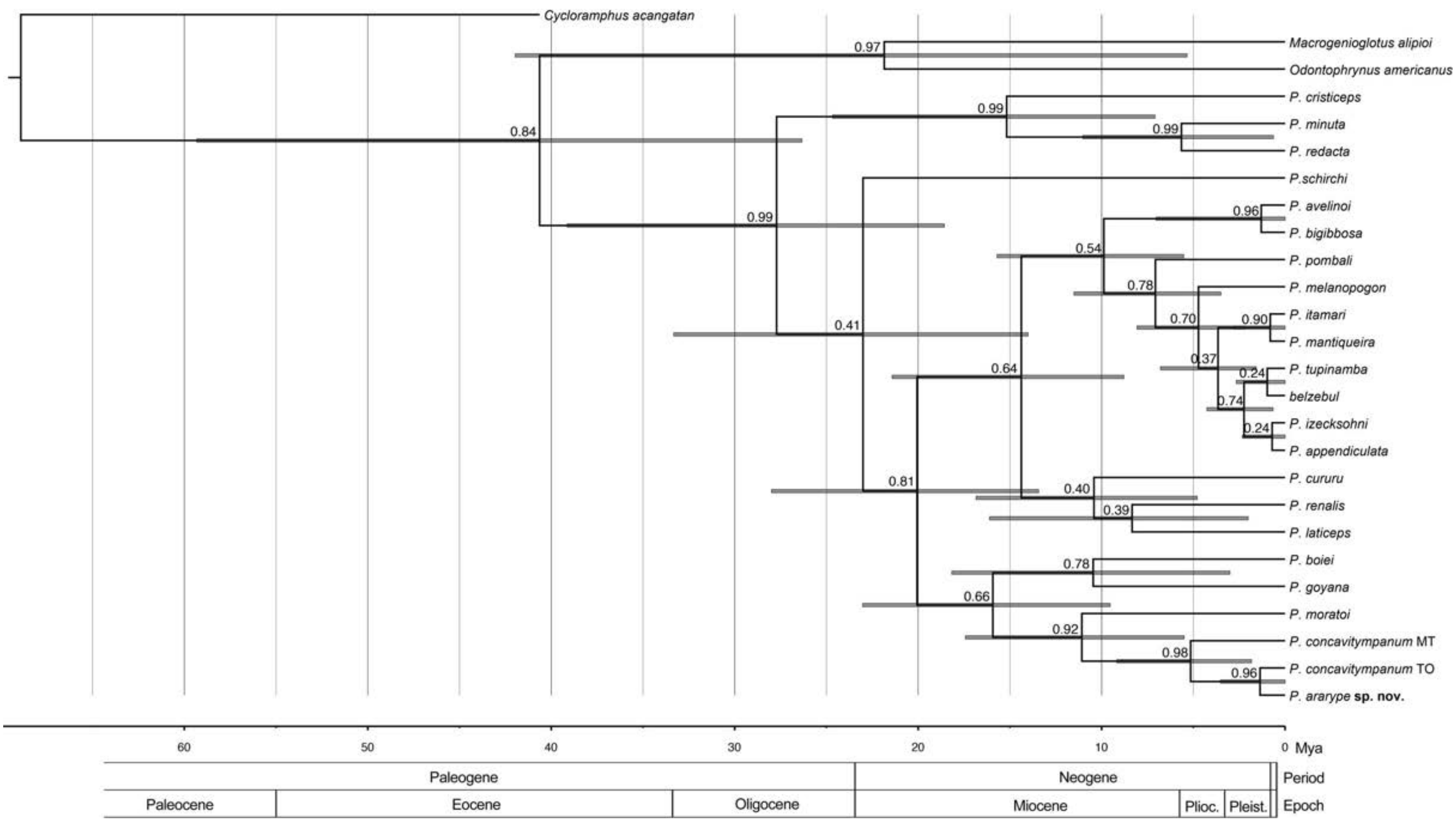


FIG. 7.—Species tree for genus *Proceratophrys* based on Bayesian analysis of the 16S and rhodopsin genes. Values above branches indicate posterior probabilities. Scale bar represents number of substitutions per site.

TABLE 4.—Uncorrected *p*-distances for 16S (inferior diagonal) and rhodopsin (superior diagonal) gene fragments among specimens representing three species of *Proceratophrys*: *ararype* sp. nov., *concavitympanum*, and *cristiceps*. Abbreviations for Brazilian states: TO = Tocantins, MT = Mato Grosso, RN = Rio Grande do Norte, CE = Ceará.

| | *Proceratophrys* species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *P. ararype* AAGARDA2736 | — | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 2 | *P. ararype* AAGARDA2741 | 0.00 | — | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 3 | *P. ararype* CHUFPE152 | 0.00 | 0.00 | — | 0.00 | 0.00 | 0.00 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 4 | *P. ararype* CHUFPE156 | 0.00 | 0.00 | 0.00 | — | 0.00 | 0.00 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 5 | *P. ararype* CHUFPE160 | 0.00 | 0.00 | 0.00 | 0.00 | — | 0.00 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 6 | *P. concavitympanum* MTR7884 Palmas, TO | 0.01 | 0.01 | 0.02 | 0.02 | 0.02 | — | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 7 | *P. concavitympanum* FMT-A11698 Aripuanã, MT | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | — | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 |
| 8 | *P. cristiceps* AAGARDA1754 Macaíba, RN | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | — | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | *P. cristiceps* AAGARDA2739 Crato, CE | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.00 | — | 0.00 | 0.00 | 0.00 |
| 10 | *P. cristiceps* AAGARDA2735 Crato, CE | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.00 | 0.00 | — | 0.00 | 0.00 |
| 11 | *P. cristiceps* GRCOLLI21987 Crato, CE | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.00 | 0.00 | 0.00 | — | 0.00 |
| 12 | *P. cristiceps* GRCOLLI22131 Crato, CE | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | — |

rivers) that are known to act as hard or semipermeable barriers for many frog species (Kaefer et al. 2013; Maia et al. 2017). Such underestimation of species diversity can have important consequences for determining phylogenetic relationships, ecology, and conservation.

*Proceratophrys ararype* occurs in the same Chapada do Araripe humid forest habitat as the critically endangered Araripe Manakin (*Antilophia bokermanni*), the endangered freshwater Crab *Kingsleya attenboroughi*, the endangered Snake *Atractus ronnie*, and the vulnerable mouse *Rhipidomys cariri* (BirdLife International 2015; Pinheiro and Santana 2016; Roberto and Loebmann 2016). Although the area is situated within the sustainable use Environmental Protected Area of Araripe Plateau, this protection category is the least restrictive under Brazilian legislation. Furthermore, this region is highly deforested and many streams have been channelized for agricultural and recreational use. These are the main threats for the humid forest on the slopes of the Araripe Plateau, and consequently, for the maintenance of water sources in the region (Linhares et al. 2010) where *P. ararype* occurs and reproduces. The conservation of these humid forests is therefore critical for the species long-term survival. Given these factors, we highlight the need of further studies on the conservation status of *P. ararype*, which could be threatened like many of the sympatric animals occurring in the Araripe plateau.

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## SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-16-00084.S1

FIG. S1.—Distribution records of individuals of Proderatophrys from Caatinga biome analyzed in the present study.

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## Appendix

### Specimens Examined

*Proceratophrys aridus*.—BRAZIL: Ceará: Milagres: MNRJ 55349, 55778–55822, 75156–75168; URCA-H 106, 142, 143.

*Proceratophrys caramaschii*.—BRAZIL: Ceará: Mucuripe: MNRJ 1419, 1420, 1680, 16470–16484, 16487–16489, 16591–16600.

*Proceratophrys concavitympanum*.—BRAZIL: Mato Grosso: Alta Floresta: ZUEC 21201. Apiacás: UFMT 7906. Aripuanã: UFMT 11697, 11699; MZUFV 9552, 9554–9556. Colniza: UFMT 6808. Juína: UFMT 6996, 7825. Paranaíta: UFMT 7534, 7963, 9882, 9990, 10038, 10041, 10046, 10054, 10067, 10109; CFBH 20675–20677; UFMS LA03, LA34, LA35, LA43, LA69; ZUEC 14505, 14506, 16011–16015, 16719, 21201. Vale São Domingos: UFMT 1834, 1836, 7882, 7885, 8319, 8320, 8377, 8380. Vila Bela da Santíssima Trindade: UFMT 4105. Pará: Canaã dos Carajás: MNRJ 90328. Parauapebas: MNRJ 90327; PUC-MG 10561, 11206. Jacareacanga: ZUEC 14505, 14506. Vitória do Xingú: UFMG 18351–18357. Rondônia: Espigão do Oeste: CFBH 5136; MZUFV 10477. Ministro Andreaza: CFBH 19818. Tocantins: Araguaína: UFMS Z36, Z37. Porto Nacional: UFMS 1146, 1147. Wanderlândia: CFBH 28521.

*Proceratophrys cristiceps*.—BRAZIL: Alagoas: Olho D'Água do Casado: UFAL 8168–8170. Piranhas: UFBA 8, 9, 43. Traipu: Serra da Mão: UFAL 8968, 9035, 9036, 9043, 9196, 9510, 9656. Bahia: Caetité: UFMG 5851. Paulo Afonso: UFPB 12114, 12119, 12122, 12123, 12128. Ceará: Aiuaba: AAGARDA 5111, 5132; URCA-H 7366, 7385, 7393, 7396, 7408, 7416, 7418. Barbalha: URCA-H 4293, 4571. Baturité: UFC3722. Crateús: URCA-H 4744. Crato: AAGARDA 2735, 2737–2740. General Sampaio: UFC 5351. Itapipoca: AAGARDA 9817, 10453–10455. Ipu: UFPB 6117–6119, 6121, 6123, 6125. Jaguaribe: AAGARDA 10176–10179, 10286, 10398–10402. Pacajus: UFC 4562. Paracuru: URCA-H 5773, 5774. Pentecoste: UFC 5001, 5018, 5019, 5193. São Gonçalo do Amarante: URCA-H 5669, 5775, 5860. Santa Quitéria: UFPB 10651, 10753–10758. Serra das Almas: UFC 32, 131, 213, 224, 3319, 3464, 3467, 3468, 3470. Serra de Ibiapaba: UFPB 6117–6126. Ubajara, Parque Nacional de Ubajara: AAGARDA 10672, 10695, 10698, 10699, 10703, 10707–10709, 10782, 10796, 10907, 10909, 10911–10914, 10961, 10974, 10981, 10983. Várzea da Conceição: UFPB 9661, 9665, 9667. Paraíba: Araruna: UFPB 8427, 8438, 8447, 8451, 8453, 8456, 8465, 8467, 8469, 8487. Boa vista: UFPB 1573–1581. Cabaceiras: UFPB 6691–6694, 11271, 11274. São José dos Cordeiros: UFPB 5866. Pernambuco: Arcoverde: UFPB 9678–9682, 9684, 9686–9688, 9692, 9701. Betânia: UFC 3331. Bezerros: UFPB 7098. Exu: URCA 1462, 1463; UFPB 7214–7217. Nascente: UFPB 9670. Ouricuri: URCA 2988, 2989. Buíque, Parque Nacional do Catimbau: AAGARDA 7706–7712, 7747, 7760, 7761, 7765, 7799, 7802, 7804, 7805, 7824, 7886, 7975, 8056, 8362, 8417, 8435, 8437–8440, 8450, 8463. Serra Talhada: UFPB 9656, 9659, 9660. Trindade: UFPB 974, 9673–9677. Piauí: Floriano: UFPI 214–2116, 222, 236. Piripiri: UFPB 10340, 10342–10346. Rio Grande do Norte: Serra Negra do Norte, Estação Ecológica do Seridó: AAGARDA 5447, 5528, 5583, 5689, 6061, 6790. João Câmara: AAGARDA 8913–8915, 9806–9811; URCA 422, 427, 483–485, 487, 488, 493, 498, 501. Macaíba, Escola Agrícola de Jundiaí: AAGARDA 1013, 1014, 1019, 1020, 1753–1771, 1773, 1776, 1778, 1786–1791, 1935, 2495, 2496, 2583, 3757, 5447, 5528, 5554, 5583, 5689, 6061, 6790, 8866–8871, 8913–8915, 9806–9811. Sergipe: Poço Redondo: UFPB 12120, 12121, 12125–12127.

*Proceratophrys huntingtoni*.—BRAZIL: Mato Grosso: Chapada dos Guimarães: UFMT 1745–1749, 11133–11135.

*Proceratophrys minuta*.—BRAZIL: Bahia: Miguel Calmon, Parque Estadual das Sete Passagens: UFBA 6229, 6230, 6716–6720, 6722, 6725, 6726.

*Proceratophrys moratoi*.—BRAZIL: São Paulo: Botucatu: ZUEC 7031–7033.

*Proceratophrys redacta*.—BRAZIL: Bahia: Morro do Chapéu: PUC-MG 7910, 7911, 7913; UFMG 6049–6057.

*Proceratophrys schirchi*.—BRAZIL: Minas Gerais: Santa Maria do Salto: PUC-MG 4021.

*Proceratophrys strussmannae*.—BRAZIL: Mato Grosso: Jauru: UFMT 5859, 6659, 7869, 7872, 7874, 7876, 7878, 7880, 7882, 7885, 7886, 8319, 8320, 8377–8380.

FIG. S1.—Distribution records of individuals of Proderatophrys from Caatinga biome analyzed in the present study