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A New Rupicolous Species of the *Pristimantis conspicillatus* Group (Anura: Brachycephaloidea: Craugastoridae) from Central Bahia, Brazil

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ABSTRACT.—We describe a new frog species of the megadiverse genus *Pristimantis* from the Chapada Diamantina, a regional designation of the Espinhaço mountain range in the state of Bahia, northeastern Brazil. We assign the new species to the genus *Pristimantis*, *P. conspicillatus* group, based on its phylogenetic position. This is the second rupicolous species of *Pristimantis* and the fourth species inhabiting northeastern Brazil. The new species is characterized by the following combination of characters: 1) dorsum background color light brown to yellowish-brown, maculated with blackish-brown marks, resembling a granite rock surface; 2) dorsum granular; 3) venter areolate; 4) dentigerous process of the vomer ovoid; 5) snout rounded or truncate in dorsal view; 6) snout rounded in profile; 7) dorsolateral folds absent; 8) finger fringes absent; 9) toe fringes weakly developed; 10) double, poorly developed nuptial pads; 11) vocal slits present in the male; 12) advertisement call composed of one note; 13) call duration 0.011–0.086 s; 14) dominant frequency varying from 2.41 to 3.49 kHz; and 15) decreasing amplitude modulation from the beginning to the end of call. We recovered the new species outside the clade containing the other three nominal species of *Pristimantis* from northeastern Brazil, as the sister species of *P. gaigei*, a species from Costa Rica, Panama, and Colombia. The new species seems to be restricted to the high-elevation areas (870–1,800 m a.s.l.) of the Chapada Diamantina, Central Bahia, Brazil. Both the genus *Pristimantis* and the *P. conspicillatus* group still lack morphological synapomorphies, and a thorough systematic review based on a stringent phylogenetic hypothesis is necessary for a better understanding of the evolution of these important lineages of Neotropical frogs.

RESUMO.—Descrevemos uma nova espécie de rã pertencente ao megadiverso gênero *Pristimantis*, oriunda da Chapada Diamantina, designação regional da Serra do Espinhaço no estado da Bahia, nordeste do Brasil. Atribuímos a nova espécie ao gênero *Pristimantis*, grupo *de P. conspicillatus*, com base em sua posição filogenética. Esta é a segunda espécie rupícola do gênero *Pristimantis* e a quarta do nordeste brasileiro. A nova espécie é caracterizada pela seguinte combinação de caracteres: 1) Coloração de fundo marrom claro a marrom-amarelado, maculada por marcas marrom-escuras, assemelhando-se à superfície de rocha granítica; 2) dorso granulado; 3) ventre areolado; 4) processo dentígero do vômer ovoide; 5) focinho arredondado ou truncado em vista dorsal; 6) arredondado em vista lateral; 7) pregas dorsolaterais ausentes; 8) fímbrias nos dedos ausentes; 9) fímbrias nos artelhos pouco desenvolvidas; 10) calosidade nupcial dupla, pouco desenvolvida; 11) fendas vocais presentes; 12) canto de anúncio composto por uma única nota; 13) duração do canto 0.011–0.086 s; 14) frequência dominante variando de 2.41 a 3.49 kHz; and 15) pico de amplitude no começo do canto, decrescendo ao longo do mesmo até alcançar o final. A nova espécie foi recuperada fora do clado que contém as outras três espécies nominais de *Pristimantis* do Nordeste brasileiro, como espécie irmã de *P. gaigei*, uma espécie da Costa Rica, Panamá e Colômbia, e parece estar restrita a áreas elevadas (870–1,800 m a.s.l.) da Chapada Diamantina, região central do estado da Bahia, Brasil. Tanto o gênero *Pristimantis* quanto o grupo de *P. conspicillatus* ainda carecem de sinapomorfias morfológicas, e uma revisão taxonômica baseada em uma hipótese filogenética robusta é necessária para melhor compreender a evolução destas importantes linhagens de rãs neotropicais.

The megadiverse genus *Pristimantis* Jiménez de la Espada, 1870 is the richest among vertebrates and currently harbors 546 species of direct-developing Neotropical frogs (Frost, 2019). This highly speciose genus is divided in 12 species groups, but most species remain unassigned to any group (Padial et al., 2014; González-Durán et al., 2017). Among these 12 groups, the *P. conspicillatus* group is the largest, comprising 35 described species (Padial et al., 2014, 2016; Oliveira et al., 2017; Barrio-Amorós et al., 2019): *P. achatinus* (Boulenger, 1898); *P. adiastolus* Duellman and Hedges, 2007; *P. avicuporum* (Duellman and Pramuk, 1999); *P. bipunctatus* (Duellman and Hedges, 2005); *P. buccinator* (Rodriguez, 1994); *P. carranguerorum* (Lynch, 1994); *P. charlottevillensis* (Kaiser et al., 1995); *P. chiastonotus* (Lynch and Hoogmoed, 1977); *P. citriogaster* (Duellman, 1992); *P. condor* (Lynch and Duellman, 1980); *P. conspicillatus* (Günther, 1858); *P. dundeei* (Heyer and Muñoz, 1999); *P. fenestratus* (Steindachner, 1864); *P. gaigei* (Dunn, 1931); *P. gutturalis* (Hoogmoed et al., 1977); *P. iiap* Padial et al., 2016; *P. incertus* (Lutz, 1927); *P. johannesdei* (Rivero and Serna, 1988); *P. koehleri* Padial and de la Riva, 2009; *P. latro* Oliveira et al., 2017; *P. lymani* (Barbour and Noble, 1920); *P. malkini* (Lynch, 1980); *P. medemi* (Lynch, 1994); *P. meridionalis* (Lehr and Duellman, 2007); *P. metabates* (Duellman and Pramuk, 1999); *P. paulodutrai* (Bokermann, 1975); *P. peruvianus* (Melin, 1941); *P. phalaroinguinis* (Duellman and Lehr, 2007); *P. ramagii* (Boulenger, 1888); *P. samaipatae* (Köhler and Jungfer, 1995); *P. skydmainos* (Flores and Rodriguez, 1997); *P. ventrigranulosus* Maciel et al., 2012; *P. vilarsi* (Melin, 1941); *P. vinhai* (Bokermann, 1975); and *P. zeuctotylus* (Lynch and Hoogmoed, 1977). The group is widely distributed across the Neotropical region, occuring from Costa Rica to southern Bolívia, extending to the Brazilian Cerrado, reaching the Atlantic Forest in northeastern Brazil. Three species of the *P. conspicillatus* group are distributed through northeastern Brazil: *P. paulodutrai*, *P. ramagii*, and *P. vinhai* (Frost, 2019).

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Field expeditions to the Chapada Diamantina, a regional designation of the Espinhaço mountain range in the state of Bahia, northeastern Brazil, allowed us to collect a distinctive new species of *Pristimantis* inhabiting the rocky mountain meadows called *Campo Rupestre* (Rocky field, in a literal translation). This species, which we describe herein by using an integrative approach, is the second rupicolous species of *Pristimantis* (the other species is *P. hoogmoedi* Kaiser et al., 2015) and the fourth species of the genus in northeastern Brazil.

MATERIALS AND METHODS

Morphology.—Specimens used in morphological analyses are housed in the following institutions: American Museum of Natural History, New York, New York, USA (AMNH); Coleção de Anfíbios Célio F. B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil (CFBH); Divisão de Anfíbios e Répteis, Museu de Zoologia da Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil (MZFS-DAR); Museu de História Natural/Museu de Zoologia da Universidade Federal da Bahia, Salvador, Bahia, Brazil (UFBA); Coleção de Anfíbios da Universidade Federal de Minas Gerais, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil (UFMG); and Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). A complete list of specimens examined is given in Appendix 1.

We took the following measurements to the nearest 0.05 mm with a digital caliper under a stereomicroscope, following Padial et al. (2016): snout–vent length (SVL), head length (HL), head width (HW), eye length (EL), eye-to-nostril distance (EN), internarial distance (IND), eye-to-eye distance (EE), tympanic membrane height (TYH), tympanic membrane length (TYL), width of disc of Finger III (FIII), width of disc of Finger IV (FIV), arm length (FA), tibia length (TL), thigh length (TH), foot length (FL), and width of disc of Toe IV (TIV). We determined the sex of the specimens by the observation of secondary sexual characteristics of male specimens (nuptial pads, vocal slits, or both) and by direct observation of the gonads or egg visibility through the belly wall in female specimens. Morphological nomenclature and characters follow previous literature on Brachycephaloidea (Heyer et al., 1990; Hedges et al., 2008; Duellman and Lehr, 2009).

Recordings and Acoustic Analysis.—Advertisement calls of 15 males belonging to the new species were recorded from the following localities in the state of Bahia, Brazil: Pico das Almas (−13.524167, −41.957778, 1,559 m a.s.l., datum WGS84 hereafter), Pico do Itobira (−13.371667, −41.879722, 1,711 m a.s.l.), and Cachoeira do Raposo (−13.606111, −41.815972, 893 m a.s.l.), all from the municipality of Rio de Contas, and municipality of Ipupiara (−11.745179, −42.469122, 1,279 m a.s.l.). All recordings were performed from 13 December 2009 to 16 December 2017, from ∼1900 h to 2400 hours, by using Marantz Professional PMD660 or PMD661 portable digital recorders at 44.1 kHz and 16-bit resolution in wav format, coupled to a Sennheiser ME66 directional microphone. The temporal and structural parameters of the calls were measured and counted on waveforms, whereas spectral parameters were obtained directly from a power spectrum. Furthermore, the waveform and spectrogram display were used to evaluate the call structure (e.g., call amplitude modulation, harmonic and pulse structure) through visual inspection. All sound analyses were performed using Raven Pro version 1.5 software (Bioacoustics Research Program, 2014). Spectrograms were produced with Fast Fourier Transform (FFT) length of 1,024 samples, overlap 89.8%, window Hanning, 3-dB filter bandwidth of 496 Hz, and window size of 256. To produce spectrogram, power spectrum, and oscillogram graphics, we used the Seewave package version 1.6.4 (Sueur et al., 2008) in the R platform version 3.3.3 (R Core Team, 2017). To ensure best spectral resolution, we configured the power spectrum with FFT length of 1,024 samples, overlap 89.8%, window Hanning, 3-dB filter bandwidth of 258 Hz, and window size of 256 without clipping. Audio files were housed in the Amphibian Sound Library of the Museu de História Natural/Museu de Zoologia da Universidade Federal da Bahia (SUFBA), Brazil, and in the acoustic repository of CFBH. We list information on the files in Appendix 2.

Eight quantitative call parameters were measured: call duration (s), inter-call interval (s), number of notes per call, note duration (s), number of pulses per note, pulse duration (s), pulse rate (pulses/s), and dominant frequency (kHz). We calculated pulse rate for each note by using the equation (pulse number − 1)/time interval between the beginning of first pulse to the beginning of last pulse (Cocroft and Ryan, 1995). The terminology used for the description of the advertisement calls (pulse, note, and call definitions) followed Köhler et al. (2017). The advertisement call of the new species was compared with the following calls available from literature: *P. achatinus* (Lynch and Myers, 1983), *P. buccinator* (Rodriguez, 1994), *P. charlottevillensis* (Kaiser et al., 1995), *P. dundeei* (Giaretta et al., 2018), *P. fenestratus* (Padial and de la Riva, 2009), *P. iiap* (Padial et al., 2016), *P. koehleri* (Padial and de la Riva, 2009), *P. latro* (Oliveira et al., 2017), *P. paulodutrai* (Bokermann, 1975; Heyer and de Carvalho, 2000), *P. ramagii* (Oitaven et al., 2017), *P. samaipatae* (Padial and de la Riva, 2009), *P. incertus* (Kaiser et al., 1995), *P. ventrigranulosus* (Maciel et al., 2012), and *P. vilarsi* (Heyer and Barrio-Amorós, 2009).

Molecular Data Acquisition and Analysis.—We extracted whole cellular DNA from liver or muscle tissue preserved in 99.5% ethanol by using a standard ammonium precipitation method (Lyra et al., 2017). We chose a fragment of the 16S ribosomal RNA gene (16S) limited by the primers 16S-AR (5′-CGCCTGTTTATCAAAAACAT-3′) and 16S-BR (5′-GACCTG GATTACTCCGGTCTGA-3′) to perform our molecular analyses (Palumbi et al., 1991). We performed PCR amplification using Taq DNA Polymerase Master Mix (Ampliqon S/A, Denmark) and Axygene Maxygene thermocyclers. The PCR program was a 3-min initial denaturing step at 95°C, followed by 35 cycles of 20 s at 95°C, 20 s at 50°C, and 45 s at 72°C, followed by a final extension step of 5 min at 72°C. We purified PCR product following Lyra et al. (2017) and sequenced it in both directions with a BigDye Terminator Cycle Sequencing Kit version 3.0 (Applied Biosystems) in an ABI 3730 automated DNA sequencer (Applied Biosystems) at Macrogen Inc. (Seoul, South Korea). Taxon sampling included all named species within the *P. conspicillatus* group with available sequences at GenBank (Appendix 3), except for *P. carranguerorum* and *P. peruvianus*. We did not use these two species because they were recovered out of the *P. conspicillatus* group in previous studies, but the taxonomic identities of the sequences available at GenBank were never confirmed (González-Durán et al., 2017). We also used nine *Pristimantis* from other species groups and five other Craugastoridae genera as outgroups: *Barycholos*, *Craugastor*, *Holoaden*, *Lynchius*, and *Yunganastes*.

We conducted sequence alignment using the software MAFFT version 7.273 (Katoh and Standley, 2013) using the E-INS-i

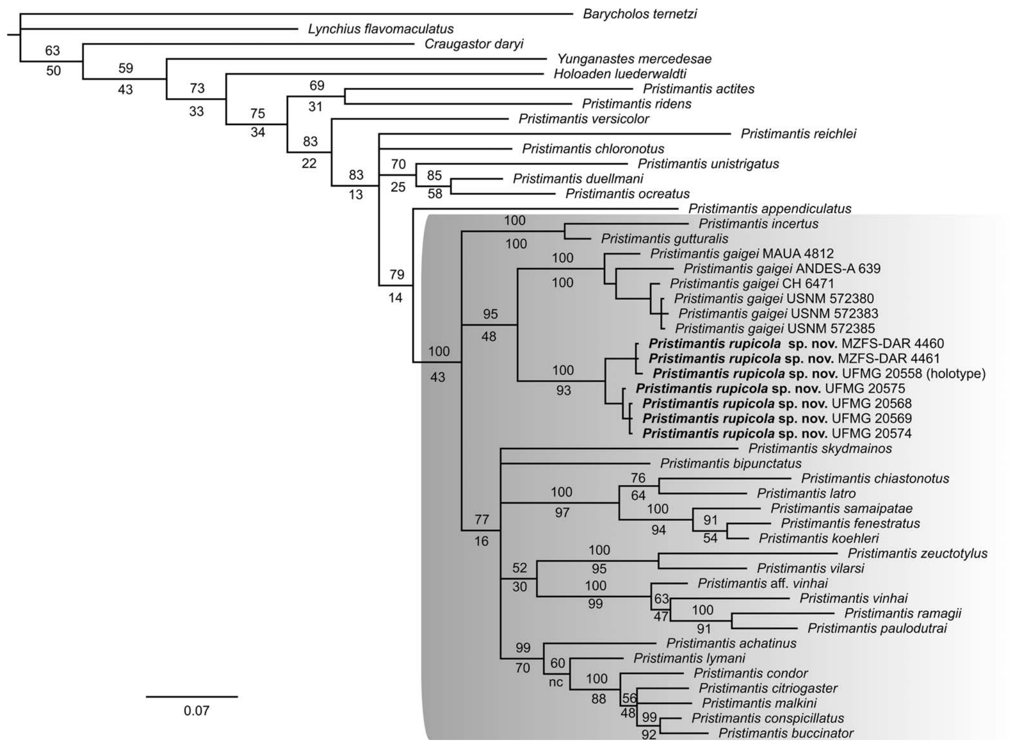

FIG. 1. The 50% majority rule consensus tree from Bayesian inference of partial 16S showing *Pristimantis rupicola* sp. nov. and its relationships within the *P. conspicillatus* group (highlighted in gray). Numbers above branches indicate posterior probabilities, and numbers below branches indicate maximum likelihood nonparametric bootstrap values. We used nc when the clade was not recovered in the maximum likelihood analysis and within-species support values are not shown.

algorithm (--genafpair command). We performed the search for the best-fitting model of nucleotide substitution using PartitionFinder 2.1.1 (Lanfear et al., 2017) using the corrected Akaike information criterion (AICc; Hurvich and Tsai, 1989) to choose the best model, considering the whole fragment as a single partition. PartitionFinder uses a maximum likelihood tree to start the analysis, and for this we chose PhyML 3.0 (Guindon et al., 2010).

To construct our phylogenetic trees, we used two optimality criteria, Bayesian inference and maximum likelihood. We performed the Bayesian analysis with MrBayes 3.2.6 (Ronquist et al., 2012), using two independent runs of 1.0×10^7 generations and four Markov chains (one cold). Parameters were sampled every 1,000 generations and burn-in was 25%. To assess run convergence, we checked the standard deviation of split frequencies (should be <0.01) and effective sample size (if <100, the parameter was considered undersampled). We conducted the maximum likelihood analysis in RAxML 8.2.10 (Stamatakis, 2014), searching the most likely tree 100 times, and performing 1,000 nonparametric bootstrap replicates.

We computed uncorrected pairwise distances with the packages APE 3.4 (Paradis et al., 2004) and SPIDER 1.3-0 (Brown et al., 2012) in the R platform version 3.3.3 (R Core Team, 2017), deleting the sites with gaps in a pairwise way (pairwise.deletion=T in the dist.dna command).

RESULTS

Phylogenetic Relationships and Genetic Distances.—The resulting best-fitting nucleotide substitution model was the general time-reversible with a proportion of invariant sites and a gamma distribution of rates across sites (GTR + Γ + I). The Bayesian inference and the maximum likelihood analyses yielded similar topologies (Fig. 1). We recovered our new species within the genus *Pristimantis*, *P. conspicillatus* group. The *P. conspicillatus* group was monophyletic with high support in the Bayesian inference analysis (100% of posterior probability), but with low support in the maximum likelihood analysis (43% of bootstrap replicates). Despite the lack of resolution in the deepest relationships among the species of the *P. conspicillatus* group, we recovered three main clades: one clade fully supported in both analyses bearing *P. incertus* and *P. gutturalis*; one clade with *P. gaigei* and *P. rupicola* sp. nov. with high support in the Bayesian inference analysis (95% of posterior probability), but low support in the maximum likelihood analysis (48% of bootstrap replicates); and one clade bearing the remaining species of the *P. conspicillatus* group. This clade was low supported in both analyses (77% of posterior probability and 16% of bootstrap replicates). Inside this large clade, we recovered the species from northeastern Brazil, *P. paulodutrai*, *P. ramagii*, and *P. vinhai*, with high support in both analyses (100% of posterior probability and 99% of bootstrap replicates). We did not recover *P. vinhai* as monophyletic, although with low support (63% of posterior probability and 47% of bootstrap replicates). Thus, we considered one of the lineages as a different species in the genetic distance analysis.

The pairwise genetic distances of the 16S among the species of the *P. conspicillatus* group varied from 2.7% (minimum distance between *P. fenestratus* and *P. koehleri*) to 22.2% (maximum distance between *P. chiastonotus* and *P. ramagii*; Table 1). As in our phylogenetic analyses, the closest species to *P. rupicola* sp. nov. was *P. gaigei* (5.0–8.8%). The genetic distance between *P. rupicola* sp. nov. and its congeners from northeastern Brazil (recovered in another clade in our phylogenetic analyses) varied

TABLE 1. Uncorrected pairwise genetic distances (given in percentage) of mitochondrial 16S ribosomal RNA gene fragment within (bold, only maximum value shown) and among species from the *P. conspicillatus* species group. Numbers below and left are minimum distances and numbers above and right are maximum distances among species.[a]

	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 – *P. rupicola* sp. nov.	7	**2.7**	12.6	13.3	13.8	16.9	11.7	11.4	12.6	13.8	8.8	14.0	12.8	13.1	12.4	11.4	14.5	16.8	13.0	13.6	12.9	11.2	12.2	9.6	17.0
2 – *P. achatinus*	3	8.4	**4.2**	13.0	11.3	18.3	9.9	9.8	9.8	13.9	13.2	15.8	12.7	15.0	8.0	9.7	16.2	19.0	14.2	13.5	14.1	11.2	14.1	12.2	19.3
3 – *P. bipunctatus*	4	11.6	7.8	**3.5**	11.7	19.1	11.1	10.3	10.3	14.9	13.8	15.2	12.7	16.2	10.5	10.5	17.1	18.2	14.0	11.4	13.3	12.5	14.5	12.9	18.4
4 – *P. buccinator*	5	12.5	6.1	10.2	**0.4**	18.6	5.6	6.4	3.2	14.3	13.6	16.0	13.7	15.2	7.6	5.6	17.0	18.4	13.7	12.5	13.5	12.3	16.1	13.1	18.6
5 – *P. chiastonotus*	49	15.2	13.2	16.2	16.8	**2.1**	17.7	16.6	17.2	11.1	15.1	19.5	11.4	12.5	16.9	18.3	20.7	22.2	12.2	19.1	18.7	16.8	20.5	18.0	20.4
6 – *P. citriogaster*	1	11.1	5.7	9.8	5.1	16.2	**NA**	5.5	4.0	13.8	11.5	13.6	12.1	13.5	5.5	4.3	17.0	17.7	12.8	11.4	11.9	11.4	14.6	12.1	18.3
7 – *P. condor*	1	10.8	5.7	9.1	6.4	15.5	5.5	**NA**	4.5	14.3	11.4	14.6	11.7	13.2	6.4	5.7	15.1	16.8	12.7	10.8	12.3	10.8	14.1	10.7	16.8
8 – *P. conspicillatus*	1	12.0	5.0	9.5	3.0	15.5	4.0	4.5	**NA**	14.3	12.8	14.9	12.9	14.0	5.5	4.4	17.3	17.7	12.1	11.0	12.5	11.0	14.9	12.3	17.4
9 – *P. fenestratus*	7	12.3	9.9	13.7	13.2	9.7	13.2	13.4	13.6	**0.6**	14.0	16.9	3.0	11.2	12.3	13.7	16.6	17.8	5.9	15.5	13.9	14.6	13.8	12.4	19.1
10 – *P. gaigei*	9	5.0	8.4	9.8	10.3	12.0	8.8	7.7	9.2	9.4	**3.5**	15.8	13.1	10.8	12.8	10.8	12.4	13.7	12.4	14.9	12.5	10.8	13.1	10.6	17.8
11 – *P. gutturalis*	1	13.7	12.1	14.9	15.7	18.7	13.6	14.6	14.9	16.9	11.1	**NA**	16.4	17.2	14.6	13.0	21.2	21.4	16.1	17.5	7.7	12.4	17.7	15.3	16.5
12 – *P. koehleri*	5	11.5	9.5	12.3	13.0	10.4	12.1	11.7	12.9	2.7	9.6	16.4	**0.0**	9.7	11.2	12.5	16.4	17.6	4.4	14.2	12.8	12.4	12.2	11.1	19.4
13 – *P. latro*	39	11.3	9.5	14.0	14.5	9.3	13.0	12.2	13.4	9.5	7.7	16.4	9.3	**NA**	13.6	13.2	15.8	17.8	9.7	16.8	14.0	12.5	13.6	10.5	19.3
14 – *P. lymani*	1	11.8	4.8	10.1	6.8	15.8	5.5	6.4	5.5	11.7	9.2	14.6	11.2	13.0	**NA**	6.5	16.0	16.1	11.5	9.7	12.9	10.8	14.1	11.5	15.2
15 – *P. malkini*	1	10.9	6.1	9.1	5.3	17.1	4.3	5.7	4.4	13.0	8.2	13.0	12.5	12.7	6.5	**NA**	16.8	17.2	12.7	11.0	10.9	11.2	15.0	11.8	19.2
16 – *P. paulodutrai*	6	10.6	9.0	12.6	12.7	17.6	12.7	11.2	12.7	12.6	7.1	17.6	12.3	12.6	11.9	12.7	**2.6**	8.8	16.9	19.0	17.8	13.1	10.9	8.3	18.3
17 – *P. ramagii*	4	12.1	10.3	13.5	14.4	18.6	13.9	13.1	13.5	13.9	8.8	18.2	13.3	13.8	12.5	13.7	5.9	**2.0**	16.3	21.4	18.8	13.9	11.6	9.5	17.3
18 – *P. samaipatae*	4	12.2	10.1	13.4	13.2	11.2	12.8	12.7	12.1	5.3	9.6	16.1	4.4	9.1	11.5	12.7	13.0	12.6	**0.0**	14.4	12.4	11.4	13.1	11.8	17.8
19 – *P. skydmainos*	1	12.8	9.9	10.4	12.0	18.1	11.4	10.8	11.0	14.8	12.1	17.5	14.2	16.0	9.7	11.0	15.0	16.1	14.4	**NA**	15.5	13.4	16.7	15.5	18.1
20 – *P. incertus*	1	12.0	12.1	12.5	13.3	17.3	11.9	12.3	12.5	13.4	10.2	7.7	12.8	13.1	12.9	10.9	13.8	14.8	12.4	15.5	**NA**	11.9	14.6	13.1	18.7
21 – *P. vilarsi*	6	10.1	8.6	11.2	11.8	16.0	11.4	10.8	11.0	13.7	8.0	12.4	12.4	11.9	10.8	11.2	9.7	10.8	11.4	13.4	11.9	**0.0**	12.6	9.5	12.6
22 – *P. vinhai*	9	10.4	9.9	12.8	14.1	16.8	13.3	12.5	13.7	11.5	8.8	16.6	11.1	11.3	12.7	13.2	7.1	7.1	12.1	15.3	13.4	10.8	**6.0**	7.3	18.4
23 – *P.* aff. *vinhai*	1	9.0	7.8	12.0	12.7	16.2	12.1	10.7	12.3	11.6	6.9	15.3	11.1	9.8	11.5	11.8	6.5	7.1	11.8	15.5	13.1	9.5	5.6	**NA**	15.1
24 – *P. zeuctotylus*	47	14.3	11.4	15.3	15.7	16.9	15.4	14.9	14.7	16.4	11.4	15.4	16.9	17.0	12.9	16.8	13.9	13.7	15.3	16.6	16.8	10.9	15.2	13.2	**2.2**

[a] *n* = number of sequences; NA = not applicable.

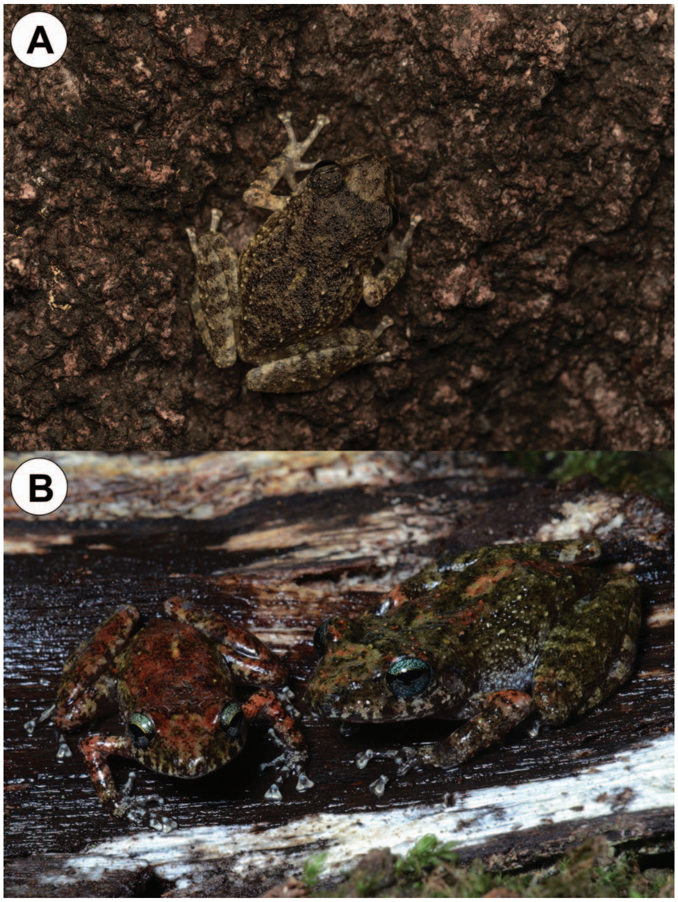

FIG. 2. Three specimens of *Pristimantis rupicola* sp. nov. in life. (A) Individual lying on a rock and showing its highly camouflaged dorsal pattern (not collected). (B) Paratypes of *P. rupicolus* sp. nov. (MZFS-DAR 4460–4461, adult male and adult female, respectively) showing the bluish-tone eye present in some specimens. Photo credits: (A) F. Leal; (B) D. J. Santana.

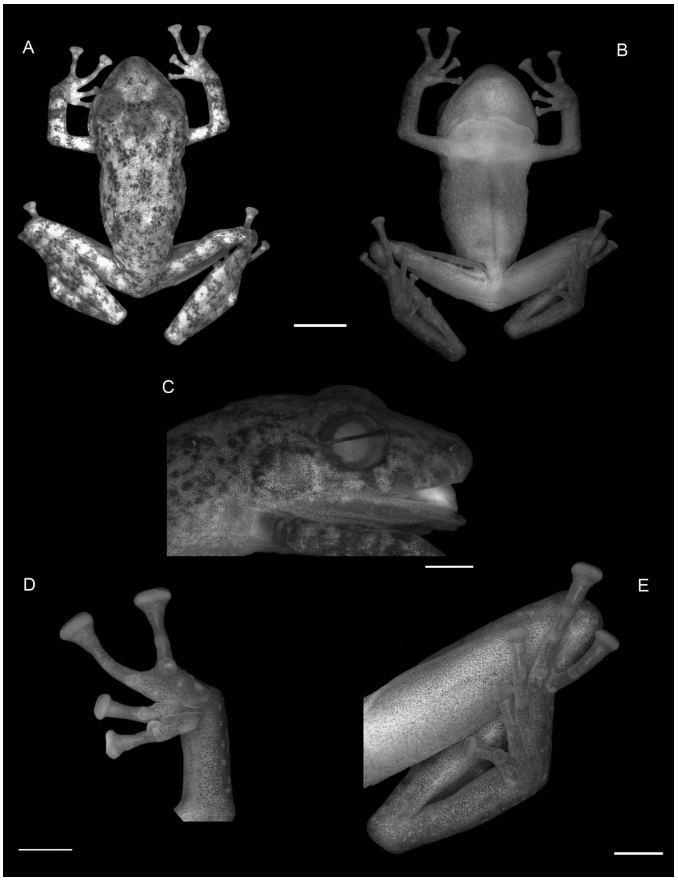

FIG. 3. Holotype of *Pristimantis rupicola* sp. nov. (UFMG 20558). (A) Dorsal view, (B) ventral view, (C) snout in profile, (D) left hand, and (E) left foot in ventral views. Scale bar = 5 mm (A and B) and 2 mm (C–E).

from 9.0 to 16.8% (*P.* aff. *vinhai*, minimum distance, and *P. ramagii*, maximum distance, respectively).

Pristimantis **rupicola** sp. nov.

(Figs. 2–4)

(Zoobank ID: lsid:zoobank.org:act:ADD691C4-A31944BF-8852-3D112757E4D3)

Holotype.—UFMG 20558, adult male. Vale do Queiroz, Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil (−13.520169, −41.950404; 1,554 m a.s.l.; datum WGS-84), collected by F. Leal and F. S. F. Leite on 12 December 2017.

Paratypes (n = 43).—MZFS-DAR 4460–4461 (adult male and adult female, respectively), municipality of Piatã, state of Bahia, Brazil (−13.152700, −41.764900, 1,263 m a.s.l.), collected by D. J. Santana, F. M. Magalhães, I. Andrade, and R. Silveira-Filho in March 2014. UFMG 4414–4421, 4453, and 4478–4484 (4415 juvenile, the others adult males), Brumadinho, Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil (respectively, −13.524190, −41.957736, 1,559 m a.s.l.; −13.511661, −41.949478, 1,461 m a.s.l.; −13.484903, −41.964981, 1,631 m a.s.l.), collected by F. S. F. Leite, M. R. Lindemann, and R. B. Mourão on 9–12 January 2010. UFMG 4501–4504 and 4515–4516 (4503 adult female, 4504 juvenile, the others adult males), Caiambola, Serra do Itobira, municipality of Rio de Contas, state of Bahia, Brazil (respectively, −13.371536, −41879676, 1,711 m a.s.l.; −13.375039, −41.894072, 1597 m a.s.l.), collected by F. S. F. Leite, P. D. P. Pinheiro, and F. Fernandes on 11–13 December 2009. UFMG 5968–5969 (respectively juvenile and adult male), Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil (−13.513120, −41.952874, 1,506 m a.s.l.), collected by F. S. F. Leite on 2 September 2008. UFMG 7806, 7823 (adult males), Caiambola, Serra do Itobira, municipality of Rio de Contas, state of Bahia, Brazil (respectively, −13.372808, −41.895650, 1,595 m a.s.l.; −13.370157, −41.878599, 1,662 m a.s.l.) and UFMG 7836–7842 (adult males), Mato Grosso, Rio de Contas, state of Bahia, Brazil (−13.419974, −41.836784, 1,285 m a.s.l.), collected by T. L. Pezzuti, L. O. Drummond, B. Imai, and L. Rodrigues on 10–12 January 2010. UFMG 20568–20570 and 20571–20575 (adult males), Serra do Buriti do Ouro, municipality of Ipupiara, state of Bahia, Brazil (respectively, −11.745179, −42.469122, 1,279 m a.s.l.; −11.740716, −42.473133, 1,304 m a.s.l.), collected by F. Leal and F. S. F. Leite on 15 and 16 December 2017.

Diagnosis.—*Pristimantis rupicola* sp. nov. is distinguished from all other species of the *P. conspicillatus* group by the following combination of characteristics: 1) dorsum background color light brown to yellowish-brown, maculated with blackish-brown marks, resembling a granite rock surface (Fig. 2); 2) dorsum granular; 3) venter areolate; 4) dentigerous process of the vomer small, ovoid; 5) snout rounded or truncate in dorsal view (Fig. 3); 6) rounded in profile (Fig. 3); 7) dorsolateral folds absent; 8) finger fringes absent; 9) toe fringes weakly developed; 10) double, poorly-developed nuptial pads; 11) vocal slits present in

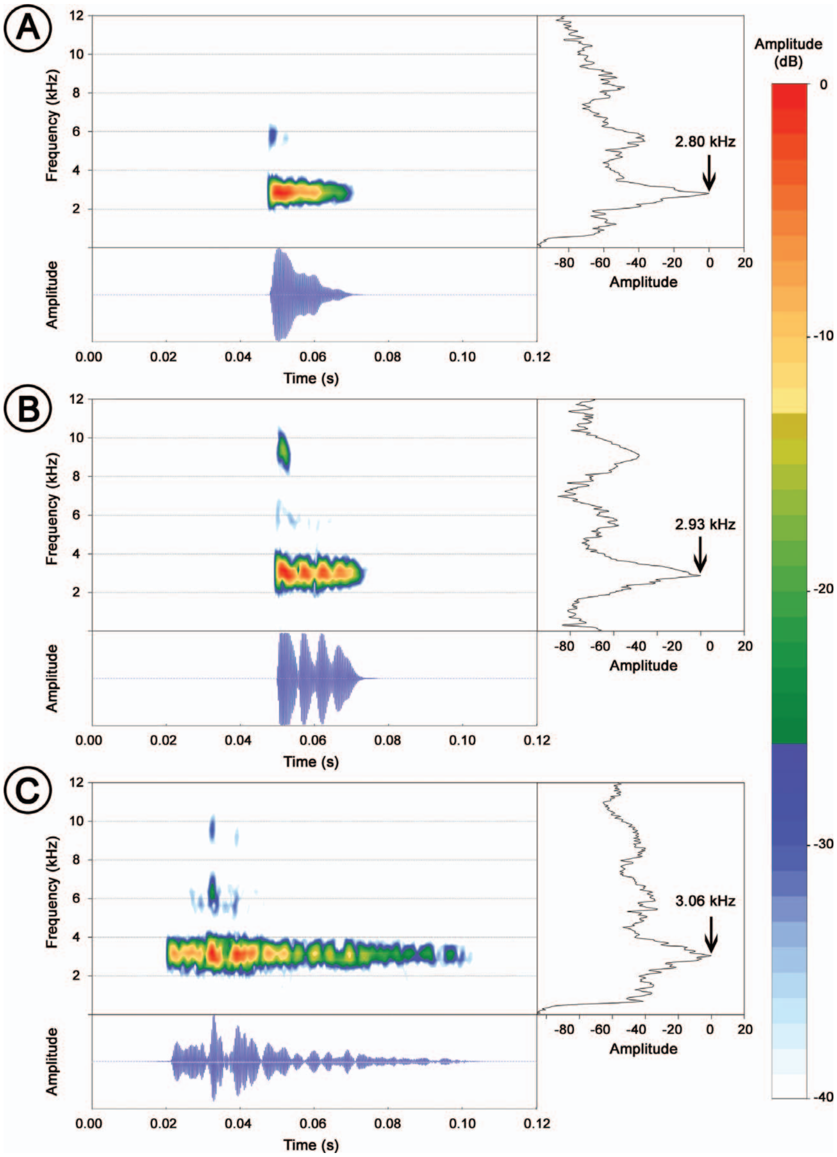

FIG. 4. Advertisement call of *Pristimantis rupicola* sp. nov. recorded in the municipalities of Rio de Contas and Ipupiara, state of Bahia, Brazil, on 12 January 2010 and 12–15 December 2017. Spectrogram (above), power spectrum (right side) featuring the dominant frequency of the call, and oscillogram (below) of (A) one call (= one short note) without pulses (FSFL 11, adult male); (B) one call (= one short note) having four pulses (FSFL 4); and (C) one call (= one long note) having pulses of irregular duration (FSFL 10).

the males; 12) advertisement call (Fig. 4) composed of one note; 13) call duration 0.011–0.086 s; 14) dominant frequency varying from 2.41 to 3.49 kHz; and 15) peak amplitude at the beginning of the call, decreasing rapidly to the end.

Pristimantis rupicola sp. nov. differs from all other members of the *P. conspicillatus* group by having its dorsal surface resembling a granitic stone (other species in the *P. conspicillatus* group without dorsal surface resembling a granitic stone). By the granular dorsum, *P. rupicola* sp. nov. is distinguished from *P. achatinus*, *P. adiastolus*, *P. bipunctatus*, *P. buccinator*, *P. carrangueroru*m, *P. charlottevillensis*, *P. chiastonotus*, *P. citriogaster*, *P. condor*, *P. conspicillatus*, *P. dundeei*, *P. fenestratus, P. gaigei*, *P. gutturalis*, *P. iiap*, *P. koehleri*, *P. meridionalis*, *P. samaipatae*, *P. ventrigranulosus*, *P. vilarsi* (dorsum finely shagreen to coarsely shagreen in these species; Hoogmoed et al., 1977; Lynch and Hoogmoed, 1977; Lynch, 1994; Kaiser et al., 1995; Lynch and Duellman, 1997; Duellman and Pramuk, 1999; Duellman and Hedges, 2005, 2007; Lehr and Duellman, 2007; Maciel et al., 2012; Padial et al., 2016), *P. lymani*, *P. malkini*, *P. peruvianus*, *P. vinhai* (shagreen with tubercles in these species; Lynch, 1980; Duellman and Pramuk, 1999; Duellman and Lehr, 2009), *P. avicuporum*, *P. johannesdei*, *P. metabates*, and *P. phalaroinguinis* (smooth or smooth with tubercles in these species; Rivero and Serna, 1988; Duellman and Pramuk, 1999; Duellman and Lehr, 2007). The areolate venter distinguishes *P. rupicola* sp. nov. from *P. achatinus*, *P. buccinator*, *P. charlottevillensis*, *P. chiastonotus*, *P. citriogaster*, *P. condor*, *P. conspicillatus*, *P. fenestratus*, *P. gaigei*, *P. gutturalis*, *P. johannesdei*, *P. latro*, *P. lymani*, *P. malkini*, *P. metabates*, *P. peruvianus*, *P. phalaroinguinis*, *P. samaipatae* (smooth in these species; Hoogmoed et al., 1977; Lynch and Hoogmoed, 1977; Lynch, 1980; Rivero and Serna, 1988; Rodriguez, 1994; Kaiser et al., 1995; Köhler and Jungfer, 1995; Lynch and Duellman, 1997; Duellman and Pramuk, 1999; Duellman and Lehr, 2007, 2009; Oliveira et al., 2017), *P. dundeei*, *P. iiap*, *P. incertus*, *P. ventrigranulosus*, *P. vinhai* (slightly granular or granular in these species; Rivero, 1961; Maciel et al., 2012; Padial et al., 2016), *P.*

koehleri, and *P. skydmainos* (granular posteriorlaterally in these species; Flores and Rodríguez, 1997; Padial and de la Riva, 2009). By the ovoid dentigerous process of the vomer, *P. rupicola* sp. nov. is distinguished from *P. achatinus*, *P. avicuporum*, *P. carranguerorum*, *P. charlottevillensis*, *P. citriogaster*, *P. condor*, *P. conspicillatus*, *P. dundeei*, *P. fenestratus*, *P. gaigei*, *P. gutturalis*, *P. johannesdei*, *P. lymani*, *P. medemi*, *P. peruvianus* (dentigerous process of the vomer triangular in these species; Hoogmoed et al., 1977; Rivero and Serna, 1988; Lynch, 1994; Kaiser et al., 1995; Lynch and Duellman, 1997; Duellman and Pramuk, 1999; Duellman and Lehr, 2009), *P. meridionalis*, and *P. vinhai* (rounded in these species; Lehr and Duellman, 2007). The snout rounded or truncate in dorsal view distinguishes *P. rupicola* sp. nov. from *P. achatinus*, *P. citriogaster*, *P. condor*, *P. conspicillatus*, *P. lymani*, *P. medemi*, *P. meridionalis*, *P. ramagii*, *P. zeuctotylus* (snout subacuminate in dorsal view in these species; Lynch and Hoogmoed, 1977; Lynch, 1994; Lynch and Duellman, 1997; Duellman and Pramuk, 1999; Duellman and Lehr, 2009), *P. chiastonotus*, *P. dundeei*, *P. fenestratus*, *P. gaigei*, *P. malkini*, *P. vinhai* (acuminate in these species; Lynch and Hoogmoed, 1977; Lynch, 1980), *P. carranguerorum* (obtuse; Lynch, 1994), *P. charlottevillensis* (trapezoid; Kaiser et al., 1995), *P. gutturalis* (suboval; Hoogmoed et al., 1977), and *P. incertus* (elliptical; Rivero, 1961). By its rounded snout in profile, *P. rupicola* sp. nov. is distinguished from *P. adiastolus* and *P. bipunctatus* (snout nearly truncate in profile in these species; Duellman and Hedges, 2005, 2007). The absence of dorsolateral folds distinguishes *P. rupicola* sp. nov. from *P. adiastolus*, *P. avicuporum*, *P. bipunctatus*, *P. buccinator*, *P. conspicillatus*, *P. iiap*, *P. latro*, *P. malkini*, *P. meridionalis*, *P. peruvianus*, and *P. skydmainos* (present in these species; Padial et al., 2016; Oliveira et al., 2017). The absence of finger fringes distinguishes *P. rupicola* sp. nov. from *P. avicuporum*, *P. carranguerorum*, *P. conspicillatus*, *P. johannesdei*, *P. latro*, *P. lymani*, *P. medemi*, *P. meridionalis*, *P. metabates*, *P. peruvianus* (present in these species; Rivero and Serna, 1988; Lynch, 1994; Duellman and Pramuk, 1999; Duellman and Lehr, 2009; Oliveira et al., 2017), *P. charlottevillensis*, *P. fenestratus*, and *P. skydmainos* (weakly developed in these species; Kaiser et al., 1995; Flores and Rodríguez, 1997). The toes of *P. rupicola* sp. nov. bear weakly developed fringes, which distinguishes this species from *P. adiastolus*, *P. avicuporum*, *P. chiastonotus*, *P. citriogaster*, *P. gutturalis*, *P. phalaroinguinis*, *P. ramagii*, *P. vilarsi* (absent in these species; Hoogmoed et al., 1977; Lynch and Hoogmoed, 1977; Lynch and Duellman, 1997; Duellman and Pramuk, 1999; Duellman and Lehr, 2007, 2009), *P. dundeei*, *P. metabates*, and *P. samaipatae* (well-developed toe fringes in these species; Köhler and Jüngfer, 1995; Duellman and Pramuk, 1999). By the double, poorly developed nuptial pads, *P. rupicola* sp. nov. is distinguished from *P. adiastolus*, *P. charlottevillensis*, *P. meridionalis*, *P. metabates*, *P. paulodutrai*, *P. phalaroinguinis*, *P. ramagii*, *P. vinhai* (nuptial pads absent in these species; Kaiser et al., 1995; Duellman and Pramuk, 1999; Duellman and Hedges, 2007; Duellman and Lehr, 2007; Lehr and Duellman, 2007), *P. bipunctatus*, *P. buccinator*, *P. iiap*, *P. skydmainos*, *P. ventrigranulosus*, and *P. vilarsi* (nuptial pad single in these species; Rodríguez, 1994; Flores and Rodríguez, 1997; Lehr et al., 2006; Duellman and Lehr, 2009; Maciel et al., 2012; Padial et al., 2016). Finally, the presence of vocal slits distinguishes *P. rupicola* sp. nov. from *P. gaigei*, *P. lymani*, *P. meridionalis*, and *P. phalaroinguinis* (vocal slits absent in these species; Duellman and Lehr, 2007, 2009; Lehr and Duellman, 2007).

The advertisement call of *P. rupicola* sp. nov. (Fig. 4; Table 2) is distinguished by having a lower call duration (0.011–0.086 s); in *P. dundeei* (0.136–0.642 s), *P. fenestratus* (0.157–0.458 s), *P. koehleri* (0.173–0.644 s), *P. latro* (0.402–0.581 s), *P. incertus* (0.128–0.160 s), *P. ventrigranulosus* (0.202–0.411 s), and *P. vilarsi* (0.521 s). The dominant frequency (2.67–3.49 kHz) distinguishes *P. rupicola* sp. nov. from *P. buccinator* (3.56 kHz), *P. charlottevillensis* (4.00 kHz), and *P. paulodutrai* (3.5–4.0 kHz). The single note per call of *P. rupicola* sp. nov. distinguishes it from *P. dundeei* (2–12 notes), *P. fenestratus* (2–4 notes), *P. koehleri* (3–8 notes), *P. latro* (7 notes), *P. incertus* (4 notes), *P. ventrigranulosus* (4–7 notes), and *P. vilarsi* (8 notes). Amplitude modulation of *P. rupicola* sp. nov. has a peak at the beginning, but decreases rapidly until the end. This feature of amplitude modulation differs from the pattern described for several species in the *P. conspicillatus* group, with the highest amplitude centered at midpoint of the call (e.g., *P. buccinator*, *P. dundeei*, *P. fenestratus*, *P. koehleri*, *P. samaipatae*, and *P. vilarsi*; Padial et al., 2016).

Description of the Holotype.—An adult male with subgular vocal sac, vocal slits, and nuptial pads. Head as long as wide; snout broadly rounded in dorsal view and short rounded in profile; nostril flat, oriented laterally; canthus rostralis distinct, straight in dorsal view; loreal region slightly concave; lips not flared; posterior half of upper eyelid covered by low sparse small granules; no cranial crests. Supratympanic fold prominent, long, bordering the dorsal portion of tympanic membrane; annulus distinct, its upper portion concealed by skin; tympanic membrane distinct, nearly rounded (tympanum length 116% of tympanum height), its length 48% of eye length; a pair of nearly rounded postrictal tubercles. Choanae rounded, separated by distance approximately seven times the diameter of a choana; dentigerous process of vomers small, slightly prominent, ovoid in shape, situated posteromedially to choanae, bearing teeth; vocal sac subgular, moderately expanded; vocal slits placed posterolaterally, their sizes about one fourth of the jaw length. Skin of dorsal surfaces and posterior parts of hind limbs smooth, with a few sparse low tubercles, dorsum granular; throat smooth, belly areolate; occipital folds absent; dorsolateral folds absent; discoidal and thoracic folds conspicuous.

A line of small, low ulnar tubercles; palmar tubercle bifid, flat, heart-shaped, its size equal to elongate, prominent thenar tubercle; a single conic supernumerary tubercle on the basis of each finger, conic; subarticular tubercles prominent, conical; finger tips enlarged and truncated, larger on fingers III and IV; fingers lacking lateral fringes; relative length of fingers III > IV > II > I; double nuptial pad as skin thickening on the posterior half of the thenar tubercle and as a rounded skin thickening on the opposite side of proximal subarticular tubercle of each thumb.

Toes long and slender, foot length 41% of SVL; heel and tarsus lacking tubercles; tarsal fold barely distinct, narrow; inner metatarsal tubercle ovate, prominent, larger than outer; outer metatarsal tubercle rounded, barely distinct; supernumerary tubercles small, conical; subarticular tubercles conical, prominent; fringes present, weakly developed; basal toe webbing absent; toe tips truncate, moderately developed; ungual flap not indented, circumferential grooves evident; relative length of toes IV > V > III > II > I; Toe V reaching the midpoint of ultimate subarticular tubercle of Toe IV and Toe III reaching midpoint of penultimate subarticular tubercle of Toe IV.

Dorsal and lateral surfaces background cream colored, with several sparse dark-brown dots and blotches. On the dorsal surfaces of the limbs the blotches are distributed forming stripes. Ventral surface cream colored with several sparse dark-brown spots. The spots get more concentrated on the ventral surfaces of the hands, arms, shanks, tarsi, and feet. Dorsal stripes are absent, but other patterns usually found on species of

Table 2. Measurements of acoustic parameters of the advertisement call for 15 adult males of *P. rupicola* sp. nov. Values are mean ± standard deviation (minimum–maximum).

Call ID	Call duration (s)	Inter-call interval (s)	No. of pulses per note	Pulse duration (s)	Pulse rate (pulses/s)	Dominant frequency (kHz)
FSFL 10[a] ($n = 11$ calls)	0.076 ± 0.008 (0.056–0.086)	2.05 ± 0.15 (1.74–2.24)	16.7 ± 2.3 (12–20)	0.005 ± 0.002 (0.002–0.011)	224.8 ± 27.4 (183.1–253.7)	3.02 ± 0.03 (2.97–3.06)
FSFL 4[b] ($n = 14$ calls)	0.021 ± 0.005 (0.012–0.026)	2.14 ± 0.24 (1.84–2.77)	3.9 ± 0.3 (3–4)	0.006 ± 0.002 (0.004–0.013)	202.9 ± 6.0 (200.0–214.3)	2.89
FSFL 9[b] ($n = 11$ calls)	0.048 ± 0.003 (0.042–0.053)	3.54 ± 0.82 (2.73–5.12)	10.0 ± 1.3 (8–4)	0.005 ± 0.002 (0.002–0.010)	211.8 ± 30.8 (166.7–282.1)	3.18 ± 0.08 (3.06–3.27)
FSFL 1 ($n = 12$ calls)	0.030 ± 0.004 (0.023–0.035)	3.16 ± 0.73 (2.75–5.30)	8.7 ± 1.1 (7–10)	0.004 ± 0.001 (0.002–0.009)	299.3 ± 40.2 (233.3–375)	3.35 ± 0.17 (3.10–3.49)
FSFL 2 ($n = 10$ calls)	0.020 ± 0.001 (0.019–0.022)	2.36 ± 0.48 (1.97–3.34)	7.7 ± 0.8 (7–9)	0.003 ± 0.001 (0.002–0.004)	379.1 ± 36.5 (333.3–421.1)	3.11 ± 0.23 (2.67–3.32)
FSFL 3 ($n = 14$ calls)	0.022 ± 0.004 (0.014–0.033)	2.58 ± 0.38 (1.97–3.38)	9.1 ± 1.6 (5–11)	0.003 ± 0.001 (0.002–0.005)	439.9 ± 42.7 (344.8–500)	2.82 ± 0.10 (2.71–3.14)
FSFL 5 ($n = 13$ calls)	0.016 ± 0.002 (0.011–0.019)	3.07 ± 0.29 (2.68–3.62)	2.9 ± 0.7 (2–4)	0.006 ± 0.004 (0.003–0.015)	274.3 ± 57.0 (181.8–333.3)	3.19 ± 0.05 (3.10–3.27)
FSFL 6 ($n = 14$ calls)	0.022 ± 0.005 (0.016–0.030)	2.73 ± 0.13 (2.59–3.01)	5.3 ± 1.5 (4–8)	0.004 ± 0.001 (0.002–0.006)	240.6 ± 18.4 (214.3–280)	3.05 ± 0.02 (3.01–3.06)
FSFL 7 ($n = 12$ calls)	0.072 ± 0.005 (0.065–0.086)	2.49 ± 0.41 (1.98–3.46)	20.6 ± 1.4 (18–23)	0.004 ± 0.002 (0.002–0.010)	284.7 ± 20.2 (242.9–308.8)	2.72 ± 0.05 (2.67–2.84)
FSFL 8 ($n = 10$ calls)	0.025 ± 0.003 (0.021–0.029)	3.16 ± 0.29 (2.80–3.65)	5.7 ± 0.8 (5–7)	0.005 ± 0.001 (0.003–0.008)	242.6 ± 8.4 (227.3–250)	3.10 ± 0.01 (3.06–3.10)
FSFL 11 ($n = 11$ calls)	0.023 ± 0.002 (0.020–0.027)	3.13 ± 0.89 (2.38–5.10)				2.78 ± 0.04 (2.71–2.80)
FSFL 12 ($n = 11$ calls)	0.031 ± 0.003 (0.024–0.034)	2.91 ± 0.31 (2.35–3.32)				3.01
UFBA 14385 ($n = 12$ calls)	0.022 ± 0.005 (0.013–0.028)		3.8 ± 2.1 (2–6)		250	2.71 ± 0.28 (2.41–3.27)
Unvouchered 2 ($n = 5$ calls)	0.019 ± 0.003 (0.013–0.022)		4.4 ± 0.9 (3–5)		244.5 ± 44.3 (166.7–272.7)	3.43 ± 0.04 (3.36–3.45)
Unvouchered 3 ($n = 8$ calls)	0.021 ± 0.001 (0.020–0.024)		5.8 ± 0.4 (5–6)		311.8 ± 24.4 (266.7–333.3)	3.20 ± 0.16 (3.06–3.45)

[a] Holotype.

[b] Paratype.

TABLE 3. Descriptive statistics and body proportions (ratios) of measurement variables for adult males and females from the type-series of *P. rupicola* sp. nov. and measurements of the holotype. See text for abbreviations. Data are given as minimum–maximum (mean ± SD) where appropriate. Measurements are in millimeters.

	Holotype (adult male, UFMG 20558)	Adult males (*n* = 39)	Adult females (*n* = 2)
SVL	23.4	18.1–28.2 (22.7 ± 2.5)	30.7–33.4
HL	9.4	7.5–12.3 (9.3 ± 1.2)	12.1–13.6
HW	9.4	7.4–12.2 (9.2 ± 1.1)	12.1–13.4
EL	3.5	2.4–4.4 (3.1 ± 0.5)	3.5–4.2
EN	3.0	1.9–3.4 (2.7 ± 0.4)	3.4–4.2
IND	2.1	1.5–2.6 (2.0 ± 0.3)	2.3–2.5
EE	5.2	3.5–6.8 (5.0 ± 0.7)	5.9–6.8
TYH	1.5	1.2–2.8 (1.7 ± 0.3)	2.1–2.4
TYL	1.7	1.1–2.9 (1.7 ± 0.3)	2.1–2.6
FIII	1.4	1.0–1.8 (1.4 ± 0.2)	1.5–1.9
FIV	1.5	1.1–1.9 (1.4 ± 0.2)	1.5–1.9
FA	4.7	3.7–6.8 (5.1 ± 0.7)	7.3–7.3
TL	13.2	10.3–15.7 (12.8 ± 1.4)	17.2–18.6
TH	12.6	9.3–15.2 (12.2 ± 1.5)	16.4–16.5
FL	9.7	7.8–11.9 (9.8 ± 1.1)	13.2–14.3
TIV	1.3	0.6–1.7 (1.2 ± 0.2)	1.3–1.6
TL/SVL	0.6	0.5–0.6 (0.6 ± 0.0)	0.6
FL/SVL	0.4	0.4–0.5 (0.4 ± 0.0)	0.4
HL/HW	1.0	0.9–1.1 (1.0 ± 0.0)	1.0
EN/EL	0.8	0.8–1.0 (0.9 ± 0.1)	1.0
EL/HW	0.4	0.3–0.4 (0.3 ± 0.0)	0.3
TYL/TYH	1.2	0.8–1.2 (1.0 ± 0.1)	1.0–1.1
TYL/EL	0.5	0.4–0.7 (0.5 ± 0.1)	0.6

the *P. conspicillatus* group such as supratympanic, canthal, and intraocular stripes seem to be absent or at least difficult to define because of the unique dorsal pattern of *P. rupicola* sp. nov. Measurements of the holotype are given in Table 3.

Variation.—Adult females are larger than adult males (male SVL = 18.1–28.2 mm; female SVL = 30.7–33.4 mm). Snout may be truncate in dorsal view and Finger I is either slightly smaller, equal to, or slightly larger than Finger II. In some specimens the dark-brown blotches form a W-shaped mark on dorsum, at the shoulder girdle. Descriptive statistics and body proportions (ratios) of measurement variables are provided in Table 3.

Color in Life.—In life, dorsum background color light brown to yellowish-brown, maculated with blackish-brown marks, resembling a granite rock surface (Fig. 2). In some specimens there are also shades of rust. The ventral surfaces are pinkish-white with dark brown spots. Most specimens exhibit bluish-toned eyes, but some of them bear yellowish-toned eyes.

Etymology.—The specific name is derived from the Latin "rupes," "rupis," meaning rock, and "cola," meaning dweller. The name is used in reference to the habits of the new species, which is commonly found among rocks of the *Campo Rupestre* environment of the Chapada Diamantina.

Distribution.—*Pristimantis rupicola* sp. nov. occurs in the highlands of the Chapada Diamantina, state of Bahia, Brazil, from ~870 to almost 1,800 m of elevation, in the municipalities of Ipupiara, Piatã, and Rio de Contas (Fig. 5).

Natural History.—Adult males of *P. rupicola* sp. nov. call at night, exposed or hidden in rock crevices of the *Campo Rupestre* rock outcrops (never perched on grassl or shrub vegetation), with scarce or no vegetation, near or far from streams or other kinds of water bodies. At "Cachoeira do Raposo" (Raposo Waterfall), individuals called over rocks inside a gallery forest bordering the waterfall; there were also individuals calling on the stonewall, up to ~3 m above ground. At Pico das Almas and Itobira, the species occurs in sympatry with *Pristimantis* sp., a species probably phylogenetically related to *P. ramagii*, which usually

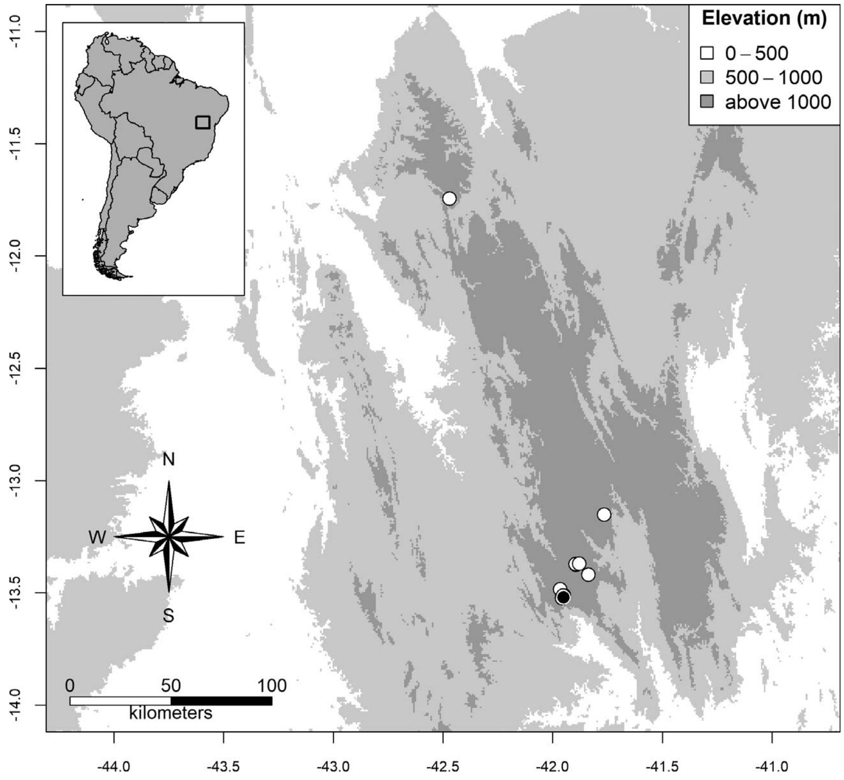

FIG. 5. Geographic distribution of *Pristimantis rupicola* sp. nov. Black circle indicates the type locality (Vale do Queiroz, Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil).

calls at the border of gallery forests or shrub vegetation associated to marshes and rarely calls on rock outcrops as *P. rupicola* sp. nov. Males can form small choruses, respond to playback, and are easily heard from a considerable distance.

Advertisement Call.—Based on calls of 15 males UFMG 20558 (holotype), UFMG 4480, UFMG 4516 (paratypes), UFBA 14385, and 11 unvouchered specimens. The advertisement calls of *P. rupicola* sp. nov. consist of a single note, pulsed or not, showing amplitude modulation characterized by energy decreasing from the beginning to the end of each call (Fig. 4). The call duration (= note duration) lasted from 0.011 to 0.086 s ($x = 0.031 \pm 0.019$ s, $n = 168$ calls) being emitted with inter-call intervals from 1.74 to 5.30 s ($x = 2.76 \pm 0.64$ s, $n = 138$ calls). Pulsed notes were composed of 2–23 pulses ($x = 9 \pm 5$, $n = 126$ notes) with pulse duration from 0.002 to 0.015 s ($x = 0.004 \pm 0.002$ s, $n = 433$ pulses), and pulse rate from 166.7 to 500 pulse/s ($x = 283.3 \pm 79.1$ pulse/s, $n = 123$ calls). Peaks of dominant frequency located in the first band of energy, from 2.41 to 3.49 kHz ($x = 3.01 \pm 0.23$ s, $n = 168$ calls). The second and the third band of energy were separated, but not well emphasized, ranging from 4.0 to 6.9 kHz (x to $= 5.85 \pm 0.50$ s, $n = 115$ calls) and from 8.09 to 10.47 kHz (x to $= 8.98 \pm 0.56$ s, $n = 67$ calls), respectively.

Suggested Vernacular Name.—Rock-Dwelling Robber Frog.

Remarks.—Most specimens of *P. rupicola* sp. nov. exhibit bluish-toned eyes (Fig. 1B), feature that seems unique among members of the *P. conspicillatus* group. However, as it was not a character present in all specimens that we have collected, we preferred not to include it in the species diagnosis.

DISCUSSION

Pristimantis rupicola seems to be restricted to the *Campo Rupestre*, occurring in areas >870 m a.s.l. of the Chapada Diamantina. The species seems to be broadly distributed along the Chapada Diamantina (Fig. 5); however, it was not registered in any strictly protected areas (equivalent to International Union for Conservation of Nature [IUCN] category II; IUCN, 1994). Its habitat is very specific, and it is constantly threatened by uncontrolled land use and occupation, fire, cattle breeding, and unregulated tourism (Leite et al., 2012).

The Espinhaço mountain range is one of the widest in South America, extending 1,300 km across eastern Brazil, being only smaller than the Andes. It harbors one of the most diverse high-altitude Neotropical ecosystems, the *Campo Rupestre*. Despite occupying such a small area (<0.8% of the Brazilian territory), the *Campo Rupestre* harbors >15% (>5,000 species) of country plant diversity (Silveira et al., 2016). The *Campo Rupestre* is a montane, grassy-shrubby vegetation mosaic typical of the Espinhaço mountain range, growing mainly over quartzitic formation, with rocky outcrops and patches of transitional vegetation such as gallery forests and relictual hilltop forests (Vasconcelos, 2011; Silveira et al., 2016). The compilation of the endemic anurans from the Espinhaço mountain range listed 39 species (Leal et al., 2020). Therefore, with the description of *P. rupicola*, 40 anuran species should be considered endemic to the Espinhaço mountain range.

Pristimantis rupicola is the second known rupicolous species among the almost 550 species of the genus *Pristimantis*, besides *P. hoogmoedi* (Kaiser et al., 2015). The latter is known only from its type locality, the southern slopes of Cerro Humo, Península de Paria, Venezuela, distant ~3,500 km from the Chapada Diamantina, and was not assigned to any species group at the time of the species description. These two species are likely nonrelated, and the rupicolous habit is probably convergent. However, testing this hypothesis with a phylogenetic approach is necessary. The dorsal color pattern in *P. hoogmoedi* is highly variable, ranging from relatively plain to "extravagantly" patterned (Kaiser et al., 2015). All the patterns bear reticulations or other markings, and although we did not analyze specimens and the authors do not mention patterns, just like in *P. rupicola*, the patterns may resemble a rock surface (Kaiser et al., 2015:figs. 8 and 9).

Surprisingly, we recovered *P. rupicola* outside the clade bearing the species from northeastern Brazil (i.e., *P. paulodutrai*, *P. ramagii*, and *P. vinhai*), as the sister species of *P. gaigei*. The two species are very distinct from each other, in several aspects. *Pristimantis gaigei* inhabits lowland tropical forests from southwestern Costa Rica, eastern Panamá, and central Colombia (Frost, 2019), distant >4,000 km from the *Campo Rupestre* of the Chapada Diamantina. We are not aware of any sister species pair with the same distribution, but another pair with a similar gap in its distribution (~3,500 km) is *Barycholos pulcher*, from the lowlands of Ecuador, and *Barycholos ternetzi*, from the Brazilian Cerrado (Hedges et al., 2008). Other taxa with similar gaps are the sister genera *Craugastor* and *Haddadus* and the clade composed of *Barycholos*, *"Eleutherodactylus" bilineatus*, and *Noblella*, but these taxa are above the species level. One pronounced morphological difference between the two species is that the dorsum of *P. gaigei* is either dark with yellow or orange stripes, mimicking Poison Dart Frogs from the genus *Phyllobates* (Toledo and Haddad, 2009) or brownish and leaf-like, whereas *P. rupicola* has a rock-like dorsum. Other morphological differences are (characteristics of *P. rupicola* inside parentheses): *P. gaigei* has acuminate snout in dorsal view (rounded), large, triangular dentigerous process of the vomer (small ovoid), dorsum shagreened (granular), venter smooth (areolate), and vocal slits absent (present). Although we recovered this sister relationship with high support only in the Bayesian inference analysis (95% of posterior probability, against 48% of bootstrap replicates in the maximum likelihood analysis), it is noteworthy because we recovered the remaining species from northeastern Brazil monophyletic with high support in both analyses (100% of posterior probability and 99% of bootstrap replicates). Nonetheless, it is necessary to perform a phylogenetic analysis with more molecular markers and more species to clarify this unusual phylogenetic relationship.

The genus *Pristimantis*, despite being recovered as monophyletic in several molecular phylogenetic analyses (Pyron and Wiens, 2011; Canedo and Haddad, 2012; Pinto-Sánchez et al., 2012; Padial et al., 2014; González-Durán et al., 2017), still lacks morphological synapomorphies (Hedges et al., 2008; Padial et al., 2014), and its species were assigned to the genus based on either phylogenetic position or overall similarities in external morphology. Likewise, the monophyly of the *P. conspicillatus* group as it is currently known (sensu Padial et al., 2014) is based party on the molecular phylogenetic position of some of its members and party on overall similarities in external morphology. We have therefore assigned *P. rupicola* to the genus *Pristimantis* and to the *P. conspicillatus* group based solely on its phylogenetic position. Although *P. rupicola* shares some phenotypic characters usually attributed as diagnostic of to the *P. conspicillatus* group, such as the presence of a tarsal fold, distinct tympanic membrane, and advertisement call composed of pulsatile and amplitude-modulated notes (Padial et al., 2016), it also has some morphological features that contradict previous diagnostic features for the group. *Pristimantis rupicola* has a granular dorsum, areolate venter, and Finger I may be slightly shorter or slightly longer than Finger II (dorsal skin shagreen without keratinized tubercles, venter smooth or granular, and Finger I longer than or equal Finger II in the rest of the species of the *P. conspicillatus* group; Padial et al., 2014, 2016).

We now raise to 36 the number of species in the *P. conspicillatus* group, 13 of these species with untested phylogenetic positions. It is one of the most broadly distributed *Pristimantis* groups, occurring through Central America, the Amazon basin, Brazilian Cerrado, Atlantic Forest, and *Campo Rupestre*. The morphological inconsistencies, the low phylogenetic knowledge, and the broad distribution of the *P. conspicillatus* group highlight the need of a thorough systematic review of the group, based on a stringent phylogenetic hypothesis, encompassing as many species as possible.

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Appendix 1

Specimens Examined

Pristimants dundeei.—BRAZIL: Mato Grosso Do Sul: CFBH 7283–7284, Costa Rica. CFBH 20068, Três Lagoas.

Pristimantis fenestratus.—BRAZIL: Amazonas: CFBH 16660, 16664, Manaus.

Pristimantis gaigei.—PANAMÁ: Coclé: USNM 523379–523381, El Copé, north of Parque Nacional General Omar Torrijos. PANAMÁ: USNM 140649, Chilibre, near twilight zone of Chilibre cave. USNM 325055, Madden Forest, George Green Park.

Pristiamantis malkini.—PERU: Loreto: AMNH 94228–94230 (pictures only; holotype and two paratypes), Estirón, Río Ampiyacu.

Pristimantis paulodutrai.—BRAZIL: Bahia: CFBH 1456, Cachoeira. CFBH 4465–4467, 11963, 11965–11966, 27714, Ilhéus. CFBH 21119, 32353, Uruçuca.

Pristimantis ramagii.—BRAZIL: Bahia: CFBH 9651–9655, 9657–9663, 9665–9670, Salvador, Bahia Federal University (UFBA) campus. PERNAMBUCO: UFMG 113–120, Recife.

Pristimantis vinhai.—BRAZIL: Bahia: UFMG 19855–19856, 19858, Arataca, Parque Nacional Serra das Lontras. CFBH 27922–27923, 27929, 27933, Bonito. CFBH 32097, 32549, Camacan, Serra Bonita. CFBH 32470, 32479–32480, 35728, Ilhéus, Fazenda Provisão. CFBH 27652, 27658, 28646, 28649, Jequié. CFBH 32400–32401, 32406, 32411–32413, 32415, Uruçuca, Fazenda Bonfim. CFBH 3785, Wenceslau Guimarães, Estação Ecológica Nova Esperança.

Appendix 3

Accession Numbers of Sequences Included in the Phylogenetic and Genetic Distance Analyses

Terminals included in the phylogenetic analyses only: *Barycholos ternetzi*.—KU495148; *Craugastor daryi*.—EF493531; *Holoaden luederwaldt*.—EU186710; *Lynchius flavomaculatus*.—EU186667; *Pristimantis actites*.—EF493696; *Pristimantis appendiculatus*.—EF493524; *Pristimantis chloronotus*.—AY326007; *Pristimantis duellmani*.—AY326003; *Pristimantis ocreatus*.—EF493682; *Pristimantis reichlei*.—EF493707; *Pristimantis ridens*.—EF493355; *Pristimantis unistrigatus*.—EF493387; *Pristimantis versicolor*.—EF493389; *Yunganastes mercedesae*.—FJ539066.

All the following terminals were included in the genetic distance analysis. Accession numbers in bold were also included in the phylogenetic analyses: *Pristimantis achatinus*.—**EF493660**, JN371033, JN991420; *Pristimantis bipunctatus*.—**EF493702**, KY006089, KY006890, KY594758; *Pristimantis buccinator*.—EU712630, EU712631, **KY652650**, MG820139, MG820140; *Pristimantis chiastonotus*.—EU201060, EU201061, JN691265–**JN691273**, JN691274–JN691311; *Pristimantis citriogaster*.—**EF493700**; *Pristimantis condor*.—**EF493701**; *Pristimantis conspicillatus*.—**EF493529**; *Pristimantis fenestratus*.—EU192256, EU192273–**EU192276**, EU192277, EU712632; *Pristimantis gaigei*.—**FJ784385**, FJ784412, FJ784461, FJ784487, **FJ784490**, **JN991447**, **JN991448**, **JN991449**, **JN991450**; *Pristimantis gutturalis*.—**JN691313**; *Pristimantis koehleri*.—**EU192278**–EU192282; *Pristimantis latro*.—KX242519–**KX242521**, KX242522–KX242525, KX925980–KX926011; *Pristimantis lymani*.—**EF493392**; *Pristimantis malkini*.—**EU186663**; *Pristimantis paulodutrai*.—JX267296, JX267297, JX267299, **JX267360**, JX267484, KU495302; *Pristimantis ramagii*.—JX267318, **JX267319**, JX267380, KU495303; *Pristimantis rupicolus*.—**MN954203–MN954209**; *Pristimantis samaipatae*.—**EU192289**–EU192292; *Pristimantis skydmainos*.—**EF493393**; *Pristimantis incertus*.—**EU186650**; *Pristimantis vilarsi*.—**KP149278**, KP149333, KP149334, KP149384, KP149391, KP149438; *Pristimantis vinhai*.—JX267343, JX267362–JX267365, JX26736491, MN954210, **MN954211**, MN954212; *Pristimantis* aff. *vinhai*.—**JX267492**; *Pristimantis zeuctotylus*.—EF376082–EU376083, EU201059, JN691222–**JN691259**, JN691260–JN691264, JQ742171.

Appendix 2. Information on sound recordings.

Call ID	Voucher	Temp. (°C)	Locality in Bahia, Brazil	Microphone	Recorder
SUFBA 410	—	21.1	Rio de Contas	K6/ME66	PMD 661
SUFBA 411	UFBA 14385	21.1	Rio de Contas	K6/ME66	PMD 661
SUFBA 412	—	21.1	Rio de Contas	K6/ME66	PMD 661
FSFL 1	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 2	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 3	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 4	UFMG 4480	—	Rio de Contas	K6/ME66	PMD 660
FSFL 5	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 6	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 7	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 8	—	—	Rio de Contas	K6/ME66	PMD 660
FSFL 9	UFMG 4576	—	Rio de Contas	K6/ME66	PMD 660
FSFL 10	UFMG 20558	—	Rio de Contas	K6/ME66	PMD 660
FSFL 11	—	—	Ipupiara	K6/ME66	PMD 660
FSFL 12	—	—	Ipupiara	K6/ME66	PMD 660