



When the tail shakes the snake: phylogenetic affinities and morphology of *Atractus badius* (Serpentes: Dipsadidae), reveals some current pitfalls on the snake's genomic age

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Abstract

Many anuran species remain to be formally named and described in Amazonia, notably in the Guiana Shield, and particularly in megadiverse groups such as *Pristimantis*. Several species in the Guiana Shield region have been confused with *Pristimantis marmoratus* and *P. ockendeni*. *Hylodes grandoculis*, a taxon previously placed in the synonymy of *P. marmoratus*, may be available for one of these species. To disentangle this confusing situation, we examined the external morphology and osteology (via μ -CT scans) of the holotype of *H. grandoculis*, the holotype of *Pristimantis marmoratus*, and of recently collected material for which we also analyzed molecular, acoustic, and morphological variation. We concluded that some populations from Suriname and northern Pará, Brazil, are distinct from *P. marmoratus* and correspond to *Pristimantis grandoculis*. Other populations, from French Guiana, are closely related to *P. grandoculis* but their status remains ambiguous. Finally, some populations, from French Guiana and Amapá, Brazil, are conspicuously distinct from both *P. marmoratus* and *P. grandoculis* and are described herein as *P. crepitaculus* sp. nov. A third species, belonging to a “trans-amazon complex”, occurs in southern Suriname, Guyana, and Brazil and remains undescribed. *Pristimantis grandoculis* and related populations from French Guiana lack external tympanum, columella, pharyngeal ostia, vocal slits and do not vocalize. This represents a rare, perhaps unique, example of a deaf and mute species of frogs from the Amazonian lowlands.

Keywords (separated by '-') Amazonia - Amphibia - Morphology - Tomography

Footnote Information



ORIGINAL ARTICLE

Back from the deaf: integrative taxonomy revalidates an earless and mute species, *Hylodes grandoculis* van Lidth de Jeude, 1904, and confirms a new species of *Pristimantis* Jiménez de la Espada, 1870 (Anura: Craugastoridae) from the Eastern Guiana Shield

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Abstract

Many anuran species remain to be formally named and described in Amazonia, notably in the Guiana Shield, and particularly in megadiverse groups such as *Pristimantis*. Several species in the Guiana Shield region have been confused with *Pristimantis marmoratus* and *P. ockendeni*. *Hylodes grandoculis*, a taxon previously placed in the synonymy of *P. marmoratus*, may be available for one of these species. To disentangle this confusing situation, we examined the external morphology and osteology (via μ -CT scans) of the holotype of *H. grandoculis*, the holotype of *Pristimantis marmoratus*, and of recently collected material for which we also analyzed molecular, acoustic, and morphological variation. We concluded that some populations from Suriname and northern Pará, Brazil, are distinct from *P. marmoratus* and correspond to *Pristimantis grandoculis*. Other populations, from French Guiana, are closely related to *P. grandoculis* but their status remains ambiguous. Finally, some populations, from French Guiana and Amapá, Brazil, are conspicuously distinct from both *P. marmoratus* and *P. grandoculis* and are described herein as *P. crepitaculus* sp. nov. A third species, belonging to a “trans-amazon complex”, occurs in southern Suriname, Guyana, and Brazil and remains undescribed. *Pristimantis grandoculis* and related populations from French Guiana lack external tympanum, columella, pharyngeal ostia, vocal slits and do not vocalize. This represents a rare, perhaps unique, example of a deaf and mute species of frogs from the Amazonian lowlands.

Keywords Amazonia · Amphibia · Morphology · Tomography

Introduction

Pristimantis Jiménez de la Espada, 1870 is the most species-rich genus among all vertebrates, currently containing more than 570 species mostly distributed throughout Amazonia,

the Andes, the Chocó, and Pantepui (Frost, 2021), and, albeit more marginally, in Central America, the Caribbean, the Cerrado, and the Atlantic Forest. Species in this genus are being named at a fast pace, with over 133 species described

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in the last decade, and over 220 species since 2000 (Frost, 2021). This, along with diversity estimates based on DNA sequence data (e.g. Trevisan et al., 2020; Vacher et al., 2020), suggests a vast number of unnamed species in this genus.

Many *Pristimantis* species occur at very narrow altitudinal ranges and have small distributions (Duellman & Lehr, 2009). This pattern is most striking not only along Andean slopes and in the Pantepui region, but also in some lowland areas (e.g. Fouquet et al., 2013; Kok, 2013). Direct mode of development (endotrophic larvae that hatch as froglets) and narrow bioclimatic niches have been suggested as possible causes of high micro-endemism in this group (Gonzalez-Voyer et al., 2011; Vences & Wake, 2007). As a corollary, half of the 445 *Pristimantis* species evaluated by the International Union for Conservation of Nature (IUCN) are considered endangered (IUCN, 2020). It is therefore important to improve our knowledge of the actual diversity and distribution of *Pristimantis* species.

Pristimantis marmoratus (Boulenger, 1900) and *P. ockendeni* (Boulenger, 1912) have for long been used to designate multiple populations of superficially similar, hard to identify, small brown *Pristimantis* species of the “*unistrigatus* group” (sensu Hedges et al., 2008, see discussion in Kok et al., 2018). In the Guiana Shield lowlands more specifically, *P. marmoratus* has been reported from northern Brazil, in the state of Pará (Ávila-Pires et al., 2010), Guyana (Ernst et al., 2005, 2006, 2007), French Guiana (Lescure & Marty, 2000), and Suriname (Ouboter & Jairam, 2012), whereas *P. ockendeni* has been reported from the Reserva Florestal Adolpho Ducke (RFAD) in the Amazonas state of Brazil (Lima et al., 2006). However, Kok et al. (2018) clearly demonstrated that the range of *P. marmoratus* (type locality “foot of Mount Roraima”, Venezuela, ca. 1067 m) is restricted to the eastern Pantepui uplands and highlands between 600 and 1800 m above sea level (asl), and Elmer and Cannatella (2008) suggested that the range of *P. ockendeni* (type locality “La Union, Rio Huacamayo, Carabaya, [Departamento Puno,] Peru, ca. 600 m”) is restricted to the Andean foothills of south-eastern Peru. Therefore, the Guiana Shield lowland populations that were previously identified as *P. marmoratus* and *P. ockendeni* likely remain unnamed, except for at least some “*P. marmoratus*” populations from Suriname for which a name is available: *Hylodes grandoculis* van Lidth de Jeude, 1904. The species was described based on a single specimen from central Suriname (“the basin and the sources of the Coppename”) and is considered a synonym of *P. marmoratus* since Frost (1985). Several species co-occur in the region, and the conspecificity of the holotype of *H. grandoculis* with recently collected material needs, therefore, to be clarified.

Vacher et al. (2020) delimited three major lineages corresponding to populations previously identified as *P. marmoratus* or *P. ockendeni*: (1) *Pristimantis* cf. *marmoratus*, occurring in the easternmost part of the region (state of Amapá in Brazil and French Guiana) and corresponding to *Pristimantis* sp. 1 of Fouquet et al. (2013) and Kok et al. (2018); (2) *Pristimantis* cf. *ockendeni*, occurring in southern Suriname and central Guyana (*Eleutherodactylus marmoratus* of Ernst et al., 2005, 2006, 2007); and (3) *Pristimantis* sp. “Guianas”, occurring in French Guiana, in southern Amapá state (Brazil), Suriname, and at the border between Guyana and the state of Pará, Brazil, corresponding to *Pristimantis* sp. 4 of Fouquet et al. (2013) and Kok et al. (2018).

To (1) disentangle this confusing situation and determine if one of these lineages would correspond to *Hylodes grandoculis*, and (2) facilitate the description of potential related species, we examined the external morphology and osteology (via μ -CT scans) of the holotype of *H. grandoculis*, of the holotype of *Pristimantis marmoratus*, and of recently collected material for which we analyzed genetic, acoustic, and morphological variation.

Material and methods

Field work and deposition of specimens

We undertook extensive field work in French Guiana, Guyana, the Brazilian states of Amapá and Amazonas, and in Suriname (Bakhuis, Taffleberg, and Sipaliwini), including areas nearby the type locality of *Hylodes grandoculis*, collecting specimens and tissue samples, and recording advertisement calls and ecological data of numerous *Pristimantis* populations (Fig. 1). Frogs were collected by hand and killed with an intraperitoneal injection of Xylocaine® (lidocaine hydrochloride). All specimens were individually tagged and fixed in 10% formalin before being transferred to a solution of 70% ethanol for permanent storage. Newly collected specimens were deposited in the Museum National d’Histoire Naturelle (Paris, France) (MNHN-RA-2020.0092–118), Museu Paraense Emílio Goeldi (MPEG 41819–41825), and the National Zoological collection of Suriname (NZCS A1210–1212). Other specimens examined are deposited in various zoological collections (Appendices 1 and 2).

Molecular analyses

We gathered 190 16S sequences of species of the “*Pristimantis unistrigatus* group” from the eastern Guiana Shield and the Pantepui region, as well as of populations south of the Amazon River previously identified as *P. cf. ockendeni* and closely related to Guiana Shield populations according to

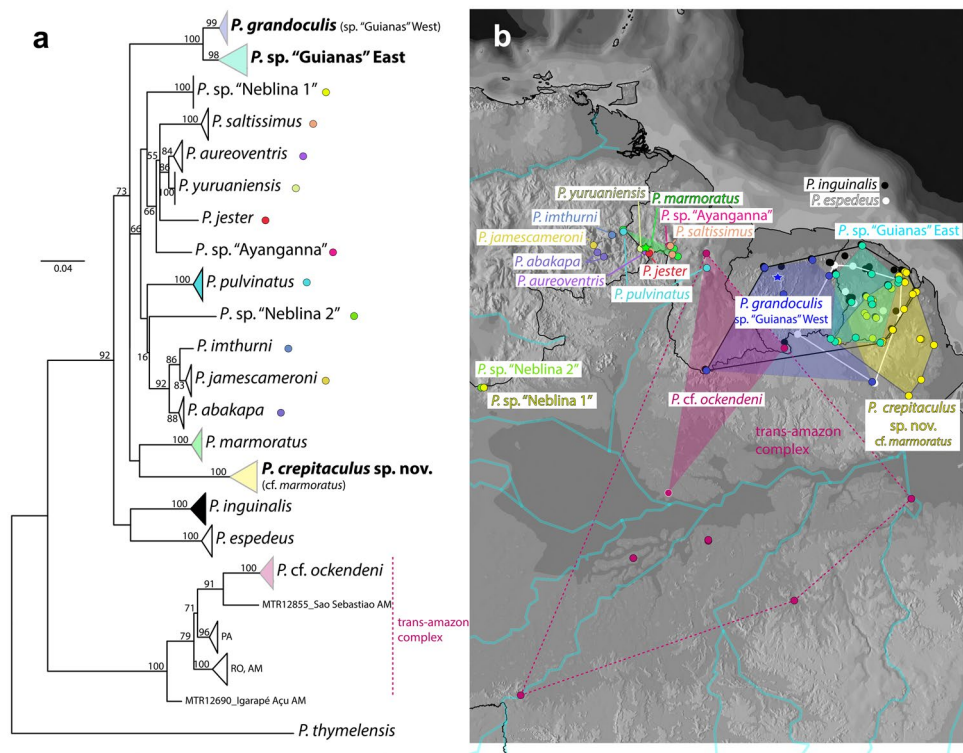


Fig. 1 **a** Maximum Likelihood phylogenetic tree obtained from the analysis of 191 sequences of 12S-16S (2548 bp) of *Pristimantis*. Bootstraps > 50% are indicated on the left side of the nodes. For sake of clarity, branches within species are collapsed. Only the species occurring in the lowlands are coloured in the tree according to the map. **b** Distribution of the different species included in the molecular dataset. The range of the species occurring in the lowlands is depicted by filled polygons (except *P. espedeus* and *P. inguinalis* that are not

filled for clarity purpose). The population of *P. cf. ockendeni* from RFAD (Manaus region) is only tentatively assigned to the same species as Guyana and Suriname populations since it is only documented by pictures and a call recording, and is indicated with a circle with white contour. The type locality of *Pristimantis grandoculis* is indicated by a blue filled star as well as the type locality of *P. marmoratus* with a green star

Vacher et al. (2020) (Appendix 1). We employed BLASTN to verify that no other 16S sequence deposited on GenBank after the work of Vacher et al. (2020) clustered with the species used in this study. Twenty-eight sequences were newly generated while the other sequences were retrieved from GenBank (Appendix 1). We completed these data with 13 sequences of 12S, eight retrieved from GenBank and five newly generated. Genomic DNA was extracted from tissue samples (muscle or liver) using either the Wizard® Genomic DNA Purification Kit (Promega; Madison, WI, USA) or the DNeasy® Blood & Tissue Kit (Qiagen; Hilden, Germany) following the manufacturer's protocols. We amplified targeted loci by standard PCR protocols and then used Sanger sequencing (primers 16RF: TATCCCTAGGGTAACTTG; 16FR: TTACCAAAAACA TCGCCT from Salducci et al., 2005). These sequences were aligned with the mitogenome of *P. thymelensis* (JX564889, which served as the outgroup), on the MAFFT7 online server under default parameters except the E-INS-i strategy, which is designed for sequences with multiple conserved domains and long gaps (Katoh et al., 2017). We trimmed the alignment to keep only regions where sequences overlap, resulting in

a final alignment of 2548 base pairs (bp). We investigated the phylogenetic relationships among a total of 191 terminals under maximum likelihood (ML), applying a GTRCAT model with RAXML v.8.2.4 (Stamatakis, 2014). All RAXML analyses were performed on the CIPRES Science Gateway online server (Miller et al., 2010). Non-parametric bootstrapping values (Felsenstein, 1985) were estimated using 1,000 pseudoreplicates.

Morphometric analysis

We examined 67 adult specimens (45 males, 22 females, among which 27 were included in our molecular dataset) of *P. cf. marmoratus* [*P. sp. 1* of Fouquet et al. (2013) and Kok et al. (2018), 13 males, 3 females], *P. cf. ockendeni* (8 males, 6 females), and *Pristimantis* sp. "Guianas" from Suriname (4 males, no females) and from French Guiana (13 males, 13 females) [*P. sp. 4* of Fouquet et al. (2013) and Kok et al. (2018)], and the holotype of *Hylodes grandoculis* (Appendix 2). The other specimens were a priori assigned to one of these species when they were collected from the same or nearby

populations and after morphological examination. Sex was determined either in the field via calling activity, or in the laboratory by examining the condition of vocal slits, nuptial pads, and gonads. We measured 18 variables; abbreviations for measurements are as follows: SVL—snout-vent length; TiL—tibia length; FeL—femur length; TaL—tarsus length; FL—foot length (from outer edge of metatarsal tubercle to the tip of toe IV); HeL—head length; HW—head width; Ind—internarial distance; IOD—interorbital distance; EN—eye-nostril distance (straight line distance between anterior corner of eye and nostrils); ED—horizontal eye diameter; TD—horizontal tympanum length; FD—disc width of Finger III; 4TD—disc width of Toe IV; ETS—eye-tip of snout distance (straight line distance between the anterior corner of eye and tip of snout); 1FiL—length of Finger I (from proximal edge of palmar tubercle to the tip of Finger I); 2FiL—length of Finger II (from proximal edge of palmar tubercle to the tip of Finger II); HL—hand length (from distal edge of palmar tubercle to the tip of Finger III).

Measurements were taken using a digital caliper to the nearest 0.01 mm. Mean and ranges were rounded to the nearest 0.1 mm (all measurements by AF, except for MPEG specimens, measured by PP). We examined the variation of morphometric data among adult males through a principal component analysis (PCA) via FactoMineR package in R v.3.2.4 (Lê et al., 2008; R Development Core Team, 2016). To control for variation in body size among individuals, we performed additional analyses on a size-corrected dataset (residuals) obtained by linear-regressing the original morphometric measures of each variable on SVL (Strauss, 1985).

3D microtomography

We investigated the osteological variation across adult males of *P. cf. marmoratus*, *Pristimantis* sp. “Guianas” and the holotypes of *Hylodes grandoculis* (RMNH 4467) and *P. marmoratus* (BMNH 1947.2.16.92). Specimens were scanned using an EasyTom 150 (at kV = 40–70, resolution < 20 µm) from the MRI platform of ISEM (Institute of Evolutionary Sciences of Montpellier), except the holotype of *H. grandoculis* which was scanned using a CT/Zeiss Xradia at the Leiden Naturalis Biodiversity Center, and the holotype of *P. marmoratus* that was scanned using a Metris X-Tek HMX ST 225 System at the Natural History Museum, London. Segmentation of the full skeleton and of the cranium was done using Avizo (FEI Visualization Sciences Group, Burlington, MA, USA) and Biomedisa (Lösel et al., 2000). µ-CT scans and surface renderings will be deposited at www.morphosource.org upon manuscript acceptance.

Acoustic analysis

We gathered six call recordings of males of *Pristimantis* cf. *marmoratus* (including one track file from Marty & Gaucher, 1999). To our knowledge, *Pristimantis* sp. “Guianas” has never been observed calling and no recording is available. The external tympanum and pharyngeal ostia are absent in that species, and males lack vocal slits. The calls of *P. cf. marmoratus* consist in series of short notes, and we measured seven call variables from waveforms using Audacity v.2.1.1 following Köhler et al. (2017): call length, silence between calls, number of notes, note length, silence between the two first notes, silence between the two last notes, dominant frequency (taken with a spectral slice over the entire note). Whenever possible, up to four measurements of each variable were taken per recorded male, and the average was considered as a single measurement. Call recordings will be deposited at www.sonotheque.mnhn upon manuscript acceptance.

Results

Phylogenetic relationships

The relationships among species inferred from the ML analysis are poorly supported at several nodes (Fig. 1). However, sequences from individuals corresponding to the different putative species form strongly supported clades. The populations previously identified as *P. cf. ockendeni* from the Guiana Shield (Suriname and Guyana) form a clade related to several populations south of the Amazon River, which we hereafter refer to as the “trans-amazon complex”. The Guiana Shield populations are more closely related to a single specimen from São Sebastião, Rio Abacaxis, Amazonas (*p* distance = 5.4%, Table 3). The “trans-amazon complex” is highly divergent from other Guiana Shield species, and is more closely related to western Amazonian species, although probably not directly related to *P. ockendeni* (Vacher et al., 2020). *Pristimantis* cf. *marmoratus* is circumscribed to the easternmost part of the Guiana Shield and forms a poorly supported clade with *P. marmoratus* sensu stricto. *Pristimantis* sp. “Guianas” samples form a strongly supported clade with uncertain relationships and are subdivided into two main lineages (*p* distance = 4.5%, Table 3), one occurring in the west (Suriname, the Amapá and Pará states in Brazil) and the other one in the east (French Guiana). The geographic range of the western lineage of *Pristimantis* sp. “Guianas” encompasses the type locality of *P. grandoculis*.

263 **Morphometric analyses**

264 The PCA based on raw morphometric measurements provided two first components accounting for 63.4% of the total
 265 variation (Fig. 2a). The first component explains 46.7% of the variation, and variable coefficients are all highly and
 266 positively correlated. Overall, the variation along the first
 267 principal component (PC) axis is related to body size; since
 268 the three species largely overlap on this variable, they also
 269 do along this axis. The variation along the second axis is

notably related to differences in TiL and FL (negatively correlated with PC2) and ED (positively correlated with PC2) and segregates populations of *Pristimantis* sp. “Guianas”, which largely overlap, from the other species that only partly overlap with each other. The holotype of *P. grandoculis* is positioned within the western populations of *Pristimantis* sp. “Guianas”.

The PCA based on size-corrected morphometric measurements provided two first components accounting for 48.1% of the total variation (Fig. 2b). The variation along the first

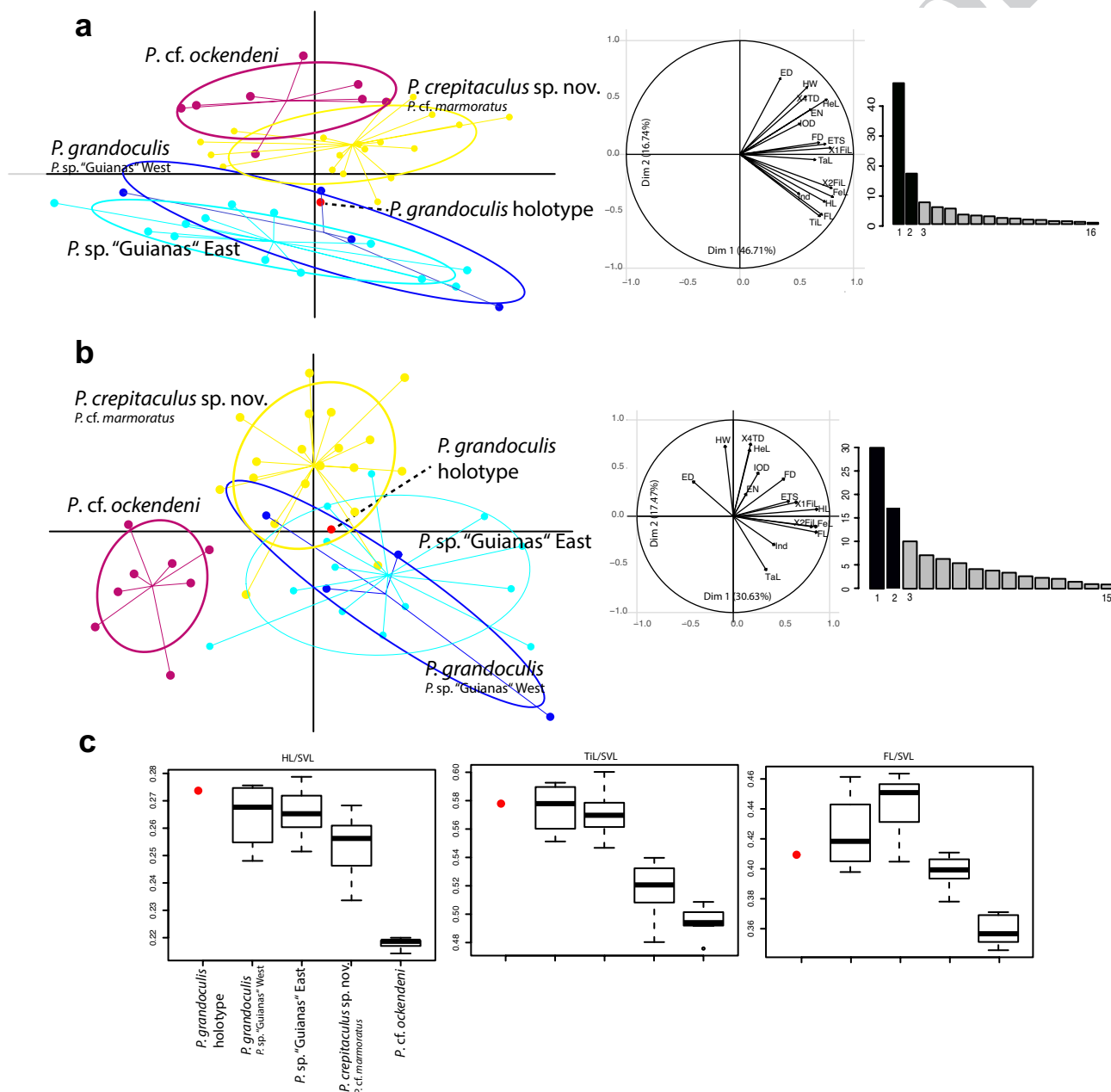


Fig. 2 **a** PCA based on 17 external body measurements (without TD) across 43 *Pristimantis* males. **b** PCA based on 16 size-corrected (residuals of the linear regression of the measurements on SVL) external body measurements. **c** Boxplots of ratio between three measurements on SVL

axis is notably related to differences in HL, FeL and FL (positively correlated with PC1), and ED (negatively correlated with PC1) and segregates *Pristimantis* cf. *ockendeni* from the other species that only partly overlap with each other (eastern and western populations of *Pristimantis* sp. “Guianas” completely overlap). The variation along the second axis is notably related to differences in HW (positively correlated with PC2) and TaL (negatively correlated with PC2) and partly segregates *P.* sp. “Guianas” from *P.* cf. *marmoratus*. The holotype of *P. grandoculis* is positioned within populations of *P.* sp. “Guianas” but also within *P.* cf. *marmoratus*.

The examination of the ratios between the aforementioned variables and SVL (Fig. 2c) shows limited overlap across species particularly considering HL/SVL and TiL/SVL. Moreover, the ratios displayed by the holotype of *P. grandoculis* are always within the range of French Guiana and Suriname populations of *P.* sp. “Guianas” and only marginally overlaps with the range of the other species.

Taxonomic conclusion

External morphology and osteology (see below) strongly suggest that the western populations that have been identified as *Pristimantis* sp. “Guianas” [*P.* sp. 4 of Fouquet et al. (2013) and Kok et al. (2018)] correspond to *Hylodes grandoculis*. This species is geographically disjunct and phylogenetically distinct from *P. marmoratus* sensu stricto based on molecular data (Fig. 1; see also Kok et al., 2018). Our morphological and osteological data also unambiguously confirm the non-conspecificity of *P. marmoratus* and *H. grandoculis*. Therefore, we formally rescue *H. grandoculis* from the synonymy of *P. marmoratus*, and herein provide an amended diagnosis of *Pristimantis grandoculis* n. comb. (van Lidth de Jeude, 1904) based on the examination of the holotype and four adult specimens from Suriname. It must be mentioned that the specimens of *Pristimantis* sp. “Guianas” from French Guiana, although morphologically very similar to *P. grandoculis*, form a distinct, closely related clade that upon the examination of a sufficient number of adult specimens (not currently available) could be either considered conspecific or a distinct species and will be hereafter referred to as *P.* sp. “Guianas” East. The easternmost species previously reported as *Pristimantis* sp. 1 (Kok et al., 2018) and *Pristimantis* cf. *marmoratus* (Vacher et al., 2020) is also morphologically clearly distinct from *P. grandoculis* and all known congeners in the area and is formally described and named herein as *P. crepitaculus* sp. nov. The “trans-amazon complex”, in which some populations have been erroneously identified as *P. ockendeni*, will be treated elsewhere.

Species accounts

Pristimantis grandoculis (van Lidth de Jeude, 1904)

- Hylodes grandoculis* van Lidth de Jeude, 1904
Eleutherodactylus marmoratus Hoogmoed, in Frost, 1985
Eleutherodactylus marmoratus Avila-Pires et al., 2010
Pristimantis marmoratus Ouboter & Jairam, 2012
Pristimantis sp. 4 Jairam, 2019
Pristimantis sp. “Guianas” Vacher et al., 2020

Holotype. RMNH 4467. Type locality: “the basin and the sources of the Coppename”, interior of Surinam. van Lidth de Jeude stated that the specimen was collected “Sept. 10th 1901” during the Coppename expedition (Anonymous). The expedition took place between August and late November 1901 “we went up the Coppename then the two rivers that form it until they become unseaworthy even for the korjales (boats) of the natives (3°57’N)”. These indications suggest that the specimen was collected at the farthest point reached by the expedition and that 3.9500°N 56.7543°W are plausible coordinates for the type locality.

Referred specimens. MNHN-RA-2020.0118 (field no. AF3435), an adult male collected by A. Fouquet, S. Cally and R. Jairam on 30 April 2015 at Bakhuis Mountains, Suriname (4.7246°N 56.7638°W, ~200 m asl; Fig. 3). NZCS A1212, an adult male collected by P. Ouboter and V. Kadosoe on 20 August 2013 at Tafelberg, Suriname (3.8049°N 56.1539°W ~500 m asl); NZCS A1210-11, two adult males collected by R. Jairam and D. Baêta on 23 June 2016 at Lely Mountain, Suriname (4.4158°N 54.6498°W, ~600 m asl).

Definition. *Pristimantis grandoculis* is characterized by the following unique combination of characters: (1) SVL small, adult males 16.5 ± 1.1 mm (range 14.7–17.9 mm, $n=5$) (Table 1), female unknown; (2) dorsal skin tuberculate, with two pairs of enlarged tubercles on the scapular region embedded in a W-shaped scapular fold, ventral skin granular particularly on the femoral region; (3) external tympanum absent, tympanic membrane not differentiated and obscured by supratympanic fold on the posterodorsal edge of tympanum, tympanic annulus indistinct; (4) pharyngeal ostia absent; (5) columella absent; (6) tibia length 55–59% of SVL; (7) snout broadly rounded in profile and dorsal view; (8) each upper eyelid with two prominent tubercles; (9) choanae round and small (0.3 mm for MNHN-RA-2020.0118), dentigerous processes of vomers oblique, narrowly separated, each bearing 3–5 odontophores; (10) vocal slits absent, vocal sac absent; (11) one unpigmented whitish nuptial pad located on the preaxial side of the thenar tubercle on each thumb in male; (12) FI much shorter than FII, reaching

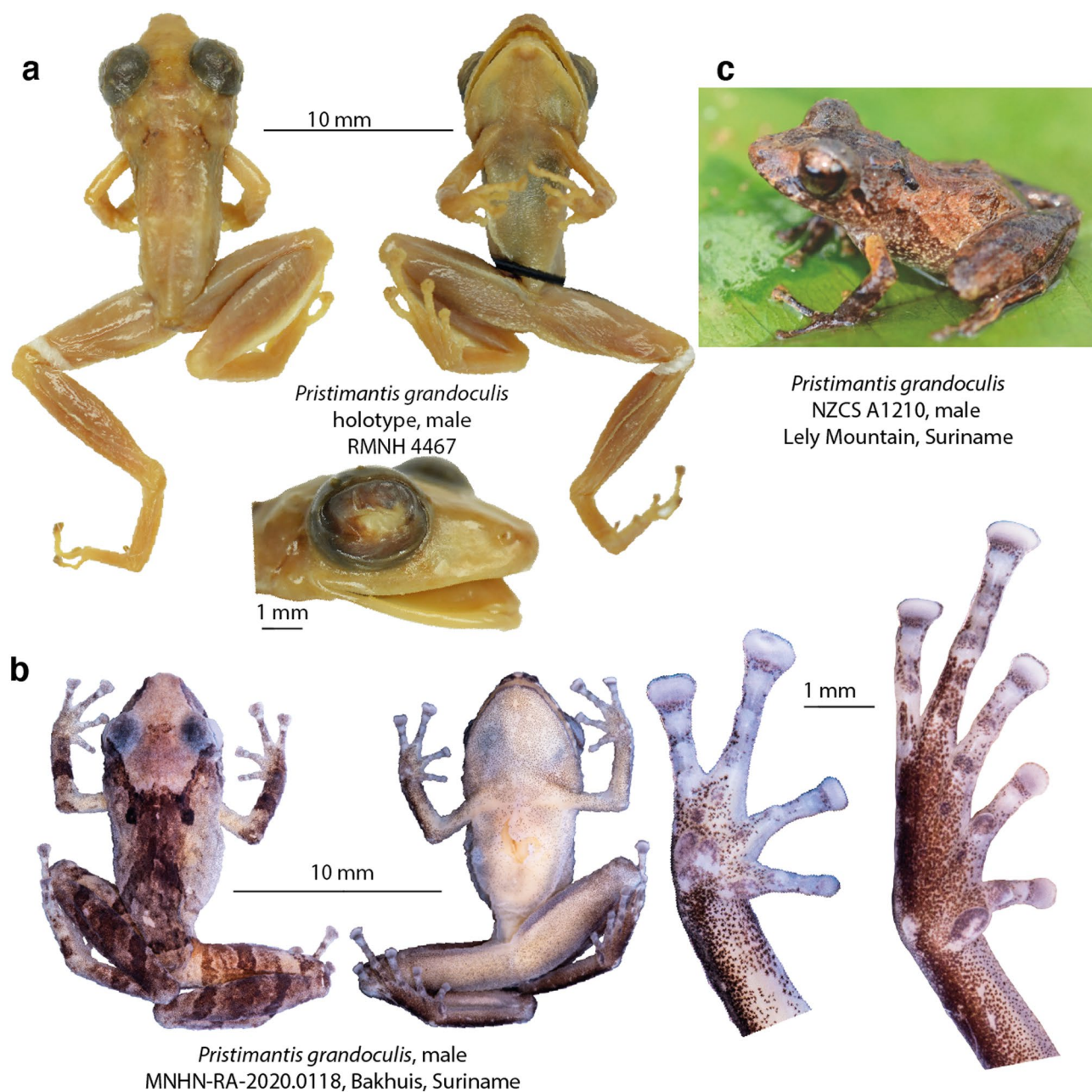


Fig. 3 **a** Dorsal, ventral, and lateral (head) views of the holotype (RMNH 4467) of *P. grandoculis* from Coppename River, Suriname. **b** Dorsal and ventral views and hand and foot of a recently collected

specimen of *P. grandoculis* (MNHN-RA-2020.0118) from Bakhuis, Suriname. **c** A photograph in life of another recently collected specimen *P. grandoculis* (NZCS A1210)

subarticular tubercle of FII; (13) fingers with preaxial fringes on FII and III; (14) finger discs broadly expanded, elliptical, thenar tubercle oval, palmar often broken in three distinct tubercles; (15) three enlarged ulnar tubercles often flat and barely visible; (16) axillary tubercles (sensu Myers & Donnelly, 2001) absent; (17) tarsal fold absent but tubercles present; (18) toes basally webbed between TII–IV with preaxial fringes on TII–V; (19) calcars absent, inner metatarsal tubercle oval, outer metatarsal tubercle round; (20) dorsal

colouration mostly chestnut brown, but highly variable in colour and pattern, ventral colouration translucent brownish grey with small cream spots, mostly on chest, throat suffused with black melanophores and scattered with small irregular cream blotches; (21) iris golden with a copper horizontal band, absence of vertical streak; (22) posterior surface of thighs and groin dark grey in life and brown in preservative, absence of yellow spot on groin.

Table 1 Morphometric variables

	SVL	TiL	FeL	TaL	FL	HeL	HW	Ind	IOD	EN	ED	TD	FD	4TD	ETS	IFiL	2FiL	HL
<i>P. crepitaculus</i> sp. nov	17.0	8.8	8.3	5.3	6.8	6.5	6.4	1.6	2.0	2.2	2.5	0.9	0.9	0.9	3.2	2.1	2.4	4.3
	15.7	8.0	7.5	4.9	6.1	6.0	5.7	1.5	1.8	1.9	2.3	0.7	0.7	0.8	2.9	1.8	2.1	3.9
	18.3	9.4	9.2	5.9	7.3	7.1	6.9	1.8	2.3	2.6	2.9	1.1	1.0	1.1	3.6	2.5	2.7	4.7
F (n=3)	23.4	11.4	10.8	6.7	9.1	8.5	8.4	2.0	2.4	2.9	3.1	1.1	1.2	1.3	4.3	3.0	3.5	5.5
	22.9	10.9	10.3	6.4	8.9	8.3	7.7	1.8	2.4	2.9	2.7	0.9	1.1	1.2	4.0	2.8	3.1	5.1
	23.9	11.8	11.0	7.0	9.5	8.6	9.0	2.2	2.5	3.0	3.3	1.3	1.2	1.3	4.5	3.2	4.0	5.8
<i>P. cf. ockendeni</i>	17.4	8.6	7.8	5.4	6.3	6.4	6.2	1.7	2.0	2.2	2.6	0.8	0.8	0.8	3.0	2.0	2.2	3.8
	16.2	8.2	7.1	5.1	5.8	5.9	5.7	1.6	1.8	2.1	2.4	0.7	0.7	0.8	2.8	1.8	2.0	3.6
	18.4	9.1	8.3	5.9	6.8	6.8	6.7	1.8	2.1	2.3	2.8	0.9	1.0	1.0	3.2	2.2	2.4	4.1
F (n=6)	24.1	11.4	10.4	6.9	8.2	8.4	8.6	2.1	2.7	3.0	3.2	1.0	1.1	1.2	4.1	2.6	3.0	5.1
	21.4	10.7	10.0	6.5	7.9	7.6	7.5	1.9	2.6	2.8	3.1	0.8	1.0	1.0	3.9	2.2	2.6	4.7
	25.7	12.2	11.5	7.3	8.6	9.6	9.6	2.3	3.1	3.2	3.4	1.2	1.2	1.3	4.5	2.9	3.6	5.4
<i>P. sp. "Guianas" East</i>	16.0	9.1	8.4	5.2	7.1	5.8	5.5	1.7	2.0	2.0	2.3	NA	0.8	0.8	3.1	2.0	2.4	4.2
	14.7	8.2	7.2	4.6	5.9	5.3	4.7	1.4	1.7	1.7	2.1	NA	0.7	0.6	2.8	1.7	1.9	3.7
	17.5	10.4	9.4	5.9	8.0	6.5	6.5	1.9	2.2	2.5	2.5	NA	0.9	0.9	3.4	2.4	2.9	4.8
F (n=13)	22.5	12.0	11.1	6.6	9.6	8.1	8.2	2.1	2.5	2.9	3.2	NA	1.1	1.1	4.3	2.8	3.2	5.9
	20.6	11.1	10.5	6.0	8.7	7.4	7.2	1.8	2.1	2.5	2.7	NA	0.9	0.9	4.1	2.5	2.7	5.3
	25.0	13.1	12.7	7.3	10.6	9.3	9.0	2.3	2.8	3.4	3.5	NA	1.4	1.4	4.7	3.2	3.9	6.4
<i>P. grandoculis</i>	16.5	9.5	8.2	5.4	7.0	6.1	6.1	1.8	1.9	2.0	2.5	NA	0.8	0.8	3.1	2.0	2.5	4.4
	14.7	8.7	7.3	4.9	6.1	5.5	5.6	1.7	1.9	1.8	2.3	NA	0.8	0.7	2.8	1.8	1.9	3.8
	17.9	10.5	9.0	6.4	7.7	6.5	6.4	1.9	2.0	2.2	2.7	NA	0.9	0.9	3.4	2.4	3.0	4.9
F (n=0)																		

Morphological comparisons with other Guiana Shield lowlands *Pristimantis* of the “*unistrigatus* group”.

Pristimantis grandoculis can mainly be distinguished from *P. espedeus* by its smaller body size (SVL range in males = 14.7–17.9 mm vs. 20.7–24.8 in *P. espedeus*); external tympanum absent (vs. visible in *P. espedeus*) and dark grey groin colouration in life (vs. reddish in *P. espedeus*).

Pristimantis grandoculis can mainly be distinguished from *P. inguinalis* by dark grey groin colouration in life (vs. bright yellow inguinal mark in *P. inguinalis*); external tympanum absent (vs. visible in *P. inguinalis*) and translucent brownish grey ventral colouration with small cream spots (vs. entirely black in *P. inguinalis*).

All the other known Guiana Shield species of the “*unistrigatus* group” occur in the Pantepui region and are generally associated with highlands (i.e. > 700 m elevation; Fouquet et al., 2013; Kok et al., 2018). *Pristimantis grandoculis* was previously confused (and considered a synonym) with *P. marmoratus*, one of these Pantepui species, from which it can immediately be distinguished by iris colour in life (black vertical streak running across the iris in *P. marmoratus* vs. no such streak in *P. grandoculis*) and absence of columella and vocal slits (vs. present in *P. marmoratus*). Among the other *Pristimantis* species found at mid-elevation in Pantepui, *P. grandoculis* can mainly be distinguished from *P. jester* (Means & Savage, 2007) by having preaxial fringes on FII and III (absent in *P. jester*), toes basally webbed between TII–IV with preaxial fringes on TII–V (webbing and fringes on toes absent in *P. jester*) and by iris colour in life (golden to copper in *P. grandoculis* vs. upper 2/5 of iris blue-grey in *P. jester*); from *P. saltissimus* (Means & Savage, 2007) by tympanum condition (external tympanum absent, with indistinct tympanic annulus in *P. grandoculis* vs. distinct with distinct tympanic annulus in *P. saltissimus*), by having preaxial fringes on FII and III (absent in *P. saltissimus*) and toes basally webbed between TII–IV with preaxial fringes on TII–V (webbing and fringes on toes absent in *P. saltissimus*); from *P. guaiquinimensis* (Schlüter & Rödder, 2007; see also Kok & Barrio-Amorós, 2013) mostly by tympanum condition (external tympanum absent, with indistinct tympanic annulus in *P. grandoculis* vs. distinct with distinct tympanic annulus in *P. guaiquinimensis*); from *P. sarisarinama* (Barrio-Amorós & Brewer-Carías, 2008) mostly by the absence of vocal slits in males (present in *P. sarisarinama*); from *P. pulvinatus* (Rivero, 1968) mostly by smaller body size in males (14.7–17.9 mm in *P. grandoculis* vs. 23.0–26.1 mm in *P. pulvinatus*) and distinct vomerine teeth (indistinct or absent in *P. pulvinatus*); and from *P. memorans* (Myers & Donnelly, 1997) mostly by the absence of vocal slits in males (present in *P. memorans*), and tympanum condition (external tympanum absent, with indistinct tympanic annulus in *P. grandoculis* vs. distinct with distinct tympanic annulus in *P. memorans*).

Variation. The holotype is relatively well preserved. However, it is highly discoloured, and overall tuberculation is difficult to assess. Proportions are similar among the five specimens examined; the amount of tuberculation on the skin varies, especially on the dorsum and lateral surfaces of the body. Colour pattern is variable across the recently collected specimens. NZCS A1210 has a dark band running along the canthus rostralis which is absent in the other specimens (Fig. 2C). The W-shaped scapular mark is well-developed anteriorly but less so posteriorly compared to the other specimens. An interorbital band darker than the dominant background is often present as well as dark bands on the arms and legs but all these markings are variable in sharpness across specimens.

Osteology of the holotype (RMNH 4467). Cranium (Fig. 4). *Shape and proportions.* The skull is well ossified, widest posterior to the orbit at the level of the articulation of the maxilla with the quadratojugal. The rostrum is moderate, the braincase is broad.

Neurocranium and dorsal investing bones. The nasals (separated medially from one another and covering all the nasal capsules dorsally), frontoparietals, parasphenoid and neopalatines are co-ossified with the sphenethmoid. The frontoparietal and prootic are fused. Ventrally, the prootics are fused with the parasphenoid alae. The exoccipitals are fused. The dorsal surface of the otic capsule is ossified. Frontoparietal crests are absent and the frontoparietal fontanelle is exposed. The septomaxilla is roughly spiralled, the medial ramus extending posterodorsal to the posterior ramus; the anterior ramus is thick; the lateral ramus is oblique with a long acuminate posterolateral extension; the posterior ramus extends from the middle of the lateral ramus ventromedially. The columellae (stapes) are absent.

Ventral investing bones. The parasphenoid cultriform process extends anteriorly from the anterior edge of the otic capsule and is co-ossified with the sphenethmoid. The parasphenoid alae are moderately long (about half of the length of the cultriform process), perpendicular to the anteroposterior body axis, broadening slightly laterally. The vomers are fused with the sphenethmoid; each vomer is composed of an arcuate bone bordering the anteromedial, medial, and posterior margins of the choana. The prechoanal ramus is expanded medially and anteriorly and bears a ventral flange along its medial edge. The postchoanal process is narrow and acuminate, slightly posteriorly curved. Well-developed dentigerous processes extend posteromedially from the union of the pre- and postchoanal processes. Each dentigerous process bears three teeth and is broadly separated from its counterpart medially. The neopalatine is fused with the maxilla distally. This complex is fused with the parasphenoid medially.

Maxillary arcade. The maxillary arcade bears many small teeth on the premaxilla and maxilla. The arcade is

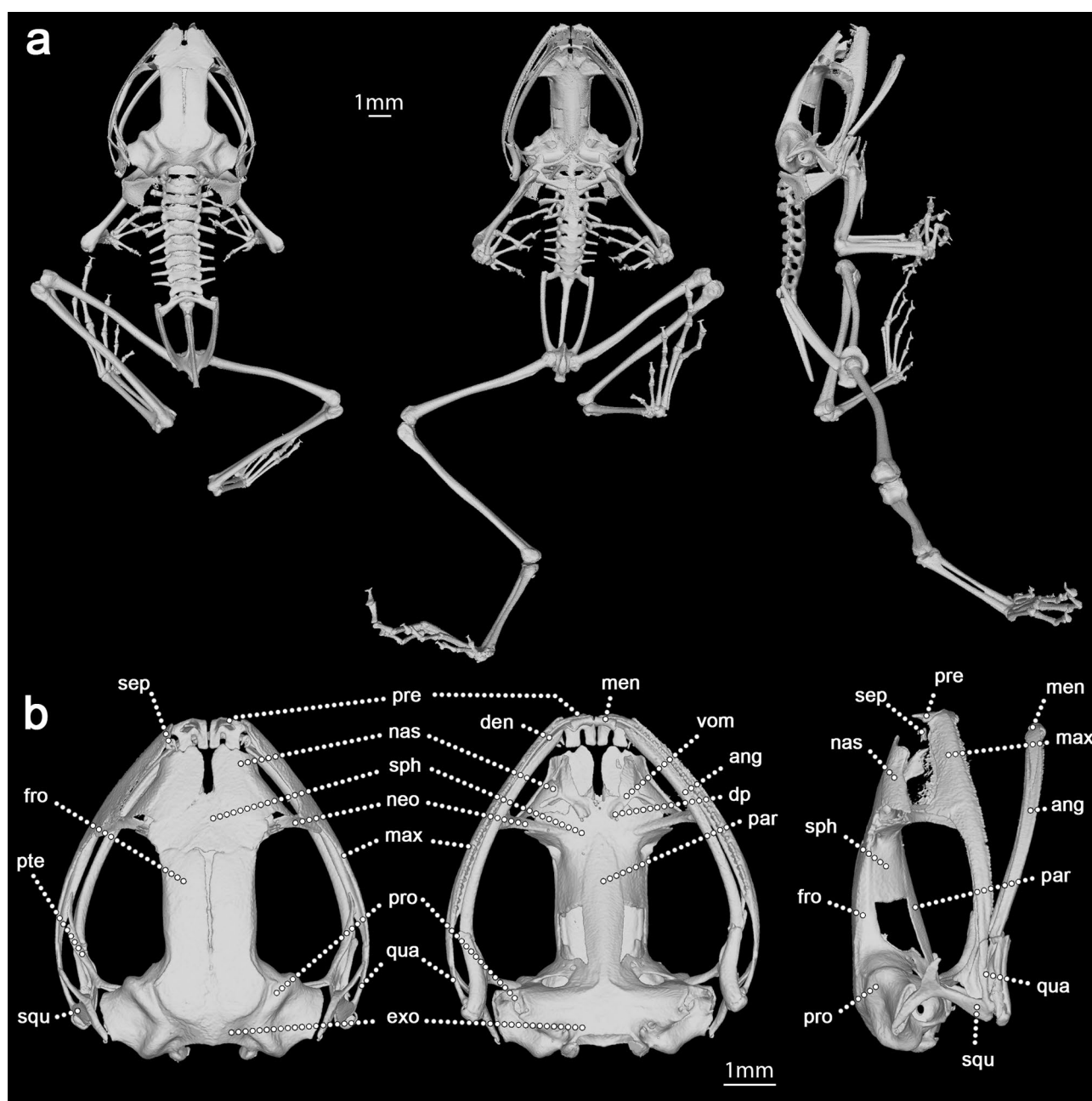


Fig. 4 Volumetric renderings of μ -CT scans of the skeleton of the holotype of *Pristimantis grandoculis* (RMNH 4467). **a** Full skeleton in dorsal (left), ventral (middle), and lateral (right) views. **b** Skull in dorsal (left), ventral (middle), and lateral (right) views. Abbreviations: ang—angulosplenic, den—dentary, dp—dentigerous process, exo—

exoccipital, fro—frontal, max—maxillary, men—mentomeckelian, nas—nasal, neo—neopalatine, par—parasphenoid, pre—premaxillary, pro—prootic, pte—pterygoid, qua—quadratojugal, sep—septomaxilla, sph—sphenethmoid, squ—squamosal, vom—vomer

complete and connected to the slender quadratojugal. The premaxillae are separated medially, and their anterodorsal alary process is weakly divergent from the midline. The pars palatina is broad, with two well-defined processes: the medial (palatine) process is relatively narrow and runs roughly parallel toward its contralateral; the lateral process is broader. The premaxilla and maxilla are in lateral contact

via a simple juxtaposition. The maxilla is long, with a broad pars palatina along its lingual margin and a moderately developed pars facialis.

Suspensory apparatus. The triradiate pterygoid bears a slightly curved anterior ramus with a sculpted ventrolateral face, oriented anterolaterally toward the maxilla, with which it articulates at approximately the mid-length of the orbit.

The pterygoid is fused to the maxilla. The medial and posterior face of the medial rami of the pterygoid are about equal in length. The medial ramus is broader than the posterior and its posterior face is strongly sculpted. The lateral end of the medial ramus overlaps the lateral edge of the prootic. The quadratojugal is long, laterally curved, and slender, articulating anteriorly with the maxilla. It has a bulbous posteroventral process and articulates dorsally with the ventral ramus of the squamosal. The squamosal is dorsally bifurcated, broad, and sculpted, extending anterodorsomedially from the quadratojugal to the level of the otic capsule; the zygomatic ramus is short, whereas the otic ramus is long, almost reaching the posterior end of the skull.

Mandible. The mandible is slim and edentate. The mentomeckelians are small and arcuate in ventral view, medially and laterally broadened, and in narrow contact medially. The dentary is short and thin, posteriorly acuminate, and overlaps the angulosplenial for about a quarter of its length. Dentary is in contact with the angulosplenial posteriorly. The angulosplenial is long and arcuate, laterally slightly grooved. The coronoid process is weak.

Hyoid. The bony posteromedial processes of the hyoid are expanded proximally and separated from one another. No ossified parahyoid is present.

Axial skeleton (Fig. 4).

Vertebral column. The vertebral column has eight procoelous, presacral vertebrae. The vertebrae have complete neural arches and low neural processes. Atlas (presacral I) and presacral II are fused medially and laterally. The transverse processes of presacrals II–III are slightly expanded distally, thicker, and broader than those of other presacrals. The transverse processes of presacrals II and III are oriented ventrolaterally (II anteriorly, III posteriorly), whereas those of presacrals IV–VIII extend dorsolaterally (IV–VII posteriorly, VIII anteriorly). The relative lengths of the transverse processes and sacral diapophyses are: III > IV > Sacrum > V ≈ VI ≈ VII ≈ VIII > II. The sacral diapophyses are slightly expanded distally. The urostyle has a well-developed dorsal ridge that extends along half its length.

Pectoral girdle. The zonal portion has well-ossified coracoids, clavicles, scapulae, and cleithra. The clavicles are long, slender, and oriented anteromedially; the medial tips are narrowly separated from one another and located anteriorly from the level of anterolateral end of the clavicle that articulates with the scapula; the coracoid is long and flared, with its sternal end slightly broader than its glenoid end. The scapula is long with a prominent pars acromialis that is not separated from the pars glenoidalis. The scapula is about one and a half the length of the clavicle. The cleithrum is ossified, well-developed, anteriorly thicker, thinning posteriorly. The suprascapula is unossified.

Pelvis girdle. The long, slender iliac shafts bear dorsolateral crests throughout their length. The overall length of the

girdle is more than two times the width between the anterior ends of the iliac shafts. The iliac prominence is broad and low, and pubes mineralized.

Manus and pes. The phalangeal formulae for the hand and foot are standard, 2–2–3–3 and 2–2–3–4–3, respectively. Terminal phalanges strongly T-shaped. Ossified prepollex and prehallux visible.

Natural history. Our data suggest that *Pristimantis grandoculis* is terrestrial and scansorial. Males were often found perched on low vegetation (0.5–1.5 m above the ground), at dusk, in a position suggesting calling activity. However, acoustic activity has never been observed neither in Suriname nor in French Guiana for *P. sp.* “Guianas” East (despite being locally abundant). It is noteworthy that both groups of populations also lack a columella and that external tympanum is absent in all specimens examined. Juveniles have been found on the leaf litter during the day, and this is also where juveniles, females and amplexant pairs of *P. sp.* “Guianas” East have been found in French Guiana suggesting that the reproduction takes place there. The species inhabits pristine *terra firme* forests from 50 to 700 m asl, generally along the slopes of small massifs.

Distribution. *Pristimantis grandoculis* occurs throughout the interior of Suriname (not along the coastal band), on the southern border of Guyana with Brazil (Acari mountains), and along the border between the Brazilian states of Pará and Amapá. The species probably extends further in southern Suriname and northern Pará state, Brazil. Phylogenetically related populations occur in French Guiana (*Pristimantis sp.* “Guianas” East), the Maroni River separating these two groups of genetically divergent populations. The taxonomic status of this group of populations needs to be clarified when additional material becomes available. In French Guiana, *P. sp.* “Guianas” East occurs throughout the territory except the Approuague-Oyapock interfluvium and is probably absent from northern Amapá state in Brazil. This pattern of distribution strikingly mirrors that of *Anomaloglossus surinamensis* (Vacher et al., 2017) and *Pipa aspera* (Vacher et al., 2020), both species displaying similar geographical boundaries and deep genetic structures along the Maroni River. Interestingly, *Pristimantis sp.* “Guianas” East only overlaps with *P. cf. marmoratus* (*Pristimantis sp.* 1) in the southern half of French Guiana. Likewise, the distribution of *A. surinamensis* only weakly overlaps with that of *A. blanci* (Fouquet et al., 2018). Both are pairs of sister species with similar ecology and body size.

Pristimantis crepitaculus sp. nov.

Pristimantis marmoratus Lescure & Marty, 2000

Pristimantis marmoratus Fouquet et al., 2007

Pristimantis marmoratus Dewynter et al., 2008

Pristimantis marmoratus Fouquet et al., 2012

Pristimantis sp. 1 Fouquet et al., 2013
Pristimantis sp. 1 Kok et al., 2018
Pristimantis sp. 1 Fouquet et al., 2019
Pristimantis cf. *marmoratus* Vacher et al., 2020

Holotype. MNHN-RA-2020.0102 (field no. AF2786), an adult male, collected by Antoine Fouquet, Maël Dewynter & Nicolas Vidal on 26 February 2015 at Mitaraka, French Guiana (2.2358 N 54.4493 W, ~200 m asl; Fig. 5).

Paratypes. Twenty-eight specimens (18 males and three females) from French Guiana and the state of Amapá, Brazil: MNHN-RA-2020.0092–0112; MPEG 41819–41825 (Appendix 2).

Etymology. The specific epithet is a latinised adjective referring to the call structure of the new species, which sounds like a rattle (*crepitaculum*).

Definition. The new species is characterized by the following unique combination of characters: (1) SVL small, adult males 17.0 ± 0.8 mm (range 15.7–18.3 mm, $n=11$) and adult females 23.4 ± 0.5 mm (range 22.9–23.9 mm, $n=3$) (Table 1); (2) dorsal skin tuberculate, two pairs of enlarged tubercles on the scapular region embedded in a W-shaped scapular fold, ventral skin granular particularly on the femoral region; (3) tympanum visible, tympanic membrane not or only poorly differentiated, tympanic annulus partially visible externally obscured by supratympanic fold on the posterodorsal edge of tympanum, tympanum c.a. 1/3 of eye length; (4) pharyngeal ostia present; (5) columella present; (6) tibia length 48–54% of SVL; (7) snout broadly rounded in profile and slightly acuminate in dorsal view; (8) each upper eyelid with two prominent tubercles; (9) choanae round and small (0.5 mm for the holotype), dentigerous processes of vomers oblique, narrowly separated, each bearing 2–4 small odontophores; (10) vocal slits present, vocal sac median, subgular; (11) one unpigmented whitish nuptial pad located on the preaxial side of the thenar tubercle on each thumb in male; (12) FI slightly shorter than FII, reaching disc of FII; (13) fingers without lateral fringes; (14) finger discs broadly expanded, elliptical, thenar tubercle ovoid, palmar tubercle ill-defined; (15) three enlarged ulnar tubercles often flat and barely visible; (16) axillary tubercles (sensu Myers & Donnelly, 2001) absent; (17) small tarsal tubercles present; (18) toes without lateral fringes but with weak lateral keels, webbing rudimentary basal between TII–V; (19) calcars absent, inner metatarsal tubercle oval, much larger than the round outer tubercle; (20) dorsal colouration highly variable from greenish to brownish with various patterns, ventral colouration light grey with small black spots denser on throat and legs; (21) iris reddish to copper with a darker horizontal band and a black vertical streak; (22) posterior surface of thighs and groin dark grey in life and brown in preservative, lack of yellow circumscribed spot on groin; (23) anterior surface of arms, posterior surface of flanks and dorsal surface of thighs often yellow in reproductive males; (24) advertisement

call characterized by series (0.50–0.75 s long) of 6–12 very short notes (0.02–0.05 s long) with a dominant frequency ranging between 3.2–3.6 kHz and emitted every 5.4–8.6 s; (25) male calling activity exclusively crepuscular, usually upside down on tree trunks of low diameter.

Morphological comparisons with other Guiana Shield lowlands *Pristimantis* of the “*unistrigatus* group”. *Pristimantis crepitaculus* sp. nov. can mainly be distinguished from *P. espedeus* by its smaller body size (SVL range in males = 15.7–18.3 mm vs. 20.7–24.8 in *P. espedeus*); dark grey groin colouration in life (vs. reddish in *P. espedeus*); and advertisement call composed of more notes and higher dominant frequency (> 6 notes and > 3.1 kHz).

Pristimantis crepitaculus sp. nov. can mainly be distinguished from *P. inguinalis* by dark grey groin colouration in life (vs. bright yellow inguinal mark in *P. inguinalis*); light grey ventral colouration with small black spots (vs. entirely black in *P. inguinalis*); and advertisement call composed of series of notes (vs a single note in *P. inguinalis*).

Pristimantis crepitaculus sp. nov. can mainly be distinguished from *P. grandoculis* by visible tympanum (external tympanum absent in *P. grandoculis*); more tuberculate dorsal skin; enlarged tubercles on eyelids being equally distant from the eye (vs. posterior tubercles closer to the eye in *P. grandoculis*); fingers and toes without fringes (fringed in *P. grandoculis*), smaller tibia length (48–54% of SVL vs. 58–60%); and presence of vocal slits in males (absent in *P. grandoculis*).

All the other species of the *unistrigatus* group known from the Guiana Shield occur in the Pantepui region and are generally associated with highlands (i.e. > 700 m elevation; Fouquet et al., 2013; Kok et al., 2018). One of these Pantepui species, *P. marmoratus*, is possibly its closest relative. *Pristimantis crepitaculus* sp. nov. can mainly be distinguished from *P. marmoratus* by its fingers and toes without fringes (fringes present in *P. marmoratus*) and its advertisement call composed of a series of notes (vs. a single note in *P. marmoratus*). Among the other *Pristimantis* species found at mid-elevation in Pantepui, *P. crepitaculus* sp. nov. can mainly be distinguished from *P. jester* (Means & Savage, 2007) by the presence of a tympanum (absent in *P. jester*), from *P. saltissimus* (Means & Savage, 2007) by iris colour in life (black vertical streak running across the iris in *P. crepitaculus* vs. no such streak in *P. saltissimus*), from *P. guaiquinimensis* (Schlüter & Rödder, 2007) by its smaller body size (females 32.4–33.6 mm in *P. guaiquinimensis* [see Kok & Barrio-Amorós, 2013] vs. 22.9–23.9 mm in *P. crepitaculus* sp. nov.), a distinct tympanum (weakly distinct in *Pristimantis crepitaculus* sp. nov.), from *P. sarisarinama* (Barrio-Amorós & Brewer-Carías, 2008) by iris colour in life (black vertical streak running across the iris in *P. crepitaculus* sp. nov. vs. no such streak in *P. sarisarinama*), and distinct vocalization (1–2, rarely 3 notes in *P. sarisarinama*

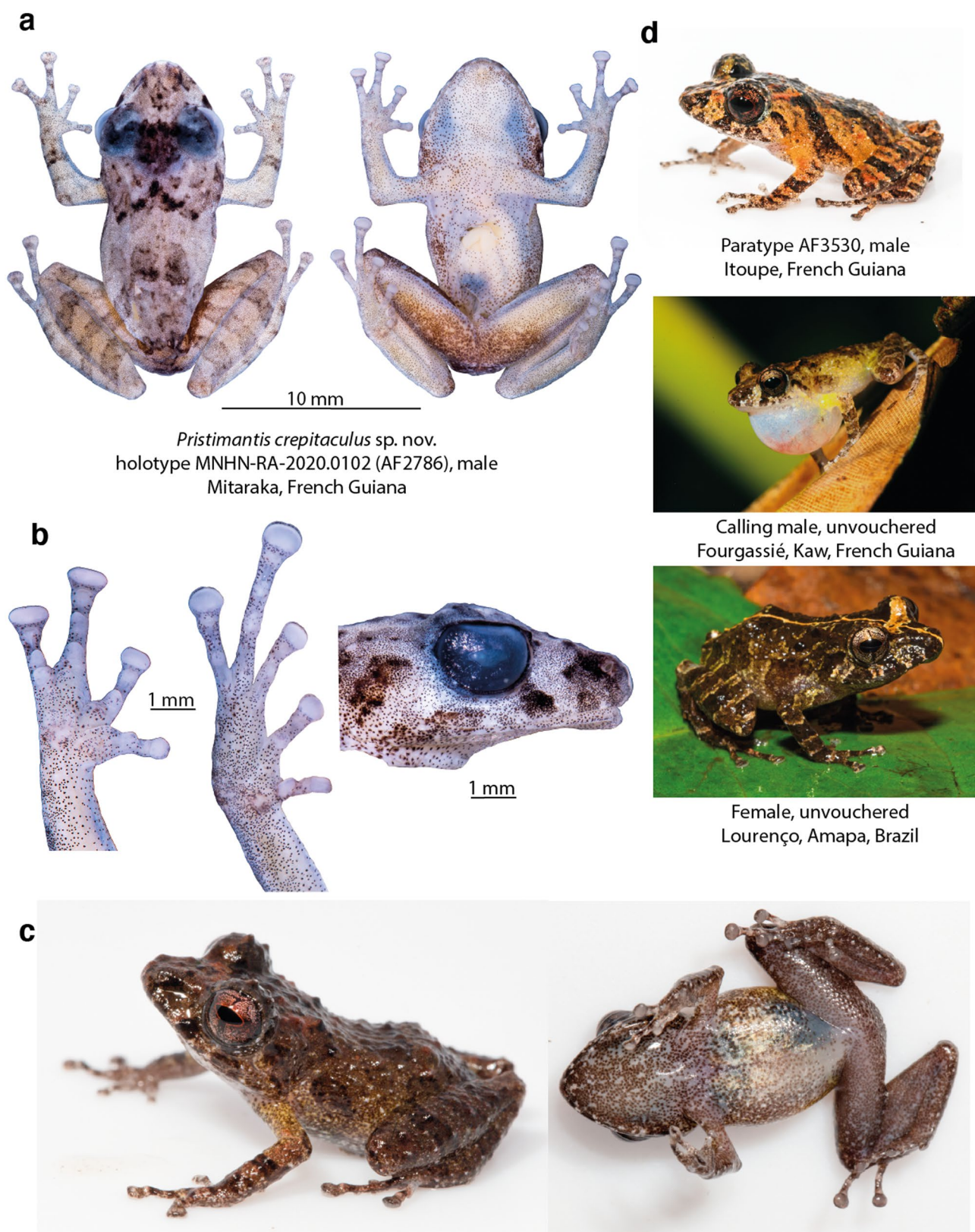


Fig. 5 **a** Holotype of *Pristimantis crepitaculus* sp. nov. in dorsal, ventral views. **b** Hand, foot and lateral view of the head. **c** Photographs of the holotype in life. **d** Several photographs of additional specimens in life

vs. 6–12 notes in *P. crepitaculus* sp. nov.), from *P. pulvinatus* (Rivero, 1968) by its smaller body size (males 23.0–26.1 mm in *P. pulvinatus* vs. 15.7–18.3 mm in *P. crepitaculus* sp. nov.) and distinct vomerine teeth (indistinct or absent in *P. pulvinatus*), from *P. memorans* (Myers & Donnelly, 1997) by iris colour in life (black vertical streak running across the iris in *P. crepitaculus* sp. nov. vs. no such streak in *P. memorans*), a shorter inter-note interval (0.05–0.12 s in *P. crepitaculus* sp. nov. vs. 0.20–0.29 s in *P. memorans*), and by the posterior thigh surface being dark grey in life (vs. blackish with yellow flecking in *P. memorans*).

Description of the Holotype. An adult male, SVL 15.8 mm. Head only slightly longer than wide, widest at corner of the mouth; snout slightly acuminate in dorsal and round in lateral views; canthus rostralis distinctly concave; nostrils nearly elliptical, directed almost completely laterally; interorbital region flat, loreal area slightly concave. Eyes large and protuberant, directed laterally, diameter of eyes much larger than tympanum diameter ($ED/TD = 3.0$), pupil elliptical. Supratympanic fold slightly distinct; tympanum small, ovoid, tympanic membrane completely covered by skin, but tympanic annulus distinct anteriorly and ventrally, covered by the *M. depressor mandibulae* posteriorly and dorsally. Vocal sac present, single, subgular, extending towards pectoral region between forearms. Choanae small (0.5 mm), round, not concealed by palatal shelf, larger than vomerine odontophores; a pair of small vomerine odontophores present; tongue ovoid, posteriorly free; vocal slits present, extending diagonally from lateral base of tongue to almost to the angle of the jaw.

Arms slender, not hypertrophied; lateral margins of arm and forearm free of fringes, folds, but with three tubercles; finger discs elliptical, expanded in all fingers, disc on FI the smallest, on FIII the largest; relative lengths of fingers $I < II < IV < III$; subarticular tubercles round, narrower than finger width; fringes absent on all fingers. Subarticular tubercles present on all fingers, one on FI and FI, two on FIII and FIV; all subarticular tubercles round and about the same size; inner metacarpal (thenar) tubercle present, oval; outer metacarpal tubercle large, W-shaped, ill-defined. Webbing between fingers absent.

Legs relatively long and slender, with rows of large and flat tubercles on tarsus and postaxially on foot (but lacking fringes or folds). All toes well developed, with expanded, elliptical, medium sized discs; discs on TIV and TV the largest, those on TI and TII the smallest; relative lengths of toes $I < II < III < V < IV$. Toes lacking fringes. Subarticular tubercles present on all toes; one tubercle present on TI, TII, and TV, two tubercles on TIII, three on TIV; all subarticular tubercles round, similar in size. Inner metatarsal tubercle oval; outer metatarsal tubercle small, round.

Skin on dorsum, head, dorsal surfaces of limbs, flanks, and groin tuberculate with enlarged tubercles on the scapular

region and on eyelids, posterior surface of the dorsum, and dorsal surface of hindlimbs. Skin on the gular region smooth; chest, belly and undersurfaces of limbs granular. Cloacal opening directed posteriorly; cloacal region lacking tubercles.

Colour of holotype in life. Dorsal colour dark brown with V-shaped black band on the scapular region, a large middorsal black blotch and an ill-defined black blotch near groin (Fig. 5). Black bands and blotches located in the interorbital region, on the loreal region, the nasal region, below the eyes and the tympanic region. Interorbital region and V-shaped scapular mark delimited anteriorly by reddish bands. Lower flank as dorsum with a black blotch. Axillary region and upper arm yellow. Lower arm as dorsum with two black transversal bands. Dorsal colouration of legs as dorsum with four black transversal bars on thigh, four on tibia and three on tarsus. Throat background grey covered with minute black melanophores; belly skin grey covered with small cream spots and by black melanophores that become sparse near groin; ventral surfaces of thighs and arms as throat. Iris with copper metallic pigmentation and pupil ring interrupted dorsally and ventrally by transversal pigmentation (Fig. 5).

Colour of holotype in preservative. After four years in 70% ethanol, colours of the specimen faded, notably glandular supracarpal pad and throat pigmentation (Fig. 5). The snout is dorsally dark brown and well-delimited by a transversal light grey interorbital band extending on half of the eyelids. Posteriorly, the interorbital region is covered by a dark brown band. A V-shaped dark brown mark is well-defined on the scapular region posteriorly followed by two oblique traversal dark brown bands. Similar, transversal dark brown bands are present on the arms, hands and legs and feet (for more details see Fig. 5a).

Variation in the type series. Proportions vary little among the 21 paratypes. Males are smaller than females (15.7–18.3 mm vs. 22.9–23.9). The amount of tuberculation on the skin varies, especially on the dorsum and flanks. Outer metatarsal tubercle is always present, but its size/visibility vary among specimens.

Colour pattern is highly variable among specimens and several patterns are observed. A pattern similar to the holotype (middorsal and interorbital bands) is present in female MNHN-RA-2020.0104 and in males MNHN-RA-2020.0110 and MPEG 41821. A white band between the anterior corner of the eyes is present in most individuals but some specimens have less conspicuous markings (e.g. MNHN-RA-2020.0102, MNHN-RA-2020.0107). The scapular V-shaped mark is light grey in a few specimens (MNHN-RA-2020.0101, MNHN-RA-2020.094) or reddish (MNHN-RA-2020.0102, MNHN-RA-2020.0109) and display brightly coloured upper arms and posterior portions of flanks in life. Two specimens (MNHN-RA-2020.0098 and

MPEG 41825) have a large well-defined cream spot on top of the snout and another one (MNHN-RA-2020.0100) has a light brown scapular mark posteriorly prolonged along the back forming a Y-shaped pattern delimited by darker flanks. Two specimens, one male (MPEG 41823) and one female (MPEG 41821) have large cream blotches on the dorsum.

Osteology of the holotype (MNHN-RA-2020.0102).
Cranium (Fig. 6). *Shape and proportions.* The skull is widest posterior to the orbit at the level of the articulation of the maxilla with the quadratojugal. The rostrum is moderate, the braincase is broad.

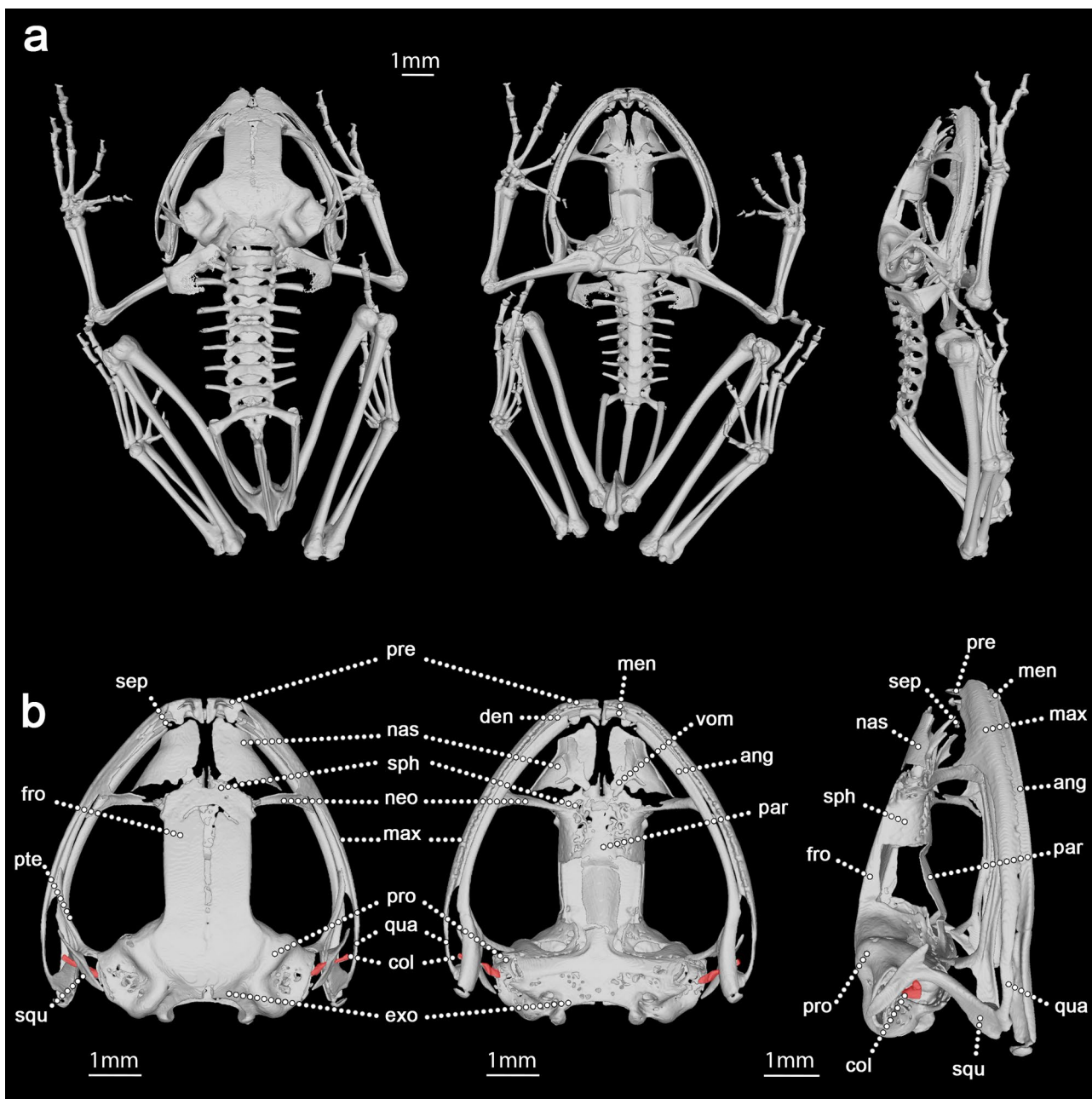


Fig. 6 Volumetric renderings of μ -CT scans of the skeleton of the holotype of *Pristimantis crepitaculus* (MNHN-RA-2020.0102). **a** Full skeleton in dorsal (left), ventral (middle), and lateral (right) views. **b** Skull in dorsal (left), ventral (middle), and lateral (right) views. Columnellae are highlighted in red. Abbreviations: ang—angulosplenic,

col—columnella, den—dentary, exo—exoccipital, fro—frontal, max—maxillary, men—mentomeckelian, nas—nasal, neo—neopalatine, par—parasphenoid, pre—premaxillary, pro—prootic, pte—pterygoid, qua—quadratojugal, sep—septomaxilla, sph—sphenethmoid, squ—squamosal, vom—vomer

Neurocranium and dorsal investing bones. The nasals are broadly separated from one another and from the sphenethmoid; they cover most of the nasal capsules dorsally. The frontoparietals are well developed, co-ossified with the sphenethmoid. Frontoparietal crests are absent and the frontoparietal fontanelle (T-shaped) is exposed. The parasphenoid and neopalatines are co-ossified with the sphenethmoid. The frontoparietal and prootic are fused. Ventrally, the prootics are fused with the parasphenoid alae. The exoccipitals are fused. The dorsal surface of the otic capsule is mostly ossified. The septomaxilla is roughly spiralled, the medial ramus extending posterodorsal to the posterior ramus; the anterior ramus is thick; the lateral ramus is oblique with a long acuminate posterolateral extension; the posterior ramus extends from the middle of the lateral ramus ventromedially. The columellae (stapes) are well ossified, formed by the synostotic fusion of the long, thin pars media plectri (stylus) and the pars interna plectri (baseplate), which is curved.

Ventral investing bones. The parasphenoid cultriform process extends anteriorly from the anterior edge of the otic capsule and is co-ossified with the sphenethmoid. The parasphenoid alae are moderately long (about half of the length of the cultriform process), perpendicular to the anteroposterior body axis, broadening slightly laterally. The vomers are in narrow contact with the sphenethmoid; each vomer is composed of an arcuate bone bordering the anteromedial, medial, and posterior margins of the choana. The prechoanal ramus is expanded medially and anteriorly and bears a ventral flange along its medial edge. The postchoanal process is narrow and acuminate, slightly anteriorly curved. Well-developed dentigerous processes extend posteromedially from the union of the pre- and postchoanal processes, left process bears two small odontophores. Each dentigerous process is broadly separated from its counterpart medially. The neopalatine is narrowly in contact with the maxilla distally. This complex is fused with the parasphenoid medially.

Maxillary arcade. The maxillary arcade bears many small teeth on the premaxilla and maxilla. The arcade is complete and connected to the slender quadratojugal. The premaxillae are separated medially, and their anterodorsal alary process is weakly divergent from the midline. The pars palatina is broad, with two well-defined processes: the medial (palatine) process is relatively narrow and runs roughly parallel toward its contralateral; the lateral process is broader. The premaxilla and maxilla are in lateral contact via a simple juxtaposition. The maxilla is long, with a broad pars palatina along its lingual margin and a moderately developed pars facialis.

Suspensory apparatus. The triradiate pterygoid bears a slightly curved anterior ramus with a sculpted ventrolateral face, oriented anterolaterally toward the maxilla, with which it articulates at approximately the mid-length of the orbit. This pterygoid is fused to the maxilla. The medial

and posterior face of the medial rami of the pterygoid are about equal in length. The medial ramus is broader than the posterior and its posterior face is strongly sculpted. The lateral end of the medial ramus overlaps the lateral edge of the prootic. The quadratojugal is long, laterally curved, and slender, articulating anteriorly with the maxilla. It has a bulbous posteroventral process and articulates dorsally with the ventral ramus of the squamosal. The squamosal is dorsally bifurcated, broad, and sculpted, extending anterodorsomedially from the quadratojugal to the level of the otic capsule; the zygomatic ramus is very short, whereas the otic ramus is long, almost reaching the posterior end of the skull.

Mandible. The mandible is slim and edentate. The mentomeckelians are small and arcuate in ventral view, medially and laterally broadened, and medially separated. The dentary is short and thin, posteriorly acuminate, and overlaps the angulosplenial for about a quarter of its length. Dentary is not in contact with the angulosplenial posteriorly. The angulosplenial is long and arcuate, laterally slightly grooved. The coronoid process is weak.

Hyoid. The bony posteromedial processes of the hyoid are expanded proximally and separated from one another. No ossified parahyoid is present.

Axial skeleton (Fig. 6).

Vertebral column. The vertebral column has eight procoelous, presacral vertebrae. The vertebrae have complete neural arches and low neural processes. Atlas (presacral I) and presacral II are fused medially and laterally. The transverse processes of presacrals II–III are slightly expanded distally, thicker, and broader than those of other presacrals. The transverse processes of presacrals II and III are oriented ventrolaterally (II anteriorly, III slightly posteriorly), whereas those of presacrals IV–VIII extend dorsolaterally (IV–V posteriorly, VI–VIII anteriorly). The relative lengths of the transverse processes and sacral diapophyses are: Sacrum > III > IV > V \approx VI \approx VII \approx VIII > II. The sacral diapophyses are slightly expanded distally. The urostyle has a well-developed dorsal ridge that extends along most of its length.

Pectoral girdle. The zonal portion has well-ossified coracoids, clavicles, scapulae, and cleithra. The clavicles are long, slender, and oriented anteromedially; the medial tips are in contact and located anteriorly from the level of anterolateral end of the clavicle that articulates with the scapula; the coracoid is long and flared, with its sternal end slightly broader than its glenoid end. The coracoids overlap medially. The scapula is long with a prominent pars acromialis that is not separated from the pars glenoidalis. The scapula is about one and a half the length of the clavicle. The cleithrum is ossified, well-developed, anteriorly thicker, thinning posteriorly. The suprascapula is unossified.

Pelvis girdle. The long, slender iliac shafts bear dorsolateral crests throughout their length. The overall length of the

girdle is more than two times the width between the anterior ends of the iliac shafts. The iliac prominence is broad and low, and pubes mineralized.

Manus and pes. The phalangeal formulae for the hand and foot are standard, 2–2–3–3 and 2–2–3–4–3, respectively. Terminal phalanges strongly T-shaped. Ossified prepollex and prehallux visible.

Advertisement call. Six specimens calling from the underwood vegetation were recorded from about 2 m away at air temperatures between 23–25 °C and 90–100% relative humidity. Descriptive statistics of call parameters are presented in Table 2. *Pristimantis crepitaculus* sp. nov. emits every 7.04 s on average (range 5.44–8.62) series (call length mean = 0.59, range 0.50–0.75 s) of 6–12 short notes (note length mean = 0.004 s; range 0.003–0.006 s). These notes are emitted with increasing inter-note intervals within the call (mean 1st interval = 0.068 s; range 0.054–0.085 s; mean 2nd interval = 0.102 s; range 0.078–0.125 s). The notes have a clear harmonic structure (i.e. with extensive amount of energy in the harmonics). The dominant frequency is 3.50 kHz on average (range 3.16–3.91 kHz) with a slight upward modulation within the call (ca. 0.2 kHz) (Fig. 7, Table 2).

Natural history. *Pristimantis crepitaculus* sp. nov. is a scansorial species. Males were found calling perched on low vegetation (0.5–2.0 m above the ground). Calling activity was limited to a short period (about 1 h) at dawn and early night. Calling, males often adopt a position head down along the trunks, small twigs, or leaves. They form groups of 2–10 males usually spaced by at least 2 m between individuals. Juveniles and females are very rarely found, but at least one female (MPEG 41825) was collected very close to a calling male (MPEG 41824, calling from a leaf at about 2 m above ground). The species inhabits *terra firme* forests from 50 to 700 m asl and seems to particularly thrive near ecotones, such as tree falls, clear-cuts, roads, rivers, maybe because the penetrating light allows denser understory cover and thus more abundant calling sites.

Distribution. The species is apparently endemic to the easternmost part of the Guiana Shield lowlands, i.e. throughout the Amapá state of Brazil and French Guiana (at the exception of the northwest part of the territory). It occurs in the upper Maroni region, which corresponds to the border with Suriname, and probably extends at least in southeastern Suriname, like other species that are also endemic to the easternmost part of the Guiana Shield (e.g. *Amazophrynella*

teko, *Boana dentei*, *Pristimantis gutturalis*). However, it is unlikely that the range of *P. crepitaculus* sp. nov. extends to the Coppename river.

Discussion

Species diversity, endemism, and biogeography of the Eastern Guiana Shield

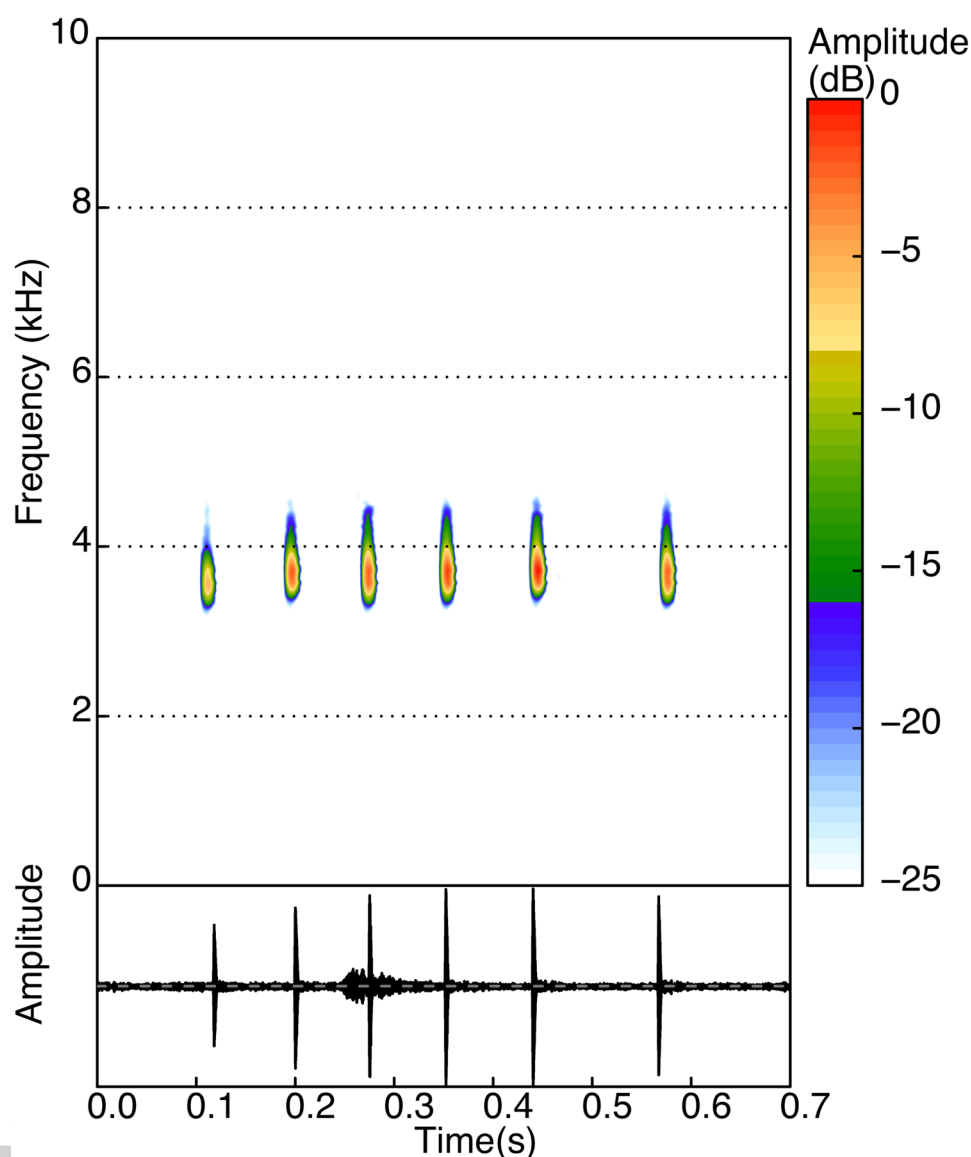
As a further step from Kok et al. (2018), the present study clarifies the understanding of the megadiverse genus *Pristimantis* in the Guiana Shield, and of overall anuran diversity pattern in the region. Many anuran species remain to be described and named in Amazonia and notably in the Guiana Shield region, as suggested by almost all studies exploring particular groups (e.g. Gehara et al., 2014; Fouquet et al., 2015; Kok et al., 2017; Jaramillo et al., 2020) and molecular diversity (Vacher et al., 2020). The fact that many Amazonian frog species are circumscribed to particular and often relatively small subregions within Amazonia is progressively unveiling as taxonomic progresses are being made. Vacher et al. (2020) notably identified three bioregions within the Guiana Shield, one in the easternmost part, one in the southern part, and one in the western part. The distributions of *P. espedeus*, *P. crepitaculus*, *P. sp.* “Guianas” East, and *P. grandoculis* in the eastern portion, of *P. cf. ockendeni* in the southern, and of *P. marmoratus*, *P. pulvinatus*, and *P. saltissimus* in the western portions strongly corroborate this pattern. The determining factors of this pattern remain ambiguous, but probably originate from both historical climatic and landscape changes and current bioclimatic heterogeneity, notably the fact that the easternmost part of the Guiana notably receives more precipitation seasonally than other parts of the region (Silva et al., 2018; Vacher et al., 2020) (Table 3).

A few lineages remain to be investigated for a better understanding of their taxonomic status, such as *Pristimantis* sp. “Guianas” East and the five lineages forming what we call a “trans-amazon complex” (*P. cf. ockendeni*). These candidate species require a thorough and integrative systematic review. Although *P. grandoculis* and *P. sp.* “Guianas” East are morphologically very similar (the latter also lacking a columella and external tympanum, see Fig. 8), the degree of divergence on the 16S fragment that we used is >4% suggesting that these groups of populations may correspond to

Table 2 Acoustic variables

		Call length	Inter-call	Note length	Inter-note 1	Inter-note 2	Dom. Freq	Nb notes
<i>P. crepitaculus</i> sp. nov.	Mean (n = 6)	0.586	7.038	0.004	0.068	0.109	3497	7.9
	Min	0.504	5.440	0.003	0.054	0.078	3163	6
	Max	0.752	8.623	0.006	0.085	0.125	3908	12

Fig. 7 Sonograms and oscillograms on a 0.7-s window of a characteristic call of *Pristimantis crepitaculus* sp. nov. from Oiapoque, Amapá, Brazil (paratype, MPEG 41823)



distinct species (Fouquet et al., 2007; Vieites et al., 2009). However, the lack of acoustic data and the low number of available specimens from Suriname so far hamper any taxonomic decision about *P.* sp. “Guianas” East. *Pristimantis* diversity in the Pantepui region also requires further investigation, as notably illustrated by candidate species from La Neblina, Mount Ayanganna, Mount Wokomung (B. Means, pers. comm.). Probably many more yet undocumented isolated lineages occur in poorly explored areas of Pantepui, including isolated tepui summits. A larger-scaled phylogenetic investigation is needed to test whether a Guiana Shield clade of *Pristimantis* might have diversified in situ. A few groups have been documented to have extensively diversified throughout the Guiana Shield lowlands and highlands such as *Anomaloglossus* (Vacher et al., 2017), and *Otophryne* (Fouquet et al., 2021). These cases are nonetheless relatively rare since most lowland amphibians have diversified

throughout Amazonia. The *Pristimantis* species belonging to the “*unistrigatus* group” could represent an additional case of Guiana Shield restricted clade, whose monophyly and timing of diversification would be worth investigating.

The case of the “trans-amazon complex” (*P.* cf. *ockendeni*) is definitively no less complex. It is most certainly a lineage apart from the other species of the Guiana Shield that most likely originated from western Amazonian ancestors and secondarily dispersed to the Guiana Shield across the Amazon River. Similar and possibly concomitant trans-Amazon dispersals are documented in *Allobates* (*A.* aff. *tapajos* Réjaud et al., 2020) and *Boana* (*Boana* gr. *albopunctata* Fouquet et al., 2021), *Synapturanus* (Fouquet et al., 2021), *Scinax* (Ferrão et al., 2016). From 9 million years ago (Ma) onwards, the Amazon basin has been draining eastward into the Atlantic Ocean and the Amazon River was forming a barrier for South-North dispersal around

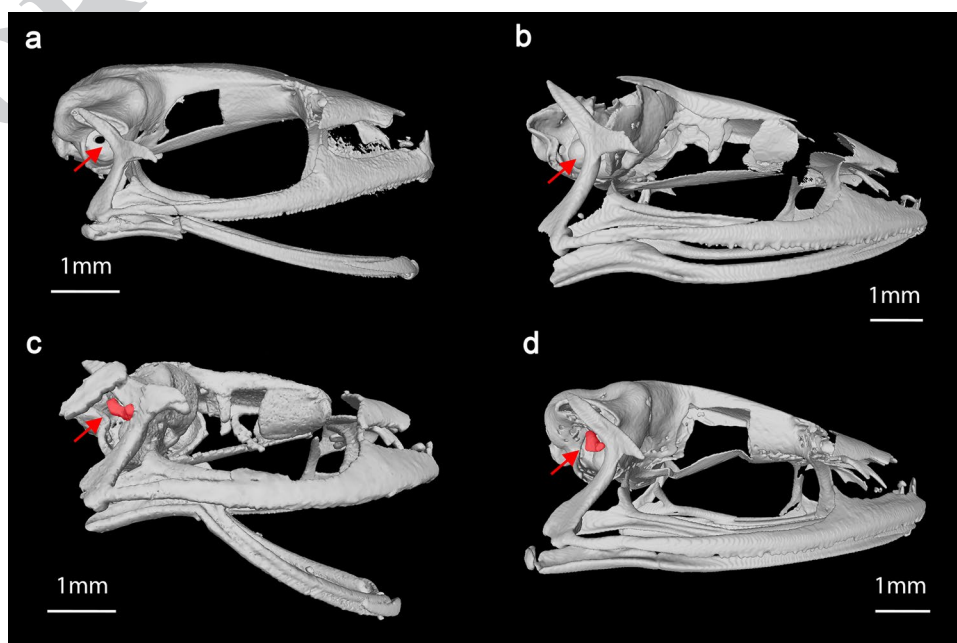
Table 3 Mean pairwise *p* distance

<i>P. crepitaculus</i> sp. nov.																				
<i>P. marmoratus</i>	0.116																			
<i>P. grandoculis</i>	0.126	0.118																		
<i>P. sp</i> “Guianas” East	0.123	0.120	0.045																	
<i>P. cf. ockendeni</i>	0.207	0.202	0.184	0.184																
<i>P. cf. ockendeni</i> Abacaxis 2	0.183	0.184	0.168	0.168	0.054															
<i>P. cf. ockendeni</i> PA	0.187	0.193	0.167	0.171	0.061	0.061														
<i>P. cf. ockendeni</i> RO, AM	0.201	0.193	0.177	0.173	0.073	0.074	0.045													
<i>P. cf. ockendeni</i> Abacaxis 1	0.185	0.180	0.164	0.165	0.073	0.071	0.047	0.054												
<i>P. abakapa</i>	0.106	0.080	0.096	0.088	0.184	0.167	0.172	0.168	0.152											
<i>P. imthurni</i>	0.112	0.087	0.097	0.088	0.184	0.167	0.176	0.176	0.158	0.036										
<i>P. jamescameroni</i>	0.107	0.089	0.098	0.087	0.186	0.169	0.171	0.165	0.147	0.026	0.023									
<i>P. pulvinatus</i>	0.112	0.099	0.102	0.099	0.180	0.165	0.167	0.174	0.161	0.063	0.068	0.060								
<i>P. aureoventris</i>	0.108	0.082	0.102	0.086	0.189	0.167	0.175	0.181	0.165	0.053	0.058	0.060	0.063							
<i>P. yuruaensis</i>	0.117	0.082	0.100	0.083	0.190	0.168	0.179	0.181	0.165	0.053	0.055	0.058	0.059	0.015						
<i>P. inguinalis</i>	0.138	0.121	0.137	0.131	0.187	0.178	0.179	0.180	0.151	0.094	0.110	0.101	0.116	0.107	0.115					
<i>P. saltissimus</i>	0.123	0.115	0.126	0.108	0.207	0.179	0.198	0.198	0.186	0.075	0.082	0.077	0.077	0.059	0.053	0.133				
<i>P. jester</i>	0.130	0.099	0.101	0.093	0.186	0.169	0.175	0.179	0.163	0.070	0.067	0.072	0.074	0.042	0.043	0.120	0.077			
<i>P. sp.</i> “Ayanganna”	0.120	0.079	0.109	0.099	0.195	0.173	0.186	0.191	0.175	0.065	0.070	0.072	0.067	0.038	0.041	0.115	0.067	0.060		
<i>P. espedeus</i>	0.138	0.121	0.139	0.142	0.199	0.179	0.187	0.197	0.178	0.110	0.131	0.121	0.111	0.111	0.116	0.137	0.129	0.133	0.114	
<i>P. sp.</i> “Neblina 1”	0.129	0.095	0.116	0.100	0.185	0.164	0.176	0.182	0.164	0.077	0.079	0.079	0.069	0.059	0.051	0.119	0.083	0.077	0.064	0.114
<i>P. sp.</i> “Neblina 2”	0.131	0.116	0.119	0.115	0.184	0.170	0.168	0.185	0.177	0.077	0.077	0.083	0.089	0.072	0.072	0.120	0.097	0.089	0.089	0.140
																				0.085

5 Ma. The processes that may have fostered multiple trans-Amazon dispersals around 5 Ma remain highly speculative. Considerable uncertainty remains about the timing and amplitude of historical topographic, hydrological, and vegetational changes in Amazonia (Albert et al., 2018; Bicudo et al., 2019; Hoorn et al., 2017; Latrubesse et al., 2010). The sediment discharge in the Amazon fan was relatively modest until 5 Ma and vastly increased in the Pliocene–Pleistocene

(Hoorn et al., 2017; Alberts et al., 2018). The lower course of the Amazon River may have become an impassable barrier for these taxa only from the Miocene–Pliocene boundary onward. Moreover, this period also coincides with vegetational and climatic changes, notably the expansion of grasslands not only in the Andes and the Cerrado but also within Amazonia (Kirschner & Hoorn, 2019).

Fig. 8 Volumetric renderings of μ -CT scans of the skull (in lateral view) of the holotype of *Pristimantis grandoculis* (a; RMNH 4467), a specimen of *P. grandoculis* from Suriname (b; MNHN-RA-2020.0118), the holotype of *P. marmoratus* (c; BMNH 1947.2.16.92), and the holotype of *P. crepitaculus* sp. nov. (d; MNHN-RA-2020.0102). Absence/presence of columellae (highlighted in red) is pointed by a red arrow



1082 Osteological comparisons

1083 At this stage, comprehensive osteological comparisons
 1084 among species in the “*unistrigatus* group” are impossible
 1085 due to the paucity of data, as the osteology of most of these
 1086 species has not been described or illustrated. However, our
 1087 osteological investigation of the holotypes of *P. marmoratus*
 1088 and *P. grandoculis* unambiguously confirms the non-
 1089 conspecificity of these taxa. The main diagnostic osteo-
 1090 logical characters are the lack of a columella and a more
 1091 ossified skull in *P. grandoculis* (Figs. 4, 6 and 8). The skull
 1092 of MNHN-RA-2020.0118 is, however, poorly ossified, which
 1093 could be an artefact of preservation as suggested by the lack
 1094 of ossification of the brain case for instance. The skull of the
 1095 holotype of *P. grandoculis*, although that specimen was col-
 1096 lected in 1904, is still strongly ossified. Unfortunately, further
 1097 comparisons with the holotype of *P. marmoratus* are made
 1098 difficult by the poor quality of the μ -CT scans, and we refrain
 1099 to describe its osteology until more μ -CT scans of additional
 1100 specimens of *P. marmoratus* sensu stricto are available. Spa-
 1101 tial distribution, external morphology, and osteological data
 1102 converge in suggesting the conspecificity of the populations
 1103 previously identified as *P. sp.* “Guianas” from Suriname and
 1104 *P. grandoculis*. The absence of a columella in *P. grandoculis*
 1105 is in line with the absence of vocal slit, pharyngeal ostia,
 1106 and calling activity in that species (see below). The sister
 1107 species (population from French Guiana) also lacks a colu-
 1108 mella and external tympanum. A complete investigation of
 1109 the osteology of the “*unistrigatus* group” would certainly be
 1110 of taxonomic/evolutionary interest.

1111 Vertical niche partitioning among species 1112 and related traits on limbs

1113 Juveniles, females, and amplexant pairs of *Pristimantis* sp.
 1114 “Guianas” East (sister to *P. grandoculis*) are often found on the
 1115 leaf litter, suggesting that the reproduction takes place directly
 1116 either on the ground or at low height in the vegetation. In con-
 1117 trast, females of *P. crepitaculus*, *P. espedeus*, *P. inguinalis* and
 1118 *P. cf. ockendeni* are rarely seen. Males of *Pristimantis* sp. “Gui-
 1119 anas” East are also found on the ground but more frequently
 1120 perched at low height in the underwood at night. However,
 1121 juveniles of *P. espedeus* are also frequently seen on the ground
 1122 as are juveniles of *Pristimantis* sp. “Guianas” East, but during
 1123 the day. Small-bodied, terrestrial, and nocturnal anurans are
 1124 very rare (Pough & Magnusson, 1992), possibly because preda-
 1125 tors such as spiders are very abundant in the leaf litter at night
 1126 (Magnusson, 2016). Among the species of the “*unistrigatus*
 1127 group” occurring in the Guiana Shield lowlands, *Pristimantis*
 1128 *grandoculis* and *P. sp.* “Guianas” East can be considered as
 1129 the lowest in terms of vertical partitioning. Vertical niche par-
 1130 titioning in *Pristimantis* has already been described notably
 1131 in western Ecuador (Lynch & Duellman, 1997; Guyasamin &

Funk, 2009) and in *Pristimantis*, *Craugastor*, and *Diasporus* in
 Costa Rica (Miyamoto, 1982). These converging observations
 strengthen the idea that vertical partitioning among *Pristimantis*
 species is frequent, even at low elevations such as in the Ama-
 zonian lowlands, and may even play a direct role in speciation. **AQ4** 6

It is noteworthy that *Pristimantis grandoculis* and *P. sp.*
 “Guianas” East have longer limbs (TL, TiL, FL) and more
 terrestrial habits than scansorial *P. crepitaculus*, *P. cf. ock-*
endeni and arboreal *P. inguinalis* and *P. espedeus*, species.
 These differences in limb proportions may be related to
 jumping ability (Citadini et al., 2018; Emerson, 1985; Zug,
 1972). We hypothesize that long distance jumping perfor-
 mance may be selected in a leaf litter and scansorial environ-
 ment which is relatively free of obstacles and that may be
 risky because predators are abundant in the leaf litter (Pough
 & Magnusson, 1992), whereas scansorial and arboreal spe-
 cies require less power but more agility in dense vegetation. **AQ5** 8

Lack of ear and of calling activity

Males of *P. grandoculis* and *P. sp.* “Guianas” East were
 often found perched on the vegetation in a position sug-
 gesting calling activity. However, acoustic activity has never
 been heard in that clade, neither in Suriname nor in French
 Guiana (despite being locally abundant), and these are the
 only species in the Guiana Shield lowlands with unknown
 call. Moreover, tympanum, columella, pharyngeal ostia,
 and vocal slits are all absent in that clade. These observa-
 tions suggest that *P. grandoculis* may be both deaf and mute.
 The loss of hearing structures has occurred multiple times
 throughout the evolutionary history of anurans (Jaslow
 et al., 1988; Boistel et al., 2013; Pereyra et al., 2016). It is
 particularly common in Bufonidae with 30% of the species
 being earless (Pereyra et al., 2016). It is also common in Ter-
 rarana (Hedges et al., 2008; Padial et al., 2014; Goutte et al.,
 2017; Von May et al., 2018) and is particularly prevalent
 in several clades distributed at high elevations (e.g. *Bryo-*
phryne, *Phrynopus*; Duellman & Lehr, 2009). Only a few
Pristimantis of the “*unistrigatus* group” have been reported
 to lack tympanum and vocal slits (e.g. *P. imthurni* and *P.*
jamescameroni, see Kok, 2013; *P. yaviensis*, see Myers &
 Donnelly, 1996). However, these *Pristimantis* do call. As
 a matter of fact, most earless frogs, although anatomically
 deaf, still call and can perceive acoustic signals via other
 organs (e.g. Boistel et al., 2013; Goutte et al., 2017). But
 only a few frog species have been reported to be mute in
 addition to be deaf. Most of these frogs are living near noisy
 environments such as streams and advertise via other cues
 such as visual or chemical signalling (Toledo et al., 2015).
 The cases of a dull-coloured Amazonian lowland species
 such as *P. grandoculis* being deaf and mute are remarkable.
 Hypotheses regarding the loss of ear and of acoustic activity
 in this species remain open. **AQ6** 2

Appendix 1 Molecular data

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	JQ742162	<i>Pristimantis</i>	<i>abakapa</i>		VUB3749	Abakapa-tepui	Venezuela	5.1892	-62.2944
NA	JQ742163	<i>Pristimantis</i>	<i>abakapa</i>		VUB3750	Angasima-tepui	Venezuela	5.0431	-62.0808
NA	JQ742151	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3741	Roraima-tepui	Guyana	5.2500	-60.7167
NA	JQ742152	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3748	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742153	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3742	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742154	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3747	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742155	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3744	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742156	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3745	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742157	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3746	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742158	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3743	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	JQ742159	<i>Pristimantis</i>	<i>aureoventris</i>		VUB3499	Wei-Assipu-tepui	Guyana	5.2175	-60.7058
NA	KDQF01000101	<i>Pristimantis</i>	<i>espedeus</i>	AF0265		Nouragues	French Guiana	4.0917	-52.7000
NA	KDQF01000107	<i>Pristimantis</i>	<i>espedeus</i>	AF0277	R116	Nouragues	French Guiana	4.0917	-52.7000
NA	KDQF01000108	<i>Pristimantis</i>	<i>espedeus</i>	AF0278	R117	Nouragues	French Guiana	4.0917	-52.7000
NA	KDQF01000150	<i>Pristimantis</i>	<i>espedeus</i>	AF0576		Ioupe	French Guiana	3.0250	-53.0800
NA	KDQF01000422	<i>Pristimantis</i>	<i>espedeus</i>	AF1156	R118	Trinité	French Guiana	4.6025	-53.4143
NA	KDQF01000423	<i>Pristimantis</i>	<i>espedeus</i>	AF1157		Trinité	French Guiana	4.6025	-53.4143
NA	KDQF01000439	<i>Pristimantis</i>	<i>espedeus</i>	AF1190	R119	Trinité	French Guiana	4.6025	-53.4143
NA	KDQF01000446	<i>Pristimantis</i>	<i>espedeus</i>	AF1203	R120	Trinité	French Guiana	4.6025	-53.4143
NA	KDQF01000452	<i>Pristimantis</i>	<i>espedeus</i>	AF1219		Trinité	French Guiana	4.6025	-53.4143
NA	KDQF01000570	<i>Pristimantis</i>	<i>espedeus</i>	AF1520	R121	Grande Montagne Tortue	French Guiana	4.2927	-52.3495
NA	KDQF01000571	<i>Pristimantis</i>	<i>espedeus</i>	AF1521	R122	Grande Montagne Tortue	French Guiana	4.2927	-52.3495
NA	KDQF01000572	<i>Pristimantis</i>	<i>espedeus</i>	AF1522	R123	Grande Montagne Tortue	French Guiana	4.29273	-52.3495
NA	KDQF01000952	<i>Pristimantis</i>	<i>espedeus</i>	AF2430		Nassau	Suriname	4.8041	-54.5555
NA	KDQF01000953	<i>Pristimantis</i>	<i>espedeus</i>	AF2431		Nassau	Suriname	4.8041	-54.5555

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	KDQF01000955	<i>Pristimantis</i>	<i>expedeus</i>	AF2433		Nassau	Suriname	4.8041	-54.5555
NA	KDQF01001020	<i>Pristimantis</i>	<i>expedeus</i>	AF2616		Atachi Bakka	French Guiana	3.5444	-53.9128
NA	KDQF01001025	<i>Pristimantis</i>	<i>expedeus</i>	AF2629		Atachi Bakka	French Guiana	3.5444	-53.9128
NA	KDQF01001028	<i>Pristimantis</i>	<i>expedeus</i>	AF2632		Atachi Bakka	French Guiana	3.5444	-53.9128
NA	KDQF01001048	<i>Pristimantis</i>	<i>expedeus</i>	AF2670		Alikéné	French Guiana	3.2156	-52.3980
NA	KDQF01001057	<i>Pristimantis</i>	<i>expedeus</i>	AF2684		Alikéné	French Guiana	3.2156	-52.3980
NA	KDQF01001058	<i>Pristimantis</i>	<i>expedeus</i>	AF2685		Alikéné	French Guiana	3.2156	-52.3980
NA	KDQF01001061	<i>Pristimantis</i>	<i>expedeus</i>	AF2690		Alikéné	French Guiana	3.2157	-52.3973
NA	KDQF01001062	<i>Pristimantis</i>	<i>expedeus</i>	AF2694		Alikéné	French Guiana	3.2157	-52.3973
NA	KDQF01001063	<i>Pristimantis</i>	<i>expedeus</i>	AF2695		Alikéné	French Guiana	3.2157	-52.3973
NA	KDQF01001529	<i>Pristimantis</i>	<i>expedeus</i>	AG268		Lucifer	French Guiana	4.7774	-53.9475
NA	KDQF01001653	<i>Pristimantis</i>	<i>expedeus</i>	AG507		Saul	French Guiana	3.7193	-53.4128
NA	KDQF01001654	<i>Pristimantis</i>	<i>expedeus</i>	AG508	R124	Saul	French Guiana	3.7193	-53.4128
NA	KDQF01002024	<i>Pristimantis</i>	<i>expedeus</i>	BNP2908		RAP Basecamp 1	Suriname	2.5269	-55.7700
JN690706	JN691314	<i>Pristimantis</i>	<i>expedeus</i>	CM395		Lucifer	French Guiana	4.7774	-53.9475
NA	KDQF01003878	<i>Pristimantis</i>	<i>expedeus</i>	PG477	R131	Kotika	French Guiana	3.9333	-54.1972
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>expedeus</i>	PG524	R132	Pic Coudreau de l'Est	French Guiana	3.3005	-52.9493
NA	KDQF01004301	<i>Pristimantis</i>	<i>expedeus</i>	ST300		Parna Tumucumaque	AP	0.9091	-53.2285
NA	KDQF01004302	<i>Pristimantis</i>	<i>expedeus</i>	ST301		Parna Tumucumaque	AP	0.9091	-53.2285
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>expedeus</i>	ST315		Parna Tumucumaque	AP	0.9091	-53.2285
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>imthurni</i>	PK3671		Ptari-tepui	Venezuela	5.7639	-61.8112
NA	KDQF01000063	<i>Pristimantis</i>	<i>inguinalis</i>	AF0157		Brownsberg	Suriname	4.9365	-55.1948
NA	KDQF01000248	<i>Pristimantis</i>	<i>inguinalis</i>	AF0803		Kaw	French Guiana	4.5507	-52.1610
NA	KDQF01000253	<i>Pristimantis</i>	<i>inguinalis</i>	AF0813		Savane Virginie	French Guiana	4.1959	-52.1490

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	KDQF01000256	<i>Pristimantis</i>	<i>inguinalis</i>	AF0820		Chutes Voltaire	French Guiana	5.0312	-54.0878
NA	KDQF01000295	<i>Pristimantis</i>	<i>inguinalis</i>	AF0883		Nouragues	French Guiana	4.0850	-52.6810
NA	KDQF01000514	<i>Pristimantis</i>	<i>inguinalis</i>	AF1386		Aratai	French Guiana	3.9909	-52.5902
NA	KDQF01000523	<i>Pristimantis</i>	<i>inguinalis</i>	AF1415		Savane Virginie	French Guiana	4.1959	-52.1490
NA	KDQF01000556	<i>Pristimantis</i>	<i>inguinalis</i>	AF1498		Nouragues	French Guiana	4.0848	-52.6806
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF1503		Grande Montagne Tortue	French Guiana	4.2927	-52.3496
NA	KDQF01000609	<i>Pristimantis</i>	<i>inguinalis</i>	AF1626		Saul	French Guiana	3.5732	-53.1985
NA	KDQF01000814	<i>Pristimantis</i>	<i>inguinalis</i>	AF2054		Sipaliwini	Suriname	2.1751	-56.0832
NA	KDQF01000937	<i>Pristimantis</i>	<i>inguinalis</i>	AF2398		Nassau	Suriname	4.8170	-54.6037
NA	KDQF01000954	<i>Pristimantis</i>	<i>inguinalis</i>	AF2432		Nassau	Suriname	4.8041	-54.5555
NA	KDQF01001019	<i>Pristimantis</i>	<i>inguinalis</i>	AF2613		Atachi Bakka	French Guiana	3.5520	-53.9509
NA	KDQF01001043	<i>Pristimantis</i>	<i>inguinalis</i>	AF2659		Alikéné	French Guiana	3.2091	-52.4020
NA	KDQF01001121	<i>Pristimantis</i>	<i>inguinalis</i>	AF2858		Mitaraka	French Guiana	2.2358	-54.4493
NA	KDQF01001229	<i>Pristimantis</i>	<i>inguinalis</i>	AF3083		Mitan G	French Guiana	2.6284	-52.5540
NA	KDQF01001402	<i>Pristimantis</i>	<i>inguinalis</i>	AF3404		Bakhuis	Suriname	4.6837	-56.7721
NA	KDQF01001416	<i>Pristimantis</i>	<i>inguinalis</i>	AF3432		Bakhuis	Suriname	4.6837	-56.7721
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF3531		Itoupe	French Guiana	3.0230	-53.0955
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF3772		Voltzberg	Suriname	4.6817	-56.1857
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF4777		Galbao	French Guiana	4.4880	-52.0445
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF5402		Camp Savane Roche Dachine	French Guiana	3.4696	-53.2300
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF5448		Trois-Saut	French Guiana	2.1969	-52.9017
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	AF5524		Haute Courcibo	French Guiana	4.4723	-53.2459
NA	KDQF01001509	<i>Pristimantis</i>	<i>inguinalis</i>	AG102		Kaw	French Guiana	4.5710	-52.2206

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	KDQF01001519	<i>Pristimantis</i>	<i>inguinalis</i>	AG225		Trinité	French Guiana	4.6709	−53.2843
JN690710	JN691317	<i>Pristimantis</i>	<i>inguinalis</i>	AG229		Trinité	French Guiana	4.6709	−53.2843
NA	KDQF01001538	<i>Pristimantis</i>	<i>inguinalis</i>	AG291		Trinité	French Guiana	4.6025	−53.4143
NA	KDQF01001595	<i>Pristimantis</i>	<i>inguinalis</i>	AG424		Atachi Bakka	French Guiana	3.6553	−53.8440
NA	KDQF01001643	<i>Pristimantis</i>	<i>inguinalis</i>	AG491		Saul	French Guiana	3.7193	−53.4128
NA	KDQF01001691	<i>Pristimantis</i>	<i>inguinalis</i>	AM015		Inini Tolenga	French Guiana	3.6632	−53.9283
NA	KDQF01002875	<i>Pristimantis</i>	<i>inguinalis</i>		MPEG30059	Serra do Acari. N ESEC Grão Pará	PA	1.2854	−58.6959
NA	KDQF01002876	<i>Pristimantis</i>	<i>inguinalis</i>		MPEG30060	Serra do Acari. N ESEC Grão Pará	PA	1.2854	−58.6959
NA	KDQF01003609	<i>Pristimantis</i>	<i>inguinalis</i>		MTR24299	Oiapoque	AP	3.8794	−51.7710
NA	KDQF01003778	<i>Pristimantis</i>	<i>inguinalis</i>		NZCS51	Brownsberg	Suriname	4.9365	−55.194826
NA	KDQF01004105	<i>Pristimantis</i>	<i>inguinalis</i>	QM0406		Montagne de fer	French Guiana	5.4074	−53.5548
NA	KDQF01004107	<i>Pristimantis</i>	<i>inguinalis</i>	QM0426		Montagne de fer	French Guiana	5.4074	−53.5548
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>inguinalis</i>	QM1074		Gaa_Kaba	French Guiana	4.4509	−54.4117
NA	JQ742170	<i>Pristimantis</i>	<i>inguinalis</i>		VUB3626	Cacao Mountain	French Guiana	4.5667	−52.4667
EU186739	EU186721	<i>Pristimantis</i>	<i>jamescameroni</i>	SBH268110		Bolivar, Aprada-tepui	Venezuela	5.4243	−62.4208
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>jamescameroni</i>		IRSNB4163	Bolivar, Aprada-tepui	Venezuela	5.4243	−62.4208
NA	JQ742169	<i>Pristimantis</i>	<i>jester</i>		VUB3493	Maringna-tepui	Guyana	5.21524	−60.5834
NA	MF037223	<i>Pristimantis</i>	<i>marmoratus</i>	CPI10703		Mt. Wokomung	Guyana	5.1175	−59.8225
EU186734	EU186716	<i>Pristimantis</i>	<i>marmoratus</i>		ROM43302	Mt. Wokomung	Guyana	5.1175	−59.8225
EU186741	EU186723	<i>Pristimantis</i>	<i>marmoratus</i>		KU181015	km 127, El Dorado- Santa Elena de Uairen Rd	Venezuela	5.8983	−61.4428
NA	JQ742166	<i>Pristimantis</i>	<i>marmoratus</i>		VUB3485	Kaiteur NP	Guyana	5.2686	−59.7686
NA	JQ742167	<i>Pristimantis</i>	<i>marmoratus</i>		VUB3491	Maringna-tepui	Guyana	5.2152	−60.5834
NA	KDQF01002108	<i>Pristimantis</i>	<i>marmoratus</i>	BNP3814		Bay Camp	Guyana	5.0112	−59.63930
NA	KDQF01002109	<i>Pristimantis</i>	<i>marmoratus</i>	BNP3815		Bay Camp	Guyana	5.0112	−59.6393
NA	KDQF01002110	<i>Pristimantis</i>	<i>marmoratus</i>	BNP3816		Bay Camp	Guyana	5.0112	−59.6393
NA	JQ742164	<i>Pristimantis</i>	<i>pulvinatus</i>		VUB3751	Iwokrama	Guyana	4.6714	−58.6850

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	JQ742165	<i>Pristimantis</i>	<i>pulvinatus</i>		VUB3674	La Escalera	Venezuela	5.9158	-61.4347
NA	KDQF01004007	<i>Pristimantis</i>	<i>pulvinatus</i>	PK3509		Iwokrama	Guyana	4.6720	-58.6840
EU186692	EU186692	<i>Pristimantis</i>	<i>saltrissimus</i>		ROM43913	Mt. Ayanganna	Guyana	5.3996	-59.9505
EU186693	EU186693	<i>Pristimantis</i>	<i>saltrissimus</i>		ROM43310	Mt. Wokomung	Guyana	5.1175	-59.8225
NA	JQ742168	<i>Pristimantis</i>	<i>saltrissimus</i>		VUB3490	Maringma-tepui	Guyana	5.2152	-60.5834
JN690708	JN691315	<i>Pristimantis</i>	<i>crepitaculus</i>	AF0021		Saul	French Guiana	3.6256	-53.2072
NA	KR811102	<i>Pristimantis</i>	<i>crepitaculus</i>	AF0563		Savane Virginie	French Guiana	4.1959	-52.1490
NA	KR811105	<i>Pristimantis</i>	<i>crepitaculus</i>	AF0757		St Georges	French Guiana	3.8112	-51.8896
NA	KDQF01000316	<i>Pristimantis</i>	<i>crepitaculus</i>	AF0910	MNHN-RA-2020.0093	Pic Coudreau du Sud	French Guiana	2.2534	-54.3534
NA	KDQF01000366	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1014		Saul	French Guiana	3.6359	-53.2726
NA	KDQF01000382	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1046		Saul	French Guiana	3.6112	-53.2886
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1387	MNHN-RA-2020.0094	Aratai	French Guiana	3.9909	-52.5902
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1388	MNHN-RA-2020.0095	Aratai	French Guiana	3.9909	-52.5902
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1598	MNHN-RA-2020.0097	Nouragues	French Guiana	4.0848	-52.6806
NA	KDQF01000601	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1607	MNHN-RA-2020.0100	Saul	French Guiana	3.5732	-53.1985
NA	KDQF01000749	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1921	MNHN-RA-2020.0101	Flat de la Waki	French Guiana	3.0840	-53.4107
NA	KDQF01000754	<i>Pristimantis</i>	<i>crepitaculus</i>	AF1941		Flat de la Waki	French Guiana	3.0836	-53.4121
NA	KDQF01001103	<i>Pristimantis</i>	<i>crepitaculus</i>	AF2786	MNHN-RA-2020.0102	Mitaraka	French Guiana	2.2358	-54.4493
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF2799	MNHN-RA-2020.0103	Mitaraka	French Guiana	2.2358	-54.4493
NA	KDQF01001186	<i>Pristimantis</i>	<i>crepitaculus</i>	AF3002		Mémora D	AP	3.3129	-52.1804
NA	KDQF01001205	<i>Pristimantis</i>	<i>crepitaculus</i>	AF3047		Mitan G	French Guiana	2.6284	-52.5540
NA	KDQF01001276	<i>Pristimantis</i>	<i>crepitaculus</i>	AF3161	MNHN-RA-2020.0108	Mitan D	AP	2.6276	-52.5419
NA	KDQF01001437	<i>Pristimantis</i>	<i>crepitaculus</i>	AF3539	MNHN-RA-2020.0092	Itoupe	French Guiana	3.0230	-53.0955
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF5399		Camp Saut Richard	French Guiana	3.47363	-53.2086

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	XXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	AF5440		Trois-Saut	French Guiana	2.1969	-52.9017
JN690707	EU201063	<i>Pristimantis</i>	<i>crepitaculus</i>	AG_BM110		Kaw3	French Guiana	4.5481	-52.1519
NA	KDQF01001542	<i>Pristimantis</i>	<i>crepitaculus</i>	AG321		Kaw	French Guiana	4.5161	-52.1005
NA	KDQF01001568	<i>Pristimantis</i>	<i>crepitaculus</i>	AG378		Montagne Maripa	French Guiana	4.4088	-52.34301
NA	KDQF01001645	<i>Pristimantis</i>	<i>crepitaculus</i>	AG494		Saul	French Guiana	3.7193	-53.4128
NA	KDQF01001886	<i>Pristimantis</i>	<i>crepitaculus</i>	BOAM048		Borne 4	French Guiana	2.3709	-53.7728
NA	KDQF01002129	<i>Pristimantis</i>	<i>crepitaculus</i>	CAAM15		Montagne Cacao	French Guiana	2.3491	-53.2160
NA	EU201062	<i>Pristimantis</i>	<i>crepitaculus</i>	CM077		Trois-Sauts	French Guiana	2.2480	-52.8746
NA	KDQF01002243	<i>Pristimantis</i>	<i>crepitaculus</i>	CM171		Trijonction	French Guiana	2.3333	-54.6000
NA	KDQF01002504	<i>Pristimantis</i>	<i>crepitaculus</i>	FL04		Plote PPBIO	AP	0.9793	-51.6149
NA	KDQF01002521	<i>Pristimantis</i>	<i>crepitaculus</i>	FTA128		Rio Vila Nova	AP	0.4493	-52.0221
NA	KDQF01002528	<i>Pristimantis</i>	<i>crepitaculus</i>	FTA165		Rio Amapá Grande	AP	2.1271	-51.1913
NA	KDQF01002543	<i>Pristimantis</i>	<i>crepitaculus</i>	FTA239		Rio Amapá Grande	AP	2.1271	-51.1913
NA	XXXXXXX	<i>Pristimantis</i>	<i>crepitaculus</i>	FTA96		Rio Vila Nova	AP	0.4493	-52.0221
NA	KDQF01003282	<i>Pristimantis</i>	<i>crepitaculus</i>	MTR13884		Lourenço	AP	2.32361	-51.6453
NA	KDQF01003293	<i>Pristimantis</i>	<i>crepitaculus</i>	MTR13930		Lourenço	AP	2.32361	-51.6453
NA	KR811104	<i>Pristimantis</i>	<i>crepitaculus</i>	MTR24285		Lourenço	AP	2.3216	-51.6109
NA	KR811103	<i>Pristimantis</i>	<i>crepitaculus</i>	MTR24300		Oiapoque	AP	3.8794	-51.7710
NA	KDQF01003952	<i>Pristimantis</i>	<i>crepitaculus</i>	PG748		St Georges	French Guiana	3.8061	-51.8934
NA	KDQF01004462	<i>Pristimantis</i>	<i>crepitaculus</i>	WAAM011		Flat de la Waki	French Guiana	3.18341	-53.4775
NA	KDQF01003322	<i>Pristimantis</i>	sp. Neblina 1	MTR15532		São Gabriel da Cachoeira	AM	0.7195	-66.0878
NA	KDQF01003323	<i>Pristimantis</i>	sp. Neblina 1	MTR15534		São Gabriel da Cachoeira	AM	0.7195	-66.0878
NA	KDQF01003325	<i>Pristimantis</i>	sp. Neblina 2	MTR15536		São Gabriel da Cachoeira	AM	0.7195	-66.0878
NA	KDQF01000102	<i>Pristimantis</i>	sp. "Guianas" East	AF0266		Nouragues	French Guiana	4.0917	-52.7000
NA	KDQF01000103	<i>Pristimantis</i>	sp. "Guianas" East	AF0268		Nouragues	French Guiana	4.0917	-52.7000

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	KDQF01000104	<i>Pristimantis</i>	sp. "Guianas" East	AF0272		Nouragues	French Guiana	4.0917	-52.700
NA	KDQF01000354	<i>Pristimantis</i>	sp. "Guianas" East	AF0978		Saul	French Guiana	3.6359	-53.2726
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	AF1360		Grande Montagne Tortue	French Guiana	4.2927	-52.3496
NA	KDQF01000558	<i>Pristimantis</i>	sp. "Guianas" East	AF1505		Grande Montagne Tortue	French Guiana	4.2927	-52.3496
NA	KDQF01001024	<i>Pristimantis</i>	sp. "Guianas" East	AF2625		Atachi Bakka	French Guiana	3.5444	-53.9128
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	AF2626		Atachi Bakka	French Guiana	3.5444	-53.9128
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	AF2818		Mitaraka	French Guiana	2.2358	-54.4493
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	AF5414		Savane Roche Dachine	French Guiana	3.4696	-53.2298
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	AF5525		Haute Courcibo	French Guiana	4.4723	-53.2459
NA	KDQF01001850	<i>Pristimantis</i>	sp. "Guianas" East	BOAM001		Borne 4	French Guiana	2.3709	-53.7728
NA	KDQF01001860	<i>Pristimantis</i>	sp. "Guianas" East	BOAM012		Borne 4	French Guiana	2.3709	-53.7728
NA	KDQF01002249	<i>Pristimantis</i>	sp. "Guianas" East	CM184		Trijonction	French Guiana	2.3333	-54.6000
JN690709	JN691316	<i>Pristimantis</i>	sp. "Guianas" East	CM317		CisameG	French Guiana	4.1833	-52.3667
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	QM0423		Montagne de fer	French Guiana	5.4074	-53.5548
NA	XXXXXXXXXX	<i>Pristimantis</i>	sp. "Guianas" East	QM1073		Gaa Kaba	French Guiana	4.4520	-54.4193
XXXXXXXXXX	KDQF01004305	<i>Pristimantis</i>	sp. "Guianas" East	ST310		Parna Tumucumaque	AP	0.9091	-53.2285
NA	KDQF01004306	<i>Pristimantis</i>	sp. "Guianas" East	ST311		Parna Tumucumaque	AP	0.9091	-53.2285
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>grandoculis</i>	UFRJA024	NZCS A1211	Lelygebergte	Suriname	4.4158	-54.6498
NA	XXXXXXXXXX	<i>Pristimantis</i>	<i>grandoculis</i>	UFRJA023	NZCS A1210	Lelygebergte	Suriname	4.4158	-54.6498
NA	KDQF01002880	<i>Pristimantis</i>	<i>grandoculis</i>		MPEG30085	Serra do Acari	PA	1.2854	-58.6959
NA	KDQF01002881	<i>Pristimantis</i>	<i>grandoculis</i>		MPEG30088	Serra do Acari	PA	1.2854	-58.6959
NA	KDQF01003777	<i>Pristimantis</i>	<i>grandoculis</i>		NZCS50	Brownsberg	Suriname	4.9366	-55.1948
NA	KDQF01003795	<i>Pristimantis</i>	<i>grandoculis</i>		NZCS A1019	Tafelberg	Suriname	3.8049	-56.1539
NA	KDQF01003796	<i>Pristimantis</i>	<i>grandoculis</i>		NZCS A1212	Tafelberg	Suriname	3.8049	-56.1539

12S access	16S access	Genus	Species	Voucher	Voucher2	Locality	Country	lat	lon
NA	KDQF01001388	<i>Pristimantis</i>	<i>grandoculis</i>	AF3365		Bakhuis	Suriname	4.6562	−56.7865
NA	KDQF01001400	<i>Pristimantis</i>	<i>grandoculis</i>	AF3402		Bakhuis	Suriname	4.6837	−56.7721
NA	KDQF01001403	<i>Pristimantis</i>	<i>grandoculis</i>	AF3408		Bakhuis	Suriname	4.6837	−56.7721
NA	KDQF01001417	<i>Pristimantis</i>	<i>grandoculis</i>	AF3435	MNHN-RA-2020.0118	Bakhuis	Suriname	4.6837	−56.7721
EU186676	EU186676	<i>Pristimantis</i>	sp. Ayangana		ROM40164	Mt. Ayangana	Guyana	5.3995	−59.9505
XXXXXXXXXX	KDQF01004221	<i>Pristimantis</i>	cf. <i>ockendeni</i>		SMNS11989	Mabura Hill forest reserve	Guyana	5.1553	−58.6997
XXXXXXXXXX	KDQF01004222	<i>Pristimantis</i>	cf. <i>ockendeni</i>		SMNS11990	Mabura Hill forest reserve	Guyana	5.1553	−58.6997
XXXXXXXXXX	KDQF01004223	<i>Pristimantis</i>	cf. <i>ockendeni</i>		SMNS11994	Mabura Hill forest reserve	Guyana	5.1553	−58.6997
XXXXXXXXXX	KDQF01000865	<i>Pristimantis</i>	cf. <i>ockendeni</i>	AF2155		Sipaliwini	Suriname	2.02682	−56.1256
NA	KDQF01003210	<i>Pristimantis</i>	cf. <i>ockendeni</i>	MTR12690		Igarapé Açu, Rio Abacaxis	AM	−4.3442	−58.6350
NA	KDQF01001829	<i>Pristimantis</i>	cf. <i>ockendeni</i>	BM153		UHE Belo Monte, Vitória do Xingu, Rio Xingu	PA	−2.9506	−51.9366
NA	KDQF01004256	<i>Pristimantis</i>	cf. <i>ockendeni</i>	SMS155		Campo Catuquira	AM	−4.9136	−61.1092
NA	KDQF01004257	<i>Pristimantis</i>	cf. <i>ockendeni</i>	SMS156		Campo Catuquira	AM	−4.9136	−61.1092
NA	KDQF01002705	<i>Pristimantis</i>	cf. <i>ockendeni</i>	JOG847		MINA PALITO	PA	−6.3173	−55.7986
NA	KDQF01003224	<i>Pristimantis</i>	cf. <i>ockendeni</i>	MTR12855		São Sebastião, Rio Abacaxis	AM	−4.3089	−58.6364
NA	KDQF01000889	<i>Pristimantis</i>	cf. <i>ockendeni</i>	AF2257		Sipaliwini	Suriname	2.0244	−56.1251
NA	KDQF01002605	<i>Pristimantis</i>	cf. <i>ockendeni</i>	H2773		UHE Jirau	RO	−9.4459	−64.8247
NA	JQ742160	<i>Pristimantis</i>	<i>yuruaniensis</i>		VUB3717	Yuruani-tepui	Venezuela	5.3139	−60.8639
NA	JQ742161	<i>Pristimantis</i>	<i>yuruaniensis</i>		VUB3720	Yuruani-tepui	Venezuela	5.3139	−60.8639

Appendix 2 Specimens examined and types

Genus	Species	Museum	Field N	Sex	Type	Locality	Country	Lat	Lon	Collector	Date	Acoustic	DNA
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0093	AF0910	F	Paratype	Pic Coudreau du Sud	French Guiana	2.2534	-54.3534	M. Blanc	01_02_2013		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0104	AF2815	F	Paratype	Miaraka	French Guiana	2.2358	-54.4493	A. Fouquet - M. Dewynter - N. Vidal	28_02_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0105	AF2816	F	Paratype	Miaraka	French Guiana	2.2358	-54.4493	A. Fouquet - M. Dewynter - N. Vidal	28_02_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0094	AF1387	M	Paratype	Aratai	French Guiana	3.9909	-52.5902	A. Fouquet - J. Devillechabrolle	16_12_2013		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0095	AF1388	M	Paratype	Aratai	French Guiana	3.9909	-52.5902	A. Fouquet - J. Devillechabrolle	16_12_2013		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0096	AF1597	M	Paratype	Nouragues	French Guiana	4.0848	-52.6806	E. Courtois	09_02_2014		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0097	AF1598	M	Paratype	Nouragues	French Guiana	4.08489	-52.6806	E. Courtois	09_02_2014		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0098	AF1599	M	Paratype	Nouragues	French Guiana	4.08489	-52.6806	E. Courtois	09_02_2014		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0099	AF1606	M	Paratype	Saul	French Guiana	3.5732	-53.1985	A. Fouquet - E. Courtois - J.P. Vacher	20_02_2014	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0100	AF1607	M	Paratype	Saul	French Guiana	3.5732	-53.1985	A. Fouquet - E. Courtois - J.P. Vacher	20_02_2014	MNHN-SO- 2021-XXX	XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0101	AF1921	M	Paratype	Flat de la Waki	French Guiana	3.0840	-53.4107	J.P. Vacher	07_04_2014		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0102	AF2786	M	Holotype	Miaraka	French Guiana	2.2358	-54.4493	A. Fouquet - M. Dewynter - N. Vidal	26_02_2015	MNHN- SO-2019-23	XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0103	AF2799	M	Paratype	Miaraka	French Guiana	2.2358	-54.4493	A. Fouquet - M. Dewynter - N. Vidal	27_02_2015		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0106	AF2860	M	Paratype	Miaraka	French Guiana	2.2358	-54.4493	A. Fouquet - M. Dewynter - N. Vidal	04_03_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0107	AF3054	M	Paratype	Miran G	French Guiana	2.6284	-52.5540	A. Fouquet - P. Nunes	20_03_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0108	AF3161	M	Paratype	Miran D	AP	2.6276	-52.5419	A. Fouquet - P. Nunes	23_03_2015		XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0109	AF3530	M	Paratype	Ioupe	French Guiana	3.0230	-53.0955	A. Fouquet - E. Courtois - B. Villette - M. Dewynter	06_01_2016	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0092	AF3539	M	Paratype	Ioupe	French Guiana	3.0230	-53.0955	A. Fouquet - E. Courtois - B. Villette - M. Dewynter	06_01_2016	MNHN-SO- 2021-XXX	XXXXXXXXXX
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0110	AF3548	M	Paratype	Ioupe	French Guiana	3.02218	-53.1105	A. Fouquet - E. Courtois - B. Villette - M. Dewynter	06_01_2016		

Genus	Species	Museum	Field N	Sex	Type	Locality	Country	Lat	Lon	Collector	Date	Acoustic	DNA
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0111	AF3664	M	Paratype	Ioupe	French Guiana	3.0256	-53.0525	A. Fouquet – E. Courtois – B. Villette – M. Dewynter	11_01_2016		
<i>Pristimantis</i>	<i>crepitaculus</i>	MNHN- RA-2020.0112	AF3687	M	Paratype	Ioupe	French Guiana	3.0230	-53.0955	A. Fouquet – E. Courtois – B. Villette – M. Dewynter	14_01_2016		
<i>Pristimantis</i>	<i>grandoculis</i>	MNHN- RA-2020.0118	AF3435	M		Bakhuis	Suriname	4.7246	-56.7638	A. Fouquet – S. Cally – R. Jairam	30_04_2015		
<i>Pristimantis</i>	<i>grandoculis</i>	RMNH 4467		M	Holotype	Coppename	Suriname						
<i>Pristimantis</i>	<i>grandoculis</i>	NZCSA1212		M		Tafleberg	Suriname	3.8049	-56.1539	P. Ouboter – V. Kadosoe			
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,819	PLVP 289	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	04_12_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,820	PLVP 290	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	05_12_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,821	PLVP 301	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	05_12_2015		
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,822	PLVP 352	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	06_12_2015	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,823	PLVP 353	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	06_12_2015	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,824	PLVP 354	M	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	06_12_2015	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>crepitaculus</i>	MPEG 41,825	PLVP 355	F	Paratype	Oiapoque	Brazil	3.79889	-51.87993	P. Peloso – L. Brandão	06_12_2015		
<i>Pristimantis</i>	<i>grandoculis</i>	NZCS A1210	UFRJA023	M		Lely Mountain	Suriname	4.2667	-54.7333	R. Jairam – D. Baeta			
<i>Pristimantis</i>	<i>grandoculis</i>	NZCS A1211	UFRJA024	M		Lely Mountain	Suriname	4.2667	-54.7333	R. Jairam – D. Baeta			
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MNHN- RA-2020.0113	AF2155	F		Sipaliwini	Suriname	2.0268	-56.1256	A. Fouquet – J.P. Vacher	23_04_2014		XXXXXXXXXX
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MNHN- RA-2020.0114	AF2258	F		Sipaliwini	Suriname	2.0244	-56.1251	A. Fouquet – J.P. Vacher	27_04_2014		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MTD47769		F		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	18 08 2010		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11990		F		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	25 04 2003		XXXXXXXXXX
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11991		F		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	25 04 2003		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11995		F		Mabura Hill forest reserve	Guyana	5.15538	-58.6997	R Ernst	01 06 2004		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MNHN- RA-2020.0115	AF2255	M		Sipaliwini	Suriname	2.0244	-56.12518	A. Fouquet – J.P. Vacher	27_04_2014	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MNHN- RA-2020.0116	AF2256	M		Sipaliwini	Suriname	2.02449	-56.1251	A. Fouquet – J.P. Vacher	27_04_2014		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MNHN- RA-2020.0117	AF2289	M		Sipaliwini	Suriname	2.0334	-56.1318	A. Fouquet – J.P. Vacher	30_04_2014	MNHN-SO- 2021-XXX	
<i>Pristimantis</i>	<i>cf. ockendeni</i>	MTD47770		M		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	18 08 2010		

Genus	Species	Museum	Field N	Sex	Type	Locality	Country	Lat	Lon	Collector	Date	Acoustic	DNA
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11987		M		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	18 11 2002		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11989		M		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	17 04 2003		XXXXXXXXXX
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11993		M		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	26 03 2004		
<i>Pristimantis</i>	<i>cf. ockendeni</i>	SMNS11994		M		Mabura Hill forest reserve	Guyana	5.1553	-58.6997	R Ernst	01 06 2004		XXXXXXXXXX

Appendix 3 Call records list

1196

Pristimantis crepitaculus

1197

- PLPDR 126 (MPEG 41822), Paratype, Oiapoque – 1198
Amapá, Brazil 1199
PLPDR 128 (MPEG 41823), Paratype, Oiapoque – 1200
Amapá, Brazil 1201
track59 Marty and Gaucher (NA), Kaw montain – French 1202
Guiana 1203
160106_0692 (AF3530), Itoupé – French Guiana 1204
160106_0693(AF3539), Holotype, Itoupé – French Guiana 1205
LS110010 (AF1606), Saul Limonade – French Guiana 1206

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Availability of data and material All new DNA sequences, call record- 1238
ings, and μ -CT scans will be deposited upon manuscript acceptance. 1239

Declarations 1240

Ethics approval Experiments have been conducted in accordance with 1241
relevant national legislation on the use of animals for research. 1242

Competing interests The authors declare no competing interests. 1243

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