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**Amended diagnosis and redescription of *Pristimantis marmoratus*
(Boulenger, 1900) (Amphibia: Craugastoridae),
with a description of its advertisement call and notes
on its breeding ecology and phylogenetic relationships**

Philippe J.R. KOK^{1,*}, Raheleh DEZFOULIAN², D. Bruce MEANS³,
Antoine FOUQUET⁴ & César L. BARRIO-AMORÓS⁵

^{1,2}Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel,
2 Pleinlaan, B-1050 Brussels, Belgium.

³Coastal Plains Institute and Land Conservancy, 1313 Milton Street, Tallahassee, Florida 32303, USA.

⁴Laboratoire Écologie, Évolution, Interactions des Systèmes Amazoniens (USR 3456 LEEISA),
Université de Guyane, CNRS Guyane, Cayenne, French Guiana.

⁵Doc Frogs Expeditions, Apartado Postal 220-8000, San José, Pérez Zeledón,
San Isidro del General, 11901 Costa Rica.

*Corresponding author: philippe.kok@vub.be

²Email: r.dezfouliau@gmail.com

³Email: means@bio.fsu.edu

⁴Email: fouquet.antoine@gmail.com

⁵Email: cesarlba@yahoo.com

¹[urn:lsid:zoobank.org:author:62BA0CB3-FB94-407F-90A1-06AB6401B911](https://zoobank.org/author:62BA0CB3-FB94-407F-90A1-06AB6401B911)

²[urn:lsid:zoobank.org:author:3A962C0A-0E66-4683-B18E-B2D7342A347A](https://zoobank.org/author:3A962C0A-0E66-4683-B18E-B2D7342A347A)

³[urn:lsid:zoobank.org:author:1D1D6AAE-EF92-4F19-92AF-59CE393CB0E9](https://zoobank.org/author:1D1D6AAE-EF92-4F19-92AF-59CE393CB0E9)

⁴[urn:lsid:zoobank.org:author:F60FCBAF-0F63-4BFA-8827-FD87D569885C](https://zoobank.org/author:F60FCBAF-0F63-4BFA-8827-FD87D569885C)

⁵[urn:lsid:zoobank.org:author:7D6F60FB-056A-487E-A135-34B21302DE43](https://zoobank.org/author:7D6F60FB-056A-487E-A135-34B21302DE43)

Abstract. The frog *Pristimantis marmoratus* was originally described as *Hylodes marmoratus* by George A. Boulenger in 1900 based on a single specimen reported to have been collected at the foot of Mount Roraima in Guyana in 1898. We herein discuss the exact location of the type locality of *P. marmoratus* and provide a redescription of the species based on new material from Kaieteur National Park and from the slopes of Maringma-tepui in Guyana. We also describe the previously unknown vocalization and breeding ecology of the species, and conducted an exploratory molecular analysis of the phylogenetic relationships within the genus *Pristimantis* represented by the members of the “*unistrigatus* species group” in the Guiana Shield. *Pristimantis marmoratus* is a small-sized species mainly distinguished from its known Guiana Shield congeners by the combination of F I < II, SVL ≤ 20.4 in males, presence of vocal slits in males, granular/pustulate dorsal skin with well-developed scapular ridges, basal webbing between fingers, fringes on fingers and toes, crossed iris, diffuse yellow or pale green wash on groin, and absence of flashy colour on axillary/pre-axillary region. The advertisement call consists of a single note repeated at a rate of ca 11 calls/min with a dominant frequency ranging from 2756 to 3101 Hz.

Pristimantis marmoratus is primarily arboreal, exclusively active at dusk, and probably restricted to the pristine rainforests of the Pantepui uplands and highlands, east of the Gran Sabana between ca 600 and 1800 m above sea level. Preliminary molecular analyses recovered *Pristimantis marmoratus* as sister to an unnamed species from the Eastern Guiana Shield. On grounds of the newly established distributional extent we suggest maintaining the IUCN conservation status as Least Concern.

Keywords. Anura, Guiana Shield, Pantepui, Systematics, Terrarana.

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Introduction

Pristimantis marmoratus (Boulenger, 1900) is the oldest described Guiana Shield member of what has later been referred to as the “*unistrigatus* group” (see Hedges *et al.* 2008; Kok *et al.* 2011; Kok 2013). As often with old descriptions, the original description of *Hylodes marmoratus* is not comprehensive enough to allow for an unambiguous diagnosis of the species compared to most of the many other members of the genus. Consequently, many available phylogenetic analyses have been based on misidentified specimens and are thus misleading for the position of *P. marmoratus* *sensu stricto*.

Pristimantis marmoratus is currently reported as widespread in the Guiana Shield, occurring from Amazonian Venezuela to French Guiana (e.g., Rivero 1961; Lescure 1976; Lescure 1981; Barrio-Amorós 1998; Lescure & Marty 2001; MacCulloch & Lathrop 2009; Avila-Pires *et al.* 2010; Ouboter & Jairam 2012; Frost 2016). MacCulloch *et al.* (2010) mentioned that the species also occurs in Amazonas State in Brazil, and described it as being “*a terrestrial leaf-litter species found in tropical lowland and montane forest. It breeds by direct development, but the egg deposition site is not known. It is adaptable to human intervention*”. However, some recent works challenged the view of *P. marmoratus* being as widespread as currently reported, and suggested instead that the name could have been applied to a number of undescribed species (e.g., Fouquet *et al.* 2007, 2013, Kok 2013). The name *marmoratus* seems to have been occasionally used for any small brown, hard to identify *Pristimantis* in north-eastern South America, and the lack of comparative specimens from close to the type locality has prevented the improvement of the species diagnosis.

As mentioned earlier, the briefness of some original species descriptions is clearly an obstacle to accurate species identification. Too brief descriptions contribute to the confusion among morphologically similar taxa and make new species descriptions more challenging (see e.g., example Kok *et al.* 2006; Kok *et al.* 2013; Fouquet *et al.* 2016). Loose descriptions also prevent the correct evaluation of conservation recommendations because identification problems affect the accuracy of the species distribution. Therefore, we believe it is an important prerequisite to redescribe these poorly defined taxa and redefine their exact geographical distribution, ultimately facilitating the description of still unnamed related taxa.

Based on new material collected in western and west-central Guyana, and direct comparison with the holotype of *Pristimantis marmoratus* (BMNH 1947.2.16.92, formerly 99.3.25.19), we here provide a morphological redescription and amended diagnosis of the species. We also describe the call of *P. marmoratus* for the first time, report on its previously unknown breeding ecology, discuss an exploratory molecular analysis of the phylogenetic relationships within the genus *Pristimantis* represented by the members of the “*unistrigatus* species group” occurring in the Guiana Shield, and examine the IUCN Red List Category of the species.

All *Pristimantis* species from the Guiana Shield highlands have historically been assigned to the “*unistrigatus* species group” (*sensu* Hedges *et al.* 2008). Although Padial *et al.* (2014) considered these species as unassignable to any group (the *unistrigatus* group being polyphyletic), we find taxonomically practical to use this artificial grouping as a working basis to compare the Guiana Shield *Pristimantis* species having the first finger shorter than the second with other *Pristimantis* species groups in the area.

On the type locality of *Pristimantis marmoratus* (Boulenger, 1900)

According to Boulenger (1900), the holotype of *Pristimantis marmoratus* is “*from the foot of Mt. Roraima, 3500 feet*” (ca 1067 m elevation) in Guyana. The specimen was collected by F.V. McConnell and J.J. Quelch, two British biologists and explorers, during an expedition to the summit of Mount Roraima led between August and October 1898. Although – according to our knowledge – the exact route taken by McConnell and Quelch during that trip is not illustrated on any map, their itinerary can be inferred from the literature. In correspondence between McConnell and Boulenger (Boulenger 1900), the former stated: “*The specimens were obtained by Mr. J. J. Quelch and myself on our second expedition to Roraima in August, September, and October, 1898. The route taken on this occasion was by the Mazaruni and Curubung rivers to the Falls of Macrobah, a boat-journey of twenty days, and thence by land to a point on the Upper Mazaruni where that river flows at a height of 1300 feet. Small bark-canoes were here obtained, and after three days’ journey up the Cako and Aruparu we arrived at the commencement of the trail to Roraima. With the exception of the last twenty miles, the whole journey, which occupied forty days, lay through thick forest.*”

Shortly after, Brown *et al.* (1901) mentioned the following about McConnell and Quelch’s expedition: “*... the Kako was paddled up until a point was reached about twenty miles north-east of Roraima, and thence, leaving the canoes, a track through dense forest was taken until, in the second week of October, the south-eastern face of the mountain was reached.*”

Quelch (in Chubb 1921) provided a detailed overview of their itinerary (unfortunately not mapped). However, it is often difficult to locate some of the small creeks, waterfalls, and Amerindian settlements he mentioned. It nevertheless leaves no doubt that the expedition reached the southern edge of Roraima from the east, travelling through Guyana, then entering Brazil most likely south, or slightly east, of Maringma-tepui, and finally entering Venezuela. Quelch (in Chubb 1921) wrote: “*... and it was with great joy that we at last came out on continuous savannah, and from a high elevation had the great range of mountains in full view – the vertical-walled Roraima before us, with smaller Roraimas on the right; the rugged pile of Marima behind; and the beautiful Sun Mountain, with its peaked dome, its terraced slopes and sharp edges, with varying light and shade all over it, away on our left; and far away in the blue distance the high plateaux of Brazil.*” This, and the fact that Quelch mentions that the expedition team crossed the Cotinga River (which lies in the extreme north of the Roraima State of Brazil), indicates that the team entered Venezuela northwest of Uei-tepui (also known as Cerro El Sol, called “Sun Mountain” by Quelch, and which indeed has a peaked dome).

The path taken by Quelch and McConnell thus likely passed south of Maringma-tepui in Guyana and from there proceeded west up the Cotinga River in Brazil and then into what is now part of La Gran Sabana in Venezuela following well-travelled Amerindian trails that Schomburgk used. They probably ascended Kukenán River to a point about 8.0 km from the southern cliffs of Mt. Roraima, which is at 3500 feet elevation, and by the late 1920s was forested (Tate 1930). If 3500 feet elevation is reasonable, this is the closest approach to Mt. Roraima at that elevation and we believe near where the type locality must be. Today the rainforest has long since been converted into low diversity grassland by frequent Amerindian burning at all seasons.

Phelps (1938) correctly stated that the collection reported in Boulenger (1900) from Guyana was actually obtained in Venezuela.

Material and methods

Fieldwork and deposition of specimens

The newly collected specimens of *Pristimantis marmoratus* are from close to the type locality, namely the slopes of Maringma-tepui (5°12'38" N, 60°33'59" W, 1060–1376 m elevation, ca 15 km airline from Mt. Roraima; Fig. 1), Cuyuni-Mazaruni District, Guyana, where two adult males and one juvenile were secured in November 2007, and from a locality named Amu Trail in the south-eastern part of Kaieteur National Park (5°08' N, 59°24' W, ca 150 km airline from Mt. Roraima, ca 630 m elevation; Fig. 1), Potaro-Siparuni District, Guyana where four adult individuals (three males, one female) were collected in June 2006. Specimens were collected by hand, euthanized by immersion in a 2% Xylocaine solution, fixed in 10% formalin for several days and then transferred to 70% ethanol for permanent storage. A piece of liver and/or thigh muscle was taken from specimens prior to fixation and preserved in 95% ethanol for later molecular analyses. Specimens were deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) and tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel.

Morphology

The terminology for morphological characters mostly follows Duellman & Lehr (2009) and most recent *Pristimantis* descriptions from the Guiana Shield (e.g., Kok 2013; Fouquet *et al.* 2013). Colour in life is described from digital photographs and field notes. Sex and maturity were determined by the presence/absence of vocal slit(s). All morphometric data were taken from the preserved specimens by

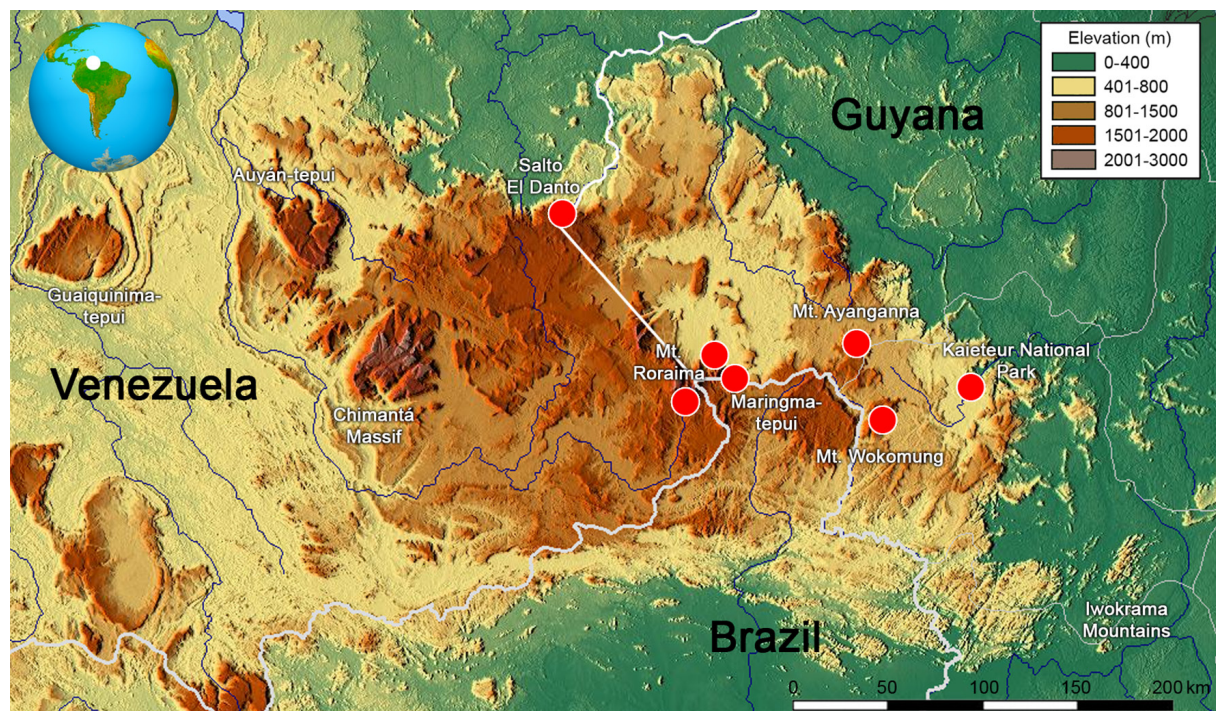


Fig. 1. Map of the Eastern Pantepui District showing the known distribution of *Pristimantis marmoratus* (Boulenger, 1900). Red dots denote localities of confirmed occurrence based either on museum specimens or colour photographs.

the same person (RD; except for the holotype: taken by PJRK) to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital caliper.

Abbreviations and standard measurements for adults are as follows:

EL	=	eye length
EN	=	eye to naris distance from anterior corner of eye to posterior margin of naris
FL	=	foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV
HAND	=	hand length from proximal edge of palmar tubercle to tip of Finger III
HL	=	head length from angle of jaw to tip of snout
HW	=	head width at level of angle of jaws
IN	=	internarial distance
IO	=	interorbital distance
SL	=	snout length from anterior corner of eye to tip of snout
SVL	=	snout-vent length
TIL	=	tibia length from outer edge of flexed knee to heel
TYM	=	greatest length of tympanum from its anterior margin to its posterior margin
WFD	=	width of disc on Finger III
WTD	=	width of disc on Toe IV

The newly acquired specimens were assigned to *Pristimantis marmoratus* based on morphological congruence with the holotype. Molecular sequence data from these specimens (two of them already available at GenBank) were used to reassign misidentified specimens (see Table 1). Because of the cryptic nature of this group, and to avoid adding more confusion, we restricted the number of specimens used in the redescription to specimens for which identification was unambiguously confirmed by molecular data on mitochondrial 16S sequences (see DNA barcoding below and Appendix 3). Specimens for which molecular data were unavailable and that we identified with confidence as *Pristimantis marmoratus* based on photographs and/or museum specimens were used to infer the distribution of the species, but were omitted from the morphological measurements and analysis.

Bioacoustics

The advertisement call of *Pristimantis marmoratus* was recorded at a distance of ca one meter from two calling males collected in Kaieteur National Park: IRSNB 14471 recorded on 26 Jun. 2006 at 6:30 pm, and IRSNB 14472 recorded on 28 Jun. 2006 at 6:00 pm. Calls were recorded on a Maxell DM60 digital audiotape using a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder. Call motivation was deemed high since several males were calling at the same location at regular intervals; air temperature at the call sites was measured with a Hanna digital pH/thermometer and was 24°C. Only three (IRSNB 14471) and 13 (IRSNB 14472) calls could be recorded. We followed a note-centred approach (Köhler *et al.* 2017), and calls were analysed at a sampling rate of 44100Hz using the software Raven v. 1.4 (Charif *et al.* 2010). Temporal variables measured are some of those summarized in Kok & Kalamandeen (2008) and included: call duration; inter-call silent interval (end of one call to beginning of the next); and call rate (number of calls per minute). The dominant frequency of the note (frequency where most sound energy is concentrated within the whole power spectrum) was calculated in Raven v. 1.4 using the “Max Freq (Hz)” measurement tool (Charif *et al.* 2010). Oscillograms and spectrograms were obtained using Raven v. 1.4 and Seewave v. 1.6.4 (Sueur *et al.* 2008) in the R statistical computing environment (R Development Core Team 2015).

Molecular phylogenetic analysis

A comprehensive phylogenetic analysis of the large polyphyletic “*unistrigatus* species group” (Hedges *et al.* 2008) is beyond the scope of this paper, instead we conducted an exploratory molecular analysis of the phylogenetic relationships within the genus *Pristimantis* represented by the members of the

Table 1. Reidentified terminal species names of GenBank. Accession numbers in bold represent *Pristimantis marmoratus* (Boulenger, 1900). Asterisks highlight sequences of specimens we examined and that correspond to the morphology of the holotype.

GenBank accession number	Original name	Voucher specimen	Reidentified name
EU186723	<i>Pristimantis pulvinatus</i>	KU 181015	<i>Pristimantis marmoratus</i> (Boulenger, 1900)
EU186716	<i>Pristimantis</i> sp.	ROM 43302	<i>Pristimantis marmoratus</i> (Boulenger, 1900)
JQ742166*	<i>Pristimantis</i> aff. <i>pulvinatus</i> A	IRSNB 14471	<i>Pristimantis marmoratus</i> (Boulenger, 1900)
JQ742167*	<i>Pristimantis</i> aff. <i>pulvinatus</i> A	IRSNB 12862	<i>Pristimantis marmoratus</i> (Boulenger, 1900)
JQ742339*	<i>Pristimantis</i> aff. <i>pulvinatus</i> A	IRSNB 12862	<i>Pristimantis marmoratus</i> (Boulenger, 1900)
JQ742164	<i>Pristimantis</i> aff. <i>pulvinatus</i> B	IRSNB 15786	<i>Pristimantis pulvinatus</i> (Rivero, 1968)
JQ742338	<i>Pristimantis</i> aff. <i>pulvinatus</i> B	IRSNB 15786	<i>Pristimantis pulvinatus</i> (Rivero, 1968)
JQ742165	<i>Pristimantis</i> aff. <i>pulvinatus</i> B	IRSNB 15634	<i>Pristimantis pulvinatus</i> (Rivero, 1968)
EU201063	<i>Pristimantis marmoratus</i>	“110BM”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
JN690707	<i>Pristimantis marmoratus</i>	“110BM”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
JN690708	<i>Pristimantis marmoratus</i>	“21AF”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
JN691315	<i>Pristimantis marmoratus</i>	“21AF”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
JN692010	<i>Pristimantis marmoratus</i>	“21AF”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
EU186692	<i>Pristimantis marmoratus</i>	ROM 43913	<i>Pristimantis saltissimus</i> (Means & Savage, 2007)
EU201062	<i>Pristimantis marmoratus</i>	“77MC”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
EU201063	<i>Pristimantis marmoratus</i>	“110BM”	<i>Pristimantis</i> sp. 1 (Fouquet <i>et al.</i> 2013)
JQ742170	<i>Pristimantis</i> cf. <i>marmoratus</i>	VUB 3626	<i>Pristimantis inguinalis</i> (Parker, 1940)
JQ742342	<i>Pristimantis</i> cf. <i>marmoratus</i>	VUB 3626	<i>Pristimantis inguinalis</i> (Parker, 1940)

“*unistrigatus* group” of Hedges *et al.* (2008) occurring in the Guiana Shield. This was with the aim of testing whether *P. marmoratus* is distinct from all other regional members of the group for which molecular data are available. To do so, we retrieved all the 16S sequences available at GenBank for members of that group in the Guiana Shield, including two sequences of specimens that we assigned to *P. marmoratus* based on morphology, and a sequence of *P. chiastonotus* Lynch & Hoogmoed, 1977 (*conspicillatus* group) to be used as outgroup. These 39 sequences were aligned with MAFFT v. 7 (Katoh & Standley 2013) and overlapped over 438 base pairs (bp), which were used for the phylogenetic analysis. We conducted a Bayesian analysis (BA) with MrBayes v. 3.1 (Huelsenbeck & Ronquist 2001) using the GTR+I+G substitution model as determined by jModeltest v. 2.0 (Darriba *et al.* 2012). The BA consisted of a 10×10^6 generations run starting with random trees and 4 Markov chains (one cold) sampled every 1000 generations. Adequate burn-in (the first 1000 sampled generations) was determined by examining likelihood scores of the heated chains for convergence on stationarity as well as the effective sample size of values in Tracer v. 1.5 (Rambaut & Drummond 2007). All parameters had effective sample sizes (ESS) largely over 200. Results were visualized and edited in FigTree v. 1.4.1 (Rambaut 2014). We considered relationships to be strongly supported when posterior probabilities were equal to or higher than 0.95.

We also calculated p-distances (pairwise deletion) among major lineages recovered from the phylogenetic analysis using MEGA 5 (Tamura *et al.* 2011).

DNA barcoding

DNA barcoding was used to unambiguously confirm the morphological identification of specimens that we assigned to the nominal species, and for which DNA sequences were not yet available at GenBank. Total genomic DNA was extracted from liver or thigh muscle using the Qiagen DNeasy® Tissue Kit following the manufacturer's instructions. The targeted "barcoding" fragment of 16S rDNA (ca 560 bp; Vences *et al.* 2005) was amplified and sequenced using the primers described by Simon *et al.* (1994) as modified by Bossuyt & Milinkovitch (2000) under previously described PCR conditions (Roelants *et al.* 2007). PCR products were checked on a 1% agarose gel and were sent to BaseClear (Leiden, The Netherlands) for purification and sequencing. These new sequences have been deposited in GenBank under the accession numbers MF037218-MF037223 (Appendix 3).

Taxonomy follows Padial *et al.* (2014). Institutional acronyms follow Frost (2016).

Results

Order Anura Fischer von Waldheim, 1813
 Superfamily Brachycephaloidea Günther, 1858
 Family Craugastoridae Hedges, Duellman & Heinicke, 2008
 Genus *Pristimantis* Jiménez de la Espada, 1870

Pristimantis marmoratus (Boulenger, 1900)

Figs 2–5, 6D

Diagnosis

Pristimantis marmoratus (Boulenger, 1900) has historically been assigned to the polyphyletic "unistrigatus species group" (*sensu* Hedges *et al.* 2008), which is mainly characterized by having Finger I shorter than II, Toe V longer than III, extending to the distal edge of the distal subarticular tubercle of Toe IV when toes are adpressed, and by the absence of cranial crests and the presence of vomerine teeth. *Pristimantis marmoratus* is characterized by the following unique combination of characters:

- (1) body small, adult males 17.6–20.4 mm SVL (n = 5), adult female 27.9 mm SVL (n = 1);
- (2) dorsal skin granular/pustulate, usually with distinctly enlarged tubercles (less pustulate in female), belly skin granular (granules not as closely set as in areolate skin *sensu* Duellman & Lehr 2009), sometimes becoming smooth in preservative;
- (3) presence of well-developed oblique scapular ridges in males (less prominent in female);
- (4) tympanum present, tympanic membrane not or only poorly differentiated, and tympanic annulus only partially visible externally, obscured by supratympanic fold, TYM 22–34% of EL;
- (5) small pharyngeal ostia present;
- (6) TIL 1.9–2.0 times HAND;
- (7) snout rounded to subovoid in dorsal view, slightly sloping in profile, *canthus rostralis* nearly straight in dorsal view, rounded in cross section, loreal region concave, flaring slightly at upper lip;
- (8) upper eyelid granular, with 1–3 distinctly enlarged tubercles on each eyelid;
- (9) choanae small, round, dentigerous processes of vomers small, sometimes barely visible or even not detectable, slightly oblique, ovoid, posterior and medial to choanae, each bearing 3–5 teeth when present;
- (10) presence of vocal slits in male, vocal sac single, subgular;
- (11) tongue cordiform;
- (12) one unpigmented whitish nuptial pad located on the preaxial side of the thenar tubercle on each thumb in male, a second pad is sometimes present (on one thumb or on both) on the preaxial side of the first subarticular tubercle;

- (13) Finger I shorter than II, FI 75–83% of FII in males, 86% of FII in female;
- (14) fingers basally webbed, with moderately developed lateral fringes, usually more conspicuously developed preaxially on Finger II;
- (15) palmar tubercle V-shaped, often broken in three distinct tubercles;
- (16) axillary tubercles (*sensu* Myers & Donnelly 2001) absent;
- (17) small ulnar tubercles present, in line;
- (18) small tarsal tubercles present, 1–3 slightly enlarged calcar tubercles present;
- (19) inner metatarsal tubercle oval, about 3–4 times the size of the round, projecting outer metatarsal tubercle;
- (20) Toe V longer than III, extending to the distal edge of the distal tubercle on Toe IV when toes are adpressed;
- (21) toes with lateral fringes, best developed preaxially on Toes II–IV, webbing basal between Toes II–V;
- (22) discs broadly expanded, elliptical;
- (23) in life, main dorsal colour pattern ranges from large, weakly visible, dark brown or grey-brown blotches to nearly uniformly brownish grey, ventral colouration ranges from whitish to grey or dark brown with series of tiny, dark brown punctuations and light grey flecking;
- (24) in preservative, main dorsal colour pattern similar to when alive, but with the melanin more prominent, revealing large, indistinct blotches or more or less uniformly distributed medium brown colour, ventral colouration consists in a uniformly distributed series of tiny, warm brown punctuations on the chin, belly and undersurfaces of the legs, feet and toes;
- (25) in life, anterior and lower posterior surfaces of thighs brown to dark brown with light grey flecking (brown with white flecking in preservative);
- (26) in life, diffuse yellow or pale green wash (white in preservative) on groin and absence of flashy colour on axillary/pre-axillary region;
- (27) in life, iris pale gold to bronze with fine black reticulations, a median horizontal brown to reddish brown bar, and a vertical streak running across the iris;
- (28) advertisement call consists in a single note repeated at a rate of ca 11 calls/min with a dominant frequency ranging from 2756 to 3101 Hz;
- (29) males call exclusively at dusk, usually upside down on mossy tree trunks of low diameter;
- (30) known elevational distribution ca 600 to 1800 m.

Material examined

Holotype

VENEZUELA: ♂, Bolívar State, foot of Mount Roraima, F.V. McConnell and J.J. Quelch leg., Aug.–Oct. 1898 (BMNH 1947.2.16.92, formerly 99.3.25.19).

Other material

GUYANA: 2 ♂♂, 1 juvenile, Cuyuni-Mazaruni District, slopes of Maringma-tepui, Philippe J.R. Kok leg., 20–22 Nov. 2007 (IRSNB 12862, IRSNB 17916, IRSNB 17939); 3 ♂♂, 1 ♀, Potaro-Siparuni District, Kaieteur National Park, Philippe J.R. Kok leg., 26–28 Jun. 2006 (IRSNB 14471-74).

The holotype (BMNH 1947.2.16.92, formerly 99.3.25.19; Fig. 2) is an adult male with large vocal slits (gender of the holotype was not provided in the original description).

Description of adult

Measurements are provided in Table 2. Adult males 17.6–20.4 mm SVL (n = 5), distinctly smaller than adult female 27.9 mm SVL (n = 1). Head slightly longer than wide, wider than body; HW 36–41% of SVL; HL 37–45% of SVL; cranial crests absent. Snout longer than eye length (SL 102–133% of EL), rounded to subovoid in dorsal view, slightly sloping in profile; *canthus rostralis* nearly straight in

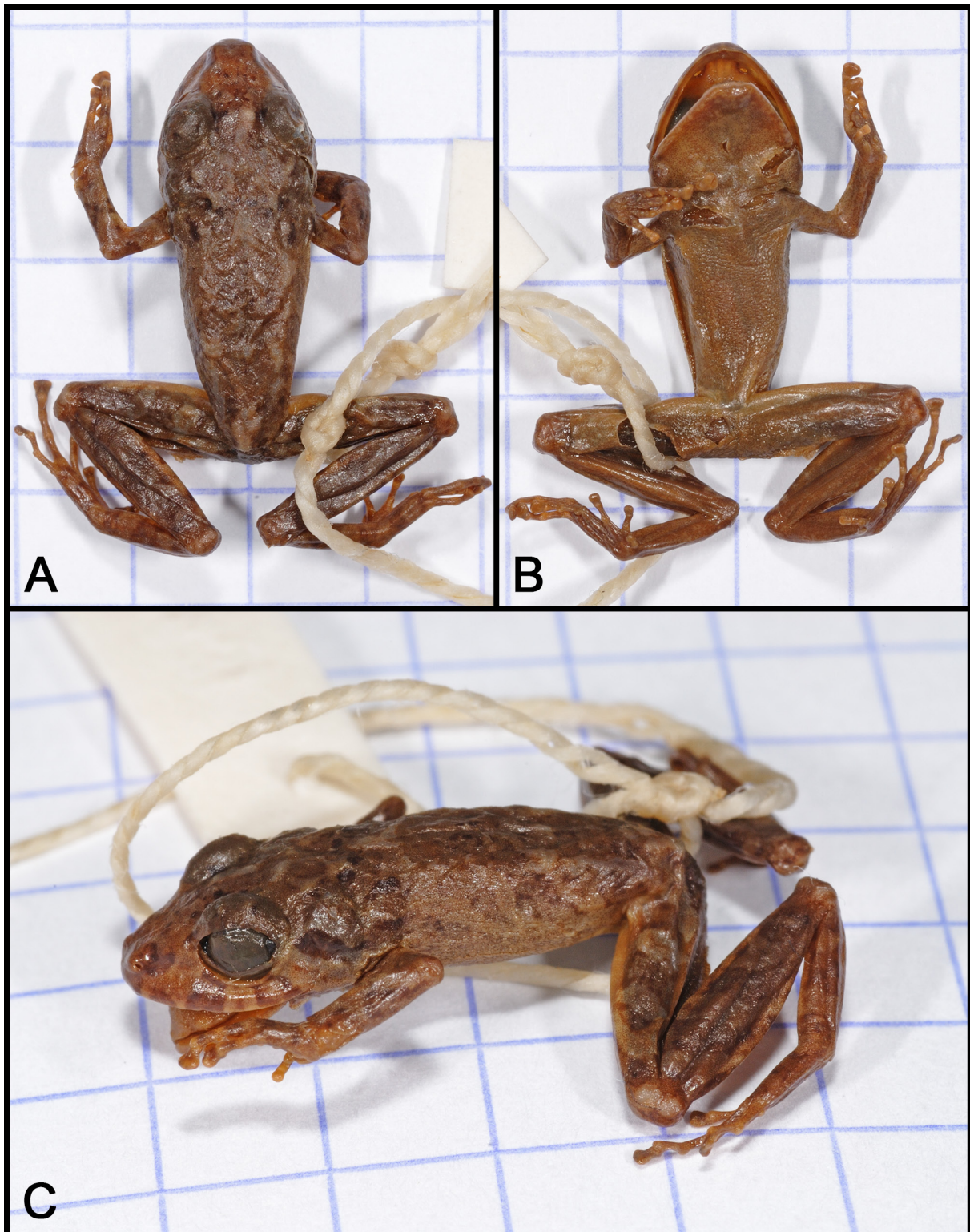


Fig. 2. *Pristimantis marmoratus* (Boulenger, 1900). Preserved adult ♂, holotype (BMNH 1947.2.16.92). A. Dorsal view. B. Ventral view. C. Dorsolateral view. Grid squares = 5 mm. Photographs by PJRK.

Table 2. Measurements (in mm) of the holotype of *Pristimantis marmoratus* (Boulenger, 1900) and new specimens assigned to the nominal species (see text for details).

Voucher	Holotype, BMNH 1947.2.16.92	IRSNB 14471	IRSNB 14472	IRSNB 14473	IRSNB 17939	IRSNB 12862	IRSNB 14474	IRSNB 17916
Gender	♂	♂	♂	♂	♂	♂	♀	Juvenile
SVL	17.9	19.4	19.0	17.6	20.4	20.2	27.9	11.3
HL	7.1	8.2	7.0	7.9	8.2	8.9	11.0	5.1
HW	6.4	7.0	7.1	6.8	7.7	8.3	10.2	4.5
SL	3.0	2.4	3.3	3.3	3.6	3.4	4.6	1.8
EN	1.9	2.4	3.1	2.4	2.6	2.6	3.0	1.3
IN	1.7	1.8	1.8	1.8	2.0	1.7	2.5	0.6
EL	2.7	3.6	2.8	2.8	3.5	3.4	3.5	1.9
IO	2.3	2.1	2.5	1.9	2.3	2.1	2.6	1.5
TYM	0.7	1.1	0.7	0.7	0.7	0.9	1.3	0.4
HAND	4.8	5.7	5.7	5.3	5.6	6.1	7.4	2.7
WFD	0.9	1.1	1.1	1.0	1.2	1.1	1.5	0.6
FL	7.1	8.4	8.3	7.6	8.2	10.1	9.0	4.3
WTD	0.8	1.1	1.0	1.1	1.3	1.0	1.3	0.6
TIL	9.7	10.8	10.9	10.2	11.0	11.9	14.0	5.9

dorsal view, rounded in cross section, loreal region concave, flaring slightly at upper lip; EN 80–110% of EL. Nares protuberant, directed posterolaterally, visible in front, dorsal and usually ventral views. Widest upper eyelid width equal or subequal to interorbital distance. Upper eyelid granular, with 1–3 distinctly enlarged tubercles on each eyelid. Tympanum present, tympanic membrane not or only poorly differentiated, tympanic annulus only partially visible externally, obscured by supratympanic fold, TYM 22–34% of EL; small pharyngeal ostia present. Choanae small, round, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers small, sometimes barely visible or even not detectable (e.g., in IRSNB 14473 on both sides, in IRSNB 17939 on left side, in IRSNB 14471 on right side), slightly oblique, ovoid, posterior and medial to choanae, each bearing 3–5 teeth when present. Tongue cordiform, slightly longer than wide, posterior half free. Vocal slits present in male, vocal sac single, subgular.

Dorsal skin texture fairly variable (probably depending on activity, as observed in several species of the genus; see for example Guayasamin *et al.* 2015), from granular to pustulate, including on head, usually with distinctly enlarged tubercles (dorsal skin less pustulate in female); well-developed oblique scapular ridges in males (less prominent in female); middorsal raphe not, or barely, detectable; supratympanic fold conspicuous in life, slightly arched, originating at posterior corner of eye, failing to reach shoulder; large post-riatal tubercles present; a weak dermal fold often present along upper flank; flanks granular. Throat surface smooth; upper chest smooth; weak thoracic fold; belly skin granular, those granules not as closely set as in so-called areolate skin (*sensu* Duellman & Lehr 2009), sometimes becoming smooth in preservative; weak discoidal fold anterior to groin; posteroventral thigh and cloacal region areolate; cloacal sheath absent.

Hand length 26–30% of SVL. Finger I 75–83% of FII in males, 86% of FII in female. Relative length of fingers III > IV > II > I; adpressed Finger I fails to reach proximal edge of digital pad of Finger II; adpressed Finger IV reaches beyond distal subarticular tubercle. One unpigmented whitish (translucent when wet) nuptial pad located on preaxial side of thenar tubercle on each thumb in male, a second

pad is sometimes present (on one thumb or on both) on preaxial side of first subarticular tubercle. Fingers basally webbed, with moderately developed lateral fringes, usually more conspicuously developed preaxially on Finger II. Finger discs broadly elliptical, broader than long, circumferential groove conspicuous; disc on Finger III ca three times as wide as distal end of adjacent phalanx. Palmar tubercle V-shaped, usually pigmented, often broken in three distinct small tubercles; thenar tubercle large, ovoid, protuberant; supernumerary tubercles few, large, subequal to subarticular tubercles, round and protuberant: subarticular tubercles large, round and protuberant, one each on FI and FII, two each on FII and FIV (Fig. 3). Ulnar tubercles small, in line. Axillary tubercles absent.

Hind limbs moderate in length, heels slightly overlap when held at right angles to sagittal plane; TIL 50–59% of SVL; FL 32% of SVL in female, 40–50% of SVL in males. Relative length of toes IV > V > III > II > I; tip of Toe V extends to distal edge of distal tubercle on Toe IV when toes are adpressed. Lateral fringes on all toes, best developed preaxially on Toes II–IV; webbing basal between Toes II–V. Toe discs subequal to finger discs, WTD/WFD 0.9; toe discs broadly expanded, elliptical, broader than long, circumferential groove conspicuous. Inner metatarsal tubercle elongate, oval, about 3–4 times size of round, projecting outer metatarsal tubercle; subarticular tubercles round, large and protuberant; supernumerary plantar tubercles small, low and round, increasing in size distally (Fig. 3). One to three slightly enlarged calcar tubercles present; outer tarsal tubercles few, low, barely detectable in preservative; inner tarsal fold short, straight to slightly curved.

Colour in life

The dorsal pattern of living specimens ranges from large, weakly visible, dark brown or grey-brown blotches to nearly uniformly brownish grey. Dorsolaterally, the pair of oblique scapular ridges is light grey on top and edged with black pigment, running from the level of the posterior of the eye to the level of the armpit. One specimen (IRSNB 14473) has distinct beige oblique lateral stripes running from tip of snout (where they fuse) to groin. Top of the forearm with a single, medial, dark brown band about one-third to one-half the width of the forearm; top of the thigh with three wide dark brown bands alternating with three light grey or reddish brown bands, all continuing onto the top of the tarsus. Diffuse yellow or paler green wash on groin. A dark blotch runs from over the ear to the angle of the mouth and two wide, dark vertical patches span from the eye to the upper lip (Fig. 4). *Canthus rostralis* not set off by colour from the snout or upper lip as in some other *Pristimantis* (e.g., in *P. pulvinatus*, see Fig. 4). Iris pale gold to bronze with fine black reticulations, a median horizontal brown to reddish brown bar, and a vertical streak running across the iris (Fig. 4). The ventral pattern is fairly variable and may change depending on light intensity, varying from whitish to grey or dark brown with series of tiny, dark brown punctuations and light grey flecking, the latter mostly on the belly. Skin on belly is translucent with some organs visible through it. Anterior and lower posterior surfaces of thighs are brown to dark brown with light grey flecking. Palms and soles are grey to dark brown.

Colour in preservative

Dorsal colour in specimens after ca 10 years in preservative is similar to when alive, but with the melanin more prominent, revealing the large, indistinct blotches on some specimens and a more or less uniformly distributed medium brown colour on others. Relatively distinct light areas in the shape of a V extend backward from the posterior of the orbit with the apex of the V terminating at the scapular ridges at the level of the insertion of the forelimbs; margins of the light V patch are usually edged with black pigment. The dark transverse bands on the forearm and legs described for living frogs are much more pronounced in preserved specimens. Anterior and lower posterior surfaces of thighs are light brown with white flecking. The diffuse yellow/pale green wash on the groin present in life becomes immaculate white in preservative. Ventral colouration is a uniformly distributed series of tiny, warm brown punctuations on the chin, belly, and undersurfaces of the legs, feet, and toes (Fig. 5). The preserved holotype (> 115 years



Fig. 3. *Pristimantis marmoratus* (Boulenger, 1900). Ventral view of left hand and left foot of a male (top), and ventral view of right hand and right foot of a female (below), both from Kaieteur National Park, Guyana. Photographs by PJRK.

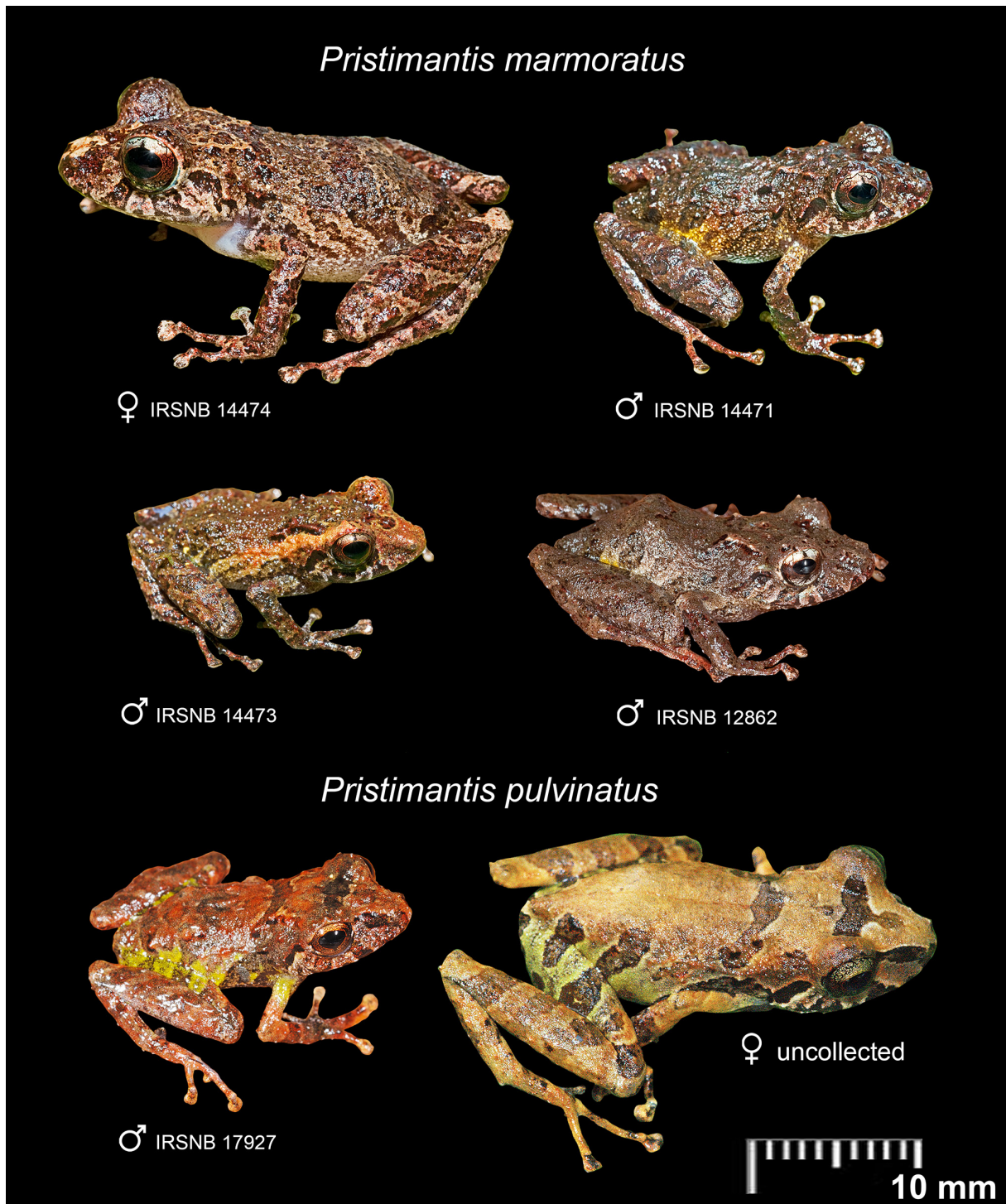


Fig. 4. *Pristimantis marmoratus* (Boulenger, 1900) (four individuals at the top) and *P. pulvinatus* (Rivero, 1968) (two individuals below). Intraspecific variation in dorsal colour pattern and sexual dimorphism in living specimens. Note: the subtle hint of green visible on the lower body and legs of some specimens of *P. marmoratus* is due to a reflection of the substrate (green leaf). Photographs by PJRK, except the uncollected *P. pulvinatus*, which is by CBA.

in preservative, Fig. 2) has a similar colour pattern as the other specimens examined, except that its skin has turned completely brown dorsally and ventrally, and some markings have faded.

Colour in juvenile

The colour pattern of one live juvenile (Fig. 6D) was similar to that of the adults, except that a wide band of black pigment wrapped around the anterior one-third of the body from the middle of the belly to between the eyes and the top the orbits, including the forearms and feet. Another blotch of black pigment covered one-fifth of the posterior of the back and cloaca as well as on the opposing parts of the heels and tips of the knees. Light brown colour with a faint stippling of tiny dark brown dots formed a dorsal saddle between the darkly pigmented areas and coloured the entire snout, top of the hind limbs, a roundish blotch over the ear, and on top of the two small warty scapular ridges. As in the adults, three medium brown, transverse crossbands are evident on top of all three segments of the hind limbs, continuing from the sides of the body. Two prominent, black-pigment-fringed, medium brown dorsoventral streaks run from the bottom of each orbit to the upper lip. As in adults, the iris is bronze with fine black reticulations, a median horizontal reddish brown bar and a vertical streak running across the iris. The ventral parts of the juvenile were completely black covered by light grey and light greenish brown flecks.

Sexual dimorphism

Sexual dimorphism is evident in size (Figs 4–5), with the only known adult female being much larger than adult males (max. 20.4 mm SVL in males vs 27.9 mm SVL in female), and by the presence of 1–2 whitish nuptial pads in males. Since only one female is known, possible sexually dimorphic characters are hard to evaluate, but we nevertheless note differences in the dorsal skin texture (less tuberculate in the female, with less prominent oblique scapular ridges; Figs 4–5). No evident sexual dichromatism is detected, although the only known female has a large whitish unpigmented blotch on the lower throat and upper chest, which is absent in males (Fig. 5). Compared to SVL, hands and tibia are slightly longer in males than in the only known female (HAND 27–30% vs 26% of SVL in female; TIL 54–59% vs 50% of SVL in female), and feet are longer in males than in the only known female (FL 40–50% vs 32% of SVL in female). No additional significant difference was detected in other size ratios.

Comparison with other species from the Guiana Shield

The combination of $FI < II$, $SVL \leq 20.4$ in males, presence of vocal slits in males, granular/pustulate dorsal skin with well-developed scapular ridges, basal webbing between fingers, fringes on fingers and toes, crossed iris, diffuse yellow or pale green wash on groin, absence of flashy colour on axillary/pre-axillary region, and absence of conspicuous canthal stripe immediately distinguish *Pristimantis marmoratus* from all described congeners reported from the Guiana Shield, lowlands included.

More specifically compared to the 23 described species of *Pristimantis* currently reported from the Guiana Shield uplands and highlands (i.e., between ca 400 and 2900 m elevation), *Pristimantis marmoratus* is immediately distinguished from *P. abakapa* Rojas-Runjaic, Salerno, Señaris & Pauly, 2013, *P. aureoventris* Kok, Means & Bossuyt, 2011, *P. auricarens* (Myers & Donnelly, 2008), *P. cantitans* (Myers & Donnelly, 1996), *P. dendrobatoides* Means & Savage, 2007, *P. imthurni* Kok, 2013, *P. jamescameroni* Kok, 2013, *P. jester* Means & Savage, 2007, *P. marahuaka* (Fuentes-Ramos & Barrio-Amorós, 2004), *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías & McDiarmid, 2010, *P. saltissimus* Means & Savage, 2007, *P. yaviensis* (Myers & Donnelly, 1996), and *P. yuruniensis* Rödder & Jungfer, 2008, by the presence of large vocal slits in males (absent in the aforementioned species); from *P. guaiquinimensis* (Schlüter & Rödder, 2007) (male unknown, see Kok & Barrio-Amorós 2013) mainly in having granular/tuberculate skin (smooth to finely granular in *P. guaiquinimensis*), fringes on fingers and toes (absent in *P. guaiquinimensis*), basal webbing between most fingers and toes

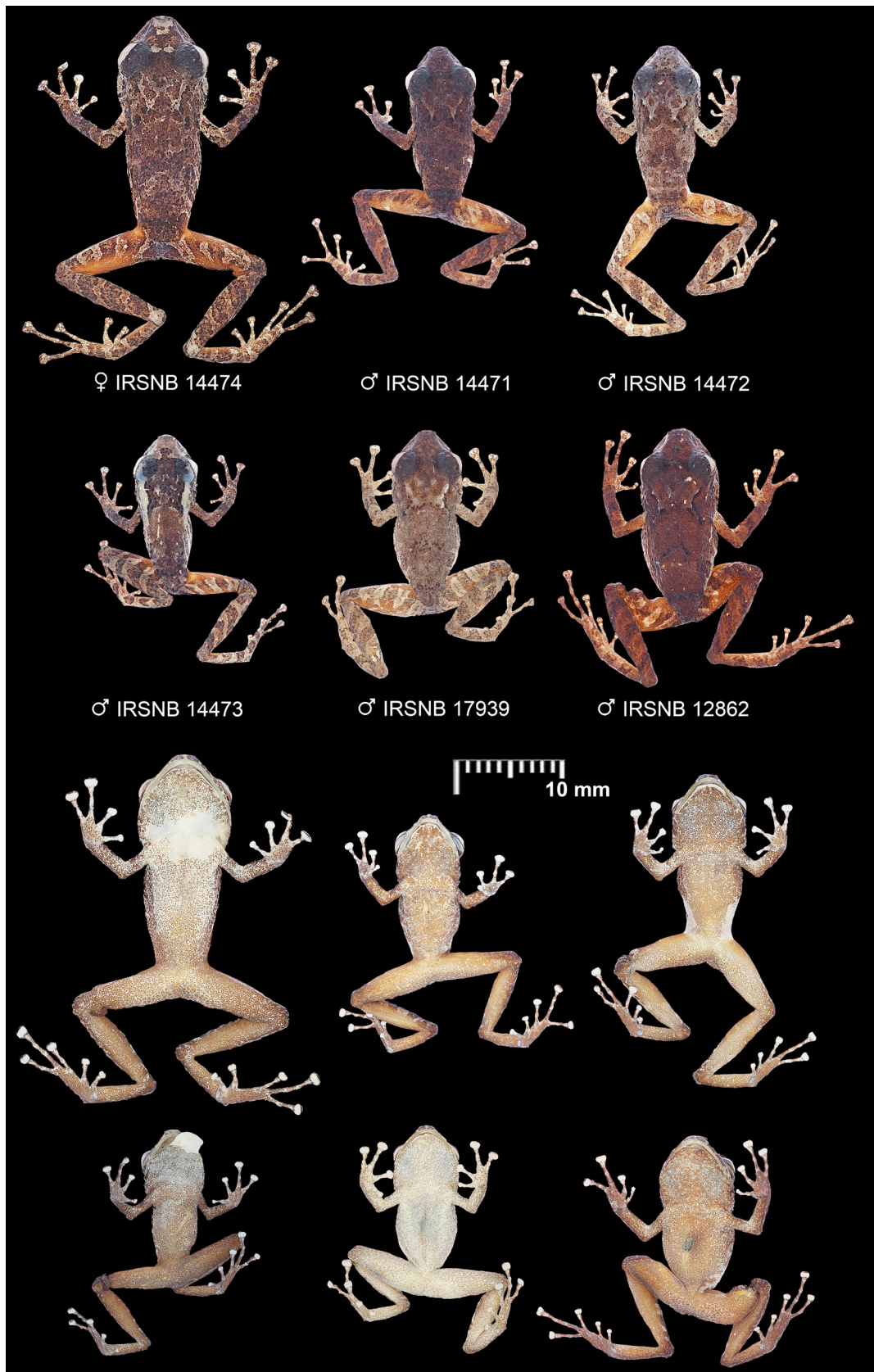


Fig. 5. *Pristimantis marmoratus* (Boulenger, 1900). Intraspecific variation in dorsal (top) and ventral (below) colour patterns in preserved specimens. Photographs by PJRK.

(absent), and smaller SVL in female (27.9 mm in *P. marmoratus* vs 32.4–34.7 in *P. guaiquinimensis*); and from *P. vilarsi* (Melin, 1941) and *P. zeuctotylus* (Lynch & Hoogmoed, 1977) mainly in having $FI < II$ ($FI > II$ in *P. vilarsi* and *P. zeuctotylus*). The remainder seven described *Pristimantis* species found in the Guiana Shield uplands and highlands also have vocal slits in males. Compared to those, *P. marmoratus* is mainly distinguished from *P. avius* (Myers & Donnelly, 1997) (endemic to the Sierra Tapirapécó, Amazonas State, Venezuela) by its smaller size (17.6–20.4 mm SVL in males, 27.9 mm SVL in female in *P. marmoratus* vs 20.0–24.0 mm SVL in males, 31.0–33.0 mm SVL in females in *P. avius*), absence of yellow or orange colouring on ventral surface (present in *P. avius*), presence of a vertical streak running across the iris (absent in *P. avius*), and presence of fringes on fingers and toes (absent in *P. avius*); from *P. cantitans* (Myers & Donnelly, 1997) (endemic to Cerro Yaví, Amazonas State, Venezuela) mainly by its much smaller size (17.6–20.4 mm SVL in males, 27.9 mm SVL in female in *P. marmoratus* vs 24.9–34.5 mm SVL in males, 31.9–44.7 mm SVL in females in *P. cantitans*), presence of a vertical streak running across the iris (absent in *P. cantitans*), diffuse yellowish/pale green colouration on groin and absence of colourful marking on posterior thigh surface (*P. cantitans* has the posterior thigh surface blackish with yellow flecking, and with a rose wash in the groin, anterior thigh, and concealed

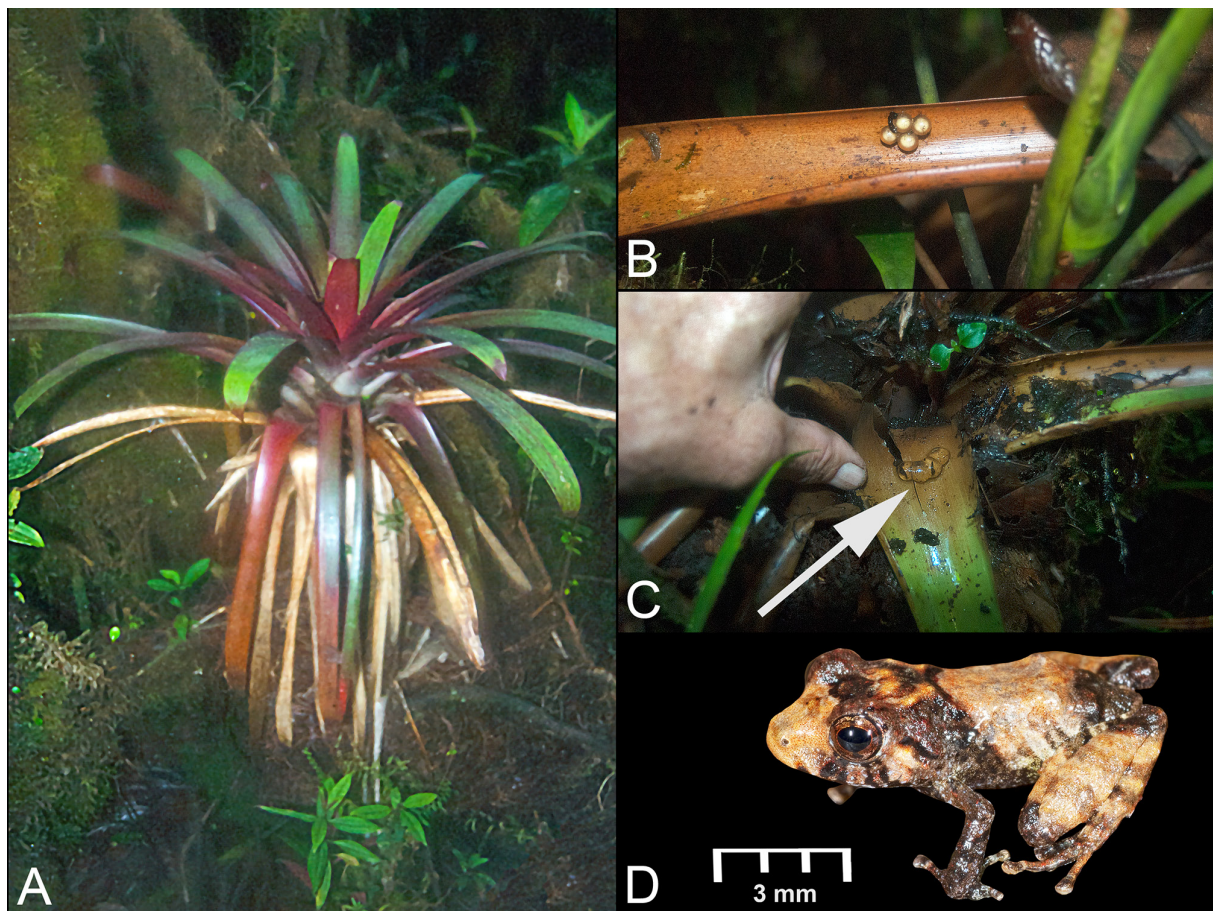


Fig. 6. A. *Guzmania* cf. *sphaeroidea* (André) André ex Mez, an arboreal bromeliad species used as egg deposition site by *Pristimantis marmoratus* (Boulenger, 1900) in the Wokomung Massif. B. Egg clutch of *Pristimantis marmoratus* deposited on a leaf of the arboreal bromeliad *Guzmania* cf. *sphaeroidea* in the Wokomung Massif. C. Egg clutch of *Anomaloglossus beebei* (Noble, 1923) (white arrow) deposited in the phytotelmata of the same plant as in B. D. Dorsolateral view of IRSNB 17916, 11.3 mm SVL, a juvenile of *P. marmoratus* collected on the slopes of Maringma-tepui, Guyana. Photographs A–C by DBM, D by PJRK.

portion of the shank); from *P. espedeus* Fouquet, Martinez, Courtois, Dewynter, Pineau, Gaucher, Blanc, Marty & Kok, 2013 (reported only between 200 and 700 m elevation in French Guiana) mainly by its smaller size (17.6–20.4 mm SVL in males, 27.9 mm SVL in female in *P. marmoratus* vs 20.7–24.8 mm SVL in males, 29.4 mm SVL in female in *P. espedeus*), diffuse yellowish/pale green colouration on groin (*P. espedeus* has the anterior surface of thighs and groin reddish), no sharp demarcation between dorsal and flank colours (present in *P. espedeus*) and presence of a vertical streak running across the iris (absent in *P. espedeus*); from *P. memorans* (Myers & Donnelly, 1997) (reported only from the Sierra Tapirapécó in Amazonas State, Venezuela, and adjacent Amazonas State in Brazil) by the presence of fringes on fingers and toes (absent in *P. memorans*), presence of a vertical streak running across the iris (absent in *P. memorans*) and in having a diffuse yellowish/pale green colouration on groin (absent in *P. memorans*); from *P. pruinatus* (Myers & Donnelly, 1996) (known only from Cerro Yaví, Amazonas State, Venezuela) by the presence of fringes on fingers and toes (absent in *P. pruinatus*), in having the tip of Toe V extending to the distal edge of the distal tubercle on Toe IV when toes are adpressed (extends only midway to proximal edge of ultimate subarticular tubercle on Toe IV in *P. pruinatus*), presence of a vertical streak running across the iris (absent in *P. pruinatus*), absence of dark orange brown on ventral surface and anterior and posterior thigh surfaces (present in *P. pruinatus*), and discernible dorsal colour pattern in preservative (dorsum patternless, blackish grey in *P. pruinatus*); from *P. pulvinatus* (Rivero, 1968), reported from the uplands of the Gran Sabana region of south-eastern Venezuela to adjacent western Guyana, therefore sympatric with *P. marmoratus*, mainly in having a vertical streak running across the iris (upper part of streak absent in *P. pulvinatus*, see Fig. 4), prominent scapular ridges in males (absent or usually fainter in *P. pulvinatus*, see Fig. 4), *canthus rostralis* not conspicuously marked (dark canthal stripe present in *P. pulvinatus*, see Fig. 4), absence of broad, conspicuous, dorsal dark bands between eyes and between axilla (usually present in *P. pulvinatus*, see Fig. 4 and Rivero 1968: fig. 1), and in lacking any flashy colour on axillary/pre-axillary region (present, green in *P. pulvinatus*, see Fig. 4); and from *P. sarisarinama* Barrio-Amorós & Brewer-Carías, 2008 (endemic to Sarisariñamatepui, Bolívar State, Venezuela) mainly by the presence of fringes on fingers and toes (absent in *P. sarisarinama*), in having a vertical streak running across the iris (absent in *P. sarisarinama*) and in having a diffuse yellowish/pale green colouration on groin (absent in *P. sarisarinama*).

Advertisement call

Temporal structure

The advertisement call of *Pristimantis marmoratus* consists of a single, unpulsed (tonal) note repeated at a rate of 11.25–11.87 calls/min. Mean call duration is 0.0184 ± 0.002 s (0.016–0.023 s). The inter-call silent interval is relatively uniform and has a mean of 6.011 ± 0.9 s and a range of 5.023–7.958 s (Figs 7–8).

Spectral structure

Four to five harmonics are developed, with the dominant frequency located in the first (fundamental) harmonic (mean: 3047 ± 121 Hz; range: 2756–3101 Hz) (Figs 7–8). Calls show a downward followed by a slightly upward frequency modulation (Fig. 8).

Comparison with other *Pristimantis* calls in the Guiana Shield uplands and highlands

To the best of our knowledge, only three uplands/highlands *Pristimantis* species for which documented calls are known produce a single note per call: *P. aureoventris* from above 2200 m elevation on Wei-Assiputepui and on the highest slopes of Mt. Roraima (Kok *et al.* 2011), *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías & McDiarmid, 2010 from above 2300 m elevation on Churi-tepui, and *P. yuruanensis* Rödder & Jungfer, 2008 from above 2300 m on Yuruaní-tepui. The call of *P. aureoventris* mainly differs in having a lower dominant frequency (2180–2430 Hz vs 2756–3101 Hz in *P. marmoratus*), and a higher call rate (18 calls/min vs ca 11 calls/min in *P. marmoratus*). The call of *P. muchimuk* is longer (0.027–0.062 s vs 0.016–0.023 s in *P. marmoratus*) and emitted at a much faster pace (> 100 calls/min vs ca 11

calls/min in *P. marmoratus*). The call of *P. yuruaniensis* is longer (0.093–0.139 s vs 0.016–0.023 s in *P. marmoratus*) and the dominant frequency is at 1980 Hz (2756–3101 Hz in *P. marmoratus*).

Interestingly, the call of *Pristimantis marmoratus* is extremely similar to the call of *P. inguinalis* (Parker, 1940), a species known from the lowlands of the eastern Guiana Shield, east of the Essequibo River. Both species have an unpulsed single note call with a dominant frequency within the same range. Based on our analysis of a call of *P. inguinalis* provided in Marty & Gaucher (1999) and partial data from Fouquet *et al.* (2013), the only differences found are (1) a slightly longer call length in *P. inguinalis* (0.023–0.032 s vs 0.016–0.023 s in *P. marmoratus*); (2) a slightly higher call rate in *P. inguinalis* (17.91 calls/min vs 11.25–11.87 calls/min in *P. marmoratus*); and (3) a slightly shorter inter-call silent interval

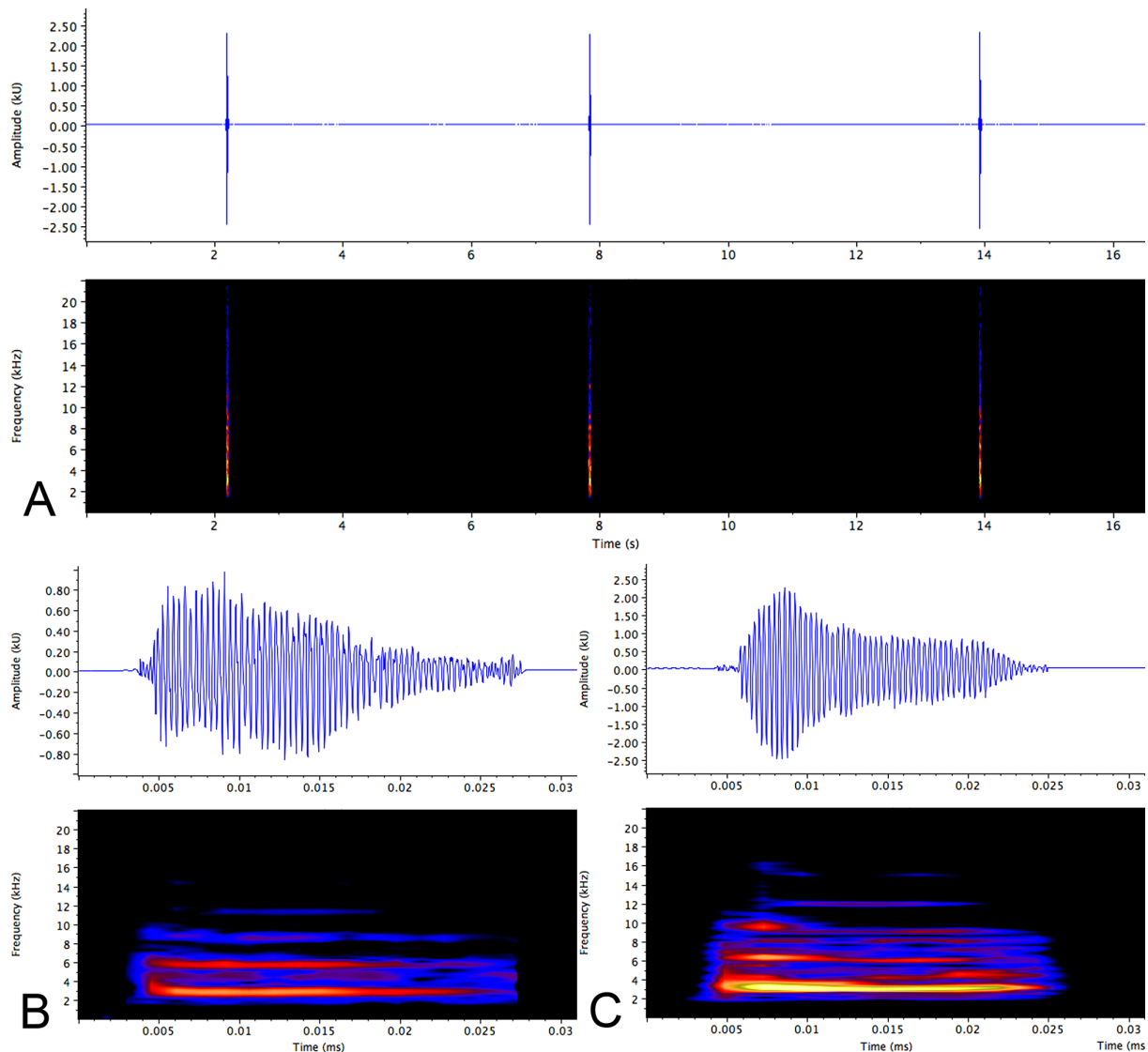


Fig. 7. Vocalization of *Pristimantis marmoratus* (Boulenger, 1900); oscillograms and spectrograms obtained using Raven v. 1.4. **A.** Oscillogram (top) and spectrogram (below) of three calls of IRSNB 14472 from Kaieteur National Park, Guyana (ca 16 s recording). **B.** Expanded oscillogram (top) and spectrogram (below) of one call of IRSNB 14471 from Kaieteur National Park, Guyana. **C.** Expanded oscillogram (top) and spectrogram (below) of one call of IRSNB 14472 from Kaieteur National Park, Guyana. Calls recorded at a temperature of 24°C.

in *P. inguinalis* (3.16–3.85 s vs 5.02–7.96 s in *P. marmoratus*). See Discussion for further comments about distribution and phylogenetic relationships; see also fig. 6 in Fouquet *et al.* (2013) for comparison.

Distribution

Pristimantis marmoratus is currently known only from – west to east – the La Escalera region in Venezuela, the southern base of Mount Roraima in Venezuela (type locality) and the north-eastern base of Mount Roraima in Guyana (Double Drop Falls), the slopes of Maringma-tepui along the border between Guyana and Brazil, Mount Ayanganna in Guyana (MacCulloch & Lathrop 2009), the Wokomung Massif in Guyana and Kaieteur National Park in Guyana (Fig. 1). The species occurs between ca 600 and 1800 m above sea level, and is probably restricted to the pristine submontane and montane rainforests of the Pantepui uplands and highlands, east of the Gran Sabana, i.e., the Eastern Pantepui District of

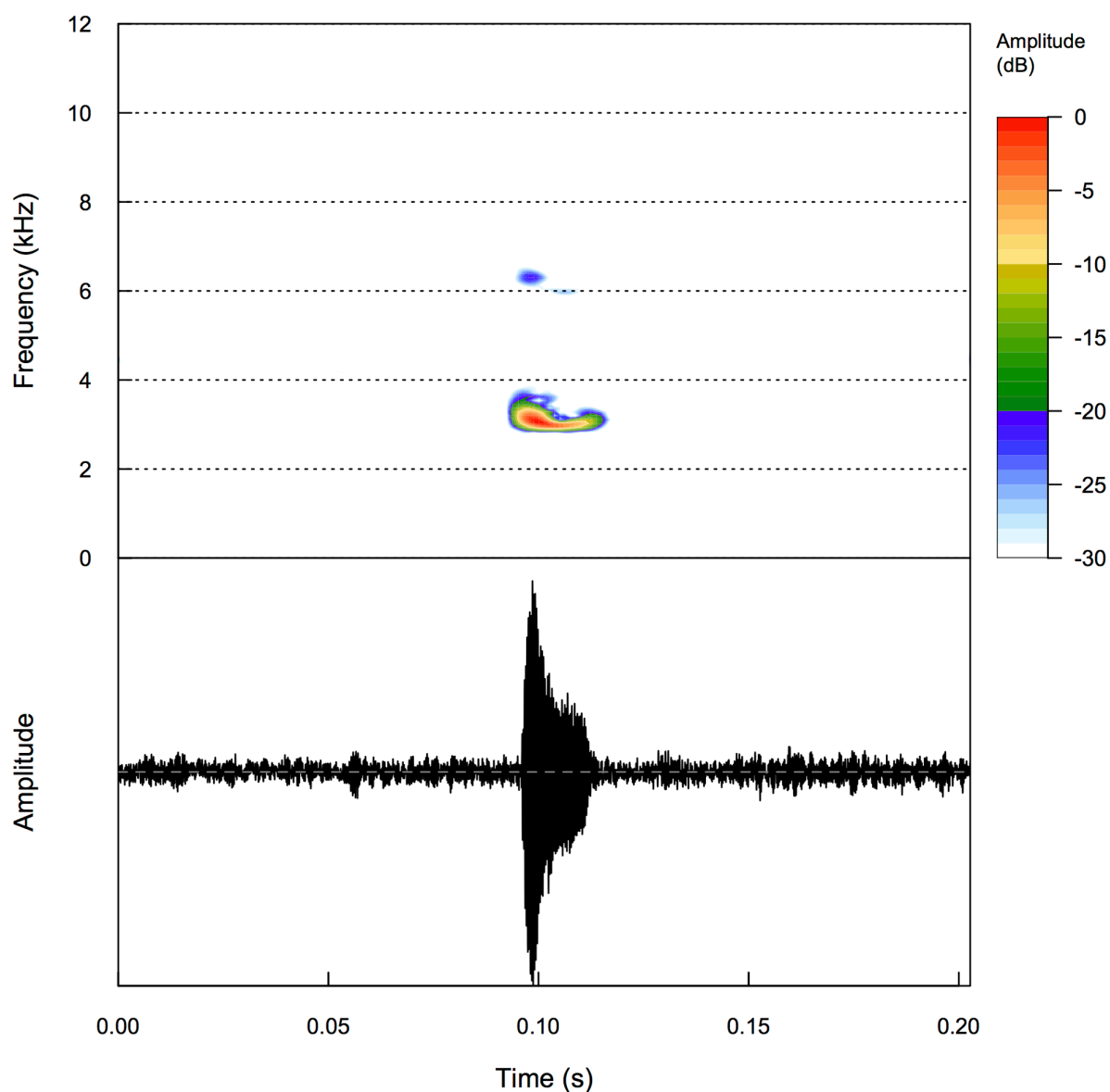


Fig. 8. Vocalization of *Pristimantis marmoratus* (Boulenger, 1900); oscillogram and spectrogram obtained using Seewave v. 1.6.4 in R. Spectrogram (top) and oscillogram (below) of one call of IRSNB 14472 from Kaieteur National Park, Guyana. Call recorded at a temperature of 24°C.

McDiarmid & Donnelly (2005). Its occurrence in northern Brazil is very likely, since parts of the slopes of Maringma-tepui are in Brazil (Fig. 1).

Natural history

All specimens were found in undisturbed submontane or montane rainforest (Fig. 9), active on small trees 50–300 cm above the ground, exclusively at dusk. *Pristimantis marmoratus* is not a common species; only a few specimens have been found at each locality of occurrence. Males were found calling (in June and November) upside down from mossy tree trunks of low diameter (< 10 cm) between 120 and 300 cm above the ground, except one male (IRSNB 14473), which was calling from the top of a green leaf 50 cm above the ground. The “upside down” call posture is also found in the closely related *P. sp. 1* of Fouquet *et al.* (2013) (as recovered in our preliminary molecular phylogenetic analysis, see below), and in *P. espedeus* and *P. inguinalis*.

In June 2012, which corresponds to the rainy season in the area, a cluster of four *Pristimantis marmoratus* eggs (Fig. 6B) was found by one of us (DBM) attached to the inside part of a leaf of a bromeliad, *Guzmania cf. sphaeroidea* (André) André ex Mez (Fig. 6A), 150 cm above the ground, on Mount Kopinang, Wokomung Massif, near the top of Kamana Falls at about 1600 m elevation (04°59'58" N, 59°52'49" W). Molecular analyses confirmed conspecificity of these eggs with *P. marmoratus* (Appendix 3). The large, white eggs did not have visibly developed embryos. After photographing



Fig. 9. Habitat of *Pristimantis marmoratus* (Boulenger, 1900). **Left.** Submontane rainforest in Kaieteur National Park at ca 630 m elevation. **Right.** Montane rainforest on the slopes of Maringma-tepui, Guyana at ca 1376 m elevation. Photographs by PJRK.

and preserving the eggs, the small plant was investigated for inhabitants of the aquatic portion of the phytotelmata. Immediately a small frog jumped out and disappeared into the deep ground litter, and eggs and tadpoles of *Anomaloglossus beebei* (Noble, 1923) were found in the water of the phytotelmata of the same small bromeliad and in the water of five other bromeliads nearby (egg/frog identifications confirmed by molecular analyses). *Pristimantis marmoratus* and *Anomaloglossus beebei* thus share the same bromeliad as an oviposition site on the Wokomung Massif (Fig. 6C). Other *Pristimantis* species found in syntopy with *P. marmoratus* were *P. dendrobatoides* (above 1600 m elevation), *P. jester* (above 1300 m elevation), *P. saltissimus* (above 1000 m elevation), and *P. pulvinatus* (above 1000 m elevation).

Phylogenetic relationships

Other *Pristimantis* species have often been confused with *Pristimantis marmoratus* (see below and Table 1). Available phylogenetic analyses using samples from misidentified specimens are thus unreliable for that taxon (e.g., Hedges *et al.* 2008; Pyron & Wiens 2011; Canedo & Haddad 2012; Kok *et al.* 2012; Padial *et al.* 2014; Mendoza *et al.* 2015; see below).

Our molecular phylogenetic analysis based on a single mitochondrial gene (16S) of correctly identified – or reidentified – specimens of the *Pristimantis* “*unistrigatus* group” in the Guiana Shield recovered *Pristimantis marmoratus* as unambiguously distinct from all the other included members of the group (Fig. 10). The gene fragment we used is short and many members of the “*unistrigatus* group” occurring outside the Guiana Shield have not been included. Therefore, our analysis remains limited in deciphering the phylogenetic position and affinities of *P. marmoratus* with the other species of the genus. Nevertheless, our analysis recovered *P. marmoratus* as the sister species (with strong support, $pp = 0.98$) of an unnamed *Pristimantis* species from the lowlands of French Guiana and Amapá State (Brazil), called *P. sp. 1* by Fouquet *et al.* (2013). However, the lowest genetic distances (0.077) are found between *P. marmoratus* and other Pantepui species (*P. abakapa* and *P. sp. Ayanganna*, see Table 3).

Discussion

Confusion between *Pristimantis marmoratus* and similar or undescribed species has been common in the literature. This is not surprising because in preservative some species are very hard (if not impossible) to distinguish since some important diagnostic characters may disappear (e.g., colour pattern, colour of iris, skin texture). Reports of *P. marmoratus* in French Guiana by Lescure (1981) for example, and later by Lescure & Marty (2001), correspond to at least two different undescribed lowland species (Fouquet *et al.* 2013); reports of *P. marmoratus* from the slopes of Marahuaka-tepui, Amazonas State in Venezuela (Rivero 1961), the Mabura Hill Forest Reserve in central Guyana (Ernst *et al.* 2005), Suriname (Ouboter & Jairam 2012), Amapá State in Brazil (Dias Lima 2008) and northern Pará State in Brazil (Avila-Pires *et al.* 2010) are most probably the result of misidentifications with other related species.

Kok *et al.* (2012, suppl. info.) presented a molecular phylogenetic tree showing that two specimens of “*P. pulvinatus*” from La Escalera in Venezuela (type locality of the species) fall into two different clades, suggesting the occurrence of two morphologically similar species in that region. In fact, Duellman’s (1997) report of *P. pulvinatus* in La Escalera, is based on both *P. pulvinatus* and *P. marmoratus* (KU18105 was not examined by us, but is reidentified here as *P. marmoratus* based on molecular data); Hedges *et al.* (2008) provided a sequence of *P. pulvinatus* from La Escalera, Venezuela, based on a misidentified specimen of *P. marmoratus* (KU18105, see above) and a sequence of *P. marmoratus* from Guyana based on a misidentified specimen of *P. saltissimus*; Kok & Kalamandeen’s (2008) report of *P. inguinalis* from Kaieteur National Park, Guyana, is exclusively based on specimens of *P. marmoratus* (these authors have been confused by the extreme similarity of the calls of these species and by the yellowish wash on the groin in *P. marmoratus*); Pyron & Wiens (2011) inferred the phylogenetic position of *P. marmoratus*

based on two misidentified specimens, one being *P. saltissimus* and the other one being the *P. sp. 1* of Fouquet *et al.* (2013); Kok *et al.* (2012) provided a sequence of *P. cf. marmoratus* from French Guiana based on a misidentified juvenile specimen of *P. inguinalis*; Cole *et al.* (2013, plate 17 E) provided a photograph of *P. marmoratus* from Guyana that corresponds to *P. saltissimus*, and a photograph of *P. saltissimus* from Guyana (plate 17 F) that corresponds to *P. marmoratus*. Canedo & Haddad (2012), Padial *et al.* (2014) and Mendoza *et al.* (2015) inferred the phylogenetic position of *P. marmoratus* based on a sample assigned to *P. saltissimus*. Several incorrect identifications thus occur in GenBank; reidentifications are provided in Table 1.

Because the report of *Pristimantis inguinalis* from Kaieteur National Park in Guyana (Kok & Kalamandeen 2008) is in error (see above), the distribution of *P. inguinalis* is likely restricted to the eastern Guiana Shield lowlands, east of the Essequibo River (Guyana).

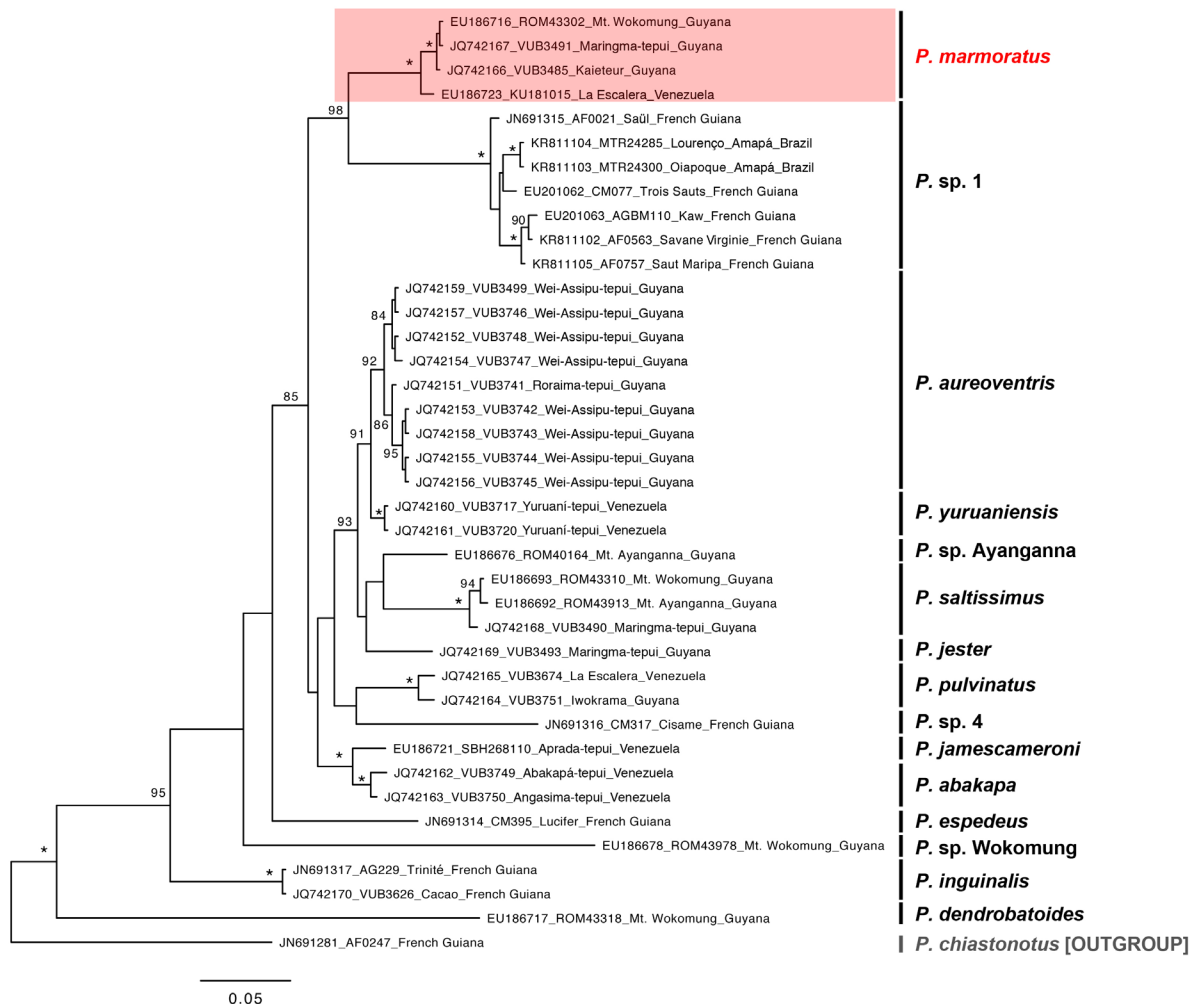


Fig. 10. Phylogenetic relationships within the *Pristimantis* “*unistrigatus* group” in the Guiana Shield as recovered in the MrBayes analysis (438 bp of the 16S rRNA gene sequence). Values at each node represent statistical support (* = 0.99 or 1). *Pristimantis marmoratus* (Boulenger, 1900) is highlighted in red.

Table 3. Mean genetic distances (p-distances) among major lineages of the *Pristimantis* “*unistrigatus* group” in the Guiana Shield using pairwise deletion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>P. marmoratus</i>														
2 <i>P. abakapa</i>	0.077													
3 <i>P. sp. Ayanganna</i>	0.077	0.063												
4 <i>P. aureoventris</i>	0.080	0.053	0.036											
5 <i>P. yuruaniensis</i>	0.080	0.053	0.038	0.015										
6 <i>P. jamescameroni</i>	0.089	0.026	0.072	0.063	0.060									
7 <i>P. pulvinatus</i>	0.097	0.064	0.064	0.063	0.060	0.062								
8 <i>P. jester</i>	0.099	0.077	0.063	0.047	0.048	0.084	0.078							
9 <i>P. inguinalis</i>	0.113	0.104	0.116	0.113	0.121	0.114	0.121	0.126						
10 <i>P. saltissimus</i>	0.113	0.077	0.067	0.059	0.053	0.078	0.078	0.079	0.140					
11 <i>P. espedeus</i>	0.115	0.112	0.119	0.121	0.124	0.127	0.116	0.145	0.133	0.136				
12 <i>P. sp. 1</i>	0.121	0.108	0.123	0.108	0.115	0.109	0.116	0.137	0.133	0.129	0.143			
13 <i>P. sp. 4</i>	0.126	0.102	0.113	0.102	0.099	0.101	0.106	0.106	0.138	0.126	0.144	0.138		
14 <i>P. sp. Wokomung</i>	0.183	0.168	0.164	0.160	0.171	0.161	0.155	0.176	0.173	0.182	0.168	0.188	0.167	
15 <i>P. dendrobatoides</i>	0.211	0.217	0.206	0.210	0.216	0.219	0.220	0.216	0.213	0.216	0.204	0.219	0.203	0.216

Given our results, the taxonomic status of *Hylodes grandoculis* Van Lidth de Jeude, 1904 [a synonym of *P. marmoratus* according to Hoogmoed (in Frost 1985)] from the Coppename basin in Suriname should be reassessed.

Pristimantis marmoratus is currently listed as Least Concern (LC) “in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining to qualify for listing in a more threatened category” (MacCulloch *et al.* 2010). Our study indicates that *P. marmoratus* has a more restricted range than previously thought, and we cannot confirm any tolerance to habitat modification (the species is restricted to pristine submontane and montane rainforests within its known range). However, since the distribution of *P. marmoratus* spans over relatively untouched areas of the Eastern Pantepui District and no decline could be demonstrated so far, we suggest maintaining its IUCN conservation status as LC, a category that applies to taxa that do not qualify (and are not close to qualifying) as Threatened or Near Threatened (IUCN Standards and Petitions Subcommittee 2016).

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Appendix 1

Additional material examined

Pristimantis abakapa: VENEZUELA, Estado Bolívar, Abakapá-tepui, IRSNB 15868 (topotypic specimen).

Pristimantis aureoventris: GUYANA, Cuyuni-Mazaruni District, Wei-Assipu-tepui, IRSNB 4152 (holotype), IRSNB 4153-54 (2 paratopotypes).

Pristimantis auricarens: VENEZUELA, Estado Bolívar, Auyán-tepui, A-164951-53 (3 paratopotypes), A-164936-50, A-164954 (16 paratypes).

Pristimantis avius: VENEZUELA, Estado Amazonas, Pico Tamacuari, A-131481 (holotype).

Pristimantis cantitans: VENEZUELA, Estado Amazonas, Cerro Yaví, A-143359-61 (3 paratopotypes).

Pristimantis dendrobatoides: GUYANA, Potaro-Siparuni District, Wokomung Massif, USNM 563662 (holotype), IRSNB 15918 (topotypic specimen).

Pristimantis espedeus: FRENCH GUIANA, Municipality of Régina, Montagne Grande Tortue, R121 (holotype).

Pristimantis guaiquinimensis: VENEZUELA, Estado Bolívar, Guaiquinima-tepui, SMNS 8004.1 (holotype), SMNS 8004.2 (paratype), SMNS 8005 (holotype of *P. tepuiensis*).

Pristimantis imthurni: VENEZUELA, Estado Bolívar, Aprada-tepui, IRSNB 4165 (holotype).

Pristimantis inguinalis: GUYANA, East Berbice-Corentyne District, New River, BMNH 1939.1.1.1 (holotype), BMNH 1939.1.1.2 (paratype).

Pristimantis jamescameroni: VENEZUELA, Estado Bolívar, Aprada-tepui, IRSNB 4140 (holotype), IRSNB 4161-64 (4 paratopotypes).

Pristimantis jester: GUYANA, Potaro-Siparuni District, Wokomung Massif, USNM 563631 (holotype); Cuyuni-Mazaruni District, slopes of Maringma-tepui, IRSNB 15867, IRSNB 15916-17.

Pristimantis memorans: VENEZUELA, Estado Amazonas, Pico Tamacuari, A-131466 (holotype).

Pristimantis pruinatus: VENEZUELA, Estado Amazonas, Cerro Yaví, A-143362-63 (2 paratopotypes).

Pristimantis pulvinatus: VENEZUELA, Estado Bolívar, La Escalera, IRSNB 15654; GUYANA, Cuyuni-Mazaruni District, slopes of Maringma-tepui, IRSNB 17927.

Pristimantis saltissimus: GUYANA, Potaro-Siparuni District, Wokomung Massif, USNM 563639 (holotype), IRSNB 15644-53 (10 topotypic specimens).

Pristimantis yaviensis: VENEZUELA, Estado Amazonas, Cerro Yaví, A-143364-76 (13 paratopotypes), A-159161-63.

Pristimantis yuruanensis: VENEZUELA, Estado Bolívar, Yuruaní-tepui, IRSNB 15638-41 (4 topotypic specimens), SMNS 09855 (paratype).

Appendix 2

GenBank accession numbers of samples used in the molecular phylogenetic analysis. Samples in boldface represent specimens corresponding to the morphology of the holotype of *Pristimantis marmoratus* (Boulenger, 1900).

Species	Locality	Country	GenBank (16S)
<i>P. abakapa</i>	Abakapá-tepui	Venezuela	JQ742162
<i>P. abakapa</i>	Angasima-tepui	Venezuela	JQ742163
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742159
<i>P. aureoventris</i>	Roraima-tepui	Guyana	JQ742151
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742153
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742158
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742155
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742156
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742157
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742154
<i>P. aureoventris</i>	Wei-Assipu-tepui	Guyana	JQ742152
<i>P. dendrobatoides</i>	Mt. Wokomung	Guyana	EU186717
<i>P. espedeus</i>	Lucifer	French Guiana	JN691314
<i>P. inguinalis</i>	Trinité, Crique Grand Leblond	French Guiana	JN691317
<i>P. inguinalis</i>	Cacao Mountain	French Guiana	JQ742170
<i>P. jamescameroni</i>	Aprada-tepui	Venezuela	EU186721
<i>P. jester</i>	Maringma-tepui	Guyana	JQ742169
<i>P. marmoratus</i>	Mt. Wokomung	Guyana	EU186716
<i>P. marmoratus</i>	Kaieteur National Park	Guyana	JQ742166
<i>P. marmoratus</i>	Maringma-tepui	Guyana	JQ742167
<i>P. marmoratus</i>	La Escalera	Venezuela	EU186723
<i>P. pulvinatus</i>	La Escalera	Venezuela	JQ742165
<i>P. pulvinatus</i>	Iwokrama	Guyana	JQ742164
<i>P. saltissimus</i>	Mt. Wokomung	Guyana	EU186693
<i>P. saltissimus</i>	Mt. Ayanganna	Guyana	EU186692
<i>P. saltissimus</i>	Maringma-tepui	Guyana	JQ742168
<i>P. sp. 1</i>	Saül	French Guiana	JN691315
<i>P. sp. 1</i>	Savane Virginie	French Guiana	KR811102
<i>P. sp. 1</i>	St Georges, Saut Maripa	French Guiana	KR811105
<i>P. sp. 1</i>	Montagne de Kaw	French Guiana	EU201063
<i>P. sp. 1</i>	Trois Sauts	French Guiana	EU201062
<i>P. sp. 1</i>	Amapá, Lourenço	Brazil	KR811104
<i>P. sp. 1</i>	Amapá, Oiapoque	Brazil	KR811103
<i>P. sp. 4</i>	Cisame	French Guiana	JN691316
<i>P. sp. Ayanganna</i>	Mt. Ayanganna	Guyana	EU186676
<i>P. sp. Wokomung</i>	Mt. Wokomung	Guyana	EU186678
<i>P. yuruanensis</i>	Yuruaní-tepui	Venezuela	JQ742160
<i>P. yuruanensis</i>	Yuruaní-tepui	Venezuela	JQ742161

Appendix 3

GenBank accession numbers of available and newly generated (in bold) 16S sequences of *Pristimantis marmoratus* (Boulenger, 1900).

Voucher	Species	Locality	Country	GenBank
IRSNB 14471	<i>P. marmoratus</i>	Kaieteur National Park	Guyana	JQ742166
IRSNB 14472	<i>P. marmoratus</i>	Kaieteur National Park	Guyana	MF037218
IRSNB 14473	<i>P. marmoratus</i>	Kaieteur National Park	Guyana	MF037219
IRSNB 14474	<i>P. marmoratus</i>	Kaieteur National Park	Guyana	MF037220
IRSNB 12862	<i>P. marmoratus</i>	Maringma-tepui	Guyana	JQ742167
IRSNB 17916	<i>P. marmoratus</i>	Maringma-tepui	Guyana	MF037221
IRSNB 17939	<i>P. marmoratus</i>	Maringma-tepui	Guyana	MF037222
CPI 10703 (egg)	<i>P. marmoratus</i>	Wokomung Massif	Guyana	MF037223
KU 181015	<i>P. marmoratus</i>	La Escalera	Venezuela	EU186723
ROM 43302	<i>P. marmoratus</i>	Wokomung Massif	Guyana	EU186716