



Research article

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Two new charismatic *Pristimantis* species (Anura: Craugastoridae) from the tepuis of “The Lost World” (Pantepui region, South America)

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Abstract. Two new colourful species of direct-developing frogs of the genus *Pristimantis* are described from the summit of two isolated tepuis (sandstone table mountains) in the Eastern Pantepui District of the Guiana Shield highlands. *Pristimantis jamescameroni* sp. nov. is described from the summit of Aprada-tepui from 2557-2571 m elevation, and *P. imthurni* sp. nov. is described from the summit of Ptari-tepui at 2471 m elevation. Both species share the absence of a differentiated tympanic membrane and external tympanic annulus (but presence of tiny pharyngeal ostia), the presence of nuptial pads in males, and the presence of lateral fringes on fingers and toes, a combination of characters that immediately distinguishes them from all other known Pantepui congeners. The two new species are morphologically similar to each other and are phylogenetically closely related, but they can be distinguished based on colour pattern and morphological characters such as head proportions, dorsal skin texture, and condition of the supratympanic fold. The IUCN conservation status of the new species is considered as Endangered (EN) owing to their apparent very restricted ranges. The number of described *Pristimantis* species occurring exclusively on tepui (and faunistically related granitic mountains) summits and upper slopes now reaches eleven.

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

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Introduction

The outstanding biogeographic region where the tepuis (a word used to describe South American table mountains consisting of Precambrian sandstone) and the faunistically related granitic mountains occur, was named Pantepui by Mayr & Phelps (1967) in their seminal study on the origin of the bird fauna of the south Venezuelan highlands. The Pantepui region (Fig. 1A) lies in the northwestern part of the Guiana Shield and is traditionally seen as one of the foremost centres of endemism in the Neotropics (Berry *et al.* 1995; Davis *et al.* 1997). Historically, Pantepui has often been limited to the upper slopes and summits

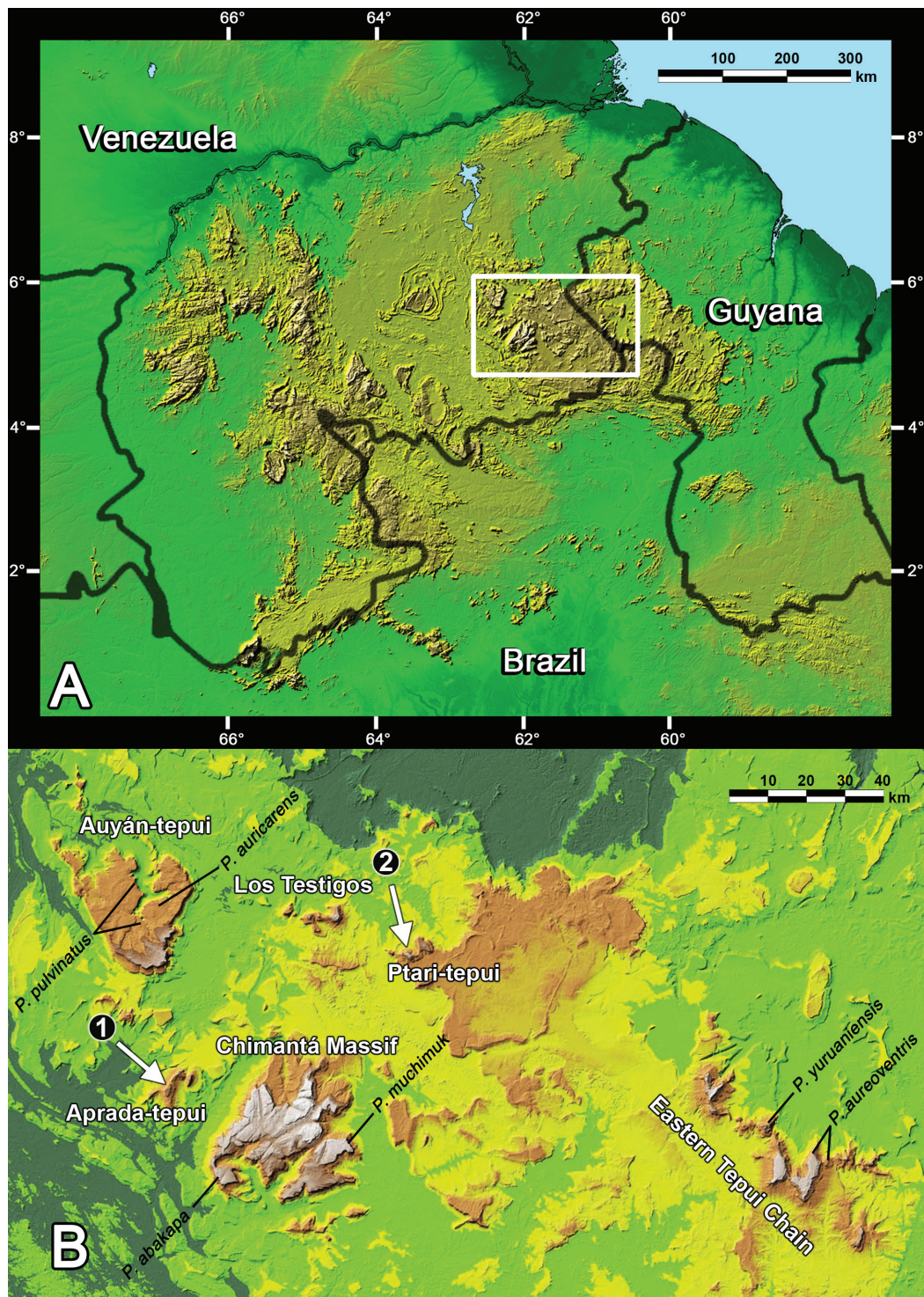


Fig. 1. A. Map of the Pantepui region, located in the western part of the Guiana Shield. The white rectangle corresponds to the area enlarged in (B). B. Distribution of known tepui summit *Pristimantis* species occurring east of the Rio Caroní in Venezuela and in western Guyana: *P. aureoventris* (Wei-Assipu-tepui and upper slopes of Mount Roraima), *P. yuruanensis* (Yuruaní-tepui), *P. muchimuk* (Churí-tepui), *P. abakapa* (Abakapá-tepui), *P. auricarens* and *P. pulvinatus* (Auyán-tepui); (1) Aprada-tepui, type locality of *Pristimantis jamescameroni* sp. nov. (area enlarged in Fig. 6A); (2) Ptari-tepui, type locality of *Pristimantis imthurni* sp. nov. (area enlarged in Fig. 6B).

of the Guiana Shield highlands covering a total surface of about 5000 km², with an altitudinal range of 1,500–3,014 m above sea level (Mayr & Phelps 1967; Rull & Nogué 2007). Nonetheless, Steyermark (1982), followed by Kok *et al.* (2012) and Kok (2013), expanded the original definition of Pantepui to include the intervening Pantepui lowlands (200–400 m asl) and uplands (400 - *ca.* 1200 m asl), which better reflects the biogeography and the past and current biotic interactions in the area (Kok 2013).

The Scottish writer Sir Arthur Conan Doyle was the first to coin the expression “The Lost World” in the title of his famous fiction novel published in 1912, in which he depicts an extraordinary expedition to an isolated table mountain in the tropical jungle of northern South America in search of dinosaur-like creatures and a forgotten civilisation (Doyle 1912). Doyle was largely inspired by the account of an expedition of the Royal Geographical Society of London to the summit of Mount Roraima in 1884, led by Sir Everard im Thurn (McDiarmid & Donnelly 2005; Dalziel 2007).

The vertical walls of tepuis can reach 1000 m, which makes most of these mountains isolated horizontally from one another, but also vertically from their surroundings. In addition to physiographic isolation, current edaphic, climatic and ecological factors contribute to further isolate most tepui tops from the surrounding savannah and tropical forest.

Kok *et al.* (2012) demonstrated that, despite their current unique geomorphology, the tepuis were insufficient barriers to local (*i.e.*, within Pantepui) gene flow, leading to a low genetic diversity among most tepui summit amphibians and reptiles. The same authors suggested that single-tepui endemism might not be as common as previously stated, since some tepui summit species, described as being single-tepui endemics, turned out to be synonyms of more widespread taxa (*e.g.*, in the genera *Anomaloglossus* and *Tepuihyla*, see for instance Kok *et al.* 2013 and Jungfer *et al.* 2013). Evolutionary processes in the area remain puzzling given that on the one hand, species previously reported as highly restricted often also occur on nearby tepuis, or in some cases in the surrounding uplands (*Tepuihyla*), and on the other hand, some populations occurring on different tepui summits and identified as a single species turned out to be complexes of distinct taxa phenotypically hard to distinguish from one another (*e.g.*, in the genus *Stefania*, Kok pers. obs.). Kok *et al.*'s (2012) discovery has a potentially strong implication for the taxonomic status of several described tepui species and highlights the difficulty of taxonomic decisions in the region, which until now was often strongly influenced by the unique topography of the area, and probably also by the legacy of Doyle's novel. However, from a conservation point of view it is crucial to delimitate species and species' distributions as accurately as possible, especially in these mountainous areas reported as particularly sensitive to global warming (Nogué *et al.* 2009).

The frog genus *Pristimantis* is the most speciose vertebrate genus, with more than 450 nominal species currently recognized (Frost 2013). Twenty of these described species are distributed in Pantepui (Kok & Barrio-Amorós 2013; Rojas-Runjaic *et al.* 2013), nine of them stated as being restricted to tepui summits and tepui upper slopes (*sensu* Kok 2013; Rojas-Runjaic *et al.* 2013). These numbers do not include the many putative undescribed and highly restricted species (at least 15), reported from the region by McDiarmid & Donnelly (2005) and still waiting to be named.

New material was recently obtained from several poorly explored tepuis, which confirms the occurrence of two distinct, unnamed *Pristimantis* species on Aprada-tepui and Ptari-tepui, respectively, two isolated tepuis located east of the Río Caroní, in the Eastern Pantepui District, Bolívar state, Venezuela. These new species are described below and their IUCN Red List Category is discussed.

Material and methods

Fieldwork and deposition of specimens

Tepui summits harbour fragile ecosystems and extreme care was taken to ensure a minimum impact on the environment (*e.g.*, no waste was left, vegetation was not damaged and turned rocks were replaced as they were found whenever possible). Specimens were collected by hand and euthanized by immersion in a 2% lidocaine solution (Linisol), fixed in 10% formalin for a few days and transferred to 70% ethanol for permanent storage. A piece of liver and/or thigh muscle was taken from most 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). Tissue samples were deposited in the Amphibian Evolution Lab, Biology Department at the Vrije Universiteit Brussel (VUB). Coordinates and elevations of the collection localities were acquired using a Garmin Global Positioning System unit and referenced to map datum WGS84.

Morphology

Terminology for morphological characters mostly follows Lynch & Duellman (1997), Savage *et al.* (2004), Kok & Kalamandeen (2008), Means & Savage (2007), Duellman & Lehr (2009), and Kok *et al.* (2011). All morphometric data were taken from the preserved specimens to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper. For ease of comparison, descriptions mainly follow the pattern of recent descriptions in the genus (*e.g.*, Myers & Donnelly 2008; Barrio-Amorós *et al.* 2010; Kok *et al.* 2011; Rojas-Runjaic *et al.* 2013).

Classical measurements for the genus were taken and are abbreviated as follows:

EL	=	eye length, horizontal distance from the posterior margin to the anterior margin of the eye
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 I	=	length of Finger I from proximal edge of palmar tubercle to tip of finger
HAND II	=	length of Finger II from proximal edge of palmar tubercle to tip of finger
HAND III	=	length of Finger III from proximal edge of palmar tubercle to tip of finger, also equivalent to hand length
HAND IV	=	length of Finger IV from proximal edge of palmar tubercle to tip of finger
HL	=	head length from angle of jaw to tip of snout
HW	=	greatest width of the head
IN	=	internarial distance, taken between the median margins of the nares
IO	=	interorbital distance, taken between the inner margins of the orbits
SL	=	snout length from anterior corner of eye to tip of snout
SVL	=	snout-vent length, from tip of snout to posterior margin of vent
TIL	=	tibia length from outer edge of flexed knee to heel
WFD	=	width of disc on Finger III
WTD	=	width of disc on Toe IV

Colour pattern in life was taken from field notes and was later refined based on high definition colour digital photographs. Sex and maturity were determined by dissection and direct examination of gonads, and by examination of secondary sexual characters (such as nuptial pads in males). Internal soft anatomy was examined by dissection of preserved specimens.

Taxonomy follows Pyron & Wiens (2012). Institutional acronyms follow Frost (2013).

Results

Generic allocation of the new species

No identifiable morphological synapomorphy supporting the genus *Pristimantis* (Hedges *et al.* 2008) has been proposed yet. The new taxa are assigned to the genus *Pristimantis* based on molecular phylogenetic relationships (Kok *et al.* 2012, Kok pers. obs., August 2012) as well as on their morphological characteristics, which fall within the range of other *Pristimantis* species (see diagnoses).

Class Amphibia Gray, 1825
Order Anura Fischer von Waldheim, 1813
Family Craugastoridae Hedges, Duellman & Heinicke, 2008
Subfamily Pristimantinae Pyron & Wiens, 2011

Pristimantis jamescameroni sp. nov.

Figs 2-5, Table 1

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Eleutherodactylinae series b (in part) – Gorzula & Señaris 1999: 55 + plate 46.

Eleutherodactylus sp. B – McDiarmid & Donnell, 2005: 514 [table 18A.1], 524.

Pristimantis sp. – Hedges *et al.* 2008: 179.

Pristimantis sp. “Aprada” – Kok *et al.* 2012: Suppl. Information: 13.

Definition and diagnosis

A small species of the genus *Pristimantis* currently not assigned to any species group, but morphologically most similar to species of the polyphyletic *unistrigatus* species group (*sensu* Hedges *et al.* 2008, see also discussion in Kok *et al.* 2011) mainly characterized in 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. The new species is characterized by the following unique combination of characters: (1) body small, male 22.8 mm SVL, females 26.3-27.5 mm (n=3); (2) dorsal skin shagreen, belly skin coarsely areolate; (3) tympanum absent (tympanic membrane not differentiated and tympanic annulus not visible externally); (4) tiny pharyngeal ostia present; (5) snout rounded to subovoid in dorsal view, rounded to slightly sloping in profile, *canthus rostralis* nearly straight in dorsal view, rounded in cross section, loreal region slightly concave, flaring slightly at upper lip; (6) upper eyelid shagreen with 1-2 distinctly enlarged tubercles on each eyelid; (7) choanae small, oval, dentigerous processes of vomers very small, barely visible, slightly oblique, ovoid to triangular, posterior and medial to choanae, each bearing 1-5 teeth; (8) absence of vocal slits in male; (9) tongue cordiform; (10) two large, mostly unpigmented nuptial pads on each thumb in male; (11) Finger I shorter than II; (12) fingers with lateral fringes, best developed preaxially on Fingers II-III; (13) ulnar tubercles absent or inconspicuous, when present low, not forming a distinct line; (14) tarsal tubercles absent, one inconspicuous calcar tubercle present; (15) inner metatarsal tubercle oval, about four times the size of the round, projecting outer metatarsal tubercle; (16) Toe V longer than III, extending to the distal edge of the distal tubercle on Toe IV when toes are adpressed; (17) toes with lateral fringes, best developed preaxially on Toes III-IV, webbing basal between Toes IV-V; (18) in life main dorsal background colouration is orange to orangish dark brown, either with irregular dark brown chevrons or a darker middorsal band, and/or a light middorsal stripe, ventral colouration is white with brown reticulation and an orange patch posteriorly; (19) in preservative dorsal background colouration is light to dark brown, either with irregular brown chevrons or a darker middorsal band, and/or a light middorsal stripe, ventral colouration is cream with brown reticulation.

Etymology

The specific epithet is a noun in the genitive case, honouring the Canadian film director, producer, environmentalist and explorer Mr. James F. Cameron in recognition of his efforts to alert the general public to environmental problems through pioneering high quality “blockbuster” movies and adventurous documentaries. James Cameron also encourages people to go vegan (a diet excluding animal products), one of the effective ways to reduce human environmental impacts such as global climate change, identified as a serious threat to tepuis ecosystems (see Nogué *et al.* 2009).

Material examined

Holotype

VENEZUELA: an adult male collected by Philippe J. R. Kok, 15 Jun. 2012 at 08h18, summit of Aprada-tepui, Bolívar state, 5°24'42"N, 62°27'00" W, 2570 m elevation, IRSNB 4160 (field number PK 3636).

Paratopotypes (n=4)

VENEZUELA: three adult females (IRSNB 4161-63, field numbers PK 3632, PK 3637, PK 3635) and one juvenile (IRSNB 4164, field number PK 3639), collected by Philippe J. R. Kok (except IRSNB 4161, collected by Brad Wilson) 14-15 Jun. 2012, all from the summit of Aprada-tepui between 2557-2571 m elevation.

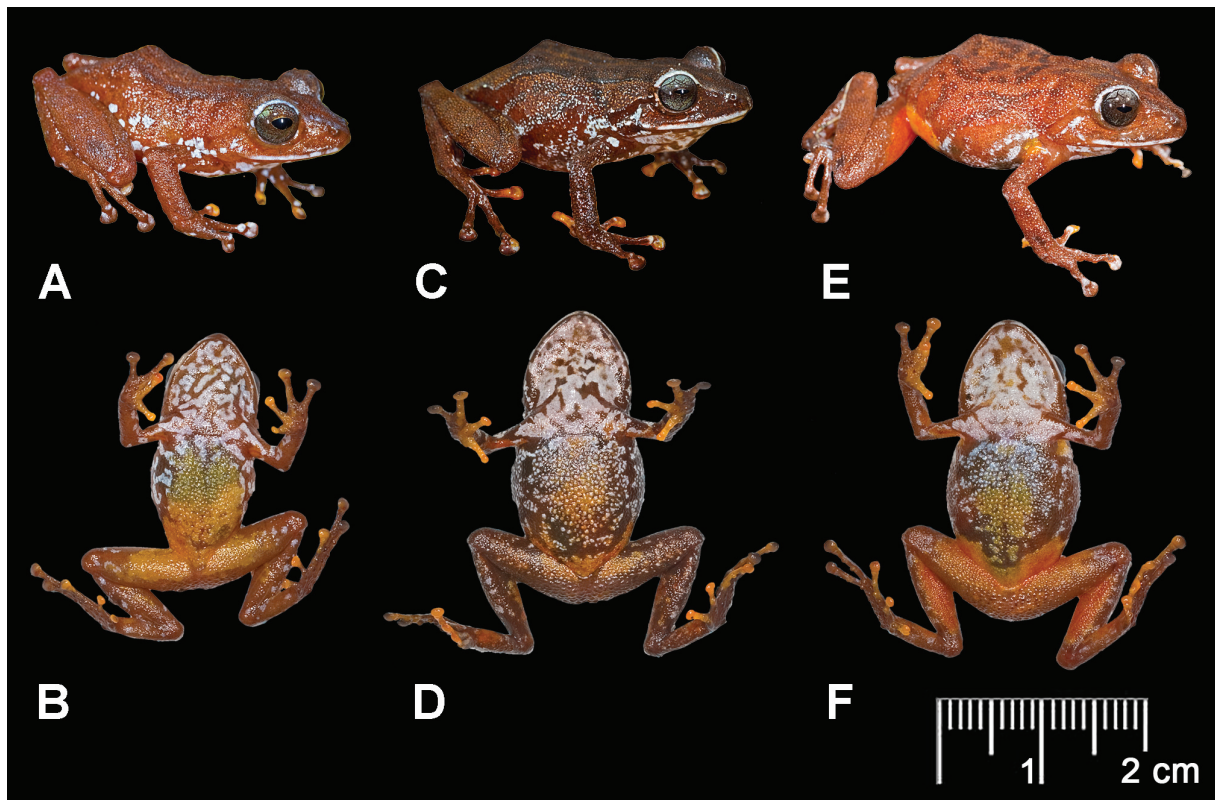


Fig. 2. *Pristimantis jamescameroni* sp. nov. Intraspecific variation in dorsal and ventral colour pattern in living specimens. **A.** Dorsolateral view of the ♂ holotype (IRSNB 4160). **B.** Ventral view of the same specimen. **C.** Dorsolateral view of a ♀ paratype (IRSNB 4163). **D.** Ventral view of the same specimen. **E.** Dorsolateral view of a ♀ paratype (IRSNB 4162). **F.** Ventral view of the same specimen. Photographs by the author.

Description of the holotype

An adult male 22.8 mm SVL (Figs 2A-B, 3, 4D, H, see Table 1 for measurements), in very good condition, except a large scar under the right thigh where a piece of muscle was removed prior to preservation. Head slightly longer than wide (HW 94.7% of HL), wider than body; HW 39.0% of SVL; HL 41.2% of SVL; cranial crests absent. Snout longer than eye length (SL 117.1% of EL), rounded to subovoid in dorsal view, rounded to slightly sloping in profile; *canthus rostralis* nearly straight in dorsal view, rounded in cross section, loreal region slightly concave, flaring slightly at upper lip; eye-naris distance shorter than eye length (EN 71.4% of EL). Nares slightly protuberant, directed posterolaterally, visible in frontal and dorsal views. Widest upper eyelid width narrower than interorbital distance (upper eyelid width 82.7% of IO), upper eyelid shagreen with 1-2 enlarged tubercles on each eyelid. Tympanum absent (tympanic membrane not differentiated and tympanic annulus not visible externally); tiny pharyngeal ostia present. Supratympanic fold conspicuous in life, slightly arched, originating at posterior corner of eye, failing to reach shoulder; post-riental tubercles evident. Choanae small, oval, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers very small, barely visible, slightly oblique, ovoid to triangular, posterior and medial to choanae, each bearing 3-4 teeth. Tongue cordiform, slightly longer than wide, rounded posteriorly, posterior half free. Vocal slits and vocal sac absent.



Fig. 3. *Pristimantis jamescameroni* sp. nov. Ventral view of left hand and left foot of the ♂ holotype (IRSNB 4160). Photographs by the author.

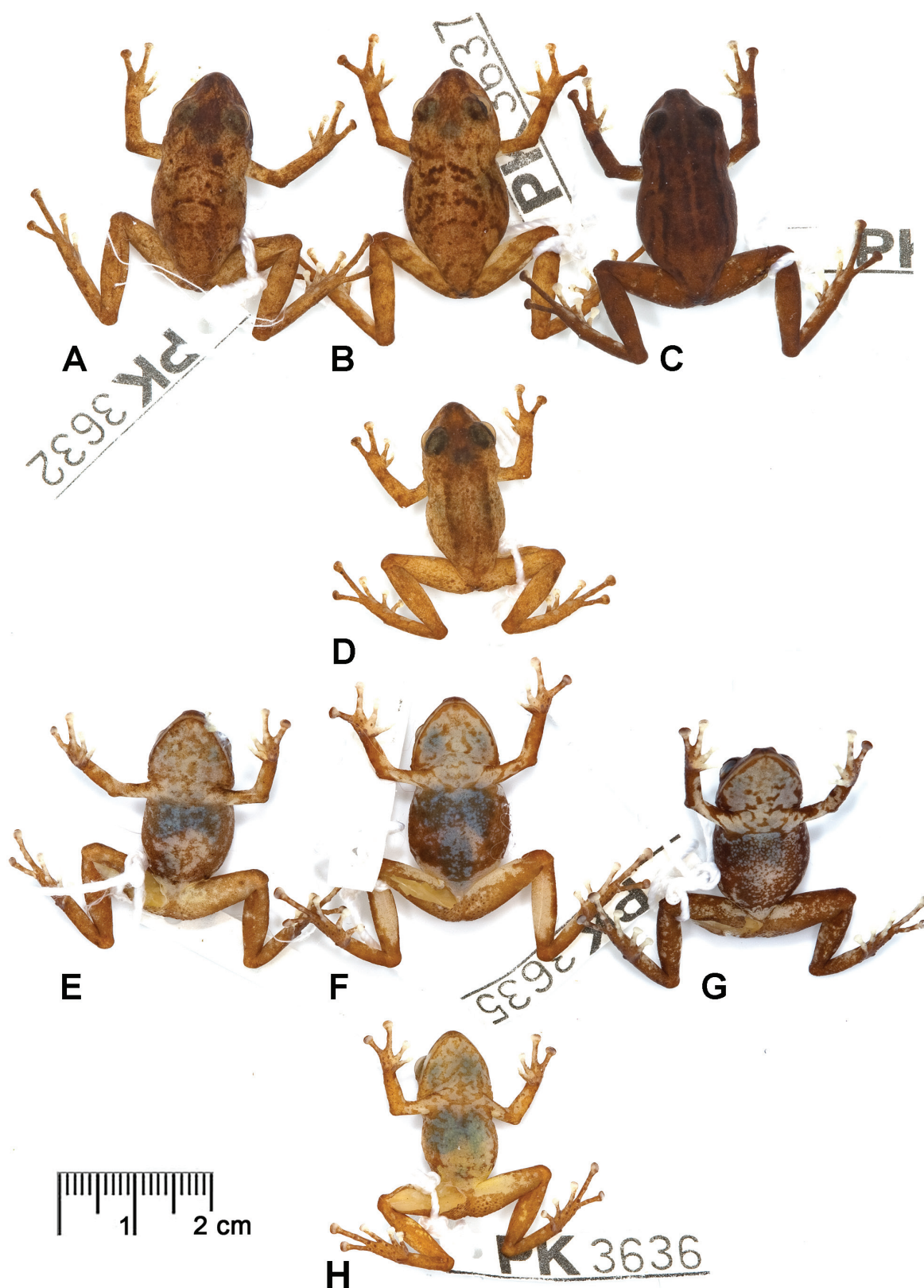


Fig. 4. *Pristimantis jamescameroni* sp. nov. Intraspecific variation in dorsal (above) and ventral (below) colour pattern in preserved specimens. **A, E.** ♀ paratype (IRSNB 4161). **B, F.** ♀ paratype (IRSNB 4162). **C, G.** ♀ paratype (IRSNB 4163). **D, H.** ♂ holotype (IRSNB 4160). Photographs by the author.

Dorsal skin shagreen, including on head; middorsal raphe detectable; no dermal folds or ridges visible on dorsal surface; flanks granular. Throat surface shagreen; upper chest shagreen, slightly “wrinkled”; weak thoracic fold; belly skin coarsely areolate; weak discoidal fold anterior to groin; posteroventral thigh and cloacal region coarsely areolate; cloacal sheath absent.

Hand length 27.2% of SVL. Finger I 80.0% of II. 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 the intercalary cartilage of Finger III on the left side, the base of the disc of Finger III on the right side. Two large, not connected, non-spinous, mostly unpigmented (translucent when wet, white when dry) nuptial pads on each thumb, one extending along the preaxial surface of the thenar tubercle and invading most of it, the other one extending along the dorsal and the preaxial surface of the thumb. Lateral fringes on all fingers, best developed preaxially on Fingers II-III (Fig. 3). Finger discs broadly expanded, elliptical, broader than long, circumferential groove conspicuous, distal edge of disc rounded; disc of Finger III 2.1 times wider than the distal end of the adjacent phalanx. Palmar tubercle large, poorly defined, not fully pigmented, deeply bifid; thenar tubercle large, protuberant, ovoid; supernumerary tubercles few, large (almost equal in size to the subarticular tubercles), slightly protuberant; subarticular tubercles large, round and protuberant, one each on FI and FII, two each on FIII and FIV. Ulnar tubercles few, inconspicuous, forming an ill-defined line; presence of a small antebrachial tubercle.

Hind limbs moderate in length, heels slightly overlap when held at right angles to sagittal plane; TIL 50.4% of SVL; FL 41.7% of SVL. Relative length of Toes IV > V > III > II > I; tip of Toe V extends to the distal edge of the distal subarticular tubercle on Toe IV; tip of Toe III extends to the distal edge of the penultimate subarticular tubercle on Toe IV on the left side, to the proximal half of the penultimate subarticular tubercle on Toe IV on the right side. Lateral fringes on all toes, best developed preaxially on Toes III-IV; webbing basal between Toe IV-V (Fig. 3). Toe discs mostly equal in size to finger discs, WTD/WFD = 1; toe discs broadly expanded, elliptical, broader than long, circumferential groove conspicuous, distal edge of disc rounded. Inner metatarsal tubercle elongate, oval, about four times the size of the projecting, round outer metatarsal tubercle; subarticular tubercles round, large and protuberant; supernumerary plantar tubercles small, low and round, increasing in size distally. Single, inconspicuous and very small round calcar tubercle; no outer tarsal tubercles detectable; inner tarsal fold not detectable.

Colour of holotype in life (see Fig. 2A-B)

Dorsal background colour orangish brown covered with numerous tiny white flecks, top of head slightly darker; inconspicuous darker (than adjacent dorsum) middorsal band outlined by ill-defined dark brown dorsolateral lines; irregular white band on the *canthus rostralis*; bluish white line on outer edge of upper eyelids; upper lips white; most post-riatal tubercles white; enlarged tubercles on eyelids light brown. Flanks orangish brown, with numerous tiny white flecks and some irregular white spots of variable sizes; groins, anterior thighs, and armpits bright orange. Arms and legs coloured as dorsal surfaces, with a few small irregular white spots on upper arms and on the distal part of tarsi. Throat, chest, and lower flanks white with brown anastomosed reticulation; belly and most of the undersurface of thighs bright orange; undersurface of distal thighs, shanks, and tarsi brown with a few small irregular white spots; posterior surface of thighs and cloacal area brown. Upper face of hands and feet orangish brown, except tip of Fingers I-II, which is bright orange, and tip of toes, which is whitish. Palms and soles brown; undersurface of Fingers I-III bright orange, including discs; undersurface of tip of Toes I-III bright orange including discs. Iris silver with dark brown venation and an ill-defined, broad horizontal brownish stripe; greenish silver spot on the posterior upper part of the iris.

Table 1. Sex, measurements (in mm), and HL/SVL ratio of type specimens of *Pristimantis jamescameroni* sp. nov. and *Pristimantis imthurni* sp. nov. Abbreviations are defined in the text.

Character	<i>Pristimantis jamescameroni</i> sp. nov. Aprada-tepui					<i>Pristimantis imthurni</i> sp. nov. Ptari-tepui
	IRSNB 4160	IRSNB 4161	IRSNB 4162	IRSNB 4163	IRSNB 4164	IRSNB 4165
Sex	Male	Female	Female	Female	Juvenile	Male
SVL	22.8	27.0	27.5	26.3	18.3	22.9
HL	9.4	10.9	11.2	10.9	8.0	8.7
HL/SVL	41.2%	40.3%	40.7%	41.4%	43.7%	38.0%
HW	8.9	10.1	10.3	9.9	7.4	8.5
SL	4.1	4.5	4.7	4.3	3.3	3.7
EN	2.5	2.9	2.9	2.7	2.0	2.4
IN	2.1	2.5	2.4	2.5	2.1	2.3
EL	3.5	3.3	3.4	3.2	2.1	3.3
IO	2.6	2.9	2.9	3.0	2.4	2.7
HAND I	3.6	4.2	4.2	4.0	3.1	3.9
HAND II	4.5	4.7	4.5	5.1	3.4	4.4
HAND III	6.2	6.7	6.6	6.6	4.8	6.2
HAND IV	4.8	5.3	4.9	5.6	3.7	4.9
WFD	1.3	1.3	1.3	1.4	1.0	1.3
FL	9.5	10.5	10.4	10.6	7.4	9.3
WTD	1.3	1.3	1.5	1.5	1.0	1.4
TIL	11.5	13.2	12.7	12.8	9.9	11.5

Colour of holotype in preservative (see Fig. 4D, H)

After 13 months in 70% ethanol (July 2013), orangish brown faded to light brown. Orange and white faded to cream. Dorsal pattern turned generally more conspicuous. Brown reticulation on throat, chest, and lower flanks faded to light brown. Granules in the cloacal area, as well as subarticular and supernumerary tubercles became dark brown. Discs are greyish brown.

Sexual dimorphism and variation among paratypes

See Table 1 for measurements of the type series, and Figs 2, 4, 5 for intraspecific variation. Sexual dimorphism evident in size, with adult females being larger than the adult male (26.3-27.5 vs. 22.8 mm SVL), and by the presence of two nuptial pads in the male. A sexual dichromatism in belly colouration seems to occur, with the presence of an orange spot restricted to the middle area of the belly in living females, whereas the orange area covers the belly, the posterior part of the ventral surface, and the undersurface of thighs in a more continuous way in the living male (see Fig. 2B, D, F). Hands and feet slightly longer in the male than in the females (HAND III 27.2% vs. 24.0-25.1% of SVL; FL 41.7% vs. 37.8-40.3% of SVL). No additional significant difference is detected in other size ratios. No significant variation in skin texture occurs among the preserved specimens, but in life IRSNB 4163 (adult female, Fig. 2C) had a conspicuous dorsolateral fold extending from behind the eye to the end of the body; that fold totally disappeared in preservative. Eyelid tubercles are more difficult to detect in preserved specimens and range from 1 to 2 on each eyelid. Number of teeth on dentigerous processes of vomers

varies from 2 to 6. Weak thoracic and discoidal folds detectable in IRSNB 4163 (female) and IRSNB 4164 (juvenile), not seen in the other paratypes. Tip of Toe V fails to reach the distal edge of the distal subarticular tubercle on Toe IV on the left side in IRSNB 4161 (female) only.

Colour pattern variable. In life, dorsal background colouration varies from bright orange to orangish dark brown, usually covered with tiny white flecks; dorsal pattern varies from irregular brown chevrons (*e.g.*, in IRSNB 4161 and IRSNB 4162) to a slightly darker (than adjacent dorsum) middorsal band outlined by ill-defined dark brown dorsolateral lines (*e.g.*, in IRSNB 4160) and/or a pale middorsal stripe (*e.g.*, in IRSNB 4163); pattern on flanks varies from a few irregular oblique white (*e.g.*, IRSNB 4163) or brown/white (*e.g.*, IRSNB 4162) stripes to white spots (holotype); colour of ventral reticulation varies from brown to dark brown; inconspicuous transverse bands on arms and legs occur in two female paratypes (IRSNB 4162 and IRSNB 4163). Enlarged tubercles on eyelids are usually white (light brown in the holotype). The juvenile (IRSNB 4164, Fig. 5) has a complex and more marked dorsal pattern consisting of a greyish brown interorbital line preceded by a greyish brown circle and followed by a wide W-shaped marking outlined by greyish brown in the scapular region; the W-shaped marking is followed by a greyish brown arch, itself followed by two back to back C-shaped light grey lines. It also differs from adults in having an irregular greyish band on the *canthus rostralis*, the upper lip not completely white, granules in the loreal region, dark brown labial stripes, the supratympanic fold underlined by a dark brown band, brown transverse bands on the forearm, and reddish transverse bands on the legs. Iris varies from silver or greenish silver to bronze, with dark brown venation and an ill-defined, broad horizontal brownish stripe.



Fig. 5. *Pristimantis jamescameroni* sp. nov. Juvenile specimen (IRSNB 4164, 18.3 mm SVL). Photograph by the author.

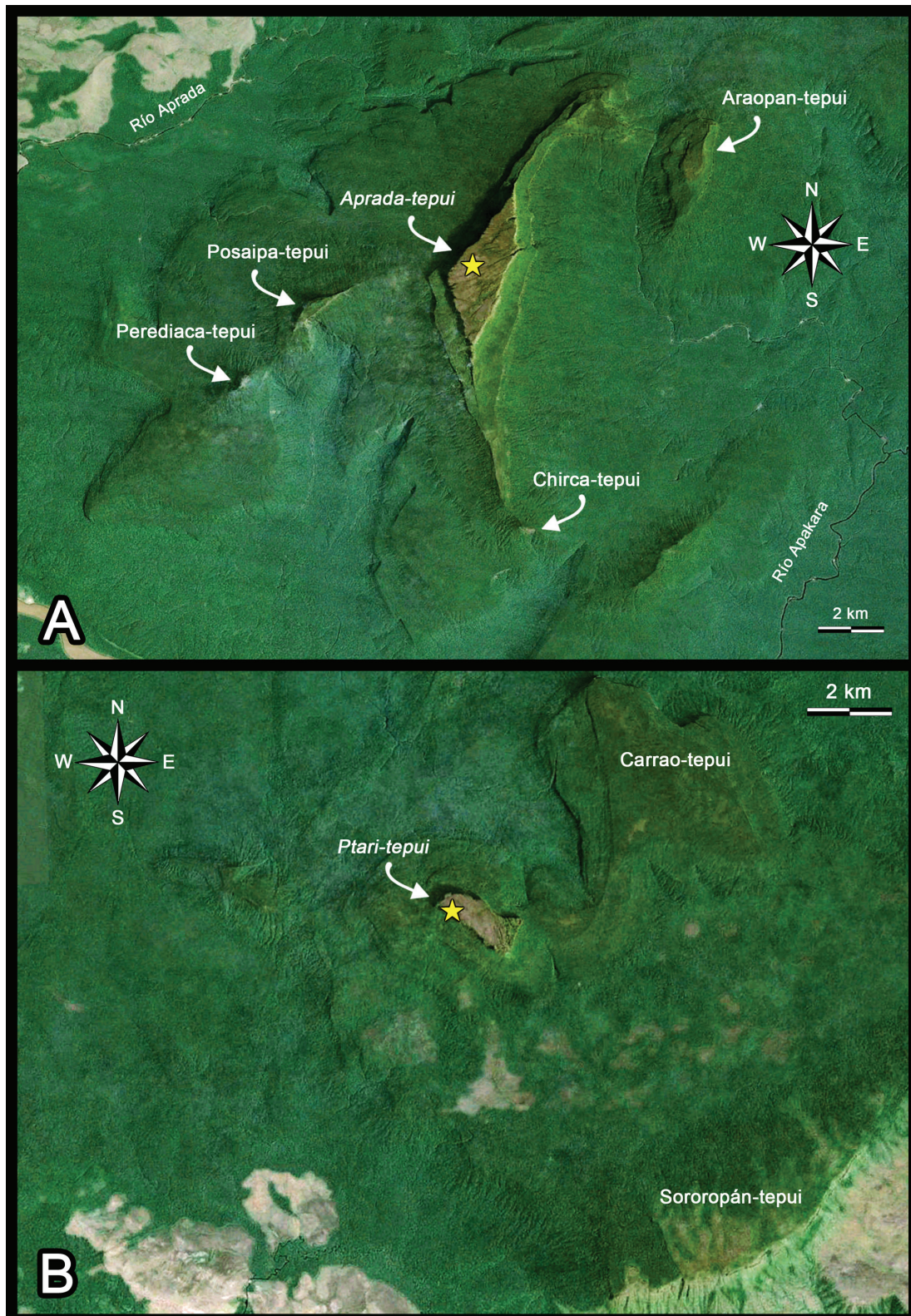


Fig. 6. A. Satellite map of the Aprada massif, showing the location of Aprada-tepui and neighbouring smaller table mountains. Yellow star indicates the type locality of *Pristimantis jamescameroni*. B. Satellite map of the Ptari massif, showing the location of Ptari-tepui and neighbouring mountains. Yellow star indicates the type locality of *Pristimantis imthurni*. Satellite maps © Google Maps.

Morphological comparisons with congeneric species

Available data suggest that tepui summit *Pristimantis* species have relatively restricted distributions in the Guinea Shield highlands; therefore, comparisons with congeners only focus on *Pristimantis* species known to occur in the Pantepui region (as defined by Kok 2013). Comparisons of external character states are based both on original descriptions and examination of museum specimens (see Appendix for material examined).

Twenty species of *Pristimantis* are currently reported from the Pantepui region: *P. aureoventris* Kok, Means & Bossuyt, 2011, only known from the summit of Wei-Assipu-tepui and the upper slopes of Mount Roraima, Cuyuni-Mazaruni District, Guyana; *P. abakapa* Rojas-Runjaic, Salerno, Señaris & Pauly, 2013, described from the summit of Abakapá-tepui, Bolívar state, Venezuela; *P. auricarens* (Myers & Donnelly, 2008), known only from Auyán-tepui, Bolívar state, Venezuela; *P. avius* (Myers & Donnelly, 1997), reported from Pico Tamacuari, Amazonas state, Venezuela; *P. cantitans* (Myers & Donnelly, 1996), known from Cerro Yaví and Cerro Yutajé, Amazonas state, Venezuela; *P. dendrobatooides* Means & Savage, 2007, only known from the Wokomung massif, Potaro-Siparuni District, Guyana; *P. guaiquinimensis* (Schlüter & Rödder, 2007), described from Guaiquinima-tepui, Bolívar state, Venezuela; *P. jester* Means & Savage, 2007, known from the Wokomung massif, Potaro-Siparuni District, Guyana, and the slopes of Maringma-tepui, Cuyuni-Mazaruni District, Guyana (Kok, pers. obs. 2007); *P. marahuaka* (Fuentes-Ramos & Barrio-Amorós, 2004), endemic to Cerro Marahuaka, Amazonas state, Venezuela; *P. marmoratus* (Boulenger, 1900), reported as widespread in the Guiana Shield from eastern Venezuela to French Guiana and northern Brazil (Frost 2013), but several species may hide under this name; *P. memorans* (Myers & Donnelly, 1997), known only from the Sierra Tapirapecó, Amazonas state, Venezuela; *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías & McDiarmid 2010, apparently endemic to the summit of Churí-tepui, Bolívar state, Venezuela; *P. pruinatus* (Myers & Donnelly, 1996), known only from Cerro Yaví, Amazonas state, Venezuela; *P. pulvinatus* (Rivero, 1968), reported from the Gran Sabana region and Auyán-tepui, Bolívar state, Venezuela to western Guyana (Frost 2013), but more than one species may hide under this name (see Kok *et al.* 2012); *P. saltissimus* Means & Savage, 2007, known from the Wokomung massif, Potaro-Siparuni District, Guyana, and the slopes of Maringma-tepui, Cuyuni-Mazaruni District, Guyana (Kok pers. obs. 2007); *P. sarisarinama* Barrio-Amorós & Brewer-Carías, 2008, endemic to Sarisariñama-tepui, Bolívar state, Venezuela; *P. vilarsi* (Melin, 1941), known from upper Amazonian Brazil, Colombia, Venezuela and Peru (Frost 2013); *P. yaviensis* (Myers & Donnelly, 1996), reported from Cerro Yaví and Cerro Yutajé, Amazonas state, Venezuela; *P. yuruaniensis* Rödder & Jungfer, 2008, known with certainty only from the summit of Yuruani-tepui, Bolívar state, Venezuela (possible occurrence on the neighbouring Kukenán-tepui, see Mägdefrau & Mägdefrau 1994; Rödder & Jungfer 2008; Kok *et al.* 2011); and *P. zeuctotylus* (Lynch & Hoogmoed, 1977), widespread in northeastern South America (Frost 2013).

Pristimantis jamescameroni sp. nov. is most easily distinguished from *P. abakapa*, *P. aureoventris*, *P. avius*, *P. cantitans*, *P. dendrobatooides*, *P. guaiquinimensis*, *P. marmoratus*, *P. memorans*, *P. pruinatus*, *P. pulvinatus*, *P. saltissimus*, *P. sarisarinama*, *P. vilarsi*, *P. yuruaniensis* and *P. zeuctotylus* by lacking a differentiated tympanic membrane and an external tympanic annulus (at least one of these structures is detectable in the latter 15 species). It further differs from *P. vilarsi* and *P. zeuctotylus* in having Finger I < II (Finger I > II in *P. vilarsi* and *P. zeuctotylus*).

Pristimantis jamescameroni sp. nov. is immediately distinguished from *P. auricarens*, *P. jester*, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis* (the only known Pantepui “earless” *Pristimantis*) in having conspicuous lateral fringes on fingers and toes (absent or limited to a weak keel in the latter 5 species).

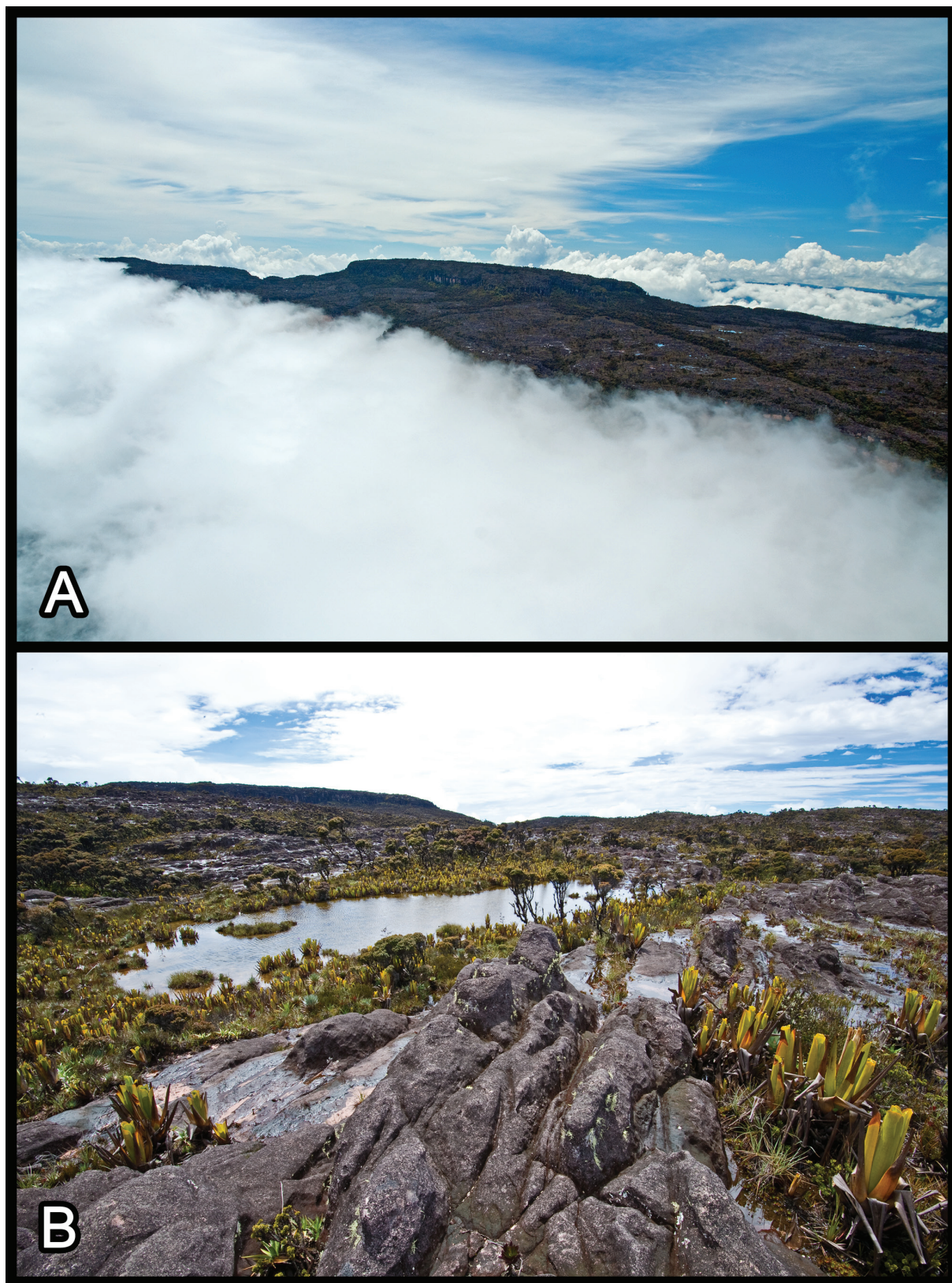


Fig. 7. **A.** The summit of Aprada-tepui lying above the clouds, photographed from a helicopter looking to the SW (2 May 2011). **B.** Summit of Aprada-tepui (15 Jun. 2012). Photographs by the author.

Distribution and ecology

Pristimantis jamescameroni sp. nov. is only known from the summit of Aprada-tepui (Figs 1B, 6A, 7A-B), Bolívar state, Venezuela, where it occurs from 2557 to 2571 m elevation. Aprada-tepui lies in the Aprada massif (Fig. 6A), in the Chimantá subdistrict (McDiarmid & Donnelly 2005). It is located ca. 22 km NW of the Chimantá massif and ca. 30 km S of Auyán-tepui (airline). According to the GPS, Aprada-tepui reaches a maximal elevation of about 2575 m above sea level. The summit area of Aprada-tepui is ca. 4.3 km², and is mainly covered by open rock vegetation and small islands of tepui forests (Huber 1995, Fig. 7B); it is characterized by a high number of small lakes (Fig. 7B) and some deep canyons.

Aside from the male holotype, which was collected by day on the ground while calling in a small shallow rock crevice, hidden by the vegetation, all specimens were collected under rocks. Other males were heard calling very sporadically from shallow rock crevices by day, but could not be located. As in most other tepui summit *Pristimantis*, the new species is not abundant and individuals are difficult to collect. The only other anuran reported from the summit of Aprada-tepui is *Stefania satelles* Señaris, Ayarzagüena & Gorzula, 1997, which occurs in higher density and might partly feed on *P. jamescameroni* sp. nov. (pers. obs.).

Pristimantis imthurni sp. nov.

Figs 8-10, Table 1

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Eleutherodactylus sp. H – McDiarmid & Donnelly 2005: 514 [table 18A.1], 521.

Definition and diagnosis

A small species of the genus *Pristimantis* currently not assigned to any species group, but morphologically most similar to species of the polyphyletic *unistrigatus* species group (*sensu* Hedges *et al.* 2008, see also discussion in Kok *et al.* 2011) mainly characterized in 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. The new species is characterized by the following unique combination of characters: (1) body small, male 22.9 mm SVL; (2) dorsal skin smooth, belly skin coarsely areolate; (3) tympanum absent (tympanic membrane not differentiated and tympanic annulus not visible externally); (4) tiny pharyngeal ostia present; (5) snout broadly rounded in dorsal view and in profile, *canthus rostralis* nearly straight in dorsal view, rounded in cross section, loreal region concave, flaring slightly at upper lip; (6) upper eyelid smooth with one barely distinct enlarged tubercle; (7) choanae very small, round, dentigerous processes of vomers inconspicuous, ovoid, posterior and medial to choanae, each bearing 3-4 teeth; (8) absence of vocal slits in male; (9) tongue cordiform; (10) two large, broadly connected, mostly unpigmented nuptial pads on each thumb in male; (11) Finger I shorter than II; (12) fingers with lateral fringes, best developed preaxially on Fingers II-III; (13) ulnar tubercles absent; (14) tarsal tubercles absent, one inconspicuous calcar tubercle present; (15) inner metatarsal tubercle oval, about four times the size of the round, projecting outer metatarsal tubercle; (16) Toe V longer than III, extending to the distal edge of the distal tubercle on Toe IV when toes are adpressed; (17) toes with lateral fringes, best developed preaxially on Toes III-IV, webbing basal between Toes IV-V; (18) in life dorsal background colouration is vivid yellow with a chocolate brown middorsal stripe and chocolate brown flanks, ventral colouration is translucent brown with a few white spots and flecks; (19) in preservative dorsal background colouration is pale yellow with a light brown middorsal stripe and light brown flanks, ventral colouration is light grey with a few white spots and flecks.

Etymology

The specific epithet is a noun in the genitive case, honouring Sir Everard F. im Thurn (1852-1932), British colonial official, author, explorer, botanist, and photographer. Everard im Thurn was the first to climb a major tepui (Mount Roraima in December 1884), along with British surveyor Harry Perkins, a Pomeron Amerindian named Gabriel, and five other unnamed Amerindians (Dalziell 2007). Im Thurn's expedition on Roraima and his numerous discoveries were partly eclipsed by the popular novel that they inspired: "The Lost World" by Sir Arthur Conan Doyle (see Introduction; Dalziell 2007).

Material examined

Holotype

VENEZUELA: an adult male collected by Philippe J. R. Kok, 20 Jun. 2012 at 20h37, summit of Ptari-tepui, Bolívar state, 5°46'09" N, 61°49'02" W, 2471 m elevation, IRSNB 4165 (field number PK 3671).

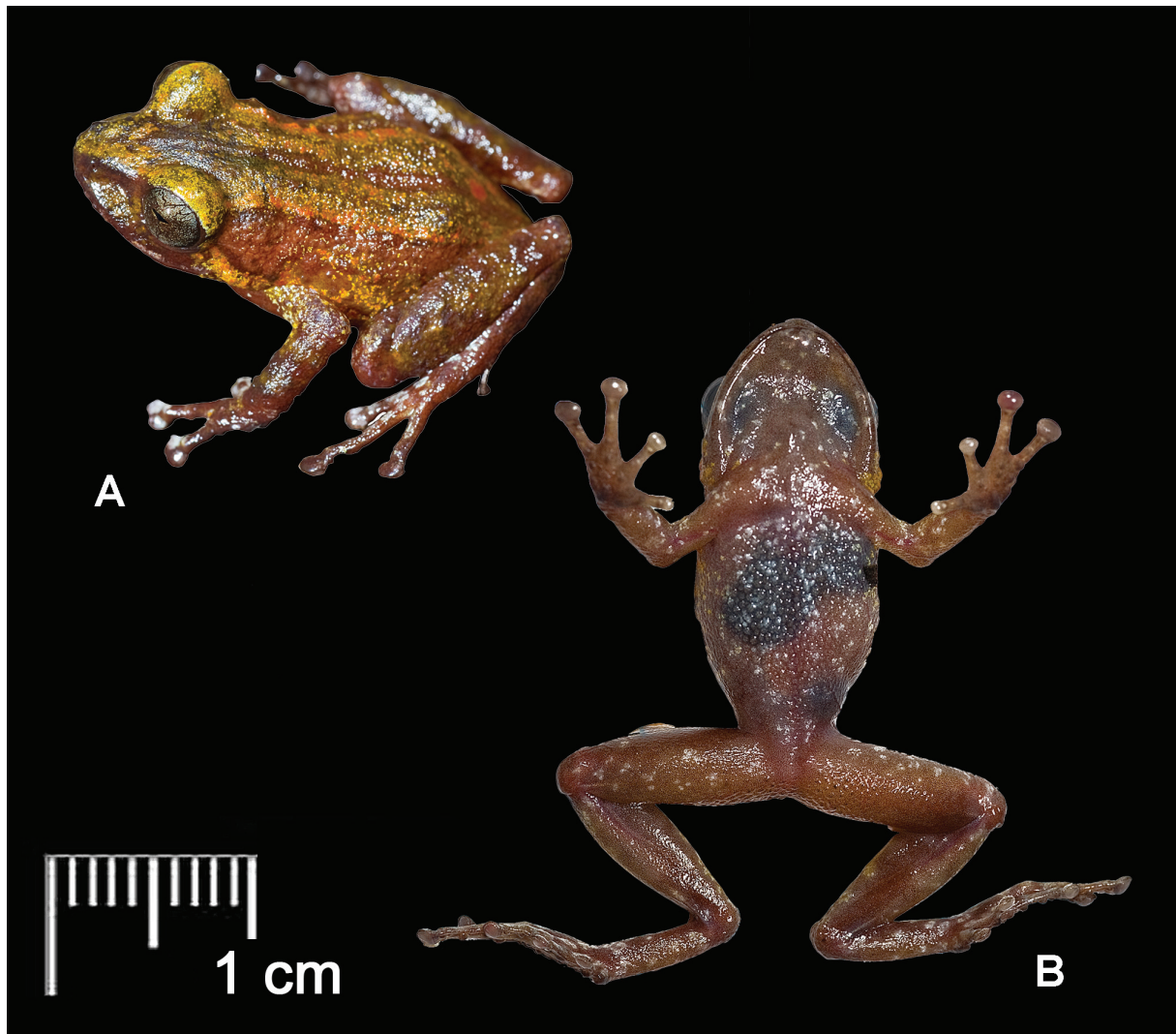


Fig. 8. *Pristimantis imthurni* sp. nov. in life. A. Dorsolateral view of the ♂ holotype (IRSNB 4165). B. Ventral view of the same specimen. Photographs by the author.

Morphological comparisons with congeneric species

For the same reasons mentioned above, comparisons with congeners only focus on the 21 *Pristimantis* species known to occur in the Pantepui region.

Pristimantis imthurni sp. nov. is most easily distinguished from *P. abakapa*, *P. aureoventris*, *P. avius*, *P. cantitans*, *P. dendrobatoides*, *P. guaiquinimensis*, *P. marmoratus*, *P. memorans*, *P. pruinatus*, *P. pulvinatus*, *P. saltissimus*, *P. sarisarinama*, *P. vilarsi*, *P. yuruaniensis*, and *P. zeuctotylus* by lacking a differentiated tympanic membrane and an external tympanic annulus (at least one of these structures is detectable in the latter 15 species). It further differs from *P. vilarsi* and *P. zeuctotylus* in having Finger I < II (Finger I > II in *P. vilarsi* and *P. zeuctotylus*).

Pristimantis imthurni sp. nov. is immediately distinguished from *P. auricarens*, *P. jester*, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis* in having lateral fringes on most fingers and toes (absent or limited to a weak keel in the latter 5 species).

By lacking a differentiated tympanic membrane and an external tympanic annulus, and in having lateral fringes on fingers and toes, *Pristimantis imthurni* sp. nov. is morphologically most similar to *P. jamescameroni* sp. nov., described earlier in this paper. These two species are mainly distinguished based on distinct dorsal and ventral colour patterns (compare Fig. 2 with Fig. 8), skin texture (smooth in *P. imthurni* sp. nov. vs. shagreen in *P. jamescameroni* sp. nov.), condition of the supratympanic fold (inconspicuous in *P. imthurni* sp. nov. vs. conspicuous in *P. jamescameroni* sp. nov.), and head proportion (shorter, with a more rounded snout in *P. imthurni* sp. nov.). Besides being morphologically reliably diagnosable, the two species are currently geographically isolated (isolated lineage segments).



Fig. 9. *Pristimantis imthurni* sp. nov. Ventral view of left hand and left foot of the ♂ holotype (IRSNB 4165). Photographs by the author.

Description of the holotype

An adult male 22.9 mm SVL (Figs 8-10, see Table 1 for measurements), in very good condition, except a large scar under the right thigh where a piece of muscle was removed prior to preservation. Head slightly longer than wide (HW 97.7% of HL), wider than body; HW 37.1% of SVL; HL 38.0% of SVL; cranial crests absent. Snout longer than eye length (SL 112.1% of EL), broadly rounded in dorsal view and in profile; *canthus rostralis* nearly straight in dorsal view, rounded in cross section, loreal region concave, flaring slightly at upper lip; eye-naris distance shorter than eye length (EN 72.7% of EL). Nares slightly protuberant, directed posterolaterally, visible in frontal and dorsal views. Widest upper eyelid width narrower than interorbital distance (upper eyelid width 81.5% of IO), upper eyelid smooth with one barely visible enlarged tubercle on each eyelid. Tympanum absent (tympanic membrane not differentiated and tympanic annulus not visible externally); tiny pharyngeal ostia present. Supratympanic fold inconspicuous in life, barely visible and fragmented in preservative, slightly arched, apparently originating at posterior corner of eye, failing to reach shoulder; a few low and small post-riental tubercles. Choanae very small, round; dentigerous processes of vomers inconspicuous, ovoid, posterior and medial to choanae, each bearing 3-4 teeth. Tongue cordiform, slightly wider than long, rounded posteriorly, posterior one-third free. Vocal slits and vocal sac absent.

Dorsal skin smooth, including on head; middorsal raphe barely detectable in preservative, well visible in life; no dermal folds or ridges visible on dorsal surface; flanks slightly granular. Throat and upper chest surfaces smooth; no thoracic fold detectable; belly skin coarsely areolate; no discoidal fold detectable; posteroventral thigh and cloacal region coarsely areolate; cloacal sheath absent, two distinctly enlarged tubercles below cloaca.

Hand length 27.1% of SVL. Finger I 88.6% of II. 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 proximal edge of digital pad of Finger III. Two large, broadly connected, non-spinous, mostly unpigmented (translucent when wet, white when dry) nuptial pads on each thumb, extending from the preaxial surface of the thenar tubercle and invading most of it, along the dorsal and the preaxial surface of the thumb. Lateral fringes on all fingers, best developed preaxially on Fingers II-III (Fig. 9). Finger discs expanded, elliptical, broader than long, circumferential groove conspicuous, distal edge of disc rounded; disc of

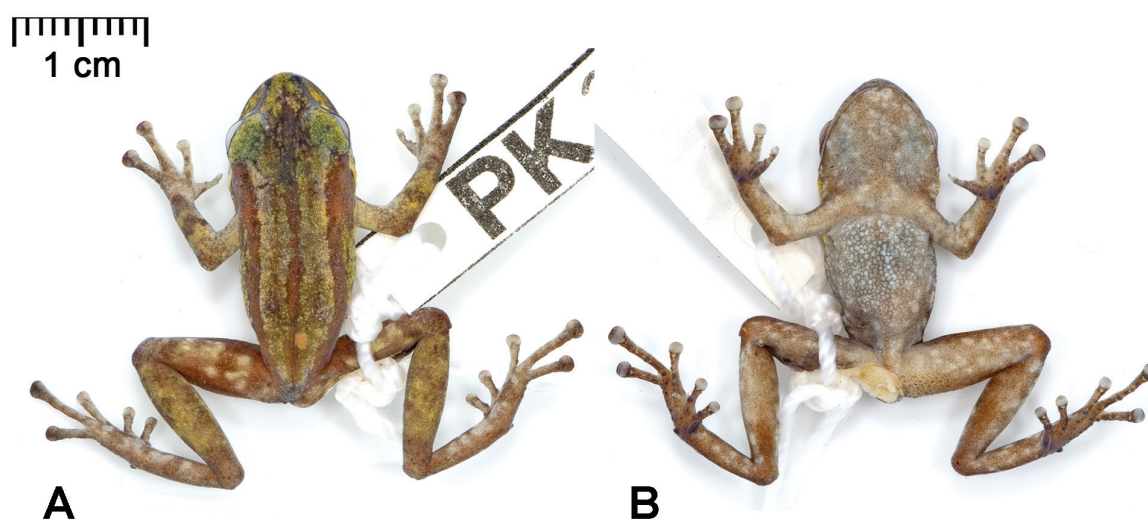


Fig. 10. *Pristimantis imthurni* sp. nov. in preservative. A. Dorsol view of the ♂ holotype (IRSNB 4165). B. Ventral view of the same specimen. Photographs by the author.

Finger III 1.8 times wider than the distal end of the adjacent phalanx. Palmar tubercle large, well defined, fully pigmented, deeply bifid; thenar tubercle large, protuberant, ovoid; supernumerary tubercles few, of variable sizes, slightly protuberant; subarticular tubercles large, round and protuberant, one each on FI and FII, two each on FIII and FIV. Ulnar tubercles absent; presence of a small antebrachial tubercle.

Hind limbs moderate in length, heels slightly overlap when held at right angles to sagittal plane; TIL 50.2% of SVL; FL 40.6% of SVL. Relative length of Toes IV > V > III > II > I; tip of Toe V extends to the distal edge of the distal subarticular tubercle on Toe IV; tip of Toe III extends to the distal edge of the penultimate subarticular tubercle on Toe IV. Lateral fringes on all toes, best developed preaxially on Toes III-IV (Fig. 9); webbing basal between Toe IV-V. Toe discs slightly larger in size than finger discs, WTD/WFD = 1.08; toe discs expanded, elliptical, broader than long, circumferential groove conspicuous, distal edge of disc rounded. Inner metatarsal tubercle elongate, oval, about four times the size of the projecting, round outer metatarsal tubercle; subarticular tubercles round, large and protuberant; supernumerary plantar tubercles small, low and round, increasing in size distally. Single, inconspicuous, very small, round calcar tubercle; no outer tarsal tubercles detectable; inner tarsal fold not detectable.

Colour of holotype in life (see Fig. 8)

Dorsal background colouration vivid yellow, top of head greyish brown; chocolate brown middorsal stripe and chocolate brown band on flanks; ill-defined, irregular reddish orange dorsolateral line; a few reddish orange blotches on the posterior part of the dorsum; a few reddish orange minute speckles on flanks; brown facemask; enlarged tubercle on eyelid whitish. Lower flanks yellow; groins, anterior thighs, and armpits brown. Arms and legs greyish brown with a few ill-defined white and dark yellow blotches. Ventral surfaces translucent greyish brown with a few irregular white spots and flecks; posterior surface of thighs and cloacal area brown. Upper face of hands and feet greyish brown with a few white and yellow markings; upper face of tip of fingers white; upper face of tip of Toes I-III white, brown on Toes IV-V. Palms, soles, undersurface of fingers and toes brown; discs greyish brown. Iris silver with dark brown venation and an ill-defined broad horizontal brownish stripe.

Colour of Holotype in preservative (see Fig. 10)

After 13 months in 70% ethanol (July 2013). Vivid yellow faded to pale yellow. Chocolate brown and brown faded to light brown; top of head is dark brown; ill-defined white and dark yellow blotches on arms and legs are slightly more conspicuous and form irregular, ill-defined transverse bands; dorsal pattern turned generally more conspicuous. Ventral colouration is light grey with a few white spots and flecks. Granules in the cloacal area, as well as subarticular and supernumerary tubercles became dark brown. Discs are grey.

Distribution and ecology

Pristimantis imthurni sp. nov. is only known from the summit of Ptari-tepui (Figs 1B, 6B, 11), Bolívar state, Venezuela, where it occurs at 2471 m elevation. Ptari-tepui lies in the Ptari massif, in the Los Testigos subdistrict (McDiarmid & Donnelly 2005). It is located ca. 47 km NE of the Chimantá massif, and ca. 22 km SE of Kamarkawarai-tepui (airline). According to the GPS, Ptari-tepui reaches a maximal elevation of about 2471 m above sea level. The summit area of Ptari-tepui is ca. 1 km² and is dominated by flat open rock surfaces and small islands of low meadow-like tepui vegetation (Huber 1995; Fig. 11B).

The male holotype – and single specimen collected – was found at night while calling partly concealed in the muddy soil in a small vegetation patch. A few other males were heard calling very sporadically from other small vegetation islands by day or night, but could not be located. *Pristimantis imthurni* sp. nov.

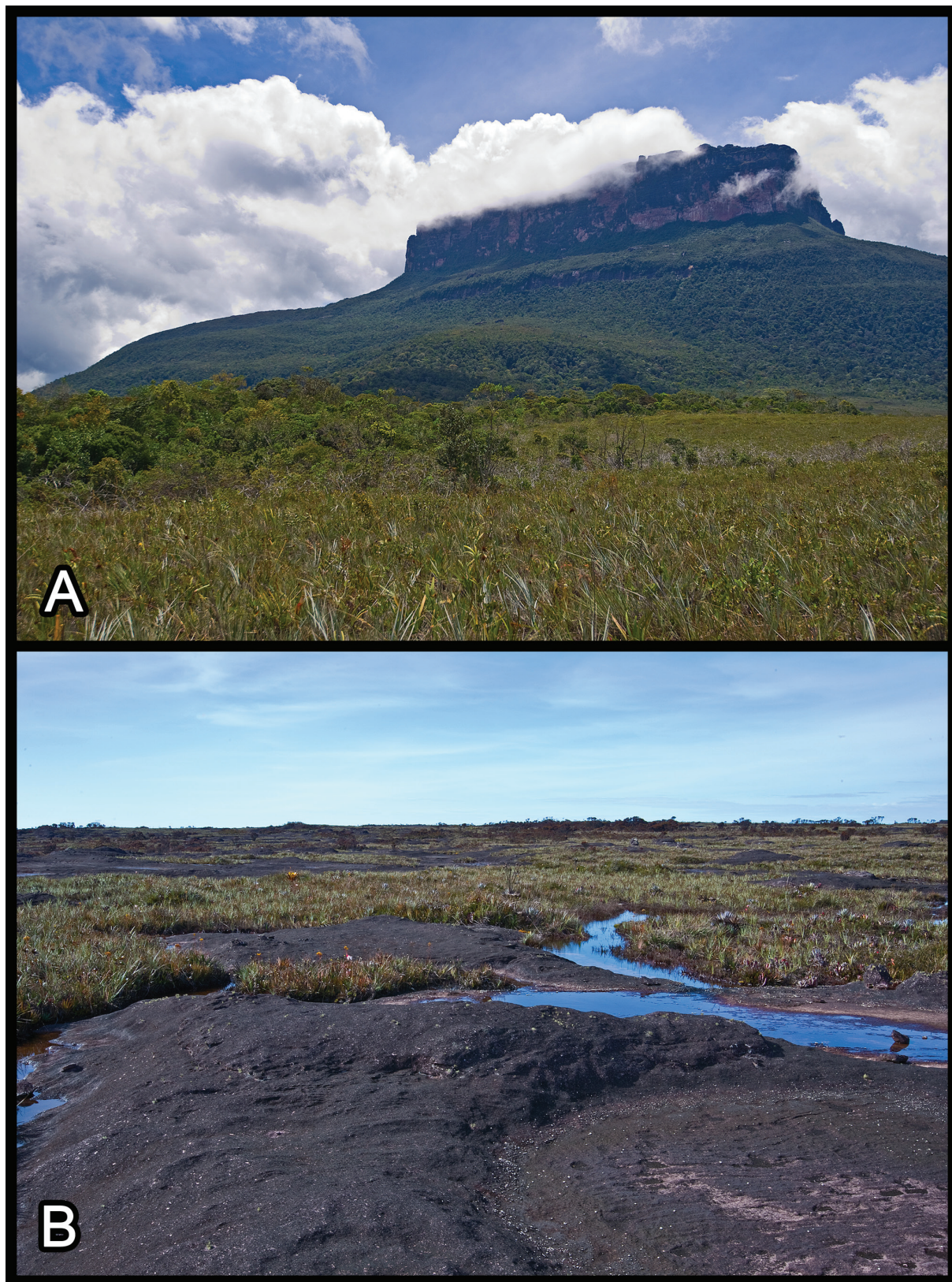


Fig. 11. A. Ptari-tepui, photographed from the surrounding savannah looking to the NE (21 Jun. 2012).
B. Summit of Ptari-tepui (21 Jun. 2012). Photographs by the author.

is not abundant. The only other anuran reported from the summit of Ptari-tepui is *Tepuihyla rimarum* Ayarzagüena, Señaris & Gorzula, 1993, which apparently also occurs in low density (pers. obs.).

Discussion

Although *Pristimantis imthurni* sp. nov. and *P. jamescameroni* sp. nov. are not the geographically closest tepui summit species (both new species occur on very isolated tepui summits separated from each other by a distance of *ca.* 50 km airline), they are recovered as sister species in preliminary phylogenetic analyses based on mtDNA (pers. obs., August 2012). Unfortunately, the lack of genetic data from several tepui summit *Pristimantis* species (e.g., *P. auricarens*, *P. muchimuk*) prevents any concluding phylogenetic inferences at this point. It should be noted that DNA sequences of *P. jamescameroni* sp. nov. have been used in previous molecular phylogenies under the name “*Pristimantis* sp” (Hedges *et al.* 2008) and “*Pristimantis* sp Aprada” (Kok *et al.* 2012), both confirming the generic allocation of the species.

McDiarmid & Donnelly (2005) listed no less than 20 undescribed *Pristimantis* species from the Guiana Shield highlands (under the genus name *Eleutherodactylus*, from sp. A to T). Since that publication, only five of these 20 species have been named: *Pristimantis* sp. C from Auyán-tepui was described as *P. auricarens* by Myers & Donnelly in 2008, *P.* sp. E from Yuruaní-tepui was described as *P. yuruaniensis* by Rödder & Jungfer in 2008, *P.* sp. G from Sarisariñama-tepui was described as *P. sarisarinama* by Barrio-Amorós & Brewer-Carías in 2008, *P.* sp. S from Guaiquinima-tepui was described as *P. guaiquinimensis* by Schlüter & Rödder in 2007, and *P.* sp. T from Cerro Marahuaka was described as *P. marahuaka* by Fuentes-Ramos & Barrio-Amorós in 2004 (thus slightly before the opus of McDiarmid & Donnelly was published). Three new species, not listed in McDiarmid & Donnelly (2005), were recently described from additional localities (*P. abakapa*, *P. aureoventris*, and *P. muchimuk*). The present paper describes two of the still unnamed species listed in McDiarmid & Donnelly (2005), *P.* sp. B and *P.* sp. H, still leaving 13 species to be named from the Pantepui region. Ten of these species occur in the Amazonas state of Venezuela (seven are reported from Cerro La Neblina, a huge massif located at the border with Brazil), three are from tepuis in the Bolívar state of Venezuela (the descriptions of two of them being in progress, Barrio-Amorós, pers. comm.).

The number of described *Pristimantis* species occurring exclusively on tepui (and faunistically related granitic mountains) summits and upper slopes now reaches eleven.

Although there is currently no evidence of continuing decline, given their apparent very restricted ranges (*ca.* 1 km² for *Pristimantis imthurni* sp. nov., less than 5 km² for *P. jamescameroni* sp. nov.) and the reported sensitivity of tepui ecosystems to global warming (see Nogué *et al.* 2009), it is suggested that *Pristimantis imthurni* sp. nov. and *P. jamescameroni* sp. nov. be classified as “Endangered” (EN) in accordance with criteria B1 a-b (iii) and B2 a-b (iii) of the IUCN Red List of Threatened Species (2001).

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Appendix: 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 (paratopotypes).

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

Pristimantis jester: GUYANA, Cuyuni-Mazaruni District, slopes of Maringma-tepui, IRSNB 15867, IRSNB 15916-17.

Pristimantis marmoratus: GUYANA, Cuyuni-Mazaruni District, foot of Mount Roraima, BMNH 1947.2.16.92 (formerly 99.3.25.19) (holotype).

Pristimantis pulvinatus: VENEZUELA, Estado Bolívar, La Escalera, IRSNB 15654.

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

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