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A NEW HIGHLAND SPECIES OF *PRISTIMANTIS* JIMÉNEZ DE LA
ESPADA, 1871 (ANURA: STRABOMANTIDAE) FROM THE PANTEPUI
REGION, NORTHERN SOUTH AMERICA

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Abstract

A new strabomantid frog of the genus *Pristimantis* Jiménez de la Espada, 1871 is described from the Eastern Pantepui Region, Guiana Shield, northern South America. The new species, *Pristimantis aureoventris* **sp. nov.**, is known so far from two neighbouring tepuis, namely Wei Assipu Tepui (type locality) at the border between Guyana and Brazil and Mount Roraima in Guyana, and occurs between 2210–2305 m elevation. The new taxon is distinguished from all known congeners by the following combination of characters: Finger I < II; tympanum distinct; basal webbing between Toes IV–V; broad lateral fringes on fingers and toes; ventral skin areolate; vocal slits absent in male; two non-spinous whitish nuptial pads and vocal sac present in male; high degree of pattern polymorphism; throat, chest, and belly golden yellow, usually with reddish brown to dark brown mottling; internal organs little or not visible through the ventral skin in life. The call of the new species consists of bouts of a single amplitude-modulated (decreasing to the end) note repeated at a rate of *ca.* 18 notes/min with a dominant frequency ranging from 2180 to 2430 Hz.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout



INTRODUCTION

The genus *Pristimantis* Jiménez de la Espada, 1871 was resurrected by Heinicke *et al.* (2007), who split the speciose genus *Eleutherodactylus* into three genera on the basis of molecular evidence: *Eleutherodactylus* was restricted to the “Caribbean Clade”, the members of the “South American Clade” were allocated to the genus *Pristimantis*, whereas the members of the “Middle American Clade” were allocated to the genus *Craugastor*. Soon after, further molecular support for this hypothesis was provided by Hedges *et al.* (2008), who allocated *Pristimantis* and 16 additional genera previously placed in the family Brachycephalidae by Frost *et al.* (2006) in the new family Strabomantidae.

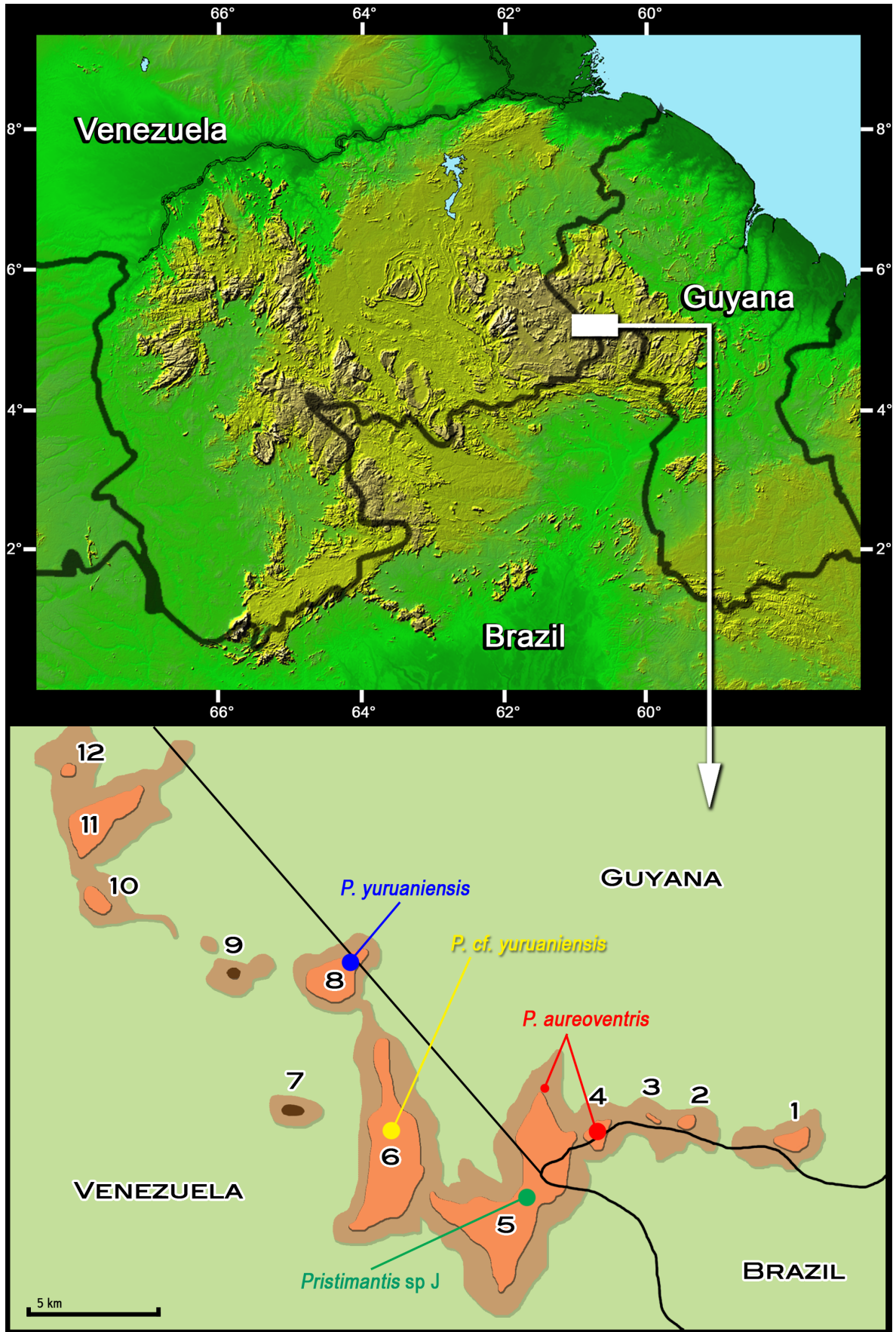
Recently, Heinicke *et al.* (2009) erected the new family Ceuthomantidae and the new genus *Ceuthomantis* to accommodate a new species from the Pakaraima Mountains of Guyana (*C. smaragdinus* Heinicke, Duellman, Trueb, Means, MacCulloch & Hedges, 2009), and proposed the placement of *Pristimantis aracamuni* (Barrio-Amorós & Molina, 2006) and *P. cavernibardus* (Myers & Donnelly, 1997) in the new family and genus based on morphological similarities. Barrio-Amorós (2010) then described *Pristimantis cf. cavernibardus* from Sarisariñama Tepui as *Ceuthomantis duellmani*.

To date, the genus *Pristimantis* contains more than 430 described species, 21 of which are distributed in the Pantepui region (Barrio-Amorós *et al.* 2010, Frost 2011), a biogeographic province referring to the complex of mountains (most of them called “tepui”) mainly derived from the sandstone of the Roraima Group in southern Venezuela, northwestern Guyana and northern Brazil (McDiarmid & Donnelly 2005) (Fig. 1). Among these 21 species, six only seem to be restricted to tepui summits and upper slopes, occurring above 2000 m elevation [*i.e.* *P. cantitans* (Myers & Donnelly, 1996), *P. pruinatus* (Myers & Donnelly, 1996), and *P. yaviensis* (Myers & Donnelly, 1996) from 2150 m on Cerro Yaví, *P. marahuaka* (Fuentes-Ramos & Barrio-Amorós, 2004) from 2450 m on Cerro Marahuaka, *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías and McDiarmid, 2010 from 2325 m on Churi Tepui in the Chimanta Massif, and *P. yuruaniensis* Rödder and Jungfer, 2008 from 2300 m on Yuruani Tepui].

According to McDiarmid & Donnelly (2005), several tepui summit *Pristimantis* species are still awaiting description, and only a few of the 20 unnamed species they listed were recently described (*e.g.* *Pristimantis auricarens* Myers & Donnelly, 2008 from Auyantepui and *P. yuruaniensis* from Yuruani Tepui).

Wei Assipu Tepui, sometimes called “Little Roraima”, is a poorly explored table-top mountain reaching *ca.* 2260 m elevation, located *ca.* 2 km airline (summit to summit distance) east of Mount Roraima at the border between Guyana and Brazil. An expedition to the summit of the tepui in November 2009 resulted in the discovery of an additional, distinctive *Pristimantis* species, which was also collected on the upper slopes of Mount Roraima. The new taxon is described below.

Figure 1. (next page). Map of the Pantepui region, with enlarged white rectangle corresponding to the Eastern Tepui Chain: 1 = Maringma Tepui, 2 = Yakontipu, 3 = Appokailang, 4 = Wei Assipu Tepui, 5 = Mount Roraima, 6 = Kukenan Tepui, 7 = Achipo Tepui, 8 = Yuruani Tepui, 9 = Guadacapiapu Tepui, 10 = Karaurin Tepui, 11 = Ilu Tepui, 12 = Tramen Tepui. Areas in orange indicate summits higher than 2000 m elevation; areas in dark brown indicate summits lower than 2000 m; areas in light brown indicate tepui slopes above 1500 m elevation.



MATERIAL AND METHODS

Specimens were collected by hand and euthanized by immersion in 2% Xylocaine. Tissue (a piece of liver or thigh muscle) was removed from most specimens and preserved in 95-100% ethanol. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens have been 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, Vrije Universiteit Brussel (VUB) (see Appendix for material examined).

Coordinates and elevations were acquired using a Garmin 60CSx Global Positioning System unit and referenced to map datum WGS84.

Terminology for morphological characters mostly follows Lynch & Duellman (1997), Savage *et al.* (2004), Kok & Kalamandeen (2008), and Duellman & Lehr (2009). 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, the description mainly follows the pattern of recent descriptions in the genus (*e.g.* Myers & Donnelly 2008, Barrio-Amorós *et al.* 2010). Classical measurements for the genus were taken and abbreviated as follows: (1) snout-vent length, from tip of snout to posterior margin of vent (SVL); (2) head length from angle of jaw to tip of snout (HL); (3) greatest width of the head (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance, taken between the median margins of the nares (IN); (7) eye length, horizontal distance from the anterior margin to the posterior margin of the eye (EL); (8) interorbital distance, taken between the median margins of the orbits (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (11) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (12) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (13) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (14) width of disc on Finger III (WFD); (15) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (16) width of disc on Toe IV (WTD); (17) tibia length from outer edge of flexed knee to heel (TIL).

Colour pattern in life was taken from field notes and colour digital photographs. Sex and maturity were determined by the presence or absence of nuptial pads (once it was established that adult males of the new species have nuptial pads) or by dissection and direct examination of gonads when sex remained doubtful. Internal soft anatomy was examined by dissection of preserved specimens.

Comparisons of external character states are based both on original descriptions and examination of museum specimens (see Appendix for material examined).

Recordings of advertisement calls were taken in the field at a distance of less than 1 m from the calling male with a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder using Maxell DM60 digital audiotape (holotype) or with a Sennheiser ME66/K6 microphone attached to a Marantz PMD661 solid state recorder (uncollected *Pristimantis yuruaniensis* recorded for comparison purpose). The calls were analysed at a sampling rate of 44100 Hz using Raven Pro version 1.4 software (Charif *et al.*, 2010).

Temporal variables measured included: call duration (= note duration); inter-call interval (beginning of one call to beginning of the next); and call rate (= number of calls per minute). The dominant (emphasized) frequency of the note was measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 150 Hz). Air temperature at the call sites was measured with a Hanna digital pH/thermometer.

Because preliminary molecular analyses based on a fragment of *ca.* 550 base pairs of the 16S rRNA gene (the authors, unpublished data) indicate that syntopic specimens from the summit of Wei Assipu Tepui cluster into two morphologically undifferentiated clades separated by 0.89–1.25% uncorrected pairwise distance (divergence within each of these clades varies from 0–0.36%) we decided to select specimens of one of these two clades to serve as the type series, assigning the others and specimens for which molecular data are unavailable to “referred specimens” (see Discussion).

Taxonomy follows Hedges *et al.* (2008). Institutional acronyms follow Frost (2011).

NEW SPECIES DESCRIPTION

Pristimantis aureoventris sp. nov.

Figs. 2–7; Table 1

Holotype. IRSNB 4152 (field number PK 2152), an adult male collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 17 November 2009 at 20h00, summit of Wei Assipu Tepui, Cuyuni-Mazaruni District, Guyana (05° 13' 05"N, 060° 42' 15"W, 2210 m elevation).

Paratopotypes (n=2). IRSNB 4153 (field number PK 2066), a female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 3 November 2009, and IRSNB 4154 (field number PK 2087), a subadult female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 4 November 2009.

Referred specimens (n=10). IRSNB 15821–22 (field numbers PK 2162–63), females; IRSNB 15820, IRSNB 15823 (field numbers PK 2085, PK 2086), males; IRSNB 15824–27 (field numbers PK 2107–08, PK 2114, PK 2117), males; IRSNB 15637 (field number PK 2158), a very small juvenile, all collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry on the summit of Wei Assipu Tepui between 3–19 November 2009. IRSNB 15643 (field number CPI 10484), a male collected by D. Bruce Means, 17 November 2006, from *ca.* 300 m below the base of the ultimate cliff of the northern “Prow” of Mount Roraima, Cuyuni-Mazaruni District, Guyana (05° 15'N, 060° 43'W, 2305 m elevation).

Etymology. The specific name *aureoventris* is a noun in apposition derived from the Latin words “*aureus*” meaning golden, and “*ventris*” meaning venter, and refers to the golden ventral face of the new species.

Generic allocation. To date, there is no identifiable morphological synapomorphy supporting the genus *Pristimantis* (Hedges *et al.* 2008). We assign the new taxon to the

genus *Pristimantis* based on molecular phylogenetic relationships (the authors, unpublished data) as well as on its morphological characteristics, which fall into the range of other *Pristimantis* species.

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 non-monophyletic *unistrigatus* species group (*sensu* Hedges *et al.* 2008, see Discussion) 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 combination of characters: (1) dorsal skin shagreened to slightly granular, rarely with some conical tubercles, faint middorsal raphe in life, ventral skin areolate; (2) tympanum distinct, less than half the size of the eye; (3) snout rounded to subovoid in dorsal view, rounded to slightly sloping in profile, canthus rostralis nearly straight to concave, round; (4) upper eyelid smooth to slightly granular, usually with one or two distinctly enlarged tubercles on each eyelid; (5) choanae small, oval, dentigerous processes of vomers small, oblique, V-shaped, posterior and medial to choanae, each bearing 2–5 teeth; (6) absence of vocal slits in males, but presence of a shallow vocal sac and of two white non-spinous nuptial pads; (7) Finger I shorter than II; (8) fingers with broad lateral fringes; (9) ulnar tubercles low, inconspicuous, not forming a distinct line in preservative, but more conspicuous in life, sometimes forming a row; (10) tarsal tubercles low, inconspicuous, not forming a distinct line, calcar tubercles present, not pronounced; (11) inner metatarsal tubercle oval, two to four times the size of the round outer metatarsal tubercle; (12) toes with broad lateral fringes, webbing basal between Toes IV–V, Toe V longer than III, usually surpassing the proximal edge of the distal tubercle on Toe IV when toes are adpressed; (13) in life dorsal colouration highly variable, ranging from light golden brown, medium or dark brown to dark brown with two broad light brown longitudinal stripes mottled with dark brown and finely edged by a cream line; a W-shaped marking may be present on scapula; ill-defined light brown oblique bands are usually present on flanks with similarly coloured ill-defined cross-bands on legs; broad light greyish brown bands may be present on flanks, dark brown dorsolateral bands may be present as well; a faint dark interorbital bar is usually visible; the snout is sometimes paler than body with some dark markings; a dark brown to black postocular stripe across upper and posterior parts of tympanum is present in most specimens; the groin is usually black or brown, sometimes with some small golden spots; a conspicuous reddish orange flashmark on groin may be visible; arms and legs often have a reddish or orangish tint. In preservative dorsal colouration brown to dark brown, the same patterns as described in life faded, but are still visible; (14) males 19.6–22.7 mm SVL, females 24.0–29.0 mm.

Compared to the 21 *Pristimantis* species distributed in the Pantepui region, *P. aureoventris* is immediately distinguished from *P. stegolepis* (Schlüter & Rödder, 2007), *P. vilarsi* (Melin, 1941), and *P. zeuctotylus* (Lynch & Hoogmoed, 1977) in having $FI < II$ ($FI > II$ in *P. stegolepis*, *P. vilarsi* and *P. zeuctotylus*); from *P. auricarens*, *P. jester* Means and Savage, 2007, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis* in having a distinct tympanum (indistinct in *P. auricarens*, *P. jester*, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis*); from *P. avius* (Myers & Donnelly, 1997), *P. cantitans*, *P. inguinalis* (Parker, 1940), *P. marmoratus* (Boulenger, 1900), *P. memorans* (Myers & Donnelly, 1997), *P. pruinatus*, *P.*

pulvinatus (Rivero, 1968), and *P. sarisarinama* Barrio-Amorós and Brewer-Carías, 2008 in lacking vocal slits in male (vocal slits present in male of *P. avius*, *P. cantitans*, *P. inguinalis*, *P. marmoratus*, *P. memorans*, *P. pruinatus*, *P. pulvinatus*, and *P. sarisarinama*); from *P. dendrobatoides* Means and Savage, 2007 in having lateral fringes on fingers and toes (absent in *P. dendrobatoides*), in having a shagreened to slightly granular dorsal skin (covered with large granular tubercles in *P. dendrobatoides*), and by the presence of nuptial pads in male (absent in *P. dendrobatoides*); from *P. guaiquinimensis* (Schlüter & Rödder, 2007) and *P. tepuiensis* (Schlüter & Rödder, 2007) by its much smaller size in adult male (male SVL max 22.7 mm [n=8] in *P. aureoventris* vs. 33.6 mm [n=2] in *P. guaiquinimensis*, and 34.7 mm [n=1] in *P. tepuiensis*), by the presence of nuptial pads in male (absent in *P. guaiquinimensis* and *P. tepuiensis*), by the presence of vomerine teeth (absent in *P. guaiquinimensis* and *P. tepuiensis*), and in having lateral fringes on fingers and toes (absent in *P. guaiquinimensis* and *P. tepuiensis*); from *P. saltissimus* Means and Savage, 2007 in having lateral fringes on fingers and toes (absent in *P. saltissimus*), and by the presence of nuptial pads in male (absent in *P. saltissimus*); from *P. yuruaniensis* by its smaller size in adult female (female SVL max 29.0 mm [n=3] in *P. aureoventris* vs. 32.2 mm [n=5] in *P. yuruaniensis*), by having the ventral part golden yellow in life, usually with reddish brown to dark brown mottling, opaque with internal organs not, or barely visible through the skin (ventral part whitish, orangish or brown speckled with minute brownish dots in life, translucent, internal organs well visible through the skin in *P. yuruaniensis*), by having a higher degree of pattern polymorphism, and by having a less tuberculate skin.

Description of the Holotype. An adult male 20.4 mm SVL (Fig. 2) in very good condition of preservation, except a few small scars on back and upper arms. Head slightly longer than wide (HW 90.4% of HL), wider than body, HW 39.9% of SVL, cranial crests absent. Snout rounded in dorsal view, slightly sloping in profile; canthus rostralis nearly straight, round, loreal region slightly concave, sloping outward to lip; nares slightly protuberant, directed posterolaterally. Upper eyelid width narrower than IO; upper eyelid slightly granular with two barely discernible enlarged tubercles on each eyelid (better visible in life). Tympanum distinct, but not conspicuous, slightly obscured posteriorly, vertically oval, TYM 29% of EL, separated from eye by about half its length; supratympanic fold originating at corner of eye, failing to reach shoulder, slightly arched; small postrictal tubercles evident. Choanae small, oval, slightly kidney-shaped, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers slightly smaller than choanae, oblique, V-shaped, posterior and medial to choanae, each bearing 3 to 4 teeth. Tongue much longer than wide, rounded posteriorly, posterior 2/3 free. Vocal slits absent, shallow subgular vocal sac present, seemingly not very distensible.

Dorsal skin shagreened, almost smooth on head; middorsal raphe faint; no scapular folds or ridges visible; dorsal surfaces of limbs shagreened; flanks granular. Throat smooth; venter areolate (coarsely granular); posteroventral thigh and cloacal region areolate; weak discoidal fold anterior to groin; ulnar tubercles low, inconspicuous, not forming a distinct line in preservative, but more visible in life with three of them more prominent, forming a row.

Finger I 85% of II; relative length of adpressed fingers III > IV > II > I; adpressed Finger I failing to reach proximal edge of subdigital pad of Finger II; broad pre- and postaxial lateral fringes on fingers; presence of two whitish non-spinous nuptial pads, one

adjacent to thenar tubercle and having about the same size, the other on the posterodorsal side of the thumb, having about the same size as the subarticular tubercle on Finger I. Finger discs expanded, with wide digital pads, broader than long, slightly rounded; distal median edge rounded. Palmar tubercle large, deeply bifid, V-shaped; thenar tubercle large, ovoid; subarticular tubercles large, round; supernumerary tubercles present, relatively large and protuberant (Fig. 3).

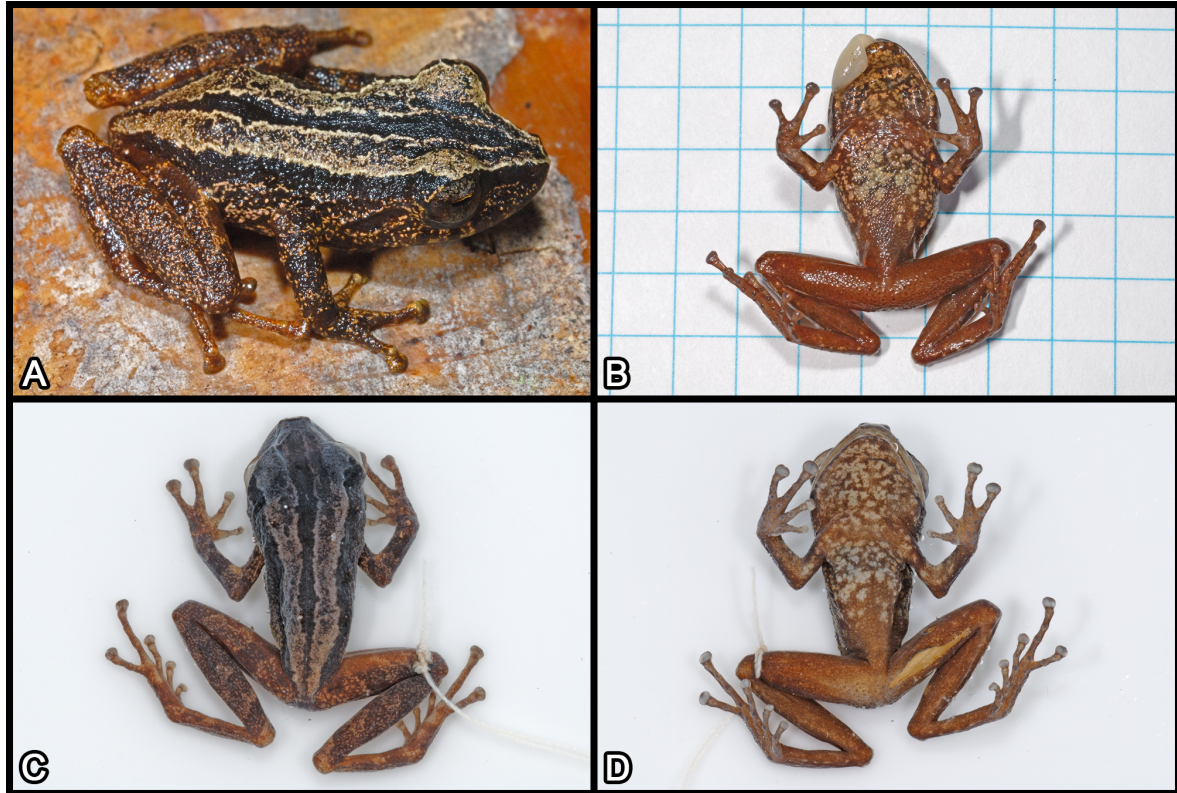


Figure 2. *Pristimantis aureoventris* sp. nov. A: Dorsolateral view of the male holotype in life (IRSNB 4152, 20.4 mm SVL). B: Ventral view of the anaesthetized holotype. C: Dorsal view of the preserved holotype. D: Ventral view of the preserved holotype. Photographs by Philippe J.R. Kok.

Hind limbs relatively long; heels overlap when held at right angles to sagittal plane; TIL 55.7% SVL; FL 45.8% SVL. Relative length of adpressed toes IV > V > III > II > I; tip of Toe V extends to distal edge of ultimate subarticular tubercle of Toe IV, tip of III to the distal edge of the penultimate subarticular tubercle of IV. Toe discs as wide or narrower than finger discs, WFD/WTD = 1.11, with wide digital pads. Toes with broad pre- and postaxial lateral fringe, except on Toe I where fringes are barely visible; webbing basal between Toes IV-V. Inner metatarsal tubercle elongate, oval, about twice the size of the round outer metatarsal tubercle; supernumerary plantar tubercles low and round; subarticular tubercles large and protuberant. Calcar tubercles indistinct. Tarsal tubercles low, inconspicuous, not forming a distinct line; inner tarsal fold not visible (Fig. 3).



Figure 3. *Pristimantis aureoventris* sp. nov. Ventral views of left hand (left) and left foot (right) of the male holotype (IRSNB 4152, 20.4 mm SVL). Scale bars = 1 mm (left) and 1.5 mm (right). Photographs by Philippe J.R. Kok.

Measurements of the Holotype (mm). SVL 20.4; HL 9.0; HW 8.2; SL 3.5; EN 2.3; IN 1.8; EL 3.2; IO 2.5, TYM 0.9; HAND I 3.6; HAND II 4.2; HAND III 5.8; HAND IV 4.7; WFD 1.1; FL 9.4; WTD 1.0; TIL 11.4.

Colour of the Holotype in life. Dorsal ground colour dark brown with two broad light brown longitudinal stripes mottled with dark brown and finely edged by a cream line, extending from tip of snout to vent. Flanks dark brown with ill-defined light brown oblique bands; limbs adorned with similarly coloured ill-defined cross-bands. Arms and legs have a reddish tint. Broad dark brown postocular stripe across upper and posterior parts of tympanum, not contacting eye and failing to reach shoulder; broad dark brown canthal stripe; ill-defined dark brown labial bars from eye to upper lip. Posterior and anterior surfaces of thighs reddish brown, slightly mottled with golden. Throat, chest, and upper belly golden yellow with reddish brown mottling, lower belly and under surfaces of limbs

reddish brown; internal organs not visible through the skin. Palms and soles dark brown. Iris greenish bronze, with fine black venation and a median horizontal reddish streak (Fig. 2).

Colour of the Holotype in preservative. After 14 months in preservative, patterns and colours faded, but remain roughly the same. The golden ventral colour and the light brown stripes and bands became greyish. Arms and legs still have a slightly reddish tint (Fig. 2).

Variation. See Table 1 for measurements, and Figs. 4–6 for intrapopulational variation.

The most striking variation occurs in colour and pattern, which are very variable among living individuals (Fig. 4). The holotype is the only specimen having a striped dorsal pattern. Among the other specimens available, the dorsal colouration in life ranges from light golden brown (*e.g.* IRSNB 15823, adult male) to dark brown (*e.g.* IRSNB 15827, adult male), sometimes with a W-shaped marking on scapula (*e.g.* IRSNB 15820 and IRSNB 15643, adult males, and IRSNB 4154, subadult female). One male (IRSNB 15825) has a dark brown dorsum with broad light greyish brown bands on flanks; two individuals (IRSNB 4153, adult female, and IRSNB 15826, adult male) have a brownish dorsum with ill-defined dark brown dorsolateral bands. The ill-defined light brown oblique bands on flanks and the similarly coloured ill-defined cross-bands on legs may be absent (*e.g.* IRSNB 15820, adult male). A faint dark interorbital bar is usually visible (absent in the holotype), this bar being conspicuous in IRSNB 4154 (subadult female). In three individuals (IRSNB 4154, subadult female, IRSNB 15824 adult male, IRSNB 15825, adult male) the snout is paler than body (tan) with some dark markings (a black inverted triangle in IRSNB 4154). A dark brown to black postocular stripe across upper and posterior parts of tympanum is present in all specimens from Wei Assipu Tepui, that stripe is poorly detectable in the Roraima specimen. Groin is usually black or brown, sometimes with some small golden spots; one male (IRSNB 15827) had a conspicuous reddish orange flashmark on its groin in life (Fig. 7), which became white after preservation. Arms and legs usually have a reddish or orangish tint; IRSNB 15824 (adult male) had the posterior and anterior surfaces of thighs, the tibio-tarsal articulation, and part of the feet including Toes III–IV bright red; IRSNB 15825 (adult male) had the tibio-tarsal articulation distinctly paler (light grey) than the legs (dark brown); IRSNB 4154 (subadult female) had the anterior surface of thighs, the posterior surface of shanks, and part of the feet including Toes III–IV orange, a similar pattern is visible in IRSNB 15826 (adult male), but much less vivid. In other specimens, the posterior and anterior surfaces of thighs are reddish brown to dark brown, slightly mottled with golden. Under surfaces of limbs are reddish brown to dark brown, often heavily spotted with golden. Mottling on venter varies from reddish brown to dark brown, almost black, and is variably extensive; two individuals (IRSNB 15823, adult male from Wei Assipu Tepui, and IRSNB 15643, adult male from Mount Roraima, see Figs. 4, 6) lack mottling on venter. Due to the golden colouration of the venter, internal organs are little (IRSNB 15822, adult female) or not (holotype and other specimens) visible through the ventral skin in life (Figs. 2, 4). Iris colouration is variable, some individuals lack the median horizontal reddish streak (*e.g.* IRSNB 15822, adult female); IRSNB 15820 (adult male) has a blue-green iris (Fig. 4). In preservative all specimens became darker and variation in colour and pattern is less visible, but is still discernible (Fig. 5).

Character	Males Wei Assipu Tepui (n=7)	Females Wei Assipu Tepui (n=3)	Subadult female Wei Assipu Tepui (n=1)	Male Mount Roraima (n=1)
SVL	21.6 ± 0.8 (20.4–22.7)	26.8 (24.0–29.0)	17.7	19.6
HL	9.2 ± 0.3 (8.6–9.6)	11.6 (10.7–12.2)	7.4	8.4
HW	8.5 ± 0.3 (7.9–8.8)	10.4 (9.7–11.2)	6.8	8.3
SL	3.8 ± 0.2 (3.5–4.1)	4.5 (4.5–4.6)	3.1	3.8
EN	2.5 ± 0.2 (2.2–2.6)	3.1 (2.9–3.3)	2.1	2.4
IN	2.0 ± 0.1 (1.8–2.2)	2.2	1.8	1.9
EL	3.1 ± 0.2 (2.9–3.3)	3.3 (3.1–3.5)	2.1	3.1
IO	2.6 ± 0.2 (2.3–2.9)	3.2 (3.1–3.3)	2.0	2.5
TYM	1.1 ± 0.1 (0.9–1.3)	1.4	1.0	0.8
HAND I	3.7 ± 0.2 (3.4–4.0)	4.9 (4.4–5.4)	3.0	3.3
HAND II	4.4 ± 0.2 (4.2–4.8)	5.6 (5.2–6.0)	3.4	3.8
HAND III	6.1 ± 0.2 (5.8–6.3)	8.0 (7.0–8.1)	4.7	5.1
HAND IV	4.9 ± 0.2 (4.6–5.2)	6.1 (5.8–6.4)	3.8	4.1
WFD	1.1 ± 0.1 (1.0–1.3)	1.3 (1.2–1.4)	0.7	1.0
FL	9.4 ± 0.3 (9.0–9.6)	11.6 (10.9–12.0)	7.4	8.1
WTD	1.1 ± 0.1 (1.0–1.2)	1.4 (1.3–1.6)	0.6	1.0
TIL	11.7 ± 0.2 (11.4–12.1)	14.9 (14.8–15.5)	9.5	10.5

Table 1. Measurements (in mm) of specimens of *Pristimantis aureoventris* sp. nov. Abbreviations are defined in the text. Mean ± SD (when sample > 3) are followed by the range in parentheses.

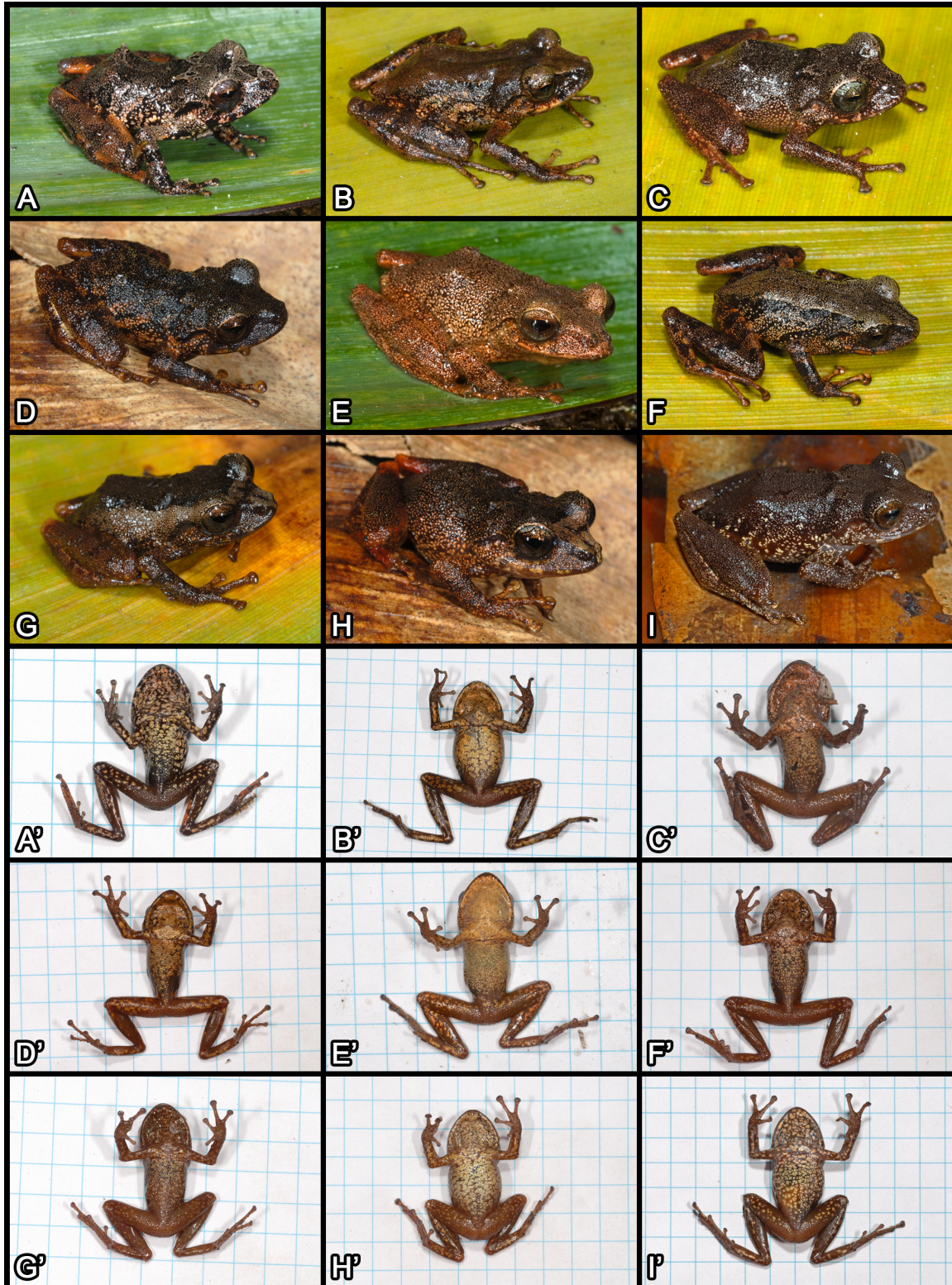


Figure 4. *Pristimantis aureoventris* sp. nov. Intrapopulation variation in dorsal and ventral colour in living specimens from Wei Assipu Tepui. A-A': IRSNB 4154, subadult female, 17.7 mm SVL. B-B': IRSNB 4153, adult female, 24.0 mm SVL. C-C': IRSNB 15820, adult male, 21.4 mm SVL. D-D': IRSNB 15827, adult male, 22.3 mm SVL. E-E': IRSNB 15823, adult male, 22.6 mm SVL. F-F': IRSNB 15826, adult male, 22.7 mm SVL. G-G': IRSNB 15825, adult male, 20.9 mm SVL. H-H': IRSNB 15824, adult male, 21.0 mm SVL. I-I': IRSNB 15822, adult female, 27.3 mm SVL. Photographs by Philippe J.R. Kok.

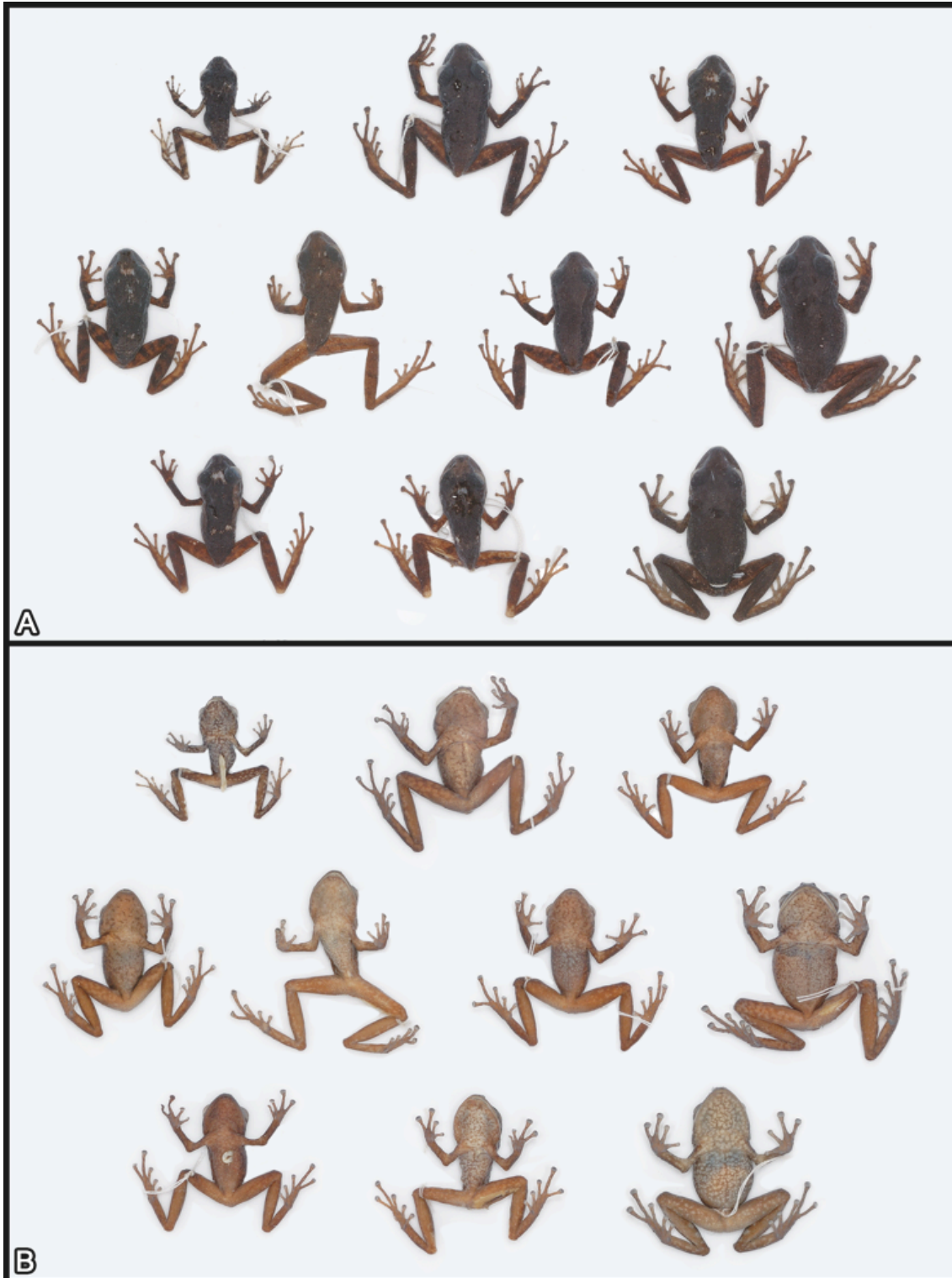


Figure 5. *Pristimantis aureoventris* sp. nov. Intrapopulation variation in dorsal (above) and ventral (below) colour in preserved specimens from Wei Assipu Tepui. First row, from left to right: IRSNB 4154, subadult female, 17.7 mm SVL, IRSNB 4153, adult female, 24.0 mm SVL, IRSNB 15820, adult male, 21.4 mm SVL. Second row, from left to right: IRSNB 15827, adult male, 22.3 mm SVL, IRSNB 15823, adult male, 22.6 mm SVL, IRSNB 15826, adult male, 22.7 mm SVL, IRSNB 15821, adult female, 29.0 mm SVL. Third row, from left to right: IRSNB 15825, adult male, 20.9 mm SVL, IRSNB 15824, adult male, 21.0 mm SVL, IRSNB 15822, adult female, 27.3 mm SVL. Photographs by Philippe J.R. Kok.

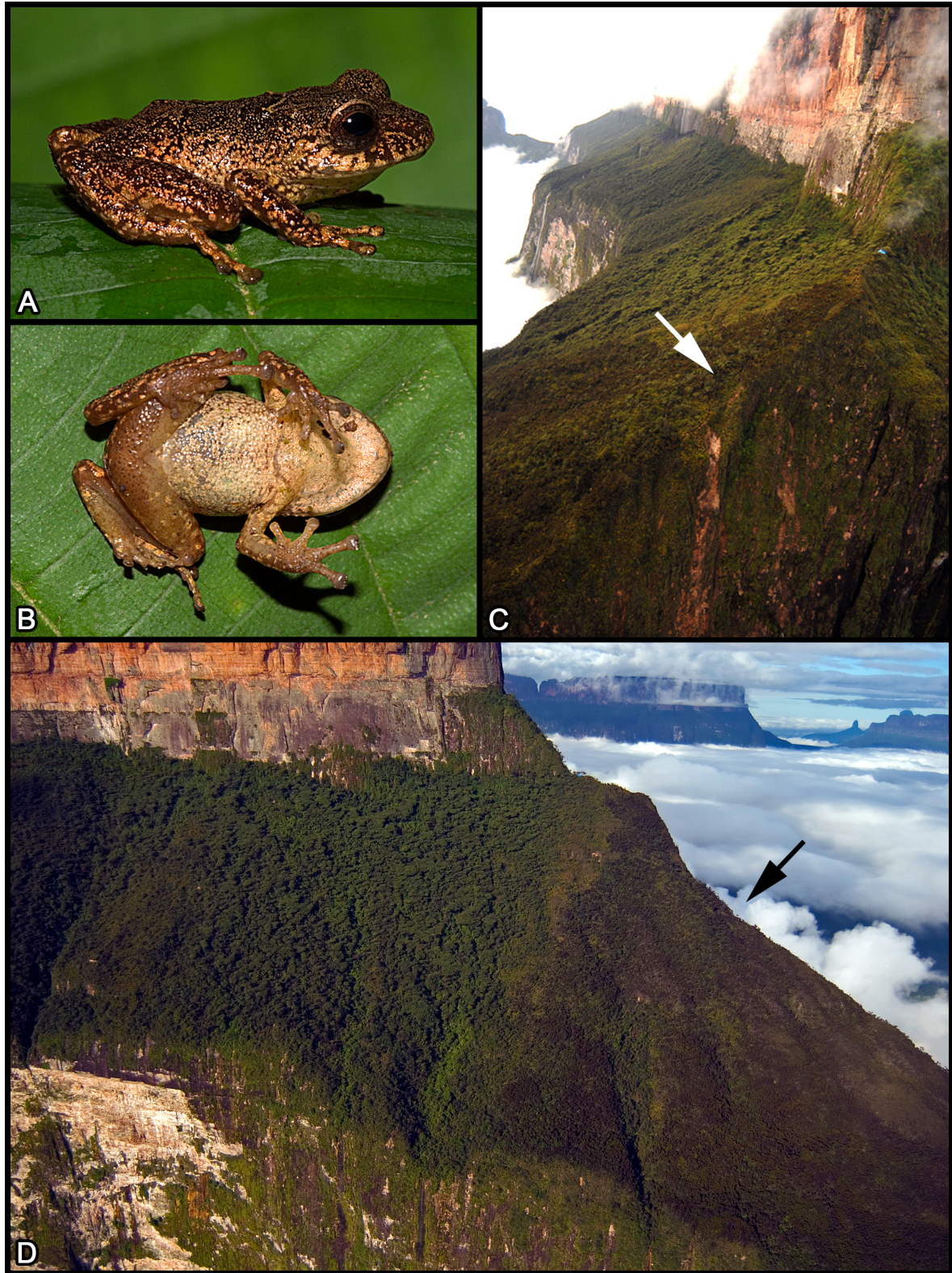


Figure 6. *Pristimantis aureoventris* sp. nov. A: Dorsolateral view of IRSNB 15643, 19.6 mm SVL, male referred specimen from the upper slopes of Mount Roraima. B: Ventral view of the same specimen while alive. C, D: Aerial photographs of the base of the ultimate cliff of the northern Prow of Mount Roraima, arrows indicate the exact place where the specimen was collected; a small part of Wei Assipu Tepui is visible on the upper left on image C. Photographs by D. Bruce Means.



Figure 7. *Pristimantis aureoventris* sp. nov. Groin region showing the conspicuous reddish orange flashmark in the adult male IRSNB 15827. Photograph by Philippe J.R. Kok.

Dorsal skin texture is slightly variable, most individuals having the dorsal skin shagreened to slightly granular. One specimen however (IRSNB 15827, adult male) has small conspicuous conical tubercles on anterior dorsum and legs, as is the case in the tiny (7.1 mm SVL) referred juvenile (IRSNB 15637). Few small conical tubercles are also visible on legs of most of the specimens. Small scapular tubercles were visible in seven individuals of both sexes in life (IRSNB 15822–24, IRSNB 15827, IRSNB 15643), but these tubercles are barely seen on the preserved animals and are absent in the holotype. Eyelid tubercles can be conspicuous (*e.g.* in IRSNB 15824, adult male) or barely visible (*e.g.* in IRSNB 15820, adult male).

Number of teeth on dentigerous processes of vomers varies from two to five; they are absent in the very small juvenile (IRSNB 15637).

A weak discoidal fold anterior to groin is visible only in the holotype and in two other specimens (IRSNB 15826, adult male, IRSNB 4153, adult female).

The tip of Toe V fails to reach the distal edge of the ultimate subarticular tubercle of Toe IV on both sides in one female (IRSNB 4153), and on one side in four individuals of both sexes (IRSNB 15822–24, IRSNB 15643).

No obvious sexual dimorphism is noted, except in size (females are larger than males).

Other differences among available specimens are considered minor.

Advertisement call. The following description is based on a sample of 21 advertisement calls from the male holotype (IRSNB 4152), recorded on the summit of Wei Assipu Tepui (05° 13' 05"N, 060° 42' 15"W, 2210 m elevation), on 17 November 2009 at 20h00, air temperature 15.0°C. The male was calling concealed between the basal leaves of an *Orectanthe sceptrum* (Xyridaceae) growing *ca.* 150 cm above the ground on the wall of a 300-cm deep small crevice.

Temporal structure. The advertisement call of *Pristimantis aureoventris* consists of a soft, single, unpulsed note (perceived by the human ear as a small drop falling in the water). Calls are apparently emitted in bouts of about 20 calls (variation of the number of calls in each bout is unknown). The call rate was 18 calls/min based on a 1-min period. The mean call duration is 0.021 ± 0.002 and varies from 0.017 to 0.023 s. The inter-call interval is rather uniform and has a mean of 3.097 ± 0.275 and a range of 2.730–3.610 s (Fig. 8A).

Spectral structure. Three harmonics are apparently developed, with the fundamental frequency dominating (mean: 2295, range: 2180–2430 Hz) (Fig. 8A). The third harmonic contains slightly more sound energy than the second. The three harmonics show a feeble “U-shaped” frequency modulation (Fig. 8A).

Comparisons. Unfortunately, very few detailed descriptions of *Pristimantis* advertisement calls are available from the highlands of the Pantepui region. Myers and Donnelly (1996) provided analyses of unvouchered calls of different individuals of two highland *Pristimantis* species (tentatively assigned to *P. cantitans* and *P. pruinatus*) from Cerro Yaví, a massif located *ca.* 680 km W airline from Wei Assipu Tepui, and Rödder and Jungfer (2008) described the call of *P. yuruaniensis* from Yuruani Tepui located *ca.* 19 km airline NW from Wei Assipu Tepui.

The call of *P. aureoventris* mostly differs from the calls described from Cerro Yaví in call duration and fundamental frequency: call duration varies from 0.017 to 0.023 s in *P. aureoventris* vs. 0.047 to 0.075 s in the type I call (presumably *P. cantitans*) and vs. 0.028 to 0.056 s in the type II call (presumably *P. pruinatus*) of Myers and Donnelly (1996); fundamental frequency varies from 2180–2430 Hz in *P. aureoventris* vs. 1520–1720 Hz in the type I call and vs. 2440–2660 Hz in the type II call of Myers and Donnelly (1996).

To the human ear, the call of *P. yuruaniensis* sounds more or less similar to that of *P. aureoventris*, but higher-pitched. Analysis indicates differences in note duration (0.017–0.023 s in *P. aureoventris* vs. 0.093–0.139 s in *P. yuruaniensis*), in fundamental frequency (2180–2430 Hz in *P. aureoventris* vs. 1860–2080 Hz in *P. yuruaniensis*), in inter-call interval (2.730–3.610 s in *P. aureoventris* vs. 0.504–1.968 s in *P. yuruaniensis*), and in harmonics structure (three harmonics showing a feeble “U-shaped” frequency modulation in *P. aureoventris* vs. five indistinctly modulated harmonics in *P. yuruaniensis*). Additionally, the distribution of sound energy decreases progressively through the higher harmonics in *P. yuruaniensis*, while in *P. aureoventris* the third harmonic contains slightly more sound energy than the second (compare Fig. 8A with Fig. 8B). Some of these variations could be caused by intrinsic parameters (*e.g.* size variation, see Duellman & Trueb 1986). Apparent similarity between calls of Pantepui *Pristimantis* species might be interpreted as a plesiomorphic trait.

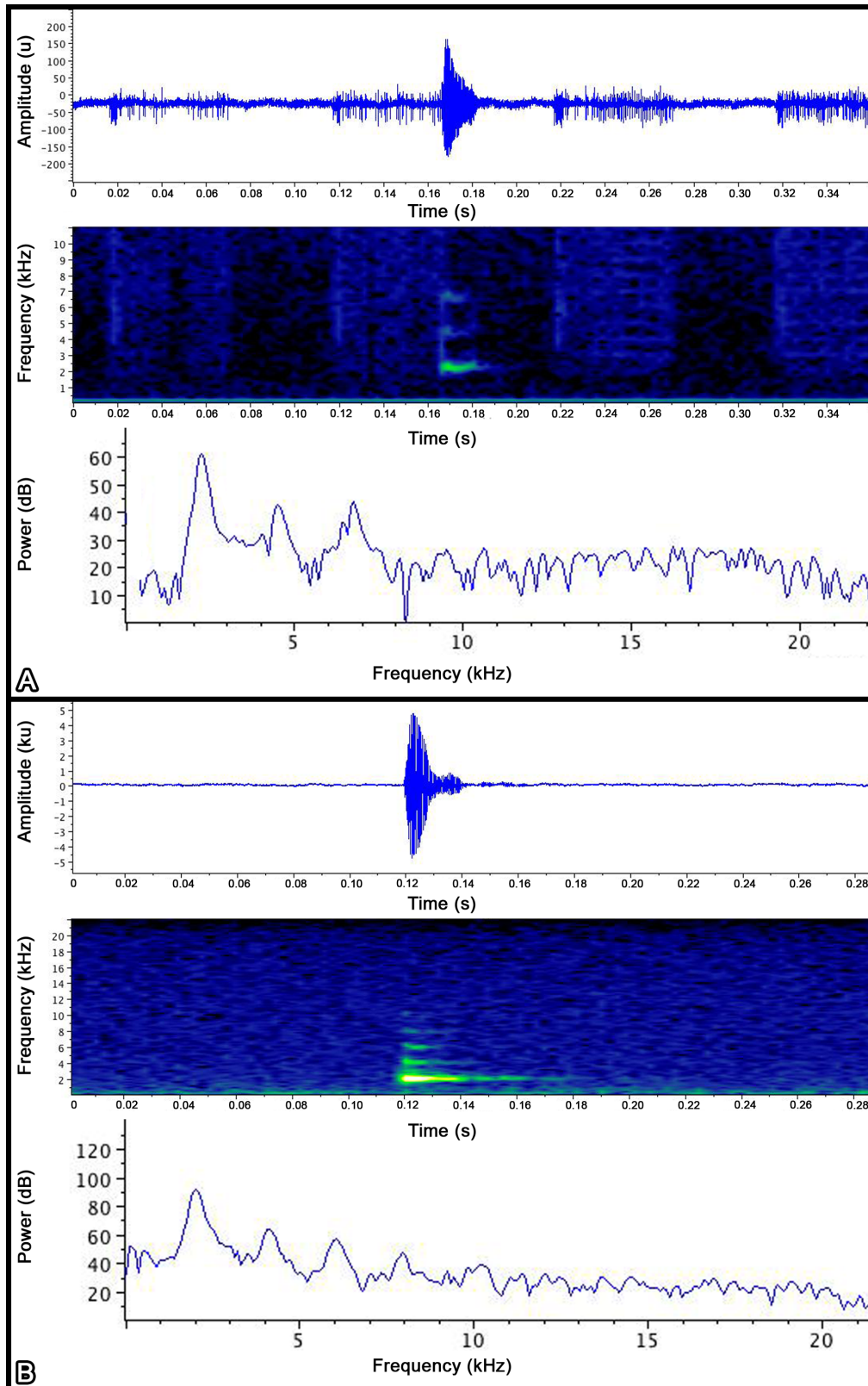


Figure 8. A. Vocalisation of *Pristimantis aureoventris* sp. nov. Oscillogram, spectrogram, and power spectrum of one call of the male holotype recorded at 15.0°C temperature. B. Vocalisation of *Pristimantis yuruaniensis*. Oscillogram, spectrogram, and power spectrum of one call of a topotypic uncollected male recorded at 15.0°C temperature.

Distribution and ecology. *Pristimantis aureoventris* is currently known only from the type locality—the summit of Wei Assipu Tepui (at 2210 m elevation) at the border between Guyana and Brazil—and from near the base of the ultimate cliff of the northern “Prow” of Mount Roraima in Guyana at about 2305 m elevation (Figs. 1, 6, 9). According to the GPS, Wei Assipu Tepui reaches a maximum elevation of *ca.* 2260 m above sea level. Wei Assipu Tepui summit area is about 3 km² and is level with a large number of fractures, some of them very deep and impassable without the use of climbing equipment—like the “Sima de los Guácharos”, which is more than 100 m deep (see Carreño *et al.* 2002). The Wei Assipu Tepui summit vegetation is the classic “tepui vegetation”, with large areas of coarse herbs mixed with woody subshrubs on peat soils, some quaking bogs and extensive patches of dwarf forests dominated by *Bonnetia roraimae* (Theaceae). The terrestrial bromeliads *Brocchinia tatei* and *B. reducta* are especially abundant, as well as *Stegolepis guianensis* (Rapateaceae), *Orectanthe sceptrum* (Xyridaceae), and *Heliamphora nutans* (Sarraceniaceae). Temperature and hygrometry were recorded from the summit of Wei Assipu Tepui between 9–11 November 2009. A thermo-hygrometer was placed under a small rock in a bare rock area on the summit. The maximum temperature recorded was 29°C (day), the minimum temperature recorded was 13°C (night). Maximum hygrometry recorded was 74% (night), minimum hygrometry was 24% (day). Temperature in the base camp (located under two very large boulders, close to a small forest) was as low as 11°C at night and hygrometry reached 98% during misty nights and mornings. Few rains occurred during our stay in November 2009, which was mostly very dry.

Culminating at 2810 m elevation, Mount Roraima is the highest tepui and second highest point in the Pantepui region (after Pico de la Neblina in the southwest, which reaches about 3000 m elevation). Roraima summit plateau area is about 34 km². The plateau is very rocky and its vegetation is very sparse. The reader is referred to Huber (1995a, b) for description of the vegetation and physical features of Mount Roraima.

Mount Roraima and Wei Assipu Tepui are very close to each other (about 2 km airline between summits) and the vegetation at the Roraima site was similar to that on Wei Assipu Tepui, but on an inclined talus slope (see below).

Pristimantis aureoventris was found to be mainly nocturnal. Four specimens collected on Wei Assipu Tepui, including the calling male holotype, were found concealed between the basal (brown) leaves of *Orectanthe sceptrum* (Xyridaceae); four other specimens (including the tiny juvenile) were collected between brown leaves at the base of *Brocchinia tatei* (Bromeliaceae); one female was found sitting on bare rock at night; a subadult female was collected at night, sitting on a branch of a small tree about 100 cm above the ground; and one specimen was collected by chance, while escaping from dense vegetation.

The individual from near the base of the ultimate cliff of Mount Roraima's northern “Prow” was taken about 10h00 as it jumped across a trail among dense tank bromeliads (*Brocchinia tatei*) and woody subshrubs in what MacInnes (1974) called the El Dorado Swamp. The “swamp” is a patch of tepui summit vegetation dominated by *Bonnetia roraimae*, *Brocchinia tatei*, *Heliamphora nutans*, *Utricularia humboldtii*, *Stegolepis guianensis*, *Orectanthe sceptrum*, and other plants that grow on the inclined, flattish ridge that extends about 1 km north beyond the end of the “Prow” between elevations 1850 and 2200 m (Fig. 6). A completely different forest vegetation dominated by several species of broad-leaved angiosperms including a *Schefflera* sp., Leguminosae, Clusiaceae, palms, and tree ferns of the genus *Cyathea*, with understory shrubs of Melastomataceae, grows at the

same elevations leading south on the talus slope below the eastern cliff of Mount Roraima all the way to a small saddle connecting Mount Roraima to Wei Assipu. Two nights of collecting in this cliff-base forest did not turn up frogs of any species.



Figure 9. A. Aerial photograph of Wei Assipu Tepui (right) and Mount Roraima (left). B. Aerial photograph of Wei Assipu Tepui, Mount Roraima is well visible on the upper left. C. Summit of Wei Assipu Tepui. D. Typical vegetation in which specimens of *Pristimantis aureoventris* sp. nov. were collected. E. Clutch of four eggs in a dead pitcher of a *Heliophora nutans* plant (pitcher removed from original location for photographic purpose). F. Close-up photograph of the four eggs inside the pitcher. Photographs by Philippe J.R. Kok.

Males call at night, hidden in plants among dense vegetation and are usually exceedingly difficult to locate. None of the several males heard calling was exposed. The species is apparently abundant, but specimens are difficult to collect. We are aware of two previous expeditions on the summit of Wei Assipu Tepui during which amphibians were collected (see for instance Villarreal *et al.* 2002), but none of them found *Pristimantis*

aureoventris.

Two clutches of eggs were found on the summit of Wei Assipu Tepui, both were in a dead (brown) pitcher at the base of two different *Heliamphora nutans* plants (Sarraceniaceae). Genomic DNA was extracted from one egg of each clutch, and DNA barcoding established conclusively adult and egg conspecificity (0% uncorrected pairwise distance). The first clutch was found on 5 November 2009 in a plant growing at the bottom of a small, very humid crevice (*ca.* 300 cm deep) and contained five eggs measuring 5.25–5.62 mm. The second clutch was found on 7 November 2009, at the edge of another small, very humid crevice (*ca.* 600 cm deep) and contained four eggs measuring 5.53–6.10 mm (Fig. 9).

Discussion. The new taxon is morphologically most similar to species assigned to the artificial *unistrigatus* species group (*sensu* Hedges *et al.* 2008). Considering that the *unistrigatus* group is largely non-monophyletic (see for instance Hedges *et al.* 2008: 15), we prefer not to include the new species in it. It is expected that further molecular and morphological data will indicate that the Pantepui species *sensu stricto* (*i.e.* highland species) are well distinct from the original *unistrigatus* group of Lynch (1976) and that of Lynch and Duellman (1997).

Among described *Pristimantis* species, the geographically closest highland species to *P. aureoventris* is *P. yuruaniensis*, which occurs on the summit of Yuruani Tepui, about 19 km (airline) NW of Wei Assipu Tepui (see Fig. 1). Both taxa inhabit very similar environments, and although superficially similar, these highland species diverge in some morphological characters (*i.e.* size, skin condition) and colour pattern, including the fact that *P. aureoventris* exhibits a high degree of pattern polymorphism, while *P. yuruaniensis* is a poorly variable species, with a distinct sexual dichromatism (males are light orangish brown, females are dark brown, see Fig. 10). Additionally, the ventral face of *P. yuruaniensis* in life is translucent, whitish, orangish or brown speckled with minute brownish dots, with internal organs well visible through the skin; conversely, that of *P. aureoventris* is opaque, golden yellow with reddish brown to dark brown mottling, with internal organs little or not visible through the skin (compare Fig. 4 with Fig. 10). Another interesting difference resides in the tongue morphology, *P. yuruaniensis* having a broad, short round tongue, rarely slightly longer than broad (only one of the five specimens examined has the tongue slightly longer than wide), whereas the tongue of *P. aureoventris* is very long, always much longer than wide. According to the data available, the number of eggs laid by each species is different: 4–5 in *P. aureoventris* vs. 9 in *P. yuruaniensis* (PJKR pers. obs., Rödder & Jungfer 2008). Furthermore, although more or less similar to the human ear, their calls are significantly different. We consider both species distinct because they are geographically isolated (isolated lineage segments), morphologically reliably diagnosable and have different advertisement calls.

Mägdefrau & Mägdefrau (1994) and Rödder & Jungfer (2008) suggested the presence of *P. yuruaniensis* on the summit of Kukenan Tepui (located 10 km airline SE to Yuruani Tepui), mostly based on overall similarities of specimens and identical call (although apparently none of the Kukenan specimens were collected). The specimen from Kukenan Tepui reported as *P. cf. yuruaniensis* illustrated in Rödder & Jungfer (2008: 64) might belong to a still undescribed species and more investigations are needed before confirming the occurrence of *P. yuruaniensis* on Kukenan Tepui.

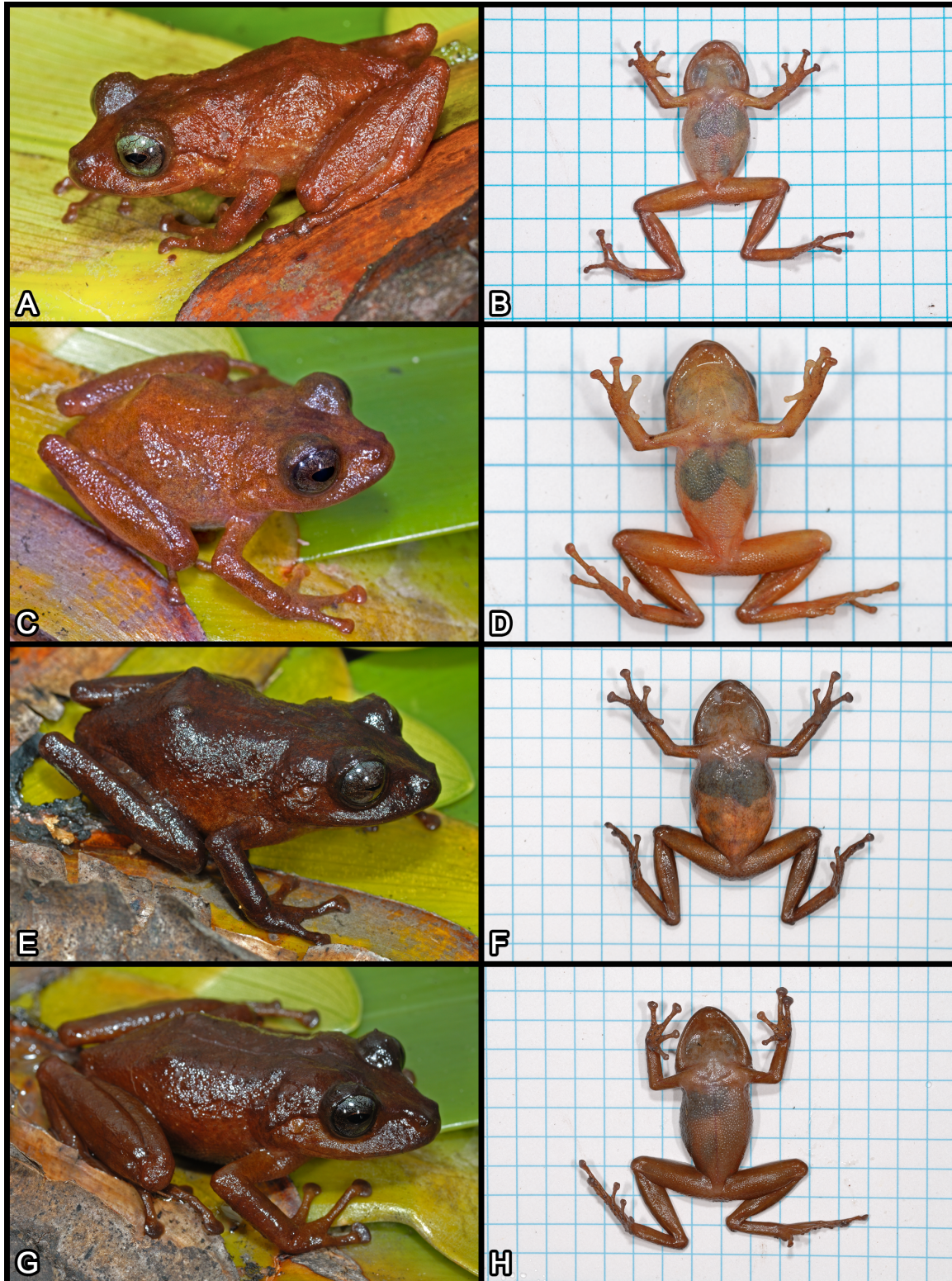


Figure 10. *Pristimantis yuruaniensis* from the type locality (Yuruani Tepui). Intrapopulation variation and sexual dichromatism in dorsal and ventral colour in living specimens. A: Dorsolateral view of the male IRSNB 15640, 23.8 mm SVL. B: Ventral view of the same specimen. C: Dorsolateral view of the male IRSNB 15641, 24.0 mm SVL. D: Ventral view of the same specimen. E: Dorsolateral view of the female IRSNB 15638, 32.1 mm SVL. F: Ventral view of the same specimen. G: Dorsolateral view of the female IRSNB 15639, 32.2 mm SVL. H: Ventral view of the same specimen. Photographs by Philippe J.R. Kok.

Because it might mislead future new species descriptions and comparisons, it should be noted that the original description of *Pristimantis yuruaniensis* (Rödder & Jungfer 2008) contains errors, some probably attributable to the poor state of preservation of the type series. Examination of one paratype (SMNS 09855, an adult female) as well as four additional topotypic specimens (IRSNB 15638–39, adult females, IRSNB 15640–41, adult males) shows that (character states reported in the original description of *P. yuruaniensis* are between parentheses): *P. yuruaniensis* has an areolate ventral skin in life (“smooth”), dentigerous processes of vomers bear 1–6 teeth (“no vomerine dentigerous processes”, although the paratype SMNS 09855 has 3–5 teeth on each vomer), vocal slits absent in males, presence of two whitish nuptial pads on thumb (characters unknown because no male was available), fingers with broad lateral fringes (“fingers without lateral keels”), toes with broad lateral fringes (“toes without lateral keels”, although fringes are well visible on the paratype SMNS 09855), basal webbing between Toes IV–V (“no webbing”). Additionally, figure 4B in Rödder & Jungfer (2008: 65) suggests that in *P. yuruaniensis* Toe V is almost equal to Toe III when toes are adpressed. This is contradicted by examination of the paratype SMNS 09855 and the additional topotypic specimens mentioned above, in which Toe V reaches at least the proximal edge of the distal subarticular tubercle on Toe IV, and is distinctly longer than Toe III.

McDiarmid & Donnelly (2005) reported an undescribed *Pristimantis* species from the summit of Mount Roraima (“*Eleutherodactylus* sp J”). Although there seems to be morphological differences between “*Eleutherodactylus* sp J” and *Pristimantis aureoventris* (César Barrio-Amorós, pers. comm), we have not examined specimens from the summit of Roraima and tissue samples from these specimens are unavailable. We therefore cannot exclude that these taxa are conspecific.

The presence of at least one same anuran species on both Mount Roraima and Wei Assipu Tepui has been reported (*Oreophrynella quelchii*, see Villarreal *et al.* 2002), and the occurrence of the same *Pristimantis* species on both of these neighbouring tepuis is not surprising. However it still remains unknown why some species sometimes occur on two or more different tepui summits, while some seem restricted to a single summit.

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APPENDIX. ADDITIONAL MATERIAL EXAMINED

Pristimantis dendrobatoides.— Guyana: *Potaro-Siparuni District*: Wokomung Massif, USNM 563662 (holotype), USNM 563661 (paratopotype), USNM 564161–64, ROM 43317 (paratypes).

Pristimantis inguinalis.— Guyana: *East Berbice-Corentyne District*: New River, BMNH 1947.2.16.6 (formerly 1939.1.1.1) (holotype), BMNH 1947.2.16.7 (formerly 1939.1.1.2) (paratype).

Pristimantis jester.— Guyana: *Potaro-Siparuni District*: Wokomung Massif, USNM 563631 (holotype), USNM 563632 (paratopotype), USNM 563633, ROM 43303, ROM 43306 (paratypes).

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, USNM 563639 (holotype), USNM 563634–37, USNM 563640–41, USNM 563644–45 (paratopotypes), USNM 563638, USNM 563642–43, USNM 563646–51, USNM 563665–79 (paratypes), IRSNB 15644–53 (topotypic specimens).

Pristimantis yuruaniensis.— Venezuela: *Estado Bolívar*: Yuruani Tepui, IRSNB 15638–41 (topotypic specimens), SMNS 09855 (paratype).

