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A new species of the genus *Pristimantis* (Amphibia, Craugastoridae) associated with the moderately evelated massifs of French Guiana

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Abstract

We describe a new *Pristimantis* from French Guiana, northern South America, which is mainly distinguished from known phenotypically related congeners (*i.e.* species from the polyphyletic *unistrigatus* species group) occurring at low and middle elevations in the Guiana Shield by the combination of a distinct tympanum, a lower ratio of tibia *vs*. hand length, a reddish groin region, and a distinct advertisement call consisting of clusters of generally four short notes. The new species inhabits pristine primary forests on the slopes of isolated massifs reaching more than 400 m elevation, and seems not to occur below *ca*. 200 m above sea level. Such a sharp altitudinal limit suggests a strong influence of thermal variation on the distribution of the species, and therefore a potential sensitivity to climate change. With only nine isolated populations documented so far, the new species should be prioritized for conservation. Historical climate fluctuations during the Quaternary are likely responsible for the distribution pattern of the new species.

Key words: Climate change, Conservation, Endemism, Guiana Shield, Taxonomy, Terrarana.

Introduction

The number of amphibian species described each year is increasing and this trend shows no sign of slowing (Köhler *et al.* 2005; Giam *et al.* 2011). These new species are essentially detected in tropical regions (Giam *et al.* 2011), especially in South America (Jenkins *et al.* 2013), and often from highlands or altitudinal gradients (McDiarmid & Donnelly 2005; Duellman & Lehr 2009; Kok *et al.* 2012). Amphibians are particularly tied to narrow thermal and hygrometric conditions (Buckley & Jetz 2007), and they generally display poor dispersal abilities (Smith & Green 2005). It has been demonstrated that thermal tolerance of tropical ectotherms is overall narrower than for temperate ones (Deutsch *et al.* 2008; Buckley *et al.* 2012). In the context of climate change, these species could be at particular risk of decline (Lips *et al.* 2003; Pounds *et al.* 2006; Whitefield *et al.* 2007). Therefore, an unknown proportion of undescribed species are threatened or may have already gone extinct, especially in the tropical highlands. Using currently recognized ranges of nominal species, Foden *et al.* (2013) suggested that amphibians of western Amazonia and the eastern Guiana Shield are the most exposed and sensitive to climate change. Given that naming species is crucial for species conservation (Angulo & Icochea 2010) it is urgent that species in these areas be described.

Among the South American direct-developing frogs (Terrarana)—and vertebrates in general—the genus *Pristimantis* is the most species-rich, containing more than 450 species to date (Heinicke *et al.* 2007; Hedges *et al.* 2008; Frost 2013), with many species still undescribed, notably from the Guiana Shield highlands (McDiarmid & Donnelly 2005, Kok 2013). A large proportion of the newly described species in the genus occur at very narrow

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altitudinal ranges (Duellman & Lehr 2009), along the slopes of the Andes and in the Pantepui region.A peculiar reproductive mode and ability to colonize high elevations encompassing a large variety of ecosystems are likely responsible for the large proportion of microendemics in this group (Gonzalez-Voyer *et al.* 2011). As a corollary, about one third of *Pristimantis* species are considered endangered and another third is Data Deficient according to IUCN criteria (IUCN 2013).

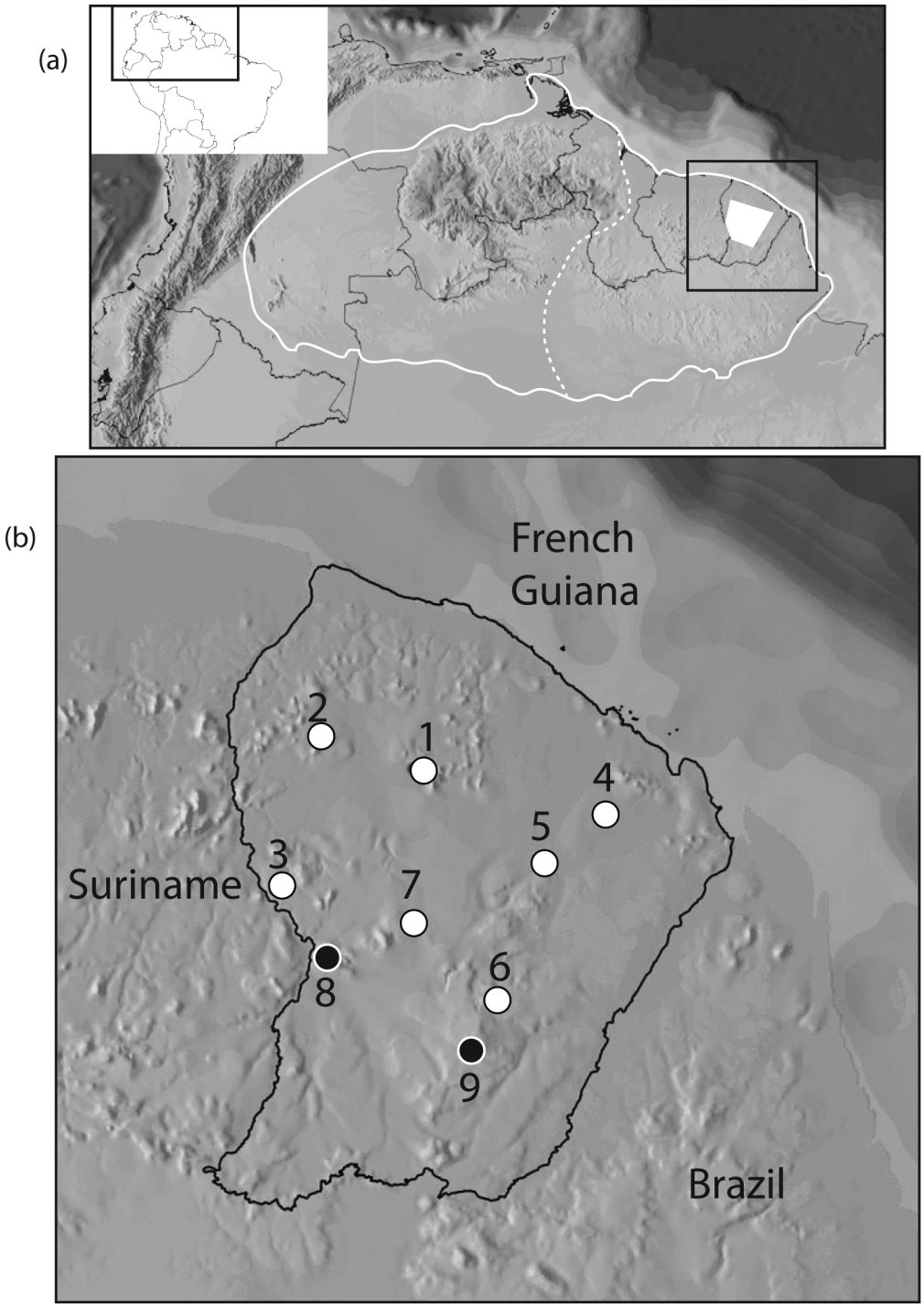

FIGURE 1. Map showing documented populations of *Pristimantis espedeus* **sp. nov.** (a) The Guiana Shield is delimited by a white line and the eastern part is separated from the western by a dotted line. A white convex polygon delimits the documented range of *Pristimantis espedeus* **sp. nov.** (b) A focus on French Guiana with white dots indicating populations for which vouchers exist (1: Réserve Naturelle de la Trinité, 2: Mont Lucifer, 3: Mont Kotika, 4: Montagne Grande Tortue (type locality), 5: Réserve Naturelle des Nouragues, 6: Pic Coudreau, 7: Monts Belvédère); black dots indicate populations without collected material (8: Monts Atachi-Bacca, 9: Mont Itoupé).

The eastern part of the Guiana Shield consists of hilly landscapes mostly covered by pristine lowland rainforest, with only a few massifs reaching more than 400 m elevation. Despite these hills being modest in elevation, a new species of *Pristimantis* (phenotypically related to the polyphyletic *unistrigatus* group) strictly associated with these uplands was discovered at nine locations in French Guiana. All known populations are located between *ca.* 200–700 m elevation on single massifs that always reach more than 400 m above sea level (Fig. 1). We herein describe this new species, and discuss its conservation status.

Material and methods

Fieldwork and deposition of specimens. A total of seventeen calling males and one female were collected at dawn by hand at seven localities in French Guiana: Réserve Naturelle de la Trinité (3 specimens), Mont Lucifer (1 specimen), Mont Kotika (7 specimens), Montagne Grande Tortue (3 specimens), Réserve Naturelle des Nouragues (2 specimens), Pic Coudreau (1 specimen), and Monts Belvédère (1 specimen). Based on call data, the species was also detected up to *ca.* 700 m elevation at two additional locations (Monts Atachi-Bacca and Mont Itoupé) (Fig. 1). Sex was confirmed by the presence of vocal slits in males.

Frogs were euthanized using an injection of Xylocaïne® (lidocaïne chlorhydrate). Tissue samples (a piece of liver) were removed and stored in 100% ethanol, while specimens were tagged and fixed (using formalin 10%) before being transferred in 70% ethanol for permanent storage. Type specimens were deposited in the collection JAGUARS IPG (Institut Pasteur de Guyane)/Kwata FR973A (Cayenne, French Guiana).

Morphology. We follow Pyron and Wiens (2011) and Frost (2013) in using Craugastoridae as the family level clade containing *Pristimantis*. The new species is unambiguously assigned to the genus *Pristimantis* based on molecular phylogenetic relationships (Fouquet *et al*. 2012).

Eighteen measurements were taken with a digital calliper to the nearest 0.01 mm and rounded to the nearest 0.1 mm, following the method of Kok *et al.* (2011). Abbreviations for measurements are as follows: SVL = snout-vent length; TiL = tibia length; FeL = femur length; TaL = tarsus length; FL = foot length (from outer edge of metatarsal tubercle to the tip of toe IV); HeL = head length (from angle of jaw to tip of snout); HW = head width; Ind = internarial distance; IOD = interorbital distance; EN = eye-nostril distance (straight line distance between anterior corner of eye and nostril); ED = horizontal eye diameter; TD = horizontal tympanum length; FD = disc width of Finger III; 4TD = disc width of Toe IV; ETS = eye-tip of snout distance (straight line distance between the anterior corner of eye and tip of snout); 1FiL = length of Finger I (from proximal edge of palmar tubercle to the tip of Finger I); 2FiL = length of Finger II (from proximal edge of palmar tubercle to the tip of Finger II); HL = hand length (from proximal edge of palmar tubercle to the tip of Finger III).

Morphologically, the new species is most similar to members of the polyphyletic *unistrigatus* species group (*sensu* Hedges *et al.* 2008), which is extremely diverse (n=193 species *sensu* Hedges *et al.* 2008) and contains species displaying a very cryptic morphological evolution. Therefore, we consider that direct comparison with all the nominal species of the group is unrealistic and poorly informative (see Discussion for further comments). Consequently, we compared specimens of the new species with (1) specimens of the three other *Pristimantis* species of the *unistrigatus* group occurring in French Guiana (one described, two as yet unnamed, see below and Appendix); (2) the other nominal species of this species group occurring at mid-elevation in the Guiana Shield (thus, excluding tepui summit species); and (3) taxa phylogenetically closely related to the new species according to the molecular analysis of Fouquet *et al.* (2012). Morphological comparisons are based both on original descriptions and examination of museum specimens (see Appendix for material examined).

In order to determine which morphometric measurements could be used to discriminate between the four species occurring in French Guiana we used a Multiple Discriminant Function Analysis (MDFA) using the package ade4 (Dray & Dufour 2007) developed for the R platform (http://cran.r-project.org/). We included only males in the analysis because no or too few females were available for three out of four of the species analysed [17 *P. espedeus* **sp. nov**.; 13 *P.* sp. 1; 11 *P. inguinalis* (Parker, 1940); 5 *P.* sp. 4]. We performed the statistical analysis using (1) raw data and (2) residuals of the linear regression of the variable *vs*. SVL, in order to correct for the size effect on the differences among groups.

Bioacoustics. Recordings were obtained from three specimens (two unvouchered specimens and the holotype) from three localities (Nouragues, Trinité, Montagne Grand Tortue) using an EDIROL R-09HR recorder. Calling

specimens, lying head down about 1–2 m high on tree trunks, were recorded at dusk at a distance of about 2–3 m from their calling sites. We also obtained recordings of two of the three other species of the *unistrigatus* group occurring in French Guiana. Temperature at the time of recordings was between 22 and 23°C. Calls were analyzed at a sampling rate of 44,100 Hz using Audacity (http://audacity.sourceforge.net/). For each variable, six samples of each recording were measured: call duration (beginning of first to the end of the last note of a call); note duration (beginning of the note to the end of the note); number of notes per call (a call is here defined as a series of identical notes emitted in groups between longer silent intervals); silent intervals (end of one call to the beginning of the next); internote interval (end of one note to beginning of the next); and call rate (= number of calls per minute estimated using a 15 s segment) (Kok & Kalamandeen 2008). Peak of the dominant frequency of the note and of the two main harmonics were measured from a spectral slice taken through six entire calls for each recording (using the Blackman window function at a 3 dB filter bandwidth of 120 Hz) (Kok & Kalamandeen 2008). Spectrograms and oscillograms were generated using the package Seewave (Sueur *et al.* 2008) in the R software.

Results

New species description

Pristimantis espedeus sp. nov.
(Figs 2, 4–5, Table 1)

Eleutherodactylus sp. 1 Marty & Gaucher (1999)
Eleutherodactylus sp. 2 Lescure & Marty (2001)
Pristimantis sp. 2 Dewynter *et al.* (2008); Fouquet *et al.* (2012)

Holotype. R121 (AF1520), an adult male collected by EC and AF in Montagne Grande Tortue, (4.30901, -52.357163; 370 m elevation), municipality of Régina, French Guiana, on 13 June 2013 at 18h40. The specimen was recorded and photographed prior to capture (Fig. 2).

Paratypes (n=17)**.** R116–117 (AF0277–0278), two males collected on 10 May 2007 near the Nouragues station in the Réserve Naturelle des Nouragues (4.091667, -52.7; 390 m elevation), municipality of Régina, French Guiana; R118–120 (AF1156, 1190, 1203), three males collected between 24 April and 3 May 2013 near the Aya camp in the Réserve Naturelle de la Trinité (4.619673, -53.408797; 320 m elevation), municipality of St Elie, French Guiana; R122–123 (AF1521–1522), two males collected with the holotype; R124 (AG508) a male collected on 15 December 2012 in Monts Belvédère (3.719347, -53.412809; 350 m elevation), municipality of Saül, French Guiana; R125–131 (PG452–455, 475–477), seven males collected on 1 February 2005 in Montagne Kotika (3.933333, -54.1972222; 370 m elevation), municipality of Papaïchton, French Guiana; R132 (PG524), a male collected on 27 March 2006 on Pic Coudreau (3.306667, -53.1472222; 400 m elevation), municipality of Saül, French Guiana; and R133 (AG270), a female collected on 12 November 2005 in Mont Lucifer (4.766667, -53.9166667; 370 m elevation), municipality of St Laurent du Maroni, French Guiana (Fig. 1).

Etymology. The specific name is considered a noun in apposition and derives from the old Norman language *espedeus* meaning "special" referring to the peculiar ecology and call of the new species (see Advertisement call, and Distribution and ecology sections below). Moreover, *espedeus* phonetically resembles "sp. 2" in French, which is how the species has been named for almost two decades.

Definition and Diagnosis. The new species is characterized by the following unique combination of characters: (1) SVL small, adult males 23.0 ± 1.1 mm (range 20.7–24.8 mm, n=17), adult female 29.4 mm (n=1) (Table 1); (2) dorsal skin granular, slightly more granular posteriorly, with a few enlarged tubercles sometimes forming a W-shaped scapular fold and/or dorsal dermal folds, dorsal skin less tuberculate in females, ventral skin granular; (3) tympanic membrane differentiated, tympanic annulus visible externally, supratympanic fold obscuring upper and posterodorsal edges of tympanum, tympanum 40% of eye length; (4) tibia length 1.9 X hand length (5) snout broadly rounded in profile and dorsal view; (6) each upper eyelid with two prominent tubercles; (7) choanae round and large (0.7 mm for the holotype), dentigerous processes of vomers oblique, narrowly separated, each bearing four teeth; (8) vocal slits present, vocal sac median, subgular, nuptial pads rugous translucid, barely visible, located on the dorsal surface of the proximal segment of Finger I; (9) Finger I shorter

than the second, 72% of Finger II; (10) fingers and toes with lateral fringes; (11) axillary tubercle absent; (12) ulnar tubercles barely visible or absent; (13) calcars absent, heel tubercles absent, inner metatarsal tubercle oval, much larger than the round outer tubercle; (14) discs broadly expanded, elliptical with broad lateral fringes, outer tubercle round, palmar tubercle heart-shaped; (15) in preservative, dorsum tan, gray and brown, three colour patterns exist: dorsally banded, dorsolaterally banded, and streaked, ventral colouration creamish white with small dark spots becoming denser on throat; (16) iris golden or silver with a dark copper horizontal band; (17) anterior surface of thighs and groin reddish in life and brown in preservative, fingers and toes with red spots in life, lack of yellow circumscribed spot on groin; (18) advertisement call characterized by clusters (0.2–0.5 s long) of 3–5 very short notes (0.02–0.03 s long) with a dominant frequency ranging between 2.7–2.8 kHz and emitted every 1.6–5.3 s; (19) calling activity exclusively crepuscular; (20) occurring at elevations between 200–700 m elevation on massifs reaching >400 m.

TABLE 1. Summary of mean measurements of the type series and sympatric *Pristimantis* species of the *unistrigatus* group from French Guiana. Abbreviations are explained in the text.

		SVL	TiL	FeL	TaL	FL	HeL	HW	Ind	IOD
P. espedeus **sp. nov.**	M (17)	22.95	12.46	11.69	6.32	9.72	8.56	8.23	2.11	2.51
	sd	1.07	0.68	0.53	0.46	0.49	0.41	0.33	0.21	0.23
	F (1)	29.40	16.30	16. 00	8.30	13.40	11.20	11.00	2.50	3.50
	sd	NA	NA	NA	NA	NA	NA	NA	NA	NA
P. inguinalis	M (11)	20.23	10.34	9.90	5.48	8.12	7.60	7.07	1.74	2.04
	sd	1.09	0.66	0.67	0.45	0.49	0.36	0.51	0.17	0.17
P. sp. 1	M (13)	17.66	9.51	9.01	5.09	7.35	6.69	5.95	1.62	2.06
	sd	1.08	0.46	0.58	0.18	0.52	0.59	0.50	0.20	0.17
	F (2)	22.20	11.50	11. 00	6.40	8.95	8.4	7.45	1.80	2.3
	sd	0.42	0.42	0.28	0. 00	0.07	0.14	0.49	0.14	0. 00
P. sp. 4	M (5)	16.36	9.36	8.68	5.32	7.38	6.28	5.30	1.74	1.96
	sd	0.85	0.57	0.54	0.43	0.37	0.33	0.46	0.17	0.22
	F (6)	22.69	12.20	11.47	7.10	9.57	8.43	7.85	2.05	2.52
	sd	1.57	0.51	0.67	1.24	1.43	0.58	0.47	0.21	0.17

TABLE 1. (Continued)

		EN	ED	TD	FD	4TD	ETS	1FiL	2FiL	HL
P. espedeus **sp. nov.**	M (17)	2.74	3.06	1.19	1.39	1.29	4.05	3.01	4.19	6.56
	sd	0.26	0.22	0.25	0.09	0.11	0.24	0.49	0.49	0.41
	F (1)	4.30	4.01	2.30	1.70	1.60	5.20	4.50	6.10	8.60
	sd	NA	NA	NA	NA	NA	NA	NA	NA	NA
P. inguinalis	M (11)	2.44	2.83	0.97	1.10	1.02	3.49	2.47	3.31	5.62
	sd	0.27	0.12	0.09	0.12	0.10	0.25	0.15	0.15	0.34
P. sp. 1	M (13)	2.18	2.52	0.85	0.78	0.75	3.24	2.21	2.94	4.63
	sd	0.32	0.21	0.14	0.12	0.13	0.19	0.24	0.34	0.24
	F (2)	3.00	2.80	0.95	1.00	1.00	4.15	2.60	3.40	5.25
	sd	0.00	0.00	0.21	0.14	0.14	0.35	0.00	0.28	0.49
P. sp. 4	M (5)	2.10	2.32	0.62	0.84	0.80	3.18	2.00	2.58	4.48
	sd	0.32	0.25	0.04	0.11	0.12	0.23	0.23	0.28	0.33
	F (6)	3.05	3.33	0.73	1.15	1.20	4.34	2.85	3.65	6.02
	sd	0.22	0.14	0.10	0.18	0.14	0.21	0.33	0.58	0.34

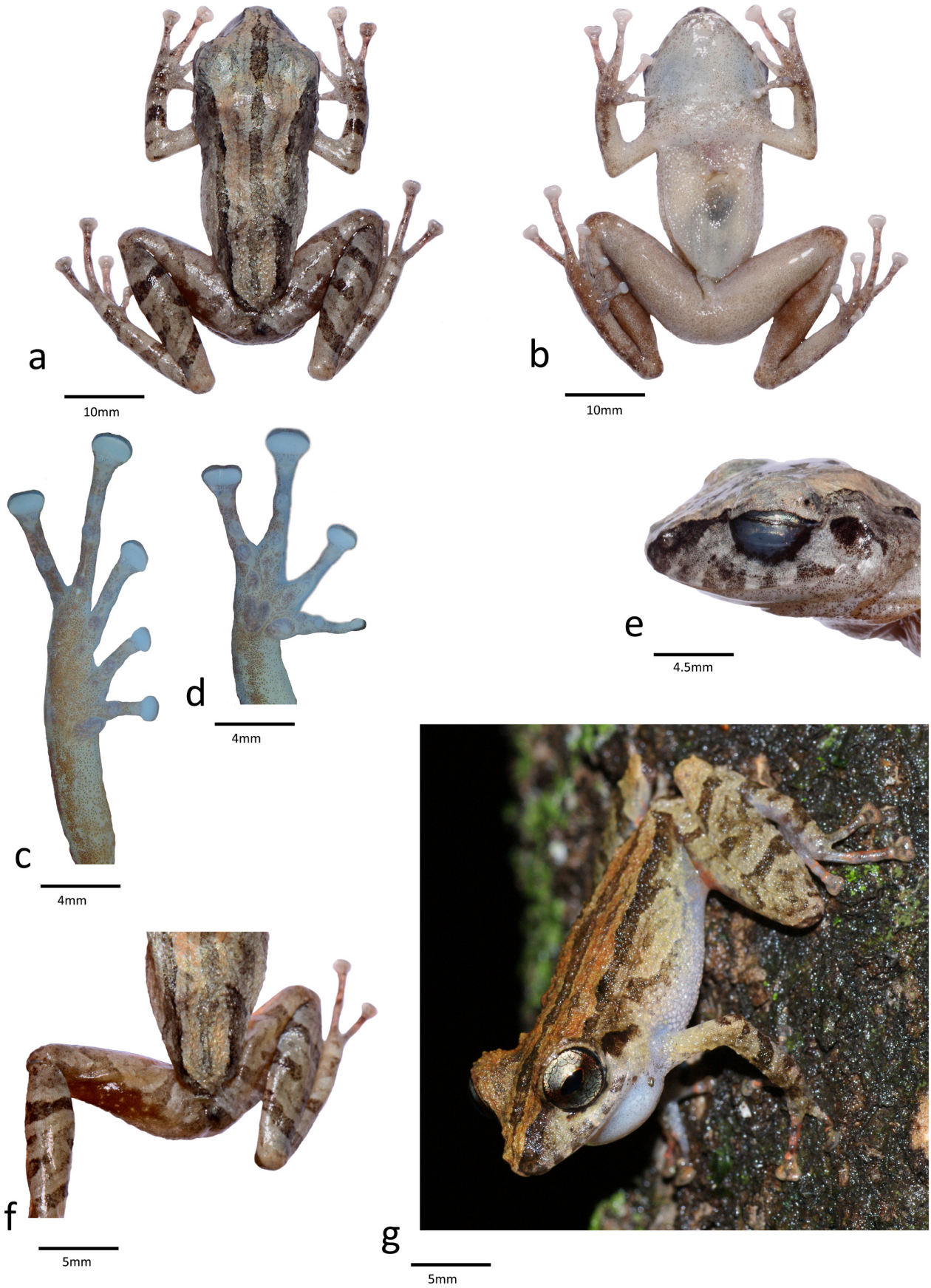

FIGURE 2. Holotype (R121) of *Pristimantis espedeus* **sp. nov.** (a) dorsal view, (b) ventral view, (c) right foot, (d) right hand, (e) head in lateral view, (f) posterior face of thigh in preservative, (g) holotype calling.

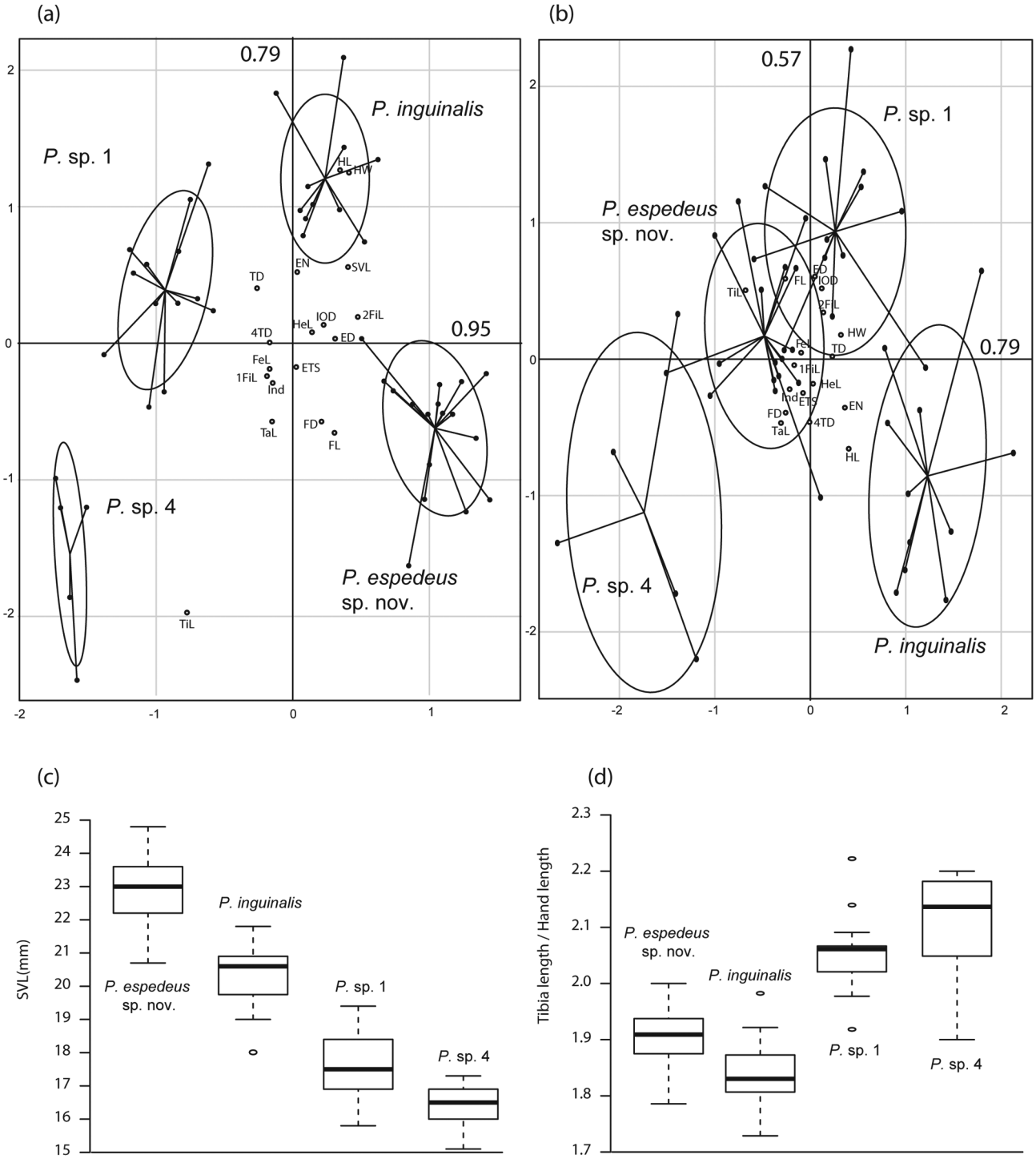

FIGURE 3. Plots of discriminant scores from MDFA based on (a) raw morphological measurements (b) residual from the different measurement and SVL taken on the four *Pristimantis* spp. of the *unistrigatus* group occurring in French Guiana. Eigen value of each axis is indicated on the right and on the top. We plotted (c) the distribution of SVL for each species and given the results from the two MDFA (d) the ratio between TiL and HL.

Morphological comparisons with congeneric species. Using the raw data, MDFA clearly segregates well the four species (Fig. 3a). Three variables notably contribute to the discrimination in opposite ways: HL and HW on the one hand, and TiL on the other. When the MDFA is based on the residuals, discrimination is less clear, especially between *Pristimantis espedeus* **sp. nov**. and *P.* sp. 1 (Fig. 3b), suggesting that most of the morphological variation is size-based between these species (Fig. 3c). Nevertheless, the variables HL and TiL still contribute appreciably and in opposite ways. Therefore, we plotted the ratio between these two variables. In *P. espedeus* **sp.**

nov. and *P. inguinalis*, TiL is less than 50% of HL, while it accounts for > 50% in most specimens of *P.* sp. 1 and *P.* sp. 4 (Fig. 3d, Table 2).

TABLE 2. Canonical weights of each variable on the first two axes using raw data and residuals. Abbreviations are explained in the text.

	DS1	DS2	DS1	DS2
SVL	0.4043	0.5580	NA	NA
TiL	-0.7746	-1.9648	-0.6692	0.4986
FeL	-0.1695	-0.1890	-0.0789	0.0382
TaL	-0.1515	-0.5637	-0.3078	-0.4620
FL	0.3052	-0.6559	-0.2620	0.5919
HeL	0.1286	0.0694	0.0285	-0.1716
HW	0.4113	1.2443	0.3068	0.1673
Ind	-0.1468	-0.2853	-0.2139	-0.2204
IOD	0.2258	0.1345	0.1168	0.5189
EN	0.0329	0.5226	0.3617	-0.3499
ED	0.3033	0.0341	0.0474	0.6010
TD	-0.2631	0.4032	0.2167	0.0198
FD	0.2103	-0.5731	-0.2493	-0.3794
4TD	-0.1623	0.0055	-0.0085	-0.4549
ETS	0.0228	-0.1668	-0.0766	-0.2485
1FiL	-0.1890	-0.2406	-0.1557	-0.0419
2FiL	0.4760	0.1926	0.1273	0.3304
HL	0.3386	1.2663	0.4022	-0.6587

Compared to the three other species of the *unistrigatus* group occurring in French Guiana (*i.e. Pristimantis inguinalis*, *P.* sp. 1 and *P.* sp. 4, the last two were previously partly misidentified with *P. marmoratus* in French Guiana *e.g.* in Lescure & Marty 2001), *Pristimantis espedeus* **sp. nov.** differs mainly by its larger SVL in males: mean of 23.0 mm (n=17) in *P. espedeus* **sp. nov.** *vs*. mean of 20.2 mm (n=11) in *P. inguinalis*, mean of 17.7 mm (n=13) in *P.* sp. 1, and mean of 16.4 mm (n=5) in *P.* sp. 4 (Table 1; Fig. 3). *Pristimantis espedeus* **sp. nov.** further differs from *P.* sp. 1 and *P.* sp. 4 by its red-orange inner thighs and groin in life (dark grey in *P.* sp. 1 and *P.* sp. 4), a more granular skin, a less clear W-shaped scapular fold, a proportionally larger head (Fig. 4), a less acuminate snout, more prominent tubercles on arms, larger finger discs, and a heart-shaped palmar tubercle (elliptical in *P.* sp. 1 and *P.* sp. 4). From *P. inguinalis* the new species mainly differs by its red-orange inner thighs and groin in life (a bright, well circumscribed yellow spot in *P. inguinalis*), and a cream ventral colouration (black in *P. inguinalis*).

From the species of the *unistrigatus* group reported to occur below *ca.* 700 m elevation in the Guiana Shield [*i.e. P. ockendeni* (Boulenger, 1912) and *P. marmoratus* (Boulenger, 1900)], *P. espedeus* **sp. nov.** is readily diagnosable by its body size: *P. ockendeni* is larger (adult female holotype = 34.0 mm *vs.* 29.4 mm in *P. espedeus* **sp. nov.** female), and *P. marmoratus* is obviously smaller (adult male holotype [with large vocal slits present] = 18.0 mm *vs.* min. 20.7 mm in *P. espedeus* **sp. nov.** males). *Pristimantis espedeus* **sp. nov.** further differs from *P. ockendeni* by its reddish groin and thighs (absent in *P. ockendeni*), and from *P. marmoratus* by its cream venter (the preserved holotype of *P. marmoratus* has a dark grey venter suggestive of a dark ventral colouration in life). *Pristimantis ockendeni* from Manaus (Lima *et al.* 2006) apparently corresponds to a still undescribed species given its smaller body size compared to the holotype of *P. ockendeni*, and can be easily distinguished from *P. espedeus* **sp. nov.** by call characteristics (see below). Three other species associated with the name *P. ockendeni* have been described by Elmer and Cannatella (2008) from the lowlands of Ecuador and do not correspond to *P. espedeus* **sp. nov.** given their smaller SVL and the absence of reddish colour on groin and thighs.

All the other species of the *unistrigatus* group known from the Guiana Shield occur in the Pantepui region and are generally associated with highlands (*i.e.* >700 m elevation). Among the *Pristimantis* species found at mid-

elevation in Pantepui, *P. espedeus* **sp. nov.** can mainly be distinguished from *P. jester* (Means & Savage, 2007) by the presence of a tympanum (absent in *P. jester*) and presence of fringes on fingers (absent in *P. jester*), from *P. saltissimus* (Means & Savage, 2007) by a slightly larger body size (16 mm–27.1 mm in *P. saltissimus vs.* 20.7–29.4 mm in *P. espedeus* **sp. nov.**), a large, prominent tympanum (present, but indistinct in *P. saltissimus*), and presence of fringes on fingers (absent in *P. saltissimus*), from *P. guaiquinimensis* (Schlüter & Rödder, 2007) by its smaller body size (females 32.4–33.6 mm in *P. guaiquinimensis* [see Kok & Barrio 2013] *vs.* 29.4 mm in *P. espedeus* **sp. nov.** female), a distinct tympanum (weakly distinct), and presence of fringes on fingers (absent), from *P. sarisarinama* (Barrio-Amorós & Brewer-Carias, 2008) by the presence of nuptial pads in males (reported to be absent in *P. sarisarinama*), tubercles on eyelids (absent in *P. sarisarinama*), and distinct vocalisation (1–2, rarely 3 notes in *P. sarisarinama vs.* 3–5 notes in *P. espedeus* **sp. nov.**), from *P. pulvinatus* (Rivero, 1968) by its slightly smaller body size (males 23.0–26.1 mm in *P. pulvinatus vs.* 20.7–24.8 mm in *P. espedeus* **sp. nov.**) and distinct vomerine teeth (indistinct or absent in *P. pulvinatus*), from *P. memorans* (Myers & Donnelly, 1997) by the presence of fringes on fingers (absent in *P. memorans*) and a higher internote interval (0.20–0.29 s in *P. memorans vs.* 0.066–0.124 s in *P. espedeus* **sp. nov.**).

Pristimantis espedeus **sp. nov.** can also be distinguished from the upper Amazonian species of the *unistrigatus* group *Pristimantis lirellus* (Dwyer, 1995), *P. croceoinguinis* (Lynch, 1968), and *P. imitatrix* (Duellman, 1978), with which it shares phylogenetic affinities according to previous analyses (Fouquet *et al*. 2012) as well as from *P. carvalhoi* (Lutz & Kloss, 1952) and *P. variabilis* (Lynch, 1968) that are related to the previous species according to Dwyer (1995), by the absence of a bright yellow spot in the groin region [present in the aforementioned species according to Dwyer (1995)], and in having a reddish groin region instead.

Description of Holotype (Figs. 2, 4–5)**.** An adult male 23.8 mm SVL in excellent condition. Head longer than wide (HW 8.4 mm, HeL 9.3 mm; HL 90.3% of HeL), cranial crests not detectable. In dorsal view, snout longer than eye length (ETS 130% of ED), broadly rounded, canthus rostralis straight and loreal region slightly concave, eye-naris distance slightly shorter than eye length (EN 94% of ED). Nares slightly protuberant, directed posterolaterally, visible from frontal and dorsal views. Upper eyelid tubercles slightly prominent on the granular skin. Tympanum distinct, 1.6 mm long, *ca.* 50% of eye length (3.3 mm). Supratympanic fold conspicuous in life, originating at posterior corner of eye, failing to reach shoulder; post-rictal tubercles absent. Vocal sac present. Throat and under surface of thighs smooth, belly granular; posteroventral surface of thigh and cloacal region granular; cloacal sheath absent. Dentigerous processes of the vomers oblique, narrowly separated, each bearing four teeth. Vocal slits visible on the floor of the mouth. Dorsal skin granular (more granular posteriorly) with enlarged tubercles, including dermal folds on dorsal portion of the flanks.

Hand length 29% of SVL. Finger I 79% 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. Large, barely visible rugous translucid nuptial pad on the dorsal surface of the proximal segment of Finger I. Lateral fringes on all fingers, best developed pre-axially on Fingers II and III (Fig. 3). Finger discs broadly expanded, elliptical, broader than long, circumferential groove conspicuous, distal edge of disc rounded; disc of Finger III (1.4 mm) 2.1 times wider than t distal end of adjacent phalanx. Palmar tubercle large, well defined, not fully pigmented, deeply bifid; thenar tubercle large, protuberant, ovoid; supernumerary tubercles few, large (almost equal in size to subarticular tubercles), slightly protuberant; subarticular tubercles large, round and protuberant, one each on FI and FII, two each on FIII and FIV.

Hind limbs moderate in length, heels slightly overlap when held at right angles to sagittal plane; TiL 54% of SVL; FL 44% 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 proximal half of the penultimate subarticular tubercle on Toe IV. Lateral fringes on all toes, best developed pre-axially on Toes III–IV; webbing basal between Toe IV–V (Fig. 2c). 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. Calcars absent; no outer tarsal tubercles detectable in preservative; inner tarsal fold not detectable.

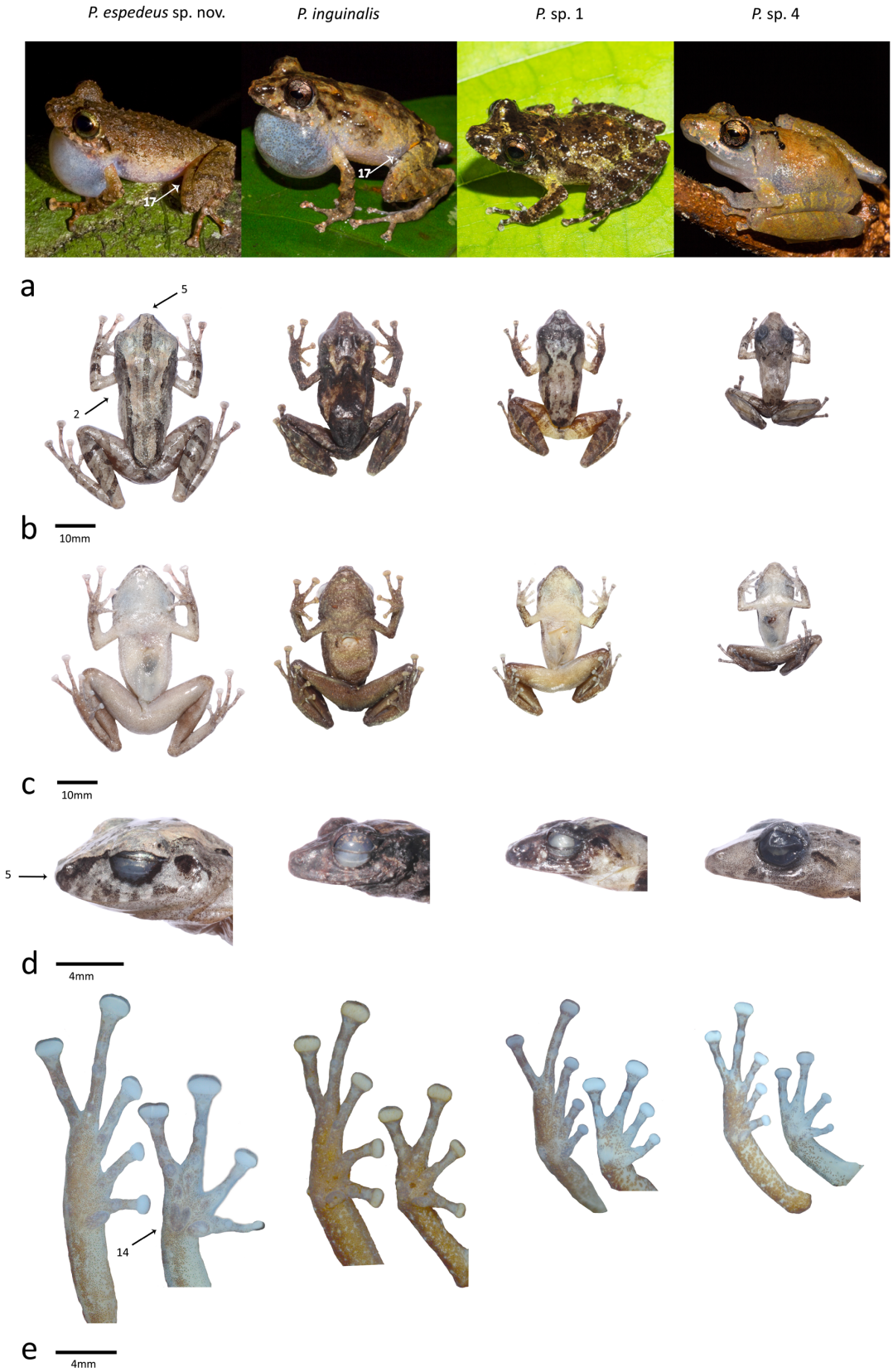

FIGURE 4. Comparison between the four *Pristimantis* species of the *unistrigatus* group occurring with certainty in French Guiana. The four specimens are adult males. *P. espedeus* **sp. nov.** holotype: R121 (AF1520), *P. inguinalis*: R179 (AF804), *P.* sp. 1: R189 (AF757) and *P.* sp. 4: R211 (AF1030). (a) Photographs of living specimens (unreferenced); (b) dorsal view; (c) ventral view; (d) lateral view of head; (e) ventral view of hand and foot. Some characters of the diagnosis are indicated by arrows and corresponding numbers.

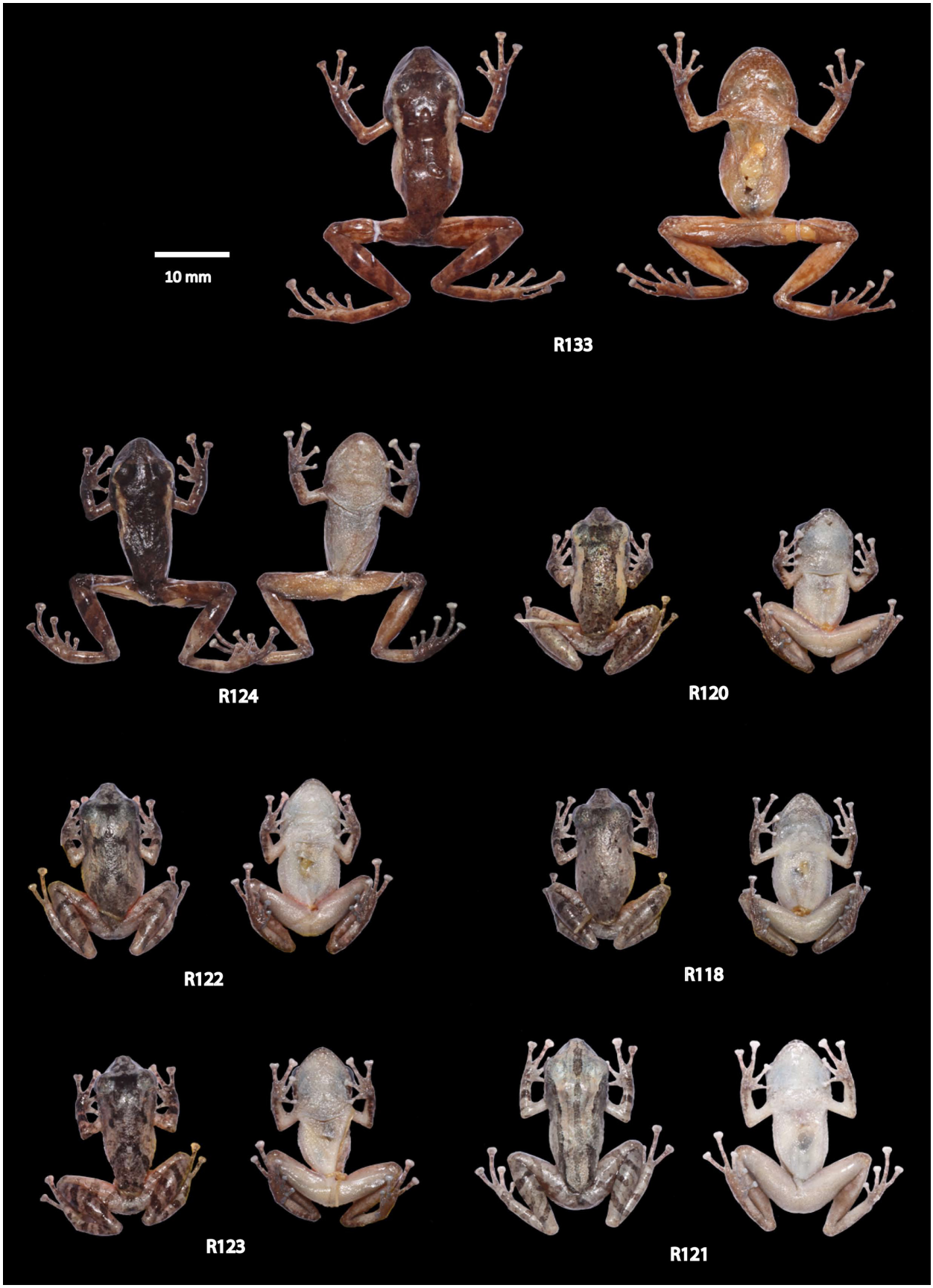

FIGURE 5. Variation among the type series of *Pristimantis espedeus* **sp. nov.** in preservative. R133 (AG270) is the only female collected and R121 (AF1520) is the holotype.

Colour of the Holotype in preservative (Fig. 2a–f)**.** Dorsal background colour light brown, with a broad dark brown vertebral stripe extending from snout to vent, and two large laterodorsal dark brown bands extending from anterior corner of eye to cloaca. Two dark brown bands on the forearms and three well-defined brown bands on shanks and tarsi, ill-defined bands on thighs. Cloacal area dark brown. Five ill-defined dark bands on the upper lip and the loreal region; black supratympanic ridge obscuring upper part of tympanum; black band extending from tip of snout, tapering to anterior corner of eye. Dark stripe on lower edge of orbit. Ventral colouration creamish white with small dark spots denser on throat and thighs.

Colour of the Holotype in life (Fig. 2g)**.** Dorsal background colour chestnut brown, with a broad dark brown stripe extending from snout to vent flanked by two large laterodorsal dark brown bands extending from anterior corner of eye to cloaca. Dorsal half of flanks yellowish brown with ill-defined oblique dark brown reticulations. Loreal region yellowish brown with a series of ill-defined greyish brown markings on the upper lip. Arms and legs yellowish brown with transversal dark bands. Groin and anterior surface of thighs bright red. Red markings also visible on fingers and toes. Belly creamish white with yellowish granular tubercles; throat similarly coloured, but with small dark brown spots.

Variation. *Pristimantis espedeus* is highly polychromatic dorsally. Three main patterns exist: a dorsally banded morph (cf. holotype), a dorsolaterally banded morph (two dorsolateral reddish brown bands in life; R120, 124, 133 in Fig. 5), and a streaked morph (with more or less well-defined chevron-like markings; R118, 122, 123 in Fig. 5). A W-shaped dark brown scapular fold is sometimes visible particularly in the streaked morph.
Sexual dimorphism can be evaluated based on the only female collected. The female is much larger than the largest male, the skin is less granular, and thumbs lack nuptial pads. Female colouration is similar to the dorsolaterally banded morph observed in some males. No additional significant difference was detected.

Advertisement call (Fig. 6, Table 3)**.** The following description is based on three recordings, one of the holotype (Montagne Grande Tortue) and two from uncollected individuals from the Réserve Naturelle des Nouragues and the Réserve Naturelle de la Trinité, respectively.

TABLE 3. Bioacoustic variables (mean and sd) in populations of *Pristimantis espedeus* **sp. nov.** from three localities. The poor quality of the recording of the holotype (Montagne Grande Tortue) does not allow measurements of the note duration, internote intervals, and frequency of harmonics.

	Nouragues	Trinité	Montagne Grande Tortue
Call duration (s)	0.34 (0.12)	0.39 (0.02)	0.27 (0.01)
Note duration (s)	0.02 (0.00)	0.02 (0.00)	NA
Notes/call	3.83 (0.98)	4 (0.00)	3 (0)
Silent interval (s)	3.61 (1.12)	3.45 (1.32)	2.58 (0.25)
Internote interval (s)	0.09 (0.02)	0.10 (0.02)	NA
Calls/min	12	20	20
Dominant Frequency (Hz)	2803 (19.26)	2696 (8.52)	2798 (12.74)
2nd harmonic (Hz)	5566 (50.73)	5348 (9.09)	NA
3rd harmonic (Hz)	8430 (41.56)	8063 (19.99)	NA

The advertisement call consists of short clusters (X=0.33 s; range=0.24–0.5 s) of generally 4 (3 to 5) short notes (X=0.02 s; range=0.019–0.025 s) having an internote interval of 0.09 s (range=0.066–0.124 s) emitted between silent intervals of 3.21 s (range=1.58–5.29 s) (Fig. 6).

The spectral structure consists of three harmonics, with the fundamental frequency dominating (X=2.7 kHz, range=2.68–2.84 kHz, Fig. 6). Two secondary harmonics are visible (but not shown in Fig. 6), having a frequency of *ca.* 5.4 and 8.2 kHz, respectively.

The vocalization of *Pristimantis espedeus* **sp. nov.** is easily distinguished from that of the two sympatric species with known advertisement calls (the call of *P.* sp. 4 remains undocumented): *P. inguinalis* emits a single note of *ca.* 3 kHz every 3–5 s, and *P.* sp. 1 emits clusters of 7–10 very short notes of *ca.* 4 kHz. The species of the *unistrigatus* group occurring in Manaus referred to as *P. ockendeni* by Lima *et al.* (2006) emits shorter clusters (0.20–0.25 s) of 4–5 notes with higher dominant frequency (3.8 kHz).

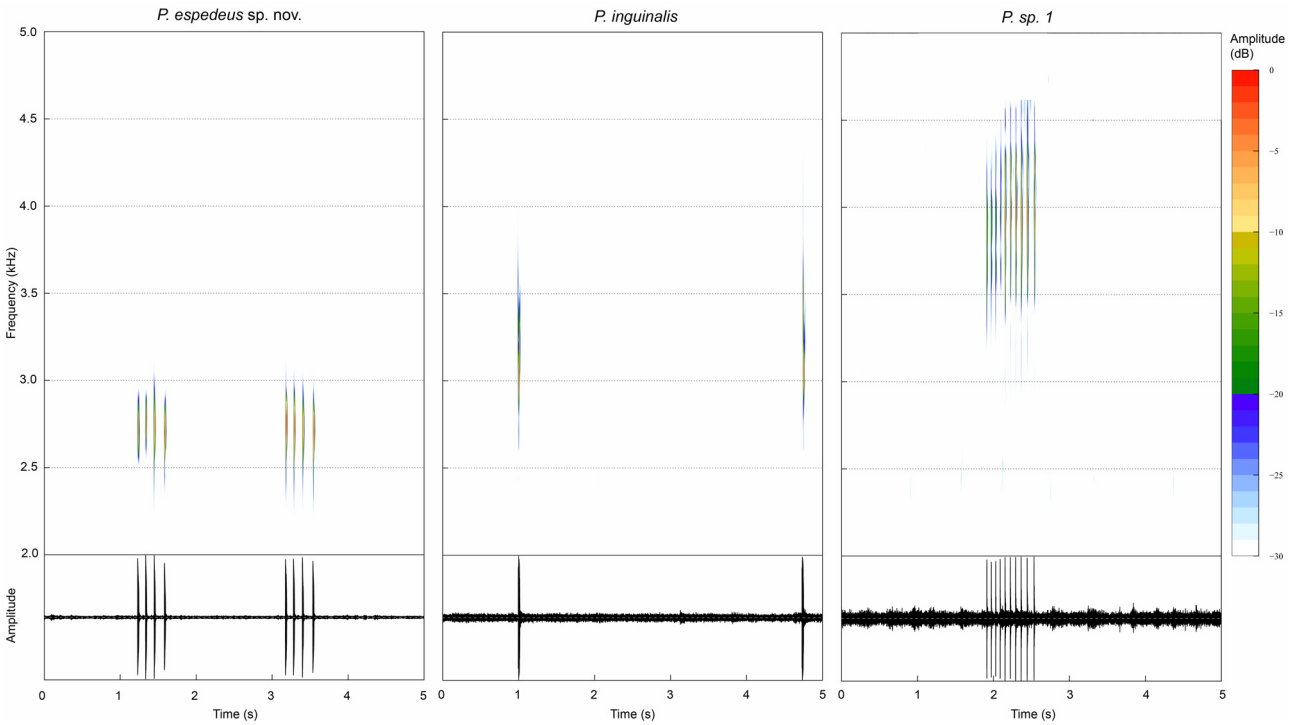

FIGURE 6. Spectrograms (above) and oscillograms (below) of the calls of three species of the *unistrigatus* group occurring in French Guiana; the call of *P.* sp. 4 is unknown. For ease of comparison spectrograms show dominant frequencies only.

Distribution and ecology. The nine known populations of *Pristimantis espedeus* **sp. nov.** are located in the Réserve Naturelle des Nouragues, the Réserve Naturelle de la Trinité, the Réserve Biologique Lucifer Dékou-Dékou (Mont Lucifer), Mont Itoupé, Montagne Kotika, Monts Atachi-Bacca, Monts Belvédère, Pic Coudreau and Montagne Grande Tortue, respectively (Fig. 1). Interestingly, the new species has not been detected from other massifs harbouring apparently suitable habitats such as Pic Matécho, Mont Galbao and Massif du Mitaraka. *Pristimantis espedeus* **sp. nov.** may occur on other massifs such as Montagne Bellevue de l'Inini, Montagne Française and possibly Lely and Nassau mountains in Suriname. All the documented populations seem completely isolated from one another by a very sharp altitudinal limit, (*ca*. 200 m elevation minimum).

Pristimantis espedeus **sp. nov.** is arboreal and only found in forests from 200 to 700 m elevation on massifs >400 m. Calling activity is limited to dusk and dawn, from *ca.* 18h00 to 19h00 and from 5h30 to 6h30; males call head down on the trunks, between 0.5 and 2 m above the ground (Fig. 2g). Although the species seems predominantly arboreal, an amplectant pair and several juveniles were observed in the leaf litter by two of us (PG and AF, respectively). Calling activity is more intense at the beginning of the rainy season (January-March), significantly decreasing afterwards and apparently ends in June. The peculiar distribution of the new species suggests possible endemism to the Eastern Guiana Shield. *Pristimantis espedeus* **sp. nov.** occurs syntopically with *P.* sp. 4, and rarely with *P. inguinalis* as well as with species belonging to other species groups [*P. chiastonotus*, *P. zeuctotylus*, *P. gutturalis*, *P. aff. zimmermanae* (*P.* sp. 3 in Lescure & Marty 2001)]

Discussion

Lescure and Marty (2001) listed several undescribed species of *Pristimantis* from French Guiana including the new species described herein. They also mention the occurrence of four additional species of the *unistrigatus* group: *Pristimantis marmoratus*, *P. inguinalis*, *P.* sp. 1 and *P.* sp. 4. The species that Lescure and Marty (2001) refer to as *P. marmoratus* corresponds in fact to two different lowland species (herein called *P.* sp. 1 and *P.* sp. 4). The species these authors called *P.* sp. 1 and *P.* sp. 4 remain of confusing identity given the mention of a white inguinal spot in *P.* sp. 1, a large body size and the absence of a W-shaped scapular fold in *P.* sp. 4. They also mention an additional undescribed species, *P.* sp. 3, which belongs to the *lacrimosus* group and is probably related to *P. zimmermannae*

(Heyer & Hardy, 1991). *Pristimantis marmoratus* has been described from >1000 m asl on the lower slopes of Mount Roraima in Guyana, and although the species was subsequently reported from Venezuela (Rivero 1961), French Guiana (Lescure & Marty 2001; Dewynter *et al.* 2008; Fouquet *et al.* 2007, 2012), Suriname (Ouboter & Jairam 2012), Amapá state in Brazil (Dias Lima 2008) and northern Pará state in Brazil (Avila-Pires *et al.* 2010), we doubt that it occurs in the eastern part of the Guiana Shield. Reports of *P. marmoratus* outside the Guiana Shield highlands could be erroneous given the altitude at which the holotype was collected (*ca.* 1067 m), while *P.* sp. 1 and *P.* sp. 4 for example (both previously identified as *P. marmoratus* in Lescure & Marty 2001) are exclusively found from 50 to 600 m elevation. The exact distribution of *P. marmoratus,* thus, remains uncertain, and it is likely that the name has been applied to an undetermined number of undescribed species. Given the ambiguity surrounding the material identified so far as *P. marmoratus* we refrain from describing *P.* sp. 1 and *P.* sp. 4 until more data are available.

Pristimantis espedeus **sp. nov.** has been recovered as the sister species of *P. inguinalis* (Fouquet et al. 2012), a species endemic to the eastern Guiana Shield. These two species share many similarities such as arboreal habits, the behaviour of generally calling head down along trunks, large expanded finger discs, similar tibia/hand ratio and the bright mark on the groin region (though of different colour and shape). However, *P. inguinalis* generally calls from higher sites in trees, generally 4–6 m above the ground, and its calling activity extends later during the night night (limited to dusk and dawn in *P. espedeus* **sp. nov.**). *Pristimantis inguinalis* is found from sea level to *ca.* 600 m elevation, but is generally absent where *P. espedeus* **sp. nov.** occurs. The two other species of the *unistrigatus* species group occurring with certainty in French Guiana are smaller and distinctly less arboreal: *P.* sp. 1 calls from lower sites (0.5–2 m), and *P.* sp. 4 is generally found on the leaf litter or on small branches 1–2 m above the ground. Their proportionally longer tibia and smaller hand may be linked to these ecological differences. *Pristimantis* sp. 4 is often found in syntopy with *P. espedeus* **sp. nov.**, which is not the case of *P.* sp. 1 that prefers ecotonal forest at low elevation. These four species form a clade with western Amazonian species (Fouquet *et al.* 2012), but their relationships are ambiguous and it is possible that the four species occurring in French Guiana form a clade endemic to the eastern Guiana Shield.

Given the larger number of amphibian species remaining to be described and the number of species threatened by extinction, it is likely that many species are currently vanishing before even being noticed. The proportion of localized *Pristimantis* endemics in highlands is striking (Duellman & Lehr 2009), and these species are particularly sensitive to climate change (Lips *et al.* 2003; Pounds *et al.* 2006; Whitefield *et al.* 2007). *Pristimantis espedeus* **sp. nov.** belongs to this category; moreover, this species illustrates how altitude-adapted species may occur in an otherwise largely lowland landscape. *Pristimantis espedeus* **sp. nov.** is endemic to French Guiana (and possibly adjacent areas) and only occurs on a few isolated massifs >400 m high. Such a narrow niche is particularly interesting and suggests that very subtle thermal variations can be sufficient to bound species distributions. Given this narrow altitudinal range, we can expect that slight climatic changes could reduce its range even more, and it is therefore important to monitor these populations. How many localized endemics associated with such modest uplands exist across Amazonia? The conservation status of 422 species of *Pristimantis* was evaluated and more than one third are considered threatened (9 CR, 90 EN, 61 VU) and another 128 remain Data Deficient (IUCN 2013). Given that the extent of occurrence of the new species is likely <20,000 km^2, that no more than 10 populations are currently known, and that global climate change could negatively affect these populations in the forthcoming years, we consider that *P. espedeus* **sp. nov.** meets the IUCN criteria to be categorized as "Vulnerable" (VU) (IUCN 2001).

The patchy distribution of *Pristimantis espedeus* **sp. nov.** is intriguing, but not unique in the Guiana Shield (see for example the distribution of the colubrid snake *Chironius challenger* Kok, 2010 that is also apparently restricted to a specific altitudinal limit with disjunct populations). We hypothesize that the distribution pattern of *P. espedeus* **sp. nov.** is shaped by unfavourable climatic conditions below *ca.* 200 m asl. During colder cycles of the Pleistocene (Colinvaux *et al.* 2000; Mayle *et al.* 2004) this species may have been more broadly distributed, allowing range expansion and gene flow across the range. Subsequently, populations of *P. espedeus* **sp. nov.** may have been isolated in patches when temperature increased. Phylogeographical analysis in combination with niche modelling is necessary to test such a hypothesis. So far the phylogeography of only open habitat organisms (*Dendropsophus gaucheri* [Fouquet *et al.* 2011]; *Manihot* species [Duputié *et al.* 2009]) and lowland frog species (12 different taxa [Fouquet *et al.* 2012], *Dendrobates* [Noonan & Gaucher 2006]; *Atelopus* [Noonan & Gaucher 2005]) have been studied in the eastern Guiana Shield. Some of these forest dwelling species are also associated with the presence of massifs, but none is as remarkably associated with these modest uplands as *P. espedeus*.

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Literature cited

Angulo, A. & Icochea, J. (2010) Cryptic species complexes, widespread species and conservation: lessons from Amazonian frogs of the *Leptodactylus marmoratus* group (Anura: Leptodactylidae). *Systematics and Biodiversity*, 8, 357–370. http://dx.doi.org/10.1080/14772000.2010.507264

Avila-Pires, T.C.S., Hoogmoed, M.S. & Rocha, W.A. (2010) Notes on the vertebrates of northern Pará, Brazil: a forgotten part of the Guianan Region, I. Herpetofauna. *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, 5 (1), 13–112. http://dx.doi.org/10.5123/s1981-81142008000200001

Barrio-Amorós, C.L. & Brewer-Carias, C. (2008) Herpetological results of the 2002 expedition to Sarisariñama, a tepui in Venezuelan Guayana, with the description of five new species. *Zootaxa*, 1942, 1–68.

Boulenger, G.A. (1900) Batrachians. *In*: Lankester, E.R. (Ed.), Report on a collection made by Messrs. McConnell, F.V. & Quelch J.J. at Mount Roraima in British Guiana. Transactions of the Linnean Society of London, 2nd series. *Zoology*, 8, 55–56. http://dx.doi.org/10.1111/j.1096-3642.1900.tb00308.x

Boulenger, G.A. (1912) Descriptions of new batrachians from the Andes of South America, preserved in the British Museum. *Annals and Magazine of Natural History*, 10, 185–191. http://dx.doi.org/10.1080/00222931208693215

Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of Amphibian richness. *Proceedings of the Royal Society B-Biological Sciences*, 274, 1167–1173. http://dx.doi.org/10.1098/rspb.2006.0436

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21, 873–885. http://dx.doi.org/10.1111/j.1466-8238.2011.00737.x

Colinvaux, P.A., De Oliveira, P.E. & Bush, M.B. (2000) Amazonian and Neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews,* 19, 141–169. http://dx.doi.org/10.1016/s0277-3791(99)00059-1

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Science of the USA*, 105, 6668–6672. http://dx.doi.org/10.1073/pnas.0709472105

Dewynter, M., Marty, C., Blanc, M., Gaucher, P., Vidal, N., Frétey, T., de Massary, J.-C. & Fouquet, A. (2008) Liste des Amphibiens et des Reptiles de Guyane. Available online: http://www.chelidae.com/pdf/dewynter2008.pdf/ (accessed 16 August 2013)

Dias Lima, J. (2008) A herpetofauna do Parque Nacional do Montanhas do Tumucumaque, Amapá, Brasil, Expedições I a V. *In*: Bernard, E. (Ed.), Inventários Biológicos Rápidos no Parque Nacional Montanhas do Tumucumaque, Amapá, Brasil. *RAP Bulletin of Biological Assessment* 48. Conservation International, Arlington, pp. 38–50.

Dray, S. & Dufour, A.-B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22 (4), 1–20.

Duellman, W.E. (1978) Three new species of *Eleutherodactylus* from Amazonian Peru (Amphibia: Anura: Leptodactylidae). *Herpetologica*, 34, 264–270. http://dx.doi.org/10.1655/03-24

Duellman, W.E. & Lehr, E. (2009) *Terrestrial-Breeding Frogs (Strabomantidae) in Peru.* Natur und Tier-Verlag, Naturwissenschaft, Münster, 382 pp.

Duputié, A., Deletre, M., De Granville, J.J. & Mckey, D. (2009) Population genetics of *Manihot esculenta ssp flabellifolia* gives insight into past distribution of xeric vegetation in a postulated forest refugium area in northern Amazonia. *Molecular Ecology*, 18, 2897–2907.
http://dx.doi.org/10.1111/j.1365-294x.2009.04231.x

Dwyer, C.M. (1995) A new species of *Eleutherodactylus* from Peru (Anura: Leptodactylidae). *Amphibia-Reptilia*, 16, 245–256.
http://dx.doi.org/10.1163/156853895x00046

Elmer, K.R. & Cannatella, D.C. (2008) Three new species of leaflitter frogs from the upper Amazon forests: cryptic diversity within *Pristimantis "ockendeni"* (Anura: Strabomantidae) in Ecuador. *Zootaxa*, 1784, 11–38.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vie, J-C., Akcakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Sekercioglu, C.H. & Mace, G.M. (2013) Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all Birds, Amphibians and Corals. *PLoS ONE*, 8 (6), e65427.
http://dx.doi.org/10.1371/journal.pone.0065427

Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M. & Gemmell, N.J. (2007) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS ONE*, 2 (10), e1109.
http://dx.doi.org/10.1371/journal.pone.0001109

Fouquet A., Noonan, B., Blanc, M. & Dill Orrico, V.G. (2011) Phylogenetic position of *Dendropsophus gaucheri* (Lescure & Marty 2000) highlights the need for an in-depth investigation of the phylogenetic relationships of *Dendropsophus* (Anura: Hylidae). *Zootaxa*, 3035, 59–67.

Fouquet, A., Noonan, B.P., Rodrigues, M.T., Pech, N., Gilles, A. & Gemmell, N.J. (2012) Multiple quaternary refugia in the eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. *Systematic Biology*, 61, 461–489.

Frost, D.R. (2013) Amphibian Species of the World: an Online Reference. Version 5.6 (9 January 2013), American Museum of Natural History, New York, USA. Available from: http://research.amnh.org/herpetology/amphibia/index.html (accessed 25 August 2013)

Gonzalez-Voyer, A., Padial, J.M., Castroviejo-Fisher, S., de la Riva, I. & Vila, C. (2011) Correlates of species richness in the largest Neotropical Amphibian radiation. *Journal of Evolutionary Biology*, 24 (5), 931–942.
http://dx.doi.org/10.1111/j.1420-9101.2011.02243.x

Giam, X., Scheffers, B.R., Sodhi, N.S., Wilcove, D.S., Ceballos, G. & Ehrlich, P.R. (2011) Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. *Proceedings of the National Academy of Sciences B*, 279, 67–76.
http://dx.doi.org/10.1098/rspb.2011.0433

Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008) New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737, 1–182.

Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the USA*, 104, 10092–10097.
http://dx.doi.org/10.1073/pnas.0611051104

Heyer, W.R. & Hardy, L.M. (1991) A new species of frog of the *Eleutherodactylus lacrimosus* assembly from Amazonia, South America (Amphibia: Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington*, 104, 436–447.

IUCN (2001) IUCN Red List Categories and Criteria. Version 3.1. Available from: http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria/ (accessed 16 August 2013)

IUCN (2013) IUCN Red List of Threatened Species. Version 2013.1. Available from: http://www.iucnredlist.org (accessed 26 August 2013)

Jenkins, C.N, Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the USA*, 110 (28), E2602–E2610.
http://dx.doi.org/10.1073/pnas.1302251110

Köhler, J., Vieites, D.R., Bonett, R.M., Garcia, F.H., Glaw, F., Steinke, D. & Vences, M. (2005) New Amphibians and global conservation: A boost in species discoveries in a highly endangered vertebrate group. *Bioscience*, 55, 693–696.
http://dx.doi.org/10.1641/0006-3568(2005)055[0693:naagca]2.0.co;2

Kok, P.J.R. (2010) A new species of *Chironius* Fitzinger, 1826 (Squamata: Colubridae) from the Pantepui region, northeastern South America. *Zootaxa*, 2611, 31–44.

Kok, P.J.R. (2013) Two new charismatic *Pristimantis* species (Anura: Craugastoridae) from the tepuis of the "Lost World" (Pantepui region, South America). *European Journal of Taxonomy*, 60, 1–24.
http://dx.doi.org/10.5852/ejt.2013.60

Kok, P.J.R. & Kalamandeen, M. (2008) *Introduction to the Taxonomy of the Amphibians of Kaieteur National Park, Guyana, Abc Taxa:* A Series of Manual Dedicated to Capacity Building in Taxonomy and Collection Management [Brussels, Belgium], Belgian Development Corporation, 1–288.

Kok, P.J.R., Means, D.B. & Bossuyt, F. (2011) A new highland species of *Pristimantis* Jiménez de la Espada, 1871 (Anura: Strabomantidae) from the Pantepui region, northern South America. *Zootaxa*, 2934, 1–19

Kok, P.J.R., MacCulloch, R.D., Means, D.B., Roelants, K., Van Bocxlaer, I. & Bossuyt, F. (2012) Low genetic diversity in tepui summit vertebrates. *Current Biology*, 22, R589–R590.
http://dx.doi.org/10.1016/j.cub.2012.06.034

Lescure, J. & Marty, C. (2001 "2000") *Atlas des Amphibiens de Guyane*. Patrimoines Naturels. Muséum national d'Histoire Naturelle, Paris, 45, pp. 388.

Lima, A.P., Magnusson, W.E., Menin, M., Erdtmann, L.K., Rodrigue, D.J., Keller, C. & Hödl, W. (2006) *Guia de sapos da Reserva Adolpho Ducke – Amazônia Central / Guide to the frogs of Reserva Adolpho Ducke* – Central Amazonia. Áttema, Manaus, 168 pp.

Lips, K.R., Reeve, J.D. & Writters, L.R. (2003) Ecological traits predicting Amphibian population declines in Central America. *Conservation Biology*, 17 (4), 1078–1088.
http://dx.doi.org/10.1046/j.1523-1739.2003.01623.x

Lutz, B. & Kloss, G.R. (1952) Anfíbios anuros do alto Solimões e Rio Negro. Apontamento sôbre algumas formas e suas vicariantes. *Memórias do Instituto Oswaldo Cruz. Rio de Janeiro*, 50, 625–678.
http://dx.doi.org/10.1590/s0074-02761952000100020

Lynch, J.D. (1968) Two new frogs of the genus *Eleutherodactylus* from eastern Ecuador (Amphibia: Leptodactylidae). *Journal of Herpetology*, 2, 129–135.

Marty, C. & Gaucher, P. (1999) *Guide sonore des Amphibiens Anoures de Guyane*. CD audio. CEBA, Mens.

Mayle, F.E., Beerling, D.J., Gosling, W.D. & Bush, M.B. (2004) Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Proceedings of the National Academy of Sciences,* 359, 499–514.
http://dx.doi.org/10.1098/rstb.2003.1434

Means, D.B. & Savage, J.M. (2007) Three new malodorous rainfrogs of the genus *Pristimantis* (Anura: Brachycephalidae) from the Wokomung Massif in west-central Guyana, South America. *Zootaxa*, 1658, 39–55.

McDiarmid, R.W. & Donnelly, M.A. (2005) The herpetofauna of the Guayana Highlands: Amphibians and Reptiles of the Lost World. *In*: Donnelly, M.A., Crother, B.I., Guyer, C., Wake, M.H. & White, M.E. (Eds.), *Ecology and Evolution in the Tropics: A Herpetological Perspective*. University of Chicago Press, Chicago, Illinois, pp. 461–560.

Myers, C.W. & Donnelly, M.A. (1997) A tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil: Report from the Phipps Tapirapecó Expedition. *American Museum Novitates*, 3213, 1–71.

Ouboter, P.E. & Jairam, R. (2012) *Amphibians of Suriname*. Brill Academic Publishers, Leiden, 376 pp.

Noonan, B.P. & Gaucher, P. (2005) Phylogeography and demography of Guianan harlequin toads (*Atelopus*): Diversification within a refuge. *Molecular Ecology*, 14 (10), 3017–3031.
http://dx.doi.org/10.1111/j.1365-294x.2005.02624.x

Noonan, B.P. & Gaucher, P. (2006) Refugial isolation and secondary contact in the dyeing poison frog *Dendrobates tinctorius. Molecular Ecology*, 15 (14), 4425–4435.
http://dx.doi.org/10.1111/j.1365-294x.2006.03074.x

Parker, H.W. (1940) Undescribed anatomical structures and new species of Reptiles and Amphibians. *Annals and Magazine of Natural History,* 5, 257–274.
http://dx.doi.org/10.1080/00222934008527045

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread Amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167.
http://dx.doi.org/10.1038/nature04246

Rivero, J.A. (1961) Salientia of Venezuela. *Bulletin of the Museum of Comparative Zoology*, 126, 1–207.

Schlüter, A. & Rödder, D. (2007) "2006" Three new frogs of the genus *Eleutherodactylus* (Amphibia, Leptodactylidae) from Guaiquinima Table Mountain, Bolivar, Venezuela. *Herpetotropicos*, 3, 88–99.

Smith, M.A. & Green, D.M. (2005) Dispersal and the metapopulation paradigm in Amphibian ecology and conservation: are all Amphibian populations metapopulations? *Ecography*, 28, 110–128.
http://dx.doi.org/10.1111/j.0906-7590.2005.04042.x

Sueur, J., Aubin, T. & Simonis, C. (2008) Equipment review: Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, 18 (2), 213–226.
http://dx.doi.org/10.1080/09524622.2008.9753600

Whitefield, S.M., Bell. K.E., Philippi, T., Saas, M., Bolanos. F., Chaves, G., Savage, J.M. & Donnelly, M.A. (2007) Amphibian and Reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the USA*, 104 (20), 8352–8356.
http://dx.doi.org/10.1073/pnas.0611256104

APPENDIX. Additional material examined.

Pristimantis inguinalis: **Brazil**, Amapá, Oiapoque, R186 (MTR24299); **Guyana**, East Berbice-Corentyne District, New River, BMNH 1939.1.1.1 (holotype), BMNH 1939.1.1.2 (paratype); **French Guiana**, Roura, Patawa, R1788-9 (AF0803–04), Régina, Savane Virginie, R180 (AF0813), St Laurent du Maroni, Chutes Voltaires, R181 (AF0820), Régina, Réserve des Nouragues, R182 (AF0883), St Elie, Reserve de la Trinité, R183 (AF1186), R184 (AF1221), Maripasoula, Inini Tolenga, R185 (AM0015); **Suriname**, Brokopondo, Brownsberg Nature Park, R177 (AF0157).

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

Pristimantis sp. 1: **Brazil**, Amapá, Lourenço, R195 (MTR24229), R196 (MTR24285), Amapá, Oiapoque, R197 (MTR24300); **French Guiana**, Saül, R187 (AF0021), Régina, Savane Virginie, R188 (AF0563), St Georges, Saut Maripa, R189 (AF0757), R199 (PG0748), Roura, Patawa, R190-1 (AF0798–99), Saül, Mont Galbao, R192-3 (AF1014, AF1046), Maripasoula, Borne 4, R194 (BOAM048), Maripasoula, Flat de la Waki, R200 (WAAM011), Camopi, Toponowini, R198 (PG0311).

Pristimantis sp. 4: **French Guiana**, Régina, Réserve des Nouragues, R201-3 (AF0272, AF0876–77), Maripasoula, Pic Coudreau, R204 (AF0910), Saül, Mont Galbao, R205-11 (AF0978, AF0997, AF1004–06, AF1025, AF1030), Maripasoula, Borne 4, R212-4 (BOAM001, BOAM012, BOAM017).