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Two new *Pristimantis* (Anura: Strabomantidae) of the *P. lacrimosus* species group from the eastern Guiana Shield lowlands

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Abstract. Many anuran species remain to be formally named and described in Amazonia, notably in the Guiana Shield and particularly in megadiverse groups such as *Pristimantis*. These descriptions are urgently needed to include species in local conservation and protection policies. In French Guiana, two species of *Pristimantis* of the *P. lacrimosus* group have been reported as *Pristimantis* sp. 3 and *Pristimantis* sp. 5. Using integrative taxonomy, we compared these two species with all other species of the *lacrimosus* group and confirmed their status as distinct species. Herein, we describe *Pristimantis fouqueti* sp. nov. and *Pristimantis flavus* sp. nov., both endemic to the eastern Guiana Shield lowlands.

Keywords. Amazonia, Amphibia, bioacoustics, integrative taxonomy, rain frogs.

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Introduction

With almost 615 described species (Frost 2025), the genus *Pristimantis* Jiménez de la Espada, 1870 is the most species-rich genus of vertebrate. New species of *Pristimantis* are being discovered and described on a regular basis, and this already impressive number keeps increasing every year. Widespread in the Neotropics, from Honduras and some Caribbean islands to northern Argentina and the Atlantic Forest in Brazil (Frost 2025), the genus is particularly diverse in the Andes (Lehr & Duellman 2009). Several systematic and taxonomic studies revealed the Guiana Shield as another source of species of *Pristimantis* (Means & Savage 2007; Kok *et al.* 2011; Fouquet *et al.* 2013; Kok 2013; Means *et al.* 2023).

The *Pristimantis lacrimosus* group currently contains 41 species distributed in Central America, through the Pacific Basin of Ecuador to the Amazonian Basin (Ron *et al.* 2020; Carrión-Olmedo & Ron 2021; Means *et al.* 2023). The largest diversity of the group is found in the Amazon basin (Ron *et al.* 2020). But the picture changes in the eastern Amazonia: while the Brazilian Shield has no described species within the group, the Guiana Shield harbours two species of the *P. lacrimosus* group, viz. *Pristimantis zimmermanae* (Heyer & Hardy, 1991) and *P. kalamandeenae* Means, Heinicke, Hedges, MacCulloch & Lathrop, 2023. Ron *et al.* (2020) redefined the *P. lacrimosus* group and suggested that the clade likely originated in the Chocoan forests of the Pacific basin of Ecuador and Colombia before colonizing Amazonia, thus probably having reached the eastern Amazon only recently. Even though this possible recent colonization could have limited the diversification, thus the number of current species, it is known that there are still at least a few undescribed species in this region (Vacher *et al.* 2020).

The genus *Pristimantis* is famous for having multiple 'cryptic' species hiding under a single name (e.g., Padial *et al.* 2009; Fouquet *et al.* 2022b; Mônico *et al.* 2024), and *P. zimmermanae* seems to be one of those species. Although its original description includes only material from the type locality, there are specimens from several localities (i.e., Brazil: Rio Branco, Acre; Serra do Navio, Amapá; Jaru and Alto Paraíso, Rondônia; Colombia: Puerto Nariño, Amazonas) used as referred material for its characterization and distribution (Heyer & Hardy 1991). Heyer & Hardy (1991) mentioned themselves that specimens of *P. zimmermanae* from Serra do Navio, for example, have distinctive traits and deserve further taxonomic evaluation.

Here, we describe two new species of the *P. lacrimosus* group from the eastern Guiana Shield, which were previously reported as *Pristimantis* sp. 3 or *P.* aff. *zimmermanae* (e.g., Lescure & Marty 2001; Vacher *et al.* 2020; Lescure *et al.* 2022; Fouquet *et al.* 2024) and *Pristimantis* sp. 5 or *P*. cf. *pluvialis* (e.g., Vacher *et al.* 2020; Lescure *et al.* 2022; Fouquet *et al.* 2024). Our descriptions are integrative, combining molecular, morphological and acoustic data. Besides, *Pristimantis zimmermanae* from the type locality is included for the first time in a molecular phylogeny.

Material and methods

Fieldwork and specimens deposition

Extensive field work has been undertaken in French Guiana during the last 20 years in an effort to better understand the extraordinary diversity of this region. Individuals of the two new species of *Pristimantis* described herein were obtained from several localities in French Guiana, with one additional specimen collected by A. Fouquet, S.M. Souza and J. Lima in the state of Amapá, Brazil. Two adult males of *P. zimmermanae* were collected by A.T. Mônico and I.Y. Fernandes on 27 December 2019, from the type locality, i.e., Manaus, state of Amazonas, Brazil, (2°26′55″ S, 59°55′45″ W). These specimens are critical since the phylogenetic position of *P. zimmermanae* remains unknown and some undescribed species might hide under that name. All specimens were collected by hand and sacrificed with an intraperitoneal injection of Xylocaine® (lidocaine hydrochloride). A piece of liver or thigh muscle was taken from the specimens prior to fixation and preserved in 95% ethanol for subsequent molecular analyses. Specimens were then individually tagged and fixed in 10% formalin before being transferred into a solution of 70% ethanol for permanent storage. Newly collected specimens were deposited in the Muséum national d'Histoire naturelle (MNHN-RA – Paris, France) and in the Museu de Zoologia da Universidade de São Paulo (MZUSP – São Paulo, Brazil). The two specimens of *P. zimmermanae* were deposited in the Herpetological Collection of Instituto Nacional de Pesquisas da Amazônia (INPA-H Manaus, Brazil).

DNA extraction, amplification and sequencing

Genomic DNA was extracted from tissues (muscle or liver) of two individuals of *Pristimantis* sp. 5 (also reported as *P.* cf. *pluvialis*, see above) from two localities: (i) "Pic Coudreau du Sud" and (ii) "Mitaraka", in French Guiana; and five individuals of *Pristimantis* sp. 3 (also reported as *P. zimmermanae*, see above) from five localities: (i) "Nouragues", (ii) "Saül" (juvenile, not included in morphometric analysis and not deposited as a specimen), (iii) "Kaw", (iv) "Trinité", in French Guiana, and (v) "Oiapoque", Amapá State, in Brazil. We also extracted genomic DNA of the two individuals of *Pristimantis zimmermanae* from the type locality (Manaus, Brazil) using PureLink™ Genomic DNA (Invitrogen by Thermo Fisher Scientific, Carlsbad, CA, USA).

Using polymerase chain reaction (PCR), we amplified a fragment of the 16S ribosomal mitochondrial RNA gene (16S), with the primers 16Saf (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi 1996) and a fragment of the nuclear recombination activating gene 1 (RAG1) with the primers R182 (5′-GCCATAACTGCTGGAGCATYAT-3′) and R270 (5′-AGYAGATGTTGCCTGGGTCTTC-3′) (Heinicke *et al.* 2007) for the nine specimens mentioned above and under the conditions described by Mônico *et al.* (2022). PCR amplifications were confirmed on a 1% agarose gel before being purified using the PEG 8000 protocol (Sambrook & Russell 2001) and Sanger sequenced along both strands (using the same primers used for PCR) on an ABI PRISM 3130XL sequencer (Thermo Fisher). Sequences were subjected to BLAST searches (Altschul *et al.* 1997) against the NCBI databases to make sure that the target genes had been amplified. Newly generated sequences were deposited in GenBank, and accession numbers are available in Appendix 1.

Sequence alignment and phylogenetic analyses

New sequences were included in a data set containing homologous sequences of 16S and RAG1 retrieved from GenBank. Sequences retrieved from GenBank are detailed in Appendix 1. We selected sequences used in the most recent phylogenetic analyses that involved individuals of the *Pristimantis lacrimosus* group and related species (Ron *et al.* 2020), along with *Tachiramantis prolixodiscus* (Lynch, 1978) (SBH 268371) as the outgroup. In total, 131 sequences (Appendix 1) of the two genes were selected (93 for 16S and 38 for RAG1), corresponding to 93 terminals. We aligned sequences of each gene separately, using the MAFFT online server under the E-INS-i strategy for the 16S gene and the G-INS-i for RAG1 (Katoh & Standley 2013). The final matrix was concatenated in Mesquite (Maddison & Maddison 2000) and consisted of 1165 bp (554 pb for 16S; and 611 pb for RAG1).

Best-fit evolutionary models and partition schemes were determined through ModelFinder (Kalyaanamoorthy *et al.* 2017) using four partitions: one for the 16S and one for each codon of RAG1. The best evolutionary models for partitions in the concatenated matrix were: TIM2+F+R3 for 16S, K2P for RAG1 1st position, and HKY+F+G4 for RAG1 2nd and 3rd codons. Phylogenetic relationships were reconstructed under Maximum Likelihood inference (ML). The ML tree was inferred using IQTREE (Nguyen *et al.* 2015) as implemented in the webserver http://iqtree.cibiv.univie.ac.at (Trifinopoulos *et al.* 2016). Clade support was estimated with 20 000 ultrafast bootstrap replications (Hoang *et al.* 2018), 1000 maximum iterations, and a minimum correlation coefficient of 0.99. We calculated the uncorrected pairwise genetic distances (*p*-distance) and Kimura-two-parameter distance (Kimura 1980) across populations of the new species and closely related species using MEGA 11 (Tamura *et al.* 2021). Genetic distances were calculated using pairwise deletion.

Morphological data

We examined four adult specimens of *Pristimantis* sp. 3 from French Guiana and one from Amapá, and seven adult specimens of *Pristimantis* sp. 5 from French Guiana. All examined individuals were included in the phylogenetic analysis with the addition of one juvenile from French Guiana. Sex was determined either in the field via calling activity, or in the laboratory by examining the condition of vocal slits and gonads. We measured 18 morphometric variables, abbreviated as follows: snout-vent length (SVL); head width (HW); head length (HL); internarial distance (IND); interorbital distance (IOD); eye-nostril distance (EN; straight line distance between anterior corner of eye and nostrils); snout length (SL; straight line distance between the anterior corner of eye and tip of snout); horizontal eye diameter (ED); tympanum length (TD); femur length (FL); tibia length (TL); tarsus length (TaL); hand length (HaL; from distal edge of palmar tubercle to the tip of Finger III); length of Finger I (L1F; from proximal edge of palmar tubercle to the tip of Finger I); length of Finger II (L2F; from proximal edge of palmar tubercle to the tip of Finger II); disc width of Finger III (W3FD); foot length (FoL; from outer edge of metatarsal tubercle to the tip of Toe IV); and disc width of Toe IV (W4FD). The definitions, diagnoses, and descriptions of the type series mostly follow the scheme of Carrión-Olmedo & Ron (2021) for ease of comparison. See also Duellman & Lehr (2009) and Carrión-Olmedo & Ron (2021) for the morphological character states used in the descriptions.

Bioacoustical analyses

We gathered six call recordings of males of *Pristimantis* sp. 3 and three call recordings of males of *Pristimantis* sp. 5. We measured nine bioacoustics variables using the Raven Pro ver. 1.6.5 software (K. Lisa Yang Center for Conservation Bioacoustics 2024), following Köhler *et al.* (2017): number of notes per call (NN); call duration (CD); silence between calls (SBC); note duration (ND); silence between notes (SBN); call rate (CR, calls per minute); minimum frequency (LF); maximum frequency (HF); and dominant frequency (DF). Whenever possible, up to four measurements of each variable were taken per recorded male, and the average was considered as a single measurement. Call recordings have been deposited at www.sonotheque.mnhn.fr (Appendix 2).

Interspecific comparisons

We compared our specimens with adults of all 39 nominal species of the *Pristimantis lacrimosus* group (sensu Ron *et al.* 2020; Carrión-Olmedo & Ron 2021): *P. acuminatus* (Shreve, 1935), *P. amaguanae* Ron, Carrión, Caminer, Sagredo, Navarrete, Ortega, Varela-Jaramillo, Maldonado-Castro & Terán, 2020, *P. aureolineatus* (Guayasamin, Ron, Cisneros-Heredia, Lamar & McCracken, 2006), *P. bromeliaceus* (Lynch, 1979), *P. calima* Ospina-Sarria & Duellman, 2019, *P. crucifer* (Boulenger, 1899), *P. degener* (Lynch & Duellman, 1997), *P. ecuadorensis* Guayasamin, Hutter, Tapia, Culebras, Peñafiel, Pyron, Morochz, Funk & Arteaga-Navarro, 2017, *P. enigmaticus* Ortega-Andrade, Rojas-Soto, Valencia, Espinosa de los Monteros, Morrone, Ron & Cannatella, 2015, *P. eremitus* (Lynch, 1980), *P. galdi* Jiménez de la Espada, 1870, *P. jorgevelosai* (Lynch, 1994), *P. lacrimosus* (Jiménez de la Espada, 1875), *P. latericius* Batallas & Brito, 2014, *P. limoncochensis* Ortega-Andrade, Rojas-Soto, Valencia, Espinosa de los Monteros, Morrone, Ron & Cannatella, 2015, *P. mendax* (Duellman, 1978), *P. mindo* Arteaga-Navarro, Yánez-Munoz & Guayasamin, 2013, *P. moro* (Savage, 1965), *P. nankints* Ron, Carrión, Caminer, Sagredo, Navarrete, Ortega, Varela-Jaramillo, Maldonado-Castro & Terán, 2020, *P. nyctophylax* (Lynch, 1976), *P. olivaceus* (Köhler, Morales, Lötters, Reichle & Aparicio, 1998), *P. omeviridis* Ortega-Andrade, Rojas-Soto, Valencia, Espinosa de los Monteros, Morrone, Ron & Cannatella, 2015, *P. ornatissimus* (Despax, 1911), *P. padiali* Moravec, Lehr, Pérez-Peña, López, Gagliardi-Urrutia & Arista-Tuanama, 2010, *P. pardalinus* (Lehr, Lundberg, Aguilar & von May, 2006), *P. petersi* (Lynch & Duellman, 1980), *P. petersioides* Carrión-Olmedo & Ron, 2021, *P. pluvialis* Shepack, von May, Ttito & Catenazzi, 2016, *P. pseudoacuminatus* (Shreve, 1935), *P. pulchridormientes* Chávez & Catenazzi, 2016, *P. rhodostichus* (Duellman & Pramuk, 1999), *P. romeroae* Ron, Carrión, Caminer, Sagredo, Navarrete, Ortega, Varela-

Table 1. Interspecific and intraspecific genetic distances across *Pristimantis flavus* sp. nov., *P. fouqueti* sp. nov. and closely related species. Uncorrected p-distances (%; lower diagonal) and Kimura-2-parameter (%; upper diagonal) for sequences in a matrix with 554 characters from 16S rRNA.

	Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	*P. flavus* sp. nov.	**0.3**	12.7	11.8	9.3	9.8	11.4	9.1	5.1	9.7	7.0
2	*P. fouqueti* sp. nov.	14.2	**0.3**	14.1	11.9	12.0	13.5	12.3	11.1	11.8	12.2
3	*P. zimmermanae*	13.1	16.0	**0.2**	7.1	10.0	10.8	9.0	10.6	11.6	10.2
4	*P. olivaceus*	10.0	13.3	7.6	**n/c**	8.1	11.3	8.3	8.7	10.5	8.0
5	*P. pulchridormientes*	10.8	13.4	11.0	7.6	**0.0**	7.1	9.0	8.6	9.6	9.2
6	*P. loeslein*	12.6	15.3	11.9	10.3	7.7	**0.0**	9.5	9.9	10.9	10.5
7	*P. kalamandeenae*	9.9	13.7	9.8	7.8	8.3	10.3	**n/c**	7.8	8.2	8.3
8	*P. pluvialis*	5.4	12.3	11.6	9.4	9.3	10.8	8.3	**0.0**	8.3	5.9
9	*P. zorro*	9.0	10.7	10.6	9.7	8.9	10.0	7.7	7.8	**0.0**	8.6
10	*P. aureolineatus*	7.4	13.5	11.5	8.5	10.0	11.5	8.9	6.2	9.3	**n/c**

Jaramillo, Maldonado-Castro & Terán, 2020, *P. royi* (Morales, 2007), *P. schultei* (Duellman, 1990), *P. subsigillatus* (Boulenger, 1902), *P. tantanti* (Lehr, Torres-Gastello & Suárez-Segovia, 2007), *P. waoranii* (McCracken, Forstner & Dixon, 2007), *P. zimmermanae*, and *P. zorro* Rivera-Correa & Daza, 2020. In addition to these, we also compared them with the most recently described *P. kalamandeenae* and *P. loeslein* Castillo-Urbina, Vences, Aguilar-Puntriano, Glaw & Köhler, 2023. Comparisons were based either on manuscripts of original descriptions or redescriptions. Finally, detailed morphological and acoustic comparisons were restricted to the closest phylogenetically related species.

Results

Phylogenetic relationships and genetic distances

The two new species are nested within the *Pristimantis lacrimosus* group (Fig. 1). *Pristimantis lacrimosus* is the sister species of the clade where the new species are nested. This clade is formed by species from western Amazonia (i.e., *P. aureolineatus*, *P. loeslein*, *P. olivaceus*, *P. pluvialis*, *P. pulchridormientes*, and *P. zorro*) and from the Guiana Shield (i.e., *P. zimmermanae* and *P. kalamandeenae*). *Pristimantis* sp. 5 is recovered sister to *P. pluvialis* with an interspecific *p*-distance of 5.4%, while *Pristimantis* sp. 3 is recovered sister to *P. zorro* with an interspecific *p*-distance of 10.7% (Table 1). Both new species are genetically distinct from *P. kalamandeenae* and *P. zimmermanae* sensu stricto, the most geographically closest taxon (Guiana Shield), with *p*-distance of 13.1 and 9.9% compared to *Pristimantis* sp. 5, and of 16.0 and 13.7% compared to *Pristimantis* sp. 3, respectively (Table 1).

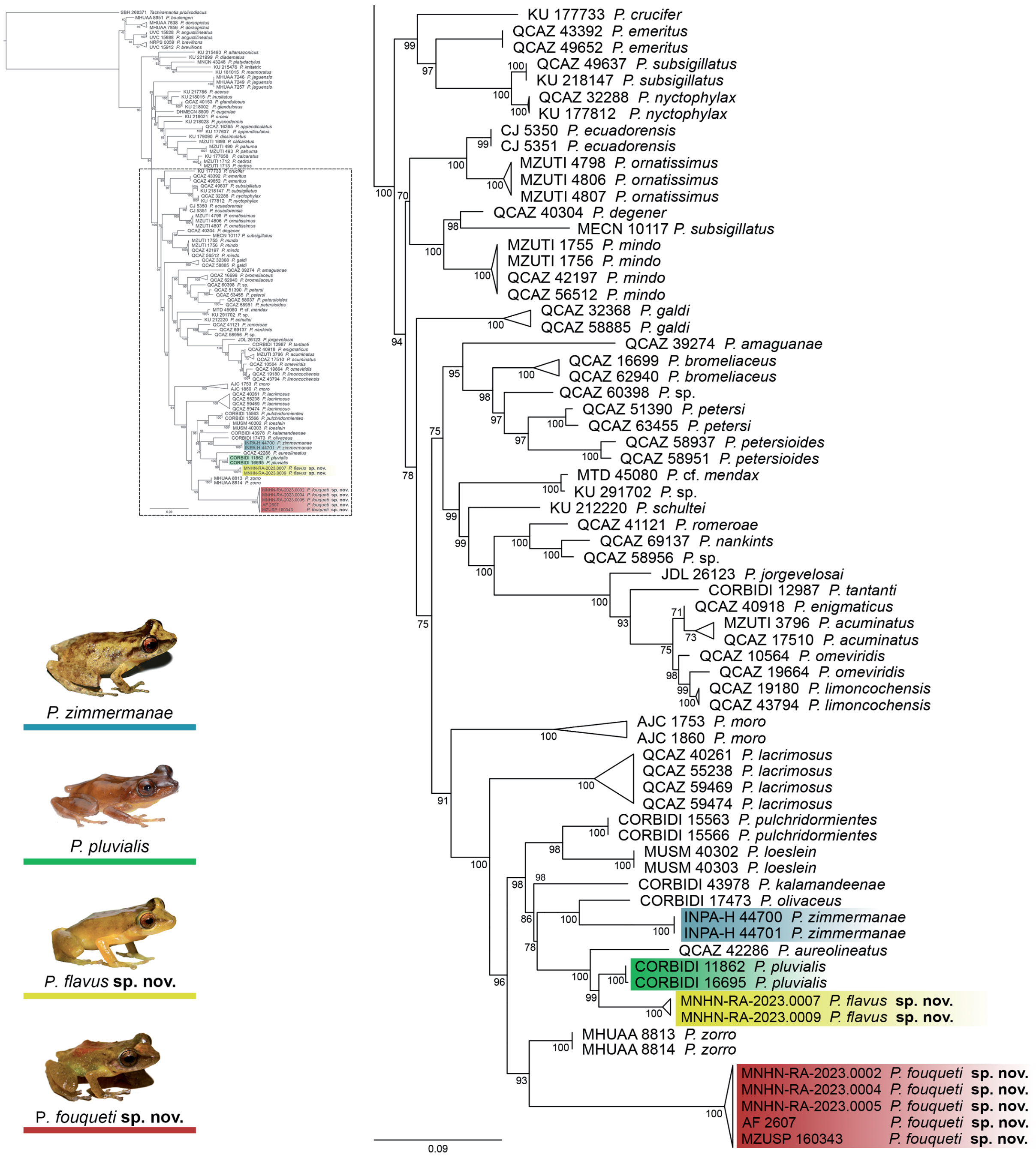

Fig. 1. Phylogenetic relationships of the *Pristimantis lacrimosus* species group inferred from a concatenated dataset of one mtDNA (16S) and one nuDNA (RAG-1) gene (1165 bp) using Maximum Likelihood. Non-parametric bootstrap supports (IQ-TREE) are provided at nodes. Species names are preceded by specimens voucher numbers. Photos by A. Fouquet (*P. flavus* sp. nov. and *P. fouqueti* sp. nov.), A. Shepack (*P. pluvialis*) and A.T. Mônico (*P. zimmermanae*).

Taxonomy

Class Amphibia Linnaeus, 1758
Order Anura Fischer Von Waldheim, 1813
Family Strabomantidae Hedges, Duellman & Heinecke, 2008
Genus *Pristimantis* Jiménez de la Espada, 1870

Pristimantis flavus sp. nov.

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Figs 2–5

Pristimantis sp. nov. – Blanc 2016: 330.
Pristimantis aff. *pluvialis* – Fouquet *et al.* 2019a: 367; 2024: 480. — Vacher *et al.* 2020: table s1.
Pristimantis sp. 5 – Dewynter *et al*. 2020: 32; 2021: 32. — Lescure *et al*. 2022: 7.

Diagnosis

The assignment of the new species to the *Pristimantis lacrimosus* species group is based on molecular phylogeny (Fig. 1) and the presence of hyperdistal subarticular tubercles (see Ron *et al.* 2020). *Pristimantis flavus* sp. nov. is characterized by the following combination of characters: (1) skin on dorsum smooth with scattered tubercles, gular region smooth, belly and ventral surface of the thighs slightly granular; discoidal fold absent; dorsolateral folds absent; (2) tympanic membrane and tympanic annulus present, round, its length 34–38% of eye diameter; (3) snout moderate in length, subacuminate in dorsal view, truncate in lateral view; loreal region slightly concave; (4) interorbital region flat, broader than upper eyelid; cranial crests absent; upper eyelid tubercles present; (5) dentigerous processes of vomers absent; (6) males with vocal slits, nuptial pads absent; vocal sac large and subgular; (7) Finger I slightly shorter than Finger II; discs of digits expanded; discs rounded on fingers I and II, and truncate on fingers III and IV; (8) fingers without lateral fringes; palmar tubercle diffuse, thenar tubercle almost triangular, both the same size; hyperdistal subarticular tubercles present; (9) four to five ulnar tubercles, low and rounded, aligned; (10) heel smooth; three tarsal tubercles, ovoid, aligned; inner tarsal fold absent; (11) inner metatarsal tubercle ovoid, three times the size of round outer metatarsal tubercle; supernumerary plantar tubercles present; (12) toes without lateral fringes; basal toe webbing absent; Toe V longer than Toe III (disc on Toe III reaches the medial subarticular tubercle on Toe IV, while disc on Toe V reaches the distal subarticular tubercle on Toe IV); hyperdistal subarticular tubercles present; toes discs less expanded than the fingers discs (discs rounded on toes I and II, and truncate on fingers III–V); (13) in life, dorsal surfaces of body and limbs bright yellow, with a distinct dark brown interorbital line; canthal stripe and supratympanic fold darker; lips vivid yellow; flanks paler than dorsum; gular region bright yellow with brown melanophores; chest yellow; belly light yellow; iris copper with an ill-defined dark copper horizontal streak; (14) SVL 18.6–21.8 mm (n = 7) in males, female unknown; and (15) advertisement call consisting of 1–4 short notes, with duration of 37–81 ms, and a dominant frequency at 2.799–3.187 Hz.

Etymology

The specific epithet ‘*flavus*’ is an adjective that refers to the yellow coloration of males in life.

Type material

Holotype

FRENCH GUIANA • adult ♂, SVL 19.3 mm; Maripasoula municipality, collected at Massif du Mitaraka; 2°14′08″ N, 54°26′57″ W; 330 m a.s.l.; datum WGS-84; 26 Feb. 2015; A. Fouquet, M. Dewynter and N. Vidal leg.; MNHN-RA-2023.0010 (field no. AF2782).

Paratypes

FRENCH GUIANA – **Maripasoula municipality** • 3 adult ♂♂; Pic Coudreau du Sud; 2°15′12″ N, 54°21′12″ W; 382 m a.s.l.; datum WGS-84; 11 Feb. 2013; M. Blanc leg.; MNHN-RA-2023.0006 to MNHN-RA-2023.0008 (field numbers AF915 to AF917, respectively) • 3 adult ♂♂; same locality as for holotype; 2–27 Feb. 2015; A. Fouquet, M. Dewynter and N. Vidal leg.; MNHN-RA-2023.0009, MNHN-RA-2023.0011, MNHN-RA-2023.0012 (field numbers AF2764, AF2783 and 2782, respectively).

Description of the holotype (MNHN-RA-2023.0010, field number AF 2752; Figs 2, 3A, 4A)

Adult male, 19.3 mm SVL; head narrower than body, 22.8% of SVL; head wider than long; head width 36.3% of SVL; snout subacuminate in dorsal view, truncate in lateral view; loreal region slightly concave; eye large, 61.4% of head length, its diameter 1.23 times its distance from the nostril; nostrils protuberant, situated close to snout; canthus rostralis weakly concave in dorsal view, slightly rounded in profile; loreal region slightly concave; lips rounded; dorsal surface of head smooth, lacking tubercles; upper eyelid width smaller than interorbital distance; interorbital region flat; tympanic annulus present, rounded, tympanic membrane present but undifferentiated; postrictal ridges or tubercles absent. Choanae ovoid, small, positioned anterior and laterally, widely separated from each other, not concealed by palatal shelf of maxilla; dentigerous processes of vomers present, oblique.

Skin on dorsum and flanks smooth with few scattered tubercles; gular region smooth; belly and ventral surface of the thighs slightly areolate; discoidal folds absent; dorsolateral folds absent. Three ulnar tubercles, discrete and rounded; palmar tubercle almost triangular, same size as diffuse thenar tubercle;

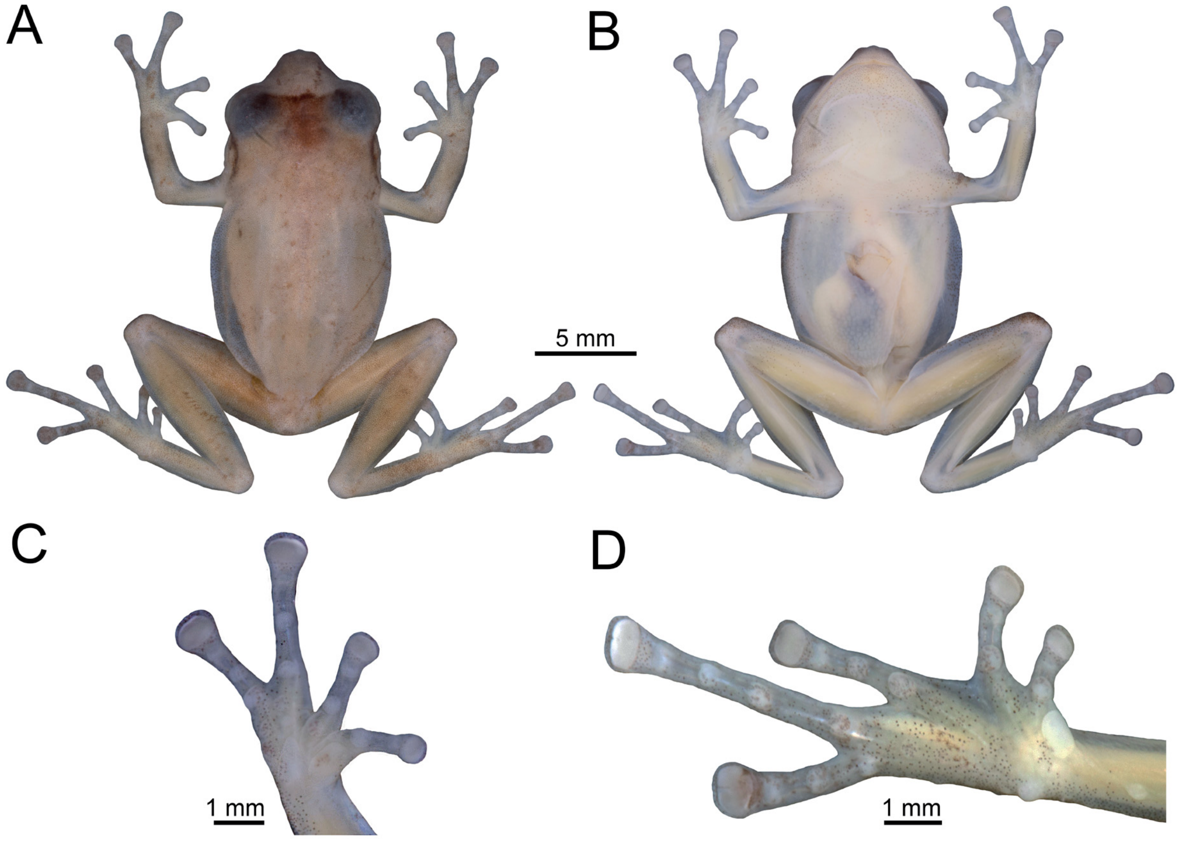

Fig. 2. *Pristimantis flavus* sp. nov., preserved holotype, ♂ (MNHN-RA-2023.0010, field number AF 2782) from Mitaraka, French Guiana. **A**. Dorsal view. **B**. Ventral view. **C**. Right hand. **D**. Right foot. Photographs by Antoine Fouquet.

Table 2. Morphometric measurements in millimeters of adults of *Pristimantis flavus* sp. nov. and *P. fouqueti* sp. nov. Values express mean ± standard deviation (range). Measurement abbreviations are defined in Material and methods.

Measurements	***Pristimantis flavus*** **sp. nov.**		***Pristimantis fouqueti*** **sp. nov.**		
	Holotype	♂♂ (n = 7)	**Holotype**	♂♂ (n = 4)	♀ (n = 1)
SVL	19.3	20.5 ± 1.2 (18.6–21.8)	18.9	19.4 ± 0.4 (18.9–19.8)	25.6
HW	7.0	7.1 ± 0.3 (6.7–7.8)	6.8	6.9 ± 0.2 (6.6–7.1)	9.7
HL	4.4	4.9 ± 0.4 (4.3–5.2)	4.9	4.9 ± 0.3 (4.6–5.3)	6.2
IND	1.5	1.5 ± 0.2 (1.2–1.7)	1.4	1.4 ± 0.1 (1.3–1.5)	2.2
IOD	2.7	2.7 ± 0.3 (2.5–3.3)	2.4	2.5 ± 0.3 (2.3–2.9)	2.9
EN	1.4	1.8 ± 0.3 (1.4–2.2)	1.8	1.8 ± 0.1 (1.7–1.9)	2.2
SL	2.0	2.3 ± 0.2 (2.0–2.5)	2.1	2.2 ± 0.1 (2.1–2.3)	3.2
ED	2.3	2.6 ± 0.2 (2.3–2.8)	2.4	2.5 ± 0.1 (2.4–2.5)	3.2
TD	0.9	0.9 ± 0.1 (0.8–1.0)	0.6	0.8 ± 0.1 (0.7–0.9)	1.0
FL	9.1	9.7 ± 0.5 (8.9–10.2)	8.9	9.0 ± 0.5 (8.4–9.5)	10.8
TL	10.1	10.2 ± 0.6 (9.2–11.0)	9.3	9.5 ± 0.4 (9.0–10.1)	11.8
TaL	4.7	5.2 ± 0.6 (4.4–5.9)	4.8	5.0 ± 0.3 (4.8–5.5)	6.6
HaL	5.4	5.7 ± 0.3 (5.3–6.0)	5.5	5.2 ± 0.2 (5.0–5.5)	6.0
L1F	3.0	2.9 ± 0.2 (2.6–3.1)	2.8	2.7 ± 0.3 (2.5–3.1)	3.2
L2F	3.6	3.6 ± 0.2 (3.3–3.8)	3.3	3.3 ± 0.3 (3.0–3.6)	3.9
W3FD	0.9	1.0 ± 0.1 (0.8–1.2)	0.8	0.9 ± 0.1 (0.8–1.0)	1.2
FoL	8.4	8.6 ± 0.4 (8.1–9.2)	7.8	8.0 ± 0.5 (7.4–8.4)	9.6
W4TD	0.9	1.0 ± 0.1 (0.9–1.2)	0.9	0.9 ± 0.1 (0.9–1.0)	1.1

supernumerary palmar tubercles present; subarticular tubercles prominent, ovoid in ventral view, rounded in lateral view; hyperdistal subarticular tubercles present; fingers lacking lateral fringes; fingers length when adpressed, 3 > 4 > 2 > 1; discs of digits expanded, rounded on fingers I and II, and truncate on fingers III and IV, pads with strongly defined circumferential grooves. Tibia length 52.3% of SVL; foot length 43.5% of SVL; hindlimbs surfaces shagreen, posterior surface granular; heel lacking tubercles; tarsus with three tubercles, ovoid, aligned; inner metatarsal tubercle ovoid, three times the size of rounded outer metatarsal tubercle; inner tarsal fold absent; supernumerary plantar tubercles present, but poorly visible; subarticular tubercles rounded; hyperdistal subarticular tubercles present; toes lacking lateral fringes; basal toe webbing absent; toes discs less expanded than the fingers discs, rounded on toes I and II, and truncate on fingers III–V; toes ventral pads strongly defined by circumferential grooves; toe lengths, when adpressed, 4 > 5> 3 > 2 > 1. All morphometric measurements are provided in Table 2.

Color of holotype. In life, background color yellow; snout vivid yellow, a distinct dark brown interorbital bar present; canthal stripe and supratympanic folds diffuse, dark brown; lips vivid yellow; flanks paler than dorsum and translucent (Fig. 3A); gular region bright yellow with small brown melanophores, which fade and disappear in the central part of the throat; chest yellow; belly light yellow, translucent; ventral surfaces of forearms and hindlimbs light yellow dorsal surfaces with scattered brown melanophores (Fig. 4A); iris copper, with fine dark brown reticulation and an ill-defined dark copper horizontal streak. After nine years in preservative (ethanol 70%), the dorsum background color turned reddish beige with a dark brown interorbital bar; canthal stripe and supratympanic fold dark brown; venter cream and translucent; ventral surface of limbs with scattered small melanophores (Fig. 2).

Intraspecific variation

Dorsal color varies depending on light and/or temperature conditions; individuals are paler at night than during the day (Fig. 3). The dorsal color pattern of some individuals had a more discrete loreal coloration (Fig. 3C) and some individuals had a lighter interorbital bar (Fig. 3B). The ventral coloration varies from light yellow to yellow, and the melanophores in the gular region vary in size (Fig. 4). Although the

Fig. 3. Male individuals of *Pristimantis flavus* sp. nov. in life. **A**. Holotype (MNHN-RA-2023.0010). **B**. Paratype (MNHN-RA-2023.0009). **C**. Paratype (MNHN-RA-2023.0011). Photographs by Antoine Fouquet.

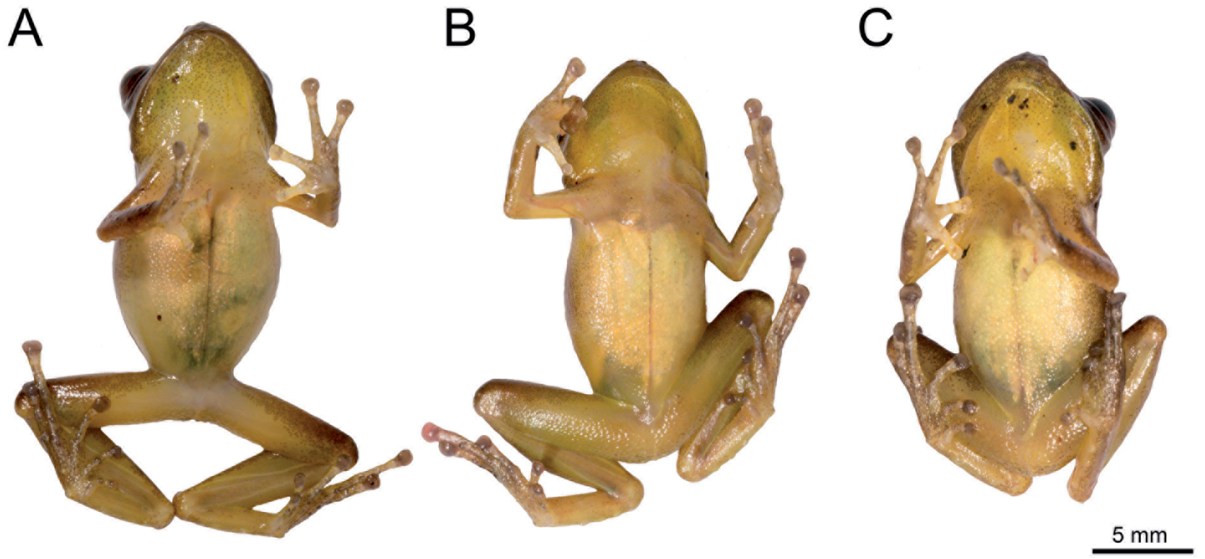

Fig. 4. Ventral coloration of *Pristimantis flavus* sp. nov. in life. **A**. Holotype (MNHN-RA-2023.0010). **B**. Paratype (MNHN-RA-2023.0009). **C**. Paratype (MNHN-RA-2023.0011). Photographs by Antoine Fouquet.

general dorsal tubercles pattern remains the same, the individuals displayed changes in the size of the tubercles during handling, going from prominent to flat (Fig. 3). Dentigerous process of vomer varies in size from medium to very small, almost indiscernible in some individuals.

Advertisement call

The advertisement call of *Pristimantis flavus* sp. nov. (n = 4 males) consists of short and powerful 'tk' sounds, similar to tongue clicks (Fig. 5). It is composed of 1–4 notes (n = 69 calls) – most commonly consisting of two notes (n = 34). Call length ranges from 42–851 ms and depend on the number of notes [i.e., calls of a single note are 61 ± 2 ms (42–85 ms), calls of two notes are 289 ± 6 ms (182–431 ms), calls of three notes are 432 ± 8 ms (340–548 ms), while calls of four notes are 749 ± 9 ms (683–851 ms)].

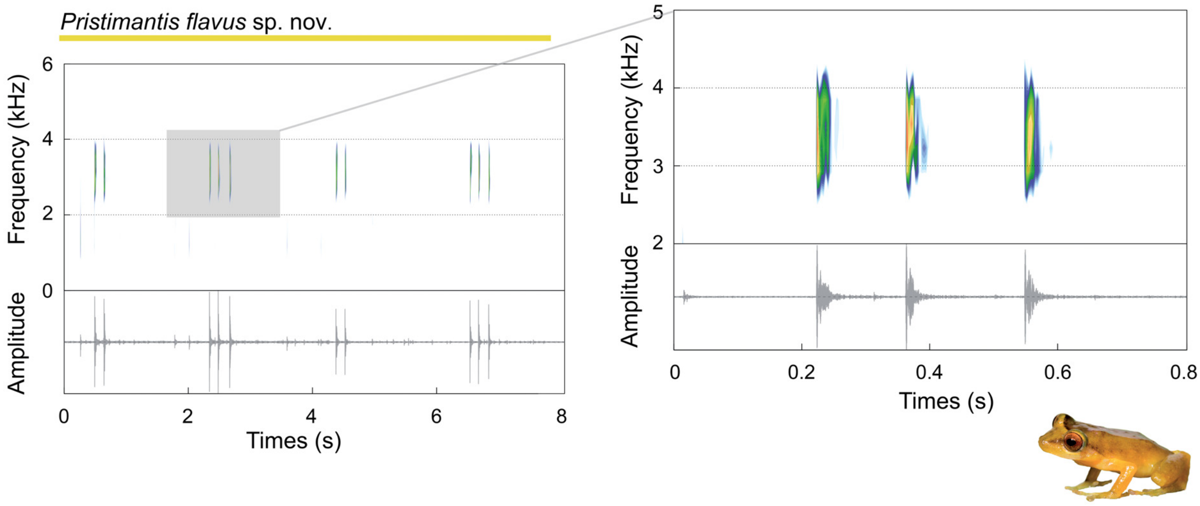

Fig. 5. Advertisement call of *Pristimantis flavus* sp. nov., holotype (MNHN-RA-2023.0010) recorded at Mitaraka, French Guiana.

Table 3. Acoustic traits of the call of *Pristimantis flavus* sp. nov. summarized according to call arrangements. Temporal and spectral traits are presented in milliseconds and Hz, respectively. Abbreviations: CD = call duration; DF = dominant frequency; HF = maximum frequency; LF = minimum frequency; ND = note duration; SBC = silence between calls; SBN = silence between notes; SD = standard deviation.

Call arrangement		CD	SBC	ND	SBN	LF	HF	DF
1 note (n = 15)	**mean**	61	931	61	–	2.530	3.405	2.960
	SD	2	23	2	–	66	190	136
	min	42	509	42	–	2.402	3.207	2.813
	max	85	1.226	85	–	2.591	3.753	3.101
2 notes (n = 34)	**mean**	289	1.379	49	181	2.541	3.516	2.986
	SD	6	52	1	5	51	165	128
	min	182	813	37	101	2.425	3.216	2.799
	max	431	2.690	65	269	2.604	3.730	3.144
3 notes (n = 12)	**mean**	432	1.341	45	160	2.569	3.482	2.963
	SD	8	53	3	5	54	254	115
	min	340	873	41	100	2.476	3.200	2.887
	max	538	2.273	49	220	2.657	3.719	3.095
4 notes (n = 8)	**mean**	749	1.201	44	191	2.554	3.207	2.963
	SD	9	19	0.1	3	41	38	114
	min	683	1.030	42	168	2.517	3.184	2.882
	max	851	1.406	45	227	2.599	3.250	3.095

Regardless of the number of notes, the silence between calls is relatively homogeneous, with an average of 1.246 ± 47 ms (509–2.690 ms). The notes are tonal and short, with a note length of 49 ± 11 ms (37–81 ms), and silence between notes of 176 ± 5 ms (101–269 ms). Males were found calling in chorus, typically calling for about one minute starting with a single note and gradually increasing the number of notes towards to the end of the call at a rate of 43 ± 4 (38–46) calls per minute. They then remain silent for another minute before starting to call again. This behaviour was observed throughout the night. Calls were emitted with a minimum frequency of 2.545 ± 54 Hz (2.402–2.657 Hz), maximum frequency of 3.457 ± 199 Hz (3.184–3.753 Hz) and dominant frequency of 2.987 ± 125 Hz (2.799–3.187 Hz) (Fig. 5). Temporal and spectral traits summarized, according to individual call arrangement, are presented in Table 3.

Differential diagnosis

Morphology

Pristimantis flavus sp. nov. is distinguished by its smaller SVL in males (18.6–21.8 mm) from the following close relatives: *P. calima* (24.0 mm; Ospina-Sarria & Duellman 2019), *P. degener* (22.2 mm; Lynch & Duellman 1997), *P. ecuadorensis* (25.4 mm; Guayasamin *et al.* 2017), *P. jorgevelosai* (24.3–29.8 mm; Lynch 1994), *P. kalamandeenae* (22.1 mm; Means *et al.* 2023), *P. latericius* (22.2–25.1 mm; Duellman & Lehr 2009), *P. mindo* (24.49–27.4 mm; Arteaga-Navarro *et al.* 2013), *P. nyctophylax* (21.9–31.4 mm; Lynch 1976), *P. padiali* (26.5 mm; Moravec *et al.* 2010), *P. pluvialis* (21.8–26.9 mm; Shepack *et al.* 2016), *P. romeroae* (23.8 mm; Ron *et al.* 2020), *P. schultei* (23.5–26.6 mm; Duellman 1990); and larger SVL in males than *P. amaguanae* (16.3 mm; Ron *et al.* 2020) and *P. pseudoacuminatus* (12.7–17.6 mm; Duellman & Lehr 2009).

The bright yellow to tan dorsal coloration readily distinguishes *P. flavus* sp. nov. from all species with greenish dorsal coloration: *P. acuminatus* (greenish yellow; Ortega-Andrade *et al.* 2015), *P. amaguanae* (olive green or olive brown; Ron *et al.* 2020), *P. aureolineatus* (olive green; Guayasamin *et al.* 2006), *P. bromeliaceus* (pale green to olive; Lynch 1979), *P. calima* (dull green, reddish brown, or olive brown; Ospina-Sarria & Duellman 2019), *P. ecuadorensis* (greenish yellow with transverse black stripes; Guayasamin *et al.* 2017), *P. enigmaticus* (greenish yellow; Ortega-Andrade *et al.* 2015), *P. galdi* (green; Duellman & Lehr 2009), *P. limoncochensis* (greenish yellow; Ortega-Andrade *et al.* 2015), *P. loeslein* (yellowish green to olive-green; Castillo-Urbina *et al.* 2023), *P. moro* (green with reddish head; Savage 2002), *P. nankints* (lime green to olive green; Ron *et al.* 2020), *P. olivaceus* (olive green; Köhler *et al.* 1998), *P. omeviridis* (greenish yellow; Ortega-Andrade *et al.* 2015), *P. padiali* (bright green to yellowish green; Moravec *et al.* 2010), *P. petersioides* (dark greenish brown, olive green, to pale yellowish green; Carrión-Olmedo & Ron 2021), *P. pseudoacuminatus* (green marbled with brown; Duellman & Lehr 2009), *P. rhodostichus* (green with red and tan marks; Duellman & Pramuk 1999), *P. tantanti* (green with white spots; Lehr *et al.* 2007) and *P. zorro* (light green to green-yellow; Rivera-Correa & Daza 2020).

The new species is further distinguished from *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. moro* (Savage 2002) and *P. tantanti* (Lehr *et al.* 2007) by the presence of a tympanic annulus; from *P. amaguanae* (Ron *et al.* 2020), *P. enigmaticus* (Ortega-Andrade *et al.* 2015), *P. kalamandeenae* (Means *et al.* 2023), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. padiali* (Moravec *et al.* 2010) and *P. tantanti* (Lehr *et al.* 2007) by the presence of vocal slits in males; from *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2006), *P. calima* (Ospina-Sarria & Duellman 2019), *P. crucifer* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. eremitus* (Lynch 1980a), *P. galdi* (Duellman and Lehr 2009), *P. jorgevelosai* (Lynch 1994), *P. lacrimosus* (Duellman & Lehr 2009), *P. latericius* (Duellman & Lehr 2009), *P. loeslein* (Castillo-Urbina *et al.* 2013), *P. pardalinus* (Lehr *et al.* 2006), *P. romeroae* (Ron *et al.* 2020) and *P. waoranii* (McCracken *et al.* 2007) by the absence of nuptial pads; and from *P. amaguanae* (Ron *et al.* 2020), *P. mendax* (Duellman, 1978), *P. pulchridormientes* (Chávez & Catenazzi 2016) and *P. zimmermanae* (Heyer & Hardy 1991) by the presence of dentigerous processes of vomers.

Pristimantis flavus sp. nov. is distinguished from all species in the group by its unique combination of body tubercles, i.e., the presence of upper eyelid tubercles vs absence in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2007), *P. degener* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. enigmaticus* (Ortega-Andrade *et al.* 2015), *P. kalamandeenae* (Means *et al.* 2023), *P. lacrimosus* (Duellman & Lehr 2009), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. moro* (Savage, 2002), *P. nankints* (Ron *et al.* 2020), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. ornatissimus* (Lynch 1970), *P. padiali* (Moravec *et al.* 2010), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. schultei* (Duellman 1990), *P. subsigillatus* (Lynch 1980b), *P. tantanti* (Lehr *et al.* 2007), *P. waoranii* (McCracken *et al.* 2009) and *P. zorro* (Rivera-Correa & Daza 2020); the presence of ulnar tubercles vs absent in *P. bromeliaceus* (Lynch 1979), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. lacrimosus* (Duellman & Lehr 2009), *P. ornatissimus* (Lynch 1970), *P. petersi* (Lynch & Duellman 1980), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. romeroae* (Ron *et al.* 2020), *P. royi* (Morales 2007), *P. subsigillatus* (Lynch 1980b) and *P. zorro* (Rivera-Correa & Daza 2020); and the presence of tarsal tubercles vs absence in *P. amaguanae* (Ron *et al.* 2020), *P. degener* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. galdi* (Duellman & Lehr 2009), *P. lacrimosus* (Duellman & Lehr 2009), *P. mendax* (Duellman 1978), *P. mindo* (Arteaga-Navarro *et al.* 2013), *P. ornatissimus* (Lynch 1970), *P. pluvialis* (Shepack *et al.* 2016), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. waoranii* (McCracken *et al.* 2007) and *P. zorro* (Rivera-Correa & Daza 2020).

Bioacoustics

There is little information about the vocalization of the *P. lacrimosus* species group, though we gathered information for 15 of them. The advertisement call of *Pristimantis flavus* sp. nov. is composed of 1–4 notes and it is distinguished from all the following species with single note calls: *P. aureolineatus* (McCracken & Forstner 2006), *P. bromeliaceus*, *P. lacrimosus*, *P. latericius* (Batallas-Revelo & Brito-M 2014), *P. loeslein* (Castillo-Urbina *et al.* 2023), *P. mindo* (Arteaga-Navarro *et al.* 2013), *P. petersi*, *P. petersioides* (Carrión-Olmedo & Ron 2021), *P. pluvialis* (Shepack *et al.* 2016), *P. royi* (Morales 2007), *P. zimmermanae* (Heyer & Hardy 1991) and *P. zorro* (Rivera-Correa & Daza 2020). The advertisement call of *Pristimantis flavus* has less notes than that of *P. galdi* (7–9 notes; Batallas-Revelo & Brito-M 2023), and has shorter notes (37–81 ms) compared to those of *P. bromeliaceus* (140–142 ms), *P. lacrimosus* (139–167 ms; Batallas-Revelo & Brito-M 2014), *P. loeslein* (98–110 ms; Castillo-Urbina *et al.* 2023), *P. mindo* (approx. 300 ms; Arteaga-Navarro *et al.* 2013), *P. petersi* (310–490 ms), *P. petersioides* (110–390 ms; Carrión-Olmedo & Ron 2021) and longer notes than that of *P. royi* (24–26 ms; Morales 2007).

The advertisement call of *Pristimantis flavus* sp. nov. is distinguished by the higher dominant frequency (2.799–3.187 Hz) from that of *P. galdi* (2.190–2.580 Hz; Batallas-Revelo & Brito-M 2023), *P. pluvialis* (2.312–2.756 Hz; Shepack *et al.* 2016), *P. subsigillatus* (1.961–2.033 Hz; Arteaga-Navarro *et al.* 2013) and by the lower dominant frequency from that of *P. bromeliaceus* (4.130–4.470 Hz; Batallas-Revelo & Brito-M 2014), *P. eremitus* (4.049–5.168 Hz; Hutter *et al.* 2016), *P. latericius* (4.260-4.470 Hz; Batallas-Revelo & Brito-M 2014), *P. petersi* (3.820–4.242 Hz), *P. petersioides* (4.122–4.837 Hz; Carrión-Olmedo & Ron 2021), *P. royi* (3.270–3.360 Hz; Morales 2007) and *P. zimmermanae* (3.485–4.222 Hz; Heyer & Hardy 1991). The advertisement call of *Pristimantis flavus* has a lower call rate (38–46 calls/min) than that of *P. zimmermanae* (62 calls/min; Heyer & Hardy 1991) and a higher call rate than that of *P. bromeliaceus* (9–34 calls/min; Batallas-Revelo & Brito-M 2014), *P. lacrimosus* (4–9 calls/min), *P. latericius* (8–30 calls/min; Batallas-Revelo & Brito-M 2014), *P. petersi* (4–9 calls/min) and *P. petersioides* (1–26 calls/min; Carrión-Olmedo & Ron 2021).

The advertisement call parameters of *Pristimantis flavus* sp. nov. are indistinguishable from those of *P. pulchridormientes*, the number of notes (1–4 vs 2–5) and dominant frequency (2.799–3.187 Hz vs 2.531–3.094 Hz; Chávez & Catenazzi 2016). However, information on other acoustic parameters would help to further differentiate these species based on their call. Unfortunately, no information is available regarding the minimum and maximum frequencies, call rate, note/call duration or inter-note/call intervals in *P. pulchridormientes*.

Distribution, natural history and conservation

The new species is only known from two localities in southern French Guiana and its ecology is mostly unknown. Males of *Pristimantis flavus* sp. nov. were captured on the Mitaraka massif (Fig. 6), calling at night from 3–5 m above the ground on leaves and bamboo in the outcrops located on the edge of the lowland forest, or on the plateau. On the "Pic Coudreau du Sud", the males were observed calling in small groups of 5–10 individuals, from 2–6 m above the ground, in dense vegetation (e.g., vines, windfall, bamboo) and often positioned under a leaf. A male was observed, calling on a leaf, upside down; another was perched in a *Clusia* L. plant at the edge between a woodland and a rocky savannah area, while a group of males was calling in a nearby transition forest. The species is nocturnal and arboreal like all species of the *lacrimosus* group. *Pristimantis flavus* probably has a wider distribution in the interior of the Guiana Shield, at least in southern French Guiana as well as in the south-east part of Suriname and northern Pará State, in Brazil (see Fig. 12). We do not have sufficient data to categorize the new species following the criteria of the International Union for Conservation of Nature (IUCN), therefore we suggest it to be Data Deficient (DD).

Fig. 6. Forests in the surroundings of the Mitaraka massif – French Guiana, inhabited by *Pristimantis flavus* sp. nov. Photography by Maël Dewynter.

Pristimantis fouqueti sp. nov.

urn:lsid:zoobank.org:act:09E34CA5-ACE6-464D-9874-13C82410A7AB

Figs 7–10

Eleutherodactylus zimmermanae – Heyer & Hardy 1991: 442.
Pristimantis sp. 3 – Lescure & Marty 2000: 220–221. — Lescure *et al.* 2022: 7.
Pristimantis zimmermanae – Taucce *et al*. 2022: 103.
Pristimantis cf. *zimmermanae* – Fouquet *et al.* 2019a: 467; 2024: 480. — Vacher *et al.* 2020: table s1.

Diagnosis

The assignment of the new species to the *Pristimantis lacrimosus* species group is based on molecular phylogeny (Fig. 1) and the presence of hyperdistal subarticular tubercles (see Ron *et al.* 2020). *Pristimantis fouqueti* sp. nov. is characterized by the following combination of characters: (1) skin on dorsum shagreen with scattered tubercles, gular region smooth, belly areolate with enlarged tubercles; discoidal fold absent; dorsolateral folds absent; (2) tympanic membrane and tympanic annulus present, round, 27–34% of eye diameter; (3) snout moderate in length, acuminate in dorsal view, protruding in lateral view; loreal region concave; (4) three to five small upper eyelid tubercles; interorbital region flat, broader than upper eyelid; cranial crests absent; (5) dentigerous processes of vomers absent; (6) males with vocal slits, nuptial pads absent, vocal sac medium to large; (7) Finger I shorter than Finger II; discs of digits rounded, broader on Finger IV; (8) fingers lacking lateral fringes; thenar tubercle barely visible, palmar tubercle heart shaped, two times the size of thenar; hyperdistal subarticular tubercles present; (9) three ulnar tubercles, discrete and rounded; (10) heel shagreen lacking tubercles; four to five tarsal tubercles, elliptical, aligned; inner tarsal fold absent; (11) inner metatarsal tubercle ovoid and small, two times the size of round outer metatarsal tubercle; supernumerary plantar tubercles present, but poorly visible; (12) toes lacking lateral fringes; basal toe webbing absent; Toe V longer than Toe III; hyperdistal subarticular tubercles present; all discs expanded, truncate; (13) in life, dorsal surfaces of body and limbs yellowish to greenish brown, with a distinct but diffuse dark brown interorbital line posterior to a light brown triangle on snout; canthal stripe and supratympanic fold dark brown; two large dark brown scapular tubercles on each side of the dorsum, large reddish brown patch usually present on the middle of the back; flanks paler than dorsum and translucent; gular region yellow with brown melanophores; belly cream, translucent with whitish tubercles; iris light copper brown, with an ill-defined horizontal dark reddish intraocular streak; (14) SVL 18.9–19.8 mm (n = 4) in males, and 25.6 mm in female (n = 1); and (15) advertisement call consisting of a single note with a duration of 73–115 ms, silence between calls of 520–848 ms and a dominant frequency at 4.031–4.307 Hz.

Etymology

The specific epithet '*fouqueti*' is a noun in the genitive case, honoring our friend and colleague Antoine Fouquet for his invaluable contribution to the amphibian systematics in the Guiana Shield in general and in French Guiana in particular.

Type material

Holotype

FRENCH GUIANA • adult ♂, SVL 18.9 mm; Régina municipality, Kaw Mountain, collected at Patawa camp; 4°32′48″ N, 52°09′06″ W; 233 m a.s.l.; datum WGS-84; 14 Mar. 2012; A. Fouquet, E.A. Courtois and P. Gaucher leg.; MNHN-RA-2023.0003 (field no. PG705).

Paratypes

BRAZIL – **Amapá State** • 1 adult ♂; Oiapoque municipality; 3°52′45″ N, 51°46′15″ W; 40 m a.s.l.; 13 Dec. 2012; A. Fouquet leg.; MZUSP 160343 (field no. MTR24136).

FRENCH GUIANA – **Régina municipality** • 1 adult ♀; Nouragues (Inselberg Camp); 4°05′43″ N, 52°40′43″ W; 330 m a.s.l.; datum WGS-84; 10 May 2007; A. Fouquet leg.; MNHN-RA-2023.0002 (field no. AF264) • 1 adult ♂; same locality as for holotype; A. Fouquet, E.A. Courtois and P. Gaucher leg.; MNHN-RA-2023.0004 (field no. PG706). – **Mana municipality** • 1 adult ♂; Trinité (near Aya Camp); 4°36′09″ N, 53°24′51″ W; 120 m a.s.l.; 1 May 2013; A. Fouquet and E.A. Courtois leg.; MNHN-RA-2023.0005 (field no. AF1189)

Referred material

FRENCH GUIANA • 1 adult ♂; Camp Saut Richard, Saül; 3°28′25.1″ N 53°12′30.8″ W; 5 Mar. 2019; Antoine Fouquet; (field no. AF AF5394) (this specimen was used only for molecular data) • 1 juv.; Atachi Bakka; 3°32′48″ N, 53°54′46″ W; 4 Feb. 2015; Benoit Villette and Jean-Pierre Vacher leg.; (field no. AF2607). (Specimen without repository number. Original specimen used to molecular analysis, only pictures remaining for reference).

Description of the holotype (MNHN-RA-2023.0003, field no. PG705; Figs 7, 8A, 9A)

Adult male, 18.9 mm SVL; head wider than body, 25.9% of SVL; head wider than long; head width 36.0% of SVL; snout acuminate in dorsal view, protruding in lateral view; loreal region concave; eye large, 49.0% of head length, its diameter 1.14 times its distance from the nostril; nostrils protuberant, situated close to snout; canthus rostralis concave in dorsal view, slightly rounded in profile; loreal area concave; lips rounded; dorsal surface of head smooth and upper eyelids with minute tubercles; upper eyelid width smaller than interorbital distance; tympanic annulus present, rounded, tympanic membrane present but undifferentiated; postrictal ridges or tubercles absent; choanae round, small; dentigerous processes of vomers absent.

Skin on dorsum shagreen with scattered tubercles; two large scapular tubercles on each side of the dorsum; no dorsolateral folds; flanks smooth; gular region smooth; belly areolate with scattered tubercles; discoidal folds absent. Three ulnar tubercles, discrete and rounded; palmar tubercle heart-shaped, two times the size of a barely visible thenar tubercle; discrete supernumerary palmar tubercles present; subarticular tubercles prominent, ovoid in ventral view, rounded in lateral view; hyperdistal subarticular tubercles present; fingers lacking lateral fringes; fingers length when adpressed, 3 > 4 > 2 > 1; discs of digits expanded, rounded, broader on Finger IV, pads with defined circumferential grooves. Tibia length 49.2% of SVL; foot length 41.3% of SVL; upper and posterior surfaces of hindlimbs shagreen; heel lacking tubercles; tarsus with four tubercles, elliptical, aligned; inner metatarsal tubercle ovoid, and small, two times the size of rounded outer metatarsal tubercle; supernumerary plantar tubercles present but poorly visible; subarticular tubercles rounded; hyperdistal subarticular tubercles present; toes lacking lateral fringes; basal toe webbing absent; discs of toes expanded, truncate; toes ventral pads poorly defined by circumferential grooves; toe lengths, when adpressed, 4 > 5 > 3 > 2 > 1. All morphometric measurements are provided in Table 2.

COLOR OF HOLOTYPE. In life, dorsal background color greenish brown; distinct but diffuse dark brown interorbital line posterior to a light brown triangle on snout; large reddish brown patch on the middle of the back; canthal stripe and supratympanic fold dark brown; scapular tubercles dark brown; posterior flanks greenish and translucent; gular region yellow with small brown melanophores; belly cream, translucent with whitish tubercles; ventral surfaces of forearms and hindlimbs pale yellow with brown melanophores; distinct dark brown spot on the ventral surface of right knee; iris light copper brown, with fine, dense, dark brown reticulation, an ill-defined dark reddish intraocular streak is continuous with the

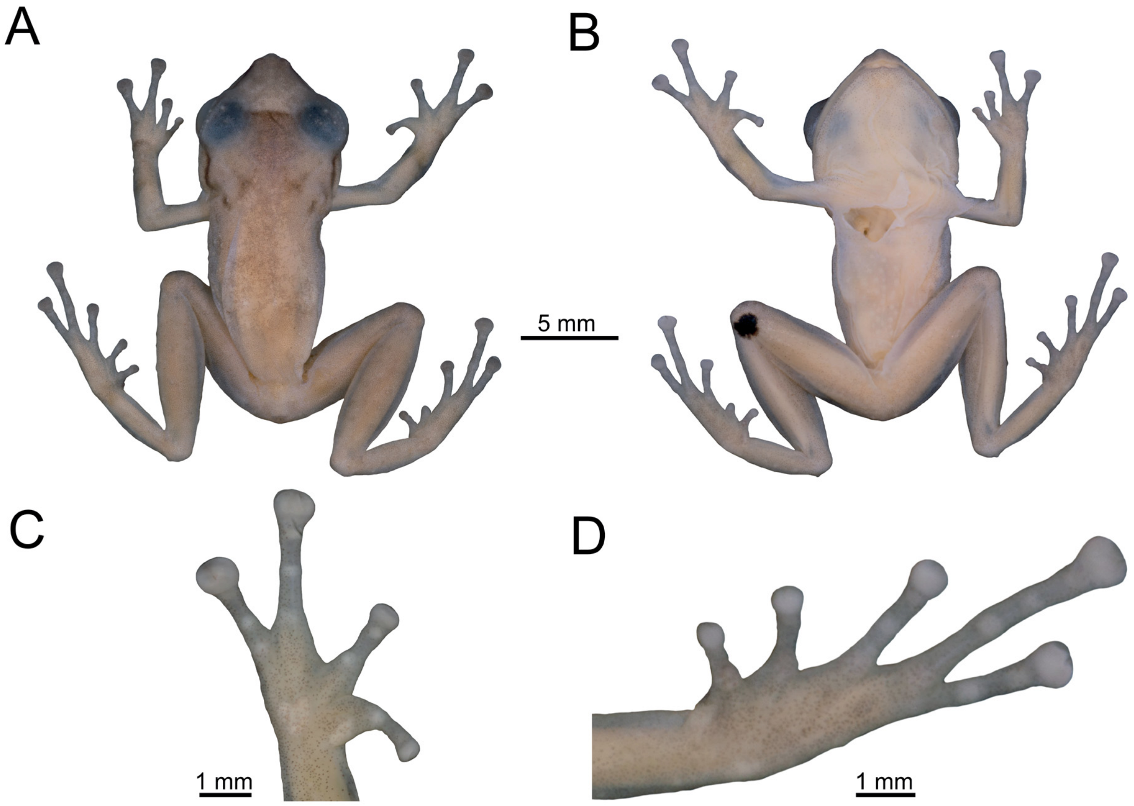

Fig. 7. *Pristimantis fouqueti* sp. nov., preserved holotype, ♂ (MNHN-RA-2023.0003, field no. PG705) from Mitaraka, French Guiana. **A**. Dorsal view. **B**. Ventral view. **C**. Right hand. **D**. Left foot. Photographs by Antoine Fouquet.

dark brown canthal stripe. After twelve years in preservative (ethanol 70%), the dorsal background color became brownish cream with a darker brown interorbital region, dark brown scapular tubercles, and dark brown canthal stripe and supratympanic fold; venter cream and translucent; ventral surface of limbs with small melanophores, denser under hands and feet; distinct dark brown spot under the right knee.

Intraspecific variation

The color of individuals changes depending on light or temperature conditions, varying from yellow during the night to brown during the day (Fig. 8). The color pattern varied between individuals, some had a very distinct reddish-brown spot on the back (Fig. 8A, C), but the dorsal coloration could be more uniform as in the holotype (Fig. 8A) or marked by brown spots bordering dorsal tubercles (Fig. 8B). The ventral color varies from cream yellow in individuals active at night to light brown during daytime

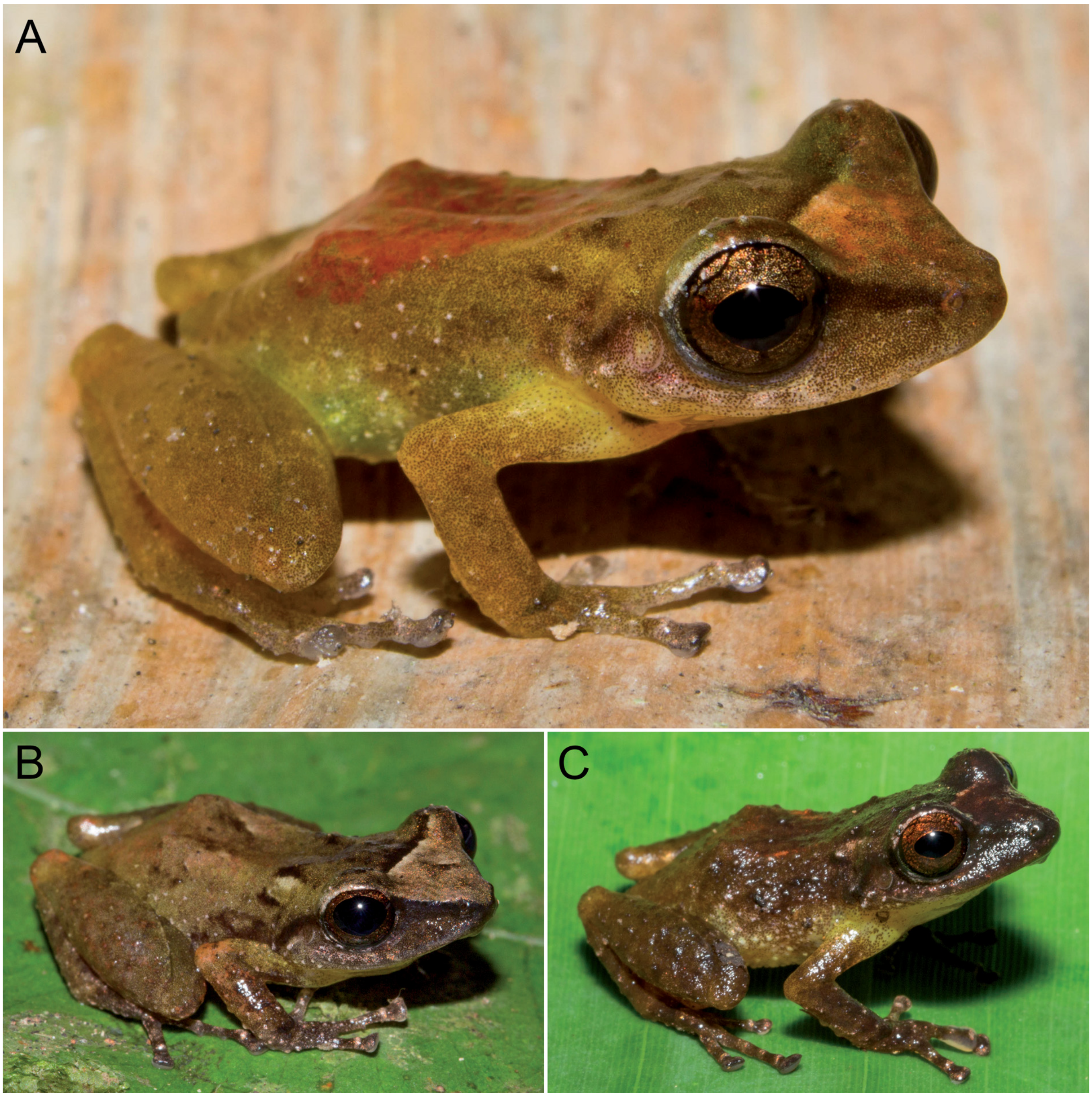

Fig. 8. Male individuals of *Pristimantis fouqueti* sp. nov. in life. **A**. Holotype (MNHN-RA-2023.0003). **B**. Paratype (MZUSP 160343). **C**. Paratype (MNHN-RA-2023.0005). Photographs by Antoine Fouquet.

(Fig. 9) the same can be observed in the condition of the white tubercles on the belly, which are more apparent when individuals are active. Although the general dorsal tubercles pattern remains the same, the observed individuals displayed remarkable changes in the size of the tubercles during handling, going from conspicuous tubercles to flat tubercles (Fig. 8). The female (AF0264) coloration was recorded only during the day, being dark uniform brown on the dorsum and light brown on the venter. A juvenile (AF2607) had a strikingly different coloration than the adults, the dorsum and limbs were greenish yellow, with patches of light to dark brown, the interorbital line and the dark brown scapular tubercles separated by a paler area were present, hands and feet were cream with brown markings and the venter was whitish translucent, with the characteristic white tubercles of the species.

Advertisement call

Males of *Pristimantis fouqueti* sp. nov. produce long series of short, high-pitched, whistled calls (Fig. 10). The advertisement call (n = 3 males) is composed of a single tonal note (n = 60 calls) with a duration of 90 ± 10 ms (73–115 ms) and silence between calls of 669 ± 90 ms (520–848 ms). Calls are emitted with a minimum frequency of 3.870 ± 93 Hz (3.770–3.991 Hz), a maximum frequency of 4.293 ± 77 Hz (4.198–4.417 Hz) and a dominant frequency of 4.138 ± 91 Hz (4.031–4.307 Hz). Males have been observed calling both in choruses and individually, at a rate of 78 ± 6 (72–84) calls per minute, and call intensity increasing on rainy nights. Temporal and spectral traits are summarized for to each analyzed individual in Table 4.

Differential diagnosis

Morphology

Pristimantis fouqueti sp. nov. is distinguished by a smaller SVL (18.9–19.8 mm) in males from those of the following close relatives: *P. acuminatus* (20.91–24.01 mm; Ortega-Andrade *et al.* 2015), *P. aureolineatus* (19.7–28.8 mm; Guayasamin *et al.* 2007), *P. calima* (24.0 mm; Ospina-Sarria & Duellman 2019), *P. degener* (22.2 mm; Lynch & Duellman 1997), *P. ecuadorensis* (25.4 mm; Guayasamin *et al.* 2017), *P. jorgevelosai* (24.3–29.8 mm; Lynch 1994), *P. kalamandeenae* (22.1 mm; Means *et al.* 2023), *P. latericius* (22.2–25.1 mm; Duellman & Lehr 2009), *P. loeslein* (20.5–23.3 mm; Castillo-Urbina *et al.* 2023), *P. mendax* (19.4–21.7 mm; Duellman 1978), *P. mindo* (2.49–27.4 mm; Arteaga-Navarro *et al.* 2013), *P. nankints* (19.6 mm; Ron *et al.* 2020), *P. nyctophylax* (21.9–31.4 mm; Lynch 1976),

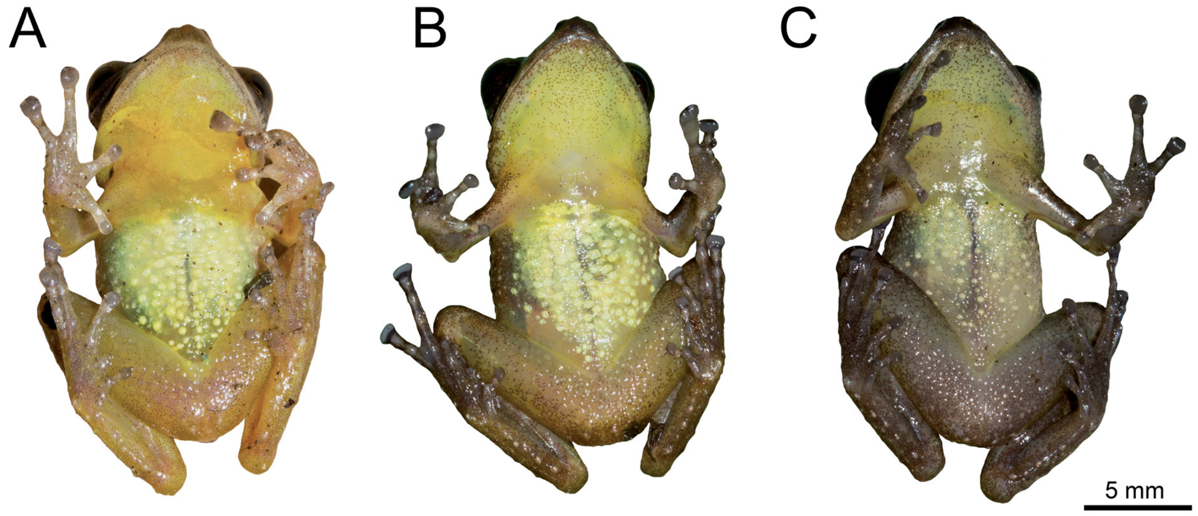

Fig. 9. Ventral coloration of males of *Pristimantis flavus* sp. nov. in life. **A**. Holotype (MNHN-RA-2023.0003). **B**. Paratype (MZUSP 160343). **C**. Paratype (MNHN-RA-2023.0005). Photographs by Antoine Fouquet.

Table 4. Acoustic traits of the advertisement call of *Pristimantis fouqueti* sp. nov. by analyzed individual. Temporal and spectral traits are presented in milliseconds and Hz, respectively. Abbreviations: CD = call duration; DF = dominant frequency; HF = maximum frequency; LF = minimum frequency; SBC = silence between calls; SD = standard deviation.

individual		CD	SBC	LF	HF	DF
Holotype MNHN-RA-2023.0003 (n = 20 calls)	**mean**	86	635	3.785	4.209	4.059
	SD	2	57	11	9	26
	min	84	544	3.771	4.197	4.041
	max	88	727	3.799	4.221	4.115
Paratype MNHN-RA-2023.0005 (n = 18 calls)	**mean**	94	718	3.966	4.371	4.226
	SD	12	96	18	27	22
	min	74	527	3.931	4.320	4.221
	max	114	848	3.991	4.417	4.307
Paratype MZUSP 160343 (n = 22 calls)	**mean**	87	637	3.783	4.235	4.060
	SD	9	75	10	15	51
	min	73	520	3770	4.210	4.031
	max	96	768	3806	4.258	4.214

P. ornatissimus (19.5–25.0 mm; Lynch 1970), *P. padiali* (26.5 mm; Moravec *et al.* 2010), *P. pardalinus* (21.1–26.7 mm; Lehr *et al.* 2006), *P. pluvialis* (21.8–26.9 mm; Shepack *et al.* 2016), *P. pulchridormientes* (19.1–21.9 mm; Chávez & Catenazzi 2016), *P. rhodostichus* (19.3 mm; Duellman & Pramuk, 1999), *P. romeroae* (23.8 mm; Ron *et al.* 2020), *P. royi* (20.1 mm; Morales 2007), *P. schultei* (23.5–26.6 mm; Duellman 1990), *P. subsigillatus* (19.3–28.5 mm; Lynch 1980b), *P. tantanti* (19.6–21.9 mm; Lehr *et al.* 2007), *P. waoranii* (19.7–21.2 mm; McCracken *et al.* 2009), *P. zimmermanae* (19.1–21.2 mm; Heyer & Hardy, 1991) and *P. zorro* (19.5–21.5 mm; Rivera-Correa & Daza 2020); and a larger SVL in males than those of *P. amaguanae* (16.3 mm; Ron *et al.* 2020) and *P. pseudoacuminatus* (12.7–17.6 mm; Duellman & Lehr 2009).

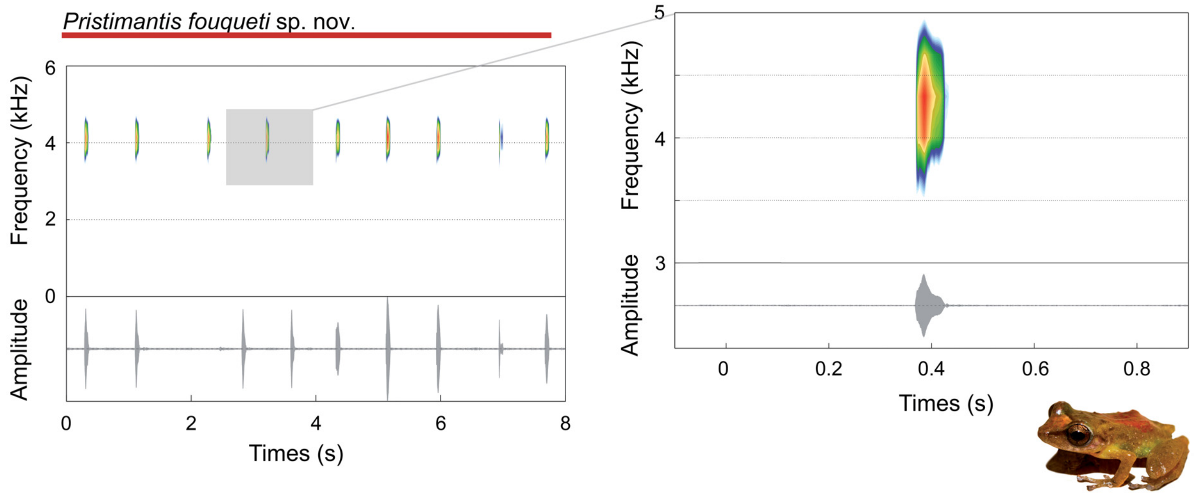

Fig. 10. Advertisement call of *Pristimantis fouqueti* sp. nov., holotype, ♂ (MNHN-RA-2023.0003) recorded at Patawa camp, Kaw Mountain, French Guiana.

The new species is distinguished by the presence of a tympanic annulus vs absent in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. moro* (Savage 2002) and *P. tantanti* (Lehr *et al.* 2007); by the presence of vocal slits in males vs absent in *P. amaguanae* (Ron *et al.* 2020), *P. enigmaticus* (Ortega-Andrade *et al.* 2015), *P. kalamandeenae* (Means *et al.* 2023), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. padiali* (Moravec *et al.* 2010) and *P. tantanti* (Lehr *et al.* 2007); by the absence of nuptial pads vs presence in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2006), *P. calima* (Ospina-Sarria & Duellman 2019), *P. crucifer* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. eremitus* (Lynch 1980a), *P. galdi* (Duellman & Lehr 2009), *P. jorgevelosai* (Lynch 1994), *P. lacrimosus* (Duellman & Lehr 2009), *P. latericius* (Duellman & Lehr 2009), *P. loeslein* (Castillo-Urbina *et al.* 2013), *P. pardalinus* (Lehr *et al.* 2006), *P. romeroae* (Ron *et al.* 2020) and *P. waoranii* (McCracken *et al.* 2007); by the absence of discoidal folds vs presence in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2006), *P. calima* (Ospina-Sarria & Duellman 2019), *P. crucifer* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. galdi* (Duellman & Lehr 2009), *P. latericius* (Duellman & Lehr 2009), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. loeslein* (Castillo-Urbina *et al.* 2023), *P. nyctophylax* (Lynch 1976), *P. olivaceus* (Köhler *et al.* 1998), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. ornatissimus* (Lynch 1970), *P. padiali* (Moravec *et al.* 2010), *P. petersi* (Lynch & Duellman 1980), *P. petersioides* (Carrión-Olmedo & Ron 2021), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. rhodostichus* (Duellman & Pramuk 1999), *P. royi* (Morales 2007) and *P. waoranii* (McCracken *et al.* 2009); and by the absence of dentigerous processes of vomers vs presence in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2006), *P. calima* (Ospina-Sarria & Duellman 2019), *P. bromeliaceus* (Lynch 1979), *P. crucifer* (Lynch & Duellman 1997), *P. degener* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. enigmaticus* (Ortega-Andrade *et al.* 2015), *P. eremitus* (Lynch 1980a), *P. flavus* sp. nov. (this study), *P. galdi* (Duellman & Lehr 2009), *P. jorgevelosai* (Lynch 1994), *P. kalamandeenae* (Means *et al.* 2023), *P. lacrimosus* (Duellman & Lehr 2009), *P. latericius* (Duellman & Lehr 2009), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. loeslein* (Castillo-Urbina *et al.* 2013), *P. mindo* (Arteaga-Navarro *et al.* 2013), *P. moro* (Savage 2002), *P. nankints* (Ron *et al.* 2020), *P. nyctophylax* (Lynch 1976), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. ornatissimus* (Lynch 1970), *P. padiali* (Moravec *et al.* 2010), *P. pardalinus* (Lehr *et al.* 2006), *P. petersi* (Lynch & Duellman 1980), *P. petersioides* (Carrión-Olmedo & Ron 2021), *P. pluvialis* (Shepack *et al.* 2016), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. rhodostichus* (Duellman & Pramuk 1999), *P. romeroae* (Ron *et al.* 2020), *P. royi* (Morales 2007), *P. schultei* (Duellman 1990), *P. subsigillatus* (Lynch 1980b), *P. tantanti* (Lehr *et al.* 2007), *P. waoranii* (McCracken *et al.* 2009) and *P. zorro* (Rivera-Correa & Daza 2020).

Pristimantis fouqueti sp. nov. is further distinguished by its unique combination of body tubercles, i.e., the presence of upper eyelid tubercles vs absence in *P. acuminatus* (Ortega-Andrade *et al.* 2015), *P. aureolineatus* (Guayasamin *et al.* 2007), *P. degener* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. enigmaticus* (Ortega-Andrade *et al.* 2015), *P. kalamandeenae* (Means *et al.* 2023), *P. lacrimosus* (Duellman & Lehr 2009), *P. limoncochensis* (Ortega-Andrade *et al.* 2015), *P. moro* (Savage 2002), *P. nankints* (Ron *et al.* 2020), *P. omeviridis* (Ortega-Andrade *et al.* 2015), *P. ornatissimus* (Lynch 1970), *P. padiali* (Moravec *et al.* 2010), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. schultei* (Duellman 1990), *P. subsigillatus* (Lynch 1980b), *P. tantanti* (Lehr *et al.* 2007), *P. waoranii* (McCracken *et al.* 2009) and *P. zorro* (Rivera-Correa & Daza 2020); the presence of ulnar tubercles vs absence in from *P. bromeliaceus* (Lynch 1979), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. lacrimosus* (Duellman & Lehr 2009), *P. ornatissimus* (Lynch 1970), *P. petersi* (Lynch & Duellman 1980), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. romeroae* (Ron *et al.* 2020), *P. royi* (Morales 2007), *P. subsigillatus* (Lynch 1980b) and *P. zorro* (Rivera-Correa & Daza 2020); and the presence of tarsal tubercles vs absence in *P. amaguanae* (Ron *et al.* 2020), *P. degener* (Lynch & Duellman 1997), *P. ecuadorensis* (Guayasamin *et al.* 2017), *P. galdi* (Duellman & Lehr 2009), *P. lacrimosus* (Duellman & Lehr 2009), *P. mendax* (Duellman 1978), *P. mindo* (Arteaga-Navarro *et al.* 2013), *P. ornatissimus* (Lynch 1970), *P. pluvialis* (Shepack *et al.* 2016), *P. pseudoacuminatus* (Duellman & Lehr 2009), *P. pulchridormientes* (Chávez & Catenazzi 2016), *P. waoranii* (McCracken *et al.* 2007) and *P. zorro* (Rivera-Correa & Daza 2020).

Bioacoustics

The advertisement call of *Pristimantis fouqueti* sp. nov. is composed of a single note and thus differs from that of all species with multiple-note calls such as *P. eremitus* (2–9 notes; Hutter *et al.* 2016), *P. flavus* sp. nov. (1–4 notes; this study), *P. galdi* (7–9 notes; Batallas-Revelo & Brito-M 2023) and *P. pulchridormientes* (2–5 notes; Chávez & Catenazzi 2016). The advertisement call of *Pristimantis fouqueti* is shorter (73–115 ms) compared to those of *P. bromeliaceus* (140–142 ms), *P. lacrimosus* (139–167 ms; Batallas-Revelo & Brito-M 2014), *P. mindo* (approx. 300 ms; Arteaga-Navarro *et al.* 2013), *P. petersi* (310–490 ms), *P. petersioides* (110–390 ms; Carrión-Olmedo & Ron 2021), and longer compared to those of *P. aureolineatus* (15–42 ms; McCracken & Forstner 2006), *P. pluvialis* (23–58 ms; Shepack *et al.* 2016), *P. royi* (24–26 ms; Morales 2007) and *P. zimmermanae* (approx. 50 ms; Heyer & Hardy 1991).

The advertisement call of *Pristimantis fouqueti* sp. nov. is also distinguished by a higher dominant frequency (4.031–4.307 Hz) from *P. flavus* sp. nov. (2.799–3.187 Hz; this study), *P. galdi* (2.190–2.580 Hz; Batallas-Revelo & Brito-M 2023), *P. lacrimosus* (3.050–3.100 Hz; Batallas-Revelo & Brito-M 2014), *P. loeslein* (2.744–3.021 Hz; Castillo-Urbina *et al.* 2023), *P. mindo* (2.698–2.919 Hz; Arteaga-Navarro *et al.* 2013), *P. pluvialis* (2.312–2.756 Hz; Shepack *et al.* 2016), *P. pulchridormientes* (2.531–

Fig. 11. Forests in the surroundings of the Inselberg Nouragues – French Guiana, inhabited by *Pristimantis fouqueti* sp. nov. Photography by Elodie Courtois.

3.094 Hz; Chávez & Catenazzi 2016), *P. royi* (3.270–3.360 Hz; Morales 2007), *P. subsigillatus* (1.961–2.033 Hz; Arteaga-Navarro *et al.* 2013) and *P. zorro* (2.842–3.186 Hz; Rivera-Correa & Daza 2020); and by a higher call rate (72–84 calls/minutes) from *P. aureolineatus* (17–40 calls/min; McCracken & Forstner 2006), *P. bromeliaceus* (9–34 calls/min; Batallas-Revelo & Brito-M 2014), *P. flavus* (38–46 calls/min; this study), *P. lacrimosus* (4–9 calls/min), *P. latericius* (8–30 calls/min; Batallas-Revelo & Brito-M 2014), *P. petersi* (4–9 calls/min), *P. petersioides* (1–26 calls/min; Carrión-Olmedo & Ron 2021) and *P. zimmermanae* (62 calls/min; Heyer & Hardy 1991).

Distribution, natural history and conservation

Very little information is available on this species, as it has been rarely observed due to its arboreal habits. However, it has been detected in many localities in French Guiana thanks to its characteristic call (Dewynter *et al.* 2021). It is a nocturnal species calling in trees and palm trees at heights exceeding 2 m. *Pristimantis fouqueti* sp. nov. seems to prefer forest edges such as 'chablis' (openings made by fallen trees) or the edges of inselbergs ('savane-roche'; Fig. 11). Some individuals, including the female, were found during the day in bromeliads located 1–2 m above the ground, suggesting that this species could use bromeliads at least as daytime refuges and possibly as breeding sites. This species appears to be distributed throughout French Guiana and is also present in the state of Amapá in Brazil (Fig. 12). Its occurrence in Suriname is likely, but remains unconfirmed.

The species inhabits primary and secondary forests, as well as forest edges. Despite the difficulty in collecting individuals, its populations are locally abundant. Therefore, we suggest the species to be listed as "Least Concern" according to the criteria of the International Union for Conservation of Nature (IUCN).

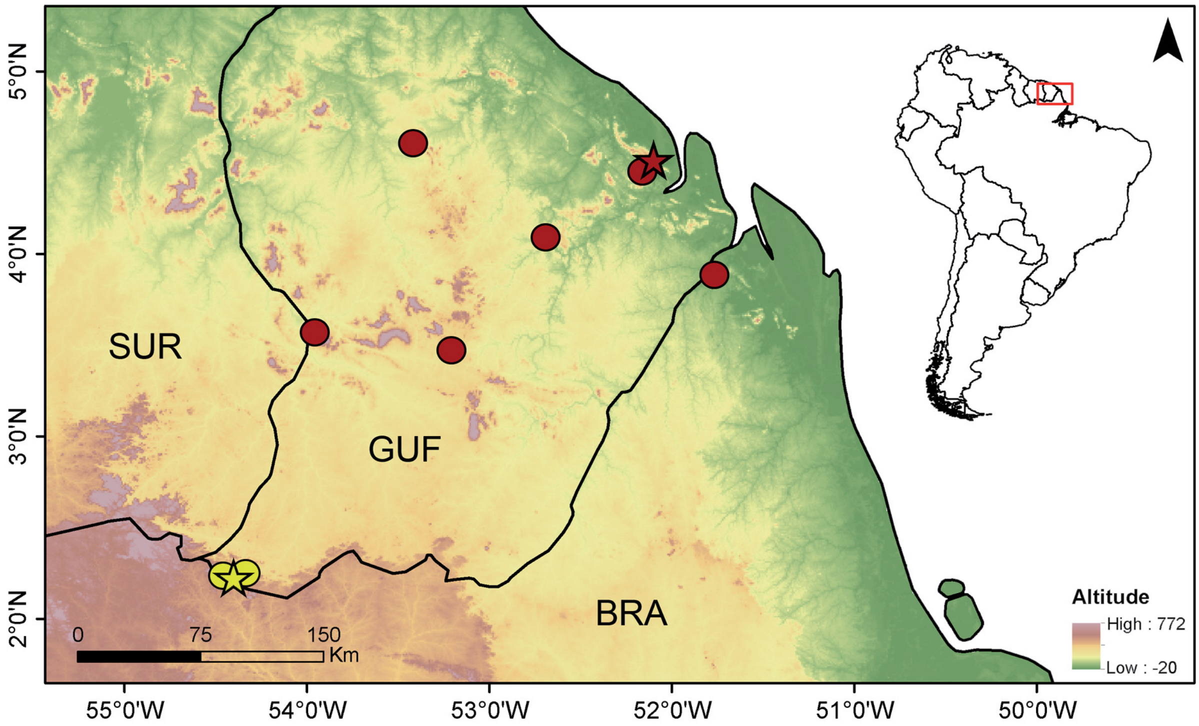

Fig. 12. Geographic distribution of *Pristimantis flavus* sp. nov. (yellow circles) and *P. fouqueti* sp. nov. (red circles). Stars indicate the type localities of each species.

Discussion

Our phylogenetical analyses improve the knowledge of the *P. lacrimosus* group and sister relationships within the clade of the new species. We included material of *P. zimmermanae* from the type locality for the first time in a phylogeny. The previous report of the species in a phylogenetic context was in Means *et al.* (2023) but that specimen turned out to be in fact *P. fouqueti* sp. nov. (AF1189, voucher MNHN-RA-2023.0005, see above). The topology of the *P. lacrimosus* group as inferred from our study diverges from previous works, mostly because most of the species used here were never included in any phylogenetical analyses before (Ron *et al.* 2020; Castillo-Urbina *et al.* 2023; Means *et al.* 2023). *Pristimantis lacrimosus* is the sister species of the clade where the new species are nested. This clade is composed of eight already described species (*P. pulchridormientes*, *P. loeslein*, *P. kalamandeenae*, *P. olivaceus*, *P. zimmermanae*, *P. aureolineatus*, *P. pluvialis*, *P. zorro*) and the two species described here. The clade seems to display a unique biogeographic pattern that should receive attention in future works. While a greater number of species seems to have diversified in the western Amazonia and Guiana Shield (*P. kalamandeenae*, *P. olivaceus*, *P. zimmermanae*, *P. aureolineatus*, *P. pluvialis* and *P. flavus*), its sister species are in the Andes (*P. pulchridormientes* and *P. loeslein*). Surprisingly, *P. fouqueti* (Guiana Shield) forms a branch with *P. zorro* (Northern Andes) that is sister to all the other species. This suggests that there was more than one independent dispersal into the Guiana Shield within the clade, a similar scenario as observed in the *Allobates trilineatus* clade (Réjaud *et al.* 2020).

The eastern part of the Guiana Shield harbors a singular biodiversity and has been suggested as a distinct bioregion based on the distribution of several amphibian lineages (Vacher *et al.* 2020). Our results suggest that *Pristimantis flavus* sp. nov. and *P. fouqueti* sp. nov. may be endemic to this region. The known distribution of *P. flavus* is restricted to only two localities in the Tumuk-Humak Mountains on the border between French Guiana and Brazil, ranging from 330 to 380 m a.s.l. Its occurrence is similar to that of *Anomaloglossus mitaraka* Fouquet *et al.*, 2019 (Fouquet *et al.* 2019b; Dewynter *et al.* 2021). Its presence in other areas, especially within Brazil and Suriname, and possible endemism to these mountain ranges need to be further evaluated. In contrast, *P. fouqueti* is more widespread, mirroring the distribution of other endemic anurans, such as *Allobates granti* (Kok *et al.*, 2006), *A. ripicolus* Fouquet, Ferrão & Jairam, 2023 (Fouquet *et al.* 2023), *Amazophrynella teko* Rojas-Zamora *et al.*, 2018 (Moraes *et al.* 2022), *Anomaloglossus baeobatrachus* (Boistel & Massary, 1999) (Vacher *et al.* 2017), *Pipa aspera* Müller, 1924 (Fouquet *et al.* 2022a), *Pristimantis chiastonotus* (Lynch & Hoogmoed, 1977), *P. gutturalis* (Hoogmoed, Lynch & Lescure, 1977) (Fouquet *et al.* 2022b), *P. crepitaculus* Fouquet *et al.*, 2022 and *P. espedeus* Fouquet *et al.*, 2013 (Mônico *et al.* 2024). Several widespread *Pristimantis* have been shown to actually be species complexes (e.g., Fouquet *et al.* 2022b; Mônico *et al.* 2024). A more integrative approach (using morphology, genetics and bioacoustics for example) has been useful to solve such cases (Padial *et al.* 2010; Páez & Ron 2019). In the original description of *P. zimmermanae*, Heyer & Hardy (1991) already mentioned that the specimen from Serra do Navio, Amapá, Brazil (WCAB 2315) was distinct from the other specimen of *P. zimmermanae* in some morphological characters. Although a careful evaluation of that specimen is required, there is a possibility that it is conspecific with *Pristimantis fouqueti*. Likewise, the original description of *P. zimmermanae* highlighted substantial morphological variation across localities, and all the referred material should be reviewed in future taxonomic works.

Studying species of the *P. lacrimosus* group is particularly difficult due to the scarcity of material available, which is largely explained by their arboreal habits, many of them being only found in the forest canopy (Guayasamin *et al.* 2006; McCracken & Forstner 2014). Their peculiar ecology makes them difficult to observe and collect. Consequently, most species in the *P. lacrimosus* group still lack a description of their advertisement call and many species within the group have been described based on very few individuals [e.g., *P. amaguanae* (Ron *et al.* 2020), *P. kalamandeenae* (Means *et al.* 2023), *P. padiali* (Moravec *et al.* 2010), and *P. tantanti* (Lehr *et al.* 2006)]. Moreover, since most specimens are detected by their call, females are rarely included in type series. Further studies are still needed to improve our knowledge of the phenology and ecology of the newly described species, as well as to better understand their distribution and conservation status.

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Appendices

Appendix 1 (continued on next three pages). Species of *Pristimantis* Jiménez de la Espada, 1870 and *Tachiramantis* Heinicke, Barrio-Amorós & Hedges, 2015 used in phylogenetic analyses, with respective voucher, GenBank acession number and references.

Species	Voucher	GenBank accession number		Reference
		16S	RAG1	
P. acerus	KU217786	EF493678	–	Heinicke *et al.* (2007)
P. acuminatus	MZUTI3796	MT508751	–	unpublished
P. acuminatus	QCAZ17510	MH516156	–	Waddell *et al.* (2018)
P. altamazonicus	KU215460	EF493670	–	Heinicke *et al.* (2007)
P. amaguanae	QCAZ39274	MT636529	MT636522	Ron *et al.* (2020)
P. angustilineatus	UVC15828	JN371034	KT898302	Mendoza *et al.* (2015)
P. angustilineatus	UVC15888	JN104677	KT898303	Garcia-R *et al.* (2012)
P. appendiculatus	KU177637	EF493524	–	Heinicke *et al.* (2007)
P. appendiculatus	QCAZ16365	MK881401	MK881315	Páez & Ron (2019)
P. aureolineatus	QCAZ42286	MT636509	MT635626	Ron *et al.* (2020)
P. boulengeri	MHUAA8951	KU724435	–	Rivera-Correa & Daza (2016)
P. brevifrons	NRPS0059	JN991433	–	Pinto-Sanchez *et al.* (2012)
P. brevifrons	UVC15912	JN370970	–	Garcia-R *et al.* (2012)
P. bromeliaceus	QCAZ16699	MT636505	MT635618	Ron *et al.* (2020)
P. bromeliaceus	QCAZ62940	MT636512	–	Ron *et al.* (2020)

Species	**Voucher**	**GenBank accession number**		**Reference**
		16S	**RAG1**	
P. calcarulatus	KU177658	EF493523	–	Heinicke *et al.* (2007)
P. calcarulatus	MZUTI1898	KT210167	–	Hutter & Guayasamin (2015)
P. cedros	MZUTI1712	KT210157	–	Hutter & Guayasamin (2015)
P. cedros	MZUTI1713	KT210155	–	Hutter & Guayasamin (2015)
P. crucifer	KU177733	EU186718	–	Hedges *et al.* (2008)
P. degener	QCAZ40304	MW567376	MW451761	Carrión-Olmedo & Ron (2021)
P. diadematus	KU221999	EU186668	–	Hedges *et al.* (2008)
P. dissimulatus	KU179090	EF493522	–	Heinicke *et al.* (2007)
P. dorsopictus	MHUAA7638	KP082874	–	Rivera-Prieto *et al.* (2014)
P. dorsopictus	MHUAA7856	KU724439	–	Rivera-Correa & Daza (2016)
P. ecuadorensis	CJ5351	KX785344	–	Guayasamin *et al.* (2017)
P. ecuadorensis	CJ5350	KX785343	–	Guayasamin *et al.* (2017)
P. enigmaticus	QCAZ40918	MT636520	MT635636	Ron *et al.* (2020)
P. eremitus	QCAZ43392	MK881460	–	Carrión-Olmedo & Ron (2021)
P. eremitus	QCAZ49652	MW567366	MW451732	Carrión-Olmedo & Ron (2021)
P. eugeniae	QCAZ52367	MW567353	MW451743	Carrión-Olmedo & Ron (2021)
P. flavus sp. nov.	MNHN-RA-2023.0007	KDQF01000321	–	Vacher *et al.* (2020)
P. flavus sp. nov.	MNHN-RA-2023.0009	KDQF01001091	–	Vacher *et al.* (2020)
P. fouqueti sp. nov.	MNHN-RA-2023.0002	JN691312	–	Fouquet *et al.* (2012)
P. fouqueti sp. nov.	MNHN-RA-2023.0005	KDQF01000438	–	Vacher *et al.* (2020)
P. fouqueti sp. nov.	AF2607	KDQF01001017	–	Vacher *et al.* (2020)
P. fouqueti sp. nov.	MNHN-RA-2023.0004	KDQF01003941	–	Vacher *et al.* (2020)
P. fouqueti sp. nov.	MZUSP 160343	KDQF01003578	–	Vacher *et al.* (2020)
P. galdi	QCAZ32368	EU186670	EU186746	Hedges *et al.* (2008)
P. galdi	QCAZ58885	MW567355	MW451756	Carrión-Olmedo & Ron (2021)
P. glandulosus	KU218002	EF493676	–	Heinicke *et al.* (2007)
P. glandulosus	QCAZ40153	MK881431	MK881333	Páez & Ron (2019)
P. imitatrix	KU215476	EF493667	–	Heinicke *et al.* (2007)

Species	Voucher	GenBank accession number		Reference
		16S	RAG1	
P. inusitatus	KU218015	EF493677	–	Heinicke *et al.* (2007)
P. jaguensis	MHUAA7246	KP082868	–	Rivera-Prieto *et al.* (2014)
P. jaguensis	MHUAA7249	KP082870	–	Rivera-Prieto *et al.* (2014)
P. jaguensis	MHUAA7257	KP082872	–	Rivera-Prieto *et al.* (2014)
P. jorgevelosai	JDL26123	DQ195461	–	Ron *et al.* (2020)
P. lacrimosus	QCAZ55238	MT636518	MT635629	Ron *et al.* (2020)
P. lacrimosus	QCAZ40261	MT636524	MT635623	Ron *et al.* (2020)
P. lacrimosus	QCAZ59469	MT636516	MT635632	Ron *et al.* (2020)
P. lacrimosus	QCAZ59474	MT636517	MT635633	Ron *et al.* (2020)
P. limoncochensis	QCAZ19180	MT636532	MT635620	Ron *et al.* (2020)
P. limoncochensis	QCAZ43794	MT636525	MT635627	Ron *et al.* (2020)
P. loeslein	MUSM30402	OR725032	–	Castillo-Urbina *et al.* (2023)
P. loeslein	MUSM30403	OR725033	–	Castillo-Urbina *et al.* (2023)
P. marmoratus	KU181015	EU186723	–	Hedges *et al.* (2008)
P. cf. *mendax*	MTD45080	EU186659	–	Hedges *et al.* (2008)
P. mindo	MZUTI1755	KF801582	–	Arteaga-Navarro *et al.* (2013)
P. mindo	MZUTI1756	KF801581	–	Arteaga-Navarro *et al.* (2013)
P. mindo	QCAZ56512	MT636522	MT635630	Ron *et al.* (2020)
P. mindo	QCAZ42197	MT636531	MT635625	Ron *et al.* (2020)
P. moro	AJC1753	JN991453	JQ025192	Pinto-Sanchez *et al.* (2012)
P. moro	AJC1860	JN991454	JQ025191	Pinto-Sanchez *et al.* (2012)
P. nankints	QCAZ69137	MT636514	MT635635	Ron *et al.* (2020)
P. nyctophylax	QCAZ32288	MT636519	MT635621	Ron *et al.* (2020)
P. nyctophylax	KU177812	EF493526	EF493425	Heinicke *et al.* (2007)
P. olivaceus	CORBIDI17473	KX155579	–	Carrión-Olmedo & Ron (2021)
P. omeviridis	QCAZ10564	MK881398	MK881312	Páez & Ron (2019)
P. omeviridis	QCAZ19664	MZ430008	MZ560986	Zumel *et al.* (2021)
P. orcesi	KU218021	EF493679	–	Heinicke *et al.* (2007)
P. ornatissimus	MZUTI4798	KU720463	–	unpublished
P. ornatissimus	MZUTI4807	KX785342	–	Guayasamin *et al.* (2017)
P. ornatissimus	MZUTI4806	KX785341	–	Guayasamin *et al.* (2017)
P. pahuma	MZUTI490	KT210159	–	Hutter & Guayasamin (2015)

Species	**Voucher**	**GenBank accession number**		**Reference**
		16S	**RAG1**	
P. pahuma	MZUTI493	KT210158	–	Hutter & Guayasamin (2015)
P. petersi	QCAZ51390	MZ219640	MZ219636	Carrión-Olmedo & Ron (2021)
P. petersi	QCAZ63455	MW567369	MW451725	Carrión-Olmedo & Ron (2021)
P. petersioides	QCAZ58937	MW567336	MW451758	Carrión-Olmedo & Ron (2021)
P. petersioides	QCAZ58951	MW567339	MW451741	Carrión-Olmedo & Ron (2021)
P. platydactylus	MNCN43248	EU192255	–	Padial *et al.* (2007)
P. pluvialis	CORBIDI11862	KX155577	KY962769	Shepack *et al.* (2016)
P. pluvialis	CORBIDI16695	KX155578	KY962770	Shepack *et al*. (2016)
P. pulchridormientes	CORBIDI15563	KX664106	–	Chávez & Catenazzi (2016)
P. pulchridormientes	CORBIDI15566	KX664107	–	Chávez & Catenazzi (2016)
P. pycnodermis	KU218028	EF493680	–	Heinicke *et al.* (2007)
P. romeroae	QCAZ41121	MT636507	MT635624	Ron *et al.* (2020)
Pristimantis sp.	QCAZ60398	MT636515	MT635634	Ron *et al.* (2020)
Pristimantis sp.	ROM43978	EU186678	–	Ron *et al.* (2020)
Pristimantis sp.	KU291702	EF493351	–	Ron *et al.* (2020)
P. schultei	KU212220	EF493681	–	Heinicke *et al.* (2007)
P. subsigillatus	KU218147	EF493525	–	Heinicke *et al.* (2007)
P. subsigillatus	MECN10117	KF801580	–	Arteaga-Navarro *et al.* (2013)
P. subsigillatus	QCAZ49637	MT636521	MT635628	Ron *et al.* (2020)
P. tantanti	CORBIDI12987	MN128402	–	Ron *et al.* (2020)
P. urani	MHUAA7471	KU724442	–	Ron *et al.* (2020)
P. zimmermanae	INPA-H 44700	PV246549	PV254902	This study
P. zimmermanae	INPA-H 44701	PV246550	PV254901	This study
P. zorro	MHUAA8813	MT747833	–	Rivera-Correa & Daza (2016)
P. zorro	MHUAA8814	MT747834	–	Rivera-Correa & Daza (2016)
T. prolixodiscus	SBH 268371	KP297385	KP297387	Heinicke *et al.* (2015)

Appendix 2. List of call recordings by species and localities (voucher).

Pristimantis flavus sp. nov.

MNHN-SO-2024-3525 — Mitaraka, French Guiana (MNHN-RA-2023.0010, holotype)
MNHN-SO-2024-3526 — Pic Coudreau du Sud, French Guiana (MNHN-RA-2023.0006)
MNHN-SO-2024-3525 — Mitaraka, French Guiana (MNHN-RA-2023.0009)
MNHN-SO-2024-3529 — Mitaraka, French Guiana (MNHN-RA-2023.0011)

Pristimantis fouqueti sp. nov.

MNHN-SO-2024-3527 — Kaw, French Guiana (MNHN-RA-2023.0003, holotype)
MNHN-SO-2024-3528 — Trinità, French Guiana (MNHN-RA-2023.0005)
MNHN-SO-2024-3530 — Amapá State, Brazil (MZUSP 160343)