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A new species of *Pristimantis* (Anura, Strabomantidae) from the state of Acre, Brazil

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Abstract. *Pristimantis* is the amphibian genus with the largest number of described species yet harbouring many species still to be named, notably in Amazonia. Here, I describe a member of the *P. diadematus* species complex from southwestern Amazonia in Brazil based on external morphology. The species is most similar to *P. divnae*, a species from southern Peru, but diagnosable from it by the combination of the following characters: presence of nuptial pads and tympanum, smaller body size (SVL 19.5-23.5 mm in males, 27.8-30.6 mm in females), and absence of yellow marks in both the inguinal region and shanks. The new species occupies the same habitats as the syntopic *P. altamazonicus*, another member of the *P. diadematus* species complex. Based on an extensive literature review, a new composition of the *P. diadematus* species complex is proposed and discussed.

Key words: Amazonia, diversity, frog, morphology, nuptial pads

Introduction

It seems at first thought rash to add other names to this already densely overpopulated genus but no other course seems practicable (Barbour & Dunn 1921, p. 161).

A century after Thomas Barbour and Emmett Dunn's statement, discoveries of new species of *Pristimantis* Jiménez de la Espada, 1870 are still made at a rapid pace. Reyes-Puig & Mancero (2022) compiled trends, biases, and relevant information about the country of origin of taxonomists working on *Pristimantis*, as well as studied geographic regions, finding that recent focus on western Amazonian species is slowly reducing the Linnean shortfall. A temporal analysis of species descriptions based on the speed of taxonomic progress allows estimating that around 180 species of *Pristimantis* frogs will probably be named and described during the next decade in this region alone (Reyes-Puig & Mancero 2022).

Amazonia extends across nine countries, with almost 60% of the biome contained within the borders of Brazil. With this enormous land surface, Brazilian Amazonia is little known regarding *Pristimantis* diversity. During the 127 years between 1864 and 1991, only three species were described based on material collected in Brazilian Amazonia (Steindachner 1864, Lutz & Kloss 1952, Heyer & Hardy 1991). A discrepancy between species richness and the country area has become more evident in the last two decades. Nine species of *Pristimantis* have been described from Ecuadorian Amazonia (Guayasamin et al. 2006, McCracken et al. 2007, Elmer & Cannatella 2008, Ortega-Andrade & Valencia 2012, Ortega-Andrade & Venegas 2014, Ortega-Andrade

et al. 2015, 2021, Ron et al. 2020); eight species from Peruvian Amazonia (Lehr et al. 2007, 2009, 2010, Morales 2007, Lehr & von May 2009, Moravec et al. 2010, Padial et al. 2016a, Shepack et al. 2016) and two species from Bolivian Amazonia (Padial & De la Riva 2009).

In Brazil, the known taxonomic diversity of Amazonian *Pristimantis* has approximately doubled in recent years. Over only the last five years, six new species were described (Oliveira et al. 2017a, 2020a, Fouquet et al. 2022a, Mônico et al. 2022, 2023). However, these advances have been geographically biased. No species has been described from western Brazilian Amazonia, despite discovering new country records from Brazil coming from this region (Souza 2009, Melo-Sampaio & Souza 2010, Bernarde et al. 2011, López-Rojas et al. 2013). The concentration of these new records in recent years is indicative that the western Brazilian Amazonia remains poorly documented regarding its *Pristimantis* fauna. Notably, several species thought to be widely distributed have recently been found to represent species complexes (Ortega-Andrade et al. 2015, Ron et al. 2020, Fouquet et al. 2022b). Moreover, analysing holotypes of poorly known species underrepresented in museums allowed the resurrection of previously synonymised taxa (Ortega-Andrade & Venegas 2014, Ortega-Andrade et al. 2015, Waddell et al. 2018).

Historical overview of the *Pristimantis unistrigatus* species group

The *P. unistrigatus* group (formerly *Eleutherodactylus unistrigatus* group) was proposed by Lynch (1974) and defined as follows: heads of 'normal' width (head width 30-40% of snout-vent length), skin of abdomen coarsely areolate, first finger shorter than second, all digits bearing discs on narrowly to broadly dilated pads, the fold of skin above the disc not markedly indented or notched distally, tympanum frequently obscured or concealed beneath skin (rarely absent), and having narrow prevomerine odontophores that are oblique or slanted in some species to triangular in outline in others (rarely not visible; never arch-like and broad).

Lynch (1976), in trying to accommodate species whose morphological characters did not allow clear assignment into other species groups of *Pristimantis*, may have used the name *unistrigatus* group without strictly observing the group's initial definition. Lynch (1979) discussed the putative relationships within the *unistrigatus* group, recognizing nine intragroups but without naming them. Lynch & Duellman (1980) clarified the composition of those intragroups into 16 assemblies: *acuminatus*, *celator*, *crucifer*, *curtipes*, *devillei*, *diadematus*, *frater*, *glandulosus*, *lacrimosus*, *nigrogriseus*, *pugnax*, *pyrrhomerus*, *rubicundus*, *surdus*, *trachyblepharis* and *unistrigatus*. It is worth noting that the *diadematus* assembly, according to Lynch & Duellman (1980), comprises species from Andean slopes and adjacent Amazonian lowlands: *E. altamazonicus*, *E. carvalhoi*, *E. croceoinguinis*, *E. diadematus*, *E. martiae* and *E. platydactylus*.

Lynch (1980) recognized 15 species of the *unistrigatus* group in Amazonia: *E. acuminatus*, *E. altamazonicus*, *E. carvalhoi*, *E. croceoinguinis*, *E. diadematus*, *E. lacrimosus*, *E. martiae*, *E. ockendeni*, *E. orphnolaimus*, *E. paululus*, *E. pseudoacuminatus*, *E. quaquaversus*, *E. trachyblepharis*, *E. variabilis*, and *E. ventrimarmoratus*. Savage (1987) proposed that the assemblies of Lynch & Duellman (1980) should be treated as species groups. The *unistrigatus* group remained unaltered during the 80s until Hedges & Schlüter (1992) recognised *E. diadematus* as a separate group, promoting some additions of species previously allocated in the former *unistrigatus* group based on external similarities. Hedges & Schlüter (1992) included six nominal species in their *E. diadematus* species group: *E. altamazonicus*, *E. diadematus*, *E. eurydactylus*, *E. nigrogriseus*, *E. platydactylus*, and *E. ventrimarmoratus*, based mainly on the very large digital tips, relatively short hind limbs, tuberculate dorsum, dorsal scapular "W" (except in *E. nigrogriseus*), and conspicuous dark bars on the legs. Rodríguez & Duellman (1994) pointed out similarities between *E. diadematus* and *E. altamazonicus* from Northern Peru.

Lehr et al. (2006) described *E. cruciocularis* and *E. flavobracatus*, comparing both species with *E. altamazonicus*. They also reported the first record of *E. eurydactylus* out of its type locality and highlighted the previous misidentification they made as *E. diadematus*. Heinicke et al. (2007) removed *Pristimantis* from the synonymy of *Eleutherodactylus* based on molecular evidence. Hedges et al. (2008) retrieved the *P.* (*Pristimantis*) *unistrigatus* species group as polyphyletic (i.e. a non-natural group) and proposed a definition similar to that of Lynch & Duellman (1997). Rocha (2016) redefined the *P. unistrigatus* group restricting to the following species: *P. bogotensis*, *P. delius*, *P. frater*, *P. gryllus*, *P. juanchoi*, *P. libraries*, *P. lynchi*, *P. martiae*, *P. miyatai*, *P. ockendeni*, *P. paisa*, *P. palmeri*, *P. ptochus*, *P. suetus*, *P. taeniatus*, *P. uisae*, *P. unistrigatus*, *P. yukpa* and *P. zophus*.

Posteriorly, Lehr & von May (2009) described *P. divnae*, highlighting its similarity with *P. diadematus* and *P. eurydactylus*, and tentatively assigned it to the *P. unistrigatus* group. Lehr et al. (2009) described *P. orcus* and noted the morphological similarities among *P. altamazonicus*, *P. diadematus*, *P. eurydactylus*, *P. orcus*, *P. ventrimarmoratus*, and *P. divnae* (treated as *Pristimantis* sp.), suggesting that these species are phylogenetically related. Rocha (2016) resurrected the *P. diadematus* group based on both molecular and morphological data to include five nominal species (*P. altamazonicus*, *P. diadematus*, *P. eurydactylus*, *P. orcus*, *P. ventrimarmoratus*) and nine candidate species. Rocha (2016) also defined the *P. diadematus* group as follows: vocal slits absent; finger I < II; digital discs expanded; digital pads with circumferential grooves; ungual flaps of digital discs not notched; subarticular tubercles single, conical, and projecting; venter areolate (smooth in *P. diadematus*); dorsolateral folds absent; odontophores oval and oblique (triangular in *P. ventrimarmoratus*); toe webbing absent (basal in *P. altamazonicus*, and in *P. orcus* on toes II-V); inner tarsal fold present (unknown in *P. diadematus*); cranial crests absent; toe V reaches distal subarticular tubercle of toe IV; marbling of bright colours (red, yellow, pink, green) or white with dark bars in the inguinal region. Currently, the *P. diadematus* group, as originally conceived, is known to be polyphyletic (Rocha 2016).

Phylogenetic evidence provided by Pinto-Sánchez et al. (2012) and Mendonza et al. (2015) supports the existence of cryptic species under the name *P. altamazonicus* in western Amazonia. Ortega-Andrade & Venegas (2014), Padial et al. (2014), Ortega-Andrade et al. (2021), Waddell et al. (2018), Moravec et al. (2020) mentioned cryptic species in both the *P. carvalhoi* and *P. imitatrix* complexes and also the existence of cryptic species related to *P. diadematus* and *P. vent/rimarmoratus* restricted to western Amazonia and adjacent Andean slopes in Peru and Ecuador. Because of the morphological similarities among *P. altamazonicus*, *P. diadematus*, *P. eurydactylus*, *P. orcus*, *P. ventrimarmoratus*, and *P. divnae*, Lehr et al. (2009) hypothesized a phylogenetic relationship between those species, which should thus compose a new species group. Padial et al. (2016b) surveyed the Alto Purus National Park and reported *P.* aff. *divnae* from the vicinity of Puerto Breu, *P.* aff. *platydactylus* 1 from the River Cocama, 2.5 km above PCV Cocama, and *P.* cf. *orcus* from the River Sepahua, camp 2. The two latter sites are close to the border with the state of Acre, Brazil. Villacampa-Ortega et al. (2017) found *P.* sp1/cf. *diadematus* from *P. diadematus* group in Manu Learning Center. Moraes et al. (2022) pointed out the existence of a *P.* cf. *diadematus* from Reserva Extrativista Baixo Juruá, Amazonas, Brazil, and argued that identification from congeners such as *P. eurydactylus* is hampered by unclear species limits and diagnoses.

This scenario of putative undescribed diversity in western Brazilian Amazonia led me to examine in detail the *Pristimantis* material deposited in the Herpetological Collection of the Universidade Federal do Acre (UFAC-RB), a significant collection for this region and rich in specimens of the genus. These examinations revealed a new species of the *P. diadematus* species group (as defined by Rocha 2016), formally described and name herein.

Material and Methods

Morphological examinations and comparisons relied on specimens preserved in 10% formalin and stored in 70% ethanol. Specimens were sexed based on external sexual characteristics (e.g. the presence of vocal sacs and nuptial pads), presence of vocal slits (although males of certain species may lack them), and internally by the condition of the gonads. Descriptions of colouration in life were based on photos taken in the field. Specimens examined are listed in the Appendix 1. The description of diagnostic characters follows Duellman & Lehr (2009). The following measurements were taken with digital callipers under a stereomicroscope and rounded to the nearest 0.1 mm: snout-vent length (SVL), tibia length (TL), foot length (FL; distance from proximal margin of inner metatarsal tubercle to tip of toe IV), head length (HL; from angle of jaw to tip of snout), head width (HW; width at level of angle of jaw), eye diameter (ED), interorbital distance (IOD), upper eyelid width (UEW), internarial distance (IND), eye-nostril distance (END; straight line distance between anterior corner of orbit and posterior margin of external nares). Fingers were numbered pre-axially to post-axially from I-IV. Comparative lengths of toes III and V were determined when both were adpressed against toe IV; lengths of fingers I and II were estimated when adpressed against each other.

Results

Taxonomic account

Pristimantis paulogabrieli sp. nov., Figs. 1-4

Pristimantis diadematus López-Rojas et al. 2015 (Table 3): 25.

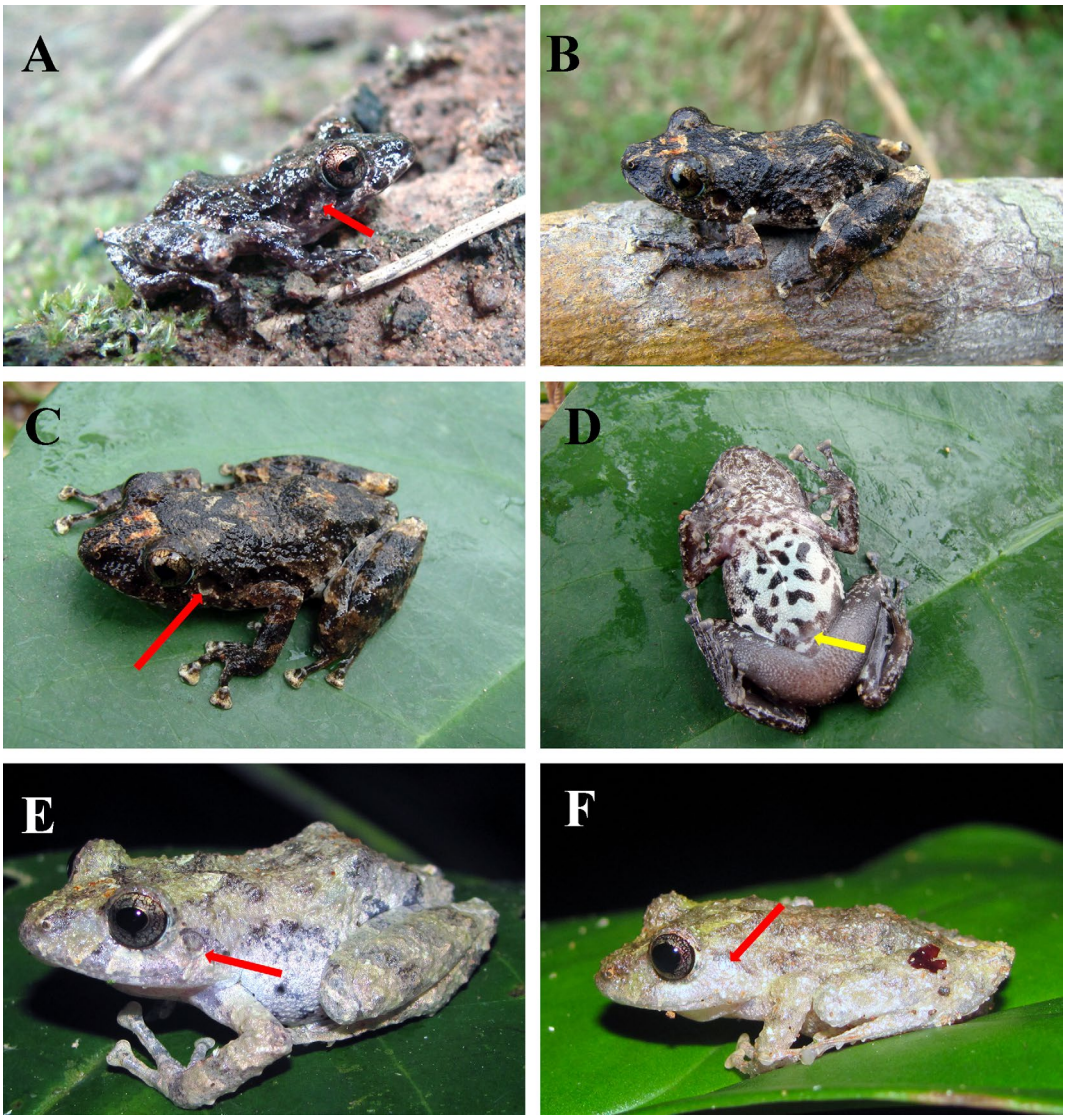

Fig. 1. *Pristimantis paulogabrieli* sp. nov. in life. Daytime photos (A-D) male paratype UFAC-RB 9668 (field series UFAC-RB 4423) (A), female holotype UFAC-RB 9669 (field series UFAC-RB 4424) (B-D). Night colouration: female paratype UFAC-RB 5737 (E) and unvouchered (F). Red arrows indicate tympanum and yellow arrow indicates discoidal fold.

Holotype: UFAC-RB 9669 (field series UFAC-RB 4424). Adult female, collected in Fazenda Experimental Catuaba, municipality of Senador Guiomard, state of Acre, Brazil (10°04.933′ S, 67°37.550′ W datum: WGS84; 183 m a.s.l.), on 25 October 2008 by P.R. Melo-Sampaio and N.M. Venâncio.

Paratypes: (n = 10): UFAC-RB 4172, adult male, collected in Fazenda São Jorge I, municipality of Sena Madureira, state of Acre, Brazil (9°26.183′ S, 68°37.317′ W 223 m a.s.l.) on June 2008 by D.B. Miranda, S. de Albuquerque and N.M. Venâncio. UFAC-RB 9668 (field series UFAC-RB 4423), adult male with the same data as holotype. UFAC-RB 4852-4853, adult male and female respectively, from the type locality, collected on 9 and 10 November 2007 by M.B. de Souza, N.M. Venâncio and T.R.B. da Silva. UFAC-RB 9670, a juvenile from the type locality, collected by P.R. Melo-Sampaio and J.M.L. Maciel on 30 May 2013. UFAC-RB 9671, an adult male from the type locality, collected on 15 June 2016 by J.S. Araújo. UFAC-RB 5050, an adult male from the type locality collected on 19 or 20 November 2007 by T.A.A. da Costa, M.L.T. Rodrigues, N.M. Venâncio, T.R.B. da Silva and M.B. de Souza. UFAC-RB 5737, an adult female from the type locality, collected on 21 July 2012 by P.R. Melo-Sampaio and J.M.L. Maciel. UFAC-RB 5863 and UFAC-RB 5969, adult males collected in Reserva Extrativista Chico Mendes, municipality of Brasiléia, state of Acre, Brazil (10°44.468′ S, 69°20.221′ W datum: SAD69; 267 m a.s.l.) by D.P.F. de França on October 2011 and June 2012 respectively.

Diagnosis: The new species, *P. paulogabrieli*, is diagnosed by the following combination of

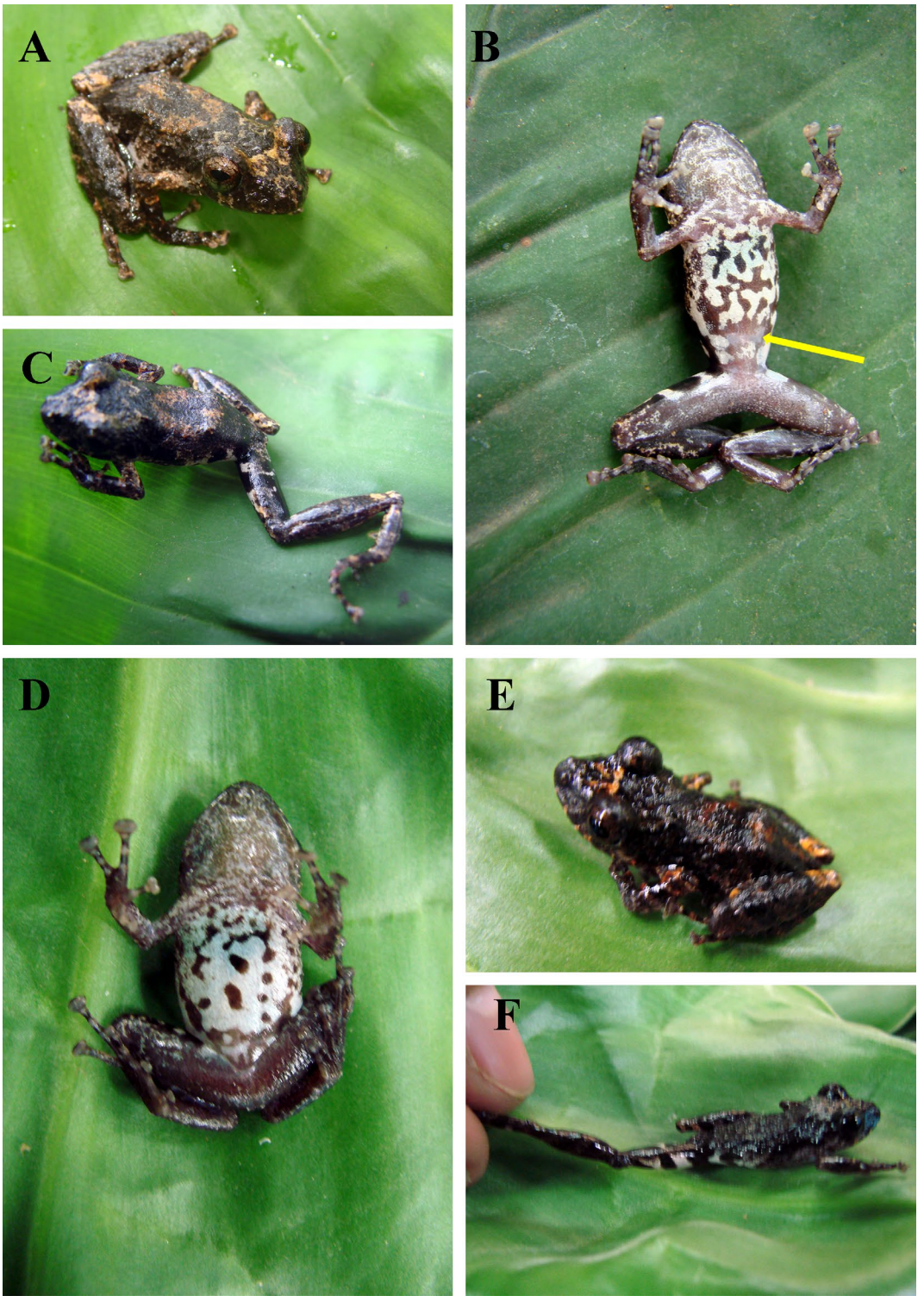

Fig. 2. *Pristimantis paulogabrieli* sp. nov. in life. (A-C) dorsal, lateral and ventral view of the body male paratype (UFAC-RB 5050); (D-F) ventral, dorsal and lateral view of the body male paratype (UFAC-RB 4852). The yellow arrow indicates discoidal fold.

characters: 1) skin on dorsum shagreen with scattered minute tubercles; dorsolateral fold absent; skin on venter areolate; discoidal fold present; 2) tympanic annulus visible, tympanic membrane present; 3) snout subacuminate in dorsal view, rounded in lateral view; 4) upper eyelid with minute tubercles, upper eyelid smaller than IOD, cranial crests absent; 5) dentigerous processes of vomers oblique low; 6) males with nuptial pads, but lacking vocal sac and vocal slits; 7) postrictal tubercles present; 8) finger I shorter than finger II, discs on fingers III and IV broad, rounded; 9) fingers with narrow lateral fringes; 10) ulnar tubercles present; 11) outer surfaces of tarsus without tubercles; 12) heel without minute

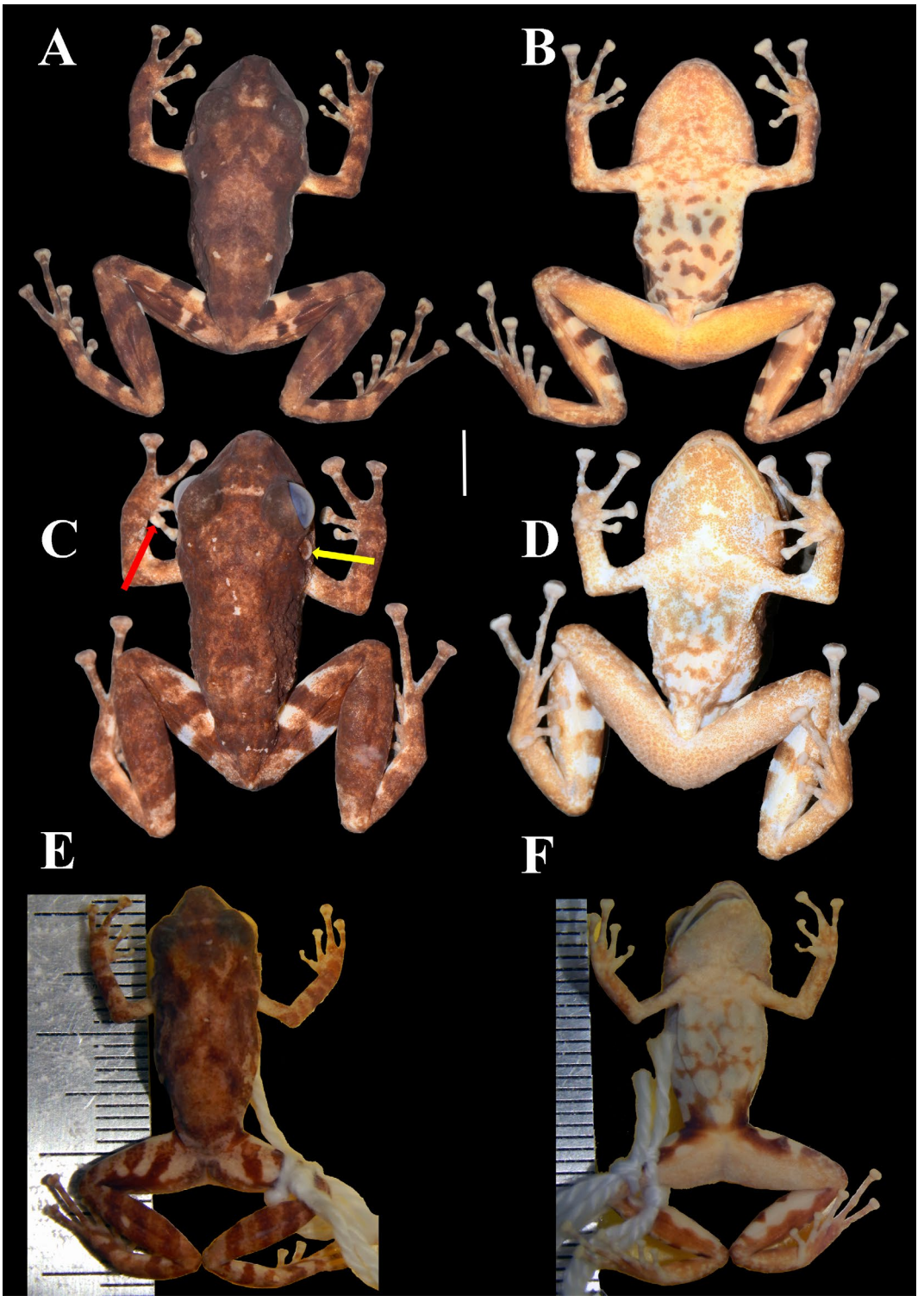

Fig. 3. Comparisons between *Pristimantis paulogabrieli* female holotype UFAC-RB 9669 (A-B), male paratype UFAC-RB 4853 (C-D) and *P. divnae* holotype MUSM 19990 (E-F). Red arrow indicates nuptial pad and yellow arrow indicates tympanum, both characters present in *P. paulogabrieli* and absent in *P. divnae*.

tubercle; 13) short, inner tarsal fold present; 14) inner metatarsal tubercle ovoid, four and half times the size of ovoid outer metatarsal tubercle; 15) few supernumerary plantar tubercles present; 16) toes with narrow lateral fringes; 17) basal toe webbing present between toes III and IV; 18) toe V much longer than toe III, toe discs broad, rounded, slightly smaller than discs on fingers; 19) in ethanol, dorsum brown with dark brown W-shaped mark on scapula and a dark brown chevron; 20) chest and belly cream with dark brown blotches, throat cream with few dark brown blotches and many minute dark brown spots; 21) SVL in adult males 19.5-23.5 mm (n = 8), females 27.8-30.6 mm (n = 2).

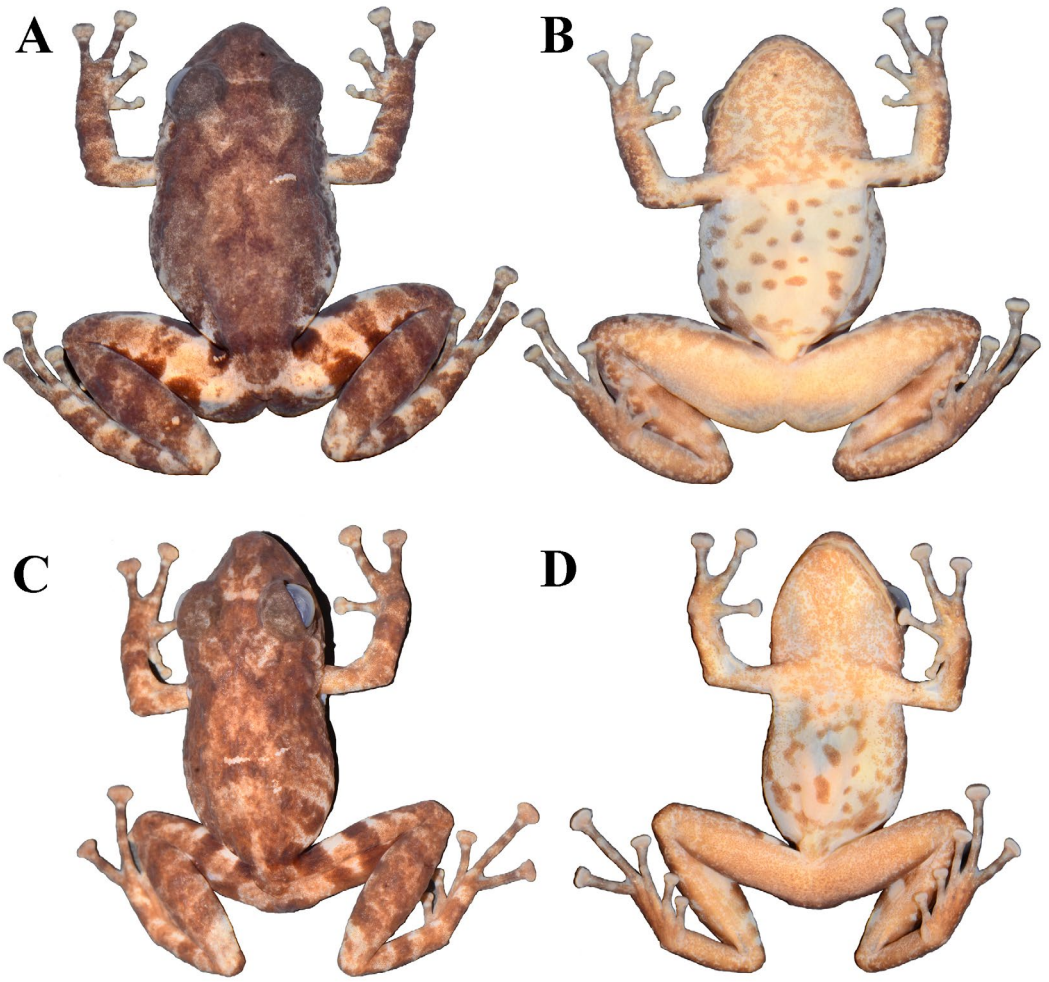

Fig. 4. Phenotypic variation in preservative *Pristimantis paulogabrieli*. Male paratype UFAC-RB 4172 (A-B), male paratype UFAC-RB 4852 (C-D).

Comparisons: In the absence of molecular data, I diagnose *P. paulogabrieli* from other western Amazonian *Pristimantis*, namely those occurring in Brazil's state of Acre, northern Bolivia, and south-eastern Peru. These species belong to the *conspicillatus*, *danae*, *lacrimosus*, and *unistrigatus* species groups (Padial et al. 2014, Ron et al. 2020, Carrión-Olmedo & Ron 2021) or have not been assigned to any group.

Species in the *P. danae* species group (*P. reichlei* Padial & De la Riva, 2009; *P. toftae* Duellman, 1978) differ from *P. paulogabrieli* by having a light venter and orange spots in the dorsal surface of thighs. *Pristimantis toftae* is also distinguished from *P. paulogabrieli* by the absence of dorsolateral folds and presence of a white line on the throat.

Species in the *P. lacrimosus* group (*P. acuminatus* Shreve, 1935; *P. aureolineatus* Guayasamin, Ron, Cisneros-Heredia, Lamar & McCracken, 2006; *P. lacrimosus* Jiménez de la Espada, 1875; *P. tantanti* Lehr, Torres-Gastello & Suárez-Segovia, 2007; *P. zimmermanae* Heyer & Hardy, 1991) differ from *P. paulogabrieli* in having an acuminate snout, smooth dorsal skin, and round and ovate finger and toe discs (Ron et al. 2020, Carrión-Olmedo & Ron 2021).

Species in the *P. conspicillatus* group (*P. buccinator* Rodríguez, 1994; *P. chiastonotus* Lynch & Hoogmoed, 1977; *P. conspicillatus* Günther, 1858; *P. fenestratus* Steindachner, 1864; *P. koehleri* Padial & De la Riva, 2009; *P. malkini* Lynch, 1980; *P. peruvianus* Melin, 1941; *P. skydmainos* Flores & Rodríguez, 1997) differ from *P. paulogabrieli* by having finger I larger than finger II and small dorsolateral ridges. Furthermore, *P. buccinator* and *P. skydmainos* have a middorsal spot fin-like tubercle in the latter (absent in *P. paulogabrieli*). *P. conspicillatus* and *P. peruvianus* are also distinctive in having yellow spotted posterior surfaces of thighs.

Species from the *P. unistrigatus* group: the absence of bold marked or spotted venter distinguishes *P. delius* (Duellman & Mendelson, 1995), *P. luscombei* (Duellman & Mendelson, 1995), and *P. ockendeni*

Table 1. Comparisons between *Pristimantis paulogabrieli* sp. nov. and congeners from *P. diadematus* group.

		P. altamazonicus	*P. brevicrus*	*P. diadematus*	*P. divnae*	*P. eurydactylus*	*P. orcus*	*P. paulogabrieli*
male	SVL (mm)	17.1-19.8	17.0-24.4	21.4-27.4	22.8-23.4	22.7-25.5	20.0-25.1	19.5-23.5
female		28.4-30.1	27.2-35.0	35.4-44.5	unknown	38.0-38.8	32.6-36.5	27.8-30.6
W-mark shaped on scapula		+	+	+	+	+	+	+
Tympanic annulus		+	-	+	+	+	+	+
Tympanic membrane		+	-	+	-	+	+	+
Discoidal fold		-	+	+	+	+	+	+
Lateral fringes on fingers and toes		+	+	+	+	+	+	+
Tarsal fold		+	+	+	+	+	+	+
Vocal slits		-	-	-	-	-	+	-
Nuptial pads		+	-	+	-	-	+	+
Iris with T-shaped mark		+	+	+	+	+	+	+
Live colouration of the groin		Red to bright orange with black mottling	Bluish white to yellowish white colour with black mottling	Bluish-white, yellowish, tan, pink, or pale green with diagonal dark brown bars	Yellow with brown marks	Creamy white with brown marks	White or whitish blue and black	White with bold black marks

Table 2. Measurements of type series from *Pristimantis paulogabrieli* sp. nov. All measures are in mm.

VOUCHER	SEX	SVL	TL	HL	IND	IOD	EW	HW	FL	E-N	ED	TY	STATUS
UFAC-RB 4172	M	23.5	11.9	7.6	2.1	1.9	2.4	9.0	10.2	2.8	3.2	1.3	PARATYPE
UFAC-RB 4852	M	21.8	11.2	7.7	1.9	2.3	2.1	8.1	9.8	2.9	3.0	1.6	PARATYPE
UFAC-RB 4853	M	22.5	11.9	7.9	2.1	2.2	2.1	8.7	10.8	3.1	3.1	1.3	PARATYPE
UFAC-RB 5050	M	22.3	11.9	8.2	2.0	2.3	2.3	7.3	9.8	2.6	2.8	1.2	PARATYPE
UFAC-RB 5737	F	30.6	16.6	10.1	2.8	3.0	2.9	11.4	13.4	3.6	2.9	1.8	PARATYPE
UFAC-RB 5863	M	24	12.4	7.9	2.3	2.3	2.3	8.6	9.5	2.9	3.0	1.5	PARATYPE
UFAC-RB 5969	M	22.9	12.6	8.5	2.3	2.5	2.3	8.9	10.9	3.3	3.3	1.5	PARATYPE
UFAC-RB 6541	M	24.3	12.3	8.3	2.2	2.3	2.3	8.5	9.7	2.6	2.7	1.7	PARATYPE
UFAC-RB 9668	M	19.5	10.9	6.9	1.5	2.2	1.9	7.2	8.5	2.3	2.8	0.9	PARATYPE
UFAC-RB 9669	F	27.8	14.9	9.8	2.7	2.7	2.3	10.9	12.6	3.4	3.5	1.6	HOLOTYPE
UFAC-RB 9671	M	21.7	10.5	7.8	1.9	2.4	3.2	8.5	9.1	2.8	3.2	1.3	PARATYPE

(Boulenger, 1912) from the new species. We note that Brito-Zapata et al. (2021) do not support the classification of this species group, finding *P. ockendeni* strongly supported as nested into the *P. orestes* species group.

The remaining western Amazonian *Pristimantis* species, which have not been assigned to any species group, share with *P. paulogabrieli* finger I < II. However, the presence of a yellow inguinal spot distinguishes *P. academicus* Lehr, Moravec & Gagliardi-Urrutia, 2010, *P. carvalhoi* (B. Lutz in Lutz & Kloss (1952)), and *P. variabilis* (Lynch, 1968) from the new species.

Among the western Amazonian species of the *P. diadematus* complex, *P. altamazonicus* (Barbour & Dunn, 1921), *P. diadematus* (Jiménez de la Espada, 1875), *P. eurydactylus* (Hedges & Schlüter, 1992), *P. orcus* (Lehr, Catenazzi & Rodríguez, 2009), and *P. ventrimarmoratus* (Boulenger, 1912) are the most similar to the new species (Duellman & Lehr 2009, Lehr et al. 2009, Ortega-Andrade et al. 2021, see Table 1 for comparisons). In the comparisons below, the condition of the species compared to the new species is presented in parentheses unless otherwise stated. *Pristimantis paulogabrieli* differs from *P. ventrimarmoratus* in having a tympanic annulus (absent) and smaller size with maximum SVL 23.5 in males and 30.6 mm in females (up to 25.5 mm SVL in males and 43.8 mm in females). *Pristimantis paulogabrieli* differs from *P. altamazonicus* in having a white venter with bold black marks (venter cream heavily stippled with grey) and a white groin with bold black marks (red to bright orange with black mottling). *Pristimantis paulogabrieli* differs from *P. diadematus* in having smaller SVL, absence of coloured marks on groin (SVL up to 27.0 mm and 44.5 mm in males and females respectively, and bluish-white, yellowish tan, pink or pale green). *Pristimantis paulogabrieli* differs from *P. eurydactylus* in having maximum SVL of 30.6 mm (up to 35.3 mm SVL in females), head without cranial crest (cranial crest or tubercular W-shaped present), and by presence of discoidal fold (absent). *Pristimantis paulogabrieli* is most similar to *P. divnae* but differs from it by having a conspicuous tympanic annulus and membrane (barely visible or absent in *P. divnae*); males have nuptial pads (absent) and a white groin (yellow) and males are smaller 22.5 mean SVL (19.5-23.5 mm) than *P. divnae* (23.1 mean SVL (22.8-23.4 mm)). Furthermore, *P. paulogabrieli* has TL/SVL > 0.50 (in *P. divnae*, < 0.50).

Description of holotype: UFAC-RB 9669 (field series UFAC-RB 4424). Head wider than body, shorter than wide; head width 39.2% of SVL; head length 35.2% of SVL; cranial crest absent; snout subacuminate in dorsal view, moderately rounded in lateral view; eye diameter 102.9% of eye-nostril distance; nostrils slightly protuberant, directed laterally; canthus rostralis weakly concave in dorsal view, rounded in cross-section; loreal region slightly concave; lips rounded; upper eyelid without tubercles; upper eyelid width 85.2% of IOD; narrow distinct supratympanic fold extending from posterior edge of upper eyelid, curved at the level of arm insertion; tympanic annulus visible, tympanic membrane present; postrictal tubercles present on both sides of head. Choana large, rounded, not concealed by palatal shelf of maxilla; dentigerous process of vomer oblique with five teeth; tongue ovoid, longer than wide, slightly notched posteriorly, half free.

Skin of dorsum shagreen with small scattered tubercles; dorsolateral folds absent; skin on flanks smooth; skin on venter weakly areolate, on thighs areolate; discoidal fold present, most evident posteriorly; cloacal sheath short; cloacal tubercles absent. Ulnar tubercles present; outer palmar tubercle bifid and low, thenar tubercle ovoid; subarticular tubercles well defined, rounded in ventral view and subconical in lateral view; one supranumerary tubercle on base of fingers II and IV, rounded and ovoid respectively, smaller than subarticular tubercles; fingers with narrow lateral fringes, most prominent basally between fingers; finger I shorter than finger II; discs on fingers broadly expanded, approximately 2× the size of phalanx anterior to it; discs rounded; ventral pads of fingers well defined in the tips by circumferential grooves, barely differentiated posteriorly.

Hind limbs long, slender, tibia length 53.6% of SVL; foot length 45.3% of SVL; upper surfaces of hind limbs shagreen with small tubercles; anterior and posterior surfaces of thighs smooth, dorsal surfaces weakly areolate; tubercle absent on heel; outer surface of tarsus with two minute tubercles; inner tarsal fold short, low; inner metatarsal tubercle ovoid, 4× the size of round outer metatarsal tubercle; subarticular tubercles well-defined, rounded in ventral view, subconical in lateral view; one supernumerary plantar tubercle on base of toes II-V; toes with narrow lateral fringes; basal webbing between toe III and IV, IV and V; discs rounded broadly expanded, but slightly smaller than those on fingers; toes having ventral pads well defined by circumferential grooves; relative lengths of toes: I < II < III < V < IV; toe V much longer than toe III. White and black blotches or bars

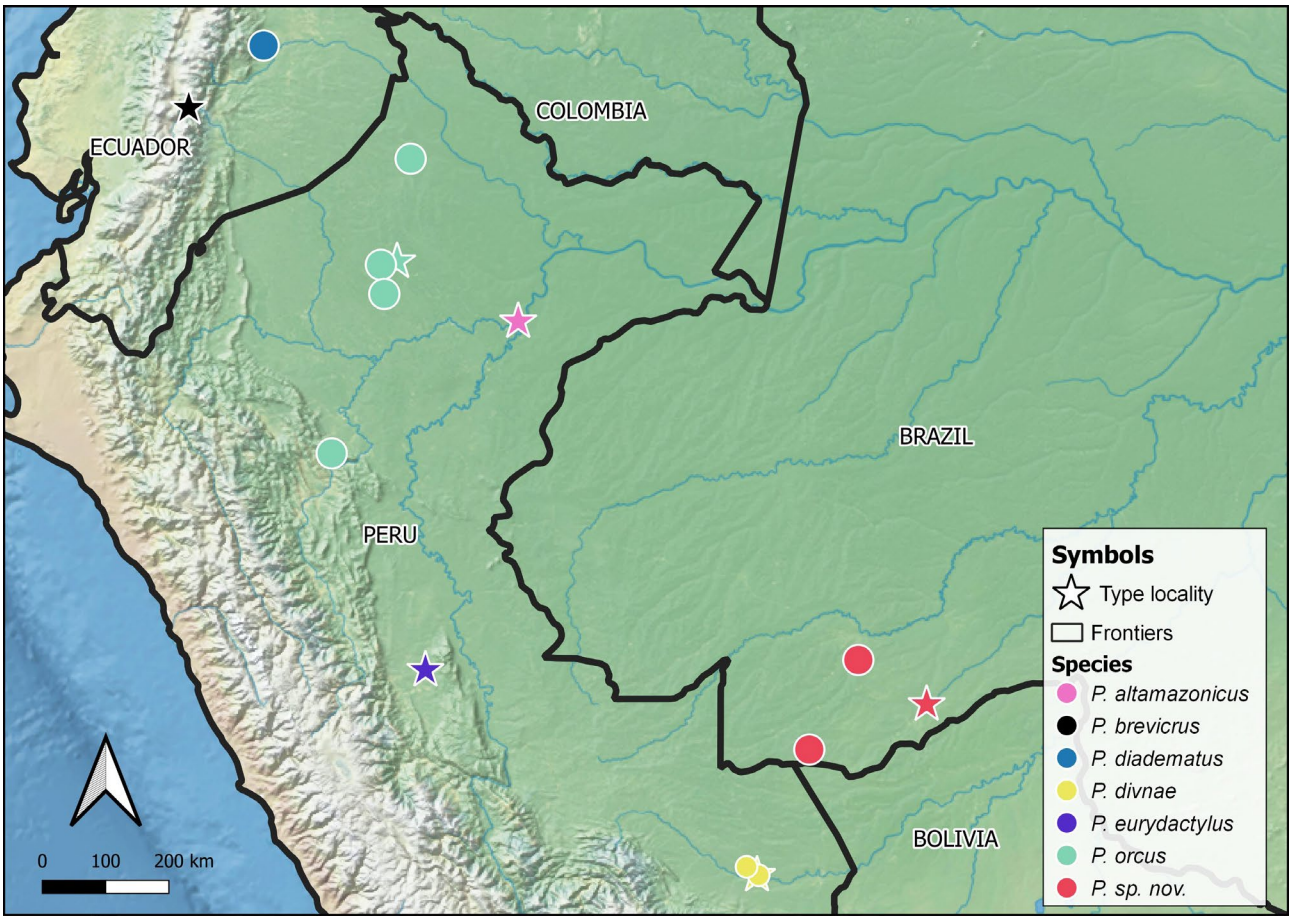

Fig. 5. Distribution of *Pristimantis diadematus* species complex indicating type localities (star): *P. altamazonicus* (pink), *P. brevicrus* (black), *P. diadematus* (blue), *P. divnae* (yellow), *P. eurydactylus* (indigo), *P. orcus* (aqua), and *P. paulogabrieli* sp. nov. (red).

on the groin and on concealed surfaces of the shanks, and a white venter with dark brown blotches.

Holotype measurements: Measurements in millimetres. Snout-vent length 27.8; tibia length 14.9; foot length 12.6; head length 9.8; head width 10.9; internarial distance 2.7; interorbital distance 2.7; eyelid width 2.3; eye-nostril distance 3.4; eye diameter 3.5; tympanum diameter 1.6.

Colouration of holotype in preservative: Snout with dark brown chevron open anteriorly followed by pale cream 'extracted molar tooth-shaped' with crown caudally directed; head with tan interorbital bar; dorsum greyish-tan with dark brown 'W' on scapular region with paired scapular tubercle (one in each extremity); sacral region with dark brown chevron with opening directed caudally. Arms greyish brown with one tan to brown bar on forearms. Hands with dark brown 'bracelet' tan coloured in the fist, with fingers similar in colouration; thighs with medial dark brown transversal bar; tibia brown with three diagonal dark brown bars; inner toes with colouration similar to outer toes. Lateral of head brown, canthal stripe absent, dark brown supratympanic stripe present; upper lip greyish tan with two dark brown bars below eye; iris black; margin of upper lip with four irregular cream spots on each side of head; flanks lighter than dorsum, with two diagonal bars, the posterior being a continuation of the dorsal chevron on the groin; groin white cream with dark brown blotch; anterior surfaces of thighs cream with three dark brown blotches, medial one larger than the others and fused with the transversal bar; concealed posterior surfaces of thighs tan to dark brown; dark brown triangular area around cloaca; concealed surfaces of shanks with three dark brown stripes; dark brown hexagonal blotch in the heels; fingers and toes tips tan with greyish tan discs.

Colouration of holotype in life: Snout with bronze 'molar tooth-shaped' spot anterior to another orange to reddish 'molar tooth-shaped' spot followed by interorbital band; upper lip with dark and pale bars; dorsum rusty brown with darker brown spots, orange to reddish in the middle and at level of the sacrum; flanks dark grey with white mottling; groin white and black; hidden surfaces of thighs white and black; hidden surfaces of tibias white and black; throat grey with fine white mottling, chest and belly dark grey

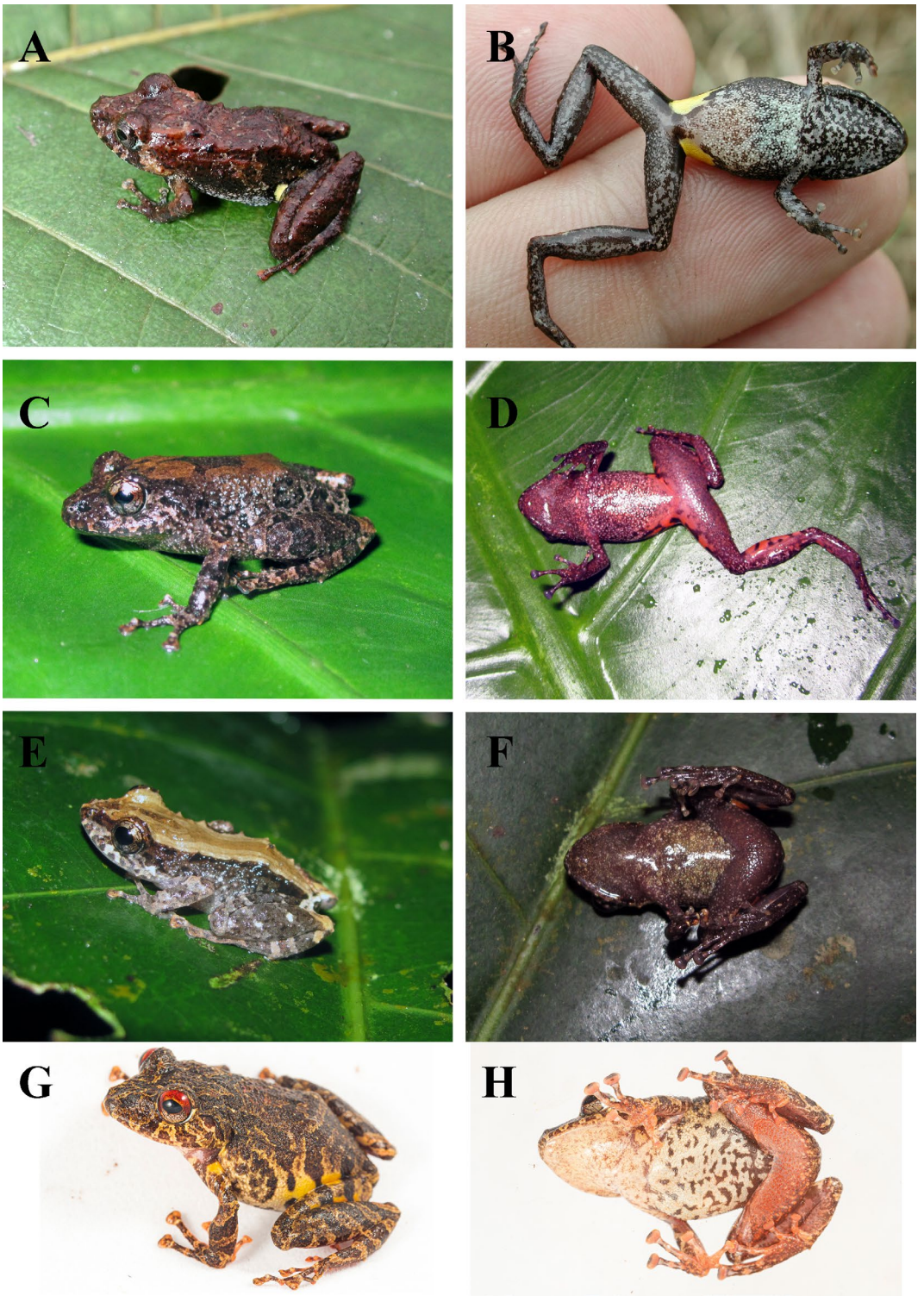

Fig. 6. *Pristimantis* species similar to *P. paulogabrieli* in dorsal and ventral views: holotype of *P. academicus* MUSM 27634 (A-B) by Jiří Moravec. *P. altamazonicus* UFAC-RB 5745 (C-D) and UFAC-RB 5786 (E-F). *Pristimantis diadematus* CORBIDI 21897 (G-H) by Germán Chávez.

with white mottling; extremities brown, tips of fingers and toes pale grey; iris greenish bronze with black reticulation, reddish copper medially with vertical black bar below pupil forming a 'T' shape (Fig. 1B-D).

Variation: regarding colouration patterns in preservative, paratype UFAC-RB 4853 has an inconspicuous W-shaped scapular mark. Nuptial pads on dorsal and medial surfaces of thumb tan to cream-coloured. The venter of males has spots smaller than those of females. The female paratype UFAC-RB 6541 is coloured sepia dorsally. The molar tooth-shaped spot is well-marked in UFAC-4852 (Fig. 2A) and UFAC-RB 5050 (Fig. 2E), barely visible

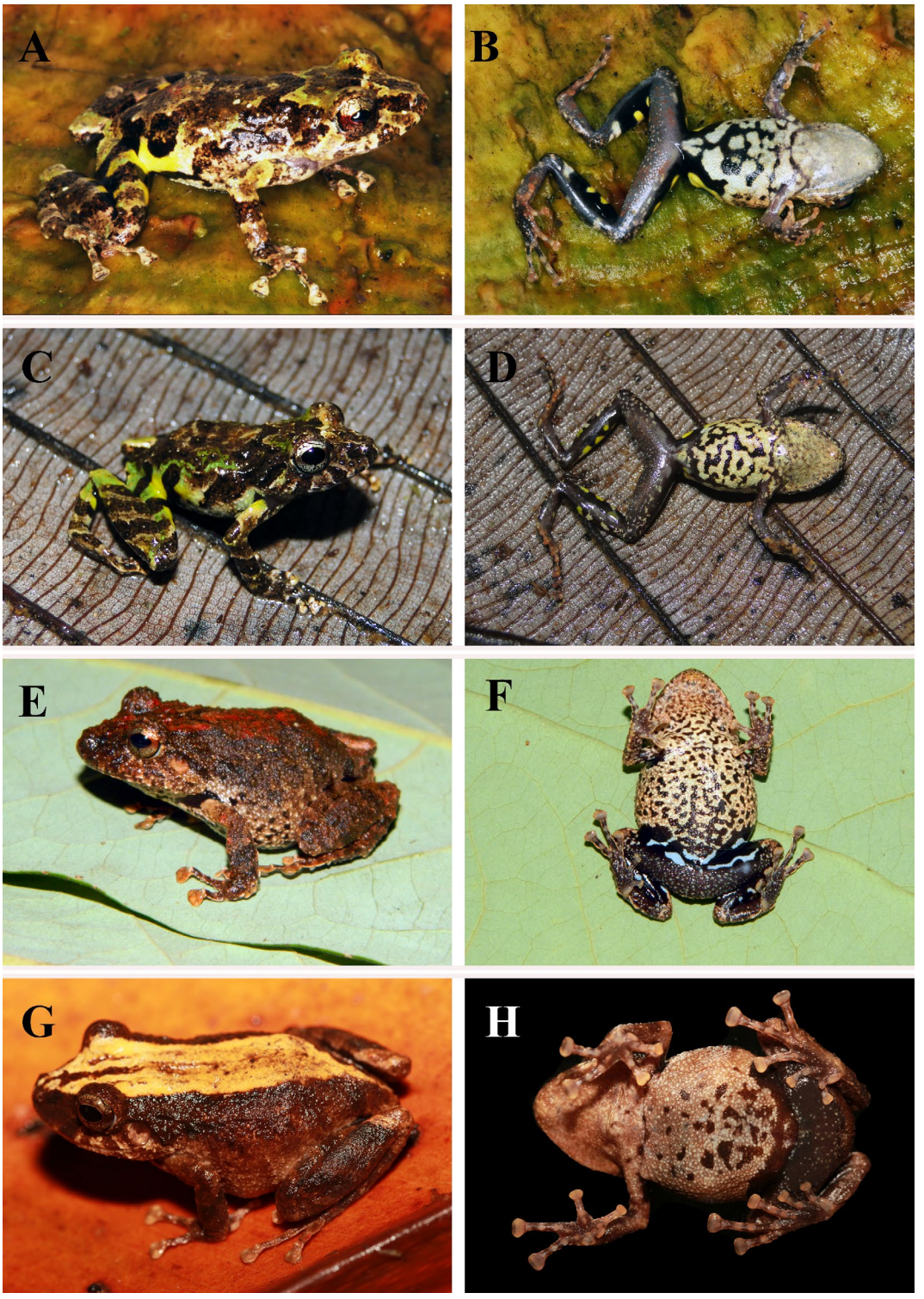

Fig. 7. *Pristimantis diadematus* species group in dorsolateral and ventral views: *P. divnae* unvouchered (A-B) by Juan Carlos Chaparro, and CORBIDI 13230 (C-D) by Pablo Venegas; *P. orcus* UFAC-RB 6040 (E-F) by Jhon Jairo López-Rojas and CORBIDI 12326 (G-H) by Germán Chávez.

in preservative in paratypes UFAC-4853 (Fig. 4A) and UFAC-RB 4172 (Fig. 4E). In life, paratype UFAC-RB 9668 (field series UFAC-RB 4423) has subocular spots distinct, bifurcating to form an inverted 'Y' shape, with five brown spots on the lips. The irises are gold with bronze vermiculation with a horizontal red streak and vertical bar forming a 'T' shape in UFAC-RB 4423 (Fig. 1A) or cross in UFAC-RB 5737 (Fig. 1E). Measurements of the morphological characters are presented in Table 2.

Etymology: The specific epithet is a patronymic name for my beloved son, Paulo Gabriel Silva Melo Sampaio.

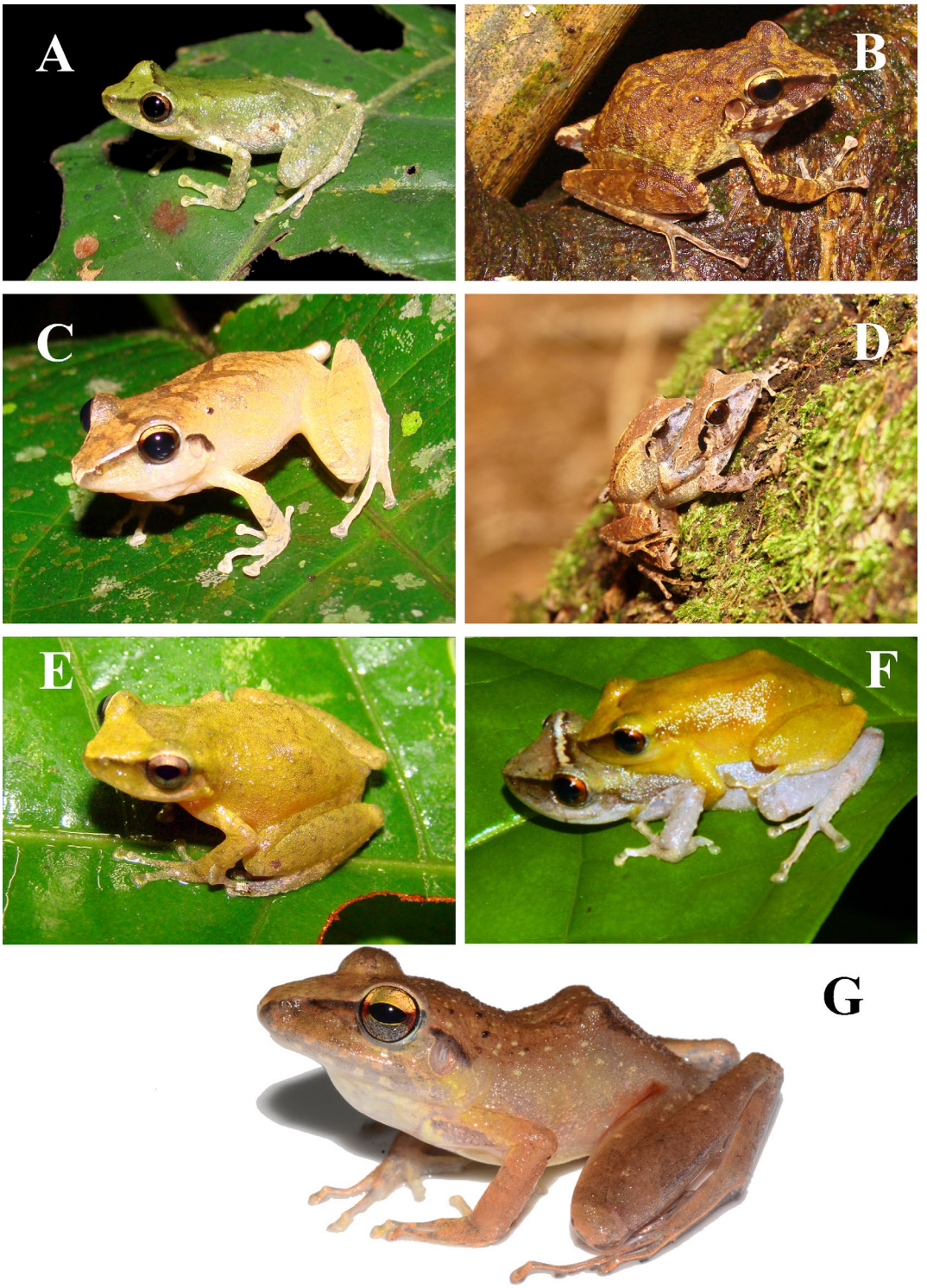

Fig. 8. Syntopic species with *Pristimantis paulogabrieli*: *P.* aff. *acuminatus* UFAC-RB 5649 (A), *P.* aff. *fenestratus* uncollected (B), *P. reichlei* uncollected (C), *P. skydmainos* uncollected (D), *P.* gr. *lacrimosus* UFAC-RB 4584 (E) and amplectant pair uncollected (F) and *P.* aff. *conspicillatus* (field number PRMS-1100) (G). Photo F by Jhon Jairo López Rojas.

Distribution and natural history

Pristimantis paulogabrieli lives in lowland open forest with bamboo in southwestern Amazonia (Fig. 5). This vegetation is dominated by scansorial and thorny bamboo *Guadua weberbaueri*, allowing sunlight to pass through the canopy, thus differing from closed-canopy Amazonian forest (dense forest). Specimens were selectively collected in forest habitats logged over the last 15-25 years, 0.5 m to 2 m high on vegetation. From 2008 to 2010 colleagues and I sampled the type locality monthly in the dry season and weekly or biweekly in the wet season, but we have yet to hear

males calling. López-Rojas et al. (2015) studied the structure of the *Pristimantis* assemblage occurring at Fazenda Experimental Catuaba, but the new species was not recorded. The new species occurs with low abundance, which seems correlated with more closed canopy (López-Rojas et al. 2015). At the type locality, this species is syntopic with *P. altamazonicus* (Figs. 6C-F) and probably sympatric with *P. divnae* and *P. orcus* (Fig. 7) through its distribution. Other syntopic species also were found with *P. paulogabrieli* such as *P.* aff. *acuminatus*, *P.* aff. *fenestratus*, *P. reichlei*, *P. skydmainos P.* gr. *lacrimosus* and *P.* aff. *conspicillatus* (Figs. 8A-G).

Discussion

Pristimantis paulogabrieli is the first species of the *P. diadematus* species complex described from Acre, Brazil. Its morphological similarity with sympatric species is restricted to the dorsal pattern, particularly the W-shaped scapular mark, suggesting *P. divnae* and *P. orcus* are probably the closest relatives of the new species, though well differentiated by many traits. The morphological similarities between *P. paulogabrieli* and members of the *P. diadematus* group (such as *P. divnae*) are congruent with the most recent phylogenies incorporating DNA data (e.g. Ortega-Andrade et al. 2021). Future analyses incorporating molecular information from the new species and species currently assigned to the *P. diadematus* species complex, namely *P. altamazonicus*, *P. brevicrus*, *P. diadematus*, and *P. orcus*, will allow investigating the relationships within this clade. Waddell et al. (2018) and Ortega-Andrade et al. (2021) have identified candidate species similar to *P. altamazonicus*, *P. brevicrus* and *P. diadematus*. Documenting this diversity will benefit from intensive herpetofaunal sampling, with implications for conservation given the landscapes in western Amazonia are increasingly fragmented (Silveira et al. 2020, Souza et al. 2020).

More broadly, some comments on the composition of *Pristimantis* species groups are warranted. Multiple terminals assigned to *P. platydactylus* have been inferred as phylogenetically nested among *P. ashaninka*, *P. llojsintuta*, *P.* cf. *carvalhoi*, *P. salaputium* and other species with inguinal spots (Rocha 2016, Moravec et al. 2020, Chávez et al. 2021, Ortega-Andrade et al. 2021). Therefore, I recommend removing *P. platydactylus* from the *P. diadematus* group because Rocha (2016) included this species in the *P. marmoratus* group. I propose an amendment to the *P. diadematus* species complex with the following species in its composition: *P. altamazonicus*, *P. brevicrus*, *P. diadematus*, *P. divnae*, *P. eurydactylus*, *P. orcus*, *P. paulogabrieli* and *P. ventrimarmoratus*.

The incorporation of molecular data has supported the identification of undescribed species diversity in many Amazonian frog clades. Nevertheless, phenotypic characters remain more readily available to scientists in the Global South, who have spearheaded and stepped up to the formidable challenge of discovering and documenting new species in the megadiverse tropical countries. In the absence of molecular data, alternative sources of information like behaviour (Rodríguez 1994) and fixed morphological traits (e.g. presence or absence of tympanum, colour in life, and nuptial pads) have been and continue to be deemed as sufficient to distinguish new species of *Pristimantis* (Lehr et al. 2006, Ortega-Andrade et al. 2015, 2021). To continue this effort while genetic data remain limited, properly uncovering the likely immense diversity of Amazonian *Pristimantis* frogs will require a detailed analysis of external morphology. This endeavour implies providing adequate figures and comparisons and standardisation of the nomenclature of phenotypic traits to avoid and minimize the current confusion in this group. This effort will also benefit from incorporating appropriate sample sizes, as species described from single or few specimens have a higher risk of leading to taxonomic oversplitting due to overlapping variation in examined traits (Guayasamin et al. 2015). Such practices will be instrumental to reduce taxonomic confusion in *Pristimantis*, which is illustrated by several examples: the holotype of *Pristimantis luscombei*, erroneously described as male by Duellman & Mendelson (1995); the description did not include an illustration of the holotype, while specimens referred to that taxon were later found to be *P. myktos* (Ortega-Andrade & Venegas 2014); *P. achuar* (Elmer & Cannatella, 2008) whose described holotype also appears as a paratype (QCAZ 25463) (P.R. Melo-Sampaio, pers. observ.) and lacking comparisons with *P. luscombei*, of which it proved to be a synonym (Ortega-Andrade & Venegas 2014); *P. latro* (Oliveira et al. 2017a) whose description is confusing and whose paratypes are listed as both paratype and paratopotypes (LZATM 742, LZATM 748, LZATM 751); 'paratypes' that do not appear in the type series (Oliveira et al. 2017b); and *P. giorgii*, *P. moa*, *P. pictus* and *P. pluvian*, Oliveira et al. (2020a), described without standardisation of morphological traits and providing incomplete figures (Oliveira et al. 2020b). As pointed out by Lynch (1976), the large number of names applied to frogs of this genus may have contributed to a certain reluctance of herpetologists to become involved with

their systematics. This diversity of names, however, comes from the immense species diversity of this group. Future studies should focus on discriminating nominal species from those that represent currently unrecognized *Pristimantis* species. I hope that the description of *P. paulogabrieli* contributes to this vital effort.

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Data Availability Statement

The data supporting this study are available in Appendix 1.

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Appendix 1. Material examined.

Pristimantis academicus: MUSM 27634 holotype; MUSM 27635 paratype (photographs).

Pristimantis altamazonicus: UFAC-RB 1672, UFAC-RB 4194, UFAC-RB 4736-4737, UFAC-RB 5745, UFAC-RB 5761, UFAC-RB 5765, UFAC-RB 5786, UFAC-RB 5966, UFAC-RB 6083, UFAC-RB 6279, UFAC-RB 6437.

Pristimantis carvalhoi: UFAC-RB 3578, UFAC-RB 3613-3614, UFAC-RB 3622, UFAC-RB 4187-4190.

Pristimantis diadematus: Peru: UFAC-RB 3569, UFAC-RB 3595 UFAC-RB 3606-3607. Brazil: Acre: UFAC-RB 881, UFAC-RB 1678-1679, UFAC-RB 1976, UFAC-RB 2222-2224, UFAC-RB 3806, UFAC-RB 4218, UFAC-RB 4219, UFAC-RB 5008, UFAC-RB 5382, UFAC-RB 5643, UFAC-RB 6658.

Pristimantis divnae: MUSM 19990 holotype (photographs). Rondônia: UFAC-RB 8203.

Pristimantis eurydactylus: MUSM 14000 paratype (photographs).

Pristimantis orcus: UFAC-RB 6040, UFAC-RB 6050-6051.

Pristimantis platydactylus: BMNH 1947.2.15.91-96 syntypes. IZUC 000765 = UCMZ 8601 (holotype of *Eleutherodactylus bockermanni*) (photographs).

Pristimantis ventrimarmoratus: BMNH 1947.2.15.73-76 syntypes (photographs).

NOMENCLATURAL ACTS REGISTRATION

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