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Molecular and Morphological Assessment of Rain Frogs in the *Pristimantis orestes* Species Group (Amphibia: Anura: Strabomantidae) with the Description of Three New Cryptic Species from Southern Ecuador

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Abstract: We review the species content of the *Pristimantis orestes* group and, by integrating genetic and morphological data, we distinguish and describe three new cryptic species from the subpáramos of southern Ecuadorian Andes. Genetically, these new species are most related to *P. matildae* and the other species of the *P. colodactylus* subgroup; however, in morphology, they are strikingly different from them, especially in terms of the shape of the body, having less-compressed heads and bodies. Additionally, they differ by their ecology, having arboreal habits in contrast with their bromeliad specialist sister species of the subgroup. The new species are also easily distinguished from the species of the *P. orestes* and *P. simonbolivari* subgroups, mainly by the lack of tympanum, longer snouts, and longer fingers and toes, and coloration. *Pristimantis sagedunneae* has a shagreen dorsum, subacuminate to rounded snout in dorsal view, Toe V longer than Toe III, and a brownish gray coloration of the dorsum with blackish or dark brown bars and an intense red coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces; *P. paladines* has a tuberculate dorsum, acuminate to subacuminate snout, Toe V longer than Toe III, and dorsum of various shades of brown, reddish brown, greenish brown, green, or reddish orange with dark, blackish bars and orange or reddish brown coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces; *P. numbala* has a shagreen dorsum, rounded to broadly rounded snout, Toe V much longer than Toe III, reddish brown coloration of the dorsum with dark brown bars and reddish brown coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces. All three species have very small distribution ranges of less than 20 km^2 located in the western limit of Parque Nacional Podocarpus, at altitudes between 2,800–3,100 m. Finally, we briefly discuss the current species composition of the group, the role that natural history might have in determining the shape of the bodies, and the cryptic diversity and distribution pattern of some of the species in southern Ecuador.

Key words: Abra de Zamora; Amphibians; Direct-developing frogs; DNA; Reserva Numbala; Reserva Tapichalaca; Tropical Andes

The neotropical genus of direct-developing frogs *Pristimantis* Jiménez de la Espada 1870 (Amphibia: Anura: Strabomantidae) is the largest among vertebrates, encompassing as of July 2022 592 species (Frost 2022), and with many more being still undescribed. This genus is distributed in Central and South America; however, most of the species are encountered in the Andean regions of Colombia, Ecuador, and Peru (Kieswetter and Schneider 2013).

With the continuous species descriptions, already in the 1970s arose the need to organize and classify in some way the many species of the genus. Thus, John D. Lynch (1976) proposed a series of species groups for the many species then known from South America (at that point known as *Eleutherodactylus*) and attempted to organize the species group arrangement for the entire genus. One such arrangement, proposed in 1997, was the *Pristimantis orestes* species group (Lynch and Duellman 1997).

At that time, the *P. orestes* group contained only three species (Lynch and Duellman 1997), distributed in páramos and high-altitude cloud forests in Ecuador: *P. orestes* (Lynch 1979), *P. simonbolivari* (Wiens and Coloma 1992), and *P. vidua* (Lynch 1979). By 2008, in the group were included 14 species; to the previous three being added 11 Peruvian species (see Hedges et al. 2008; Duellman and Lehr 2009). However, by 2014 only four species of these were included in the comprehensive Terrarana phylogenetic revisions, and only two (*P. orestes* and *P. simonbolivari*) clustered together to form a group (see Hedges et al. 2008; Padial et al. 2014). Two other species were later added to the *P. orestes* species group: *P. bambu* Arteaga-Navarro and Guayasamin 2011 and *P. mazar* Guayasamin and Arteaga 2013.

Brito et al. (2017a) redefined the group and added to it *P. andinognomus* Lehr and Coloma 2008, the newly described *P. muranunka*, and two additional species (which currently remain undescribed). They removed the Peruvian species *P. melanogaster* (Duellman and Pramuk 1999) and *P. simonsii* (Boulenger 1900), and noticed that *P. orestes* is incorrectly defined, being actually represented by three different species in their tree. *Pristimantis tiktik* Székely et al. 2018 was added to the group and Urgilés et al. (2019) clarified the identity of *P. orestes*, using for the first time genetic material from the type locality, and included *P. saturninoi* Brito et al. 2017b and two new species, *P. cajanuma* and *P. quintanai*, into the group.

By using samples from the type locality, Abra de Zamora, Székely et al. (2020) redescribed *P. vidua* and *P. colodactylus* (Lynch 1979) and confirmed their belonging to the group, and added two new species, *P. samaniegoi* and *P. matildae*. Also, in order to facilitate the analysis of the group, the authors recognized three large subgroups (lineages) of species (Fig. 1): the *P. orestes* subgroup (with *P. andinog-*

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FIG. 1.—Morphological diversity in the *Pristimantis orestes* species group. *Pristimantis orestes* subgroup: (A) *P. vidua* MUTPL 156, SVL = 26.8 mm, adult female from Bosque Protector Washapamba, Loja Province, 3,003 m; (B) *P. cajanuma* MUTPL 347, SVL = 22.0 mm, female paratype from Cajanuma entrance to the Parque Nacional Podocarpus, Loja Province, 3,042 m; (C) *P. orestes* MUTPL 242, SVL = 20.7 mm, adult male from Vía Urdaneta - Tutupali, Loja Province, 2,960 m. *Pristimantis simonbolivari* subgroup: (D) *P. tiktik* MUTPL 247, SVL = 20.2 mm, female paratype from Vía Urdaneta - Tutupali, Loja Province, 3,108 m; (E) *P. quintanai* ZSFQ 4130, adult male from Rivera, Cañar Province, 3,050 m (photo by Juan C. Sánchez-Nivicela); (F) *P. samaniegoi* MUTPL 357, SVL = 20.1 mm, female holotype from Cajanuma entrance to the Parque Nacional Podocarpus, Loja Province, 3,258 m. *Pristimantis colodactylus* subgroup: (G) *P. colodactylus* MUTPL 311, SVL = 20.2 mm, adult female from Abra de Zamora, Loja Province, 2,822 m; (H) *P. muranunka* MUTPL 652, SVL = 19.9 mm, adult male from Cerro Plateado, Zamora Chinchipe Province, 2,409 m; (I) *P. matildae* MUTPL 366, SVL = 20.8 mm, female paratype from Abra de Zamora, Loja Province, 2,817 m; (J) *P. sagedunneae* MUTPL 597, SVL = 21.7 mm, female paratype from Cajanuma entrance to the Parque Nacional Podocarpus, Loja Province, 2,991 m; (K) *P. paladines* MUTPL 1151, SVL = 19.5 mm, female paratype from Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca, Zamora Chinchipe Province, 2,880 m; (L) *P. numbala* MUTPL 1178, SVL = 23.2 mm, female paratype from Reserva Numbala, Zamora Chinchipe Province, 2,861 m. All specimens are from Ecuador.

nomus, *P. orestes*, *P. vidua*, *P. cajanuma*, and an undescribed species), the closely related *P. simonbolivari* subgroup (with *P. tiktik*, *P. saturninoi*, *P. simonbolivari*, *P. bambu*, *P. mazar*, *P. quintanai*, *P. samaniegoi*, and two undescribed species) and the morphologically distinct, bromeliad specialist, *P. colodactylus* subgroup (with *P. matildae*, *P. colodactylus*, *P. muranunka*, and an undescribed species). Thus, by 2020, the *P. orestes* species group contained 14 species and 4 undescribed species, all from the Andes of central and southern Ecuador. Herein we describe three new cryptic species of the *P. colodactylus* subgroup from southern Ecuador; these new species are morphologically different from the congeners of the other two subgroups, but also from all sister species in the *P. colodactylus* subgroup, from which they additionally differ in their arboreal habits.

Materials and Methods

Specimen Collection and Study Site

Specimens were collected during several field expeditions carried out between May 2015 and May 2022 in Abra de Zamora (Loja Province, southern Ecuador; 3.9922°S, 79.1455°W; datum = WGS84 in all cases; 2,812 m a.s.l.), the Cajanuma sector of Parque Nacional Podocarpus (Loja Province; 4.1128°S, 79.1767°W, 2,991 m), the Cerro Toledo sector of Parque Nacional Podocarpus (Loja and Zamora Chinchipe provinces; 4.3796°S, 79.1124°W, 3,080 m), Reserva Numbala (Zamora Chinchipe Province; 4.4065°S, 79.0885°W, 2,875 m), Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca (Zamora Chinchipe Province; 4.4472°S, 79.1459°W, 2,880 m), and Reserva Tapichalaca (Zamora Chinchipe Province; 4.4861°S, 79.1529°W, 2,915 m). Intensive visual encounter surveys and auditory surveys were made, both during the day and during the night (1200 to 0200 h) in all the sampled areas.

The study sites (Fig. 2) are located inside or in the close vicinity of Parque Nacional Podocarpus, southern Ecuador (Loja and Zamora Chinchipe provinces). The park was declared in 1982 and comprises an area of 146,289 ha; it has a very irregular topography covering altitudes from 900 to 3,650 m, with large areas of diverse natural habitats (Rahbek et al. 1995; Ordóñez-Delgado et al. 2019), and it is part of the Tropical Andes hotspots, the richest in biodiversity on the planet (Myers et al. 2000). The area sampled for our study has an altitudinal range between 2,800 and 3,100 m and consists of subpáramo or evergreen elfin forest (Homeier et al. 2008).

We used the following terms for ranking species relative abundance (as presented in Székely et al. 2020): common—when the species presence was detected (seen or heard), in the proper habitat, in large or moderate numbers, on more than 50% of the sampling days/nights; uncommon—when the species presence was detected in moderate or small numbers, on 25–50% of the sampling days/nights; rare—when the species presence was detected in small numbers on less than 25% of the sampling days/nights.

All collected specimens were photographed alive, euthanized using 20% benzocaine, fixed in 10% formalin, and stored in 70% ethanol. Tissue samples for genetic analyses were preserved in 96% ethanol. Examined specimens (listed in the type-series and Appendix I) are housed at Museo de Zoología, Universidad Técnica Particular de Loja, Loja, Ecuador (MUTPL), Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ), and Museo de Zoología, Universidad Tecnológica Indoamérica, Quito, Ecuador (MZUTI).

Molecular Analyses

Genomic extraction, amplification, and sequencing were as described in Székely et al. (2020); the newly generated DNA sequences were deposited in GenBank (Appendix II). For the phylogenetic analysis we used sequences of two mitochondrial ribosomal genes (12S and 16S rRNA) and one nuclear gene (recombination-activating gene 1 [RAG-1]) from 43 individuals of 21 species corresponding to 19 different localities from Ecuador (Appendix II), representing all the currently confirmed species of the *Pristimantis orestes* species group (GenBank-available sequences and 25 new sequences generated by this study). As outgroups, we used *Pristimantis ceuthospilus*, *P. diadematus*, *P. imitatrix*, *P. rhodoplichus*, *P. unistrigatus*, and *P. wiensi*. The tree was rooted with *P. galdi*.

We edited, assembled, and aligned (MAFFT algorithm with the G-INS-i iterative refinement method; Katoh and Standley 2013) the sequences using the program Geneious Prime (v2022.2.2, Biomatters Ltd., Auckland, New Zealand). We inspected visually, in PhyDE v0.9971 (Müller et al. 2010), the edited alignments of 12S, 16S, and RAG-1 sequences to correct potential alignment errors, concatenated them into a single matrix, and then used them for the phylogenetic analyses. The phylogenetic analyses were based on a 2,733-base pair (bp) dataset (901 bp for 12S, 1,193 bp for 16S, and 639 bp for RAG-1). The aligned and concatenated matrix is available at https://dx.doi.org/10.5281/zenodo.7262263. We conducted Basic Local Alignment Search Tool (BLAST) searches to identify similar sequences of 12S, 16S, and RAG-1 in GenBank and used FastTree v2.1 (Price et al. 2010) to build an exploratory tree with most of the available Ecuadorian *Pristimantis* sequences in order to determine the relationships of the new species. Both the BLAST searches and the FastTree indicated that the new species are part of the *P. orestes* species group.

Phylogenetic relationships were inferred using both Maximum Likelihood and Bayesian Inference. We used PartitionFinder v2.1.1 (Lanfear et al. 2017) to select the best partition scheme based on the corrected Akaike Information Criterion (AICc) for model selection. PartitionFinder identified three partition schemes (best model in parentheses): 12S and 16S (GTR+I+G), RAG-1 1st and 2nd position (F81+G), and RAG-1 3rd position (HKY+G). Maximum Likelihood analyses were conducted in GARLI v2.1 (Zwickl 2006), performing 1,000 tree searches (four independent searches, two with the "streefname" set to random and two set to stepwise, with 250 replicates each) and node support assessed with 1,000 bootstrap replicates. Bayesian Inference analysis was implemented in MrBayes v3.2.6 (Ronquist et al. 2012), the Markov Chain Monte Carlo runs being performed twice, independently, for 50 million generations, with trees sampled every 1,000 generations until convergence ($P < 0.001$), and consensus trees were summarized after discarding the initial 25% as burn-in. More details about how tree searches were performed are presented in Székely et al. (2020).

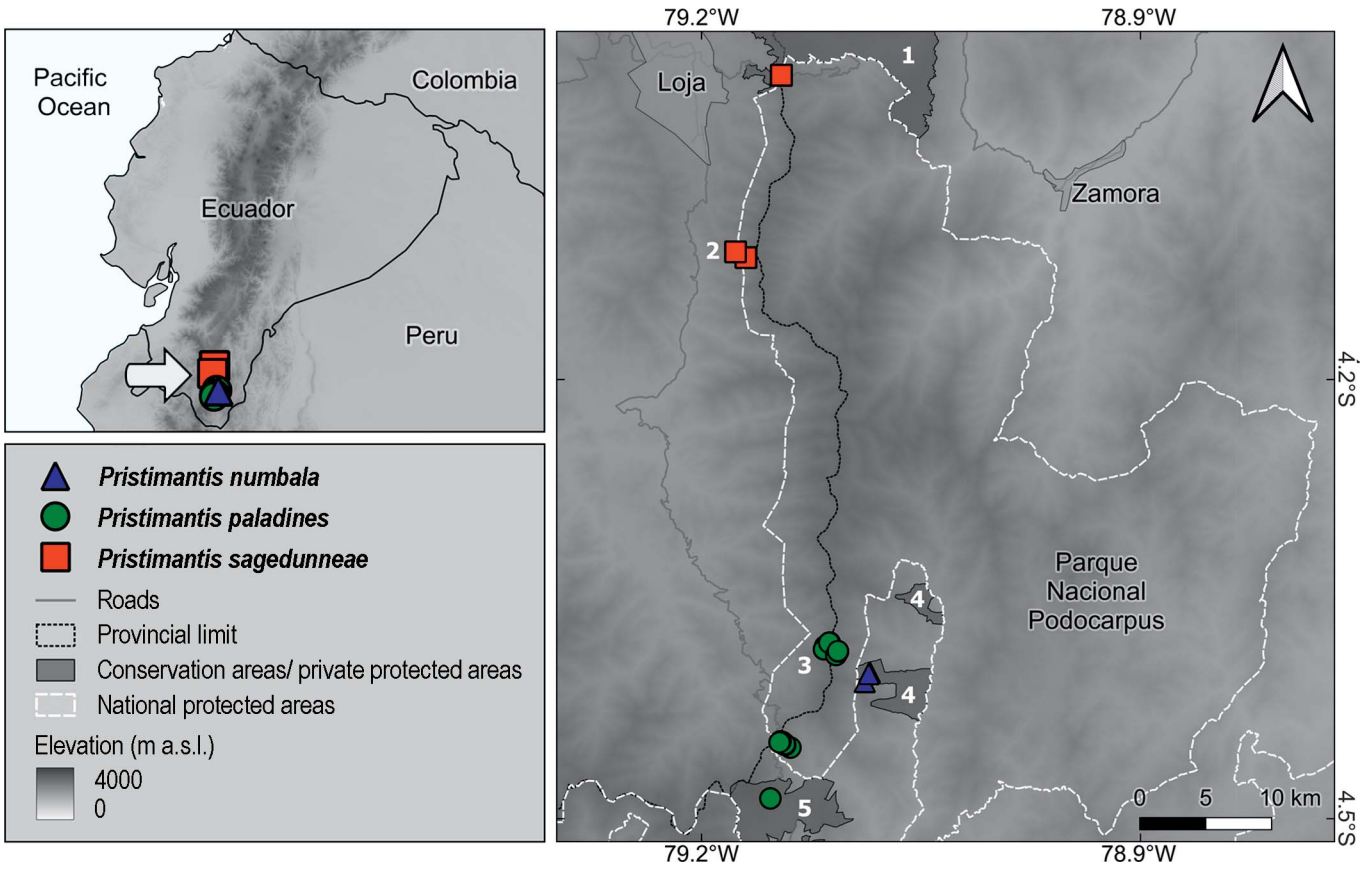

Fig. 2.—Distribution of the three new species. Records are based on specimens deposited at the Museo de Zoología, Universidad Técnica Particular de Loja, Loja, Ecuador (MUTPL) and field data. The numbers represent important sampling areas: (1) Abra de Zamora; (2) Cajanuma sector of Parque Nacional Podocarpus; (3) Cerro Toledo sector of Parque Nacional Podocarpus; (4) Reserva Numbala; (5) Reserva Tapichalaca.

We a priori regarded that a tree node had strong support when its bootstrap value was >75 and its Bayesian posterior probability was >0.95, moderate support for 50–75 and 0.90–0.95, and weak support or nonresolved for values lower than 50 and 0.90, respectively. Uncorrected genetic p-distances were calculated for 16S with MEGA6 (Tamura et al. 2013) and are presented in Supplemental File S1, available online.

Morphological Analyses

For the description of qualitative and quantitative morphological characters, as well as the format of the description, we largely follow Duellman and Lehr (2009). Sex was determined by gonadal inspection. Juveniles and subadults were distinguished from the adults by the smaller size, slightly more tuberculate skin, and condition of oviducts and/or ovarian eggs (Duellman and Lehr 2009). As suggested by Duellman and Lehr (2009), we designated the large tubercle at the base of Finger I (thumb) as the thenar tubercle, and the usually much larger and commonly bifurcate (partially divided distally) tubercle at the base of Fingers III and IV as the palmar tubercle. Based on Lynch and Duellman (1997), we classified the relative lengths of toes V and III as follows: Toe V is slightly longer than Toe III when the tip of Toe V does not reach the proximal edge of the distal subarticular tubercle on Toe IV, when they are adpressed; Toe V is longer than Toe III when its tip reaches the proximal edge of the distal subarticular tubercle in Toe IV but does not extend to its distal edge; Toe V is much longer than Toe III if the tip of Toe V reaches, or extends beyond, the distal edge of the distal subarticular tubercle on Toe IV. Coloration of live specimens was based on field notes and digital photographs. We refer to coloration in life unless otherwise stated.

For comparison of several important features we used predetermined categories, due to the fact that the available morphometric data is limited to a relatively small number of specimens or missing altogether. Thus, the body size (relative size inside the *P. orestes* species group) was defined as: minute (when the largest recorded female snout–vent length [SVL] is smaller than 21 mm); small (female SVL smaller than 23 mm); medium (female SVL smaller than 25 mm); and large (female SVL larger than 25 mm). Snout length was defined as: very short (when the average eye–nostril distance [END] is less than 8% of the SVL); short (average END is less than 9% of the SVL); and long (average END is more than 9% of the SVL). Finger III length (or hand length) was defined as: very short (when the average length of Finger III is less than 22% of the SVL); short (average length of Finger III is less than 24% of the SVL); medium (average length of Finger III is less than 26% of the SVL); long (average length of Finger III is less than 28% of the SVL); and very long (average length of Finger III is larger than 28% of the SVL). Toe IV length (or foot length) was defined as: very short (when the average length of Toe IV is less than 38% of the SVL); short (average length of Toe

IV is less than 40% of the SVL); medium (average length of Toe IV is less than 46% of the SVL); long (average length of Toe IV is less than 48% of the SVL); and very long (average length of Toe IV is larger than 48% of the SVL). Tympanum was defined as: present (tympanic membrane absent but tympanic annulus evident or both tympanic membrane and annulus present) or absent (both tympanic annulus and tympanic membrane absent).

All adult specimens were weighted (body mass) before euthanasia using a MyWeigh Triton T3 portable scale with 0.01 g precision. Measurements of the preserved specimens were taken under a stereo microscope, with a Vernier caliper, and rounded to the nearest 0.1 mm. Specimens were measured for the following morphometric variables: (1) SVL, distance from the tip of snout to posterior margin of vent; (2) head width, widest portion of the head, measured at level of jaw articulation; (3) head length, distance from the tip of snout to posterior angle of jaw articulation; (4) interorbital distance, distance between the inner margins of the orbits; (5) internarial distance, distance between the inner edges of the narial openings; (6) upper eyelid width, the perpendicular distance to the outer edge of the eyelid; (7) eye diameter, distance between anterior and posterior borders of eye; (8) END, distance from posterior margin of nostril to anterior margin of eye; (9) thigh length, length of thigh from vent to knee; (10) tibia length, length of flexed leg from knee to heel; (11) foot length (length of Toe IV), distance from proximal margin of inner metatarsal tubercle to tip of Toe IV; (12) hand length (length of Finger III), distance from proximal edge of palmar tubercle to the tip of Finger III (Székely et al. 2020). Additionally, we defined and measured the (13) head height, as the highest portion of the head, measured at level of jaw articulation, and (14) body height, the highest portion of the body, measured at level of the iliosacral articulation. Measurements are given as mean ± SD. All raw measurements are presented in File S2.

To evaluate the differences in the shape of animals in relation to their preferred microhabitat, we classified the species in categories according to their phylogenetic subgroup, i.e., *P. simonbolivari* (includes *P. tiktik* and *P. samaniegoi*), *P. orestes* (*P. andinognomus*, *P. cajanuma*, *P. orestes*, and *P. vidua*), but dividing the *P. colodactylus* subgroup into two separate categories based on their microhabitat: bromeliad *P. colodactylus* (*P. colodactylus*, *P. matildae*, and *P. muranunka*) and arboreal *P. colodactylus* (*P. numbala*, *P. paladines*, and *P. sagedunnae*). As proxies for the shape of individuals, we calculated the head ratio (head height/SVL) and body ratio (body height/SVL). Comparison of these parameters between the four categories of species was done through analysis of variance (ANOVA) tests, after checking that the normality (Q–Q plot inspection) and homogeneity of variance (Levene's test) assumptions were met; if ANOVA tests were significant, we followed with Tukey's honestly significant difference (HSD) post hoc. To check for differences in morphological traits between pair of species, we used Mann–Whitney *U*-tests (due to low sample sizes), using only the measurements from females. All statistical analysis was performed in IBM SPSS Statistics v25 (IBM SPSS Statistics, Armonk, NY), with a significance level of $\alpha = 0.05$.

Results

Phylogeny

The Bayesian and Maximum likelihood phylogenetic trees showed almost the same topology, with minor differences in the position of some of the unresolved branches, with stronger Bayesian Inference support for some of the tree nodes (Fig. 3). Similar to Brito et al. (2017a), Urgilés et al. (2019), and Székely et al. (2020), we recovered the *Pristimantis orestes* species group as monophyletic, with strong support (bootstrap values = 100%; posterior probabilities = 1) in both analyses. Also, the three subgroups (*P. orestes*, *P. simonbolivari*, and *P. colodactylus*, sensu Székely et al. 2020) have strong support in both analyses. Additionally, the new tree has a similar topology with the one presented in Székely et al. (2020), with some small differences in the position of the unresolved branches of the *P. orestes* and *P. simonbolivari* subgroups.

The three new species are part of the *P. colodactylus* subgroup and form, together with their sister species *P. matildae*, a strongly supported clade (bootstrap values = 99.6%; posterior probabilities = 1); the exact relationship between the new species remains nonresolved (Fig. 3). Uncorrected genetic p-distances for the gene 16S of the new species and their sister species, *P. matildae*, ranges between 2.4% and 4.9%; the distances from the other species of the *P. colodactylus* subgroup ranges between 6.0% and 10.5%, and from the species of the *P. orestes* and *P. simonbolivari* subgroups between 7.5% and 13.0% (File S1).

Uncorrected genetic p-distances between the new species are as follows: between *P. sagedunneae* and *P. paladines* range from 2.0% to 2.8%; between *P. sagedunneae* and *P. numbala* range from 4.3% to 4.9%; and between *P. paladines* and *P. numbala* range from 3.4% to 4.4%. As for the intraspecific uncorrected genetic p-distances, these did not surpass 0.2% for *P. sagedunneae*, 0.7% for *P. paladines*, and 0.1% for *P. numbala* (File S1).

Morphology

Our morphometric analysis suggests that the bromeliad specialist species from the *P. colodactylus* subgroup have a different body shape by having both flatter heads (ANOVA $F_{3,122} = 48.86$, $P < 0.001$; Fig. 4; Table 1) and slender (more-compressed) bodies (ANOVA, $F_{3,122} = 14.19$, $P < 0.001$; Fig. 5; Table 1) compared to both the species in the other two subgroups and to the newly described arboreal sister species. The three new species have a body shape more similar to the species of the *P. orestes* and *P. simonbolivari* subgroups than to their bromeliad sister species from the *P. colodactylus* subgroup (Figs. 1, 4, 5).

Taxonomy

Pristimantis ***sagedunneae*** sp. nov.
(Figs. 6–9)

Holotype.—MUTPL 500 (Field no. SC 230; Figs. 6–8), an adult female from Ecuador, Loja Province, Abra de Zamora (3.9922°S, 79.1455°W), 2,812 m, collected by P. Székely and F. Stănescu on 13 November 2018.

Paratypes (4 females, 1 juvenile).—MUTPL 1094 (Field no. SC 1206), MUTPL 1095 (Field no. SC 1207; Figs. 9B, E, H), two adult females and MUTPL 1096 (Field no. SC 1208; Fig. 9C, F, I), a juvenile, collected from the

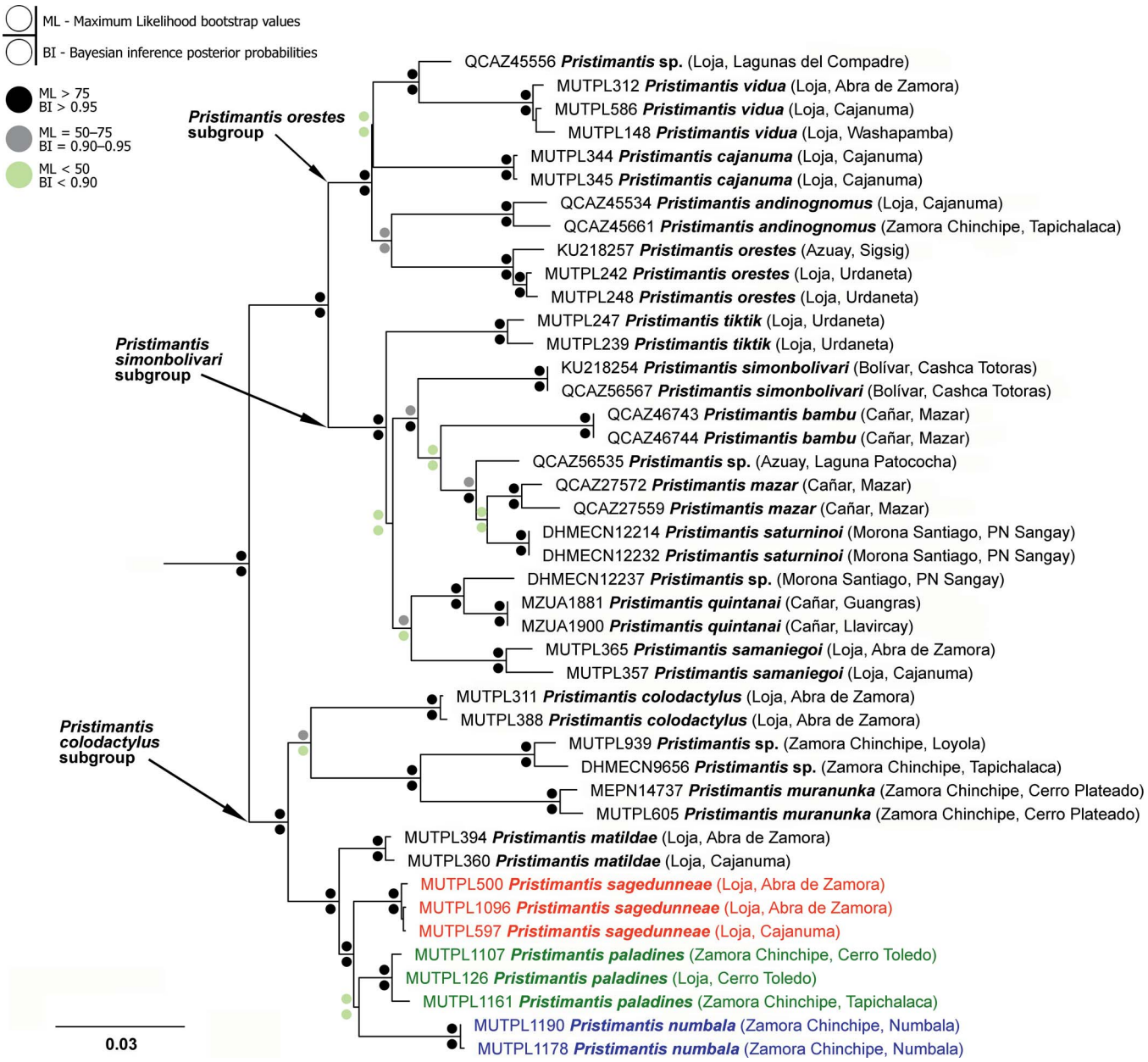

FIG. 3.—Maximum likelihood phylogram of the *Pristimantis orestes* species group based on 2,733 base pairs of concatenated mitochondrial DNA from 12S and 16S, and nuclear DNA from RAG-1 gene fragments. Outgroup is not shown. The catalog number, species name, province, and short locality name of the vouchers are shown next to each terminal; all samples are from Ecuador (associated data are listed in Appendix II).

type locality by P. Székely, D. Székely, D. Armijos-Ojeda and A. Jara-Guerrero on 4 June 2021; MUTPL 597 (Field no. SC 252; Fig. 9A, D, G), adult female, from Loja Province, Cajanuma entrance to the Parque Nacional Podocarpus, on Los Miradores trail (4.1128°S, 79.1767°W), 2,991 m, collected by P. Székely on 12 January 2019; MUTPL 911 (Field no. SC 421), adult female, from Loja Province, Cajanuma entrance to the Parque Nacional Podocarpus, on Los Miradores trail (4.1167°S, 79.1697°W), 2,861 m, collected by S. Hualpa-Vega and D. Hualpa-Vega on 8 December 2019.

Diagnosis.—We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 3) and on the general morphological similarity to other members of the genus. *Pristimantis sagedunneae* is a medium-sized species (among the *P. orestes* group; Table 2), distinguished by the following combination of traits: (1) skin on dorsum shagreen with some scattered tubercles (feature more evident in life); skin on venter areolate; discoidal fold present; dorsolateral folds absent; flanks usually with longitudinal lateral folds on anterior half; low middorsal fold present; (2) tympanic annulus and tympanic membrane absent; supratympanic fold present; (3) snout subacuminate to rounded in dorsal view, rounded in profile; canthus rostralis concave in dorsal view, rounded in profile; (4) upper eyelid bearing one larger tubercle and several small tubercles (feature more evident in life), it's width about 68% of interorbital distance; cranial crests absent; (5) dentigerous processes of vomers concealed in buccal mucosa; each process bearing three to five teeth; (6) condition of vocal sacs, vocal slits, and nuptial pads

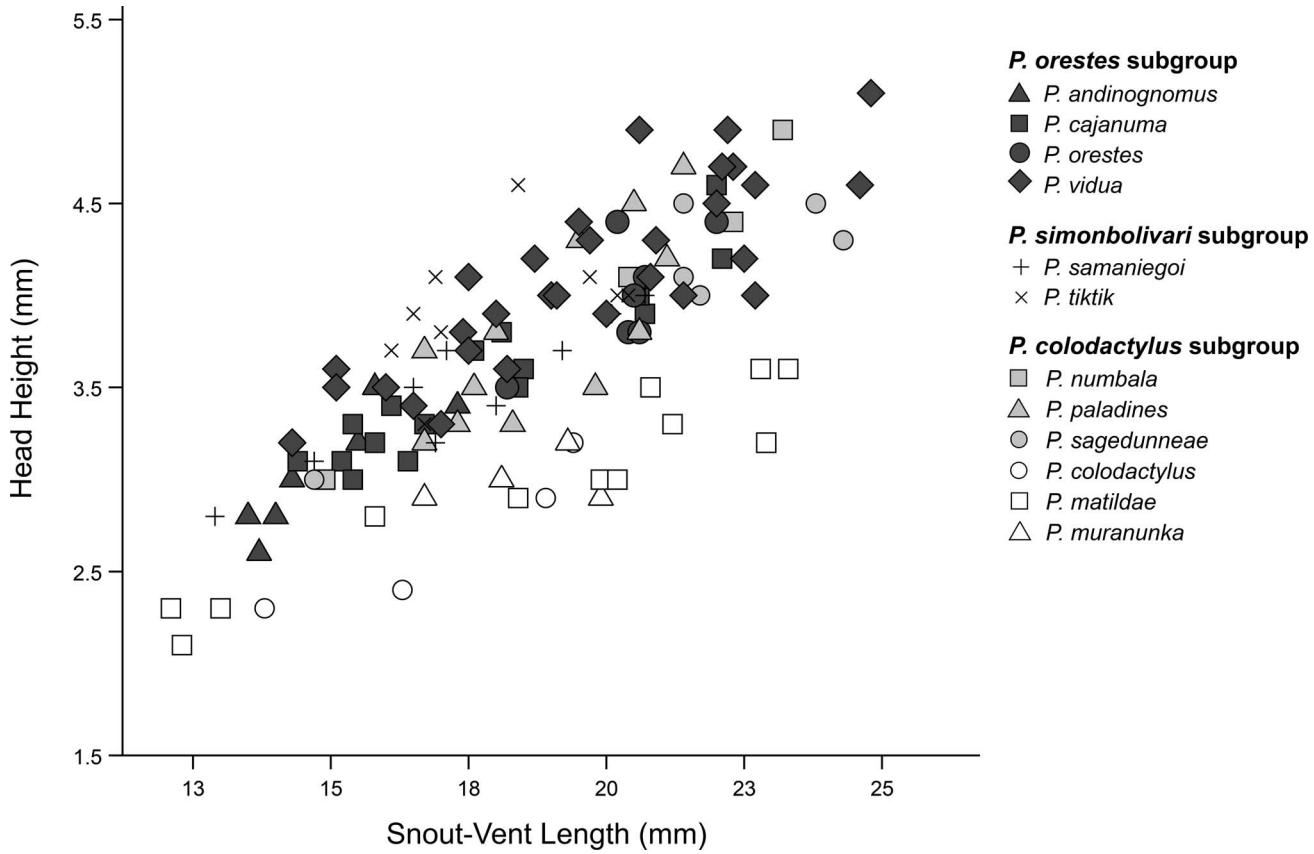

Fig. 4.—Relationship between head height and SVL in the three subgroups of the *Pristimantis orestes* species group. Among the *P. colodactylus* subgroup, *P. colodactylus*, *P. matildae*, and *P. muranunka* are bromeliad specialists (open symbols), while *P. numbala*, *P. paladines*, and *P. sagedunneae* are arboreal species.

unknown; (7) Finger I shorter than Finger II; discs on fingers broadly expanded, truncate; circumferential grooves present; (8) fingers bearing lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present; palmar tubercle divided into a larger (inner) and a smaller (outer) tubercle(s); thenar tubercle elliptical, same size with the inner palmar tubercle; (9) ulnar tubercles present (feature more evident in life); (10) heel with one to three large tubercles and several small tubercles (feature more evident in life); outer edge of tarsus with row of small tubercles (feature more evident in life); inner tarsal fold present; (11) inner metatarsal tubercle broadly ovoid, about 3× to 4× the size of subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present; (12) toes bearing broad lateral fringes; webbing basal; Toe V longer than Toe III; discs on toes broadly expanded, truncate, about same size as those on fingers; circumferential grooves present; (13) in life, dorsum brownish gray, with blackish or dark brown bars that on the middle of the back conjoin in >X or XXX-like shapes; flanks, dorsal surfaces of arms, and of hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs, groin, and concealed limb surfaces red or intense red; head with a wide, black-bordered light interorbital bar, dark labial bars, and dark supratympanic stripes; venter and ventral surfaces of hindlimbs and arms pinkish white or pinkish gray, with or without dark markings on the throat; iris bronze with black reticulations and a median, wide, horizontal dark red streak; (14) SVL 21.4–24.3 mm in adult females (22.5 ± 1.41, n = 5); males unknown.

Comparisons with similar species.—*Pristimantis sagedunneae* is morphologically very different from the brome-

Table 1.—Pairwise comparisons between species subgroups (post hoc Tukey's honestly significant difference tests) for head height/SVL (shown above the diagonal) and body height/SVL (shown under the diagonal) ratios. Bolded text indicates significant differences with an $\alpha = 0.05$. The species included in the analysis are: *Pristimantis colodactylus* subgroup bromeliad species (*P. colodactylus*, *P. matildae*, and *P. muranunka*), *P. colodactylus* subgroup arboreal species (*P. numbala*, *P. paladines*, and *P. sagedunnae*), *P. simonbolivari* subgroup (*P. tiktik* and *P. samaniegoi*), and *P. orestes* subgroup (*P. andinognomus*, *P. cajanuma*, *P. orestes*, and *P. vidua*).

	P. colodactylus subgroup, bromeliad species	*P. colodactylus* subgroup, arboreal species	*P. simonbolivari* subgroup	*P. orestes* subgroup
P. colodactylus subgroup, bromeliad species		**$P < 0.0001$**	**$P < 0.0001$**	**$P < 0.0001$**
P. colodactylus subgroup, arboreal species	**$P = 0.001$**		**$P = 0.043$**	$P = 0.253$
P. simonbolivari subgroup	**$P = 0.001$**	$P = 0.991$		$P = 0.469$
P. orestes subgroup	**$P < 0.0001$**	$P = 0.249$	$P = 0.515$	

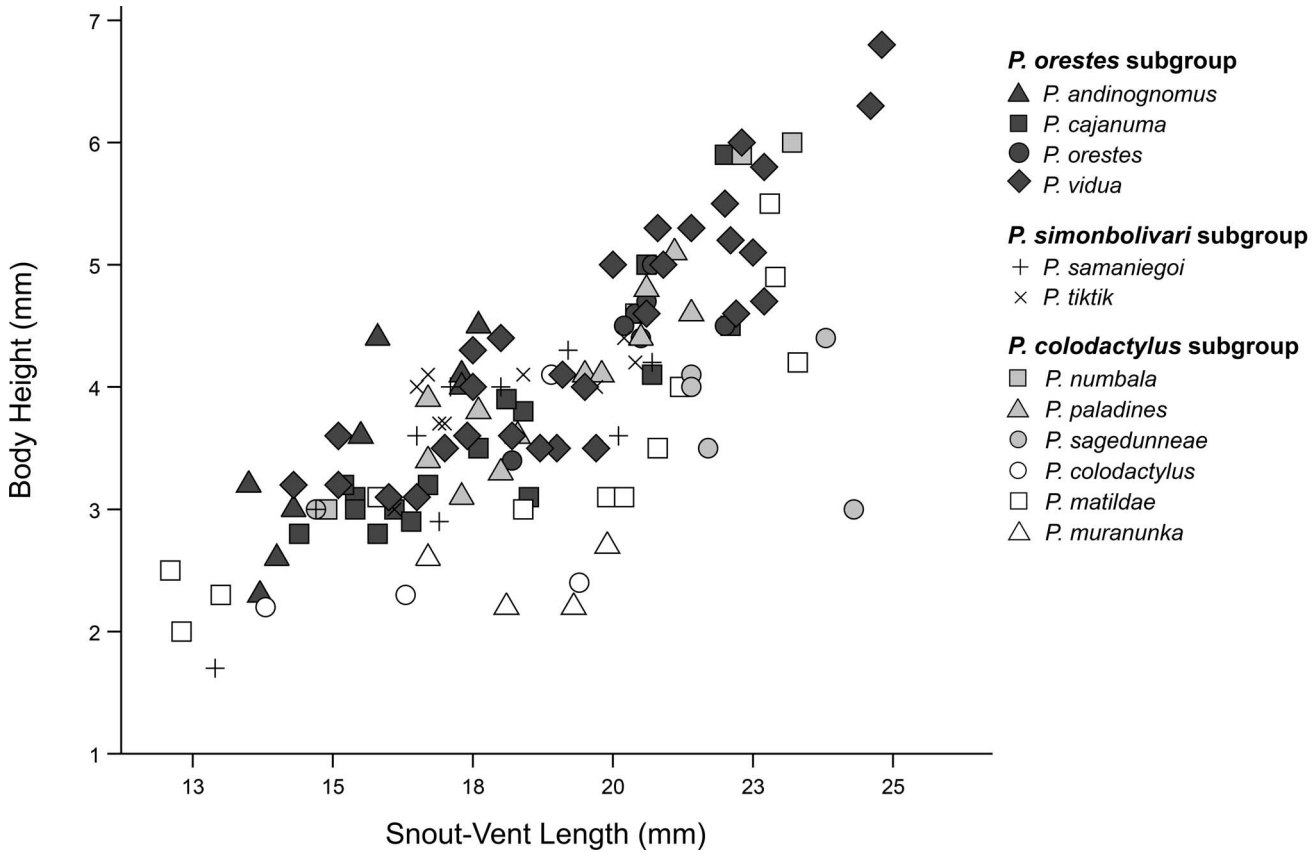

FIG. 5.—Relationship between body height and SVL in the three subgroups of the *Pristimantis orestes* species group. Among the *P. colodactylus* subgroup, *P. colodactylus*, *P. matildae*, and *P. muranunka* are bromeliad specialists (open symbols), while *P. numbala*, *P. paladines*, and *P. sagedunneae* are arboreal species.

liad specialist species of the *P. colodactylus* subgroup, being distinguished mainly by the general habitus, with not compressed body and head, much longer fingers and toes and the general coloration, and from the other species of the *P. orestes* group, mainly by the much longer fingers and toes and the general coloration (Figs. 1, 4, 5; Table 2). It is most similar to the other two new species, *P. paladines* and *P. numbala*.

From the 17 species that are currently included in the *P. orestes* group, only 6 species lack tympanic annuli and membranes: *P. samaniegoi*, *P. colodactylus*, *P. matildae*, *P. paladines*, *P. numbala*, and *P. sagedunneae* (Table 2). However, *P. sagedunneae* differs from *P. samaniegoi* by its larger size (SVL $>$ 21 mm vs. SVL $<$ 20.7 mm in *P. samaniegoi*), longer snout (END $>$ 2.1 mm vs. END $<$ 1.8 mm), longer fingers (Finger III length $>$ 6.3 mm vs. Finger III length $<$ 5.1 mm), longer toes (Toe IV length $>$ 10.1 mm vs. Toe IV length $<$ 8.3 mm), discs on fingers and toes broadly expanded (vs. slightly expanded), and by different coloration pattern, with blackish or dark brown bars that on the middle of the back conjoin in >X or XXX-like shapes and with large areas of the dorsal surfaces of thighs, groin, and concealed limb surfaces being red or intense red (vs. dorsum, flanks, dorsal surfaces of hindlimbs and arms dark brown with various white, irregular spots and dark gray venter in females). Within the *P. colodactylus* subgroup, *P. sagedunneae* can be distinguished from *P. muranunka* by the lack of tympanic annulus and tympanic membrane (vs. present in *P. muranunka*), and from *P. colodactylus* and *P. matildae* by having a noncompressed body and head (vs. compressed; Figs. 4 and 5; Table 1), longer fingers (Finger III length $>$ 6.3 mm vs. Finger III length $<$ 4.4 mm in *P. colodactylus* and $<$ 6.1 mm in *P. matildae*), longer toes (Toe IV length $>$ 10.1 mm vs. Toe IV length $<$ 7.5 mm in *P. colodactylus* and $<$ 9.8 mm in *P. matildae*), and by the typical red coloration present on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. concealed coloration missing in *P. colodactylus* and *P. matildae*; Table 2).

The three new species are morphologically similar and difficult to distinguish. However, there are several important features that can be used to identify each of them (Table 3). Thus, *P. sagedunneae* can be distinguished from *P. paladines* by its larger size (Mann–Whitney $U = 1$, $n_1 = n_2 = 5$, $P = 0.02$), shagreen dorsum (vs. tuberculate in *P. paladines*), low middorsal fold (vs. elevated, or tall middorsal fold that has usually several larger tubercles scattered along its length), the intense red coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. orange or reddish brown coloration), and the lack of green in the dorsal coloration (vs. frequently green present in the dorsal coloration). From *P. numbala*, *P. sagedunneae* can be distinguished by the subacuminate to rounded snout (vs. rounded to broadly rounded snout in *P. numbala*), the relative length of the toes, with Toe V longer than Toe III (vs. Toe V much longer than Toe III), the intense red

Fig. 6.—Adult female holotype of *Pristimantis sagedunneae* in life (MUTPL 500, SVL = 21.4 mm) from Abra de Zamora, Loja Province, 2,812 m: (A) dorsolateral view; (B) ventral view; (C) dorsal view.

coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. reddish brown coloration), and the lack of green in the dorsal coloration (vs. frequently green present in the dorsal coloration).

Description of holotype.—Adult female (MUTPL 500; Figs. 6–8), with small whitish eggs, head wider than body, wider than long, head length 82% of head width, head width 38% of SVL; head length 31% of SVL; snout long (END 10% of SVL), rounded in dorsal view and in profile, with small rostral papilla at tip of snout; canthus rostralis concave in dorsal view, rounded in profile; loreal region slightly convex; eye diameter larger than END; nostrils slightly protuberant, oriented posteriorly; lips not flared; cranial crests absent; upper eyelid bearing one larger tubercle and several small

Fig. 7.—Adult female holotype of *Pristimantis sagedunneae* in preservative (MUTPL 500, SVL = 21.4 mm) from Abra de Zamora, Loja Province, 2,812 m: (A) dorsal view; (B) ventral view; (C) lateral view.

tubercles (feature more evident in life); width of upper eyelid 69% of interorbital distance; tympanic annulus and tympanic membrane absent; supratympanic fold present; two large, rounded postrictal tubercles, separated by a large space between them; choanae large, round, partially concealed by palatal shelf of maxillary arch; dentigerous processes of vomers concealed in buccal mucosa but with process from the right side bearing three teeth; tongue longer than wider, slightly notched posteriorly, posterior half not adherent to floor of mouth.

Skin on dorsum shagreen with some scattered tubercles (feature more evident in life); thin, low middorsal fold starting at tip of snout and ending at cloaca; dorsolateral folds absent; flanks with longitudinal lateral folds on anterior half; skin on chest, belly, ventral surfaces of thighs areolate; thoracic fold absent, discoidal fold weak; cloacal region bordered ventrally by several small tubercles.

Ulnar tubercles present (trait more visible in life); outer palmar tubercle prominent, divided into a larger (inner) and a smaller (outer) tubercle(s); thenar tubercle elliptical, same size with inner palmar tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all fingers; supernumerary palmar tubercles rounded, large, just slightly smaller than subarticular tubercles; fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, truncate; all fingers bearing pads well defined by circumferential grooves.

Hindlimbs long, slender; tibia length 52% of SVL; foot length 50% of SVL; heel with two large and several small tubercles (trait more visible in life); outer edge of tarsus with row of small tubercles (trait more visible in life); inner edge of tarsus bearing short fold; inner metatarsal tubercle broadly ovoid, about 3× subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present in all toes; supernumerary plantar tubercles rounded or oval, smaller than subarticular tubercles; toes bearing lateral fringes; webbing basal; discs on toes broadly expanded, truncate, smaller than those on fingers; toes with ventral pads well defined by circumferential grooves; relative length of toes I <II < III < V < IV; Toe V longer than Toe

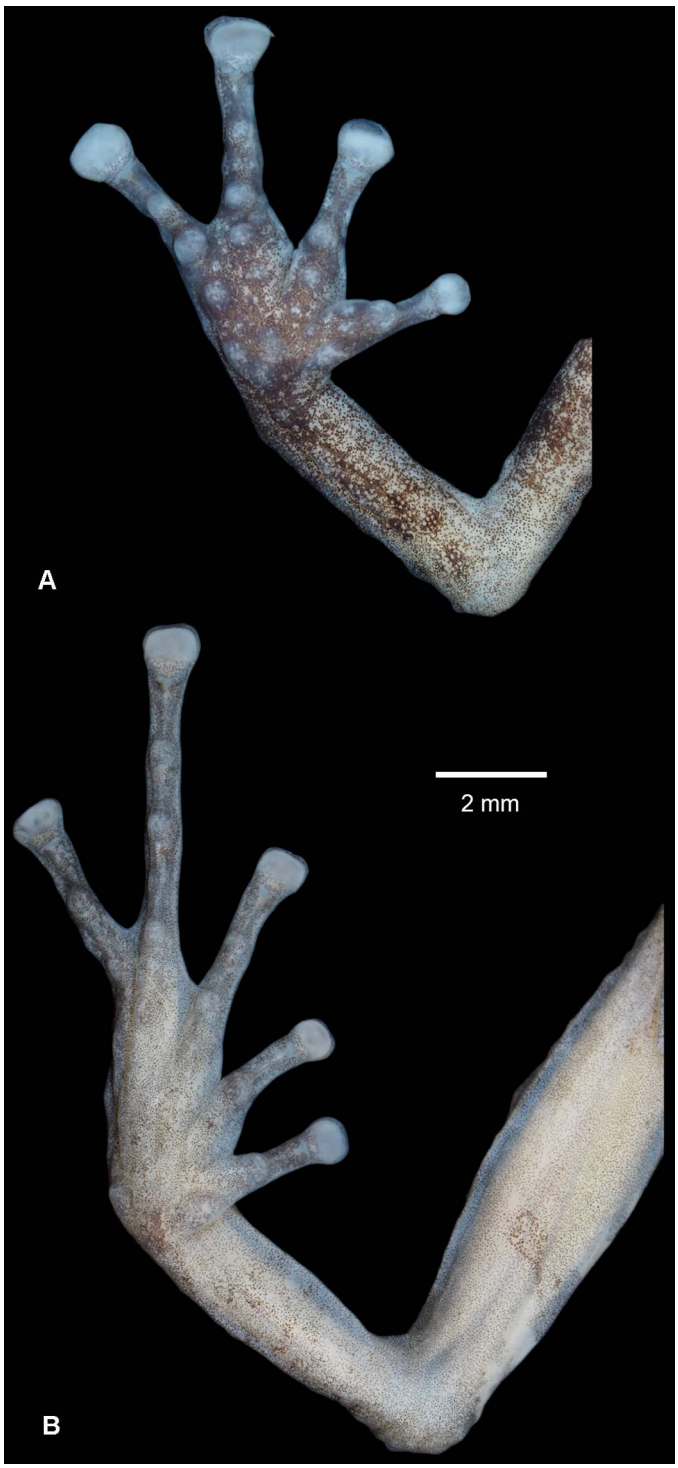

Fig. 8.—Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of female holotype *Pristimantis sagedunneae* (MUTPL 500, SVL = 21.4 mm) in preservative.

III (tip of Toe III extends beyond proximal edge of penultimate subarticular tubercle on Toe IV, tip of Toe V barely extends beyond proximal edge and not reaches distal edge of distal subarticular tubercle on Toe IV).

Coloration of holotype.—In life (Fig. 6): dorsum pinkish/brownish gray, with dark, blackish bars that on the middle of the back conjoin in a >X-like shape; flanks with wide, dark transverse bars; dorsal surfaces of arms and hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs, groin, and concealed limb surfaces are intense red; head with wide, black bordered light (whitish yellow), butterfly shaped interorbital bar, dark labial bars and dark supratympanic stripes; venter and ventral surfaces of hindlimbs and arms pinkish white or pinkish gray; throat white; iris bronze with black reticulations and a median, wide, horizontal dark red streak.

In preservative (Fig. 7): dorsum brownish gray with dark brown bars; flanks, dorsal surfaces of arms and hindlimbs brownish gray with dark transverse bars; head with black-bordered whitish yellow interorbital bar, dark labial bars and dark supratympanic stripes; venter, ventral surfaces of arms, and throat predominantly brown or dark brown; ventral surfaces of hindlimbs whitish yellow.

Measurements of holotype (in mm).—SVL 21.4; head width 8.1; head length 6.6; interorbital distance 2.6; internarial distance 2.1; upper eyelid width 1.8; eye diameter 2.4; END 2.1; thigh length 10.2; tibia length 11.2; foot length 10.6; hand length 6.3.

Body mass of holotype.—0.91 g.

Variation.—Morphometric variation is shown in Table 4. The dark, blackish bars that conjoin on the middle of the back have various forms, such as >X, XX, XXX, or W-like shapes, and were unique for each of the encountered individuals. These characteristic patterns formed by the bars probably can be used for the individual photographic identification. Of all encountered animals, paratype MUTPL 597 (Fig. 9A, D, G) had the most-intense red coloration of the dorsal surfaces of thigh, groin, and concealed limb surfaces. This specimen had also the largest areas colored with red, having even the toes and fingertips red (Fig. 9A). The iris of the paratype MUTPL 1095 (Fig. 9B) had a very light coloration, being almost white, except for the horizontal dark red streak. The sole encountered juvenile (paratype MUTPL 1096) had just a little bit of the dorsal surfaces of thighs and groins colored with red (Fig. 9C). We suspect that, as the individuals mature, the intensity of the color and the superficies covered with red increases in this species.

Advertisement call.—Unknown.

Etymology.—The specific name *sagedunneae* is a noun in the genitive case and honors Sage Dunne, in recognition of her passion for Andean wildlife and her family's invaluable support of conservation work in Ecuador. Of particular importance is their contribution to the amphibian conservation in the Sangay-Podocarpus connectivity corridor, Ecuador's first ecological corridor, which protects 567,067 ha of high-elevation páramo grasslands and cloud forest ecosystems, as well as chains of lakes and wetlands, with unique biological diversity and endemism.

Common English name.—Sage Dunne's Rain Frog.

Common Spanish name.—Cutín de Sage Dunne.

Distribution.—*Pristimantis sagedunneae* is known only from Abra de Zamora and about 13 km to the south, from the Cajanuma sector of Parque Nacional Podocarpus (Fig. 2). All the specimens from Abra de Zamora were encountered in only one very small area (less than 50 m^2) and in Cajanuma only on the Los Miradores trail. We were not able to encounter this species in adjacent areas, with similar ecosystems, despite intensive fieldwork carried out since 2016. The specimens were encountered at an altitudinal

FIG. 9.—Color variation in life for individuals of *Pristimantis sagedunneae*, in dorsolateral or lateral, dorsal, and ventral views. (A, D, G) MUTPL 597, SVL = 21.7 mm, adult female paratype from the Cajanuma entrance to the Parque Nacional Podocarpus, Loja Province, 2,991 m; (B, E, H) MUTPL 1095, SVL = 23.8 mm, adult female paratype from Abra de Zamora, Loja Province, 2,812 m; (C, F, I) MUTPL 1096, SVL = 14.7 mm, juvenile paratype from Abra de Zamora, 2,812 m.

range between 2,800 and 3,000 m in subpáramo ecosystems (Homeier et al. 2008).

Natural history.—This is a rare species, or at least with a very low detectability. Between 2016 and 2022 we encountered only seven specimens of *P. sagedunneae*, and during only 4 d out of more than 50 d of fieldwork in the area. All animals were encountered during the night, perching on moss-covered branches or leaves, from 40 cm up to 2 m high, in habitats with shrubby vegetation. No individual was encountered inside bromeliads. Unfortunately, despite intensive searches, we were not able to hear or encounter any males. Sympatric frog species include *Pristimantis* aff. *andinognomus*, *P. cajanuma*, *P. matildae*, *P. samaniegoi*, *P. versicolor* (Lynch 1979), and *P. vidua*.

Conservation status.—*Pristimantis sagedunneae* is known from only two close localities, from an estimated area of less than 10 km^2. Although both localities are inside a nationally protected area, we recommend that this species be categorized as Endangered following the B1ab(iii,iv,v)+2ab(iii,iv,v) International Union for Conservation of Nature (IUCN) criteria (IUCN 2001) because: (1) its Extent of Occurrence (EOO) and Area of Occupancy (AOO) are estimated to be less than 10 km^2; (2) it is known from only a few individuals and only from two localities; and (3) its habitats could be affected in the near future, as they are situated in the vicinity of densely populated areas (Ordóñez-Delgado et al. 2020).

Pristimantis ***paladines*** sp. nov.
(Figs. 10–14)

Holotype.—MUTPL 1159 (Field no. SC 1260; Figs. 10–12), an adult female from Ecuador, Zamora Chinchipe Province, Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca (4.4472°S, 79.1459°W), 2,880 m, collected by P. Székely, D. Székely, D. Armijos-Ojeda, and L. Carrión on 27 August 2021.

Paratypes (4 females, 5 males and 2 subadults).—MUTPL 1151 (Field no. SC 1252; Fig. 13A, D, G), MUTPL 1155 (Field no. SC 1256), MUTPL 1160 (Field no. SC 1261; Fig. 13B, E, H), and MUTPL 1161 (Field no. SC 1262; Fig. 13C, F, I), four females collected with the holotype; MUTPL 122, MUTPL 123, MUTPL 125 (Fig. 14A, D, G), three adult

Table 2.—Comparison of several important features of the currently confirmed species of the *Pristimantis orestes* group. For the definition of the categories see Morphological Analyses in the Material and Methods section. Special coloration: refers to some kind of distinctive coloration (in females or both sexes), either ventral or dorsal spots, or markings in axilla, groin, or on concealed limb surfaces. ? = Indicates that we lack information or that the available data are uncertain due to incomplete measurements and/or possible identification errors. *Incorrectly defined as slightly expanded in Székely et al. 2020. SVL = snout–vent length; END = eye–nostril distance.

	Body size	Snout length	Finger III length	Toe IV length	Relative lengths of toes	Discs on fingers and toes	Tympanum	Vocal slits	Special coloration	Source
Pristimantis orestes subgroup										
P. vidua	Large (females SVL up to 26.8 mm)	Very short (END about 7.8% of SVL)	Medium (length of Finger III about 24.5% of SVL)	Short (length of Toe IV about 39.6% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Present	Present	No	This study
P. cajanuma	Small (females SVL up to 22.1 mm)	Short (END about 8.5% of SVL)	Long (length of Finger III about 27.3% of SVL)	Long (length of Toe IV about 46.7% of SVL)	Toe V slightly longer than Toe III	Expanded, rounded	Present	Present	Yes	This study
P. andinognomus	Minute (females SVL up to 17.9 mm)	Very short (END about 7.7% of SVL)	Short (length of Finger III about 23.4% of SVL)	Medium (length of Toe IV about 41.8% of SVL)	Toe V much longer than Toe III	Slightly expanded, rounded	Present	Present	Yes	This study
P. orestes	Large (females SVL up to 27.2 mm)	Short (END about 8.4% of SVL)	Short (length of Finger III about 23.0% of SVL)	Short (length of Toe IV about 39.9% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Present	Present	Yes	This study
Pristimantis simonbolivari subgroup										
P. tiktik	Minute (females SVL up to 20.4 mm)	Short (END about 8.0% of SVL)	Short (length of Finger III about 22.9% of SVL)	Short (length of Toe IV about 39.0% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Present	Present	Yes	This study
P. simonbolivari	Small (females SVL up to 22.0 mm)	Very short? (END about 7.6% of SVL)	?	?	?	Slightly expanded, rounded	Present	Present	Yes	Wiens and Coloma 1992
P. bambu	Large (females SVL up to 26.4 mm)	Short? (END about 9.0% of SVL)	Medium? (length of Finger III about 24.9% of SVL)	Medium? (length of Toe IV about 44.7% of SVL)	Toe V slightly longer than Toe III	Expanded, rounded to truncate	Present	Present	Yes	Arteaga-Navarro and Guayasamin 2011
P. mazar	Medium (females SVL up to 23.7 mm)	?	Short? (length of Finger III about 23.9% of SVL)	Short? (length of Toe IV about 39.0% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Present	Present	Yes	Guayasamin and Arteaga 2013
P. saturninoi	Small (females SVL up to 21.5 mm)	Short? (END about 8.4% of SVL)	Long? (length of Finger III about 26.0% of SVL)	Medium? (length of Toe IV about 41.6% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Present	Present	Yes	Brito et al. 2017b
P. quintanai	Small (females SVL up to 21.8 mm)	Very short (END about 7.5% of SVL)	Medium (length of Finger III about 24.3% of SVL)	Medium (length of Toe IV about 41.1% of SVL)	Toe V longer than Toe III	Expanded, rounded	Present	Present	Yes	This study
P. samaniegoi	Minute (females SVL up to 20.7 mm)	Short (END about 8.7% of SVL)	Short (length of Finger III about 23.5% of SVL)	Short (length of Toe IV about 38.6% of SVL)	Toe V slightly longer than Toe III	Slightly expanded, rounded	Absent	Present	Yes, in females	This study
Pristimantis colodactylus subgroup										
P. colodactylus	Minute (females SVL up to 20.7 mm)	Long (END about 9.2% of SVL)	Very short (length of Finger III about 21.6% of SVL)	Very short (length of Toe IV about 36.1% of SVL)	Toe V much longer than Toe III	Slightly expanded, rounded	Absent	Absent	No	This study
P. muranunka	Medium (females SVL up to 23.3 mm)	Long (END about 9.2% of SVL)	Short (length of Finger III about 22.7% of SVL)	Short (length of Toe IV about 38.5% of SVL)	Toe V longer than Toe III	Slightly expanded, rounded	Present	Absent	No	Brito et al. 2017a and this study
P. matildae	Medium (females SVL up to 23.3 mm)	Long (END about 9.1% of SVL)	Medium (length of Finger III about 25.2% of SVL)	Medium (length of Toe IV about 40.2% of SVL)	Toe V much longer than Toe III	Broadly expanded*, truncate	Absent	Absent	No	This study
P. sagedunneae	Medium (females SVL up to 24.3 mm)	Long (END about 10.1% of SVL)	Very long (length of Finger III about 28.4% of SVL)	Very long (length of Toe IV about 48.4% of SVL)	Toe V longer than Toe III	Broadly expanded, truncate	Absent	?	Yes	This study
P. paladines	Small (females SVL up to 21.4 mm)	Long (END about 9.6% of SVL)	Very long (length of Finger III about 28.6% of SVL)	Very long (length of Toe IV about 48.7% of SVL)	Toe V longer than Toe III	Broadly expanded, truncate	Absent	Absent	Yes	This study
P. numbala	Medium (females SVL up to 23.2 mm)	Long (END about 9.6% of SVL)	Very long (length of Finger III about 28.9% of SVL)	Very long (length of Toe IV about 48.3% of SVL)	Toe V much longer than Toe III	Broadly expanded, truncate	Absent	?	Yes	This study

TABLE 3.—Morphological trait comparison among the three new species. SVL = snout–vent length.

	Pristimantis sagedunneae	*Pristimantis paladines*	*Pristimantis numbala*
Relative body size	Medium	Small	Medium
Snout shape (in dorsal view)	Subacuminate to rounded	Acuminate to subacuminate	Rounded to broadly rounded
Relative head width	Head width about 37% of SVL	Head width about 38% of SVL	Head width about 40% of SVL
Canthus rostralis (in dorsal view)	Concave	Weakly concave to straight	Concave
Large tubercles on upper eyelid	One	Two to three	One
Relative width of upper eyelid	Width of upper eyelid about 68% of interorbital distance	Width of upper eyelid about 72% of interorbital distance	Width of upper eyelid about 83% of interorbital distance
Loreal region	Slightly convex	Slightly convex	Flat
Choanae	Large, round, partially concealed by palatal shelf of maxillary arch	Large, round, partially concealed by palatal shelf of maxillary arch	Large, oval, not concealed by palatal shelf of maxillary arch
Dentigerous processes of vomers	Concealed in buccal mucosa	Inconspicuous, oblique, ovoid or triangular, separated medially by distance lower than the width of processes	Evident, oblique, ovoid, separated medially by distance equal or slightly lower to the width of processes
Skin texture on dorsum	Shagreen with some scattered tubercles	Tuberculate, with numerous scattered large tubercles	Shagreen with some scattered tubercles
Middorsal fold	Low	Evident (tall), usually with several larger tubercles scattered along its length	Low
Thenar tubercle size	The same size with the inner palmar tubercle	Larger than the inner palmar tubercle	Larger than the inner palmar tubercle
Supernumerary palmar tubercles	Rounded, large, just slightly smaller than subarticular tubercles	Rounded, small, much smaller than subarticular tubercles	Oval, large, smaller than subarticular tubercles
Large tubercles on the heel	One to three	Two to three	One
Outer edge of tarsus	With a row of small tubercles	With a row of large, conical tubercles	With or without a row of small tubercles
Relative lengths of toes	Toe V longer than Toe III	Toe V longer than Toe III	Toe V much longer than Toe III

males, and MUTPL 124, MUTPL 126 two subadults from Loja Province, the Cerro Toledo sector of Parque Nacional Podocarpus (4.3796°S, 79.1124°W), 3,080 m collected by P. Székely and D. Székely on 10 May 2016; MUTPL 1107 (Field no. SC 1210; Fig. 14B, E, H) and MUTPL 1109 (Field no. SC 1212; Fig. 14C, F, I), two adult males from Zamora Chinchipe Province, the Cerro Toledo sector of Parque Nacional Podocarpus (4.3857°S, 79.1066°W), 3,104 m collected by P. Székely and D. Székely on 26 June 2021.

Diagnosis.—We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 3) and on the general morphological similarity to other members of the genus. *Pristimantis paladines* is a small species (among the *P. orestes* group; Table 2), distinguished by the following combination of traits: (1) skin on dorsum tuberculate with numerous scattered large tubercles (in life the tuberculated texture of the skin is more evident); skin on venter areolate; discoidal fold present; dorsolateral folds absent; flanks usually with longitudinal lateral folds on anterior half; middorsal fold evident, tall, usually with several larger tubercles scattered along its length (feature more evident in life); (2) tympanic annulus and tympanic membrane absent; supratympanic fold present; (3) snout acuminate to subacuminate in dorsal view, rounded in profile; canthus rostralis weakly concave to straight in dorsal view, rounded in profile; (4) upper eyelid bearing two to three large tubercles and several small tubercles (feature more evident in life), its width about 72% of interorbital distance in females and 81% of interorbital distance in males; cranial crests absent; (5) dentigerous processes of vomers inconspicuous, oblique, ovoid or triangular, separated medially by a distance smaller than the width of processes; each process

TABLE 4.—Body measurements of adults of the three new *Pristimantis* species. Body mass (in grams), snout–vent length (SVL) (in mm), and morphological proportions (in percentages). Values are given as mean ± SD (range). Raw measurements are presented in File S2. Female body mass includes eggs. *n = 4. END = eye–nostril distance; — indicates missing data.

	Pristimantis sagedunneae		*Pristimantis paladines*		*Pristimantis numbala*	
Character	Females (n = 5)	Males	Females (n = 5)	Males (n = 5)	Females (n = 3)	Males
Body mass	0.90 ± 0.09 (0.83–1.03)*	—	0.88 ± 0.18 (0.66–1.10)	0.50 ± 0.04 (0.45–0.55)	0.98 ± 0.16 (0.79–1.08)	—
SVL	22.5 ± 1.41 (21.4–24.3)	—	20.5 ± 0.82 (19.5–21.4)	17.4 ± 0.73 (16.7–18.3)	21.9 ± 1.43 (20.4–23.2)	—
Head width/SVL	36.7 ± 0.97 (35.4–37.9)	—	37.6 ± 0.91 (36.4–38.5)	35.9 ± 1.60 (34.1–38.3)	39.8 ± 0.87 (38.8–40.4)	—
Head length/SVL	31.6 ± 0.70 (30.8–32.7)	—	33.6 ± 2.04 (31.6–36.4)	31.2 ± 1.04 (30.1–32.3)	32.8 ± 0.95 (31.9–33.8)	—
Head height/SVL	19.1 ± 1.23 (17.7–21.0)	—	20.0 ± 2.02 (17.7–22.1)	19.9 ± 1.69 (18.0–22.2)	20.3 ± 0.72 (19.7–21.1)	—
END/SVL	10.2 ± 0.61 (9.7–11.2)	—	9.5 ± 0.51 (8.9–10.1)	9.7 ± 0.43 (9.2–10.2)	9.6 ± 0.21 (9.4–9.8)	—
Head length/head width	86.2 ± 3.49 (81.5–89.7)	—	89.2 ± 3.61 (85.9–94.7)	86.9 ± 2.19 (84.4–89.8)	82.5 ± 1.52 (81.1–84.1)	—
Upper eyelid width/interorbital distance	67.7 ± 2.82 (63.0–70.4)	—	72.0 ± 2.32 (70.4–76.0)	81.4 ± 5.11 (72.7–85.0)	82.8 ± 4.12 (80.0–87.5)	—
Body height/SVL	17.0 ± 2.87 (12.3–19.2)	—	22.1 ± 1.53 (20.7–24.2)	19.9 ± 2.18 (17.9–23.4)	25.0 ± 2.16 (22.5–26.5)	—
Tibia length/SVL	50.0 ± 1.91 (47.9–52.3)	—	50.6 ± 1.17 (49.1–52.3)	51.3 ± 2.56 (47.4–54.5)	51.4 ± 2.41 (49.1–53.9)	—
Foot length/SVL	48.4 ± 2.54 (44.9–50.9)	—	48.8 ± 1.36 (47.2–50.8)	48.6 ± 2.75 (43.9–51.1)	48.3 ± 0.81 (47.4–49.0)	—

Fig. 10.—Adult female holotype of *Pristimantis paladines* in life (MUTPL 1159; SVL = 20.6 mm); from Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca, Zamora Chinchipe Province, 2,880 m: (A) dorsolateral view; (B) ventral view; (C) dorsal view.

bearing two to five teeth; (6) males without vocal sacs, vocal slits, and nuptial pads; (7) Finger I shorter than Finger II; discs on fingers broadly expanded, truncate; circumferential grooves present; (8) fingers bearing lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present; palmar tubercle usually not divided or only partially divided into a larger (inner) and a smaller (outer) tubercle(s); thenar tubercle elliptical, larger than inner palmar tubercle; (9) ulnar tubercles present (feature more evident in life); (10)

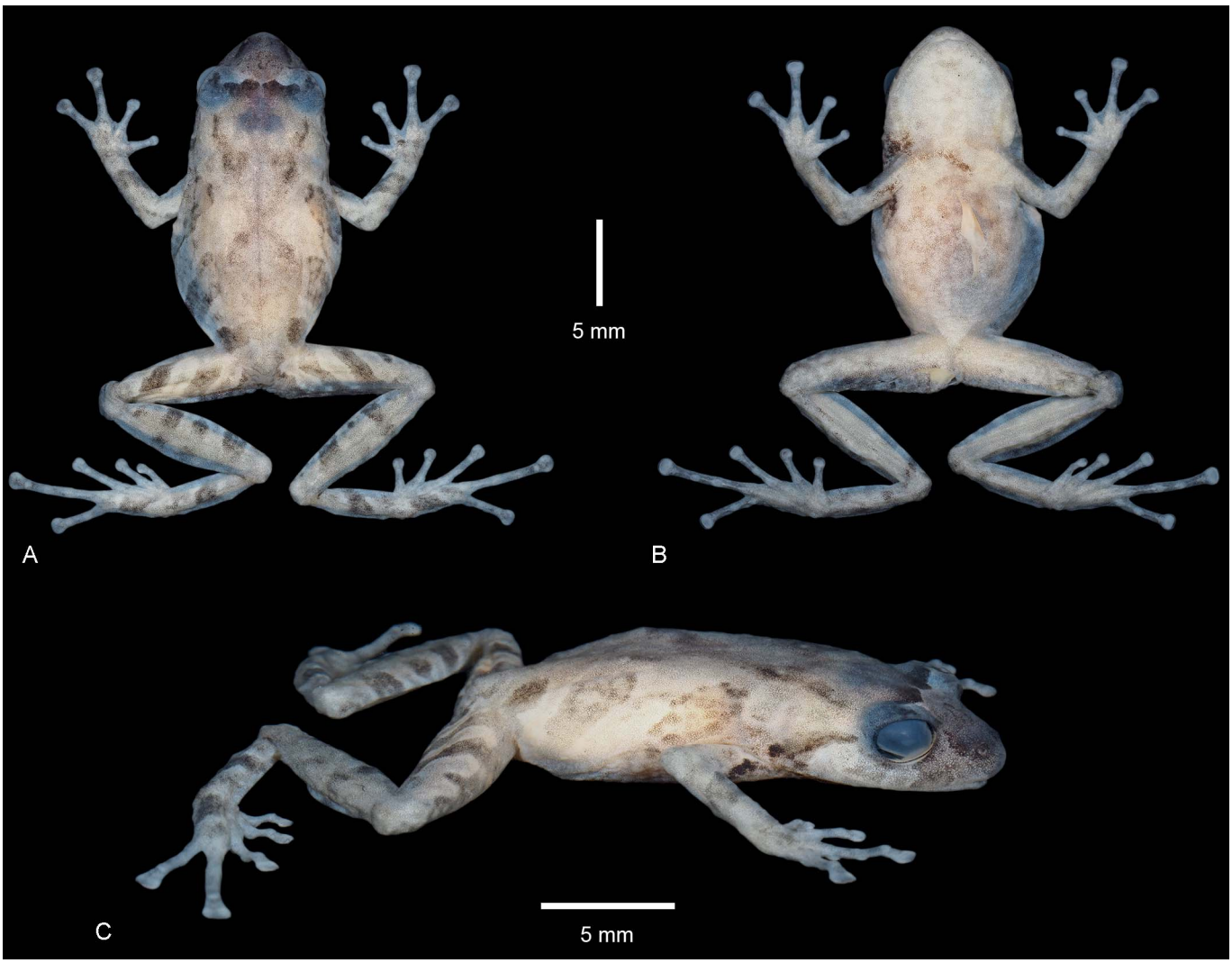

FIG. 11.—Adult female holotype of *Pristimantis paladines* in preservative (MUTPL 1159; SVL = 20.6 mm); from Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca, Zamora Chinchipe Province, 2,880 m: (A) dorsal view; (B) ventral view; (C) lateral view.

heel with two to three large tubercles and several small tubercles (feature more evident in life); outer edge of tarsus with row of large, conical tubercles (feature more evident in life); inner tarsal fold present; (11) inner metatarsal tubercle broadly ovoid, about 2× to 3× the size of subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present; (12) toes bearing broad lateral fringes; webbing basal; Toe V longer than Toe III; discs on toes broadly expanded, truncate, slightly smaller than those on fingers; circumferential grooves present; (13) in life, dorsum of various shades of brown, reddish brown, greenish brown, green or reddish orange with, dark, blackish bars, with or without X or W markings on the back; flanks, dorsal surfaces of arms and of hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs, groin, concealed limb surfaces and sometimes of dorsum orange or reddish brown; head usually with dark, blackish interorbital markings, dark labial bars and dark supratympanic stripes; venter and ventral surfaces of hindlimbs and arms pinkish white or pinkish gray, with or without dark markings on the throat; iris bronze with fine black reticulations and a median, wide, horizontal dark red streak; (14) SVL 19.5–21.4 mm in adult females (20.5 ± 0.82, $n = 5$) and 16.7–18.3 mm in adult males (17.4 ± 0.73, $n = 5$).

Comparison with similar species.—*Pristimantis paladines* is morphologically very different from the bromeliad specialist species of the *P. colodactylus* subgroup, being distinguished mainly by the general habitus, with not compressed body and head, longer fingers and toes, and the general coloration, and from the other species of the *P. orestes* species group, mainly by the much longer fingers and toes and the general coloration (Figs. 1, 4, 5; Table 2). It is most similar to the other two newly described species, *P. sagedunneae* and *P. numbala*.

Pristimantis paladines differs from *P. samaniegoi* by its longer snout (END > 1.9 mm vs. END < 1.8 mm), longer fingers (Finger III length > 5.4 mm vs. Finger III length < 5.1 mm), longer toes (Toe IV length > 9.7 mm vs. Toe IV length < 8.3 mm), discs on fingers and toes broadly expanded (vs. slightly expanded), and by different coloration pattern with dark, blackish bars, with or without X or W

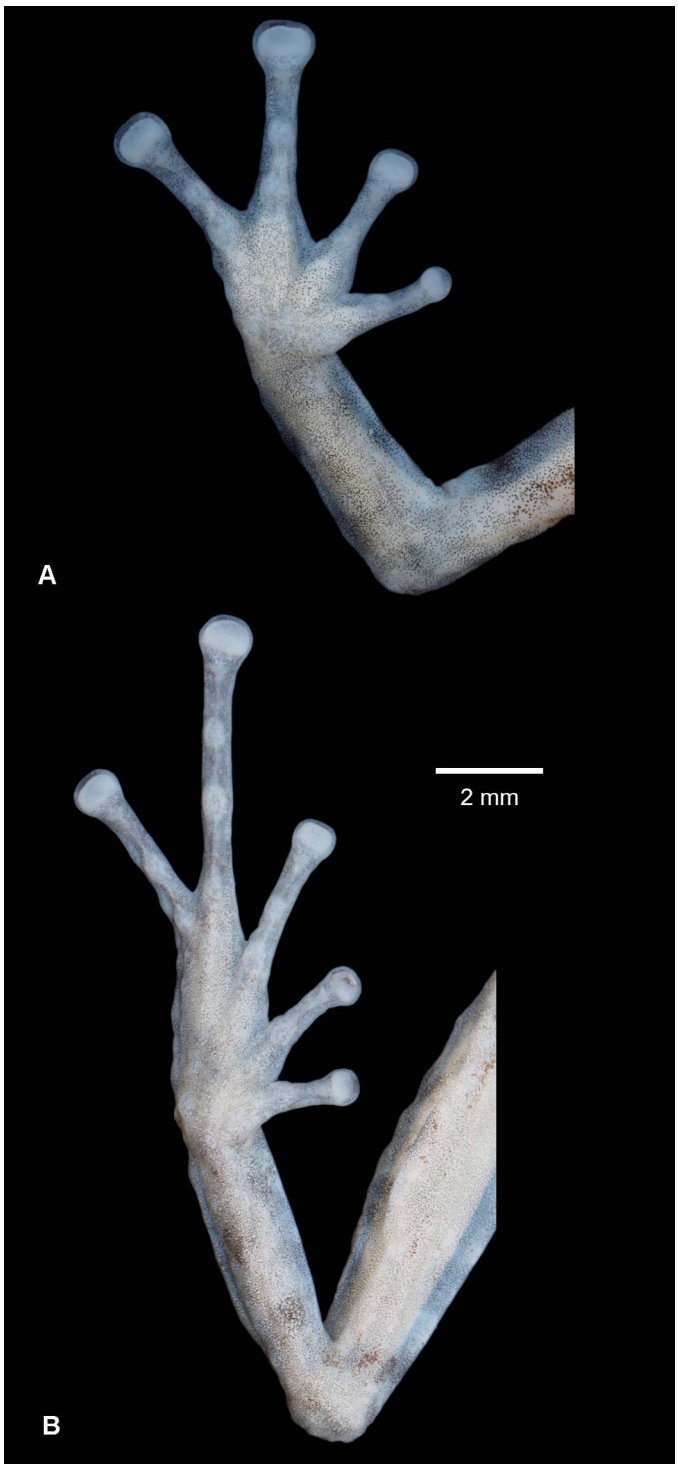

Fig. 12.—Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of female holotype *Pristimantis paladines* (MUTPL 1159; SVL = 20.6 mm) in preservative.

markings on the back and with large areas of the dorsal surfaces of thighs, groin, concealed limb surfaces, and sometimes of the dorsum orange or reddish brown (vs. dorsum, flanks, dorsal surfaces of hindlimbs, and arms dark brown with various white, irregular spots and dark gray venter in females). Within the *P. colodactylus* subgroup, *P. paladines* can be distinguished from *P. muranunka* by the lack of tympanic annulus and tympanic membrane (vs. present in *P. muranunka*), and from *P. colodactylus* and *P. matildae* by having a noncompressed body and head (vs. compressed; Table 1; Figs. 4, 5), longer fingers (Finger III length $>$ 5.4 mm vs. Finger III length $<$ 4.4 mm in *P. colodactylus*), longer toes (Toe IV length $>$ 9.7 mm vs. Toe IV length $<$ 7.5 mm in *P. colodactylus*), and by the typical orange or reddish brown coloration present on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. concealed coloration missing in *P. colodactylus* and *P. matildae*; Table 2).

There are several important features that can be used to distinguish *P. paladines* from its sister species (Table 3). Thus, *P. paladines* differs from *P. sagedunneae* by its smaller size (Mann–Whitney $U = 1$, $n_1 = n_2 = 5$, $P = 0.02$), tuberculate dorsum (vs. shagreen in *P. sagedunneae*), tall middorsal fold that has usually several larger tubercles scattered along its length (vs. low middorsal fold, without tubercles), orange or reddish brown coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. intense red coloration), and frequently green present in the dorsal coloration (vs. lack of green in the dorsal coloration). *Pristimantis paladines* differs from *P. numbala* by the acuminate to subacuminate snout (vs. rounded to broadly rounded snout in *P. numbala*), the tuberculate dorsum (vs. shagreen dorsum), tall middorsal fold that usually has several larger tubercles scattered along its length (vs. low middorsal fold, without tubercles), and shorter relative length of the toes, with Toe V longer than Toe III (vs. Toe V much longer than Toe III).

The dorsum skin texture can be used only for identification in life, as all three new species have the ability to change their skin texture similarly to *P. mutabilis* (Guayasamin et al. 2015). Furthermore, in preserved specimens the texture of the skin, and particularly the shape of the tubercles, is significantly modified by the preservation process (the tubercles become less conspicuous). Nevertheless, the tuberculate dorsum is an evident distinction between *P. paladines* and its sister species.

Description of holotype.—Adult female (MUTPL 1159; Figs. 10–12), with large white-yellow eggs, head narrower than body, wider than long, head length 87% of head width, head width 36% of SVL; head length 32% of SVL; snout long (END 10% of SVL), subacuminate in dorsal view and rounded in profile, with small rostral papilla at tip of snout; canthus rostralis weakly concave in dorsal view, rounded in profile; loreal region slightly convex; eye diameter larger than END; nostrils slightly protuberant, oriented posteriorly; lips not flared; cranial crests absent; upper eyelid bearing two larger tubercles and several small tubercles (trait more visible in life); width of upper eyelid 70% of interorbital distance; tympanic annulus and tympanic membrane absent; supratympanic fold present; one large, rounded postrictal tubercle; choanae large, round, partially concealed by palatal shelf of maxillary arch; dentigerous processes of vomers inconspicuous, slightly smaller than the choanae, oblique, situated posterior and median to choanae, triangular in outline, separated medially by distance equal to half of width of processes, each process bearing three to four teeth; tongue just slightly longer as wide, not notched posteriorly, posterior half not adherent to floor of mouth.

FIG. 13.—Color variation in life for females of *Pristimantis paladines*, in lateral or dorsolateral, dorsal, and ventral views. Paratypes from Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca, Zamora Chinchipe Province, 2,880 m: (A, D, G) MUTPL 1151, SVL = 19.5 mm; (B, E, H) MUTPL 1160, SVL = 19.8 mm; (C, F, I) MUTPL 1161, SVL = 21.1 mm.

Skin on dorsum tuberculate with numerous scattered large tubercles (trait more visible in life); evident, tall, middorsal fold starting at tip of snout and ending at cloaca (trait more visible in life); dorsolateral folds absent; flanks with longitudinal lateral folds on anterior half; skin on chest, belly, ventral surfaces of thighs areolate; thoracic and discoidal folds present, weak; cloacal region bordered laterally by one tubercle on each side and ventrally by several small tubercles.

Ulnar tubercles present (trait more visible in life); outer palmar tubercle prominent, partially divided into a larger (inner) and a smaller (outer) tubercle(s); thenar tubercle elliptical, larger than inner palmar tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present in all fingers; supernumerary palmar tubercles rounded, small, much smaller than subarticular tubercles; fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, truncate; all fingers bearing pads well defined by circumferential grooves.

Hindlimbs long, slender; tibia length 51% of SVL; foot length 49% of SVL; heel with two large and several small tubercles (trait more visible in life); outer edge of tarsus with row of large, conical tubercles (trait more evident in life); inner edge of tarsus bearing short fold; inner metatarsal tubercle broadly ovoid, about 2× subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present in all toes; supernumerary plantar tubercles inconspicuous; toes bearing broad lateral fringes; webbing basal; discs on toes broadly expanded, truncate, slightly smaller than those on fingers; toes with ventral pads well defined by circumferential grooves; relative length of toes I <II < III < V < IV; Toe V longer than Toe III (tip of Toe III extends beyond proximal edge of penultimate subarticular tubercle on Toe IV, tip of Toe V barely extends beyond proximal edge and does not reach distal edge of distal subarticular tubercle on Toe IV).

Coloration of holotype.—In life (Fig. 10): dorsum greenish brown with dark bars and X and W dark markings on middle of the back; flanks with wide, dark transverse bars;

Fig. 14.—Color variation in life for males of *Pristimantis paladines*, in lateral or dorsolateral, dorsal, and ventral views. Paratype from the Cerro Toledo sector of Parque Nacional Podocarpus, Loja Province, 3,080 m: (A, D, G) MUTPL 125, SVL = 16.7 mm. Paratypes from the Cerro Toledo sector of Parque Nacional Podocarpus, Zamora Chinchipe Province, 3,104 m: (B, E, H) MUTPL 1107, SVL = 18.0 mm, (C, F, I) MUTPL 1109, SVL = 17.3 mm.

dorsal surfaces of arms and hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs and of groin are orange; head with wide, whitish yellow interorbital bar, which is bordered posteriorly by dark, blackish markings, dark labial bars, and dark supratympanic stripes; venter and ventral surfaces of hindlimbs and arms pinkish gray; the skin on right side of abdomen almost translucent, revealing the whitish yellow coloration of the large eggs; throat pinkish gray; iris bronze with fine black reticulations and a median, wide, horizontal dark red streak.

In preservative (Fig. 11): dorsum brownish gray with dark brown bars; flanks, dorsal surfaces of arms and hindlimbs brownish gray with dark transverse bars; head with dark interorbital markings, dark labial bars and dark supratympanic stripes; venter, ventral surfaces of arms, hindlimbs, and throat predominantly whitish yellow, with some small brownish markings.

Measurements of holotype (in mm).—SVL 20.6; head width 7.5; head length 6.5; interorbital distance 2.7; internarial distance 1.8; upper eyelid width 1.9; eye diameter 2.2; END 2.0; thigh length 9.9; tibia length 10.4; foot length 10.1; hand length 5.7.

Body mass of holotype.—0.96 g.

Variation.—Morphometric variation is shown in Table 4. Besides the evident size difference between the females and males (females being significantly larger), there are no noticeable distinction between the sexes. Some individuals, like the female paratype MUTPL 1160 (Figs. 13B, E), had the entire back reddish orange, or others, like the female paratype MUTPL 1161 (Figs. 13C, F), had a predominantly green dorsum with additional reddish orange coloration. Some individuals (like the MUTPL 123, MUTPL 1155 or MUTPL 1160 paratypes) had several smaller or larger white spots scattered on the dorsum, head, or dorsal surfaces of arms and legs (Figs. 13B, E). The male paratype MUTPL 125 had a very particular coloration with a wide, whitish yellow middorsal stripe (Figs. 14A, D).

Advertisement call.—Unknown.

Etymology.—The specific name *paladines* is a noun in apposition and honors the Paladines family from the city of Loja, in particular Félix Humberto Paladines Paladines

(1938–2022), for his valuable contribution to the academic and cultural fields and for safeguarding the history and identity of southern Ecuadorian people. In addition, it constitutes recognition of the remarkable work carried out by his children, Renzo, Bruno, Pedro, and Maria Gabriela, who created the nongovernmental organization Naturaleza y Cultura Internacional (NCI), a consolidated organization dedicated to the protection of wildlife in Latin America where it has managed to protect, to date, more than 8.5 million hectares of tropical forest in various countries.

Common English name.—Paladines Rain Frog.

Common Spanish name.—Cutín de Paladines.

Distribution.—*Pristimantis paladines* is known from three nearby localities: the Cerro Toledo sector of the Parque Nacional Podocarpus, then from about 10 km to the south, inside Parque Nacional Podocarpus in the vicinity of Reserva Tapichalaca, and from another 5 km further in the south in the Reserva Tapichalaca (Fig. 2). The specimens were encountered at an altitudinal range between 2,800 and 3,100 m in subpáramo ecosystems (Homeier et al. 2008).

Natural history.—This is a common and locally abundant species. Individuals were encountered during the night, perching on moss-covered branches or leaves or on moss-covered walls near the road, sometimes next to small streams, at heights ranging from the soil level up to 1.5 m high, in habitats with shrubby vegetation. No individual was encountered inside bromeliads. Also, no calling males were heard. Sympatric frog species include *Pristimantis andinognomus*, *P. atratus* (Lynch 1979), *P. versicolor*, and three undescribed species of *Pristimantis*.

Conservation status.—*Pristimantis paladines* is a common and locally abundant species known currently from only three close localities, from an estimated area of less than 20 km^2. All known localities are inside national or private protected areas and its habitat currently does not face any major threats. Nonetheless, we recommend that this species is categorized as Near Threatened following the IUCN criteria, due to its very small Extent of Occurrence (EOO).

Pristimantis ***numbala*** sp. nov.
(Figs. 15–18)

Holotype.—MUTPL 1190 (Field no. SC 1284; Figs. 15–17), an adult female from Ecuador, Zamora Chinchipe Province, Reserva Numbala (4.4065°S, 79.0885°W), 2,875 m, collected by S. Hualpa-Vega, P. Székely, and D. Székely on 3 September 2021.

Paratypes (2 females and 1 juvenile).—MUTPL 1191 (Field no. SC 1285; Figs. 18C, F, I), a juvenile collected with the holotype; MUTPL 1178 (Field no. SC 1271; Figs. 18A, D, G), MUTPL 1179 (Field no. SC 1272; Figs. 16B, E, H), two females, from Reserva Numbala (4.4005°S, 79.0854°W), 2,861 m, collected by P. Székely, D. Székely, and S. Hualpa-Vega on 2 September 2021.

Diagnosis.—We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 3) and on the general morphological similarity to other members of the genus. *Pristimantis numbala* is a medium-sized species (among the *P. orestes* group; Table 2), distinguished by the following combination of traits: (1) skin on dorsum shagreen with some scattered tubercles (feature more evident in life); skin on venter areolate; discoidal fold present; dorsolateral folds absent; flanks usually with longitudinal lateral folds on anterior half; low middorsal fold present (feature more evident in life); (2) tympanic annulus and tympanic membrane absent; supratympanic fold present; (3) snout rounded to broadly rounded in dorsal view, rounded in profile; canthus rostralis concave in dorsal view, rounded in profile; (4) upper eyelid bearing one larger tubercle and several small tubercles (feature more evident in life), it's width about 83% of interorbital distance; cranial crests absent; (5) dentigerous processes of vomers evident, oblique, ovoid, separated medially by distance equal or slightly smaller than the width of processes; each process bearing four to six teeth; (6) condition of vocal sacs, vocal slits, and nuptial pads unknown; (7) Finger I shorter than Finger II; discs on fingers broadly expanded, truncate; circumferential grooves present; (8) fingers bearing lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present; palmar tubercle usually not divided or only partially divided into a larger (inner) and a smaller (outer) tubercle(s); thenar tubercle elliptical, larger than inner palmar tubercle; (9) ulnar tubercles present (feature more evident in life); (10) heel without or with one larger tubercle and several small tubercles (feature more evident in life); outer edge of tarsus with or without row of small tubercles (feature more evident in life); inner tarsal fold absent or present; (11) inner metatarsal tubercle broadly ovoid, about 2× to 3× the size of subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present; (12) toes bearing lateral fringes; webbing basal; Toe V much longer than Toe III; discs on toes broadly expanded, truncate, about same size or slightly smaller as those on fingers; circumferential grooves present; (13) in life, dorsum reddish brown, with dark brown bars and X markings on the back; flanks grey, pinkish grey, or green, with wide, dark transverse bars; dorsal surfaces of arms and of hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs, groin, and concealed limb surfaces reddish brown; head with black interorbital markings, dark labial bars and black supratympanic stripes; venter, throat, and ventral surfaces of hindlimbs and arms pinkish white or pinkish gray with blackish markings; iris bronze with fine black reticulations and a median, wide, horizontal dark red streak; (14) SVL 20.4–23.2 mm in adult females (21.9 ± 1.43, $n = 3$); males unknown.

Comparison with similar species.—*Pristimantis numbala* is morphologically very different from the bromeliad specialist species of the *P. colodactylus* subgroup, being distinguished mainly by the general habitus, with not compressed body and head, much longer fingers and toes, and the general coloration, and from the other species of the *P. orestes* group mainly by the much longer fingers and toes and the general coloration (Figs. 1, 4, 5; Table 2). It is most similar to the other two new species, *P. sagedunneae* and *P. paladines*.

Pristimantis numbala differs from *P. samaniegoi* by its longer snout (END > 2.0 mm vs. END < 1.8 mm), longer fingers (Finger III length > 6.1 mm vs. Finger III length < 5.1 mm), longer toes (Toe IV length > 10.0 mm vs. Toe IV length < 8.3 mm), discs on fingers and toes broadly expanded (vs. slightly expanded), and by different coloration

Fig. 15.—Adult female holotype of *Pristimantis numbala* in life (MUTPL 1190, SVL = 22.3 mm) from Reserva Numbala, Zamora Chinchipe Province, 2,875 m: (A) lateral view; (B) ventral view; (C) dorsal view.

pattern with dark brown bars and X markings on the back and with large areas of the dorsal surfaces of thighs, groin, and concealed limb surfaces reddish brown (vs. dorsum, flanks, dorsal surfaces of hindlimbs and arms dark brown with various white, irregular spots and dark gray venter in females). Within the *P. colodactylus* subgroup, *P. numbala* can be distinguished from *P. muranunka* by the lack of tympanic annulus and tympanic membrane (vs. present in *P. muranunka*) and from *P. colodactylus* and *P. matildae* by having a noncompressed body and head (vs. compressed;

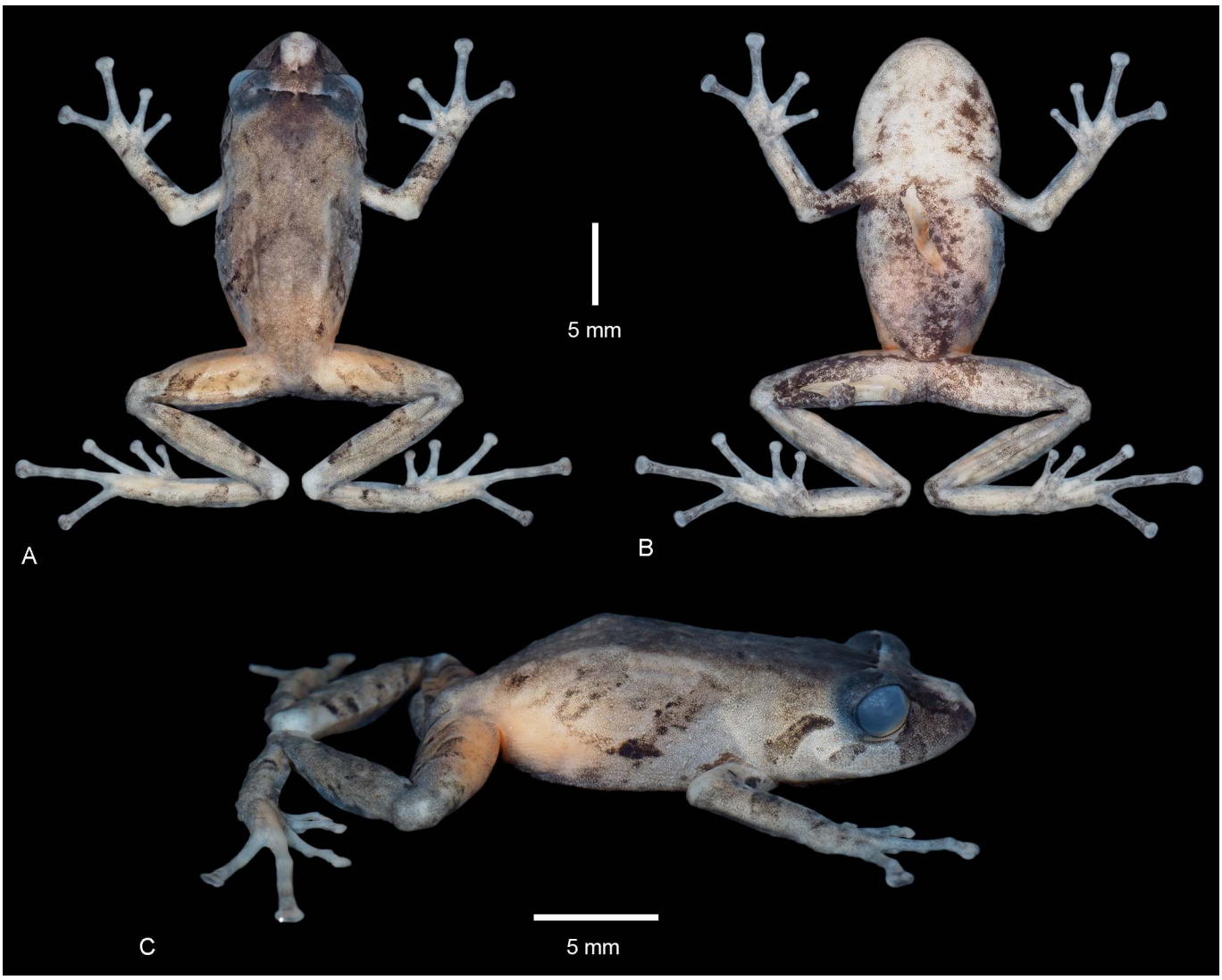

FIG. 16.—Adult female holotype of *Pristimantis numbala* in preservative (MUTPL 1190, SVL = 22.3 mm) from Reserva Numbala, Zamora Chinchipe Province, 2,875 m: (A) dorsal view; (B) ventral view; (C) lateral view.

Figs. 4, 5; Table 1), longer fingers (Finger III length > 6.1 mm vs. Finger III length < 4.4 mm in *P. colodactylus*), longer toes (Toe IV length > 10.0 mm vs. Toe IV length < 7.5 mm in *P. colodactylus* and < 9.8 mm in *P. matildae*), and by the typical reddish brown coloration present on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. concealed coloration missing in *P. colodactylus* and *P. matildae*; Table 2).

There are several important features that can be used to distinguish *P. numbala* from its sister species (Table 3). Thus, *P. numbala* differs from *P. sagedunneae* by the rounded to broadly rounded snout (vs. subacuminate to rounded snout in *P. sagedunneae*), the relative length of the toes, with Toe V much longer than Toe III (vs. Toe V longer than Toe III), the reddish brown coloration on the dorsal surfaces of thighs, groin, and concealed limb surfaces (vs. intense red coloration), and frequently green present in the dorsal coloration (vs. lack of green in the dorsal coloration). *Pristimantis numbala* differs from *P. paladines* by the rounded to broadly rounded snout (vs. acuminate to subacuminate snout in *P. paladines*), the shagreen dorsum (vs. tuberculate dorsum), low middorsal fold (vs. tall middorsal fold, that has usually several larger tubercles scattered along its length), and the relative length of the toes, with Toe V much longer than Toe III (vs. Toe V longer than Toe III).

Description of holotype.—Adult female (MUTPL 1190; Figs. 15–17), with large white eggs, head slightly wider than body, wider than long, head length 81% of head width, head width 40% of SVL; head length 33% of SVL; snout long (END 9% of SVL), rounded in dorsal view and in profile, with small rostral papilla at tip of snout; canthus rostralis concave in dorsal view, rounded in profile; loreal region flat; eye diameter larger than END; nostrils slightly protuberant, oriented posteriorly; lips not flared; cranial crests absent; upper eyelid bearing one larger tubercle and several small tubercles (trait more visible in life), width of upper eyelid 80% of interorbital distance; tympanic annulus and tympanic membrane absent; supratympanic fold present; two (on the right side) and one (on the left side) larger, rounded

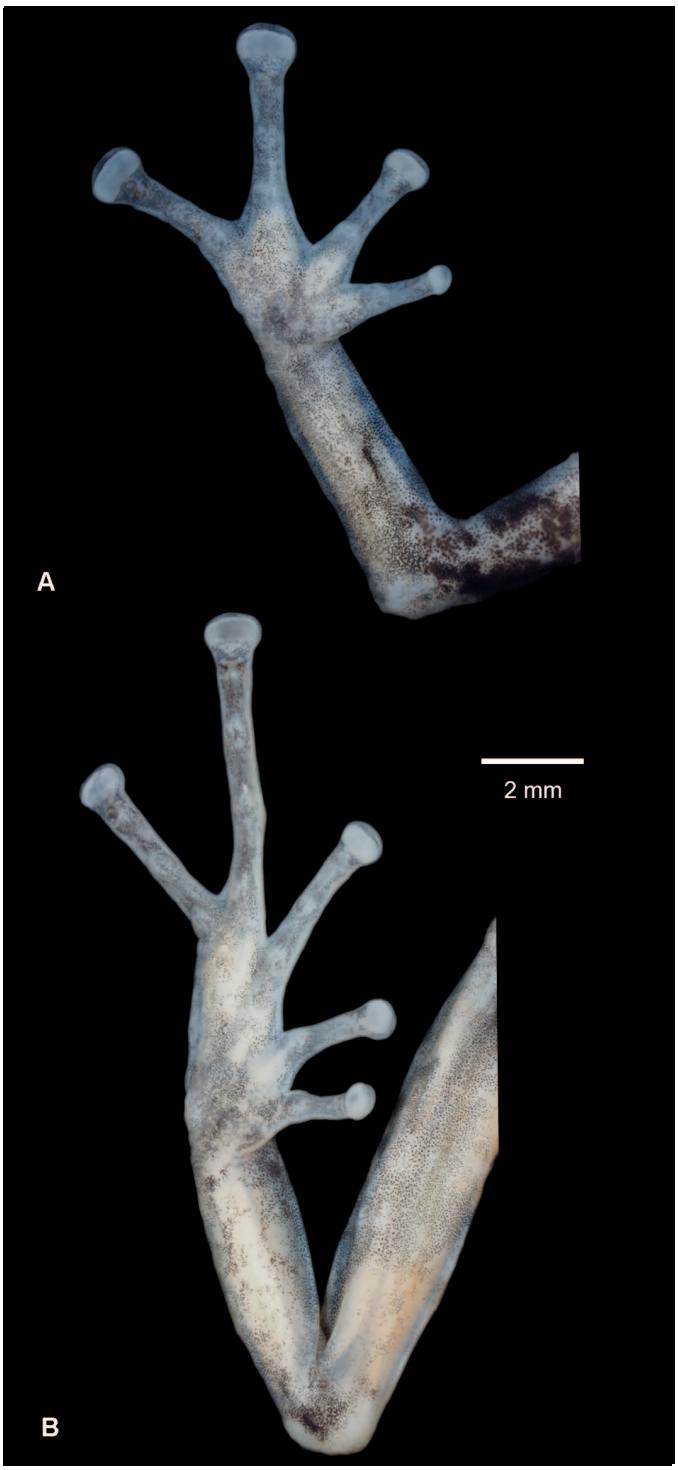

Fig. 17.—Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of female holotype *Pristimantis numbala* (MUTPL 1190, SVL = 22.3 mm) in preservative.

postrictal tubercles; choanae large, oval, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers evident, slightly smaller than the choanae, oblique, situated posterior and median to choanae, ovoid in outline, separated medially by distance equal to width of processes, each process bearing four to five teeth; tongue just slightly longer than wide, slightly notched posteriorly, posterior half not adherent to floor of mouth.

Skin on dorsum shagreen with some scattered tubercles (feature more evident in life); thin, low middorsal fold starting at tip of snout and ending at cloaca (feature more evident in life); dorsolateral folds absent; flanks with longitudinal lateral folds on anterior half; skin on chest, belly, ventral surfaces of thighs areolate; thoracic and discoidal fold present; cloacal region bordered ventrally by two larger tubercles.

Ulnar tubercles present (feature more evident in life); outer palmar tubercle prominent, not divided; thenar tubercle elliptical, larger than the inner part of outer tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present in all fingers; supernumerary palmar tubercles inconspicuous; fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, truncate; all fingers bearing pads well defined by circumferential grooves.

Hindlimbs long, slender; tibia length 51% of SVL; foot length 49% of SVL; heel with one large and several small tubercles (trait more visible in life); outer edge of tarsus with row of small tubercles (trait more visible in life); inner edge of tarsus without fold; inner metatarsal tubercle broadly ovoid, about 2× subconical (in profile) outer metatarsal tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present in all toes; supernumerary plantar tubercles oval, smaller than subarticular tubercles; toes bearing lateral fringes; webbing basal; discs on toes broadly expanded, truncate, slightly smaller than those on fingers; toes with ventral pads well defined by circumferential grooves; relative length of toes I <II < III < V < IV; Toe V much longer than Toe III (tip of Toe III extends beyond proximal edge of penultimate subarticular tubercle on Toe IV, tip of Toe V extends beyond distal edge of distal subarticular tubercle on Toe IV).

Coloration of holotype.—In life (Fig. 15): dorsum reddish brown with some dark markings on the back; flanks pinkish grey and green and with wide, dark transverse bars; dorsal surfaces of arms and hindlimbs with dark transverse bars; large areas of dorsal surfaces of thighs, groin, and concealed limb surfaces reddish brown; head with black interorbital marking, whitish yellow snout, dark labial bars, and black supratympanic stripes; venter, throat, and ventral surfaces of hindlimbs and arms pinkish gray with blackish markings; iris bronze with fine black reticulations and a median, wide, horizontal dark red streak.

In preservative (Fig. 16): dorsum brownish gray with dark brown bars; flanks, dorsal surfaces of arms, and hindlimbs brownish gray with dark transverse bars; groin and dorsal surfaces of thighs yellowish orange; head with dark interorbital markings, whitish yellow snout, dark labial bars and dark supratympanic stripes; venter, ventral surfaces of arms, hindlimbs, and throat whitish yellow, with dark brownish markings.

Measurements of holotype (in mm).—SVL 22.3; head width 9.0; head length 7.3; interorbital distance 2.5; internarial distance 2.1; upper eyelid width 2.0; eye diameter 2.6; END 2.1; thigh length 10.8; tibia length 11.4; foot length 10.8; hand length 6.4.

FIG. 18.—Color variation in life for paratypes of *Pristimantis numbala*, in lateral or dorsolateral, dorsal, and ventral views. Adult females from Reserva Numbala, Zamora Chinchipe Province, 2,861 m: (A, D, G) MUTPL 1178, SVL = 23.27 mm; (B, E, H) MUTPL 1179, SVL = 20.4 mm. Juvenile from Reserva Numbala, Zamora Chinchipe Province, 2,875 m: (C, F, I) MUTPL 1191, SVL = 14.9 mm.

Body mass of holotype.—1.06 g.

Variation.—Morphometric variation is shown in Table 4. None of the paratypes had so much of their dorsum colored in reddish brown as in the case of the holotype. Also, in the case of the paratypes, the dark brown markings on the dorsum, flanks, and dorsal surfaces of arms and of hindlimbs were more evident (contrasting) than in the holotype. The paratype MUTPL 1178 was the only one that did not have a whitish yellow snout (Figs. 18A, D).

Advertisement call.—Unknown.

Etymology.—The specific name *numbala* is a noun in apposition and refers to Reserva Numbala, an important private protected area managed by the NGO Naturaleza y Cultura Internacional. The reserve was established in 2006, with the main aim of conserving the last remnants of romerillo (*Retrophyllum rospigliosii* and *Prumnopitys harmsiana*, Podocarpaceae) forests, which are represented here by some of the last, giant trees of these species. The reserve protects 1,800 ha of subpáramo and montane cloud forest and is home to an important diversity of birds, amphibians, mammals, and plants. It is located between the two isolated extensions of the southern part of Parque Nacional Podocarpus, guaranteeing the connectivity needed for the preservation of the biological diversity of the national park and its area of influence.

Common English name.—Numbala Rain Frog.

Common Spanish name.—Cutín de Numbala.

Distribution.—*Pristimantis numbala* is known only from Reserva Numbala and its immediate proximity (Fig. 2). Specimens were encountered at an altitudinal range between 2,860 and 2,880 m in a subpáramo ecosystem (Homeier et al. 2008).

Natural history.—This is an uncommon species. However, this is an incomplete assessment because we were able to carry out only four collecting expeditions in the reserve and we encountered the species only during one of the field trips. We found merely a couple of individuals, all females. The animals were encountered during the night, perching on moss-covered branches or leaves, from the soil up to 1 m high, in habitats with shrubby vegetation. No individual was encountered inside bromeliads. Sympatric frog species include *Pristimantis andinognomus*, *P. atratus*, *P. cryptome-*

las (Lynch 1979), *P. versicolor*, and two undescribed species of *Pristimantis*.

Conservation status.—*Pristimantis numbala* is currently known only from one locality with a very small estimated area of about 300 m^2. Because we lack sufficient data to make an assessment, we consider this species to be Data Deficient following the IUCN criteria.

Discussion

Overview of the *Pristimantis orestes* Species group

The description of these three new species brings the total number of species in the *P. orestes* group to 17, with an additional four species that are currently undescribed (Fig. 3). Additionally, Brito et al. (2017a) identified some morphological similarities between *P. muranunka* and *P. proserpens* (Lynch 1979), *P. paquishae* Brito et al. 2014, and *P. tinajillas* Urgilés et al. 2014. Based on their morphology, these species could belong to this group; however, because no reliable morphological synapomorphies are known for the *P. orestes* group, future work is needed to clarify their phylogenetic relationships and determine their association with the group. Nonetheless, there remain many more species from this group that are currently lacking formal description (at least 15 species; PS, personal observation). Thanks to the work published during the last 6 yr, we have a clearer image regarding the species composition of the *P. orestes* group in central and southern Ecuador; all the currently known species being distributed in Andean montane forests, subpáramos, and páramos.

Unfortunately, the situation of the Peruvian species is unknown, as there is not even one species molecularly confirmed to belong to the group. Thus, from the 11 Peruvian species included originally (Hedges et al. 2008; Duellman and Lehr 2009), *P. atrabracus* (Duellman and Pramuk 1999), *P. chimu* Lehr 2007, *P. cordovae* (Lehr and Duellman 2007), *P. corrugatus* (Duellman et al. 2006), *P. melanogaster*, *P. pataikos* (Duellman and Pramuk 1999), *P. pinguis* (Duellman and Pramuk 1999), *P. seorsus* Lehr 2007, *P. simonsii*, *P. stictoboubonus* (Duellman et al. 2006), and *P. ventriguttatus* Lehr and Köhler 2007, DNA sequences were available for only two (*P. melanogaster* and *P. simonsii*); their analysis determined the removal of these species from the group. In 2012, two more species were tentatively added to the group (*P. mariaelenae* Venegas and Duellman 2012 and *P. stipa* Venegas and Duellman 2012), but they also lack molecular data. The group presence is certain, at least for northern Peru, close to the Ecuadorian border. Specimens identified as *P. colodactylus* from there (Lynch 1979; Lehr and Duellman 2007) are probably closely related, undescribed species, because *P. colodactylus* is endemic to Abra de Zamora, much further in the north (Székely et al. 2020). Also, *P. muranunka* might be present because the known populations of this species are very close to the Peruvian border.

Microhabitat–Body Shape Relationship

Our results suggest that the arboreal species of the *P. orestes* and *P. simonbolivari* subgroups share a characteristic body shape, with short snouts, robust (chubby) bodies, relatively narrow heads, proportionately short limbs, and narrow and rounded digital discs, as observed by Lynch and Duellman (1997) in their original diagnosis of the *P. orestes* group (Fig. 1). In contrast, the bromeliad specialist species from the *P. colodactylus* subgroup—*P. colodactylus*, *P. muranunka*, and *P. matildae* (Figs. 1G–I)—have a strikingly distinct body shape (Székely et al. 2020). These species are characterized by a different habitus, with longer snouts, slender (compressed) bodies, and flatter heads (Figs. 1, 4, 5; Tables 1 and 2). Herein we infer that the divergence in general shape of the *colodactylus* lineages from the typical *orestes* shape is due to life in different microhabitats, and that these body features are probably the result of the adaptation to the life inside the overlapping rosette of leaves of the bromeliads. On the other hand, the robust (chubby), short-legged body shape that characterizes the *orestes* and *simonbolivari* subgroups is considered an adaptation to the life in moss layer and herbaceous vegetation by some authors (Lehr et al. 2017).

It is important to mention that the measurements that we used for the height of head and body are not ideal, as the shape of the body can suffer important changes due to the preservation process. Alternative, more-precise methods, such as landmark-based geometric morphometrics or osteological measurements on high resolution microcomputed tomography scans, should be employed in order to confirm our initial findings. Also, specimens from all the species of the group (we had data for 12 of the 17 species) should be included in future analyses, and probably measurements on lives specimens (or scaled, good quality photographs of live specimens), in order to correctly define and measure the shape of the head and body. Nevertheless, our preliminary analysis confirms that the bromeliad specialist species have flatter (compressed) body planes compared with the arboreal species of the group.

Although phylogenetically closely related with them, the three new arboreal species described here are morphologically dissimilar from the bromeliad specialist sister species, having less-compressed heads and bodies, and they display evident markings on thighs, groin, and concealed limb surfaces (Fig. 1; Table 2). On the other hand, the new species seem to be different also from all the species of the *P. orestes* and *P. simonbolivari* subgroups, mainly by the longer snouts (a character that is shared with their sister bromeliad species) and longer fingers and toes (Table 2), having somewhat intermediary body shapes (Fig. 1).

Cryptic Diversity in Southern Ecuador

The results of the 2021 Ecuadorian amphibian Red List assessment (Ortega-Andrade et al. 2021) showed that 57% of the species (363 species out of the 635 assessed) are threatened, the main causes being habitat loss, the expansion of the agricultural/cattle raising frontier, and other anthropogenic threats (roads, human settlements, and mining/oil activities), as well as potential synergic effects with climate change and emergent diseases. Also, most threatened species were found to be in Andean montane forest and páramo ecosystems, with nearly 10% of them located outside protected areas. The authors of the assessment highlighted that the incomplete taxonomic delimitation, especially in megadiverse countries like Ecuador, has the potential to seriously impact amphibian conservation. Widely distributed species complexes, which are often assessed as Least Concern, sometimes include cryptic taxa that might be

facing particular conservation threats (Ortega-Andrade et al. 2021). In this context, it is especially important to increase the research efforts toward the description of new species, and particularly delimit cryptic species, in order to correctly evaluate extinction risks and implement adequate conservation actions.

The high-altitude Andes are characterized by high levels of endemism and speciation for anuran fauna, despite a relatively low species richness (Bernal and Lynch 2008; Garcia-R et al. 2014; Guarnizo et al. 2015; Mendoza et al. 2015). Proposed main drivers for this high diversification rate in the *Pristimantis* are related to low dispersion abilities, a high degree of specialization to microhabitats, and ecological opportunities due to absence of other lineages (Mendoza et al. 2015; Hutter et al. 2017). The *P. orestes* species group evolution in our study area is such an example: at least nine species and four potential new species are present here, taking into account only the samples taken from a few localities, from a mountain range that has less than 50 km in a straight line (from Abra de Zamora to Reserva Tapichalaca) and at altitudes between 2,700–3,300 m.

The amphibian species that inhabit the mountain range from Abra de Zamora to Reserva Tapichalaca exhibit a particular pattern in their distribution (Fig. 2). This mountain range represents the western limits of Parque Nacional Podocarpus and consists of evergreen upper montane forest (on altitudes usually between 2,100 to 2,700 m) and subpáramo or evergreen elfin forest (on the crest, between 2,700 and 3,700 m; Homeier et al. 2008). The crest heights fluctuate between 2,700 to 3,700 m, with an average of around 3,200 m, with its highest altitudes being encountered toward the southern half of the distance, nearby the famous complex of around 50 glacial lakes known as Lagunas del Compadre.

Thus, some of the species encountered in the Abra de Zamora/ Cajanuma area are replaced by morphologically and ecologically similar, but genetically different, species in the Cerro Toledo sector of the national park. This is the case of *Pristimantis andinogigas* Yánez-Muñoz et al. 2019, *P. sagedunneae*, and *Lynchius flavomaculatus* (Parker 1938) from Abra/ Cajanuma and *P. chomskyi* Páez and Ron 2019, *P. paladines*, and an undescribed species of *Lynchius* (Székely et al. 2020) from Cerro Toledo, respectively. However, we have additional evidence that the same situation applies to several undescribed species of *Pristimantis* (three of them from the *P. orestes* species group), and probable is the case of *P. andinognomus* and *P. versicolor*, which need careful revisions (Székely et al. 2020). In these cases, the genetic distance varies between 2% and 3%, which is lower than the conservative 3% genetic distance threshold proposed to identify candidate species in anurans (Fouquet et al. 2007; Vieites et al. 2009). However, ample evidence produced in recent years confirms that this is an overly prudent limit (Caminer and Ron 2014; Guayasamin et al. 2019), especially in young evolutionary radiations such as *Pristimantis* (Garcia-R et al. 2014; Ortega-Andrade et al. 2015; Páez and Ron 2019). Moreover, the Andean *Pristimantis* species are known to have small distribution ranges, and the few exceptions might be artefacts of incorrect species delimitation, as evidenced by recent studies (Páez and Ron 2019; Urgilés et al. 2019; Székely et al. 2020; Zumel et al. 2022).

Not all species from our study area follow this distribution pattern. Species such as *P. vidua* reach their southern limit in Abra de Zamora/ Cajanuma, while others such as *P. balionotus*, *P. cajanuma*, *P. colodactylus*, or *P. percultus* are known, for now, only from this relatively small area (Székely et al. 2020). Additionally, the distribution of *P. numbala* is intriguing, as this species is genetically more distant from the nearby *P. paladines* in Cerro Toledo than *P. paladines* is from its sister species from further north, *P. sagedunneae* (Fig. 2). Probably the population of *P. numbala* from Reserva Numbala represents the species' north-western limits and almost reaches *P. paladines* distribution flanks. Nonetheless, as we lack any data from inside the Parque Nacional Podocarpus (mostly due to the inaccessibility and remoteness of the area), we do not have the information to back up this hypothesis. It is imperative to collect additional information, especially from the unexplored areas situated between the Cajanuma and Cerro Toledo sectors, as well as from the remote areas inside the national park, in order to understand the distribution of the amphibians in this biodiversity hotspot.

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Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/HERPMONOGRAPHS-D-22-00002.1.S1 and https://doi.org/10.1655/HERPMONOGRAPHS-D-22-00002.1.S2.

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Appendix I

Additional Specimens Examined

Pristimantis andinognomus (25).—ECUADOR: Zamora Chinchipe: Reserva Tapichalaca (QCAZ 26964, 26965, 27033, 29248, 35374, 35375, 35377, 35378, 45614, 45621, 45622, 45623, 45656, 45659, 45661, 45662; MUTPL 338–340, 743, 744); Parque Nacional Podocarpus nearby Reserva Tapichalaca (MUTPL 1153, 1157); Reserva Numbala (MUTPL 1170, 1173).

Pristimantis aff. *andinognomus* (24).—ECUADOR: Loja: Abra de Zamora (MUTPL 206–209); Bosque Protector Washapamba (MUTPL 157–162, 167); Huacapamba (MUTPL 384, 386, 387); Parque Nacional Podocarpus - Cajanuma (MUTPL 348–351; 1097); Parque Nacional Podocarpus - El Palto (MUTPL 989); Reserva Madrigal del Podocarpus (MUTPL 193–195); San Lucas, Acacana (MUTPL 1123).

Pristimantis bambu (29).—ECUADOR: Cañar: La Libertad, Reserva Mazar (MZUTI 3373, 3378, 3420; QCAZ 68126, 68127, 68131, 68133–68143, 68145, 68147, 68151, 68154, 68161, 68329, 68335, 68342, 68374, 68375, 68402); Zamora Chinchipe: Yacuambi, Imbana (QCAZ 54356).

Pristimantis cajanuma (15).—ECUADOR: Loja: Parque Nacional Podocarpus - Cajanuma (MUTPL 343–347, 352, 353, 355, 573, 583, 584, 591–594).

Pristimantis colodactylus (4).—ECUADOR: Loja: Abra de Zamora (MUTPL 311, 388, 675, 732).

Pristimantis aff. *colodactylus* (1).—ECUADOR: Zamora Chinchipe: Reserva Tapichalaca (MUTPL 742).

Pristimantis matildae (12).—ECUADOR: Loja: Abra de Zamora (MUTPL 366, 394, 731, 733); Parque Nacional Podocarpus - Cajanuma (MUTPL 360–362, 813); Parque Nacional Podocarpus - El Palto (MUTPL 990, 992–994).

Pristimantis aff. *matildae* (17).—ECUADOR: Loja: Parque Nacional Podocarpus - Cerro Toledo (MUTPL 527, 682–689, 817); Zamora Chinchipe: Parque Nacional Podocarpus, nearby Reserva Tapichalaca (MUTPL 1152, 1154, 1156, 1158); Reserva Numbala (MUTPL 1192–1194).

Pristimantis mazar (37).—ECUADOR: Cañar: El Tambo (QCAZ 2569); La Libertad, Reserva Mazar (MZUTI 3418, 3488; QCAZ 27493, 27503–27505, 27507, 27508, 27511, 27514, 27519, 27553–27555, 27560, 27563, 27565, 32619, 49750, 49764, 68334, 68344, 68353, 68368, 68383, 68386, 68387, 68391, 68392, 68394–68397, 68405, 68409, 68413).

Pristimantis muranunka (4).—ECUADOR: Zamora Chinchipe: Cerro Plateado (MUTPL 652); Reserva Cerro Plateado (MUTPL 605, 606, 643).

Pristimantis aff. *muranunka* (1).—ECUADOR: Zamora Chinchipe: Loyola (MUTPL 939).

Pristimantis orestes (8).—ECUADOR: Azuay: Vía Sigsig - Gualaquiza (QCAZ 40783); Bosque Protector Shincata (MUTPL 787, 799, 800); Loja: Vía Urdaneta - Tutupali (MUTPL 242, 248, 249, 1060).

Pristimantis aff. *orestes* (50).—ECUADOR: Azuay: Cooperativa Bellarica (QCAZ 52584); El Guillan, Hacienda de la Universidad del Azuay (QCAZ 59019–59021, 61872–61874, 61877); En el camino entre Gualaceo y Plan de Milagro (QCAZ 27056); Matanga (QCAZ 29134); Vía Susudel - Cuenca, a aproximadamente 1 km de Susudel (MZUTI 706); Yumate, Shoupshe (QCAZ 46991); 8 km sur de La Paz en Panamericana (QCAZ 45935); Cañar: La Libertad, Reserva Mazar (QCAZ 27482, 27498, 27513, 27559, 27563, 27606–27608, 28136, 32611, 32613–32615, 49753, 68129, 68358); Chimborazo: Río Atillo (QCAZ 3341); El Oro: Chillacocha (QCAZ 45093, 45096); Loja: Bosque Protector Washapamba (QCAZ 40804; MUTPL 136–142, 172); Parque Nacional Podocarpus (QCAZ 4974); Saraguro (QCAZ 58567–58570); Morona Santiago: Límite Provincial entre Azuay y Morona Santiago, vía Sigsig - Cutchil - Oriente, 25 km este de Sigsig (QCAZ 3443–3446).

Pristimantis proserpens (1).—ECUADOR: Zamora Chinchipe: Rio Blanco (MUTPL 403).

Pristimantis samaniegoi (9).—ECUADOR: Loja: Abra de Zamora (MUTPL 365, 660, 674, 676, 777); Parque Nacional Podocarpus - Cajanuma (MUTPL 356–358); Reserva Madrigal del Podocarpus (MUTPL 1075).

Pristimantis aff. *samaniegoi* (9).—ECUADOR: Zamora Chinchipe: Reserva Numbala (MUTPL 1176, 1177, 1180–1183, 1185–1187).

Pristimantis simonbolivari (40).—ECUADOR: Azuay: Cuenca, Baños (QCAZ 37665–37670); Bolívar: Bosque Protector Cashca Totoras (QCAZ 932, 939, 942, 12932, 13755, 13759, 13763, 16819, 16823, 16830, 16832, 16925, 25107, 25108, 25113, 25120, 25121, 25123, 30893, 35747–35749, 36669, 37665–37670, 42591, 42594, 42598, 49361); 12 km este de Guaranda, carretera Guaranda - Riobamba (QCAZ 1497).

Pristimantis tiktik (9).—ECUADOR: Loja: Vía Urdaneta - Tutupali (MUTPL 239, 240, 245–247, 251, 252, 276, 277).

Pristimantis vidua (21).—ECUADOR: Loja: Abra de Zamora (MUTPL 295, 296, 312, 496, 501, 805); Bosque Protector Washapamba (MUTPL 143–150, 164, 173); Parque Nacional Podocarpus - Cajanuma (MUTPL 492, 581, 586, 590); Reserva Madrigal del Podocarpus (MUTPL 488).

Appendix II.—Voucher, GenBank accession numbers, and locality for the *Pristimantis* specimens used in the phylogenetic analysis. All specimens are from Ecuador. *Incorrectly labeled as DHMECN 3112 in Table 1 of Brito et al. (2017a) and in GenBank. Bold letters mark the sequences generated by the present study; — indicates missing data.

Species	Voucher number	GenBank accession no.			Locality
		12S	16S	RAG1	
P. andinognomus	QCAZ45534	—	KY967669	KY967688	Loja, Parque Nacional Podocarpus, guardianía Cajanuma
P. andinognomus	QCAZ45661	—	KY967671	KY967690	Zamora Chinchipe, Reserva Tapichalaca
P. bambu	QCAZ46743	—	KY967674	KY967692	Cañar, Reserva Mazar
P. bambu	QCAZ46744	—	KY967659	KY967693	Cañar, Reserva Mazar
P. cajanuma	MUTPL344	MK993331	MK604535	—	Loja, Parque Nacional Podocarpus, Cajanuma
P. cajanuma	MUTPL345	MK993331	MK604535	MK602184	Loja, Parque Nacional Podocarpus, Cajanuma
P. colodactylus	MUTPL311	MT764340	MT764804	MT810309	Loja, Abra de Zamora
P. colodactylus	MUTPL388	MT778072	MT762200	MT810310	Loja, Abra de Zamora
P. matildae	MUTPL360	MT778081	MT762201	MT810319	Loja, Parque Nacional Podocarpus, Cajanuma
P. matildae	MUTPL394	MT778084	MT762202	MT810322	Loja, Abra de Zamora
P. mazar	QCAZ27559	—	KY967664	KY967683	Cañar, Reserva Mazar, La Libertad
P. mazar	QCAZ27572	JF906315	KY967666	KY967685	Cañar, Reserva Mazar, La Libertad
P. muranunka	MEPN14737	—	KY967661	KY967680	Zamora Chinchipe, Reserva Cerro Plateado
P. muranunka	MUTPL605	MT778085	MT764807	MT810323	Zamora Chinchipe, Reserva Cerro Plateado
P. numbala	MUTPL1178	**OP290789**	**OP290796**	**OP302834**	Zamora Chinchipe, Reserva Numbala
P. numbala	MUTPL1190	—	**OP290797**	**OP302835**	Zamora Chinchipe, Reserva Numbala
P. orestes	KU218257	EF493388	EF493388	—	Azuay, 7 km E Sigsig
P. orestes	MUTPL242	MT778087	MK604538	MK602185	Loja, 11 km NE Urdaneta
P. orestes	MUTPL248	MK993330	MK604539	MK602186	Loja, 11 km NE Urdaneta
P. paladines	MUTPL126	**OP290790**	**OP290798**	—	Loja, Parque Nacional Podocarpus, Cerro Toledo
P. paladines	MUTPL1107	**OP290791**	**OP290799**	**OP302836**	Zamora Chinchipe, Parque Nacional Podocarpus, Cerro Toledo
P. paladines	MUTPL1161	**OP290792**	**OP290800**	**OP302837**	Zamora Chinchipe, Parque Nacional Podocarpus nearby Reserva Tapichalaca
P. quintanai	MZUA.AN.1881	MK993335	MK604541	MK602188	Cañar, Comunidad Guangras
P. quintanai	MZUA.AN.1900	MK993336	MK604544	MK602189	Cañar, Llavircay
P. sagedunneae	MUTPL500	**OP290793**	**OP290801**	**OP302838**	Loja, Abra de Zamora
P. sagedunneae	MUTPL597	**OP290794**	**OP290802**	**OP302839**	Loja, Parque Nacional Podocarpus, Cajanuma
P. sagedunneae	MUTPL1096	**OP290795**	**OP290803**	**OP302840**	Loja, Abra de Zamora
P. samaniegoi	MUTPL357	MT778091	MT764810	MT810328	Loja, Parque Nacional Podocarpus, Cajanuma
P. samaniegoi	MUTPL365	MT778092	MT764811	MT810329	Loja, Abra de Zamora
P. saturninoi	DHMECN12214	MK993328	MK604532	—	Morona Santiago, Parque Nacional Sangay
P. saturninoi	DHMECN12232	MK993327	MK604533	—	Morona Santiago, Parque Nacional Sangay
P. simonbolivari	KU218254	EF493671	EF493671	—	Bolívar, Bosque Protector Cashca Totoras
P. simonbolivari	QCAZ56567	—	KY967676	KY967695	Bolívar, Bosque Protector Cashca Totoras
P. tiktik	MUTPL239	MH668274	MH668275	MH708575	Loja, 21 km E Urdaneta
P. tiktik	MUTPL247	MH668161	MH668276	MH708576	Loja, 14 km E Urdaneta
P. vidua	MUTPL148	MT778096	MT764812	MT810333	Loja, Bosque Protector Washapamba
P. vidua	MUTPL312	MT778098	MT764815	MT810336	Loja, Abra de Zamora
P. vidua	MUTPL586	MT778106	MT764823	MT810344	Loja, Parque Nacional Podocarpus, Cajanuma
Pristimantis sp.	DHMECN12237	MK993329	MK604534	—	Morona Santiago, Parque Nacional Sangay
Pristimantis sp.	DHMECN9656*	—	KY967658	KY967677	Zamora Chinchipe, Reserva Tapichalaca
Pristimantis sp.	MUTPL939	**MZ702105**	**MZ702090**	**MZ706290**	Zamora Chinchipe, Loyola
Pristimantis sp.	QCAZ45556	—	KY967670	KY967689	Loja, Parque Nacional Podocarpus, Lagunas del Compadre
Pristimantis sp.	QCAZ56535	—	KY967675	KY967694	Azuay, Laguna Patococha