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OXFORD

Original Article

Three new bamboo-specialist frogs of the genus *Pristimantis* (Amphibia: Anura: Strabomantidae) from Southern Ecuador reveal patterns of parallel evolution

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ABSTRACT

Based on an integrative taxonomical approach, using morphological and bioacoustics data, we redefine *Pristimantis atratus*, using specimens from the type locality, and describe three new related species from the southern Ecuadorian Andes. Phylogenetic analyses place *P. atratus* and the new species within the *Pristimantis phoxocephalus* species group of the subgenus *Huicundomantis*. We consider these four taxa as bamboo-specialist species because they exhibit distinctive morphological traits that mimic the leaves of Andean bamboo and show strong microhabitat fidelity to bamboo-dominated ecosystems. Our results provide evidence for parallel evolution of three clades of *Pristimantis* that share these adaptations. Two are nested in the subgenus *Huicundomantis* and are distributed on the eastern slopes of the Andes, and the third, in the subgenus *Trachyphrynus*, *Pristimantis devillei* species group, on the western slopes. Our findings highlight the ecological specialization and convergent morphological adaptations of some Andean *Pristimantis* species to bamboo-dominated habitats, revealing the importance of these ecosystems for amphibian diversity and evolution.

Keywords: phylogenetic systematics; Andes; amphibian; Neotropics; biodiversity; convergent evolution

INTRODUCTION

The Neotropical genus *Pristimantis* Jiménez de la Espada, 1870 (Amphibia: Anura: Strabomantidae) is the most species-rich genus among vertebrates, comprising 622 described species as of August 2025 (Frost 2025), with many more awaiting formal description. The need to organize and classify the growing number of *Pristimantis* species became evident as early as the 1970s, when John D. Lynch (1976) proposed a series of species groups for the South American representatives of the genus (then classified under *Eleutherodactylus*). Although species groups are informal classifications, they are very useful in managing species-rich genera, such as *Pristimantis*. They help with the organization of species based on shared genetic, morphological, or ecological features and play an important role in guiding taxonomic discussions and the description of new species.

In Ecuador, the 262 species of *Pristimantis* currently reported are organized into 14 such species groups: *anaiae* (Ortega *et al.* 2022, Reyes-Puig *et al.* 2024), *boulengeri* (González-Durán *et al.* 2017, Bejarano-Muñoz *et al.* 2022), *conspicillatus* (Lynch and Duellman 1997, Fouquet *et al.* 2022), *cryptomelas* (Páez and Ron 2019), *devillei* (Lynch and Duellman 1997, Padial *et al.* 2014), *lacrimosus* (Lynch and Duellman 1997, Ron *et al.* 2020), *miktos* (Ortega *et al.* 2022), *myersi* (Lynch and Duellman 1997, Franco-Mena *et al.* 2023, Yánez-Muñoz *et al.* 2025), *orcesi* (Lynch and Duellman 1997, Sánchez-Nivicela *et al.* 2020), *orestes* (Lynch and Duellman 1997, Brito *et al.* 2017, Székely *et al.* 2023),

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phoxocephalus (Páez and Ron 2019), *ridens* (Hedges *et al.* 2008, Reyes-Puig *et al.* 2020), *rubicundus* (Hedges *et al.* 2008, Reyes-Puig *et al.* 2020), and *unistrigatus* [Lynch 1976, Zumel *et al.* 2022 (for the *trachyblepharis* clade), Mônico *et al.* 2024]. Some of these species groups are currently placed within three subgenera: *cryptomelas*, *miktos*, and *phoxocephalus* groups are included in *Huicundomantis* (Páez and Ron 2019); *ridens* and *rubicundus* in *Hypodictyon* (Hedges *et al.* 2008); and *boulengeri*, *devillei*, and *myersi* in *Trachyphrynus* (Franco-Mena *et al.* 2023). Still, 88 Ecuadorian species of *Pristimantis* remain unassigned to any species group, primarily owing to the lack of molecular data (56 species) or the absence of a revision and formal group description.

The subgenus *Huicundomantis* was described by Páez and Ron (2019), who initially included 23 species. These comprised *Pristimantis philipi* (Lynch & Duellman, 1995); five species assigned to the newly established *cryptomelas* species group: *Pristimantis cryptomelas* (Lynch, 1979), *Pristimantis gagliardoi* Bustamante & Mendelson, 2008, *Pristimantis muscosus* (Duellman & Pramuk, 1999), *Pristimantis spinosus* (Lynch, 1979), and the newly described *Pristimantis nangaritza*; and 17 species placed in the newly created *phoxocephalus* species group: *Pristimantis atratus* (Lynch, 1979), *Pristimantis balionotus* (Lynch, 1979), *Pristimantis hampatusami* Yánez-Muñoz *et al.*, 2016, *Pristimantis percultus* (Lynch, 1979), *Pristimantis phoxocephalus* (Lynch, 1979), *Pristimantis tinguichaca* Brito *et al.*, 2016, *Pristimantis versicolor* (Lynch, 1979), and 10 newly described species: *Pristimantis atillo*, *Pristimantis chomskyi*, *Pristimantis gloria*, *Pristimantis jimenezi*, *Pristimantis lutzae*, *Pristimantis multicolor*, *Pristimantis teslai*, *Pristimantis torresi*, *Pristimantis totoroi*, and *Pristimantis verrucolatus*. In 2019, *Pristimantis andinogigas* Yánez-Muñoz *et al.*, 2019 was described, and in 2021 *Pristimantis lojanus* Székely *et al.*, 2021 was added to the subgenus, both species being included in the *phoxocephalus* group. Ortega *et al.* (2022) created a new group and incorporated it to the subgenus, the *P. miktos* species group, with *Pristimantis miktos* Ortega-Andrade & Venegas, 2014, *Pristimantis mallii* Reyes-Puig *et al.*, 2019, and the newly described *Pristimantis tamia*. Finally, Sánchez-Nivicela *et al.* (2024) elucidated the molecular identity of *Pristimantis ruidus* and included it within the subgenus *Huicundomantis*, identifying it as the sister species of *P. philipi*. Currently, the subgenus *Huicundomantis* contains 29 species (Table 1) and seven undescribed, candidate new species.

The name *Huicundomantis* (the word 'huicundo' or 'huicundu' comes from Quechua, meaning epiphytic plants, especially bromeliads such as those in the genus *Guzmania*) was proposed because these frogs are frequently found inside bromeliad plants (Páez and Ron 2019). Our review of the limited ecological data available for these species revealed that 16 are facultative users of bromeliads (using them as daytime refuges alongside other microhabitats), 12 show no association with bromeliads, and only one species (*P. balionotus*) can currently be considered a bromeliad specialist (Table 1). In the case of *P. balionotus*, in a mark–recapture study conducted over 8 months, the 145 observed individuals (juveniles, subadults, and adults) were encountered exclusively in bromeliads (Villavicencio Asanza 2025). Thus, we define a 'bromeliad specialist' as a species that relies on bromeliads throughout its life, consistently inhabiting them rather than merely using them as temporary daytime refuges. This concept closely resembles the term bromeligenous, which is used to describe species that spend their entire life cycle within bromeliads and rely exclusively on them as breeding sites (Peixoto 1995, Sabagh *et al.* 2017). However, given that *Pristimantis* are direct-developing frogs, they probably do not depend on bromeliads in such a strict manner.

Among the *Huicundomantis* species not associated with bromeliads, some exhibit special adaptations to life on other types of vegetation. Herein, we redefine *P. atratus s.s.* by providing, for the first time, sequences from the type locality (Suro Rancho in Morona Santiago province) and a description of its advertisement call, and we describe three new, morphologically very similar species. These four *Pristimantis* (*Huicundomantis*) species are associated with Andean bamboos and share a distinctive body shape and coloration, which closely mimic the bamboo leaves. Furthermore, we recognize the same morphological features in another group of similar *Pristimantis* from a different subgenus and interpret these as patterns of parallel phenotypic evolution, i.e. the independent evolution of similar traits in closely related lineages (Futuyma 1986, Schluter *et al.* 2004).

MATERIALS AND METHODS

Ethics statement

This study was carried out in strict accordance with the guidelines for use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists, the Herpetologists' League and the Society for the Study of Amphibians and Reptiles. Research permits were issued by the Ecuadorian Ministry of Environment (MAE-DNB-CM-2015-0016, MAAE-ARSFC-2020-0727, MAATE-DBI-CM-2021-0181, MAATE-ARSFC-2023-0063, and MAATE-ARSFC-2024-1019).

Specimen collection and study site

Specimens were collected during several field expeditions carried out between April 2017 and June 2025 in Abra de Zamora (Loja province, southern Ecuador; 3.9912°S, 79.1454°W; datum WGS84; 2815 m a.s.l.), the Cerro Toledo sector of Parque Nacional Podocarpus (Zamora Chinchipe provinces; 4.3865°S, 79.1074°W, 3087 m a.s.l.), Reserva Numbala (Zamora Chinchipe province; 4.4035°S, 79.0883°W, 2936 m a.s.l.), Reserva Tapichalaca (Zamora Chinchipe province; 4.4878°S, 79.1489°W, 2678 m a.s.l.), Parque Nacional Yacuri (Zamora Chinchipe province; 4.7753°S, 79.4110°W, 3104 m a.s.l.), and Río Sangola, at ~30 km north-east from the village of Chito (Zamora Chinchipe province; 4.8416°S, 78.9278°W, 2422 m a.s.l.). For habitat description, we follow the Ecosystem Classification System of Continental Ecuador, developed by the Ecuadorian Ministry of Environment (MAE 2013).

Pristimantis atratus specimens were collected in January 2024 from the type locality, Suro Rancho in Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño (Morona Santiago province; 3.0090°S, 78.6201°W, 2798 m a.s.l.). Additionally, in order to collect specimens and observe the ecosystem in the type locality of *Pristimantis yumbo* Yánez-Muñoz *et al.*, 2010, Bosque Protector Tandacato (Pichincha province; 0.2203°S, 78.6977°W, 2868 m a.s.l.), we visited the site in December 2023. Sampling consisted of intensive visual encounter and auditory surveys, both diurnal and nocturnal, in all sampled areas.

Table 1. Comparison of key morphological and ecological traits between the three new species and the currently recognized members of the *Huicundomantis* subgenus.

Species	Size	Bromeliad specialists	Tympanum	Vocal slits	Dorsolateral folds	Lateral folds	Special coloration	Source
Pristimantis philipi	Small (33.7 mm)	No	Absent	Absent	Absent	Absent	Yes	Lynch and Duellman (1995)
Pristimantis ruidus	Medium (39.8 mm)	No	Absent	Absent	Absent	Absent	No	Lynch (1979), Sánchez-Nivicela *et al.* (2024)
***Pristimantis miktos* group**								
Pristimantis mallii	Small (34.3 mm)	Facultative	Present	Present	Absent	Absent	No	Reyes-Puig *et al.* (2019)
Pristimantis miktos	Small (29.2 mm)	No	Present	Absent	Absent	Absent	No	Ortega-Andrade and Venegas (2014)
Pristimantis tamia	Small (29.9 mm)	No	Present	Absent	Absent	Absent	No	Ortega *et al.* (2022)
***Pristimantis cryptomelas* group**								
Pristimantis cryptomelas	Large (45.7 mm)	Facultative	Present	Absent	Absent	Present	Yes	Székely *et al.* (2020)
Pristimantis gagliardoi	Small (33.6 mm)	No	Present	Absent	Absent	Present	No	Bustamante and Mendelson III (2008)
Pristimantis muscosus	Large (46.1 mm)	No	Present	Present	Absent	Present	Yes	Duellman and Pramuk (1999), Páez and Ron (2019), this study
Pristimantis nangaritza	Small (32.4 mm)	No	Present	Present	Absent	Present	No	Páez and Ron (2019)
Pristimantis spinosus	Small (35.3 mm)	No	Present	Absent	Absent	Present	Yes	Lynch (1979), this study
***Pristimantis phoxocephalus* group**								
Pristimantis andinogigas	Large (50.5 mm)	Facultative	Present	Present	Absent	Absent	No	Yánez-Muñoz *et al.* (2019), this study
Pristimantis atillo	Small (35.3 mm)	Facultative	Present	Present	Absent	Absent	No	Páez and Ron (2019)
Pristimantis atratus	Small (27.3 mm)	No, bamboo specialists	Present	Present	Absent	Absent	Yes	Lynch (1979), this study
Pristimantis balionotus	Small (32.4 mm)	Yes	Present	Present	Absent	Absent	Yes	Székely *et al.* (2020), Villavicencio Asanza (2025)
Pristimantis chomskyi	Large (44.3 mm)	Facultative	Present	Present	Absent	Absent	No	Páez and Ron (2019), this study
Pristimantis chusquea	Small (31.3 mm)	No, bamboo specialists	Present	Present	Absent	Absent	Yes	This study
Pristimantis gloria	Small (35.8 mm)	Facultative	Present	Present	Absent	Absent	No	Páez and Ron (2019)
Pristimantis hampatusami	Medium (37.6 mm)	Facultative	Present	Present	Absent	Present	Yes	Székely *et al.* (2016, Yánez-Muñoz *et al.* (2016)
Pristimantis jimenezi	Medium (37.4 mm)	Facultative	Present	Present	Absent	Present	Yes	Páez and Ron (2019)
Pristimantis lojanus	Large (44.3 mm)	No	Present	Present	Absent	Absent	No	Székely *et al.* (2021)
Pristimantis lutzae	Small (33.9 mm)	No	Present	Present	Absent	Present	No	Páez and Ron (2019)
Pristimantis multicolor	Medium (40.5 mm)	Facultative	Present	Present	Absent	Absent	No	Páez and Ron (2019)
Pristimantis oculolineatus	Small (28.5 mm)	No, bamboo specialists	Present	Present	Present	Present	Yes	This study
Pristimantis percultus	Medium (38.2 mm)	Facultative	Present	Absent	Absent	Absent	No	Székely *et al.* (2020)
Pristimantis phoxocephalus	Medium (39.9 mm)	Facultative	Present	Present	Absent	Present	Yes	Páez and Ron (2019)

(Continued)

Table 1. Continued.

Species	Size	Bromeliad specialists	Tympanum	Vocal slits	Dorsolateral folds	Lateral folds	Special coloration	Source
Pristimantis teslai	Medium (28.2)[a]	No	Present	Present	Absent	Absent	No	Páez and Ron (2019), this study
Pristimantis tinguichaca	Small (31.7 mm)	Facultative	Present	Present	Absent	Absent	No	Brito *et al.* (2016)
Pristimantis torresi	Medium (39.5 mm)	Facultative	Present	Present	Absent	Present	Yes	Páez and Ron (2019)
Pristimantis totoroi	Small (34.3 mm)	Facultative	Present	Present	Absent	Present	No	Páez and Ron (2019)
Pristimantis translucidus	Small (24.9)[a]	No, bamboo specialists	Present	Present	Absent	Absent	Yes	This study
Pristimantis verrucolatus	Large (47.5 mm)	Facultative	Present	Present	Absent	Present	No	Páez and Ron (2019)
Pristimantis versicolor	Small (32.2 mm)	Facultative	Present	Absent	Absent	Absent	No	Székely *et al.* (2020)

Size (relative size in the subgenus): small, when the largest recorded individual snout–vent length (SVL) is <36 mm; medium, SVL is >36 mm and <42 mm; or large, SVL is >42 mm. Based on female size ([a]except where no female is known). In parenthesis, maximum reported SVL value.
Bromeliad specialist: yes, relies on bromeliads throughout its life, consistently inhabiting them rather than merely using them as temporary daytime refuges; facultative, using bromeliads as temporary daytime refuges together with other microhabitats as trees, shrubs, rocks, or logs; or no, not associated with bromeliads.
Tympanum: present, tympanic membrane absent but tympanic annulus evident, or both tympanic membrane and annulus present; or absent, both tympanic annulus and tympanic membrane absent.
Special coloration: refers to some kind of distinctive coloration, either ventral or dorsal spots, or markings in axilla, groin, or on concealed limb surfaces.

For ranking the relative abundance of species, we used the following terms: common, when the species presence was detected (seen or heard), in the proper habitat, in large or moderate numbers, on >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; and rare, when the species presence was detected in small numbers on <25% of the sampling days/nights (Székely *et al.* 2020).

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 are presented in Appendix 1. Institutional abbreviations are as follows: KU (Biodiversity Institute, University of Kansas, Lawrence, KS, USA), MUTPL (Museo de Zoología, Universidad Técnica Particular de Loja, Loja, Ecuador), NMNH (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador), and USNM (United States National Museum, Smithsonian Institution, Washington, DC, USA).

Molecular analyses

Genomic extraction, amplification, and sequencing were as described by Székely *et al.* (2020); the newly generated DNA sequences were deposited in GenBank (Appendix 2). For the phylogenetic analysis, we used sequences of two mitochondrial ribosomal genes (12S and 16S ribosomal RNA) and one nuclear gene (recombination-activating gene 1, *RAG-1*) from 75 specimens of 39 species or candidate species (29 described, 7 undescribed, candidate new species, and the 3 new species described herein) corresponding to 46 different localities from Ecuador and one from Peru (Appendix 2); these samples (GenBank-available sequences and 41 new sequences generated by this study) represent all the currently confirmed species of the *Huicundomantis* subgenus of *Pristimantis* (*sensu* Ortega *et al.* 2022). As outgroups, we used the species from Sánchez-Nivicela *et al.* (2024), and the tree was rooted with *Pristimantis unistrigatus* (Günther, 1859).

The sequences were edited, assembled, and aligned (MAFFT algorithm with the G-INS-i iterative refinement method; Katoh and Standley 2013) in Geneious Prime (v.2025.0.3, Biomatters Ltd, Auckland, New Zealand); the 12S, 16S, and *RAG-1* aligned sequences were inspected visually to correct alignment errors in PhyDE (Müller *et al.* 2010), concatenated into a single matrix, then used for the phylogenetic analyses (Székely *et al.* 2023). The analyses were based on a 2425 bp pair dataset (925 bp for 12S, 886 bp for 16S, and 614 bp for *RAG-1*); the aligned and concatenated matrix is available at https://doi.org/10.5281/zenodo.16898580.

Phylogenetic relationships were inferred using both maximum likelihood (ML) and Bayesian inference (BI). We used PartitionFinder v.2.1.1 (Lanfear *et al.* 2017) to select the best partition scheme with the Bayesian information criterion as a model of selection; PartitionFinder identified three partition schemes (best model in parentheses): 12S and 16S (GTR+I+G), *RAG-1* first and third codon position (F81+I+G), and *RAG-1* second codon position (K80+G). The ML analyses were conducted in IQ-TREE 2 (Minh *et al.* 2020). We performed two different runs, in order to test the topologies of the trees: one run with the default settings in IQ-TREE, in which the program determined the best-fitting model for our alignment (TIM2+F+I+R3 under the Bayesian information criterion), and with the -bnni option (optimized, hill-climbing nearest neighbour interchange, search) in order to reduce the risk of overestimating the branch supports of the ultrafast bootstrap (UFBoot), with 100000 bootstrap replicates for the SH-like approximate likelihood ratio branch test (SH-aLRT; Guindon *et al.* 2010) and with 100000 ultrafast bootstrap replicates (UFBoot; Hoang *et al.* 2018) to assess the branch support; and a second run with the default settings, but the branch support evaluated with 1000 standard non-parametric bootstrap

(Boot; Felsenstein 1985) searches. The BI analysis was implemented in MrBayes v.3.2.6 (Ronquist *et al.* 2012), with the Markov chain Monte Carlo runs being performed twice, independently, for 10 million generations, with trees sampled every 1000 generations; convergence of the runs was assessed from the average split frequency of standard deviations ($P < .001$) and by checking the potential scale reduction factors (~1.0) for all model parameters; consensus trees were summarized after discarding the initial 25% as burn-in (Székely *et al.* 2023).

Additionally, to position the species of interest within the appropriate species groups, we analysed 16S ribosomal RNA sequences from all Ecuadorian *Pristimantis* species available in GenBank (204 species). For this analysis, we used an unpartitioned 1292 bp dataset, with one representative sequence per species. Phylogenetic relationships among species groups were inferred using an ML approach implemented in IQ-TREE 2, under default parameters.

A priori, we regarded that a tree node had 'strong support' when its bootstrap (Boot) value was >75 and its Bayesian posterior probability (PP) was >.95, 'moderate support' for 50–75 and .90–.95, and 'weak support' or non-resolved for values <50 and .90, respectively (Székely *et al.* 2023); clades were considered strongly supported when UFBoot was ≥95 and SH-aLRT ≥80 (Guindon *et al.* 2010, Hoang *et al.* 2018). Uncorrected genetic p-distances were calculated using a trimmed 864 bp fragment of 16S, excluding regions with extensive gaps. The analysis was performed in MEGA6 (Tamura *et al.* 2013) using the pairwise deletion option. The results are presented in the Supporting Information (File S1).

Morphological characterization

We largely followed the definitions provided by Lynch and Duellman (1997) and Ospina-Sarria and Duellman (2019), in addition to the format of the description proposed by Duellman and Lehr (2009). Sex was determined by gonadal inspection and the presence of external sexual characters, such as the vocal sacs and slits of the males. Coloration of live specimens was based on digital photographs.

All adult specimens were weighed (body mass, BM) before euthanasia using a My Weigh Triton T3 portable scale with 0.01 g precision. Measurements were taken under a stereo microscope, with Vernier callipers, and rounded to the nearest 0.1 mm. Specimens were measured for the following morphometric variables: (i) snout–vent length (SVL), distance from the tip of snout to posterior margin of vent; (ii) head width (HW), widest portion of the head, measured at level of jaw articulation; (iii) head length (HL), distance from the tip of snout to posterior angle of jaw articulation; (iv) interorbital distance (IOD), the shortest distance between the inner margins of the orbits; (v) internarial distance (IND), distance between the inner edges of the narial openings; (vi) upper eyelid width (EW), greatest width of the upper eyelid margins; (vii) eye diameter (ED), horizontal distance between anterior and posterior corners of the eye; (viii) eye–nostril distance (EN), distance from posterior margin of nostril to anterior corner of eye; (ix) snout length (SL), distance from tip of snout to anterior corner of eye; (x) snout–nostril distance (SN), distance from tip of the snout to edge of the narial opening; (xi) tympanum diameter (TD), greatest horizontal distance between peripheral borders of tympanic annulus; (xii) thigh length (THL), length of thigh from vent to knee; (xiii) tibia length (TL), length of flexed leg from knee to heel; (xiv) foot length (FL), distance from proximal margin of inner metatarsal tubercle to tip of toe IV; (xv) forearm length (FLL), length of forearm from the flexed elbow to proximal edge of palmar tubercle; and (xvi) hand length (HAL), distance from proximal edge of palmar tubercle to tip of finger III. Measurements are given as the mean ± SD.

For comparison of the body size, we used predetermined categories, because the available morphometric data are limited to a relatively small number of specimens or missing altogether. Thus, the body size (relative size in the *Huicundomantis* subgenus) was defined as follows: small (when the largest recorded female SVL is <36 mm); medium (female SVL of >36 mm and <42 mm); and large (female SVL >42 mm).

Bioacoustic characterization

The calls were recorded in the field using an Olympus LS-11 Linear PCM Recorder, with a RØDE NTG2 condenser shotgun microphone or with a Xiaomi Redmi 9A smartphone with Lavalier GL-119 omnidirectional condenser microphone, at 44.1 kHz sampling frequency and 16-bit resolution, in WAV file format. Air temperature and humidity were measured with a data logger (Lascar Electronics, model EL-USB-2-LCD, accuracy: ±0.5°C; ±5%). All analysed call recordings are deposited in original form, full length, at Fonoteca UTPL (record IDs are provided in Supporting Information, File S2). Acoustic analysis was conducted using Raven Pro v.1.6 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology). We measured the temporal parameters from the oscillograms and the spectral parameters from spectrograms obtained with the Hanning window function, Discrete Fourier Transform (DFT): 512 samples, 3 dB filter bandwidth: 124 Hz, and a 50% overlap (Székely *et al.* 2020).

The terminology and procedures for measuring call parameters follow Cocroft and Ryan (1995), Toledo *et al.* (2015), and Köhler *et al.* (2017), with a note-centred approach to distinguish between a call and a note (*sensu* Köhler *et al.* 2017). The following temporal and spectral parameters were measured and analysed: (i) call duration, i.e. the time from the beginning to the end of a call (for multi-note calls; in the case of single-note calls, this is the same as a note duration); (ii) inter-call interval, i.e. the interval between two consecutive calls, measured from the end of one call to the beginning of the consecutive call; (iii) call rate, i.e. number of calls per minute, measured as the time between the beginning of the first call and the beginning of the last call; (iv) note duration, i.e. the duration of a single note within a call, measured from beginning to the end of the note; (v) inter-note interval, i.e. the interval between two consecutive notes within the same call, measured from the end of one note to the beginning of the consecutive note; (vi) note rate, i.e. number of notes per second, measured as the time between the beginning of the first note and the beginning of the last note; (vii) dominant frequency, i.e. the frequency containing the highest sound energy, measured along the entire call; and (viii) the 90% bandwidth, reported as frequency 5% and frequency 95%, or the minimum and maximum frequencies, excluding the 5% below and above the total energy in the selected call (Székely *et al.* 2020).

Given that the data violated both the normal distribution (Shapiro–Wilk test, $P < .05$ for all parameters) and

homoscedasticity (Levene test, $P < .05$ for all parameters) assumptions, we assessed interspecific differences in call parameters (note duration, inter-note interval, note rate, peak frequency, 5% frequency, and 95% frequency) by performing non-parametric Kruskal–Wallis tests. Significant results were followed by pairwise Wilcoxon rank-sum *post hoc* tests, with Bonferroni correction for multiple comparisons. All statistical analyses were carried out in R v.4.3.2 (R Core Team 2025).

RESULTS

Phylogenetic analyses

The BI and the two ML phylogenetic trees showed almost the same topology, with only minor differences in the position of some of the unresolved branches. The BI tree presented relatively higher branch support, and in the case of ML, the UFBoot tree proved to be most conservative (having overall smaller support values) compared with the non-parametric Boot tree (Fig. 1). Consistent with the findings of Páez and Ron (2019), Ortega *et al.* (2022), and Sánchez-Nivicela *et al.* (2024), we recovered the subgenus *Huicundomantis* as monophyletic, with strong support (SH-aLRT = 97.9%; UFBoot = 99%; Boot = 97%; PP = 1). However, as shown in our phylogenetic tree (Supporting Information, Fig. S1), and similarly to Sánchez-Nivicela *et al.* (2024), the basal terminals within *Huicundomantis* are represented by the clade comprising *P. philipi* and *P. ruidus*, rather than the *P. miktos* group. Nonetheless, this topology remains unresolved owing to the lack of branch support.

Our results show that *P. atratus s.s.* (sampled from the type locality), along with two newly identified sister species, forms a strongly supported clade (SH-aLRT = 100%; UFBoot = 100%; Boot = 100%; PP = 1). This clade is only distantly related to the taxon previously considered to be *P. atratus*, which, upon closer examination, was revealed to be an undescribed species. We formally describe this taxon further below as *Pristimantis oculolineatus* (Fig. 1). *Pristimantis atratus s.s.* and the three new species belong to the *P. phoxocephalus* species group (Supporting Information, Fig. S1), which in our phylogenetic tree had a strong support (SH-aLRT = 97.6%; UFBoot = 97%; Boot = 90%; PP = 1), consistent with the trees of Páez and Ron (2019), Ortega *et al.* (2022), and Sánchez-Nivicela *et al.* (2024). The relationship between *P. atratus s.s.* and its two new sister species remains unresolved, with our branch topologies merely suggesting closer ties to *Pristimantis chusquea* (with moderate support in the ML analysis, Boot = 52) than to *Pristimantis translucidus* (Fig. 1).

Uncorrected genetic p-distances for 16S between *P. atratus s.s.* and its sister species (*P. chusquea* and *P. translucidus*) range between 2.5% and 4.2%. In contrast, the genetic distances between these species and *P. oculolineatus* are notably higher, ranging from 6.6% to 8.2%. As for the intraspecific genetic p-distances, these did not exceed 0.3% in *P. atratus*, 0.4% in *P. chusquea*, 0% in *P. translucidus*, and 0.1% in *P. oculolineatus* (Supporting Information, File S1).

Bioacoustic analyses

All evaluated sound parameters revealed significant differences between species (Kruskal–Wallis, note duration $\chi_3^2 = 280.25$; inter-note interval $\chi_3^2 = 84.58$; note rate $\chi_3^2 = 98.26$; peak frequency $\chi_3^2 = 238.93$; 50% frequency $\chi_3^2 = 239.28$; 95% frequency $\chi_3^2 = 143.13$; all $P < .001$). *Post hoc* tests retained significant differences between pairwise comparisons of species (all $P < .001$), with two exceptions: call duration between *P. chusquea* and *P. translucidus* ($P = .99$) and 95% frequency between *P. oculolineatus* and *P. translucidus* ($P = .99$). The advertisement calls of *P. atratus s.s.* and the three new species are so distinct that they can be distinguished readily by ear (Fig. 2). Detailed sonograms for each species are provided in their respective sections.

Parallel evolution in Andean *Pristimantis*

Pristimantis atratus s.s. and its sister species (*P. chusquea* and *P. translucidus*) share distinctive morphological traits that enable effective camouflage on the leaves of native Andean bamboo (family Poaceae, genus *Chusquea* Kunth). Specifically, their light dorsal coloration, ranging from cream to yellowish brown or darker brown, combined with dark brown stripes or irregular spots and the presence of numerous low dermal ridges on the dorsum that mimic the leaf texture, closely resembles the dry leaves of *Chusquea* (Fig. 3). We found that these species are almost exclusively associated with bamboo shrubs, primarily found within the 'Southern montane evergreen forest of the eastern Andes' ecosystem, at elevations ranging from 2400 to 2900 m a.s.l. Herein, we define these species as 'bamboo specialist', because they are found almost exclusively on bamboo shrubs or within ecosystems dominated by *Chusquea* species, and their distinctive bamboo leaf-mimicking body shape suggests a strong microhabitat fidelity. Their distant relative, *P. oculolineatus* (Fig. 1), shares the same morphological traits, also being a bamboo specialist, and the northern populations inhabit the same ecosystem type. Further south, this species is also associated with bamboo shrubs found within the 'High montane evergreen shrubland of the páramos from southern Ecuador' ecosystem, generally occurring at slightly higher elevations that reach 3100 m a.s.l. These four species belonging to the *P. phoxocephalus* species group are the only currently known *Pristimantis* species distributed along the eastern slopes of the Andes (Fig. 4) that exhibit this distinctive bamboo leaf-mimicking habitus.

On the western slopes of the Andes (Fig. 4), members of a different subgenus exhibit the same morphological features associated with life on *Chusquea* leaves: the dorsal coloration, ranging from cream to yellowish brown or darker brown, combined with dark brown stripes or irregular spots, and the presence of numerous low dermal ridges on the dorsum. This is the case for *P. yumbo* and an undescribed species, *P.* aff. *yumbo*, which appears to be very similar [QCAZ 58450, listed as '*P. yumbo*' in the online database Anfibios del Ecuador (Ron *et al.* 2024) and in GenBank]. These two species belong to the deeply divergent subgenus *Trachyphrynus* and are part of the *devillei* species group (Fig. 5). *Pristimantis yumbo* is so similar to *P. atratus* (Fig. 6) that, when it was described, the authors noted that '…both species are very similar in their external morphology and appear to be closely related. They could apparently be sister species separated by vicariance, as both occupy montane cloud forest ecosystems at similar elevations' (Yánez-Muñoz *et al.* 2010). Indeed, the ecosystem type inhabited by *P. yumbo* and its close relative is the 'Montane evergreen forest of the western Andes', at elevations ranging from 2400 to 2900 m a.s.l., which essentially represents the counterpart of the

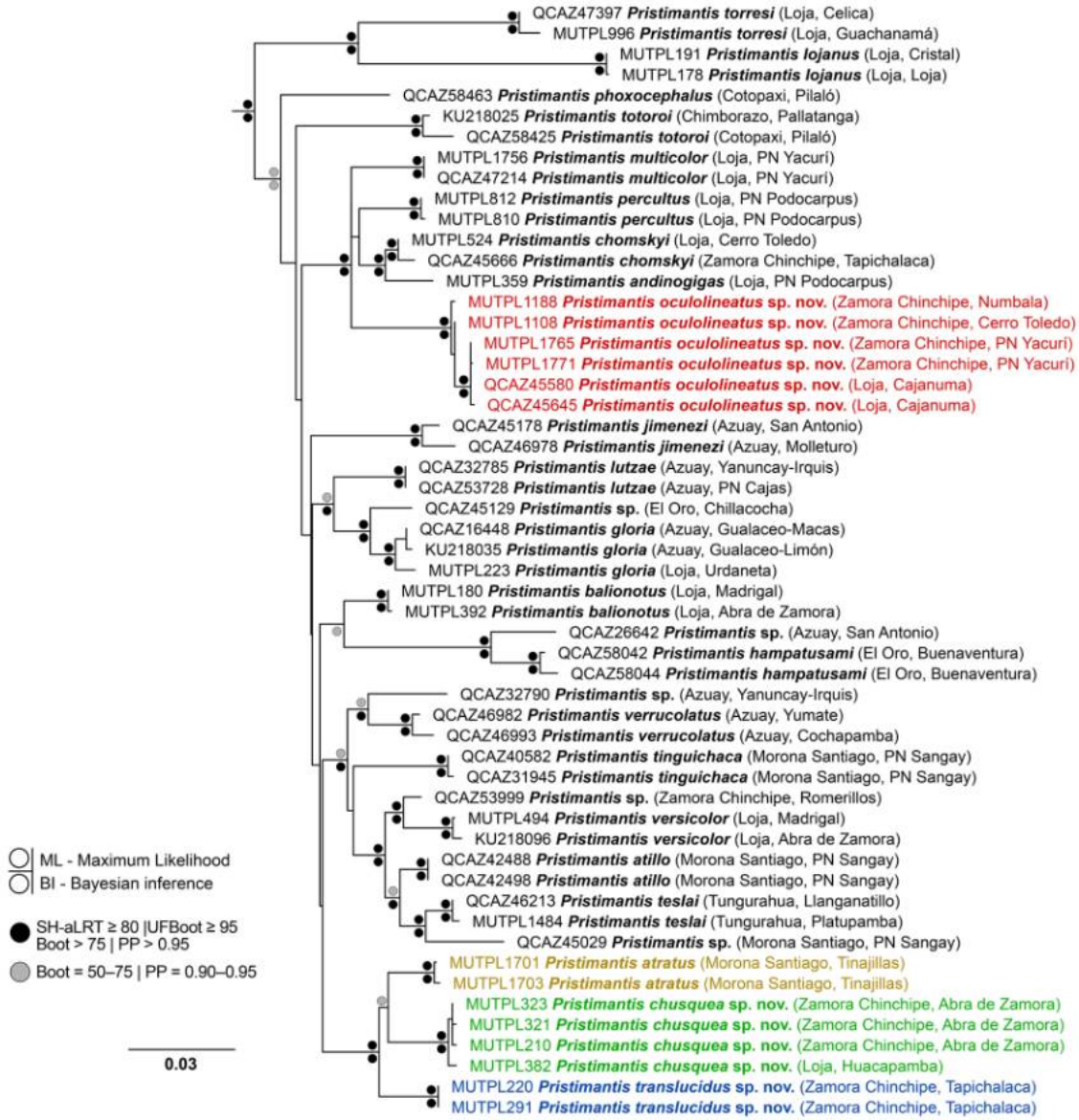

Figure 1. Maximum likelihood phylogram of the *Pristimantis phoxocephalus* species group based on 2425 bp dataset of concatenated mitochondrial DNA from 12S and 16S, and nuclear DNA from *RAG-1* gene fragments. The outgroup is not shown; the tree was rooted with *Pristimantis unistrigatus* [the complete tree of the *Pristimantis* (*Huicundomantis*) subgenus is provided in Supporting Information, Fig. S1]. The catalogue 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 2). Abbreviations: SH-aLRT, SH-like approximate likelihood ratio branch test; UFBoot, ultrafast bootstrap; Boot, standard non-parametric bootstrap; PP, Bayesian posterior probability.

ecosystem inhabited by the *Huicundomantis* bamboo-specialist species on the eastern slopes of the Andes.

The impressive morphological resemblance observed between the eastern Andean bamboo specialists and their western congeners suggests a case of parallel evolution. Despite belonging to distinct subgenera (*Huicundomantis* and *Trachyphrynus*, respectively) and species groups (*phoxocephalus* and *devillei*), these taxa independently evolved similar external traits (that allow them to mimic bamboo leaves) in response to analogous ecological pressures. Their similarity in morphology and habitat preference, along with their geographical split across the eastern and western slopes of the Andes, supports the hypothesis that these adaptations are the result of parallel evolutionary processes rather than shared ancestry.

SYSTEMATIC ACCOUNTS

Family Strabomantidae Hedges *et al.*, 2008
Genus *Pristimantis* Jiménez de la Espada, 1870

Pristimantis atratus (Lynch, 1979)
(Figs 7, 8)

Eleutherodactylus atratus—Lynch (1979).
Eleutherodactylus (Eleutherodactylus) atratus—Lynch (1996), Lynch and Duellman (1997).
Pristimantis atratus—Heinicke *et al.* (2007).
Pristimantis (Pristimantis) atratus—Hedges *et al.* (2008).

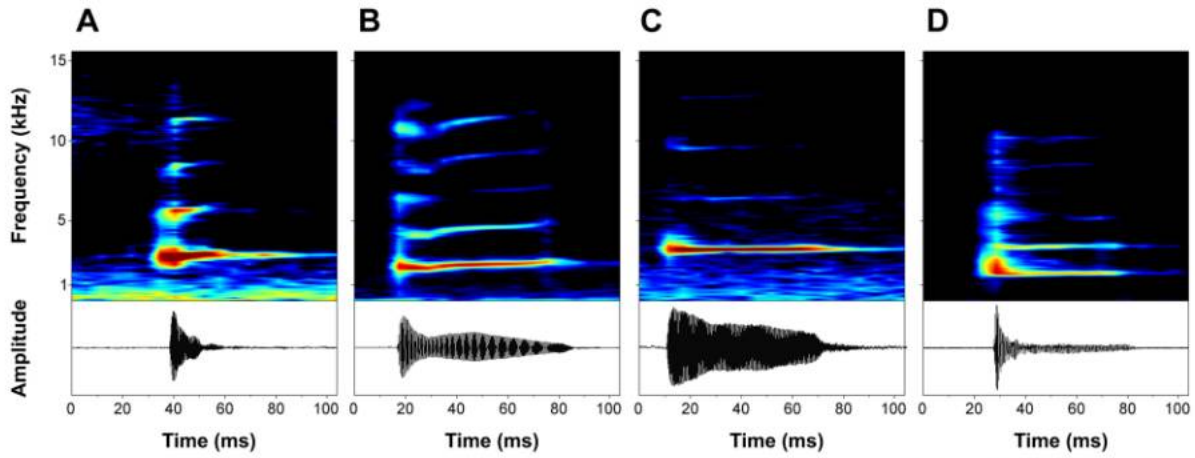

Figure 2. Comparative sonograms of the four bamboo specialist species: A, *Pristimantis atratus s.s.* (FUTPL-A-1001); B, ***Pristimantis chusquea*** (FUTPL-A-1041); C, ***Pristimantis translucidus*** (FUTPL-A- 377); and D, ***Pristimantis oculolineatus*** (FUTPL-A-546).

Figure 3. ***Pristimantis chusquea*** on leaves of Andean bamboo (genus *Chusquea*) from Abra de Zamora, Zamora Chinchipe Province. Note the similar coloration and the presence of numerous low dermal ridges on the dorsum that mimic the leaf texture.

Common English name: Black-thighed rainfrog.

Common Spanish name: Cutín de muslo negro.

Etymology: Latin, meaning dressed in black, in reference to the black areas on the concealed surfaces (Lynch 1979).

Holotype: USNM 199675 (Supporting Information, Figs S3, S4), an adult female from Ecuador, Provincia Morona Santiago, Suro Rancho, 2683 m a.s.l., collected by James A. Peters on 23 August 1962.

Paratypes: USNM 199679–199682, collected with the holotype; USNM 199683–199689, between Sapote and Suro Rancho, 2604–2622 m a.s.l.

Amended definition: A small-sized species of *Pristimantis* in the subgenus *Huicundomantis* (Table 1) as inferred from the phylogenetic relationships (Fig. 1), characterized by the following combination of traits: (1) skin on dorsum shagreen, usually bearing numerous low ridges (trait more evident in life); skin on venter areolate; discoidal fold present; dorsolateral folds absent; low mid-dorsal fold present; (2) tympanic annulus evident and tympanic membrane differentiated, its length ~39% of the length of eye; supratympanic fold present, slightly concealing the upper edge of tympanum; (3) snout subacuminate in dorsal view, rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; (4) upper eyelid bearing one to three larger tubercles (trait more evident in life), ~63% IOD in one female and 67% IOD in males; cranial crests inconspicuous, low; (5) dentigerous processes of vomers oblique, ovoid, separated medially by distance larger than the width of processes; each process bearing three to five teeth; (6) males with pigmented subgular vocal sac and round vocal slits; (7) finger I shorter than finger II; discs on fingers broadly expanded, rounded; circumferential grooves present; (8) fingers with lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present (trait more evident in life);

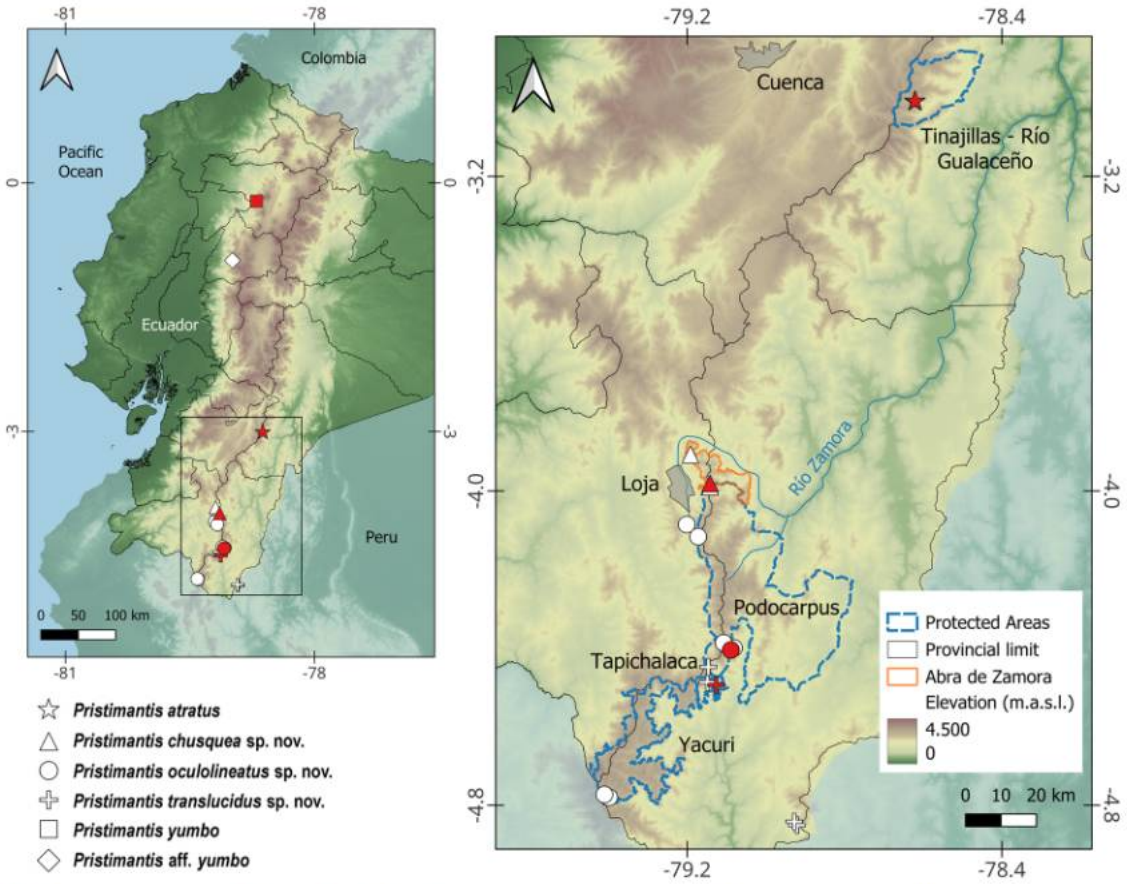

Figure 4. Distribution of the currently known Ecuadorian *Pristimantis* species considered bamboo specialists. Type localities are indicated in red. Records are based on specimens deposited at the Museo de Zoología, Universidad Técnica Particular de Loja (MUTPL), Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), and authors' field data.

palmar tubercle bifid, larger than thenar tubercle; thenar tubercle oval to elliptical; (9) ulnar tubercles present (trait more evident in life); (10) heel with one larger, conical tubercle (trait more evident in life); outer edge of tarsus with a row of tubercles (trait more evident in life); inner tarsal fold present; (11) inner metatarsal tubercle ovoid, about two- to three times the size of round outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present (trait more evident in life); (12) toes bearing lateral fringes; webbing basal; toe V longer than toe III; discs on toes broadly expanded, rounded, about same size as those on fingers; circumferential grooves present; (13) in life, dorsum cream to yellowish brown, with or without pale to dark brown stripes; flanks yellowish brown, sometimes with black blotches; venter whitish cream with small dark flecks; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces white, yellow, or orange with large black blotches; iris golden, without reticulations, and a median, brownish streak; (14) SVL 27.3 mm in one adult female (Lynch 1979) and 20.7–24.0 mm in adult males (22.4 ± 1.66 mm, $N = 3$).

Variation: Morphometric variation is shown in Table 2. Coloration does not differ between sexes. Most of the encountered individuals were either uniformly coloured with small dark brown spots, like the uncollected female (Fig. 8A, B) and male MUTPL 1701 (Fig. 8C, D), or inconspicuously striped, like the male MUTPL 1703 (Fig. 7) and subadult MUTPL 1702 (Fig. 8G, H). The male MUTPL 1703 had also a wide darker mid-dorsal band (Fig. 7). The male specimen MUTPL 1735 exhibited a highly atypical coloration, characterized by an intensely reddish brown dorsum with distinct orange spotting (Fig. 8E, F). The large, black-blotched areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces varied from white to intense orange (Figs 7, 8).

Vocalizations: For the description of the *P. atratus* call, we analysed seven call samples of four males, all recorded at the type locality, Suro Rancho in Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño, Morona Santiago Province, in 2024. Descriptive statistics of the acoustic variables are provided in Table 3 (detailed information on each of the recordings is provided in Supporting Information, File S2).

Pristimantis atratus has an advertisement call characterized by short, metallic 'tic' sounds (notes) repeated over a period of time. The calls are typically composed of two to three notes (Fig. 9); however, in some instances, the call can contain up to five distinct notes. The calls consistently begin as single-noted calls that at some point increase in complexity, incorporating two to three notes in subsequent calls. The calls that contain four to five notes are probably emitted during social interactions, triggered by the nearby presence of a female or a competitive vocalizing male

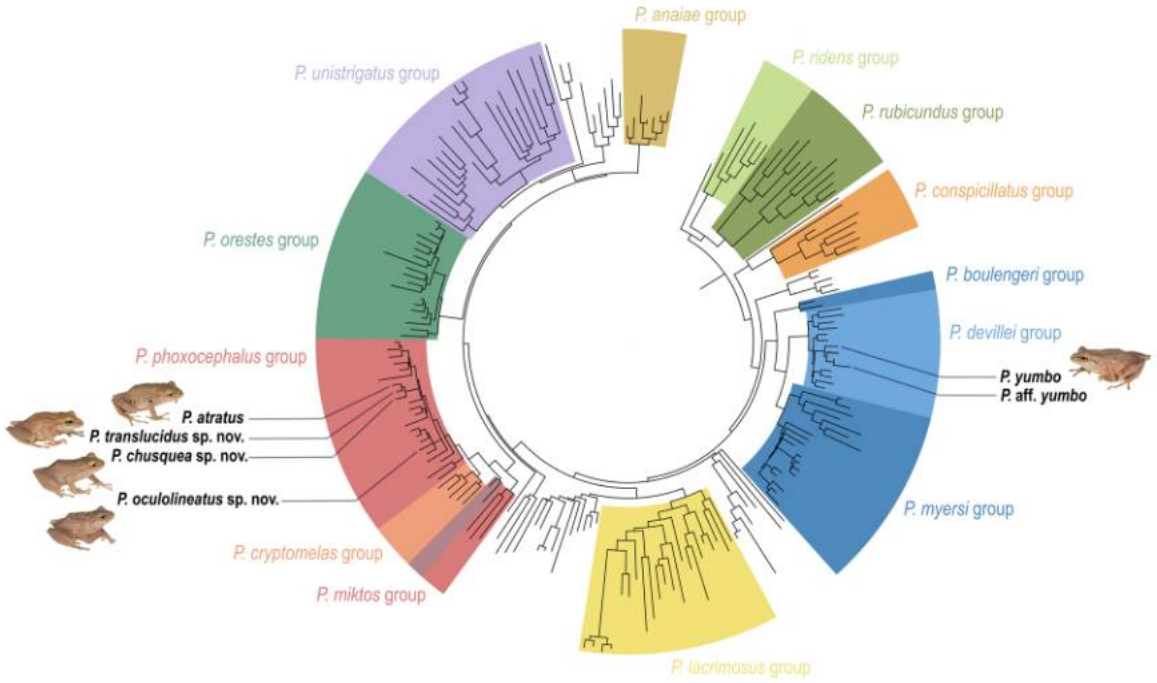

Figure 5. Maximum likelihood phylogram of all the currently available Ecuadorian *Pristimantis* species, organized by their respective species groups. Bamboo-specialist species are highlighted. The analysis is based on 1292 bp 16S mitochondrial DNA gene fragments from 204 species retrieved from GenBank. *Pristimantis phoxocephalus*, *Pristimantis cryptomelas*, and *Pristimantis miktos* species groups are included in the subgenus *Huicundomantis*; *Pristimantis boulengeri*, *Pristimantis devillei*, and *Pristimantis myersi* in subgenus *Trachyphrynus*. The detailed phylogram is provided in the Supporting Information (Fig. S2).

Figure 6. Bamboo-specialist *Pristimantis* species, from the eastern slopes of the Andes (A, ***Pristimantis chusquea***, MUTPL 1793, from Zamora Chinchipe Province, Abra de Zamora) and the western slopes of the Andes (B, *Pristimantis yumbo*, MUTPL 1683, from the type locality, Pichincha Province, Tandacato).

(probably courtship calls *sensu* Wells 2007). The notes within each call are structurally and temporally very similar, although the first note of the series is usually slightly longer. The calls are characterized by a mean duration of 0.244 s (in the case of double-noted calls, whereas quintuple-noted calls can last ≤0.842 s), a mean inter-call interval of 8.1 s, and a mean call rate of 5.1 calls/min (Table 3). The notes are tonal sounds, short, characterized by a mean duration of 0.027 s, a mean inter-note interval of 0.189 s, and a mean note rate of 4.6 notes/s. The mean dominant frequency of the call was 2827.3 Hz, with a mean 90% bandwidth of 2708.9–3014.6 Hz (Table 3). The fundamental frequency is not recognizable, but usually up to four harmonics are visible.

Distribution: For now, *P. atratus* is confirmed molecularly only from its type locality, Suro Rancho in Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño, Morona Santiago Province, but it is very probably distributed further to the north, as suggested by the records available on the online database Anfibios del Ecuador (Ron *et al.* 2024) and Amphibians of Ecuador encyclopedia (Coloma and Duellman 2025).

Natural history: James A. Peters and his associates collected the specimens from the type series in August 1962; they encountered calling males at night on bushes and by day caught individuals of both sexes beneath rocks and logs along the trail between Gualaceo and General Plaza (Lynch 1979). At the type

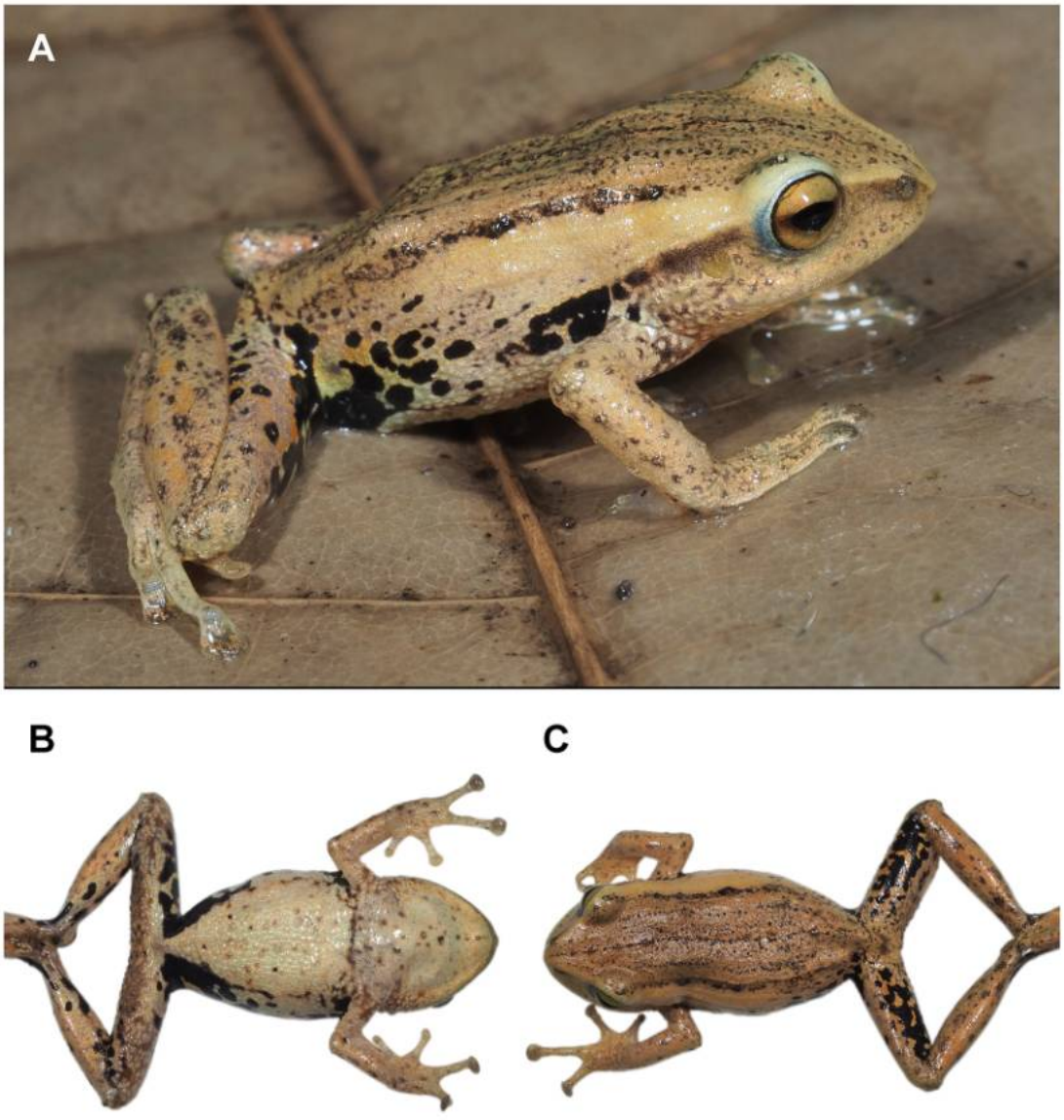

Figure 7. *Pristimantis atratus s.s.* (MUTPL 1703; adult male; SVL 20.7 mm) from the type locality, Suro Rancho, Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño, Morona Santiago Province: A, dorsolateral view; B, ventral view; and C, dorsal view.

locality, on one night (20 January 2024), we encountered many calling males, almost exclusively on leaves of Andean bamboos (*Chusquea* sp.), from 50 cm above the ground up to 2.5 m high. The general habitus of this species closely mimics dry *Chusquea* leaves, allowing it to blend seamlessly into its environment and making it difficult to detect, especially when the animals are inactive or not calling.

Conservation status: Pristimantis atratus is currently categorized as Vulnerable (IUCN 2025). However, this assessment was done by considering also the records from Loja and Zamora Chinchipe Provinces that, in fact, belong to different species, described below. Based on the information presented in the present work (redefinition of the species and restriction of its distribution to Morona Santiago Province) and the general lack of information on population size and geographical range, we suggest assigning *P. atratus* to the Data Deficient category following the International Union for Conservation of Nature (IUCN) criteria (IUCN 2001). In order to update the species conservation status, it is essential to collect populational and new distribution data from Morona Santiago but also its neighbouring provinces (mainly Azuay and Chimborazo), where this species might be present.

Remarks: Lynch (1979) provides a detailed description of this species and a black and white photograph. Our definition concurs with the majority of the morphological characters described by Lynch, but we complemented the description with traits that are more evident in life. One difference is that we consider that the fingers have lateral fringes, in contrast to the lack of them as described by Lynch. The author himself mentions in the 'Description' section of his paper that the fingers are 'lacking lateral fringes' but are 'keeled laterally'. This is most probably only a subjective difference, because Lynch and Duellman (1997) mention in the definition of these characters that '… there is a continuum from keels to fringes, and in some cases

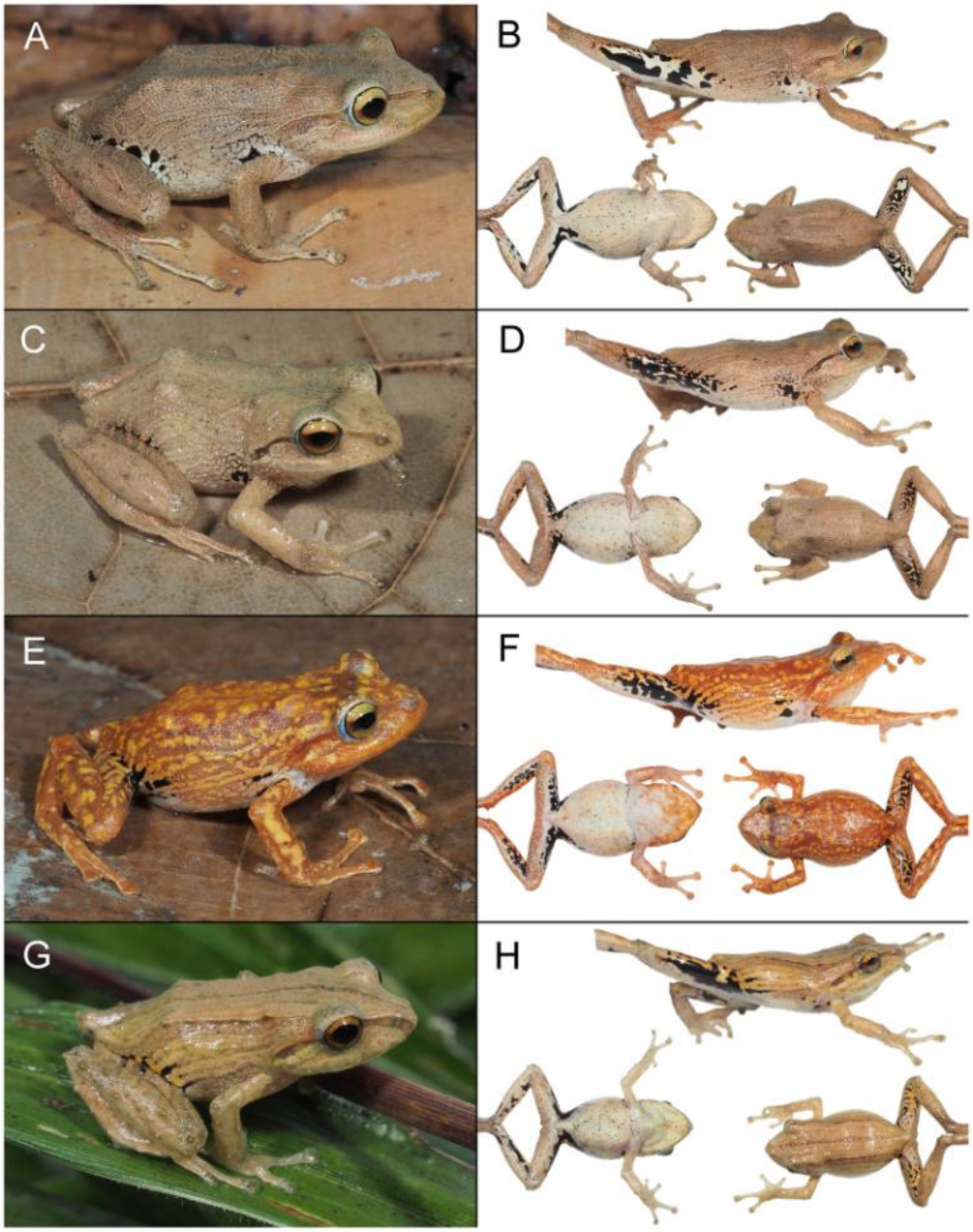

Figure 8. Colour variation in life for individuals of *Pristimantis atratus s.s.*, in dorsolateral, lateral, ventral, and dorsal views. A, B, uncollected adult female. C, D, MUTPL 1701 (adult male, SVL 22.6 mm). E, F, MUTPL 1735 (adult male, SVL 24.0 mm). G, H, MUTPL 1702 (subadult, SVL 16.8 mm). All individuals are from the type locality, Suro Rancho in Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño, Morona Santiago Province.

the distinction is arbitrary'. Also, Lynch mentions that no enlarged postrictal tubercles are present; however, in all examined specimens we observed two larger, rounded postrictal tubercles. Finally, the specimen KU 165236 (fig. 3A) depicted in the original description (Lynch 1979) was collected from Abra de Zamora and thus it is, in fact, *P. chusquea* and not *P. atratus*.

The diagnosis provided herein is based on specimens from the original description (*USNM 199675*, 199679–82, and 199683–89) and one subadult (MUTPL 1702), three adult males (MUTPL 1701, 1703, and 1735), and an uncollected female, from the type locality.

Pristimantis chusquea sp. nov.

(Figs 10–15)

ZooBank registration: urn:lsid:zoobank.org:act:758D367C-339E-43A4-9EA4-5D791B1AB884

Common English name: Chusquea rain frog.

Common Spanish name: Cutín de chusquea.

Etymology: The specific epithet *chusquea* is a noun in apposition and refers to the genus *Chusquea*, a group of native evergreen Andean

Table 2. Body measurements of adults *Pristimantis atratus s.s.* and the three new species.

Character	*Pristimantis atratus*		*Pristimantis chusquea*		*Pristimantis translucidus*	*Pristimantis oculolineatus*	
	Females	Males	Females	Males	Males	Females	Males
	($N=1$)[a]	($N=3$)	($N=1$)	($N=6$)	($N=5$)	($N=2$)	($N=3$)
Body mass (BM)		0.78 ± 0.07 (0.70–0.83)	2.3	1.44 ± 0.24 (1.14–1.86)	0.98 ± 0.13 (0.86–1.15)[b]	1.56–1.86	1.44 ± 0.13 (1.29–1.53)
Snout–vent length (SVL)	27.3	22.4 ± 1.66 (20.7–24.0)	31.3	26.7 ± 0.79 (25.5–27.8)	24.0 ± 0.91 (22.5–24.9)	26.9–28.5	25.6 ± 1.51 (23.9–26.7)
Head width (HW)	10.0	8.6 ± 0.50 (8.1–9.1)	11.2	9.7 ± 0.20 (9.4–10.0)	8.4 ± 0.23 (8.1–8.6)	10.2–11.1	10.0 ± 0.55 (9.4–10.4)
Head length (HL)	9.6	7.4 ± 0.70 (6.7–8.1)	10.1	8.7 ± 0.29 (8.3–9.0)	7.7 ± 0.23 (7.3–7.9)	9.3–9.7	8.9 ± 0.47 (8.4–9.3)
Interorbital distance (IOD)	3.2	2.8 ± 0.21 (2.6–3.0)	3.7	3.3 ± 0.20 (3.0–3.6)	2.9 ± 0.13 (2.7–3.0)	3.3–3.5	3.2 ± 0.10 (3.1–3.3)
Internarial distance (IND)		2.0 ± 0.15 (1.9–2.2)	2.8	2.4 ± 0.08 (2.2–2.4)	2.1 ± 0.05 (2.1–2.2)	2.3–2.4	2.3 ± 0.10 (2.2–2.4)
Upper eyelid width (EW)	2.0	1.9 ± 0.26 (1.6–2.1)	3.2	2.4 ± 0.17 (2.2–2.6)	2.0 ± 0.11 (1.9–2.2)	2.7–2.8	2.7 ± 0.15 (2.5–2.8)
Eye diameter (ED)	3.2	2.9 ± 0.29 (2.6–3.1)	3.5	3.2 ± 0.20 (3.0–3.5)	2.9 ± 0.17 (2.6–3.0)	3.0–3.1	3.1 ± 0.44 (2.6–3.4)
Eye–nostril distance (EN)	2.7	2.3 ± 0.23 (2.0–2.4)	2.8	2.5 ± 0.05 (2.5–2.6)	2.2 ± 0.09 (2.1–2.3)	3.0–3.1	2.7 ± 0.15 (2.5–2.8)
Snout length (SL)		3.5 ± 0.38 (3.1–3.8)	4.8	4.3 ± 0.17 (4.1–4.6)	3.8 ± 0.10 (3.7–3.9)	4.7–4.8	4.3 ± 0.06 (4.3–4.4)
Snout–nostril distance (SN)		1.3 ± 0.15 (1.1–1.4)	2.0	1.8 ± 0.14 (1.6–2.0)	1.5 ± 0.08 (1.4–1.6)	1.7	1.7 ± 0.12 (1.6–1.8)
Tympanum diameter (TD)	1.2	1.2 ± 0.15 (1.0–1.3)	1.6	1.3 ± 0.15 (1.0–1.4)	1.2 ± 0.11 (1.1–1.4)	1.4–1.6	1.5 ± 0.06 (1.4–1.5)
Thigh length (THL)		10.3 ± 0.46 (9.9–10.8)	13.2	11.9 ± 0.55 (11.3–12.5)	10.8 ± 0.36 (10.4–11.3)	12.7–13.8	12.4 ± 0.84 (11.4–12.9)
Tibia length (TL)	13.7	11.1 ± 0.87 (10.6–12.1)	15.0	13.5 ± 0.39 (12.8–13.8)	12.2 ± 0.66 (11.2–12.8)	13.7–15.2	13.6 ± 0.75 (12.8–14.3)
Foot length (FL)		10.2 ± 0.25 (9.9–10.4)	14.4	12.9 ± 0.69 (11.8–13.7)	10.9 ± 0.55 (9.9–11.2)	13.0–14.5	12.9 ± 0.55 (12.4–13.5)
Forearm length (FLL)		5.5 ± 0.53 (5.1–6.1)	7.1	6.6 ± 0.25 (6.2–6.8)	5.6 ± 0.36 (5.2–6.0)	6.6–7.1	6.7 ± 0.25 (6.4–6.9)
Hand length (HAL)		6.6 ± 0.23 (6.5–6.9)	9.1	7.9 ± 0.50 (7.2–8.5)	6.9 ± 0.36 (6.5–7.3)	8.5–9.7	8.2 ± 0.15 (8.0–8.3)
HW/SVL	36.6	37.6–39.1	35.8	34.5–36.9	34.4–36.0	37.9–38.9	38.6–39.5
HL/SVL	35.2	32.3–33.8	32.3	31.7–33.3	31.3–32.4	34.0–34.6	34.1–35.4
EN/SVL	9.9	9.7–10.6	8.9	9.0–9.9	9.1–9.5	10.9–11.2	10.1–10.6
SL/SVL		15.0–16.4	15.3	14.7–16.9	15.2–16.4	16.8–17.5	16.1–18.0
HL/HW	96	82.7–89.0	90.2	87.5–92.7	89.5–94.0	87.4–91.2	88.3–89.4
EN/HL	28.1	29.6–32.9	27.7	28.1–31.0	28.6–29.5	32.0–32.3	29.7–30.1
SL/HL		38.5–46.9	47.5	46.6–51.8	48.1–50.7	49.5–50.5	47.3–51.2
SN/HL		16.4–17.8	19.8	18.2–22.2	17.9–20.5	17.5–18.3	17.2–21.4
ED/HL	33.3	38.3–42.5	34.7	33.3–39.3	35.6–39.0	32.0–32.3	31.0–37.4
EW/IOD	62.5	61.5–70.0	86.5	61.1–81.3	66.7–81.5	80.0–81.8	80.6–84.8
EN/ED	84.4	76.9–77.4	80.0	71.4–86.7	73.3–82.1	100	79.4–96.2
TD/ED	37.5	38.5–41.9	45.7	30.3–46.7	40.0–46.7	46.7–51.6	41.2–57.7
THL/SVL		45.0–47.8	42.2	41.5–47.3	43.6–46.2	47.2–48.4	47.7–49.0
TL/SVL	50.2	46.9–51.2	47.9	47.5–52.3	49.4–52.0	50.9–53.3	50.9–54.4
FL/SVL		43.3–47.8	46.0	45.3–51.3	44.0–46.1	48.3–50.9	48.3–51.9
FLL/SVL		23.5–25.4	22.7	22.3–26.0	22.0–24.2	24.5–24.9	25.1–26.8
HAL/SVL		28.8–31.4	29.1	27.0–31.8	27.4–29.5	31.6–34.0	30.7–33.5

Body mass (in grams), measurements (in millimetres) and morphological proportions (as percentages). Values are given as the mean ± SD (range). Female body mass includes eggs.
[a]Measurements of the holotype from Lynch 1979.
[b]$N=4$.

Table 3. Quantitative description of the advertisement calls (mean ± SD, range, and *N*) of *Pristimantis atratus s.s.* and the three new species.

Characteristic	*Pristimantis atratus* (4)	*Pristimantis chusquea* (4)	*Pristimantis translucidus* (7)	*Pristimantis oculolineatus* (5)
Notes per call	1–5 (usually 2 or 3)	1–6 (usually 2)	1–14 (usually 2 or 3)	1–3 (usually 1)
Double-noted call duration (s)	0.244 ± 0.02 (0.215–0.295) *N* = 14	0.356 ± 0.02 (0.336–0.398) *N* = 41	0.352 ± 0.03 (0.294–0.459) *N* = 27	0.471 ± 0.02 (0.444–0.500) *N* = 4
Inter-call interval (s)	8.1 ± 1.17 (6.1–10.6) *N* = 20	11.6 ± 2.90 (6.8–16.8) *N* = 39	8.7 ± 2.97 (3.7–16.6) *N* = 47	3.7 ± 1.11 (2.0–7.1) *N* = 75
Call rate (calls/min)	5.1 ± 1.20 (3.5–6.5) *N* = 7	4.7 ± 0.79 (3.9–6.0) *N* = 6	5.8 ± 1.28 (3.7–8.0) *N* = 9	15.3 ± 3.41 (11.5–20.6) *N* = 5
Note duration (s)	0.027 ± 0.008 (0.015–0.048) *N* = 90	0.067 ± 0.005 (0.055–0.079) *N* = 91	0.067 ± 0.01 (0.043–0.085) *N* = 200	0.057 ± 0.005 (0.045–0.076) *N* = 107
Inter-note interval (s)	0.189 ± 0.03 (0.114–0.249) *N* = 63	0.223 ± 0.01 (0.204–0.266) *N* = 41	0.199 ± 0.04 (0.102–0.287) *N* = 134	0.278 ± 0.04 (0.220–0.373) *N* = 26
Note rate (notes/s)	4.6 ± 0.43 (3.4–5.1) *N* = 34	3.4 ± 0.16 (3.0–3.6) *N* = 41	3.6 ± 0.33 (2.4–4.5) *N* = 57	2.9 ± 0.31 (2.3–3.2) *N* = 15
Dominant frequency (Hz)	2827.3 ± 133.6 (2670.1–3100.8) *N* = 40	2181.0 ± 75.1 (2067.2–2239.5) *N* = 53	3168.0 ± 220.3 (2842.4–3703.7) *N* = 82	1817.6 ± 71.6 (1722.7–1981.1) *N* = 88
Frequency 5% (Hz)	2708.9 ± 133.7 (2583.9–2928.5) *N* = 40	2055.8 ± 87.8 (1894.9–2239.5) *N* = 53	3082.9 ± 221.5 (2756.3–3617.6) *N* = 82	1644.4 ± 75.7 (1550.4–1808.8) *N* = 88
Frequency 95% (Hz)	3014.6 ± 178.8 (2756.3–3359.2) *N* = 40	2382.5 ± 41.2 (2325.6–2411.7) *N* = 53	3281.5 ± 223.5 (2928.5–3876.0) *N* = 82	3200.6 ± 314.5 (2411.7–3531.4) *N* = 88

The number of recorded individuals is given in parentheses after the species name.

bamboos (family Poaceae) that dominate the habitat in which this species lives; the general appearance of the species mimics the dry leaves of this bamboo. The name *chusquea* originates from the Northern Andean indigenous Chibcha language and it means 'reed'.

Holotype: MUTPL 210 (Figs 10–13A), an adult male from Ecuador, Zamora Chinchipe Province, Abra de Zamora, on the old Loja-Zamora road (3.9809°S, 79.1420°W; datum WGS84), 2706 m a.s.l., collected by Paul Székely and Diana Székely on 16 May 2017.

Paratypes (nine: five males, one female, and three juveniles): MUTPL 321, a juvenile, MUTPL 322, an adult male, and MUTPL 323, an adult female from Zamora Chinchipe Province, Abra de Zamora, on the old Loja-Zamora road (3.9846°S, 79.1437°W), 2737 m a.s.l., collected by Paul Székely and Diana Székely on 4 April 2018; MUTPL 382 (field no. SC 185), a juvenile from Loja Province, Abra de Zamora, Huacapamba (3.9082°S, 79.1918°W), 2687 m a.s.l., collected by Paul Székely, Diana Székely, and Diego Armijos on 4 August 2018; MUTPL 1793 (field no. SC 3935), MUTPL 1794 (field no. SC 3936), and MUTPL 1795 (field no. SC 3937), three males from Zamora Chinchipe Province, Abra de Zamora, on the old Loja-Zamora road (3.9838°S, 79.1436°W), 2728 m a.s.l., collected by Paul Székely and Diana Székely on 26 June 2024; MUTPL 1796 (field no. SC 3938), a juvenile and MUTPL 1797 (field no. SC 3939), an adult male from Loja Province, Abra de Zamora, Huacapamba (3.9049°S, 79.1897°W), 2709 m a.s.l., collected by Paul Székely, Diana Székely, Diego Armijos, and Eddie Jaramillo on 6 July 2024.

Definition: We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 1) and on the general morphological similarity to other members of the genus. *Pristimantis chusquea* is a small-sized species (among the *Huicundomantis* subgenus; Table 1) characterized by the following combination of characters: (1) skin on dorsum shagreen, usually bearing numerous low ridges (trait more evident in life); skin on venter areolate; discoidal fold present; dorsolateral folds absent; low mid-dorsal fold usually absent; (2) tympanic annulus evident and tympanic membrane differentiated, its length ~41% of the length of eye; supratympanic fold present, slightly concealing the upper edge of tympanum; (3) snout acuminate in dorsal view, rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; (4) upper eyelid bearing one larger tubercle (trait more evident in life), ~87% IOD in one female and 73% IOD in males; cranial crests inconspicuous, low; (5) dentigerous processes of vomers oblique, ovoid to triangular, separated medially by distance equal to or smaller than the width of processes; each process bearing five to ten teeth; (6) males with pigmented subgular vocal sac, large vocal

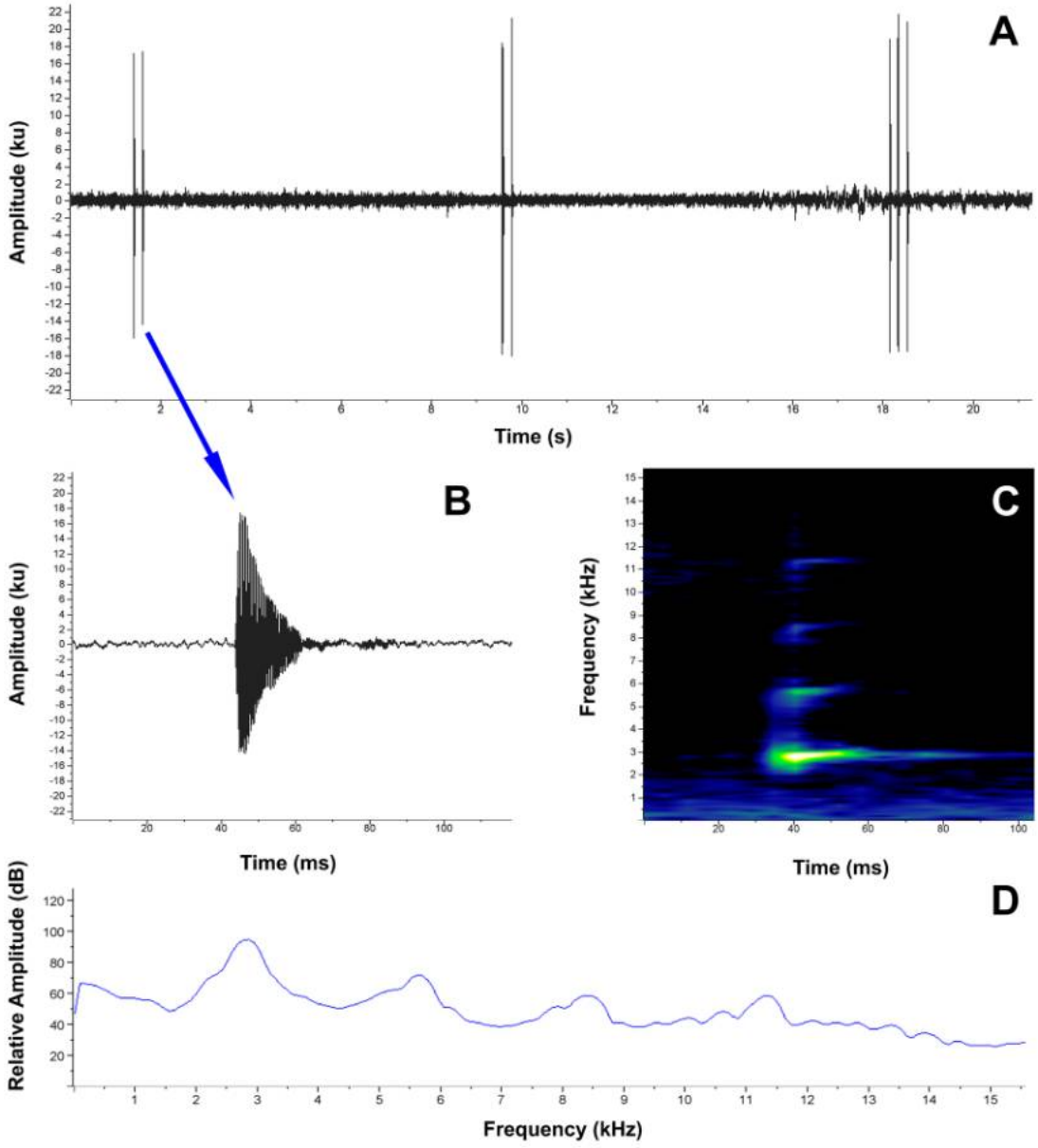

Figure 9. Advertisement call of *Pristimantis atratus s.s.* (FUTPL-A-1001): A, oscillogram of three calls, with double- and triple-noted (last one) calls; B, oscillogram of a note; C, spectrogram of a note; and D, power spectrum of a note.

slits and white nuptial pads (trait more evident in life); (7) finger I shorter than finger II; discs on fingers broadly expanded, rounded; circumferential grooves present; (8) fingers with lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present (trait more evident in life); palmar tubercle inconspicuous, bifid; thenar tubercle large, elliptical, sometimes merged with the subarticular tubercle of finger I; (9) ulnar tubercles present (trait more evident in life); (10) heel with one large, conical to very large, fleshy and curved tubercle; outer edge of tarsus with a row of tubercles (trait more evident in life); inner tarsal fold present; (11) inner metatarsal tubercle ovoid, about three times the size of round outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present (trait more evident in life); (12) toes bearing lateral fringes; webbing basal; toe V longer than toe III; discs on toes broadly expanded, rounded, about same size as those on fingers; circumferential grooves present; (13) in life, dorsum cream, beige, yellowish brown to dark brown, with or without pale to dark brown stripes or spots; flanks whitish, cream or yellowish brown; venter whitish cream with small dark flecks; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces white, yellow, or orange with large black blotches; iris yellow ocher to orange, with a median brownish streak, without reticulations; (14) SVL 31.3 mm in one adult female and 25.5–27.8 mm in adult males (26.7 ± 0.79 mm, $N = 6$).

Comparison with similar species: Pristimantis chusquea is morphologically very different from the majority of species of the *Huicundomantis* subgenus and all other Ecuadorian *Pristimantis* species, owing to its particular habitus and coloration that mimics the dry

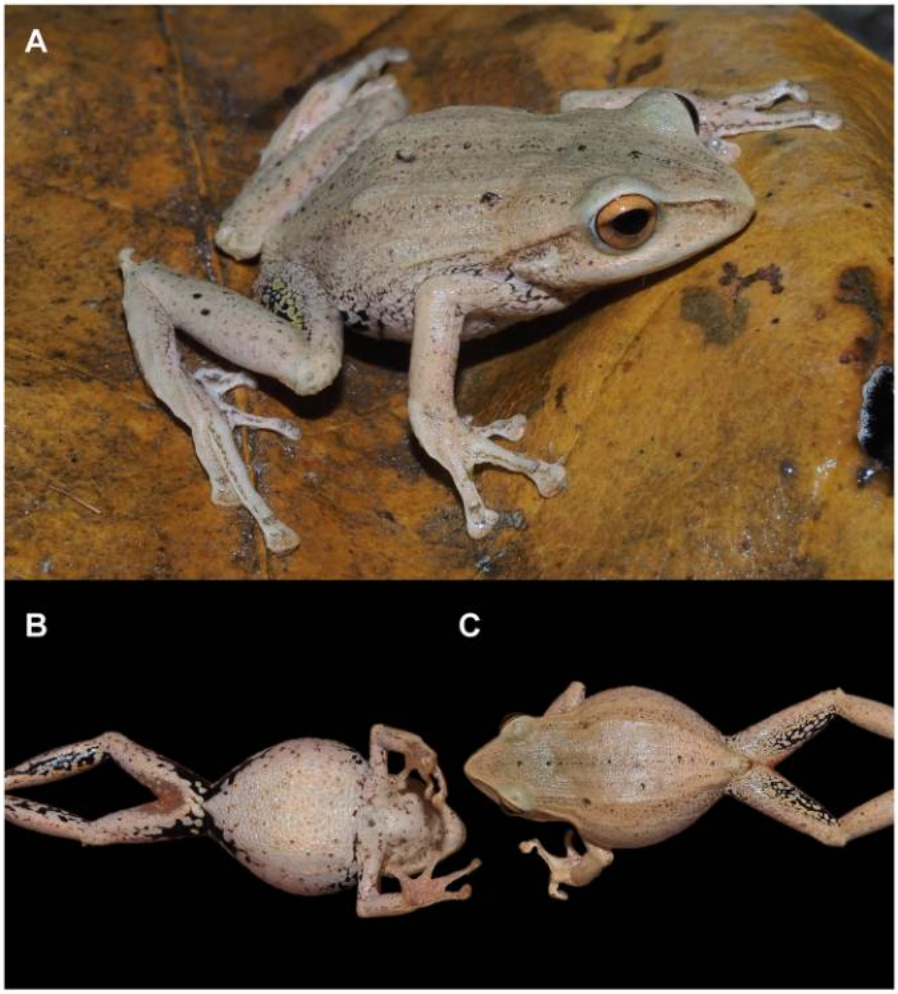

Figure 10. Holotype of ***Pristimantis chusquea*** (*MUTPL 210*; adult male; SVL 27.8 mm) in life, from Abra de Zamora, Zamora Chinchipe Province: A, dorsolateral view; B, ventral view; and C, dorsal view.

Chusquea leaves. In particular, the combination of the cream to yellowish brown dorsal coloration, the dorsum with the low ridges, the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, and the large tubercles on the upper eyelids and heels easily distinguish this species from its congeners. It bears a greater resemblance to *P. yumbo*, *P. atratus*, and the other two new species.

Pristimantis chusquea can be distinguished easily from *P. yumbo* by the presence of the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces (vs. lack of any black markings in *P. yumbo*) and the uniform yellow ocher to orange iris coloration (vs. iris golden with a reddish copper centre in *P. yumbo*).

Pristimantis chusquea is most similar to *P. atratus* and the other two new species, *P. translucidus* and *P. oculolineatus*, from which it can be distinguished by several important morphological characters (Table 4). Thus, *P. chusquea* differs from *P. atratus* by its larger size (SVL and BM range not overlapping; Table 2), longer, acuminate snout (vs. shorter, subacuminate in *P. atratus*; SL/HL and SN/HL range not overlapping; Table 2), large to very large fleshy heel tubercles (vs. smaller heel tubercles in *P. atratus*), and yellow ocher to orange iris (vs. golden in *P. atratus*; Figs 7, 8). *Pristimantis translucidus* can be distinguished from *P. chusquea* by the smaller size (vs. larger size in *P. chusquea*; SVL and BM range basically not overlapping; Table 2), the unpigmented/translucent vocal sac in the males (vs. pigmented vocal sac in *P. chusquea*; Figs 13, 14), smaller heel tubercles (vs. large to very large fleshy heel tubercles in *P. chusquea*), and the cream iris coloration (vs. yellow ocher to orange iris in *P. chusquea*). *Pristimantis oculolineatus* can be distinguished easily from *P. chusquea* by the striped iris (vs. iris without reticulations in *P. chusquea*), the presence of thick dorsolateral and lateral folds (vs. dorsolateral and lateral folds absent in *P. chusquea*), the coarsely pustulated flanks (vs. smooth flanks in *P. chusquea*), smaller heel tubercles (vs. larger heel tubercles in *P. chusquea*), toe V much longer than toe III (vs. toe V longer than toe III in *P. chusquea*), and the coloration on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces with smaller dark brown or black blotches or reticulations (vs. black blotches larger in *P. chusquea*). Finally, all these four species differ significantly by their advertisement calls (see call descriptions below).

Pristimantis tinguichaca (a species of the *Huicundomantis* subgenus) superficially resembles in coloration *P. chusquea* but lacks the typical low ridges on the dorsum and the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb

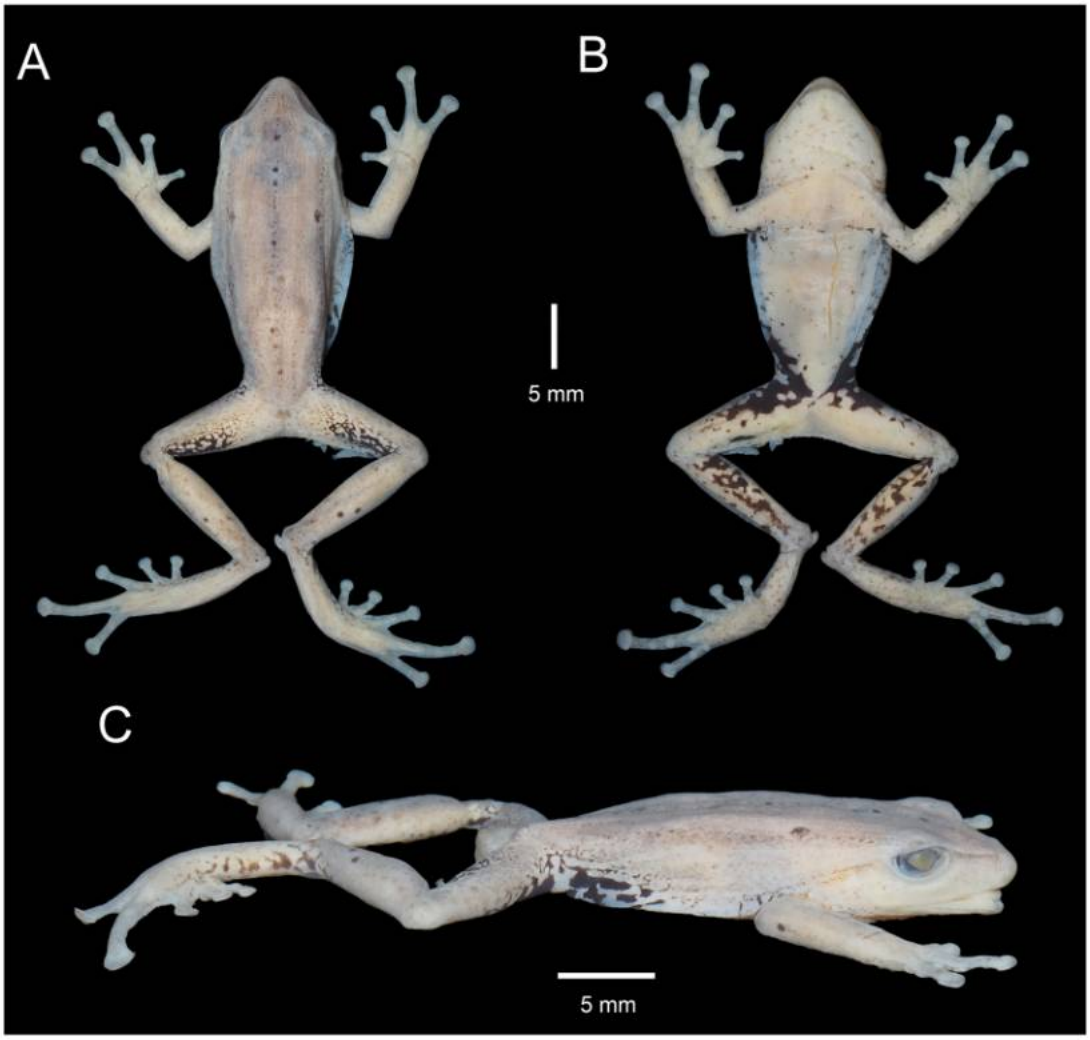

Figure 11. Holotype of ***Pristimantis chusquea*** (*MUTPL 210*; adult male; SVL 27.8 mm) in preservative, from Abra de Zamora, Zamora Chinchipe Province: A, dorsal view; B, ventral view; and C, lateral view.

surfaces; also, the advertisement call of this species is very different from the call of *P. chusquea* (Brito *et al.* 2016).

Description of the holotype: Adult male (*MUTPL 210*; Figs 10–13A), head narrower than body, wider than long, HL 92% of HW, HW 35% of SVL, HL 32% of SVL; snout long (SL 15% of SVL; SL 47% of HL; EN 28% of HL; SN 18% of HL), acuminate in dorsal view and rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; loreal region slightly concave; ED much larger than EN; nostrils slightly protuberant, oriented posteriorly; lips not flared; cranial crests inconspicuous, low, barely visible; upper eyelid bearing one larger tubercle (trait more visible in life; Fig. 13A); EW 77% of IOD; tympanic annulus evident and tympanic membrane differentiated; thick supratympanic fold present, slightly concealing the upper margin of the tympanum (Fig. 10A); TD 30% of ED; two larger, rounded postrictal tubercles; choanae large, oval, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers prominent, larger than the choanae, oblique, situated posterior and median to choanae, triangular in outline, separated medially by distance smaller than the width of processes, each process bearing five teeth; tongue longer than wide, slightly notched posteriorly, posterior half not adherent to floor of mouth; large vocal slits at the angles of the mouth, near the margin of jaw; subgular vocal sac pigmented (Figs 10B, 13A).

Skin on dorsum shagreen with numerous low ridges (trait more visible in life); mid-dorsal fold absent; dorsolateral folds absent; skin on belly and posteroventral surfaces of thighs areolate; thoracic and discoidal folds present; cloacal region bordered ventrally by two large and several small tubercles.

Ulnar tubercles present (trait more visible in life); outer palmar tubercle inconspicuous, bifid; thenar tubercle elliptical, large; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all fingers; supernumerary palmar tubercles rounded, smaller than subarticular tubercles (trait more visible in life); white nuptial pads present on finger I (trait more visible in life); fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, rounded; all fingers bearing pads well defined by circumferential grooves (Fig. 12A).

Hindlimbs long, slender; THL 42% of SVL; TL 52% of SVL; FL 49% of SVL; heel with a very large, fleshy, and curved tubercle (Figs 10A, 11); outer edge of tarsus with a row of small, conical tubercles (trait more evident in life); inner edge of tarsus bearing

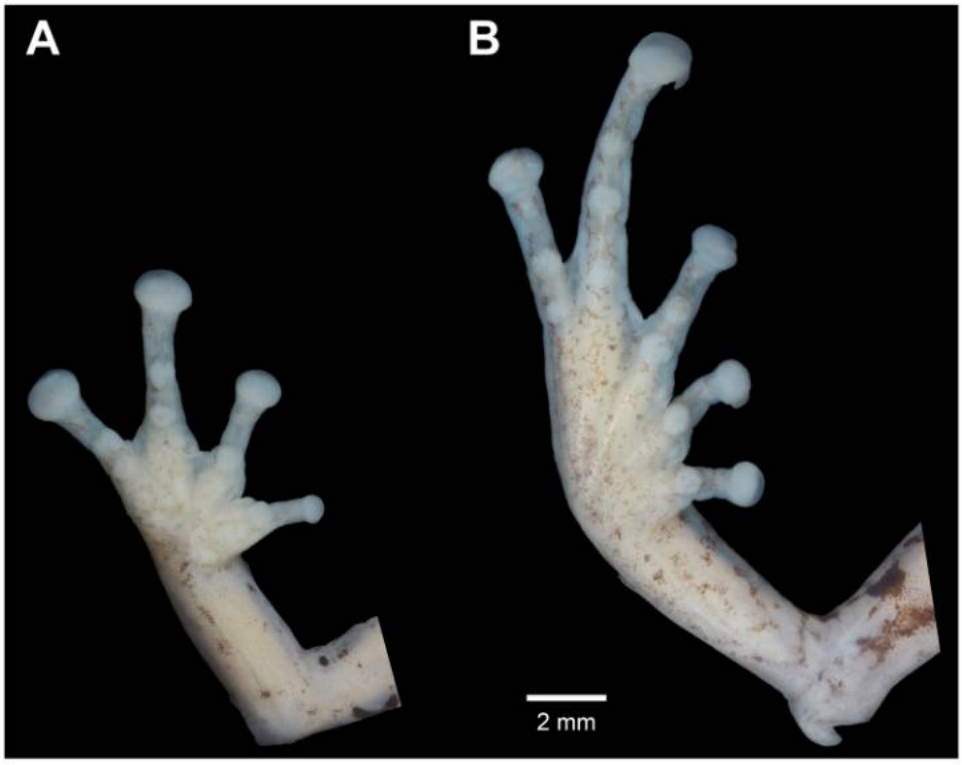

Figure 12. Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of male holotype ***Pristimantis chusquea*** (*MUTPL 210*; SVL 27.8 mm) in preservative.

Figure 13. Vocal sac differences in the three new species. A, pigmented vocal sac of male holotype ***Pristimantis chusquea*** (*MUTPL 210*; SVL 27.8 mm; Abra de Zamora, Zamora Chinchipe Province). B, unpigmented/translucent vocal sac of male holotype ***Pristimantis translucidus*** (*MUTPL 220*; SVL 24.4 mm; Reserva Tapichalaca, Zamora Chinchipe Province). C, partly inflated, pigmented vocal sac of male holotype ***Pristimantis oculolineatus*** (*MUTPL 1188*; SVL 26.3 mm; Reserva Numbala, Zamora Chinchipe Province).

a short fold; inner metatarsal tubercle ovoid, about three times rounded outer metatarsal tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all toes; supernumerary plantar tubercles rounded, smaller than subarticular tubercles (trait more visible in life); toes bearing lateral fringes; webbing basal; discs on toes broadly expanded, rounded, about same size as those on fingers; toes with ventral pads well defined by circumferential grooves (Fig. 12B); 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 reache distal edge of distal subarticular tubercle on toe IV).

Coloration of holotype: In life (Fig. 10): dorsum, upper parts of flanks, dorsal surfaces of hindlimbs and arms beige, with small dark brown irregular spots; lower parts of flanks whitish with dark brown to black blotches; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces white and yellow with large black blotches; head with faint light brown canthal and supratympanic stripes; throat, venter, and ventral surfaces of hindlimbs and arms whitish cream with small dark flecks; iris orange, with a median brownish streak, without reticulations.

In preservative (Fig. 11): dorsum brownish grey with black irregular spots; dorsal surfaces of arms and of hindlimbs yellowish grey; lower parts of flanks whitish grey with black blotches; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb

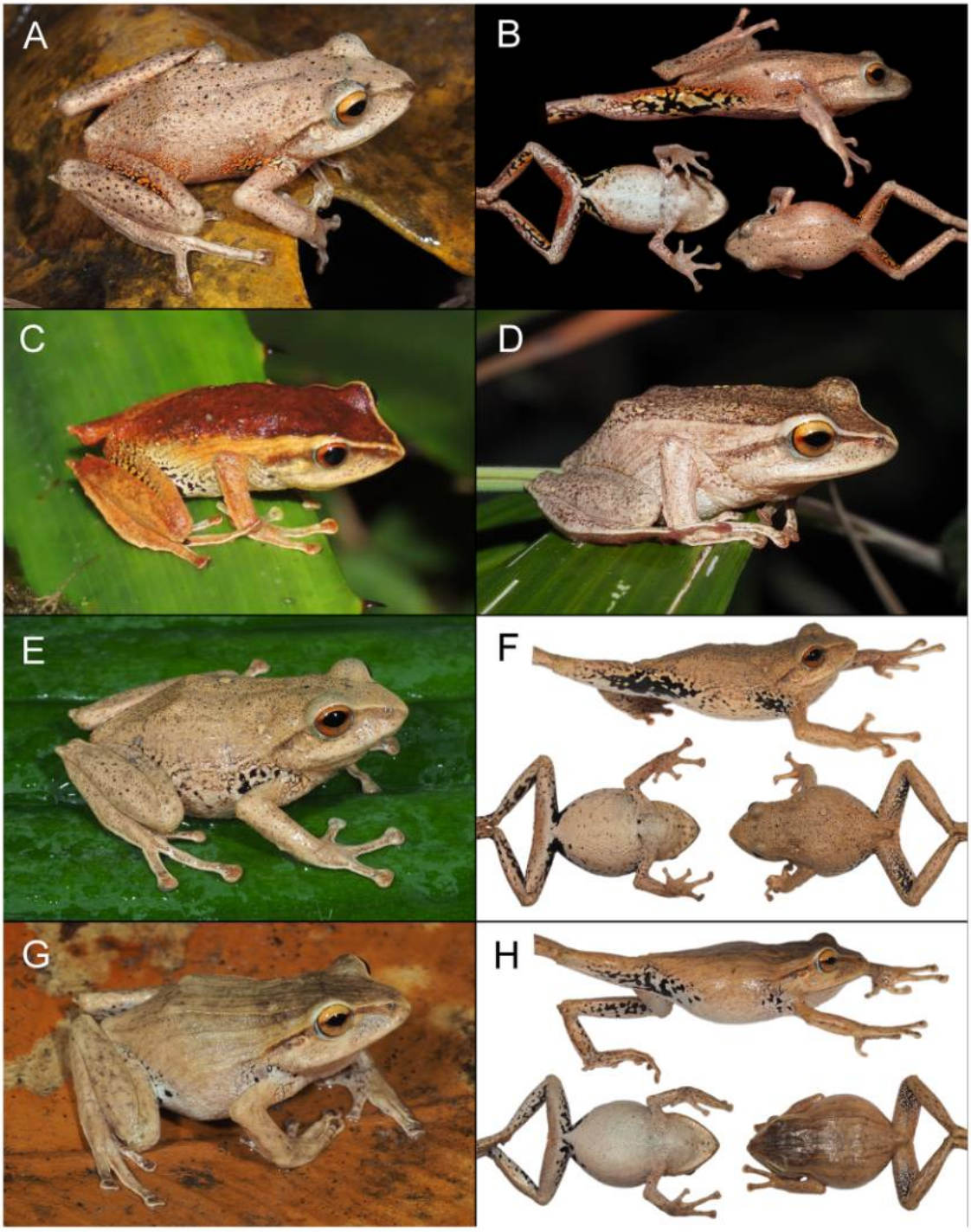

Figure 14. Colour variation in life for adult males of ***Pristimantis chusquea***, in dorsolateral, lateral, ventral, and dorsal views. A, B, MUTPL 322, SVL 25.5 mm, paratype from Abra de Zamora, Zamora Chinchipe Province. C, uncollected, from Abra de Zamora, Zamora Chinchipe Province. D, uncollected, from Huacapamba, Loja Province. E, F, MUTPL 1794, SVL 26.2 mm, paratype from Abra de Zamora, Zamora Chinchipe Province. G, H, MUTPL 1797, SVL 27.2 mm, paratype from Huacapamba, Loja Province.

surfaces whitish grey with large black blotches; throat, venter, and ventral surfaces of hindlimbs and arms whitish yellow with small black flecks.

Measurements of holotype (in millimetres): SVL 27.8; HW 9.6; HL 8.8; IOD 3.4; IND 2.4; EW 2.6; ED 3.3; EN 2.5; SL 4.1; SN 1.6; TD 1.0; THL 11.6; TL 13.2; FL 12.6; FLL 6.2; and HAL 7.5.

Body mass of holotype: 1.86 g.

Variation: Morphometric variation is shown in Table 2. Coloration does not differ between sexes. Most of the encountered individuals were either uniformly coloured with dark brown spots, like MUTPL 323 (Fig. 14A, B), MUTPL 1794 (Fig. 14E, F), and MUTPL 321 (Fig. 15E, F), or striped, like MUTPL 1797 (Fig.

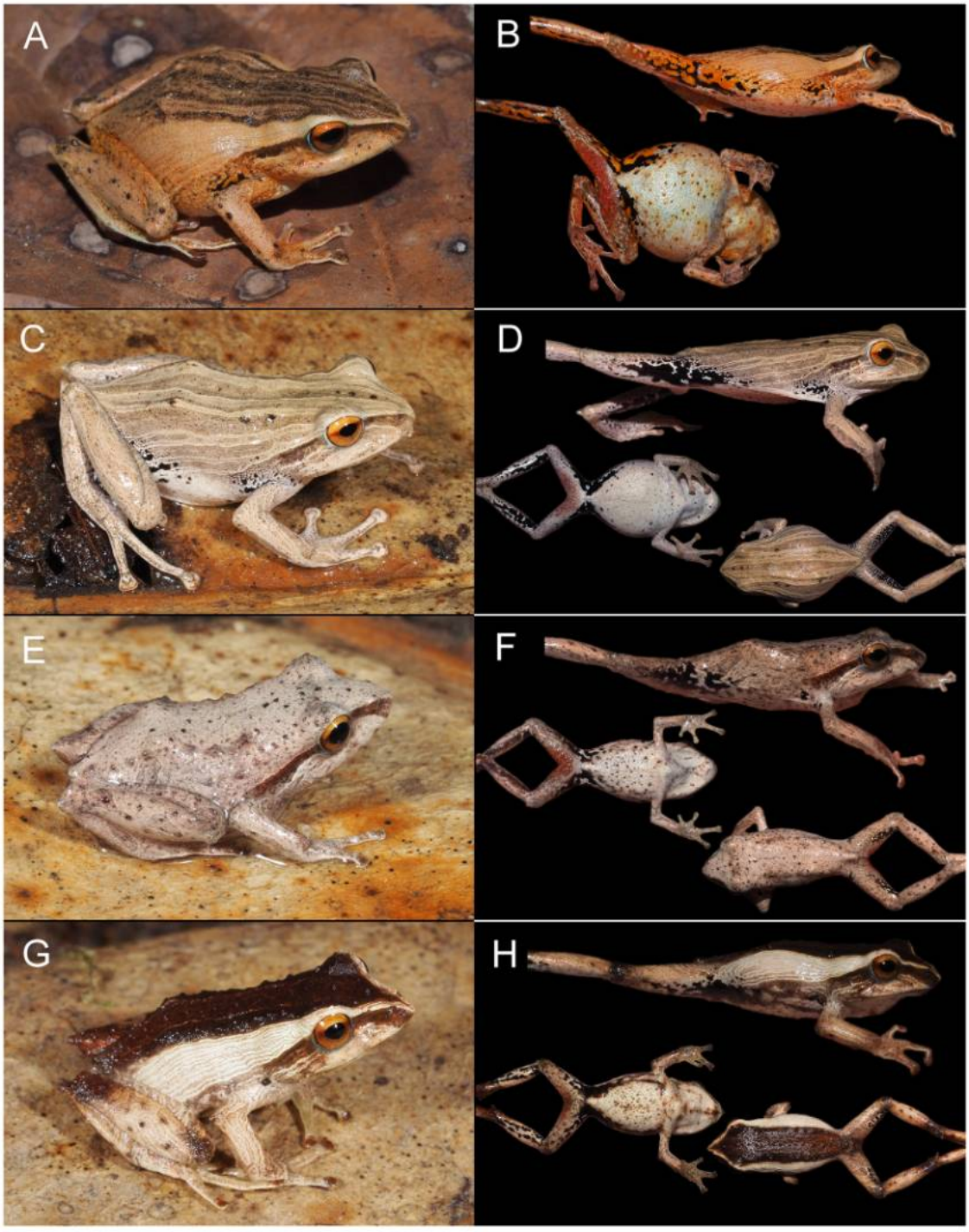

Figure 15. Colour variation in life for individuals of ***Pristimantis chusquea***, in dorsolateral, lateral, ventral, and dorsal views. A, B, uncollected adult female from Abra de Zamora, Zamora Chinchipe Province. C, D, MUTPL 323, SVL 31.3 mm, adult female paratype from Abra de Zamora, Zamora Chinchipe Province. E, F, MUTPL 321, SVL 14.4 mm, juvenile paratype from Abra de Zamora, Zamora Chinchipe Province. G, H, MUTPL 382, SVL 15.8 mm, juvenile paratype from Huacapamba, Loja Province.

14G, H), an uncollected female (Fig. 15A, B), and MUTPL 323 (Fig. 15C, D). Some individuals had a wide darker mid-dorsal band that varied from a brownish reticulation (Fig. 14D) to reddish brown (Fig. 14C) or dark brown, like MUTPL 382 (Fig. 15G, H). The large black-blotched areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces varied from white, yellow, to intense orange (Figs 14, 15). The juveniles already presented the characteristic black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, but lacked any yellow or orange coloration (Fig. 15E, F, G, H). The iris coloration varied from yellow ocher to dark orange (Figs 14, 15).

Vocalizations: For the description of the call of *P. chusquea*, we analysed seven call samples from four males, all recorded in Abra

Table 4. Main morphological trait differences between *Pristimantis atratus s.s.* and the three new species.

Trait	*Pristimantis atratus*	*Pristimantis chusquea*	*Pristimantis translucidus*	*Pristimantis oculolineatus*
Snout shape (in dorsal view) and relative size	Subacuminate, shorter	Acuminate, longer	Acuminate, longer	Acuminate, longer
Flanks texture	Smooth	Smooth	Smooth	Pustulated
Dorsolateral and lateral folds	Absent	Absent	Absent	Prominent, thick
Mid-dorsal fold	Present	Usually absent	Absent	Usually absent
Vocal sac	Pigmented	Pigmented	Unpigmented/ translucent	Pigmented
Heel tubercles, relative size and shape	Medium, conical	Large, conical to very large, fleshy and curved	Medium to large, conical	Medium, conical
Relative lengths of toes	Toe V longer than toe III	Toe V longer than toe III	Toe V longer than toe III	Toe V much longer than toe III
Dark markings of thighs, groin, axilla, and concealed limb surfaces	Large, black blotches	Large, black blotches	Large, black blotches	Small, dark brown or black blotches or reticulations
Iris coloration	Golden, without reticulations	Yellow ocher to orange, without reticulations	Cream, without reticulations	Whitish, with reticulations/stripes

de Zamora, Zamora Chinchipe Province, in 2019 and 2024. Descriptive statistics of the acoustic variables are provided in Table 3 (detailed information on each of the recordings is provided in Supporting Information, File S2).

Pristimantis chusquea has an advertisement call characterized by short whistle-like sounds (notes) repeated over a period of time, very similar to the call of *P. balionotus* (Székely *et al.* 2020). The calls are typically composed of two notes (Fig. 16); however, in some instances the call can contain up to six distinct notes. The calls consistently begin as single-noted calls that at some point become double-noted calls. The calls that contain three to six notes are probably emitted during social interactions, triggered by the nearby presence of a female or a competitive vocalizing male (probably courtship calls *sensu* Wells 2007). The notes within each call are structurally and temporally very similar, although the first note of the series is usually slightly longer.

The calls are characterized by a mean duration of 0.356 s (in the case of double-noted calls, whereas the calls with six notes can last ≤1.248 s), a mean inter-call interval of 11.6 s, and a mean call rate of 4.7 calls/min (Table 3). The notes are tonal sounds, relatively long, characterized by a mean duration of 0.067 s, a mean inter-note interval of 0.223 s, and a mean note rate of 3.4 notes/s. The mean dominant frequency of the call is 2181.0 Hz, with a mean 90% bandwidth of 2055.8–2382.5 Hz (Table 3). The fundamental frequency is not recognizable, but up to six harmonics are visible.

The advertisement call of *P. chusquea* is very different from the call of *P. atratus* and easily distinguished (Fig. 2). The call of *P. atratus* consists of metallic 'tic' sounds, whereas *P. chusquea* produces calls that are more whistle-like (longer duration notes). Thus, the calls differ significantly in call duration, note duration, note rate, and frequencies (Table 3; Figs 2, 9, 16). Also, the call of *P. chusquea* can be distinguished readily from that of *P. tinguichaca* by its whistle-like sound, in contrast to the metallic clicking sounds produced by *P. tinguichaca*, which also exhibits a significantly lower dominant frequency (Brito *et al.* 2016).

Distribution: Pristimantis chusquea is currently known from only two close localities inside the biodiversity hotspot Abra de Zamora (Ordóñez-Delgado *et al.* 2020): on the old Loja-Zamora road and Huacapamba (Fig. 4). Specimens were encountered at an elevational range between 2663 and 2784 m a.s.l. in a 'Southern montane evergreen forest of the eastern Andes' ecosystem.

Natural history: This is an uncommon species. All animals were encountered during the night, almost exclusively on *Chusquea* leaves (the dense bamboo patches found along the roads), from 30 cm above the ground up to 2 m high. Lynch (1979) mentions that in 1975 William E. Duellman found four individuals in terrestrial bromeliads in Abra de Zamora; despite our intensive fieldwork in the area since 2016, we never encountered this species in bromeliads, probably because we mostly worked during the night, when the animals are active and not hidden (possibly in bromeliads). Calling males were heard year-round, being more active during rainy nights. The animals are well camouflaged and difficult to detect, especially if they are not active. Sympatric frog species include *P.* aff. *andinognomus* and *P. versicolor* (Lynch 1979); however, only *P. versicolor* was encountered sometimes on *Chusquea* leaves.

Conservation status: Pristimantis chusquea is known from only two close localities, near the city of Loja and a protected area (Parque Nacional Podocarpus), from an estimated area of <12 km^2. Thus, based on the available information, we recommend that *P. chusquea* be categorized as Endangered following the IUCN criteria B1ab(i, ii, iii, iv)+2ab(i, ii, iii, iv) (IUCN 2001) because: (i) its extent of occurrence is estimated to be <8.5 km^2 and the area of occupancy <12 km^2; (ii) it is known from only two locations; and (iii) its habitats could be affected in the near future, because they are situated in the vicinity of densely populated areas and mostly outside protected areas (Ordóñez-Delgado *et al.* 2020).

Remarks: Uncorrected genetic p-distances between *P. chusquea* and its closest relatives range between 3.6%–4.2% (*P. atratus*) and 3.5%–3.9% (*P. translucidus*); the genetic distance between *P. chusquea* and *P. oculolineatus* ranges from 6.9% to 8.2% (Supporting Information, File S1).

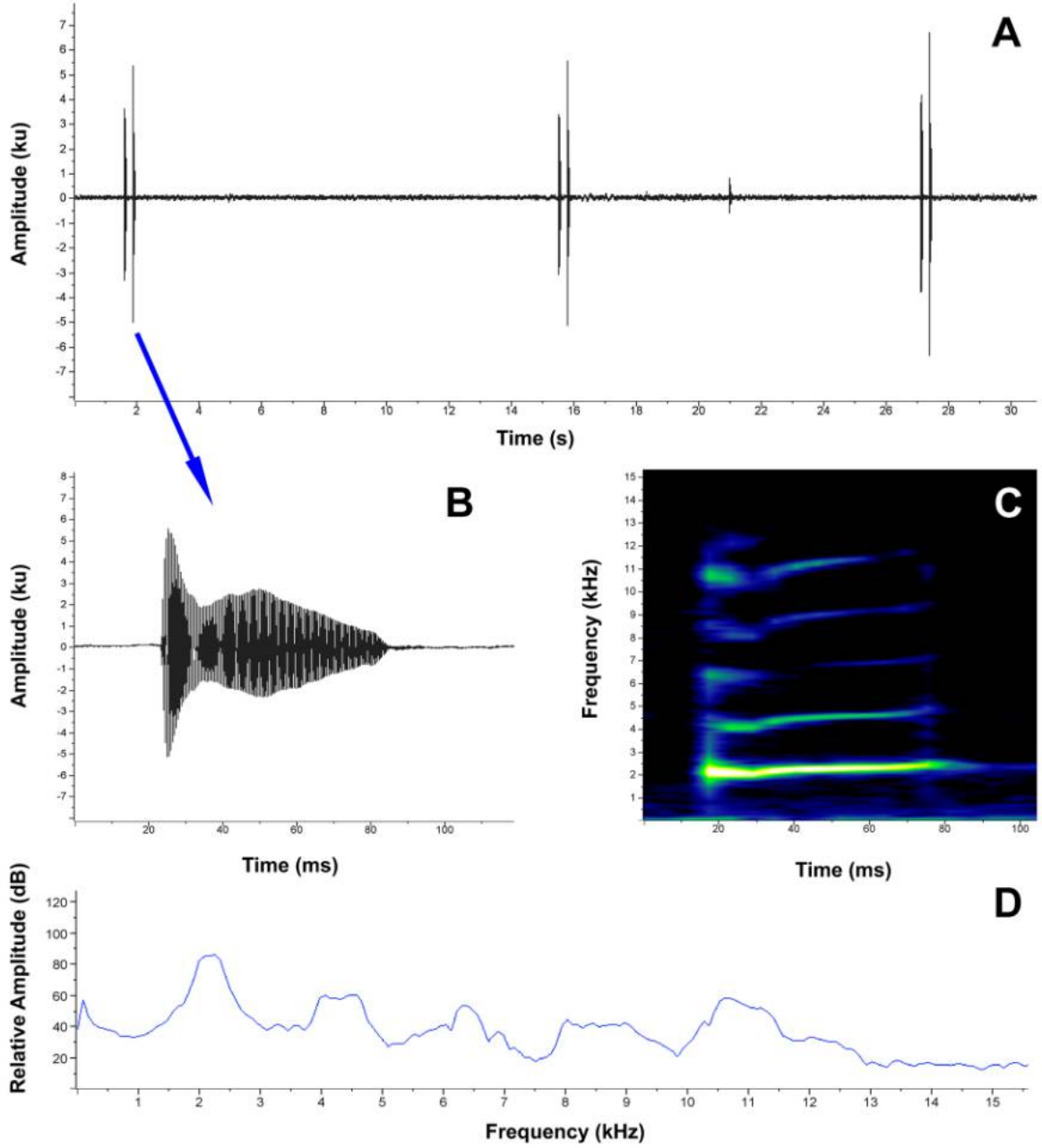

Figure 16. Advertisement call of ***Pristimantis chusquea*** (paratype MUTPL 1795, FUTPL-A-1041): A, oscillogram of three double-noted calls; B, oscillogram of a note; C, spectrogram of a note; and D, power spectrum of a note.

***Pristimantis translucidus* sp. nov.**

(Figs 13B, 17–20)

ZooBank registration: urn:lsid:zoobank.org:act:56A9C758-B7D0-4FD1-B397-C69BED517BE8

Common English name: Translucent rain frog.

Common Spanish name: Cutín translúcido.

Etymology: The specific epithet *translucidus* is derived from Latin, meaning 'translucent' or 'allowing light to pass through' and refers to the particular semi-transparent subgular vocal sac that easily distinguishes this species from its morphologically similar sister species. The name is used as an adjective in the masculine form.

Holotype: MUTPL 220 (Figs 13B, 17–19), an adult male from Ecuador, Zamora Chinchipe Province, Reserva Tapichalaca (4.4939°S, 79.1264°W; datum WGS84), 2433 m a.s.l., collected by Paul Székely and Diana Székely on 23 April 2017.

Paratypes (six: four males and two juveniles): MUTPL 291, a juvenile from Zamora Chinchipe Province, Reserva Tapichalaca (4.4931°S, 79.1315°W), 2600 m a.s.l., collected by Diego Armijos on 5 December 2017; MUTPL 1709 (field no. SC 1972), a juvenile from Zamora Chinchipe Province, Reserva Tapichalaca, Sendero Tapir (4.4878°S, 79.1489°W), 2678 m a.s.l., collected by Paul Székely and Diana Székely on 5 February 2024; MUTPL 1858 (field no. SC 463), an adult male from Zamora Chinchipe Province, nearby Río Sangola, at ~30 km north-east from the village

of Chito (4.8508°S, 78.9209°W), 2568 m a.s.l., collected by Santiago Hualpa on 17 December 2024; MUTPL 1874 (field no. SC 3961), an adult male from Zamora Chinchipe Province, Reserva Tapichalaca, Sendero Tapir (4.4880°S, 79.1489°W), 2672 m a.s.l., collected by Paul Székely and Diana Székely on 1 February 2025; MUTPL 1970 (field no. SC 3295) and MUTPL 1971 (field no. SC 3296), two adult males from Zamora Chinchipe Province, nearby Río Sangola, at ~30 km north-east from the village of Chito (4.8416°S, 78.9278°W), 2422 m a.s.l., collected by Santiago Hualpa on 9 June 2025.

Definition: We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 1) and on the general morphological similarity to other members of the genus. *Pristimantis translucidus* is a small-sized species (among the *Huicundomantis* subgenus; Table 1) characterized by the following combination of characters: (1) skin on dorsum shagreen, usually bearing numerous low ridges (trait more evident in life); skin on venter areolate; discoidal fold present; dorsolateral folds absent; low mid-dorsal fold absent; (2) tympanic annulus evident and tympanic membrane differentiated, its length ~43% of the length of eye; supratympanic fold present, slightly concealing the upper edge of tympanum; (3) snout acuminate in dorsal view, rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; (4) upper eyelid bearing one larger tubercle (trait more evident in life), ~71% IOD in males; cranial crests inconspicuous, low; (5) dentigerous processes of vomers oblique, ovoid to triangular, separated medially by distance equal to or slightly larger than the width of processes; each process bearing three to six teeth; (6) males with an unpigmented/translucent subgular vocal sac and vocal slits; (7) finger I shorter than finger II; discs on fingers broadly expanded, rounded; circumferential grooves present; (8) fingers with lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present (trait more evident in life); palmar tubercle inconspicuous, bifid; thenar tubercle large, elliptical; (9) ulnar tubercles present (trait more evident in life); (10) heel with one large conical tubercle; outer edge of tarsus without tubercles; inner tarsal fold present; (11) inner metatarsal tubercle ovoid, about two times the size of round outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present (trait more evident in life); (12) toes bearing lateral fringes; webbing basal; toe V longer than toe III; discs on toes broadly expanded, rounded, slightly smaller than those on fingers; circumferential grooves present; (13) in life, dorsum cream, beige to yellowish brown, with pale to dark brown stripes; flanks whitish, cream, or yellowish brown, sometimes with black blotches; venter whitish cream with small dark flecks; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces white or yellow with large black blotches; iris cream, with a median brownish streak, without reticulations; and (14) SVL 22.5–24.9 mm in adult males (24.0 ± 0.91 mm, $N = 5$); females unknown.

Comparison with similar species: Pristimantis translucidus is morphologically very different from the majority of species of the *Huicundomantis* subgenus and all the Ecuadorian *Pristimantis* species, owing to its particular habitus and coloration that mimics the dry *Chusquea* leaves. In particular, the combination of the cream to yellowish brown dorsal coloration, the dorsum with the low ridges, the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, and the large tubercles on the upper eyelids and heels easily distinguish this species from its congeners.

Pristimantis translucidus is most similar to *P. atratus* and the other two new species, *P. chusquea* and *P. oculolineatus*, from which it can be distinguished by several important morphological characters (Table 4). Thus, *P. translucidus* differs from *P. atratus* by the longer, acuminate snout (vs. shorter, subacuminate in *P. atratus*; SL/HL and SN/HL range not overlapping; Table 2) and the unpigmented/translucent vocal sac in the males (vs. pigmented vocal sac in *P. atratus*). *Pristimantis translucidus* differs from *P. chusquea* by the smaller size (vs. larger size in *P. chusquea*; SVL and BM range basically not overlapping; Table 2), the unpigmented/translucent vocal sac in the males (vs. pigmented vocal sac in *P. chusquea*; Fig. 13), smaller heel tubercles (vs. large to very large fleshy heel tubercles in *P. chusquea*), and the cream iris coloration (vs. yellow ocher to orange iris in *P. chusquea*). *Pristimantis oculolineatus* can be distinguished easily from *P. translucidus* by the striped iris (vs. iris without reticulations in *P. translucidus*), the presence of thick dorsolateral and lateral folds (vs. dorsolateral and lateral folds absent in *P. translucidus*), the coarsely pustulated flanks (vs. smooth flanks in *P. translucidus*), toe V much longer than toe III (vs. toe V longer than toe III in *P. translucidus*), and the coloration on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces with smaller, dark brown or black blotches or reticulations (vs. black blotches larger in *P. translucidus*). Additionally, all these four species differ significantly by their advertisement calls (see the call descriptions).

Pristimantis translucidus differs significantly from *P. yumbo* by the presence of the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces (vs. lack of any black markings in *P. yumbo*) and the uniform cream iris coloration (vs. iris golden with a reddish copper centre in *P. yumbo*), and from *P. tinguichaca* by the presence of the black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces (vs. lack of any black markings in *P. tinguichaca*), the cream iris (vs. red iris in *P. tinguichaca*), and the advertisement call (Brito *et al.* 2016).

Description of the holotype: Adult male (*MUTPL 220*; Figs 17–19), head narrower than body, wider than long, HL 92% of HW, HW 36% of SVL, HL 32% of SVL; snout long (SL 16% of SVL; SL 49% of HL; EN 29% of HL; SN 20% of HL), acuminate in dorsal view and rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; loreal region slightly concave; ED larger than EN; nostrils slightly protuberant, oriented posteriorly; lips not flared; cranial crests inconspicuous, low, barely visible; upper eyelid bearing one larger tubercle (trait more visible in life; Fig. 17A); EW 82% of IOD; tympanic annulus evident and tympanic membrane differentiated; supratympanic fold present, slightly concealing the upper margin of the tympanum (Fig. 17A); TD 47% of ED; one large, elongated postrictal tubercle; choanae large, oval, partly concealed by palatal shelf of maxillary arch; dentigerous processes of vomers prominent, larger than the choanae, oblique, situated posterior and median to choanae, ovoid in outline, separated medially by distance almost equal to the width of processes, each process bearing three to five teeth; tongue longer than wide, slightly notched posteriorly, posterior half not adherent

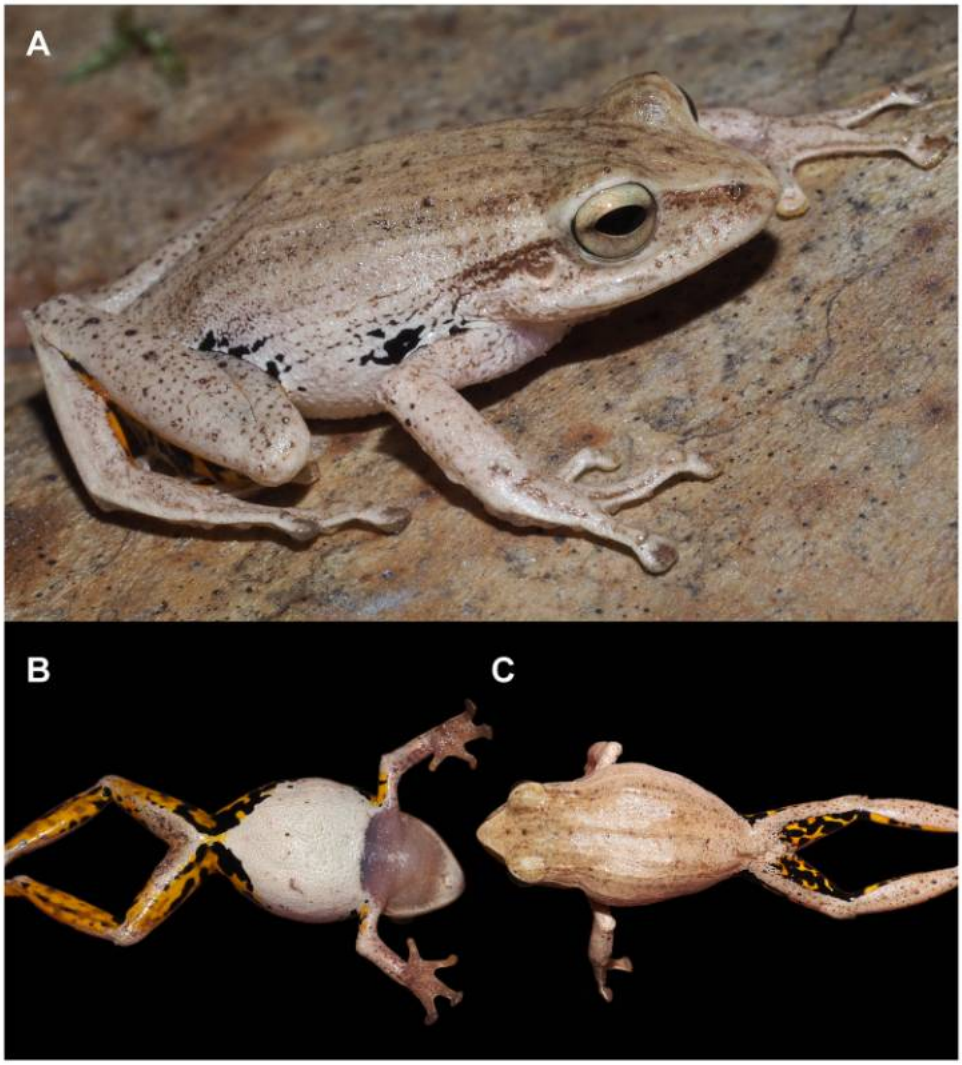

Figure 17. Holotype of ***Pristimantis translucidus*** (*MUTPL 220*; adult male; SVL 24.4 mm) in life, from Reserva Tapichalaca, Zamora Chinchipe Province: A, dorsolateral view; B, ventral view; and C, dorsal view.

to floor of mouth; vocal slits at the angles of the mouth; subgular vocal sac unpigmented/translucent (Figs 13B, 17B).

Skin on dorsum shagreen with numerous low ridges (trait more visible in life); mid-dorsal fold absent; dorsolateral folds absent; skin on belly and posteroventral surfaces of thighs areolate; thoracic and discoidal folds present; cloacal region bordered ventrally by two large and several small tubercles.

Ulnar tubercles present (trait more visible in life); outer palmar tubercle inconspicuous, bifid; thenar tubercle elliptical, large; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all fingers; supernumerary palmar tubercles rounded, smaller than subarticular tubercles (trait more visible in life); fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, rounded; all fingers bearing pads well defined by circumferential grooves (Fig. 19A).

Hindlimbs long, slender; THL 44% of SVL; TL 52% of SVL; FL 46% of SVL; heel with a large conical tubercle (Fig. 18); outer edge of tarsus lacking tubercles; inner edge of tarsus bearing a short fold; inner metatarsal tubercle ovoid, about two times oval outer metatarsal tubercle; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all toes; supernumerary plantar tubercles rounded, smaller than subarticular tubercles (trait more visible in life); toes bearing lateral fringes; webbing basal; discs on toes broadly expanded, rounded, slightly smaller than those on fingers; toes with ventral pads well defined by circumferential grooves (Fig. 19B); 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 not reaches distal edge of distal subarticular tubercle on toe IV).

Coloration of holotype: In life (Fig. 17): dorsum brownish beige, with inconspicuous dark brown stripes and dark brown irregular spots; dorsal surfaces of hindlimbs and arms beige, with dark brown irregular spots; lower parts of flanks white with black blotches; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces yellow with large black blotches; head with wide, discontinuous, light brown canthal and supratympanic stripes; throat pinkish; venter and ventral surfaces of thighs white with small dark flecks; iris cream, with a median brownish streak, without reticulations.

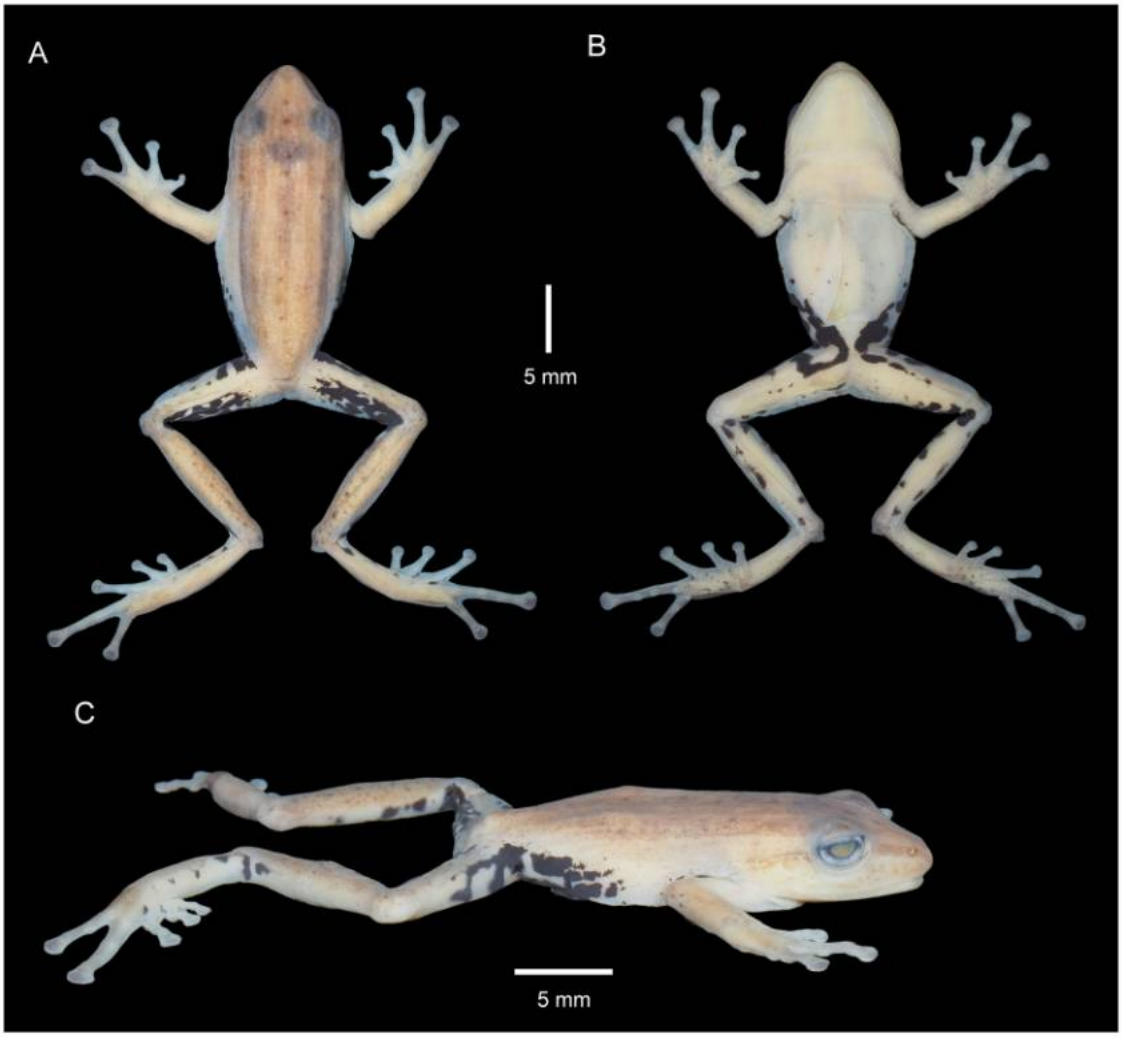

Figure 18. Holotype of ***Pristimantis translucidus*** (*MUTPL 220*; adult male; SVL 24.4 mm) in preservative, from Reserva Tapichalaca, Zamora Chinchipe Province: A, dorsal view; B, ventral view; and C, lateral view.

In preservative (Fig. 18): dorsum reddish brown, with inconspicuous blackish stripes and blackish irregular spots; dorsal surfaces of hindlimbs and arms cream, with dark brown irregular spots; lower parts of flanks yellowish white with black blotches; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces yellowish white with large black blotches; throat, venter, and ventral surfaces of hindlimbs and arms whitish yellow with small black flecks.

Measurements of holotype (in millimetres): SVL 24.4; HW 8.6; HL 7.9; IOD 2.7; IND 2.1; EW 2.2; ED 3.0; EN 2.3; SL 3.9; SN 1.6; TD 1.4; THL 10.8; TL 12.7; FL 11.2; FLL 5.9; and HAL 7.2.

Body mass of holotype: 1.15 g.

Variation: Morphometric variation is shown in Table 2. Most of the encountered individuals were striped like the males MUTPL 1874 (Fig. 20A, B) and MUTPL 1970 (Fig. 20C, D) or the juvenile MUTPL 1709 (Fig. 20G, H). The juvenile MUTPL 291 had a wide dark green mid-dorsal band and evident dark brown canthal and supratympanic stripes (Fig. 20E, F). The large black-blotched areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces varied from white to yellow (Fig. 20). All encountered adult males had translucent vocal sacs. The juveniles presented some of the characteristic black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, but generally lacked the yellow coloration (Fig. 20F, H). The iris varied from light cream to dark cream (Fig. 20).

Vocalizations: For the description of the call of *P. translucidus* we analysed seven call samples from seven males, six calls being recorded in Reserva Tapichalaca, Zamora Chinchipe Province, in 2017 and 2024, and one near to Río Sangola, Zamora Chinchipe Province, in 2025. Descriptive statistics of the acoustic variables are provided in Table 3 (detailed information on each recording is provided in Supporting Information, File S2).

Pristimantis translucidus has an advertisement call characterized by long, sharp 'tic' sounds (notes) repeated over a period of time, most similar to the call of *P. atratus*. The calls are typically composed of two to three notes (Fig. 21); however, in some instances the call can contain ≤14 distinct notes. The calls consistently begin as single-noted calls that at some point increase in complexity, incorporating two to three notes in subsequent calls. The calls that

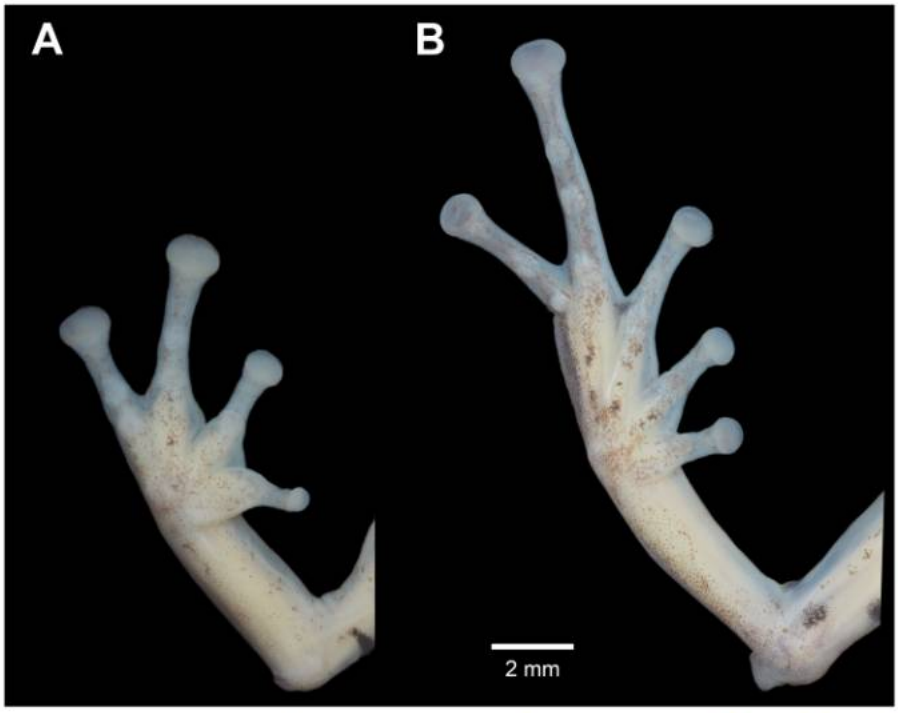

Figure 19. Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of male holotype ***Pristimantis translucidus*** (*MUTPL 220*; SVL 24.4 mm) in preservative.

contain 4–14 notes are probably emitted during social interactions, triggered by the nearby presence of a female or a competitive vocalizing male (probably courtship calls *sensu* Wells 2007). The notes within each call are structurally and temporally very similar, although the first note of the series is usually slightly longer.

The calls are characterized by a mean duration of 0.352 s (in the case of double-noted calls, whereas the calls with 14 notes can last ≤3.405 s), a mean inter-call interval of 8.7 s, and a mean call rate of 5.8 calls/min (Table 3). The notes are tonal sounds, relatively long, characterized by a mean duration of 0.067 s, a mean inter-note interval of 0.199 s, and a mean note rate of 3.6 notes/s. The mean dominant frequency of the call is 3168.0 Hz, with a mean 90% bandwidth of 3082.9–3281.5 Hz (Table 3). The fundamental frequency is not recognizable, but up to five harmonics are visible.

The advertisement call of *P. translucidus* is similar to the call of *P. atratus* but can be distinguished by its longer call and note durations and by its higher frequencies (Table 3; Figs 2, 9, 21). Although *P. translucidus* and *P. chusquea* share some similar call characteristics, such as call and note duration, their vocalizations are easily distinguishable; *P. chusquea* produces more whistle-like calls, whereas *P. translucidus* emits sounds that resemble sharp tics, making them readily identifiable even by ear. Also, the call of *P. translucidus* has higher frequencies (Table 3; Figs 2, 16, 21). The advertisement call of *P. translucidus* differs markedly from that of *P. tinguichaca*, primarily by its significantly higher dominant frequencies (Brito *et al.* 2016).

Distribution: Pristimantis translucidus is currently known from three localities: two closely situated, one inside Parque Nacional Podocarpus and a second one in Reserva Tapichalaca; and a third locality, at ~45 km to the south-east in straight line, on the mountains bordering Río Sangola, at ~30 km north-east of the village of Chito (Fig. 4). Based on the topography of the region and the distributional gap between these known localities, we assume that additional populations are likely to occur in areas with suitable habitat. Additionally, owing to the proximity of the Río Sangola population to the Peruvian border, it is likely that *P. translucidus* also occurs in adjacent areas of northern Peru. Specimens were encountered at an elevational range between 2422 and 2895 m a.s.l. in 'Southern montane evergreen forest of the eastern Andes' and 'Montane shrubland and grassland of the Cordillera del Cóndor' ecosystems.

Natural history: This is an uncommon species. All animals were encountered during the night, predominantly on *Chusquea* leaves (in the dense bamboo patches), from 20 cm above the ground up to 3 m high. Calling males were heard in January, February, April, and June, being more active during rainy nights. The animals on the bamboo patches are well camouflaged and difficult to detect, especially if they are not active. Sympatric frog species include *Pristimantis andinognomus* Lehr & Coloma, 2008, *Pristimantis galdi* Jiménez de la Espada, 1870, and two undescribed *Pristimantis* species, but only *P. translucidus* was found on bamboo leaves.

Conservation status: Pristimantis translucidus is known from three localities in an estimated area of 54 km^2. Two of the localities are inside protected areas, one national (Parque Nacional Podocarpus) and one privately owned (Reserva Tapichalaca, managed by the NGO Fundación Jocotoco) but the third location, Río Sangola, is in a mining concession area that is likely to be severely impacted by mining activities in the near future. Thus, based on the available information, we recommend that *P. translucidus* be categorized as Endangered following the IUCN criteria B1ab(i,

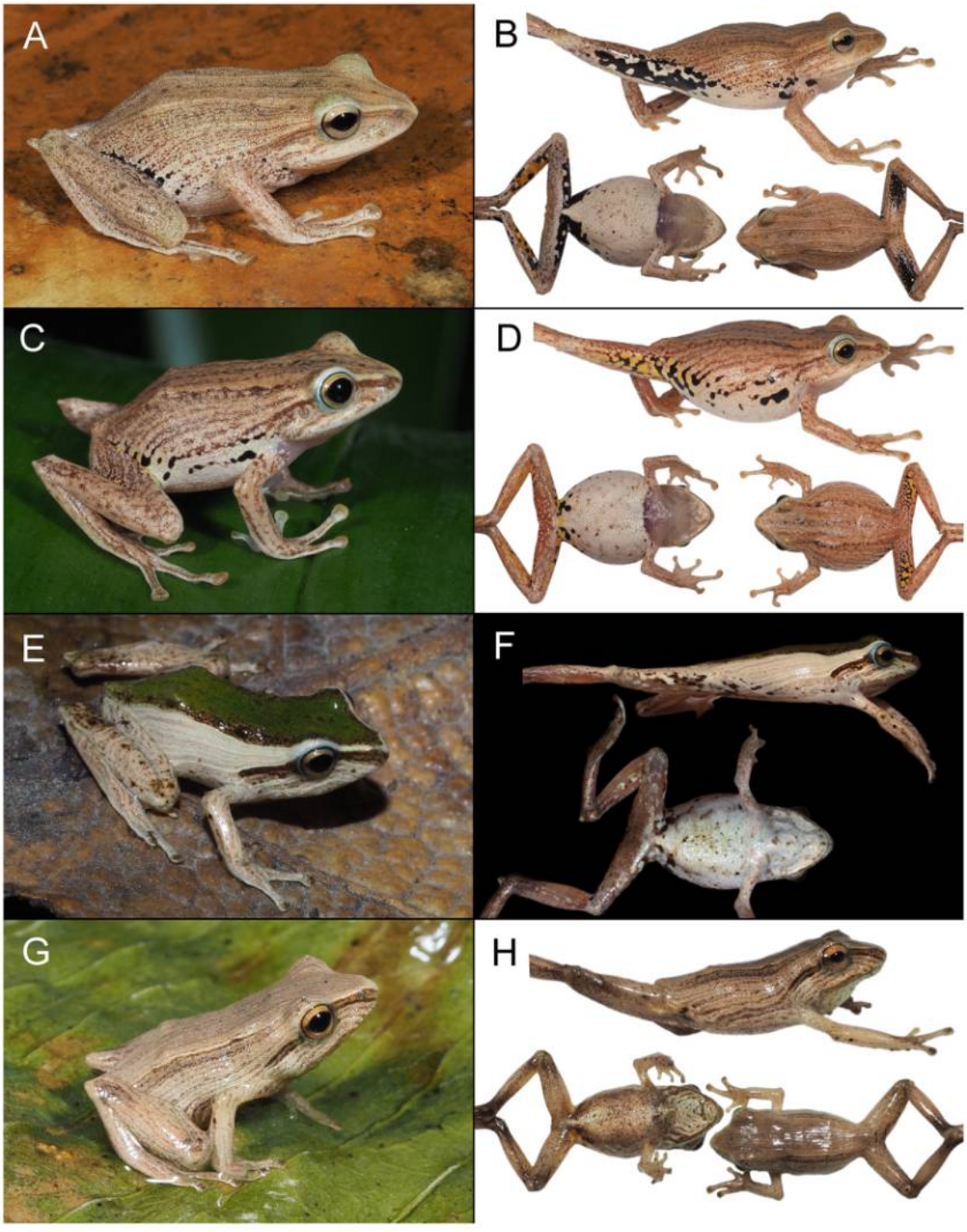

Figure 20. Colour variation in life for individuals of ***Pristimantis translucidus***, in dorsolateral, lateral, ventral, and dorsal views. A, B, MUTPL 1874, SVL 24.9 mm, adult male paratype from Reserva Tapichalaca, Zamora Chinchipe Province. C, D, MUTPL 1970, SVL 24.3 mm, adult male paratype from Río Sangola, Zamora Chinchipe Province. E, F, MUTPL 291, SVL 14.9 mm, juvenile paratype from Reserva Tapichalaca, Zamora Chinchipe Province. G, H, MUTPL 1709, SVL 11.6 mm, juvenile paratype from Reserva Tapichalaca, Zamora Chinchipe Province.

ii, iii, iv)+2ab(i, ii, iii, iv) (IUCN 2001) because: (i) its extent of occurrence is estimated to be <54 km^2 and the area of occupancy <16 km^2; (ii) it is known from only three locations; and (iii) its habitats could be affected in the near future, because some of its populations are located within a mining concession area.

Remarks: Uncorrected genetic p-distances between *P. translucidus* and its closest relatives range between 2.5%–3.1% (*P. atratus*) and 3.5%–3.9% (*P. chusquea*); the genetic distance between *P. translucidus* and *P. oculolineatus* ranges from 6.6% to 7.3% (Supporting Information, File S1).

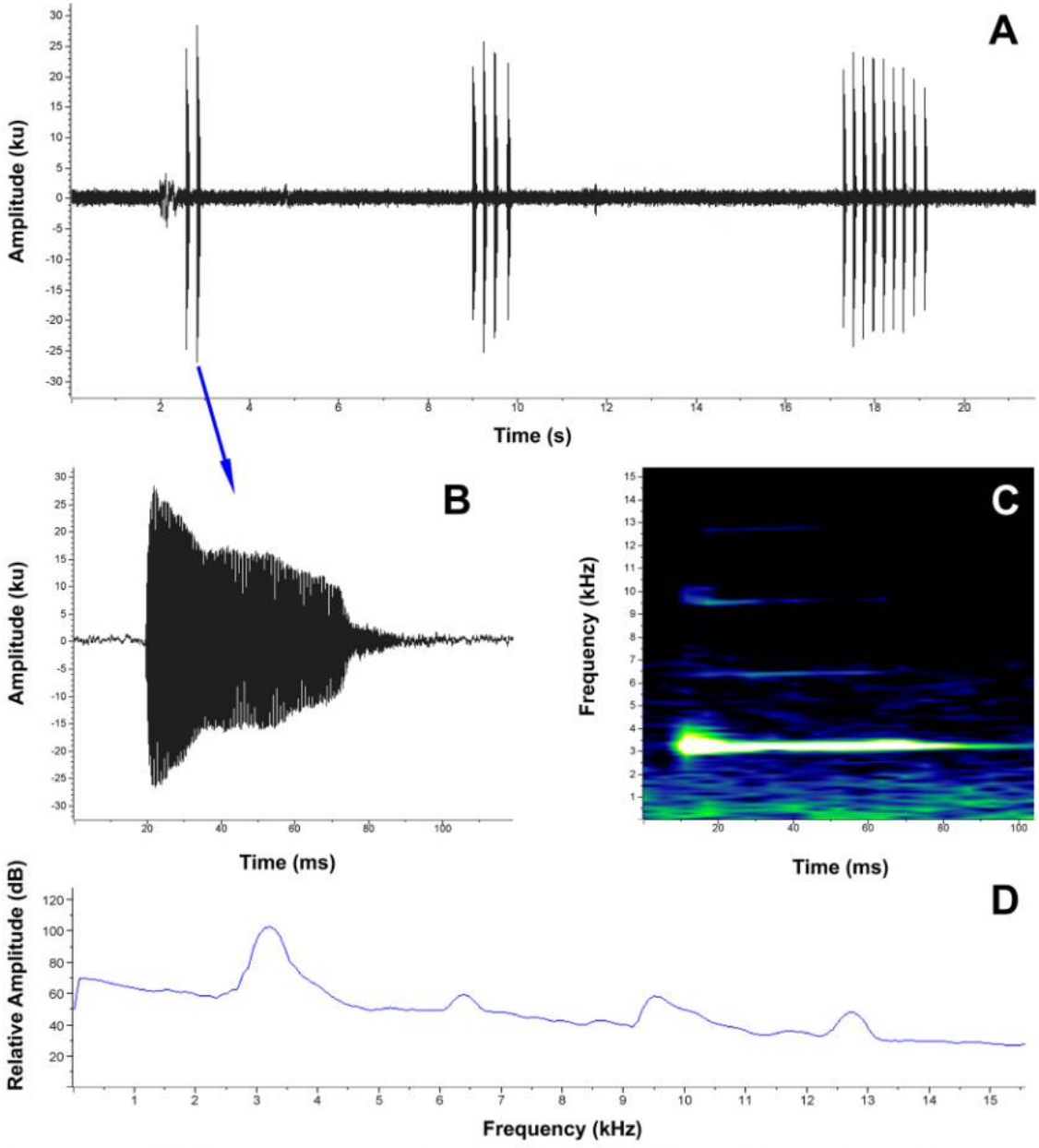

Figure 21. Advertisement call of ***Pristimantis translucidus*** (holotype *MUTPL 220*, FUTPL-A-377): A, oscillogram of three calls, with double-noted, quadruple-noted, and nine-noted calls; B, oscillogram of a note; C, spectrogram of a note; and D, power spectrum of a note.

***Pristimantis oculolineatus* sp. nov.**

(Figs 13C, 22–26)

ZooBank registration: urn:lsid:zoobank.org:act:C45E7013-280F-457A-BD69-7A3D3F648F4B

Pristimantis atratus—Páez and Ron (2019).
Pristimantis atratus—Székely *et al.* (2020).
Pristimantis atratus—Székely *et al.* (2021).
Pristimantis atratus—Ortega *et al.* (2022).
Pristimantis atratus—Portik *et al.* (2023).
Pristimantis atratus—Sánchez-Nivicela *et al.* (2024).

Common English name: Striped-eyed rain frog.

Common Spanish name: Cutín de ojos rayados.

Etymology: The specific epithet *oculolineatus* is derived from the Latin words *oculus*, meaning 'eye', and *lineatus*, meaning 'lined' or 'striped', and refers to the distinctive striped iris that easily distinguishes this species from morphologically similar species. The name is used as an adjective in the masculine form.

Holotype: MUTPL 1188 (field no. SC 1282; Figs 13C, 22–24), an adult male from Ecuador, Zamora Chinchipe Province, Reserva Numbala (4.4047°S, 79.0892°W; datum WGS84), 2946 m a.s.l., collected by Paul Székely, Diana Székely, and Santiago Hualpa on 3 September 2021.

Paratypes (ten: two males, two females, two subadults, and four juveniles): MUTPL 1108 (field no. SC 1211), a juvenile from Zamora Chinchipe Province, the Cerro Toledo sector of Parque Nacional

Podocarpus (4.3865°S, 79.1074°W), 3087 m a.s.l., collected by Paul Székely and Diana Székely on 26 June 2021; MUTPL 1184 (field no. SC 1277), an adult male from Zamora Chinchipe Province, Reserva Numbala (4.4035°S, 79.0883°W), 2936 m a.s.l., collected by Paul Székely, Diana Székely, and Santiago Hualpa on 2 September 2021; six specimens from Zamora Chinchipe Province, Parque Nacional Yacuri, collected by Dan Cogălniceanu, Paul Székely, and Jhony Arboleda on 26 April 2024: MUTPL 1758 (field no. SC 3904) and MUTPL 1761 (field no. SC 3907), two juveniles (4.7784°S, 79.4040°W), 3047 m a.s.l., MUTPL 1763 (field no. SC 3909), a juvenile and MUTPL 1765 (field no. SC 3911), an adult male (4.7786°S, 79.4047°W), 3051 m a.s.l., MUTPL 1766 (field no. SC 3912), a subadult female (4.7787°S, 79.4068°W), 3059 m a.s.l., and MUTPL 1771 (field no. SC 3917), a subadult female (4.7780°S, 79.4080°W), 3069 m a.s.l.; MUTPL 1869 (field no. SC 3954), an adult female from Zamora Chinchipe Province, Parque Nacional Yacuri, (4.7753°S, 79.4110°W), 3104 m a.s.l., collected by Paul Székely and Diana Székely on 24 December 2024; MUTPL 1871 (field no. SC 3957), an adult female from Zamora Chinchipe Province, Parque Nacional Yacuri, (4.7787°S, 79.4033°W), 3029 m a.s.l., collected by Paul Székely and Diana Székely on 25 December 2024.

Definition: We assign this species to *Pristimantis* based on phylogenetic evidence (Fig. 1) and on the general morphological similarity to other members of the genus. *Pristimantis oculolineatus* is a small-sized species (among the *Huicundomantis* subgenus; Table 1) characterized by the following combination of characters: (1) skin on dorsum shagreen with scattered tubercles, usually bearing numerous low ridges (trait more evident in life); flanks coarsely pustulated; skin on venter areolate; discoidal fold present; prominent, thick dorsolateral and lateral folds present; low mid-dorsal fold usually absent; (2) tympanic annulus evident and tympanic membrane differentiated, its length ~49% of the length of eye; prominent supratympanic fold present, slightly concealing the upper edge of tympanum; (3) snout acuminate in dorsal view, rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; (4) upper eyelid bearing one larger tubercle (trait more evident in life), ~81% IOD in females and 83% IOD in males; cranial crests inconspicuous, low; (5) dentigerous processes of vomers oblique, ovoid to triangular, separated medially by distance smaller than the width of processes; each process bearing four to eight teeth; (6) males with pigmented subgular vocal sac and large vocal slits; (7) finger I shorter than finger II; discs on fingers broadly expanded, rounded; circumferential grooves present; (8) fingers with lateral fringes; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary palmar tubercles present (trait more evident in life); palmar tubercle bifid, larger than thenar tubercle; thenar tubercle elliptical; (9) ulnar tubercles present (trait more evident in life); (10) heel with one larger, conical tubercle; outer edge of tarsus with a row of tubercles (trait more evident in life); inner tarsal fold present; (11) inner metatarsal tubercle ovoid, about three times the size of round outer metatarsal tubercle; subarticular tubercles prominent; hyperdistal subarticular tubercles present; supernumerary plantar tubercles present (trait more evident in life); (12) toes bearing lateral fringes; webbing basal; toe V much longer than toe III; discs on toes broadly expanded, rounded, about same size as those on fingers; circumferential grooves present; (13) in life, dorsum cream, beige to yellowish brown, with or without pale to dark brown stripes or spots; flanks cream or yellowish brown; venter whitish cream with small dark flecks; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces yellow or orange, with small dark brown or black blotches or reticulations; iris whitish, with reticulations/stripes and a median brownish streak; and (14) SVL 26.9–28.5 mm in adult females ($N = 2$) and 23.9–26.7 mm in adult males (25.6 ± 1.51 mm, $N = 3$).

Comparison with similar species: Pristimantis oculolineatus is morphologically different from the majority of species of the *Huicundomantis* subgenus and all other Ecuadorian *Pristimantis* species, owing to its particular habitus and coloration that mimics the dry *Chusquea* leaves. In particular, the combination of the cream to yellowish brown dorsal coloration, the dorsum with the low ridges, the black blotches or reticulations on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, and the large tubercles on the upper eyelids and heels easily distinguish this species from its congeners.

Pristimantis oculolineatus is most similar to *P. atratus* and the other two new species, *P. chusquea* and *P. translucidus*, from which it can be distinguished easily by several important morphological characters (Table 4). Mainly the whitish reticulated/striped iris, the thick dorsolateral and lateral folds, the coarsely pustulated flanks, in addition to the advertisement call distinguish *P. oculolineatus* from its similar-looking congener species. Additionally, *P. oculolineatus* differs from *P. atratus* by the larger size (vs. smaller size in *P. atratus*; SVL and BM range basically not overlapping; Table 2), longer, acuminate snout (vs. shorter, subacuminate in *P. atratus*; SL/HL and SN/HL range basically not overlapping; Table 2), toe V much longer than toe III (vs. toe V longer than toe III in *P. atratus*), and the coloration on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces with smaller, dark brown or black blotches or reticulations (vs. black blotches larger in *P. atratus*). The detailed comparisons with *P. chusquea* and *P. translucidus* have been presented in the corresponding sections above.

Pristimantis oculolineatus differs significantly from *P. yumbo* by the whitish reticulated/striped iris (vs. iris golden with a reddish copper centre and without reticulations in *P. yumbo*) and the presence of the black blotches or reticulations on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces (vs. lack of any black markings in *P. yumbo*), and from *P. tinguichaca* by the presence of the black blotches or reticulations on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces (vs. lack of any black markings in *P. tinguichaca*), the whitish reticulated/striped iris (vs. red iris in *P. tinguichaca*), and the advertisement call (Brito *et al.* 2016).

Description of the holotype: Adult male (*MUTPL 1188*; Figs 13C, 22–24), head slightly wider than body, wider than long, HL 89% of HW, HW 40% of SVL, HL 35% of SVL; snout long (SL 17% of SVL; SL 47% of HL; EN 30% of HL; SN 17% of HL), acuminate in dorsal view and rounded in profile; canthus rostralis straight in dorsal view, rounded in profile; loreal region slightly concave; ED larger than EN; nostrils slightly protuberant,

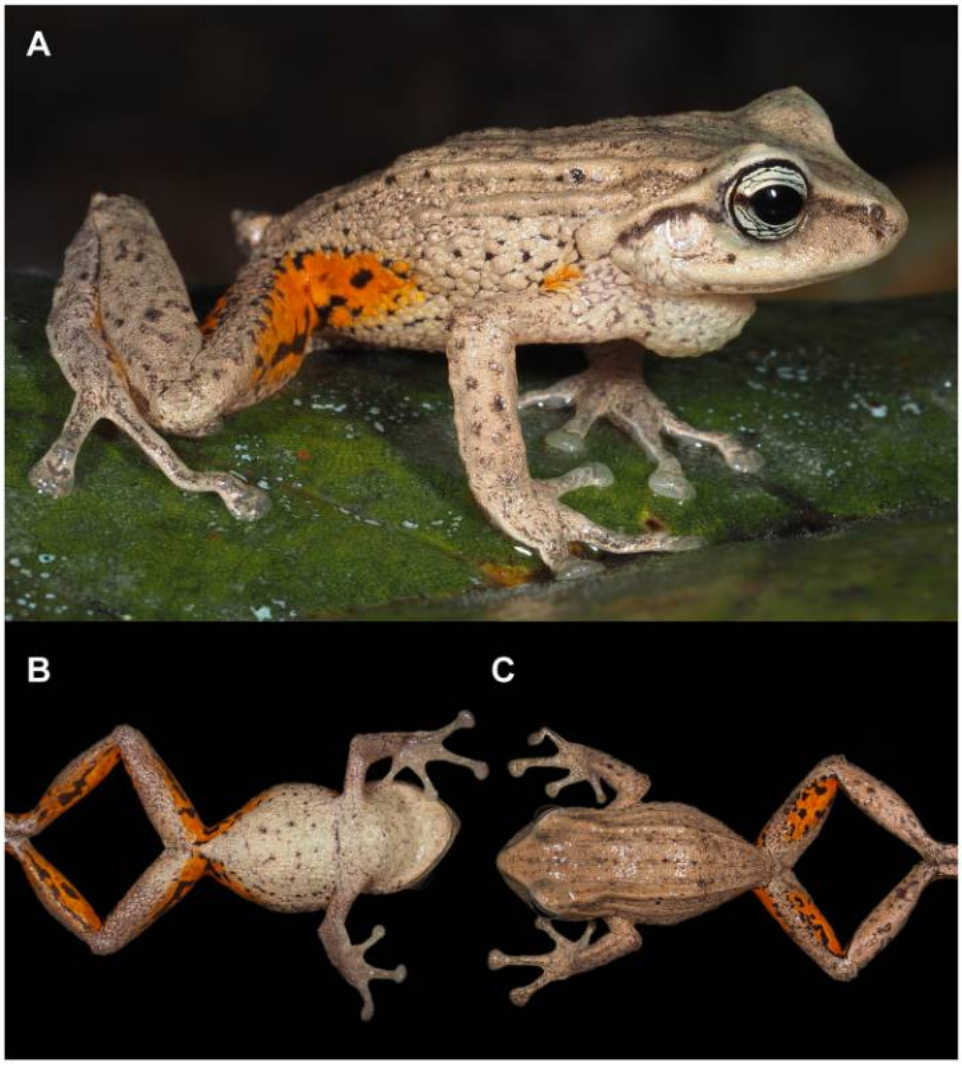

Figure 22. Holotype of ***Pristimantis oculolineatus*** (*MUTPL 1188*; adult male; SVL 26.3 mm) in life, from Reserva Numbala, Zamora Chinchipe Province: A, dorsolateral view; B, ventral view; and C, dorsal view.

oriented posteriorly; lips not flared; cranial crests inconspicuous, low, barely visible; upper eyelid bearing one larger tubercle (trait more visible in life; Fig. 22A); EW 84% of IOD; tympanic annulus evident and tympanic membrane differentiated; thick supratympanic fold present, slightly concealing the upper margin of the tympanum (Fig. 22A); TD 46% of ED; two large, elongated postrictal tubercles; choanae large, oval, partly concealed by palatal shelf of maxillary arch; dentigerous processes of vomers prominent, slightly larger than the choanae, oblique, situated posterior and median to choanae, triangular in outline, separated medially by a distance smaller than the width of processes, each process bearing three teeth; tongue longer than wide, prominently notched posteriorly, posterior half not adherent to floor of mouth; large vocal slits at the angles of the mouth; subgular vocal sac pigmented (Figs 13C, 22A, B).

Skin on dorsum shagreen, with scattered tubercles and numerous low ridges (trait more visible in life); flanks coarsely pustulated (Fig. 22A); mid-dorsal fold absent; dorsolateral and lateral folds prominent, thick (Fig. 22A, C); skin on belly and posteroventral surfaces of thighs coarsely areolate; thoracic and discoidal folds present; cloacal region not bordered by distinct tubercles.

Ulnar tubercles present (trait more visible in life); outer palmar tubercle bifid, partly divided into a larger (inner) and a smaller (outer) tubercles; thenar tubercle elliptical, large; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all fingers; supernumerary palmar tubercles rounded, smaller than subarticular tubercles (trait more visible in life); fingers bearing lateral fringes; relative length of fingers I < II < IV < III; discs on fingers broadly expanded, rounded; all fingers bearing pads well defined by circumferential grooves (Fig. 24A).

Hindlimbs long, slender; THL 49% of SVL; TL 54% of SVL; FL 51% of SVL; heel with a large conical tubercle (Figs 22, 23); outer edge of tarsus with a row of tubercles (trait more evident in life); inner edge of tarsus bearing a short fold; inner metatarsal tubercle ovoid; outer metatarsal tubercle inconspicuous; subarticular tubercles prominent, round and rounded in section; hyperdistal subarticular tubercles present on all toes; supernumerary plantar tubercles rounded, smaller than subarticular tubercles

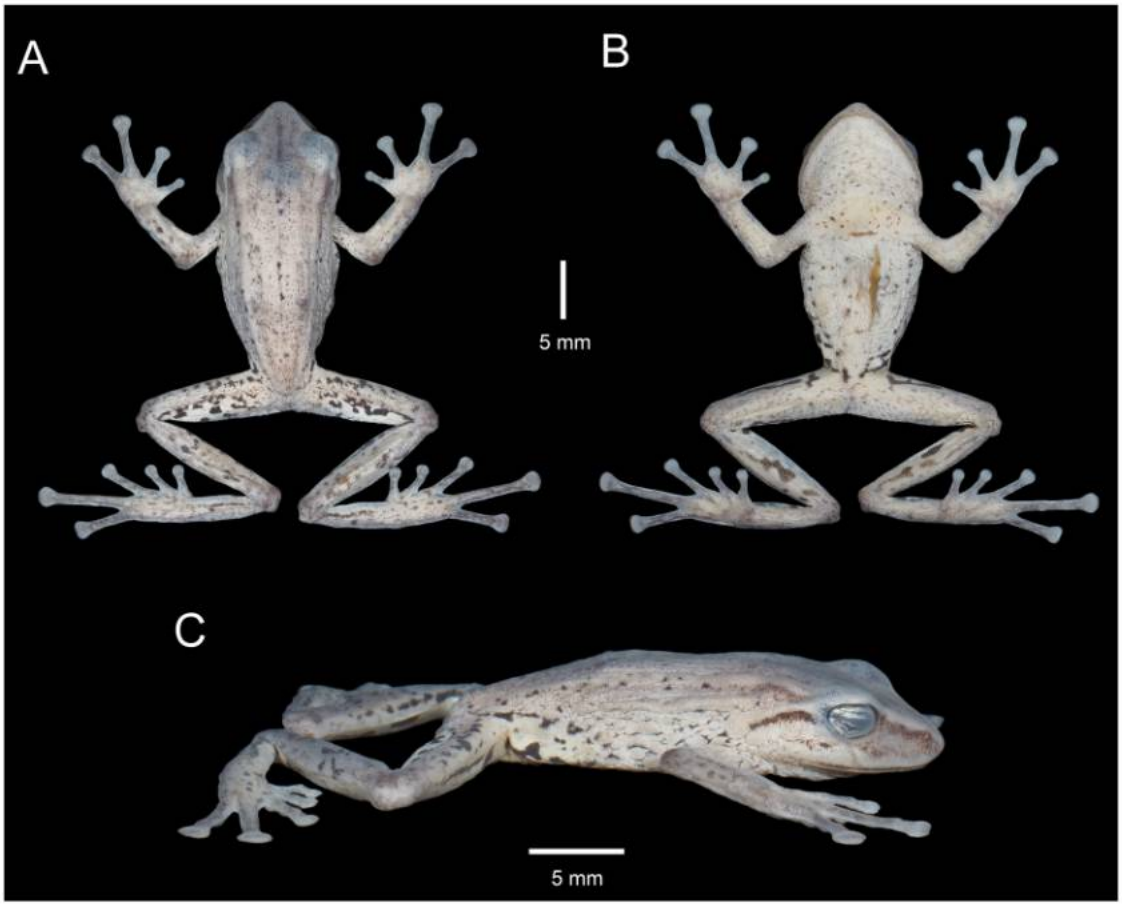

Figure 23. Holotype of ***Pristimantis oculolineatus*** (*MUTPL 1188*; adult male; SVL 26.3 mm) in preservative, from Reserva Numbala, Zamora Chinchipe Province: A, dorsal view; B, ventral view; and C, lateral view.

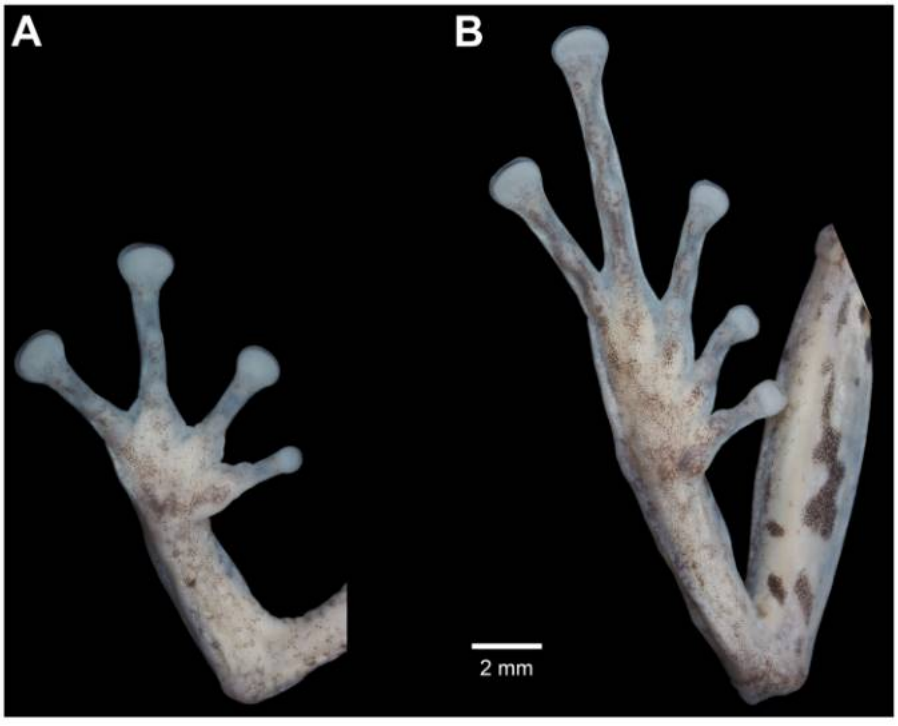

Figure 24. Details of the palmar surface of the hand (A) and plantar surface of the foot (B) of male holotype ***Pristimantis oculolineatus*** (*MUTPL 1188*; SVL 26.3 mm) in preservative.

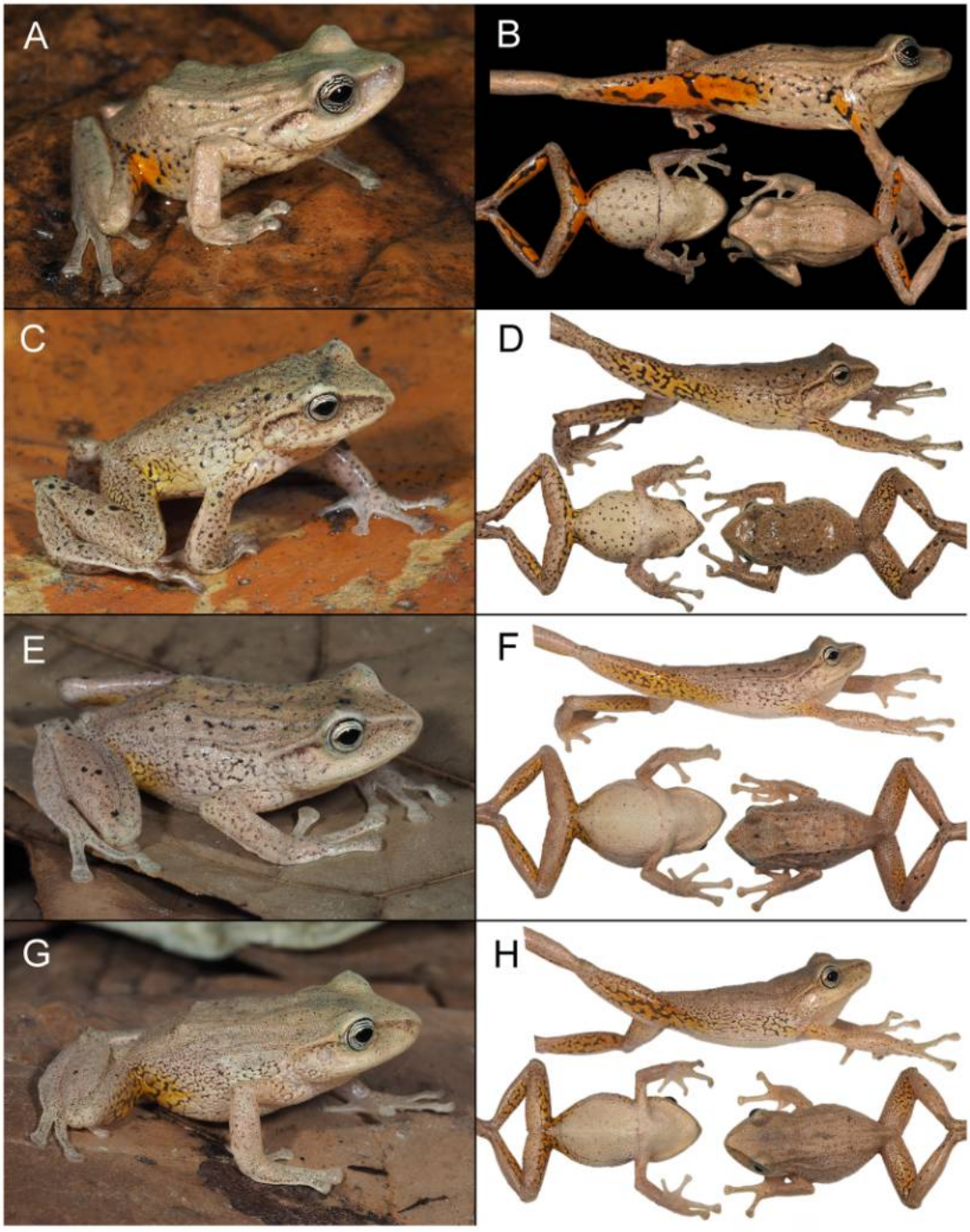

Figure 25. Colour variation in life for individuals of ***Pristimantis oculolineatus***, in dorsolateral, lateral, ventral, and dorsal views. A, B, MUTPL 1184, SVL 26.7 mm, adult male paratype from Reserva Numbala, Zamora Chinchipe Province. C, D MUTPL 1765, SVL 23.9 mm, adult male paratype from Parque Nacional Yacuri, Zamora Chinchipe Province. E, F, MUTPL 1869, SVL 28.5 mm, adult female paratype from Parque Nacional Yacuri, Zamora Chinchipe Province. G, H, MUTPL 1871, SVL 26.9 mm, adult female paratype from Parque Nacional Yacuri, Zamora Chinchipe Province.

(trait more visible in life); toes bearing lateral fringes; webbing basal; discs on toes broadly expanded, rounded, about same size as those on fingers; toes with ventral pads well defined by circumferential grooves (Fig. 24B); 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. 22): dorsum and dorsal surfaces of hindlimbs and arms dark beige, with inconspicuous darker brown stripes and black irregular spots; lower parts of flanks slightly lighter, with black irregular spots; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces intense orange with small black blotches; head with dark brown canthal and supratympanic stripes; throat, venter, and ventral surfaces of hindlimbs and arms light beige with small irregular black

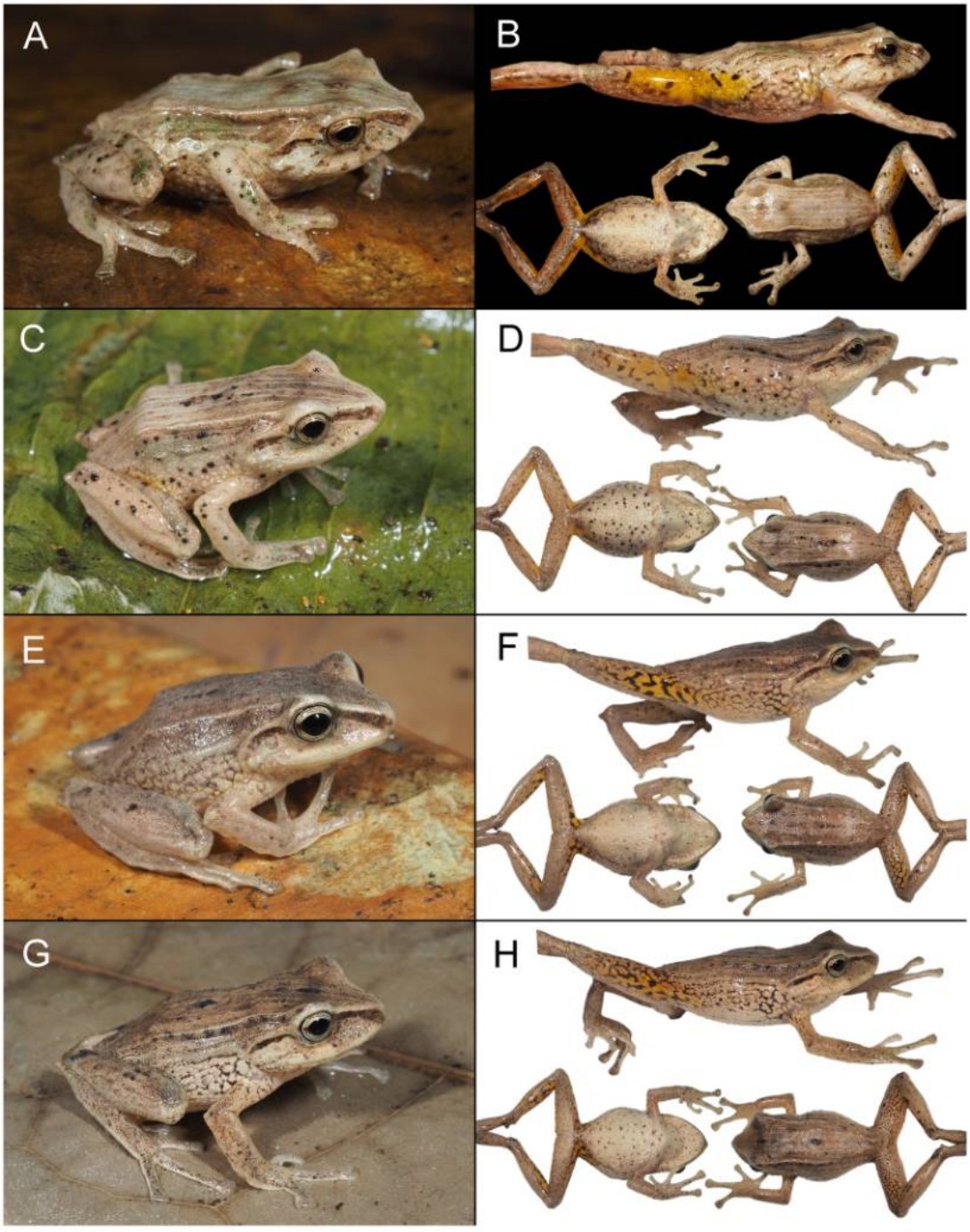

Figure 26. Colour variation in life for individuals of ***Pristimantis oculolineatus***, in dorsolateral, lateral, ventral, and dorsal views. A, B, MUTPL 1108, SVL 15.2 mm, juvenile paratype from Cerro Toledo, Zamora Chinchipe Province. C, D, MUTPL 1761, SVL 15.1 mm, juvenile paratype from Parque Nacional Yacuri, Zamora Chinchipe Province. E, F, MUTPL 1763, SVL 19.2 mm, juvenile paratype from Parque Nacional Yacuri, Zamora Chinchipe Province. G, H, MUTPL 1771, SVL 23.7 mm, subadult female paratype from Parque Nacional Yacuri, Zamora Chinchipe Province.

spots; iris white, with black reticulations/stripes and a median dark brown streak.

In preservative (Fig. 23): dorsum and dorsal surfaces of hindlimbs and arms grey, with inconspicuous blackish stripes and black irregular spots; lower parts of flanks yellowish white with irregular black spots; large areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces yellowish white with small black blotches; throat, venter, and ventral surfaces of hindlimbs and arms whitish yellow with small irregular black spots.

Measurements of holotype (in millimetres): SVL 26.3; HW 10.4; HL 9.3; IOD 3.2; IND 2.4; EW 2.7; ED 3.3; EN 2.8; SL 4.4; SN 1.6; TD 1.5; THL 12.9; TL 14.3; FL 13.5; FLL 6.9; and HAL 8.3.

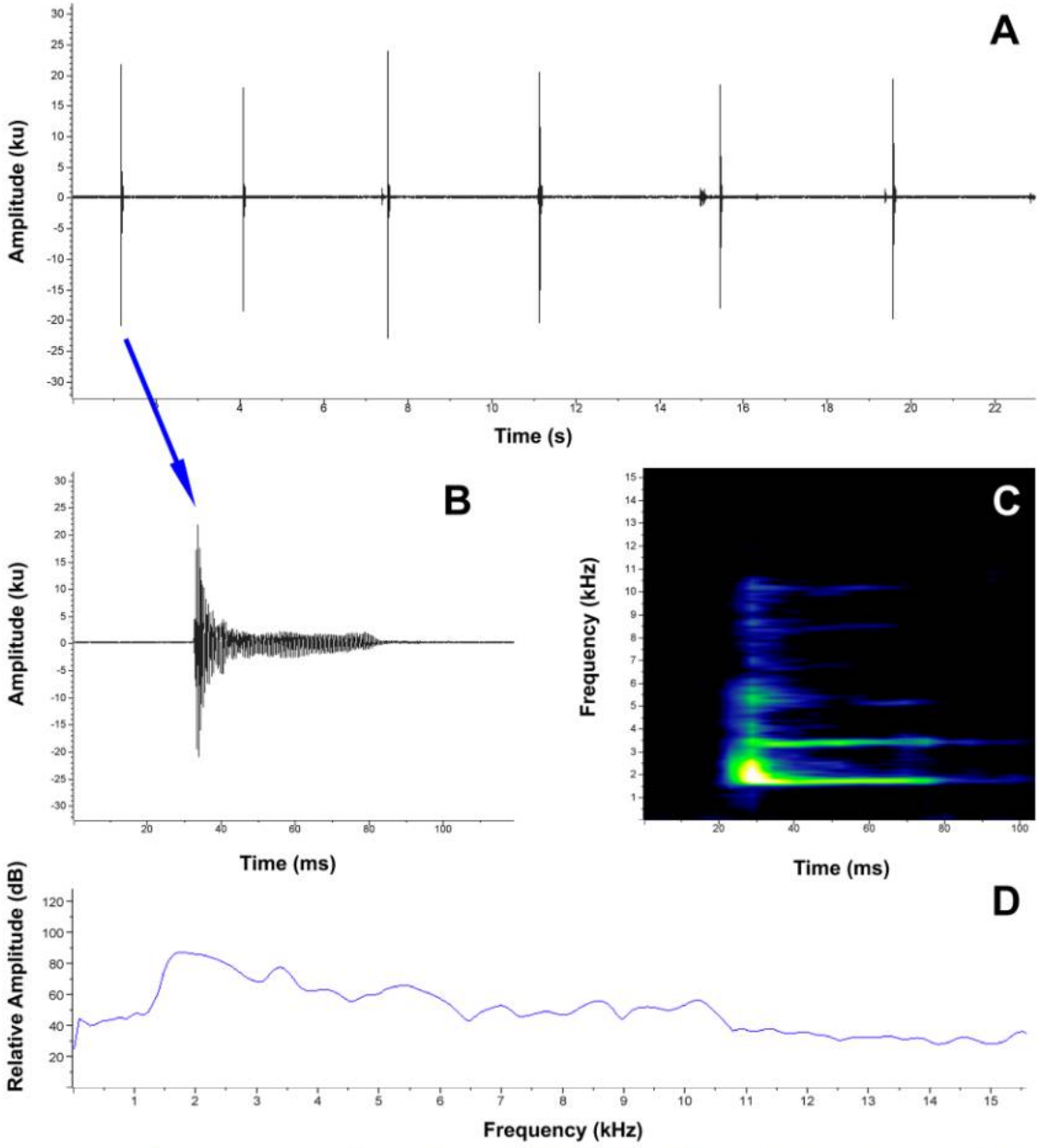

Figure 27. Advertisement call of ***Pristimantis oculolineatus*** (holotype *MUTPL 1188*, FUTPL-A-546): A, oscillogram of a section of six calls, with single-noted calls; B, oscillogram of a note; C, spectrogram of a note; and D, power spectrum of a note.

Body mass of holotype: 1.51 g.

Variation: Morphometric variation is shown in Table 2. Coloration does not differ between sexes. Most of the encountered individuals were uniformly coloured with dark irregular spots, like the males MUTPL 1184 (Fig. 25A, B) and MUTPL 1765 (Fig. 25C, D) or the females MUTPL 1869 (Fig. 25E, F) and MUTPL 1871 (Fig. 25G, H). However, the black-blotched areas of dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces varied from various shades of yellow to intense orange (Fig. 25). Some individuals, like MUTPL 1108 (Fig. 26A, B), MUTPL 1761 (Fig. 26C, D), and 1771 (Fig. 26G, H), had inconspicuous stripes on their dorsum. The juveniles and subadults already presented the characteristic blackish blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces, accompanied by the yellow coloration (Fig. 26). The iris coloration varied from white to light cream (Figs 25, 26).

Vocalizations: For the description of the call of *P. oculolineatus* we analysed five call samples from five males, four calls being recorded in Reserva Numbala, Zamora Chinchipe Province, in 2021, and one in Parque Nacional Yacuri, Zamora Chinchipe Province, in 2024. Descriptive statistics of the acoustic variables are provided in Table 3 (detailed information on each recording is provided in Supporting Information, File S2).

Pristimantis oculolineatus has an advertisement call characterized by long, raspy 'tic' sounds (notes) repeated over a period of time. The calls are typically composed of only one note, and rarely by two or three notes (Fig. 27). As in the case of its similar sister species, the calls that contain more than one note are probably

emitted during social interactions, triggered by the nearby presence of a female or a competitive vocalizing male (probably courtship calls *sensu* Wells 2007).

The calls are characterized by a mean duration of 0.471 s (in the case of double-noted calls), a mean inter-call interval of 3.7 s, and a mean call rate of 15.3 calls/min (Table 3). The notes are tonal sounds, relatively long, characterized by a mean duration of 0.057 s, a mean inter-note interval of 0.278 s, and a mean note rate of 2.9 notes/s. The mean dominant frequency of the call is 1817.6 Hz, with a mean 90% bandwidth of 1644.4–3200.6 Hz (Table 3). The fundamental frequency is not recognizable, but up to six harmonics are visible.

The advertisement call of *P. oculolineatus* is highly distinctive, characterized by its raspy 'tic' sounds, low dominant frequency, and broad spectral range (the 90% bandwidth), which make it easily distinguishable from the calls of its morphologically similar sister species. Thus, the call of *P. oculolineatus* differs from that of *P. atratus* by the longer call duration, shorter inter-call interval, higher call rate, longer note duration, lower note rate, lower dominant frequency, and by typically consisting of a single note (Table 3; Figs 2, 9, 27); from the call of *P. chusquea* it differs by the longer call duration, shorter inter-call interval, higher call rate, lower note rate, lower dominant frequency, and by typically consisting of a single note (Table 3; Figs 2, 16, 27); from the call of *P. translucidus* it differs by the longer call duration, higher call rate, lower dominant frequency, and by typically consisting of a single note (Table 3; Figs 2, 21, 27). Finally, the call of *P. oculolineatus* differs from that of *P. tinguichaca* by the longer, raspy 'tic' sounds and lower dominant frequency (Brito *et al.* 2016).

Distribution: Pristimantis oculolineatus is currently known from three disjunct localities in southern Ecuador (Fig. 4). The first is in the Cajanuma sector of Parque Nacional Podocarpus and its immediate surrounding areas outside the park, the second locality lies ~33 km to the south (straight line) in Reserva Numbala, and the third is situated ~54 km further south, in Parque Nacional Yacuri. Based on the topography of the region and the large distributional gap between these known localities, we assume that additional populations are likely to occur in areas with suitable habitat. Additionally, owing to the proximity of the Parque Nacional Yacuri population to the Peruvian border, it is possible that *P. oculolineatus* also occurs in adjacent areas of northern Peru. Specimens were encountered at an elevational range between 2523 and 3116 m a.s.l. in 'Southern montane evergreen forest of the eastern Andes' and 'High montane evergreen shrubland of the páramos from southern Ecuador' ecosystems.

Natural history: This is a common species, at least in Reserva Numbala and Parque Nacional Yacuri, where we encountered several calling males, subadults, and juveniles. The records from the Cajanuma population belong to the Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ) and are from 2009 (Ron *et al.* 2024). Despite the close vicinity of this population to the city of Loja and our ongoing fieldwork since 2016 in the area, we did not locate any additional individuals.

All animals were encountered during the night, predominantly on *Chusquea* leaves (in the dense bamboo patches along the trails and roads), from 30 cm above the ground up to 2 m high. Calling males were heard in September and December, being more active during rainy nights. The animals on the bamboo patches are well camouflaged and difficult to detect, especially if they are not active. Sympatric frog species, but not on the bamboo leaves, include *P. versicolor* and several undescribed *Pristimantis* species.

Conservation status: Pristimantis oculolineatus is known from three localities in an estimated area of 990 km^2. All three localities are inside protected areas, two national (Parque Nacional Podocarpus and Parque Nacional Yacuri) and one privately owned (Reserva Numbala, managed by the NGO Naturaleza y Cultura Internacional). Thus, taking into consideration that this is a common species, has a relatively large extent of occurrence, almost all the known populations are inside protected areas, and the fact that we did not identify any significant current or foreseeable threats that could affect its extent and/or quality of habitat, we consider this species to be Least Concern following the IUCN criteria.

Remarks: Pristimantis oculolineatus is part of a strongly supported clade (SH-aLRT = 99.9%; UFBoot = 100%; Boot = 100%; PP = 1) formed by *P. multicolor*, *P. percultus*, *P. chomskyi*, and *P. andinogigas*, but its kinship to these species remains non-resolved (Fig. 1). Members of this group share the coarsely pustulated texture on the flanks and the reticulated iris. Uncorrected genetic p-distances between *P. oculolineatus* and its closest relatives range between 4.5%–4.7% (*P. multicolor*), 3.4%–4.2% (*P. percultus*), 3.4%–4.2% (*P. chomskyi*), and 4.3%–4.6% (*P. andinogigas*); the genetic distance between *P. oculolineatus* and *P. atratus* ranges from 6.7% to 7.9% (Supporting Information, File S1).

DISCUSSION

The type locality of *Pristimantis atratus*

In order to clarify the molecular identity of *P. atratus*, we collected samples from its type locality, Suro Rancho in Morona Santiago Province, where James A. Peters and his associates collected several specimens in 1962. James A. Peters made various visits to Ecuador (1958–59, 1962, 1966, 1969, and 1972–73; Irish and Zug 1982). His collections, deposited at NMNH, represented a huge contribution to the knowledge of Neotropical herpetofauna, mostly reptiles, but also helped to clarify the taxonomy of genera such as *Atelopus* (Peters 1973), *Caecilia* and *Epicrionops* (Taylor and Peter 1974), *Hyloxalus* (Rivero 1991) and *Pristimantis* (Lynch 1979). His fieldwork included transects in southern Ecuador, on the eastern slopes of the Andes, an area almost unknown at the time, which remains poorly explored in terms of herpetofauna even now (Sánchez-Nivicela *et al.* 2023).

The type locality, 'Suro Rancho, Provincia Morona-Santiago, Ecuador, 2683 m', benefits from a more detailed description and a map in the study by Peters (1973). Suro Rancho (also called Gualecenita and Surorancho) was a 'tambo', a single house that functioned as an inn on what was a mule trail crossing the páramos between Gualaceo and Plan de Milagro; the road became open to vehicular transit from Gualaceo to Surorancho in 1963 (Urdiales González 2016) and to Limón Indanza in 1968 (Castro Zaruma 2021). It is worth noting that in the Andes, the terms 'suro' or 'zuro' are commonly used to refer to bamboo of the genus *Chusquea*. It is probable that the place derives its name from the abundance of

this plant, which also constitutes the preferred habitat of *P. atratus*. Today, Suro Rancho is merely a toponym recognized only by the local residents within the former protected area Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño. This protected area (located in the canton Limón Indanza) was created in 2002 and represented one of the few examples in the country of decentralized environmental management, being administered by the Gobierno Autónomo Descentralizado Municipal (GADM) de Limón Indanza. In November 2024, the Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño was officially incorporated into the Río Negro Sopladora National Park, resulting in the expanded protected area now known as the Parque Nacional Río Negro Sopladora—Tinajillas Río Gualaceño.

Bamboo-specialist species

The Andean bamboo *Chusquea* (Poaceae) is the most diverse genus of Neotropical woody bamboos, with ~198 described species (Clark *et al.* 2022). These bamboos occur primarily in montane forests and high-elevation grasslands and tend to occupy specialized habitats, such as Andean páramos, Brazilian campos de altitude, *Araucaria* forests, *Nothofagus* forests, and the pine–oak forests of Mexico (Fisher *et al.* 2014). Many *Chusquea* species are able to colonize areas disturbed naturally or by humans aggressively (Judziewicz *et al.* 1999), also being able to inhibit germination of surrounding plants by creating a thick leaf litter (Tol and Cleef 1994) or by limiting understorey light (Giordano *et al.* 2009). This is why the presence and high coverage of Andean bamboo is often considered an indication of deforestation or forest degradation (Veblen 1982). However, bamboo plays an important role in the natural dynamics of forest ecosystems, contributing to the maintenance of the structure and species composition of plants and animals (Caviedes and Ibarra 2017). In some cases, it may even act as a primary driver of tree regeneration cycles (Holz and Veblen 2006).

Regarding the fauna inhabiting *Chusquea*-dominated ecosystems, we have records mainly for insect, bird, and mammal species that use the bamboo as shelter or for feeding (Greeney *et al.* 2008, Celis-Diez *et al.* 2011, Jacobs *et al.* 2012, Cockle and Areta 2013, Seifert *et al.* 2016, Ibarra *et al.* 2018, Areta *et al.* 2023). In the case of amphibians, most available records mention *Chusquea* only as one among several plant species characterizing the ecosystems where these species occur. In general, little is known about the effects of bamboo presence or absence on anuran community composition, despite the fact that it contributes to habitat heterogeneity, offering unique microhabitats or resources that can support distinct amphibian communities (Blair and Doan 2009, Lopez-Rojas *et al.* 2015, Saboyá-Acosta *et al.* 2025). Moreover, there are very few records of species that inhabit almost exclusively *Chusquea*-dominated ecosystems and virtually no documented cases of species exhibiting specific adaptation to life in these environments. For example, *Pristimantis bambu* Arteaga-Navarro & Guayasamin, 2011, an Ecuadorian species found in leaf litter and low vegetation within regrowth montane forest dominated by bamboo (hence the name), does not appear to have any particular morphological features specifically linked to life on *Chusquea* leaves. In the case of *Rhinoderma darwinii* Duméril & Bibron, 1841, a species characterized by a pointed snout and cryptic coloration, it has been reported that individual coloration varies depending on the substrate, with some individuals even resembling bamboo leaves (Crump 2002, Ibarra *et al.* 2018). However, although this species has also been recorded in *Chusquea*-dominated ecosystems (Ibarra *et al.* 2018), its special morphological adaptations are more suited to life in leaf litter rather than to the bamboo leaves.

Most of our observations involved individuals perched on Andean bamboo shrubs, and even in cases where they were found on leaves of other plant species, they were always located within ecosystems dominated by *Chusquea* species. We believe that the bamboo-specialist *Pristimantis* species presented in our study exhibit strong microhabitat fidelity to *Chusquea*-dominated ecosystems, a pattern that appears to be linked to their distinctive morphological traits. Their general body shape, cryptic coloration, and the presence of numerous dermal ridges on the dorsum, mimicking the texture of bamboo leaves, enable these frogs to achieve effective camouflage within the bamboo shrubs. It is important to mention that not all the preserved specimens bear the characteristic low dorsal ridges of these species, because this character is mostly evident in life and tends to be inconspicuous or even lost during the preservation process. Additionally, we think that the bamboo-specialist *Pristimantis* species have the ability to change their skin texture in a similar manner to *Pristimantis mutabilis* Guayasamin *et al.*, 2015. We observed that the few specimens encountered on other types of vegetation (generally on smooth leaves, in contrast to the ridged *Chusquea* leaves) or maintained in captivity in plastic bags for longer periods of time tended to have a smoother dorsum, without the low ridges.

To our knowledge, no other Ecuadorian species have these morphological features that mimic bamboo leaves. Our results provide evidence for parallel evolution of three clades of *Pristimantis* that share these adaptations. Two are nested in the subgenus *Huicundomantis*, *phoxocephalus* species group, and the third in the subgenus *Trachyphrynus*, in the *devillei* species group (Fig. 5). At a smaller scale, the case of *P. atratus*, its sister species, and the more distant relative *P. oculolineatus* is particularly interesting because they are distributed on the eastern slopes of the Andes and mostly share the same type of ecosystem (Fig. 4). However, these bamboo-specialist species differ significantly in morphology even if they share the general bamboo leaf-mimicking habitus, because they maintain the general characteristics unique to their respective clades. Thus, *P. oculolineatus* has the characteristic pustulated texture on the flanks (warty or glandular according to other authors: Páez and Ron 2019, Yánez-Muñoz *et al.* 2019) and the reticulated iris like its sister species, *P. andinogigas*, *P. chomskyi*, *P. multicolor*, and *P. percultus*. In contrast, *P yumbo* and its close relative are members of a markedly distant and different, geographically isolated clade of *Pristimantis*, being distributed on the western slopes of the Andes (Fig. 4). These species do not exhibit the particular black blotches on the dorsal surfaces of thighs, groin, axilla, and concealed limb surfaces characteristic to the *Huicundomantis* species; it is currently unknown whether these markings are related in any way to the life on the bamboo leaves. These cases highlight the role of bamboo-dominated montane ecosystems in shaping the phenotypic traits and ecological specialization in anurans.

Biogeography

The newly described species inhabit a region characterized by complex topography and ecological heterogeneity, which is likely to have contributed to their evolutionary divergence (García-Rodríguez *et al.* 2021). Southern Ecuador, particularly the transition zone between the Andes and the Amazon, presents

a mosaic of biogeographical barriers that can restrict gene flow and promote allopatric speciation (Duellman 1999, Hazzi *et al.* 2018). One such barrier is the valley of Río Zamora (Krabbe 2008, Bonaccorso 2009), which separates the range of *P. atratus* from that of the newly described species located further south, at a straight-line distance of >110 km (Fig. 4). Its deeply incised topography disrupts the continuity of montane forest habitats, potentially limiting dispersal (Beck *et al.* 2008). Additionally, Río Zamora, together with Río Jubones, marks the northern limit of the Huancabamba Depression (Weigend 2004), a region long recognized as a major biogeographical barrier for certain Andean organisms (Duellman 1999, Hazzi *et al.* 2018) or a migration corridor (Quintana *et al.* 2017), but also a centre of origin and diversification for others (Torres-Carvajal *et al.* 2020).

Regarding the new species, the situation appears to be more complex, particularly owing to incomplete distribution data. The amphibian fauna inhabiting the mountain range from Abra de Zamora to the Cerro Toledo sector of the Parque Nacional Podocarpus and Reserva Tapichalaca shows a particular pattern in the distribution (Székely *et al.* 2023). Notably, some species found in the Abra de Zamora area are replaced by morphologically and ecologically similar, yet genetically different, species in the Cerro Toledo/Tapichalaca sector. This seems to be the case for *P. chusquea* and *P. translucidus*: *P. chusquea* is known only from Abra de Zamora, and the northernmost records of *P. translucidus* are from the southern limits of the Podocarpus national park (Fig. 4). *Pristimantis translucidus* is likely to have a continuous distribution extending south-east towards the Río Sangola population (Fig. 4), located in the Cordillera del Cóndor. Suitable habitats between Río Sangola and Tapichalaca, at elevations between 2400 and 2900 m a.s.l., might include connecting mountain ranges, such as the Cordillera de Paredones, which could harbour additional populations of this species.

In contrast, *P. oculolineatus*, the morphologically similar but distant relative of *P. chusquea* and *P. translucidus*, has a comparatively wider distribution. This species occupies a broad, ~100-km-long and probably continuous range, stretching from Parque Nacional Yacuri to the vicinity of Abra de Zamora, at elevations between 2500 and 3100 m a.s.l. (Fig. 4). The distribution of *P. oculolineatus* might overlap with that of *P. translucidus* around Tapichalaca and Numbala, and possibly with *P. chusquea* near Abra de Zamora, in the Cajanuma sector of Parque Nacional Podocarpus. Nevertheless, we did not find these species occurring syntopically at either location. In order to gain a better understanding of the distribution and to uncover patterns of diversification and speciation among these species, additional data are needed, particularly from unexplored areas. This is especially true for *P. atratus*, a species for which distributional data remain limited. Finally, the distribution records from Paquisha, located at the northeastern limits of Zamora Chinchipe province, presented in the Amphibians of Ecuador encyclopedia (Coloma and Duellman 2025), are likely to correspond to a different, probably undescribed species.

CONCLUSION

The discovery and description of three new bamboo-specialist *Pristimantis* species, alongside the redefinition of *P. atratus*, reveal a remarkable case of parallel evolution in Andean frogs. These species exhibit similar morphological traits consistent with adaptation to the life on Andean bamboo, despite belonging to distinct phylogenetic lineages. Their ecological specialization emphasizes the narrow niche occupied by some *Pristimantis* from the Ecuadorian Andes and reveals the importance of bamboo-dominated ecosystems for amphibian diversity and evolution.

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SUPPLEMENATRY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest in relation to this work.

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DATA AVAILABILITY

The data underlying this article are available in the manuscript, its Supporting Information, and in the Zenodo repository (https://doi.org/10.5281/zenodo.16898580).

APPENDICES

APPENDIX 1. ADDITIONAL SPECIMENS EXAMINED.

Pristimantis andinogigas (1). ECUADOR: LOJA PROVINCE, Parque Nacional Podocarpus—Cajanuma (MUTPL 359).

Pristimantis balionotus (14). ECUADOR: LOJA PROVINCE, Abra de Zamora (MUTPL 292, 297, 391, 392, 677); Reserva Madrigal del Podocarpus (MUTPL 180, 487, 489–491); ZAMORA CHINCHIPE PROVINCE, Estación Científica San Francisco (MUTPL 1673, 1674, 1676, 1678).

Pristimantis chomskyi (10). ECUADOR: LOJA PROVINCE, Parque Nacional Podocarpus—Cerro Toledo (MUTPL 113–116, 121, 524–526, 816); ZAMORA CHINCHIPE PROVINCE, Reserva Tapichalaca (MUTPL 1783).

Pristimantis cryptomelas (16). ECUADOR: LOJA PROVINCE, Abra de Zamora (MUTPL 135, 470, 471); Bosque Protector Washapamba (MUTPL 167–171); Loja, Huacapamba (MUTPL 380, 381, 383, 385); Parque Nacional Podocarpus—Cajanuma (MUTPL 493); San Lucas (MUTPL 1121); ZAMORA CHINCHIPE PROVINCE, Reserva Numbala (MUTPL 1174); Parque Nacional Yacuri (MUTPL 1774).

Pristimantis curtipes (1). ECUADOR: CARCHI PROVINCE, Reserva Ecológica El Ángel (MUTPL 1950).

Pristimantis devillei (1). ECUADOR: NAPO PROVINCE, Parque Nacional Cayambe-Coca (MUTPL 1303).

Pristimantis gloria (56). ECUADOR: AZUAY PROVINCE, Vía Gualaceo—Plan de Milagro, Loma de la Virgen (1623); LOJA PROVINCE, Vía Urdaneta-Tutupali (MUTPL 222–238, 250); MORONA SANTIAGO PROVINCE, Bosque Protector Jima (MUTPL 39–72); Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño (MUTPL 1624); ZAMORA CHINCHIPE PROVINCE, Belen, Bosque Protector Shincata (MUTPL 801).

Pristimantis lojanus (32). ECUADOR: LOJA PROVINCE, Cristal, Reserva El Cristal (MUTPL 191, 192, 280); Loja (MUTPL 14–23, 108, 176–179, 628, 935, 936, 1030, 1076); Parque Nacional Podocarpus—Cajanuma (MUTPL 923); San Lucas (MUTPL 704, 1026).

Pristimantis multicolor (1). ECUADOR: LOJA PROVINCE, Parque Nacional Yacuri (MUTPL 1756).

Pristimantis muscosus (4). ECUADOR: ZAMORA CHINCHIPE PROVINCE, La Canela (MUTPL 1553); Reserva Cerro Plateado (MUTPL 619, 637); Reserva Tapichalaca (MUTPL 741).

Pristimantis percultus (3). ECUADOR: LOJA PROVINCE, Parque Nacional Podocarpus—Cajanuma (MUTPL 810–812).

Pristimantis ruidus (1). ECUADOR: AZUAY PROVINCE, Reserva Quitahuaycu (MUTPL 1613).

Pristimantis spinosus (3). ECUADOR: MORONA SANTIAGO PROVINCE, Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño (MUTPL 1638, 1639, 1699).

Pristimantis teslai (3). ECUADOR: TUNGURAHUA PROVINCE, El Triunfo (MUTPL 1425); Patate (MUTPL 1484, 1489).

Pristimantis torresi (5). ECUADOR: EL ORO PROVINCE, Nudillo (MUTPL 1847, 1876); LOJA PROVINCE, Guachanamá, El Apretadero (MUTPL 996–998).

Pristimantis versicolor (23). ECUADOR: LOJA PROVINCE, Abra de Zamora (MUTPL 112, 293, 294, 313, 389, 390, 497); Loja, Huacapamba (MUTPL 806); Parque Nacional Podocarpus—Cajanuma (MUTPL 910); Parque Nacional Podocarpus—El Palto (MUTPL 991); Ramos Urcu (MUTPL 719); Reserva Madrigal del Podocarpus (MUTPL 494); ZAMORA CHINCHIPE PROVINCE, Abra de Zamora (MUTPL 1522); Estación Científica San Francisco (MUTPL 1615, 1842); La Canela (MUTPL 1563, 1566); Reserva Cerro Plateado (MUTPL 653); Reserva Numbala (MUTPL 1175); Reserva Tapichalaca (MUTPL 738–740, 1787).

Pristimantis vertebralis (1). ECUADOR: PICHINCHA PROVINCE, Bosque Protector Tandacato (MUTPL 1682).

Pristimantis yumbo (1). ECUADOR: PICHINCHA PROVINCE, Bosque Protector Tandacato (MUTPL 1683).

APPENDIX 2. VOUCHER NUMBER, GENBANK ACCESSION NUMBERS, AND LOCALITY FOR THE *PRISTIMANTIS* (*HUICUNDOMANTIS*) SPECIMENS USED IN THE PHYLOGENETIC ANALYSIS. BOLD LETTERS MARK THE SEQUENCES GENERATED BY THE PRESENT STUDY.

		GenBank accession no.			
Species	**Voucher number**	**12S**	**16S**	**RAG-1**	**Locality**
Pristimantis andinogigas	MUTPL359	MT764339	MT756022	MT810305	Ecuador: Loja, Parque Nacional Podocarpus, Cajanuma
Pristimantis atillo	QCAZ42488		MK881440	MK881340	Ecuador: Morona Santiago, Parque Nacional Sangay, Lagunas de Atillo
Pristimantis atillo	QCAZ42498		MK881444	MK881344	Ecuador: Morona Santiago, Parque Nacional Sangay
Pristimantis atratus	MUTPL1701	**PX210004**	**PX209072**	**PX222693**	Ecuador: Morona Santiago, 'Suro Rancho', Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño
Pristimantis atratus	MUTPL1703	**PX210005**	**PX209073**	**PX222694**	Ecuador: Morona Santiago, 'Suro Rancho', Área Ecológica de Conservación Municipal Tinajillas Río Gualaceño
Pristimantis balionotus	MUTPL180	MT778069	MT756023	MT810306	Ecuador: Loja, Reserva Madrigal del Podocarpus
Pristimantis balionotus	MUTPL392	MT778071	MT756025	MT810308	Ecuador: Loja, Abra de Zamora
Pristimantis chomskyi	MUTPL524	MZ678943	MZ678934	MZ700220	Ecuador: Loja, Parque Nacional Podocarpus, Cerro Toledo
Pristimantis chomskyi	QCAZ45666		MK881476	MK881369	Ecuador: Zamora Chinchipe, Reserva Tapichalaca
Pristimantis chusquea	MUTPL210	**PX210006**	**PX209074**	**PX222695**	Ecuador: Zamora Chinchipe, Abra de Zamora
Pristimantis chusquea	MUTPL321	**PX210007**	**PX209075**	**PX222696**	Ecuador: Zamora Chinchipe, Abra de Zamora
Pristimantis chusquea	MUTPL323	**PX210008**	**PX209076**	**PX222697**	Ecuador: Zamora Chinchipe, Abra de Zamora
Pristimantis chusquea	MUTPL382	**PX210009**	**PX209077**	**PX222698**	Ecuador: Loja, Huacapamba
Pristimantis cryptomelas	MUTPL135	MT778073	MT756026	MT810311	Ecuador: Loja, Abra de Zamora
Pristimantis cryptomelas	MUTPL168	MT778075	MT756028	MT810313	Ecuador: Loja, Bosque Protector Washapamba
Pristimantis gagliardoi	QCAZ42575		MK881456	MK881355	Ecuador: Morona Santiago, Parque Nacional Sangay, Ranger Station, Tinguichaca river
Pristimantis gagliardoi	QCAZ46738		MK881480	MK881372	Ecuador: Cañar, Reserva Mazar
Pristimantis gloria	KU218035	EF493348	EF493348		Ecuador: Azuay, 8.1 km W Morona Santiago border, Gualaceo-Limón road
Pristimantis gloria	MUTPL223	MT778079	MT756032	MT810317	Ecuador: Loja, 21 km E Urdaneta
Pristimantis gloria	QCAZ16448		MK881402	MK881316	Ecuador: Azuay, Gualaceo-Macas road
Pristimantis hampatusami	QCAZ58042		MK881504	MK881387	Ecuador: El Oro, Reserva Buenaventura
Pristimantis hampatusami	QCAZ58044		KX525478	KX525472	Ecuador: El Oro, Reserva Buenaventura
Pristimantis jimenezi	QCAZ45178		MK881468	MK881362	Ecuador: Azuay, San Antonio, Parque Nacional Cajas border
Pristimantis jimenezi	QCAZ46978		MK881482	MK881374	Ecuador: Azuay, Molleturo, Zadracay river
Pristimantis lojanus	MUTPL178	MZ678945	MZ678936	MZ700222	Ecuador: Loja, Loja, Quebrada San Simon
Pristimantis lojanus	MUTPL191	MZ678946	MZ678937	MZ700223	Ecuador: Loja, Cristal
Pristimantis lutzae	QCAZ32785		MK881421	MK881326	Ecuador: Azuay, Bosque Protector Yanuncay-Irquis, Páramo de Quimsacocha
Pristimantis lutzae	QCAZ53728		MK881495		Ecuador: Azuay, Parque Nacional Cajas, El Capo, Laguna Toreadora
Pristimantis mallii	QCAZ45744	MZ330729	MZ241492		Ecuador: Pastaza, Reserva Comunitaria Ankaku
Pristimantis mallii	QCAZ45770	MZ330730	MZ241496	MZ332932	Ecuador: Pastaza, Reserva Comunitaria Ankaku
Pristimantis miktos	GGU807		KP064151		Peru: Loreto, Nanay, Lote 123
Pristimantis miktos	QCAZ55445		MZ241510	MK391383	Ecuador: Orellana, Parque Nacional Yasuní, Tambococha
Pristimantis multicolor	MUTPL1756		**PX209078**	**PX222699**	Ecuador: Loja, Parque Nacional Yacuri
Pristimantis multicolor	QCAZ47214		MK881489		Ecuador: Loja, Parque Nacional Yacuri, Laguna Negra
Pristimantis muscosus	QCAZ54857		MK881501	MK881386	Ecuador: Zamora Chinchipe, Reserva Tapichalaca
Pristimantis nangaritza	QCAZ41710		MK881436	MK881336	Ecuador: Zamora Chinchipe, Alto Nangaritza PF, Las Orquídeas, Tepuy forest

Species	Voucher number	GenBank accession no. 12S	16S	RAG-1	Locality
Pristimantis oculolineatus	MUTPL1108	**PX210011**	**PX209080**	**PX222701**	Ecuador: Zamora Chinchipe, Parque Nacional Podocarpus, Cerro Toledo
Pristimantis oculolineatus	MUTPL1188	**PX210010**	**PX209079**	**PX222700**	Ecuador: Zamora Chinchipe, Reserva Numbala
Pristimantis oculolineatus	MUTPL1765	**PX210012**	**PX209081**	**PX222702**	Ecuador: Zamora Chinchipe, Parque Nacional Yacuri
Pristimantis oculolineatus	MUTPL1771	**PX210013**	**PX209082**	**PX222703**	Ecuador: Zamora Chinchipe, Parque Nacional Yacuri
Pristimantis oculolineatus	QCAZ45580		MK881471	MK881364	Ecuador: Loja, Cajanuma
Pristimantis oculolineatus	QCAZ45645		MK881473	MK881366	Ecuador: Loja, Parque Nacional Podocarpus, Cajanuma
Pristimantis percultus	MUTPL810	MT778088	MT756034	MT810325	Ecuador: Loja, Parque Nacional Podocarpus, Cajanuma
Pristimantis percultus	MUTPL812	MT778089	MT756035	MT810326	Ecuador: Loja, Parque Nacional Podocarpus, Cajanuma
Pristimantis philipi	KU217863	EF493672	EF493672		Ecuador: Azuay, 4 km W Laguna Toreadora, nearby Parque Nacional Cajas
Pristimantis philipi	QCAZ37537		MK881426	MK881331	Ecuador: Azuay, Parque Nacional Cajas
Pristimantis phoxocephalus	QCAZ58463		MK881507	MK881390	Ecuador: Cotopaxi, Pilaló surroundings
Pristimantis ruidus	DHMECN19106	PP725379	PP723736	PP731015	Ecuador: Azuay, Quitahuaycu reserve
Pristimantis ruidus	MUTPL1613	PP725380	PP723737	PP731016	Ecuador: Azuay, Quitahuaycu reserve
Pristimantis spinosus	KU218052	EF493673	EF493673		Ecuador: Morona Santiago, 10.6 km W Plan de Milagro
Pristimantis tamia	QCAZ59630	MZ330735	MZ241526	MZ332958	Ecuador: Pastaza, Parque Nacional Llanganates, Comunidad Zarentza
Pristimantis tamia	QCAZ59643	MZ330736	MZ241528	MZ332960	Ecuador: Pastaza, Parque Nacional Llanganates, Comunidad Zarentza
Pristimantis teslai	MUTPL1484	**PX210014**	**PX209083**	**PX222704**	Ecuador: Tungurahua, Patate, Sendero Platupamba
Pristimantis teslai	QCAZ46213		MK881478		Ecuador: Tungurahua, Llanganatillo, Parque Nacional Llanganates border
Pristimantis tinguichaca	QCAZ31945		MK881418	MK881323	Ecuador: Morona Santiago, Parque Nacional Sangay, San Vicente
Pristimantis tinguichaca	QCAZ40582		MK881433	MK881334	Ecuador: Morona Santiago, Parque Nacional Sangay, Lagunas de Atillo
Pristimantis torresi	MUTPL996	MZ678947	MZ678938	MZ700224	Ecuador: Loja, Guachanamá, El Apretadero
Pristimantis torresi	QCAZ47397		MK881492	MK881380	Ecuador: Loja, Celica-Alamor road
Pristimantis totoroi	KU218025	EF493349	EF493349		Ecuador: Chimborazo, 70 km W Riobamba via Pallatanga
Pristimantis totoroi	QCAZ58425		MK881505	MK881388	Ecuador: Cotopaxi, Pilaló surroundings
Pristimantis translucidus	MUTPL220	**PX210015**	**PX209084**	**PX222705**	Ecuador: Zamora Chinchipe, Reserva Tapichalaca
Pristimantis translucidus	MUTPL291	**PX210016**	**PX209085**	**PX222706**	Ecuador: Zamora Chinchipe, Reserva Tapichalaca
Pristimantis verrucolatus	QCAZ46982		MK881483	MK881375	Ecuador: Azuay, Yumate, Shoupshe
Pristimantis verrucolatus	QCAZ46993		MK881485	MK881377	Ecuador: Azuay, Cochapamba
Pristimantis versicolor	KU218096	EF493389	EF493389	EF493431	Ecuador: Loja, Abra de Zamora
Pristimantis versicolor	MUTPL494	MT778095	MT756038	MT810332	Ecuador: Loja, Reserva Madrigal del Podocarpus
Pristimantis sp.	QCAZ26642		MK881409		Ecuador: Azuay, San Antonio de Chaucha
Pristimantis sp.	QCAZ32790		MK881423	MK881328	Ecuador: Azuay, Bosque Protector Yanuncay-Irquis, Páramo de Quimsacocha
Pristimantis sp.	QCAZ45029		MK881461		Ecuador: Morona Santiago, Parque Nacional Sangay, Etén, Rio Culebrillas
Pristimantis sp.	QCAZ45129		MK881462	MK881358	Ecuador: El Oro, Chillacocha
Pristimantis sp.	QCAZ45720		MZ241490	MZ332927	Ecuador: Pastaza, Reserva Comunitaria Ankaku
Pristimantis sp.	QCAZ45945		MZ241502	MZ332938	Ecuador: Pastaza, Reserva Comunitaria Ankaku
Pristimantis sp.	QCAZ53999		MK881496		Ecuador: Zamora Chinchipe, Yacuambi, Romerillos
Pristimantis sp.	QCAZ58855		MZ241514	MZ332949	Ecuador: Morona Santiago, Parque Nacional Sangay, Sardinayacu

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