diversity

MDPI

Article

Four New Species of Direct-Developing Frogs, Genus *Oreobates* (Anura: Strabomantidae), from Peru †

Pablo J. Venegas [1,2,*], James W. Ttito [2,3,4], Luis A. García-Ayachi [1,2], Michael Gulman [2], Juan D. Valencia [2] and Alessandro Catenazzi [2,5]

[1] Rainforest Partnership, 4005 Guadalupe St., Austin, TX 78751, USA; luisalberto@rainforestpartnership.org
[2] Instituto Peruano de Herpetología (IPH), Augusto Salazar Bondy 136, Urb. Higuereta, Surco, Lima 15038, Peru; titonina18@gmail.com (J.W.T.); michaelgulman@gmail.com (M.G.); cca.god7991@gmail.com (J.D.V.); acatenazzi@gmail.com (A.C.)
[3] Centro de Investigación VERTEBRATE, Universidad Nacional San Antonio Abad del Cusco, Av. de La Cultura 733, Cusco 08003, Peru
[4] Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco, Plaza de Armas S/N, Cusco 08000, Peru
[5] Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
* Correspondence: pablo@rainforestpartnership.org
† urn:lsid:zoobank.org:pub:7E1A5548-0B13-4B32-B31C-986CDF53B6B5.

Abstract

The Peruvian Andes harbor one of the most geographically complex and biologically diverse regions of the Tropical Andes, yet several microbasins and mountain ridges remain poorly surveyed for amphibians. Here, we describe four new species of the terrestrial-breeding frog genus *Oreobates* from the departments of Amazonas, San Martín and Huánuco, Peru, based on morphology, coloration, and molecular phylogenetic analyses. The new species inhabit humid montane and premontane forests of the upper basin of the Huallaga River. The new taxa differ from congeners by combinations of body size, skin texture, digital morphology, coloration, and iris pattern. Phylogenetic analyses recovered the new species within distinct lineages of *Oreobates*, supporting their recognition as independent evolutionary entities. Our results further highlight the role of Andean topography, especially dry inter-Andean valleys associated with the Marañón, Apurímac, and Mantaro systems, as important barriers shaping diversification in Andean amphibians. These discoveries emphasize the underestimated diversity of *Oreobates* in the Peruvian Yungas and reinforce the importance of continued taxonomic exploration of the Andean ecosystems.

Keywords: Andes; biogeographic barrier; diversification; Huallaga River; inter-Andean valley; Marañón River; phylogenetic relationships; Terrarana; Yungas ecorregion

Check for updates

Academic Editor: Michel Baguette

Received: 18 May 2026
Revised: 16 July 2026
Accepted: 24 July 2026
Published: 30 July 2026

Copyright: © 2026 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license.

1. Introduction

The Tropical Andes biodiversity hotspot, extending along the Andean mountain range from Venezuela to Bolivia, is widely recognized as the most biodiverse region on Earth [1]. Within this region, the transition between the Andes and the Amazon Basin along the eastern Andean versant, also called the Yungas ecoregion [2] harbors exceptionally high amphibian species richness and endemism [3,4]. The pronounced environmental heterogeneity across these elevational gradients promotes diversification in Neotropical amphibians by fostering speciation, coexistence, and the persistence of distinct evolutionary lineages [5,6].

Terrarana is a clade of New World terrestrial-breeding frogs characterized by direct development, in which embryos develop into miniature versions of adults, bypassing a free-living larval stage, a reproductive mode that is thought to facilitate their diversification in terrestrial and montane environments [7–9]. This group comprises more than 30% of Neotropical anuran diversity (1297 species) and approximately 17% of described amphibian species worldwide [10]. Although Terrarana reach their highest species richness in the Tropical Andes, largely driven by the diversification of the genus *Pristimantis*, their generic diversity is broadly distributed across the Neotropics [10]. Thirteen genera of Terrarana occur in the Tropical Andes (i.e., *Bryophryne*, *Microkayla*, *Noblella*, *Phyllonastes*, *Qosqophryne*, *Urkuphryne*, *Niceforonia*, *Lynchius*, *Oreobates*, *Phrynopus*, *Pristimantis*, *Strabomantis*, and *Yunganastes*), of which only seven are endemic to the region (i.e., *Bryophryne*, *Microkayla*, *Qosqophryne*, *Urkuphryne*, *Lynchius*, *Phrynopus*, and *Yunganastes*) [10–17].

One of these Terrarana taxa, the genus *Oreobates* (Jiménez de la Espada, 1872), currently comprises 27 recognized species, occurring from the lower Andean slopes to the upper Amazon Basin, ranging from Colombia southward to northern Argentina and eastward to western Brazil [10]. More than half of the known species (19) occur in the Yungas between 800 and 3000 m elevation, primarily in humid to semi-humid montane forests along the eastern Andean versant, except for seven species restricted to lowland habitats below 700 m [15,18–21], and the single species *Oreobates ayacucho* restricted tohigh-Andean grassland (puna) above 3400 m [12,15]. This distributional pattern suggests that geographic isolation, together with divergent selective pressures across elevational gradients, has shaped the evolutionary and demographic history of *Oreobates*, with limited transitions between lowland and montane habitats. In this context, adaptation to higher elevations may promote disjunct distributions, reduced effective population sizes, and restricted gene flow, thereby facilitating speciation [4].

Given the apparent high rates of diversification of *Oreobates* in the Yungas, and considering that many areas remain poorly explored due to their inaccessibility, it is likely that additional species persist in undersurveyed regions. This is further supported by the limited representation of many described species in scientific collections, which constrains a comprehensive understanding of the genus' diversity, distribution, and morphological variation [15,18,19].

Here, we contribute to the understanding of *Oreobates* diversity by describing four new species based on morphological and phylogenetic evidence. These species are identified from specimens collected during herpetological expeditions conducted since 2018 in previously unexplored areas along the Amazonian slope of the northern Central Andes of Peru, specifically in the departments of Amazonas, San Martín, and Huánuco.

2. Materials and Methods

2.1. Field Techniques and Permits

This study was carried out in accordance with the guidelines for use of live amphibians and reptiles in field research [22]. Specimens collected for this study are covered by the following research permits (given by the Ministerio de Agricultura) that include permanent scientific collection of live specimens: RD-067-2019-MINAGRI-SERFOR-DGGSPFFS, RD-179-2022-DGGSPFFS-DGSPFS, and RD-D000149-2024-MIDAGRI-SERFOR-DGGSPFFS-DGSPFS.

The four new species of *Oreobates* described herein were collected during rapid herpetological inventories carried out in the departments of San Martín and Huánuco, northeastern Peru, from 2018 to 2025. We collected frogs by hand using the complete species inventory technique [23], during slow night walks (19:00 to 03:00 h) along streams and within the forest using headlamps. Collected specimens were anesthetized and euthanized with an

overdose of 20% benzocaine gel applied to their ventral surfaces [24]. Tissue samples were taken before fixation, removing a portion of liver through a ventral cut on the right anterior side of the venter or by clipping the entire left foot, and stored in 96% ethanol. We then fixed specimens with formalin for 24 h and subsequently stored them in 70% ethanol. Voucher specimens are deposited in the herpetological collection of CORBIDI in Lima, Peru. Coordinates and elevation were taken with a GPSmap 62st, Garmin Ltd., Olathe, AR, USA (set to WGS84 datum).

2.2. Morphology

The format for the descriptions follows Padial et al. [15] for *Oreobates*. The terminology and definition of diagnostic characters follow Duellman and Lehr [12]. Sex was determined by the presence of vocal slits and by direct gonadal inspection. Measurements were taken with digital calipers and rounded to the nearest 0.1 mm. We measured SVL (snout–vent length), TL (tibia length), FL (foot length, distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), HL (head length, obliquely from angle of jaw to tip of snout), HW (head width, at level of angle of jaw), ED (eye diameter, distance between the anterior and posterior borders of the visible eye), IOD (interorbital distance, distance between the medial edge of the orbits), EW (upper eyelid width, length of the visible eye along the outer edge of eyelid), IND (internarial distance, distance between the inner edges of nares), EN (eye–nostril distance, distance between the anterior corner of orbit and the posterior margin of nares). Fingers and toes are numbered preaxially to postaxially from I to IV and I to V, respectively. Comparative lengths of Toes III and V were determined when both were adpressed against Toe IV; lengths of Fingers I and II were compared when adpressed against each other. We obtained morphological data for the comparison of *Oreobates amarakaeri*, *O. gemcare*, and *O. machiguenga* from Padial et al. [15], *O. lundbergi* from Lehr [25], and *O. pereger* from Duellman and Lehr [12]. Specimens examined are listed in Appendix A.

2.3. DNA Extraction, Amplification, and Sequencing

To assess relationships with the most closely related species, we performed phylogenetic analyses using concatenated fragments of the mitochondrial genes 12S and 16S rRNA, the protein-coding mitochondrial gene cytochrome c oxidase subunit I (COI), the nuclear protein-coding gene recombination-activating protein 1 (RAG1), and the tyrosinase precursor (Tyr). We extracted DNA from muscle tissue of specimens CORBIDI 20361, 20362, 23749, 28465, 28467, 28690, 28694, 28925, and 28936 from the type series of the four species described in this study, and of a paratype of *O. colanensis*. We used a commercial extraction kit (IBI Scientific, Peosta, IA, USA). We followed standard protocols for primers, DNA amplification, and sequencing [7,16,26,27]. Polymerase chain reaction (PCR) amplifications were performed on a ProFlex thermal cycler (Applied Biosystems, Thermo Fisher Scientific, Waltham, MA, USA) using previously tested protocols [27,28]. PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) and sent to MCLAB (San Francisco, CA, USA) for sequencing. Newly generated sequences were deposited in GenBank (Appendix B).

2.4. Phylogenetic Analyses

Our analysis comprised newly generated sequences from 9 specimens. We downloaded sequences of 42 additional specimens from closely related species (from BLASTN implemented in Geneious R11, version 11.1.5, Biomatters Ltd., Auckland, New Zealand, with searches performed through the NCBI BLAST service) or morphologically similar, congeneric species and the species *Lynchius tabaconas*, *Niceforonia elassodiscus*, and *Leptodactylus bolivianus* (used as outgroup taxa) from GenBank. We used Geneious R11, version

11.1.5 (Biomatters, http://www.geneious.com/) to assemble pair-end reads, to generate a consensus sequence, and to align our novel and GenBank sequences within Geneious using MAFFT v7.017 and default parameters [29]. We trimmed the aligned sequences to a length of 1015 bp for 12S, 596 bp for 16S, 687 bp for COI, 682 bp for RAG, and 552 bp for Tyr. Our analysis included 51 terminals.

For phylogenetic inference using maximum likelihood, we used the partitioning scheme and evolutionary models previously used in phylogenetic analyses of Holoadeninae [16,27]. The first partition subset included both the 12S and 16S sequences with the substitution model GTR + I + G. The remaining five subsets were partitioned by codon position as follows (substitution model in parentheses): one subset including the first codon position of COI (SYM + I + G), one subset including the second codon position of COI (F81 + I), one subset including the third codon position of COI (GTR + G), one subset including the first and second codon positions of RAG1 and the first and second codon positions of Tyr (GTR + I + G), and one subset including the third codon position of both RAG1 and Tyr (K80 + G).

We used Maximum Likelihood (ML) to infer the phylogenetic relationships of the study species. A concatenated alignment of 3538 bp, including the five loci, was used for the ML analysis. We used IQ-TREE v1.6.12 [30] on the concatenated dataset, and estimated branch support using the ultrafast bootstrap (UFBoot) described in Minh et al. [31] (10,000 bootstrap replicates). The log-likelihood of the consensus tree was −20,685.88. Finally, we used iTol v.5 to visualize and edit the tree [32].

We additionally calculated genetic distances for the mitochondrial 16S rRNA fragment to further support species delimitation. Although no universally accepted cutoff exists for defining species boundaries based on 16S rRNA divergence. Fouquet et al. [33] proposed that distances of 3% or greater are indicative of distinct species. Fouquet et al. [33] further supported this criterion, noting that most allopatric species distributed in the Guianas and other regions of South America exhibit genetic distances ranging from 3% to 6%. This pattern is also consistent with results from well-sampled mitochondrial datasets, in which Fouquet et al. [33] found that most taxa showing divergences below 3% warranted synonymization. One advantage of using the 16S rRNA gene is that it represents the most widely sequenced genetic marker for *Oreobates* and more generally frog taxonomy [33–35]. We calculated uncorrected p-distances, defined as the proportion of nucleotide sites differing between pairs of sequences, using MEGA version 12 [36], and made the resulting data available on Figshare (Table S1).

2.5. Taxonomy

Our taxonomic conclusions are based on an integrative frame composed of the observation of morphological features and color patterns, as well as the inferred phylogenetic relationships [37]. We considered the combination of these data as species delimitation criteria following a general lineage or unified species concept [38,39].

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new name contained in the electronic version is effectively published under that Code from the electronic edition alone. This published work and its nomenclatural acts have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is urn:lsid:zoobank.org:pub: 7E1A5548-0B13-4B32-B31C-986CDF53B6B5 (available online: https://zoobank.org/References/7e1a5548-0b13-4b32-b31c-986cdf53b6b5, accessed on 20 July 2026).

3. Results

3.1. Phylogenetic Relationships

The phylogenetic tree inferred in this study (Figure 1), the most complete to date for *Oreobates*, recovered the genus *Oreobates* as monophyletic with strong support (UFBoot = 100) and as the sister to *Lynchius tabaconas* with high support (UFBoot = 99). Within *Oreobates*, a well-supported basal split (UFBoot = 100) separates *O. lundbergi* from the remaining species, which are arranged into three principal clades. Two species, *O. lehri* and *O. sanctaecrucis*, appear to be non-monophyletic, each represented by two distinct terminals. In the case of *O. lehri*, neither sequence originates from the type locality, raising the possibility that both may be misidentified and instead correspond to undescribed species. The Genbank sequences of two other specimens identified as *O. lehri* (JF809952 and FJ539069) are of *O. gemcare*. Overall, our topology is congruent with previously published phylogenies of *Oreobates* [15,18,19,21,40], which were primarily based on single mitochondrial markers (e.g., 16S) or reduced multilocus datasets.

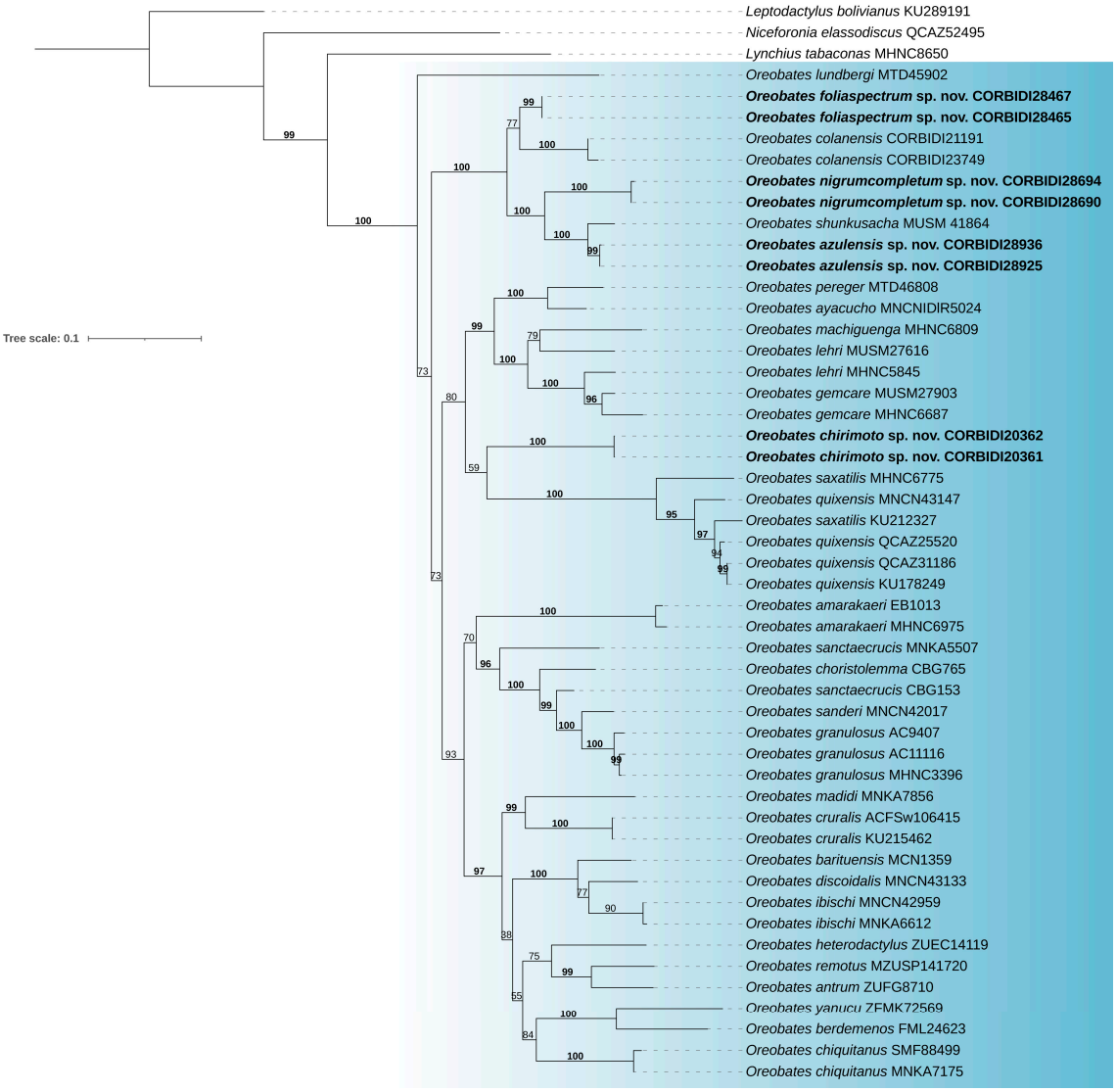


Figure 1. Phylogenetic relationships within *Oreobates* inferred with Maximum Likelihood; see Materials and methods for details. Nodal supports displayed are the non-parametric bootstrap support.

Three of the new species described here were recovered within one of these clades with strong support (UFBoot = 100). This clade comprises five species and includes the following relationships: (*O. foliaspectrum* sp. nov. + *O. colanensis*) (UFBoot = 77), sister to a subclade formed by *O. nigrumcompletum* sp. nov. and (*O. shunkusacha* + *O. azulensis* sp. nov.) (UFBoot = 100 for both nodes). All newly described species are recovered within this clade with high support.

Oreobates chirimoto sp. nov. is recovered as sister to the clade containing *O. quixensis* and *O. saxatilis*, although with low support (UFBoot = 59). This latter pair is supported as sister species (UFBoot = 80) and together form the sister group of a well-supported subclade comprising species primarily distributed in the southern Peruvian Yungas (i.e., *O. ayacucho*, *O. lehri*, *O. machiguenga*, *O. gemcare*, and *O. pereger*).

3.2. Species Account

3.2.1. *Oreobates azulensis* sp. nov.

urn:lsid:zoobank.org:act: 3162003A-EDB7-4960-BBBE-51D6DCA8627F (available online: https://zoobank.org/NomenclaturalActs/3162003a-edb7-4960-bbbe-51d6dca8627f, accessed on 20 July 2026).

Figures 2 and 3.

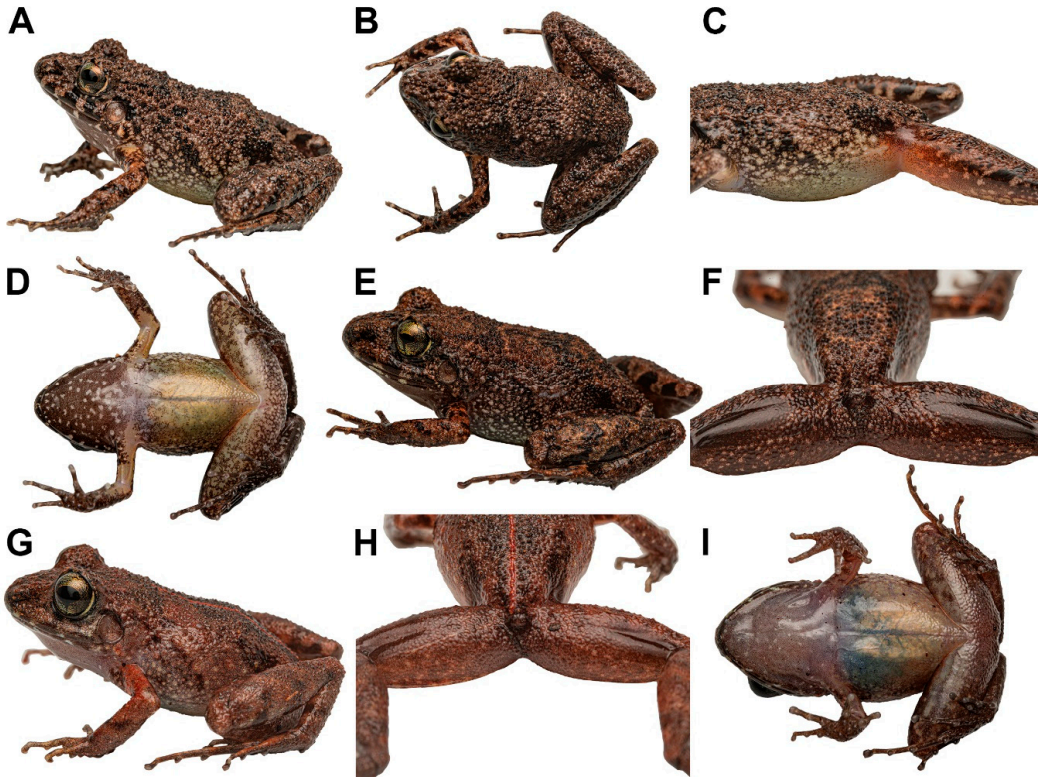


Figure 2. *Oreobates azulensis* sp. nov. in life: (**A**) dorsolateral, (**B**) dorsal, (**C**) groin and anterior surface of thighs, and (**D**) ventral surface of holotype (CORBIDI 28935), SVL 20 mm; (**E**) dorsolateral view and (**F**) posterior surface of thighs of adult male (CORBIDI 28930), SVL 22 mm; (**G**) dorsolateral view, (**H**) posterior surface of thighs, and (**I**) ventral view of (CORBIDI 28927), SVL 22 mm. Photographs by James W. Titto.

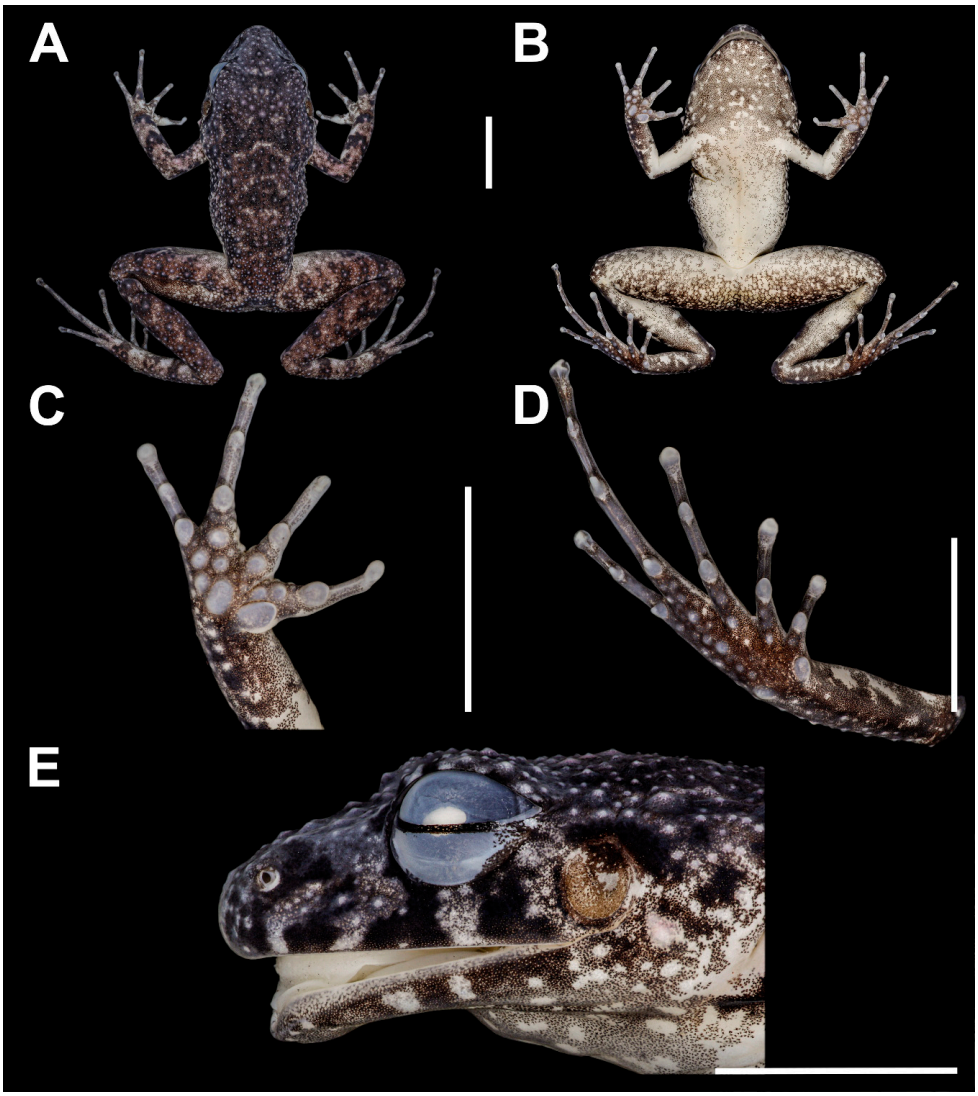


Figure 3. Preserved holotype of *Oreobates azulensis* sp. nov. (CORBIDI 28935) in dorsal view (**A**), ventral view (**B**), palm (**C**), sole (**D**), and head in lateral view (**E**). Scale bar 5 mm. Photographs by Luis A. García-Ayachi.

Holotype. CORBIDI 28935, an adult male, from Valle Azpusana—Alto Consuelo, Pucuyacu district, Leoncio Prado province, Huánuco department, Peru (8.5701° S, 76.0743° W, 1750 m), collected on 21 July 2025 by James W. Ttito and Michael Gulman.

Paratypes. CORBIDI 28934, 28936, two adult female, collected with the holotype; CORBIDI 28925, subadult female and CORBIDI 28926, adult male (8.5823° S, 76.0838° W, 1461 m); CORBIDI 28927 adult male (8.5761° S, 76.0777° W, 1654 m); CORBIDI 28928, juvenile male (8.5762° S, 76.0777° W, 1641 m); CORBIDI 28929, adult male (8.5749° S, 76.0769° W, 1695 m); CORBIDI 28930, adult male (8.5735° S, 76.0765° W, 1735 m); CORBIDI 28931, adult male (8.5725° S, 76.0757° W, 1741 m); CORBIDI 28932, adult male (8.5723° S, 76.0757° W, 1754 m); CORBIDI 28933, adult male (8.5712° S, 76.0757° W, 1763 m). All specimens from Valle Azpusana—Alto Consuelo, Pucuyacu district, Leoncio Prado province, Huánuco department, Peru, collected in July 2025 by James W. Ttito and Michael Gulman.

Diagnosis. *Oreobates azulensis* (Figure 2) is easily distinguished from the rest of congeners by the following combination of characters: (1) fingertips and toe tips rounded, not expanded; (2) vocal slits absent; (3) nuptial pad present; (4) belly and ventral surface of thighs tan-cream with faint brown reticulations; and (5) dorsum covered by keratinized pointed granules gently heterogenous in size.

Oreobates azulensis lacks vocal slits like six other species from the Peruvian Andes (i.e., *O. chirimoto* sp. nov., *O. colanensis*, *O. foliaspectrum* sp. nov., *O. lundbergi*, *O. nigrumcompletum* sp. nov., and *O. shunkusacha*). *Oreobates azulensis* differs from these species (characters between parentheses) (see Table 1) by having the belly and ventral surface of thighs tan-cream with faint brown reticulations (yellow in *O. chirimoto;* belly dark brown with white flecks and thighs red in *O. colanensis*; orange or brownish orange with brown reticulations or blotches in *O. foliaspectrum*; gray or flesh colored in *O. lundbergi*; and deep brown or black in *O. nigrumcompletum*). In addition, *O. azulensis* differs from *O. colanensis* by lacking a dorsolateral fold (present), and from *O. chirimoto*, *O. lundbergi* and *O. shunkusacha* by having the dorsum covered with pointed granules heterogeneous in size (covered by round granules with scattered enlarged flat warts in *O. chirimoto*, smooth with scattered tubercles in *O. lundbergi*, and covered by round or subconical granules homogeneous in size in *O. shunkusacha*).

Table 1. Qualitative morphological traits and SVL of *Oreobates azulensis* sp. nov., *O. chirimoto* sp. nov., *O. foliaspectrum* sp. nov., *O. nigrumcompletum* sp. nov., and similar species from Peru. Coloration corresponds to live individuals.

Character	*O. azulensis* sp. nov.	*O. chirimoto* sp. nov.	*O. colanensis*	*O. foliaspectrum* sp. nov.
Vocal slits	Absent	Absent	Absent	Absent
Dorsolateral fold	Absent	Absent	Present	Absent
Canthus rostralis in dorsal view	Sinuous	Sinuous	Concave	Sinuous
Dorsal texture	Keratinized pointed granules, gently heterogeneous in size	Round granules with scattered enlarged round and conical warts	Finely granular with pointed warts	Pointed granules, homogeneous in size
Ventral patter	Throat brown with white spots, belly cream, thighs cream with brown reticulations	Throat brown with cream spots, belly and thighs yellow or yellowish cream	Throat reddish brown, belly brown with white spots and flecks, thighs reddish brown	Throat brown with cream or tan spots, belly and thighs orange with brown reticulations or brown with orange blotches or cream spots
Axillary glands	Absent	Absent	Absent	Absent
Basal webbing Toe III–IV	Absent	Absent	Absent	Absent
Finger III–IV tips	Round, not expanded	Round, not expanded	Round, barely expanded	Round, not expanded
Axilla/groin/posteior surface of thigh	Brown	Orange or brownish orange	Dark brown with yellowish cream or white blotches	Brownish orange or brown with cream flecks
Iris color	Coppery with fine brown reticulations	Gold with thin brown reticulations	Iris gold with a brown stripe in the middle	Bicolored, upper half of iris red and lower half greenish bronze bearing brown reticulations

Table 1. *Cont.*

Character	*O. azulensis* sp. nov.	*O. chirimoto* sp. nov.	*O. colanensis*	*O. foliaspectrum* sp. nov.
SVL (in mm)	♂ 19–22; ♀ 31–34	♂ 25; ♀ 29–30	♂ 21–22; ♀ unknown	♂ 23–26; ♀ 30–32
Character	***O. lundbergi***	***O. nigrumcompletum* sp. nov.**	***O. shunkusacha***	***O. amarakaeri***
Vocal slits	Absent	Absent	Absent	Present
Dorsolateral fold	Absent	Absent	Absent	Absent
Canthus rostralis in dorsal view	Concave	Sinuous	Sinuous	Straight
Dorsal texture	Smooth with few scattered tubercles	Keratinized granules, mostly pointed, gently heterogeneous in size	Round to subconical granules, homogeneous in size	Round or slightly pointed warts, heterogeneous in size
Ventral patter	Gray or flesh-colored and thighs tan	Dark brown to black without marks	Cream to pinkish cream with dark or faint brown mottling	Gray with orange blotches and/or cream and white dots
Axillary glands	Absent	Absent	Absent	Absent
Basal webbing Toe III–IV	Absent	Absent	Absent	Absent
Finger III–IV tips	Nearly truncate, not expanded	Round, not expanded	Round, barely expanded	Round, slightly expanded
Axilla/groin/posteior surface of thigh	Tan	Dark brown	Dark brown or tan	Orange
Iris color	Bronze with black reticulations	Dark brown densely spotted with gold flecks bearing a thin gold circumpupillary ring	Greenish-golden with black reticulations	Golden strongly marbled with black
SVL (in mm)	♂ 37; ♀ 39–48	♂ 22–26; ♀ 28–34	♂ 24–26; ♀ 37–41	♂ 20–30
Character	***O. cruralis***	***O. gemcare***	***O. granulosus***	***O. machiguenga***
Vocal slits	Present	Present	Present	Present
Dorsolateral fold	Absent	Absent	Absent	Absent
Canthus rostralis in dorsal view	Sinuous	Straight	Convex or sinuous	Convex
Dorsal texture	Low round granules with enlarged round warts	Shagreen with enlarged granules and low warts, heterogeneous in size	Granular with keratinized round granules and slightly enlarged warts	Round to conical granules, homogeneous in size
Ventral patter	Throat and chest gray with cream spots, belly cream or grayish cream, thighs brownish gray with cream spots	Cream with brown mottling or reticulations	Throat and chest purple or brown with yellow or white spots, belly yellow	Throat white with orange blotches, belly white, thighs orange
Axillary glands	Present	Present	Present	Absent

Table 1. *Cont.*

Character	*O. azulensis* sp. nov.	*O. chirimoto* sp. nov.	*O. colanensis*	*O. foliaspectrum* sp. nov.
Basal webbing Toe III–IV	Absent	Absent	Absent	Present
Finger III–IV tips	Truncate, expanded	Truncate or round, narrow	Round, slightly expanded	Round, slightly expanded
Axilla/groin/posteior surface of thigh	Brown	Orange	Orange	Orange
Iris color	Pale bronze with fine black reticulations	Golden with a bronze horizontal medial streak	Bronze with black reticulations	Bronze with black reticulations
SVL (in mm)	♂ 20–30; ♀ 24–33	♂ 31–34; ♀ 39	♂ 22–28; ♀ 34–39	♀ 32
Character	***O. quixensis***		***O. saxatilis***	
Vocal slits	Present		Present	
Dorsolateral fold	Absent		Absent	
Canthus rostralis in dorsal view	Sinuous		Sinuous	
Dorsal texture	Small granules intermixed with prominent round or pointed warts, heterogeneous in size		Small round granules with scattered enlarged round warts	
Ventral pattern	Grayish white with brown reticulations, thighs tan		White or whitish cream with or without faint brown reticulations, thighs orange	
Axillary glands	Absent		Absent	
Basal webbing Toe III–IV	Absent		Absent	
Finger III–IV tips	Round, slightly expanded		Round, slightly expanded	
Axilla/groin/posteior surface of thigh	Brown, some specimens with a pinkish hue on groin		Orange	
Iris color	Bronze or silver with black reticulations		Bronze or silver with an orange hue	
SVL (in mm)	♂ 35–48; ♀ 47–63		♂ 44–50; ♀ 50–63	

Oreobates azulensis shares a brown, granular dorsal surface with *O. amarakaeri*, *O. cruralis*, *O. gemcare*, *O. granulosus*, *O. machiguenga*, *O. quixensis*, and *O. saxatilis*, but can be distinguished from these species by the following characteristics (Table 1): basal membrane between Toe III and IV absent (present in *O. machiguenga*); tips of Finger III and IV round and not expanded (slightly expanded and truncate in *O. cruralis*); dorsum covered by pointed granules heterogenous in size (round granules and flat slightly enlarged warts in *O. amarakaeri*; round and conical granules homogenous in size in *O. machiguenga*; shagreen with enlarged round granules and low warts in *O. gemcare*; round granules and small or enlarged flat warts in *O. granulosus*; low round granules and scattered enlarged flat warts in *O. cruralis*; round or pointed small granules intermixed with prominent round or pointed warts in *O. quixensis*; round granules with scattered prominent flat or subconical warts in *O. saxatilis*); axillary glands absent (present in *O. cruralis*, *O. gemcare*, and *O. granulosus*); axilla, groin and posterior surface of thighs brown (orange in *O. amarakaeri*, *O. gemcare*, *O. machiguenga* and *O. saxatilis*); belly and ventral surface of thighs tan or brownish cream with faint brown reticulations (grayish white with brown reticulations and ventral surface of thighs tan in *O. quixensis*; and white or whitish cream with or without faint brown

reticulations and ventral surface of thigh orange or creamy orange in *O. saxatilis*); and iris coppery with fine brown reticulations (light bronze dorsally and silver ventrally with black reticulations in *O. quixensis*, and bronze or silver bearing black reticulations and an orange hue dorsally in *O. saxatilis*).

In addition, *O. azulensis* is noticeably smaller than *O. quixensis* and *O. saxatilis* (SVL 19–22 mm in males and 31–34 mm in females of *O. azulensis* versus 35–48 mm in males and 47–63 mm in females of *O. quixensis*, and 44–50 mm in males and 50–63 mm in females of *O. saxatilis*).

Characterization. A small species of *Oreobates* (SVL 19–22 mm in eight adult males and 23–34 mm in four adult females) characterized as follows: (1) skin of dorsum and limbs granular, covered by keratinized pointed granules gently heterogeneous in size; ventrolateral region areolate; occipital fold absent or present as a \ /-shaped fold; dorsolateral fold absent; skin on throat, chest, belly, anteroventral surface of thighs, and groin smooth; posterior and ventral surfaces of thighs areolate; discoidal fold absent or ill-defined; postrictal glands present, distinct, conical; (2) tympanic membrane and annulus distinct, large, about 47–57% of eye length; supratympanic fold present, ill-defined; (3) head wider than long; snout short, rounded in dorsal and lateral views; canthus rostralis weak, straight or barely sinuous in dorsal view, slightly curved in profile; (4) cranial crests absent; upper eyelid covered with pointed granules; (5) dentigerous processes of vomers large, prominent, triangular, moderately separated, situated posteromedial to choanae (posterior margin at level of choanae), bearing 6–7 vomerine teeth; (6) males lacking vocal slits and vocal sacs; nuptial pads present; (7) hands with long and slender fingers; Finger I barely longer than or equal in length to Finger II; subarticular tubercles conical, larger on inner fingers than on outer fingers; supernumerary tubercles conspicuous, rounded, smaller than subarticular tubercles; fingertips rounded, bearing ill-defined circumferential grooves; ungual flaps absent; lateral fringes and keels on fingers absent; (8) ulnar region bearing pointed granules; (9) heel bearing pointed granules; tubercles on tarsus absent; (10) inner metatarsal tubercle ovoid, prominent, 2–3 times the size of the conical and inclined outer metatarsal tubercle; subarticular tubercles prominent, conical; supernumerary tubercles conspicuous, much smaller than subarticular tubercles, rounded; (11) toes long and slender (foot length 52–58% SVL); lateral fringes and webbing absent; Toe V reaching proximal margin or middle of second subarticular tubercle of Toe IV; Toe III reaching middle or distal margin of second subarticular tubercle of Toe IV; toe tips rounded, not expanded, lacking ungual flaps and circumferential grooves; (12) axillary glands absent; (13) in life, dorsal surface bronze or brown with irregular dark brown marks; labial bars dark brown with light brown or cream interspaces; supratympanic fold dark brown; tympanic membrane darker than surrounding skin; two diagonal stripes on flanks present; axillae, groin, anterior and posterior surfaces of thighs, and hidden surfaces of shanks brown; throat and chest brown with white or cream spots; belly and ventral surfaces of thighs tan or brownish cream, with or without faint brown reticulations; iris coppery with fine brown reticulations and sclera brownish cream.

Description of holotype. Adult male (CORBIDI 28935) with a moderately robust body and in a good state of preservation, with a portion of liver removed through a ventral cut on the right anterior side of the venter and preserved as a tissue sample for molecular analyses (Figure 3). Skin of dorsum, flanks, and limbs covered by keratinized pointed granules gently heterogeneous in size; occipital fold absent; ventrolateral region areolate; dorsolateral fold absent; skin on throat, chest, belly, and anteroventral surfaces of thighs smooth; discoidal fold barely visible; posterior and posteroventral surfaces of thighs areolate; groin smooth. Head wider than long (Head Length = 38% SVL; Head Width = 40% SVL). Snout rounded in dorsal and lateral views; canthus rostralis weak, straight in dorsal

view and slightly curved in profile; lips rounded, not flared. Nostrils not protuberant, slightly directed dorsolaterally. Loreal region concave. Eye of moderate size, its diameter 12% SVL. Tympanic membrane evident, lighter in coloration than surrounding skin; tympanum conspicuous, oval, diameter 6% SVL. Supratympanic fold thin, obscuring upper and posterior margins of tympanum. Postrictal glands present, protuberant, conical, one enlarged on each side. Dentigerous processes of vomers prominent, triangular, moderately separated from each other; each process bearing 6–7 scattered teeth. Vocal slits and vocal sac absent. Choanae large, half-moon shaped, not concealed by palatal shelf of maxillary arch. Tongue large, cordiform, with anterior two-thirds attached to floor of mouth. Forearms slender, bearing indistinct low ulnar tubercles. Fingers slender; fingertips rounded, bearing ill-defined circumferential grooves. Nuptial pad present on Finger I as a distinct unpigmented patch. Relative lengths of fingers II < I < IV < III. Fingers lacking dermal fringes; webbing absent. Subarticular tubercles small, conical. Supernumerary tubercles present, prominent, rounded, heterogeneous in size. Palmar tubercle prominent, deeply bifid. Inner metacarpal tubercle prominent, elliptical. Hind limbs slightly robust; tibia length 57% SVL; foot length 57% SVL. Heel bearing pointed granules; outer edge of tarsus bearing conical granules. Inner metatarsal tubercle prominent, ovoid, twice size of conical outer metatarsal tubercle; plantar surface bearing numerous distinct small supernumerary tubercles heterogeneous in size; subarticular tubercles well defined, conical, small. Toes lacking lateral fringes; toe tips rounded, lacking circumferential grooves and ungual flaps. Relative lengths of toes I < II < III < V < IV; Toe V barely reaching proximal margin of second subarticular tubercle of Toe IV; Toe III reaching middle of second subarticular tubercle of Toe IV; toe webbing absent.

Measurements (in mm) of the holotype. SVL 20.5; tibia length 11.7; foot length 11.7; head length 7.8; head width 8.2; eye diameter 2.5; tympanic diameter 1.3; IOD 2.3; upper eyelid width 1.9; internarial distance 2.1; eye-nostril distance 2.4.

Coloration in life (Figure 2A–D). Dorsal surface light brown including the sides of head; dorsum with dark brown marks and two irregular dark brown diagonal stripes on flanks, and scattered whitish flecks on ventrolateral region, limbs bearing dark brown bars; lips bearing distinct dark brown bars with whitish interspaces; groins and axillae brownish orange, posterior surface of thighs brown, and hidden surface of shank cream bearing brown bars. Ventral surface, throat and chest brown bearing whitish spots; belly, thighs, and arms tan with faint brown reticulations; palms and soles brown. Irises coppery with brown reticulations and pupil with a ventral black notch. Sclera brownish cream.

Coloration in 70% ethanol (Figure 3). Dorsal surface dusty brown, darker than in life, with lighter marks. Axillae and groins cream-tan, posterior surface of thighs dusty brown with cream flecks, hidden surface of shanks cream with brown bars. Throat brown with cream spots; the rest of ventral surfaces cream or cream-tan with a light brown mottling.

Variation. Eight adult males are smaller (SVL 19–22 mm) than the four adult females (SVL 23–34 mm). Sexually dimorphic characters such as nuptial pads are present in male specimens. See Table 2 for measurements and proportions of the type specimens. Coloration and pattern are identical in all specimens (Figure 2).

Distribution and natural history. *Oreobates azulensis* is known only from two localities in the Huallaga River basin, at elevations between 1450 and 1770 m, Huánuco department, central Peru (Figure 4). The distribution of this species lies within the buffer zone of Cordillera Azul National Park and in the Ucayali moist forests ecoregion according to Olson et al. [2]. The specimens were collected in the leaf litter at night, between 19:00 and 03:00 h, on steep slopes and narrow summits covered by primary premontane forest. Other sympatric anuran species collected were *Pristimantis* aff. *lirellus*, *Pristimantis* sp. (*P. lacrimosus* group), *Strabomantis* sp., *Pristimantis* sp., and *Rhinella lilyrodriguezae*.

Table 2. Variation in morphological measurements (in mm) of the type series of *Oreobates azulensis* sp. nov., *O. chirimoto* sp. nov., *O. foliaspectrum* sp. nov., and *O. nigrumcompletum* sp. nov. Mean ± SD is given in parentheses following the range if applicable. See text for abbreviations.

	***O. azulensis* sp. nov.**		***O. chirimoto* sp. nov.**		***O. foliaspectrum* sp. nov.**		***O. nigrumcompletum* sp. nov.**	
	♂ (*n* = 8)	♀ (*n* = 2)	♂ (*n* = 1)	♀ (*n* = 2)	♂ (*n* = 3)	♀ (*n* = 4)	♂ (*n* = 6)	♀ (*n* = 3)
SVL	19.9–22.9 (21.3 ± 1.1)	31.7–34.6	25.2	29.2–30.9	23.7–26.4 (24.7 ± 1.4)	30.2–33.0 (32.1 ± 1.3)	22.4–26.1 (24.2 ± 1.3)	28.5–34.9 (32.3 ± 3.4)
TL	11.4–12.2 (11.8 ± 0.3)	18.5–19.2	15.3	18.5–18.7	17.3–18.3 (17.9 ± 0.5)	21.8–23.6 (22.6 ± 0.7)	11.8–13.5 (12.4 ± 0.6)	15.3–16.8 (16.0 ± 0.8)
FL	11.1–12.4 (11.8 ± 0.4)	18.4–18.6	13.1	15.6–15.7	13.9–14.2 (14.0 ± 0.2)	17.4–18.1 (17.8 ± 0.3)	11.9–13.5 (12.7 ± 0.6)	16.3–16.9 (16.5 ± 0.3)
HL	7.3–8.7 (8.1 ± 0.5)	11.9–12.6	8.5	9.8–9.9	9.4–10.0 (9.7 ± 0.3)	10.8–12.2 (11.7 ± 0.6)	9.2–9.7 (9.5 ± 0.2)	11.6–12.9 (12.4 ± 0.7)
HW	7.9–9.4 (8.6 ± 0.6)	12.8–13.8	10.3	12.1–12.3	9.3–9.8 (9.4 ± 0.3)	11.4–12.9 (12.2 ± 0.7)	9.4–10.5 (9.9 ± 0.4)	12.0–14.0 (13.3 ± 1.2)
ED	2.5–3.2 (2.9 ± 0.3)	3.8–4.3	3.1	3.2–3.4	2.9–3.7 (3.3 ± 0.4)	3.7–4.1 (3.9 ± 0.2)	3.4–3.9 (3.6 ± 0.2)	3.9–4.7 (4.4 ± 0.4)
IOD	1.9–2.4 (2.3 ± 0.2)	3.8–3.8	2.7	2.8–3.0	2.1–2.6 (2.4 ± 0.3)	3.0–3.4 (3.3 ± 0.2)	2.2–2.9 (2.5 ± 0.2)	2.7–3.5 (3.0 ± 0.4)
EW	1.9–2.1 (2.0 ± 0.1)	2.7–2.8	2.1	2.4–2.4	2.1–2.3 (2.1 ± 0.1)	2.6–2.9 (2.8 ± 0.2)	2.3–2.6 (2.4 ± 0.1)	2.7–3.1 (3.0 ± 0.2)
IND	2.1–2.5 (2.3 ± 0.1)	3.2–3.3	2.6	2.9–3.0	2.4–2.9 (2.7 ± 0.2)	3.0–3.6 (3.3 ± 0.2)	2.2–2.6 (2.3 ± 0.1)	2.7–2.9 (2.8 ± 0.1)
E-N	2.4–2.8 (2.6 ± 0.2)	3.8–4.1	3	3.6–3.8	3.2–3.5 (3.3 ± 0.1)	3.7–4.7 (4.2 ± 0.5)	2.7–3.1 (3.0 ± 0.2)	3.5–4.2 (3.9 ± 0.4)
TY	1.3–1.8 (1.5 ± 0.2)	2.0–2.2	1.9	1.6–1.7	1.0–1.2 (1.1 ± 0.1)	1.4–1.7 (1.5 ± 0.1)	1.5–1.9 (1.7 ± 0.2)	1.7–1.9 (1.8 ± 0.1)
TL/SVL	0.52–0.58 (0.55 ± 0.02)	0.55–0.58	0.6	0.61–0.63	0.69–0.75 (0.72 ± 0.03)	0.69–0.72 (0.70 ± 0.02)	0.50–0.53 (0.51 ± 0.01)	0.44–0.55 (0.50 ± 0.06)
FL/SVL	0.53–0.58 (0.55 ± 0.02)	0.54–0.58	0.52	0.51–0.53	0.54–0.59 (0.57 ± 0.03)	0.54–0.58 (0.55 ± 0.02)	0.52–0.55 (0.53 ± 0.01)	0.47–0.57 (0.51 ± 0.05)
HL/SVL	0.37–0.39 (0.38 ± 0.01)	0.36–0.38	0.34	0.32–0.34	0.37–0.41 (0.39 ± 0.02)	0.36–0.37 (0.36 ± 0.01)	0.37–0.41 (0.39 ± 0.01)	0.37–0.41 (0.39 ± 0.02)
HW/SVL	0.40–0.42 (0.41 ± 0.01)	0.40–0.40	0.41	0.39–0.42	0.37–0.39 (0.38 ± 0.01)	0.37–0.39 (0.38 ± 0.01)	0.40–0.43 (0.41 ± 0.01)	0.40–0.42 (0.41 ± 0.01)
HW/HL	1.02–1.08 (1.06 ± 0.02)	1.07–1.10	1.21	1.23–1.25	0.93–1.00 (0.97 ± 0.04)	1.01–1.06 (1.04 ± 0.02)	1.02–1.08 (1.04 ± 0.03)	1.04–1.10 (1.07 ± 0.03)
E-N/ED	0.77–0.95 (0.89 ± 0.06)	0.97–0.99	0.96	1.12–1.14	0.91–1.09 (1.02 ± 0.10)	0.98–1.23 (1.07 ± 0.11)	0.76–0.89 (0.82 ± 0.05)	0.87–0.91 (0.89 ± 0.02)
EW/IOD	0.83–1.07 (0.89 ± 0.09)	0.70–0.73	0.76	0.80–0.87	0.81–0.98 (0.91 ± 0.09)	0.80–0.88 (0.85 ± 0.04)	0.81–1.03 (0.94 ± 0.08)	0.88–1.13 (1.01 ± 0.13)
TY/ED	0.47–0.63 (0.54 ± 0.05)	0.47–0.57	0.61	0.49–0.50	0.33–0.36 (0.35 ± 0.02)	0.36–0.43 (0.39 ± 0.03)	0.42–0.54 (0.48 ± 0.04)	0.38–0.42 (0.40 ± 0.02)

Etymology. The specific epithet refers to the Cordillera Azul mountain range, where this species was discovered.

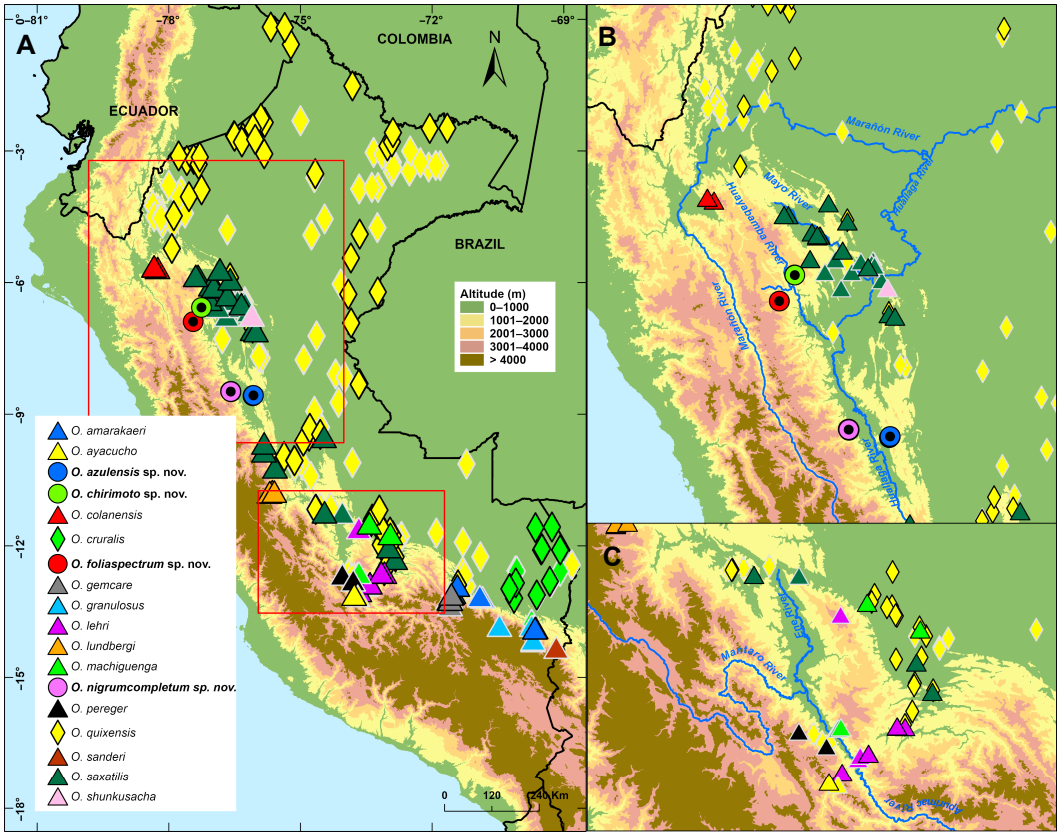


Figure 4. Map showing the distribution of the genus *Oreobates* in Peru, including the new species described herein: (**A**) Peru; (**B**) the Marañón and Huallaga basins; and (**C**) the Mantaro, Apurímac, and Ene basins. Symbols with black outlines represent examined specimens; symbols with gray outlines represent literature records; and symbols with a black dot correspond to the type localities of new species. Red outlines in (**A**) corresponding to the area of (**B**) and (**C**).

3.2.2. *Oreobates chirimoto* sp. nov.

urn:lsid:zoobank.org:act: 437BEDBD-5CE8-4FF4-A916-BC833C6DB0D3 (available online: https://zoobank.org/NomenclaturalActs/437bedbd-5ce8-4ff4-a916-bc833c6db0d3, accessed on 20 July 2026).

Figures 5 and 6.

Holotype. CORBIDI 20362, an adult female from Nuevo Chirimoto, Huicungo district, Mariscal Caceres Province, San Martin department, Peru (6.5687° S, 77.2564° W; 1942 m), collected by L. A. Garcia Ayachi and J. Gamboa on 13 December 2018.

Paratypes. An adult male and female, CORBIDI 20361 and 20386, respectively, collected with the holotype.

Diagnosis. *Oreobates chirimoto* (Figure 5) is easily distinguished from the rest of congeners by the following combination of characters: (1) fingertips and toe tips narrowly rounded; (2) vocal slits and nuptial pads absent; (3) belly and ventral surface of thighs yellow; and (4) dorsum covered by round granules with scattered enlarged round and conical warts.

Oreobates chirimoto shares with six species from the Peruvian Andes (i.e., *O. azulensis* sp. nov., *O. colanensis*, *O. foliaspectrum* sp. nov., *O. lundbergi*, *O. nigrumcompletum* sp. nov., and *O. shunkusacha*) the lack of vocal slits. *Oreobates chirimoto* is easily distinguished from these species (characters between parentheses) (Table 1) by having the belly and ventral surface of thighs yellow (tan-cream with brown reticulations *O. azulensis*; belly dark brown with white flecks and thighs red in *O. colanensis*; orange or brownish orange with brown reticulations or blotches in *O. foliaspectrum*; gray or flesh colored in *O. lund-*

bergi; deep brown or black in *O. nigrumcompletum*; and cream with dark brown mottling in *O. shunkusacha*). In addition, *O. chirimoto* differs from *O. azulensis*, *O. lundbergi*, *O. nigrumcompletum*, and *O. shunkusacha* by lacking nuptial pads (present), from *O. colanensis* by lacking dorsolateral fold (present), and from *O. azulensis*, *O. lundbergi*, *O. nigrumcompletum*, and *O. shunkusacha* by having the dorsum covered with rounded granules and scattered enlarged round and conical warts (pointed granules gently heterogenous in size in *O. azulensis* and *O. nigrumcompletum*, smooth with scattered tubercles on *O. lundbergi*, and round or subconical granules homogenous in size without enlarged warts in *O. shunkusacha*).

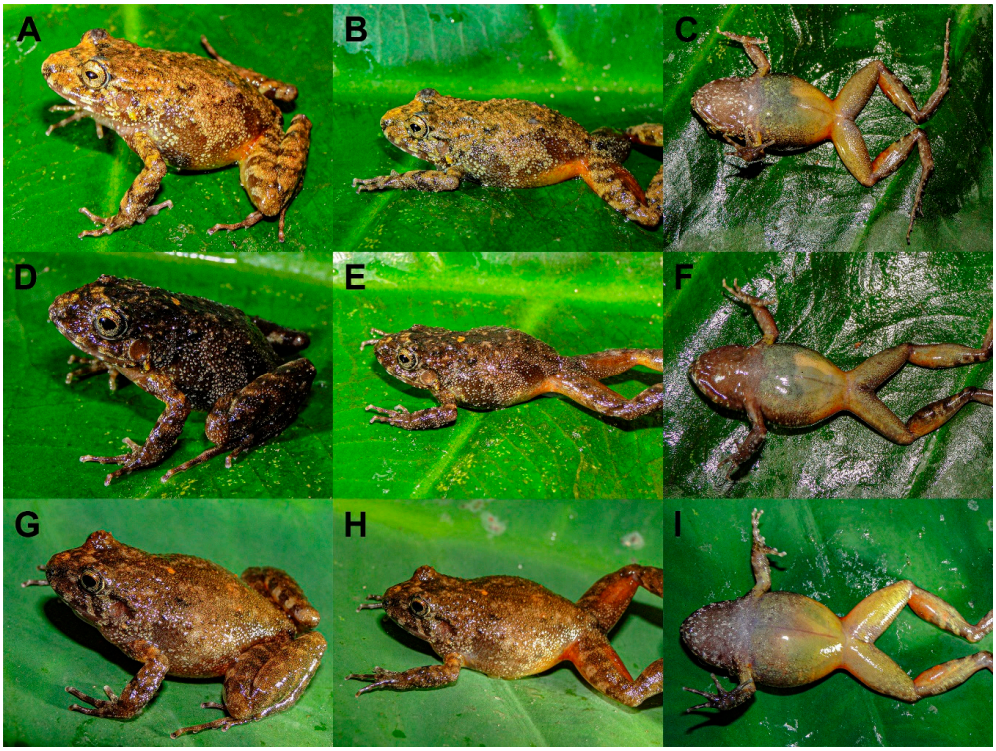


Figure 5. *Oreobates chirimoto* sp. nov. in life: (**A**) dorsolateral, (**B**) groin and posterior surface of thighs coloration, and (**C**) ventral views of holotype (CORBIDI 20362), SVL 29.2 mm; (**D**) dorsolateral, (**E**) groin and posterior surface of thighs, and (**F**) ventral views of adult male CORBIDI 20361, SVL 25 mm; (**G**) dorsolateral, (**H**) groin and posterior surface of thighs, and (**I**) ventral views of adult female CORBIDI 20386, SVL 30 mm. Photographs by Luis A. García-Ayachi.

Due to the brown dorsal coloration and the dorsal surface covered by granules, *O. chirimoto* can be confused superficially with *O. amarakaeri*, *O. cruralis*, *O. gemcare*, *O. granulosus*, *O. machiguenga*, *O. quixensis*, and *O. saxatilis*. Nevertheless, *O. chirimoto* differs from the aforementioned species (character of the former species in parenthesis) by the following features (see Table 1): canthus rostralis sinuous in dorsal view (straight in *O. amarakaeri* and *O. gemcare*, and convex in *O. machiguenga*); basal membrane between Toe III and IV absent (present in *O. machiguenga*); tips of Finger III and IV narrowly rounded (slightly expanded and truncate in *O. cruralis*); dorsum covered by round granules with scattered enlarged flat warts (round and conical granules without enlarged warts in *O. machiguenga*; round granules in *O. granulosus*; round or subconical small granules intermixed with prominent round and subconical warts in *O. quixensis*; round small granules with scattered prominent flat or subconical warts in *O. saxatilis*); axillary glands absent (present in *O. cruralis*, *O. gemcare*, and *O. granulosus*); belly and ventral surface of thighs yellow with or without faint brown reticulations (dark or light gray with orange blotches and/or cream and white dots, and ventral surface of thighs orange in *O. amarakaeri*; belly white or cream with brown reticulations in *O. cruralis*; cream with brown reticulations and

ventral surface of thighs orange in *O. gemcare*; yellow with white spot in some individuals and ventral surface of thighs orange or tan in *O. granulosus*; white and ventral surface of thighs orange in *O. machiguenga*; grayish white with brown reticulations and ventral surface of thighs tan in *O. quixensis*; white or whitish cream with or without faint brown reticulations and ventral surface of thigh orange or creamy orange in *O. saxatilis*); and iris golden with fine brown reticulations (light bronze dorsally and silver ventrally with black reticulations in *O. quixensis*, and bronze or silver bearing black reticulations and an orange hue dorsally in *O. saxatilis*).

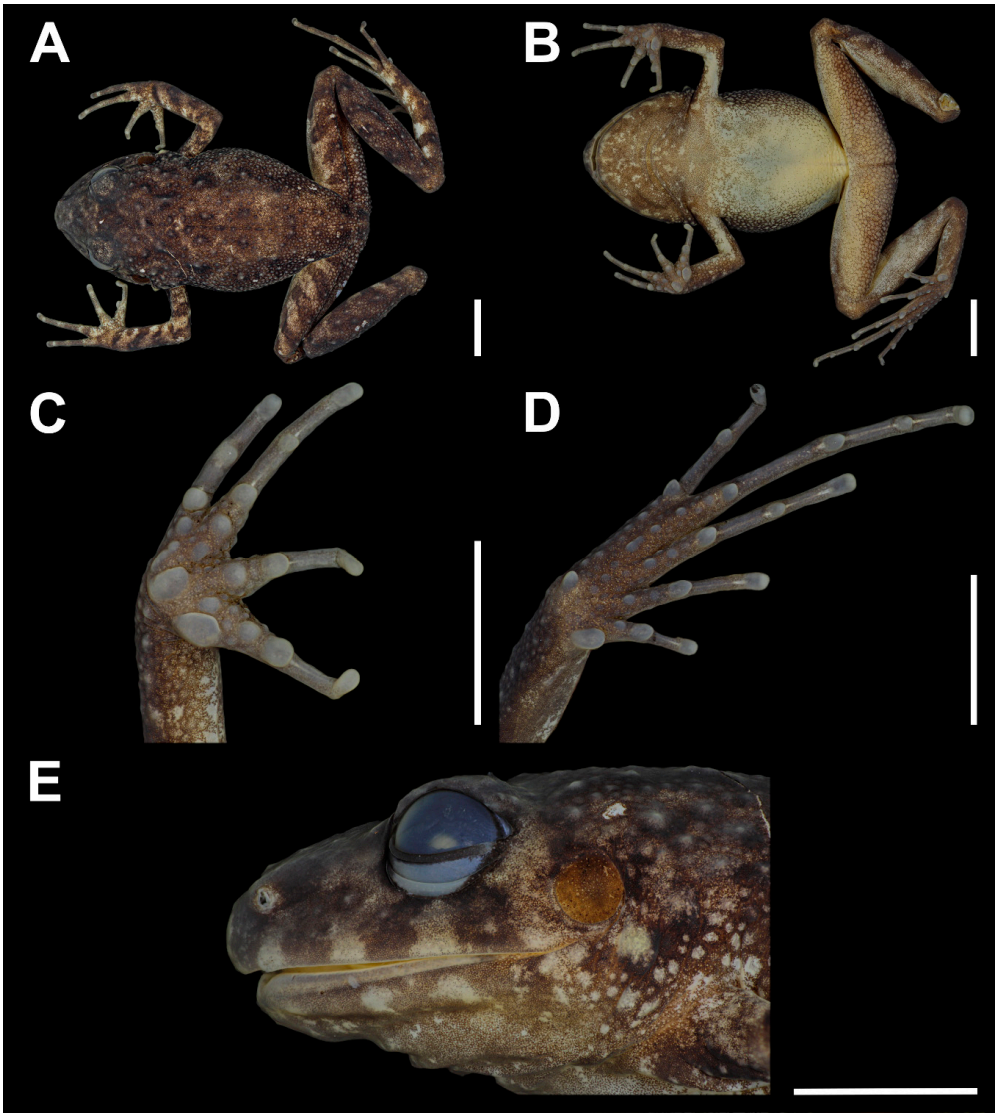


Figure 6. Preserved holotype of *Oreobates chirimoto* sp. nov. (CORBIDI 20362) in dorsal view (**A**), ventral view (**B**), palm (**C**), sole (**D**), and head in lateral view (**E**). Scale bar 5 mm. Photographs by Luis A. García-Ayachi.

Oreobates pereger possesses the belly and ventral surface of thighs yellow; however, *O. chirimoto* is easily distinguished by having the dorsum covered with granules and scattered enlarged warts (smooth), Finger I barely larger than Finger II (Finger I shorter than Finger II), and snout rounded in dorsal view (subacuminate).

Characterization. A small species of *Oreobates* (SVL of an adult males 25 mm and 29–30 mm in two adult females) characterized as follows: (1) skin of dorsum and limbs granular, round granules splattered with enlarged round and conical warts, flanks areolate; occipital fold absent; dorsolateral fold absent; skin on throat, chest and belly smooth;

posterior and ventral surfaces of thighs areolate and groin smooth; discoidal fold absent; postrictal gland present, protuberant, conical; (2) tympanic membrane and annulus distinct, large, about 49–61% of length of eye; supratympanic fold present, thin; (3) head wider than long; snout short, round in dorsal view and in lateral view; canthus rostralis weak, sinuous in dorsal view, slightly curved in profile; (4) cranial crests absent; upper eyelid covered with conspicuous round granules; (5) dentigerous process of the vomers large, prominent, ovoid in shape, narrowly separated, situated posteromedial to choanae (posterior margin at level of choanae), bearing 3 and 6 vomerine teeth; (6) male specimen lacking vocal slits and vocal sacs, nuptial pads absent; (7) hands with long and slender fingers, first finger barely longer than second; subarticular tubercles conical, large on inner fingers and small on outer fingers; supernumerary tubercles conspicuous, round and conical, some smaller and others larger than subarticular tubercles; fingertips round, narrow, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) ulnar region bearing small, round tubercles; (9) heel bearing granules, tubercles on tarsus absent; (10) inner metatarsal tubercle ovoid, prominent, 3 to 4 times the size of conical and inclined outer metatarsal tubercle; subarticular tubercles, prominent, conical, supernumerary tubercles conspicuous, much smaller than subarticular tubercles, some round and other conical; (11) toes long and slender (foot length 51–53% SVL), lateral fringes and webbing absent; toe V reaching the proximal margin of the second subarticular tubercle of toe IV; toe III reaching the middle or distal margin of the second subarticular tubercle of toe IV; tips of toes narrow, rounded, ungual flap and circumferential groove absent; (12) axillary glands absent; (13) in life, dorsal surface light brown with faint darker marks or dark brown with lighter marks, dark brown labial bars and dark bars on limbs present, flanks splattered with cream or dirty cream flecks; axillae, groins, anterior and posterior surfaces of thighs orange; throat and chest brown with cream spots; belly and ventral surface of thighs yellow, and ventral surface of shanks yellow with faint orange blotches; palms and soles brown; iris gold with thin brown reticulations and pupil with a ventral black notch; sclera grayish cream.

Description of holotype. Adult female (CORBIDI 20362) with a robust body and in a good state of preservation, with the left foot removed and preserved as a tissue sample for molecular analyses (Figure 6). Skin of dorsum and limbs covered by small round granules, splattered with enlarged flat warts; flanks areolate; dorsolateral fold absent; skin on throat and chest smooth and belly weakly areolate; discoidal fold absent; posterior and ventral surfaces of thighs and groin areolate. Head wider than long (Head Length = 34% of SVL; Head Width = 41% of SVL). Snout rounded in dorsal and lateral views; canthus rostralis weak, slightly sinuous from above and curved in profile; lips rounded, not flared. Nostrils not protuberant, directed laterally. Loreal region concave. Eye of moderate size, its diameter 11% of SVL. Tympanic membrane evident, lighter in color than surrounding skin; tympanum conspicuous, oval, diameter 6% of SVL. Supratympanic fold ill-defined, obscuring upper and posterior margins of tympanum. Postrictal gland present, protuberant, conical. Dentigerous processes of vomers prominent, ovoid, narrowly separated from each other; each process bears 6 teeth along its proximal edge. Choanae large, oval, not concealed by palatal shelf of maxillary arch. Tongue large, cordiform, with its anterior three-quarters attached to the floor of the mouth. Forearms slender, bearing two to three ulnar low tubercles. Fingers slender; fingertips narrow with rounded tips and lacking circumferential groove. Relative lengths of fingers I > II < IV > III. Fingers lacking dermal fringes; webbing absent. Subarticular tubercles small and conical. Supernumerary tubercles present, distinct, some round and others conical, heterogeneous in size. Palmar tubercle prominent, deeply bifid. Inner metacarpal tubercle prominent and elliptical. Hind limbs robust; tibia length 63% SVL; foot length 53% SVL. Heel bearing small granules; tarsal tubercles indistinct.

Inner metatarsal tubercle prominent, ovoid, three to four times the size of the conical outer metatarsal tubercle; plantar surface with a lot of distinct small supernumerary tubercles heterogeneous in size; subarticular tubercles well defined, conical, and small. Toes lacking lateral fringes; toe tips narrowly rounded, lacking circumferential grooves. Relative length of toes I < II < III > V < IV; toe V reaching the proximal margin of the second subarticular tubercle of toe IV; toe III reaching the distal margin of the second subarticular tubercle of toe IV; toe webbing absent.

Measurements (in mm) of the holotype. SVL 29.2; tibia length 18.5; foot length 15.6; head length 9.9; head width 12.3; eye diameter 3.4; tympanic diameter 1.7; IOD 3.0; upper eyelid width 2.4; internarial distance 2.9; eye-nostril distance 3.8.

Coloration in life (Figure 5A–C). Dorsum light brown with darker marks including dark brown labial bars with whitish cream interspaces, suprainguinal dark blotch, dark blotches on flanks, and bars on limbs, scattered cream flecks on flanks; axilla, groins, anterior and posterior surface of thighs orange; ventral surface, throat and chest brown with cream spots, belly and ventral surface of thighs yellow, shanks yellow with faint orange blotches, tarsus brown with cream spots, palms and soles brown. Iris golden with thin brown reticulations and pupil with a ventral black notch. Sclera cream.

Coloration in 70% ethanol (Figure 6). Dorsum dark brown with faint lighter marks, flanks and posterior third of dorsum covered by dusty cream granules; throat and chest brown with dirty cream spots, belly cream, ventral surface of thighs cream with a faint brown fine reticulation, shanks cream with faint brown transversal bars; forearms, tarsus, palms and soles brown.

Variation. The only known single adult male is smaller (SVL 25 mm) than the two adult females (SVL 29–30 mm). No dimorphic sexual character such as vocal slits and nuptial pads is present in the single male specimen. See Table 2 for measurements and proportions of the type specimens. Coloration and pattern are identical in all specimens (Figure 5).

Distribution and natural history. *Oreobates chirimoto* is known only from the type locality, Nuevo Chirimoto, in the upper basin of the Huayabamba River, at an elevation of 1940 m, San Martín department, northeastern Peru (Figure 4). The distribution of this species lies in the Peruvian Yungas ecoregion according to Olson et al. [2]. The three specimens were collected in the leaf litter, between 20:00 and 23:00 h, on a steep slope covered by montane forest dissected by black water streams, which originate in a summit covered by a dense scrubland that grows on white sand soils covered by lichens and epiphytes. Other sympatric anuran species collected were *Gastrotheca testudinea*, *Hemiphractus* sp., *Pristimantis lirellus*, and *Rhinella moralesi.*

Etymology. The specific epithet refers to the type locality, the surroundings of Nuevo Chirimoto town, where this species was discovered.

3.2.3. *Oreobates foliaspectrum* sp. nov.

urn:lsid:zoobank.org:act: 7C40660C-02E9-4D99-932F-BF7681D8F49E (available online: https://zoobank.org/NomenclaturalActs/7c40660c-02e9-4d99-932f-bf7681d8f49e, accessed on 20 July 2026).

Figures 7 and 8.

Holotype. CORBIDI 28468 and adult female, from Canaan, Huicungo district, Mariscal Cáceres province, San Martín department, Peru (6.8926° S, 77.4476° W, 2118 m); collected in July 2022 by Juan D. Valencia Málaga.

Paratypes. CORBIDI 28463, adult male (6.8931° S, 77.4465° W, 2084 m); CORBIDI 28465, adult male (6.8922° S, 77.4478° W, 2097 m); CORBIDI 28466, adult male (6.8924° S, 77.4478° W, 2100 m); CORBIDI 28467, adult female (6.8925° S, 77.4478° W, 2070 m); COR-

BIDI 28469, adult female (6.8924° S, 77.4479° W, 2087 m; CORBIDI 28470, adult female (6.8925° S, 77.4477° W, 2099 m). All specimens from Canaan, Huicungo district, Mariscal Cáceres province, San Martín department, Peru, collected on 14 July 2022 by Juan D. Valencia Málaga.

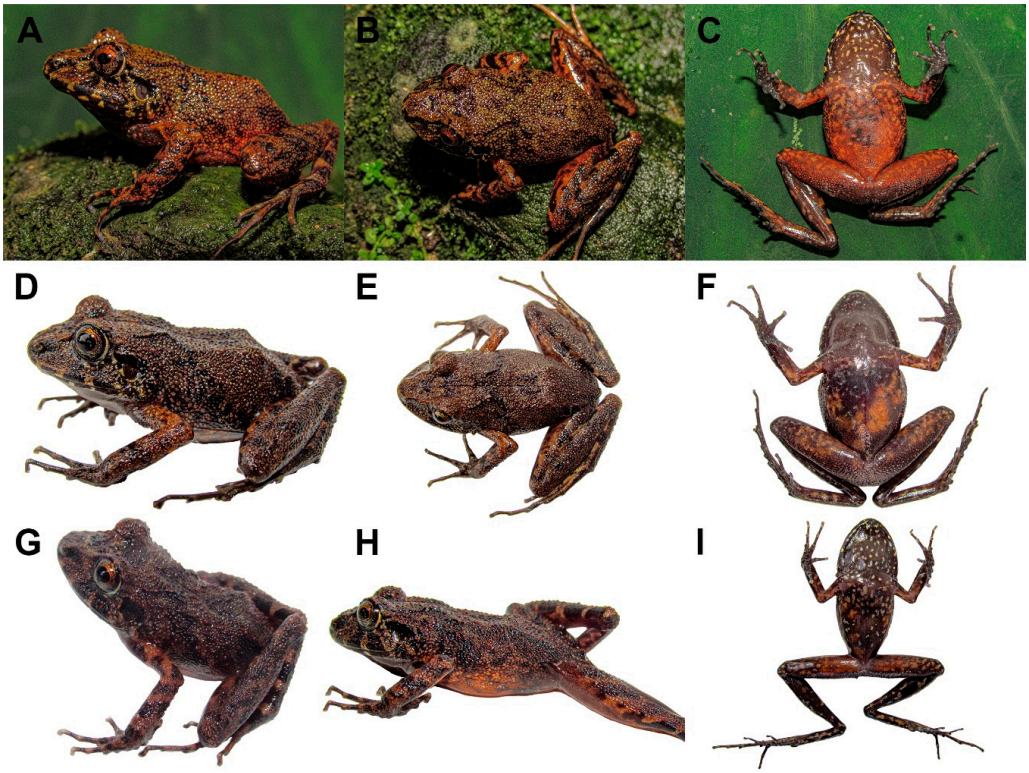


Figure 7. *Oreobates foliaspectrum* sp. nov. in life: (**A**) dorsolateral, (**B**) dorsal, and (**C**) ventral views of holotype (CORBIDI 28468), SVL 32 mm; (**D**) dorsolateral, (**E**) dorsal, and (**F**) ventral views of adult female CORBIDI 28470, SVL 30 mm; (**G**) dorsolateral and (**H**) lateral views of adult male CORBIDI 28465, SVL 26 mm; and (**I**) ventral view of adult male CORBIDI 28463, SVL 24 mm; Photographs by Juan D. Valencia.

Diagnosis. *Oreobates foliaspectrum* (Figure 7) is easily distinguished from the rest of congeners by the following combination of characters: (1) fingertips and toe tip narrowly rounded; (2) vocal slits and nuptial pads absent; (3) bicolored iris, upper half red and lower half greenish bronze with brown reticulations; (4) nearly truncate in dorsal view and nearly truncate in lateral view; (5) belly and ventral surface of thighs orange or brownish orange with brown reticulations or blotches; (6) dorsum covered by pointed granules homogenous in size; and (7) belly weakly areolate.

Oreobates foliaspectrum lacks vocal slits, like six other species from the Peruvian Andes, i.e., *O. azulensis* sp. nov., *O. chirimoto* sp. nov., *O. colanensis*, *O. lundbergi*, *O. nigrumcompletum*, and *O. shunkusacha*. *Oreobates foliaspectrum* is superficially similar to the recently described *O. shunkusacha*, which is the closest species geographically (see Table 1). Both species have the dorsal surface covered with pointed tubercles homogeneous in size, similar dorsal and ventral patterns, and a yellow sclera. However, *O. foliaspectrum* differs from *O. shunkusacha* (characters between parentheses) by having the snout gently truncate in dorsal view and lateral view (rounded), the iris red in its upper half and greenish bronze with brown reticulations in its lower half (greenish-gold with black reticulations and a dark brown circumpupillary line), the belly and ventral surface of thighs orange or brownish orange with brown reticulations or blotches (cream with dark or faint brown reticulations), and lacking nuptial pads (present).

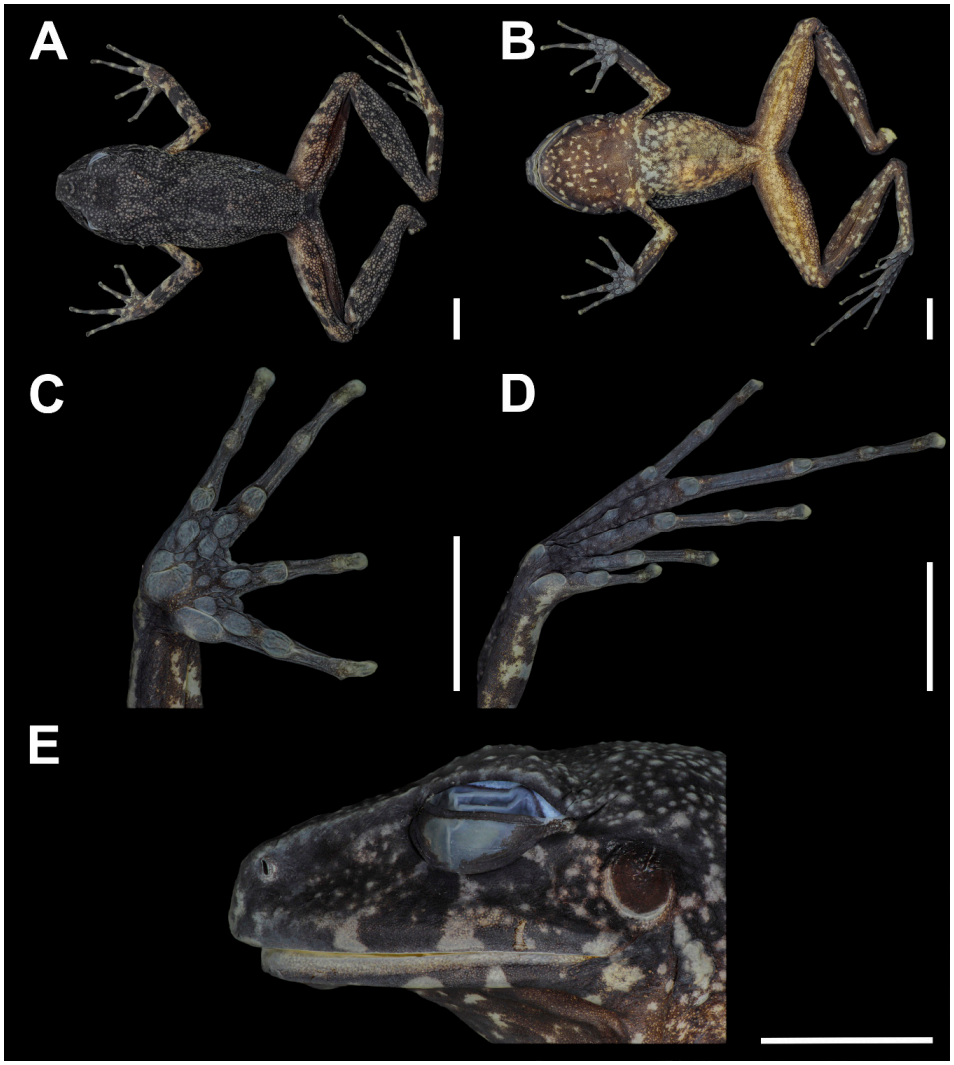


Figure 8. Preserved holotype of *Oreobates foliaspectrum* sp. nov. (CORBIDI 28468) in dorsal view (**A**), ventral view (**B**), palm (**C**), sole (**D**), and head in lateral view (**E**). Scale bar 5 mm. Photographs by Luis A. García-Ayachi.

From the other species, *O. foliaspectrum* can be easily distinguished by the following characters (see Table 1): from *O. colanensis* by lacking dorsolateral folds (present) and by lacking flash marks on hidden surfaces of body (white or cream blotches on dark brown axilla, groins, anterior and posterior surfaces of thighs, and shanks); from *O. chirimoto* by having the dorsum covered by pointed granules homogenous in size (round and heterogenous in size); from *O. lundbergi* by having the dorsum covered by pointed granules homogenous in size (smooth with scattered tubercles), by lacking nuptial pads (present), and venter weakly areolate (smooth); from *O. nigrumcompletum* by having the dorsum covered by pointed granules homogenous in size (pointed granules and gently heterogenous in size) and the venter orange with brown reticulations or blotches (deep brown or nearly black without marks); from *O. azulensis* by having the dorsum covered by pointed granules homogenous in size (pointed and heterogenous in size) and the venter orange with brown reticulations or blotches (tan-cream with brown reticulations).

Other species of *Oreobates* with orange or rosy-orange coloration in groins or hidden surfaces of hindlimbs are *O. amarakaeri*, *O. gemcare*, *O. machiguenga*, and *O. saxatilis*. However, *O. foliaspectrum* is easily distinguished from these species by the following characters (Table 1): belly orange or brownish orange bearing brown reticulations or blotches (venter dark or light gray with orange blotches or/and cream or white dots in *O. amarakaeri*, cream

with brown mottling or reticulation in *O. gemcare*, white in *O. machiguenga*, and grayish white in *O. saxatilis*); lacking axillary glands (present in *O. gemcare*); venter weakly areolate (smooth in former species); and dorsum covered by pointed granules homogenous in size (round granules and enlarged warts in *O. amarakaeri*, round granules in *O. gemcare*, round granules with scattered prominent flat or subconical warts in *O. saxatilis*).

Characterization. A medium-sized species of *Oreobates* (SVL 23–26 mm in adult males and 30–33 mm in adult females) characterized as follows: (1) skin of dorsum, flanks, and limbs granular, granules pointed and homogeneous in size; ventrolateral region areolate; occipital fold present as a \ /-shaped fold; dorsolateral fold absent; skin on throat and chest smooth, belly smooth or barely areolate; posterior and ventral surfaces of thighs areolate; groins areolate; discoidal fold present, slightly visible as a thoracic fold or laterally; postrictal gland present, subconical or conical; (2) tympanic membrane and annulus distinct, large, about 33–43% of eye length; supratympanic fold present, distinct, black; (3) head as long as wide; snout short, nearly truncate in dorsal and lateral views; canthus rostralis well defined, distinctly sinuous in dorsal view, straight in profile; (4) cranial crests absent; upper eyelid covered with pointed granules; (5) dentigerous processes of vomers large, prominent, triangular, distinctly separated, situated posteromedial to choanae (posterior margin at level of choanae), bearing 5–9 vomerine teeth; (6) males lacking vocal slits and vocal sacs; nuptial pads absent; (7) hands with distinctly long and slender fingers; Finger I longer than Finger II; subarticular tubercles conical, large on inner fingers and small on outer fingers; supernumerary tubercles distinct, heterogeneous in size, rounded, smaller than subarticular tubercles; fingertips narrowly rounded, bearing circumferential grooves and ungual flaps; lateral keels on fingers present; (8) ulnar region bearing small, low, rounded tubercles; (9) heel bearing granules; tubercles on tarsus absent; (10) inner metatarsal tubercle ovoid, prominent, 2–3 times size of conical and inclined outer metatarsal tubercle; subarticular tubercles conical, distinct; supernumerary tubercles conspicuous, heterogeneous in size, rounded, some similar in size to subarticular tubercles; (11) toes distinctly long and slender (foot length 54–59% SVL); lateral keels present and webbing absent; Toe V reaching proximal or distal margin of second subarticular tubercle of Toe IV; Toe III reaching close to or distal margin of second subarticular tubercle of Toe IV; toe tips narrowly rounded, bearing circumferential grooves and ungual flaps; (12) axillary glands absent; (13) in life, dorsum light brown with faint reddish hue bearing faint or dark brown marks, including canthal stripe, supratympanic stripe, labial bars, W-shaped scapular mark, and bars on limbs; forelimbs, ventrolateral region, anterior and posterior surfaces of thighs, shanks, tarsus, and feet with orange or reddish brown hue; throat brown with cream or tan spots; remaining ventral surfaces orange or brownish orange with brown reticulations or blotches on belly; palms and soles brown; iris bicolored, upper half red and lower half greenish bronze, bearing brown reticulations; sclera yellow or orange.

Description of holotype. Adult female (CORBIDI 28468) with relatively slender body and in a good state of preservation, with left foot removed and preserved as a tissue sample for molecular analyses (Figure 8). Skin of dorsum bearing small conical granules homogeneous in size, covering entire dorsal surface including limbs; dorsolateral fold absent; skin on throat and chest smooth, belly weakly areolate; discoidal fold absent; posterior surfaces of thighs and groin areolate. Head as long as wide (Head Length = 37% SVL; Head Width = 37% SVL). Snout nearly truncate in dorsal and lateral views; canthus rostralis distinct, sinuous in dorsal view and straight in profile; lips rounded, not flared. Nostrils not protuberant, directed laterally. Loreal region distinctly concave. Eye of moderate size, with a diameter of 13% SVL. Tympanic membrane evident, similar in coloration to surrounding skin; tympanum conspicuous, oval, diameter 5% SVL. Supratympanic fold ill-defined, obscuring upper margin of tympanum. Postrictal gland present, subconical.

Dentigerous processes of vomers conspicuous, triangular, well separated from each other; each process bearing 7 teeth along proximal edge. Choanae large, half-moon shaped, anterior quarter concealed by palatal shelf of maxillary arch. Tongue large, cordiform, with anterior two-thirds attached to floor of mouth. Forearms slender, lacking tubercles. Fingers slender; fingertips narrow, rounded, bearing circumferential grooves. Relative lengths of fingers II < I < IV < III. Fingers bearing lateral keels; webbing absent. Subarticular tubercles small, conical. Supernumerary tubercles present, well defined, rounded, small. Palmar tubercle prominent, bifid. Inner metacarpal tubercle prominent, large, elliptical. Hind limbs slender; tibia length 69% SVL; foot length 54% SVL. Heel bearing small granules; tarsal tubercles absent. Inner metatarsal tubercle prominent, ovoid, 3 times size of conical outer metatarsal tubercle; plantar surface bearing several small ill-defined supernumerary tubercles heterogeneous in size; subarticular tubercles well defined, conical, small. Toes bearing lateral keels; toe tips narrowly rounded, bearing circumferential grooves. Relative lengths of toes I < II < III = V < IV; Toe V reaching middle of second subarticular tubercle of Toe IV; Toe III reaching distal margin of second subarticular tubercle of Toe IV; toe webbing absent.

Measurements (in mm) of the holotype. SVL 32.4; tibia length 22.2; foot length 17.5; head length 11.8; head width 11.9; eye diameter 4.1; tympanic diameter 1.5; IOD 3.4; upper eyelid width 2.8; internarial distance 3.3; eye-nostril distance 4.5.

Coloration in life (Figure 7A–C). Dorsum light brown with a faint reddish hue bearing black marks consisting in scattered black spots, two thin bars on the top of snout and interorbital region, canthal stripe, supratympanic stripe, W-shaped scapular mark, and blotches on flanks; forelimbs, hands and fingers pale orange bearing deep brown bars; ventrolateral region orange; thighs orange, tibia light brown, tarsus, feet, and toes brownish cream bearing dark brown bars; axillae and groins orange, and posterior surface of thighs orange with dirty cream flecks. Ventral surface, throat and chest brown with tan spots, belly orange with brown reticulations, thighs orange with faint brown reticulations, shanks tan with dark brown bars, and palms and soles brown. Upper half of iris red and lower half greenish bronze bearing brown reticulations, and pupil with a black ventral notch. Sclera yellow.

Coloration in 70% ethanol (Figure 8). Dorsal surface grayish brown covered by grayish cream granules and grayish cream labial bars; limbs, fingers, and toes creamy tan bearing brown bars; and posterior surface of brown with creamy tan flecks. Ventral surface, throat and most of the chest brown with cream spots, belly and thighs creamy tan with brown reticulations, forelimbs creamy tan with brown marks, shanks and tarsus brown with cream spots, palms and soles brown.

Variation. In the type series, three adult males (SVL = 23–26 mm) are smaller than four adult females (SVL = 30–33 mm). See Table 2 for measurements and proportions of the type specimens. The three adult male paratypes lack vocal slits and nuptial pads. Individuals only show a slight variation in the ventral pattern. The female CORBIDI 28470 (Figure 7C) and male CORBIDI 28463 (Figure 7I) have the belly brown with tan and creamy orange blotches, and the male has white spots on the throat (Figure 7I).

Distribution and natural history observations. *Oreobates foliaspectrum* is only known from the type locality, Canan in the Huayabamba River basin, at an elevation of 2100 m, San Martín department, northeastern Peru (Figure 4). This species inhabits montane forest patches of low canopy (less than 6 m) with slender trees, tree ferns, and Chusquea bamboo that grow on poor sandy soils in a matrix of cattle ranching pastures. Specimens were collected at night between 19:00 and 12:00 h on the forest floor on a soil consisting of a deep layer of roots, leaf litter, and ferns commonly found on poor sandy soils. All specimens

collected were captured near holes formed by raised roots and quickly hid in them when they felt threatened. The forest floor showed signs of frequent cattle trampling.

According to Olson et al. [2], the distribution of *O. foliaspectrum* lies in the Peruvian Yungas ecoregion. Sympatric anuran species collected in the type locality were: *Pristimantis nephophilus*, *Pristimantis* sp. (*danae* group), *Rhinella moralesi*, and *R. margaritifera* complex.

Etymology. The specific name *foliaspectrum* is compounded by two Latin substantives, folia meaning leaf and spectrum meaning image, vision, apparition, or appearance. Referring to the rare appearance of this species (e.g., reddish eyes, long fingers and toes, and cryptic coloration) as a ghostly image that inhabits the leaf litter.

3.2.4. *Oreobates nigrumcompletum* sp. nov.

urn:lsid:zoobank.org:act: 41E40370-7D29-49E0-A536-85AC44CC5103 (available online: https://zoobank.org/NomenclaturalActs/41e40370-7d29-49e0-a536-85ac44cc5103, accessed on 20 July 2026).

Figures 9 and 10.

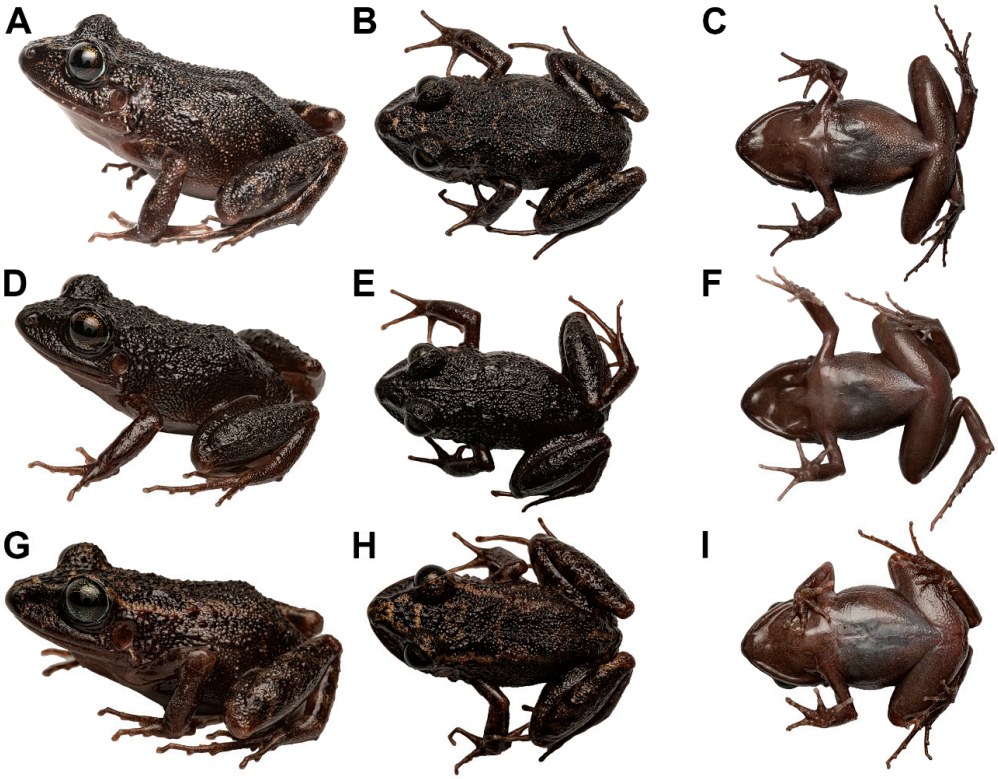


Figure 9. *Oreobates nigrumcompletum* sp. nov. in life: (**A**) dorsolateral, (**B**) dorsal, and (**C**) ventral views of holotype (CORBIDI 28691), SVL 33 mm; (**D**) dorsolateral, (**E**) dorsal, and (**F**) ventral views of adult male CORBIDI 28693, SVL 24 mm; (**G**) dorsolateral, (**H**) dorsal, and (**I**) ventral views of adult male CORBIDI 28687, SVL 26 mm. Photographs by James W. Titto.

Holotype. CORBIDI 28691, an adult female, from Finca Oso Pecho Blanco, Uchiza district, Tocache province, San Martín department, Peru (8.4846° S, 76.5873° W, 1384 m), collected on 3 August 2025 by James W. Ttito and Michael Gulman.

Paratypes. CORBIDI 28693, adult male, (8.479608° S, 76.585491° W, 1155 m); CORBIDI 28689, adult female, (8.483019° S, 76.582708° W, 1291 m); CORBIDI 28688, adult male, (8.48441° S, 76.583077° W, 1358 m); CORBIDI 28692, adult male, (8.483218° S, 76.587141° W, 1358 m); CORBIDI 28690, adult female, (8.477394° S, 76.594046° W, 1474 m); CORBIDI 28687, adult male, (8.487947° S, 76.584844° W, 1497 m); CORBIDI 28695, adult male, (8.490532° S, 76.585073° W, 1652 m); CORBIDI 28694, adult male, (8.491616° S, 76.585241° W, 1691 m).

All specimens from Finca Oso Pecho Blanco, Uchiza district, Tocache province, San Martín department, Peru; collected between 30 July and 04 August 2025 by James W. Ttito and Michael Gulman.

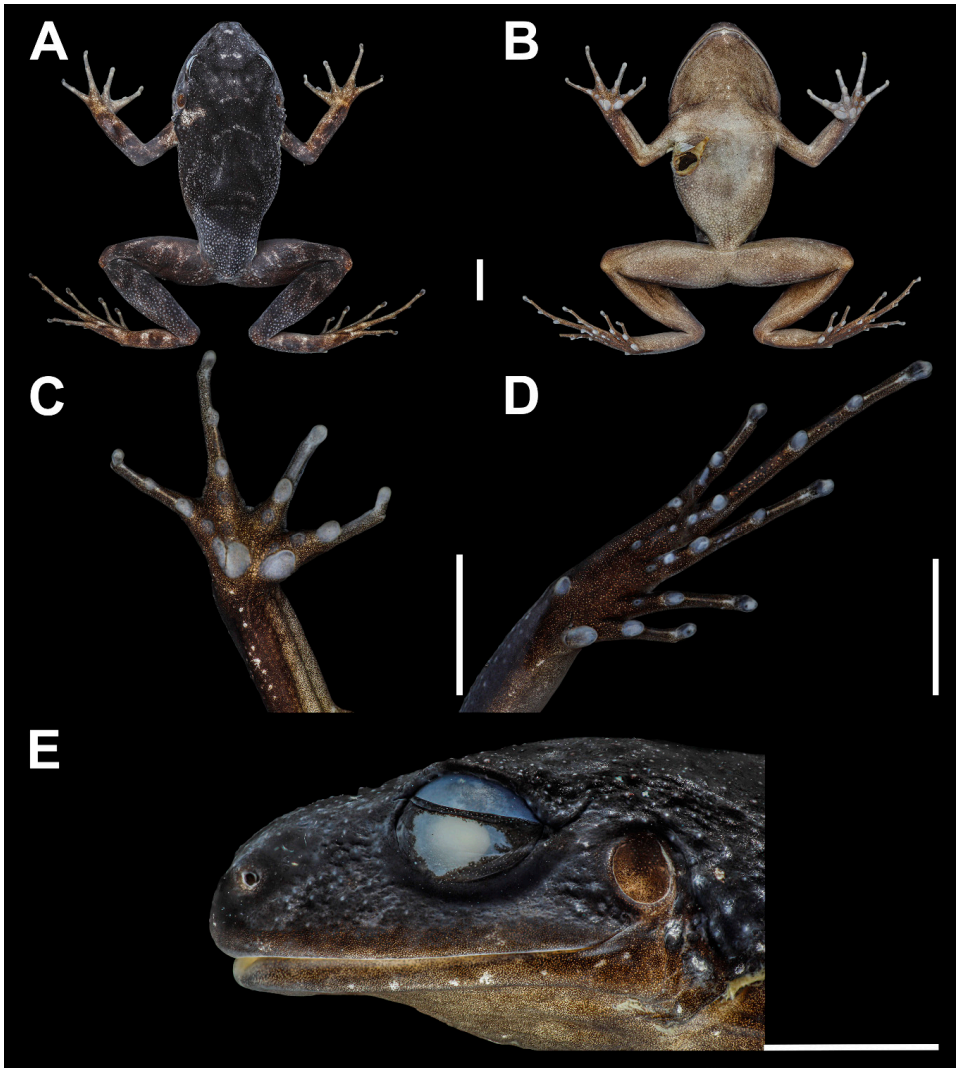


Figure 10. Preserved holotype of *Oreobates nigrumcompletum* sp. nov. (CORBIDI 28691) in dorsal view (**A**), ventral view (**B**), palm (**C**), sole (**D**), and head in lateral view (**E**). Scale bar 5 mm. Photographs by Luis A. García-Ayachi.

Diagnosis. *Oreobates nigrumcompletum* (Figure 9) is easily distinguished from the rest of congeners (27 species) by the following combination of characters: (1) tip of finger and toes rounded, not expanded; (2) vocal slits absent and nuptial pads present; (3) dorsal surface deep brown or nearly black lacking contrasting marks, only faint tan brown speckles on dorsum or tan bars on limbs in some specimens; (4) ventral surface deep brown without marks; (5) dorsum covered by mostly pointed granules, gently heterogenous in size; and (6) belly weakly areolate.

Other species of *Oreobates* from the Peruvian Andes that also share with *O. nigrumcompletum* the absence of vocal slits are: *O. azulensis* sp. nov., *O. chirimoto* sp. nov., *O. colanensis*, *O. lundbergi*, *O. shunkusacha*, and *O. foliaspectrum* sp. nov. Nevertheless, *O. nigrumcompletum* can be easily distinguished from the aforementioned species (see Table 1) by having the iris dark brown densely spotted with gold flecks bearing a thin gold circumpupillary ring (copper in *O. azulensis*, gold bearing a brown streak at the middle in *O. colanensis*, bronze with black reticulation in *O. lundbergi*, upper half of iris red and lower half greenish bronze

bearing brown reticulations in *O. foliaspectrum*, and greenish-golden with black reticulations in *O. shunkusacha*), skin of dorsum covered by pointed granules gently heterogenous in size (rounded granules with scattered round tubercles in *O. chirimoto*, dorsum smooth with few scattered tubercles in *O. lundbergi*, granules round to subconical homogenous in size in *O. shunkusacha*), and lacking dorsolateral folds (present in *O. colanensis*).

In preservative (ethanol 70%), specimens of *O. nigrumcompletum* are brown dorsally and can be confused in collections with other species with dorsal granular skin and brown dorsum such as: *O. amarakaeri*, *O. cruralis*, *O. gemcare*, *O. granulosus*, *O. machiguenga*, *O. quixensis*, and *O. saxatilis* (Table 1). However, *O. nigrumcompletum* differs from *O. machiguenga* by lacking a basal membrane between Toe III and IV, and from *O. cruralis* by having the outer fingertips round and not expanded (basal membrane between Toe III and IV present in *O. machiguenga*, and outer fingertips slightly expanded and truncate in *O. cruralis*). The dorsal surface is covered by pointed granules gently heterogeneous in size in *O nigrumcompletum*, while it is covered by round granules and slightly enlarged warts in *O. amarakaeri*, low round granules and some enlarged flat warts in *O. cruralis*, shagreen with enlarged round granules and low warts in *O. gemcare*, and round granules and small or enlarged flat warts in *O. granulosus*. Like *O. nigrumcompletum*, *O. quixensis* and *O. saxatilis* possess keratinized granules on the dorsum; however, the latter two species differ by having granules with the presence of scattered enlarged warts, giving a conspicuously heterogeneous aspect. In addition, *O. nigrumcompletum* lacks axillary glands, present in *O. cruralis*, *O. gemcare*, and *O. granulosus*. In addition, *O. nigrumcompletum,* with a SVL of 22–26 mm in males and 28–34 mm in females, is smaller than *O. quixensis* (35–48 mm in males and 47–63 mm in females) and *O. saxatilis* (44–50 mm in males and 50–63 mm in females).

Characterization. A small species of *Oreobates* (SVL 22–26 mm in adult males and 28–34 mm in adult females) characterized as follows: (1) skin of dorsum and limbs granular, granules keratinized, mostly pointed, and gently heterogeneous in size; flanks areolate; occipital fold present as a \ /-shaped fold; dorsolateral fold absent; skin on throat and chest smooth, belly weakly areolate; posterior and ventral surfaces of thighs and groins weakly areolate; discoidal fold present as a thin thoracic fold or visible posteriorly; postrictal gland present, rounded, subconical or conical; (2) tympanic membrane and annulus distinct, large, about 42–54% of eye length; supratympanic fold present, thin and ill-defined; (3) head as long as wide or slightly wider than long; snout short, rounded in dorsal and lateral views; canthus rostralis gently sinuous in dorsal view, slightly curved in profile; (4) cranial crests absent; upper eyelid covered with conspicuous round granules; (5) dentigerous processes of vomers large, prominent, triangular, distinctly separated, situated posteromedial to choanae (posterior margin at level of choanae), bearing 3–7 vomerine teeth; (6) males lacking vocal slits and vocal sacs; nuptial pads present at base of Finger I as a small unpigmented patch; (7) hands with long and slender fingers; Finger I equal in length to or barely longer than Finger II; subarticular tubercles rounded to conical, large on inner fingers and small on outer fingers; supernumerary tubercles small, rounded, smaller than subarticular tubercles; fingertips rounded, not expanded, lacking or bearing ill-defined circumferential grooves and ungual flaps; lateral fringes and keels on fingers absent; (8) ulnar region bearing small, low, rounded tubercles; (9) heel bearing granules; tubercles on tarsus absent; (10) inner metatarsal tubercle ovoid, prominent, 3 times size of conical and inclined outer metatarsal tubercle; subarticular tubercles conical, distinct; supernumerary tubercles usually ill-defined, much smaller than subarticular tubercles, rounded; (11) toes long and slender (foot length 47–57% SVL); lateral fringes and webbing absent; Toe V reaching close to or middle of second subarticular tubercle of Toe IV; Toe III reaching close to or middle of second subarticular tubercle of Toe IV; toe tips narrow, rounded, bearing ill-defined circumferential grooves and ungual flaps on outer toes; (12) axillary glands absent; (13) in life, dorsum deep brown,

nearly black, with or without faint tan markings; when present, markings consisting of scattered specks or faint dorsolateral stripes, discrete cream labial bars, and faint tan bars on limbs; hidden surfaces similar in coloration to dorsal background; ventral surfaces deep brown; iris dark brown densely spotted with gold flecks, bearing thin gold circum-pupillary ring and pupil with ventral black notch; sclera dark gray.

Description of holotype. Adult female (CORBIDI 28691) with a relatively robust body and in a good state of preservation, with a portion of liver removed through a small ventral opening on the right anterior side of the venter and preserved as a tissue sample for molecular analyses (Figure 10). Skin of dorsum and flanks granular, bearing small keratinized and mostly conical granules gently heterogeneous in size, covering entire dorsum and limbs; ventrolateral region areolate; dorsolateral fold absent; skin on throat and chest smooth, belly weakly areolate; discoidal fold present only as a weak thoracic fold; posterior and ventral surfaces of thighs and groins areolate. Head slightly wider than long (Head Length = 38% SVL; Head Width = 42% SVL). Snout rounded in dorsal and lateral views; canthus rostralis weak, slightly sinuous in dorsal view and slightly curved in profile; lips rounded, not flared. Nostrils not protuberant, directed laterally. Loreal region slightly concave. Eye of moderate size, its diameter 14% SVL. Tympanic membrane evident, lighter in coloration than surrounding skin; tympanum conspicuous, oval, diameter 6% SVL. Supratympanic fold ill-defined, obscuring upper margin of tympanum. Postrictal glands present, subconical. Dentigerous processes of vomers conspicuous, triangular, well separated from each other; each process bearing 6 teeth along proximal edge. Choanae large, half-moon shaped, anterior quarter concealed by palatal shelf of maxillary arch. Tongue large, cordiform, with anterior two-thirds attached to floor of mouth. Forearms slender, bearing small, low, rounded ulnar tubercles. Fingers slender; fingertips rounded, not expanded, lacking circumferential grooves. Relative lengths of fingers II < I < IV < III. Fingers lacking dermal fringes; webbing absent. Subarticular tubercles prominent, conical. Supernumerary tubercles present, well defined, rounded, small. Palmar tubercle prominent, deeply bifid. Inner metacarpal tubercle prominent, large, elliptical. Hind limbs slender; tibia length 50% SVL; foot length 50% SVL. Heel bearing small granules; tarsal tubercles absent. Inner metatarsal tubercle ovoid, 3 times size of conical outer metatarsal tubercle; plantar surface bearing few small ill-defined supernumerary tubercles; subarticular tubercles well defined, conical, small. Toes lacking lateral fringes; toe tips rounded, not expanded, bearing ill-defined circumferential grooves on outer toes. Relative lengths of toes I < II < III < V < IV; Toe V reaching middle of second subarticular tubercle of Toe IV; Toe III reaching distal margin of second subarticular tubercle of Toe IV; toe webbing absent.

Measurements (in mm) of the holotype. SVL 33.6; tibia length 16.8; foot length 16.9; head length 12.9; head width 13.9; eye diameter 4.6; tympanic diameter 1.9; IOD 3.5; upper eyelid width 3.0; internarial distance 2.8; eye-nostril distance 4.2.

Coloration in life (Figure 9A–C). Dorsum deep brown, nearly black, bearing inconspicuous tan marks, discrete cream labial bars, and limbs as dorsum coloration bearing faint tan bars; ventral surface deep brown including palms and soles; iris dark brown densely spotted with gold flecks bearing a thin gold circumpupillary ring and the pupil with a ventral black notch. Sclera dark gray.

Coloration in 70% ethanol (Figure 10). Dorsal surface dark brown bearing tan marks on dorsum, tan bars on limbs, and the tips of granules dusty white, more evident posteriorly and on hind limbs. Ventral surface tan.

Variation. In the type series, six adult males (SVL = 22–26 mm) are smaller than three females (SVL = 28–34 mm) and possess nuptial pads. See Table 2 for measurements and proportions of the type specimens. There is no significant morphological variation related to the skin texture or coloration between specimens. The male specimen CORBIDI 28687 possesses a faint dorsolateral stripe.

Distribution and natural history observations. *Oreobates nigrumcompletum* is only known from the Finca Oso Pecho Blanco in the Huallaga River basin, San Martín department, northeastern Peru, at elevations between 1155 and 1690 m (Figure 4). This locality lies in the Peruvian Yungas ecoregion according to Olson et al. [2]. All individuals were observed during the night, between 19:00 and 3:00 h, in the leaf litter of a steep slope covered by primary premontane forest. Sympatric species of anurans collected with *O. nigrumcompletum* were *Hemiphractus helioi*, *Pristimantis adiastolus*, *P.* aff. *lirellus*, and *P.* sp. (*lacrimosus* group), *Rhinella aff. margaritifera*, and *Strabomantis* sp.

Etymology. The specific name *nigrumcompletum* is compounded by the Latin adjectives "*nigrum*" and "completum", meaning black and complete or entire, respectively, due to the entire dark coloration of this new species.

4. Discussion

We integrated morphological traits with molecular data to describe four new species of the genus *Oreobates*, increasing the number of species in the genus to 31 species. Our phylogenetic analysis (Figure 1) of *Oreobates* is the most complete both in terms of locus and species coverage, with a 3538 bp long matrix concatenating fragments of three mitochondrial genes (16S, 12S, and COI) and two nuclear genes (RAG1 and Tyr). By employing a multilocus dataset that combines both mitochondrial and nuclear markers, our study provides a broader and more comprehensive genetic sampling than previous works, which were largely restricted to single mitochondrial markers or reduced multilocus sets. The topology recovered here (Figure 1) is congruent with previously published phylogenies of *Oreobates* [15,18,19,21,40].

In particular, our results closely resemble the maximum likelihood topology of Venegas et al. [21]. A notable difference among previous studies concerns the position of *O. lundbergi*. In our analysis, this species is recovered as the sister lineage to all remaining *Oreobates* with strong support, a result consistent with Venegas et al. [21]. In contrast, previous studies based on single-locus datasets generally placed *O. lundbergi* within internal clades, often with low support (see Padial et al. [15]; Köhler & Padial [40]; Pansonato et al. [19]; Castillo-Urbina et al. [18]), suggesting that increased gene sampling improves resolution of deeper relationships within the genus.

Overall, our phylogenetic results support the placement of all new species within *Oreobates* and corroborate their status as distinct evolutionary lineages. Although the genetic divergence between *O. azulensis* and *O. shunkusacha* (UPD = 2%) is lower than that observed among some currently recognized species (Table S1), both species are recovered as sister taxa with strong support (UFBoot = 100), despite *O. shunkusacha* being represented only by mitochondrial data (16S). Importantly, the two species are readily distinguished by dorsal skin texture, a widely used diagnostic character in *Oreobates* taxonomy (see Padial et al. [15,41]; Köhler and Padial [40]; Castillo-Urbina et al. [18]): dorsum covered by keratinized pointed granules heterogeneous in size in *O. azulensis* versus round or subconical granules homogeneous in size in *O. shunkusacha*.

The presence of keratinized tips on granules or warts on the dorsal skin has frequently been used as a diagnostic character in species of *Oreobates* [15,40,41]. However, the stability of this character remains uncertain and, in this study, we use it with caution. In some species, keratinized tips are subtle and difficult to observe (e.g., *O. granulosus*, *O. saxatilis*, *O. nigrumcompletum*), which may lead to inconsistencies among descriptions and specimen comparisons. Moreover, it remains unclear whether the development of these keratinized structures is constant throughout life or associated with reproductive condition or seasonality. Similar sexually dimorphic and seasonally expressed keratinized structures are known in other anurans, such as the nuptial labial spines of *Leptobrachium boringii*, which fall off

once the breeding season is over [42], the dorsal spicules of males in *Osteocephalus*, where these structures are linked to breeding activity and may regress outside the reproductive season [43–45], and the spiny points on top of warts of species of *Atelopus*, which vary according to sex, ontogeny, and among individuals [46,47]. Further studies are needed to determine whether dorsal keratinization in *Oreobates* is a stable taxonomic character or varies seasonally according to reproductive condition.

The four new species described herein occur in the Peruvian Yungas, at elevations from 1400 to 2100 m, reinforcing the importance of this ecoregion as a major center of diversification for *Oreobates* [4]. More than half the currently recognized species of the genus inhabit montane forests along the eastern Andean versant, particularly within the Yungas, where steep elevational gradients, habitat heterogeneity, and strong geographic isolation create favorable conditions for allopatric divergence and local adaptation [4,15,18]. Montero-Mendieta et al. [4] demonstrated that highland *Oreobates* species tend to have smaller effective population sizes and stronger genetic drift than lowland taxa, likely a consequence of habitat fragmentation in montane environments. Reduced gene flow among isolated populations, together with divergent selective pressures across elevations, may therefore promote rapid lineage diversification in these frogs. Our results are consistent with this hypothesis, as all four new species were discovered in geographically isolated montane forests that remain poorly explored and are separated by deep river valleys and rugged topography, such as in the Huallaga River Basin (see Figure 4B).

Interestingly, although *Oreobates* is highly diversified in the Yungas or montane forests of the central and southern Andes, the genus is notably absent from the montane forests of the eastern Andean slopes of Ecuador and Colombia [48,49]. In the eastern versant of the Northern Andes, only *O. quixensis* occurs, apparently extending across adjacent Amazonian lowlands and foothills rather than as part of the montane Anuran fauna [15,49]. This distributional pattern suggests that the Marañón Valley, which separates the northern Andes from the central Andes of Peru, may represent an important biogeographic barrier limiting the northward expansion of montane *Oreobates* lineages (see Figure 4B). Similar barrier effects have been documented for multiple Andean taxa, even high-mobility vertebrates such as birds, where deep dry valleys such as the Marañón interrupt humid montane forest continuity and promote lineage isolation and endemism [50–54]. Another hypothesized barrier is the Apurímac–Mantaro inter-Andean valleys in southern Peru (see Figure 4C) [55–57], which played a similar but reduced role as the barrier for southern Peruvian *Oreobates*, with a distinct clade of montane *Oreobates* occurring south of the Apurímac-Ene River (*O. gemcare*, *O. lehri*, *O. machiguenga*).

The phylogenetic relationships recovered here further support repeated diversification within the Yungas rather than a single regional radiation. Three of the new species (*O. azulensis*, *O. foliaspectrum*, and *O. nigrumcompletum*) form part of a well-supported northern Peruvian clade together with *O. colanensis* and *O. shunkusacha*, suggesting localized diversification in the montane forests of the upper Huallaga River basin (see Figure 4B). In contrast, *O. chirimoto* is recovered as sister to the *O. quixensis* + *O. saxatilis* clade and closely related to a subclade composed mainly of species distributed in the southern Peruvian Yungas (*O. ayacucho*, *O. lehri*, *O. machiguenga*, *O. gemcare*, and *O. pereger*). This pattern suggests that elevational specialization and geographic isolation have generated multiple independent diversification events across the Yungas, contributing to the high endemism observed in the genus. The discovery of four additional species in relatively limited survey areas strongly indicates that the diversity of *Oreobates* in the northern Peruvian Yungas remains underestimated. It is important to note that the phylogenetic support for *O. chirimoto* is low, and therefore its relationships should be interpreted with caution. Likewise, the

rivers mentioned as potential barriers in the Discussion will require broader geographic and genetic sampling to corroborate their role in diversification.

Finally, an additional pattern of interest is the distribution of vocal slits within *Oreobates*. The absence of vocal slits characterizes the well-supported clade containing *O. azulensis*, *O. colanensis*, *O. foliaspectrum*, *O. nigrumcompletum*, and *O. shunkusacha*, as well as *O. lundbergi* and *O. chirimoto*, which occur in different phylogenetic positions. This distribution suggests that the absence of vocal slits does not represent a synapomorphy for a single lineage, but rather a more complex evolutionary pattern involving either retention of an ancestral condition or repeated independent losses within the genus, a pattern commonly observed in the evolution of secondary sexual characters and vocal structures in anurans [58–62]. Because vocal slits are generally associated with advertisement calls, mate attraction, and territorial interactions in anurans [63–66], their absence may reflect shifts in reproductive strategies or calling behavior. Similar evolutionary lability of reproductive characters has been documented in other direct-developing frogs, where vocal sacs and vocal slits may be reduced or secondarily lost under different selective pressures [60]. Further bioacoustic and behavioral studies will be necessary to determine whether the absence of vocal slits in these species is associated with reproductive ecology and whether this character represents a stable phylogenetic signal within *Oreobates*.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18080458/s1, Table S1: Table of uncorrected p-distances across all species included in our molecular analyses using the 16S gene marker.

Author Contributions: Conceptualization, P.J.V. and A.C.; investigation, P.J.V., L.A.G.-A., A.C., M.G., J.W.T. and J.D.V.; writing—original draft preparation, P.J.V., L.A.G.-A. and A.C.; writing—review and editing, P.J.V., L.A.G.-A., A.C., M.G., J.W.T. and J.D.V.; funding acquisition, P.J.V., A.C. and J.W.T. All authors have read and agreed to the published version of the manuscript.

Funding: The fieldwork in Nuevo Chirimoto was funded by APECO through THE CRITICAL ECOSYSTEM PARTNERSHIP (CEPF) with the project: Updating the status of an endemic harlequin frog from Peru, project number CEPF-108792. Fieldwork in Cordillera Azul National Park was funded by CIMA Cordillera Azul with the project titled: "Exploring amphibians and reptiles along an altitudinal gradient (700 to 1800 m a.s.l.) in the Maronilla area (Aspuzana), a buffer zone of Cordillera Azul National Park". Fieldwork in Finca Oso Pecho Blanco was funded by the SPDA-2024 Carlos Ponce del Prado Award.

Institutional Review Board Statement: Our research was approved by IACUC-24-024 of Florida International University, Miami, FL 33199, USA.

Data Availability Statement: The table with uncorrected p-distances across all species using 16S gene alignments and script are available in the Supplemental Materials.

Acknowledgments: P.J.V. and L.A.G.-A. are especially indebted to Mariella Leo and Glen Seitz of Asociación Peruana para la Conservación de la Naturaleza (APECO) for their logistic support during the fieldwork. P.J.V. and L.A.G.-A. are also grateful to our field assistant Juan Gamboa and especially to our field guide Francisco Galoc and his hospitality. J.D.V. is indebted to Benoît Segerer, Fabrice Schmitt, Jean-François Blanc, Ombline Chabasseur, Raphaël Sane, and Alessandro Pignochi for their logistical support and companionship in the field, and especially to Artemio Chávez and his wife Francelit Espejo for their hospitality in Canaan village. J.W.T. is indebted to Yngrid Cordova for project coordination, Jorge Díaz Cotrina, the owner of Finca Oso Pecho Blanco, for their invaluable support in guiding and logistics, Yerson Cereceda Ayme, Estefany Avilés, Mauro Huamani, Alexis Antesana, and Jherick Porras Huamani for their outstanding work and constant support during field activities.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Material examined. Material deposited in the Herpetology Collection of the Centro de ornitología y Biodiversidad (CORBIDI).

Oreobates amarakaeri (*n* = 3): PERU—Cusco, Paucartambo, Piñi Piñi trocha catarata, −12.8706, −71.4273, 570 m, CORBIDI 19160l;—Madre de Dios, Manu, Manu Bio Lodge (formerly Estacion Biológica Villa Carmen), −12.89008, −71.41084, 550 m, CORBIDI 16288;—*Puno*, Carabaya, Santo Domingo, −13.84385, −69.65754, 1235 m, CORBIDI 18732.

Oreobates ayacucho (*n* = 1): PERU—Ayacucho, La Mar, Pacobamba, −13.0774, −73.7775, 3940 m, CORBIDI 19281.

Oreobates colanensis (*n* = 16): PERU—Amazonas, Utcubamba, Lechucita, −5.6311, −78.2570, 2610 m, CORBIDI 21191, 21295-96; Bagua, Refugio Copallín, −5.5960, −78.3401, 2380 m, CORBIDI 23594, 23626-27, 23630, 23633, 23636-37, 23639-40, 23674, 23749-51.

Oreobates cruralis (*n* = 17): PERU—Madre de Dios, Tahuamanu, Alegría, −12.0950, −69.0823, 320 m, CORBIDI 25985, 25934, 25953; Tahuamanu, Base 51 de Bozovich concesión de madera, −11.5870, −69.6452, 350 m, CORBIDI 15426; Tambopata, Corredor Tambopata-Manu, −12.8444, −70.0938, 240 m, CORBIDI 15137, 15147; Tambopata, El Parador, −12.9797, −70.2351, 240 m, CORBIDI 13505, 13529; Tambopata, Inotawa, −12.8093, −69.3182, 190 m, CORBIDI 05260, 05278; Tambopata, Las Piedras Amazon Center, −12.0708, −69.4993, 240 m, CORBIDI 18262, 18276, 18288, 18118, 18181; Tambopata, Tambopata Research Center, −13.1209, −69.6159, 235 m, CORBIDI 17107;—Puno, Carabaya, Parque Nacional Bahuaja Sonene- Campamento Base, −13.1949, −70.1324, 300 m, CORBIDI 13231.

Oreobates gemcare (*n* = 4): PERU—Cusco, Paucartambo, trocha canopy Wayqecha, −13.1902, −71.5864, 2950 m, CORBIDI 19453-54; Paucartambo, Esperanza, −13.1817, −71.6076, 2810 m, CORBIDI 11922; −13.17695, −71.60207, 2830, m, MUSM 27904; Paucartambo, pasando segundo túnel, −13.17892, −71.60966, 2785 m, MUSM 28029, 21151, AMNH 153085-87; −13.17554, −71.60827, 2750 m, MUSM 27885; Paucartambo, Pillahuata, −13.15722, −71.59459, 2350 m, AMNH 157013; −13.15716, −71.59750, 2370 m, MHNG 2606.46; Paucartambo, Mirador, −13.0711, −71.5639, 1640 m, CORBIDI 19480; −13.07407, −71.55608, 1750 m, MUSM 21152; −13.07388, −71.55810, 177 m, MUSM 21153; −13.06910, −71.55504, 1740, m, MUSM 27903; −13.06851, −71.55995, 1690 m, MUSM 27901.

Oreobates granulosus (*n* = 4): PERU—Cusco, Paucartambo, Adventure Trail, −13.0581, −71.5459, 1370 m, CORBIDI 17035; Paucartambo, Valle de Kosñipata, −13.0341, −71.5160, 1120 m, CORBIDI 16216;—Puno, Sandia, Santo Domingo, −13.8380, −69.6474, 1475 m, CORBIDI 18695, 18704.

Oreobates lehri (*n* = 15): PERU—Ayacucho, La Mar, Toccate, −12.9919, −73.6591, 2290 m, CORBIDI 19284;—Cusco, La Convención, Aendoshiari, −12.8174, −73.4197, 2370 m, CORBIDI 18780, 26689; La Convención, KP 129—Comunidad ochigoteni, −12.5758, −73.0900, 1690 m, CORBIDI 05398-99, 05398-99; La Convención, KP108—Alto Shima, −12.5704, −73.1622, 1543 m, CORBIDI 09688; 10597-602, 9688.

Oreobates machiguenga (*n* = 2): PERU—Cusco, La Convención, CC NN Shivancoreni, −11.6933, −72.9526, 385 m, CORBIDI 19030; La Convención, Reserva Comunal Matsiguenga, −11.4523, −73.4324, 604 m, CORBIDI 16016.

Oreobates quixensis (*n* = 125): PERU—Amazonas, Condorcanqui, Bosques en la cuenca del Río Cenepa, al norte de Santa María de Nieva, −4.4775, −77.8876, 268 m, CORBIDI 09087, 09179, 14320; Condorcanqui, Concesión de Conservación Pamau Nain, −5.2219, −77.9311, 515 m, CORBIDI 14027; Condorcanqui, Quebrada Kampankis, −4.0431, −77.5412, 325 m, CORBIDI 09510;—Cusco, La Convención, Campamento Kinteroni, −11.4936, −73.2068,

399 m, CORBIDI 07084, 07138, 07140-41; La Convención, CC NN Camaná, −11.9753, −73.1708, 606 m, CORBIDI 00346; La Convención, Distrito Echarate KP 115, −12.5670, −73.0903, 1300, CORBIDI 05998; La Convención, kinteroni, −11.5044, −73.2530, 392 m, CORBIDI 10259; La Convención, KP 15, CC NN Chokoriari, −11.9569, −72.9410, 434 m, CORBIDI 08484-85; La Convención, KP 50, CC NN Poyentimari, −12.1885, −73.0009, 725 m, CORBIDI 08272, 08537, 08547, 08566; La convención; KP 85, Monte Carmelo; −12.4445, −73.0242, 1008 m, CORBIDI 10680-81; La Convención, Mipaya, −11.5800, −73.1645, 370 m, CORBIDI 10108, 10115, 12473; La Convención, Pagoreni B (Malvinas), −11.6853, −72.9583, 442, CORBIDI 10057; La Convención, Reserva Comunal Matsiguenga, −11.3909, −73.3651, 638 m, CORBIDI 15971; La Convención, Reserva Matsiguenga, −11.4562, −73.3911, 556 m, CORBIDI 16897; La Convención, Rio Camisea, −11.7648, −72.8987, 399 m, CORBIDI 07063, 07097-99, 07115; La Convención, Santuario Nacional Megantoni, −12.2538, −72.8350, 515 m, CORBIDI 06662;—Huánuco, Puerto Inca, campamento caoba de cordillera del sira, distrito de Llullapichis, −9.5022, −74.8043, 545 m, CORBIDI 14462; Puerto Inca, Estación Biológica Panguana, Río Yuyapichis, −9.6138, −74.9356, 260 m, CORBIDI 15681, 15695; Puerto Inca, Huánuco, Puerto Inca, −9.3210, −74.7866, 1350 m, CORBIDI 16716;—Junín, Satipo, Portillo Alto—Fundo Santa Teresa, −11.1651, −74.6483, 940 m, CORBIDI 15802, 16838;—Loreto, Alto Amazonas, Campamento Mina de Sal, −5.8894, −76.6044, 300 m, CORBIDI 13758; Datem del Marañón, Distrito Morona, Pongo Chinim, −3.1130, −77.7762, 365 m, CORBIDI 11288; Datem del Marañón, Andoas, −2.6516, −76.5137, 151 m, CORBIDI 01062, 01089: Datem del Marañón, Capahuari norte, −2.6643, −76.5012, 270 m, CORBIDI 04811-13, 04839, 04852; Datem del Marañón, Pongo Chinim, −3.1130, −77.7762, 365 m, CORBIDI 09338; Datem del Marañón, San Jacinto, −2.6516, −76.5137, 151 m, CORBIDI 01102; Datem del Marañón, Sargento Puño, −3.2186, −77.5888, 208 m, CORBIDI 07494; Datem del Marañón, Sector 2, −3.1902, −77.4308, 206 m, CORBIDI 07578, 08681-82; Datem del Marañón, Sector 3, −3.1374, −77.3001, 212 m, CORBIDI 07511, 08773; Datem del Marañón, Sector 4, −3.3059, −77.3215, 210 m, CORBIDI 08708, 08724; Datem del Marañón, Sector 7, −3.8852, −77.2537, 210 m, CORBIDI 07515; Datem del Marañón, Sector 9, −3.8852, −77.2537, 210 m, CORBIDI 07517; Loreto, Andoas, −2.3511, −75.8162, 187 m, CORBIDI 04649, 04679, 04743, 04758, 04923, 04964, 05306; Loreto, Campamento San Jacinto, −2.7043, −76.3128, 273 m, CORBIDI 01511; Loreto, Jibarito, −2.7356, −76.0318, 197 m, CORBIDI 06481; 06620, 09005-6, 0905-06; Loreto, Rio Corrientes, −3.0650, −75.8264, 200 m, CORBIDI 02708, 02749; Loreto, San Jacinto, −2.3308, −75.8637, 160 m, CORBIDI 01130, 01189, 01212, 01216, 01218, 01232; Loreto, Shiviyacu, −2.4819, −76.0856, 194 m, CORBIDI 06405; Loreto, Trompeteros, −2.7948, −76.3349, 206 m, CORBIDI 05022; Maynas, Campamento Curupa, −2.8854, −73.0180, 125 m, CORBIDI 05857; Maynas, Jacamar-1, −3.5178, −74.6630, 180 m, CORBIDI 10331; Putumayo, campamento bajo algodón, −2.4853, −72.0541, 116 m, CORBIDI 17405; Putumayo, campamento medio algodón, −2.5806, −72.8934, 134 m, CORBIDI 17302; Putumayo, Campamento Piedritas, −2.7928, −72.9168, 156 m, CORBIDI 05864; Putumayo, Comunidad El Estrecho, Campamento quebrada-bufeo, −2.4803, −71.6541, 97 m, CORBIDI 17238; Putumayo, Güeppi, −0.1847, −75.3590, 220 m, CORBIDI 00179-82; Putumayo, Medio Campuya, −1.5176, −73.8162, 135 m, CORBIDI 12683; Putumayo, Redondococha, −0.5713, −75.2192, 192 m, CORBIDI 00080; Requena, Campamento Anguila, −6.2650, −73.9100, 140 m, CORBIDI 15204; Requena, Centro de Investigación Jenaro Herrera, −4.8955, −73.6508, 140 m, CORBIDI 06285-86; Requena, Comunidad Nativa Galicia, −5.4397, −73.8515, 138 m, CORBIDI 12224, 12231; Requena, Sierra del Divisor, −6.9187, −73.8461, 205 m, CORBIDI 02181-82, 02186, 02190, 02220, 02415, 02523, 02634; Requena, Zona Reservada Sierra del Divisor, −6.2136, −73.2392, 500 m, CORBIDI 03878;—Madre de Dios, Manu, Cusco, Paucartambo, Kosñipata, Pillcopata, −12.8901, −71.4108, 550 m, CORBIDI 16288;—Pasco, Oxapampa, Alto Lorencillo, −10.0603, −75.1369, 301 m, CORBIDI

27722; Pasco, Oxapampa, Nueva Kametza, −10.0569, −75.1412, 302 m, CORBIDI 27701-02; Oxapampa, San Cristobal, −9.9625, −75.3727, 378 m, CORBIDI 14712;—San Martín, Picota, Area de conservación Municipal Chambira, −7.0375, −76.0900, 679 m, CORBIDI 06387;—Ucayali, Atalaya, Pulerja, −11.1847, −73.2019, 349 m, CORBIDI 19507; Coronel Portillo, Reserva Comunal el SIRA, −9.4604, −74.5501, 1000 m, CORBIDI 17454, 17462; Coronel Portillo, Rio Abujao, −8.3025, −73.6562, 275 m, CORBIDI 12964, 12988, 13048-51.

Oreobates saxatilis (*n* = 36): PERU—Cusco, La Convención, KP 59, Pongo de Mainique, −12.2581, −72.8425, 670 m, CORBIDI 05486; La Convención, Ticumpinia Chocoriari, −11.9923, −72.9870, 579 m, CORBIDI 23205;—Huánuco, Huánuco, Rio Tambo, −9.8099, −75.8315, 1615 m, CORBIDI 09037-38; Pachitea, Santa Clara (tramo medio), −9.6295, −75.8305, 1085 m, CORBIDI 14945-46, 14948;—Junín, Satipo, Carretera Mazamari-Puerto Ocopa, −11.2002, −74.4551, 561 m, CORBIDI 08913;—Loreto, Alto Amazonas, Campamento Mina de Sal, −5.8894, −76.6044, 300 m, CORBIDI 13772; Datem del Marañón, Campamento Alto Cahuapanas, −5.6644, −76.8390, 1150 m, CORBIDI 13801;—Pasco, Oxapampa, Huampal (parte alta), −10.1761, −75.5810, 1700 m, CORBIDI 07295;—San Martín, Lamas, Rio Mayo, −6.2507, −76.6636, 688 m, CORBIDI 06339, 06341; Moyobamba, 2.4 Km al este de Calzada (ciudad), −6.0252, −77.0430, 1040 m, CORBIDI 03131; Moyobamba, Área de Conservación Municipal Mishquiyacu, −6.0588, −76.9764, 989 m, CORBIDI 03281, 03290-92, 03300-02; Moyobamba, CENTRO POBLADO DE PAITOJA, −6.3561, −77.0675, 1618 m, CORBIDI 01246; Moyobamba, MISHQUILLACU, −6.0755, −76.9764, 985 m, CORBIDI 01424, 01432, 01435; Moyobamba, Pabloyacu, −6.0651, −76.9417, 936 m, CORBIDI 03250-51, 03263; Picota, Area de conservación Municipal Chambira, −7.0375, −76.0900, 679 m, CORBIDI 06350-51, CORBIDI 06395; Picota, Parque Nacional Cordillera Azul, Puesto de control 16 Chambirillo, −7.0691, −76.0153, 1122 m, CORBIDI 08851; Rioja, Bajo Naranjillo, −5.8108, −77.3892, 844 m, CORBIDI 03331, 01396; San Martín, Bocatoma, −6.4572, −76.3485, 462 m, CORBIDI 08949;—Ucayali, Coronel Portillo, RC El Sira, al oeste de la CCNN Amaquiria, −9.4795, −74.4645, 242 m, CORBIDI 21829.

Appendix B

Table A1. Genbank accession codes for sequences used in phylogenetic analyses. Newly generated sequences are in bold.

Species	Voucher	12S	16S	COI	RAG	TYR
Oreobates amarakaeri	MHNC6975	JF809934	JF809996	NA	JF809913	JF809891
Oreobates amarakaeri	EB10.13	NA	MG820146	MG820171	NA	NA
Oreobates antrum	ZUFG8710	MH025430	MH025454	NA	MH025439	MH025448
Oreobates ayacucho	MNCN(IDlR5024)	JF809933	JF809970	NA	JF809912	JF809890
Oreobates barituensis	MCN1359	JF809935	JF809999	NA	JF809914	JF809892
Oreobates berdemenos	FML24623	NA	KJ125509	NA	NA	NA
Oreobates chiquitanus	SMF88499	NA	MW029644	NA	NA	NA
Oreobates chiquitanus	MNKA7175	JF809923	EU192296	NA	JF809902	JF809882
Oreobates choristolemma	CBG765	JF809921	FJ539067	NA	JF809900	JF809881
Oreobates colanensis	CORBIDI 21191	NA	MZ015004	**PZ287746**	PZ760909	**PZ288738**
Oreobates colanensis	CORBIDI 23749	NA	**PZ288745**	NA	NA	NA
Oreobates cruralis	KU215462	EU186666	EU186666	NA	EU186743	EU186764
Oreobates cruralis	sw1064.15	NA	MH458943	NA	NA	NA
Oreobates discoidalis	MNCN43133	JF809925	FJ539068	NA	JF809904	JF809884
Oreobates gemcare	MHNC6687	JF809930	JF809961	NA	JF809909	NA
Oreobates gemcare	MUSM27903	NA	KY652648	KY672981	KY672964	KY681069
Oreobates granulosus	AC94.07	NA	KY652649	KY672982	KY672965	KY681070
Oreobates granulosus	AC111.16	NA	MH458945	**PZ287745**	**PZ288728**	**PZ288739**
Oreobates granulosus	MHNC3396	JF809929	EU368897	NA	JF809908	JF809887

Table A1. *Cont.*

Species	Voucher	12S	16S	COI	RAG	TYR
Oreobates heterodactylus	ZUEC14119	NA	KJ125510	NA	NA	NA
Oreobates ibischi	MNKA6612	FJ438817	FJ438806	NA	NA	NA
Oreobates ibischi	MNCN 42959	NA	FJ438794	NA	NA	NA
Oreobates lehri	MUSM27616	JF809927	JF809957	NA	JF809906	NA
Oreobates lehri	MHNC5845	NA	JF809995	NA	NA	NA
Oreobates lundbergi	MTD45902	JF809928	JF809958	NA	JF809907	JF809886
Oreobates machiguenga	MHNC6809	JF809932	JF809969	NA	JF809911	JF809889
Oreobates madidi	MNKA7856	JF809922	FJ539070	NA	JF809901	NA
Oreobates pereger	MTD46808	JF809926	JF809955	NA	JF809905	JF809885
Oreobates quixensis	QZ31186	NA	MZ429970	NA	MZ560991	JF809893
Oreobates quixensis	QCAZ25520	NA	JF810002	NA	PP536411	NA
Oreobates quixensis	KU178249	EF493828	EF493662	NA	NA	NA
Oreobates quixensis	MNCN43147	NA	EU192297	NA	NA	NA
Oreobates remotus	MZUSP141720	MH025426	JN688274	NA	MH025435	MH025444
Oreobates sanctaecrucis	MNKA5507	JF809924	JF809951	NA	JF809903	JF809883
Oreobates sanctaecrucis	CBG153	NA	EU368903	NA	NA	NA
Oreobates sanderi	MNCN42017	NA	EU368904	NA	NA	NA
Oreobates saxatilis	KU212327	EU186726	EU186708	NA	EU186742	EU186763
Oreobates saxatilis	MHNC6775	JF809931	JF809962	NA	JF809910	JF809888
Oreobates shunkusacha	MUSM 41864	NA	PX125890	NA	NA	NA
Oreobates yanucu	ZFMK72569	NA	KY111322	NA	NA	NA
Oreobates azulensis	CORBIDI 28925	NA	**PZ288741**	**PZ284374**	**PZ288729**	**PZ288734**
Oreobates azulensis	CORBIDI 28936	NA	**PZ288742**	**PZ284375**	**PZ288730**	**PZ288735**
Oreobates nigrumcompletum	CORBIDI 28690	NA	**PZ288748**	**PZ284378**	**PZ288732**	**PZ288736**
Oreobates nigrumcompletum	CORBIDI 28689	NA	**PZ288749**	**PZ284379**	**PZ288733**	**PZ288737**
Oreobates chirimoto	CORBIDI 20361	NA	**PZ288743**	**PZ284376**	**PZ288727**	NA
Oreobates chirimoto	CORBIDI 20362	NA	**PZ288744**	**PZ284377**	NA	NA
Oreobates foliaspectrum	CORBIDI 28465	NA	**PZ288746**	NA	**PZ288731**	NA
Oreobates foliaspectrum	CORBIDI 28467	NA	**PZ288747**	NA	NA	NA
Lynchius tabaconas	MHNC8650	KX470774	KX470781	NA	KX470790	KX470797
Niceforonia elassodiscus	QCAZ52495	MW567328	MW567375	NA	MW451754	NA
Leptodactylus bolivianus	KU 289191	DQ158417	DQ158417	NA	DQ158343	NA

References

1. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.; Kent, J. Biodiversity Hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [CrossRef] [PubMed]
2. Olson, D.M.; Dinerstein, E.; Wikramanayake, E.D.; Burgess, N.D.; Powell, G.V.N.; Underwood, E.C.; D'Amico, J.A.; Itoua, I.; Strand, H.E.; Morrison, J.C.; et al. Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience* **2001**, *51*, 933–938. [CrossRef]
3. Hutter, C.R.; Cobb, K.A.; Portik, D.M.; Travers, S.L.; Wood, P.L., Jr.; Brown, R.M. FrogCap: A modular sequence capture probe-set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. *Mol. Ecol. Resour.* **2022**, *22*, 1100–1119. [CrossRef] [PubMed]
4. Montero-Mendieta, S.; De la Riva, I.; Irisarri, I.; Leonard, J.A.; Webster, M.T.; Vilà, C. Phylogenomics and evolutionary history of *Oreobates* (Anura: Craugastoridae) Neotropical frogs along elevational gradients. *Mol. Phylogenet. Evol.* **2021**, *161*, 107167. [CrossRef] [PubMed]
5. Perrigo, A.; Hoorn, C.; Antonelli, A. Why mountains matter for biodiversity. *J. Biogeogr.* **2020**, *47*, 315–325. [CrossRef]
6. Rahbek, C.; Borregaard, M.K.; Antonelli, A.; Colwell, R.K.; Holt, B.G.; Nogues-Bravo, D.; Rasmussen, C.M.; Richardson, K.; Rosing, M.T.; Whittaker, R.J. Building mountain biodiversity: Geological and evolutionary processes. *Science* **2019**, *365*, 1114–1119. [CrossRef] [PubMed]
7. Hedges, S.B.; Duellman, W.E.; Heinicke, M.P. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa* **2008**, *1737*, 1–182. [CrossRef]
8. Heinicke, M.P.; Lemmon, A.R.; Lemmon, E.M.; McGrath, K.; Hedges, S.B. Phylogenomic support for evolutionary relationships of New World direct-developing frogs (Anura: Terraranae). *Mol. Phylogenet. Evol.* **2018**, *118*, 145–155. [CrossRef] [PubMed]
9. Padial, J.M.; Grant, T.; Frost, D.R. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. *Zootaxa* **2014**, *3825*, 1–132. [CrossRef] [PubMed]

10. Frost, D.R.; Frost, D.R. Amphibian Species of the World: An Online Reference. Version 6.2. 2026. Available online: https://amphibiansoftheworld.amnh.org/index.php (accessed on 8 April 2026).
11. Catenazzi, A.; Mamani, L.; Lehr, E.; May, R.v. A New Genus of Terrestrial-Breeding Frogs (Holoadeninae, Strabomantidae, Terrarana) from Southern Peru. *Diversity* **2020**, *12*, 184. [CrossRef]
12. Duellman, W.E.; Lehr, E. *Terrestrial Breeding Frogs (Strabomantidae) in Peru*; Natur und Tier-Verlag GmbH: Münster, Germany, 2009; p. 382.
13. Ferro, J.M.; Taffarel, A.; Cardozo, D.; Grosso, J.; Puig, M.P.; Suárez, P.; Akmentins, M.S.; Baldo, D. Cytogenetic characterization and B chromosome diversity in direct-developing frogs of the genus *Oreobates* (Brachycephaloidea, Craugastoridae). *Comp. Cytogenet.* **2016**, *10*, 141. [CrossRef] [PubMed]
14. Motta, A.P.; Chaparro, J.C.; Pombal, J.J.P.; Guayasamin, J.M.; De la Riva, I.; Padial, J.M. Molecular Phylogenetics and Taxonomy of the Andean GenusLynchiusHedges, Duellman, and Heinicke 2008 (Anura: Craugastoridae). *Herpetol. Monogr.* **2016**, *30*, 119–142. [CrossRef]
15. Padial, J.M.; Chaparro, J.C.; Castroviejo-Fisher, S.; Guayasamin, J.M.; Lehr, E.; Delgado, A.J.; Vaira, M.; Teixeira, M., Jr.; Aguayo, R.; de la Riva, I. A revision of species diversity in the Neotropical genus *Oreobates* (Anura Strabomantidae), with the description of three new species from the Amazonian slopes of the Andes. *Am. Mus. Novit.* **2012**, *3752*, 55. [CrossRef]
16. von May, R.; Diaz, M.I.; Ttito, A.; Santa-Cruz, R.; Catenazzi, A. The Rediscovery of *Noblella peruviana* after More than 115 Years Helps Resolve the Molecular Phylogeny and Taxonomy of Noblella (Amphibia, Anura, Strabomantidae). *Diversity* **2024**, *16*, 613. [CrossRef]
17. Ortega, J.A.; Cisneros-Heredia, D.F.; Camper, J.D.; Romero-Carvajal, A.; Negrete, L.; Ron, S.R. Systematics of minute strabomantid frogs allocated to the genus *Noblella* (Amphibia: Anura) with description of a new genus, seven new species, and insights into historical biogeography. *Zool. J. Linn. Soc.* **2025**, *203*, zlae162. [CrossRef]
18. Castillo-Urbina, E.; Vences, M.; Dezetter, M.; Glaw, F.; Burgos, C.; Aliaga, L.; Torres-Ccasani, G.; Hope, S.F.; Mendoza, A.; Köhler, J. New insights into the diversity of *Oreobates* frogs (Anura: Craugastoridae): Description of a new species from the Peruvian Yungas and comments on *O. quixensis* and *O. saxatilis*. *Salamandra* **2025**, *61*, 423–441.
19. Pansonato, A.; Motta, A.; Cacciali, P.; Haddad, C.F.; Strüssmann, C.; Jansen, M. On the identity of species of *Oreobates* (Anura: Craugastoridae) from Central South America, with the description of a new species from Bolivia. *J. Herpetol.* **2020**, *54*, 393–412. [CrossRef] [PubMed]
20. Vaz-Silva, W.; Maciel, N.M.; De Andrade, S.P.; Amaro, R.C. A new cryptic species of *Oreobates* (Anura: Craugastoridae) from the seasonally dry tropical forest of central Brazil. *Zootaxa* **2018**, *4441*, 89–108. [CrossRef] [PubMed]
21. Venegas, P.J.; García-Ayachi, L.A.; Ormeño, J.; Bullard, S.; Catenazzi, A.; Motta, A.P. Two new species of terrestrial-breeding frogs (Anura: Brachycephaloidea) from Cordillera de Colán, Peru. *Neotrop. Biodivers.* **2021**, *7*, 279–296. [CrossRef]
22. Beaupre, S.J.; Jacobson, E.R.; Lillywhite, H.B.; Zamudio, K. *Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research*; American Society of Ichthyologists and Herpetologists: Norman, OK, USA, 2004; p. 43. Available online: https://www.asih.org/resources (accessed on 8 April 2026).
23. Scott, N.J. Complete species inventories. In *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*; Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1994; pp. 78–84.
24. McDiarmid, R.W. Appendix 4: Preparing amphibians as scientific specimens. In *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*; Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1994; pp. 279–286.
25. Lehr, E. A new species of the *Eleutherodactylus nigrovittatus* group (Anura: Leptodactylidae) from Andean Peru. *Herpetologica* **2005**, *61*, 199–208. [CrossRef]
26. Palumbi, S.; Martin, A.; Romano, S.; McMilan, W.O.; Stice, L.; Grabowski, G. *Simple Fool's Guide to PCR: Version 2.0*; University of Hawaii: Honolulu, HI, USA, 2002; p. 45.
27. von May, R.; Catenazzi, A.; Corl, A.; Santa-Cruz, R.; Carnaval, A.C.; Moritz, C. Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. *Ecol. Evol.* **2017**, *7*, 3257–3267. [CrossRef] [PubMed]
28. Catenazzi, A.; Ttito, A. A new species of *Psychrophrynella* (Amphibia, Anura, Craugastoridae) from the humid montane forests of Cusco, eastern slopes of the Peruvian Andes. *PeerJ* **2016**, *4*, e1807. [CrossRef] [PubMed]
29. Katoh, K.; Standley, D.M. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Mol. Biol. Evol.* **2013**, *30*, 772–780. [CrossRef] [PubMed]
30. Nguyen, L.-T.; Schmidt, H.A.; von Haeseler, A.; Minh, B.Q. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **2015**, *32*, 268–274. [CrossRef] [PubMed]
31. Minh, B.Q.; Nguyen, M.A.T.; Von Haeseler, A. Ultrafast approximation for phylogenetic bootstrap. *Mol. Biol. Evol.* **2013**, *30*, 1188–1195. [CrossRef] [PubMed]

32. Letunic, I.; Bork, P. Interactive Tree of Life (iTOL) v6: Recent updates to the phylogenetic tree display and annotation tool. *Nucleic Acids Res.* **2024**, *52*, W78–W82. [CrossRef] [PubMed]
33. Fouquet, A.; Gilles, A.; Vences, M.; Marty, C.; Blanc, M.; Gemmell, N.J. Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS ONE* **2007**, *2*, e1109. [CrossRef] [PubMed]
34. Padial, J.M.; De la Riva, I. Integrative taxonomy reveals cryptic Amazonian species of *Pristimantis* (Anura Strabomantidae). *Zool. J. Linn. Soc.* **2009**, *155*, 97–122. [CrossRef]
35. Vences, M.; Thomas, M.; Van der Meijden, A.; Chiari, Y.; Vieites, D.R. Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Front. Zool.* **2005**, *2*, 5. [CrossRef] [PubMed]
36. Kumar, S.; Stecher, G.; Suleski, M.; Sanderford, M.; Sharma, S.; Tamura, K. MEGA12: Molecular evolutionary genetic analysis version 12 for adaptive and green computing. *Mol. Biol. Evol.* **2024**, *41*, msae263. [CrossRef] [PubMed]
37. Padial, J.M.; Miralles, A.; De la Riva, I.; Vences, M. The integrative future of taxonomy. *Front. Zool.* **2010**, *7*, 16. [CrossRef] [PubMed]
38. de Queiroz, K. The general lineage concept of species, species criteria, and the process of speciation. In *Endless Forms: Species and Speciation*; Howard, D.J., Berlocher, S.H., Eds.; Oxford University Press: Oxford, UK, 1998; pp. 57–75.
39. de Queiroz, K. Species concepts and species delimitation. *Syst. Biol.* **2007**, *56*, 879–886. [CrossRef] [PubMed]
40. Köhler, J.; Padial, J.M. Description and phylogenetic position of a new (singleton) species of *Oreobates* Jiménez de la Espada, 1872 (Anura: Craugastoridae) from the Yungas of Cochabamba, Bolivia. *Ann. Carnegie Mus.* **2016**, *84*, 23–38. [CrossRef]
41. Padial, J.M.; Chaparro, J.C.; De La Riva, I. Systematics of *Oreobates* and the *Eleutherodactylus discoidalis* species group (Amphibia, Anura), based on two mitochondrial DNA genes and external morphology. *Zool. J. Linn. Soc.* **2008**, *152*, 737–773. [CrossRef]
42. Zhang, W.; Guo, Y.; Li, J.; Huang, L.; Kazitsa, E.G.; Wu, H. Transcriptome analysis reveals the genetic basis underlying the seasonal development of keratinized nuptial spines in *Leptobrachium boringii*. *BMC Genom.* **2016**, *17*, 978. [CrossRef] [PubMed]
43. Jungfer, K.-H. The taxonomic status of some spiny-backed treefrogs, genus *Osteocephalus* (Amphibia: Anura: Hylidae). *Zootaxa* **2010**, *2407*, 28–50. [CrossRef]
44. Jungfer, K.-H.; Verdade, V.K.; Faivovich, J.; Rodrigues, M.T. A new species of spiny-backed treefrog (*Osteocephalus*) from Central Amazonian Brazil (Amphibia: Anura: Hylidae). *Zootaxa* **2016**, *4114*, 171–181. [CrossRef] [PubMed]
45. Ron, S.; Pramuk, J.B. A new species of *Osteocephalus* (Anura: Hylidae) from Amazonian Ecuador and Peru. *Herpetologica* **1999**, *55*, 433–446.
46. Coloma, L.; Duellman, W.; Almendáriz, A.; Ron, S.; Teran-Valdez, A.; Guayasamin, J. Five new (extinct?) species of *Atelopus* (Anura: Bufonidae) from Andean Colombia, Ecuador, and Peru. *Zootaxa* **2010**, *2574*, 1–54. [CrossRef]
47. Peters, J.A. *The Frog Genus Atelopus in Ecuador (Anura: Bufonidae)*; Smithsonian Institution Press: Washington, DC, USA, 1973; p. 49.
48. AmphibiaWeb. Available online: https://amphibiaweb.org (accessed on 8 April 2026).
49. Coloma, L.; Duellman, W. *Amphibians of Ecuador: Craugastoridae*; CRC Press: Boca Ratón, FL, USA, 2025; Volume III, p. 522.
50. EchevarrÍA, L.Y.; Venegas, P.J.; GarcÍA-Ayachi, L.A.; Bravo, A.G.; Torres-Carvajal, O. Facing a slithery dragon: Systematics of the *Petracola ventrimaculata* (Boulenger, 1900) species complex (Squamata: Gymnophthalmidae) with description of five new species. *Zootaxa* **2026**, *5792*, 245–286. [CrossRef] [PubMed]
51. Guzman, B.K.; García-Bravo, A.; Allauja-Salazar, E.E.; Mejía, I.A.; Guzmán, C.T.; Oliva, M. Endemism of woody flora and tetrapod fauna, and conservation status of the inter-Andean Seasonally Dry Tropical Forests of the Marañón valley. *Glob. Ecol. Conserv.* **2021**, *28*, e01639. [CrossRef]
52. Hazzi, N.A.; Moreno, J.S.; Ortiz-Movliav, C.; Palacio, R.D. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 7985–7990. [CrossRef] [PubMed]
53. Weir, J.T. Implications of genetic differentiation in neotropical montane forest birds1. *Ann. Mo. Bot. Gard.* **2009**, *96*, 410–433. [CrossRef]
54. Winger, B.M.; Bates, J.M. The tempo of trait divergence in geographic isolation: Avian speciation across the Marañon Valley of Peru. *Evolution* **2015**, *69*, 772–787. [CrossRef] [PubMed]
55. Hosner, P.A.; Andersen, M.J.; Robbins, M.B.; Urbay-Tello, A.; Cueto-Aparicio, L.; Verde-Guerra, K.; Sánchez-González, L.A.; Navarro-Sigüenza, A.G.; Boyd, R.L.; Núñez, J. Avifaunal surveys of the upper Apurímac River Valley, Ayacucho and Cuzco Departments, Peru: New distributional records and biogeographic, taxonomic, and conservation implications. *Wilson J. Ornithol.* **2015**, *127*, 563–581. [CrossRef]
56. Lehr, E.; Catenazzi, A. A new species of Bryophryne (Anura: Strabomantidae) from southern Peru. *Zootaxa* **2008**, *1784*, 1–10. [CrossRef]
57. Lehr, E.; Catenazzi, A. Two new species of Bryophryne (Anura: Strabomantidae) from high elevations in southern Peru (Region of Cusco). *Herpetologica* **2010**, *66*, 308–319. [CrossRef]
58. Elias-Costa, A.J.; Faivovich, J. Convergence to the tiniest detail: Vocal sac structure in torrent-dwelling frogs. *Biol. J. Linn. Soc.* **2019**, *128*, 390–402. [CrossRef]

59. Emerson, S.B. Testing pattern predictions of sexual selection: A frog example. *Am. Nat.* **1994**, *143*, 848–869. [CrossRef] [PubMed]
60. Garcia-Gomez, I.; Pereyra, M.O.; Cabra-Garcia, J.; Ospina-Sarria, J.J. Evolutionary history of secondary sexual characters in the most species-rich genus of anurans, the direct-developing frogs of the genus *Pristimantis* (Anura: Strabomantidae). *Biol. J. Linn. Soc.* **2022**, *136*, 264–281. [CrossRef]
61. Moura, P.H.A.G.; Elias-Costa, A.J.; Nunes, I.; Faivovich, J. Diversity and evolution of the extraordinary vocal sacs of casque-headed treefrogs (Anura: Hylidae). *Biol. J. Linn. Soc.* **2021**, *134*, 423–442. [CrossRef]
62. Targino, M.; Elias-Costa, A.J.; Taboada, C.; Faivovich, J. Novel morphological structures in frogs: Vocal sac diversity and evolution in Microhylidae (Amphibia: Anura). *Zool. J. Linn. Soc.* **2019**, *187*, 479–493. [CrossRef]
63. Emerson, S.B.; Boyd, S.K. Mating vocalizations of female frogs: Control and evolutionary mechanisms. *Brain Behav. Evol.* **1999**, *53*, 187–197. [CrossRef] [PubMed]
64. Starnberger, I.; Preininger, D.; Hödl, W. The anuran vocal sac: A tool for multimodal signalling. *Anim. Behav.* **2014**, *97*, 281–288. [CrossRef] [PubMed]
65. Wells, K.D. The social behaviour of anuran amphibians. *Anim. Behav.* **1977**, *25*, 666–693. [CrossRef]
66. Wells, K.D. The effect of social interactions on anuran vocal behavior. In *The Evolution of the Amphibian Auditory System*; John Wiley and Sons: New York, NY, USA, 1988; pp. 433–454.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.