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Two new species of gymnophthalmid lizards of the genus *Petracola* (Squamata: Cercosaurinae) from the Andes of northeastern Peru, and their phylogenetic relationships

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Abstract.—The small and semi-fossorial lizards of the genus *Petracola* are distributed in the Andes from central to northern Peru, on both sides of the dry valley of the Marañón River. Very little is known about the taxonomy of *Petracola*, but it is presumed that this genus harbors a higher number of species than is currently known. Here, we used a Maximum Likelihood (ML) molecular phylogenetic analysis using concatenated fragments of four mitochondrial genes (12S, 16S, *cyt-b*, and ND4) and one nuclear gene (*c-mos*), and the revision of museum specimens, to determine the species diversity of populations of *Petracola* on both sides of the Marañón River. Our results show that *Petracola* is a monophyletic genus composed of three independent lineages. The first lineage includes two undescribed species from the right side of the Marañón River, which we describe herein. The second lineage corresponds to *P. ventrimaculatus*, and the third lineage includes *P. waka* which contains undescribed species. Among the two new species from the right side of the Marañón River, *P. amazonensis* can be identified by having only the first superciliary expanded to the dorsal surface, two pairs of genials in contact, absence of a loreal scale, venter orange with black spots forming a transverse band, absence of precloacal pores, and a maximum SVL of 43.0 mm in females; whereas *P. shurugojalcapi* can be identified by having two genials in contact, absence of a loreal scale, two discontinuous superciliaries, black venter, dorsum dark brown or black with some cream spots, and an absence of precloacal pores. The two new species increase the diversity of this genus to seven species, four of which inhabit the right side of the dry valley of the Marañón River. However, like other genera of gymnophthalmid Andean lizards, the diversity of *Petracola* is still underestimated.

Keywords. Andean lizard, Cercosaurini, dry valley, endemic species, northern Andes, Marañón River, semi-fossoriality

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Introduction

The genus *Petracola* Doan and Castoe, 2005, is a poorly studied Andean lineage of small and semi-fossorial lizards distributed in the central and northern Andes of Peru, on both margins of the dry valley of the Marañón River (DVMR) (Doan and Castoe 2005; Kizirian et al. 2008; Köhler and Lehr 2004; Uzzell 1970). The species of *Petracola* inhabit ecosystems of montane cloud forests, inter-Andean valleys, and wet *puna* at elevations from 1,889 to 3,600 m asl.

The systematics and taxonomy of *Petracola* are poorly developed, and geographic information gaps prevent an appreciation of the full diversity and distribution of the genus. The type species of *Petracola*, *P. ventrimaculatus* (Boulenger, 1900), was initially assigned to *Proctoporus* by Boulenger (1900). Previously, based on morphological characters such as the presence of smooth dorsal scales, three postparietal scales, short limbs, and the presence of entire palpebral disc, Uzzell (1970) assigned *P. ventrimaculatus* to the *Proctoporus pachyurus* group. Further analyses based on molecular data and a taxonomic

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review led to the creation of the genus *Petracola* (Castoe et al. 2004; Doan and Castoe 2005), which has been supported by recent studies (Goicoechea et al. 2012; Mamani et al. 2020, 2022; Moravec et al. 2018; Torres-Carvajal et al. 2016). Species of *Petracola* are phylogenetically related to Andean speciose lineages containing *Cercosaura*, *Potamites*, and *Proctoporus*, and minor lineages such as “*Cercosaura manicata boliviana*,” *Dendrosauridion*, *Selvasaura*, and *Wilsonosaura* (Mamani et al. 2020, 2022; Moravec et al. 2018; Rojas-Runjaic et al. 2021). Despite the increasing knowledge about high-Andean gymnophthalmids accumulated over the past decade, the diversity of gymnophthalmid species continues to be underestimated.

Currently, the genus contains five species: *Petracola angustisoma* Echevarría and Venegas, 2015; *P. labioocularis* (Köhler and Lehr, 2004); *P. pajatensis* Rodríguez and Mamani, 2020; *P. ventrimaculatus*, and *P. waka*, Kizirian, Bayefsky-Anand, Eriksson, Le and Donnelly 2008. Although Kizirian et al. (2008) hypothesized that *P. ventrimaculatus* and *P. waka* represent complexes of species, only two more species have been described since 2015 (Echevarría and Venegas 2015; Rodríguez and Mamani 2020). Moreover, this genus has a peculiar distribution on both sides of the DVMR, in which *Petracola angustisoma* and *P. pajatensis* are distributed on the right side (Echevarría and Venegas 2015; Köhler and Lehr 2004; Rodríguez and Mamani 2020), *P. waka* is distributed on the left side, and *P. ventrimaculatus* is distributed on both sides of the Marañón River (Kizirian et al. 2008).

Vicariant topographic features such as the DVMR introduce genetic barriers between populations on the two sides of the valley, promoting the diversification of lineages (Futuyma and Kirkpatrick 2017). The ornithological literature supports the hypothesis that the arid valley of the DVMR interrupts gene flow between populations and promotes allopatric speciation (Hazzi et al. 2018; Weir 2009; Winger and Bates 2015), but this hypothesis has not been tested in other biological groups, and especially in philopatric organisms such as gymnophthalmid lizards (Doan et al. 2021). Here, based on an analysis of morphological data and molecular phylogenetic relationships of four mitochondrial genes (12S, 16S, *cyt-b*, and ND4) and one nuclear gene (*c-mos*) from specimens collected on both sides of the DVMR, we evaluated the hypothesis proposed by Kizirian et al. (2008) that *Petracola ventrimaculatus* and *P. waka* are species complexes, and we describe two new species from those complexes.

Material and Methods

Data Collection and Morphology

Specimens of the new species were collected in Department Amazonas, Peru, and are deposited in the Colección Científica Pro Fauna Ayacucho (PFAUNA) and the Museo de Biodiversidad del Perú (MUBI). Specimens were collected by hand, euthanized, fixed in 10% formalin, and

stored in 70% ethanol. Tissue samples were stored in 2 ml cryogenic tubes filled with 96% ethanol. The terminology for diagnostics and format description follows Uzzell (1970), Kizirian (1996), Mamani et al. (2022), and Mamani and Rodríguez (2022). Measurements were taken with calipers to the nearest 0.1 mm. Abbreviations for measurements are as follows: SVL (snout-vent length), TL (tail length), LAL (length between arm and leg), LSA (length from the tip of snout to anterior margin of the insertion of the arm), HL (head length, from the tip of snout to posterior margin of tympanum), HW (head width, maximum width of head), HH (head height, maximum height of head), FR (frontal length), and FN (frontonasal length). Morphological data of *Petracola* species were taken from the literature (Echevarría and Venegas 2015; Kizirian et al. 2008; Köhler and Lehr 2004; Rodríguez and Mamani 2020) and the examination of voucher specimens deposited at the Museo de Historia Natural de la Universidad Nacional de San Marcos (MUSM), Lima, Peru; Museo de Biodiversidad del Perú (MUBI), Cusco, Peru; and Colección Científica Pro Fauna Silvestre (PFAUNA), Ayacucho, Peru. The specimens examined are listed in Appendix I.

DNA Extraction, Amplification, Sequencing, and Phylogenetic Reconstruction

We extracted DNA from the tissue samples of seven voucher specimens of *Petracola* (Table 1) from both sides of the DVMR. We used standard protocols (Mamani et al. 2020) to amplify fragments of the small subunit rRNA (12S), large subunit rRNA (16S), dehydrogenase subunit 4 (ND4), cytochrome b (*cyt-b*), and oocyte maturation factor gene (*c-mos*). The new DNA sequences are available in GenBank (Appendix 1; <https://www.ncbi.nlm.nih.gov/genbank/>). We obtained additional sequences of congeneric species and representative species of different gymnophthalmid genera and outgroups (following Moravec et al. 2018) from GenBank. We excluded *Petracola ventrimaculatus* (AY507894) from our data set of the gene ND4, because the sample was nested within *Cercosaura* genus in a previous exploratory analysis, suggesting a possible labeling error or contamination. The final data set contained 137 operational taxonomic units (OTU) and 2,384 bp of concatenated fragments (458 bp for 12S, 561 bp for 16S, 345 bp for *cyt-b*, 639 bp for ND4, and 381 bp for *c-mos*) (Table S1).

The genetic sequences were aligned using MUSCLE software (Edgar 2004) implemented in MEGA-X (Kumar et al. 2018). We inferred the phylogenetic relationships using a Maximum Likelihood (ML) approach in IQTREE Web server (Trifinopoulos et al. 2016). The evolution models were estimated in ModelFinder (Kalyaanamoorthy et al. 2017) and were TIM2+F+I+G4 for 12S, GTR+F+R4 for 16S, TIM2e+I+G4 for *cytb*, GTR+F+R5 for ND4, and TPM3+F+G4 for *c-mos*. Branch supports were estimated for 10,000 replicates using ultrafast Bootstrap (Hoang et al. 2018). Following Moravec et al. (2018), we used *Alopoglossus atriventris*, *Bachia bresslaui*, *B. dorbignyi*, *B. flavescens*, *Ecpleopus gaudichaudii*, *Gymnophthalmus*

Table 1. Voucher museum specimens of *Petracola* lizards, mentioning their collection locations and GenBank codes sequences used in this study. All localities are from Peru.

Species/voucher	Locality	12S	16S	ND4	cytb	c-mos
<i>P. amazonensis</i> MUBI 11473	Chiliquin, Chachapoyas, Amazonas	OR231541	OR231652	OR208583	OR198057	OR211561
<i>P. shurugojalcapi</i> MUBI 17727	La Jalca, Chachapoyas, Amazonas	OR231542	OR231653	-	OR198058	OR211562
<i>P. shurugojalcapi</i> PFAUNA 430	La Jalca, Chachapoyas, Amazonas	OR231543	OR231654	-	OR198059	OR211563
<i>P. waka</i> MUBI 2603	Baños del Inca, Cajamarca, Cajamarca	OR231544	OR231655	OR208584	OR198060	OR211564
<i>P. waka</i> MUBI 2605	Baños del Inca, Cajamarca, Cajamarca	OR231545	OR231656	OR208585	OR198061	OR211565
<i>P. waka</i> MUBI 2609	Type locality, Cajabamba, Cajamarca	OR231546	OR231657	OR208586	OR198062	-
<i>P. waka</i> MUBI 2611	Type locality, Cajabamba, Cajamarca	OR231547	OR231658	OR208587	OR198063	OR211566

leucomystax, *Rhachisaurus brachylepis*, *Riolama inopinata*, and *R. leucosticta* as outgroup taxa.

We estimated uncorrected *p*-distances between species of *Petracola* for the 16S gene using MEGA-X (Kumar et al. 2018). Genetic distances for 16S larger than 3% separate most species of gymnophthalmid lizards (Torres-Carvajal et al. 2015).

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Results

Phylogenetic Relationships and Generic Assignment

The ML tree recovered the monophyly of the ingroup Cercosaurinae (ultrafast bootstrap, UB = 100; Figs. 1 and S1). Our topology recovered the monophyly of all genera with high support, except *Proctoporus* (UB = 52). The monophyly of *Oreosaurus* was not supported, because *O. serranus* was recovered as a different lineage of *Oreosaurus*, with *Cercosaura*, “*Cercosaura manicata boliviana*,” *Dendrosauridion*, *Petracola*, *Potamites*, *Proctoporus*, and *Wilsonosaura* as its closest relatives.

The genus *Petracola* was recovered with high support (UB = 100) as sister lineage of *Cercosaura*, “*Cercosaura*

manicata boliviana,” *Dendrosauridion*, *Potamites*, *Proctoporus*, *Selvasaura*, and *Wilsonosaura* (Fig. 1). The specimens of *Petracola* from the left side of the DVMR were monophyletic, and include *P. ventrimaculatus* and *P. waka*, but the node support was low (UB = 83). Three specimens from the right side of the DVMR, including the two new species (*P. amazonensis* and *P. shurugojalcapi*), were recovered as sister lineages with high support (UB = 100) and have high uncorrected *p*-distances for the 16S gene ranging from 3.7% to 8.0% (Table 2), suggesting they might be distinct from the currently recognized taxa. Additionally, the distance between specimens of *P. waka* from the type locality (MUBI 2609, 2611) and those from Baños del Inca and Abra Gelic is 6.3–6.6%, which suggests a hidden cryptic diversity (Table 2).

Finally, our phylogeny and morphological traits such as presence of imbricate and scale-like papillae on the tongue, scales of the head without striations or rugosities, smooth dorsal scales, and absence of prefrontal scales (Doan and Castoe 2005), support the assignment to the genus *Petracola*.

Taxonomy

Petracola amazonensis sp. nov.

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Holotype. MUBI 11485, adult female (Figs. 2–4) from Upa, bridle path to Yurumarca, District of Chiliquin, Province of Chachapoyas, Department of Amazonas, Peru (6°0'9.19" S; 77°49'21.08" W; ca. 3,020 m asl), collected by Juan C. Chaparro on 23 May 2012.

Paratypes. Two specimens: A subadult male (MUBI 11473) and a subadult female (MUBI 11474) from near the type locality (5°59'40.27" S; 77°48'36.26" W; 3,250 m asl), collected by Juan C. Chaparro and Alexander Pari on 22 May 2012.

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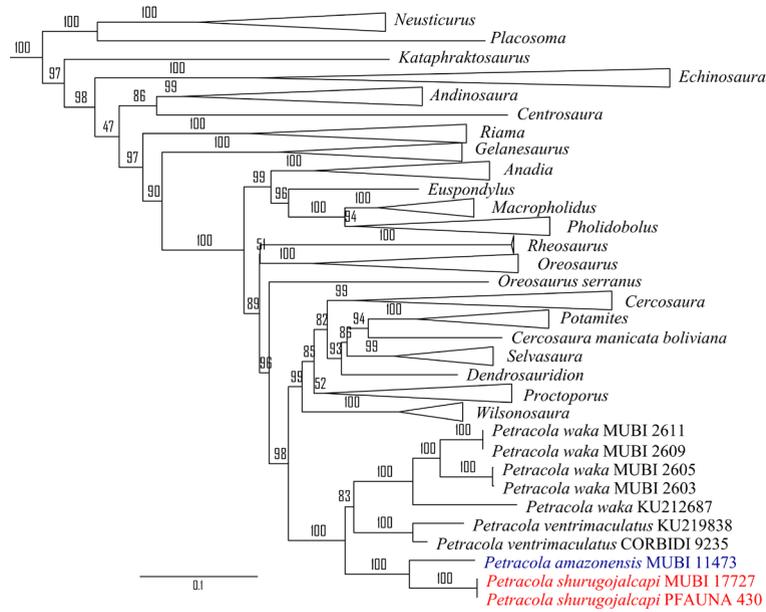


Fig. 1. Phylogenetic relationships of Cercosaurini (log likelihood = -54268.289, ultrafast bootstrap = 10,000) constructed from the data set of 2,384 nucleotides for mitochondrial genes (12S, 16S, cyt-b, and ND4) and a nuclear gene (c-mos), showing species of *Petracola* and the two new species *Petracola amazonensis* and *P. shurugoalcapu*. The numbers on the branches are ultrafast bootstraps values.

Table 2. Pairwise uncorrected *p*-distances for 16S rRNA between *Petracola* species. The asterisk (*) indicates type locality.

	1	2	3	4	5	6	7	8	9	10
(1) <i>P. ventrimaculatus</i> CORBIDI 9235	-									
(2) <i>P. ventrimaculatus</i> KU 219838	0.024	-								
(3) <i>P. waka</i> KU 212687	0.063	0.071	-							
(4) <i>P. waka</i> MUBI 2603	0.073	0.091	0.063	-						
(5) <i>P. waka</i> MUBI 2605	0.073	0.091	0.063	0.000	-					
(6) <i>P. waka</i> MUBI 2609*	0.069	0.082	0.066	0.031	0.031	-				
(7) <i>P. waka</i> MUBI 2611*	0.069	0.082	0.066	0.031	0.031	0.000	-			
(8) <i>P. shurugoalcapu</i> MUBI 17727	0.058	0.074	0.080	0.079	0.079	0.079	0.079	-		
(9) <i>P. shurugoalcapu</i> PFAUNA 430	0.058	0.074	0.080	0.079	0.079	0.079	0.079	0.000	-	
(10) <i>P. amazonensis</i> MUBI 11473	0.057	0.072	0.085	0.078	0.078	0.072	0.072	0.037	0.037	-

Etymology. The specific epithet, *amazonensis*, is an adjective in reference to the type locality in the Department of Amazonas, northern Peru.

Diagnosis: *Petracola amazonensis* is diagnosed based on the following combination of characters: (1) frontonasal longer than frontal; (2) nasoloreal suture absent; (3) two supraoculars; (4) one superciliary scale expanded on dorsal surface of head; (5) two postoculars; (6) palpebral disc transparent, entire or divided vertically in two; (7) four supralabials anterior to the posteroventral angle of the subocular; (8) 3–4 anterior infralabials; (9) four

genials in contact; (10) three rows of prelinguals; (11) dorsal body scales rectangular, smooth, juxtaposed; (12) 25–28 scales around midbody; (13) 31–32 transverse dorsal rows; (14) 18–19 transverse ventral rows; (15) 17–20 longitudinal dorsal rows; (16) 8–9 longitudinal ventral rows; (17) a continuous series of small lateral scales separate dorsals from ventral scales; (18) 2–4 posterior cloacal plate scales; (19) two anterior preanal plate scales; (20) four femoral pores per hind limb in males, two in females; (21) preanal pores absent; (22) 7–9 subdigital lamellae on finger IV; 11–14 subdigital lamellae on toe IV; (23) limbs not overlapping when

adpressed against body; (24) pentadactyl, digits clawed; and (25) coloration of female in life: dorsum is brown with numerous dark spots distributed irregularly from tip of head to tail, flanks are similar to dorsum, the chin and throat are pale orange with large black spots, venter mostly orange, with black spots on anterior part of ventral scales forming longitudinal lines (Fig. 4); coloration of males in life is unknown; in preservative the dorsum is similar to coloration in life, and venter changes from orange to cream (Fig. 2).

Petracola amazonensis can be distinguished from *P. angustisoma* and *P. pajatensis* by lacking a loreal scale (loreal scale present in *P. angustisoma* and *P. pajatensis*); from *P. labioocularis* by lacking precloacal pores and posterior subocular is not elongated downward (precloacal pores present and posterior subocular is elongated downward and separates supralabials in *P. labioocularis*); from *P. waka* by having two genials in contact, first superciliary scale, and venter is orange with black spots forming transverse bands (three genials in contact, four continuous superciliary scales, and venter is cream with some small, black spots in *P. waka*); from *P. ventrimaculatus* by having a maximum SVL in males of 43.0 mm, dorsum dark brown with some black spots not forming bands, and first superciliary only (maximum SVL in females 59.0 mm, dorsum light brown with continuous black dorsal bands, and 2–3 discontinuous superciliaries in *P. ventrimaculatus*).

Description of the holotype. Adult female, snout–vent length (SVL) 43.0 mm, tail length 42.3 mm (regenerated); head scales smooth, without striations or rugosities; rostral scale wider (1.5 mm) than tall (0.8 mm), in contact with frontonasal, nasals, and first supralabials; frontonasal longer (2.5 mm) than wide (1.7 mm), longer than frontal scale, widest in the middle, in contact with rostral, nasal, first superciliary, and frontal; prefrontal absent; frontal longer than wide, pentagonal,



Fig. 2. Holotype of *Petracola amazonensis*, female MUBI 11485 (SVL = 43.0 mm, TL = 42.3 mm).

in contact with first supraocular and frontoparietals; frontoparietal paired, polygonal (hexagonal), in contact with frontal, supraoculars, parietals, and interparietals; two supraoculars, in contact with superciliaries, frontal, frontoparietals, interparietal, and postoculars; parietals polygonal (irregular heptagon), in contact with frontoparietals, posterior supraocular, postocular, interparietal, temporals, supratemporals laterally, and with postparietals posteriorly; interparietals hexagonal, in contact with frontoparietals anteriorly, parietals laterally, and with postparietal posteriorly; two polygonal postparietals, joined in the middle by a small surface. Nasal scale entire, longer than high, in contact with first supralabial; loreal scale absent; left side with first superciliary, on right side with a posterior rudimentary posterior superciliary, first superciliaries expand on dorsal surface of head; two small preoculars; frenocular trapezoidal in contact with second supralabial; palpebral disc entire and transparent; three suboculars on right side and two on left side; two postoculars; temporals and supratemporals smooth, polygonal; four supralabials anterior to the posteroventral angle of the suboculars. Mental wider than long, in contact with the first infralabial and postmental posteriorly; postmental single, polygonal (irregular pentagonal), in contact with first and second infralabials, and first pair of genials; four genials in contact; three transversal rows of pregular scales, in the anterior row they are large; five rows of gular scales, quadrangular and circular. Dorsal scales rectangular with blunt edges, juxtaposed, smooth, 32 transverse rows; 17 longitudinal dorsal rows at midbody; a continuous series

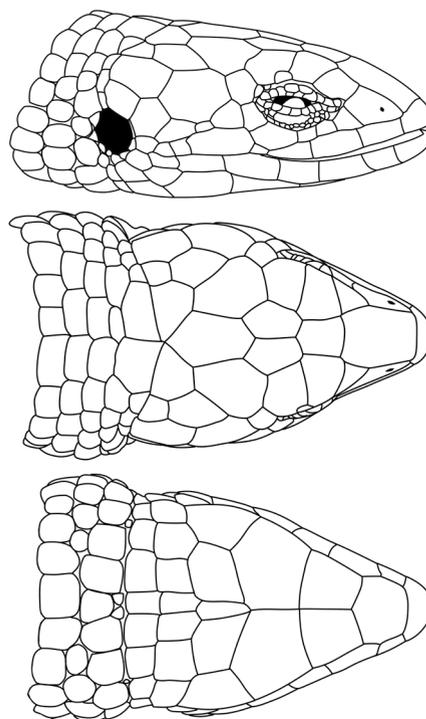


Fig. 3. Drawings of lateral, dorsal, and ventral views of the head of the holotype (MUBI 11485) of *Petracola amazonensis*.

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of small lateral scales; reduced scales at limb insertion region; 18 transverse ventral rows; eight longitudinal ventral rows at midbody; anterior and posterior preanal plate paired; scales on the tail rectangular, subimbricate, and smooth; ventral scales quadrangular, juxtaposed, and smooth. Limbs pentadactyl; digits clawed; dorsal brachial scales polygonal, imbricate, and smooth with blunt edges; ventral brachial scales small, rounded, and smooth; dorsal antibrachial scales polygonal, imbricate and smooth; ventral antibrachial scales rounded, smooth, smaller than dorsal; dorsal manus scales polygonal, smooth, imbricate; palmar scales small, rounded, and domelike; dorsal scales on fingers smooth, quadrangular, imbricate, two on finger I, three on II, five on III, five on IV, and four on V; two subdigital lamellae on finger I, five on finger II, seven on finger III, seven on finger IV, five on finger V; scales on anterodorsal surface of thigh polygonal, smooth, imbricate; scales on posterior surface of thigh small, rounded, and separated; scales on ventral surface of thighs polygonal with blunt edges, smooth, imbricate, polygonal and juxtaposed; two femoral pores on each thigh; scales on anterior surface of crus polygonal, smooth, imbricate, decreasing in size distally; scales on posterodorsal surface of crus smooth, polygonal, and imbricate; scales on ventral surface of crus polygonal, enlarged, smooth, and imbricate; scales on dorsal surface of feet polygonal, smooth, and imbricate; scales on ventral surface of feet rounded, small, and domelike; dorsal scale of toes smooth, imbricate, two on toe I, four on toe II, five on toe III, six on IV, five on toe V; four subdigital lamellae on toe I, seven on toe II, nine on toe III, 13 on toe IV, eight on toe V. Coloration in life was described in diagnosis; in preservative, dorsum, dorsal surface of head, neck, arms, and legs brown with irregular, black spots; venter, chin, neck, arms, and legs gray with black spots, on venter black spots form transverse bands (Fig. 4).



Fig. 4. Holotype in life of *Petracola amazonensis* from Upa (MUBI 11485, SVL= 43.0 mm, TL = 42.3 mm, female).

Variation. The most notable variation was the number of infraoculars: adult female with 2–3 (left-right), juvenile male with 1–2, and juvenile female with 3–3; adult female with a rudimentary posterior superciliar on the right side; juvenile male with three anterior infralabials on the right side and three postparietals; and adult female with 25 scales around body and 28 on juveniles.

Distribution and ecology. *Petracola amazonensis* is only known from the type locality, Upa near Yurumarca, from 3,020–3,250 m asl (Fig. 5), District of Chiliquin, Province of Chachapoyas, Department of Amazonas (Fig. 6). All specimens were found in grassland during March (rainy season). The specimen MUBI 11473 was found under rocks, MUBI 11474 inside bromeliads of the genus *Tillandsia*, and MUBI 11485 walking on grassland near a creek and a forest. *Petracola amazonensis* is likely diurnal and semifossorial. Syntopic Squamata species include *Stenocercus orientalis*. Tree vegetation is dominated by *Podocarpus* (Podocarpaceae), *Alnus* (Betulaceae), *Weinmannia* (Cunoniaceae), *Ceroxylon* (Arecaceae) and *Hyeronima* (Euphorbiaceae). Dominant species in the shrub layer include *Macrocarpaea* (Gentianaceae), *Munnozia* (Asteraceae), *Chusquea* (Poaceae), and *Piper* (Piperaceae); and herbs *Anthurium* (Araceae), *Tillandsia* (Bromeliaceae), orchids (Orchidaceae) and *Peperomia* (Piperaceae).

Conservation. *Petracola amazonensis* was found in a small area in the district of Chiliquin (Fig. 5), and we suspect it might be endemic to the Department of Amazonas. The type locality is 2.5–3.0 km from the Private Conservation Area “Comunal San Pablo - Catarata Gocta,” and it is very likely that the species is distributed within this conservation area. In general, the habitat where we conducted our herpetological surveys was in an acceptable state of conservation in May 2012. Given the lack of knowledge regarding its geographic distribution, we recommend that *P. amazonensis* be categorized as Data Deficient in the Red List of the International Union for Conservation of Nature (IUCN 2022).



Fig. 5. Type locality of *Petracola amazonensis*, Upa, District of Chiliquin, Province of Chachapoyas, Department of Amazonas.

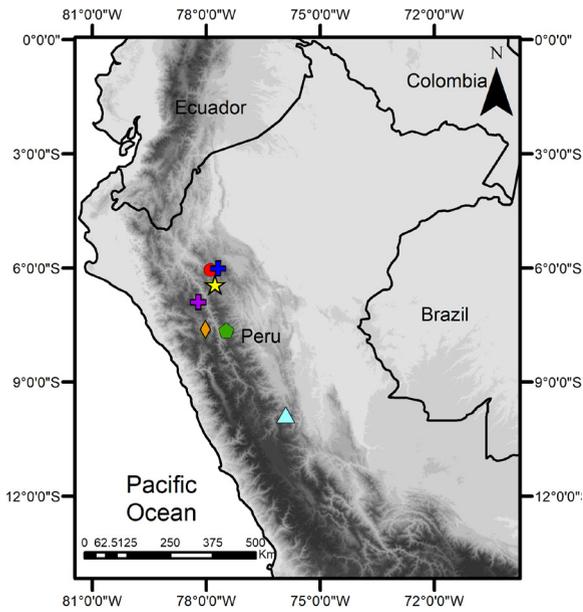


Fig. 6. Map showing the type localities of *Petracola* species: *Petracola amazonensis* (blue cross), *P. angustisoma* (red circle), *P. labioocularis* (light blue triangle), *P. pajatensis* (green pentagon), *P. shurugojalcapi* (yellow star), *P. ventrimaculatus* (purple cross), and *P. waka* (orange diamond).

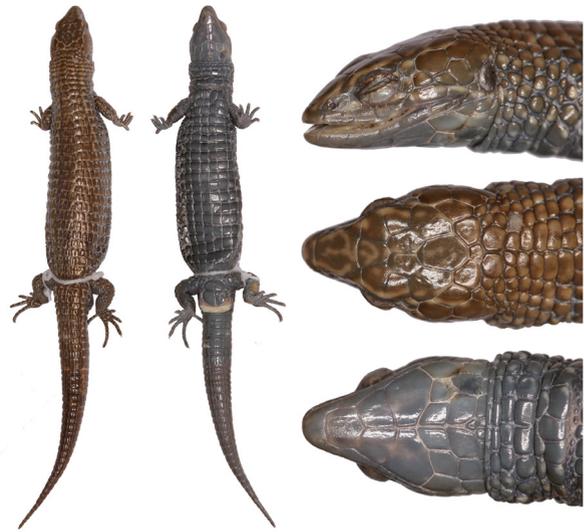


Fig. 7. Holotype of *Petracola shurugojalcapi*, adult female PFAUNA 431 (SVL = 51.0 mm, TL = 39.0 mm).

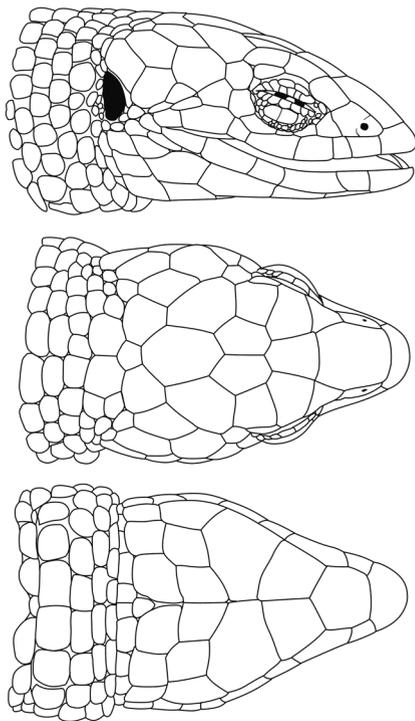


Fig. 8. Drawings of lateral, dorsal, and ventral views of the head of the holotype (PFAUNA 431) of *Petracola shurugojalcapi*.



Fig. 9. Holotype in life of *Petracola shurugojalcapi* from La Jalca Grande (PFAUNA 431, SVL = 51.0 mm, TL = 39.0 mm, adult female).

Petracola shurugojalcapi sp. nov.

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Holotype. PFAUNA 431, adult female (Figs. 7–9) from Área de Conservación Privada Llamapampa-La Jalca, District of Jalca Grande, Province of Chachapoyas, Department of Amazonas, Peru (6°25'36" S; 77°45'56" W; 2,990 m asl), collected by Victor Vargas on 30 May 2013.

Paratypes. Seven specimens: Two adult males (PFAUNA 427, MUBI 17727), subadult male (PFAUNA 432), and two adult female (PFAUNA 429, MUBI 17726) from the same place as the holotype. A male (PFAUNA 430) and female (PFAUNA 433) were collected near the type locality (6°25'36" S; 77°45'56" W; ca. 2,990 m asl).

Etymology. The specific epithet, *shurugojalcapi*, treated as a noun in apposition, is a combination of two local words: “shurugo” the local name for a gymnophthalmid lizard and “jalcapi” that means “from Jalca” in the Quechua language. The specific name was proposed by the inhabitants of La Jalca Grande.

Diagnosis. *Petracola shurugojalcapi* is diagnosed based on the following combination of characters: (1) frontonasal longer than frontal; (2) nasoloreal suture absent; (3) two supraoculars; (4) two discontinuous superciliaries, first expanded onto dorsal surface of head; (5) two postoculars; (6) palpebral disc transparent, divided vertically in two; (7) 3–4 supralabials anterior to the posteroventral angle of the subocular; (8) four anterior infralabials; (9) four genials in contact; (10) three rows of pregulars; (11) dorsal body scales rectangular, smooth, juxtaposed; (12) 29–32 scales around midbody; (13) 31–33 transverse dorsal rows; (14) 18–21 transverse ventral rows; (15) 19–23 longitudinal dorsal rows; (16) eight longitudinal ventral rows; (17) a continuous series of small lateral scales separating dorsals from ventrals; (18) 2–4 posterior cloacal plate scales; (19) two anterior preanal plate scales; (20) 5–6 femoral pores per hind limb in males, 2–3 in females; (21) preanal pores absent; (22) 8–9 subdigital lamellae on finger IV; 13–15 subdigital lamellae on toe IV; (23) limbs not overlapping when adpressed against body; (24) pentadactyl, digits clawed; (25) coloration of males in life is brown or dark brown with or without numerous cream spots distributed irregularly on flanks, and dorsum forming four discontinuous transversal lines, venter immaculate black or blackish gray; females with brown dorsum, numerous and irregular light brown or cream spot on flanks, venter blackish gray.

Petracola shurugojalcapi can be distinguished from *P. amazonensis* by having dorsum brown with irregular dark spots, venter black with lateral cream spots, and two separate superciliaries (dorsum brown or dark-brown with irregular cream spots, venter orange with black spots forming transversal bands, and only first superciliary present in *P. amazonensis*); from *P. angustisoma* and *P. pajatensis* by not having a loreal scale (loreal scale present

in *P. angustisoma* and *P. pajatensis*); from *P. labioocularis* by lacking preloacal pores and by having the posterior subocular not elongated downward (preloacal pores present and by having posterior subocular scale elongated downward and separates supralabials in *P. labioocularis*); from *P. waka* by having the palpebral disc divided vertically, two genial scales in contact, two discontinuous superciliary scales, venter black (palpebral disc entire, three genials in contact, four continuous superciliary scales, venter cream with small black spots in *P. waka*); from *P. ventrimaculatus* by having a maximum SVL in males of 51.0 mm, dorsum dark brown or black with some cream spots not forming bands, and venter dark with lateral cream spots (maximum SVL in males 71.1 mm, dorsum light brown with continuous black longitudinal bands, and venter cream with bold black transversal band in *P. ventrimaculatus*).

Description of the holotype. Adult female, snout–vent length (SVL) 51.0 mm, tail length 39.0 mm (regenerated), head scales smooth, without striations or rugosities; rostral scale wider (2.0 mm) than tall (0.9 mm), in contact with frontonasal, nasals, and first supralabials; frontonasal longer (2.5 mm) than wide (2.1 mm), longer than frontal scale, widest in the middle part, in contact with rostral, nasal, first superciliary, and frontal; prefrontal absent; frontal longer than wide, pentagonal, in contact with first superciliary, first supraocular, and frontoparietals; frontoparietal paired, polygonal (hexagonal), in contact with frontal, supraoculars, parietals, and interparietals; supraoculars two, in contact with superciliaries, frontal, frontoparietals, interparietal, and postoculars; parietals longer than wide, polygonal (irregular heptagon), in contact with frontoparietals and superior supraocular, interparietal, temporals, and supratemporals laterally, and with postparietals posteriorly; interparietals polygonal (irregularly heptagonal), in contact with frontoparietals anteriorly, with parietals laterally, and with postparietal posteriorly; three postparietals, the middle one is smaller than laterals, polygonal. Nasal scale entire, longer than high, in contact with first and second supralabials; nasal suture does not divide the nasal, the right side has upper and lower suture, but the left side only the lower; loreal scale absent; two superciliaries, discontinuous, and first expanded onto dorsal surface of head; two preoculars; frenocular trapezoidal in contact with second and third supralabial; palpebral disc transparent and divided in two; three suboculars; two postoculars; temporals smooth, polygonal; four supralabials anterior to the posteroventral angle of suboculars. Mental wider than long, in contact with first infralabials and postmental posteriorly; postmental single, polygonal (irregular heptagonal), in contact with the first and second infralabials, and the first pair of genials; four genials in contact; three transversal rows of pregular scales; six gular scale rows, quadrangular with rounded corners, and smooth. Dorsal scales rectangular, longer than wide, juxtaposed, smooth, 34 transverse rows; 20 longitudinal dorsal scale rows at midbody; a continuous series of small lateral scales; reduced scales at limb insertion region present; 20

Table 3. Morphometric measurements of *Petracola amazonensis* and *P. shurugojalcapí*. * broken tail, ** regenerated tail.

	<i>P. shurugojalcapí</i>				<i>P. amazonensis</i>	
	PFAUNA 431	PFAUNA 427	PFAUNA 430	PFAUNA 429	MUBI 17727	MUBI 11485
	Holotype	Paratype	Paratype	Paratype	Paratype	Holotype
Sex	Female	Male	Male	Female	Male	Female
SVL	51.0	48.5	44.0	47.4	50.8	43.0
LAL	26.7	24.5	24.6	26.3	26.2	21.6
LSA	15.5	19	15	14.8	18.2	14.8
TL	39.0 (**)	65.9 (**)	52.9	7.4 (*)	32.4 (**)	42.3
HL	9.3	10.7	8.9	8.4	10.5	9.3
HW	6.8	8.2	6.9	6.2	8.1	5.6
HH	5.3	6.3	5.4	5.1	6.1	4.6
FR	1.9	2.0	1.9	1.4	2	1.4
FN	2.6	2.7	2.1	2.5	2.6	2.5

transverse ventral scale rows; eight longitudinal ventral scale rows at midbody, lateral scales slightly smaller; anterior and posterior preanal plate scales paired; scales on tail rectangular, slightly subimbricate, and smooth; ventral scales quadrangular, juxtaposed, and smooth. Limbs pentadactyl; digits clawed; dorsal brachial scales polygonal, imbricate, and smooth; ventral brachial scales rounded, separate, and smooth; dorsal antebrachial scales polygonal, imbricate and smooth; ventral antebrachial scales rounded, separate, smooth, smaller than dorsal; dorsal manus scales polygonal, smooth, imbricate; palmar scales small, rounded, separate, and dome-like; dorsal scales on fingers smooth, quadrangular, imbricate, two on finger I, five on II, five on III, five on IV, and four on V; five subdigital lamellae on finger I, eight on finger II, nine on finger III, nine on finger IV, seven on finger V; scales on anterodorsal surface of thigh polygonal, smooth, imbricate; scales on posterior surface of thigh small, rounded, and separated; scales on anteroventral surface

of thigh polygonal, smooth, imbricate and posteroventral surface of thigh small, polygonal and juxtaposed; two femoral pores in both thighs; scales on anterior surface of crus polygonal, smooth, separated, decreasing in size distally; scales on posterodorsal surface of crus smooth, polygonal, separated; scales on ventral surface of crus polygonal, enlarged, smooth, and imbricate; scales on dorsal surface of toes polygonal, smooth, and imbricate; scales on ventral surface of toes rounded, small and domelike; dorsal scale of toes smooth, imbricate, two on toe I, five on toe II, six on toe III, eight on IV, seven on V; five subdigital lamellae on toe I, eight on toe II, 11 on toe III, 14 on toe IV, ten on toe V. Coloration in life, dorsum, dorsal surface of head, neck, arms, and legs brown; lateral sides of dorsum and tail with many small and irregular, cream spots; venter, ventral surface of head, neck, arms, and legs dark gray, flanks have intense cream spots. Coloration in preservative as in life, but less intense.

Variation. Adult male MUBI 17727 has two suboculars on the right side, males have 9–12 temporal scales and females 6–9, males are more robust than females; paratype PFAUNA 432, the nasal suture scale does not divide the nasal, but connects inferiorly to the nostril; in MUBI 17727, the nasal suture connects inferiorly and superiorly to the nostril; and the nasal sutures of the other paratypes do not connect with the nostril and extend posteriorly to middle part of the nostril. Morphometric characters vary by sex and are shown in Table 3.

Distribution and ecology. *Proctopopus shurugojalcapí* is known only from the type locality, Área de Conservación Privada Llamapampa-La Jalca, from 2,940–2,990 m asl (Fig. 10), District of La Jalca, Province of Chachapoyas, Department of Amazonas (Fig. 6). All specimens (eight) were found during diurnal surveys from 10:00 to 14:00 h. The new species was found in sympatry with



Fig. 10. Type locality of *Petracola shurugojalcapí*, Área de Conservación Privada Llamapampa-La Jalca, District of la Jalca Grande, Province of Chachapoyas, Department of Amazonas.

Stenocercus sp., *Liophis* sp., and frogs *Gastrotheca monticola*, *Pristimantis schultei*, *P.* cf. *corrugatus*, *P.* sp., and *Centrolene* sp. The habitat of *P. shurugojalcapi* is dominated by trees of the genera *Weinmannia*, *Clusia*, and *Symplocos*, and shrubs of the family Melastomataceae.

Conservation. *Petracola shurugojalcapi* was found during field studies in support of the establishment of the Área de Conservación Privada Llamapampa-La Jalca. The Conservation Area was established on 17 April 2015, protecting more than 26,000 ha of montane forest and wet grasslands. However, this important area is not exempt from threats such as deforestation and land use changes associated with local subsistence farming, ranching, and forest fires. Although available data indicate that this species could have a restricted distribution, adjacent areas remain unexplored and could host additional populations. Therefore, we recommend that *P. shurugojalcapi* be categorized as Data Deficient in the Red List of the International Union for Conservation of Nature (IUCN 2022).

Discussion

Our ML phylogenetic analysis recovered the monophyly of *Petracola* with respect to a clade including *Cercosaura*, *Cercosaura manicata boliviana*, *Dendrosauridion*, *Proctoporus*, *Potamites*, and *Wilsonosaura*, a result that is congruent with previous studies (Moravec et al. 2018; Rojas-Runjaic et al. 2021; Mamani et al. 2022). All generic lineages were recovered with high support, except *Proctoporus* and *Pholidobolus*. The genus *Proctoporus* has not been conclusively defined, with some studies supporting its monophyly (e.g., Goicoechea et al. 2012; Mamani et al. 2022; Sánchez-Pacheco et al. 2018; this study), while others do not (e.g., Rojas-Runjaic et al. 2021; Torres-Carvajal et al. 2016; Vásquez-Restrepo et al. 2020). In fact, the topologies of phylogenetic trees differ depending on the methods of phylogenetic reconstruction (Bayesian inference and Maximum Likelihood; Mamani et al. 2022; Moravec et al. 2018). Sánchez-Pacheco et al. (2018) showed that *Proctoporus* is monophyletic when using Maximum Parsimony approximation with either the combined data set of DNA + morphology or the dataset of DNA only. Sánchez-Pacheco et al. (2018) also recovered the monophyly of *Oreosaurus* (including *O. serranus*). However, recent studies showed that *Oreosaurus* is not monophyletic (e.g., Mamani et al. 2022; Rojas-Runjaic et al. 2021). Despite conflicting results, progress from studies using molecular phylogenetic analyses have improved tree topologies overall.

Our phylogenetic analysis recovered multiple diagnosable lineages within *Petracola*, including *P. amazonensis*, *P. shurugojalcapi* (UB=100), *P. ventrimaculatus* (UB=100), and the *P. waka* species complex (UB=100). This preliminary result shows that the species from the right side of the DVMR are an independent lineage with respect from those of the left side (*P. ventrimaculatus* and *P. waka*). However, our sampling

is considered as only preliminary (including only two species) and should be taken with caution. Finally, the phylogenetic position of two species that inhabit the right side of the DVMR, *P. angustisoma* and *P. pajatensis*, is unknown. If our hypothesis is correct, *P. angustisoma* and *P. pajatensis* should form a monophyletic lineage together with *P. amazonensis* and *P. shurugojalcapi*.

Despite the low number of localities sampled, our results supported the hypothesis proposed by Kizirian et al. (2008) that *P. ventrimaculatus* and *P. waka* are cryptic species complexes. Likewise, the populations of *P. waka* and *P. ventrimaculatus* are independent lineages at the species level with high genetic distance and should be recognized as such (Fig. 1, Table 2). Furthermore, we describe two of these species collected on the right side of the DVMR, which increases the diversity of the genus to seven species. The first available sequence of *P. waka* in GenBank (named as *Proctoporus* sp (KU212687) by Castoe et al. 2004) was collected from Abra Gelic, a remote locality (80 km) north of the type locality (Cajabamba), and we added samples from the Cajabamba and Baños del Inca 70 km northwest of the type locality. The molecular evidence suggests that specimens from both Abra Gelic and Baños del Inca belong to undescribed species that will be treated in a separate study. The landscape between these locations is heterogeneous and includes the Huamachuquino River, which is characterized by having arid vegetation (pers. obs.) that could promote vicariance.

Finally, our results suggest that the populations of *Petracola* on the right side of the DVMR are evolutionarily independent from the populations on the left side. These results are similar to those proposed for birds (Hazzi et al. 2018; Weir 2009; Winger and Bates 2015), supporting the hypothesis that the DVMR promotes allopatric speciation of Andean lineages. However, more extensive sampling is needed to determine whether all *Petracola* species on the right side are monophyletic, and to uncover the true diversity of this rarely studied group.

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Literature Cited

- Boulenger GA. 1900. Descriptions of new batrachians and reptiles collected by Mr. P.O. Simons in Peru. *Annals Magazine of Natural History* 6(7): 181–186.
- Castoe TA, Doan TM, Parkinson CL. 2004. Data partitions and complex models in Bayesian analysis: the phylogeny of gymnophthalmid lizards. *Systematic Biology* 53(3): 448–469.
- Doan TM, Castoe TA. 2005. Phylogenetic taxonomy of the Cercosaurini (Squamata: Gymnophthalmidae), with new genera for species of *Neusticurus* and *Proctoporus*. *Zoological Journal of the Linnean Society* 143(3): 405–416.
- Doan TM, Sheffer SA, Warmington NR, Evans EE. 2021. Population biology of the unusual thermoconforming lizards of the Andes Mountains of Peru (Squamata: Gymnophthalmidae). *Austral Ecology* 46: 1,039–1,051.
- Echevarría LY, Venegas PJ. 2015. A new elusive species of *Petracola* (Squamata: Gymnophthalmidae) from the Utcubamba basin in the Andes of northern Peru. *Amphibian & Reptile Conservation* 9(1) [Special Section]: 26–33 (e107).
- Edgar RC. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1,792–1,797.
- Futuyma DJ, Kirkpatrick M. 2017. *Evolution*. Sinauer Associates, Sunderland, Massachusetts, USA. 599 p.
- Goicoechea N, Padial JM, Chaparro JC, Castroviejo-Fisher S, De la Riva I. 2012. Molecular phylogenetics, species diversity, and biogeography of the Andean lizards of the genus *Proctoporus* (Squamata: Gymnophthalmidae). *Molecular Phylogenetics and Evolution* 65(3): 953–964.
- Hazzi NA, Moreno JS, Ortiz-Movliav C, Palacio RD. 2018. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 115(31): 7,985–7,990.
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS. 2018. UFBot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518–522.
- IUCN. 2022. IUCN Red List of Threatened Species. Available: <https://www.iucnredlist.org>. [Accessed: 30 January 2023].
- Kalyaanamoorthy S, Minh BQ, Wong TKF, Von Haeseler A, Jermin LS. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587–589.
- Kizirian D, Bayefsky-Anand S, Eriksson A, Le M, Donnelly MA. 2008. A new *Petracola* and re-description of *P. ventrimaculatus* (Squamata: Gymnophthalmidae). *Zootaxa* 1700(1): 53–62.
- Kizirian DA. 1996. A review of Ecuadorian *Proctoporus* (Squamata: Gymnophthalmidae) with descriptions of nine new species. *Herpetological Monographs* 10: 85–155.
- Köhler G, Lehr E. 2004. Comments on *Euspondylus* and *Proctoporus* (Squamata: Gymnophthalmidae) from Peru, with the description of three new species and a key to the Peruvian species. *Herpetologica* 60(4): 501–518.
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1,547–1,549.
- Mamani L, Cruz R, Mallqui S, Catenazzi A. 2022. Molecular phylogenetics and comparative examination of voucher specimens reveal two new species of gymnophthalmid lizards (Squamata, Gymnophthalmidae) from the Peruvian Andes, with comments on *Proctoporus guentheri* (Boettger, 1891). *Diversity* 14(3): 215.
- Mamani L, Rodríguez LO. 2022. A new species of Andean lizard, *Proctoporus* (Gymnophthalmidae: Cercosaurinae), from the highland of Parque Nacional Otishi in Peru. *Zootaxa* 5213(1): 75–85.
- Mamani L, Chaparro JC, Correa C, Alarcón C, Salas CY, Catenazzi A. 2020. A new species of Andean gymnophthalmid lizard (Squamata: Gymnophthalmidae) from the Peruvian Andes, and resolution of some taxonomic problems. *Diversity* 12(9): 361.
- Moravec J, Šmíd J, Štundl J, Lehr E. 2018. Systematics of neotropical microteiid lizards (Gymnophthalmidae, Cercosaurinae), with the description of a new genus and species from the Andean montane forests. *ZooKeys* 774: 105–139.
- Rodríguez LO, Mamani L. 2020. A new species of *Petracola* (Squamata: Gymnophthalmidae) from Rio Abiseo National Park, San Martín, Peru. *Amphibian & Reptile Conservation* 14(1) [General Section]: 140–146 (e227).
- Rojas-Runjaic FJM, Barrio-Amorós CL, Señaris JC, De la Riva I, Castroviejo-Fisher S. 2021. Discovery of an additional piece of the large gymnophthalmid puzzle: a new genus and species of stream spiny lizard (Squamata: Gymnophthalmidae: Cercosaurinae) from the western Guiana Shield in Venezuela. *Zootaxa* 4950(2): 296–320.
- Sánchez-Pacheco SJ, Torres-Carvajal O, Aguirre-Peñafiel V, Nunes PMS, Verrastro L, Rivas GA, Rodrigues MT, Grant T, Murphy RW. 2018. Phylogeny of *Riama* (Squamata: Gymnophthalmidae), impact of phenotypic evidence on molecular datasets, and the origin of the Sierra Nevada de Santa Marta endemic fauna. *Cladistics* 34: 260–291.
- Torres-Carvajal O, Lobos SE, Venegas PJ, Chávez G, Aguirre-Peñafiel V, Zurita D, Echevarría LY. 2016. Phylogeny and biogeography of the most diverse clade of South American gymnophthalmid lizards (Squamata, Gymnophthalmidae, Cercosaurinae). *Molecular Phylogenetics and Evolution* 99: 63–75.
- Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ.

Two new species of *Petracola* from Peru

2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44(W1): W232–W235.

Uzzell TM. 1970. Teiid lizards of the genus *Proctoporus* from Bolivia and Peru. *Postilla* 142: 1–39.

Vásquez-Restrepo JD, Ibáñez R, Sánchez-Pacheco SJ, Daza JM. 2020. Phylogeny, taxonomy, and distribution of the Neotropical lizard genus *Echinosaura* (Squamata: Gymnophthalmidae), with the recognition

of two new genera in Cercosaurinae. *Zoological Journal of the Linnean Society* 189(1): 287–314.

Weir JT. 2009. Implications of genetic differentiation in neotropical montane forest birds. *Annals of the Missouri Botanical Garden* 96(3): 410–433.

Winger BM, Bates JM. 2015. The tempo of trait divergence in geographic isolation: avian speciation across the Marañon Valley of Peru. *Evolution* 69(3): 772–787.



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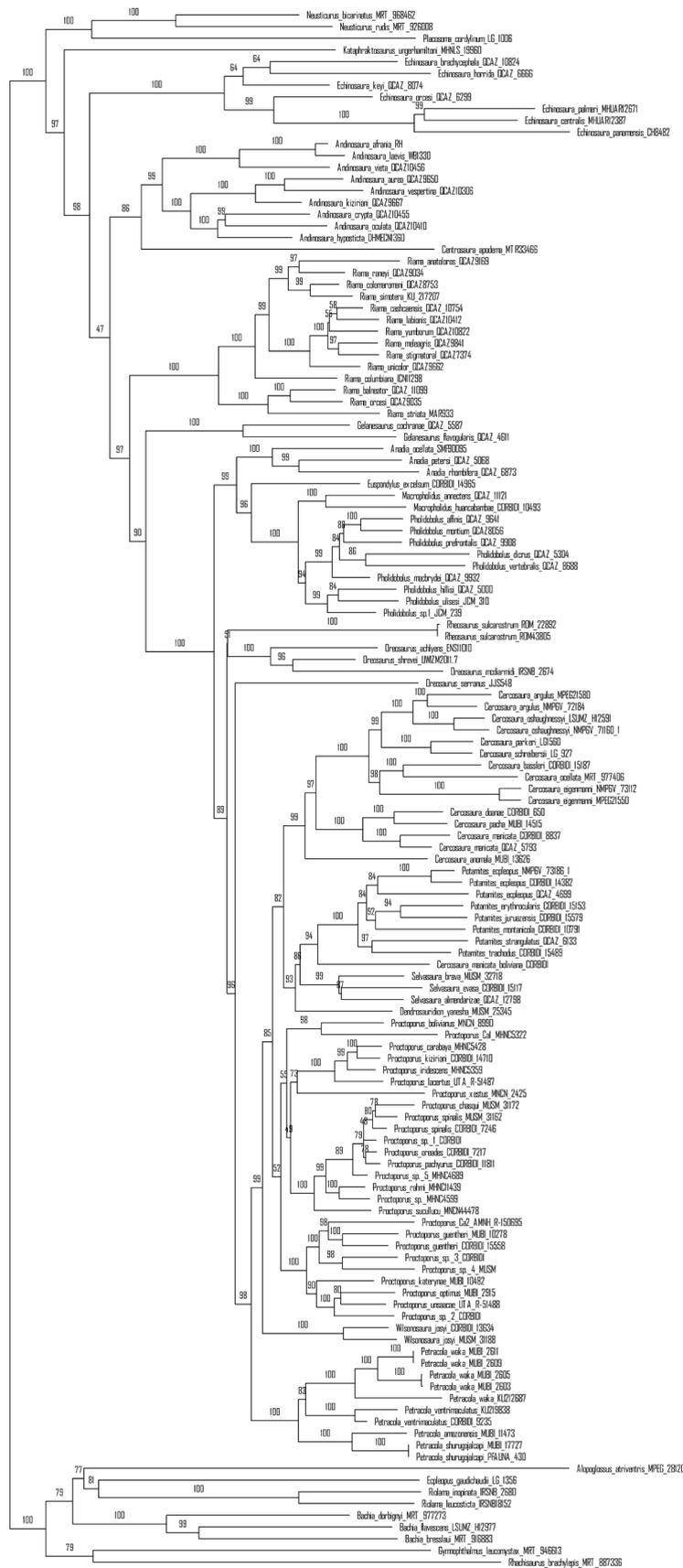


Fig. S1. Phylogenetic relationships of Cercoosaurini (log likelihood = -54268.289, ultrafast bootstrap = 10,000) constructed from the data set of 2,384 nucleotides for mitochondrial genes (12S, 16S, cyt-b, and ND4) and a nuclear gene (c-mos).