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A New Genus of Gymnophthalmid Lizard from the Central Peruvian Andes †

Luis Mamani [1,*], Víctor J. Vargas-García [2,3], Juan C. Chaparro [1], Germán Chávez [4] and Alessandro Catenazzi [5]

[1] Museo de Biodiversidad del Perú (MUBI), Cusco 08000, Peru; jchaparroauza@yahoo.com
[2] Asociación Pro Fauna Silvestre Ayacucho (PFAUNA), Ayacucho 05001, Peru; vjvargasg@gmail.com
[3] Servicio Nacional Forestal y de Fauna Silvestre (SERFOR), Lima 15076, Peru
[4] Instituto Peruano de Herpetología (IPH), Lima 15038, Peru; vampflack@yahoo.com
[5] Department of Biological Sciences, Florida International University (FIU), Miami, FL 33199, USA; acatenazzi@gmail.com
* Correspondence: luismamanic@gmail.com
† urn:lsid:zoobank.org:pub:4B01D450-D88E-467D-B404-E741B2D05476.

Abstract

The Andes harbor extraordinary species richness, but a substantial proportion of their biodiversity remains insufficiently documented. Among their most diverse lineages are lizards of the family Gymnophthalmidae, whose diversity remains underestimated. Here, we assess the phylogenetic position and taxonomic status of a poorly known group of cercosaurine lizards from the eastern slopes of the central Peruvian Andes. We examined preserved specimens from the departments of Pasco and Huánuco and obtained DNA sequences of one nuclear (*c-mos*) and four mitochondrial markers (12S, 16S, ND4, and Cytb). These sequences were combined with data retrieved from GenBank to assemble a multilocus matrix of 2290 base pairs representing 153 terminal taxa. Phylogenetic relationships were inferred under a maximum-likelihood approach. The six focal specimens formed a clade within Cercosaurini, with strong support (UFBoot = 100) for its phylogenetic placement and monophyly. This new clade is distinguished from closely related genera by a distinctive combination of external morphological characters, including the presence of precloacal pores and the third subocular extending ventrally between the supralabial scales. Based on the congruence between molecular and morphological evidence, we describe *Perusaurus* gen. nov., transfer *Petracola labioocularis* to the new genus as *Perusaurus labioocularis* comb. nov., and based on morphological evidence, we also transfer *Proctoporus laudahnae* to *Perusaurus laudahnae* comb. nov. The clade also includes at least two species awaiting formal description. The recognition of *Perusaurus* demonstrates that the evolutionary diversity of Cercosaurinae in the Peruvian Andes remains considerably underestimated.

Keywords: Andes; Cercosaurinae; Gymnophthalmidae; molecular phylogeny; new genus; Peru

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1. Introduction

Lizards of the family Gymnophthalmidae constitute one of the most diverse lineages of Neotropical lizards, comprising approximately 300 species distributed from southern Mexico to Argentina [1,2]. Although they are widely distributed across numerous regions of Central and South America, the Andes, Amazonia, and the Guiana Shield harbor the highest levels of species diversity and endemism of Gymnophthalmidae [2]. The earliest-diverging evolutionary lineages are primarily concentrated in Amazonia and the Guiana

Shield, whereas the highest speciation rates occur in the tropical Andes and adjacent lowlands [3]. This pattern is particularly evident in Cercosaurinae, the most diverse radiation within Gymnophthalmidae, which appears to have originated in the northern Andes, followed by subsequent diversification and dispersal events toward the central Andes and Amazonia [4].

The taxonomic history of Gymnophthalmidae has been particularly complex because of unstable generic taxonomy, high levels of intraspecific variation, and pronounced interspecific similarity across several lineages. These characteristics have hindered the identification of consistent diagnostic characters, because many of the traits traditionally used in the classification of the family have evolved convergently [4–7]. As a consequence of this morphological similarity, numerous semifossorial species were assigned to *Proctoporus* [8], whereas species with semiaquatic habits were grouped within *Neusticurus* [9].

Subsequently, phylogenetic analyses based on DNA sequence data clarified the evolutionary relationships among these lineages and reorganized Gymnophthalmidae taxonomy [4,6,7,10–12]. This approach also facilitated the recognition and description of new genera, including *Selvasaura* [11], *Dendrosauridion* [13], and *Wilsonosaura* [14]. Collectively, these advances highlight the importance of integrating molecular and morphological evidence to accurately delimit and classify species in groups characterized by high interspecific morphological similarity and substantial intraspecific variation.

In the central Andes of Peru, *Proctoporus laudahnae* and *Petracola labioocularis* were originally described within *Proctoporus* [15]. *Petracola labioocularis* exhibits both a continuous series of femoral pores between the hind limbs, including the precloacal pores, a condition originally described as "no scales between medialmost femoral pores," and a third subocular extending ventrally between the supralabials. In contrast, *Proctoporus laudahnae* shares only the latter character, with the third subocular extending ventrally between the supralabials, whereas the precloacal pores are separated by a pair of scales, and femoral pores are separated from precloacal pores by a narrow gap (see Figure 4 in Köhler and Lehr [15]). These characters do not correspond to the morphological pattern typically observed in *Proctoporus* or in other geographically proximate genera, such as *Euspondylus*, *Cercosaura*, *Petracola*, or *Selvasaura*. In contrast, the presence of precloacal pores has been documented in genera such as *Acratosaura*, *Bachia*, *Colobosaura*, *Leposoma*, and others distributed primarily in Amazonia [16]. Nevertheless, these genera are phylogenetically and geographically distant from the species of the central Peruvian Andes, suggesting that this combination of characters may represent an independently evolved and taxonomically informative condition within Andean lineages.

Following its description, *Proctoporus labioocularis* was transferred to *Petracola* by Doan and Castoe [6] on the basis of morphological evidence. However, Echevarría et al. [17] noted that its combination of characters and disjunct distribution are inconsistent with those of congeneric species and therefore recommended treating it as *incertae sedis* within Cercosaurinae until its phylogenetic position could be evaluated using molecular evidence. In contrast, *P. laudahnae* was included in the phylogeny of Torres-Carvajal et al. [4] based on the two specimens CORBIDI 15558 and 15743. Subsequent examination showed that the specimens had been misidentified and actually represent members of the *Proctoporus guentheri* species complex rather than true *P. laudahnae* [18]. Chávez and Chávez-Arribasplata [19] additionally reported a population from the left bank of the Huallaga River that they identified as *P. laudahnae*. However, these specimens differ from *P. laudahnae sensu stricto* in lacking a nasoloreal suture and in having 32–34 transverse dorsal scale rows, whereas *P. laudahnae* has a nasoloreal suture and 37 transverse dorsal scale rows. This combination of characters suggests that the reported population may represent a distinct, undescribed species rather

than *P. laudahnae*. Consequently, no verified genetic data are currently available for *P. laudahnae sensu stricto*, and its phylogenetic position remains unresolved.

The combination of morphological characters exhibited by *Proctoporus laudahnae* and *Petracola labioocularis*, together with the limited availability of reliable molecular evidence, has hindered efforts to clarify their phylogenetic position within Cercosaurinae. Despite preliminary morphological and molecular evidence supporting the distinctiveness of this lineage [20], its phylogenetic relationships and taxonomic status remain unresolved.

In the present study, we generated new DNA sequences from specimens identified as *Petracola labioocularis* and from additional unidentified specimens exhibiting a similar combination of morphological characters (Figures 1 and 2). We integrated these molecular data with a comparative assessment of the external morphology of the available specimens, supplemented by original species descriptions, taxonomic diagnoses, and illustrations of related taxa. Using this integrative approach, we aimed to: (1) infer their phylogenetic relationships within Cercosaurinae; (2) assess whether the analyzed specimens constitute an independent evolutionary lineage; and (3) determine whether their phylogenetic position and their combination of morphological characters support the recognition of a new genus.

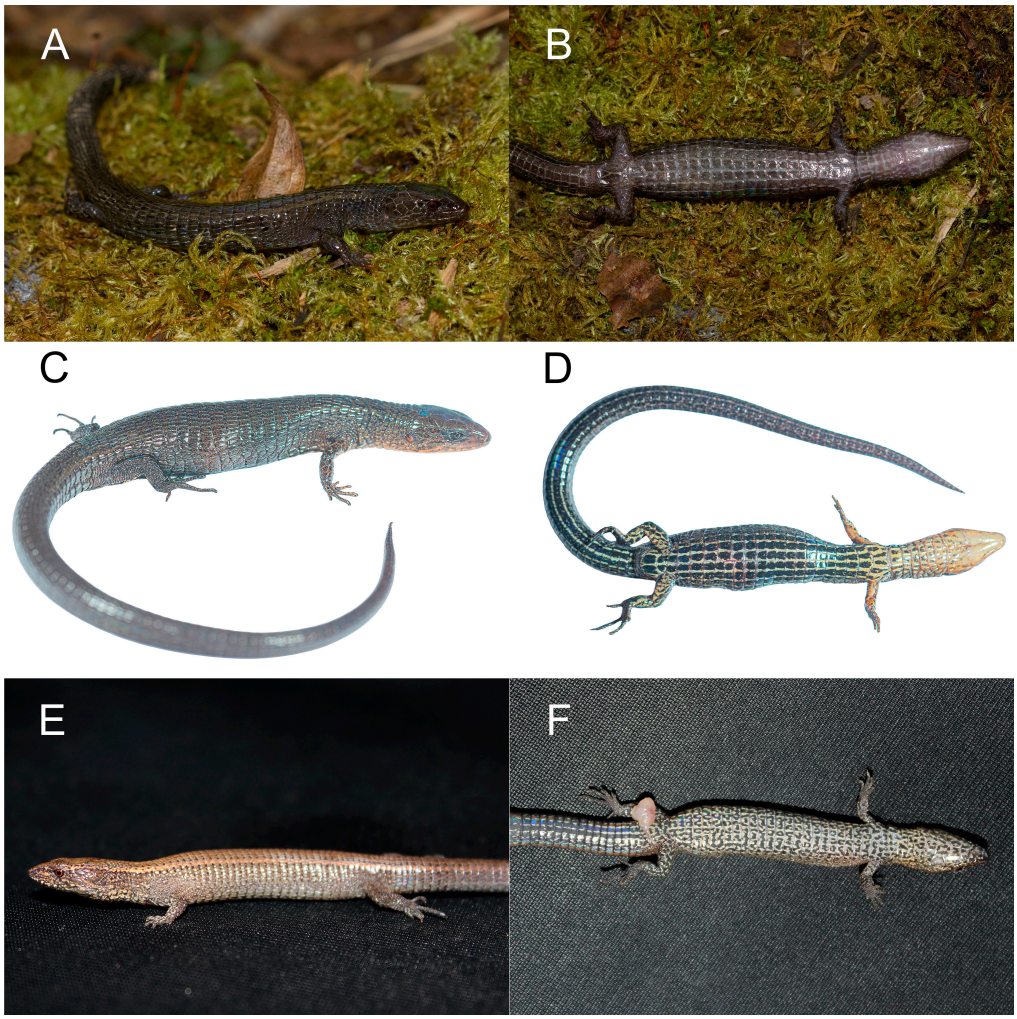


Figure 1. Lateral and ventral views of three species of *Perusaurus* gen. nov. *Perusaurus labioocularis* ((**A**,**B**), female, MUBI 14232), *Perusaurus* sp. 1 ((**C**,**D**), female, CORBIDI 16071), *Perusaurus* sp. 2 ((**E**,**F**), male, MUBI 13266).

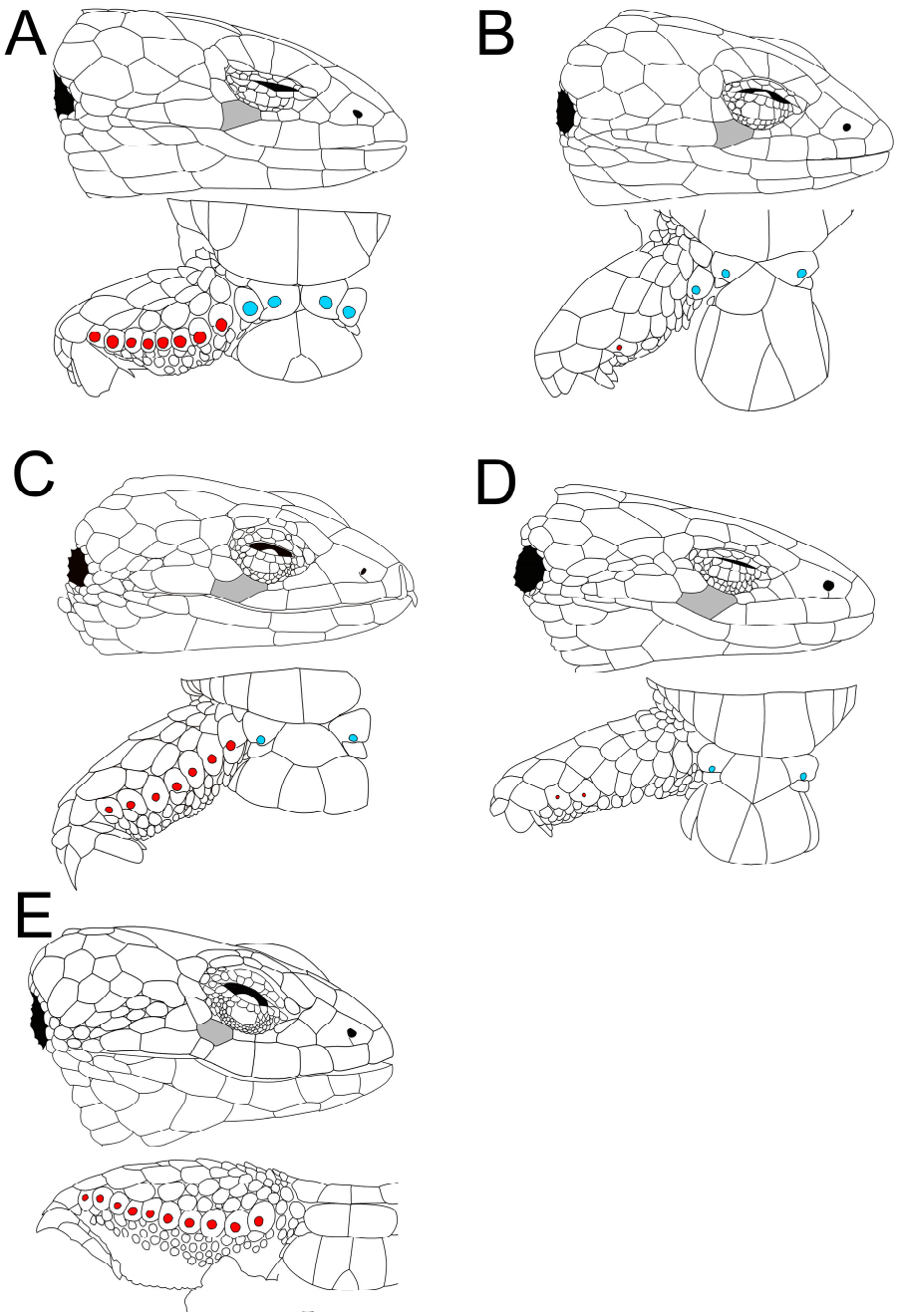


Figure 2. Drawings of the head, ventral surfaces of the hind limbs, and cloacal region of *Perusaurus labioocularis* ((**A**), male, MUBI 14252; (**B**), female, MUBI 14254), *Perusaurus* sp. 2 ((**C**), male, MUBI 13266; (**D**), female, MUBI 11462), and *Proctoporus rahmi* ((**E**), male, MUBI 4688). Gray shading indicates the third subocular, which extends ventrally between the supralabials and separates them in *Perusaurus* (**A**–**D**), but does not separate them in *Proctoporus rahmi* (**E**). Light blue indicates precloacal pores, whereas red indicates femoral pores.

2. Materials and Methods

2.1. Sampling and Morphological Characterization

We examined preserved specimens (Appendix A) and obtained tissue samples from six individuals deposited in the scientific collections of the Centro de Ornitología y Biodiversidad (CORBIDI), Museo de Biodiversidad del Perú (MUBI), and Asociación Pro Fauna Silvestre Ayacucho (PFAUNA). The specimens were collected in the central Andes of Peru, specifically in the departments of Pasco and Huánuco (Table 1, Figure 1).

Table 1. Voucher specimens, collection localities, geographic coordinates, and GenBank accession numbers for the newly generated sequences included in this study.

Species/Voucher	Locality	Coordinates	12S	16S	Cytb	ND4	*c-mos*
Perusaurus labioocularis MUBI14252	Peru: Huánuco: Chaglla: Monte Potrero	9°54′57.31″ S, 76°3′53.36″ W	QB133587	QB133589	QB174404	QB174408	QB174412
Perusaurus sp. 1 CORBIDI16071	Peru: Huánuco: Achupampa	9°43′42.70″ S, 75°56′47.80″ W	QB133586	QB133592	QB174403	QB174407	QB174413
Perusaurus sp. 1 CORBIDI16072	Peru: Huánuco: Achupampa	9°43′42.70″ S, 75°56′47.80″ W	QB133585	QB133591	QB174402	NA	QB174414
Perusaurus sp. 2 PFAUNA447	Peru: Huánuco: Ambo: Saccsahuanca	10°13′17.62″ S, 76°8′36.48″ W	QB133582	QB133590	QB174399	QB174405	QB174410
Perusaurus sp. 2 MUBI11457	Peru: Pasco: Malhuapampa	10°25′0.41″ S, 76°11′20.82″ W	QB133584	QB133588	QB174401	QB174409	QB174411
Perusaurus sp. 2 MUBI11461	Peru: Pasco: Malhuapampa	10°25′0.41″ S, 76°11′20.82″ W	QB133583	NA	QB174400	QB174406	NA

Scale characters were examined on both sides of the body using an AmScope SM-6TPZ-64S-5M stereomicroscope (AmScope, Irvine, CA, USA). Morphometric measurements were taken using a digital caliper with a precision of 0.1 mm. The terminology used to describe the external morphological characters included in the diagnosis primarily followed Uzzell [8], Kizirian [21], and Mamani and Rodríguez [22]. However, we avoided the expressions "fusion of the anterior superciliary with the first supraocular" and "fusion of the posterior subocular with a supralabial" because, based on our observations, we found no incomplete sutures or other morphological evidence supporting the interpretation of these conditions as resulting from the fusion of originally independent scales. Instead, we used the terms "first superciliary dorsally expanded" and "third subocular extending ventrally between the supralabial scales," which we consider to describe the observed configuration more precisely and objectively. Sex was determined by examination of the hemipenes and the characteristic swelling at the base of the tail in males. Morphological characters of other species and genera used for comparative purposes were obtained from the specialized literature and from the examination of specimens deposited in the three scientific collections mentioned above.

2.2. DNA Extraction and Sequencing

Genomic DNA was extracted from muscle tissue preserved in 96% ethanol using a commercial extraction kit from IBI Scientific (Dubuque, IA, USA; catalog no. B47282). We obtained 27 gene fragments comprising one nuclear gene encoding the oocyte maturation factor (*c-mos*) and four mitochondrial genes: the small and large subunits of ribosomal RNA (12S and 16S, respectively), NADH dehydrogenase subunit 4 (ND4), and cytochrome b (Cytb) (Table 1). Polymerase chain reactions (PCRs) were performed following standardized protocols using the primers listed in Table 2. PCR products were purified using ExoSAP-IT Express (Affymetrix, Santa Clara, CA, USA) and subsequently sent to MCLAB (San Francisco, CA, USA) for bidirectional sequencing. The sequences generated in this study were deposited in GenBank (Table 1). Additionally, 555 sequences representing 147 terminal taxa were retrieved from GenBank: 141 sequences of 12S, 147 of 16S, 127 of ND4, 20 of Cytb, and 120 of *c-mos* (Table S1). Outgroup selection followed the criterion proposed by Moravec et al. [11].

2.3. Sequence Alignment and Phylogenetic Analysis

Sequences for each marker were aligned independently using MUSCLE v.3.8.31 [23], as implemented in MEGA X [24]. The alignments were subsequently inspected and concatenated into a multilocus matrix comprising 2290 base pairs and including fragments of four mitochondrial genes (12S, 16S, ND4, and Cytb) and one nuclear gene (*c-mos*).

Phylogenetic reconstruction was conducted under the maximum-likelihood criterion using IQ-TREE v. 3.1.3 [25,26]. The concatenated matrix was initially divided into 11 partitions: one for each non-coding ribosomal gene, 12S and 16S, and one for each codon position of the protein-coding genes ND4, Cytb, and *c-mos*. Nucleotide substitution model selection and optimization of the partitioning scheme were performed with ModelFinder Plus using the MFP + MERGE partition-merging strategy implemented in IQ-TREE [27]. The selected scheme comprised seven final partitions (Table 3).

Node support was assessed using 100,000 ultrafast bootstrap replicates with UFBoot2 [28]. The resulting phylogenetic tree was visualized and edited in FigTree v.1.4.4 [29].

Table 2. Primers, nucleotide sequences, PCR cycling conditions, and references for the amplification of mitochondrial and nuclear loci used in this study.

Gene	Primer	Primers Sequence	PCR Cycle Conditions	Reference
12S	12S1L	CAAACTGGGATTAGATACCCCACTAT	94 °C/3 min; 33 × (95 °C/30 s, 57 °C/30 s, 72 °C/90 s); 72 °C/10 min	[30]
	12S2H	AGGGTGACGGGCGGTGTGT		
16S	16sF.0	CTGTTTACCAAAAACATMRCCTYTAGC	96 °C/3 min; 40 × (95 °C/30 s, 51 °C/60 s, 72 °C/60 s); 72 °C/10 min	[5,30]
	16sR.0	TAGATAGAAACCGACCTGGATT		
Cytb	L14841	AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA	96 °C/3 min; 40 × (95 °C/30 s, 52 °C/60 s, 72 °C/60 s); 72 °C/10 min	[31,32]
	H15149	AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA		
ND4	ND412931L	CTACCAAAAGCTCATGTAGAAGC	94 °C/5 min; 30 × (94 °C/60 s, 50 °C/60 s, 72 °C/60 s); 72 °C/10 min	[30]
	ND413824H	CATTACTTTTACTTGGATTTGCACCA		
c-mos	G73	GCGGTAAAGCAGGTGAAGAAA	96 °C/3 min; 35 × (95 °C/25 s, 52 °C/60 s, 72 °C/120 s); 72 °C/10 min	[33]
	G74	TGAGCATCCAAAGTCTCCAATC		

Table 3. Best-fit nucleotide substitution models and final partitioning scheme selected by ModelFinder for the concatenated multilocus dataset.

Nucleotide Substitution Model	Data Partition	Number of Aligned Sites
GTR + F + I + R5	12S + 16S	943
GTR + F + R7	ND4 codon positions 1 and 3	414
TPM3u + F + I + R3	ND4 codon position 2	207
TIM2e + G4	Cytb codon position 1	116
TIMe + G4	Cytb codon position 2 + *c-mos* codon positions 1 and 2	368
HKY + F + R2	Cytb codon position 3	116
K3Pu + F + G4	*c-mos* codon position 3	126

3. Results

The maximum-likelihood analysis recovered Cercosaurini as a monophyletic clade with maximum support (UFBoot = 100; Figure 3 and Figure S1). Overall, the principal internal relationships received moderate to high support. However, some deeper relationships remained weakly resolved, particularly the position of the clade comprising *Centrosaura* and *Echinosaura* relative to the remaining cercosaurines (UFBoot = 50), as well as the position of *Riama* and its internal relationships (UFBoot = 60). Our results also recovered *Proctoporus* as monophyletic (UFBoot = 71), whereas *Oreosaurus* was recovered as non-monophyletic.

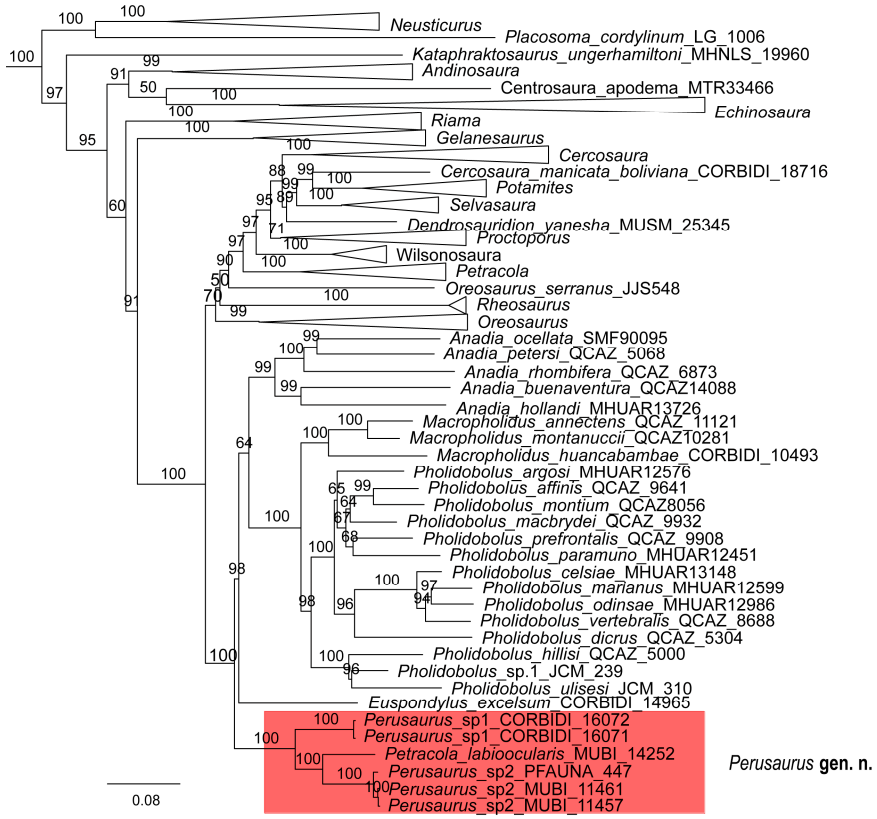


Figure 3. Maximum-likelihood phylogeny showing the position of *Perusaurus* gen. nov. within Cercosaurini (in red), inferred from a concatenated dataset of 2290 bp comprising four mitochondrial markers (12S, 16S, Cytb, and ND4) and one nuclear marker (*c-mos*). Numbers at nodes indicate ultrafast bootstrap support values based on 100,000 replicates. Log-likelihood = −58,181.9.

The six focal terminals formed a strongly supported monophyletic clade (UFBoot = 100), here recognized as *Perusaurus* gen. nov. This genus was recovered as the sister lineage to a clade comprising *Anadia*, *Macropholidus*, *Pholidobolus*, and *Euspondylus* with strong node support (UFBoot = 100). Within *Perusaurus* gen. nov., the two specimens identified as *Perusaurus* sp. 1 (CORBIDI 16071, 16072) were recovered as sister taxa with maximum support (UFBoot = 100). Similarly, the three unidentified specimens of *Perusaurus* sp. 2 (MUBI 11457, 11461, and PFAUNA 447) formed a strongly supported clade (UFBoot = 100), which was recovered as the sister group of *Petracola labioocularis* (UFBoot = 100, MUBI 14252) (Figure 3).

Morphological examination showed that the populations represented by *Perusaurus* sp. 1 and *Perusaurus* sp. 2 differ from *P. labioocularis* and *P. laudahnae* in lacking a nasoloreal suture and having keeled dorsal scales. Additional differences include variation in the number of supraocular scales and precloacal pores (Figure 2). The two populations also differ from each other in several scale counts: *Perusaurus* sp. 2 has a higher number of transverse dorsal and ventral scale rows, whereas *Perusaurus* sp. 1 exhibits lower values that partially overlap with those of the nominal species. Together, these differences in scalation, along with variation in snout–vent length, suggest that the two populations represent morphologically distinguishable entities (Table 4).

The monophyly and phylogenetic position of *Perusaurus* gen. nov., together with its distinctive combination of external morphological characters, including the presence precloacal pores and the third subocular extending ventrally between the supralabial scales (Figure 2), provide congruent lines of evidence for its recognition as an independent evolutionary lineage and support its assignment to a distinct genus. *Perusaurus labioocularis*

exhibits both diagnostic characters, including a continuous series of femoral and precloacal pores and the third subocular extending ventrally between the supralabials. In contrast, *P. laudahnae* shares the latter character but exhibits precloacal pores separated by a pair of scales, as observed in *Perusaurus* sp. 2 (Figure 2C,D). These shared morphological characteristics provide further support for the placement of *P. laudahnae* within *Perusaurus*.

Table 4. Morphological comparison among the species and candidate species of *Perusaurus*. Measurements of snout–vent length (SVL) are given in millimeters. A dash indicates unreported information. Data for *P. laudahnae* were obtained from Köhler and Lehr [15]. For *Perusaurus* sp. 1, SVL measurements were available for only one adult specimen.

Character	*Perusaurus labioocularis*	*Perusaurus laudahnae*	*Perusaurus* sp. 1	*Perusaurus* sp. 2
Sample size (N)	1 ♂, 4 ♀	2 ♂	3 ♂, 3 ♀	4 ♂, 8 ♀
SVL (mm)	♂: 55.9; ♀: 59.2–60.8	♂: 65.0	♀: 62.8	♂: 53.6–55.9; ♀: 50.2–57.6
Nasal–loreal suture	Present	Present	Absent	Absent
Postoculars	2	2	2	2–3
Supraoculars	3	3	2–3	2
Superciliaries	1–2, discontinuous	4	3–4	4
First superciliary dorsally expanded	Present	Absent	Present	Present
Palpebral disc	Vertically divided	Vertically divided	Vertically divided	Vertically divided
Anterior infralabials	3	4	3	3–4
Genial pairs in contact	4	4	4	4
Dorsal scales on neck	Smooth	Smooth	Smooth	Smooth
Dorsal body scales	Smooth	Striated	Keeled	Keeled
Scales around midbody	32–34	—	34–38	36–38
Transverse dorsal scale rows	33–35	37	32–34	44–50
Transverse ventral scale rows	19–20	20	19–20	25–27
Longitudinal dorsal scale rows	22–24	—	25–28	24–26
Longitudinal ventral scale rows	10	—	8–10	12
Precloacal pores	4	2	2	1–2
Femoral pores	♂: 7–8; ♀: 2	♂: 8	♂: 5–7; ♀: 4–6	♂: 6–7; ♀: 1

3.1. Taxonomy

Family: Gymnophthalmidae Fitzinger, 1826;
Subfamily: Cercosaurinae Gray, 1838;
Tribe: Cercosaurini Gray, 1838;
Genus: *Perusaurus* gen. nov.;
ZooBank LSID: urn:lsid:zoobank.org:act:57191E48-4B8F-437D-A738-C119A4C5AB92;
Type species: *Proctoporus labioocularis* Köhler & Lehr, 2004, *by original designation*.

3.2. Etymology

The generic name *Perusaurus* is formed by combining Peru, the country where all currently known species of the genus occur, with the Latinized Greek noun saurus, from the Ancient Greek σαῦρος (sauros), meaning "lizard." The name is masculine.

3.3. Definition

Tongue with imbricate, scale-like papillae. Head scales smooth, lacking striations or rugosities; frontonasal, frontal, and interparietal single; frontoparietals and parietals paired; nasals separated. Eyelids movable; palpebral disc vertically divided into two or three scales. Three subocular scales, with the third extending ventrally and interrupting the supralabial series. Three or four anterior infralabials; posterior gular scales slightly enlarged and quadrangular. Limbs pentadactyl; digits clawed. Dorsal scales quadrangular, elongate, smooth, striated, or keeled, subimbricate, and arranged exclusively in transverse rows; reduced scales present between the dorsal and ventral scales. Ventral scales enlarged, quadrangular, smooth, and juxtaposed. Femoral and precloacal pores present in both males and females. Tail cylindrical.

3.4. Diagnosis

Perusaurus is distinguished from other genera of Cercosaurini by a combination of morphological characters, including the presence of precloacal pores and the third subocular extending ventrally and interrupting the supralabial series. Precloacal pores are also present in some species of *Riama*, although the third subocular generally does not extend ventrally between the supralabials, except in *R. labionis*. *Perusaurus* differs from *R. labionis* in having two or three supraoculars rather than four.

3.5. Distribution

Perusaurus occurs on the eastern slopes of the central Peruvian Andes, in montane forests and inter-Andean valleys of the departments of Huánuco and Pasco, on both sides of the Huallaga River. Its known elevational distribution ranges from 2980 to 3300 m a.s.l. (Figure 4).

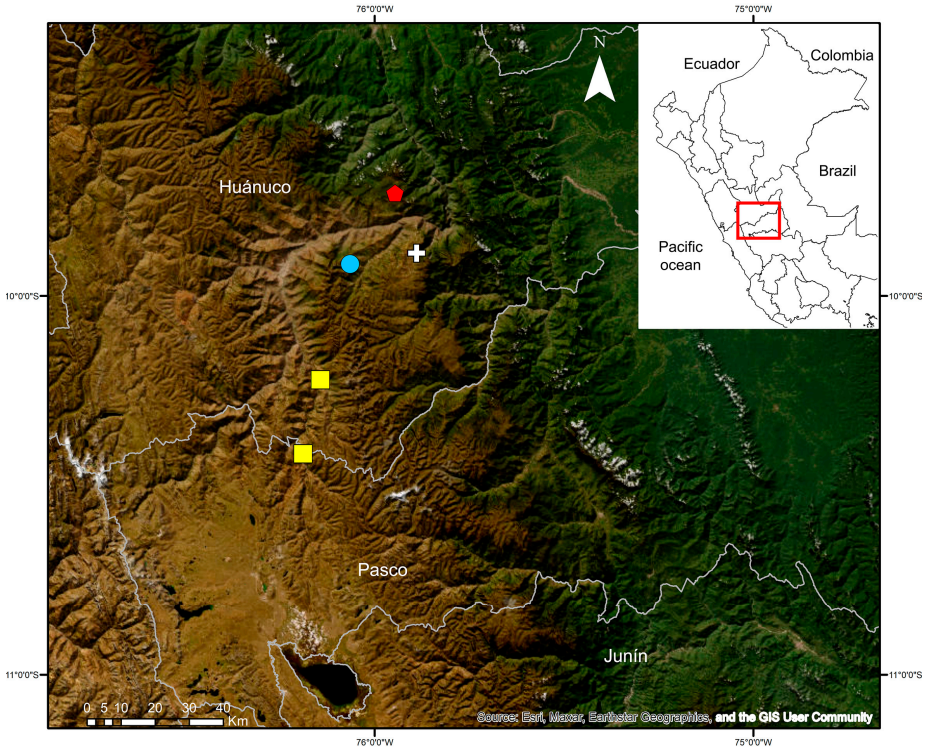


Figure 4. Geographic distribution of *Perusaurus* gen. nov. Distribution records are shown for *Perusaurus labiooccularis* (light-blue circle), *P. laudahnae* (white cross), *Perusaurus* sp. 1 (red pentagon), and *Perusaurus* sp. 2 (yellow squares). Geographic coordinates were obtained from voucher specimen records and the published literature.

3.6. Included Species

Perusaurus labioocularis (Köhler & Lehr, 2004), comb. nov., and *Perusaurus laudahnae* (Köhler & Lehr, 2004), comb. nov.

4. Discussion

Our results provide molecular and morphological evidence supporting the recognition of a new genus of gymnophthalmid lizards distributed along the eastern slopes of the central Peruvian Andes. The six terminals analyzed formed an independent monophyletic lineage that is clearly differentiated from phylogenetically related genera. This evolutionary distinctiveness is further supported by a combination of external morphological characters, including precloacal pores and the third subocular extending ventrally between the supralabial scales. Although some of these characters occur individually in other gymnophthalmids, their combined presence, together with the phylogenetic position of the clade, distinguishes this lineage from *Anadia*, *Euspondylus*, *Macropholidus*, *Pholidobolus*, and other genera of Cercosaurini (Table 5).

Table 5. Comparison of selected morphological characters of *Perusaurus* gen. nov. and geographically proximate and phylogenetically related genera of Cercosaurinae.

Characters	*Anadia*	*Macro-pholidus*	*Pholido-bolus*	*Euspon-dylus*	*Selvas-aura*	*Petracola*	*Perusa-urus*	*Procto-porus*	*Wilsono-saura*	*Riama*
Palpebral disc	Entire or vertically divided	Entire	Vertically divided	Vertically divided	Entire	Entire	Vertically divided	Entire	Entire	Vertically divided
Third subocular extending ventrally between supralabi-als	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	Absent	Usually absent
Dorsal body scales	Smooth	Smooth	Keeled	Smooth	Keeled	Smooth	Smooth, striated or keeled	Keeled	Striated or keeled	Smooth, striated or keeled
Precloacal pores	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	Absent	Present or absent
Femoral pores	Present	Present	Absent or present	Present	Present	Present	Present	Present	Present	Present

The recognition of this lineage adds to a series of recent discoveries that have substantially reshaped our understanding of cercosaurine diversity in the Andes. These include the description of the genera *Selvasaura* [11], *Dendrosauridion* [13], and *Wilsonosaura* [14], all of which were recognized through the integration of molecular evidence. Collectively, these cases indicate that several Andean species were historically assigned to different genera because of convergent similarities and the conservative nature of their external morphology, whereas phylogenetic analyses have revealed that they represent deeply divergent evolutionary lineages [4,6,7].

The integration of molecular evidence is also reflected in the recent descriptions of species of the genera *Proctoporus* [18], *Petracola* [17,34], and *Selvasaura* [35]. These studies have documented previously unrecognized diversity within relatively restricted geographic areas of the Peruvian Andes and demonstrated that even well-established genera still harbor considerably underestimated diversity. This pattern appears to be associated with the pronounced topographic and environmental heterogeneity of the eastern Andean slopes, which are characterized by deep valleys, mountain ranges, and geographically isolated montane forest formations. These geographic features may restrict dispersal and

promote prolonged isolation in small-bodied organisms with limited dispersal capacity, thereby increasing opportunities for speciation [2,3].

Consistent with this pattern, the monophyletic clade recovered in our analysis contains at least two species that remain to be formally described: *Perusaurus* sp. 1, represented by specimens CORBIDI 16071 and CORBIDI 16072, and *Perusaurus* sp. 2, represented by PFAUNA 447, MUBI 11457, and MUBI 11461. Furthermore, although the phylogenetic position of *P. laudahnae* remains unresolved because no genetic data are currently available, its morphological similarity to the species included in the clade and its geographic distribution in the central Peruvian Andes provide additional support for its assignment to *Perusaurus*.

Finally, the discovery of a genus-level lineage restricted to the central Andes has implications that extend beyond taxonomic classification. Accurate delimitation enables the recognition of evolutionary units that might otherwise remain obscured under incorrect generic assignments and is essential for assessing their distribution, endemism, and conservation status. Because several Andean species of Cercosaurini are known from only a few localities and inhabit montane ecosystems affected by habitat transformation and fragmentation, further biological inventories are needed in poorly explored regions of Pasco, Huánuco, and adjacent areas. Overall, our results not only increase the known generic diversity of Cercosaurini but also support the hypothesis that the true evolutionary diversity of lizards in the Peruvian Andes remains far from fully documented.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/taxonomy6040066/s1, Figure S1: Maximum-likelihood phylogeny of Cercosaurini inferred from a concatenated dataset of 2290 bp comprising four mitochondrial markers (12S, 16S, Cytb, and ND4) and one nuclear marker (*c-mos*). Numbers at nodes indicate ultrafast bootstrap support values based on 100,000 replicates. Log-likelihood = −58,181.9; Table S1: GenBank code accession for taxa and genes used in this study. Sequences generated in this study are indicated in bold.

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Appendix A

Specimens Examined

Perusaurus labioocularis. PERU: Huánuco: Chaglla, Monte Potrero: MUBI 14232 (adult female), MUBI 14251 (subadult female), MUBI 14252 (adult male), MUBI 14253 (adult female), and MUBI 14254 (adult female).

Perusaurus sp. 1. PERU: Huánuco: Achupampa: CORBIDI 16071 (adult female), CORBIDI 16072 (subadult male), CORBIDI 16073 (subadult female), CORBIDI 16074 (subadult male), CORBIDI 16076 (subadult male), and CORBIDI 16077 (subadult female).

Perusaurus sp. 2. PERU: Pasco: Huariaca, Malhuapampa: MUBI 11457 (adult female), MUBI 11458 (adult male), MUBI 11459 (adult female), MUBI 11461 (adult female), MUBI 11462 (adult female), MUBI 11463 (subadult male), MUBI 11464 (adult female), and MUBI 13266 (adult male). Huánuco: Ambo, Saccsahuanca: PFAUNA 446 (adult female), PFAUNA 447 (adult male), PFAUNA 448 (subadult female), and PFAUNA 449 (adult female).

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