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Molecular Phylogenetics and Comparative Examination of Voucher Museums Reveal Two New Species of Gymnophthalmid Lizards (Squamata, Gymnophthalmidae) from the Peruvian Andes, with Comments on *Proctoporus guentheri* (Boettger, 1891) [†]

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Abstract: The genus *Proctoporus* comprises cursorial and semifossorial lizards that inhabit the Andes of Argentina, Bolivia, and Peru. The taxonomy is complex, and many undescribed species and geographic gaps remain to be addressed. In this study, we use molecular phylogenetics and examine voucher museums to describe two new species of gymnophthalmid lizards from the montane forests of Cusco, on the eastern slopes of the Andes of Peru. We inferred phylogenetic relationships from concatenated sequences of four mitochondrial (12S, 16S, ND4, and Cytb) and one nuclear (c-mos) gene fragments, using a Maximum Likelihood approach and Bayesian Inference. We also examined and compared meristic traits of the specimens deposited in herpetological collections in Peru and Bolivia. Our molecular phylogeny had strong support for the monophyly of the subfamily Cercosaurinae, low support for the genus *Proctoporus*, and revealed two new taxa of *Proctoporus*. The two new species, which we name *P. katerynae* sp. nov. and *P. optimus* sp. nov., are characterized as having two rows of preocular scales and three anterior infralabials. Furthermore, we re-identified specimens assigned to *P. laudahnae* as *P. guentheri*, and we comment on the taxonomy of *P. guentheri*. Finally, we discuss how global climate change and human-caused habitat loss may threaten *P. katerynae* sp. nov. and *P. optimus* sp. nov. by the mechanism known as “Escalator to extinction”.

Keywords: cloud montane forest; escalator to extinction; endangered species; Sorata; Machu Picchu; phylogenetic relationships

1. Introduction

The genus *Proctoporus* Tschudi, 1845, is a group of semifossorial lizards that inhabit the Cordillera de los Andes, from northern Argentina to central Peru [1–5]. This genus inhabits montane forests, humid grassland, and inter-Andean valleys in the eastern slope of the Andes, from 1000 to 4200 m a.s.l. [2,3,5–7]. This genus is composed of 16 species [5,8], all of which are distributed in Peru: *Proctoporus bolivianus* (Werner, 1910), *P. carabaya* (Goicoechea, Padial, Chaparro, Castroviejo-Fisher, and De la Riva, 2013), *P. chasqui* (Chávez, Siu-Ting, Duran, and Venegas, 2011), *P. guentheri* (Boettger, 1891), *P. iridescens* (Goicoechea,

Padial, Chaparro, Castroviejo-Fisher, and De la Riva, 2013), *P. kiziriani* (Goicoechea, Padial, Chaparro, Castroviejo-Fisher, and De la Riva, 2013), *P. lacertus* (Stejneger, 1913), *P. laudhanae* (Köhler and Lehr, 2004), *P. machupicchu* Mamani (Goicoechea and Chaparro, 2015), *P. oreades* (Chávez, Siu-Ting, Duran, and Venegas, 2011), *P. pachyurus* (Tschudi, 1845), *P. rhami* (De Grijns, 1936), *P. spinalis* (Boulenger, 1911), *P. sucullucu* (Doan and Castoe, 2003), *P. unsaaca* (Doan and Castoe, 2003), and *P. xestus* (Uzzell, 1969). The presence of *P. xestus* is doubtful and was based on a list of species without reference to a voucher specimen [9]. *Proctoporus* is also distributed in Bolivia with three species (*P. bolivianus*, *P. guentheri*, and *P. xestus*), and in Argentina with one species (*P. xestus*) [3,6,7].

The taxonomic history of *Proctoporus* is complex. Before the studies by Castoe et al. [10], and Doan and Castoe [4], there were 31 species of *Proctoporus* [1]. Castoe et al. [10] analyzed the genetic sequences and demonstrated the polyphyly of *Proctoporus*, followed by Doan and Castoe [4] who rearranged the taxonomy and reduced *Proctoporus* species richness to five (*P. bolivianus*, *P. guentheri*, *P. pachyurus*, *P. unsaaca*, and *P. sucullucu*). Subsequently, other studies based on genetic data increased *Proctoporus* species richness and transferred the species previously included in *Euspondylus* to *Proctoporus* (*P. spinalis*, *P. chasqui*, *P. oreades*, and *P. rahmi*) [2,11], which raised doubts about the validity of *Euspondylus*. However, the validity of *Euspondylus* was resolved by Chávez et al. [12]. Furthermore, Torres-Carvajal et al. [11] suggested a new polyphyly of *Proctoporus*, which was corroborated by subsequent studies [13,14]. Nevertheless, the support values of nodes in these phylogenies were low, and a recent study based on four mitochondrial markers (12S, 16S, Cytb, and ND4) and one nuclear marker (c-mos) showed the monophyly of *Proctoporus* [15], confirming the findings by Goicoechea et al. [2]. Likewise, the topology of Mamani et al. [15] nested the recently described genus *Wilsonosaura* with *Proctoporus*, raising doubts about the validity of *Wilsonosaura*. Another taxonomic problem concerns *P. guentheri*, which was described by Boettger [16], based on a specimen collected by Ernesto Guenther from near Sorata in Bolivia. Unfortunately, the holotype was destroyed by bombings during the Second World War [7], and the lack of additional material from the type locality prevented re-description. Burt and Burt [17] considered *P. bolivianus* as a junior synonymy of *P. guentheri*, but Uzzell [7] recognized these species as distinct and synonymized *Oreosaurus ocellatus* and *O. anomalus* with *P. guentheri*. Sorata is the type locality for both *P. bolivianus* and *P. guentheri*. Sorata is a dry inter-Andean valley covered by scrub vegetation, which is the habitat of *P. bolivianus* [3,18], but where *P. guentheri* has not been observed. Additionally, at sites other than Sorata, *P. guentheri* was collected only in humid montane forests [6,7,19,20].

In this study, we describe two new species of semifossorial microteiid lizards of the genus *Proctoporus* from the montane forests of Cusco, based on morphological and molecular data (four mitochondrial and a nuclear gene). In addition to increasing the species richness of *Proctoporus* to 18 species, we discuss the taxonomic status of *P. guentheri*.

2. Materials and Methods

2.1. Taxon Sampling

We obtained biological tissues of five specimens deposited in the herpetological collection of the Museo de Biodiversidad del Perú (MUBI). We identified specimens MUBI 12687 from Tucantinas and MUBI 10278 from the Native Community Alto Matoriato as *P. guentheri*, and specimens MUBI 2915 and 2984 from Mesa Pelada, and MUBI 10482 from Monte Carmelo as *Proctoporus* sp. (Table 1).

Table 1. Localities, coordinates, voucher museum, and Genbank accession code.

Species	Locality	Coordinates	Voucher	12S	16S	ND4	Cytb	c-mos
<i>Proctoporus guentheri</i>	Alto Matoriato, La Convención, Cusco.	12°30'20" S/72°49'59" W	MUBI 10278	OM893811	OM893806	OM885354	OM885350	OM885358
<i>Proctoporus guentheri</i>	Tucantinas, La Convención, Cusco.	12°43'21" S/72°53'56" W	MUBI 12687	OM893812	OM893807	-	OM885351	OM885359
<i>Proctoporus kateryna</i> sp. nov.	Monte Carmelo, La Convención, Cusco.	12°22'58" S/73°4'20" W	MUBI 10482	OM893813	OM893808	OM885355	-	OM885360
<i>Proctoporus optimus</i> sp. nov.	Mesa Pelada, La Convención, Cusco.	12°56'21" S/72°35'56" W	MUBI 2915	OM893814	OM893809	OM885356	OM885352	OM885361
<i>Proctoporus optimus</i> sp. nov.	Mesa Pelada, La Convención, Cusco.	12°56'21" S/72°35'56" W	MUBI 2984	OM893815	OM893810	OM885357	OM885353	OM885362

2.2. DNA Extraction, Amplification, and Sequencing

We obtained DNA from muscle tissues preserved in 96% ethanol following the method used by Mamani et al. [16] (Table 2). We obtained sequences of fragments of four mitochondrial (small subunit rRNA, 12S; large subunit rRNA, 16S; NADH dehydrogenase subunit 4, ND4; cytochrome b, Cytb) and one nuclear gene (oocyte maturation factor gene, c-mos). We deposited all new sequences in Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>, accessed on 12 March 2021). Additionally, we obtained 212 sequences of 12S, 209 sequences of 16S, 19 sequences of Cyt b, 181 sequences of ND4, and 185 sequences of c-mos from GenBank (Table S1 in Supplementary Materials).

Table 2. List of genes, primers, and PCR cycles used in this study.

Gene	Primer	Primers Sequence (5'–3')	PCR Cycle	Reference
12S	12S1L 12S2H	CAAAGTGGGATTAGATACCCCACTAT AGGGTGACGGGCGGTGTGT	94 °C/3 min; 33 × (95 °C/30 s, 57 °C/30 s, 72 °C/90 s); 72 °C/10 min	[21]
16S	16sF.0 16sR.0	CTGTTTACCAAAAACATMRCCTYTAGC TAGATAGAAACCGACCTGGATT	96 °C/3 min; 40 × (95 °C/30 s, 51 °C/60 s, 72 °C/60 s); 72 °C/10 min	[21,22]
ND4	ND412931L ND413824H	CTACCAAAAAGCTCATGTAGAAGC CATTACTTTTACTTGGATTGACCA	96 °C/3 min; 40 × (95 °C/30 s, 52 °C/60, 72 °C/60 s); 72 °C/10 min	[23,24]
Cytb	L14841 H15149	AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA	94 °C/5 min; 30 × (94 °C/60 s, 50 °C/60 s, 72 °C/60); 72 °C/10 min	[21]
c-mos	G73 G74	GCGGTAAAGCAGGTGAAGAAA TGAGCATCCAAAGTCTCCAATC	96 °C/3 min; 35 × (95 °C/25 s, 52 °C/60 s, 72 °C/120 s); 72 °C/10 min	[25]

2.3. Phylogenetic Reconstruction

The five genetic sequences were aligned in MUSCLE [26] implemented in MEGA-X [27] and were concatenated using Mesquite V.3.61 [28]. We inferred the phylogenetic relationships of the new species using a Maximum Likelihood (ML) approach based on the concatenated matrix of nuclear and mitochondrial genes. The evolution models of sequences were estimated in ModelFinder [29] and were GTR+F+I+G4 for 12S, GTR+F+R5 for 16S, TIM2e+I+G4 for ND4, GTR+F+R5, and K2P+G4 for c-mos. We inferred a phylogenetic Maximum Likelihood tree by using the IQTREE Web server [30]. Branch supports were estimated for 10,000 replicates using ultrafast Bootstrap [31]. For Bayesian Inference (BI), we used MrBayes v3.2.1 [32] to perform a Bayesian Inference analysis via Markov Chain Monte Carlo (MCMC) with the concatenated data set using the GTR+G+I evolutionary model. The analysis consisted of four independent chains run for 10 million generations, sampled every 1000 generations. The first 25% of generations were conservatively discarded as burn-in after observing the stationarity of ln-likelihoods of trees in Tracer

v1.7.1 [33]. The convergence and mixing of chains were assessed by examining the values of the average standard deviation of split frequencies (ASDSF), expected sampling sizes (ESS), and potential scale reduction factor (PSRF) for all parameters. Following Moravec et al. [13], we used *Alopoglossus atriventris*, *Bachia barbourri*, *B. bicolor*, *B. bresslaui*, *B. dorbignyi*, *B. flavescens*, *Ecleopos gauichaudii*, *Gymnophthalmus leucomystax*, *Rhachisaurus brachylepis*, *Riolama inopinata*, and *R. leucosticta* as outgroup taxa.

2.4. Taxonomic Treatment and Review of Museum Vouchers

The terminology for diagnostic characters and format description followed Uzzell [7], Kizirian [1], and Goicoechea et al. [3], except that we defined a new diagnostic character as anterior infralabials to the infralabial scales in contact with the mental and genial scales (Figure 1). Measurements were taken with a caliper, accurate to 0.1 mm. Data for other species were taken from the literature [3,5–7,34] and through examination of the specimens deposited in the herpetological collection of the Centro de Ornitología y Biodiversidad (CORBIDI), Museo de Historia Natural Alcide d’Orbigny (MHNC-R), Museo de Biodiversidad del Perú (MUBI), Colección Boliviana de Fauna (CBF), Colección Científica Pro Fauna Silvestre Ayacucho (PFAUNA), and University of Texas Arlington Collection of Vertebrates (UTA). See Appendix A for the list of specimens examined.

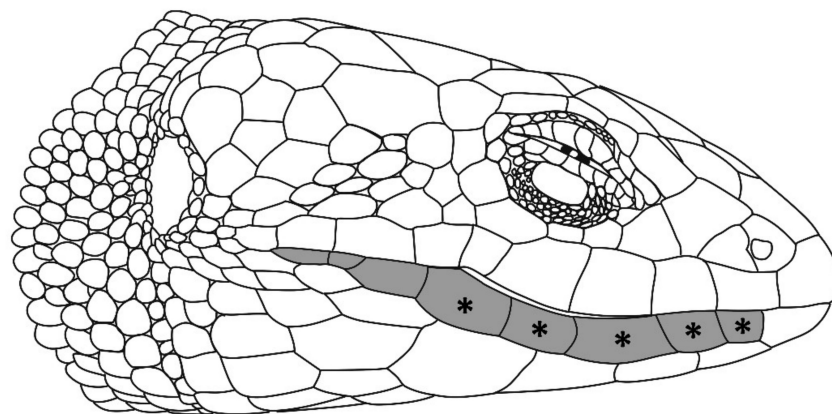


Figure 1. View of the head of the gymnophthalmid lizard (*Euspondylus caideni*, MUBI 14330) showing infralabial (gray) and anterior infralabials (*).

Nomenclatural act. 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 the nomenclatural acts it contains 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:3AA038EE-2A46-4380-B58D-DC006B2BCEEA.

3. Results

3.1. Phylogenetic Relationships

The ML and BI trees recovered the monophyly of Cercosaurinae (ultrafast bootstrap, UB = 100, PP: 1; Figures S1 and S2 respectively in Supplementary Materials). In our ML tree, most of the lineages at the genus level were strongly supported, while some lineages containing genera had low support: *Oreosaurus* + *Petracola* + *Wilsonosaura* + *Selvasaura* + *Dendrosauridion* + *Potamites* + “*Cercosaura manicata boliviana*” + *Cercosaura* + *Proctoporus* had UB = 58; *Selvasaura* + *Dendrosauridion* + *Potamites* + *Dendrosauridion* + “*Cercosaura manicata boliviana*” + *Cercosaura* + *Proctoporus* had UB = 55; *Selvasaura* + *Dendrosauridion* +

Potamites + *Dendrosauridion* + “*Cercosaura manicata boliviana*” + *Cercosaura* had UB = 53; and *Proctoporus* had UB = 49. Our BI tree was similar to the ML tree, except that many lineages were recovered with very low PP values (Figure 2). The phylogenetic relationships of *Cercosaura*, *Cercosaura manicata boliviana*, *Dendrosauridion*, *Potamites*, *Proctoporus*, *Selvasaura*, and *Wilsonosaura* were not resolved (Figure S2). In addition, our ML and BI tree did not recover the monophyly of *Oreosaurus*, *Proctoporus iridescens*, *P. guentheri*, and *P. spinalis*.



Figure 2. Phylogenetic relationship of the species described here (Log likelihood = −57,081.542 ultrafast bootstrap = 10,000). The number on the branches are posterior probability (bold) and ultrafast bootstrap values (no bold). The Maximum Likelihood and Bayesian Inference tree were constructed from a concatenated dataset of 2270 nucleotides of four mitochondrial (12S, 16S, Cytb, and ND4) and a nuclear (c-mos) gene fragments.

3.2. Specimens Voucher, Generic Assignment, and Species Reidentification

We examined museum specimens (listed in the Appendix A) of all species of *Proctoporus* from Bolivia and Peru. We considered 14 species of *Proctoporus* from Peru, but two species, *P. bolivianus* and *P. xestus*, did not have museum specimens. The presence of *P. bolivianus* was reported by Goicoechea et al. [3] based on museum specimens from Puno

(near Bolivia), but we did not find any voucher of *Proctoporus xestus* from Peru. Therefore, including the two new species described here, the richness of the genus *Proctoporus* in Peru was updated to 17.

We assigned the new specimens included in this study to *Proctoporus* based on the position on our phylogeny, and the presence of imbricate and scale-like papillae on the tongue; head scales smooth without striations or rugosities; eyelids developed with an undivided translucent disc; dorsal scales, quadrangular elongate, keeled, juxtaposed, and forming transversal series only; and posterior gulars squarish (*sensu* [10]).

Proctoporus guentheri is a semifossorial species that is characterized mainly by the presence of two enlarged preangular scales [7]. The museum specimens identified as *P. guentheri* by Doan and Castoe [6] lack enlarged preangular scales, but they have two rows of preangular scales, which are unique characters in *Proctoporus*. Two specimens identified as *P. laudahnae* (CORBIDI 15558, 15743) by Torres-Carvajal et al. [11] have two enlarged preangular scales and lack preloacal pores, were incorrectly identified as *P. guentheri*. All specimens listed in the Appendix A and specimens (MUBI 10278, and 12687) identified as being part of *P. guentheri* species complex in this study have two enlarged preangular scales. Three specimens included in this study (MUBI 2915, 2984, 10482) and specimens named as *P. guentheri* by Doan and Castoe [6] have two rows of preangular scales, which is a unique character in *Proctoporus*. These specimens include two new species of *Proctoporus* that differ in body size, presence of femoral pores in females, and number of scales around midbody (see below).

Taxonomy

Proctoporus katerynae sp. nov.

LSID: urna:lsid:zoobank.org:act:A00E62DD-1ACF-4DB4-9A4E-19FF3EF98558.

Holotype. MUBI 10482, adult female (Figures 3 and 4) from Monte Carmelo (12°22'58" S, 73°04'20" W, 1960 m a.s.l.), district Echarate, province La Convención, Department Cusco, in Peru. Collected by S. Mallqui and R. Cruz on 26 February 2010.

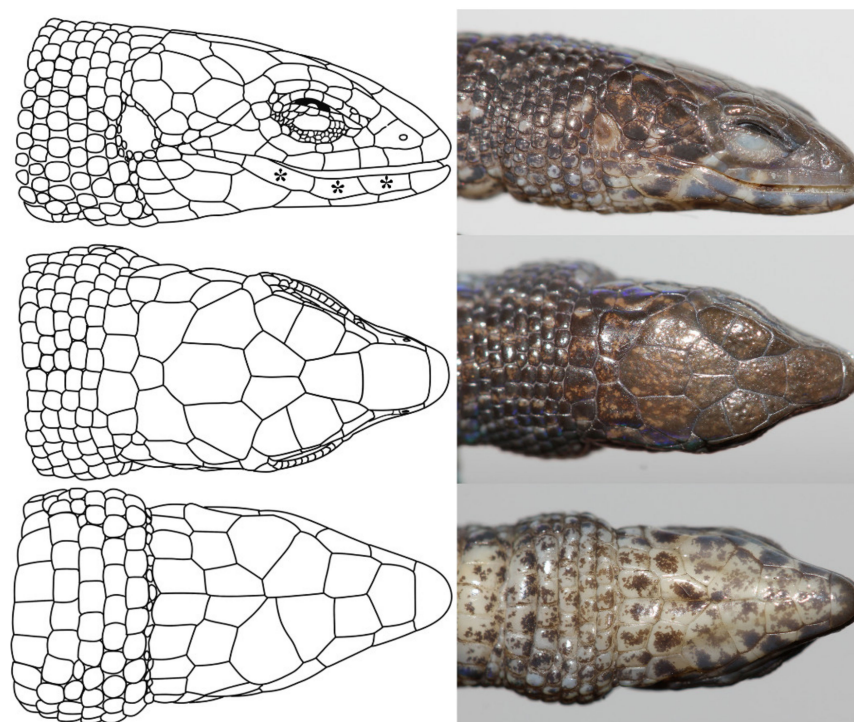


Figure 3. View of lateral, dorsal, and ventral of the holotype head of *Proctoporus katerynae* sp. nov. (MUBI 10492, SVL = 38.2 mm, TL = 58.5 mm, female). Asterisks indicate anterior infralabial scales. Drawing by R. Cruz.



Figure 4. Life specimen of the holotype of *Proctoporus katerynae* sp. nov. from Monte Carmelo (MUBI 10492, SVL = 38.2 mm, TL = 58.5 mm, female).

Paratypes—MUBI 10492 (subadult female) and MUBI 10493 (sub adult male) collected near the type locality (12°22'30" S, 73°04'47" W, 2040 m a.s.l.) and with the holotype.

Etymology—The specific epithet, *katerynae*, is patronymic for Kateryn Pino Bolaños (MUSA, Peru), in recognition of her friendship with the first author (LM), and her work for mammal conservation in Peru.

Diagnosis—(1) Frontonasal slightly longer than frontal; (2) nasoloreal suture absent; (3) three supraoculars; (4) four superciliaries; (5) three postoculars; (6) palpebral disc undivided and transparent; (7) four supralabials anterior to the posteroventral angle of the subocular; (8) three anterior infralabials; (9) four to five genials in contact; (10) two rows of preregulars; (11) dorsal body scales quadrangular, keeled, and sub imbricate; (12) 30–32 scales around midbody; (13) 31–33 transverse dorsal rows; (14) 18–19 transverse ventral rows; (15) 18–20 longitudinal dorsal rows; (16) eight longitudinal ventral rows; (17) a continuous series of small lateral scales separating dorsals from ventrals; (18) four posterior cloacal plate scales; (19) two anterior preanal plate scales; (20) seven to eight femoral pores per hind limb in a male, absent in females; (21) preanal pores absent; (22) seven to eight subdigital lamellae on finger IV; 10–12 subdigital lamellae on toe IV; (23) limbs not overlapping when adpressed against the body; (24) pentadactyl, digits clawed; (25) in one adult female, the dorsum is predominantly brown and black with tiny yellow spots of irregular distribution, the flanks of the anterior middle part of the body have yellow spots

that look like ocelli, the ventral surface is yellow with some irregular, dark mottling, and the throat is yellow with abundant dark spots; and coloration of adult males unknown. (Figure 4). Measurements are in Table 3.

Table 3. Morphometric measurements of *Proctoporus katerynae* sp. nov. and *P. optimus* sp. nov.

Measurements (mm)	<i>Proctoporus optimus</i> sp. nov.		<i>Proctoporus katerynae</i> sp. nov.		
	Males (n = 4)	Females (n = 3)	MUBI 10482 Adult Female	MUBI 10492 Juvenile Male	MUBI 10493 Juvenile Female
Snout vent length	44.7 (43.8–46.5) ± 3.3	44.9 (43–45.9) ± 1.7	38.2	27.4	19.0
Tail length	62.9 (56–70.8) ± 8.1	67.6–80.3	58.5	lost	11.6
Length between arm and leg	24.5 (23.8–26.4) ± 1.9	24.0 (22–25.5) ± 1.8	21.3	14.0	8.3
Head length to ear	9 (8.4–10.4) ± 0.8	8.4 (8–8.7) ± 0.4	7.4	5.2	4.8
Head width	6.53 (5.6–7.6) ± 0.7	6.5 (6–6.1) ± 0.1	4.8	3.8	3.1
Frontal (mm)	1.87 (1.8–2.1) ± 0.1	1.73 (1.7–1.8) ± 0.1	1.5	1.2	1.1
Frontonasal (mm)	2.1 (1.9–2.5) ± 0.2	2.07 (1.9–2.2) ± 0.2	1.8	1.4	1.1

Proctoporus katerynae sp. nov. can be distinguished from all species of *Proctoporus* (*P. bolivianus*, *P. carabaya*, *P. chasqui*, *P. iridescens*, *P. kiziriani*, *P. lacertus*, *P. laudahnae*, *P. machupicchu*, *P. oreades*, *P. pachyurus*, *P. rhami*, *P. spinalis*, *P. succullucu*, *P. unsaacae*, and *P. xestus*), except for *P. guentheri*, as having two rows of preular scales (three in all other species of *Proctoporus*), and from *P. guentheri* through the absence of a pair of enlarged preulars in contact at the midline (present in *P. guentheri*). Additionally, *P. katerynae* sp. nov. can be distinguished from *P. bolivianus*, *P. carabaya*, *P. chasqui*, *P. iridescens*, *P. kiziriani*, *P. lacertus*, *P. machupicchu*, *P. oreades*, *P. pachyurus*, *P. rhami*, *P. spinalis*, *P. succullucu*, *P. unsaacae*, and *P. xestus* by having three anterior infralabial scales (five in all species, except in *P. machupicchu*, *P. laudahnae*, and *P. unsaacae*, which have four).

Description of the Holotype

Adult female, snout-vent length (SVL) 38.2 mm, tail length 58.5 mm; head scales, smooth, without striations or rugosities; rostral scale, wider than tall, meeting supralabials on either side, above the supralabials, in contact with frontonasal, nasals, and first supralabials; frontonasal, slightly longer than wide, longer than frontal, widest posteriorly, in contact with rostral, nasals, frontal, first supraocular, and first superciliar; frontal, longer than wide, pentagonal, in contact with frontonasal, first and second supraoculars, and frontoparietals; frontoparietals, polygonal, in contact with frontal, second, and third supraoculars, parietals, and interparietal; three supraoculars, all in contact with superciliaries, third in contact with frontoparietal, parietal, and postocular; interparietal, longer than wide, heptagonal, in contact with frontoparietals, parietals, and with occipitals; parietals, irregular pentagon, in contact with frontoparietals, third supraoculars and third postocular, posteriorly with occipital, and laterally with supratemporals; three occipitals, smaller than parietals, the middle smaller than the sides; and two supratemporals. Nasal, divided by nasal suture, longer than high, and in contact with first and second supralabials; loreal incomplete; four superciliaries; two preoculars, first in contact with first superciliary and second in contact with frenocular and first subocular; frenocular, irregular pentagon, in contact with second and third supralabials, second preoculars, first subocular, and loreal scales; palpebral disc made up of a single transparent scale; three suboculars; three postoculars; 12 temporals, smooth, glossy, and polygonal; and four supralabials anterior to the posteroventral angle of the subocular. Mental, wider than long, in contact with first infralabial and postmental posteriorly; postmental, single, pentagonal, in contact with first infralabials and first pair of genials; six genials, five in contact; first pair in contact with first and second infralabials; second pair of genials in contact with second and third infralabials; the left scale of third pair of genial in contact with the second right genial; five gular scale rows; collar fold, distinct; and lateral neck scales, round, smooth, and juxtaposed. Dorsal scales, rectangular, longer than wide, juxtaposed, with single, high, rounded keel; 33 transverse dorsal rows

and 20 longitudinal dorsal rows at the midbody; continuous lateral scale series, smaller than dorsals; reduced scales at limb-insertion regions; 18 transverse ventral scale rows; eight longitudinal ventral scale rows at the midbody; anterior preanal plate scales paired; and two posterior preanal plate scales. Scales of dorsal tail, rectangular and juxtaposed; dorsal and dorsolateral caudal scales keeled; and ventral scales quadrangular and smooth. Forelimbs pentadactyl and digits clawed; dorsal brachial scales polygonal, subimbricate, and smooth; ventral brachial scales, roundish, subimbricate, and smooth; antibrachial scales polygonal, smooth; ventral antibrachial scales, smallest; dorsal manus scales, polygonal, smooth, and subimbricate; palmar scales small, rounded, juxtaposed, and domelike; and dorsal scales on fingers, smooth, quadrangular, imbricate, two on finger I, three on finger II, five on finger III, six on finger IV, and three on finger V. Hindlimbs, pentadactyl and digits clawed; scales of anterodorsal surface of thigh, large, polygonal, smooth, and subimbricate; scales on posterior surface of thigh, small, rounded, and juxtaposed; scales on ventral surface of thigh, large, rounded, flat, smooth; scales on anterior surface of crus polygonal, smooth, juxtaposed, decreasing in size distally; scales on anterodorsal surface of crus rounded and subimbricate; scales on ventral surface of crus large, smooth, flat, and subimbricate; scales on dorsal surface of toes, quadrangular, smooth, three on toe I, four on toe II, six on toe III, seven on toe IV, and five on toe V; subdigital lamellae, single distally, double proximally; and limbs not overlapping when adpressed against the body.

The coloration in life of the dorsum, head, and flanks is dark brown with irregular yellow and black spots; the venter, chin, throat, and ventral surface of the tail are cream-yellow with small and irregular black spots, and black spots are more intense in the chin, throat, and tail; and the dorsal and ventral surface of the forelimbs and hindlimbs are similar to the dorsal surface. In the preservative, the dorsum, head, flanks, and dorsal surface of the tail are dark brown with small and irregular cream spots; the venter, chin, throat, and ventral surface of the tail are cream with irregular and small brown spots; and the dorsal surfaces of forelimbs and hindlimbs are like the dorsum and the ventral surfaces are like the venter.

Distribution and ecology—The new species is only known from the type locality in Monte Carmelo, a montane cloud forest in the buffer zone of Reserva Comunal Machiguenga, southeastern Peru, at elevations of 1960–2040 m (Figure 5). These specimens were found under fallen tree trunks and under leaf litter during diurnal surveys from 11:00 a.m. to 14:00 p.m. *Proctoporus katerynae* sp. nov. was found in sympatry with *Euspondylus caideni* and *Bothrocophias andianus*.

Conservation—The habitat of *Proctoporus katerynae* sp. nov. is well preserved. However, the presence of a gas pipeline and the increase in deforestation for agriculture in nearby areas could place its conservation at risk. Likewise, global warming could threaten *P. katerynae* sp. nov. In a recent study in the montane forests of the Cerro de Pantia-colla, southeastern Peruvian Andes, Freeman et al. [35] reported that high-elevation birds declined in both range size and abundance, and common mountaintop species have disappeared over the last three decades. This reduction and extirpation of species was caused by climate warming through a mechanism known as “escalator to extinction” [36,37]. According to this mechanism, global warming increases average temperatures, forcing lowlands species to move toward higher land in order to keep living at their thermal optimum [38]. Species that can disperse move upwards, but mountaintop species have nowhere to go and, as consequence, are extirpated. Moreover, birds and flying insects and flying mammals could “jump” from lower mountaintops to close, higher mountaintops where ecological conditions may be more favorable [39]. However, the low-vagility and philopatry of organisms such as small reptiles, amphibians, and small non-flying mammals will prevent these species from being able to migrate elevationally, track their ideal climate, or “jump” across mountains, and consequently, they are more vulnerable to climate change (Figure 6). Therefore, global climate change threatens the extinction of *P. katerynae* sp. nov. and other non-flying small species that inhabit mountaintops of the tropical montane Andes.

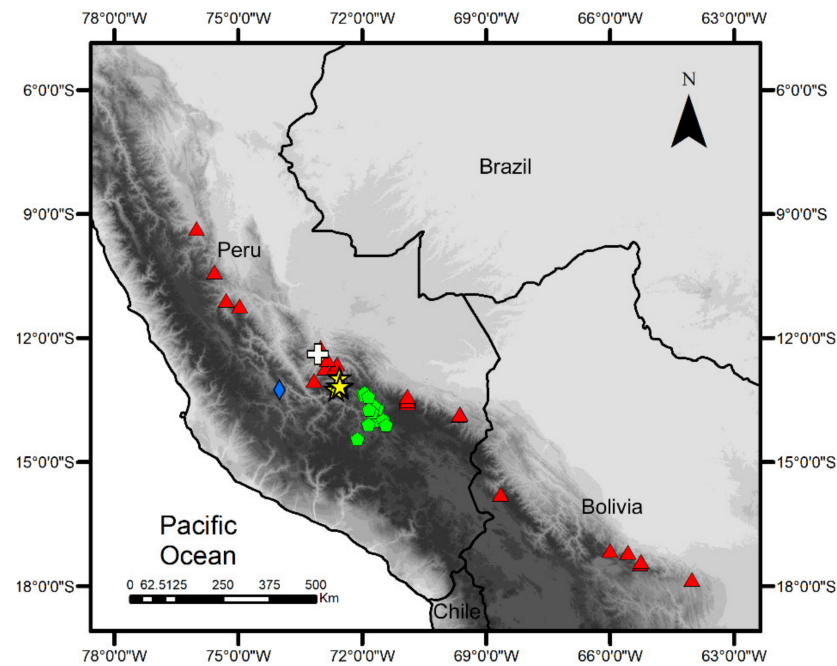


Figure 5. Distribution of *Proctoporus* species related to the two new species described in this study. *Proctoporus guentheri* species complex (red triangle), *P. katerynae* sp. nov. (white cross), *P. optimus* sp. nov. (yellow star), *P. unsaaca*e (green pentagon), and *Proctoporus* sp. “2” (blue diamond). We used voucher records and literature to obtain the coordinates of the localities.

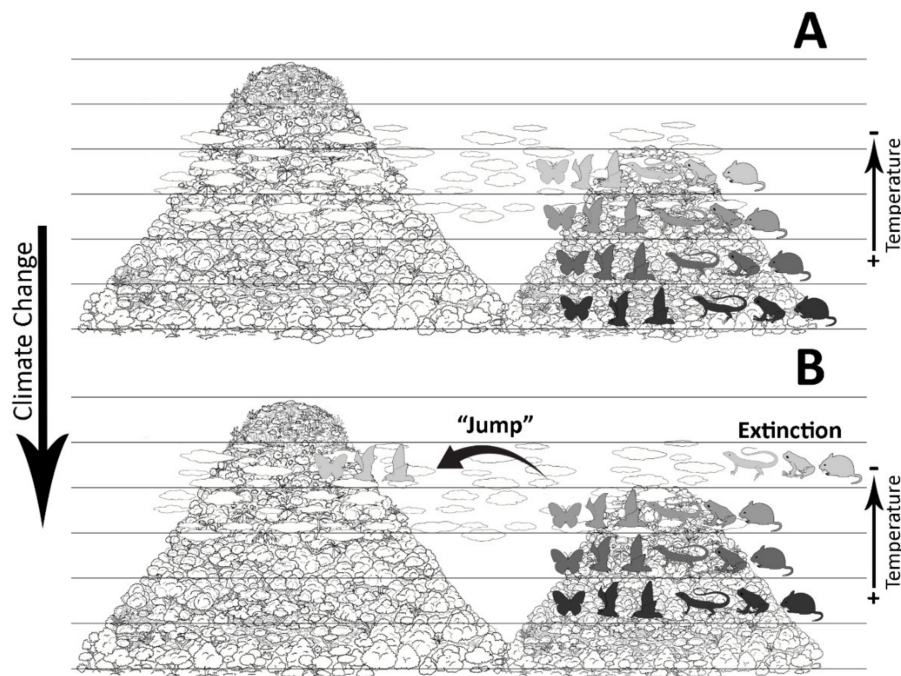


Figure 6. Global climate change warms the lower regions through altitudinal gradient, causing species migration to higher parts where the climate is ideal, causing “escalator to extinction”. Species that have a high dispersal capacity (bats, birds, and flying insects) can “jump” to an adjacent mountain, but non-flying species (frogs, lizards, and small mammals) cannot “jump” and go extinct. (A) No climate change and (B) with climate change. This figure is adapted from Chen et al. [38], Freeman et al. [35], Parmesan et al. [39], and Urban [37]. Drawing by L. Mamani and O. Armesto.

Proctoporus optimus sp. nov.

Proctoporus guentheri Doan and Castoe 2003: 434

LSID: urn:lsid:zoobank.org:act:635C6124-99F6-4369-9EC1-EA369A140DFD.

Holotype—MUBI 11119, adult male (Figures 7 and 8) from Santuario Histórico de Machu Picchu (HSM) ($13^{\circ}11'01''$ S, $72^{\circ}32'29''$ W, 2790 m a.s.l.), district Aguas Calientes, province Urubamba, department Cusco, in Peru. Collected by Luis Mamani on 13 October 2012.

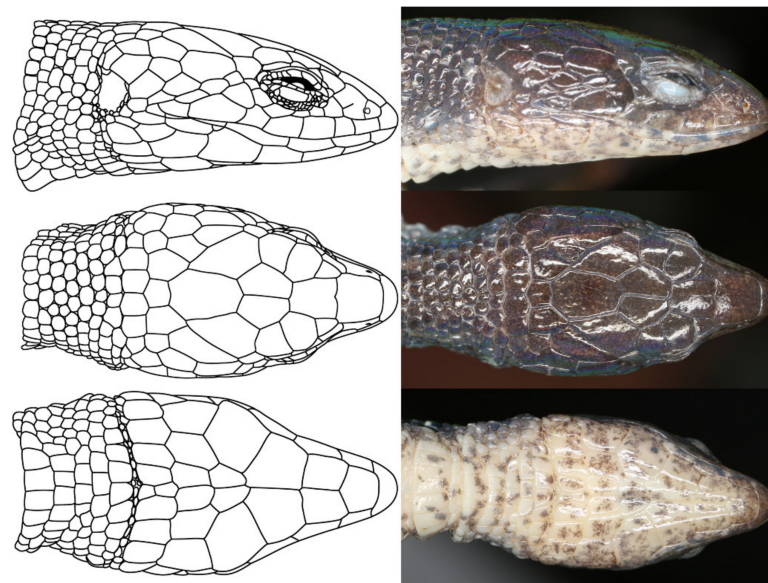


Figure 7. View of the lateral, dorsal, and ventral of the holotype head of *Proctoporus optimus* sp. nov. (MUBI 11119, SVL = 40.1 mm, TL = 69.1 mm, male). Drawing by R. Cruz.



Figure 8. Life specimen of the holotype of *Proctoporus optimus* sp. nov. (MUBI 11119, SVL = 40.1 mm, TL = 69.1 mm, male) from Santuario Histórico de Machu Picchu.

Paratypes—Four adult males (MHNC 1716, 1721, 1724, and 1731), five adult females (MHNC 1717–19, 1722, and 1729), and a subadult female (MHNC 1726) collected by Armando Mendoza Centeno and John L. Achicahuala Zegarra in April 2002, from Wiñaywayna, Santuario Histórico de Machu Picchu; two adult male (MUBI 962, 975) and two adult females (MUBI 855, 964) collected by Juan Carlos Chaparro in 1998, from Santuario Histórico de Machu Picchu, Province Urubamba. An adult male (MUBI 13133), three adult females (MUBI 12740–1 and 13133), two subadult males (MUBI 12742 and 13136), and five subadult females (MUBI 12962–3, 12744, and 13134–5) collected by Raúl Quispe Phocco in July 2013, from Sahuayaco, district Santa Teresa, province La Convención. Two adult males (MUBI 2915 and 2984) collected by Luis Mamani in October 2013, from Mesa Pelada (12°56′21″ S, 72°35′55″ W, 2780 m a.s.l.), and a male (MUBI 2809) collected by James W. Tito in January 2017, from Chuyamayo (12°58′17″ S, 72°36′02″ W, 2420 m a.s.l.), district Maranura, province La Convención. UTA R-51512, R-51515 from Chocalloc and R-51515–16 from Machu Picchu. All types were collected in the department of Cusco, Peru.

Referred specimen: UTA R-51518 from Chachabamba in the Santuario Histórico de Machu Picchu.

Etymology—The specific epithet, *optimus*, is patronymic for Optimus Prime, leader of the Autobots in the science fiction movie Transformers, in recognition of the seventh film that was filmed in Machu Picchu: Transformers: Rise of the Beasts.

Diagnosis—(1) Frontonasal longer than frontal; (2) nasoloreal suture incomplete or absent; (3) three supraoculars; (4) four superciliaries; (5) three postoculars; (6) palpebral disc, undivided and transparent; (7) four supralabials, anterior to the posteroventral angle of the subocular; (8) three anterior infralabials, occasionally four; (9) four to five genials in contact; (10) two rows of pregenials; (11) dorsal body scales, quadrangular, keeled, and sub imbricate; (12) 34–38 scales around the midbody; (13) 33–34 transverse dorsal rows; (14) 18–22 transverse ventral rows; (15) 24–27 longitudinal dorsal rows; (16) 10 longitudinal ventral rows; (17) a continuous series of small lateral scales separating the dorsals from the ventrals; (18) three to four posterior cloacal plate scales; (19) two anterior preanal plate scales; (20) six to nine femoral pores per hind limb in males and four to eight in females; (21) preanal pores absent; (22) 8–11 subdigital lamellae on finger IV; 14–17 subdigital lamellae on toe IV; (23) limbs not overlapping when against the body; (24) pentadactyl, digits clawed; (25) in adult males, the dorsum is brown with small and irregular black spots irregularly distributed; the flank is similar to the dorsum with a continuous line of conspicuous ocelli from the neck to tail; the ventral surface varies from intense orange to a combination of orange and cream; the throat is intense orange with abundant dark spots; in adult females, the dorsum is similar to males; the flanks are brown with small and irregular black spots irregularly distributed with small no conspicuous ocelli; and the ventral surface is cream with few or many more brown spots (Figure 8). Measurements are shown in Table 3.

Proctoporus optimus sp. nov. can be distinguished from all species of *Proctoporus* (*P. bolivianus*, *P. carabaya*, *P. chasqui*, *P. iridescens*, *P. kizirianii*, *P. lacertus*, *P. laudahnae*, *P. machupicchu*, *P. oreades*, *P. pachyurus*, *P. rhami*, *P. spinalis*, *P. succullucu*, *P. unsaaca*, and *P. xestus*), except for *P. guentheri* and *P. katerynae* sp. nov., as having two rows of pregenial scales (three in all other species of *Proctoporus*); from *P. guentheri* through the absence of a pair of enlarged pregenials in contact on the midline behind the second pair of genials (present in *P. guentheri*); and from *P. katerynae* sp. nov., as having 18–20 longitudinal dorsal scale rows, eight longitudinal ventral scale rows, and females having four to eight femoral pores (24–27 longitudinal dorsal scale rows, 10 longitudinal ventral scale rows, and females not having femoral pores in *P. katerynae* sp. nov.).

Description of the Holotype

Adult male, snout-vent length (SVL) 40.1 mm, tail length 69.1 mm; head scales, smooth, without striations or rugosities; rostral scale, wider than tall, meeting supralabials on either side, above the supralabials, in contact with frontonasal, nasals, and first supralabials; frontonasal, slightly longer than wide, smaller than the frontal, widest posteriorly, in contact with rostral, nasals, anteriormost supraocular, frontal and first superciliar; prefrontals

absent; frontal, longer than wide, polygonal, in contact with frontonasal, first two supraoculars, and frontoparietals; frontoparietals polygonal, in contact with frontal, second, and third supraoculars, parietals, and interparietal; three supraoculars, all in contact with superciliaries, third in contact with frontoparietal, parietal, and postocular; interparietal, longer than wide, heptagonal, in contact with frontoparietals anteriorly, with parietals laterally, and with occipitals posteriorly; parietals, irregular pentagon, anteriorly in contact with frontoparietals and third supraoculars, posteriorly with occipital, laterally in contact with supratemporal and third postocular; three occipitals, smaller than the parietals, the middle is smaller than the sides; and three supratemporals on the left side and two on the right. Nasal divided by nasal suture, longer than high, in contact with first and second supralabials; loreal, absent or incomplete; four superciliaries; two preoculars, small and separate, the first in contact with the first superciliary, nasal, and frenocular, the second in contact with the frenocular and first subocular; frenocular, pentagonal, in contact with the second and third supralabials, preoculars, and first subocular; palpebral disc made up of a single transparent scale; three suboculars; three postoculars; temporals, smooth, glossy, polygonal, 15 on the left side and 16 on the right; and four supralabials, anterior to the posteroventral angle of the subocular. Mental, wider than long, in contact with first infralabial and postmental; postmental, single, pentagonal, in contact with the first infralabials and first pair of genials; six genials, two anterior pairs in contact; first pair in contact with first and second infralabials; second pair of genials in contact with the second and third infralabials; third pair separated by two smaller median pregenials; five gular scale rows; collar fold, distinct; and lateral neck scales, round and smooth. Dorsal scales, rectangular, longer than wide, juxtaposed, with single high, rounded keel; 35 transverse dorsal rows and 24 longitudinal dorsal rows at the midbody; continuous lateral scale series, smaller than dorsals; reduced scales at limb-insertion regions; 21 transverse ventral scale rows and 10 longitudinal ventral scale rows at the midbody; anterior preanal plate scales, paired; and four posterior preanal plates. Scales of dorsal tail, rectangular and juxtaposed; dorsal and dorsolateral caudal scales, keeled and ventral; and ventral scales, quadrangular and smooth. Forelimbs, pentadactyl and digits clawed; dorsal brachial scales, polygonal, subimbricate, and smooth; ventral brachial scales, roundish, juxtaposed, and smooth; antebrachial scales, polygonal, subequal in size, smooth, and ventral antebrachial scales smallest; dorsal manus scales, polygonal, smooth, and subimbricate; palmar scales, small, rounded, and domelike; and dorsal scales on fingers, smooth, polygonal, imbricate, two on finger I, four on finger II, five on finger III, six on finger IV, three on finger V. Hindlimbs, pentadactyl and digits clawed; scales of anterodorsal surface of thigh, large, polygonal, smooth, and subimbricate; scales on posterior surface of thigh, small, rounded, and juxtaposed; scales on ventral surface of thigh, large, rounded, flat, and smooth; six femoral pores on the left leg and seven on the right; scales on anterior surface of crus, polygonal, smooth, juxtaposed, and decreasing in size distally; scales on anterodorsal surface of crus, rounded and subimbricate; scales on ventral surface of crus, large, smooth, flat, and subimbricate; scales on dorsal surface of toes, quadrangular, smooth, two on toe I, five on toe II, eight on toe III, ten on toe IV, and six on toe V; subdigital lamellae, single distally and double proximally; and limbs not overlapping when adpressed against the body.

The coloration in life of the dorsum, dorsal surface of forelimbs and hindlimbs, and head is dark brown with small and irregular black spots; the flanks are like the dorsum, but with continuous and conspicuous ocelli; the sides of the venter, chin, throat, and ventral surface of legs and tail are intense orange with small and irregular black spots; and the middle of belly is cream. In the preservative, the dorsum, head, flanks, dorsal surface of tail, forelimbs, and hindlimbs are brown, and the venter, chin, throat, ventral surface of tail, forelimbs, and hindlimbs are cream with irregular and small brown spots.

Distribution and ecology—The new species is known from the montane forest of Cusco in five localities, Historical Sanctuary of Machu Picchu, Chocalloc, Santa Teresa, and Mesa Pelada, at elevations of 1641–2780 m altitude (Figure 5). The specimens were found under fallen tree trunks, leaf litter, and rocks during diurnal assessments. *Proctoporus optimus* sp.

nov. was found in sympatry with other gymnophthalmid lizards such as *Cercosaura anomala*, *P. machupicchu*, *P. lacertus*, and *P. unsaacae* in Machu Picchu.

Conservation—*Proctoporus optimus* sp. nov. inhabit the most important, and one of the most fragile protected natural areas in Peru, in the Historical Sanctuary of Machu Picchu (HSMP). Typical human activities at HSMP include tourism, introduction of invasive species, railway traffic and operations, hydroelectric regulation, and urban growth. Tourism activities promote biodiversity loss and alter animal behavior (e.g., [40,41]), through the introduction of invasive species such as trout, dogs, and cats (e.g., [42–45]); human-transported wildlife diseases (e.g., [46]); noise emissions from vehicles and hydroelectric power operations (e.g., [47]); and running over wildlife by vehicles and railways (e.g., [48,49]). However, the precise effects of these threats on biodiversity and on populations of *P. optimus* sp. nov. have not yet been quantified.

4. Discussion

The results of our study show that comparative examination of museum specimens and molecular phylogenetic analyses are very important in order to correctly identify the species, especially species groups that have historically been underestimated, and where cryptic diversity is high, such as *Proctoporus*. In fact, *Proctoporus* previously contained many species that today belong to other highly divergent lineages, such as *Petracola* and *Riama* [4], similar to lineages of terrestrial breeding frog from the Andes that were previously included in *Phrynopus*. The use of genetic sequences allowed for the rearrangement of lineages and discovering of the cryptic diversity of the Andean group (e.g., [10,50–52]).

The result of our ML tree is congruent with recent studies [2,11,13,15,53], with some differences, such as the polyphyly of *Oreosaurus*, *Proctoporus iridescens*, *P. guentheri*, and *P. spinalis*. The topologies of Torres-Carvajal et al. [11] and Vásquez-Restrepo et al. [14] recovered the polyphyly of *Proctoporus*, in contrast to topologies of Goicoechea et al. [2], Moravec et al. [13], and Mamani et al. [15], who reported the monophyly of *Proctoporus*. These contrasting result and low support values do not support the monophyly of *Proctoporus*. Furthermore, the polyphyly recovered in both trees of *Oreosaurus*, *Proctoporus iridescens*, and *P. spinalis* must be reviewed. Moreover, *P. guentheri* was recovered in two divergent lineages, the first lineage contained *P. laudahnae*, *P. guentheri* (MUBI 10278, 12687), *P. sp.* “Ca2”, *P. sp.* “sp3”, and *P. sp.* “sp4” (all specimens collected in montane forests of Bolivia and Peru) and corresponded to *Proctoporus guentheri*, while the second lineage containing *P. unsaacae*, *P. guentheri* (UTA R-51515 and 51517), *P. optimus* sp. nov. (MUBI 2915 and 2984), and *P. katerynae* sp. nov. (MUBI 10482) was a sister lineage of *P. guentheri*.

The new species described in this study are similar, both having two rows of preangular scales and three anterior infralabial scales. We hypothesize that, according to its position within the topology of our molecular phylogenies, *P. katerynae* sp. nov. could be the ancestral species with respect to the other species (*P. optimus* sp. nov. and *P. unsaacae* and *P. sp.*) that colonized the high montane forest and arid valleys of Apurimac, Ayacucho, and Cusco. However, this biogeographical hypothesis is yet to be formally tested.

On other hand, the lineage that contains the *P. guentheri* species complex has only been reported in humid montane forest ecosystems, and not within arid ecosystems such as inter-Andean valleys [7,19,20]. In addition, it covers a latitudinal extension of more than 1500 km in a straight line from the central Andes of Peru to the central Andes of Bolivia (Figure 5). We note that this lineage is widely distributed and it has not been able to colonize the inter-Andean valleys, much less the grasslands of the humid Puna. Thermal tolerances and water stress (especially maintaining water balance during the development of the individual from egg to adult) may prevent successful colonization of the drier and warmer inter-Andean valleys. A recent study found that two species of Andean gymnophthalmid lizards (*P. succullucu* and *P. unsaacae*) in an inter-Andean valley tolerate relatively high temperatures, and may not be susceptible to temperature rise [54]. However, the high maximum temperature in the inter-Andean valley at 2870 m a.s.l. (up to 34.0 °C) might promote local adaptation to higher temperatures. In contrast, moderate maximum temper-

atures (21.74 °C at 3000 m a.s.l.) in the montane forest where members of the *P. guentheri* species complex live should not select for warm tolerance [55]. Furthermore, colonization of the inter-Andean valleys by members of the *P. guentheri* species complex could also be limited by the inability to maintain water balance during the development of the individual from egg to adult. Finally, very little is known about the biology of the gymnophthalmid lizards that mainly inhabit the Andes mountains and that may be potentially sensitive to ongoing global climate change.

The result of our study demonstrates that there is a long way to go to resolve the taxonomy of *Proctoporus*, especially the taxonomy of *P. guentheri*, which still does not have a neotype and has long been causing taxonomic problems. Uzzell [7] synonymized *Oreosaurus ocellifer* described from the Marcapata valley and *O. anomalus* from the San Miguel valley, both in southeastern Peru, with *P. guentheri*. Our topology recovered two specimens (CORBIDI 14692 and 14693) from the Marcapata Valley and a specimen from the Cordillera de Vilcabamba (MUBI 12687) located ~20 km northeast of the San Miguel valley as sister lineages. These two lineages could correspond to the previously recognized *O. ocellifer* and *O. anomalus*, although more research is required to reassess their taxonomic status. Specifically, the absence of genetic sequences and specimens of *P. guentheri* from the type locality hinders a resolution of the taxonomy of these lineages.

The holotype of *P. guentheri* was collected by Ernesto Guenther and deposited in the Lübeck Museum, Germany [16]. The loss of the holotype during World War II prevented the species from being characterized in detail by later studies such as those by Burt and Burt [17] and Uzzell [7], which relied on vague morphological descriptions. Burt and Burt [17], based on provenance, similarity, and number of femoral pores, hypothesized that *P. bolivianus* is synonymous with *P. guentheri*, assuming that *P. bolivianus* was described as the female of *P. guentheri*. However, Uzzell [7] reviewed a larger sample of specimens assigned to *P. guentheri*, finding conclusive differences between both species. The presence of two elongated genial scales, the row of transverse ventral scales (26 in *P. bolivianus* and 17–20 in *P. guentheri*), and the row of transverse dorsal scales (37–45 in *P. bolivianus* and 29–35 in *P. guentheri*) supported the separation of both species. The original description of the species did not use the genial scales as diagnostic characters. Boettger [16] mentioned that *P. guentheri* has four pairs of submental scales (genials), where three anterior scales are joined in the middle and the posteriors are separated, but is highly probable that the third and fourth pair of posterior scales have been confused with the pregenial scales. We observe that species of the genus *Proctoporus* do not possess these characteristics, except for "*Cercosaura manicata boliviana*", but Boettger [16] did not refer to this species. *Proctoporus machupicchu* and some specimens of *P. bolivianus* are characterized by having three pairs of bonded genials, but the fourth row of genials is absent. All specimens we examined and assigned to *P. guentheri* possess two pairs of pregenials, a pair of anterior elongated greats that are attached, and a pair of posterior reduced greats that may be separate or joined (Figure 9). It is very likely that these scales were mistaken as the four pairs of genial scales. Finally, our phylogeny recovered all specimens that had a pair of elongated pregenial scales within the *P. guentheri* lineage. Furthermore, the specimens from Machu Picchu (Peru) and assigned to *P. guentheri* by Doan and Castoe [6] lack these scales, and were nested in a divergent lineage with respect to *P. guentheri* (Figure 2).

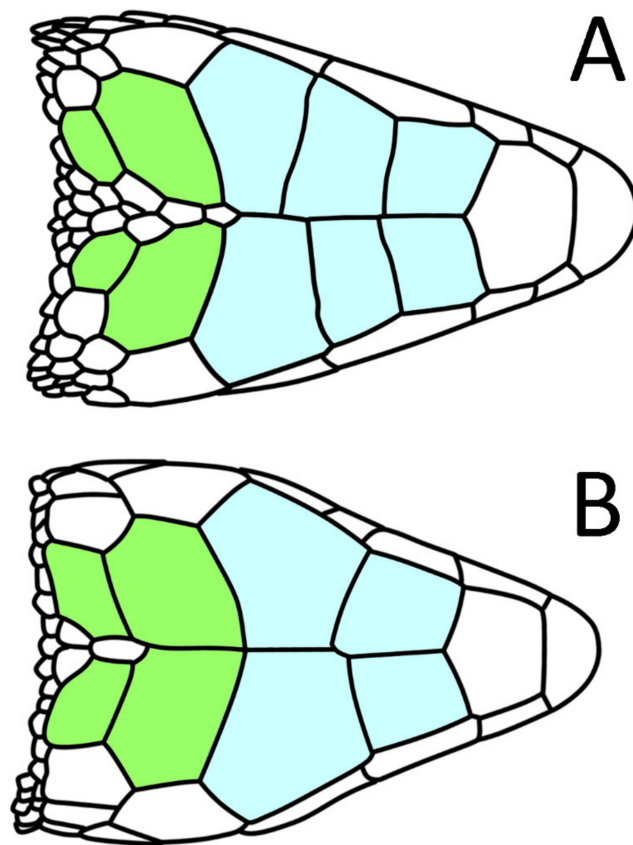


Figure 9. Ventral view of head of “*Cercosaura manicata boliviana*” ((A), CORBIDI 16500) and *Proctoporus guentheri* ((B), MHNC-R 3137). Light blue represents genial scales and light green represents enlarged pregenal scales.

All of the specimens identified in this study as *P. guentheri* come from montane forests on the eastern slope of the Andes, from central Peru to southeastern Bolivia. The type locality of Sorata is an inter-Andean, dry shrubland, which does not coincide with the characteristics of the humid montane forests. Assuming our interpretation of the description of *P. guentheri* is correct, Sorata is a very unlikely locality for *P. guentheri*, and we suggest that the designation of Sorata as a type locality is an error (Figure 10). Our claim is supported by Boettger’s list of Sorata species, many of which do not inhabit inter-Andean scrublands and dry valleys. Later studies revised Sorata’s species list and updated the species taxonomy [56–58], but did not consider the ecological aspects associated with the early records: two species of lizards (*Anolis fuscoauratus* and *Diploglossos fasciatus*), two species of amphisbaenians (*Amphisbaena darwini* and *Amphisbaena fuliginosa*), and 11 species of snakes (*Atractus emmeli*, *Dipsas cenchoa*, *D. catesbyi*, *Drepanoides anomalus*, *Erythrolamprus aescapularis*, *Leptodeira annulata*, *Mastigodryas bobdaerti*, *Micrurus spixii*, *Oxyrhopus petolarius*, *Philodryas olfersii*, and *Taeniophallus occipitalis*) that do not inhabit arid inter-Andean valleys with scrub vegetation.

If not Sorata, then what is the type locality of *P. guentheri*? Boettger [16] mentioned that the type specimens came from the “vicinity” of Sorata, which may extend many kilometers around the populated center. Furthermore, he mentioned a town called Mapiri, which is located ~68 km as the crow flies, northwest of Sorata. Mapiri is ecologically characterized by presenting a humid ecosystem of Yungas forests [58], it is located at ~660 m a.s.l. and it is likely that all the specimens collected by Günther and deposited in the Lübert Museum come from the surroundings of Mapiri. Therefore, the type locality for *P. guentheri* could be within the Yungas forests above 1000 m a.s.l. in the region between Mapiri and Sorata.



Figure 10. View of landscape of Sorata at 2700 m a.s.l., Bolivia. Photo taken by L.M. on 24 February 2012.

Finally, the designation of a neotype and type locality for *P. guentheri* will allow us to resolve the taxonomy of this widely distributed lineage and of its many cryptic species. Unfortunately, we could not find specimens assigned to *P. guentheri* in two scientific collections from Bolivia (CBF, MHNC-R) that originated in the surroundings of Mapiri. We encourage Bolivian biologists to work on the systematics and taxonomy of this species, to designate a neotype, and to document the genetic diversity of populations of *P. guentheri* and related forms.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14030215/s1>. Figure S1: Maximum likelihood tree of *Proctoporus* and other gymnophthalmid lizards. Figure S2: Bayesian Inference tree of *Proctoporus* and other gymnophthalmid lizards Table S1: List of vouchers and accession number codes of taxa used in this study available from GenBank.

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

Appendix A

Specimens Examined

Proctoporus bolivianus: BOLIVIA: LA PAZ: CBF 1507–8, 1513–4, 1519–21 (7 ♂), 1505–6, 1509–12, 1522–5 (10 ♀), 1517–8 (2 juveniles). Total = 19.

Proctoporus carabaya: PERU: PUNO: Carabaya: MUBI 5428, 5430, 11582 (3 ♂), MUBI 5422, 11579–81, 11584 (5 ♀), MUBI 5431 (juvenile); Ollachea: MUBI 11849 (1 ♂), MUBI 11850–1 (2 ♀). Total = 12.

Proctoporus chasqui: PERU: AYACUCHO: La Mar: Chuiquintirca: CORBIDI 6961–5, 6967, 8413, 8415–6, 8418–9, 8423 (12 ♂), CORBIDI 6955–6, 6968–9, 8414, 8417, 8420–2, 8424–5, 8431–2 (13 ♀) Total = 25.

Proctoporus guentheri: BOLIVIA: SANTA CRUZ: CBF 36.2, 1677–8 (3 ♂); COCHABAMBA: MHNC-R 499, 3136–7, 3139 (4 ♂), MHNC-R 3138 (1 ♀); PERU: AYACUCHO: Cajadela: CORBIDI 17876 (1 ♀); CUSCO: La Convención: Urusayhua: MUBI 13341–2 (2 ♀), 13518–20, 13325, 13327, 13622, 13642 (7 ♂); Marcapata: MUBI 5880 (1 ♀), 5878–9, 6045 (3 ♂), CORBIDI 14355, 14692 (2 ♀), 14693 (1 ♂); Paucartambo: Kosñipata: San Pedro: MUSM 27981 (1 ♀); Quellouno: MUBI 2987 (1 ♀), 2985–6 (2 ♂); Echarate: Alto Loroahuachana: MUSM 29455–6 (2 ♀), 29454 (1 ♂); Alto Sangobatea: MUSM 29449 (2 ♀); Reserva Comunal Machiguenga: MUBI 10278–9, 11188 (3 ♂); HUÁNUCO: Tingo María: La Garganta: CORBIDI 15558 (1 ♂), 14932, 14978–9 (3 ♀); Santa Rosa de Yanajanca: MUSM 39217; PASCO: Huancabamba: MUBI 14516, 14526, 14528, 14530 (4 ♀), 14518, 14525, 14529 (3 ♂); JUNÍN: Chanchamayo: San Ramón: MUSM 36484 (1 ♀), 36476 (1 ♂); PUNO: Carabaya: Ollachea: MUBI 2867. Total = 53.

Proctoporus iridescens: PERU: PUNO: Sandia: MUBI 5359, 5699 (2 ♂), MUBI 5360–1, 5421, 5700–2 (6 ♀). Total = 8.

Proctoporus kiziriani: PERU: CUSCO: Quispicanchi: Marcapata: MUBI 5369, 5859 (2 ♀); MUBI 5366–7, 5683–5, 5861 (6 ♂). Total = 8.

Proctoporus lacertus: PERU: CUSCO: Santa Teresa: MUBI 11165–67, 11169 16085–6 (6 ♂), MUBI 11168 (1 ♂); Soraypampa: MUBI 2808, 13299–302, 13311 (7 ♂), MUBI 13303–7, 13309–10 (7 ♀); Vilcabamba: MUBI 2880, 2884 (2 ♂), MUBI 2881–3, 2885–6 (5 ♀).

Proctoporus laudahnae: PERU: HUÁNUCO: Carpish: Achupampa: CORBIDI 16071, 16073, 16077 (3 ♀), CORBIDI 16074, 16076 (2 ♂), CORBIDI 16072 (Juvenile). Total = 6.

Proctoporus machupicchu: PERU: CUSCO: Aobamba: MUBI 13362, 13373 (2 ♀); Santuario Histórico de Machu Picchu: MUBI 11815 (♀); San Luis: MUBI 16307 (♂). Total = 4.

Proctoporus oreades: PERU: PASCO: Santa Barbara: CORBIDI 7219 (Holotype ♂), CORBIDI 7214, 7216–8, 7220, 7222, 7224–25 (8 paratypes ♀), CORBIDI 7215, 7221, 7229 (3 paratypes ♂), CORBIDI 7223 (juvenile). Total = 12.

Proctoporus pachyurus: PERU: JUNIN: Tarma: Cerro San Cristóbal: MUBI 4690, 4693, 4696, 4701, 4703–6 (8 ♂), 4692, 4697–8, 4700 (4 ♀); Palca: MHNSM 13882, 13890, 13893 (3 ♀) 13887–8, 13891 (3 ♂), 13889, 13893 (2 juveniles); Tarma: MHNSM 13905, 13908, 13910–11 (4 ♂), 13906–7, 13908, 13912–16 (8 ♀); Huasi Huasi: 16646–7 (2 ♂), MHNSM 16644 (1 ♀). Total = 35.

Proctoporus rhami: PERU: CUSCO: Paucartambo: Estación Biológica Wayquecha: MUBI 4555, 4577–8, 4592, 4688 (5 ♂), MUBI 4556, 4559, 4569, 4599 (4 ♀); Marcapata: MUBI 5849, 5863–6, 6065, MUSA 1516, 1515 (8 ♂); MUBI 5847–8, 5853–8, 5862, 6066–7, 6069, 12885, MUSA 1532, MUSM 30275, 30284 (16 ♀), MUSM 30293, 30296, MUBI 12877 (3 juveniles) Total = 36.

Proctoporus spinalis: PERU: PASCO: Huancabamba: MUBI 14505 (♀), 14506 (♂); Osoaplaya: CORBIDI 7234, 7237, 7240–1 (4 ♂), CORBIDI 7246 (♀); Shollet Forest: CORBIDI 11573–5 (♀); Lugar 1: CORBIDI 10177, 10232–3, 10276 (4 ♂), CORBIDI 10208, 10231 (2 ♀);

Cuevablanca: MUSM 19965 (♂), 19964 (♀); Oxapampa: MUSM 23527 (♂), 28856 (♀), MUSM 17725–6 (2 ♂), 23528 (♀). Total = 23.

Proctoporus sucullucu: PERU: CUSCO: Urubamba: Piscacucho: MUBI 2925–9, 2931–3, 2937–40, 2942, 2944 (14 ♀); Área de Conservación Privada La Verónica: MUBI 14341 (1 ♂), 14342 (1 ♀). Total = 16.

Proctoporus unsaaca: PERU: CUSCO: Andahuaylillas: Piquillacta: MUBI 12040 (1 ♀), 12038–9, 12045 (3 ♂); Calca: MUBI 12058–9, 16027–8, 16031–3, 16035 (8 ♀), 12060, 16030, 16036 (3 ♂); Calca: Colcabamba: MUBI 15392–3 (2 ♂); Coya: MUBI 12057 (1 juvenile); Taray: MUBI 12055 (1 ♀); Lamay: MUBI 12056 (1 ♂); Quispicanchi: Lucre: MUBI 12030 (1 ♀), 12029, 12031 (2 ♂); Urcos: MUBI 12917 (1 ♀); Canchis: Checacupe: MUBI 2817 (1 ♀), 2818–9, 11978 (3 ♂); Combapata: MUBI 11964, 11967 (2 ♀), 11972 (1 ♂). Total = 31.

Proctoporus xestus: BOLIVIA: LA PAZ: CBF 617–8, 622–4, 2089, 3697, 4530–2 (10 ♂), CBF 619, 1861, 2090, 2331–2 (5 ♀), CBF 625 (1 juvenile); COCHABAMBA: CBF 1694, G2-141, MHNCR 16, 204, 315, 334 (6 ♂); TARIJA: CBF 2072, 2074, 2294, 2296–7, 2303, 2753 (7 ♂), CBF 2071, 2073, 2291, 2295, 2748, 3279 (6 ♀), CBF 2298, 2749–52 (5 juvenile). Total = 40.

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