

Eleutherodactylus discoidalis

BOLIVIA: Departamento Tarija: 12.3 km NW of Entre Ríos, on the road to Tarija, MNK-A 3877-97.

Eleutherodactylus ibischi

BOLIVIA: Departamento Santa Cruz: Km 68.5 on Santa Cruz de la Sierra-Samaipata road, 750 m elevation, CBF 3341 (holotype); Km 60 on Santa Cruz de la Sierra-Samaipata road, MNK-A 6612.

Eleutherodactylus zongoensis

BOLIVIA: Departamento La Paz: Valle de Zongo, 1250 m, CBF 2503 (holotype).

Ischnocnema quixensis

BOLIVIA: Departamento Pando, CBF 2528-29; Río Negro, MNK-A 6525-27.

Ischnocnema sanctaerucis

BOLIVIA: Departamento Santa Cruz: El Chapé, 2060 m elevation, MNK-A 1198 (holotype); MNCN 42010-13.

Ischnocnema saxatilis

PERU: Departamento San Martín: Ponga de Shilcayo, about 4 km NNW of Tarapoto, 470 m (06° 31' S, 76° 53'), MHNSM 8431 (paratype).

Herpetologica, 61(3), 2005, 325-336
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PHYLOGENETIC RELATIONSHIPS OF THE GENUS
PROCTOPORUS SENSU STRICTO (SQUAMATA:
GYMNOPHTHALMIDAE), WITH A NEW SPECIES
FROM PUNO, SOUTHEASTERN PERU

TIFFANY M. DOAN^{1,4,5}, TODD A. CASTOE², AND WILFREDO ARIZÁBAL ARRIAGA³

¹*Biology Department, Vassar College, Box 555, 124 Raymond Avenue, Poughkeepsie, NY 12604-0555, USA*

²*Department of Biology, University of Central Florida, 4000 Central Florida Blvd, Orlando, FL 32816-2368, USA*

³*Museo de Historia Natural Cusco, Universidad Nacional de San Antonio Abad de Cusco, Urb. Los Angeles E-1, Cusco, Peru*

The genus *Proctoporus* sensu stricto is a poorly known gymnophthalmid lizard clade distributed across the Andes of southern Peru and Bolivia. Recent collecting efforts in central and southern Peru recovered specimens and tissues of all known members of the genus, enabling the first complete phylogeny of the genus to be constructed. In addition, a new species was found in Puno, Peru and is described herein. We analyzed DNA sequences of three mitochondrial genes using maximum parsimony and Bayesian MCMC methods to reconstruct a phylogeny of the group. The phylogeny suggests an ancient split between a newly discovered lineage from Puno and the remaining species that coincides geographically with its isolated range. *Proctoporus pachyurus* and *P. succullucu* form sister species; *P. bolivianus* forms a clade with *P. unsaaca* + *P. guentheri*. The elevationally restricted ranges of all known *Proctoporus* species likely have contributed to the high species diversity found in southern Peru. Both allopatric and parapatric modes of speciation are proposed to explain the diversification of *Proctoporus* species.

Key words: Andes; Gymnophthalmidae; New species; Peru; Phylogeny; *Proctoporus*; Puno; South America; Squamata; Taxonomy

OF THE 31 described species originally included in the genus *Proctoporus*, five were

recognized to be in the *P. pachyurus* species group by Doan and Castoe (2003) and Uzzell (1970). Through a phylogenetic study including a broad array of gymnophthalmid lizard taxa, Castoe et al. (2004) found that *Proctoporus* species did not form a monophyletic group, and that members of the *P. pachyurus* species

⁴ PRESENT ADDRESS: Department of Biology, Central Connecticut State University, 1615 Stanley Street, New Britain, CT 06050, USA.

⁵ CORRESPONDENCE: e-mail, tiffperu@yahoo.com

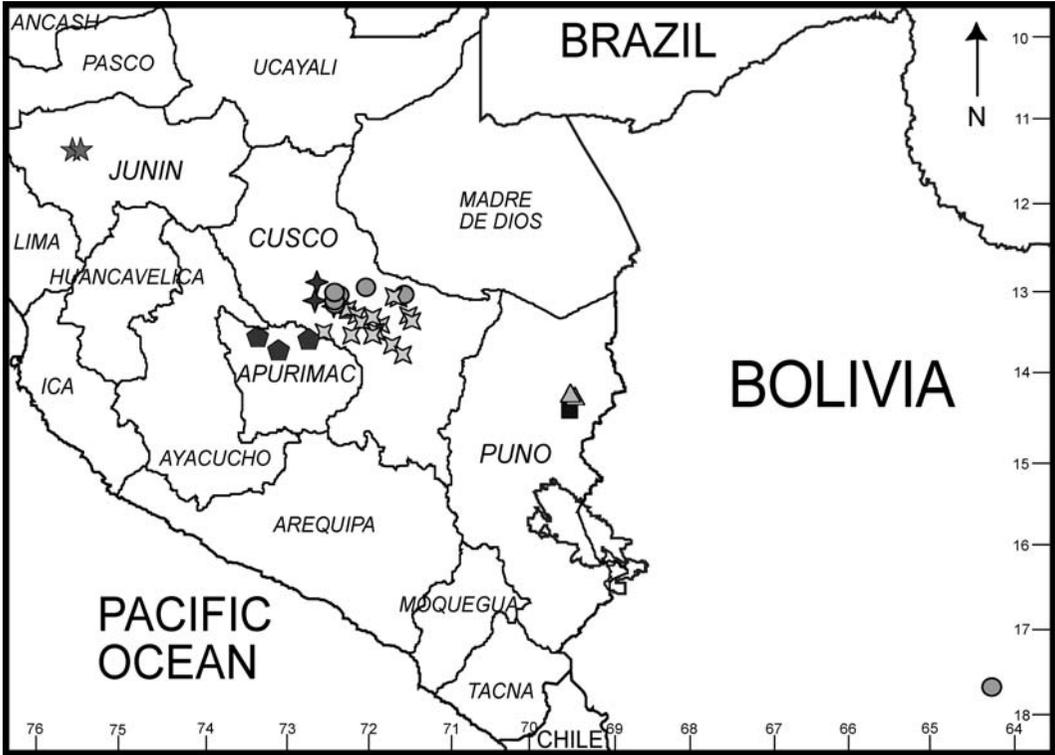


FIG. 1.—Map of southern Peru and neighboring countries depicting the sampling localities for *Proctoporus* species in this study. Country frontiers are indicated by thicker black lines. Departmental boundaries of Peru are indicated by thin grey lines; departmental names are in italics. The following symbols are used for each species: five-sided star = *P. pachyurus*; four-sided star = *P. guentheri*; pentagon = *P. succullucu*; X = *P. unsaacae*; circle = *P. bolivianus*; triangle = *P. new species*; square = *P. sp. 3*.

group did form a monophyletic group distantly related to a majority of other *Proctoporus*. Based on these data, Doan and Castoe (2005) separated the *P. pachyurus* group from all other *Proctoporus* species by removing all other species from the genus *Proctoporus* sensu stricto and placing them in separate genera. All molecular phylogenetic analyses to date, however, have not sampled the species *P. pachyurus* nor have they included all members of the species traditionally allied with *P. pachyurus* (i.e., all species of *Proctoporus* sensu stricto).

Proctoporus sensu stricto is distributed throughout the Andes of central and southern Peru and Bolivia (Doan and Castoe, 2003). Within *Proctoporus*, four species are restricted to the extreme high elevations of the central Andes, occurring 2600–4080 m above sea level (Doan, 2003; T. Doan, personal observation). The fifth species, *P. guentheri*, occurs at lower elevations (1000–3200 m; Doan, 2003). Col-

lectively, these montane species inhabit an array of Andean habitats including cloud forest and puna.

Although specimens of all currently recognized species are represented in various museums, tissues for molecular analysis only recently have become available for certain members of the genus (Castoe et al., 2004; Doan and Castoe, 2003). Recent field collections in the central and southern Peruvian Departments of Apurimac, Cusco, Junín, and Puno allowed the completion of a tissue collection of the entire genus (see map, Fig. 1), and the first complete molecular phylogenetic reconstruction of the genus. Here we combine our molecular data for *Proctoporus* with the large gymnophthalmid dataset of Castoe et al. (2004) and re-evaluate the monophyly of the newly redesignated genus. In addition to reconstructing the phylogeny of all known *Proctoporus* species, our field investigations

and subsequent analyses revealed a new lineage of *Proctoporus*. These specimens were originally identified as *P. guentheri* based on their morphology and the fact that they were first encountered at a relatively low elevation (2100 m). Subsequent morphological and molecular analyses, however, determined that this lineage is quite distinct from its congeners and that it actually consists of two separate sister species.

MATERIALS AND METHODS

Specimens of *Proctoporus* were obtained throughout the Peruvian range of the genus (Fig. 1; see Doan and Castoe, 2003, for Cusco localities). Specimens were collected by hand, euthanized, fixed in 10% formalin, and later transferred to 70% ethanol for long-term museum storage. The specimens were deposited at the University of Texas at Arlington Collection of Vertebrates (UTA) and the Museo de Historia Natural, Universidad Nacional de San Antonio Abad de Cusco (MHNC; formerly abbreviated UNSAAC) in Peru. Liver tissue was taken from all individuals and stored in tissue lysis buffer (0.5M Tris, 0.25% EDTA, 2.5% SDS).

In addition to the specimens collected in the field, supplemental museum specimens were examined from KU, MHNC, USNM, UTA, and the Gabinete de Zoología, Universidad Nacional de San Antonio Abad de Cusco (GZ). Museum abbreviations follow Leviton et al. (1985) except for MHNC and GZ. All specimens examined are listed in Appendix I. Measurements were made with a digital caliper to the nearest 0.1 mm. All anatomical terms and methods of taking meristic counts follow Kizirian (1996) except as modified by Doan (2003) and Doan and Schargel (2003).

In addition to morphological analysis of specimens, we reconstructed a three-gene molecular phylogeny of *Proctoporus* from southern Peru and included a recently collected specimen of *P. bolivianus* from Bolivia. We added our sequences to the expanded gymnophthalmid dataset of Castoe et al. (2004; which included data from Doan and Castoe, 2003; and Pellegrino et al., 2001). Our molecular sampling of *Proctoporus* included multiple individuals of each described species in the genus and three individuals of the newly discovered lineage.

Whole cellular DNA was extracted from liver tissue using the DNeasy DNA extraction kit (Qiagen). A fragment of the mitochondrial NADH dehydrogenase subunit 4 gene and adjacent tRNAs (hereafter referred to collectively as ND4) was PCR amplified using the primer pair ND4 and Leu as in Arévalo et al. (1994) for all specimens that were collected. Additionally, mitochondrial small and large ribosomal subunit genes (12S and 16S) were amplified for selected specimens as described in Parkinson (1999) and Parkinson et al. (1997). Positive PCR products were excised out of agarose electrophoretic gels and purified using the GeneClean III kit (Bio101). Purified PCR products were quantified and directly sequenced using the CEQ D Dye Terminator Cycle Sequencing (DTCS) Quick Start Kit (Beckman Coulter), run on a Beckman CEQ2000 automated sequencer.

Raw sequence chromatographs were edited using Sequencher 4.2 (2004 Gene Codes Corp.). Sequences were added to the existing alignment of gymnophthalmid lizards from Castoe et al. (2004) and aligned to this dataset by eye. These sequences were later rechecked for positive alignment based on inferred amino acid sequence (protein-coding region) in Genedoc (Nicholas and Nicholas, 1997). Gaps in alignment were treated as ambiguities for phylogenetic analyses. The final alignment consisted of a combined total of 93 OTU's and 1640 aligned positions: 860 from ND4 (including tRNAs), 331 from 12S, and 449 from 16S. All new sequences were deposited in GenBank under the accession numbers listed in Appendix II.

We reconstructed phylogenies based on the maximum parsimony (MP) criterion in PAUP* v4.0b10 (Swofford, 2002) and Bayesian (Markov Chain Monte Carlo, MCMC) phylogenetic analysis in MrBayes v3.0b4 (Ronquist and Huelsenbeck, 2003). Phylogenetic inference was conducted on the combined concatenated dataset including all three genes. For MP analyses we conducted equally-weighted parsimony searches using the heuristic strategy with 100 random taxon addition sequence replicates. Settings for MP analyses were tree bisection-reconnection branch swapping, steepest descent off, and MULTREES option on (Swofford, 2002). We assessed support for clades in MP analyses using 100 nonparamet-

TABLE 1.—Mean genetic distance between species of *Proctoporus*. Uncorrected sequence divergence is given below the diagonal (bottom-left) and Kimura-2-parameter genetic distance is given above the diagonal (top-right).

	<i>P. bolivianus</i>	<i>P. guentheri</i>	<i>P. pachyurus</i>	<i>P. subsolanus</i>	<i>P. sp. 3 Laracani</i>	<i>P. succullucu</i>	<i>P. unsaacae</i>
<i>P. bolivianus</i>		0.136	0.147	0.157	0.154	0.153	0.145
<i>P. guentheri</i>	0.122		0.133	0.136	0.142	0.140	0.100
<i>P. pachyurus</i>	0.130	0.119		0.104	0.102	0.106	0.147
<i>P. subsolanus</i>	0.138	0.122	0.096		0.101	0.138	0.157
<i>P. sp. 3 Laracani</i>	0.137	0.127	0.094	0.094		0.129	0.146
<i>P. succullucu</i>	0.137	0.126	0.097	0.124	0.117		0.154
<i>P. unsaacae</i>	0.130	0.093	0.131	0.139	0.131	0.137	

ric bootstrap (Felsenstein, 1985) pseudoreplicates with 10 random taxon addition sequence replicates implemented in PAUP*.

ModelTest version 3.0 (Posada and Crandall, 1998) was used to infer the best-fit model of evolution for the combined dataset based on both AIC and hLTR model selection criteria available in the program (see also Huelsenbeck and Crandall, 1997; Posada and Crandall, 2001). Each MCMC run employed the model selected by ModelTest (see results).

All MCMC phylogenetic reconstructions were conducted in MrBayes (Ronquist and Huelsenbeck, 2003) with vague priors (as per the program's defaults) and model parameters estimated as part of the analyses. Three heated chains and a single cold chain were used in all MCMC analyses and runs were initiated with random trees. Trees were sampled every 100 generations and majority-rule consensus phylograms and posterior probabilities for nodes were assembled from all post burn-in sampled trees. Four independent MCMC runs were conducted to confirm stationarity was reached and that no single run was trapped on local (rather than global) optima and that independent runs converged on similar stationary parameter estimates. Each independent MCMC run employed a total of 2.5 million generations, 500,000 of which were discarded as burn-in, yielding 2 million post burn-in generations per run.

RESULTS

The combined dataset consisted of 831 constant characters and 686 parsimony informative characters. Mean uncorrected genetic distances between species ranged between 9.3% and 13.8% (Table 1). The parsimony analysis resulted in 41,310 equally-parsimonious trees of 6796 steps (CI = 0.206, RI =

0.557). The strict consensus of these trees is presented in Fig. 2A with nodes receiving <50% bootstrap support shown as collapsed. Overall, the results of MP failed to resolve basal relationships among *Proctoporus* species and also failed to resolve the monophyly of the genus.

ModelTest selected the General Time Reversible (GTR; Tavaré, 1986) model with gamma distributed among-site rate variation (G; Yang, 1993) and an estimated proportion of invariant sites (I) as the best-fit model of evolution (GTR+G+I model) based on both AIC and hLTR model selection criteria. This model was used for all Bayesian MCMC runs. Independent Bayesian MCMC analyses resulted in extremely similar parameter estimates (including likelihoods and posterior probabilities) and each rapidly ascended to a stationary likelihood plateau. Thus, all post-burn-in generations from the four independent runs were combined to estimate parameters and posterior probabilities for clades. The marginal likelihood across all post-burn-in runs (total of 8 million generations, sampled every 100) had an arithmetic mean of $\ln L = -29878.92$ and a harmonic mean of $\ln L = -29906.74$. The mean and 95% credibility interval of parameters of the GTR+G+I model, based on results from the combined four MCMC runs, are as follows: $rG-T = 1.00$ (1.00–1.00), $rC-T = 3.96$ (3.23–4.71), $rC-G = 0.18$ (0.11–0.26), $rA-T = 0.56$ (0.44–0.69), $rA-G = 3.99$ (3.38–4.69), $rA-C = 0.509$ (0.41–0.63), $\pi(A) = 0.39$ (0.38–0.41), $\pi(C) = 0.28$ (0.26–0.29), $\pi(G) = 0.08$ (0.08–0.09), $\pi(T) = 0.24$ (0.23–0.26), $\gamma = 0.57$ (0.53–0.62), $\pi_{Invar.} = 0.43$ (0.40–0.46).

The Bayesian MCMC reconstruction is shown in Fig. 2B with clades receiving <50% posterior probability collapsed. Four distinct

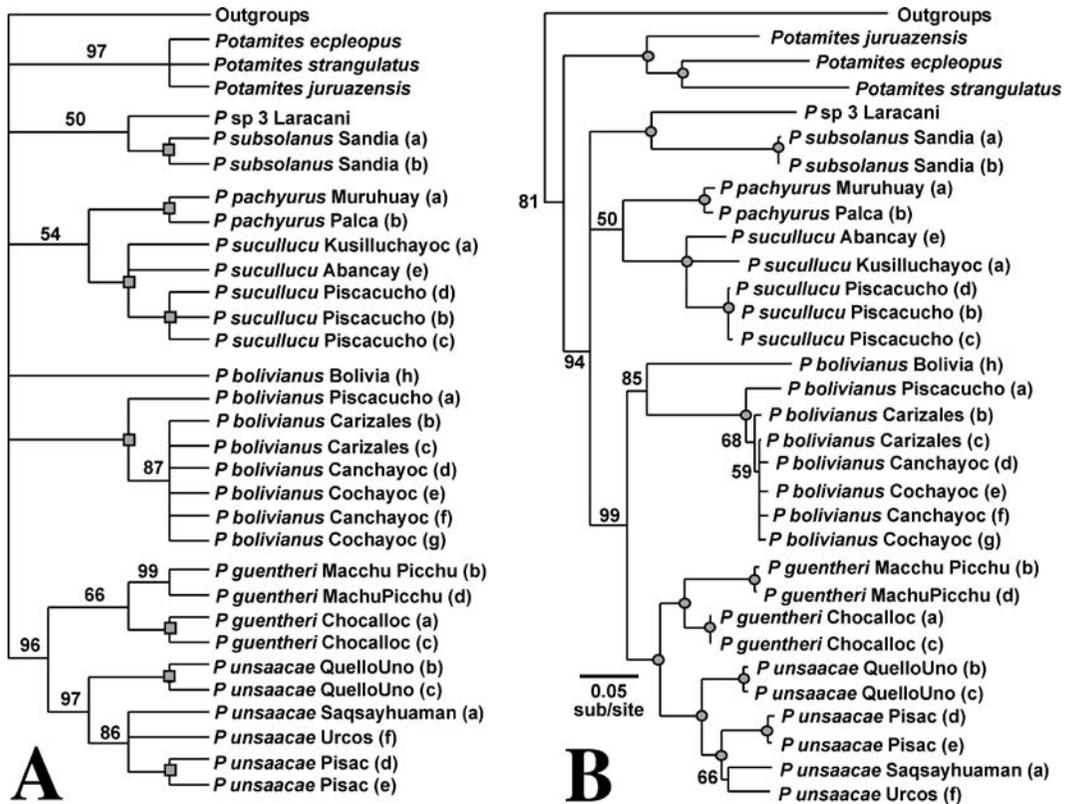


FIG. 2.—Results of phylogenetic analyses including all species of *Proctoporus* based on 1640 bases of mitochondrial DNA sequence per individual. Individuals of a species are indicated by letters in parentheses and coincide with Appendix II and Castoe et al. (2004). (A) Strict consensus of 41,310 equally parsimonious trees from maximum parsimony phylogenetic analysis with nodes collapsed if bootstrap support <50%. Bootstrap values for nodes are shown adjacent to node if $\geq 50\%$. Nodes with 100% bootstrap values are indicated with a gray square. Branch lengths are not informative. (B) Bayesian MCMC phylogenetic reconstruction phylogram based on 8 million post-burn-in generations with nodes collapsed if posterior probability support <50%. Posterior probability values for nodes are shown adjacent to node if $\geq 50\%$. Nodes with 100% posterior probability are indicated with a grey circle.

clades are evident in the Bayesian reconstruction. One clade contains an undescribed lineage of the specimens collected from Sandia and Laracani, both in the Department of Puno, Peru. A second clade contains *P. pachyurus* and *P. succullucu*. The third clade is made up of *P. bolivianus*; the final clade contains *P. guentheri* and *P. unsaaca*, recovered as the sister clade to *P. bolivianus*. Monophyly of *Proctoporus* sensu stricto is supported by 94% posterior probability. Monophyly of each individual species is supported with 100% posterior probability support except for *P. bolivianus*. One individual of *P. bolivianus* from Santa Cruz, Bolivia appears to be distantly related to other members of its species.

The maximum parsimony and Bayesian reconstructions do not have any nodes in conflict, but the parsimony tree suffers from poor resolution. Similarly, both of the reconstructions presented here are congruent with the phylogeny of Castoe et al. (2004) at all nodes.

The specimens from Puno clearly represent an undescribed clade of *Proctoporus*. Moreover, the specimens from Sandia and Laracani appear distantly related to each other with 9.4% uncorrected sequence divergence (Table 1). Additionally, the morphology of the specimens from Sandia and Laracani is quite distinct, with differences in numbers of supratympanic temporals, coloration, and the presence of a loreal scale. These two populations are separated from each other by 1000 m in elevation.

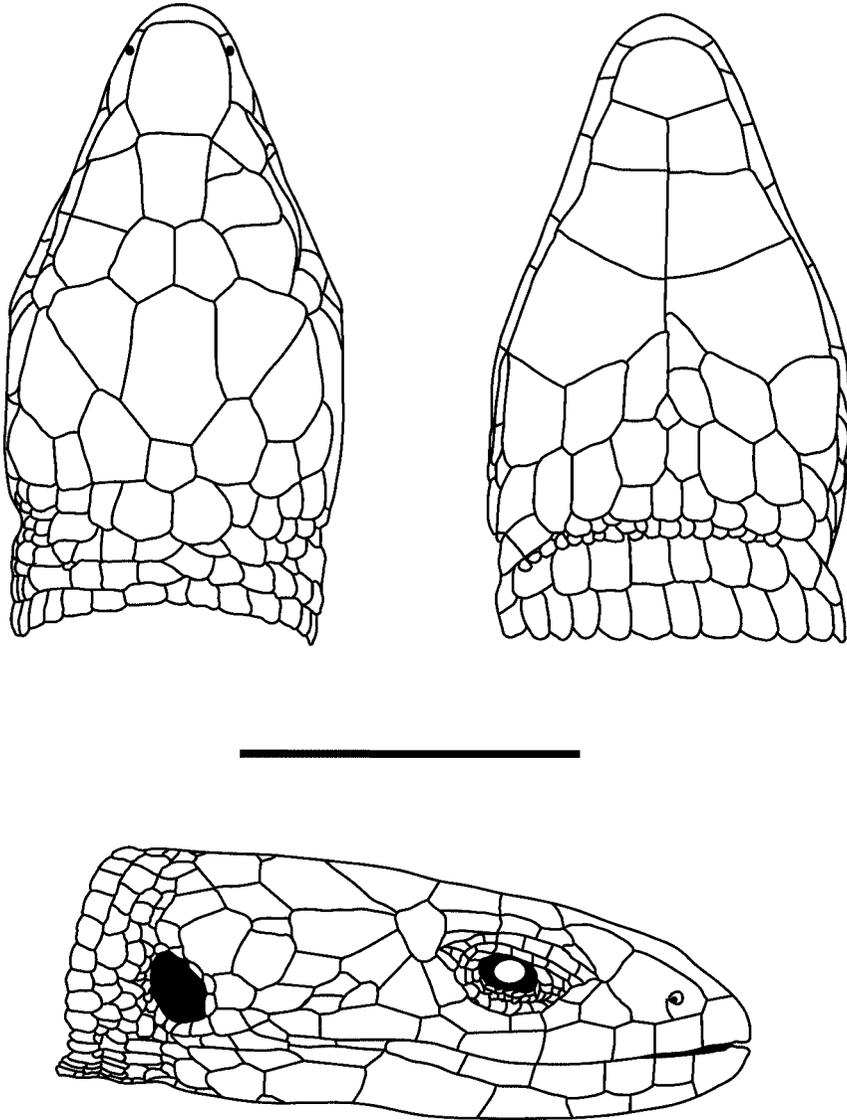


FIG. 3.—Head of the holotype of *Proctoporus subsolanus* (UTA R-52944). Top left—dorsal view; Top right—ventral view; Bottom—lateral view. Scale bar = 5 mm.

Herein, we describe the sixth species of *Proctoporus* sensu stricto from Sandia, Peru. We believe that the specimen from Laracani represents an additional distinct species, but with only one juvenile specimen collected we cannot construct a diagnosis adequate to describe that species. Therefore, we leave the Laracani specimen as an undescribed species until further collection produces an adequate type series for that lineage (*Proctoporus* sp. 3).

SYSTEMATIC ACCOUNT

Proctoporus subsolanus sp. nov.

Holotype.—UTA R-52944 (Fig. 3), a gravid adult female, from the town of Sandia (14.34275° S, 69.46274° W), Province of Sandia, Department of Puno, Peru; 2100 m; collected on 19 June 2003 by Tiffany M. Doan.

Paratypes.—UTA R-52946, an adult male; 52947, a subadult male; 52948, and MHNC

TMD1269, adult females; all from Sandia (14.35509° S, 69.46887° W); 2221 m; collected on 20 June 2003 by Todd A. Castoe and Wilfredo Arizábal Arriaga.

Referred specimens.—MHNC TMD1266, MHNC TMD1268, MHNC TMD1270, same data as paratypes.

Diagnosis.—(1) frontonasal longer than frontal; (2) supraoculars two; (3) superciliaries 3–4, first expanded onto dorsal surface of head; (4) palpebral eye-disc made up of a single, undivided scale; (5) supralabials 5–6; (6) infralabials five; (7) dorsal body scales quadrangular, with high rounded keel; (8) transverse rows of dorsals 33–37; (9) transverse ventral rows 22–24; (10) a continuous series of small lateral scales separating dorsals from ventrals; (11) posterior cloacal plate made up of six scales in both sexes; (12) femoral pores per hind limb in males 5–8, in females 0–3; (13) preanal pores absent; (14) subdigital lamellae on Toe IV 15–17; (15) limbs not overlapping when adpressed against body in adults; (16) lateral body surfaces without ocelli, or with very few in both sexes.

Specimens of *Proctoporus subsolanus* show the presence of an undivided palpebral eye-disc, which identify them as members of the genus *Proctoporus*, as opposed to *Riama* or *Petracola* (Doan and Castoe, 2005; Uzzell, 1970). *Proctoporus subsolanus* can be distinguished from *P. guentheri* and *P. pachyurus* by having two supraoculars (*P. guentheri* 3, *P. pachyurus* 4). It can be distinguished from *P. unsaaciae* by lacking a continuous series of lateral ocelli. It can be distinguished from *P. succullucu* by limbs not overlapping when adpressed. It can be distinguished from *P. bolivianus* by having the frontonasal much longer than frontal (*P. bolivianus* has frontal equal length to frontonasal). It can be distinguished from *P. sp. 3* by having fewer subdigital lamellae (21 on Toe IV in the undescribed species).

Description of holotype.—Adult female, gravid, snout–vent length (SVL) 43.6 mm, original complete tail 70.2 mm; head scales smooth, glossy, without striations or rugosities; rostral scale wider than tall, meeting supralabials on either side at above the height of supralabials, and becoming higher medially, in contact with frontonasal, nasals, and first supralabials; frontonasal longer than wide, six-

sided, anterior sutures rectangular, posterior sutures forming a 110° angle, in contact with nasals, antermost superciliary, and frontal, longer than frontal; prefrontals absent; frontal longer than wide, pentagonal, in contact with antermost superciliary on left side only, in contact with first supraocular on left side, with first and second supraoculars on right side, in contact with frontoparietals; frontoparietals hexagonal, in contact with first and second supraoculars on left and second and third supraoculars on right, in contact with parietals and interparietal; supraoculars two on left side and three on right, first supraocular on right side in contact with first superciliary only, first on left side and second on right side in contact with first three superciliaries, second on left side and third on right side in contact with fourth superciliary, parietal, and postocular; interparietal longer than wide, heptagonal, in contact with parietals and occipitals; parietals polygonal, with posterior sutures in contact with occipital, lateral sutures diagonally in contact with subequally large temporal, bordering postocular anteriorly, second supraocular, and frontoparietal; occipitals three, smaller than parietals, median smallest, extending further posteriorly than two lateral occipitals. Nasal entire with no separate loreal scale on left side, on right side a partial suture extending from ventral portion of scale into nostril, longer than high, nostril situated in anterior third of scale, in contact with first and second supralabials, first superciliary, and frenocular; four superciliaries, first expanded onto dorsal surface of head; two preoculars, first in contact with first superciliary and frenocular, second in contact with frenocular and first subocular; frenocular roughly triangular, dorsalmost corner in contact with first superciliary, in contact with second and third supralabials, first and second preoculars, and first subocular; palpebral eye-disc made up of a single transparent scale; suboculars three; postoculars two; temporals smooth, glossy, polygonal; supratympanic temporals two; supralabials five, first four supralabials to angle of jaw; infralabials five. Mental wider than long, in contact with first infralabial and postmental posteriorly; postmental single, pentagonal, posterior suture angular with point directed posteriorly, in contact with first and second infralabials and first pair of genials;

three pairs of genials, anterior pair in contact with second and third infralabials; second genials in contact with third and fourth infralabials; third pair in contact with fourth and fifth infralabials; one pair of chin shields, separated by irregular pregenials; gular scale rows seven; collar fold slightly distinct, concealing two rows of small scales; lateral neck scales round, smooth.

Dorsals rectangular, longer than wide, with anterior and posterior margins slightly convexly curved, juxtaposed, with single high rounded keel, in 37 transverse rows; some paravertebral scales irregularly arranged; longitudinal dorsal scale rows 20 at fifth transverse ventral scale row, 23 at tenth transverse ventral scale row, 24 at fifteenth transverse ventral scale row; continuous lateral scale series, two to three scales wide, smaller than dorsals, partially hidden in lateral fold, reduced scales at limb insertion regions present; transverse ventral scale rows 22; longitudinal ventral scale rows at midbody 12; anterior preanal plate scales paired; posterior preanal plate scales six, lateralmost scales small; scales on tail rectangular, juxtaposed; dorsal and dorsolateral caudal scales with keel, ventral and ventrolateral caudal scales smooth; midventral subcaudal scales wider than adjacent scales, almost square, antermost midventral subcaudal scales subimbricate.

Limbs pentadactyl; digits clawed; dorsal brachial scales polygonal, subequal in size, subimbricate, smooth; ventral brachial scales roundish, subimbricate, smooth; antebrachial scales polygonal, subequal in size, smooth, ventral antebrachial scales smallest; scales on dorsal surface of manus polygonal, smooth, subimbricate; scales on palmar surface of manus small, rounded, subimbricate, domelike; thenar scales two, smooth laterally, raised into domes medially; finger length formula $IV > III > II > V > I$; scales on dorsal surfaces of fingers smooth, quadrangular, covering dorsal half of digit, overhanging supradigital lamellae, 3 on I, 5 on II, 6 on III, 5/6 on IV, 4 on V; subdigital lamellae 5 on I, 8 on II, 9 on III, 12 on IV, 6 on V; scales at base of Finger V thicker than adjacent scales. Scales on anterodorsal surface of thigh large, polygonal, smooth, subimbricate; scales on posterior surface of thigh small, rounded, juxtaposed; scales on ventral surface of thigh large, rounded, flat,

smooth; femoral pores 2/1; preanal pores absent; scales on anterior surface of crus polygonal, smooth, juxtaposed, decreasing in size distally; scales on anterodorsal surface of crus rounded, juxtaposed; scales on ventral surface of crus large, smooth, flat, subimbricate; toe length formula $IV > III > V > II > I$; scales on dorsal surface of digits single, quadrangular, smooth, of varying sizes, overhanging supradigital lamellae, 3 on I, 5 on II, 7 on III, 11 on IV, 7 on V; subdigital lamellae single distally, double proximally, 5 on I, 8 on II, 13 on III, 16 on IV, 11 on V; limbs not overlapping when adpressed against the body, separated by eight to nine dorsal scale lengths.

Coloration in preservative.—Dorsal surface of head dark brown with lighter brown faint mottling; lateral surface of head like dorsal surface, but with more light mottling, lip irregularly barred with cream coloring; ventral surface of head yellowish cream with clumps of black stippling on each scale; pregenial region like head but with fainter stippling, medial scales lack stippling; gular region like head but with denser stippling per scale, forming longitudinal clumps. Dorsal surface of body nearly same color as head, but slightly more grey and with less mottling, two faint light brown dorsolateral longitudinal stripes originate near occiput and extend to forelimb insertions; lateral surface of body same coloration as dorsum, fading to more mottling and lighter brown near venter; ventral surface of body with yellowish cream ground color, lateralmost scales with black stippling, medialmost scales lack stippling. Limbs similar to body, dorsal surface of arms darkly mottled with dark coloration decreasing towards ventral surface, ventral surface of arms yellowish cream without black stippling, dorsal surface of legs with more mottling than body, ventral surface of legs with cream ground color and dispersed grey stippling. Dorsal tail coloration like that of body, ventral surface of tail light brown with dark brown mottling anteriorly, ground color of tail becoming orange with brown mottling posteriorly and distal portion of tail dark brown with lighter mottling (same coloration as dorsal surface).

Coloration in life.—Dorsal, lateral, and ventral surfaces are similar to coloration in preservative. Dorsolateral longitudinal stripes

can be seen to extend from occiput onto base of tail. Ventral surface of head whitish cream; ventral surface of body yellow.

Variation.—Adult females SVL 40.7–42.6 mm, adult male SVL 47.3 mm; complete original tail of adult female 63.4, no adult males with complete original tails known. The paratypes and referred specimens are very similar to the holotype with the following minor exceptions. Suparoculars on the right side of the holotype's head appear to be anomalous. No other specimens have three supraoculars. UTA R-52946 has only two occipitals that do not meet medially because the interparietal extends posteriorly and fills the space between the occipitals. UTA R-52946, 52947, and 52948 have a partial nasal suture extending into the nostril from below, but also have a second partial diagonal suture that extends from the junction with the frenocular, especially on the left side. MHNC TMD1266 has three superciliaries. In UTA R-52946, 52947, and 52948 the frenocular does not make contact with the first superciliary and three postoculars are present. In UTA R-52947 there are three preoculars. MHNC TMD1266 and TMD1268 have six supralabials. In UTA R-52947 and 52948 there are two genial pairs and two chin shield pairs; the first pair of chin shields is separated by two pregenal scales.

Coloration is quite similar among the specimens with some having a lighter dorsum and more distinct longitudinal stripes. Stippling on the venter is more distinct or greyer in some specimens and nearly absent in others. In UTA R-52946 lateral surfaces of the body are orange and the tail and hind limbs are infused with orange. The ventral surface of the body is orange laterally and the tail is pink on the original portion and dark grey on the regenerated portion. UTA R-52946 has one lateral ocellus of black surrounding a white dot anterior to the forelimb insertions. UTA R-52947 has three indistinct lateral white spots that do not form ocelli that begin anterior to the forelimb insertion and continue to approximately midbody.

Meristic variation includes: transverse dorsal rows 33–37; longitudinal dorsal rows at midbody 21–23; longitudinal ventral rows 10–12; transverse ventral rows 22–24; subdigital lamellae on Finger IV 10–14; subdigital lamellae on Toe IV 15–21.

Sexual dimorphism is slight in this species with males having wider heads (relative to SVL) and two males (UTA R-52946 and 52947) are more colorful than the females. Femoral pore number is also sexually dimorphic, with males possessing 6–8 femoral pores per leg and females having 0–3.

Distribution.—*Proctoporus subsolanus* is known only from the type locality in northern Puno, in the Sandia Province. This area lies within the Cordillera de Apolobamba, on the easternmost flank of the central Andes of southern Peru. Specimens of this species were found between 2100 and 2221 m. This slope abruptly drops into the lowland rainforest of the Tambopata National Reserve.

Habitat and ecology.—Specimens of this species were found within and around the town of Sandia often on agricultural terraces where maize and other crops were being cultivated. These areas were probably once covered in cloud forest before human occupation of the area by the Incan civilization. All specimens were found beneath stones on the ground. Stomach contents were analyzed in four specimens and consisted of coleopterans, hymenopterans (adult and larval ants), isopods, and some unknown arthropod legs. Two gravid females were found to contain two eggs each.

Etymology.—The specific epithet is a Latin adjective meaning eastern. This name refers to the species occurring on the easternmost flank of the Andes Mountains in southern Peru. The Cordillera de Apolobamba is the final mountain range before the mountains descend into the Amazon Basin.

DISCUSSION

The known range of the genus *Proctoporus* sensu stricto is restricted to the departments of Junín, Ayacucho, Apurímac, Cusco, and Puno of central and southern Peru and the departments of La Paz, Santa Cruz, and Cochabamba of western Bolivia. Species of *Proctoporus* are known to have limited altitudinal ranges, with four members of the genus inhabiting very high elevations (>4000 m; Doan, 2003; Doan and Castoe, 2003). *Proctoporus guentheri* and the new species *P. subsolanus* inhabit lower elevations (as low as 1000 m for *P. guentheri*; Doan, 2003) and forested habitats that differ greatly from those of the high Andean species.

Despite our thorough sampling in Cusco Department (see Doan and Castoe, 2003), and less extensive but widespread sampling in Apurímac, Junín, and Puno, only one locality of sympatry was found among the six species of *Proctoporus*. At the village of Ollantaytambo, Cusco, *P. sucullucu* and *P. unsaaciae* were found to occur syntopically. At this locality, all diagnostic characters appear to remain discrete between the species and no external morphological evidence of introgression is apparent (this is currently being investigated using molecular markers by the authors). These preliminary observations suggest that *Proctoporus* species retain their specific identity even in syntopic situations, implying the existence of reproductive isolating mechanisms other than geographic isolation sufficient to prevent observable interspecific geneflow.

The phylogeny of the genus suggests an ancient split between the lineage from northern Puno and the remaining species. *Proctoporus subsolanus* occurs on the cis-Andean slope where the mountains begin their plunge into the Amazon Basin. Such a distribution substantially isolates them from other members of the genus with high mountains to the west and the barren altiplano to the south.

We find no obvious biogeographic explanation to account for the patterns of diversity across the other *Proctoporus* lineages. The only species from central Peru, *P. pachyurus* is most closely related to *P. sucullucu* from Apurímac and Cusco. *Proctoporus bolivianus* forms a sister relationship with *P. unsaaciae* + *P. guentheri* (Fig. 2). *Proctoporus unsaaciae* is the most common species in Cusco, occurring at most of the sampled localities in great abundance. *Proctoporus guentheri* occurs in the same general regions as *P. bolivianus* but at lower elevations (Doan and Castoe, 2003). The ancestor of *P. unsaaciae* and *P. guentheri* may have speciated parapatrically, with populations at high elevations giving rise to *P. unsaaciae* and those at lower elevations becoming *P. guentheri*. A similar scenario may explain the diversification of the newly discovered Puno lineage whereby sister species (*P. subsolanus* and *P. sp. 3*) appear to have partitioned their altitudinal distribution. Speciation of other *Proctoporus* clades may have been allopatric, but their current distributions do not appear

bounded by any obvious extant barriers to gene flow. Overall, the level of geographic population sampling in the current study provides only cursory evidence for historical biogeographic hypotheses. Currently, we are conducting an expanded population genetic study across all available populations in the hopes of elucidating more detailed estimates of historical genetic and demographic patterns.

RESUMEN

El género *Proctoporus* sensu stricto es un clado gymnophthálmido poco conocido que está distribuido en los Andes del Perú y Bolivia. Colecciones recientes en el sur y centro del Perú registraron especímenes y tejidos de todos los miembros del género y permiten la primera filogenia completa del género. Además, encontramos una nueva especie en Puno, Perú y la describimos aquí. Analizamos las secuencias de ADN de tres genes mitocondriales con análisis de parsimonia máxima y Bayesian MCMC para construir una filogenia del grupo. La filogenia indica que una división antigua ocurrió entre el linaje de Puno y el resto de las especies. Esta división coincide geográficamente con su ámbito aislado. *Proctoporus pachyurus* y *P. sucullucu* son especies hermanas; *P. bolivianus* forma un clado con *P. unsaaciae* y *P. guentheri*. Los rangos altitudinales restringidos de todas las especies conocidas de *Proctoporus* probablemente han contribuido a la alta diversidad de las especies de *Proctoporus* del sur del Perú. Ambos modos de especiación alopatrico y parapátrico son propuestos para explicar la diversificación del género *Proctoporus*.

Acknowledgments.—This study was partially funded by grants from Women's International Science Collaboration (American Association for the Advancement of Science) to TMD and WAA and the Vassar College Collins Faculty Research Fund to TMD. We thank J. Degner, R. Ruggiero, and J. Stainkamp for their suggestions on the manuscript. We thank C. Parkinson for providing laboratory space and resources for molecular aspects of this project. We thank J. A. Campbell and C. J. Franklin for cataloging our specimens. We also thank M. Romero Pastor, R. Acero Villanes, and K. Ramirez of the Instituto Nacional de Recursos Naturales of Peru for facilitating collecting and export permits and S. J. Orenstein for laboratory assistance. In addition, we thank the personnel at the following museums for loans of material under their care: AMNH, GZ, KU, MHNC, USNM, and UTA.

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Accepted: 19 April 2005

Associate Editor: Joseph Mendelson III

APPENDIX I

Specimens Used in Morphological Analysis

Specimen localities are given according to museum catalog information. Cataloged localities and spellings were used as is without correction of errors.

Proctoporus bolivianus: BOLIVIA: *La Paz*: Murillo, Valle de Zongo, Estación Hidroeléctrica Cuti, Khuchu (UTA R-39113); *Santa Cruz*: Caballero, Canton San Juan, Amboró National Park (AMNH R-150695); PERU: *Cusco*: 500 m up road Carizales (UTA R-51485); 800 m up road Carizales (UTA R-51486–51487); Canchayoc (UTA R-51483–51484); Cerro de Puquin (GZ 0027); Cerro Machu Picchu (UTA R-51509–51511); Cochayoc (MHNC WAA5024, UTA R-51481–51482); Cosñipata (GZ 0043); Ñusta Hispania (USNM 60699–60700, 60748 [holotype of *P. obesus*]); Ollantaytambo (USNM 49549 [paratype of *P. lacertus*], 60719); 25 km NNE Paucartambo, Abra Acanacu (KU 163801, 163804, 163810–163811, 163814, 163820, 163827, 163830–163831, 163834, 163836, 163839–164740, 163842, 163846); 29 km NNE Paucartambo, Abra Acanacu (KU 13965); 31 km NNE Paucartambo, Abra Acanacu (KU 13958, 13963); Piscacucho (MHNC AC136–AC141, UTA R-51501–51508); Tincochaca (USNM 49551 [holotype of *P. lacertus*]); Torontoy (USNM 60726–60727).

Proctoporus guentheri: BOLIVIA: *La Paz*: Nor Yungas, Serranía de Bella Vista, 17 km from Carrasco towards Sapecho (UTA R-39114); PERU: *Cusco*: Chachabamba (UTA R-51518); Chocalloc (UTA R-51512–51515); Machu Picchu (KU 135157–135160, UTA R-51516–51517); 5 km WSW Santa Isabel (KU 139307, 139309); 6 km NE Santa Isabel (KU 163939); Wiñaywayna (MHNC WAA5056).

Proctoporus pachyurus: PERU: Junín: Palca (KU 135095, KU 181919–181922, 181924, 181927); NW Palca (KU 181917–181918, 181923, 181926); 1 km NW Palca (KU 181925, 181929–181931); 2 km E Palca (KU 181938–181939); 4 km W Palca (KU135096–135097); 5 km W Palca (KU135099).

Proctoporus subsolanus: PERU: Puno: Sandia, town of Sandia (UTA R-52944 [holotype], UTA R-52946, 52947, 52948 [paratypes], MHNC TMD1266, TMD1268, TMD1269 [paratype], TMD1270).

Proctoporus sucullucu: PERU: Cusco: Kusilluchayoc (MHNC WAA5006, UTA R-51478); Piscacucho (UTA R-51496 [holotype], 51497–51500 [paratypes]).

Proctoporus unsaacaе: PERU: Cusco: Pisac, Viacha (UTA R-51475–51476, 51479); QuelloUno (MHNC AC132, UTA R-51488 [holotype], 51489–51495 [paratypes]); Saqsayhuaman (GZ Valdinós3, UTA R-51477); Urcos (UTA R-51480).

Proctoporus sp. 3: PERU: Puno: Sandia, village of Laracani (UTA R-52945).

APPENDIX II *Proctoporus* Specimens Sampled for Molecular Analysis with Museum and GenBank Accession Numbers for Each Gene. Letters in parentheses refer to individuals of a species and coincide with letters from Castoe et al. (2004).

Species	Locality	Museum	ND4	12S	16S
<i>Proctoporus bolivianus</i> (h)	Bolivia: Santa Cruz: Amboró	AMNH R-150695	AY968812	AY968821	AY968828
<i>Proctoporus bolivianus</i> (d)	Peru: Cusco: Canchayoc	UTA R-51483	AY225176		
<i>Proctoporus bolivianus</i> (f)	Peru: Cusco: Canchayoc	UTA R-51484	AY225182	AY968820	AY968827
<i>Proctoporus bolivianus</i> (c)	Peru: Cusco: Carizales	UTA R-51486	AY225179		
<i>Proctoporus bolivianus</i> (b)	Peru: Cusco: Carizales	UTA R-51487	AY225180	AY507850	AY507868
<i>Proctoporus bolivianus</i> (g)	Peru: Cusco: Cochayoc	UTA R-51481	AY225181		
<i>Proctoporus bolivianus</i> (e)	Peru: Cusco: Cochayoc	UTA R-51482	AY225183		
<i>Proctoporus bolivianus</i> (a)	Peru: Cusco: Piscacucho, 3600 m	UTA R-51506	AY225175	AY507851	AY507869
<i>Proctoporus guentheri</i> (c)	Peru: Cusco: Chocallo	UTA R-51512	AY225184		
<i>Proctoporus guentheri</i> (a)	Peru: Cusco: Chocallo	UTA R-51515	AY225185	AY507849	AY507872
<i>Proctoporus guentheri</i> (d)	Peru: Cusco: Machu Picchu	UTA R-51516	AY225168		
<i>Proctoporus guentheri</i> (b)	Peru: Cusco: Machu Picchu	UTA R-51517	AY225169	AY507854	AY507873
<i>Proctoporus pachyurus</i> (a)	Peru: Junín: Muruhuay	UTA R-52949	AY968816	AY968824	AY968834
<i>Proctoporus pachyurus</i> (b)	Peru: Junín: Palca	MHNC TMD1203	AY968815	AY968823	AY968829
<i>Proctoporus subsolanus</i> (a)	Peru: Puno: Sandia	UTA R-52944	AY968814	AY968826	AY968833
<i>Proctoporus subsolanus</i> (b)	Peru: Puno: Sandia	UTA R-52946	AY968811	AY968822	AY968831
<i>Proctoporus sucullucu</i> (e)	Peru: Apurímac: Abancay	UTA R-52950	AY968817		AY968830
<i>Proctoporus sucullucu</i> (a)	Peru: Cusco: Kusilluchayoc	UTA R-51478	AY225171	AY507857	AY507878
<i>Proctoporus sucullucu</i> (d)	Peru: Cusco: Piscacucho, 3048 m	UTA R-51500	AY225188		
<i>Proctoporus sucullucu</i> (b)	Peru: Cusco: Piscacucho, 3191 m	UTA R-51496	AY225177	AY507858	AY507879
<i>Proctoporus sucullucu</i> (c)	Peru: Cusco: Piscacucho, 3300 m	UTA R-51498	AY225187		
<i>Proctoporus unsaacaе</i> (d)	Peru: Cusco: Pisac	UTA R-51475	AY225174	AY968819	
<i>Proctoporus unsaacaе</i> (e)	Peru: Cusco: Pisac	UTA R-51479	AY225172	AY968818	
<i>Proctoporus unsaacaе</i> (b)	Peru: Cusco: Quello Uno	UTA R-51488	AY225186	AY507859	AY507882
<i>Proctoporus unsaacaе</i> (c)	Peru: Cusco: Quello Uno	UTA R-51493	AY225178		
<i>Proctoporus unsaacaе</i> (a)	Peru: Cusco: Saqsayhuaman	UTA R-51477	AY225170	AY507860	AY507881
<i>Proctoporus unsaacaе</i> (f)	Peru: Cusco: Urcos	UTA R-51480	AY225173		
<i>Proctoporus</i> sp. 3	Peru: Puno: Laracani	UTA R-52945	AY968813	AY968825	AY968832