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# USING MORPHOLOGICAL AND MOLECULAR EVIDENCE TO INFER SPECIES BOUNDARIES WITHIN *PROCTOPORUS BOLIVIANUS* WERNER (SQUAMATA: GYMNOPHTHALMIDAE)

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ABSTRACT: *Proctoporus bolivianus* is a gymnophthalmid lizard species that occurs at high elevations in the Andes Mountains of southern Peru and Bolivia. Extensive morphological variation in populations collected in the Department of Cusco, Peru, suggested the presence of cryptic species. To assess this possibility, we reconstructed morphological and molecular phylogenies of 13 populations of this species and also used a character-based approach to examine the morphology in more detail. We found *P. bolivianus* to be composed of three distinct lineages that are separated by substantial genetic distances. We erect two new species to contain unnamed lineages within the *P. bolivianus* complex. These three species are found within a small geographic area and are likely differentiated because of historical geographic barriers in the extreme landscape of the central Andes.

*Key words:* Andes; Cryptic species; Cusco; Gymnophthalmidae; New species; Peru; *Proctoporus bolivianus*; *Proctoporus sucullucu*; *Proctoporus unsaacae*; South America; Squamata; Taxonomy

THE GENUS *Proctoporus* contains 27 species that range from southern Peru and Bolivia, following the Andes Mountains northward into Venezuela (Doan and Schargel, 2003; Kizirian, 1996). These montane species inhabit cloud forest, dry forest, páramo, and puna habitats throughout the central and northern Andes and associated mountain ranges (Duellman, 1979; Kizirian, 1996). Uzzell (1958, 1970) conducted two taxonomic reviews of certain members of the genus and placed some species into phenetic species groups. Kizirian (1996) performed a more extensive study of the 16 species of Ecuadorian *Proctoporus*, describing nine previously unrecognized species. Aside from these three works, few other studies examining the relationships or phylogeny of the genus have been conducted (but see Hillis, 1985). Although a molecular phylogenetic hypothesis for relationships within the family Gymnophthalmidae has recently become available (Pellegrino et al., 2001), it included no representatives of *Proctoporus*.

The *Proctoporus pachyurus* group (Uzzell, 1970) was erected to contain *P. bolivianus*, *P. guentheri*, and *P. pachyurus*, three species that occupy the southern range limit of the genus and occur from central Peru to Bolivia. As a whole, this species group is allopatric of other *Proctoporus* species, being separated from the *P. ventrimaculatus* group of northern Peru by an airline distance of over 250 km along the Andes (Uzzell, 1970). The *P. pachyurus* group was unified by the presence of a single palpebral scale over the eye, a median occipital, two or three supraoculars, and squarish pregular scales that do not form chevrons (Uzzell, 1970). Because all of the characters listed, except for the first, are found in other species of *Proctoporus*, only the undivided palpebral can be considered a synapomorphy defining the group. The status of the group has not been examined since its description.

One member of the *P. pachyurus* group, *P. bolivianus*, occurs in the Departments of Apurímac, Ayacucho, Cusco, and Puno of southeastern Peru, as well as the Department of La Paz in western Bolivia (Uzzell, 1970). Its elevational range is from 2500–4080 m (Duellman, 1979; Uzzell, 1970). *Proctoporus bolivianus* is not known to be directly sympatric (syntopic) with any other species of *Proctoporus*, but *P. guentheri* co-occurs throughout

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most of its range at lower elevations (Uzzell, 1970).

Uzzell (1970) expressed considerable confusion regarding the morphological variability among individuals of *P. bolivianus*. He synonymized three species with *P. bolivianus*: *Oreosaurus* (= *Proctoporus*) *lacertus* Stejneger, *P. longicaudatus* Andersson, and *P. obesus* Barbour and Noble. Despite the morphological variation that he found among the types of the three synonyms and other specimens throughout the range of this species, he felt data were not sufficient to warrant the recognition of a distinct species from within the specimens of *P. bolivianus*. He did, however, state that the names of the junior synonyms remained available should more data support the distinctiveness of certain forms (Uzzell, 1970).

A new collection of *P. bolivianus* specimens from Cusco, Peru, displayed a high degree of morphological diversity among individuals and among populations. Apparent patterns of morphological variation seemed to suggest the presence of unrecognized species within these southeastern Peruvian *P. bolivianus* populations. In addition to museum specimens, tissue samples of the same individuals were collected to facilitate the incorporation of molecular data in the analysis of these populations. To date, no molecular studies have been performed on the genus *Proctoporus*, largely because of the paucity of tissues in collections. Using the three methods suggested by Wiens and Penkrot (2002), we examined mtDNA and morphological phylogeny, in addition to character-based morphological approaches, to assess the taxonomic status of populations currently assigned to *P. bolivianus*. Based on the combined evidence from these sources, we herein examine species boundaries and construct a species classification congruent with the evolutionary species concept (Wiley, 1978).

## Materials and Methods

A collecting trip to the Department of Cusco, Peru, yielded 56 specimens of *Proctoporus*, including 10 *P. guentheri* and 46 *P. bolivianus*. Specimens were collected by hand, euthanized with sodium pentobarbitol, 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 of the Universidad Nacional de San Antonio Abad de Cusco (UNSAAC) in Peru. Liver tissue was taken from all individuals that were deposited at UTA and stored in 95% ethanol.

In addition to the specimens that were collected in the field, supplemental material was examined from KU, UNSAAC, USNM, UTA, and the Gabinete de Zoología of the Universidad Nacional de San Antonio Abad de Cusco (GZ). Museum abbreviations follow Leviton et al. (1985) except for UNSAAC and GZ. Specimens of all other known species of *Proctoporus* were also examined for comparison (except for *P. laevis* for which no material was available for loan). All specimens examined are listed in Appendix I.

### *Morphological Characters*

Morphological examination of specimens included the scoring of 67 external morphological characters (Appendix II) from 74 specimens. All anatomical terms and methods of taking meristic counts follow Kizirian (1996), except as modified by Doan and Schargel (2003). One of these authors (T. M. Doan) scored all of the morphological characters in order to reduce inter-observer variability (Lee, 1990). The characters used were a range of binary and multi-state, qualitative, meristic, and morphometric data and are based on the character set established by Doan (2003*a*), with some expansion of additional characters. Character 66 (green color of mid-venter) was determined by scanning the ventral surfaces of each preserved specimen on a flatbed scanner at 300 dpi. Because the specimens were fixed in formalin and preserved in alcohol, the colors may not be truly representative of their colors in life. However, all specimens were captured, collected, and preserved within 1 mo of each other and, at the time of the scanning of the specimens, had been in alcohol $<1$ yr, so that any fading or change of color would be equivalent for all specimens. The Visioneer PaperPort program was used to lighten the scans by five increments, and then the files were converted to uncompressed .tif files and input into Adobe Photoshop. The "eye dropper" tool was used

to select three scales along the mid-ventral line to determine the amount of green present (scales selected were in focus with no shading present). The median of the three measurements was recorded as the character state.

### *Molecular Characters*

The molecular analysis included at least two individuals of the *P. bolivianus* complex from all nominal available localities when possible, for a total of 19 samples of the *P. bolivianus* complex (Appendix III). Whole cellular DNA was extracted from liver tissues (stored in 95% ethanol) using DNeasy DNA extraction kits (Qiagen). A fragment of the mitochondrial NADH-subunit 4 (ND4) gene and adjacent tRNA region was amplified via standard PCR using the primer pair ND4 and Leu (Arévalo et al., 1994). The PCR conditions consisted of an initial cycle of 3-min denaturation at 94 C, 1-min annealing at 46 C, and 1-min extension at 68 C; 40 cycles of 45-s denaturation at 94 C, 45-s annealing at 48 C, and 45-s extension at 70 C; with a final 10-min extension at 72 C. Positive PCR products were purified using the Minelute PCR purification kit (Qiagen) or excised out of a low melting temperature agarose electrophoresis gel. These purified or excised PCR products were cloned using the Topo TA cloning kit (Invitrogen) according to the manufacturer's protocols. Positive clones were grown in liquid culture, and plasmids were isolated from multiple clones per individual using spin miniprep kits (Qiagen). Plasmids were sequenced using either: (1) SequiTherm EXCEL II DNA Sequencing Kit-LC with the protocols specified by the manufacturer (Epicenter Technologies), run on a LI-COR Model 4200LR DNA sequencer or (2) CEQ D Dye Terminator Cycle Sequencing (DTCS) Quick Start Kit (Beckman Coulter), run on a Beckman CEQ2000 automated sequencer according to the manufacturers' protocols.

Raw sequence chromatographs were edited and initially aligned using Sequencher 3.1 (1991–1998 Gene Codes Corporation). These sequences were later rechecked for positive alignment based on amino acid sequence (protein-coding region) and secondary structure (tRNA region; based on Flores-Villela et al., 2000 and Kumazawa and Nishida, 1993) in Genedoc (Nicholas and Nicholas, 1997). Alignment was unambiguous and two specimens (UTA R-51512 and 51515; outgroups) showed a two-base deletion within the terminal stop codon of the protein-coding region, resulting in a change in the codon sequence from TAG to TAA. No indels were inferred in the tRNA regions. Gaps in alignment were treated as ambiguities for phylogenetic analyses. All sequences were deposited in GenBank under the accession numbers listed in Appendix III.

### *Data Analysis*

We utilized the approach recommended by Wiens and Penkrot (2002) for delimiting species boundaries. Within the *P. bolivianus* complex, we examined the mtDNA phylogenies, tree-based morphological data, and character-based morphological data. Mitochondrial DNA analysis provides a power tool, given its rapid coalescence and evolutionary rate, for examining differentiation among populations or species (Drovetski, 2002; Felsenstein, 1983; Moore, 1995). Phylogenetic reconstructions of mitochondrial haplotypes may, however, be misleading in some circumstances if dispersal is biased by sex, haplotype lineage sorting is incomplete, or introgression is or has occurred (e.g., Avise, 1989; Pamilo and Nei, 1988). To assure that the correct taxonomic decisions were made, we used both morphological and mitochondrial data to reconstruct phylogenetic relationships among populations and also implemented more traditional character-based analyses of morphological data. Because we used multiple data sets, we have greater confidence in the results than a single data set would provide.

We conducted multiple separate analyses for the morphological and molecular data sets. Both morphological and molecular data sets were analyzed using PAUP* version 4.0b10 (Swofford, 2002). Phylogenetic reconstruction was accomplished using maximum parsimony (MP) only for morphological data; both MP and maximum likelihood (ML) methods were used to reconstruct phylogenies based on the molecular data. All reconstructions were rooted with *P. guentheri*, a member of the *P. pachyurus* group (sensu Uzzell, 1970).

For the MP molecular analysis, we used unweighted parsimony with branch-and-bound searches; support for nodes was

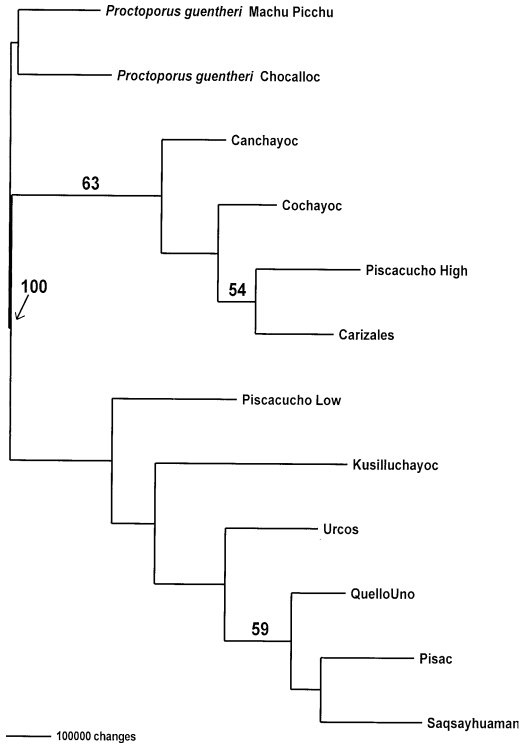


FIG. 1.—Phylogram of the most-parsimonious tree from the morphological phylogenetic reconstruction with bootstrap values greater than 50% indicated.

assessed by using 1000 nonparametric branch-and-bound bootstrap replicates (Felsenstein, 1985) implemented with PAUP*. For the ML molecular analysis, we used Model Test version 3.06 (Posada and Crandall, 1998) to determine the simplest best fit model of evolution (based on successive hierarchical log-likelihood ratio tests) and searched for optimal ML trees using this selected model with a heuristic search in PAUP*. Node support for ML trees was assessed with 100 full heuristic bootstrap pseudoreplicates.

Because there was morphological polymorphism within many of the species for each character, the generalized frequency coding method (GFC) of Smith and Gutberlet (2001) was used to create frequency subcharacters, which were used as characters for MP analysis in PAUP*. This method has been shown to be superior for utilizing polymorphic morphological and allozyme characters in phylogeny reconstruction (Bonett, 2002; Doan, 2003*a*,*b*; Smith and Gutberlet, 2001). Strict frequencies were used for unordered characters, and cumulative frequencies were used for ordered characters (Smith and Gutberlet, 2001). The unequal subcharacter-weighting scheme (USW) was employed as recommended by Smith and Gutberlet (2001). By using the GFC method, all polymorphism data were used and no information was discarded. Specimens were grouped by locality; localities used for this reconstruction were identical to those used in the molecular analyses. For the morphological analyses, we used branch-and-bound searches, and support for nodes was assessed by using 1000 nonparametric heuristic bootstrap pseudoreplicates (Felsenstein, 1985) with 100 random addition sequence replicates implemented with PAUP*. Settings for the analysis were tree bisection-reconnection branch swapping, steepest descent off and MULTREES option on (Swofford, 2002).

To compare the morphological and molecular topologies, Templeton Tests (Templeton, 1983) were implemented in PAUP*. A constraint file was generated for the morphological analysis to match the molecular topology, and the congruence between topologies was tested at a significance level of 0.05. Goldman et al. (2000) pointed out that Templeton Tests may not be valid if testing a topology known to be shorter a priori. To control for this problem with the Templeton Test, he recommended halving the $P$ value ($P/2$), which we also present here.

## RESULTS

The morphological data set provided 304 GFC subcharacters, of which 219 were parsimony informative. The morphological phylogenetic reconstruction yielded a single most-parsimonious tree (Fig. 1) of 3,281,904 weighted steps (CI = 0.483; RI = 0.408; RC = 0.197; HI = 0.517). Two major lineages are evident within this tree. One clade (which is referred to as clade A) contains specimens from Cochayoc, Canchayoc, Carizales, and Piscacucho (denoted as Piscacucho High because of two separate populations on this mountain at two different elevations). The other clade (clade B) is composed of specimens from Saqsayhuaman, Pisac, Urcos, Quello Uno, Kusilluchayoc, and Piscacucho Low.

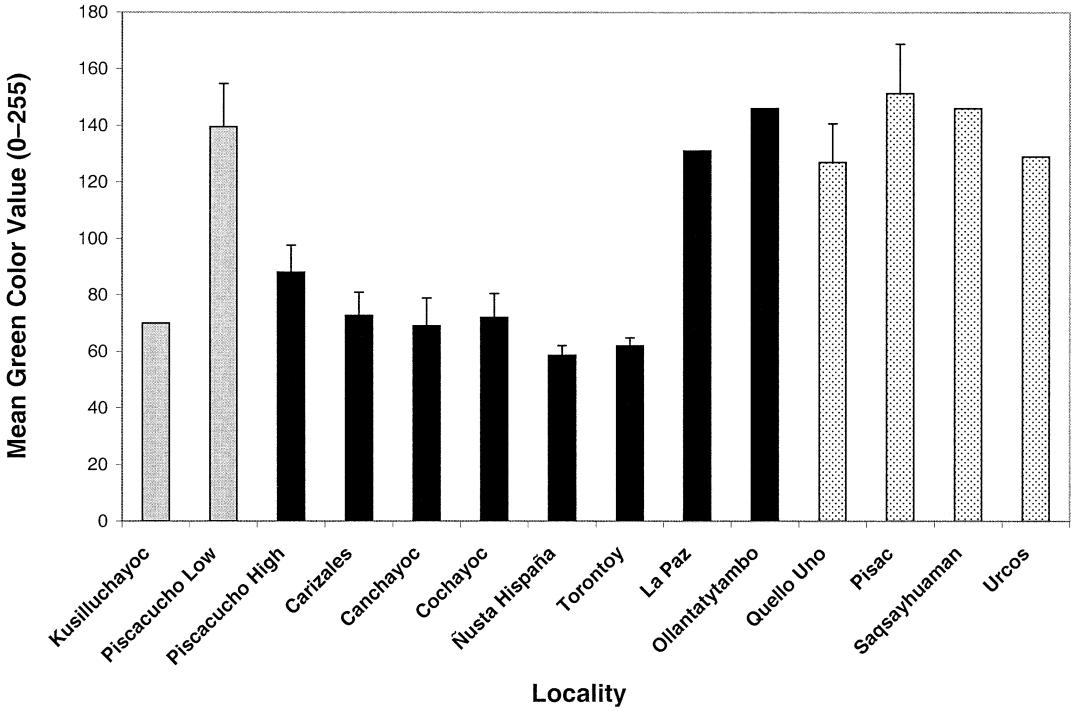


FIG. 2.—Mean green color values grouped by collection locality, with standard deviation bars indicated. Grey = *P. sucullucu*; black = *P. bolivianus*; spotted = *P. unsaacae*.

Two of the most variable morphological characters were examined in detail by locality (Figs. 2, 3). Character 66 (green color value) (Fig. 2) shows that specimens belonging to clade A in the morphological phylogeny were darker than (i.e., had lower green values than) the members of clade B. Snout-vent lengths (SVL) (Fig. 3) of males of clade A in the morphological phylogeny were longer than males of the clade B. Females of the clade A were usually longer than females of the clade B, except for some specimens from Piscacucho High.

The molecular data set provided a total of 856 characters (base pairs), 225 of which were parsimony informative. The MP molecular reconstruction yielded 10 equally parsimonious trees of 464 steps (CI = 0.718; RI = 0.878; RC = 0.630; HI = 0.282; Figure 4 depicts one of these optimal trees). The branching order of the 10 trees was identical, but relative branch lengths of specimens from Cochayoc, Canchayoc, and Carizales differed because of base change allocations at the node joined them. For the ML analysis of molecular data, the specific model of sequence evolution that best fit the data, as determined using the hLRTs method in ModelTest 3.06 (Posada and Crandall, 1998, 2001), was the Hasegawa-Kishino-Yano model with among site rate variation (HKY85 + $\Gamma$; Hasegawa et al., 1985; Yang, 1993) with the following parameters: ti/tv ratio = 3.7943; gamma shape parameter = 0.2565; base frequencies A = 0.3466, C = 0.2657, G = 0.1171, T = 0.2706. The ML reconstruction resulted in a single optimal tree with a likelihood score of -ln likelihood = 3394.06348 (parsimony-based tree statistics: CI = 0.716; RI = 0.878; RC = 0.628; HI = 0.284). The topology of the ML tree was largely identical to the MP trees and is not depicted here. The only notable difference between the ML and MP trees is that the optimal ML tree shows the sample from Urcos as the sister taxon to that from Saqsayhuaman (ML bootstrap for the corresponding node = 65%), whereas the optimal MP trees show the samples from Urcos as the sister taxon to the

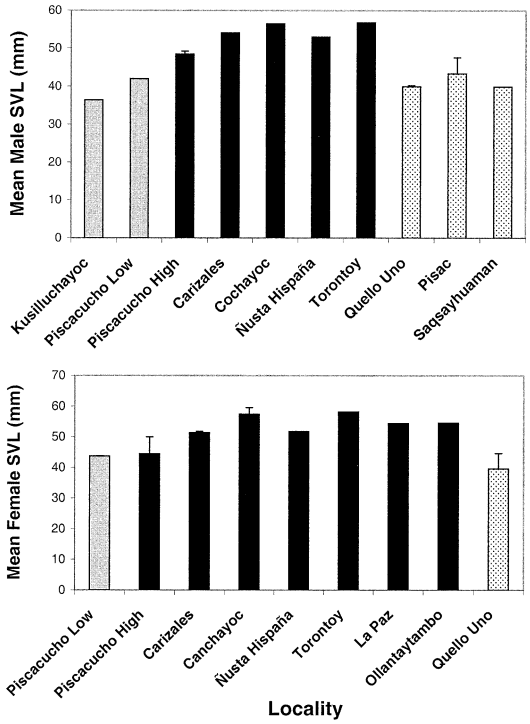


FIG. 3.—Adult male (top) and female (bottom) mean snout–vent length by collection locality, with standard deviation bars indicated. Grey = *P. sucullucu*; black = *P. bolivianus*; spotted = *P. unsaacae*. Localities are lacking when there were no specimens available of one sex.

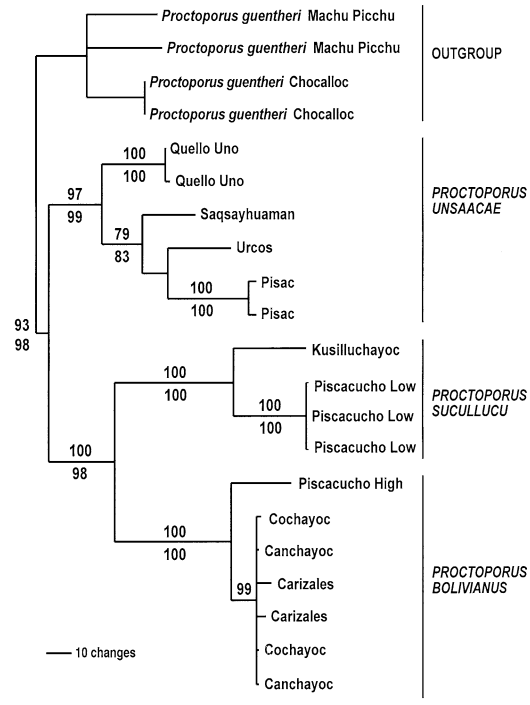


FIG. 4.—One of 10 optimal MP trees from the molecular phylogenetic reconstruction with bootstrap values greater than 50% indicated. The bootstrap values above the branches are from maximum parsimony; values below the branch are from maximum likelihood. Additional optimal MP topologies not shown differed only slightly with respect to terminal branch arrangement. The bars on the right side reflect new species designations.

Pisac sample (MP bootstrap for corresponding node = <50%).

Three distinct, well supported clades are evident in the molecular reconstructions that are associated with high bootstrap support (Fig. 4) and separated by large genetic distances (pairwise uncorrected distances and pairwise distances estimated under the HKY85 + Γ model; Table 1). The top clade (clade X) is made up of the same populations as morphological clade A (Fig. 1; Cochayoc, Canchayoc, Carizales, and Piscacucho High). The next clade (clade Y) is sister to clade X and consists of the Kusilluchayoc and Piscacucho Low populations. The bottom clade (clade Z) consists of Pisac, Urcos, Saqsayhuaman, and Quello Uno. Clades Y and Z contain the individuals belonging to clade B from the morphological reconstruction (Fig. 1).

The Templeton Test, comparing the unconstrained morphological tree and the morphological tree constrained to the topology of the molecular tree (constrained morphological tree: 3,348,688 weighted steps; CI = 0.473; RI = 0.385; RC = 0.182; HI = 0.527), demonstrated that they were not significantly different ($n$ = 107; $Z$ = –1.3303; $P$ = 0.3337; $P/2$ = 0.1669). For the purposes of discussion, we will hereafter use the molecular MP reconstruction as our preferred tree based on its high bootstrap support.

## SYSTEMATICS

Based on our phylogenetic reconstructions and character-based examinations, it is evident that *P. bolivianus* is composed of multiple evolutionary species (sensu Wiley, 1978). The molecular reconstruction (Fig. 4) identifies three natural groups within the *P. bolivianus* complex that are separated from one another by substantial genetic distances (13.4–16.3%

TABLE 1.—Mean genetic distances between sampling localities. Numbers above the shaded diagonal are distances estimated from the maximum likelihood HKY85 + Γ model employed in phylogenetic searches; those below the diagonal are uncorrected percent genetic distances.

| | Kusilluchayoc | Piscacucho Low | Piscacucho High | Carizales | Canchayoc | Cochayoc | Quello Uno | Pisac | Saqsayhuaman | Urcos | *P. guentheri* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Kusilluchayoc | | 0.090 | 0.340 | 0.317 | 0.313 | 0.317 | 0.321 | 0.312 | 0.378 | 0.304 | 0.287 |
| Piscacucho Low | 0.069 | | 0.350 | 0.315 | 0.308 | 0.310 | 0.318 | 0.309 | 0.361 | 0.312 | 0.268 |
| Piscacucho High | 0.157 | 0.161 | | 0.047 | 0.048 | 0.050 | 0.281 | 0.303 | 0.330 | 0.320 | 0.255 |
| Carizales | 0.150 | 0.151 | 0.040 | | 0.006 | 0.007 | 0.255 | 0.263 | 0.323 | 0.266 | 0.236 |
| Canchayoc | 0.148 | 0.148 | 0.040 | 0.006 | | 0.004 | 0.254 | 0.257 | 0.318 | 0.266 | 0.233 |
| Cochayoc | 0.149 | 0.149 | 0.042 | 0.007 | 0.004 | | 0.258 | 0.262 | 0.322 | 0.270 | 0.238 |
| Quello Uno | 0.151 | 0.152 | 0.144 | 0.134 | 0.134 | 0.135 | | 0.123 | 0.117 | 0.114 | 0.144 |
| Pisac | 0.147 | 0.147 | 0.150 | 0.137 | 0.135 | 0.136 | 0.085 | | 0.122 | 0.304 | 0.168 |
| Saqsayhuaman | 0.163 | 0.159 | 0.156 | 0.153 | 0.151 | 0.152 | 0.078 | 0.082 | | 0.099 | 0.212 |
| Urcos | 0.150 | 0.153 | 0.158 | 0.140 | 0.140 | 0.141 | 0.079 | 0.070 | 0.071 | | 0.150 |
| *P. guentheri* | 0.144 | 0.139 | 0.137 | 0.132 | 0.131 | 0.132 | 0.092 | 0.103 | 0.117 | 0.096 | |

mean divergence between clades; Table 1). Based on the tree topology, the haplotypes of each of the groups are exclusive and there does not appear to be gene flow among the basal lineages (Wiens and Penkrot, 2002). This finding suggests that three species are present in the complex (Table 2).

The tree-based morphological data (Fig. 1) depict one exclusive population, clade A (Canchayoc/Carizales/Cochayoc/Piscacucho High), which is separated from the other clade by basal nodes with relatively strong support (63% bootstrap) and, therefore, constitutes a distinct species. Clade B is made up of two non-exclusive population groups with basal relationships being weakly supported (<50% bootstrap support). Because of this, clade B cannot be confidently separated into two lineages with the tree-based morphological data (Table 2).

For the character-based approach, morphologies of individuals of each of the sampled populations also suggested the existence of three distinct groups (e.g., Figs. 2, 3; Table 2). Based on the results of the tree-based DNA approach and the character-based approach (with partial support from the tree-based morphological approach), we herein erect two new species to contain these distinct evolutionary lineages. Figures 2 and 3 are patterned to reflect these new species designations. Table 3 lists character state ranges for particular morphological characters of the members of the *P. pachyurus* species group. Each new species differs from all others sampled by at least 9% sequence divergence, whereas the genetic divergence within species ranges <1% to over 8% (Table 1). The level at which we have prescribed species limits likely represents a conservative estimate (based on remaining intraspecific genetic distances of 8% in the ND4 mtDNA gene). We feel that, at present, it is only prudent to describe new species in cases where all data sources concur and where sufficient numbers of individuals were available for examination. Future studies with additional material from the localities sampled herein and those in surrounding areas may allow further resolution of species boundaries within this complex.

TABLE 2.—Comparison of results of three approaches to assessing species boundaries as recommended by Wiens and Penkrot (2002) within the *Proctoporus bolivianus* species complex.

| Clade | Tree-based DNA | Tree-based morphology | Character-based morphology |
|---|---|---|---|
| 1 | Canchayoc, Carizales, Cochayoc, Piscacucho High | Canchayoc, Carizales, Cochayoc, Piscacucho High | Canchayoc, Carizales, Cochayoc, Piscacucho High |
| 2 | Kusilluchayoc, Piscacucho Low | Kusilluchayoc, Piscacucho Low, Urcos, Saqsayhuaman, Pisac, Quello Uno | Kusilluchayoc, Piscacucho Low |
| 3 | Urcos, Saqsayhuaman, Pisac, Quello Uno | | Urcos, Saqsayhuaman, Pisac, Quello Uno |

TABLE 3.—List of distinguishing characters among members of the *Proctoporus pachyurus* species group.

| | *P. bolivianus** | *P. guentheri* | *P. pachyurus* | *P. sucullucu* | *P. unsaacae* |
|---|---|---|---|---|---|
| Male adult snout–vent length (mm) | 46.9–56.8 | 40.0–44.5 | 58** | 36.5–45.0 | 31.7–46.3 |
| Female adult snout–vent length (mm) | 38.9–64.1 | 42.2–43.1 | 58** | 43.7–47.7 | 34.8–46.3 |
| Supralabials | 4–5 | 4–5 | 4–5 | 6 | 5–6 |
| Transverse dorsal rows | 34–47 | 29–36 | 47–61 | 38–46 | 36–42 |
| Transverse ventral rows | 20–27 | 18–23 | 24–27 | 24–25 | 18–26 |
| Limbs overlapping when adpressed | variable | no | no | yes | no |
| Green ventral color value | 56–146 | 111–166 | unknown | 70–158 | 115–159 |

* Excluding the holotype of *P. obesus*.
** From Uzzell (1970).

As mentioned above, three synonyms of *P. bolivianus* Werner exist. Herein, we discuss the status of each synonym based on our data and subsequently describe two novel species below.

*Proctoporus bolivianus* Werner. Many of the individuals we examined for this study are members of this species, including all of the specimens from Canchayoc, Carizales, Cochayoc, Ñusta Hispaña, Ollantaytambo, Paucartambo, high altitudes of Piscacucho, Tincochaca, Peru, and La Paz, Bolivia (for consistency only the individuals for which we had both specimens and tissues were included in the phylogeny reconstructions). The definition of this species is rather broad because of the extreme color difference of two of the specimens examined from Ollantaytambo, Peru [USNM 49549 (paratype of *O. lacertus*) and USNM 60719] in comparison with all others assigned to this species. Their coloration is very pale, as opposed to the dark brown and black of all other members of the species examined.

*Proctoporus lacertus* (Stejneger). This species was described as *O. lacertus* and placed in a genus that has long been synonymized with *Proctoporus* (Burt and Burt, 1931). After examining the holotype, a paratype, and several specimens referred to this species (Barbour and Noble, 1921), we follow Uzzell (1970) in the synonymy of *P. lacertus* with *P. bolivianus*.

*Proctoporus obesus* Barbour and Noble. This species was described from a single specimen from Ñusta Hispaña, Peru. It appears to differ greatly from other specimens captured at the same locality because of its enormous size. The specimen is damaged, which made examination of characters difficult. It differs from specimens of *P. bolivianus* in several ways. The holotype has 6 supralabials (*P. bolivianus* has 4–5) and 19 transverse ventral scale rows (*P. bolivianus* has 20–27). We estimate the SVL of the holotype to be 65.5 mm [Uzzell (1970) estimated the SVL to be 78 mm], which is larger than any other specimens of *P. bolivianus*. In addition, its head width is very large relative to other *P. bolivianus*. It seems possible that this specimen does represent a distinct species. However, without greater sample sizes, we continue to consider it a junior synonym of *P. bolivianus*.

*Proctoporus longicaudatus* Andersson. This species was described from a single specimen from Pelechuchi, Bolivia. We have not been able to examine the holotype of this species, but the original description by Andersson is quite complete. With additional information provided by Uzzell (1970), it seems clear that the holotype of this species should remain a junior synonym of *P. bolivianus*.

*Proctoporus* ***sucullucu*** sp. nov.

*Proctoporus* sp. 1: Doan, 2003*b*

*Holotype.*—UTA R-51496 (Fig. 5), a female from Piscacucho (13° 12.213′ S, 72° 22.533′ W), a small village near the town of Chilca, Province of Urubamba, Department of Cusco, Peru; 3191 m; collected on 4 June 2001 by Wilfredo Arizábal Arriaga.

*Paratypes.*—All paratypes from Piscacucho. UTA R-51497, neonate; and UTA R-51498, adult female, 3300 m; collected by Wilfredo Arizábal Arriaga on 5 June 2001; UTA R-51499, juvenile female; and UTA R-51500, adult male, 3048 m; collected by Tiffany M. Doan and Wilfredo Arizábal Arriaga on 6 June 2001.

*Referred specimens.*—UNSAAC WAA5006 and UTA R-51478 from Kusilluchayoc, Peru.

*Diagnosis.*—(1) Nasal divided, forming a pentagonal loreal scale, (2) median occipital present, (3) superciliaries four, first expanded onto dorsal surface of head, (4) palpebral eye-disc made up of a single, undivided, pigmented scale, (5) supralabials six, (6) infralabials five, (7) genials two, (8) dorsal scales quadrangular, with rounded keel, (9) transverse rows of dorsals 38–46, (10) transverse ventral rows 24–25, (11) a continuous series of small lateral scales separating dorsals and ventrals, (12) femoral pores per hind limb in males 6–8, in females 0–3, (13) preanal pores absent, (14) limbs overlapping when adpressed against the body, (15) ventral scales with grey stippling.

*Proctoporus sucullucu* is a member of the *P. pachyurus* group (Uzzell, 1970), which is united by the synapomorphy of the presence of an undivided palpebral disc. *Proctoporus sucullucu* can be distinguished by this character from all other *Proctoporus* species except those of the *P. pachyurus* group. *Proctoporus sucullucu* can be distinguished from *P. bolivianus* by having six supralabials (*P. bolivianus* has four or five). It can be distinguished from *P. guentheri* by a higher number of transverse dorsal scale rows (29–36 in *P. guentheri*; 38–46 in *P. sucullucu*). It can be distinguished from *P. pachyurus* by having fewer transverse dorsal scale rows (47–61 in *P. pachyurus*; 38–46 in *P. sucullucu*). It can be distinguished from *P. unsaacae* by limbs overlapping when adpressed.

*Description of holotype.*—Adult female, SVL 45.7 mm, tail 91.3 mm; head scales smooth, glossy; rostral scale wider than tall, meeting supralabials on either side at the height of supralabials, rising higher medially, in contact with frontonasal, anterior corner of nasals, and first supralabials; frontonasal longer than wide, rectangular with rounded corners, in contact with nasals, loreal, anteriormost superciliary, anteriormost corner of the first supraocular, and frontal, longer than frontal; prefrontals absent; frontal longer than wide, pentagonal, not in contact with anteriormost superciliary, in contact with first two supraoculars and frontoparietals; frontoparietals pentagonal, in contact with second and third supraoculars, parietals and interparietal; supraoculars three, all in contact with superciliaries, third in contact with parietal and postocular; interparietal longer than wide, heptagonal, in contact with parietals laterally, with occipitals posteriorly; parietals polygonal, with posterior tips in contact with occipital, lateral suture diagonally in contact with temporals, three anterior sutures, in contact with postocular, third supraocular, and interparietal; occipitals three, smaller than parietals, median smallest. Nasal divided, longer than wide, nostril near posterior edge of scale, in contact with first supralabial; loreal present, pentagonal, in contact with first superciliary, preocular, and frenocular posteriorly, first and second supralabials; four superciliaries, first and second slightly expanded onto dorsal surface of head; preocular present, in contact with frenocular and first subocular; frenocular trapezoidal, in contact with second and third supralabial and first and second suboculars; palpebral eye-disc made up of a single pigmented scale; suboculars four; postoculars two; temporals smooth, glossy, polygonal; supratympanic temporals two; supralabials six, first four supralabials to angle of jaw; infralabials five; mental wider than tall, in

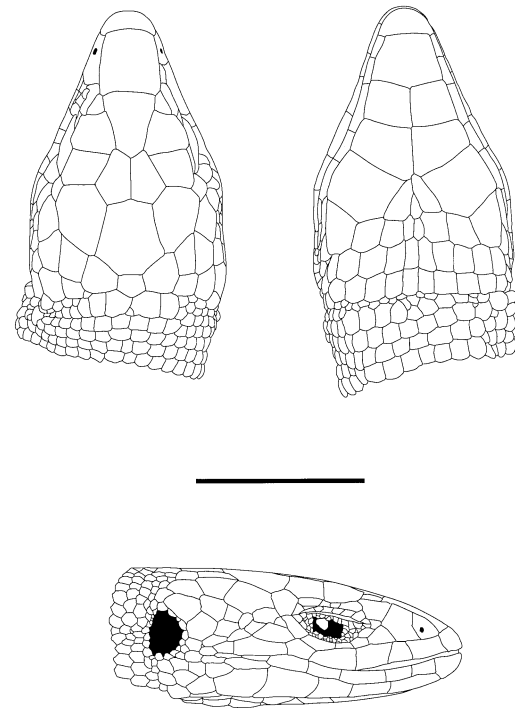

FIG. 5.—Head of the holotype of *Proctoporus sucullucu* (UTA R-51496). Upper left, dorsal view; upper right, ventral view; bottom, lateral view. Scale bar = 5 mm.

contact with first supralabials and postmental posteriorly; postmental single, pentagonal, posterior suture angular with point directed posteriorly, in contact with first and second infralabials; two pairs of genials, anterior pair quadrilateral, in contact with second and third infralabials; second genials in contact with third and fourth infralabials; one pair of chinshields not in contact medially, separated by two large and a smaller median pregular, in contact with fourth and fifth infralabials; gular scale rows eight; collar fold barely distinct; lateral neck scales round, smooth.

Dorsals rectangular with rounded corners, longer than wide, juxtaposed, with a central rounded keel, in 42 transverse rows; paravertebral scales irregularly arranged; longitudinal dorsal scale rows 18 at fifth transverse ventral scale row, 27 at tenth transverse ventral scale row, 27 at fifteenth transverse ventral scale row; continuous lateral scale series, three scales wide, smaller than dorsals, hidden in lateral fold, reduced scales at limb insertion regions present; transverse ventral scale rows 23; longitudinal ventral scale rows at midbody 10; anterior cloacal plate scales paired; posterior cloacal plate scales eight; scales on tail rectangular, juxtaposed; dorsal and dorsolateral caudal scales with low keel, ventral and ventrolateral caudal scales smooth; midventral subcaudals wider than adjacent scales.

Limbs pentadactyl; digits clawed; dorsal brachial scales polygonal, subequal in size, subimbricate, smooth; ventral brachial scales round, small, subimbricate, smooth; dorsal antebrachial scales polygonal, subequal in size, smooth, ventral antebrachial scales round, small; scales on dorsal surface of manus rounded, polygonal, smooth, subimbricate; scales on palmar surface of manus small, rounded, domelike; thenar scales keeled; scales on dorsal surface of fingers smooth, quadrangular, covering dorsal half of digit, overhanging supradigital lamellae, 3 on I, 6 on II, 8 on III, 7 on IV, 5 on V; subdigital lamellae 7 on I, 11 on II, 13 on III, 15 on IV, 9 on V; scales at base of Finger V thicker than adjacent scales; anterodorsal scales of thigh large polygonal, keeled, subimbricate; posterior thigh scales small, round, juxtaposed; ventral thigh scales large, rounded, smooth, imbricate; femoral pores and preanal pores absent; anterior crus scales polygonal, keeled, juxtaposed, decreasing in size distally, becoming rounded distally; anterodorsal crus scales rounded; ventral crus scales large, smooth, flat, imbricate; scales on dorsal surface of digits single, quadrangular, smooth, of varying sizes, overhanging supradigital lamellae single distally, double basally, 4 on I, 5 on II, 10 on III, 12 on IV, 9 on V; subdigital lamellae double, 9 on I, 10 on II, 15 on III, 19 on IV, 13 on V; limbs overlapping when adpressed against body.

*Coloration in preservative.*—Dorsal surface of head dark brown with light brown faint mottling; lateral surface of head like dorsal surface, but with faint dark brown rays originating from the orbit, three cream bars on lips; ventral surface of head cream with dark grey stippling on anteriormost scales, pregular and gular region with light grey stippling coalescing to form one indistinct blotch per scale. Dorsal surface of body same color as head, but with dark brown spots that form four indistinct stripes that extend from occiput to just posterior to forelimb insertions, with cream coloring between stripes; lateral surface of body same coloration as dorsum with one indistinct ocellus in neck region on both sides; ventral surface of body with yellowish cream ground color, each scale with grey stippling that forms an indistinct spot per scale, amount of grey increases laterally. Limbs similar to body, ventral surface of arms yellowish cream, ventral surface of legs with cream ground color and dispersed grey stippling. Coloration of dorsal and ventral surfaces of tail like that of body.

*Coloration in life.*—Same as in preservative.

*Variation.*—Adult female SVL 44.7 mm, adult male SVL 41.4–45.0 mm; original, complete tail of adult male 64.9 mm, original complete tail of adult female 60.1 mm. The paratypes and referred specimens are similar to the holotype with the several notable exceptions. Two specimens (UTA R-51478 and 51499) have two supraoculars, so that frontonasal does not touch any supraoculars and the frontal does make contact with first superciliary. Another specimen (UTA R-51498) has three supraoculars that are not arranged like the holotype—the area of the first supraocular is absent but three supraoculars fill the space of the second and third

supraoculars of the holotype. The second (anomalous) supraocular does not contact the superciliaries. In UTA R-51478, the frontonasal and frontal are of the same length. In UTA R-51498, a pair of triangular prefrontals meet in a medial point. In UTA R-51478, the frontal is heptagonal. In UTA R-51498, a triangular scale between the frontoparietals and frontal is present. In UTA R-51478 and 51498, the loreals do not contact the preocular. In UTA R-51500, seven transverse rows of gular scales are present.

Scalation of the two individuals referred to this species is anomalous. One paratype (UTA R-51498) has prefrontal scales, abnormal supraoculars, and an extra scale between the frontoparietals and frontal. As the absence of prefrontals is considered a diagnostic character of the genus *Proctoporus* (Kizirian, 1996), their presence in this specimen is troubling. However, because of the abnormal nature of many of its scale characters, together with the fact that the mtDNA sequence of this specimen is practically identical to others from the same locality, we are confident that this specimen does belong to this species. Another specimen (UTA R-51497) also demonstrates anomalous scalation not listed above. Many of the head scales of this specimen are fused. This specimen, a neonate, was collected as it was being prematurely extracted from its egg by a predatory scorpion, and it is probable that normal ontogenetic fragmentation of the head plates was incomplete.

Coloration among the paratypes and referred specimens is very similar to the holotype, with some appearing slightly darker than the holotype. One specimen (UTA R-51478) has a higher number of lateral ocelli and a much darker venter with dark grey stippling covering most of each scale. The venter of UTA R-51498 differs slightly from the holotype in that the medial scales have a reduced amount of grey stippling.

Meristic variation includes: transverse dorsal rows 38–46; longitudinal dorsal rows at midbody 21–24; longitudinal ventral rows 10–14; transverse ventral rows 24–25; subdigital lamellae on Finger IV 13–16; subdigital lamellae on Toe IV 18–21.

Sexual dimorphism is slight in this species. Femoral pore number is the most pronounced sexually dimorphic character, with males having from 6–8 on each leg, whereas females have from 0–3. Additionally, males possess wider heads than do females (relative to SVL).

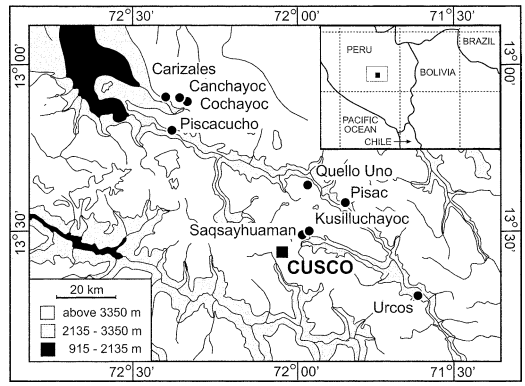


FIG. 6.—Elevational contour map, including the localities of the *Proctoporus bolivianus* complex in southern Peru. Sampling localities are marked with circles; the city of Cusco is indicated by a square. The locality of Piscacucho is composed of both Piscacucho High and Piscacucho Low sites, separated by 300–550 m in elevation.

*Distribution.*—*Proctoporus sucullucu* is known only from the Department of Cusco in southern Peru (Fig. 6). We have collected this species from Piscacucho in the west to Kusilluchayoc in the east. It has been recorded from 3048 m at Piscacucho to 3660 m at Kusilluchayoc.

*Habitat and ecology.*—This diurnal species was most often found under flat stones in disturbed grassland or pastureland. Little is known about its ecology, but, like other members of the genus, it is probably insectivorous and lays two eggs per clutch (Uzzell, 1970). At Piscacucho, a communal nest was found that contained 23 eggs of *P. sucullucu*. Several of the eggs had been broken and the embryos were being preyed upon by a scorpion. When found, UTA R-51497, a neonate, was dead and being eaten by a scorpion.

*Etymology.*—The specific epithet, *sucullucu*, an indeclinable noun, is the name of *Proctoporus* lizards in the local Quechua language.

*Remarks.*—*Proctoporus sucullucu* occurs on one of the same mountains as *P. bolivianus* (Piscacucho), with *P. sucullucu* consistently occurring at lower elevations (3048–3300 m at Piscacucho Low) than *P. bolivianus*

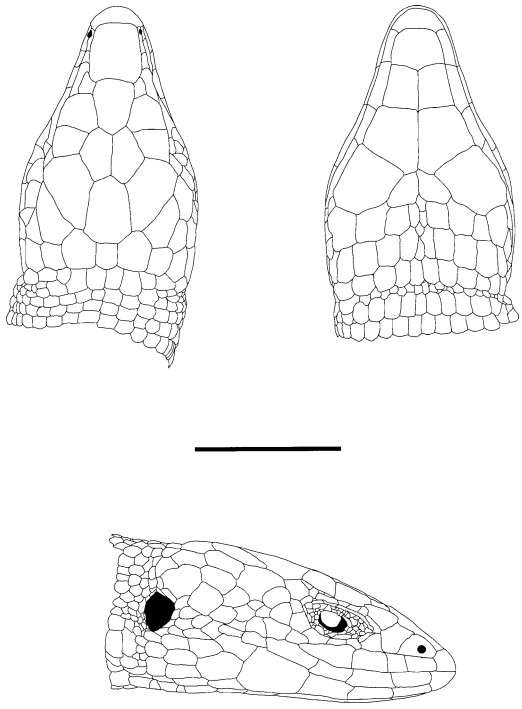

FIG. 7.—Head of the holotype of *Proctoporus unsaacae* (UTA R-51488). Upper left, dorsal view; upper right, ventral view; bottom, lateral view. Scale bar = 5 mm.

(3590–3600 m at Piscacucho High). Although they occur in close proximity (within 290 vertical m), it does not appear that these species come into direct contact.

*Proctoporus* ***unsaacae*** sp. nov.

*Proctoporus* sp. 2: Doan, 2003*b*

*Holotype.*—UTA R-51488 (Fig. 7), a female from Quello Uno (13° 21.887′ S, 71° 58.215′ W), a village near the town of Calca, Province of Calca, Department of Cusco, Peru; 3253 m; collected on 31 May 2001 by Tiffany M. Doan.

*Paratypes.*—All paratypes from Quello Uno. UTA R-51490, adult female, same data as holotype; UTA R-51489, juvenile male, 51491, adult male, and 51492, juvenile female; 3168 m; collected by Tiffany M. Doan and Wilfredo Arizábal Arriaga on 31 May 2001; UTA R-51493–94, adult males, and 51495, adult female; 3300 m; collected by Wilfredo Arizábal Arriaga and Tiffany M. Doan on 1 June 2001.

*Referred specimens.*—UNSAAC AC132; UTA R-51475–77, 51479, from Quello Uno, Pisac, Saqsayhuaman, and Urcos, Peru.

*Diagnosis.*—(1) Nasal divided, forming a pentagonal loreal scale; (2) median occipital present; (3) superciliaries four, first expanded onto dorsal surface of head; (4) palpebral eye-disc made up of a single, undivided scale; (5) genials two; (6) dorsal scales quadrangular, with low rounded keel, surrounded or not by longitudinal striations; (7) transverse rows of dorsals 36–42; (8) transverse ventral rows 18–26; (9) a continuous series of small lateral scales separating dorsals and ventrals; (10) femoral pores per hind limb in males 5–7, in females 0–3; (11) preanal pores absent; (12) limbs not overlapping when adpressed against the body in adults; (13) a continuous series of dark-centered ocelli on the lateral surface; (14) venter cream, medial scales immaculate, ventrolateral scales with dark spot centered in each scale.

Specimens of *P. unsaacae* show the presence of an undivided palpebral eye-disc, which place them in the *P. pachyurus* group (Uzzell, 1970). *Proctoporus unsaacae* can be distinguished from all other *Proctoporus* species except those in the *P. pachyurus* group by this character. *Proctoporus unsaacae* can be distinguished from *P. bolivianus* by a continuous series of lateral ocelli (in *P. bolivianus*, ocelli, if present, are faint and do not form a continuous series). It can be distinguished from *P. guentheri* by cream venter with ventrolateral scales that each have a dark spot (*P. guentheri* has yellow or orange venter without any spots). It can be distinguished from *P. pachyurus* by a lower number of transverse dorsal scale rows (47–61 in *P. pachyurus*; 36–42 in *P. unsaacae*). It can be distinguished from *P. sucullucu* by limbs not overlapping when adpressed.

*Description of holotype.*—Adult female, SVL 46.3 mm, tail 34.6 mm (regenerated); head scales smooth, glossy; rostral scale wider than tall, meeting supralabials on either side at above the height of supralabials and rising higher medially, in contact with frontonasal, nasals, and first supralabials; frontonasal longer than wide, rectangular with rounded corners, in contact with nasals, loreal, anteriormost superciliary, anteriormost corner of first supraocular, and frontal, longer than frontal; prefrontals absent; frontal longer than wide, pentagonal, anterior, and lateral sutures straight, posterior suture slightly convex, not

in contact with anteriormost superciliary, in contact with first two supraoculars and frontoparietals; frontoparietals pentagonal, in contact with second and third supraoculars, parietals, and interparietal; supraoculars three, all in contact with superciliaries, third in contact with parietal and postocular; interparietal longer than wide, hexagonal, in contact with parietals and occipitals; parietals polygonal, posterior tips in contact with occipital, lateral suture diagonally in contact with temporal, four anterior sutures, in contact with postocular, fourth superciliary, third supraocular, and interparietal; occipitals three, smaller than parietals, median smallest. Nasal divided, longer than wide, nostril in center of scale, in contact with first and second supralabials; loreal present, pentagonal, in contact with first superciliary, preocular, frenocular, and second and third supralabials; four superciliaries, first expanded onto dorsal surface of head; preocular present, in contact with first subocular; frenocular trapezoidal, in contact with third supralabial, preocular, and first and second suboculars; palpebral eye-disc made up of a single transparent scale; suboculars four; postoculars three; temporals smooth, glossy, polygonal; supratympanic temporals two; supralabials five, first four supralabials to angle of jaw; infralabials four/five; mental wider than tall, in contact with first supralabials and postmental posteriorly; postmental single, pentagonal, posterior suture angular with point directed posteriorly, in contact with first infralabials; two pairs of genials, anterior pair trapezoidal, in contact with first and second infralabials; second genials in contact with second and third infralabials; one pair of chinshields not in contact medially, separated by two large and a smaller median pregular, in contact with third and fourth/third, fourth, and fifth infralabials; gular scale rows seven; collar fold barely distinct, concealing one row of small gular scales; lateral neck scales round, smooth.

Dorsals rectangular, longer than wide, juxtaposed, with a low rounded central keel surrounded by longitudinal striations, in 38 transverse rows; some middorsal scales irregularly arranged; longitudinal dorsal scale rows 17 at fifth transverse ventral scale row, 21 at tenth transverse ventral scale row, 20 at fifteenth transverse ventral scale row; continuous lateral scale series, 2–3 scales wide, laterals much smaller than dorsals, reduced scales at limb insertion regions present; transverse ventral scale rows 24; longitudinal ventral scale rows at midbody 12; anterior cloacal plate scales paired; posterior cloacal plate scales six; scales on tail rectangular, juxtaposed; dorsal and dorsolateral caudal scales with low keel, ventral and ventrolateral caudal scales smooth; midventral subcaudals wider than adjacent scales.

Limbs pentadactyl; digits clawed; dorsal brachial scales polygonal, subequal in size, subimbricate, smooth; ventral brachial scales round, subimbricate, smooth; antebrachial scales polygonal, subequal in size, smooth, ventral antebrachial scales smallest; scales on dorsal surface of manus rounded, polygonal, smooth, subimbricate; scales on palmar surface of manus small, rounded, domelike; thenar scales keeled; scales on dorsal surface of fingers smooth, quadrangular, covering dorsal half of digit, overhanging supradigital lamellae, 3 on I, 6 on II, 7 on III, 7 on IV, 5 on V; subdigital lamellae 5 on I, 9 on II, 11 on III, 14 on IV, 8 on V; scales at base of Finger V thicker than adjacent scales; anterodorsal scales of thigh large, polygonal, smooth, subimbricate; posterior thigh scales small, round, juxtaposed; ventral thigh scales large, rounded, smooth; femoral pores 2/3, near basal part of thigh; preanal pores absent; anterior crus scales polygonal, smooth, juxtaposed, decreasing in size distally, becoming rounded distally; anterodorsal crus scales rounded, domelike; ventral crus scales large, smooth, flat, imbricate; scales on dorsal surface of digits single, quadrangular, smooth, of varying sizes, overhanging supradigital lamellae single distally, double basally, 3 on I, 6 on II, 8 on III, 12 on IV, 9 on V; subdigital lamellae double, 7 on I, 11 on II, 16 on III, 20 on IV, 15 on V; limbs not overlapping when adpressed against body.

*Coloration in preservative.*—Dorsal surface of head tan with dark brown stippling, especially at margins of scales; lateral surface of head like dorsal surface, but with dark brown and cream rays, brown rays originating from posterior edges of eye, one cream streak originating from ventroposterior edge of eye, other brown and cream streaks create barring on lips; ventral surface of head cream with

brown stippling on anteriormost scales, pregular and gular region with dark spot in center of each scale, spots lessen posteriorly. Dorsal surface of body with grayish ground color with dark brown mottling, two longitudinal brown stripes extend from occiput to midbody, two cream stripes just medial to brown stripes; lateral surface of body same coloration as dorsum with a series of ocelli with dark brown borders and cream centers, ocelli begin anterior to tympanum and end near hind limb insertion, ocelli near midbody less distinct; ventral surface of body immaculate cream medially, ventrolateral scales with one dark spot in center of each scale, gray stippling encroaches from lateral surface onto lateralmost ventral scales. Limbs similar to body, each arm with one ocellus on dorsal surface of branchial, ventral surface of arms cream with dark spots, dorsal surface of legs uniformly brown, ventral surface with cream ground color and brown stippling. Dorsal surface of tail like body, longitudinal stripes from dorsum reappear on tail, ventral surface of tail cream with brown stippling medially, brown laterally.

*Coloration in life.*—Similar to coloration in alcohol but darker overall.

*Variation.*—Adult females SVL 38.4–42.7 mm, adult males SVL 40.6–49.1 mm; complete original tail of adult males 78.4–78.5 mm, no adult females with original tails known. The paratypes and referred specimens are similar to the holotype with the following exceptions. Some specimens (UTA R-51475–77, 51479–80, and 51490–95) have two supraoculars, which results in the frontal contacting the first superciliary. In UTA R-51475, 51477, and 51492–95, there are three suboculars. In UTA R-51489, 51491–92, and 51494, there are two postoculars. In UTA R-51491–92, there are three supratympanic temporals. In UTA R-51492, there are six supralabials. In UNSAAC AC132, UTA R-51479–80, 51489, and 51491–95, there are eight transverse rows of gulars. In UTA R-51475–76, there are nine transverse rows of gulars. In UTA R-51480, there are striations on dorsal scales. Coloration is very similar among specimens, being slightly lighter or darker than the holotype, with stripes and ocelli more or less evident.

Meristic variation includes: transverse dorsal rows 36–42; longitudinal dorsal rows at midbody 18–26; longitudinal ventral rows 10–14; transverse ventral rows 19–27; subdigital lamellae on Finger IV, 11–15; subdigital lamellae on Toe IV, 16–22.

Sexual dimorphism is slight in this species with males being slightly longer and with wider heads (relative to SVL). Males are also generally darker on the ventral surface. Femoral pore number is the most sexually dimorphic trait, with males possessing 5–7 femoral pores per leg and females having 0–3.

*Distribution.—Proctoporus unsaacae* is known only from the Department of Cusco in southern Peru (Fig. 6). It is known to range from Saqsayhuaman in the west to Urcos in the east and has also been recorded from Pisac and Quello Uno. It has been recorded from 3152 m at Pisac to 3600 m at Saqsayhuaman.

*Habitat and ecology.*—This lizard species was found exclusively in human-disturbed areas and often in Incan ruins. This diurnal species was most often found under flat stones or in human-made piles of small pebbles. Little is known about the ecology of this species but, like other members of its genus, it is probably insectivorous and lays two eggs per clutch (Uzzell, 1970).

*Etymology.*—The specific epithet is an indeclinable noun in honor of the herpetological research group at the Universidad Nacional de San Antonio Abad de Cusco, a university in Cusco, Peru, commonly referred to as UNSAAC. The students and research associates of that group have contributed much to the knowledge of Andean herpetofauna. Many of them have assisted us in our studies and collected some of the paratypes and referred specimens of this species.

## Discussion

The montane lizards of the genus *Proctoporus* range over some of the most geographically dramatic topography of the western hemisphere, the central and northern Andes and adjacent ranges of South America (Kizirian, 1996). Potential barriers to gene flow over such an extreme landscape are numerous, and present taxonomic allocations for members of this genus are likely an underestimate of overall diversity within the group. This is evidenced by Kizirian (1996) in his description of nine new species from the Andes of Ecuador, as well as the findings presented

here relative to the southern Peruvian Andes. The substantial genetic divergence among populations included in this study that occur in such close proximity (Fig. 6; Table 1) infers a long history of isolation among those populations. Overall, our findings and those of Kizirian (1996) highlight the endemic nature of many *Proctoporus* species and, furthermore, suggest that lesser known portions of the Andes likely harbor undescribed *Proctoporus*.

Geographic or geologic features that might have historically influenced speciation patterns within the *P. bolivianus* complex remain unidentified. In some cases, there currently are no obvious major physical barriers between nominal taxa sampled here and their close relatives. We commonly have encountered *Proctoporus* in human-altered areas. The long history of civilization in this area of the Andes (e.g., the Incan Empire) may have drastically affected distributions of these lizard species (Duellman, 1979). In discussing the biogeography of another group of montane Andean lizards of the tribe Cercosaurini (sensu Pellegrino et al., 2001), Hillis (1985) and Hillis and Simmons (1986) demonstrated the temporally dynamic ranges of *Pholidobolus* and discussed the difficulty that such dynamics bring to inferring historical biogeography of montane taxa. Similarly, significant biogeographic boundaries that initially may have affected speciation in the *P. bolivianus* complex are unlikely to coincide with current species range extents. Until further data are collected, these considerations, together with the poorly known relationships within the genus (but see Doan, 2003*b*), prevent meaningful inferences about historical biogeography.

## Resumen

*Proctoporus bolivianus* es una especie de lagartija de la familia Gymnophthalmidae que occure a grandes elevaciones en el sur del Perú y Bolivia. Una gran variación morfológica en poblaciones colectadas en Cusco, Perú sugerió la presencia de especies crípticas. Para evaluar este fenómeno, construimos filogénias morfológicas y moleculares de 13 poblaciones de esta especie, y también examinamos caracteres morfológicos en más detalle. Encontramos que *P. bolivianus* está compuesto por tres linajes distinctos, separados por distancias genéticas grandes. Aquí describimos dos especies nuevas de estos linajes, sin nombres disponibles. Estas tres especies occurren dentro de un ámbito geográfico pequeño y probablemente evolucionaron por barreras históricas en los Andes centrales.

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## APPENDIX I

### *Specimens Used in Morphological Analysis*

Specimen localities are given according to museum catalog information. Catalogued 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); PERU: *Cusco*: 500 m up road Carizales (UTA R-51485); 800 m up road Carizales (UTA R-51486–87); Canchayoc: (UTA R-51483–84); Cerro de Puquin (GZ 0027); Cerro Machu Picchu (UTA R-51509–11); Cochayoc (UNSAAC WAA5024, UTA R-51481–82); Cosñipata (GZ 0043); Ñusta Hispaña [USNM 60699–700, 60748 (holotype of *P. obesus*)]; Ollantaytambo [USNM 49549 (paratype of *P. lacertus*), 60719]; 25 km NNE Paucartambo, Abra Acanacu (KU 163801, 163804, 163810–11, 163814, 163820, 163827, 163830–31, 163834, 163836, 163839–40, 163842, 163846); 29 km NNE Paucartambo, Abra Acanacu (KU 13965); 31 km NNE Paucartambo, Abra Acanacu (KU 13958, 13963); Piscacucho (UNSAAC AC136–AC141,

UTA R-51501–08); Tincochaca [USNM 49551 (holotype of *P. lacertus*)]; Torontoy (USNM 60726–27).

*Proctoporus guentheri:* BOLIVIA: *La Paz*: Nor Yungas, Serrania de Bella Vista, 17 km from Carrasco towards Sapecho (UTA R-39114); PERU: *Cusco*: Chachabamba (UTA R-51518); Chocalloc (UTA R-51512–15); Machu Picchu (KU 135157–60, UTA R-51516–17); 5 km WSW Santa Isabel (KU 139307, 139309); 6 km NE Santa Isabel (KU 163939); Wiñaywayna (UNSAAC WAA5056).

*Proctoporus pachyurus:* PERU: *Junín*: Palca (KU 135095, KU 181919–22, 181924, 181927); NW Palca (KU 181917–18, 181923, 181926); 1 km NW Palca (KU 181925, 181929–31); 2 km E Palca (KU 181938–39); 4 km W Palca (KU135096–97); 5 km W Palca (KU135099).

*Proctoporus sucullucu:* PERU: *Cusco*: Kusilluchayoc (UNSAAC WAA5006, UTA R-51478); Piscacucho [UTA R-51496 (holotype), 51497–500 (paratypes)].

*Proctoporus unsaacae:* PERU: *Cusco*: Pisac, Viacha (UTA R-51475–76, 51479); QuelloUno [UNSAAC AC132, UTA R-51488 (holotype), 51489–95 (paratypes)]; Saqsayhuaman (GZ Valdinos3, UTA R-51477); Urcos (UTA R-51480).

## Appendix II

### *Morphological Character Descriptions*

When character states could be validly ordered by character state intermediacy (Wilkinson, 1992), they were considered ordered (O) and the others were considered unordered (U) (for binary characters no ordering is necessary).

*Character 1:* Frontonasal condition: undivided (0); divided (1)

*Character 2 (O):* Frontonasal length: shorter than frontal (0); same length as frontal (1); longer than frontal (2)

*Character 3 (U):* Prefrontal suture: no suture because of lack of prefrontal scales (0); entire length of prefrontal scales (1); short (i.e., less than entire length of prefrontal scales) (2); point (3); suture absent (4)

*Character 4 (U):* Frontoparietal contact with which supraoculars: one/two (0); one/two/three (1); two (2); two/three (3); two/three/four (4); three (5); three/four (6); four (7); four/five (8)

*Character 5 (O):* Relative interorbital/eye–snout distance: expressed as an approximate decimal multiplied by 10. For example, if the interorbital distance were seven tenths that of the eye–snout distance, a 7 would be recorded

*Character 6 (O):* Relative eye–snout/crus length: expressed as a decimal, as in Character 5

*Character 7 (O):* Number of supraoculars

*Character 8 (O):* Relative interparietal width: anteriormost suture thinner than posteriormost suture of frontal (0); equal to frontal (1); wider than frontal (2)

*Character 9 (O):* Number of occipitals

*Character 10 (O):* Nasal condition: undivided (i.e., nasal and loreal fused) (0); incompletely divided (1); divided into separate nasal and loreal scales (2)

*Character 11:* Loreal contact with supralabial: no (0); yes (1)

*Character 12 (O):* Number of superciliaries

*Character 13 (O):* Number of eye palpebral scales of the main row

*Character 14 (O):* Number of reduced lower orbital scales on the ventralmost margin

*Character 15 (O):* Number of suboculars

*Character 16 (O):* Number of postoculars

*Character 17 (O):* Number of first anterior row of temporals

*Character 18 (O):* Number of supratympanic temporals

*Character 19 (O):* Number of reduced scales surrounding tympanum

*Character 20 (U):* Tympanum shape: half circle (0); round (1); oblong (2)

*Character 21 (O):* Number of supralabials

*Character 22 (O):* Number of scales in a row from supralabials to tympanum

*Character 23 (O):* Number of infralabials

*Character 24 (O):* Approximate number of scale organs on first supralabial, recoded as: five (0); 10 (1); 15 (2); 20 (3); 25 (4); 30 (5); 35 (6); 40 (7); 45 (8)

*Character 25 (O):* Scale organs on first infralabial: identical to Character 24

*Character 26 (O):* Number of genials

*Character 27 (O):* Number of scales in posterior transverse pregular row

*Character 28 (O):* Number of scales in medial pregular row (often not a complete row but all scales counted on the midline)

*Character 29 (O):* Number of scales in first transverse gular row

*Character 30 (O):* Number of transverse gular rows (not including reduced scales folded into the collar)

*Character 31 (O):* Number of ventral scales in the first transverse row between forelimbs

*Character 32 (O):* Number of longitudinal ventral rows at midbody

*Character 33 (O):* Number of transverse ventral rows

*Character 34 (O):* Number of scales in posteriormost transverse ventral row

*Character 35 (O):* Number of interpreanal scales

*Character 36 (O):* Number of cloacal plate rows (1 or 2)

*Character 37 (O):* Number of posterior cloacal plate scales in males

*Character 38 (O):* Number of posterior cloacal plate scales in females

*Character 39 (O):* Number of scales around base of tail

*Character 40 (O):* Number of femoral pores on one leg in males

*Character 41 (O):* Number of femoral pores on one leg in females

*Character 42 (O):* Number of total preanal pores of males

*Character 43 (O):* Number of longitudinal dorsal rows at midbody

*Character 44 (O):* Number of transverse dorsal rows

*Character 45 (U):* Dorsal scale shape: quadrangular (0); hexagonal (1); rhomboid (2); rounded rectangle (3); pyramidal (4)

*Character 46 (U):* Dorsal scale relief: smooth (0); keeled (1); striate (2); rugose (3)

*Character 47 (O):* Number of lateral scale rows at midbody

*Character 48 (O):* Lateral scale size: much smaller than dorsals (0); approximately half the size of dorsals (1); same size as dorsals (2); no differentiated lateral scales (3)

*Character 49 (O):* Number of scales in a row along the dorsal surface of forelimb from insertion to manus

*Character 50 (O):* Number of supradigital lamellae of Finger V

*Character 51 (O):* Number of subdigital lamellae of Finger IV

*Character 52 (U):* Femoral scale relief: smooth (0); keeled (1); striate/rugose (2); tuberculate (3)

*Character 53 (O):* Number of supradigital lamellae of Toe V

*Character 54 (O):* Number of subdigital lamellae of Toe IV

*Character 55:* Tubercles on subdigital lamellae of Toe IV: double (0); single (1)

*Character 56 (O):* Relative toe length of Toe V and Toe III: expressed as a decimal as in Characters 5 and 6

*Character 57 (O):* Relative brachial/crus length: expressed as a decimal as in Characters 5, 6, and 56

*Character 58:* Barred lip: no (0); yes (1)

*Character 59 (O):* Number of longitudinal dorsal stripes

*Character 60 (O):* Number of lateral ocelli in the main row

*Character 61 (O):* Ventral scale pigmentation: none (0); lateral only (1); less than 50% of each ventral scale covered by dark pigment (2); more than 50% covered by pigment (3)

*Character 62 (O):* Number of total preanal pores in females

*Character 63:* Femoral pore size: small (filling less than 60% of scale) (0); large (filling greater than 70% of scale) (1)

*Character 64 (O):* Presence of gular block (sensu Uzzell, 1970): absent (0); partial (1); fully present (2)

*Character 65 (O):* Large, flat scales on forelimb (sensu Uzzell, 1970): absent (0); partial (1); fully present (2)

*Character 66 (O):* Green color of mid-venter: expressed as a number from 0–255; values (0–255) were divided by 10 and rounded to a whole number to be used in PAUP*, reducing the number of character states from 256 to 26 to avoid having a high number of states

*Character 67 (O):* Head width at widest point divided by SVL; this character multiplied by 100 and rounded to use as whole numbers in PAUP*

## Appendix III

*Tissue Samples Used for Molecular Analysis*

| Species | Locality | Museum number | GenBank accession number |
|---|---|---|---|
| *Proctoporus bolivianus* | Peru: Cusco: Piscacucho, 3600 m | UTA R-51506 | AY225175 |
| *Proctoporus bolivianus* | Peru: Cusco: Cochayoc | UTA R-51481 | AY225181 |
| *Proctoporus bolivianus* | Peru: Cusco: Cochayoc | UTA R-51482 | AY225183 |
| *Proctoporus bolivianus* | Peru: Cusco: Canchayoc | UTA R-51483 | AY225176 |
| *Proctoporus bolivianus* | Peru: Cusco: Canchayoc | UTA R-51484 | AY225182 |
| *Proctoporus bolivianus* | Peru: Cusco: Carizales | UTA R-51486 | AY225179 |
| *Proctoporus bolivianus* | Peru: Cusco: Carizales | UTA R-51487 | AY225180 |
| *Proctoporus guentheri* | Peru: Cusco: Chocalloc | UTA R-51512 | AY225184 |
| *Proctoporus guentheri* | Peru: Cusco: Chocalloc | UTA R-51515 | AY225185 |
| *Proctoporus guentheri* | Peru: Cusco: Machu Picchu, Camino Peatonal | UTA R-51516 | AY225168 |
| *Proctoporus guentheri* | Peru: Cusco: Machu Picchu, Camino Peatonal | UTA R-51517 | AY225169 |
| *Proctoporus sucullucu* | Peru: Cusco: Kusilluchayoc | UTA R-51478 | AY225171 |
| *Proctoporus sucullucu* | Peru: Cusco: Piscacucho, 3191 m | UTA R-51496 | AY225177 |
| *Proctoporus sucullucu* | Peru: Cusco: Piscacucho, 3300 m | UTA R-51498 | AY225187 |
| *Proctoporus sucullucu* | Peru: Cusco: Piscacucho, 3048 m | UTA R-51500 | AY225188 |
| *Proctoporus unsaacae* | Peru: Cusco: Pisac, Viacha | UTA R-51475 | AY225174 |
| *Proctoporus unsaacae* | Peru: Cusco: Pisac, Viacha | UTA R-51479 | AY225172 |
| *Proctoporus unsaacae* | Peru: Cusco: Saqsayhuaman | UTA R-51477 | AY225170 |
| *Proctoporus unsaacae* | Peru: Cusco: Urcos | UTA R-51480 | AY225173 |
| *Proctoporus unsaacae* | Peru: Cusco: Quello Uno, a small settlement near Calca | UTA R-51488 | AY225186 |
| *Proctoporus unsaacae* | Peru: Cusco: Quello Uno, a small settlement near Calca | UTA R-51493 | AY225178 |

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