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A New Cryptic Species of *Stenocercus* (Squamata: Iguanidae) from the Andes of Ecuador

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Abstract

We describe a new species of *Stenocercus* from the Andes of Ecuador that previously was erroneously assigned to *S. guentheri* due to its general phenotypic similarity with this species. Based on phylogenetic analyses of mitochondrial DNA sequence data, we show that the new species is not nested within *S. guentheri* but is actually sister to *S. festae*. The new species can be distinguished from other *Stenocercus* by the combination of the following characters: imbricate scales on posterior surface of thighs, smooth ventrals, a posthumeral mite pocket consisting of a shallow depression with a wide opening (more distinct in adult specimens), small scales on occipitoparietal region, supraoculars of similar size, 62–83 scales around midbody, and no black midventral stripe or black transverse band on the ventral surface of neck in adult males.

Resumen

Describimos una especie nueva de *Stenocercus* de los Andes de Ecuador, que debido a similitud morfológica estaba erróneamente asignada a *S. guentheri*. En base a análisis filogenéticos de datos de secuencias de ADN mitocondrial, demostramos que la especie nueva no está anidada dentro de *S. guentheri* y es la especie hermana de *S. festae*. La especie nueva se puede diferenciar de otras especies de *Stenocercus* por la combinación de los siguientes caracteres morfológicos: escamas imbricadas en la superficie posterior de los muslos, ventrales lisas, bolsillo posthumeral poco profundo con una abertura ancha (más marcado en adultos), región occipitoparietal con escamas pequeñas, supraoculares de tamaño homogéneo, 62–83 escamas alrededor del cuerpo, franja medio ventral negra o banda transversal negra en el cuello ausentes.

With 61 species, *Stenocercus* [Duméril and Bibron \(1837\)](#) constitutes one of the most speciose squamate genera of South America. Most species occur along the northern and central Andes and adjacent lowlands (0–4,000 m), and a few species occur in Argentina, Brazil, Paraguay, and Uruguay ([Torres-Carvajal, 2007a](#)). The taxonomic study of collections from previously unexplored Andean regions has resulted in a remarkable number of discoveries and descriptions of new species of *Stenocercus* during the past two decades (e.g., [Cadle, 1991, 1998, 2001](#); [Avila-Pires, 1995](#); [Torres-Carvajal, 2000, 2005a,b,c, 2007b](#)), and it is very likely that a considerable number of new species will be discovered and described in the near future if exploration of similar areas continues.

Even though collections in poorly explored areas are important and often result in discoveries of highly distinctive new species, part of the biodiversity in any given region may be represented by cryptic species ([Bickford et al., 2007](#)). Morphologically indistinguishable taxa may be diagnosed with nontraditional taxonomic approaches, such as phylogenetic analyses of molecular data combined with careful examination of novel morphological characters or other sources of data. Herein, we combine evidence from morphology and phylogenetic analyses of DNA sequence data to describe a new species of *Stenocercus* that was previously confused with *S. guentheri* because of morphological similarity.

Materials and Methods

All type specimens of the new species described herein are deposited in the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ). Specimens of *Stenocercus guentheri* examined in this study are listed in Appendix 1. We follow the terminology of Torres-Carvajal (2007a) for characters included in the description. Snout–vent length (SVL) and tail length (TL) were taken with a ruler and recorded to the nearest 1 mm. All other measurements were made with digital calipers and recorded to the nearest 0.1 mm. Osteological characters were examined from digital x-ray radiographs of specimens QCAZ 9613 and QCAZ 9898 taken in a Thermo KeveX X-ray Imaging System. Clutch size was determined from x-ray radiographs. Egg volume was calculated with the formula of a prolate spheroid: $V = 4/3 \pi (\text{length}/2)(\text{width}/2)^2$. Sex was determined by noting the presence of hemipenes or sexually dichromatic characters ([Torres-Carvajal, 2000, 2007a](#)).

Differences in scale counts between the new species and *S. guentheri*, as well as differences between sexes in the new species, were evaluated with *t*-tests for normally distributed variables (i.e., Shapiro–Wilk test, $P > 0.05$). All selected variables had equal variances (i.e., *F*-test, $P > 0.001$). We used PAST 2.14 ([Hammer et al., 2001](#)) for all statistical tests.

Phylogenetic Analyses

Torres-Carvajal et al. (2006) sampled a continuous fragment of mitochondrial DNA that extends from the protein-coding gene ND1 (subunit 1 of NADH dehydrogenase) through the genes encoding tRNA^{ILE}, tRNA^{GLN}, tRNA^{MET}, ND2 (subunit 2 of NADH dehydrogenase), tRNA^{TRP}, tRNA^{ALA}, tRNA^{ASN}, the origin of light-strand replication, tRNA^{CYS}, tRNA^{TYR}, to the protein-coding gene COI (subunit I of cytochrome *c* oxidase). Following similar laboratory and alignment protocols, this fragment was sequenced for one specimen of *S. festae*, two of *S. guentheri*, and three of the new species described herein. GenBank accession numbers are provided in [Table 1](#). In addition, we used published sequences of *S. festae*, *S. guentheri*, *S. angel*, *S. chota*, and *S. ornatus* ([Table 1](#)). Complete mitochondrial sequence data were obtained for all specimens included in the analyses. The molecular data matrix contains three samples of *S. guentheri*; three of the new species; two of *S. festae*; and one each of *S. angel*, *S. chota*, and *S. ornatus*. Phylogenetic relationships were assessed under a Bayesian approach using MrBayes 3.1.2 ([Ronquist and Huelsenbeck, 2003](#)). The model of character evolution for the analyses was taken from [Torres-Carvajal et al. \(2006\)](#). To reduce the chance of converging on a local optimum, four independent analyses were performed. Each analysis consisted of 5 million generations and four Markov chains with default heating values. Parameter values for the model were estimated from the data and initiated with flat priors except for branch lengths, for which an exponential prior was used. Trees were sampled every 1,000 generations, resulting in 5,000 saved trees per analysis, of which 500 were arbitrarily discarded as “burn-in.” Stationarity was confirmed by plotting the $-\ln L$ per generation in the program Tracer 1.2 ([Rambaut and Drummond, 2003](#)). After confirming that the four analyses reached stationarity at a similar likelihood score and that the topologies were similar, the resultant 18,000 trees were used to calculate posterior probabilities for each bipartition in a maximum clade credibility tree in TreeAnnotator 1.6.1 ([Rambaut and Drummond, 2010](#)). *Stenocercus ornatus* was used as outgroup based on the topologies recovered by [Torres-Carvajal et al. \(2006\)](#) and [Torres-Carvajal \(2007c\)](#).

Systematics

***Stenocercus cadlei* sp. nov.**

Holotype

QCAZ 9898, an adult male, from 400 m on road Panamericana-Santa Lucía, 6 km N Mocha, 3,205 m (1.366°S, 78.654°W; WGS 84), collected on 4 October 2009 by O. Torres-Carvajal, P. Mafla-Endara and S. Báez.

Paratypes

Ecuador: Provincia Cañar: QCAZ 9637–9638, Cañar, 3,209 m (2.560°S, 78.931°W), collected on 25 July 2009 by P. Mafla-Endara and A. Vargas; Provincia Chimborazo: QCAZ 9902, 1.5 km road to Columbe, 3,170 m (1.884°S, 78.723°W), collected on 4 October 2009 by O. Torres-Carvajal, P. Mafla-Endara and S. Báez; QCAZ 9903–9906, 11.3 km N Palmira on Panamerican road, 3,161 m (1.981°S, 78.727°W), collected on 5 October 2009 by O. Torres-Carvajal, P. Mafla-Endara and S.

Báez; QCAZ 9613–9615, Riobamba, Pungalá, Comunidad Melán, 3,564 m (1.875°S, 78.548°W), collected on 2 August 2009 by S. Aldás-Alarcón, A. León Huisha, and S. Sanaitan Huisha; QCAZ 9623–9625, Riobamba, Pungalá, Comunidad Melán, 3,564 m (1.875°S, 78.548°W), collected on 4 August 2009 by S. Aldás-Alarcón, A. León Huisha, and Segundo Sanaitan Huisha; QCAZ 9948–9950, 2.8 km S Tixán on Panamerican road, 2,912 m (2.175°S, 78.817°W), collected on 15 October 2009 by O. Torres-Carvajal, P. Mafla-Endara, and S. Báez; QCAZ 3659–3661, 14.5 km N Tixán, Panamerican road, 3,274 m (2.05°S, 78.733°W), collected on 9 January 1997 by O. Torres-Carvajal; Provincia Cotopaxi: QCAZ 8772–8773, Apagua, 3,960 m (0.974°S, 78.936°W), collected on 7 March 2009 by F. Ayala-Varela, E. Carrillo-Ponce, and J. García; QCAZ 8059, 2 km S Chugchilán, road to Quilotoa, 2,917 m (0.806°S, 78.936°W), collected on 4 April 2010 by P. Mafla-Endara, J. P. Almeida, O. Torres-Carvajal, and S. Báez; QCAZ 6951, 8019, 10658, Laguna de Yambo, 2,634 m (1.1017°S, 78.5882°W), collected on 8 March 2006 by I. G. Tapia; 24 November 2007 by O. Torres-Carvajal; and August 2010 by L. Dután, P. Mafla-Endara, and J. P. Almeida, respectively; QCAZ 9640, Mulaló, 3,029 m (0.776°S, 78.578°W), collected on 5 August 2009 by J. P. Almeida and P. Mafla-Endara; QCAZ 1109, Parque Nacional Cotopaxi, collected on 28 September 1991 by G. Onore and L. A. Coloma; QCAZ 6994, Río Barrancas, collected on 5 November 2003 by D. Alvarado S.; QCAZ 8055, San Juan de Pasto Calle, 1,956 m (0.751°S, 78.648°W), collected on 3 April 2010 by P. Mafla-Endara, J. P. Almeida, O. Torres-Carvajal, and S. Báez; Provincia Tungurahua: QCAZ 10245–10246, Ambato, cañón del Río Ambato, 2,488 m (1.249°S, 78.606°W), collected on 15 February 2010 by O. Torres-Carvajal and S. Báez; QCAZ 9188–9189, Ambato, road to Píllaro, collected on 13 September 2007 by P. González and A. Vallejo; QCAZ 10006–10007, 10009–10010, 10014–10015, 10017, 10019, Caserío Poatug, Sector Aya Samana, 2,573 m (1.282°S, 78.491°W), collected on 21 November 2009 by S. Aldás-Alarcón and R. Toscano; QCAZ 9838, Cotaló, road to Comunidad Mucubí, 2,626 m (1.429°S, 78.517°W), collected on 20 September 2009 by A. Hurquizo, P. Mafla-Endara, and J. P. Almeida; QCAZ 9851, Patate, 2,215 m (1.311°S, 78.514°W), collected on 24 September 2009 by P. Mafla-Endara, M. Iglesias, and E. Endara; QCAZ 11016–11018, Road Guaranda-Ambato, 4,034 m (1.416°S, 78.864°W), collected on 13 October 2010 by P. A. Menendez; and QCAZ 2858, Urbina, 2,811 m (1.1433°S, 78.5546°W), collected on 8 January 1994 by L. A. Coloma and P. Moret.

Diagnosis

Stenocercus cadlei differs from all other species of *Stenocercus* except *S. angel*, *S. chota*, *S. festae*, *S. guentheri*, and *S. nigromaculatus* by having imbricate scales on posterior surface of thighs, smooth ventrals in adults, a posthumeral mite pocket consisting of a shallow depression with a wide opening (more distinct in adult specimens), small scales in occipitoparietal region, and supraoculars of similar size. Of these species, *S. nigromaculatus* is unique in having an antehumeral fold. *Stenocercus cadlei* differs from *S. angel*, *S. chota*, and *S. festae* (character states of latter three species in parentheses) by having more scales around midbody, 62–83, mean = 71.55 ± 4.86 (49–68, mean = 56.09 ± 3.71 ; 45–59, mean = 50.93 ± 2.96 ; 47–66, mean = 55.91 ± 4.85 , respectively). Some males of *S. festae* (66%) and *S. guentheri* (53%) have a distinct, sometimes medially incomplete, transverse black band on ventral surface of neck; males of the new species lack this band (Fig. 1). Both *S. guentheri* and the new species differ from *S. festae* (character states in

parentheses) in having smooth or weakly keeled ventrals in juveniles (distinctly keeled), and in lacking a black antehumeral patch in adult males (patch present). Adult males of *S. cadlei* also differ from adult males of *S. festae* and *S. guentheri* in having scattered dark flecks on the venter. Furthermore, some adult females of the new species have a bright yellow patch with a dark reticulation on the pectoral region; females of *S. festae* and *S. guentheri* lack this pattern and usually have uniformly colored venters.

Of eight scale count variables recorded in both *S. cadlei* and *S. guentheri* ([Table 2](#)), only two were normally distributed and subsequently used in *t*-tests. *Stenocercus cadlei* has fewer paravertebrals ($t = -7.698$, $df = 101$, $P < 0.001$) and more scales around midbody ($t = 4.666$, $df = 101$, $P < 0.001$) than *S. guentheri*.

Definition

(1) Maximum SVL in males 85 mm ($n = 17$); (2) maximum SVL in females 73.50 mm ($n = 24$); (3) vertebrals 45–61; (4) paravertebrals 58–79; (5) scales around midbody 62–83; (6) supraoculars 4–7; (7) internasals 3–4; (8) postrostrals 2–4; (9) loreals 3–5; (10) gulars 20–29; (11) subdigitals on Finger IV 15–23; (12) subdigitals on Toe IV 22–32; (13) posthumeral mite pocket present as a shallow depression with a wide opening; (14) postfemoral mite pocket distinct with slit-like opening; (15) parietal eye visible through interparietal cornea in 80% of specimens; (16) scales on occipitoparietal region small, keeled or multicarinate, imbricate; (17) projecting angulate temporals absent; (18) row of enlarged supraoculars occupying most of supraocular region absent; (19) scales on frontonasal region weakly imbricate anteriorly; (20) preauricular fringe present; (21) neck folds absent; (22) lateral and dorsal nuchals similar in size; (23) posterior gulars rhomboidal or cycloid, smooth, imbricate, not notched; (24) lateral and dorsal body scales similar in size; (25) vertebrals larger than adjacent paravertebrals; (26) dorsolateral crest absent; (27) ventrals smooth, imbricate; (28) scales on posterior surfaces of thighs keeled, imbricate; (29) inguinal granular pocket absent; (30) inguinal groove absent; (31) preanals not projected; (32) tail not strongly compressed laterally in adult males; (33) tail length 57–67% of total length; (34) caudal whorls per autotomic segment three; (35) caudals not spinose; (36) dark brown stripe extending anterodorsally from subocular region to supraciliaries absent; (37) dark patch extensively covering gular region of females absent; (38) dark patch extensively covering gular region of adult males absent; (39) black patch on ventral surface of neck in adult males absent; (40) dark midventral longitudinal stripe in 28% of adult males; (41) dark patches on ventral surface of thighs in adult males absent; (42) postxiphisternal inscriptional ribs not in contact midventrally, Patterns 1A and 2B of [Torres-Carvajal \(2004\)](#). The above-listed characters follow the same sequence as in [Torres-Carvajal \(2007a\)](#).

Description of Holotype

Male ([Fig. 1](#)); SVL = 85 mm; TL = 60 mm (original) + 60.7 mm (regenerated); maximum head width = 16 mm; head length = 19.6 mm; head height = 12.5 mm; scales on parietal and occipital regions small, keeled, slightly imbricate; parietal eye visible; supraoculars in six rows, keeled, slightly imbricate, subequal in size; canthals two; anterior most canthal separated from nasal by two minute scales; scales in frontonasal region slightly imbricate; internasals four; postrostrals four, two

most lateral wider than long on each side, medial postrostrals longer than wide; supralabials five; infralabials five; loreals five; lorilabials in one row; preocular not divided, in contact with posterior canthal; lateral temporals imbricate, moderately keeled; gulars in 23 rows between tympanic openings; all gulars smooth, imbricate, each bearing one apical pit; second infralabial in contact with first two sublabials; mental in contact with first pair of infralabials, first pair of postmentals, and one minute scale between postmentals; lateral and dorsal scales of body and neck keeled, imbricate; lateral scales of neck granular; scales around midbody 76; vertebrals large, in 53 rows, forming a prominent serrate vertebral crest; paravertebrals 68; ventrals smooth, imbricate; preauricular fringe short, composed of six enlarged scales; neck folds absent; limb scales keeled, imbricate, except for infrafemorals, infratibials, and supracarpals that are smooth and imbricate; lamellae on Finger IV 21; lamellae on Toe IV 30; tail not compressed laterally; caudals keeled, imbricate; basal subcaudals smooth, imbricate; posthumeral pocket shallow with wide opening; postfemoral pocket shallow, with a posteroventrally oriented slit-like opening.

Color in Life of Holotype

Dorsum yellowish green with a longitudinal series of broad, irregular dark brown transverse bands over vertebral line; bright yellow dots on flanks and lateral surface of neck, where they become brighter; dorsal surface of limbs with black reticulations; dorsal surface of head with irregular dark brown marks; subocular and loreal regions bluish green; gular region with a mixture of green and blue scales in light tones anteriorly and yellow scales posteriorly, as well as dark brown or gray scales forming a reticulate pattern that extends onto pectoral region; yellow blotch on each side of pectoral region at base of insertion of fore limb; ventral surface of body bluish green medially and yellowish green laterally, with scattered dark brown flecks; bright yellow patch covering ventral surface of hindlimbs, as well as pelvic, precloacal and postcloacal regions; ventral surface of tail yellow with scattered dark brown flecks; regenerated tail light brown.

Variation

From the scale counts and measurements presented in [Table 3](#), only scales around midbody, vertebrals, paravertebrals, and tail length/total length were normally distributed. None of these characters is different (i.e., *t*-test, $P < 0.001$) between sexes.

Some adult males differ in coloration from the holotype. Male QCAZ 9903 (SVL = 67 mm) had a cream ventral background including the gular region, with a faint yellow tint on the pectoral region; male QCAZ 9950 (SVL = 81.6 mm) lacked a yellow patch on the pelvic region and ventral surface of hindlimbs; male QCAZ 10006 had a dark brown head, with some dark green scales laterally, and a light blue (medially) and bright orange (laterally) ventral surface of body. Of 14 adult males examined, 28% had a dark midventral stripe.

An adult female (QCAZ 10015; [Fig. 1](#)) had the following coloration in life: flanks and dorsal aspect of body, limbs, and tail yellowish brown with a dark brown reticulate pattern; gular region bluish gray anteriorly and dark gray with scattered yellowish green flecks posteriorly; pectoral region bright yellow with a gray reticulate pattern; the yellow pectoral patch extends posteriorly as one

midventral and two ventrolateral stripes that faint away on the pelvic region; remaining ventral surface of body light blue; ventral surface of body, limbs, and base of tail covered by scattered black or dark brown spots; ventral surface of nonregenerated and regenerated tails salmon and light cream, respectively.

Juveniles (QCAZ 8773, 9640, 9948–49, 10017, 10019, 10246) had a dark brown dorsal background, with darker reticulations. The venter was pinkish or yellowish cream and the throat varies from light to bright yellow; the gular region was covered by a brown or black, sometimes dense, reticulation; dark scattered flecks might be present on the venter ([Fig. 1](#)).

Natural History

Some specimens of *S. cadlei* were active between 0900–1400 h on rocks, fallen logs, or moving on the ground in disturbed grasslands or crops, whereas other specimens were discovered sleeping under rocks or fallen logs after 1700 h. Most individuals were captured within 100 m from the road. Some adult males and females were found on rocks or logs exposed to the sun between 0830 and 0900 h, presumably thermoregulating. One specimen (QCAZ 9851) was found active in the shadow under a shrub at 1245 h when the air temperature was 29°C, suggesting that this species has a preference for temperatures below 29°C. Two females (QCAZ 11016–17) were found at 1435 h under the same rock with nearly 40 carabid beetles. It is unclear whether these females were feeding, cooling off, or sleeping, but this finding indicates that females of *S. cadlei* can share the same microhabitat.

Stenocercus cadlei autotomizes its tail, presumably as an escape mechanism. Adult male QCAZ 8059 autotomized its tail when captured at 0930 h. Among examined specimens, 25% of females and 38% of males had regenerated tails.

An adult female (QCAZ 9613) collected on 2 August 2009 contained one fully developed egg in each oviduct. The sizes of these eggs were 19.29 mm × 10.89 mm and 18.57 mm × 10.71 mm; their volumes were 1197.81 and 1115.29 mm³, respectively. The smallest individual examined (SVL = 43.2 mm; QCAZ 9948) was captured on 15 October 2009. Other small juveniles (i.e., SVL < 50 mm) were captured in February, March, August, October, and November, suggesting that *S. cadlei* has more than one reproductive season per year.

Phylogenetic Relationships

The phylogenetic tree inferred in this study ([Fig. 2](#)) is consistent with previous hypotheses ([Torres-Carvajal et al., 2006](#); [Torres-Carvajal, 2007c](#)) in that *S. angel*, *S. chota*, *S. festae*, and *S. guentheri* form a well-supported clade, with *S. angel* and *S. guentheri* as sister species. Nonetheless, our tree is different from previous hypotheses in that *S. chota* is not sister to the remaining three species but, rather, its position is ambiguous. The phylogenetic analyses of mitochondrial DNA sequence data in this study support *S. cadlei* as a monophyletic group strongly. Moreover, *S. cadlei* is supported strongly as sister to *S. festae* ([Fig. 2](#)) and not *S. guentheri* as expected from morphology.

Distribution

Stenocercus cadlei inhabits inter-Andean valleys and nearby paramos in Ecuador ([Fig. 3](#)). It occurs at elevations of 1,956–4,034 m in Provincias Cañar, Cotopaxi, Tungurahua, and Chimborazo. Of 61 georeferenced localities where *S. cadlei* occurs, 46 (75%) are within intervening areas; eight (13%) in North Andean montane scrub; two (4%) in montane evergreen forest; two (4%) in North Andean pluviseasonal montane forest; and one each (1.3%) in North Andean pluvial montane forest, montane paramo grassland, and geliturbated subnival paramo vegetation according to the Andean ecosystems classification of [Cuesta et al. \(2009\)](#). This species is not known to occur in sympatry with other species of *Stenocercus*.

Etymology

The specific name is a noun in the genitive case and is a patronym for John E. Cadle, who has published important contributions to the systematics of *Stenocercus* ([Cadle, 1991](#), [1998](#), [2001](#)). Cadle also made important specimen and tissue collections of *Stenocercus* from Peru, and these collections have been used in several systematic studies of these lizards.

Discussion

Most species of *Stenocercus* occur along the Andes and have narrow latitudinal ranges. This distribution suggests that geographical barriers resulting from Andean uplift events (e.g., inter-Andean valleys) have had a great impact on the diversification of this clade. Previous phylogenetic hypotheses suggest that *Stenocercus* is composed of two clades with different distribution patterns ([Torres-Carvajal et al., 2006](#); [Torres-Carvajal, 2007c](#)). One of these clades contains *S. guentheri*, and along with *S. caducus*, *S. iridescens*, and *S. roseiventris*, these species have wide latitudinal distribution ranges compared with other species in the clade ([Torres-Carvajal, 2007c](#)). Of these, *S. guentheri* (sensu [Torres-Carvajal, 2007a](#)) is the only species occurring at high altitudes, and one could argue that this species has not been affected by the same geological or climatic events (e.g., vicariant events resulting from Andean orogeny) as other high-altitude species of *Stenocercus* that have narrower distribution ranges. The results presented herein invalidate this argument and demonstrate that an incorrect taxonomic arrangement can mislead biogeographical interpretations. The recognition of southern populations of “*S. guentheri*” as a separate species restricts the latitudinal distribution of *S. guentheri*. Both this species and *S. cadlei* have narrow latitudinal ranges ([Fig. 3](#)) as do other Andean species of *Stenocercus* ([Torres-Carvajal, 2007a](#)).

High-altitude species of *Stenocercus* from the northern Andes live at altitudes that were not reached before the mid-Pliocene 3–4 million yr ago ([Simpson, 1979](#); [Aleman and Ramos, 2000](#)), suggesting that these species are products of recent speciation events. This recent age might explain why some species are so similar morphologically and suggests that some of the taxa recognized presently include cryptic species that have not been discovered yet. *Stenocercus cadlei* is an example of a cryptic species from the northern Andes that was discovered through phylogenetic analyses of molecular data and a more careful subsequent examination of morphological characters. Other

Andean taxa with an evolutionary history similar to *Stenocercus* might include cryptic species waiting to be discovered.

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Appendix 1

Additional Specimens

Stenocercus guentheri

ECUADOR: Provincia Imbabura: Atuntaqui, 0°20'1"N, 78°18'8"W, 2,387 m, QCAZ 776; 7.5 km N Otavalo on Panamerican Highway, 0°17'24"N, 78°14'24"W, 2,524 m, QCAZ 3761; Tabacundo-Mojanda road, 3,150 m, QCAZ 3793; San Miguel ravine, 1 km N Otavalo, 0°14'12"N, 78°15'22"W, 2,535 m, KU118057; Urcusiqui, 12 km NW Otavalo, 0°18'36"N, 78°20'34"W, 3,298 m; KU 118069; Otavalo, 0°13'60"N, 78°16'0"W, 2,603 m, KU 134535; San Antonio of Ibarra, 0°18'0"N, 78°7'0"W, 2,542 m, KU 134556; Lake Cuicocha, 10 km W Quiroga, 0°18'0"N, 78°22'0"W, 3,173 m, KU 134564. Provincia Pichincha: 1.6 km ENE Quito, 0°13'12"S, 78°30'0"W, 2,879 m, USNM 201236–7; 2.4 km SSE Quito, 0°13'12"S, 78°30'0"W, 2,879 m, USNM 201234, 201238; Cayambe volcano slopes, 0°2'10"N, 78°3'36"W, 3,500 m, FHGO 1136; Guayllabamba, 0°3'20"S, 78°20'25"W, 2,139 m, QCAZ 718, 777, 779, 782; Ilaló, Hacienda Chuspiyacu, 0°14'2"S, 78°23'43"W, 2,525 m, QCAZ 722; Jerusalem, 0°0'2"S, 78°22'6"W, 2,314 m, QCAZ 1323; Lloa, 0°15'0"S, 78°35'0"W, 3,060 m, QCAZ 4108; Machachi, 0°30'28"S, 78°33'46"W, 2,940 m, QCAZ 720, 736, 758, 775, 778, 780–1, 783–4; below Pacto, USNM 201239; Pintag-Antisana road, 0°22'12"S, 78°22'18"W, 2,880 m, QCAZ 2808; Pusuquí, 0°4'0"S, 78°27'0"W, 2,747 m, QCAZ 4153; Quito, 0°11'24"S, 78°29'38"W, 2,810 m, EPN 5900, QCAZ 432, 728, 737, 2857, SMF 60592, USNM 201226, 201230–3; San Antonio, 0°0'15"N, 78°27'6"W, 2,481 m, QCAZ 713–6, 738, 740–54, 1357, 1400, 2163, 2199, 58.7.25.16a, 60.6.16.18, 60.6.16.20–21 (syntypes); Uyumbicho, 0°23'0"S, 78°31'0"W, 2,668 m, QCAZ 760; 4 km W San Antonio, 0°1'0"N, 78°29'9"W, 2,550 m, KU 134610; 3.5 km E Chicho River in Los Chillos Valley, E Quito, 0°16'0"S, 78°28'60"W, 2,535 m, KU 152171; Casitagua, near Pomasqui, 0°1'60"S, 78°28'60"W, 3,089 m, QCAZ 4339; Tababela, new airport, 0°6'37"S, 78°21'35"W, 2,355 m, QCAZ 8925; Alambi hill, 0°4'035"S, 78°34'51"W, 2,934 m, QCAZ 9690; Limpiopungo, 0°36'58"S, 78°27'58"W, 3,871 m, QCAZ 10028; 20.9 km N Quito, 0°0'40"S, 78°29"W, 2,150 m, QCAZ 11062.

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TABLE 2. Summary of morphological characters, measurements (mm), and color patterns of *Stenocercus cadlei* and *S. guentheri*. Range (first line), mean \pm SD (second line), and *n* (if different from heading, third line) are given for quantitative characters.

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TABLE 3. Sexual variation in scutellation and measurements (mm) of *Stenocercus cadlei*. Range (first line), mean \pm SD (second line), and *n* (if different from heading, third line) are given.