

# A NEW SPECIES OF LIZARD RELATED TO *STENOCERCUS CADUCUS* (COPE) (SQUAMATA: IGUANIDAE) FROM PERU AND BOLIVIA, WITH A KEY TO THE "OPHRYOESSOIDES GROUP"

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**ABSTRACT.** A new species of iguanid lizard, *Stenocercus prionotus*, is described from eastern Peru and Bolivia (known range from San Martín Department, Peru, to northern La Paz and El Beni departments, Bolivia). Most localities are in the Andean foothills and immediately adjacent lowlands. *Stenocercus prionotus* is similar to several other species of *Stenocercus* with large posterior head scales, an enlarged row of supraoculars, and keeled ventral scales. These similar species are referred to as the "Ophryoessoides group" without implying that it is a monophyletic assemblage. Based on their common possession of a

unique scaly flap concealing a portion of the posthumeral mite pocket, the new species is apparently closely related to *S. caducus* (Cope), which is known from central Bolivia south to northern Argentina and Paraguay. *Stenocercus prionotus* is distinguished from *S. caducus* by having a more prominent vertebral crest and a pattern of alternating light and dark bars on the throat (rarely observed in *S. caducus*, which usually has light throat spots). These two species also occupy different physiographic regions (western Amazonian rainforest for *S. prionotus*; chaco for *S. caducus*).

Populations of *S. prionotus* from northern Peru and Bolivia. Northern populations are also broadly sympatric with two other species of the "Ophryoessoides group," *S. aculeatus* and *S. fimbriatus*. However, in southern Peru *S. prionotus* is not known to be sympatric with other species of that group. I postulate that the higher vertebral crest in northern populations of *S. prionotus* functions as a species recognition signal in the multispecies assemblages. A key to species of the "Ophryoessoides group" is provided and distributions of the species in Peru and Bolivia are summarized.

**RESUMEN.** Se describe una nueva especie de lagartija iguanida, *Stenocercus prionotus*, del Perú Oriental y de Bolivia. Se conoce la nueva especie desde el departamento de San Martín, Perú, hasta el norte de los departamentos La Paz y El Beni en Bolivia. La mayoría de las localidades se encuentran en las estribaciones andinas y adyacentes tierras bajas. *Stenocercus prionotus* es similar a varias otras especies de *Stenocercus* con grandes escamas sobre el posterior de la cabeza, una fila amplia de supraoculares, y escamas ventrales quilladas. Se refiere estas especies como el "grupo Ophryoessoides," sin implicar su monophyletismo. Basada en su posesión de un lóbulo escamoso único que oculta una porción del bolsillo antehumeral, se considera la nueva especie cercanamente relacionada a *Stenocercus caducus* (Cope), que se conoce desde Bolivia central hasta el norte de la

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Argentina y del Paraguay. *Stenocercus prionotus* se distingue de *S. caducus* al tener una cresta vertebral más prominente y un patrón de alternativas barras claras y oscuras sobre la garganta (un patrón raramente observado en *S. caducus*, que usualmente tiene manchas claras sobre la garganta).

Las poblaciones de *Stenocercus prionotus* del norte del Perú tienen una cresta vertebral más alta que la cresta en poblaciones del sur de Perú y Bolivia. Las poblaciones del norte de Perú también son ampliamente simpátricas con dos otras especies del "grupo *Ophryoessoides*," *S. aculeatus* y *S. fimbriatus*. Sin embargo, en el sur del Perú y Bolivia no se conocen localidades donde se encuentra *S. prionotus* simpátrica con otras especies del grupo. Postulo que la cresta vertebral más alto en las poblaciones norteñas de *S. prionotus* funciona como un señal para reconocimiento de especies en comunidades donde hay varias especies simpátricas. Se provee una clave para las especies del "grupo *Ophryoessoides*" y se resumen las distribuciones de las especies Peruanas y Bolivianas.

## INTRODUCTION

*Stenocercus sensu* Frost (1992), including the nominal genera *Ophryoessoides* and *Proctotretus*, is a moderately diverse assemblage of South American iguanid lizards (*sensu* Macey et al., 1997; Schulte et al., 1998) with about 50 species currently recognized. Most of the species are in the Andes and adjacent lowlands of Colombia, Ecuador, and Peru, but a few are primarily Amazonian or have distributions in the physiographically diverse terrain south of the Amazon basin. Although new species of *Stenocercus* continue to be discovered in the field, others have been known from old collections and are only now being described (e.g., Cadle, 1991, 1998; Avila-Pires, 1995). In this category is a new species from the lowlands of eastern Peru and Bolivia that has been referred erroneously to the names *aculeatus* O'Shaughnessy (1879) or *caducus* Cope (1862) in previous literature, and associated with the genera *Leioccephalus* or *Ophryoessoides* before the current understanding of these names came into use (see Etheridge, 1966; Frost, 1992). Rodriguez and Cadle (1990) left the new species nameless in a checklist pending resolution of its status. The new species is apparently closely related to *Stenocercus caducus* (Cope) and is described herein.

## MATERIALS AND METHODS

Frost (1992; see especially footnote 5) and Cadle (1991) discussed reasons for referring new species such as the one described here to *Stenocercus* Duméril and Bibron *sensu lato* (including *Ophryoessoides* Duméril and *Proctotretus* Duméril and Bibron). Externally, the new species is similar to those species that Fritts (1974) placed in *Ophryoessoides*, that is, those species with keeled ventral scales, large posterior head scales (usually including well-differentiated interparietal, parietals, postparietals, and occipitals), and one moderately to greatly enlarged supraocular row. In addition to the new species described here, species included in the "*Ophryoessoides* group" are *aculeatus* O'Shaughnessy, 1879; *caducus* Cope, 1862; *dumerilii* Steindachner, 1867; *erythrogaster* Hallowell, 1856; *fimbriatus* Avila-Pires, 1995; *huancabambae* Cadle, 1991; *iridescens* Günther, 1859; *limitaris* Cadle, 1998; *scapularis* Boulenger, 1901; *tricristatus* Duméril, 1851; and two undescribed species noted later in this paper under *Key to Species of the "Ophryoessoides group" of Stenocercus*. I use the term "*Ophryoessoides* group" as a convenience to refer to this group of phenotypically similar species without implication as to its status as a monophyletic or nonmonophyletic assemblage within *Stenocercus*.

General descriptive protocols follow Cadle (1991), who defined terminology of the scales, neck folds, and mite pockets used herein, based in part on Frost (1992). Bilateral scale counts (e.g., subdigitals) were made only on one side (the left, unless it was damaged), except for the holotype, for which both left and right counts were recorded (l, r). A summary of selected scutellational and qualitative characters for the new species and similar species from eastern Peru and Bolivia is presented in Table 1.

All measurements are in millimeters. The abbreviation SVL refers to the head-body length, from snout to vent. The con-

TABLE 1. COMPARISON OF THE SPECIES OF *STENOGERCUS* WITH KEELED VENTRAL SCALES ("OPHYDROSSOIDES" SENSU FRITTS, 1974) IN EASTERN PERU AND BOLIVIA. QUANTITATIVE CHARACTERS ARE GIVEN AS RANGE FOLLOWED BY MEAN  $\pm$  1 SD. FOR SOME CHARACTERS (E.G., INTERNASALS AND SUPRAOCULARS) THE MODE OR PERCENTAGE OF SPECIMENS WITH A PARTICULAR CHARACTER, RATHER THAN MEANS, IS GIVEN. SAMPLE SIZES (*N*) ARE GIVEN AT THE TOP OF EACH COLUMN EXCEPT WHERE THEY VARIED FOR INDIVIDUAL MEASURES (*N* ADDED PARENTHETICALLY). DATA FOR *S. HUANGCABAMBAE* ARE FROM CADLE (1991). DATA FOR *S. ACULEATUS* INCLUDE BOTH ECUADORIAN AND PERUVIAN SPECIMENS, WHICH DIFFER IN SOME QUALITATIVE AND QUANTITATIVE CHARACTERS (SEE *IS THE DISTRIBUTION OF STENOGERCUS ACULEATUS DISJUNCT?*).

	<i>Stenogercus prionotus</i> new species <i>N</i> = 55	<i>Stenogercus cadatus</i> (Cope) <i>N</i> = 43	<i>Stenogercus finbriatus</i> Avila-Pires <i>N</i> = 33	<i>Stenogercus aculeatus</i> (O'Shaughnessy) <i>N</i> = 26	<i>Stenogercus huangcambae</i> Cadle <i>N</i> > 100	<i>Stenogercus scapularis</i> (Boettger) <i>N</i> = 11
Midbody scales	36-48 40.8 $\pm$ 3.02	34-44 38.2 $\pm$ 2.10 (42)	39-51 43.8 $\pm$ 7.83	34-45 40.2 $\pm$ 3.04	37-53 43.9 $\pm$ 3.20	59-70 62.8 $\pm$ 2.86
Vertebral scales	27-39 34.2 $\pm$ 2.69	30-43 35.9 $\pm$ 5.59 (41)	37-52 43.7 $\pm$ 3.24	32-46 40.9 $\pm$ 3.57 (25)	37-51 43.4 $\pm$ 3.40	42-52 48.4 $\pm$ 2.66
Gular scales	15-22 18.5 $\pm$ 2.69	16-23 18.6 $\pm$ 1.41 (40)	17-25 20.1 $\pm$ 2.29	16-23 19.7 $\pm$ 1.85	18-28 20.9 $\pm$ 1.64	22-27 24.5 $\pm$ 1.75
Internasals	7 (60%), 6 (25%), 5 (11%), rarely 8	7 (55%), 6 (45%)	6 (40%), 5 (29%) 7 (17%), rarely 4	4 (24%), 5 (20%) 6 (40%), 7 (16%)	6 (70%), 5 (28%) rarely 4 or 7	6 (64%), 5 (36%)
Supraoculars	5, occasionally 6 (rarely 7)	5-6 (rarely 4)	4 (rarely 5 or 6)	4 (rarely 3 or 5)	3-6 (mode = 5)	3-5 (mode = 4)
Fourth finger sub- digitals	16-21	15-21	14-18	17-21	14-20	18-23
Fourth toe subdigitals	18.8 $\pm$ 1.30	17.6 $\pm$ 1.16	16.1 $\pm$ 0.83	19.2 $\pm$ 1.16	16.8 $\pm$ 1.41	20.5 $\pm$ 1.51
Tail/total length <sup>1</sup>	24-31 26.6 $\pm$ 3.64 0.69-0.74 0.72 $\pm$ 0.012 (30)	23-30 26.0 $\pm$ 1.59 0.69-0.73 0.70 $\pm$ 0.015 (21)	22-26 23.4 $\pm$ 1.17 0.64-0.67 0.66 $\pm$ 0.010 (8)	22-29 25.2 $\pm$ 1.79 0.68-0.73 0.71 $\pm$ 0.019 (6)	20-28 24.6 $\pm$ 1.56 0.65-0.71 0.68 $\pm$ 0.01	25-29 27.2 $\pm$ 1.33 0.69-0.71 0.69 $\pm$ 0.01 (6)
Maximum size (mm), SVL (total length)						
Males	89 (323)	72 (193+) <sup>2</sup>	74 (208)	93 (340)	95 (-) <sup>3</sup>	80 (249)
Females	93 (329)	93 (349)	91 (-) <sup>3</sup>	91 (295)	75 (231)	92 (297)
Posthumeral pocket	Type 4 with scaly flap	Type 4 with scaly flap	Type 4 no flap	Type 4 no flap	Type 4 no flap	Type 4 no flap
Postfemoral pocket	Type 1	Type 1	Type 1	Type 2, 3, or 5 <sup>4</sup>	Type 5	Type 3 (high frequency of Type 5)

<sup>1</sup> Juveniles < 50 mm snout-vent (SVL) were excluded because tail length seems to scale positively with body size in *Stenogercus*.

<sup>2</sup> See text (*Comparison of Stenogercus prionotus with S. cadatus*) for discussion of apparent size dimorphism in *S. cadatus*.

<sup>3</sup> Tail broken.

<sup>4</sup> See text for discussion of this variation.

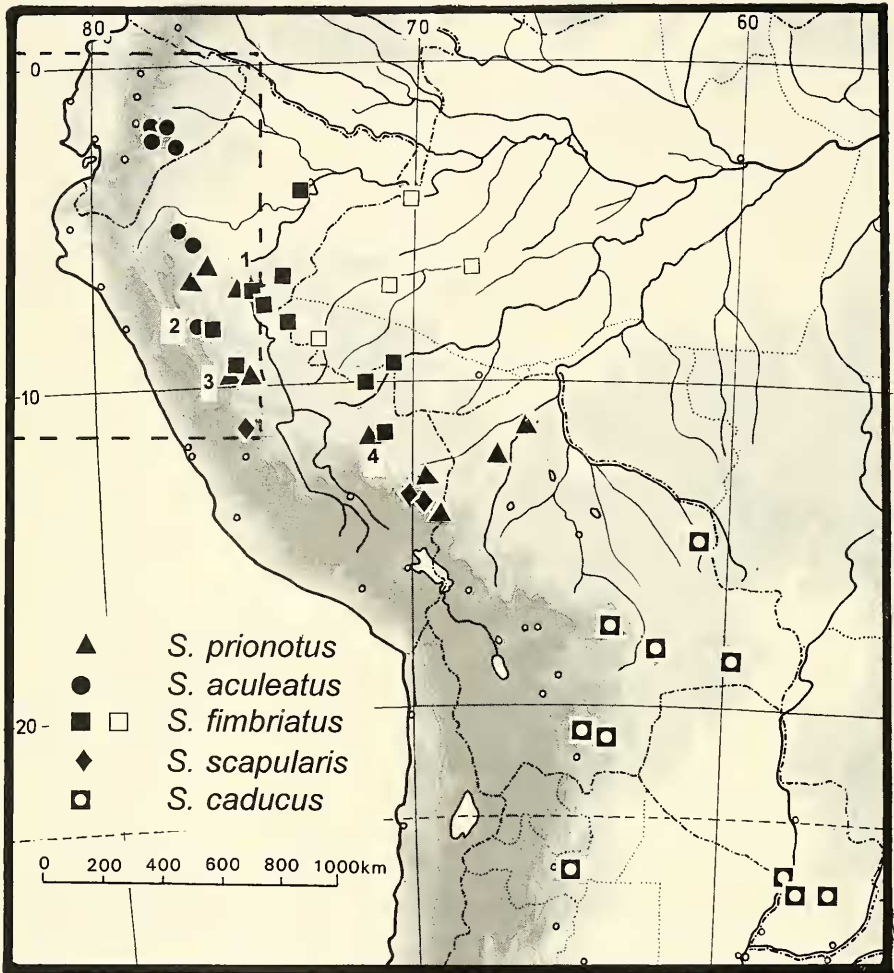


Figure 1. Distribution of species of *Stenocercus* emphasized in this paper (western South America, Ecuador to Paraguay and northern Argentina). Open symbols for *S. fimbriatus* are literature records from Avila-Pires (1995); locality for *S. caducus* in northern Argentina is the southernmost locality in Argentina reported by Cej (1993). Otherwise, all records are based on specimens examined. Numbered localities are documented or suspected cases of sympatry referred to in the text and noted in the Appendix: 1, Pampa Hermosa; 2, Pampa Seca, Río Mixiollo; 3, Tingo Maria; 4, Manu National Park. Upper left quadrant outlined with dotted line is the area shown in greater detail in Figure 2.

figurations of neck folds and mite pockets vary considerably among species of *Stenocercus* and are useful in distinguishing species. The most important qualitative characteristics of these features used herein are the following, which are discussed more fully by Cadle (1991):

*Neck and Body Folds and Crests.* In contrast to many species of *Stenocercus*, neck folds are usually absent or weakly de-

veloped in the "*Ophryoessoides* group." When present, they are better characterized as crests rather than folds because they are usually indicated by strongly keeled rows of scales instead of actual folds of skin. The position of such crests corresponds to the position of folds seen in other species of *Stenocercus*, but only two are commonly seen in the "*Ophryoessoides* group": an antehumeral crest, which

is a more or less vertical row of strongly keeled scales immediately anterior to the forelimb insertion, and usually highlighted with white scales; and a supra-auricular crest, a strongly keeled horizontal row of scales extending from the posterior temporal region to the shoulder region. All species of the “*Ophryoessoides* group” have a distinct vertebral crest formed by the strongly keeled, and often projecting, scales of the vertebral row. In addition, some of these species have a more or less prominent dorsolateral crest formed by a row of strongly keeled scales separating the flanks from the dorsum proper. The dorsolateral crest varies in length. In some species it is exceptionally long, extending from the proximal portion of the tail to the neck region, where it is confluent with the supra-auricular crest. In other species it is present only anteriorly or posteriorly.

*Posthumeral (Axillary) and Postfemoral Mite Pockets.* Type 1—pocket absent; no skin modification. Type 2—rudimentary pocket manifested by skin modification, such as bare skin, a series of wrinkles, or a shallow depression lined with scales different from surrounding body scales. Type 3—similar to Type 2, but with an overhanging fold of skin or a thickened border. Type 4—a deep pocket, usually with a broad circular opening, whose depth is greater than half the diameter of its opening. Type 5—a deep pocket with a narrow, slit-like opening and a depth greater than half the diameter of its opening. In two species discussed herein the posthumeral pocket is partially concealed by a scaly flap of skin, which I term a posthumeral or axillary flap. This structure is described more fully later.

Angulate temporal scales are distinctly enlarged, keeled scales posterior to, and in line with, the superciliary scales. When present, they form a distinct border between the posterior head scales and the lateral temporal scales, and they are morphologically distinguishable from these series (Cadle, 1991: 6–7; see Fig. 4). Angulate temporal scales are equivalent to su-

prateemporals as used in some literature (e.g., Avila-Pires, 1995). In several species of *Stenocercus* the angulate temporals are not only keeled but they bear a projecting bladeliike vane from the keels; in such cases I refer to the scales as “projecting.”

Coordinates for localities were obtained from the ornithological gazetteers of the Neotropics (Stephens and Traylor, 1983; Paynter, 1989, 1992, 1993, 1997), and from Lamas (1976), Morales and McDiarmid (1996), Schulenberg and Awbrey (1997b), and Peruvian department maps produced by the Instituto Geográfico Nacional, Lima. I also consulted the on-line versions of the Peru and Bolivia gazetteers of the U.S. Board on Geographic Names at the GEOnet® Names Server: <http://164.214.2.59/gns/html/index.html>. Bracketed data in localities are inferences from these or other cited sources. Distributions of the new species and others emphasized in this paper are given in Figures 1 and 2. Institutional abbreviations are given at the beginning of the Appendix.

## DESCRIPTION OF A NEW SPECIES OF *STENOCERCUS*

### *Stenocercus prionotus*<sup>2</sup> new species

Figures 3–7, Figure 12; Table 1

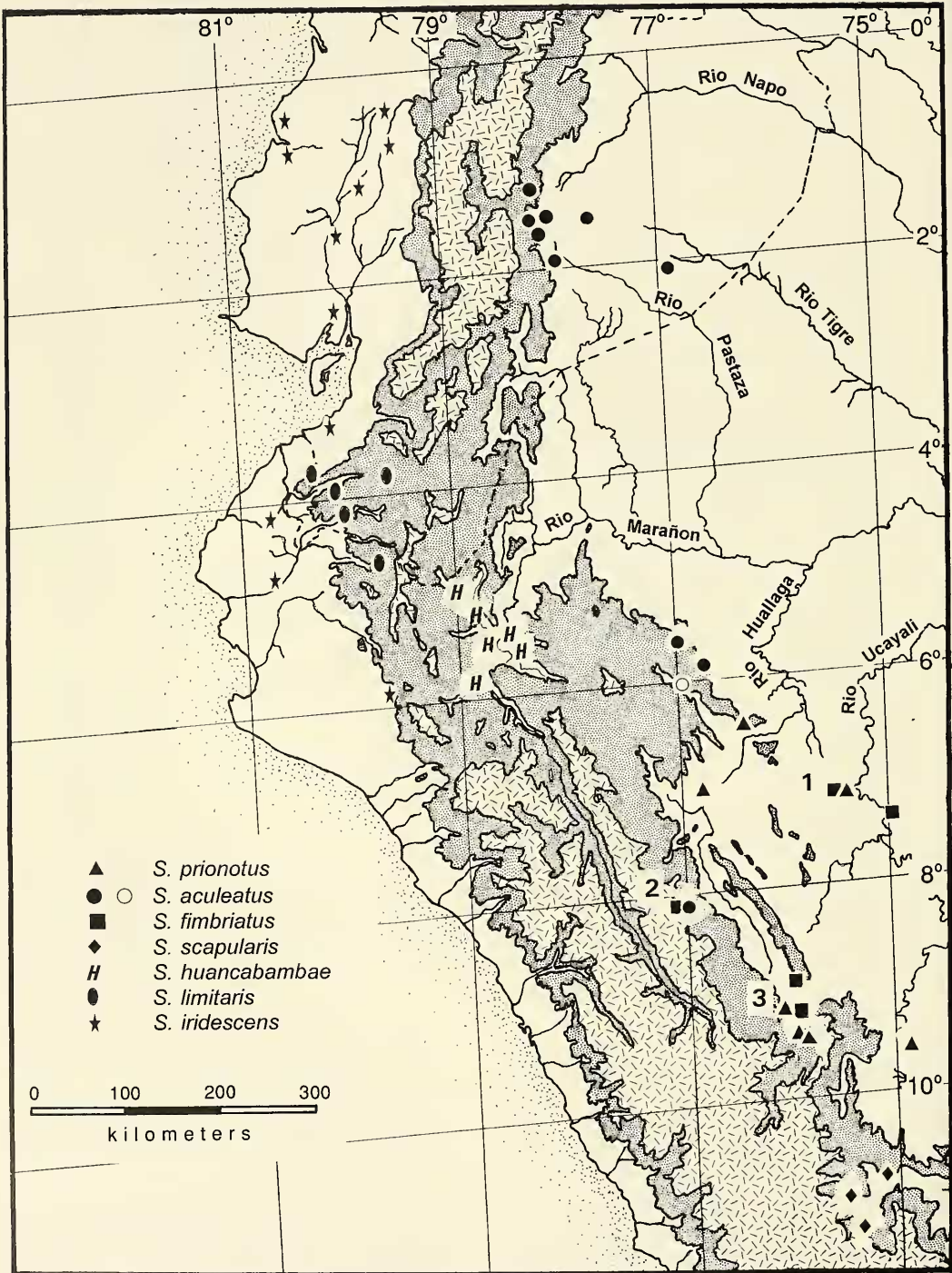
*Liocephalus caducus* (Cope, 1862): Boulenger (1898), specimen from “Barraca, Rio Madidi” [Bolivia] (BMNH 98.6.9.4) and probably two other northern Bolivian localities discussed in the text.

*Ophryoessoides caducus* (Cope, 1862): Fugler (1989: 63), specimens from San Marcos Ranch, El Beni Department, Bolivia, including ROM 12815.

*Ophryoessoides aculeatus* (O’Shaughnessy, 1879): Fugler (1983, 1986, 1989), specimens from Tumi Chucua, El Beni Department, Bolivia (USNM paratypes).

*Ophryoessoides* sp.: Rodriguez and Cadle (1990), specimen from Cocha Cashu, Manu National Park, Madre de Dios Department, Peru (MCZ 150243).

<sup>2</sup> *Stenocercus prionotus* was recognized as new by R. Etheridge, P. E. Vanzolini, and E. E. Williams many years ago. Vanzolini and Williams applied the unpublished name *Stenocercus dorsatus* to labels of many specimens in various collections.



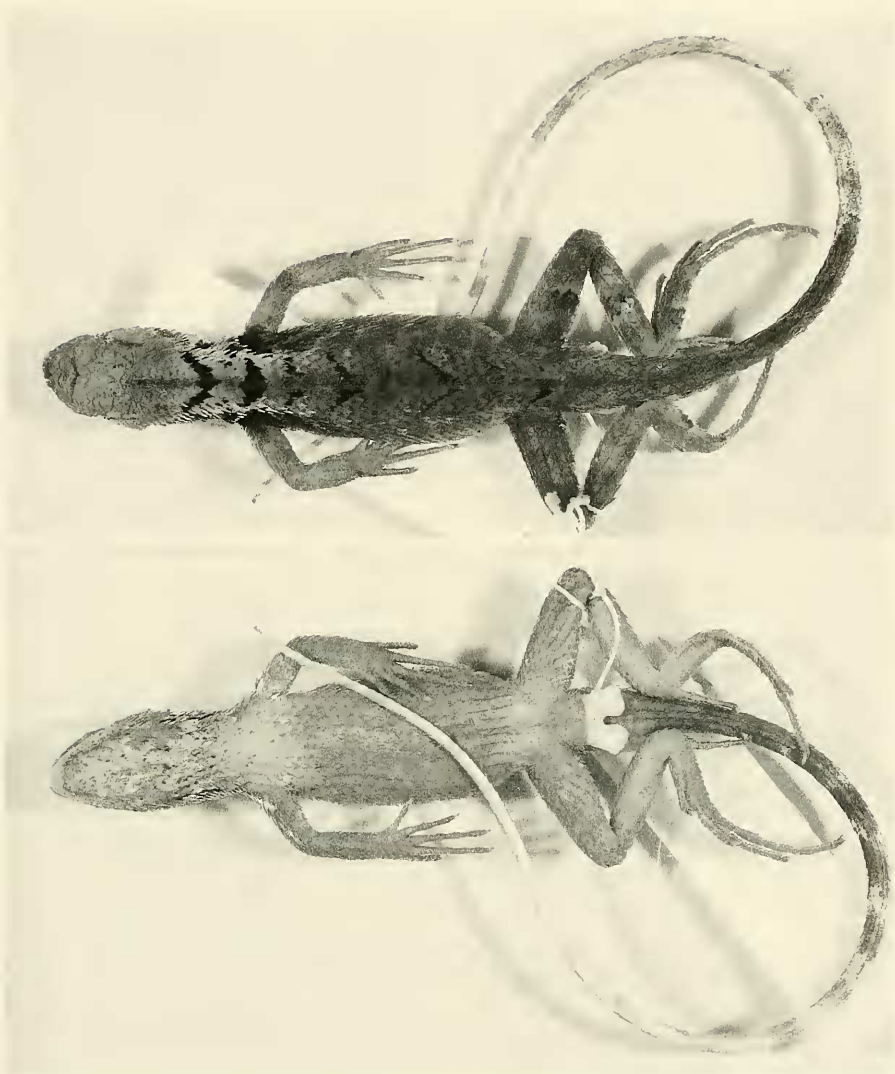


Figure 3. Dorsal and ventral views of the holotype of *Stenocercus prionotus* (USNM 193683). Approximately  $\times 0.87$ .

Figure 2. Northern Peru and Ecuador (see Fig. 1) showing distributions of species in the "Ophryossoides group." Numbered localities are documented or suspected cases of sympatry referred to in the text and the Appendix (see Fig. 1 for names). Open circle at  $06^{\circ}\text{S}$ ,  $77^{\circ}\text{W}$  is the type locality for *Stenocercus aculeatus* (Moyabamba, San Martín Department). All other localities are based on specimens examined; see Cadle (1991, 1998) for *S. iridescens*, *S. limitaris*, and *S. huancabambae*. The known distributions of all species are indicated by the localities plotted; however, the distribution of *S. iridescens* continues farther north in western Ecuador than the area covered by the map.

*Holotype* (Figs. 3–5). **United States National Museum of Natural History (USNM) 193683** (field number WCS 2421). **PERU: DEPTO. HUÁNUCO:** Jardín Botánico de la Universidad Agraria de la Selva, Tingo Maria, vicinity of Río Huallaga, 670 m elevation [09°18'S, 75°59'W]. Adult male collected 29 June 1966 by Wade C. Sherbrooke.

*Paratypes from the Vicinity of the Type Locality.* **PERU: DEPTO. HUÁNUCO:** Ca. 2 mi. by trail W. Tingo Maria, west bank of Río Huallaga in vicinity of confluence with Río Monzón, 670 m elevation (9 October 1966, W. C. Sherbrooke), **USNM 193685**. Universidad Agraria de la Selva, Tingo Maria, Río Huallaga, 670 m elevation (18 August 1967, unknown collector for W. C. Sherbrooke), **USNM 193686**. Vicinity of Cueva de las Lechuzas, ca. 3 mi. SW Tingo Maria, Río Monzón, ca. 700 m elevation (17 April 1968, Vito Yaringano for W. C. Sherbrooke), **USNM 193687**. Picuriacu, ca. 2 mi. NW Tingo Maria, Río Huallaga (20 April 1968, W. C. Sherbrooke), **USNM 193688**.

*Other Paratypes.* **PERU: DEPTO. HUÁNUCO:** Buena Vista, Valley of the Chinchao [= Río Chinchao] [approximately 9°31'S, 75°52'W] (1–15 September 1923, E[dmund] Heller), **FMNH 5582–83**. Hacienda Pampayacu [09°33'S, 75°54'W] (17 July–16 August 1936, Dr. Snonge), **MCZ 43758–59, 43761–62**. Río Llullapichis, 4–5 km upstream from Río Pachitea, 200 m elevation [09°37'S, 74°55'W] (January 1969, Hans W. Koepcke), **KU 179058**. [**DEPTO. LORETO**]: E[astern] Peru, Pampa Hermosa, near mouth of Río Cushabatay, Río Ucayali Valley, 500 ft. [152 m] [07°12'S, 75°17'W] (date unknown, H[arvey] Bassler), **AMNH 56760–64**. [**DEPTO. MADRE DE DIOS**]: Cocha Cashu Biological Station, Manu National Park [11°51'S, 71°19'W] (July 1975, John W. Fitzpatrick), **MCZ 150243**. Explorer's Inn, Tambopata Reserve, ca. 30 km (straight line) SSW Puerto Maldonado, 280 m [12°50'S, 69°17'W] (2 September–7 October 1983, native collectors), **USNM**

**247468–69, 247680**; (23 May 1986, Victor R. Morales), **USNM 269022**. [**DEPTO. PUNO**]: Prov. Sandia: Tambopata, San Juan [del Oro], 1520 m or 5000 ft. [14°12'S, 69°08'W]<sup>3</sup> (22 November–20 December 1950, Hilda H. Heller), **FMNH 64788–92, 64794–811**. [**DEPTO. SAN MARTÍN**]: Juanjui [07°11'S, 76°45'W] (collector and date unknown), **MCZ 121233**. Tarapoto, 370 m [06°30'S, 76°25'W] (25 July 1984, Rainer Schulte), **KU 212629**.

**BOLIVIA: DEPTO. BENI:** Provincia Vaccadiez, Tumi Chucua [176 m; 11°08'S, 66°10'W] (23 October–18 November 1981, Charles M. Fugler), **USNM 280246–51**. Puerto Cruzeiro, San Marcos Ranch at confluence of Ríos Isiboro and Ichoa [15°17'S, 65°45'W] (10 February 1977, J. Lovisek), **ROM 12815**. [**DEPTO. LA PAZ**]: Barraca, Río Madidi [12°35'S, 67°02'W] (1893, Luigi Balzan), **BMNH 98.6.9.4**.

*Distribution* (Fig. 1). *Stenocercus prionotus* is known from the lowlands and Andean foothills of eastern Peru and adjacent Bolivia (San Martín department, Peru, south to the Río Beni in northern Bolivia). The known elevational range is 176–1,520 m, but the highest recorded elevation is more than twice the elevation of the next lower one. Most localities in Peru are adjacent to or near the Andean foothills, and several localities in La Paz and El Beni departments, Bolivia, are unconfirmed. No specimens are known from a broad geographic hiatus between central and southern Peru (Fig. 1). See *Distribution Patterns in Stenocercus prionotus* for further discussion.

*Etymology.* The epithet *prionotus* is de-

<sup>3</sup> Hilda Heller's notes on this collection in the Karl P. Schmidt archives of the FMNH describe San Juan as the site of an agricultural station on "the left side of the Río Tambopata at 5000 feet." With some hesitancy I identify Heller's locality as the town known as San Juan del Oro, which is on the left bank of the Río Tambopata at approximately the elevation given by Heller. I have located only two other places named San Juan in Puno Department, but neither is on the Río Tambopata.



rived from the Greek adjective *prionotos* meaning jagged or serrate. The name refers to the strongly serrate vertebral crest of *Stenocercus prionotus*, which is the most obvious character distinguishing this species from its apparent closest relative, *S. caducus*.

*Data on the Holotype.* Adult male, hemipenes partially everted. SVL, 83 mm. Tail length, 201 mm. Total length, 284 mm. Tail/total length, 0.71. Vertebral scales between the occipital and the posterior margin of the hind limb, 31. Midbody scales, 42. Gular scales between the ears, 16. Internasals, 6. Subdigital scales on fourth fingers and toes, respectively, 18–18, 25–25. Color pattern well preserved: top of head brown with narrow dark brown interorbital bar extending laterally onto supraoculars; dorsum brown with narrow blackish chevrons middorsally (1 on neck, 1 above forelimbs, 2 others anterior to midbody; posterior chevrons poorly defined); dark brown scapular blotch bordered anteriorly by white antehumeral stripe; ill-defined grayish dorsolateral streaks between ear and anterior body; throat grayish with poorly defined oblique light grayish stripes; venter brown without distinct pattern.

*Definition.* A species of *Stenocercus* characterized by the following features: (1) Dorsal head scales subimbricate and strongly keeled to multicarinate; temporals keeled, imbricate or subimbricate. (2) Posterior head scales larger than anterior ones, with distinct interparietal, a pair of parietals, a pair of postparietals, and a large median occipital (often surrounded by several small irregular scales). (3) Internasals usually 7, but pattern irregular and may be 5 or 6. (4) One row of supraoculars distinctly enlarged. (5) One canthal on each side between the superciliaries and the lateralmost internasal. (6) A pair of strongly keeled angulate temporals in line on each side (rarely, 3 angulate temporals are present), each with a low projecting blade; partially or completely separated from enlarged posterior head scales

by a single row of small scales. (7) Anterior and posterior gular scales strongly keeled. (8) Parietal eye distinct. (9) Neck folds absent; a vertical, strongly keeled row of scales in the antehumeral region and occasionally a much less distinct raised series in the supra-auricular region. (10) Dorsal and ventral body scales imbricate, mucronate, strongly keeled; dorsal scales at midbody 36–48. (11) Vertebral row continuous, bearing a strongly projecting serrate crest in adults; a dorsolateral crest present on posterior body and the base of the tail. (12) Deep posthumeral pocket (Type 4) partially concealed by a scaly posthumeral flap originating on its anteroventral border; postfemoral pocket absent (Type 1). (13) Scales of posterior thigh imbricate, keeled. (14) Tail strongly compressed in adults, anteriorly with low vertebral and dorsolateral crests continuous with those of the body. (15) Dorsal coloration of males in preservative (Figs. 3, 6) brown with or without distinct chevrons; a distinct white vertical antehumeral stripe extending ventrally to the proximal ventral surface of forelimb; a large dark scapular blotch; in well-preserved specimens the throat bears oblique alternating dark and light stripes (see *Description*); females similar but pattern elements often more subdued.

#### DIAGNOSIS AND COMPARISONS

In having enlarged posterior head scales, an enlarged row of supraoculars, and strongly keeled ventral scales, *Stenocercus prionotus* is like other species in the “*Ophryoessoides* group” of *Stenocercus*. These are the species most likely to be confused with *S. prionotus*. Five other described species of the “*Ophryoessoides* group” occur in eastern Peru or Bolivia: *S. aculeatus* (O’Shaughnessey, 1879); *S. caducus* (Cope, 1862); *S. fimbriatus* Avila-Pires, 1995; *S. huancabambae* Cadle, 1991; and *S. scapularis* (Boulenger, 1901). An undescribed species occurs in the Río Marañon valley of eastern Peru (see *Key to Species of the “Ophryoessoides Group”*

of *Stenocercus*). *Stenocercus prionotus* and *S. caducus* are unique among known species of *Stenocercus* (perhaps unique within iguanids) in having deep posthumeral mite pockets (Type 4) that are partially concealed anteroventrally by a scaly flap, which may be termed a posthumeral or axillary flap (Fig. 5). *Stenocercus prionotus* and *S. caducus* are compared in greater detail below, but *S. prionotus* is distinguished from *S. caducus* (characteristics in parentheses) by: (1) a strongly projecting, serrate vertebral crest (low and scarcely projecting); (2) 2 (usually) or 3 enlarged, strongly keeled, projecting angulate temporal scales on each side (scales not greatly enlarged, less projecting); and (3) a gular pattern consisting, when evident, of oblique alternating dark and light lines or bars, or oblique light lines on a dark ground color (usually light spots on a darker ground color, unicolor, or [rarely] a pattern similar to that of *S. prionotus*).

Readily determined characters distinguishing *Stenocercus prionotus* from the other four species of the "Ophryoessoides group" known from eastern Peru and Bolivia include the extent of keeling on dorsal head and body scales, relative development of the postfemoral pockets, and the number of midbody scale rows (Table 1 and key presented later herein). *Stenocercus fimbriatus* and *S. aculeatus* are known to be sympatric with *S. prionotus* at several localities in eastern Peru. In addition to having a posthumeral flap (absent in *S. fimbriatus* and *S. aculeatus*), *S. prionotus* is distinguished from *S. fimbriatus* (characteristics in parentheses; see Avila-Pires, 1995) in having strongly keeled dorsal scales in adults (smooth or weakly keeled), a dorsolateral crest prominent only on the posterior body (prominent anteriorly and continuous with antehumeral and supra-auricular folds or crests), and in lacking "fimbriate" scales on the posterior distal portion of the thigh (present). *Stenocercus prionotus* is distinguished from *S. aculeatus* (characteristics in parentheses) in lacking a postfemoral pocket (moderate to

deep); in having strongly keeled, often multicarinate, head scales (smooth or weakly striated in adults, wrinkled in juveniles); 5–7 internasals (4–5); and only moderately enlarged supraoculars, usually 5–6 supraoculars across the widest part of the orbit (greatly enlarged, usually 4 across the orbit).

*Stenocercus prionotus* differs from *S. scapularis* (characteristics in parentheses) in lacking squarish or rectangular projecting superciliary scales (present) and in having fewer than 50 midbody dorsal scale rows (59–70 rows). *Stenocercus prionotus* differs from *S. huancabambae* (characters in parentheses) in lacking a postfemoral pocket (deep, Type 5) and in having prominent dorsolateral crests on the posterior body (weak, restricted to anterior body when present).

Two species of *Stenocercus* from western Ecuador and Peru, *S. iridescens* and *S. limitaris*, have enlarged posterior head scales and supraoculars. In contrast to *Stenocercus prionotus*, *S. iridescens* has smooth head plates, 2 canthals, a poorly developed posthumeral pocket (Type 1 or 2), and lacks keeled angulate temporals and dorsolateral crests on the body (see Cadle, 1991, fig. 10). *Stenocercus limitaris* has a deep postfemoral pocket (Type 5), 2 canthals, a single strongly keeled (but non-projecting) angulate temporal, and lacks dorsolateral crests.

Other non-Peruvian species of the "Ophryoessoides group" can be distinguished from *Stenocercus prionotus* by features in the key presented later and other superficial characters, such as the presence of 2 canthals and 4 internasals (usually) in *S. erythrogaster* (1 and 5–7 in *S. prionotus*), and enlarged, projecting pyramidal or conical postsuperciliary scales in *S. dumerilii* and *S. tricristatus* (Avila-Pires, 1995).

Other species of *Stenocercus* are distinguished from *S. prionotus* by a combination of features such as smaller head plates, smooth ventrals, and absence of dorsolateral crests. Most species of *Steno-*

*cercus* except the “*Ophryoessoides* group” have smooth or weakly keeled head plates. Other characters, such as the number of dorsal scale rows, morphology of the posthumeral and postfemoral mite pockets, extent of sexual dimorphism, and degree of differentiation of the vertebral scale row and crest also aid in distinguishing the species (see descriptions and discussion in Fritts, 1974; Cadle, 1991, 1998).

Apart from *Stenocercus fimbriatus*, *S. scapularis*, and *S. aculeatus*, two other species of *Stenocercus* are known from localities close to or sympatric with known populations of *S. prionotus*: *S. crassicaudatus* and *S. roseiventris*. These species are distinguished from *S. prionotus* by lacking prominent serrate vertebral crests (low crests may be present), having smooth ventral scales, and having prominently spinose tails with the spines arranged in distinct whorls.

## DESCRIPTION

*Head* (Fig. 4). Dorsal head scales subimbricate (a tendency to be more juxtaposed posteriorly); strongly keeled to multicarinate or wrinkled. Rostral in contact with first supralabial, first lorilabials, and a series of postrostrals. Usually 7 elongate, strongly keeled internasals between the nasals dorsally; however, the anterior dorsal head scales are very irregular and occasionally only 5 or 6 internasals are present. One canthal scale between the anterior superciliary and the lateralmost internasal, separated from the nasals by tiny postnasals. Canthus very strongly angled. Nostril in posterior portion of an elongate nasal scale, which may contact the rostral scale anteriorly or be separated from it by small postrostrals. Four or 5 strongly overlapping, elongate anterior superciliaries followed by 2 or 3 shorter posterior superciliaries slightly overlapping in the reverse direction (but more or less in a straight line). One supraocular row moderately enlarged, 2 mediocentral scales much larger than the others. Five or 6 scales across the supraocular area at its

widest part. Interparietal distinct and elongate, diamond-shaped or pentagonal (apex posteriorly). Parietal eye visible. A pair of parietals in contact behind the interparietal, flanked posterolaterally by a postparietal on each side. Postparietals separated medially by a single median transversely elongate occipital; occasionally 1 or 2 small scales are intercalated at the juncture of the parietal, postparietal, and/or occipital (e.g., Fig. 4).

Lateral temporal scales strongly keeled, imbricate to subimbricate; separated from posterior dorsal head scales on each side by 2 (occasionally 3) elongate, strongly keeled angulate temporal scales bearing a low projecting vane. Keels of adjacent angulate temporals aligned. Posterior angulate temporals separated from postparietals by 2 or 3 small scales in a longitudinal row. Anterior angulate temporals may contact postparietal and one other larger posterior head scale or be separated from them by small scales. Anterior border of ear weakly denticulated; posterior border rounded, bordered with keeled imbricate scales.

Anterior and posterior gulars strongly keeled. Mental smooth, in contact with first pair of postmentals and first pair of infralabials. Enlarged postmentals 3 or 4 on each side, only the first pair in contact medially.

*Neck and Body*. Dorsal and lateral scales of neck and body imbricate, mucronate, strongly keeled. Vertebral row produced into a prominent projecting serrate crest in adults of both sexes that is continuous from the nuchal region to the base of the tail, gradually disappearing on the anterior  $\frac{1}{4}$  to  $\frac{1}{3}$  of tail. Dorsolateral crest (a raised, strongly keeled row of scales) on posterior  $\frac{1}{3}$  of body, continuing onto base of tail. The dorsolateral crest occasionally appears very indistinctly farther anteriorly on the body, but only on the posterior body does it sharply delimit the dorsolateral (paradorsal) scales from the flank scales. Three rows of scales between dorsolateral and vertebral crests at anterior

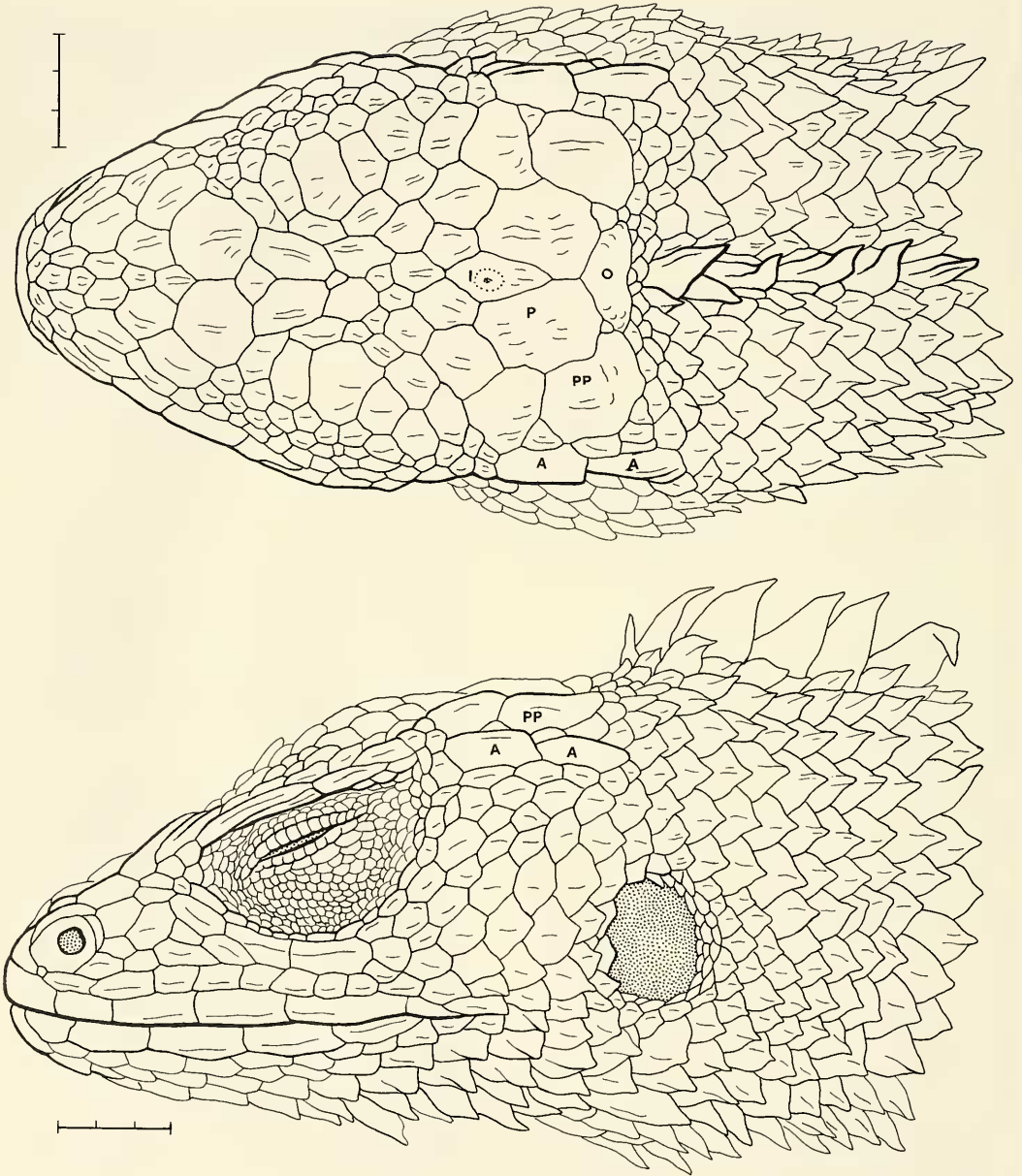


Figure 4. Head scales of the holotype of *Stenocercus prionotus* (USNM 193683) in dorsal and lateral views. Scale bars = 3 mm. To facilitate coordination with the text, the following scales are indicated on one side (interparietal and occipital are median scales): A, angulate temporal; I, interparietal; O, occipital; P, parietal; PP, postparietal.

edge of dorsolateral crest (i.e., just anterior to the pelvic region), 2 rows posteriorly (dorsal to hindlimbs); scales between the crests strongly imbricate and keeled only on posterior part of scale. Flank scales mostly fully keeled (sometimes only the posterior part of each scale), imbricate, mucronate, slightly smaller than dorsolateral scales. Ventral body scales mucronate, strongly keeled (keels running the length of the scales). Ventrals approximately the same size as the dorsolateral scales, larger than flank scales.

*Neck Folds.* Distinct neck folds absent. Poorly developed antehumeral crest present.

*Tail.* Tail strongly compressed, anteriorly bearing low projecting vertebral and dorsolateral crests continuous with those of the body. Dorsal scales moderately keeled, ventral scales strongly keeled.

*Limbs.* Dorsal and ventral scales of forelimbs, hindlimbs, and posterior thigh strongly keeled, unicarinate, mucronate; some scales of the shank larger than any thigh scales. Supradigitals and subdigitals unicarinate. Palmar scales strongly unicarinate. Plantar scales strongly unicarinate.

*Posthumeral and Postfemoral Mite Pockets.* Posthumeral mite pocket a deep cavity (Type 4) with a prominent axillary flap concealing the anteroventral aspect (Fig. 5). Postfemoral pocket absent (Type 1).

The flap associated with the posthumeral pocket projects from the anteroventral and ventral edges of the pocket. Antero-dorsally, a similar but much smaller flap is present in some specimens (e.g., Fig. 5). The posthumeral flap consists of a fleshy ridge covered anteriorly and posteriorly (or externally and internally when the flap is lying flat against the body) by keeled imbricate scales. Externally, usually 3 or 4 larger scales cover the flap ventrally and a series of much smaller scales is present dorsally. One or 2 of the larger scales are sometimes highlighted with white. When appressed against the body (i.e., against

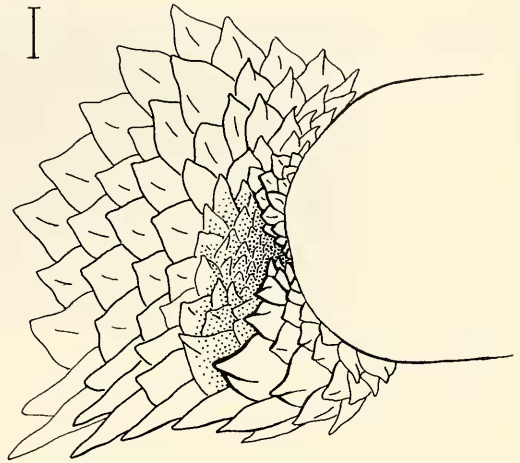


Figure 5. Posthumeral (axillary) flap of *Stenocercus prionotus* (USNM 193683, holotype). Anterior to the right. The broad oval on the right is the deflected forelimb and the posthumeral mite pocket is the heavily stippled cavity deep to the flap. The posterior border of the axillary flap is marked by the scales with heavily outlined posterior borders and it extends anteriorly to the ventral part of the forelimb. A smaller dorsal flap is also present in this specimen (small patch of heavily outlined scales on anterodorsal edge of the pocket; see text). Scale bar = 1 mm.

the opening of the posthumeral pocket) the flap conceals approximately the ventral  $\frac{1}{3}$  to  $\frac{1}{2}$  of the vertical dimension of the pocket. The flap is equally prominent in adults of both sexes and is proportionally as well developed in subadults (including hatchlings) as in adults.

*Size and Proportions.* Largest male (USNM 193683) 89 mm SVL, 323 mm total length (sample size of males with SVL  $\geq 70$  mm = 13). Largest female (KU 212629) 93 mm SVL, 329 mm total length (sample size of females with SVL  $\geq 70$  mm = 16). Tail relatively long, 69–74% of total length in adults (67–71% in juveniles).

*Coloration and Pattern of Adult Males in Life.* The following color descriptions are paraphrased from the field notes of Wade C. Sherbrooke. USNM 193683 (holotype):

Lower half of side between limbs is lavender-brown. This color extends from both sides across the belly approximately  $\frac{1}{3}$  of the way on each side, leaving a tan-brown central strip down the belly. General base color of the body is brown, darkest

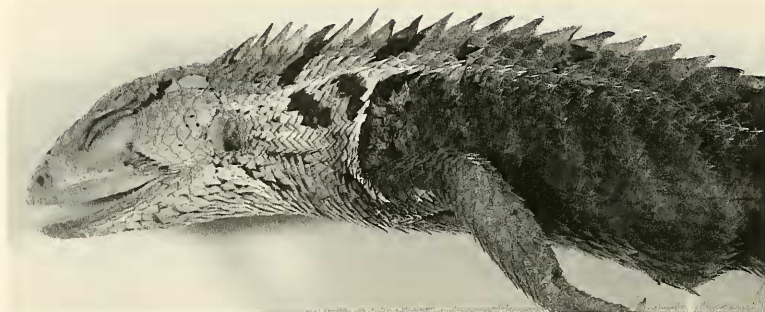


Figure 6. Lateral view of *Stenocercus prionotus* from northern Peru (USNM 193685; male, snout-vent length 76 mm). Note the high vertebral crest and the following pattern elements: dark subocular bar, dark blotches on the dorsal and lateral surfaces of the neck, pale antehumeral bar, indistinct pale dorsolateral stripe, and indistinct oblique bars on the trunk.

near the hind legs and tan just in front of the forelegs. A distinct white line runs dorsally from the top of each foreleg to three quarters of the way to the dorsal crest; it runs through a large black patch just above the forelimb. Head markings consist of a dark brown line running between the eyes on the top of the head; this continues through the eye to broaden slightly at the rear portion of the jaw. The gular area is streaked by several light cream lines. Very slight lavender tinge to all of body behind forelimbs. [Sketch in notes shows black middorsal patches that don't extend to flanks].

USNM 193685 (WCS 2543):

This specimen closely resembles [USNM 193683] in color, with one exception. There are several green spots on . . . the right dorsal surface between the limbs and on the dorsal portions of the tail behind the hind limbs and the dorsal tibio-fibula portion of the right hind leg.

*Coloration of Adult Females in Life.* Unknown.

*Coloration in Preservative (Figs. 3, 6, 7).* Specimens of *Stenocercus prionotus* vary greatly in coloration due mainly to variation in initial preservation and the length of time in preservative. Poorly preserved specimens may be more or less uniform brown all over, although obscure pattern elements are usually present. Well preserved specimens are brown dorsally with darker brown to blackish chevrons mid-dorsally. One chevron dorsal to each pair of limbs and one on the neck are usually evident, and these are darker than others that may be present. Three to five mid-dorsal chevrons are between the limbs.

Dark spots or an additional chevron are often present on the dorsal neck and usually on the base of the tail. The light antehumeral/humeral line is universally present and evidence of the dark shoulder patch is usually present (often very prominent). Flanks usually unicolor and somewhat darker than the dorsum between the dorsolateral crests; however, some specimens (e.g., KU 179058, USNM 280246) have distinct dirty white vertical bars or chevrons on the flanks (five between the limbs), and such bars appear occasionally, but more obscurely in other specimens (see Fig. 6). The dorsolateral crest is often highlighted for a variable length with a distinct or indistinct light line, giving the impression of a light dorsolateral stripe. Forelimbs more or less unicolor brown or with obscure pattern; hindlimbs brown with darker brown bands. Dark subocular bar distinct. Top of head often with an obscure or distinct dark brown interocular bar. Oblique bars on throat (Fig. 7) often visible but throat may be unicolor or have an obscure pattern. Venter of most specimens unicolor, dirty white, gray, or beige; however, some specimens (e.g., USNM 280246) have a series of irregular longitudinal dark brown streaks.

*Scale Counts and Qualitative Features (Table 1).* *Stenocercus prionotus* has relatively low midbody, vertebral, and gular scale counts. The scales are relatively large and strongly keeled over most of the body.

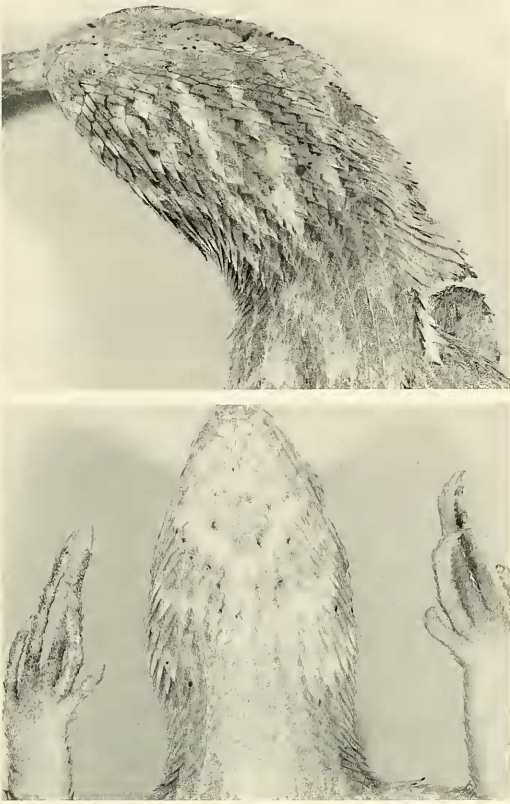


Figure 7. Gular patterns in *Stenocercus prionotus*. Top, typical throat pattern (oblique view) consisting of light and dark stripes that extend medially to the midline (USNM 193687). Bottom, specimen in which the ground color is lighter and therefore the contrasting pale stripes are less distinct (USNM 193685).

*Sexual Dimorphism.* *Stenocercus prionotus* does not exhibit strong sexual dimorphism. Males and females attain approximately the same size and have the same general pattern, but whether the coloration in life reported above for adult males pertains to females as well is unknown. The vertebral crest is only slightly more developed in males than in females of the same population but this character shows strong clinal variation (northern populations with higher crests; further discussed below). Other characters that sometimes vary between the sexes in *Stenocercus* show little variation in *S. prionotus*. Nei-

ther standard meristic counts (Table 1) nor the relative development of the posthumeral and postfemoral pockets (Types 4 and 1, respectively, in adults of both sexes and in subadults) show obvious sexual dimorphism.

#### DISTRIBUTION PATTERNS IN *STENOCERCUS PRIONOTUS*

*Absence of Stenocercus prionotus from Lowland Localities in Eastern Peru.* *Stenocercus prionotus* is widespread in the lowlands along the Andean front from northern Peru to northern Bolivia (Fig. 1). However, all Peruvian localities are close to the Andean foothills and south of the broad extension of the Cordillera Oriental separating the great bend of the Río Marañón from upper reaches of the Río Huallaga (Fig. 2). The absence of specimens in comprehensive collections from the Iquitos region (Dixon and Soini, 1986), Balta (Ucayali Department; specimens at LSUMNS and University of Arizona), and Cuzco Amazonico (Madre de Dios Department; Duellman and Salas, 1991) suggest that *S. prionotus* may be absent from the lowlands distant from the Andean foothills, at least in Peru. Similarly, collections from northern Loreto Department (Duellman and Mendelson, 1995) and northern Amazonas Department (J. E. Cadle and R. W. McDiarmid, unpublished data from the Río Cenepa and Río Santiago) suggest that *S. prionotus* does not occur north of the Río Marañón.

However, these sites have been sampled unevenly. For example, species accumulation curves for lizards at Cuzco Amazonico (Duellman and Koechlin, 1991) reached an asymptote after about 15 person-weeks of effort, whereas only 5 person-weeks were expended in northern Loreto and the species accumulation curve for the total herpetofauna showed no asymptote (Duellman and Mendelson, 1995; data not presented for lizards only). Quantitative data are not available for the other sites, but large collections are available for the Iquitos region, including more than 1,000

TABLE 2. PATTERNS OF PRESUMED SYMPATRY OF *STENOCERCUS* IN EASTERN PERU. ONLY SPECIES OF THE "OPHRYOESSOIDES GROUP" AND THE SUPERFICIALLY SIMILAR SPECIES, *S. ROSEIVENTRIS*, ARE LISTED.<sup>1</sup> LOCALITIES ARE LISTED ROUGHLY NORTH TO SOUTH; FOR PRECISE LOCALITIES SEE THE APPENDIX AND LOCALITIES FOR THE TYPE SERIES OF *S. PRIONOTUS*.

	Iquitos Region	San Martin/W. Loreto <sup>2</sup>	Pampa Hermosa	Río Mishollo	Tingo Maña	Manu <sup>3</sup>	Balta	Cuzco Amazonico	Explorer's Inn
<i>S. prionotus</i>		×	×		×	×			×
<i>S. aculeatus</i>		×		×					
<i>S. fimbriatus</i>	×		×	×	×	×	×		
<i>S. roseiventris</i>	×					×		×	×

<sup>1</sup>The only other species of *Stenocercus* known from primarily the lowlands and lower Andean foothills in this region is *S. crassicaudatus*, which lacks a projecting vertebral crest and has a very spiny tail.

<sup>2</sup>The distributions of *S. prionotus* and *S. aculeatus* overlap both altitudinally and latitudinally in northern Peru but they have not been taken together at the same locality. See Figure 2 for localities.

<sup>3</sup>In Manu National Park, *S. fimbriatus* and *S. roseiventris* are sympatric at Pakitza, whereas *S. prionotus* is known only from Cocha Cashu.

lizards obtained by Dixon and Soini (1986) and additional collections from the region made by Harvey Bassler and deposited in the AMNH. Similarly large collections resulted from the efforts of Cadle and McDiarmid in Amazonas (specimens in the MVZ and USNM). Thus, barring artifacts introduced by the difficulties of collecting cryptic rainforest lizards, *S. prionotus* seems to be absent from these sites.

Documenting and explaining patterns of absence is always difficult, but the apparent absence of *Stenocercus prionotus* from the lowlands distant from the Andes in Peru is not due to failure to collect *Stenocercus* at these localities because at least one other species of *Stenocercus* is known from each (Table 2). However, no lowland locality is known in which more than two species of the "Ophryoessoides group" of *Stenocercus* are sympatric. Of interest in this connection is that *S. prionotus* has not been taken in the upper reaches of the Río Perene and its tributaries (Junín Department), although it is known from north and south of that region. Numerous specimens of *Stenocercus* of at least five species (*S. boettgeri*, *S. crassicaudatus*, *S. formosus*, *S. scapularis*, and *S. variabilis*<sup>4</sup>)

have been collected along an elevational

tribing these specimens to "Palca, Bolivia" rather than Palca (Junín Department), Peru. One specimen I collected near Palca, Peru (MCZ 178166) is nearly identical with BMNH 1946.8.11.91 in scale counts, pattern, and qualitative characters (both of these specimens differ considerably from BMNH 1946.8.11.89 in color pattern). However, the attribution of the specimens to Peru is not without some equivocation. The types were collected by P. O. Simons (see Cadle, 1998: footnote 6), who collected in the vicinity of Palca, Peru, in March and April, 1900, although that specific locality is not listed in his published itinerary (Chubb, 1919). However, Simons's itinerary places him at "Palca, 18 miles E of La Paz" [Bolivia] on 9 November 1900 (Chubb, 1919: 5). Simons's field tags attached to the syntypes record simply "Palca 3000 m," which is close to the elevation of Palca, Peru (2,740 m), but not that in Bolivia (4,600 m). Adding to the confusion are entries in the BMNH registries for the syntypes, concerning which Colin J. McCarthy provided the following comments via e-mail:

Boulenger originally wrote "Palca Peru 3000m" but later struck through Peru and wrote "Bolivia." There are two sheets of notes (presumably from Simons) stuck in at this page of the register about the localities in the batch. With regard to Palca he has written "Palca, just S. of La Paz, Bolivia." I assume it was that information that caused Boulenger to alter his original entry!

Thus, the confusion may have originated with the note that Simons provided subsequent to cataloguing of the collection at the BMNH. In any case, no specimens resembling *S. variabilis* are definitely known from Bolivia and the only species of the genus definitely known to occur above 4,000 m is *Stenocercus chrysopygus* from northern Peru.

<sup>4</sup>Based on examination of two of the three syntypes of *Stenocercus variabilis* Boulenger (BMNH 1946.8.11.89, 1946.8.11.91) I concur with Fritts (1974: 66) that Boulenger (1901: 553) erred in as-



transect along this well-traveled route (Fritts, 1974; Cadle, 1991 and unpublished data). Thus, analysis of circumstantial distributional data suggests that the distribution of *S. prionotus* in the lowlands of eastern Peru may be influenced by the number of sympatric species of *Stenocercus*. At all localities from which *S. prionotus* has been taken, only one other species of *Stenocercus* is known (Table 2). These patterns of sympatry are discussed in the next section with reference to patterns of geographic variation in *S. prionotus*.

In contrast, the apparent restriction of *Stenocercus prionotus* to the Andean foothills and immediately adjacent lowlands in Peru does not seem related to the distribution of any major habitat type or physiographic region. Most of the extensively sampled localities (e.g., Iquitos and Cuzco Amazonico) include a variety of lowland habitats characteristic of western Amazonia. *Stenocercus prionotus* is known from both floodplain forests (Cocha Cashu) and more upland forests on river terraces in southeastern Peru (Explorer's Inn); Foster (1990) and Dallmeier et al. (1996) described these floristic communities in southeastern Peru. Thus, the apparent absence of *S. prionotus* at the localities discussed above is not due to some simple relation to local habitat availability. For example, it is unclear why *S. prionotus* was not obtained at Pakitza (Morales and McDiarmid, 1996), even though it occurs at nearby Cocha Cashu. On a broader geographic scale, the restriction of *S. prionotus* to lowlands and foothills adjacent to the Andes may be related to the present or historical influence of the Andes on the climate and vegetation (rainfall, temperature, and major soil types) of neighboring regions.

A curious and unexplained hiatus in the distribution of *Stenocercus prionotus* occurs between the vicinity of Tingo Maria-Río Lullapichis (Huánuco Department) and Cocha Cashu in Manu National Park (Madre de Dios Department), a gap of some 600 km that includes the entire up-

per reaches of the Río Ucayali-Urubamba-Ene system. Additionally, populations north and south of this gap differ in some qualitative and quantitative characters (see *Patterns of Sympatry and Geographic Variation in Stenocercus prionotus, and the Need for Additional Fieldwork*). Scattered collections (e.g., maps in Fritts, 1974; Avila-Pires, 1995), but no comprehensive herpetofaunal surveys or collections, are available from this vast region. Thus, whether the geographic hiatus is real or a sampling artifact cannot be discerned. Efforts to resolve this issue need to be made.

*Unconfirmed Bolivian Localities for Stenocercus prionotus.* Because of the previous confusion of *Stenocercus prionotus* with *S. caducus*, specimens perhaps referable to *S. prionotus* from several localities in Bolivia are unconfirmed. Boulenger (1898) reported specimens of "*Liocephalus caducus*, Cope" in the Museo Civico Storia Naturale Giacomo Doria in Genoa collected by Luigi Balzan from four localities (Balzan, 1931). I have not attempted to verify the existence of these specimens. However, one of Balzan's specimens from "Barraca, Rio Madidi" was exchanged to the BMNH (now BMNH 98.6.94), and is confirmed as *S. prionotus*. The "*Liocephalus caducus*" specimens from the other three Balzan localities are outside the known distribution of *S. caducus* but are close to other known localities for *S. prionotus* in northern Bolivia (Fig. 1). I suspect these are *S. prionotus* based on geographic location. The localities are, as listed by Boulenger (1898) (see Fig. 1), (1) "Coroico and Chulumani, Prov. Yungas, 1,600 metres alt." [La Paz Department; Coroico, 1,725 m, 16°10'S, 67°44'W; Chulumani, 1,905 m, 16°24'S, 67°31'W]. (2) "Reyes, right bank of Rio Beni" [El Beni Department, 232 m; 14°19'S, 67°23'W]. (3) "Misiones [sic] Mosetenes" [approximately 15°31'S, 67°25'W].<sup>5</sup> These

<sup>5</sup> The Moseten Indians inhabited upper reaches of the Río Beni and its tributaries in the Andean foothills of the present department of La Paz (Métraux,

localities would not be unusual for *S. prionotus*, although the first two localities are the highest elevations recorded for the species (the species occurs at 1500 m in nearby Puno Department, Peru). All are in the upper reaches of the Río Beni, whereas the two confirmed Bolivian localities for *S. prionotus* are farther north in the same drainage.

Burt and Burt (1931: 273) listed two specimens of "*Leiocephalus* [= *Stenocercus*] *scapularis*" (AMNH 22450, 22532) from Rurrenabaque, Bolivia [El Beni Department; 14°28'S, 67°34'W]. These were reidentified in 1971 by Thomas H. Fritts as *Stenocercus caducus* but they are presently missing from the AMNH collection (Linda Ford, in litt., February 1999). Rurrenabaque is very close to Balzan's locality (2) above. Based solely on presumed habitats and presently known distributions of *S. prionotus* and *S. caducus* in eastern Bolivia (see text; Fig. 1), I suspect that AMNH 22450 and 22532 are most likely *S. prionotus*. They should be reexamined if they are ever located. As an outside possibility, any of the unverified specimens from these Bolivian localities could represent *S. fimbriatus*, which is now known from southern Peru (Appendix).

#### PATTERNS OF SYMPATRY AND GEOGRAPHIC VARIATION IN *STENOCERCUS PRIONOTUS*, AND THE NEED FOR ADDITIONAL FIELDWORK

*Stenocercus prionotus* varies geographically in several characters, most notably in the height of the vertebral crest. Because

of the potential role of the crest in either intra- or interspecific communication it seems appropriate to discuss patterns of geographic variation in *S. prionotus* in the context of the distribution of other species of the "*Ophryoessoides* group." In this regard, patterns of sympatry among species of this group in Peru and Bolivia are especially relevant.

*Patterns of Sympatry of Species in the "Ophryoessoides Group."* The most complex distributional patterns for the "*Ophryoessoides* group" are in northern and central Peru, where six species occur (*Stenocercus aculeatus*, *S. fimbriatus*, *S. prionotus*, *S. huancabambae*, *S. scapularis*, and an undescribed species; Fig. 2). In contrast to the other species, *S. huancabambae* and the undescribed species occur in comparatively dry deciduous forests west of the known distributions for the other species. Their distributions probably do not overlap the other species and they will not be considered further here. Based on known latitudinal and elevational distributions, three species (*S. aculeatus*, *S. fimbriatus*, and *S. prionotus*) are probably broadly sympatric in northern Peru, although sympatry is documented only for pairs of these at three localities (Fig. 2; Table 2). The habitat preferences of the species in the region of sympatry are unknown.

Whether *Stenocercus scapularis* is sympatric with *S. prionotus* is less clear. *Stenocercus scapularis* is known from two widely separated areas in Huánuco and Puno departments (Peru) (Fig. 1; Appendix), and it seems to be elevationally parapatric to *S. prionotus* in northern Peru (Huánuco Department). In this area, *S. scapularis* occurs above 1,000 m and *S. prionotus* is not known above 700 m. In Puno Department, *S. prionotus* is known from a series obtained by Hilda Heller at San Juan del Oro (1,520 m elevation), which elevationally overlaps the distribution of *S. scapularis* in the same region (1,000–1,830 m). However, these two species have not been taken at the same lo-

1942). According to Métraux (1942: 15), by the end of the 19th century when Balzan collected his specimens the decimated population of the Mosetenes was concentrated in the three "Misiones Mosetenes" of San Miguel de Muchanes (15°14'S, 67°39'W), Santa Ana (15°31'S, 67°30'W), and Covendo (15°49'S, 67°06'W). The approximate coordinates given in the text are the average for these three sites. According to several maps with elevational contours indicated, Muchanes and Covendo are between 500 and 1,000 m and Santa Ana is less than 500 m in elevation. Mathews (1879) also discusses these missions.

cality in southern Peru. Interestingly, although the largest series of *S. prionotus* available from a single locality (San Juan del Oro) is in the elevational range of *S. scapularis*, no specimens of that species were obtained by Heller during a month-long stay at the site.

In southern Peru and Bolivia, *Stenocercus prionotus* is not known to be sympatric with other members of the "*Ophryoessoides* group." However, based on the occurrence of *S. prionotus* and *S. fimbriatus* at two nearby localities within Manu National Park (Cocha Cashu and Pakitza,<sup>6</sup> respectively), sympatry for these two species is expected along the Andean front in this region. In southern Peru and Bolivia, *S. prionotus* is also broadly sympatric with *S. roseiventris*, a large terrestrial species that is superficially similar to species of the "*Ophryoessoides* group." However, these species have been taken together at only one locality, Explorer's Inn.

To summarize these patterns of sympatry, the distributions of three species of the "*Ophryoessoides* group" overlap broadly in northern Peru. *Stenocercus prionotus* is known to be sympatric with at least one other species of the group in Huánuco and Loreto departments. No species of the "*Ophryoessoides* group" are known to be sympatric in southern Peru and Bolivia.

*Geographic Variation.* Geographic variation pertains to both quantitative and qualitative characters in *Stenocercus prionotus*. Specimens from the northern part of the range have higher average counts of midbody scales than southern specimens, which is shown graphically in Figure 8. However, there is broad overlap in the counts from opposite ends of the range. A reverse trend (lower counts in the north), occurs in the number of vertebral (dorsal crest) scales (Fig. 9); this reflects the reduced prominence, and hence small-

er scales, of the crest in southern populations. None of these differences in scale counts is statistically significant.

The height of the vertebral crest shows strong clinal variation in *Stenocercus prionotus*. Populations from northern and central Peru have higher crests than those from southern Peru and Bolivia (Fig. 10). However, the absence of specimens between Huánuco Department in central Peru and Manu National Park (Madre de Dios Department) in southern Peru (Fig. 1) makes it impossible to analyze this trend in detail. Specimens from the former region have a high crest typical of all specimens from that area and farther north, whereas specimens from Madre de Dios Department and farther south have distinctly lower crests. The crest is not strongly sexually dimorphic in either region.

Whether the transition in crest height is abrupt or gradual between central and southern Peru is unclear. Indeed, it is unclear whether intervening populations of *Stenocercus prionotus* exist. Both patterns of clinal variation have been extensively documented empirically and theoretically for many organisms (Éndler, 1977). The pattern of geographic variation in *S. prionotus* could conform to any of several in Endler's (1977: 4) classification scheme. However, present knowledge of distributions and character variation is most similar to Endler's "differentiated disjunction" pattern, wherein disjunct populations of a species diverge in one or more characters. Further speculation is not fruitful in the absence of more extensive collections from the region of disjunction in eastern Peru.

*A Hypothesis of Causation for Geographic Differentiation in the Vertebral Crest of Stenocercus prionotus.* Variation in the height of the vertebral crest is a prominent distinction between northern and southern populations of *Stenocercus prionotus*. This variation calls for an explanation while at the same time recognizing that, in the absence of experimental or field studies, ascribing causation to pat-

<sup>6</sup> The record of *Stenocercus fimbriatus* from Pakitza (Appendix) extends the known range for this species south by approximately 200 km from Balta in Ucayali Department, Peru (Avila-Pires, 1995).



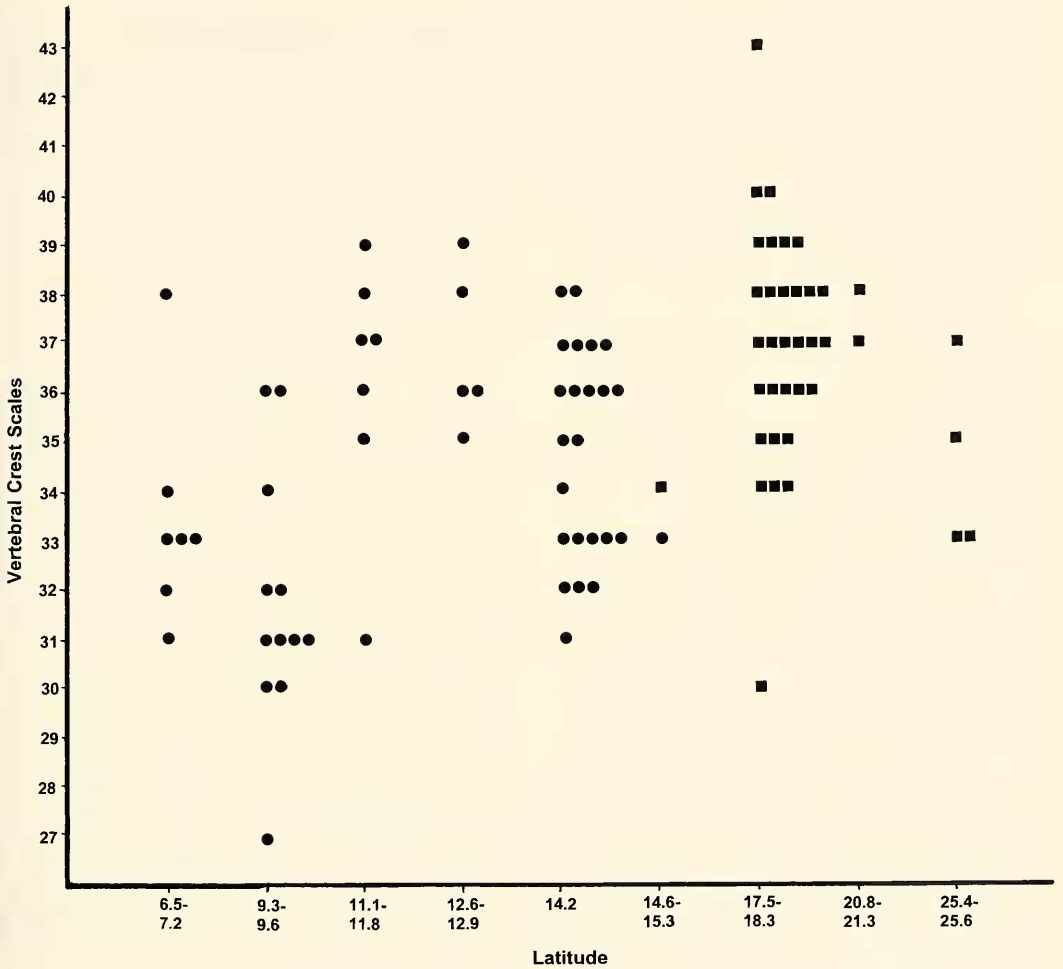


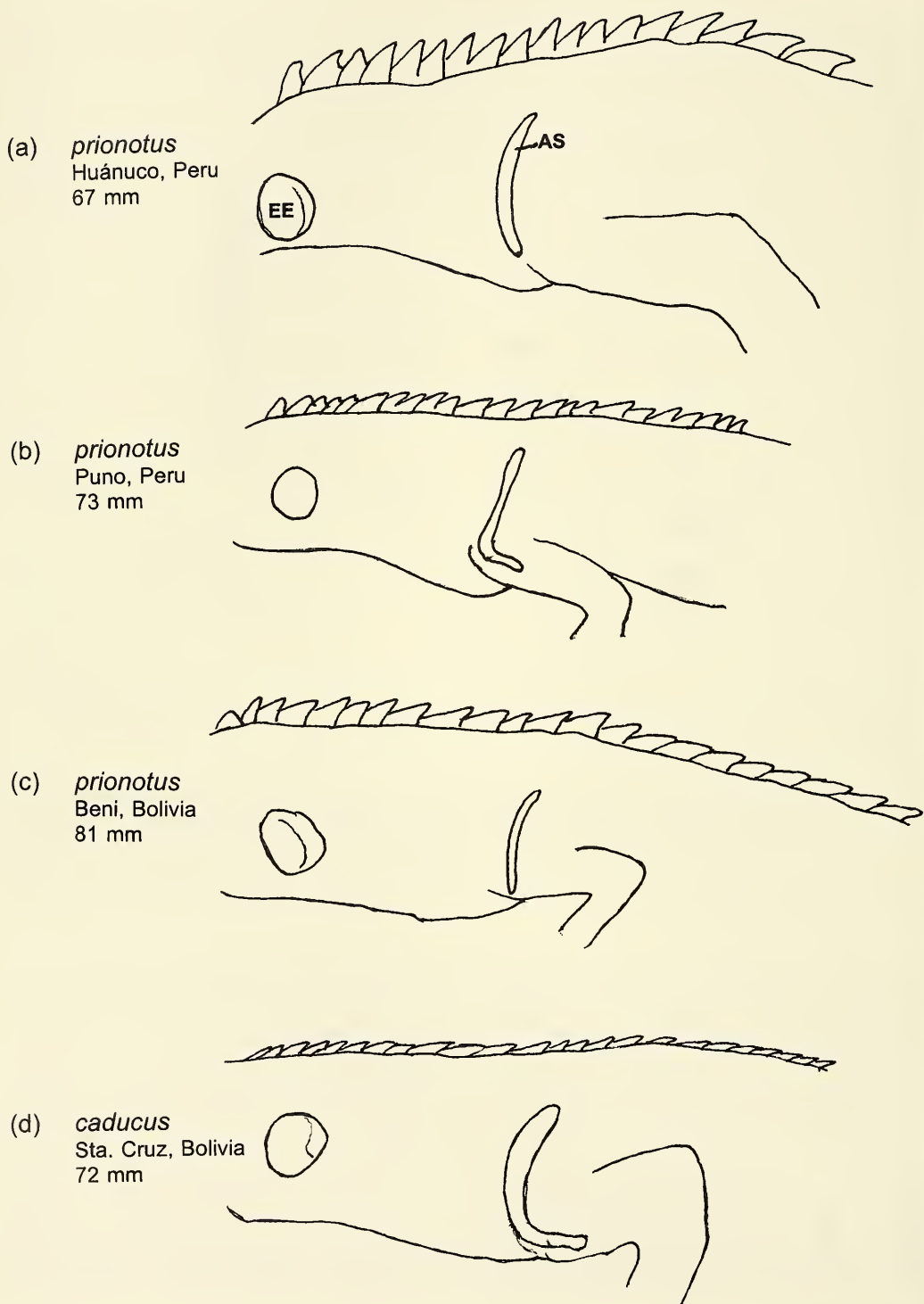
Figure 9. Geographic variation in the number of vertebral crest scales in *Stenocercus prionotus* and *S. caducus*. Symbols and axes are the same as Figure 8.

contrast, in southern Peru and northern Bolivia the distribution of *S. prionotus* overlaps only *S. scapularis* and (perhaps) *S. fimbriatus* of the “*Ophryoessoides* group,” but *S. prionotus* is not known to be sympatric with either of these species.<sup>7</sup>

<sup>7</sup> The only case of sympatry of any of these with other species of *Stenocercus* of which I am aware involves *S. prionotus* and *S. roseiventris* at Explorer's Inn (cf. Table 2), but *S. roseiventris* is phenotypically dissimilar to species of the “*Ophryoessoides* group” in having shorter limbs, different color pattern, spiny tail, and different body form.

The vertebral crest of *S. prionotus* in southern Peru and northern Bolivia is similar in development to that in allopatric populations of *S. aculeatus*.

I conjecture that the strongly developed vertebral crests of *Stenocercus prionotus* in northern Peru may be related to the presence of multiple sympatric congeners in that part of the range, and that the crest functions as a species recognition character. If true, this explanation for variation in crest height would have no precedent among lizards. The only analogous situa-



tion seems to be dewlaps in *Anolis*, in which species recognition has been postulated as a biological role for dewlap color and size in complex assemblages of these lizards (Williams and Rand, 1977; Losos and Chu, 1998).

*The Need for Additional Fieldwork.* Only field observations and experimental studies of the function of the vertebral crest in *Stenocercus prionotus* can determine whether the functional hypothesis advanced here is correct. Ideally, parallel studies should be conducted in the area of sympatry with other species of the "Ophryoessoides group," as well as in the area with no known sympatric species of that group. That design would permit an evaluation of any context-dependent use of the crest in these populations. Two sympatric species are known from the vicinity of Tingo Maria (Huánuco Department; Table 2), a very accessible area for study.

Two other reasons for additional comprehensive fieldwork on these species are indicated. First, we need documentation of the extent to which species of the "Ophryoessoides group" are sympatric or syntopic. Particular targets should be the northern part of the range of *Stenocercus prionotus*, where *S. aculeatus* and *S. fimbriatus* are known to have overlapping ranges; and Manu National Park in southern Peru, a reasonably accessible area where *S. fimbriatus* and *S. prionotus* are known to be closely allopatric (but not sympatric) on a microgeographic scale (Table 2). Second, the character differences between the northern populations of *S. prionotus* and those of southern Peru and Bolivia could indicate that two or more species reside within my concept of this species. Fieldwork concentrated in the

geographic gap between Tingo Maria and vicinity (Huánuco Department) and Cocha Cashu (Madre de Dios department), the two most proximate localities of the northern and southern population groups, is needed to verify whether intermediate populations occur. The possibility that these might be two allopatric species separated by a broad geographic gap should not be dismissed without further evaluation.

#### NATURAL HISTORY OF *STENOCERCUS PRIONOTUS*

Few natural history observations exist for *Stenocercus prionotus*. Wade C. Sherbrooke (field notes) found the holotype running in the relatively open floor of a bamboo garden at about 1200 h. USNM 193685 was taken along a trail within rainforest. Brief notes associated with the series from Explorer's Inn (Madre de Dios Department, Peru; USNM 247468–69, 247680, 269022) indicate that specimens were obtained during the day on the ground from clearings around the lodge, although USNM 269022, an adult female (91 mm SVL), was on a leaf 40 cm above the ground. MCZ 150243 was retrieved from a mist net near the edge of tall floodplain forest at Cocha Cashu. In the dry season (September–December) of a lowland rainforest in the vicinity of Tumi Chucua (Beni Department, Bolivia), Fugler (1986: table 5) found *Stenocercus prionotus* (reported as *Ophryoessoides aculeatus*) in varzea (seasonally inundated rainforest) but not in terra firme rainforests of the area; females with enlarged eggs were found in early November (Fugler, 1986: table 4).

Hilda H. Heller provided the following

←

Figure 10. Diagrammatic representation of geographic and size-related variation in the height of the vertebral crest in *Stenocercus prionotus* and *S. caducus*. Drawings were made with a camera lucida to emphasize the form and height of the vertebral crest. Sketches are drawn to an approximately uniform interval between the external ear opening (EE) and the white antehumeral stripe (AS). For each specimen the geographic location and the SVL are given (all specimens are adult males): (a) MCZ 43759, (b) FMNH 64799, (c) USNM 280250, (d) CM 970. Note especially the differences between the northern specimen of *S. prionotus* (a) compared to southern ones (b and c), especially given the size differences among these; and the differences between size-matched specimens of *S. prionotus* and *S. caducus* (b and d).

notes on the San Juan [del Oro] locality from which she obtained a series of *Stenocercus prionotus* in the early 1950s (K. P. Schmidt archives, FMNH):

Steep forest with deep undergrowth. Steep fields. Rainfall probably somewhat greater than at Pampa Grande,<sup>8</sup> due to its colder climate and steep exposure; I have no figures. Brushy second growth may be burned in fairly wide patches in August, and [the] resort is frequently made to burning, indicating a moderately dry winter period.

As of the mid-1980s very little undisturbed forest was left in the vicinity of San Juan del Oro (personal observations). Although Heller provided detailed notes on some of the snakes and frogs from her collection, she makes no specific comments about the lizards.

Most observations suggest that *Stenocercus prionotus* prefers open habitats, such as areas of human disturbance and light gaps within forests (e.g., created by trails), rather than deep rainforests. Alternatively, the observations may simply indicate the ease of observation and capture in more open habitats. A combination of cryptic coloration and escape behavior (rapid flight followed by immobility) possibly makes *S. prionotus* very difficult to observe in closed-canopy rainforest, as reported for the similar species, *S. fimbriatus* (Dixon and Soini, 1986; Avila-Pires, 1995) and *S. caducus* (Scrocchi et al., 1985).<sup>9</sup> However, we currently lack observations to support these statements for *S. prionotus*.

#### COMPARISON OF *STENOCERCUS PRIONOTUS* WITH *S. CADUCUS*

A scaly flap associated with the posthumeral pockets is a unique and unquestionably derived character shared by *Stenocercus prionotus* and *S. caducus*, which suggests that these are sister species (Figs. 5,

11).<sup>10</sup> I am unaware of a similar structure in any other lizards. Some individual variation in the precise form and size of the flap occurs in both species but it seems extremely improbable that these structures are not homologous in the two species.

Moreover, *Stenocercus prionotus* and *S. caducus* are similar in standard meristic characters (Table 1; Figs. 8, 9), and the similarity among Bolivian populations of both species has caused confusion about the identity of particular populations (see citations in the synonymy of *S. prionotus*). Geographic, ontogenetic, or individual variation of some characters within both species, especially the height of the vertebral crest and the number of midbody scale rows (Fig. 8), further clouds the distinctions between them. Differentiating the northern populations of *S. prionotus* from *S. caducus* is unequivocal and facile based solely on the size of the vertebral crest and on associated meristic counts. However, specimens of *S. prionotus* from southern Peru and northern Bolivia are more difficult to distinguish from *S. caducus*. For example, animals from populations of *S. prionotus* in southern Peru and Bolivia have less prominent vertebral crests (hence, higher vertebral scale counts), and generally lower numbers of midbody scale rows, than do specimens from northern populations (Figs. 8, 9); in these respects they are more similar to *S. caducus*. Nevertheless, even accounting for these difficulties, a combination of three qualitative characters is sufficient to distinguish *S. prionotus* from *S. caducus*, and the species

<sup>8</sup> I have been unable to localize Pampa Grande.

<sup>9</sup> Cei (1993) claimed that *Stenocercus caducus* was arboreal, but Scrocchi et al. (1985) reported the behavior of this species in more detail and stated that it was terrestrial.

<sup>10</sup> In my comparisons I have emphasized Bolivian specimens referred to *Stenocercus caducus*, whereas the type locality is "Paraguay." I have not fully convinced myself that specimens referred to this species from Bolivia, Paraguay, and Argentina are, in fact, all the same taxon. Considerable variation exists in some aspects of coloration and scale characters in these specimens. However, my concept of *S. caducus* corresponds to that used in current literature (e.g., Gallardo, 1959; Scrocchi et al., 1985; Cei, 1993). Only a thorough study of *S. caducus* across its range will resolve this issue.



may differ in patterns of sexual size dimorphism.<sup>11</sup>

*The Form of the Vertebral Crest.* Despite geographic variation in the prominence of the vertebral crest, males and females of *Stenocercus prionotus* have a distinctly projecting serrate vertebral crest extending from the nuchal region to the anterior portion of the tail (Figs. 6, 10, 12). The scales of the crest are strongly triangular in lateral view, are flaplike (i.e., they bend easily), project vertically from the dorsum, and are strongly differentiated from the adjacent dorsal scales. Although the crest is somewhat less developed in females, it is prominent in both sexes. Specimens from northern Bolivia and southern Peru have a substantially lower crest than specimens from central and northern Peru (Fig. 10). Nonetheless, the form and projection angle of the crest scales is the same as in the northern populations.

In contrast, the scales of the vertebral crest in *Stenocercus caducus* are only moderately differentiated from adjacent dorsal scales in being more strongly keeled and mucronate. The crest in *S. caducus* is only slightly projecting in males (Fig. 10) and even less so in females (Fig. 12); the crest is mainly apparent on the neck and anterior body. In *S. caducus*, the scales of the crest are stiff and prismatic, and the main axis of projection is posterior rather than vertical, as in *S. prionotus*.

Crest height in *Stenocercus* varies positively with size and thus it is critical to compare similar-sized specimens when documenting differences among population samples or species. This realization has been critical to differentiating *Stenocercus prionotus* from *S. caducus* in south-

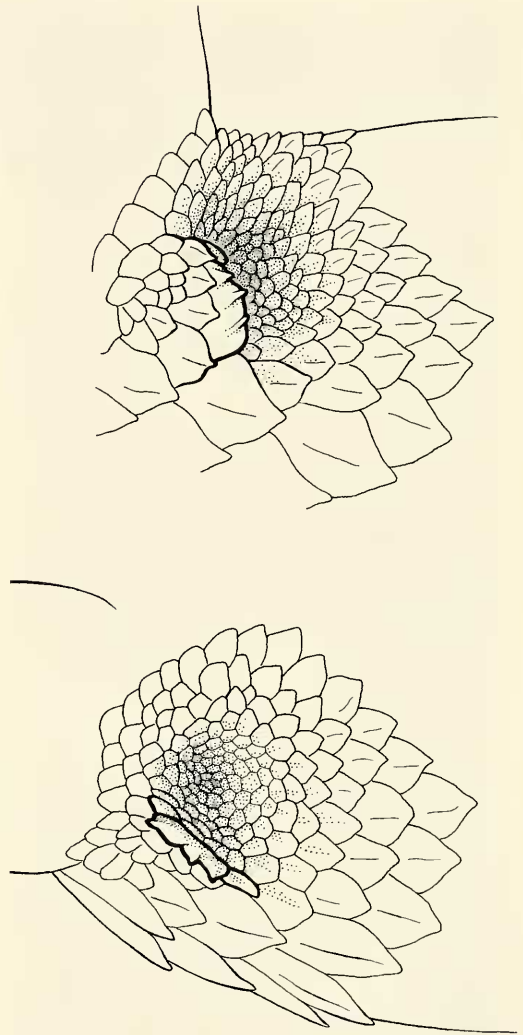


Figure 11. Axillary region of *Stenocercus caducus* showing the posthumeral flap (MCZ 34215). Anterior to the left. The posthumeral flap comprises the heavily outlined scales posteroventral to the forelimb. The opening of the posthumeral pocket is the heavily stippled area deep to the flap. Top, Posthumeral flap in its normal orientation covering the anteroventral portion of the pocket. Bottom, the flap deflected ventrally, with its posterior scales viewed from their tips. Approximately  $\times 8.5$ .

<sup>11</sup> I am uncertain how Fugler (1983, 1986, 1989) distinguished Bolivian specimens he referred to *Stenocercus aculeatus* and *S. caducus*. In 1983 and 1986 he referred specimens from Tumi Chucua (Beni, Bolivia) to *S. aculeatus*. In 1989 he listed these again, along with ROM specimens from San Marcos Ranch (Beni, Bolivia) identified as *S. caducus*. Fugler specimens from these localities that I have examined are all *S. prionotus* (see list of paratypes).

ern Peru and Bolivia. Large adult males of *S. prionotus* from southern populations are scarce in collections. For example, although only 18 specimens of *S. prionotus* are available from northern Peru, one half of these are males with SVL  $\geq 60$  mm. In

contrast, twice as many specimens each of *S. prionotus* and *S. caducus* are available from southern Peru and Bolivia. Yet, only one third of the available specimens of either species from these areas are males  $\geq 60$  mm SVL, and no males of *S. caducus* were  $>72$  mm SVL.

Figure 10 shows differences in the height of the vertebral crest in a series of males of *Stenocercus prionotus* from southern Peru and Bolivia compared with similar-sized specimens of *S. prionotus* from northern Peru and with *S. caducus* (the largest males of *S. caducus* studied were 72 mm SVL; see also Fig. 6). The trend toward lower crests in *S. prionotus* from the southern part of its range is evident, as is the difference between *S. caducus* and *S. prionotus*. A comparison of all specimens suggests that the difference in the height of the vertebral crest between *S. prionotus* and *S. caducus* males begins to be apparent by approximately 65 mm SVL and becomes pronounced at around 70–75 mm SVL. No males of *S. caducus*  $>72$  mm SVL were among the specimens examined, despite the availability of a large number of specimens from southern Bolivia, including a series of 31 specimens (10 males  $\geq 60$  mm SVL) from the vicinity of Santa Cruz. A similar contrast in crest height appears in females of the two species (Fig. 12).

*Angulate Temporal Scales.* *Stenocercus prionotus* has two (occasionally three) very strongly keeled, projecting angulate temporal scales on each side (Fig. 4). These are much larger than adjacent scales on the head and they are partially or completely separated from the large posterior head scales (parietals, postparietals, and occipital) by one row of small keeled scales (occasionally partially doubled). *Stenocercus caducus* usually has two (occasionally three) angulate temporals that are smaller and less projecting than those in *S. prionotus*. In *S. caducus* the angulate temporals may or may not be larger than adjacent posterior head scales and they are not

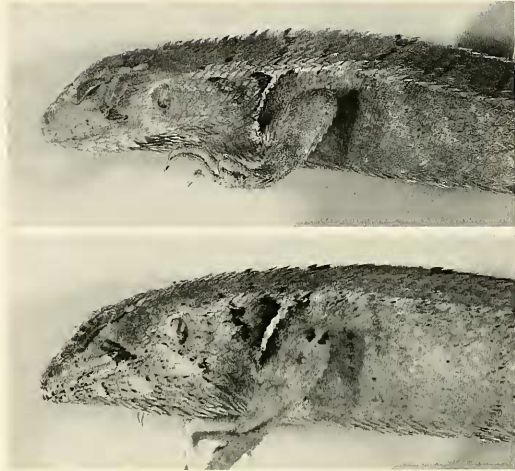


Figure 12. Size-matched females of *Stenocercus prionotus* and *S. caducus* from Bolivia. Top, *S. prionotus* (USNM 269022, snout-vent length [SVL] 91 mm). Bottom, *S. caducus* (UTA 38046, SVL 93 mm). Note the subtle difference in crest height between the two specimens and their otherwise similar patterns.

strongly differentiated from other posterior head scales.

*Color Pattern of the Gular Region.* Many specimens of *Stenocercus prionotus* have a regular pattern of alternating diagonal light and dark stripes on the throat. These usually converge closely toward the midline (Fig. 7) and are most easily visualized in preserved specimens submerged in alcohol. This pattern consists of a dark stripe beginning at a point on the lower labials in line with, but broader than, the subocular dark bar. The stripe projects posteromedially, gradually fading and blending with the ventral ground color on the neck anterior to the pectoral region. The dark stripe is bordered on either side by a distinct pale stripe. Anteriorly, this series is preceded by another dark and another pale stripe. The dark stripes are usually approximately twice as wide as the pale ones, although not always (e.g., the dark stripes are only slightly wider than the pale ones in MCZ 150243). In life the pattern may manifest itself as a series of pale stripes on a darker background (e.g., the "gular area streaked by several light

cream colored lines" in the life colors of the holotype).

The gular region appears uniform in many preserved specimens of *Stenocercus prionotus*, but I suspect this is a preservation artifact. Occasional specimens have pale spots in the pectoral region, and others are essentially unicolor and without apparent pattern (again, probably a preservation artifact).

On the other hand, the throat pattern of *Stenocercus caducus* is highly variable and irregular. When a distinctive pattern is present, it most often consists of light spots rather than alternating stripes (Fig. 13). Cope (1862) described the holotype of *S. caducus* from Paraguay as having a dark throat that was "light varied" (i.e., variegated, or spotted), and some specimens I examined have this pattern (Fig. 13). None of several color descriptions for Argentinian specimens of *S. caducus* mention stripes or spots on the throat. Scrocchi et al. (1985) described living examples as having pale spots in parallel transverse rows in the pectoral region or with pale spots on the abdomen, but did not comment on the throat pattern; Gallardo (1959) described the ventral coloration as "pale olive with some scattered pale spots; throat darker"; and Cei (1993) described the venter as "dark brownish with series of rounded pale spots, sometimes anastomosing along the length of a median line." Although no authors mention alternating light and dark stripes on the throat in *S. caducus*, UTA 38046 does have this pattern (Fig. 13). But in this specimen the stripes are confined to the lateral edges of the throat (i.e., do not closely approach the midline as in *S. prionotus*). Apart from the throat pattern, the coloration of *S. prionotus* and *S. caducus* seems to be very similar judging from descriptions of *S. caducus* in the literature (Gallardo, 1959; Scrocchi et al., 1985; Cei, 1993).

*A Possible Difference in Sexual Size Dimorphism.* Data presented in Table 1 suggests another contrast between *Stenocercus prionotus* and *S. caducus*: *S. prionotus*

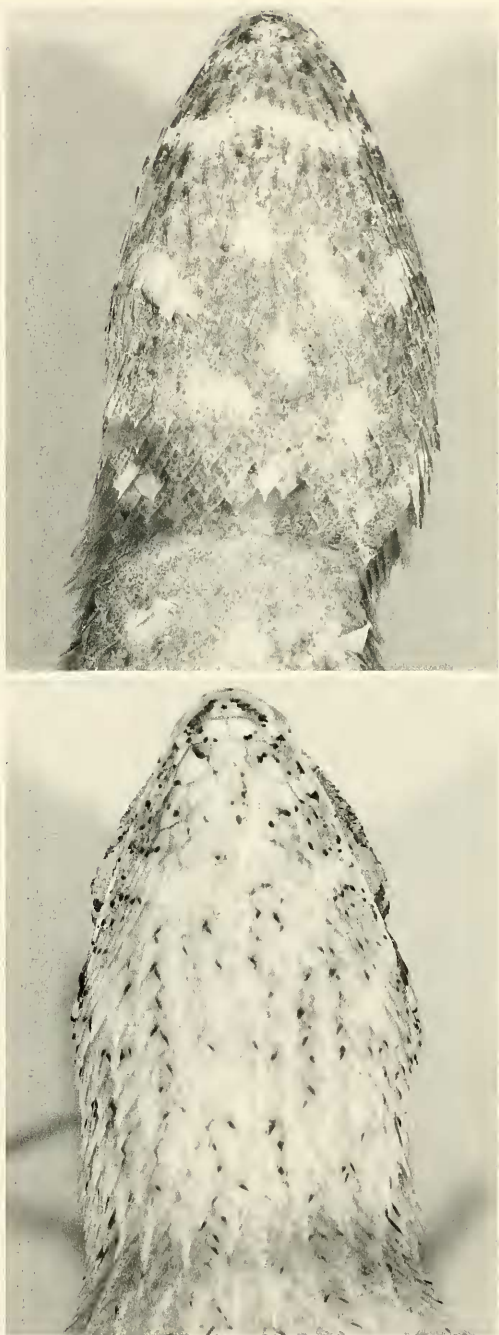


Figure 13. Gular patterns in *Stenocercus caducus*. Top, typical throat pattern consisting of light spots on a dark background (BMNH 1927.8.1.163). Bottom, variant pattern consisting of stripes confined to the lateral portion of the throat (UTA 38046). Compare to Figure 7.

is not dimorphic in the maximum sizes attained by males and females, whereas females of *S. caducus* apparently attain about 20 mm greater SVL than males. However, estimating maximum size is subject to considerable sampling error so this distinction should be considered to be only provisional. Nonetheless, males of *S. prionotus* with SVL >80 mm are known from the northern (USNM 193685) and southern (USNM 280250, BMNH 98.6.9.4) portions of its range, even though the three largest males from the largest population sample (23 specimens in FMNH from Puno Department, Peru) had an SVL of 73 mm (this sample included six adult females with an SVL of 78–89 mm).

In contrast, a sample of 39 *Stenocercus caducus* from Bolivia included 12 adult males, none of which had an SVL >72 mm; in the total sample of *S. caducus* ( $N = 43$ ) 17 females had an SVL  $\geq 80$  mm (range 80–93 mm).<sup>12</sup> Thus, unless a systematic collecting bias against males exists, the different pattern of sexual size dimorphism provides another character distinguishing *S. prionotus* and *S. caducus*. Data presented in Table 1 suggests that other species of the “*Ophryoessoides* group” may be size dimorphic (*S. fimbriatus*, *S. huancabambae*, and ?*S. scapularis*) or not (*S. aculeatus*), and either males (*S. huancabambae*) or females (*S. caducus* and *S. fimbriatus*) may attain a larger body size.

#### DISTRIBUTIONS OF *STENOCERCUS PRIONOTUS* AND *S. CADUCUS* IN EASTERN BOLIVIA

The ranges of *Stenocercus prionotus* and *S. caducus* approach one another in

eastern Bolivia, but do not overlap.<sup>13</sup> Currently, the two closest documented localities are, for *S. prionotus*, near the junction of the Río Madidi and the Río Beni (BMNH 98.6.9.4), and for *S. caducus*, many specimens from the vicinity of Santa Cruz de la Sierra (see above discussion for *S. prionotus* and Appendix; Fig. 1). *Stenocercus caducus* is also known from the Bolivia–Brazil border in the region of the Serranía de Huanchaca in northern Santa Cruz Department, Bolivia.<sup>14</sup>

I am aware of no specimens of *Stenocercus* referable to either *S. caducus* or *S. prionotus* between the Río Beni valley and roughly a line connecting Santa Cruz and the vicinity of Serranía de Huanchaca. Southeast of the Río Beni, the central part of the Beni basin (the Llanos de Mojos) is characterized by flooded savanna grasslands, palm savannas, swamps, and other habitats that are inundated for significant portions of the year; terra firme forests are restricted to somewhat elevated levees along rivers (Clapperton, 1993: 196; Hanagarth, 1993). *Stenocercus prionotus* or *S. caducus* seem unlikely to occur in this area except possibly in these gallery forests, although Fugler (1986) reported *S. prionotus* (as *Ophryoessoides aculeatus*) in seasonally flooded forest during the dry season.

*Stenocercus prionotus* and *S. caducus* probably are segregated by habitat in Bolivia and their distributions may not overlap. *Stenocercus prionotus* is associated

<sup>13</sup> All references to “*Ophryoessoides aculeatus*” in Bolivia (e.g., Fugler, 1983, 1986) that I verified have referred to *Stenocercus prionotus*. However, given the general confusion of species in this complex, some records not traced will have to be checked to rule out the possibility that they do not refer to *S. caducus* or perhaps some other species of the “*Ophryoessoides* group,” such as *S. fimbriatus* or *S. scapularis* (see *Distribution Patterns in Stenocercus prionotus*).

<sup>14</sup> See the Appendix, UTA 3S04S. Michael Harvey (personal communication) recently obtained specimens of *Stenocercus caducus* at El Refugio, a lowland locality at the southern end of the Serranía de Huanchaca (14°44'S, 61°01'W).

<sup>12</sup> These sizes are somewhat larger than those previously reported (81 mm; Gallardo, 1959; Scrocchi et al., 1985; Marcus, 1986). Cei (1993) stated that *S. caducus* reaches only 75 mm SVL in Argentina. Sexes were not given for any individual or sexed specimens in these reports.

with upper Amazonian and lower montane rainforests with annual rainfall greater than 2,000 mm in both Peru and Bolivia. On the other hand, confirmed localities of *S. caducus* are within the physiographic domain broadly referred to as chaco, including a mixture of dry forests, palm savannas, gallery forests, deciduous forests, and ecotonal areas (Scrocchi et al., 1985; Marcus, 1986; Cei, 1993). Short (1975) and Parker et al. (1993) described the diversity of chaco habitats. Gallardo (1979: table 12.1) listed *S. caducus* as a species "basically restricted to the chaco." Average annual rainfall in this area is less than 1,000 mm. *Stenocercus caducus* is known from Parque Nacional Noel Kempff Mercado and vicinity in Bolivia (see footnote 14; Harvey, 1998). This area is characterized by a complex mixture of habitat types, including deciduous forests and cerrado enclaves, and with an annual rainfall of 1,400–1,500 mm (Killeen, 1998). Harvey (1998) encountered *S. caducus* at granitic outcrops covered by semideciduous forests and more open habitats. The herpetofauna of this site is a mixture of species that are typical of Amazonian and of chaco environments (Harvey, 1998; personal observations).

The range of *Stenocercus caducus* extends outside the strictly defined chaco region (see Short, 1975, and Clapperton 1993, for discussion) on the southeastern edge of its range east of the Río Paraguay and in the Andean foothills of southern Bolivia and northern Argentina (Fig. 1). Harvey (1997) reported *S. caducus* from "subtropical wet forests" (1,150–2,050 m elevation) in southern Bolivia. He characterized *S. caducus* as a "Chacoan species that invade[s] the Andean foothills . . . [including] those distributed within the Gran Chaco or that occur in dry forests surrounding the Gran Chaco" (Harvey, 1997: 35). The montane wet forests (yungas) of this area are restricted to ridges high enough for cloud formation during much of the year (generally >1,500 m elevation), and they are surrounded by deciduous dry

forest (Schulenberg et al., 1997). The climate of this area is generally dry and it receives only about 1,200 mm of rainfall per year (Holst, 1997).

The transition between the wet rainforests of Peru and northern Bolivia (range of *Stenocercus prionotus*) and the chaco habitats (range of *S. caducus*) occurs in a very broad ecotone consisting of savannas, evergreen shrublands, and gallery forests of the Beni basin and Río Mamore drainage, from which no specimens of either *S. prionotus* or *S. caducus* have been reported. The piedmont forests of the Andes between the known ranges of *S. prionotus* and *S. caducus*, which are wetter than adjacent lowland forests because of the moderating effect of the Andes, provide one potential route for contact or overlap of their ranges.

The eastern distributional limits of *Stenocercus caducus* along the Bolivia–Brazil frontier are not well understood. I am unaware of verified records from Brazil, although the species does occur close to the Brazilian border in the vicinity of the Serranía de Huanchaca in Parque Nacional Noel Kempff Mercado. Some references to "*Stenocercus caducus*" from western Brazil (e.g., Mato Grosso State; Cope, 1887; Boulenger, 1903) likely refer instead to an undescribed species very similar to *S. caducus* (P. E. Vanzolini and E. E. Williams, personal communication; personal observations). However, the ranges of *S. caducus* and the undescribed species in eastern Bolivia–Paraguay and western Brazil are not well defined; the two species may be separated by the seasonally inundated savannas of the pantanal. Additionally, few specimens of *S. caducus* apparently exist from the chaco of northwestern Paraguay, although Aquino et al. (1996) reported specimens from Parque Nacional Defensores del Chaco (approximately 20°30'S, 60°20'W), as well as other Paraguayan localities in more mesic regions east of the Río Paraguay.

## IS THE DISTRIBUTION OF *STENOCERCUS ACULEATUS* DISJUNCT?

In the process of diagnosing *Stenocercus prionotus* I reviewed the characters and distribution of *S. aculeatus*. In addition to variation in some characters of uncertain significance, some aspects of the distribution of *S. aculeatus* seem peculiar (Fig. 2). First, the distribution of *S. aculeatus* appears to be disjunct between northern Peru and eastern Ecuador. Although the type locality is in northern Peru (Moyabamba, San Martín Department), most specimens are from eastern Ecuador (Fig. 2). The two areas from which specimens are known (Fig. 2) are separated by a broad geographic gap through which courses the main tributary of the upper Amazon, the Río Marañón. Neither *S. aculeatus* nor any other species of *Stenocercus* was obtained during herpetofaunal surveys in northern Loreto Department, Peru (Duellman and Mendelson, 1995), northern Amazonas Department, Peru (Río Cenepa and Río Santiago; J. E. Cadle and R. W. McDiarmid, unpublished data), or during a rapid biological assessment of the Cordillera del Condor region of southeastern Ecuador and northern Peru (Schulenberg and Awbrey, 1997a). *Stenocercus aculeatus* is known from many localities in adjacent regions of Ecuador.

Second, all Ecuadorian localities for *Stenocercus aculeatus* are in the drainages of the Río Pastaza and the Río Curaray. No specimens are known from the Río Napo drainage just to the north, even though no recognized physiographic or faunal break seems to separate the Río Napo drainage from the Río Curaray drainage. However, all localities that have been sampled comprehensively from the Río Napo are on the left (northern) bank of the river (e.g., Duellman, 1978; Vitt and De la Torre, 1996; unpublished list from a large collection from the Jatun Sacha Biological Station assembled and under study by Gregory Vigle). The absence of

*S. aculeatus* from Santa Cecilia (Duellman, 1978) is probably real rather than sampling error, given the intensity of collecting over several years at the site. Thus, *S. aculeatus* possibly does occur on the right (south) bank of the Río Napo and will be recorded once large collections are made there.

The apparent geographic disjunction of *Stenocercus aculeatus* between northern Peru and eastern Ecuador may correspond to some character differences among samples that should be studied more thoroughly (Cadle, unpublished data). For example, Peruvian specimens of *S. aculeatus* have very deep postfemoral pockets (Type 5) in both sexes, whereas the postfemoral pockets are more weakly developed in specimens from Ecuador (Type 2 or 3 in both sexes). Ecuadorian specimens also appear to have more scales in the vertebral row and fewer subdigital scales on the fourth toe than do Peruvian specimens. All of these impressions are based on small sample sizes (Appendix).

The significance of these differences is unclear without a more detailed study of variation among populations of *Stenocercus aculeatus*. However, one possibility is that two or more species are represented in specimens currently referred to *S. aculeatus*, in which case the distributions of individual taxa may be not be contiguous. This is analogous to the previous confusion of *S. fimbriatus* and *S. prionotus* with *S. aculeatus*. Taxonomic recognition of *S. fimbriatus* and *S. prionotus* has concomitantly reduced the geographic distribution understood for *S. aculeatus*. Consequently, a more comprehensive systematic analysis of *S. aculeatus* with special reference to a comparison of Ecuadorian and Peruvian populations is warranted. If two species are recognized, the name *Liocephalus angulifer* Werner (1901) is available for the Ecuadorian populations.

### KEY TO SPECIES OF THE "OPHYROESSOIDES GROUP" OF *STENOCERCUS*

Because of the general confusion about the species considered herein (e.g., see the

synonymy of *Stenocercus prionotus*), I provide the following key as a guide for identifications. The key will work for those species of *Stenocercus* in Peru or Bolivia with keeled ventral scales, enlarged posterior head scales, and one row of moderately to greatly enlarged supraoculars (“*Ophryoesoides* group” as used herein). I have also included the three other currently recognized species having these characteristics, *S. erythrogaster* (Hallowell), *S. dumerilii* (Steindachner), and *S. tricristatus* (Duméril), although these are not known from Peru or Bolivia and are unlikely to occur there. Character and distributional data in the key for *S. dumerilii* and *S. tricristatus* follow Avila-Pires (1995).

I also include in the key an undescribed species with keeled ventrals and enlarged head plates and supraoculars from Amazonas Department, Peru, but I am unaware of other undescribed species of the “*Ophryoesoides* group” from Peru or Bolivia. However, an undescribed species similar to *Stenocercus caducus* (but lacking a posthumeral flap) is known from western Brazil (Mato Grosso) and is not included in the key. Additional study of *S. iridescens* from the Pacific lowlands of Peru and Ecuador is needed (Cadle, 1998: footnote 4) and, as indicated above, a thorough modern study of variation in *S. aculeatus* (Amazonian Ecuador and Peru) is also warranted. Other undescribed species may reside within either of these named taxa. The key will permit identification of all Peruvian and Bolivian taxa previously confused with *S. aculeatus* (e.g., Dixon and Soini, 1975, 1986 [*S. fimbriatus*]; Fugler, 1983, 1986, 1989 [*S. prionotus*]) and *S. iridescens* (e.g., *S. huancabambae* and *S. limitaris*; see Cadle, 1991, 1998). The key also should work for Ecuadorian species, with the caveat that I have paid less attention to Ecuadorian *Stenocercus* except as necessary in conjunction with work on Peruvian species. Of the species covered, only *S. aculeatus*, *S. iridescens*, and *S. limitaris* are definitely known from Ecuador.

The key should be viewed as a means of identifying a set of phenotypically similar, but not necessarily closely related, species within *Stenocercus* in the broad sense. All other species of *Stenocercus* in Peru and Bolivia have smooth (or at most only very weakly keeled) ventrals and more fragmented supraoculars and head plates; see Fritts (1974), Frost (1992), and Cadle (1991, 1998) for discussion and illustrations. Many of these species also have granular scales on the body or posterior surface of the thigh, neither of which is present in species covered by the key. The keys and discussions in Fritts (1974) and Cadle (1991, 1998) are useful for identifying these other species.

The key assumes familiarity with characters of the mite pockets, head scales, and neck folds and crests outlined in Cadle (1991) (see also *Materials and Methods*). In most cases I have used characters that show minimal sexual dimorphism so that specimens of either sex can be identified; exceptions are noted. It is useful to keep in mind that, in most species of *Stenocercus*, scales of juveniles are more prominently keeled than in adults, even when the corresponding scales of adults, such as head scales and dorsal body scales, are smooth. Instances of possible confusion in the key are indicated. The extent of development of posthumeral and postfemoral mite pockets varies according to sex and size in many species of *Stenocercus*, although such variation seems less extensive in this set of species than in many others; I have indicated the range of variation including juveniles and adults of both sexes in the key. Summary geographic distributions are given for each species as a rough guide to known occurrences. However, these should be used cautiously as ancillary information in identifying specimens because distributions of species are sometimes poorly circumscribed. For greatest utility the key should be used in conjunction with illustrations herein and in Cadle (1991, 1998) and Avila-Pires (1995).

1. Canthal and supraciliaries forming a pronounced crest that ends in an enlarged, erect, postsupraciliary that may be distinctly pointed or blunt. Posthumeral and postfemoral mite pockets absent (Type 1 in both instances) ..... 2  
 Canthals and supraciliaries not forming a pronounced crest; no enlarged, erect post-supraciliary. Posthumeral pocket absent (Type 1) to deep (Type 4). Postfemoral pocket absent (Type 1) to deep (Type 5) ..... 3
2. Enlarged postsupraciliary distinctly pointed. Two enlarged scales above ear opening. Tibia approximately equal to thigh length ..... *Stenocercus dumerilii* (Steindachner) (northeastern Pará, Brazil)  
 Enlarged postsupraciliary blunt. No enlarged scales above ear opening; tibia distinctly shorter than thigh ..... *Stenocercus tricristatus* (Duméril) (known only from the holotype, probably from the state of Minas Gerais, Brazil)
3. Superciliary scales projecting laterally shelf-like above the orbit in adults, rectangular in dorsal view.<sup>15</sup> Midbody dorsal scale rows more than 55 (59–70). Postfemoral pocket well developed (Type 3 or 5) ..... *Stenocercus scapularis* (Boulenger) (intermediate elevations on the Andean slopes of central and southern Peru; known elevations greater than 1,000 m)  
 Superciliary scales not projecting laterally, the anterior ones elongate, strongly overlapping. Midbody dorsal scale rows fewer than 55 (30–53). Postfemoral pocket variable (Type 1, 2, 3, or 5) ..... 4
4. Posthumeral mite pocket deep (Type 4) and with an associated scaly flap extending from its anteroventral border and partially concealing it ..... 5  
 Posthumeral mite pocket absent to deep (Type 1, 2, 3, or 4) but without an associated flap ..... 6
5. Vertebral crest strongly projecting in both sexes, serrate, extending from the nuchal region to the proximal portion of the tail; its individual scales triangular, flaplike. Throat often with alternating oblique dark and light stripes. Two enlarged, strongly keeled and projecting angulate temporal scales on each side .....  
 ..... *Stenocercus prionotus* Cadle (rainforested lowlands and Andean foothills of eastern Peru and northern Bolivia)
6. A fringe of enlarged fimbriate scales on the distal posterodorsal surface of thigh. Several longitudinally oblique rows of large, strongly keeled scales on shank.<sup>16</sup> Scales between vertebral and dorsolateral crests smooth or occasionally very weakly keeled. .... *Stenocercus fimbriatus* Avila-Pires (lowlands of eastern Peru and central western Amazonian Brazil)  
 No fringe of fimbriate scales on thigh or strongly keeled oblique scales on shank. Scales between vertebral and dorsolateral crests moderately to strongly keeled at least posteriorly; dorsolateral crest may be weakly developed, but dorsal scales still strongly keeled ..... 7
7. Posthumeral mite pocket variable (Type 1, 2, 3, or 4). Postfemoral mite pocket variable (Type 1, 2, 3, or 5). Head scales smooth or keeled. Angulate temporal scales keeled, may be projecting and bladelike. Internasals usually 4 or more (occasionally 3, never 2), often irregular in pattern and shape. .... 8  
 Posthumeral mite pocket absent or weakly developed (Type 1 or 2). Postfemoral mite pocket absent (Type 1). Head scales smooth. Angulate temporal scales smooth; none bladelike and projecting. Two polygonal internasals in contact on the midline, each broader laterally than medially. .... *Stenocercus iridescens* (Günther) (Pacific lowlands and intermediate elevations of western Ecuador and northwestern Peru)
8. One to 3 strongly keeled, but nonprojecting, angulate temporal scales in line with the superciliary row between the lateral tem-

<sup>15</sup> The superciliaries in juveniles of *Stenocercus scapularis* have a more typical shape. The extent of shelf-like projection and change to a more rectangular shape seem positively correlated with body size and thus develop with age. The number of dorsal scale rows and the development of the postfemoral pocket are useful clues for subadults.

<sup>16</sup> The fimbriate scales form a projecting fringe on the distal portion of the thigh. Both the fimbriate scales and the oblique scales on the shank are relatively more prominent in juveniles than adults.



- porals and the posterior dorsal head scales.  
Two subequal canthal scales on each side.  
Head scales keeled, at least posteriorly ..... 9
- Two projecting bladelike angulate temporals  
in line with superciliary row. A single can-  
thal on each side (rarely, 2 are present but  
in that case 1 is much larger than the other).  
Head scales smooth or keeled. .... 11
9. Posthumeral pocket moderately developed  
in males (Type 2 or 3), absent in females  
(Type 1). Postfemoral pocket absent in fe-  
males (Type 1), moderate to deep in males  
(Type 3 or 5). Anterior gular scales weakly  
to strongly keeled. ....  
..... *Stenocercus erythrogaster* (Hallowell)  
(northern Colombia)
- Posthumeral and postfemoral pockets deep  
in both sexes (Types 4 and 5, respective-  
ly).<sup>17</sup> Anterior gular scales smooth to weakly  
keeled. .... 10
10. Interparietal indistinct, parietal eye not visi-  
ble. Three occipitals. Dark subocular bar  
absent. Three angulate temporals separ-  
ated from large posterior head scales by a  
row of tiny scales .... *Stenocercus* new species  
(known from a single specimen [Appendix]  
from the inter-Andean valley of the Río  
Marañón near Balsas, Amazonas Depart-  
ment, Peru)
- Interparietal distinct, parietal eye visible.  
Two occipitals. Dark subocular bar pres-  
ent. One angulate temporal much larger  
than others and in contact with at least 1  
other enlarged posterior head scale. ....  
..... *Stenocercus limitaris* Cadle  
(intermediate elevations [600–2,200 m] of the  
Andes on the Pacific versant of southwest-  
ern Ecuador and northwestern Peru)
11. Head scales smooth to slightly wrinkled in  
adults; weakly keeled, wrinkled, or rugose  
in juveniles. Prominent dorsolateral crest  
on body from neck to base of tail and con-  
tinuous with both supra-auricular crest  
and antehumeral crest. Postfemoral pock-  
et moderate to deep (Type 2, 3, or 5).  
..... *Stenocercus aculeatus* (O'Shaughnessy)  
(rainforested lowlands and intermediate ele-  
vations of northern Peru adjacent to the  
Andes and in eastern Ecuador)
- Head scales strongly keeled or multicarinate  
in juveniles and adults. Dorsolateral crest,  
when present, weak and restricted to neck  
and anterior body. Postfemoral pocket  
deep (Type 5). ....  
..... *Stenocercus huancabambae* Cadle

(dry inter-Andean valleys of the upper Río  
Marañón in Cajamarca and west central  
Amazonas departments, northern Peru)

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<sup>17</sup> An undescribed species in the next couplet of the  
key is known only from a single adult male. The dis-  
tributions of species in couplets 9 and 10 should be  
used as ancillary data for identification.

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#### APPENDIX: SPECIMENS EXAMINED

Institutional abbreviations are as follows:

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	The Natural History Museum, London
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
FMNH	The Field Museum, Chicago
KU	Natural History Museum, University of Kansas, Lawrence
LSUMNS	Louisiana State University Museum of Natural Science, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
ROM	Royal Ontario Museum, Toronto
USNM	National Museum of Natural History, Washington, D.C.
UTA	University of Texas at Arlington

Bracketed information was inferred from sources listed in the *Materials and Methods*. For specimens of other species of the "*Ophryossoides* group" examined

(*S. huancabambae*, *S. iridescens*, and *S. limitaris*), see Cadle (1991, 1998). Bold-face numbered localities 1–4 are known or suspected areas of sympatry between the species listed and *Stenocercus prionotus*. They correspond to numbered localities in Figures 1 and 2 and in the text discussion.

#### *Stenocercus aculeatus*

**ECUADOR: PROV. MORONA-SANTIAGO:** Chiguaza [ca. 1,000 m; 01°59'S, 77°58'W] (USNM 200882–84). [**PROV. NAPO/TUNGURAHUA:** Llanganates area<sup>18</sup> (FMNH 23527). **PROV. PASTAZA:** Río Pastaza, Abitagua [01°23'S, 78°05'W] (FMNH 25803–05, 26892, 28011, 28057 [=17 specimens]). Río Pastaza, Alpayacu [01°28'S, 78°07'W] (FMNH 3926–27; MCZ 8081). Canelos [01°35'S, 77°45'W; 530 m] (MCZ 38530). Montalvo, Río Bobonaza [314 m; 02°04'S, 76°58'W] (USNM 200892). [**PROV. PASTAZA:** Baños, Mera Trail [<sup>P</sup> = between Baños and Mera<sup>19</sup>; approximately 01°30'S, 78°10'W] (FMNH 28012).

**PERU: [DEPTO. LA LIBERTAD]:** E Peru, Pampa Seca, Río Mixiolla [=Río Mishollo] Valley, Upper Huallaga region, 4300 ft [2, 1,311 m; approximately 08°16'S, 76°58'W]<sup>20</sup> (AMNH 57085). [**DEPTO. LOR-**

<sup>18</sup> I have been unable to localize this. The Cordillera de los Llanganates is a high range (to >4,500 m) in the Cordillera Oriental north of the Río Pastaza (Paynter, 1993). The locality may refer to lower elevations in this range.

<sup>19</sup> Baños is a famous collecting locality at the foot of Volcán Tungurahua at 1,820 m. That would be an altitudinal record for *Stenocercus aculeatus*. I interpret the locality as stated in the FMNH catalogues as being on the trail between Baños and Mera, which is at 1,160 m. See Brown (1941) and Chapman (1926) for discussion.

<sup>20</sup> Harvey Bassler collected *Stenocercus* for the AMNH at two localities on the Río Mixiolla (=Río Mishollo): Pampa Seca and La Pinita (see *Stenocercus fimbriatus*), as listed in AMNH catalogues. The Río Mishollo originates in southeastern La Libertad Department, flows eastward, and joins the Río Huallaga in southwestern San Martín Department. The elevations given for these localities, 1,067 m and 1,311 m, indicate that they lie in the narrow stretch of the valley that straddles the boundary between La Libertad and San Martín departments (departmental maps produced by the Instituto Geográfico Nacional, Lima). I identify these localities as Pampaseca and Piñita, respectively, in extreme southeastern La Libertad Department, as indexed by Stiglich (1922). Both localities are in Ongón District and the coordinates given are those for the town of Ongón. Stiglich (1922) states that Piñita is a small village on the Quebrada Pedernal, a left tributary of the Río Mishollo. Apart from indicating that Pampaseca is a farm,

ETO]: NE Peru, Front Range between Moyabamba and Cahuapanas, 3000 ft [915 m; approximately 05°37'S, 77°00'W] (AMNH 57083). Northeastern Peru: Icuta on Balsapuerto–Moyabamba trail, 3500 ft [1,067 m; 05°58'S, 76°40'W; given as "Icuto" or "Icutu-Cuesta" by Lamas, 1976] (AMNH 56413).

### *Stenocercus caducus*

**BOLIVIA: NO SPECIFIC LOCALITY:** BMNH 1946.8.29.76 (holotype of *Leiocephalus bolivianus* Boulenger); CM 4583–84. **DEPTO. CHUQUISACA:** Sud Cinti, trail from Rinconada Bufete to El Palmar [1,170–2,000 m; approximately 20°50'S, 64°21'W] (UTA 39102). **DEPTO. SANTA CRUZ:** Buena Vista, ca. 500 m [17°27'S, 63°40'W] (MCZ 20625–26, 29023; FMNH 16165, 21486, 21511; BMNH 1927.S.1.163–164; CM 4527, 4550–51, 4558, 4587–88, 4605, 4607, 4616, 4626, 4634–36, 4641). Las Yuntas [=Las Juntas,<sup>21</sup> 18°35'S, 63°08'W] (CM 970). Provincia Chiquitos, Santiago (Serranía and nearby), 700–750 m [18°19'S, 59°34'W] (FMNH 195983). [Provincia] Chiquitos, Canton El Cerro, Finca Dos Milanos, 17°27'30"S, 62°20'00"W (UTA 38046). Provincia Sara, eastern Bolivia, 600 m [17°27'S, 63°40'W] (BMNH 1907.10.31.7–8). Provincia Sara, Santa Cruz de la Sierra [17°48'S, 63°10'W] (CM 966, 969, 1301S). Provincia Sara, Río Surutu W of Buena Vista [17°24'S, 63°51'W] (CM 4590). Provincia Sara, Río Colorado [17°38'S, 63°54'W] (CM 4598). [Provincia] Velasco, Inselbergs near Florida [14°38'S, 61°15'W] (UTA 3804S). **DEPTO. TARIJA:** Villa Montes [21°15'S, 63°30'W] (MCZ 28634). Misión San Francisco [21°15'S, 63°30'W] (BMNH 98.7.7.5; specimen collected by Alfredo Borelli, whose San Francisco = Villa Montes fide Paynter, 1992).

**PARAGUAY: [DEPTO. CAAGUAZÚ]:** Pastoreo [approximately 25°23'S, 55°52'W] (MCZ 34214–15). **[DEPTO. CENTRAL]:** Asunción [25°16'S, 57°40'W] (FMNH 9496). Colonia Nueva Italia [25°37'S, 57°30'W] (FMNH 42281).

### *Stenocercus erythrogaster*

**COLOMBIA: [DEPTO. MAGDALENA]:** Río Frio [30–450 m; 10°55'N, 74°10'W] (MCZ 29707). Santa Marta Mountains [approximately 10°50'N, 73°40'W] (MCZ 11303). Río Toribio, Hacienda "Papare," second river on road from Ciénaga to Santa Marta [11°03'N, 74°14'W] (FMNH 165153). **[DEPTO. SANTANDER]:** San Gil [1,095 m; 06°33'N, 73°08'W] (ANSP 24136, MCZ 36877).

Stiglich (1922) gives no further information about its location.

<sup>21</sup> The specimen was collected in November or December 1913 by José Steinbach, who collected at a locality known as "Las Juntas" during that same period (Paynter, 1992). The two localities are assumed to be the same. The variant spelling "Yuntas" does not appear in any sources consulted.

### *Stenocercus fimbriatus*

**PERU: NO SPECIFIC LOCALITY:** (FMNH 56070). **DEPTO. HUÁNUCO:** ca. 35 km NE Tingo Maria, Hcda. Santa Elena, ca. 1000 m [approximately 08°57'S, 76°02'W] (LSUMNS 26966–67). Approximately ½ mile E Universidad Agraria de La Selva, Tingo Maria, vicinity of Río Huallaga [3, 09°18'S, 75°59'W], USNM 193684. **[DEPTO. LA LIBERTAD]:** E Peru, La Pinita, Río Mixiolla, tributary of upper [Río] Huallaga, 3500 ft [1,067 m; approximately 08°16'S, 76°55'W; see footnote 20] (AMNH 56797–98). **[DEPTO. LORETO]:** E Peru, Contamana, Ucayali River valley [134 m; 07°15'S, 74°54'W] (AMNH 56803). E Peru, E of Contamana on trail to Contaya, 700 ft [213 m; approximately 07°15'S, 74°54'W] (AMNH 56781–82). E Peru, Pampa Hermosa, mouth of Río Cushabatay, 500 ft [152 m] [1, 07°12'S, 75°17'W] (AMNH 56788, 56790–92, 56794–96, 56801–02). Mishana, Río Nanay, Estación Biológica Caucebus, 150 m [03°53'S, 73°27'W] (USNM 222377). Mishuana [=Mishana; 150 m, 03°53'S, 73°27'W] (KU 212628). **DEPTO. MADRE DE DIOS:** Pakitza Station [Río Manu], Manu National Park [4, 11°56'S, 71°17'W] (Victor R. Morales 18235). **DEPTO. UCAYALI:** Río Curanja, Balta, approximately 300 m [approximately 10°08'S, 71°13'W] (LSUMNS 17519, 25402–04, 26720–23). Alto [Río] Purús, Alto [Río] Curanja, Igarape Champuiaco [9°34'S, 70°36'W] (MCZ 61226). Peru/Brazil frontier, Utoquinia Region, 1000 ft. [305 m; approximately 08°00'S, 74°00'W]<sup>22</sup> (AMNH 56789, 56799–800).

### *Stenocercus scapularis*<sup>23</sup>

**PERU: NO SPECIFIC LOCALITY:** (FMNH 56444). **[DEPTO. JUNÍN]:** Chanchamayo, 1200 m [approximately 11°03'S, 75°47'W] (FMNH 40608–11). Peregne, 1200 m [10°58'S, 75°13'W] (MCZ 49580–81). Tarma, Chanchamayo, 1300 m [11°25'S, 75°42'W] (FMNH 45522). **[DEPTO. PUNO]:** Sagrario, Río Quitún [approximately 1,020 m; 13°55'S, 69°41'W]

<sup>22</sup> The region referred to is north to northeast of Pucallpa. The variant spellings Utoquinia, Utoquina, and Uroquina are in the literature and are applied to a right-bank tributary of the Río Ucayali, a village on the Río Ucayali, and an airstrip on the Río Utoquinia near the Brazilian border. The entire region is less than 500 m in elevation except for a small raised area near the Brazilian border that attains nearly 800 m and that is apparently the source of the Río Utoquinia.

<sup>23</sup> The occurrence of *Stenocercus scapularis* at Rurenabaque, El Beni Department, Bolivia, as reported for two specimens in the AMNH (Burt and Burt, 1931: 273) is apparently based on a misidentification. These specimens are probably either *S. prionotus* (most likely) or *S. caducus* (see *Distribution Patterns in Stenocercus prionotus*).

(FMNH 4040S). "Camp 4" [between Santo Domingo and La Pampa; approximately 13°44'S, 69°37'W]<sup>24</sup> (FMNH 40409). Juliaca, Lake Aracona, 16,600 ft. [shipping point only; correct locality is on the right bank of the Río Inambari, 1,830 m, 13°30'S, 70°00'W]<sup>25</sup> (AMNH 1701).

<sup>24</sup> According to the field catalogue in the FMNH Mammal Division the collector, Colin Sanborn, was in Santo Domingo on 20 October 1941 and in La Pampa on 23 October (see also notes in Stephens and Traylor, 1983). The specimen FMNH 40409 was collected 21 October, and thus "Camp 4" is assumed to be between these points.

<sup>25</sup> The specimen was collected in 1900 by H. H. Keays, who collected many mammals and other vertebrates in southern Peru, primarily for the American Museum of Natural History. It is clear that most of the specimens labeled with the locality "Juliaca" (a town on the Peruvian altiplano near Lake Titicaca) actually came from farther north in the Río Inambari valley. Allen (1900: 219; 1901: 41) provides the following information:

The Museum has recently received two small collections of mammals made by Mr. H. H. Keays, at Juliaca, in southeatern Peru, a little to the westward of Lake Titicaca. Mr. Keays writes: "Our camp is situated in the loop of the Inambari River. The country is very broken, with deep narrow cañons, and is covered with a dense undergrowth of shrubs and vines, with here or there a palmetto or a cedar rising above the surrounding vegetation." He gives the altitude as 6000 feet [1,830 m], and the position as latitude 13°30' S., longitude 70° W.

... it is necessary to correct a misleading statement in my former paper in respect to the locality where the ... collections were made. Mr. Keays's post-office address was Juliaca, and through lack of explicit information, it was inferred that the Inca Mines, where he collected, were in the immediate vicinity of Juliaca ... the Inca Mines are situated about 200 miles northeast of Juliaca, on the east side of the Andes, on the Inambari River, a tributary of the Amazon, and at a much lower altitude than Juliaca. The altitude and geographical position were correctly given in the former paper, but in place of Juliaca, ... read Inca Mines.

Keays's information quoted by Allen places the locality on the right bank of the Río Inambari in the foothills of an outlying Andean spur separating the Río Inambari from upper tributaries of the Río Tambopata. I have not located a Lake Aracona and suspect that this is an error for Lake Aricoma, a high Andean lake on the route between Juliaca and the location of Keays's camp. However, it is not at all clear why this name is associated with the locality. No notes or correspondence of Keays are in the AMNH mammal department archives for further clarification (R. S.

### *Stenocercus* sp.

**PERU: DEPTO. AMAZONAS:** 17 km ENE Balsas [06°49'S, 78°00'W] (ROM 1645S).

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