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A REVISION OF LIZARDS OF THE GENUS  
*PRIONODACTYLUS*, WITH A NEW GENUS  
FOR *P. LEUCOSTICTUS* AND NOTES ON THE  
GENUS *EUSPONDYLUS* (SAURIA, TEIIDAE)

THOMAS UZZELL





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A REVISION OF LIZARDS OF THE GENUS *PRIONODACTYLUS*, WITH  
A NEW GENUS FOR *P. LEUCOSTICTUS* AND NOTES ON THE GENUS  
*EUSPONDYLUS* (SAURIA, TEIIDAE)

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(Received 2 May 1972)

ABSTRACT

*Prionodactylus* differs from *Euspondylus* in having a double row of widened gular scales and keeled hexagonal scales; it is therefore removed from synonymy with *Euspondylus*. Five species (*P. vertebralis*, *P. dicrus* new species, *P. manicatus*, *P. argulus*, and *P. eigenmanni*) are recognized. *P. dicrus* is related to *P. vertebralis*; in both, the loreal is separated from the supralabials, the subdigital lamellae are not tuberculate, and the frontonasal is not divided; *P. dicrus* differs in having two dorsolateral light stripes anteriorly that fuse to one posteriorly, rather than a single median light line throughout. *P. vertebralis* is known from Pacific Ecuador and Colombia, the Magdalena and Cauca valleys of Colombia, and from adjacent Panamá and Venezuela; *Euspondylus ampuedae* appears to be the same species (new synonymy). *P. dicrus* occurs on the Amazonian slopes of central Ecuador. *P. manicatus* has two subspecies. *P. m. manicatus*, with single tubercles on the subdigital lamellae, no median collar scale, and a divided eyelid disc, occurs in Amazonian Ecuador and northern Peru. *P. m. bolivianus*, with non-tuberculate subdigital lamellae, a median collar scale, and an undivided eyelid disc, occurs in Amazonian Bolivia and southern Peru. In both races, the loreal touches the supralabials and the frontonasal is not divided. *P. argulus* has a wide range in the Guianas and Amazonian South America, at relatively low elevations, from northern Brazil along the slopes of the Andes to Bolivia. It has a divided frontonasal, and the loreal touches the supralabials. *P. eigenmanni* occurs only in Amazonian Bolivia. It has a single frontonasal, the loreal touches the supralabials, and the subdigital lamellae may have both single and double tubercles.

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*Prionodactylus spinalis* and *P. rahmi* are placed in the genus *Euspondylus* because they do not have a double widened row of gular scales.

*Prionodactylus ocellifer* is identified as *Aspidolaemus affinis* (new synonymy).

*Riolama*, new genus, is proposed for *Prionodactylus leucostictus*. *Riolama* differs from *Prionodactylus* in not having a double row of widened gular scales, in having a superficial tympanum rather than a recessed one, in having much depressed digits, except at the tips, and in having plicae rather than folds on the anterior tip of the tongue. The plicae of the tongue indicate affinities of *Riolama* with *Ptychoglossus*, *Alopoglossus*, and *Ecpleopus*. The former two have completely plicate tongues. *Riolama* differs from *Ecpleopus* by the much depressed toes, by the complete superciliary series, and by the longitudinal rather than diagonal rows of ventral scales. *R. leucosticta* is the only known species.

Specimens of *Euspondylus maculatus* (the type species of the genus) that have been reported from Pacific coastal South America are apparently mislabelled. The species is reliably known from northern and central Amazonian Peru.

*Euspondylus stenolepis*, on account of its completely plicate tongue and smooth scales on the forelimbs, is referred to the genus *Ptychoglossus* (new combination).

Keys to *Prionodactylus* and *Euspondylus* based on these changes are included. The status of names proposed in or referred to *Euspondylus* and *Prionodactylus* is summarized.

The genus *Prionodactylus* has as relatives *Cercosaura*, *Pantodactylus*, *Aspidolaemus*, and *Pholidobolus*. *Cercosaura* is distinct in scutellation. The other genera, particularly *Aspidolaemus* and *Pantodactylus*, may not be distinguishable from *Prionodactylus*. Hemipenial features of *Pantodactylus* and *Cercosaura* distinguish the individuals for which this organ was studied from the individuals of the other genera for which hemipenes were examined.

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## I. INTRODUCTION

The genus *Euspondylus*, although one of the earliest named in Group II (Boulenger, 1885) of the family Teiidae, remains one of the most ill defined, largely because the type species of the genus, *Euspondylus maculatus* Tschudi (1845), is essentially devoid of unusual external morphological features on which a generic concept could be founded. As a result, *Euspondylus* became a wastebasket into which many other taxa could be put. As the generic concept gradually broadened, ever more distinctive taxa could be placed within it, so that by the time of Burt and Burt's (1931) study, one or more members of at least six quite distinct genera had become included. Several of these came into *Euspondylus* when the Burts merged *Prionodactylus* with *Euspondylus*. This merger seemed justified partly because of the diversity of taxa that had previously been included in *Euspondylus* and in *Prionodactylus*. Gradually, however, these diverse stocks have been removed from *Euspondylus* (Ruibal, 1952; Uzzell, 1959, 1961, 1969a, b).

The genus *Prionodactylus* can, I believe, be redefined to encompass five taxa, one of which I here describe for the first time. Definition of *Prionodactylus* requires considerable reshuffling of other taxa. I have considerable faith in some of the changes proposed here, but the collection of species that remains in *Euspondylus* still seems artificial to me. The easy work, however, appears to be done.

## ABBREVIATIONS

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology, Harvard University
MLS	Museo de La Salle, Bogotá
MNH	Muséum National d'Histoire Naturelle, Paris
NRM	Naturhistoriska Riksmuseet, Stockholm
UIMNH	University of Illinois Museum of Natural History
UKMNH	University of Kansas Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
ZMB	Zoologisches Museum, Berlin
ZSM	Zoologische Staatssammlung, Munich



II. A REVISION OF THE GENUS *Prionodactylus**Prionodactylus* O'Shaughnessy

*Prionodactylus* O'Shaughnessy, 1881, Proc. Zool. Soc. London 1881: 231.  
DEFINITION. Tongue with imbricate scalelike papillae. Snout moderate to long, blunt to pointed. Head scales without striations or rugosities; single or divided frontonasal; single frontal and interparietal; paired prefrontals and parietals; a median and two paramedian occipitals. Nostril pierced in a single or divided nasal; loreal and frenoocular present; first superciliary expanded onto dorsal surface of head or not; prefrontals in contact with loreal. Supraoculars two to four; superciliary series complete. Eyelids developed, lower with a translucent or lightly pigmented disc, divided by vertical grooves or not. Tympanum recessed, external ear opening small. Gular crease present, weak. Collar fold well developed. Gular scales flat, rectangular, the two median rows of scales, at least on the posterior part of the throat, forming a double longitudinal series of widened scales. Limbs pentadactyl; digits clawed. Forefoot with or without enlarged platelike scales along inner margin of palm between thumb and wrist; if enlarged, the medial edge projecting or not. Undersides of third and fourth toes usually with paired scales on proximal part, the inner scale usually producing a tubercle. Dorsal scales in diagonal and transverse rows, keeled, hexagonal. Lateral scales reduced in size, forming a wide band between dorsal and ventral scales; upper rows keeled. Ventral scales in transverse and longitudinal rows, smooth. Femoral pores occasionally absent in females. Preanal scales in two rows.

REMARKS. The genus *Prionodactylus* was named for the tubercles under the toes and fingers of northern populations of *P. manicatus*, the type species of the genus. In these populations, the subdigital lamellae are angled on the midline of the digit, and bear a single tubercle on the angle (Fig. 1). In

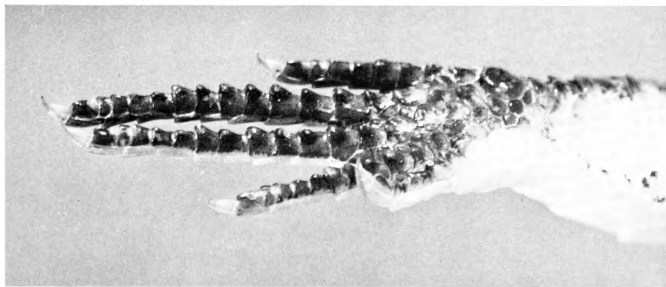


FIG. 1. Undersurface of the left forefoot of *Prionodactylus m. manicatus* (UKMNH 109819), showing the single medial tubercle of the basal lamellae of the third and fourth digits.  $\times 8$ .

southern populations of *P. manicatus* and in *P. vertebralis* and *P. dicrus* the subdigital lamellae are mostly single and are nontuberculate; in these, the subdigital lamellae at the base of the third and fourth toes are doubled, and the inner parts are swollen into tubercles. *Prionodactylus eigenmanni* has single and double tubercles, as well as simple subdigital lamellae. In *P. argulus*, most of the subdigital lamellae are paired, but not tuberculate.

The relationships of *Prionodactylus* appear to be with *Cercosaura*, *Pantodactylus*, *Aspidolaemus*, and *Pholidobolus*, with all of which it shares keeled dorsal scales and a double longitudinal row of widened gular scales. *Prionodactylus* may be distinguished from *Cercosaura* because *Cercosaura* has large rectangular keeled dorsal scales in longitudinal rows. *Pantodactylus*, as noted by Ruibal (1952: 520) may in fact be indistinguishable from *Prionodactylus*. *Aspidolaemus* and *Pholidobolus* also may be indistinguishable from *Prionodactylus*, but at present I retain them as different genera pending studies based on more than scalation.

The taxa that I recognize in the genus *Prionodactylus* may be distinguished by the following key.

- |   |                                |
|---|--------------------------------|
| 1. Frontonasal divided .....  | <i>P. argulus</i>              |
| Frontonasal single .....  | 2                              |
| 2. Loreal separated from supralabials by nasal and frenooocular .....   | 3                              |
| Loreal in contact with the supralabials .....   | 4                              |
| 3. A narrow middorsal light stripe from rostral to tail .....   | <i>P. vertebralis</i>          |
| Two narrow dorsolateral light stripes on head fusing to one at midbody .....  | <i>P. dicrus</i> , new species |
| 4. 32-35 scales around the midbody region; 13-15 subdigital lamellae under fourth toe; some subdigital lamellae with one, others with two tubercles .....         | <i>P. eigenmanni</i>           |
| 33-52 scales around the midbody region; 14-23 subdigital lamellae under fourth toe; subdigital lamellae, if tuberculate, with a single tubercle per lamella ..... | 5                              |
| 5. 2 or 3 posterior preanal scales; no median collar scale; translucent disc in lower eyelid divided into two segments .....                                      | <i>P. m. manicatus</i>         |
| 4 posterior preanal scales; a median collar scale; translucent disc in lower eyelid undivided .....   | <i>P. m. bolivianus</i>        |

Although additional work may result in subdivision of some of the taxa that I recognize, these are the basic stocks in the genus as I understand it.

*Prionodactylus vertebralis* (O'Shaughnessy)

(Fig. 2)

*Cercosaura* (*Pantodactylus*) *vertebralis* O'Shaughnessy, 1879, Ann. Mag. Nat. Hist. Ser. 5, 4: 298.

*Prionodactylus palmeri* Boulenger, 1908, Ann. Mag. Nat. Hist. Ser. 8, 2: 518.  
*Prionodactylus marianus* Ruthven, 1921, Occ. Pap. Mus. Zool. Univ. Michigan 103: 1.

(?) *Euspodylus ampuedae* Lancini, 1968, Publ. Ocas. Mus. Cienc. Nat., Zool. 12: 4.

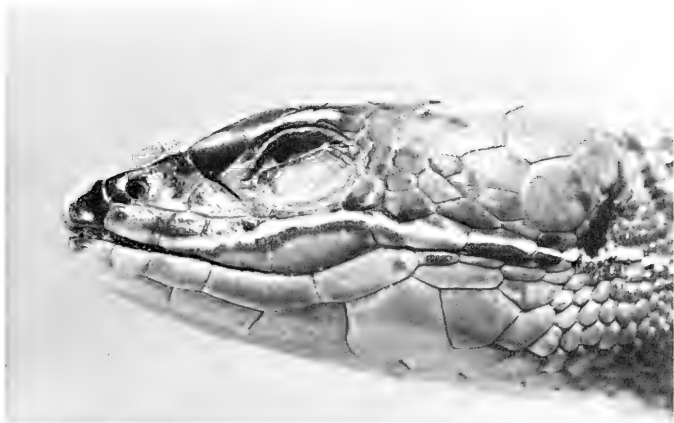


FIG. 2. Side view of the head of *Prionodactylus vertebralis* (FMNH 43799). The left loreal is fused to the nasal on this specimen.  $\times 5$ .

**HOLOTYPE.** A young female (BMNH 78.1.25.13, reregistered as 1946.8.31.35) collected by Buckley at Intac, Imbabura Province, Ecuador.

**DEFINITION.** A single frontonasal. Loreal separated from supralabials by contact between nasal and frenoocular (98%)<sup>1</sup>. Two collar scales at midline, usually widened. Lamellae under fingers not forming tubercles. Translucent disc in lower eyelid divided into 3-5 parts<sup>2</sup>, often lightly pigmented. No sexual dimorphism in femoral pore number. A conspicuous middorsal light stripe the length of the body and along the unregenerated part of the tail.<sup>3</sup>

**VARIATION.** I have examined over 200 specimens of *P. vertebralis*. There is considerable variation, within as well as between populations (Table 1).

Most of the specimens examined (88%) have three supraoculars on each side. One individual (FMNH 43806) has 4-4. Counts of 2-2 supraoculars are relatively common (39%) in the series from San Pedro, the type locality

<sup>1</sup>Loreal absent in the single Peruvian specimen (LACM 55881).

<sup>2</sup>Undivided in LACM 55881.

<sup>3</sup>Absent in LACM 55881; possibly present only in male paratype of *Euspodylus ampuedae*.

of *P. marianus*. Eight longitudinal rows of ventrals are also relatively common in the series from San Pedro (24/43); this count occurs sporadically elsewhere some 12 times.

There is some indication of a latitudinal gradient in whether or not the prefrontals are in contact at midline. They more often are in contact in the north (San Pedro, 36/41; Sonsón, 16/27, with three additional specimens having an azygous scale separating the prefrontals). Farther south, separated prefrontals are more common (Pasto, 4/4 separated; Pichincha and Cotopaxi, Ecuador, 5/9 separated). The series from "Mera" has 5/11 separated, and the series from "Zamora" has 4/6 separated.

The two extreme southern specimens, AMNH 18312 from El Oro, Ecuador, and LACM 55881 from Piura, Peru, lack prefrontal scales entirely, and thus superficially resemble members of the genus *Proctoporus*. These two specimens appear to carry to an extreme the reduction in prefrontal size associated with separation of the prefrontals.

As anomalies, occasional individuals have the median occipital missing, the loreal fused to the nasal, frontonasal asymmetrically divided, and various extra, minute head scales. These form no obvious geographic patterns.

Samples of individuals from two areas show notable variation. The specimens from San Pedro, the type locality of *P. marianus*, fall into two groups. Eight of the 10 paratypes of *P. marianus* that I have examined (UMMZ 56031, 8 specimens; CAS 54809-10) have 8 rather than 6 longitudinal rows of ventral scales. Seven have 2-2 supraoculars, and one has 2-3. These specimens also have fewer femoral pores. Nine additional specimens (MCZ 14652-57; USNM 75967, 120798; BMNH 1925.5.1.11) were collected by Hno. Nicéforo María at about the same time and place as UMMZ 56031; BMNH 1925.5.1.11 was obtained from the University of Michigan and has the same collection data as the paratypes; it probably is a paratype. These "topotypes" resemble the paratypes of *P. marianus* in having 8 longitudinal rows of ventral scales, 2-2 supraoculars in 6 individuals and a low number of femoral pores. In contrast, AMNH 32737-57 and MCZ 29860 and 46448 differ from the paratypes and similar specimens. Four of 23 have 2-2 supraoculars; 6 have 8 longitudinal rows of ventral scales; the femoral pore number is greater (Table 2). A canonical analysis (BMDO7M; Dixon 1968) based on total femoral pores, longitudinal rows of ventral scales, transverse rows of ventral and of dorsal scales, scales around midbody region, and total number of supraocular scales, groups 18 of the 19 paratypes and "topotypes" together, and 18 of the 21 "non-types" together. The first two canonical axes account for 90 per cent of the dispersion. Fig. 3 shows that the non-paratype females are very variable; they include three of the misplaced individuals. I conclude that the samples labelled San Pedro came from at least two different localities in that area.

Among the animals from near Popayán, two quite distinct forms occur. These can be separated by several scale counts and by total femoral pore number (Table 1). The specimens differ also in color, with the specimens

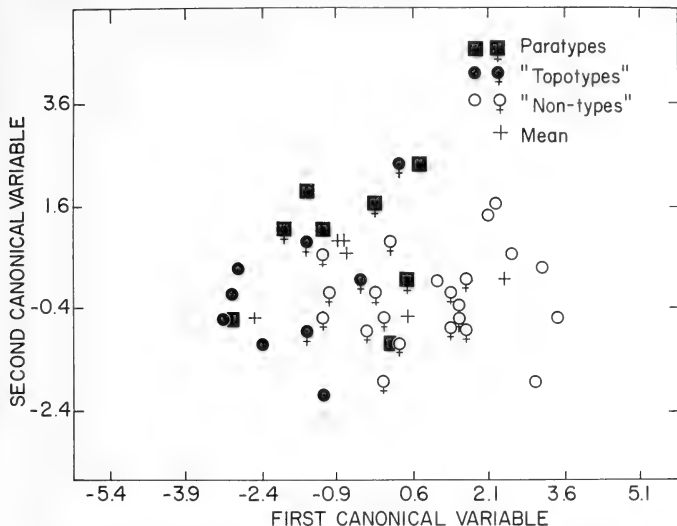


FIG. 3. Distributions and means for individuals of three groups of specimens from the type locality of *Prionodactylus marianus* (San Pedro, Colombia) along the first and second canonical axes. The characters on which the analysis was based include total femoral pores, longitudinal rows of ventral scales, transverse rows of ventral and of dorsal scales, scales around midbody region, and total number of supraoculars. The first two canonical axes account for 90 per cent of the dispersion. Paratypes include UMMZ 56031 (8 specimens) and CAS 54809-10. "Topotypes" include MCZ 14652-57, USNM 75967, 120798, BMNH 1925.5.11; the last is probably a paratype. "Non-types" include AMNH 32737-57 and MCZ 29860 and 46448.

from Popayán (1700 m) being in general much lighter in coloration than the specimens from El Tambo (2000 m). Part of the difference may be due to preservation; the El Tambo specimens appear to be formalin blackened. In the darker specimens, from El Tambo, the dark borders to the light mid-dorsal stripe are essentially straight and parallel on the head, and separated by the distance separating the supraocular series on the top of the head. In the lighter colored specimens, however, the dark borders for the median light line are much more irregular, and may run along the outer edges of the occipitals, the parietals, the supraoculars and along the canthus rostralis. Of the 10 light-colored specimens, 5 have the prefrontals separated; of the 12 darker-colored specimens, 2 have the prefrontals separated; the  $X^2$  value observed (2.79) indicates that this difference has a probability between 0.1 and 0.05 of occurring by chance.

TABLE 1. Characteristics of specimens of *Prionodactylus vertebralis*.  
 Figures represent ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital lamellae Fourth finger	Fourth toe
Panamá	8	31	18-19	35-37	15-16	18-19
2 ♂ ♂						
Colombia						
San Pedro	0-11	30-35	20-23	31-42	11-17	15-21
19 ♂ ♂	(3.7)	(32.2)	(21.1)	(36.1)	(14.3)	(17.9)
24 ♀ ♀	0-9	30-35	20-23	31-41	12-18	13-20
	(4.0)	(31.0)	(21.3)	(35.7)	(14.4)	(18.5)
Sonsón	0-6	29-34	19-23	33-42	13-17	16-22
14 ♂ ♂	(1.7)	(31.3)	(21.1)	(38.4)	(15.2)	(18.9)
13 ♀ ♀	0-6	30-34	20-24	36-41	13-19	17-22
	(2.3)	(32.0)	(22.0)	(38.0)	(15.4)	(18.9)
Yarumal	9	31	19	42	—	—
1 ♂						
1 ♀	8	30	20	40	13-14	16-18
Medellín						
1 ♂	8	33	23	41	14	19-20
4 ♀ ♀	6-7	31-35	20-22	36-44	13-15	16-21
	(6.5)	(33.0)	(20.8)	(38.5)	(14.4)	(18.2)
Río Negro	7	32	22	42	14-15	18-19
1 ♀						
Las Palmas	3-9	32	21	35-40	15-16	18-19
2 ♀ ♀						

**El Tambo**

7 ♂ ♂	11-15 (13.1)	31-33 (31.6)	17-20 (18.9)	39-45 (41.4)	14-16 (15.1)	18-21 (20.0)
5 ♀ ♀	13-16 (13.8)	30-32 (31.0)	18-20 (19.2)	40-42 (41.2)	14-16 (14.9)	17-23 (19.7)

**Popayán**

8 ♂ ♂	7-11 (8.8)	29-34 (31.1)	20-22 (20.7)	34-40 (36.9)	11-15 (13.9)	17-19 (17.9)
2 ♀ ♀	8 (8.0)	32 (32.0)	22 (22.0)	37-88 (37.5)	12-14 (13.0)	17-19 (17.7)

**Jericó**

2 ♂ ♂	5-6	31-32	19-20	40-41	14-15	17-19
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**Santa Rosa de Osos**

3 ♂ ♂	0-4 (1.3)	32-34 (33.0)	19-22 (20.7)	33-35 (33.7)	13-14 (13.3)	16-19 (17.5)
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**Río Negro**

1 ♂	6	31	20	38	14	17-18
3 ♀ ♀	6-8 (6.7)	30-33 (31.3)	20-21 (20.7)	36-43 (38.3)	13-18 (16.5)	17-21 (19.8)

**Arracachal**

2 ♀ ♀	2-3	30-32	19	33-36	14-15	19-20
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**Tolima**

15 ♂ ♂	4-8 (6.6)	31-34 (32.4)	20-22 (21.4)	31-41 (37.8)	15-17 (15.7)	17-21 (19.4)
3 ♀ ♀	8 (8.0)	30-34 (32.0)	21-22 (21.3)	34-40 (37.3)	14-16 (15.2)	18-21 (19.8)

**Quindío Mts.**

3 ♂ ♂	6-9 (7.0)	31-32 (31.7)	21 (21.0)	35-36 (35.5)	13-15 (14.2)	18-19 (18.5)
4 ♀ ♀	6-8 (7.0)	30-33 (31.7)	19-22 (21.0)	36-39 (38.3)	14-15 (14.7)	19 (19.0)

TABLE 1 (continued) Characteristics of specimens of *Prionodactylus vertebralis*.  
 Figures represent ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital lamellae Fourth finger	Fourth toe
Río Riposa						
1 ♂	9	30	19	33	14	17
Pueblorrico						
1 ♂	10	31	19	41	15	19
2 ♀♀	9	31	19-20	41-43	16-17	18-19
Pasto						
3 ♂♂	4	30-31 (30.3)	20-21 (20.3)	36-42 (38.7)	14-15 (14.6)	19-22 (20.6)
1 ♀	8	30	21	38	15	19-21
Ecuador						
Northwestern Localities						
5 ♂♂	8-14 (10.2)	30-32 (31.0)	18-21 (19.2)	35-38 (36.8)	14-16 (15.3)	19-22 (20.3)
4 ♀♀	8-11 (9.7)	29-31 (30.0)	18-20 (19.0)	35-37 (36.0)	14-17 (15.5)	19-21 (20.0)
El Chiral						
1 ♀	8	30	19	41	14-17	22
Peru						
1 ♂	0	32	22	28	13-14	18
"Zamora"						
4 ♂♂	10-13 (11.8)	30 (30.0)	18-19 (18.3)	35-38 (36.3)	12-15 (13.9)	18-20 (18.5)
2 ♀♀	6-8 (7.0)	30-33 (31.5)	18-19 (18.5)	35-37 (36.0)	12-13 (12.7)	17-18 (17.3)
"Eastern Ecuador"						
6 ♂♂	7-11 (8.8)	29-31 (30.0)	18-21 (18.8)	35-39 (36.3)	14-16 (14.6)	17-21 (19.3)
6 ♀♀	9-11 (9.8)	30-31 (30.5)	18-20 (19.3)	34-38 (36.0)	13-18 (15.2)	17-22 (19.3)



These two series were also compared in a canonical analysis using the same characters used for the San Pedro specimens (Fig. 4). The first canonical axis accounts for 91 per cent of the dispersion and for the major differences between the samples. The second canonical axis includes largely sexual dimorphism, and accounts for an additional 6 per cent of the dispersion.

In general, when other series are compared with those from near Popayán by canonical analysis, the dark specimens remain distinct. Their greatest similarity is with specimens from western Ecuador, especially in femoral pore number and number of transverse rows of ventral scales (Table 1).

The specimen from Piura, Peru (LACM 55881) is remarkable in several ways. It lacks prefrontals and loreals. It has no middorsal light line. Instead, there are dorsolateral light lines with dark borders on the head and the anterior part of the body, the lines and their borders about one dorsal scale's width wide; these lines disappear near midbody. The number of scales around

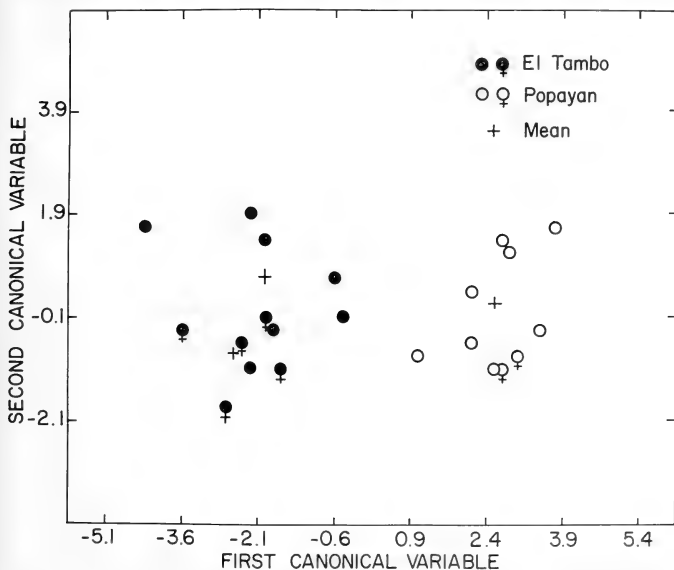


FIG. 4. Distribution and means for individuals of two groups of *Prionodactylus vertebralis* from near Popayán, Colombia, along the first and second canonical axes. The characters on which the analysis was based include total femoral pores, longitudinal rows of ventral scales, transverse rows of ventral and dorsal scales, and total number of supraoculars. The second canonical axis reflects largely sexual dimorphism. These two axes account for 97 per cent of the dispersion. The Popayán sample includes FMNH 43794-803; the El Tambo sample includes FMNH 43804-15.

the midbody is lower than in most Ecuadorian material, especially compared to AMNH 18312, from El Oro.

The absence of the middorsal light line gives this animal a pattern quite unlike that of other specimens of *P. vertebralis*. Dorsolateral light lines are, however, faintly suggested in AMNH 18312. The undivided disc in the lower eyelid may reflect the common tendency for southern species and populations of species of Group II of the Teiidae to have an undivided eyelid disc. The absence of the loreal probably results from fusion with the nasal; the pattern of scales on the side of the head resembles that seen in *P. vertebralis*, except that the first superciliary scale, rather than the loreal, is separated from the supralabials by contact between the frenoocular and nasal.

Eventually, this specimen may be referred to a distinct taxon. In the absence of additional material, and because of its similarities to AMNH 18312, which has faint dorsolateral light lines on the head and anterior part of body and which lacks prefrontals. I consider it a specimen, although highly unusual, of *P. vertebralis*.

**COLORATION.** Most specimens of this species appear to be badly blackened. In life they appear to be considerably more attractive. James A. Peters kindly described the color and pattern of two specimens from Tandayapa, Pichincha, Ecuador, that I have not examined, as follows. Middorsal stripe bronze on snout, darker between eyes, lightening to light bronze or light tan, and

TABLE 2. Characters of three groups of *Prionodactylus vertebralis* from San Pedro, Antioquia, Colombia.

	Total femoral pores	Ventral scale rows	Dorsal scale rows	Scales around midbody region
<b>Paratypes</b>				
6 ♂♂	0-6 (2.7)	20-21 (20.8)	30-34 (31.8)	31-37 (33.2)
4 ♀♀	0-5 (1.7)	20-21 (20.5)	31 (31.0)	33-38 (34.2)
<b>"Topotypes"</b>				
5 ♂♂	0-11 (2.2)	20-21 (20.4)	32-34 (32.8)	32-42 (35.2)
4 ♀♀	0-3 (0-7)	21-23 (21.5)	30-34 (32.0)	31.37 (32.7)
<b>"Non-types"</b>				
8 ♂♂	0-11 (5.7)	20-23 (21.5)	31-35 (32.0)	34-42 (39.0)
16 ♀♀	0-9 (5.3)	20-23 (21.5)	31.35 (32.9)	35-41 (37.0)

Paratypes = UMMZ 56031 (8 specimens, CAS 54809-10); "topotypes" = MCZ 14652-57, USNM 75967, 120789, BMNH 1925.5.1.11; "non-types" = AMNH 32737-57, MCZ 29680, 46448.

finally almost to white over sacrum. Three to four scales on either side of middorsal stripe jet black; rest of side olive brown. Ocelli along sides jet black, with bluish-white centers. A reddish area around first two ocelli on neck; another over sacrum and on lateral edge of tail. Ocelli all along side onto tail. Forelimb dorsally has black spots with bright yellow centers; remainder of limb olive brown. Hind limb olive brown with black mottling. Dorsum of head on either side of middorsal line black, shading to dark brown laterally. A bronze line over eye, another from nostral along labials, below tympanum to shoulder; behind the shoulder, much lighter, a dirty yellow, broken into spots each with an irregular black border. The chin and throat a soft chocolate tan; entire chest, belly, anal region, tail, and lower side of hindlimbs a vivid orangy-red, spotted and dotted with black. Ventral side of forelimbs olive-brownish. Iris a deep glowing red.

The largest male examined is 63 mm snout to vent; the largest female, 68 mm. Twenty-five males with tails intact have tail over snout-vent length ratios of 1.7–2.3, mean 1.99; 20 females have a range of 1.7–2.2, mean, 1.86.

**SEXUAL DIMORPHISM.** This species shows relatively little sexual dimorphism, since the femoral pores number about the same in males and females. There is probably considerable sexual difference in color in living individuals, but most of the material examined is badly blackened after preservation.

**REMARKS.** The holotype of *P. vertebralis* came from Intac, Imbabura, Ecuador. Although some of the locality data for specimens collected by Buckley appear to be incorrect (Peters 1955), that Intac is the correct locality is supported by recent collections of specimens from several localities close to Intac in western Ecuador (Fig. 5).

There are records of *P. vertebralis* from eastern Ecuador. AMNH 60586–97, reportedly from Mera, Tungurahua, at about 1000 m, are typical of the species; almost certainly they are incorrectly labelled.<sup>4</sup> Another record, BMNH 1933.6.24.82–87 from Zamora in Chinchipe-Zamora (Parker 1934) may be based on specimens from Loja rather than Zamora, since many of the specimens in that collection of Carrion's came from Loja.

The altitudinal range of *P. vertebralis* in Ecuador (700–1600 m) suggests that it should be confined to one side of the Andes or the other. A closely related species, found on the eastern Andean slopes, is described below. Most of the recent records for *P. vertebralis* come from the western Andean slopes. I doubt records from the eastern slopes.

The holotype of *P. palmeri* Boulenger (1908), BMNH 1909.4.30.63 (re-registered as 1946.8.31.43) is an adult female collected from San Antonio, Valle del Cauca, Colombia by M. G. Palmer. Boulenger's description and figure are excellent. The holotype falls within my concept of *P. vertebralis*.

<sup>4</sup>James A. Peters (personal communication) has drawn a similar conclusion about AMNH 49943–46, 49948–50, specimens of *Atelopus longirostris* collected by C. Ollala, and supposedly from Mera.

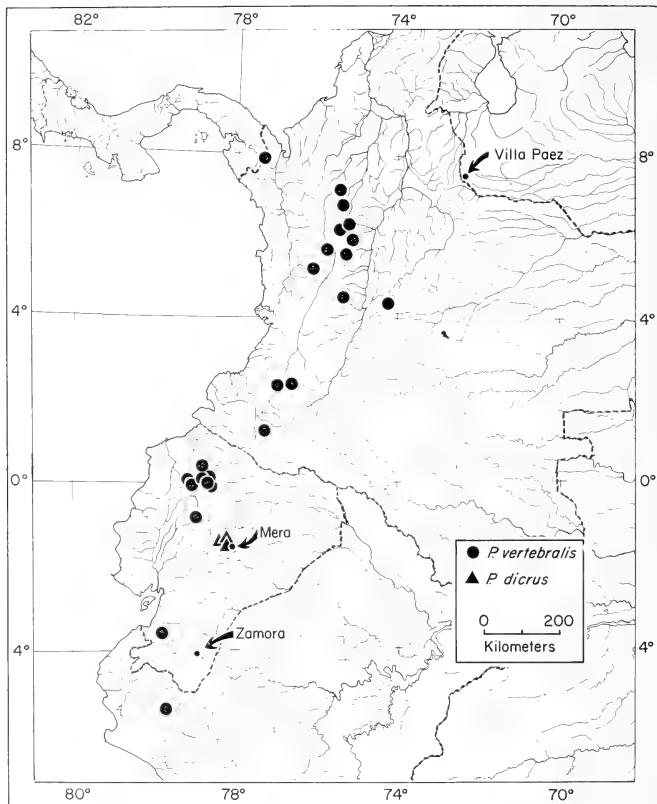


FIG. 5. Northwestern South America, showing ranges for *Prionodactylus vertebralis* and for *P. dicrus*, new species. Certain localities discussed in the text are also indicated.

UMMZ 56037, the holotype of *P. marianus* Ruthven (1921) was collected by Hno. Nicéforo María near San Pedro, Antioquia, Colombia. I have examined this specimen and it falls within my concept of *P. vertebralis*.

There is some question about the number of paratypes of *P. marianus*. Ruthven gave no indication of the number of specimens that he examined. The paratypes recorded at the University of Michigan Museum of Zoology originally included 13 catalogued as 56031. Two of these were sent to the California Academy of Sciences (CAS 54809-10); one was sent to the

Field Museum of Natural History (FMNH 109860). There are still 8 specimens catalogued as 56031 at the University of Michigan. Two of the original paratype series are thus not accounted for; one is probably BMNH 1925.5.1.11.

Although they are not included in Barbour and Loveridge's (1929) list of typical material in the Museum of Comparative Zoology, Barbour and Loveridge (1946) listed 10 specimens (MCZ 14651-60) as paratypes of *P. marianus*, and indicated that they were received as an exchange from the University of Michigan. These specimens apparently were examined by Ruthven before he described *P. marianus* (letter to T. Barbour, 10 June 1921). Ruthven clearly indicated, however, that many Colombian specimens, presumably including MCZ 1465-60, were sent by Barbour to Ruthven for identification. Ruthven identified the MCZ *Prionodactylus* as conspecific with his new form.

Ruthven stated that two of the paratypes have 3-3 supraoculars. I identify these as UMMZ 56031C and CAS 54809. Since MCZ 14653 also has 3-3 supraoculars, it seems likely that this individual, and thus the entire series, was not considered a paratype by Ruthven. If this is true, USNM 120789, listed by Cochran (1961) as a paratype of *P. marianus*, likewise is not, since it was formerly MCZ 14660.

I have been unable to examine any specimens of *Euspodylus ampuedae* Lancini (1968) and Lancini's description does not describe several features that I consider diagnostic of genera and species of teiid lizards of Group II. I believe, however, that Lancini has redescribed *Prionodactylus vertebralis*, and that *E. ampuedae* should be placed as a junior synonym of that species (new synonymy). My main reason for thinking that *E. ampuedae* is conspecific with *P. vertebralis* is the pattern of the light lip line, described by Lancini as beginning on the mental, crossing the middle of the second supralabial, the upper border of supralabials 3, 4, and 5, and continuing to below the ear opening and above the forelimb insertion. This pattern is duplicated in *P. vertebralis* (Fig. 2) and in *P. dicrus*, new species, but in no other *Prionodactylus*. Most of the other described features of *E. ampuedae* can be matched in the sample of *P. vertebralis* that I have examined. Few of these features, however, are diagnostic of any species. I interpret the two loreals to include a superior loreal separated from the supralabials by an inferior frenoocular.

Two characteristics of *E. ampuedae* suggest that the present synonymy is not correct: the number of scales around the midbody region (27-29) reported by Lancini is less than I have observed in *P. vertebralis* (31-45 in Colombian specimens); no middorsal light line was described for the holotype and female paratypes of *E. ampuedae*, although such a line is almost always present in *P. vertebralis*. Both of these differences could easily be accounted for, however; the former by a different convention in counting the scales, especially the minute lower lateral scales; the latter by desquamation of the specimens, which makes the middorsal light stripe almost invisible while leaving the lip line conspicuous. The male paratype, however, does

have a middorsal light stripe. Alternatively, *E. ampuedae* may be a distinct taxon.

*E. ampuedae* was described from Villa Paez, Estado Tachira, Venezuela (Fig. 5).

**BIOLOGY.** Virtually no biological data are available to me. One specimen from Pichincha was collected in the debris of a large log near a small, fast-flowing stream. Many of the females contain two leathery-coated eggs, one in each oviduct.

**RANGE.** Specimens of *Prionodactylus vertebralis* are known from the Pacific slopes of Ecuador and northern Peru at elevations of 700 to 1600 m above sea level, from the Cauca and Magdalena valleys of Colombia at elevations of 1500 to 2500 m, from far southern Panamá, and possibly from Estado Tachira in Venezuela.

#### Specimens Examined

COLOMBIA: ANTIOQUIA, Jericó (1967 m) USNM 84967, 92496; Las Palmas, SE of Medellín: FMNH 63824-25; Medellín (1538 m) AMNH 32758-59, 32772-73, 32775; Río Negrito; 15 km E of Sonsón: FMNH 63823; Río Negro (2120 m) AMNH 38950-53; San Pedro (2560 m) UMMZ 56031 (8 specimens), CAS 54809-10, paratypes of *Prionodactylus marianus*; BMNH 1925.5.1.11, MCZ 14652-57, 29680, 46448, USNM 75967, 120789, AMNH 32737-57; Santa Rosa de Osos (2640 m) AMNH 32766-68; Sonsón (2545 m) AMNH 32725-36, 35302, UMMZ 57702 (4), 89421 (10); Yarumal (2300 m) FMNH 63821-22. CALDAS, Pueblorrico (1560 m) BMNH 1910.7.11.19-21. CAUCA, Munchique, near El Tambo (2000 m) FMNH 43804-15; Popayán (1700 m) FMNH 43794-803. CUNDINAMARCA, Arracachal (200 m) UMMZ 131677-78. NARIÑO, Pasto (2594 m) AMNH 91768-71. TOLIMA, no other locality: UMMZ 56441 (4), 63801 (4); Quindío Mountains: MCZ 15953-57, 15959, USNM 75968. VALLE DEL CAUCA, Río Riposa Virology Field Station, USNM 151620; San Antonio (1850-2200 m) BMNH 1909.4.30.63, reregistered as 1946.8.31.43, holotype of *Prionodactylus palmeri*.

ECUADOR: COTOPAXI, below Sigchos in Toachi Valley (1000 m) USNM 193944. EL ORO, El Chiral (1350 m) AMNH 18312. IMBABURA, Intac (1000 m) BMNH 78.1.25.13, reregistered as 1946.8.31.35, holotype of *Cercosaura vertebralis*. PASTAZA, Mera (1000 m) AMNH 60586-97. PICHINCHA, Mindo (1050 m) UMMZ 119714; 3 km E of Nanegal Chico (1600 m) USNM 193946; Pacto (1000 m) USNM 193941-43; below Pacto (900 m) USNM 194065; Palma Real (900 m) USNM 193945; Pandayacu USNM 193940; Río Blanco near mouth of Río Yambi (700 m) USNM

193947; Río Caoni (200–300300 m) USNM 193939. Zamora-Chinchi, Zamora (800 m) BMNH 1933.6.24.82–87.

PANAMA. Darien, Cerro Mali UKMNH 76174–75.

PERU: Piura, 16 km E of Canchaque LACM 58811.

*Prionodactylus dicrus*, new species  
(Fig. 6)

*Euspondylus festae*, Burt and Myers, 1942:319.

HOLOTYPE. FMNH 36708, an adult female from Ecuador, Tungurahua, Matopo; 1300 m; June 1938; William Clarke-MacIntyre.

PARATYPES. FMNH 28043, 134152, USNM 193592: Ecuador, Tungurahua, Baños (1800 m); BMNH 1912.11.1.34: Topo (1500 m); AMNH 24144, CAS-SU 8253: Pastaza, Abitagua (1100–1500 m); USNM 193590–91: headwaters of Río Arajuno (about 600 m); USNM 194383: between Baños and Puyo (900 m).



FIG. 6. Side view of the head of *Prionodactylus dicrus*, new species (USNM 194383, paratype).  $\times 6$ . The loreal is separated from the supralabials by contact between the nasal and frenoocular. The light labial line is less conspicuous than in *P. vertebralis*, but follows essentially the same course.

DIAGNOSIS. A member of the genus *Prionodactylus* closely allied to *P. vertebralis* in having an undivided frontonasal and the loreal scale separated from the upper labial scales by contact between the nasal and frenoocular; these two features distinguish *P. vertebralis* and *P. dicrus* from all other species of the genus. *P. dicrus* differs from *P. vertebralis* in that it has two light lines on the snout, superciliary scales and anterior parts of the body that fuse posteriorly to form a median light line, rather than a median light line from the snout to the tail; and marked sexual dimorphism in femoral pore number (20–25 in males of *P. dicrus*, 7–11 females; 0–16 in males and females of *P. vertebralis*. Subdigital lamellae of forefoot without tubercles (Fig. 7).

DESCRIPTION OF HOLOTYPE. Rostral broadly in contact with frontonasal, narrowly in contact with nasal and first supralabial. Frontonasal wider than long. Two prefrontals forming a short median suture. Frontal length about 1.4 times breadth, in contact with prefrontals, second supraoculars, and frontoparietals. Paired prefrontals, about twice as long as broad, in contact medially. Interparietal 1.4 times as long as broad. Parietals slightly longer



FIG. 7. Underside of left forefoot of *Prionodactylus dicrus*, new species (USNM 4688, paratype) showing the nontuberculate subdigital lamellae.  $\times 7$ .



than wide, each in contact with interparietal, prefrontal, fourth supraocular, a small postocular, a lateral (narrowly) and medial temporal (broadly), and a paramedian occipital scale. A median occipital, a pair of paramedian occipitals, and a largish pair behind these that could be called postoccipitals. Four supraoculars on each side, the anteriormost small, second largest, fourth slightly larger than third. Superciliary series complete, 4 on right, 5 on left, the first not expanded onto dorsal surface of head. Nasal scale low, elongate, extending past middle of second supralabial, apparently divided on right, entire on left. A narrow, diagonally placed loreal separated from supralabials by contact between nasal and small, triangular frenoocular. Loreal bounded by nasal, prefrontal, first supraocular (narrowly), first superciliary, and frenoocular. Three (left) or 4(right) very narrow suboculars. A diagonally placed row of 3 somewhat larger postoculars. A pigmented disc in the lower eyelid, divided into four sections by vertical grooves. Seven supralabials on each side, the space between the sixth and seventh and the lateral temporal scale filled with about three longitudinal rows of elliptical scales. These and the temporal scales weakly marked with fine wrinkles. External ear opening round; tympanum deeply recessed, unpigmented, larger than external ear opening. Mental followed by 1 unpaired and 3 (left) or 4 (right) paired chin shields, all in contact with infralabials, the first (left) meeting the first and second (right) at midline, the posterior ones separated by pregonals. Pregonals (Ruibal, 1952) irregular, smooth, smallest on midline, in chevrons, not forming transverse rows. Gular crease distinct, marked by small scales. Gulars smooth, rounded posteriorly, larger in anteriormost row; a row of seven pairs of widened gular scales on midline. Collar distinct; scales smooth, rounded posteriorly, six in number including a large median pair.

Median anterior dorsal scales almost square, wrinkled; remainder of dorsal body scales elongate, hexagonal, keeled, with minute ridges that converge toward posterior tips of keel (Fig. 8); in 33 rows between occipital and posterior margin of hind limbs. Lateral scales on neck, in axilla, and in groin small granules; a weak fold from tympanum to lateral edge of collar. Lateral body scales between limb insertions in two sizes; above, a zone about 6 scales high in which larger lateral rows are intercalated between ends of transverse rows of dorsals; below, a granular series, almost a groove, three to five scales high. Ventrals smooth, quadrangular, rounded at posterior corners, in 8 longitudinal and 20 transverse rows between collar and anterior preanal scales. Two rows of smooth preanal scales, the posterior row with four elongate medial and two minute lateral scales, the 2 median widest: the anterior row with 2 relatively larger medial and 2 smaller lateral scales. Femoral pore series divided; a single pore near each knee, 2 (right) and 3 (left) minute pores near groin, the innermost virtually a preanal pore. Pores usually in center of scale.

Scales on forelimb large, very weakly keeled, weakly wrinkled on anterior and dorsal surfaces, granular beneath. Subdigital lamellae undivided, slightly swollen, but not forming a series of projections (Fig. 7). Scales along margin



FIG. 8. Dorsal scales of *Prionodactylus dicrus*, new species USNM 194383, paratype) showing keel and minute ridges converging posteriorly.  $\times 20$ .

between thumb and wrist conspicuously enlarged, with a free posterior edge. On palm scales granular. Dorsal thigh scales large, keeled and wrinkled; anterior and ventral scales smooth; posterior scales granular. Anterior shank scales large, keeled and wrinkled; ventral scales very large, smooth; posterior scales granular. A row of intercalated scales on posterior side under bases of digits one through four, the subdigital lamellae in these areas forming tubercles. Digits weakly compressed, claws relatively robust, curved. Caudal scales above, like dorsals, below, like ventrals, forming complete rings around tail.

Color and pattern generally obscure; ground color olive; a pair of thin light lines faintly discernable beginning on rostral, following canthus rostralis, superciliaries, and median temporals, becoming conspicuous on body as light bluish lines a single dorsal's width wide, gradually converging posteriorly, fusing at the nineteenth transverse row of dorsal scales, and continuing posteriorly to tip of unregenerated tail as a light line 2-3 scales wide.

Another, even thinner light line, beginning at edge of first supralabial, continuing along dorsal edge of third supralabial, across remaining supralabials to lower edge of tympanum, along the weak neck fold, along the body above the arm insertion and along upper edge of laterals almost to groin. Ventrally, a uniform lead gray.

VARIATION. A median occipital is present in all individuals, the prefrontals are in contact in all, and the loreal is separated from the infralabials in all. Eight of the specimens examined have 4-4 supraoculars; USNM 193590 and FMNH 28043 have 3-3; on the left in the former the location of a fourth, posterior supraocular is indicated by grooves that do not meet in the center of the very large third. The first supraocular is very small in all, and occupies the space on the top of the head usually filled in *Prionodactylus* by a dorsal expansion of the first superciliary; as a consequence that scale ends at the canthus rostralis. There is a pair of large median collar scales in all specimens. The femoral pores in the females number far fewer than they do in males (Table 3). The series in females is divided in all cases, with at least one essentially preanal pore and at least one near the knee. There are enough scales between these sets so that if all had pores, there would be little sexual dimorphism in total number. One specimen (USNM 193590) has 6 rather than 8 longitudinal rows of ventral scales. The largest male examined is 40 mm snout to vent, the largest female, 53 (the holotype). Other variational data are included in Table 3.

RELATIONSHIPS. The relationships of *P. dicrus* are with *P. vertebralis*. This is indicated not only by the features mentioned in the diagnosis, but also by numerous details of structure. A striking feature shared by these two taxa is the conspicuous wrinkling on many of the scales, especially the dorsal body scales (Fig. 8).

Specimens of *P. vertebralis* have been reported from the Amazonian slopes of the Andes at Mera in Pastaza (AMNH 60586-97) and from Zamora in Chinchipe-Zamora (BMNH 1933.6.24.82-87; Parker 1934). While it is possible that *P. vertebralis* is sympatric with *P. dicrus* near Mera, I doubt it. I suspect that the American Museum specimens are mislabelled. The alti-

TABLE 3. Characteristics of 10 specimens of *Prionodactylus dicrus*, new species. Figures represent ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital Fourth finger	lamellae Fourth toe
5 ♂♂	20-25 (22.2)	29-31 (30.4)	20-21 (20.8)	38-42 (40.2)	15-17 (15.8)	20-23 (21.0)
5 ♀♀	7-11 (8.4)	31-33 (31.6)	20-22 (20.8)	38-43 (40.8)	15-17 (16.0)	21-22 (21.3)

tudinal range of *P. vertebralis* in Ecuador (up to about 1600 m) suggests that it would be confined to one side or the other of the Andes. I believe it probable that the specimens reported by Parker from Zamora actually came from Loja in the province of Loja, some 50 kilometers to the west, whence much of the material collected by Carrion and reported in the same paper came; this would be more consistent with other distributional records. On the whole, I am more inclined to believe the Zamora record than the Mera record, since there are numerous collections from Mera, and no other individuals of *P. vertebralis* have turned up in that area. Additional collecting near Zamora, where the fauna is less well known, may yield new specimens of *P. vertebralis*.

The derivation of *P. dicrus* and *P. vertebralis* from a common ancestor as a result of isolation of populations on each side of the Andes seems quite likely. The time or area of the transgression by some ancestral population are not known. The patterns of *P. dicrus* and *P. vertebralis* could easily be changed one into the other. Many specimens of *P. vertebralis* have already some lightening along the superciliary series.

DERIVATION OF NAME. The name is from the Greek  $\delta\epsilon\kappa\rho\sigma$ , forked. It is used as an adjective modifying *Prionodactylus*.

RANGE. Specimens of *Prionodactylus dicrus* are known from elevations of perhaps 600 to perhaps 1800 m above sea level on the eastern Andean slopes of central Ecuador.

#### Specimens Examined

These include only the holotype and paratypes.

#### *Prionodactylus manicatus* (O'Shaughnessy)

DEFINITION. A single frontonasal. Loreal almost always in contact with frontonasal and supralabials. At least some indication of a light labial line beginning under eye and continuing to tympanum. Subdigital lamellae either smooth or with a single median tubercle.

VARIATION. I have examined 48 specimens that I refer to this species. These come from localities in Amazonian Ecuador, Peru, and Bolivia, and from the Bolivian Chaco (Fig. 9). The sample shows considerable geographic variation (Table 4); I have grouped the populations, somewhat arbitrarily, into two subspecies. Geographical variation in several characters is discussed below.

1. Posterior preanal scales. Usually females of teiid lizards of Group II have more posterior preanal scales than males have. Although there is slight

sexual dimorphism in this character in *P. manicatus*, the dominant trend is a geographical one, independent of sex. Specimens from Ecuador usually have 2 large lateral and 1 narrow median posterior preanal scale. A single male (MCZ 45779) has only 2 posterior preanals. Two females have additional slivers lateral to the 3 major preanal scales. Three posterior preanals also occur in specimens from northern and central Peru. The female from Oxapampa and the two from Divisoria have the additional lateral slivers. All 11 specimens for which I have data from Bolivia and southern Peru have 4 posterior preanals; they are almost equally wide.

2. Enlarged collar scales. Specimens from Ecuador have 2 large collar scales that form almost the entire collar. These 2 large scales form a continuation of the pairs of large gular scales, although they are wider than the widened gulars. Two widened scales also occur in AMNH 90673, from Luisiana in central Peru. The Bolivian and the remainder of the Peruvian specimens have a median and 2 paramedian collar scales of about equal size, except for UMMZ 96547 and FMNH 40424, in which the median

TABLE 4. Characters of 33 specimens of *Prionodactylus manicatus*. Figures are ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital lamellae Fourth finger	Fourth toe
<i>P. m. manicatus</i>						
Ecuador and Northern Peru						
7 ♂♂	26-30 (27.9)	39-42 (40.3)	19-20 (19.3)	43-52 (46.6)	10-13 (11.3)	14-18 (15.8)
8 ♀♀	24-28 (26.6)	37-40 (39.1)	17-20 (18.9)	37-49 (44.3)	10-12 (11.4)	14-17 (15.7)
Divisoria						
1 ♂	21	34	20	43	12	16-17
2 ♀♀	16-17	32-34	19-21	41-42	12	17-18
Oxapampa						
1 ♀	14	34	18	38	12	—
Luisiana						
1 ♀	15	36	17	40	12	17-18
<i>P. m. bolivianus</i>						
Southern Peru						
4 ♂♂	15-19 (17.0)	33-38 (36.3)	17-20 (18.7)	36-40 (38.3)	12-15 (13.6)	17-21 (19.8)
6 ♀♀	5-9 (6.8)	35-37 (35.7)	17-19 (18.5)	35-41 (37.8)	13-15 (14.2)	17-23 (20.6)
Bolivia						
1 ♂	16	36	20	36	13-14	21-22
2 ♀♀ <sup>1</sup>	3-7	35-40	18-21	33-41	14-15	20-23

<sup>1</sup>Italicized numbers indicate holotype of *P. m. bolivianus*.

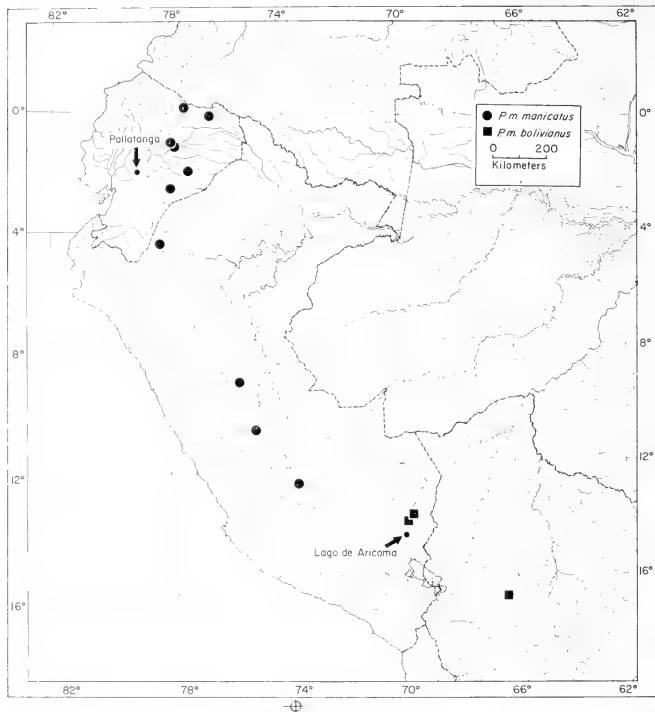


FIG. 9. Collection localities for *Prionodactylus manicatus* in Ecuador, Peru, and Bolivia. Localities mentioned in the text are also indicated.

scale is fused with one of the lateral collar scales in an asymmetrical arrangement.

3. Disc is lower eyelid. The translucent disc in the lower eyelid is unpigmented in all specimens examined. In Ecuadorian and northern and central Peruvian specimens, the disc is divided into 2 or 3 segments by vertical grooves, except for FMNH 134398. The Bolivian and southern Peruvian material has the disc in the lower eyelid undivided except for FMNH 40424 and BMNH 1946.8.31.37, one of the syntypes of *Prionodactylus okendeni*. This pattern of geographic variation, divided eyelid discs in the north, undivided ones in the south, also occurs in other widespread teiids of Group II (*Cercosaura ocellata* and *Neusticurus ecleopus*; Ruibal, 1952; Uzzell, 1964).

4. Longitudinal rows of ventral scales. The number recorded is the number of longitudinal rows at midbody not interrupted by smaller scales for at least

four transverse rows. Most of the specimens from Ecuador have 6 longitudinal rows if the criterion is strictly interpreted, but in two, the lateral rows would be counted as rows of ventrals by most observers, and a third specimen clearly has eight rows near midbody. The northern and central Peruvian specimens generally have 8 longitudinal rows, except for AMNH 90673 from Luisiana in central Peru, which has 6. Bolivian and southern Peruvian specimens have 8 longitudinal rows of ventrals except for BMNH 1946.8.31.37.

5. Coloration. In Ecuador, at one extreme of development, there is a light line from the first supralabial along the lips, through the lower edge of the external ear opening, above the arm, along the side, finally disappearing near the hind limb insertion. This light line is bordered below by dark from the third infralabial posteriorly. More usually, this band begins on the first supralabial and terminates just posterior to the forelimb insertion; it is constricted or broken where it crosses the lateral extension of the collar. The northern and central Peruvian specimens also have this less well-developed light line, broken at the collar, and stopping just posterior to the arm. The specimens from Bolivia and southern Peru have a much reduced light lateral line, beginning under the middle or posterior part of the eye, having less regular margins, and generally broken somewhere anterior to the collar. There is usually an ill-defined line above the arm insertion.

6. Subdigital lamellae. The generic name *Prionodactylus* derives from the tubercles of the subdigital lamellae of northern population (Fig. 1). Such tubercles are also present in the central Peruvian populations, although they seem less well developed; this may be partly due to the condition of these older specimens. The specimens from Bolivia and southern Peru have little or no swelling of the subdigital lamellae.

The toes of the central and southern Peruvian specimens and of the Bolivian specimens have many of the proximal subdigital lamellae doubled. When tubercles are present under the toes as in the central Peruvian specimens, it is the inner part that forms the tubercle.

7. Other characters. Table 4 lists ranges and means for several other characters. Total femoral pore number appears to decrease from north to south. Ecuadorian and northern Peruvian specimens show almost no sexual dimorphism in pore number; the dimorphism increases markedly to the south, where females have far fewer pores than males. The number of dorsal scales between occiput and posterior margin of hind limbs decreases from north to south, as does the number of scales around the midbody region. Subdigital lamellae, in contrast, increase in number from north to south.

Because the samples of animals come from separated areas, it is impossible to be certain that they are connected by series of potentially interbreeding populations. The general pattern of variation from north to south, without reversals, and the fact that the central Peruvian populations resemble the southern populations in some characters (collar scales, longi-

tudinal rows of ventral scales), the northern populations in some others (preanal scales, disc in lower eyelid, coloration), and are intermediate in yet others (femoral pores, scales around midbody region, subdigital lamellae) suggest that these populations are all conspecific. Certainly, the populations here referred to *P. manicatus* are more closely related to each other than any of them is to any other species of *Prionodactylus*. This is attested by the single frontonasal, the contact between the loreal and the supralabials, the presence of a light lip line, and the generally high number of dorsal scales and scale rows around the midbody region.

*Prionodactylus manicatus manicatus* (O'Shaughnessy)  
(Fig. 10)

*Cercosaura (Prionodactylus) manicata* O'Shaughnessy, Proc. Zool. Soc. London 1881: 231.

SYNTYPES. BMNH 80.12.8.8, reregistered as 1946.8.2.1, an adult male from Ecuador, Chimborazo, Pallatanga, received from Buckley, and BMNH 80.12.8.5-7, reregistered as 1946.8.31.15-17, three adult females from Ecuador, Pastaza, Canelos, also received from Buckley.

DEFINITION. A subspecies of *P. manicatus* distinguished by having two or three, rather than four, large posterior preanal scales, two widened collar scales at midline, the transparent disc in the lower eyelid divided into two or three sections by vertical grooves, a light lip line beginning on the first



FIG. 10. Side view of the head of *Prionodactylus manicatus manicatus* (UKMNH 109819).  $\times 5$ . The loreal is in contact both with the frontonasal and the supralabials. The light lip line is broader and straighter than in *P. vertebralis* and *P. dicrus*.



supralabial, and subdigital lamellae of toes and fingers forming a serrated series of tubercles (Fig. 1).

SEXUAL DIMORPHISM. This subspecies of *P. manicatus* shows remarkably little sexual dimorphism, although females from central Peru appear to have fewer femoral pores than the single male examined.

SIZE AND TAIL LENGTH. The largest male examined was 61 mm snout to vent; the largest female, 73 mm. Two males with tails intact have tail over snout-vent length ratios of 1.7 and 1.9, mean 1.84; four females with tails intact have tail over snout-vent length ratios of 1.4 to 1.7, means 1.55.

REMARKS. Although syntypes of *P. manicatus manicatus*, which I have examined, supposedly came from both the Pacific and the Amazonian slopes of Ecuador, the specimen from Pallatanga is undoubtedly mislabelled, as was much Buckley material reported from both Pallatanga and eastern Ecuadorian localities (Peters 1955; Uzzell 1961).

RANGE. Amazonian slopes of the Andes from central Peru north to Ecuador (Fig. 9), at elevations of 300 to perhaps 1600 m above sea level.

*Prionodactylus manicatus bolivianus* Werner  
(Fig. 11)

*Prionodactylus bolivianus* Werner, 1899, Zool. Anz. 22: 481.

*Prionodactylus Okendeni* Boulenger, 1907, Ann. Mag. Nat. Hist. ser. 7, 19: 486.

HOLOTYPE. MNHN 00.4, an adult female from the Chaco of Bolivia; the specimen was received from Werner (Guibé 1954).

DEFINITION. A subspecies of *P. manicatus* distinguished by having 4 large posterior preanal scales, 3 subequal collar scales at midline, the transparent disc in the lower eyelid not divided into sections by vertical grooves, light lip line beginning under eye, and subdigital lamellae of toes and fingers except at bases of toes 3 and 4 not forming a serrate series of tubercles.

SEXUAL DIMORPHISM. Females have far fewer femoral pores than males, but little other sexual dimorphism is evident. The males I have examined have 2 or 3 black ocelli with light centers, but these are ill defined. Boulenger (1907) reported ocelli in male syntypes of *P. okendeni*.

SIZE AND TAIL LENGTH. The largest male examined was 56 mm snout to vent; the largest female, 58 mm. Two females with intact tails have tail over snout-vent length ratios of 1.7 to 2.1, mean 1.91.

REMARKS. I have examined the holotype of *P. bolivianus*. The description offered by Werner is adequate. I count 4 femoral pores on the right side,



FIG. 11. Side view of the head of *Prionodactylus manicatus bolivianus* (FMNH 40422).  $\times 6$ . The loreal is in contact with the supralabials, the small, oval disc in the lower eyelid is not divided, and the light lip line is absent beneath and in front of the eye.

3 on the left; these are weakly developed. There are 3 supraoculars on each side; the first superciliary is expanded onto the dorsal side of the head. The loreal is in contact with both the frontonasal and the supralabials. The small oval translucent disc in the lower eyelid is undivided. There is an even number of collar scales at midline, and they are not particularly widened. There is a light middorsal area 2-3 scales wide bordered by dark stripes that end on the tail. Virtually all of these features can be found in the specimens referred to *P. M. bolivianus*.

I have also examined a second specimen (ZSM 66/1920) identified by Werner as *P. bolivianus*. It is an adult male, purchased from Werner in 1920, and collected by Schluter in Bolivia in 1907. This individual has 8 longitudinal rows of ventral scales, three large posterior preanals, 3-3 supraoculars, a small undivided oval disc in the lower eyelid, the first superciliary expanded onto the dorsal surface of the head, the loreal in contact with both the frontonasal and the supralabials, and 3 subequal collar scales at midline.

The only definite statements about range in Bolivia are Werner's locality in Chaco, and a specimen (UMMZ 69547) from the Departamento de Cochabamba. I suspect that the Chaco is too dry for this species, but the fauna of Bolivia is too ill known for this to be more than conjecture.

Many specimens of *Opipеuter xestus* in collections from Bolivia have been labelled *Prionodactylus bolivianus*; they differ from the holotype of *P. bolivianus* in being totally devoid of keeling on the scales, rather than

strongly keeled especially on the dorsal and lateral body and caudal scales. Werner did not mention keeling in his description of *P. bolivianus* but such keeling is implied by his generic placement of the taxon. The undivided disc in the lower eyelid of *P. m. bolivianus* is small, oval, and translucent, whereas in *O. xestus* it is relatively enormous, nearly circular, and transparent (Uzzell 1969).

The syntypes of *Prionodactylus okendeni* Boulenger (1907) are BMNH 1905.5.31.2-8, reregistered as 1946.8.31.36-42, from Puno, Oconeque, at about 1750 m above sea level, and 1902.11.28.3, from Peru, Puno, Santo Domingo, about 1500 m above sea level. I have examined these specimens, but only data on 1946.8.31.37 are included in the discussion of variation and in Table 4. The description by Boulenger places the syntypes within the variation that I have observed in southern Peruvian specimens. I know of no characters that will distinguish the syntypes of *Prionodactylus okendeni* from the Bolivian material identified by Werner as *P. bolivianus*. I therefore consider *P. okendeni* a junior synonym of *P. bolivianus* Werner (cf. Peters and Donoso-Barros 1970).

AMNH 1705-06, recorded as from Lake Aracona, Juliaca, Peru, probably came from near Santo Domingo in Puno, Peru (cf. Dunn 1942, Uzzell 1970).

RANGE. Specimens of *P. m. bolivianus* are known from the Department de Puno in southern Peru south to the Departamento de Cochabamba or possibly the Chaco of Bolivia, at elevations of about 1200-17500 m above sea level (Fig. 9).

#### Specimens Examined

##### *Prionodactylus m. manicatus*

ECUADOR: NAPO: Río Licuna USNM 194066; Río Pindo USNM 194068; Puerto Libre, Río Aguarico (570 m) UKMNH 119405-7; Puerto Napo (463 m) UIMNH 55781; Santa Cecilia (340 m) UKMNH 109817-18, 119408-09; Río Viclano USNM 194067. PASTAZA, Río Pastaza between Canelos and Río Marañón MCZ 37261. MORONA-SANTIAGO, between Río Pastaza and Río Santiago MCZ 45779.

PERU: AMAZONAS: Río Cenipa Valley AMNH 56494. CUZCO, Río Apurímac, Luisiana (500 m) AMNH 90673. HUANUCO, Divisoria (1300-1600 m) FMNH 55986-88. PASCO, Oxapampa (1800 m) FMNH 134398.

##### *Prionodactylus m. bolivianus*

BOLIVIA: no other locality: ZSM 66/1920. CHACO: MNHN 00.4, holotype of *Prionodactylus bolivianus*; DEPARTAMENTO COCHABAMBA: UMMZ 69547. PERU, PUNO (Carabaya) Santo Domingo (1862 m) FMNH 40420-25;

(Sandía) Oconeque (1956 m) BMNH 1905.5.31.3, reregistered as 1946. 8.31.37, syntype of *Prionodactylus okendeni*; Juliaca, Lake Aracona (=Lago de Aricoma) AMNH 1705-06.

*Prionodactylus eigenmanni* Griffin

*Prionodactylus eigenmanni* Griffin, 1917, Ann. Carnegie Museum 11: 316.

HOLOTYPE. An adult female (CM 918) collected by José Steinbach in the Provincia de Sara, Beni, Bolivia, 400 m above sea level.

DEFINITION. A single frontonasal. Loreal in contact with frontonasal and supralabials. Two large collar scales. Subdigital lamellae of three kinds (Fig. 12): simple, with a median tubercle, or with two lateroventral tubercles.



FIG. 12. Undersurface of the right forefoot of *Prionodactylus eigenmanni* (BMNH 1927.8.1.152), showing the single and double tubercles of the subdigital lamellae.  $\times 18$ .

Translucent disc in lower eyelid oval, not divided into segments by vertical grooves. Marked sexual dimorphism in femoral pore number. No conspicuous dorsal light lines; no continuous light line along supralabials.

VARIATION. I have examined the holotype and six other individuals. There is very little variation (Table 5). All specimens have a median occipital, six transverse rows of ventral scales, 3-3 supraoculars, the first superciliary expanded onto the dorsal surface of the head, an undivided translucent disc in the lower eyelid, and two very wide collar shields at midline.

In addition to the sexual dimorphism in femoral pore number, the single female examined has four rather than two posterior preanals. Griffin interchanged anterior and posterior preanals in his description.

The largest male examined is 38 mm snout-to-vent; the largest female, 40. Three males with intact tails have tail over snout-vent length ratios of 1.2 to 1.4, mean 1.30.

REMARKS. Burt and Burt (1931) placed this species in the synonymy of *P. bolivianus* Werner. I have examined the holotype of *P. bolivianus*; *P. eigenmanni* is quite distinct.

RANGE. Amazonian slopes of Bolivia between 200 and 400 m above sea level (Fig. 13).

#### Specimens Examined

BOLIVIA: BENI, Yacuma, Rurrenabaque (227 m): AMNH 22537-38; Provincia de Sara (200-400 m): CM 981, holotype. SANTA CRUZ, Ichilo, Buena Vista (400 m): MCZ 24887, BMNH 1927.8.1.151-152.

#### *Prionodactylus argulus* (Peters)

*Cercosaura* (*Pantodactylus*) *argulus* Peters, 1862, Abh. Akad. Wiss. Berlin 1862: 184.

*Prionodactylus oshaughnessyi* Boulenger, 1885, Cat. Liz. British Mus. 2: 392.

*Prionodactylus holmgreni* Andersson, 1914, Ark. för Zool. 9 (3): 9.

*Prionodactylus columbiensis* Werner, 1916, Zool. Anz. 47: 306.

TABLE 5. Characters of seven specimens of *Prionodactylus eigenmanni*. Figures represent ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital lamellae Fourth finger	Fourth toe
6 ♂♂	12-15 (13.0)	32-35 (33.0)	17-19 (17.8)	29-31 (29.8)	9-11 (10.0)	13-15 (14.2)
1 ♀	0	32	18	30	10-10	13-14

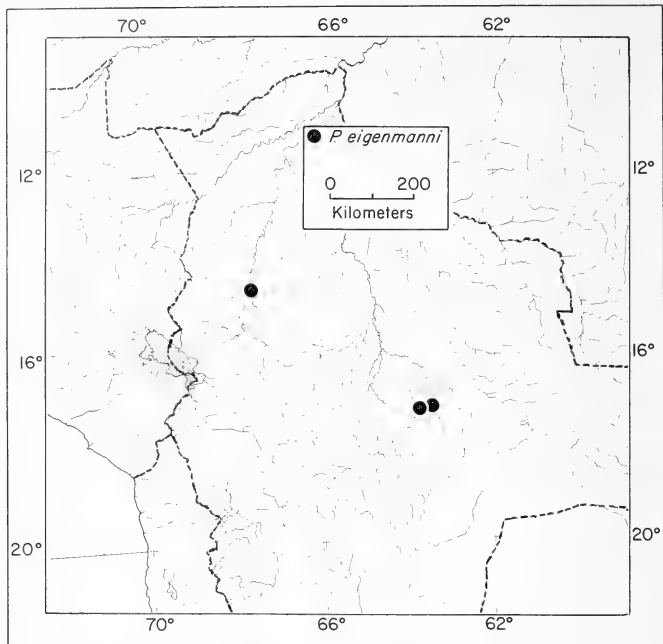


FIG. 13. Bolivia, showing localities for *Prionodactylus eigenmanni*.

**HOLOTYPE.** ZMB 4555, an adult male from the mountainous regions around Santa Fe de Bogotá, Cundinamarca, Colombia collected by Liedig.

**DEFINITION.** Frontonasal divided. Loreal in contact with frontonasal and supralabials. Two or three large collar scales at midline. Subdigital lamellae mostly divided but not tuberculate except at bases of toes 1–4. Translucent disc in lower eyelid divided into two pieces by a vertical groove. Marked sexual dimorphism in femoral pore number. Usually a pair of dorsolateral light line; supralabials light, the light area continued posteriorly as a lateral light line through external ear opening and above forelimb.

**VARIATION.** *P. argulus* is a wide-ranging species, but I have seen relatively few specimens from the northeastern and southwestern parts of its range (Fig. 14). For the characters that I have investigated, there seems to be little geographic variation (Table 6). Virtually all specimens have a median occipital, although it is irregular in several specimens. In UMMZ 68087, it is fused to one of the paramedian occipitals. The loreal is in contact with

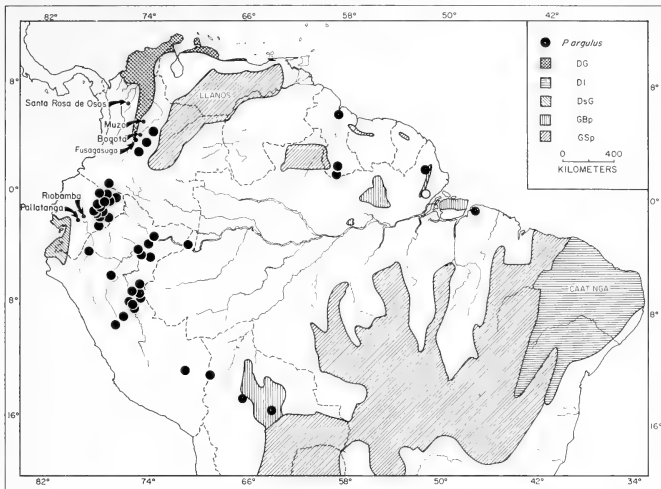


FIG. 14. Northern South America showing savannah and grassland formations, and localities for *Prionodactylus argulus*. Open symbols are literature records. Certain localities discussed in the text are indicated. Abbreviations: DG, broadleaf deciduous trees and grass; Di, broadleaf deciduous trees, plants sufficiently far apart so that they frequently do not touch; DsG, broadleaf deciduous shrub forms, minimum height 3 feet, with grass; GBp, grass with broadleaf evergreen trees growing singly or in groups or patches; GSp, grass with semideciduous trees growing singly or in groups or patches.

the supralabials in all specimens. The supraoculars mostly number 3–3; occasional specimens have 4 or 2 on one side, 3 on the other. The first superciliary is expanded onto the dorsal surface of the head in all specimens, but the area on the dorsal surface varies considerably. The translucent disc in the lower eyelid is divided into two parts by vertical grooves. Some 14 specimens from various localities lack a median collar scale and thus have an even rather than an odd number of collar scales.

Most of the specimens examined have 6 longitudinal rows of ventral scales. In the small sample from Bolivia, including the holotype of *P. holmgreni*, all specimens have 8 longitudinal rows of ventral scales. These far-southern specimens also possibly have a slightly larger number of dorsal and ventral scale rows, and a lower number of scales around the midbody region. The samples are, however, very small, and similar counts also occur in the far northeast. Because of the general absence of distinction in scale counts, I see no present merit in recognizing a southern race of *P. argulus*.

The samples from Colombia seem distinctive in some counts, particularly in their lower numbers of dorsal scale rows. The interpretation of these data

TABLE 6. Characters of 73 specimens of *Prionodactylus argulus*.  
 Figures represent ranges and, in parentheses, means.

	Total femoral pores	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Subdigital Fourth finger	lamellae Fourth toe
<b>Brazil</b>						
1 ♂	20	39	19	34	16-17	21-22
1 ♀	0	42	20	37	17-18	22
<b>Guyana</b>						
1 ♂	16	38	20	33	15-16	20-21
2 ♀ ♀	4-5 (4.5)	37-40 (38.5)	(18-20) (19.0)	32-33 (32.5)	15-16 (15.7)	19-21 (20.0)
<b>Colombia</b>						
<b>Meta</b>						
4 ♂ ♂	14-16 (15.5)	31-36 (33.5)	18-20 (19.0)	29-33 (31.5)	14-16 (15.3)	18-21 (19.5)
3 ♀ ♀	7-11 (9.0)	33-35 (34.0)	18-19 (18.3)	30-32 (31.0)	15-16 (15.2)	19-22 (20.7)
<b>Putumayo</b>						
1 ♂	14	32	18	30	16	18-19
<b>Miscellaneous</b>						
4 ♂ ♂	15-16 (15.3)	31-34 (32.7)	17-20 (18.7)	29-30 (29.7)	14-16 (15.0)	18-20 (19.2)
1 ♀	7	33	20	30	13	16
<b>Ecuador<sup>1</sup></b>						
14 ♂ ♂	12-23 (18.8)	38-42 (39.6)	16-21 (18.6)	30-39 (34.3)	13-18 (15.5)	18-22 (19.4)
13 ♀ ♀	4-13 (10.1)	38-43 (41.1)	17-21 (18.0)	32-39 (35.5)	14-18 (15.9)	17-24 (19.9)
<b>Peru</b>						
<b>Loreto and San Martin</b>						
17 ♂ ♂	13-25 (17.0)	37-44 (39.9)	18-23 (19.9)	31-41 (33.6)	13-18 (15.3)	18-23 (19.9)
5 ♀ ♀	4-15 (9.8)	36-45 (41.2)	19-20 (19.2)	31-41 (36.8)	14-17 (15.7)	18-21 (19.6)
<b>Huánuco</b>						
2 ♂ ♂	16-20	37-43	19-21	36-37	16-18	20-22
1 ♀	7	43	19	36	16-17	20-22
<b>Madre de Dios</b>						
1 ♂	12	38	22	32	14-15	18-20
<b>Bolivia</b>						
2 ♂ ♂ <sup>2</sup>	13-15	42	22	32	16	20-22
2 ♀ ♀	2	41-44	21	31	15-18	18-21

<sup>1</sup>Based on AMNH 32724, 60630, 89831; BMNH 80.12.8.17, 1946-8.31.18, 1956.1.15.91; MLS 372 (Colombia) UIMNH 65701-2, 04-15; UKMNH 98604-05; UMMZ 84745, 84846 (1), 90771, USNM 193949-50.

<sup>2</sup>Holotype of *P. holmgreni* italicized.



is confused by some doubts about the origin of some of the specimens. The specimens that supposedly came from west of the eastern range of the Andes seem no more distinct from other populations than those that certainly come from Amazonian Colombia. Thus, even though the dorsal counts given by Werner for his *P. columbiensis* are lower than those Werner gave for conspecific nominal taxa that have Amazonian ranges, the data do not permit recognition of a Magdalena Valley race, both because the western specimens are not distinct from the Amazonian specimens from Colombia, and because the total Colombian sample is only very weakly distinguished from the remainder of the populations.

**SEXUAL DIMORPHISM.** The greatest sexual dimorphism is in color. Mature males have one to several light-centered, dark-bordered ocelli along the sides of the body beginning in the shoulder region. Such ocelli are absent or at most faint in the females and young. The number of femoral pores also shows sexual dimorphism; where appreciable samples have been examined, the highest total counts for the females overlap the lowest total counts for males (Table 6).

**REMARKS.** The holotype of *Cercosaura argulus* (ZMB 4555) is an adult male. I have examined the specimen. Peters' (1862) description is very good. The holotype is unusual in having the prefrontals separated from each by an anterior extension of the frontal. I have not seen this condition elsewhere in the specimens I refer to this taxon, but the holotype is so similar to the material examined in so many other features that I consider this distinction an anomaly.

*Prionodactylus oshaughnessyi* was distinguished from *P. argulus* by Boulenger (1885) primarily, I believe, because of the anomalous separation of the prefrontals in Peters' holotype. Boulenger also listed other differences in scale dimension and number. I have examined the syntypes of *P. oshaughnessyi* (BMNH 80.12.8.1 from Pallatanga, and 80.12.8.14-16, recatalogued as 1946.8.31.18-20), a male and two females from Canelos. These specimens fall within my concept of *P. argulus*. All the syntypes were collected by Buckley; the specimen labelled Pallatanga, like much other Buckley material from Pallatanga, is undoubtedly mislabelled (Peters, 1955; Uzzell, 1961).

Through the courtesy of Greta Vestergren, I have examined the holotype of *Prionodactylus holmgreni*, an adult male (NRM 3226) collected by N. Holmgren at San Fermín, in La Paz (Caupolican), about 850 m above sea level. I consider *P. holmgreni* a junior synonym of *P. argulus* (cf. Peters and Donoso-Barros, 1970). Although this and the other Bolivian material examined show slight differences from the rest of the material referred to *P. argulus*, I do not presently believe that any purpose is served by recognition of a distinct southern subspecies of *P. argulus*, although the name *holmgreni* remains available should that course later prove useful.

Burt and Burt (1931) considered *P. holmgreni* a subspecies of *P. okendeni*. *P. okendeni*, however, differs in having a single frontonasal, rather than a divided one, and belongs with *P. manicatus*. The specimens identified by the Burt's as *P. o. holmgreni* (AMNH 22740-41, 38955-62) are *Opipeteer xestus*.

*Prionodactylus columbiensis* Werner (1916) was described from a specimen purportedly from the Cañón de Tolima. I have been unable to locate the holotype. Werner described the specimen in enough detail so that it clearly may be placed with the rest of the material that I identify as *Prionodactylus argulus*. Especially, the divided frontonasal and the presence of a lateral light line are characteristic of *P. argulus* rather than any of the other species of *Prionodactylus*.

The number of scales around the midbody region in *P. columbiensis*, according to Werner's key, varies from 25 to 29; the holotype had 25. I have not seen specimens with this few scales (Table 6). All of the other data given by Werner can, however, be matched within the specimens I refer to *P. argulus*.

Werner gave no indication of the sex of the holotype. The presence of two large posterior preanal scales suggests that it was a male; most females have more than two posterior preanals. Most males, especially individuals as long as Werner's holotype (50 mm snout-to-vent) have at least one well-marked ocellus on the side of the body, but Werner mentioned none.

*Prionodactylus argulus* is basically an Amazonian drainage species (Fig. 14). In Colombia, most of the recent records are from the lower Amazonian slopes. I have examined 9 specimens from these areas. In addition, however, I have examined the following specimens from west of the easternmost Andes in Colombia: MLS 373 (Humbo near Muzo, Boyacá), MCZ 42190 and 61157 (Muzo, Boyacá), MCZ 22014 (Bogotá, Cundinamarca), AMNH 32769 (Santa Rosa de Osos, Antioquia), and UMNZ 131628 (Fusagasugá, Cundinamarca). The holotype of *P. argulus* reportedly came from the mountainous surroundings of Bogotá. The holotype of *P. columbiensis* reportedly came from the Cañón de Tolima.

Dunn (1944) was almost certainly correct in his surmise that *P. argulus* is not part of the herpetofauna of the Bogotá region. AMNH 32769 had been identified (Burt and Burt, 1931) as one of a series of *P. vertebralis* from Santa Rosa de Osos, and almost surely some error in record keeping accounts for the locality data of this specimen. Since *P. argulus* is basically a lowland Amazonian form, I doubt that it crosses the easternmost Andes either near Andalucia or at the Paso de los Cruces, both of which are at about 1800 m. The records are, however, too numerous to reject out of hand, and I have indicated these western localities on the range map for *P. argulus* (Fig. 14). Verification that *P. argulus* does not occur in the Magdalena valley is needed. Regardless, there is nothing distinctive about the specimens from these western localities, which are listed in Table 6 as miscellaneous Colombian localities.

AMNH 14561-62, 23328, and 32724, supposedly from Riomamba, Chimborazo Province, Ecuador, are probably mislabelled.

RANGE. Specimens of *Prionodactylus argulus* are known from elevations from about 100 m above sea level to perhaps 1600 m above sea level at the periphery of the Amazon basin from Bolivia north and east to Amapá in Brazil.

#### Specimens Examined

BOLIVIA. BENI (Ichillo), Buena Vista (400 m) UMMZ 60600. COCHABAMBA: UMMZ 68087-88 (Cundinamarca), Monteredondo (1420 m) ZSM 63/1959 (2 specimens). LA PAZ (Caupolican), San Fermín (700-100 m) NMNH 3226, holotype of *Prionodactylus holmgreni*.

BRAZIL. AMAPÁ, upper Rio Lunier, Tumuc-Humac (Tumucumaque; 100-200 m) MNHN 1899.73. PARÁ, Utinga, near Belém (100-200 m) ZSM 203/1911.

COLOMBIA. AMAZONAS, Puerto Nariño (280 m) MLS 372. ANTIOQUIA, Santa Rosa de Osos: AMNH 32769. BOYACA, Garagoa (1634 m) MCZ 31860; Humbo, near Muzo: MLS 373; Muzo: MCZ 42190, 61157. ?CUNDINAMARCA, Bogotá: ZMB 4555, holotype of *Cercosaura argulus*, MCZ 22014; Fusagasugá (1800 m) UMMZ 131680; META, Acacias MLS 375; Caño Guayapa, tributary of Río Guejar (400 m) FMNH 81316, UMMZ, 131682; upper Río Guejar near San Juan de Arama (400 m) UMMZ 131679; Villavicencio (450 m) MCZ 31606-07, 31859; MLS 376. PUTUMAYO, Puerto Asis MLS 374. VAUPES, upper Río Apaporis, tributary of Río Caquetá: UMMZ 131681.

ECUADOR. No other locality: AMNH 38954. Eastern Ecuador: AMNH 89831. CHIMBORAZO, Pallatanga: BMNH 80.12.8.17, syntype of *Prionodactylus oshaughnessyi*; Riobamba (2250 m) AMNH 14561-62, 23328, 32724. MORONA-SANTIAGO, between Río Pastaza and Río Santiago: MCZ 45780. NAPO, Cuyabeno (227 m): UIMNH 65707; Limón Cocha (200-500 m) UIMNH 65701-02, 65704-05, 65708-13, 65715, UKMNH 98604-05, 119429; 2.5 km S of Ongota: UMMZ 123893; Puerto Libre, Río Aguarico (570 m) UKMNH 119425-28; San Francisco (1200 m) UMMZ 84746 (4 specimens), 84747 (7), UIMNH 65714; Santa Cecilia (340 m) UKMNH 105384-85, 109820-22, 112227, 119410-24; near Tena (500 m) UMMZ 84745. PASTAZA, Alpayacu UMMZ 90771; Anga Cocha, Río Bobonaza AMNH 60630; 2.5 km downstream from Cabaceras, Río Bobonaza (550 m) USNM 193949; Canelos (700 m) BMNH 80.12.8.14, reregistered as 1946.8.31.18, syntype of *Prionodactylus oshaughnessyi*; 6 km W of Canelos (700 m) UKMNH 119432; Río Conambo (300 m) USNM 193953;

Mera (1140 m) UKMNH 119430-31; upper Río Pastaza (800 m) USNM 193952; 2.5 km SE of Puyo (800 m) USNM 193948; Sarayacu (400 m) MCZ 37710; BMNH 1956.1.15.91; Veracruz, 10 km E of Puyo (900 m) USNM 193950-51, UKMNH 119433.

GUYANA. Essiquibo, Bartica District (10 m) AMNH 21265; Marudi (250 m) AMNH 61386; Shudikar-wau (300 m) AMNH 61434.

PERU. No other locality: AMNH 56293. AMAZONAS, mouth of Río Santiago (100-200 m) AMNH 56285, 56291; HUÁNUCO, Divisoria (1300-1600 m) FMNH 55983-85; Hacienda Pampayacu (750 m) MCZ 43767. LORETO, Cerros de Contaya, E of Contamana (100-200 m) AMNH 56297; Cerro Azul (100-200 m) FMNH 55982; Iquitos (100 m) AMNH 56299; Isla Cedro (100-200 m) AMNH 56292; mouth of Río Aquaytia (100-200 m) AMNH 56286; Río Bombo, upper Río Tapiche Valley (100-200 m) AMNH 56221; mouth of Río Napo, Lago Mirano region (100-200 m) AMNH 56295-96; mouth of Río Tigre (100-200 m) AMNH 56493; upper Río Utoquinia (200-500 m) AMNH 56280; Pucallpa (100-200 m) MCZ 45878; San Regis (100-200 m) AMNH 56294; Utoquinia-Tapiche region: AMNH 56281-83; Yarinacocha (100-200 m) FMNH 55981. MADRE DE DIOS, Avispa (1000 m) FMNH 154832. SAN MARTIN, Juan del Monte, AMNH 56394.

#### Hemipenes of Species of *Prionodactylus*

I have examined hemipenes of all five species of *Prionodactylus*. Members of this genus, like most species of Boulenger's (1885) Group II of the family Teiidae, have calcareous spinules in the flounces of the hemipenis. I have developed a technique for examining these (Figs. 14-21). The hemipenis is dissected free from the tail; for consistency, I have used the left organ if possible. The organ is washed in several changes of distilled water, soaked briefly (several hours) in 0.5% KOH, stained in a solution of Alizarin Red S in 1% KOH for 12 to 24 hours, destained in several rinses of distilled water (by the time unbound dye is removed, excess KOH is also removed) and stored in 70% alcohol. Staining is more uniform and more rapid if the organ is slit before being stained. For uniformity, I have slit the organ along the length of the sulcus spermaticus from its attachment at the cloacal wall to the end of the undivided section of the hemipenis. Additional slitting beyond this point, both medially to separate the two lobes, and laterally, to open up each lobe, allows the internal pattern to be examined. The organ loses little of its integrity in the KOH solution, and may be manipulated with forceps so that the details, especially those hidden beneath the median welt, may be examined.

The feature most objectively viewed is the pattern of the calcareous spinules. At the tip of the organ, the two lobes form a series of complex folds,

but these are difficult to examine, and easily destroyed or damaged while slitting the lobes. I have placed little emphasis on variation in this part of the organ.

Because the illustrations are based on slit and spread preparations, it should be pointed out that in the intact organ, the spinous areas on either side of the median welt form two distinct pouches. Before dissection, the sulcus is in contact with the median welt, and in cross section, the undivided part of the organ has a C-shaped space, with the median welt inside the C.

There are numerous slight differences in the hemipenes examined. Since I have examined only one from each species, it is not possible at this time to be certain that the differences do not reflect individual or seasonal differences rather than species-specific differences.

The hemipenis of *P. vertebralis* (Fig. 15A) has a series of chevron-shaped flounces with calcareous spinules in both the lateral (left) and medial (right) pockets. The apices of the chevrons are basal and lie beneath the free edge of the median welt when the organ is slit along the sulcus spermaticus. There are 22 complete chevrons in the lateral pocket, plus two incomplete ones at the base of the organ; there are 21 complete and one incomplete chevron in the medial pocket. Teeth are present across the apices of the chevrons, but in the distal 4 or 5 chevrons, the apex is occupied by an enlarged tooth, usually with lateral spurs (Fig. 15B, C). These spurs have not been seen in other species of Group II. The spinules in the flounces are relatively uniform in size (Fig. 15D). The base of the median welt has a series of five tooth-bearing flounces that continue across it (Fig. 15E). The teeth in these vary considerably in size, being smallest in the basal rows, and at the lateral edges of each row; the teeth in the distalmost of these five rows are slightly smaller than the teeth in the row basal to it.

The hemipenis of *P. dicrus* (Fig. 16A) is generally similar to that of *P. vertebralis*. There are 14 toothed flounces in the lateral pocket, and 15 in the medial pocket. The chevron-shaped flounces lack teeth at the apices (Fig. 16B); there are five short rows of teeth across the base of the median welt (Fig. 16C); the teeth are larger medially, smaller at the ends of the rows. The teeth of the third and fourth rows from the base are larger than those of the remaining rows.

In the hemipenis of *Prionodactylus m. manicatus* (Fig. 17A), the toothed flounces form chevron-shaped structures; teeth are continuous across the apex. There is, however, no enlarged tooth at the apex of the distal chevrons. The chevrons number 23 in the lateral pocket, 24 in the medial. There are three complete and one incomplete rows of teeth across the base of the median welt (Fig. 17B). The teeth are larger medially, and larger in the distal rows.

In the hemipenis of *Prionodactylus argulus* (Fig. 18A) the flounces do not form complete chevrons; this is conspicuously true of the basal flounces (Fig. 18B). These toothed flounces number 18 in the lateral pocket, 17 in the medial pocket. A single complete row of teeth crosses the base of the median

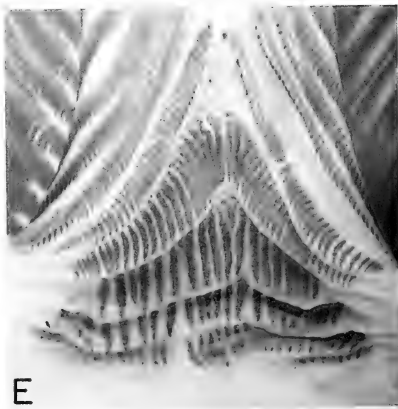
A



B



C



D

E

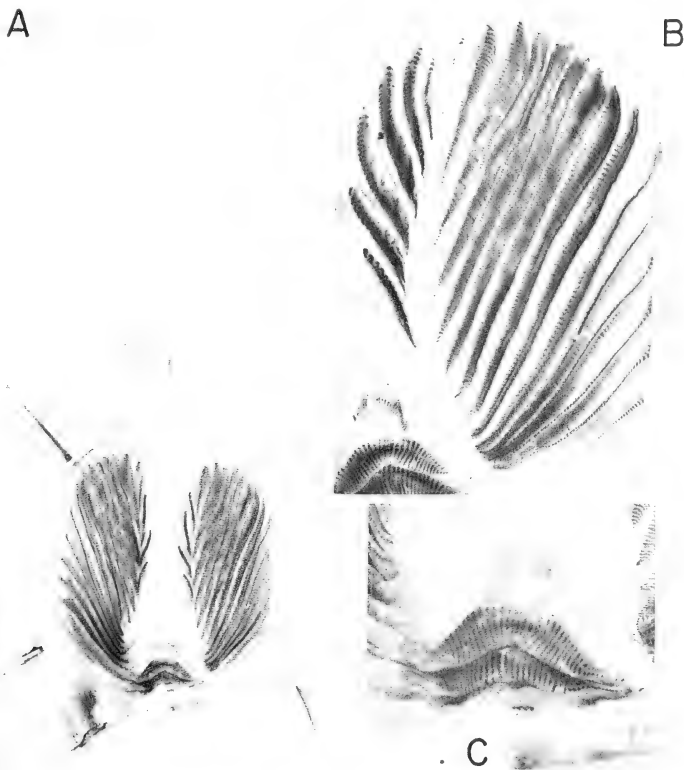


FIG. 16 (above). Structure of the left hemipenis of *Prionodactylus dicrus*, new species (FMNH 28043). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 10$ . B) The median welt pulled back to reveal the apices of the chevron-shaped flounces; the teeth are not continuous across the apex, and there are no enlarged teeth at the apex.  $\times 22$ . C) The short rows of teeth in flounces that cross the base of the median welt.  $\times 33$ .

FIG. 15 (left). Structure of the left hemipenis of *Prionodactylus vertebralis* (USNM 193939). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 7$ . B) The median welt pulled back to reveal the apices of the chevron-shaped flounces.  $\times 16$ . C) Details of the enlarged teeth at the apices of the distal chevrons of the medial pocket.  $\times 43$ . D) Details of the teeth in the arms of the chevrons.  $\times 43$ . E) The short rows of teeth in flounces crossing the base of the median welt.  $\times 16$ .

welt (Fig. 18C), but there is also a partial row, and there are one or two isolated teeth.

In *Prionodactylus eigenmanni*, the hemipenis has 14 toothed flounces in the lateral pocket, 15 in the medial pocket. These flounces are chevron shaped, with teeth complete across the apices. There is no enlarged tooth at the apex of the chevron. There are 4 short rows across the base of the median welt, and part of a fifth. The teeth in these are largest medially, smallest at the ends of the rows. The teeth of the middle rows are larger.

In general, the hemipenial structures in *Prionodactylus* thus seem to be rather similar. There are differences in the few organs examined. Some of these, such as number of rows of flounces, are associated with body size; there are more flounces with teeth in *P. vertebralis* and *P. m. manicatus*, the two largest taxa. The enlarged teeth at the apices of the chevrons of *P. vertebralis* are the most distinctive feature observed in the series.

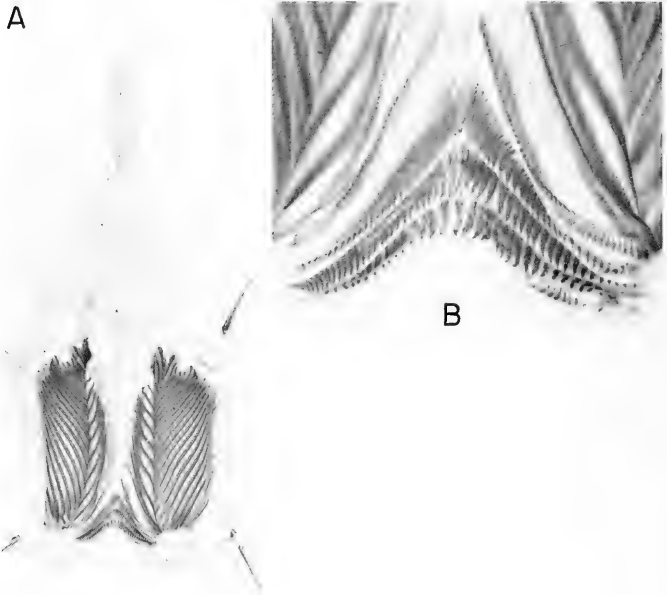


FIG. 17. Structure of the hemipenis of *Prionodactylus manicatus manicatus* (FMNH 45779). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 6$ . B) The short rows of teeth in flounces that cross the base of the median welt.  $\times 17$ .





FIG. 18. Structure of the left hemipenis of *Prionodactylus argulus* (FMNH 81316). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 6.5$ . B) Detail of the flounces in the basal part of the medial pocket, showing the absence of teeth at the apices of the chevrons.  $\times 34$ . C) The short row of teeth in the flounces crossing the base of the median welt.  $\times 34$ .

Figures 20–22 show hemipenial structures of individuals of three related genera. The hemipenis of *Pantodactylus schreibersii* is very distinctive in comparison to the hemipenes of species of *Prionodactylus*. There are 15 tooth-bearing flounces in both the lateral and medial pockets (Fig. 20A). Teeth are absent across the apices of the chevrons, especially basally; in this, there is some similarity to the hemipenis of *P. argulus* (Fig. 18B). In marked distinction, however, the teeth of the basal five flounces of the left pocket are much larger than those of the distal flounces (Fig. 20B). The teeth in the short rows crossing the base of the medial welt also seem to be relatively much larger than the corresponding teeth in species of *Prionodactylus* (Fig. 20C).

The hemipenis of *Cercosaura ocellata* (Fig. 21) also shows some distinctive features. There are 12 chevron-shaped tooth bearing flounces in the lateral pocket, and 17 in the medial pocket. Three rows of teeth that cross the base of the median welt are continuous with 3 of the more basal chevrons in each pocket (Fig. 21B). This condition has not been seen in *Prionodactylus* or the other genera discussed here.

The hemipenis of *Aspidolaemus affinis* (Fig. 22) seems rather like that of several forms of *Prionodactylus*, especially *P. vertebralis* and *P. m. manicatus*. There are 27 tooth-bearing flounces in the lateral and 28 in the medial pocket. Most of these form chevrons that are toothed across the apex; there is no enlarged tooth at the apex. There are 4 short rows of teeth across the base of the median welt. In addition, the ends of two of the incomplete basal chevrons are essentially joined on the median welt by an enlarged tooth (Fig. 22B). The general similarity of the hemipenis of *P. vertebralis*, *P. m. manicatus*, and *Aspidolaemus affinis* can be observed in comparing Figures 15, 17 and 22.

#### Relationships within the Genus *Prionodactylus*

Within *Prionodactylus*, the closest pair of species clearly seems to be *P. vertebralis* and *P. dicrus*. These share nontuberculate subdigital lamellae on the fingers, an undivided frontonasal, a loreal separated from the supralabials, minutely ridged dorsal scales, a distinctive light lip line, and parts of the dorsal pattern: the posterior middorsal light line of *P. dicrus* resembles that of *P. vertebralis*. The anterior pair of dorsolateral stripes on the head and anterior part of the body of *P. dicrus* is paralleled in some *P. vertebralis* by light lines on the superciliary scales. This pair seems clearly to represent two daughter species derived from a single ancestral species.

*P. manicatus* seems in many ways related to *P. vertebralis* and *P. dicrus*. after formaldehyde preservation, some degree of minute ridging on the dorsal scales, the nontuberculate subdigital lamellae on the forelimbs of *P. m. bolivianus*, and the light lip line, especially of *P. m. manicatus*. *P. manicatus* has a much higher number of scales around the midbody region, and in *P. manicatus*, the loreal is in contact with the supralabials.

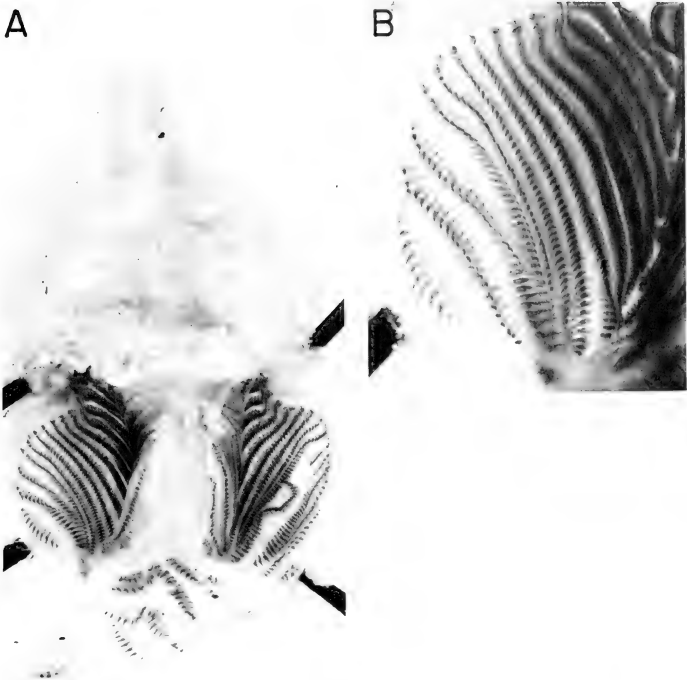


FIG. 19. Structure of the hemipenis of *Prionodactylus eigenmanni* (BMNH 1927. 8.1.152). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing the general arrangement of the frounces in the lateral (left) and medial (right) pockets.  $\times 12$ . B) The median welt pulled back to show the teeth continuing across the apices of the frounces in the lateral pocket, and details of the spinules.  $\times 27$ .

*Prionodactylus argulus* and *P. eigenmanni* seem rather alike, but this general impression results from their both being brownish rather than blackish when preserved; the venter in both is light. This perhaps reflects altitude, and possibly is related to insolation, rather than closeness of common ancestry. Indeed, *P. manicatus* in general occurs at altitudes ranging between those of *P. argulus* and *P. eigenmanni* on the one hand and those of *P. vertebralis* and *P. dicrus* on the other, and is considerably less uniformly black beneath than the two higher elevation forms, although blacker than the lower elevation forms.

*P. argulus* seems to be closer to *P. vertebralis*, *P. dicrus*, and particularly

*P. manicatus* in that it has a light lip; this forms a line only posteriorly where it is bordered beneath by a dark line. *P. argulus* has the loreal in contact with the supralabials, but is particularly distinctive in its longer snout and divided frontonasal.

*Prionodactylus eigenmanni* also has the loreal in contact with the supralabials, but it has an undivided frontonasal. The single and double tubercles on the subdigital lamellae set this species apart from the others in the genus.

The arrangement of the loreal and of the frontonasal both appear to be related to snout length. *P. dicrus* and *P. vertebralis*, in which the loreal is separated from the supralabials, have, relative to body size, the shortest snouts in the genus. The three species in which the loreal touches the supralabial series have relatively longer snouts. The longest snouted species, *P. argulus*, also has the frontonasal divided. Divided frontonasals are unusual in Group II of the Teiidae, and do not occur in all long-snouted forms, for example, *Anadia* and *Placosoma*. A divided frontonasal does occur, however, in the longer-snouted forms of *Echinosaura*.

#### Relationships to Other Genera

Ruibal (1952: 520) pointed out that *Pantodactylus* and *Prionodactylus* are closely related, in fact, perhaps not distinguishable. Among the species of *Prionodactylus*, *P. argulus* seems closest to *Pantodactylus*. They share, among other features, the general brownish color in preservation, a lined pattern, at least in some forms of *Pantodactylus*; and a light venter. More importantly, both *Pantodactylus schreibersii* and *Prionodactylus argulus* have all but the distal subdigital lamellae of the toes and fingers divided into two parts, although not tuberculate. There is possibly some confirmation of a relationship in the structure of the hemipenis, in the absence of teeth at the apices of the basal chevrons (Figs. 18B, 20A). The enlarged teeth in the basal chevrons of *Pantodactylus* is, however, quite distinctive.

*Cercosaura* also seems to be closer to *P. argulus* or *P. eigenmanni* than to the other species of *Prionodactylus*, but is a very distinctive animal, and apparently not particularly close to any *Prionodactylus*.

*Aspidolaemus affinis* appears in its general features to be closer to the high-elevation species of *Prionodactylus*, *P. vertebralis* and *P. dicrus*, than to other members of the genus. This similarity, however, in such features as the generally dark coloration, and slightly pigmented disc in the lower eyelid, may well reflect adaptations to high elevations. Some suggestion of affinity occurs in the hemipenial structure, in the numerous flounces with teeth in them and the larger number of short, tooth-bearing folds across the base of the median welt. There is some similarity to *P. manicatus* as well: the loreal in *A. affinis* touches the supralabials, and there are dorsolateral light lines, ill marked, in both.

These notes are very tentative. A study of skeletal and muscular features would shed much light on the affinities of this complex group of lizards.

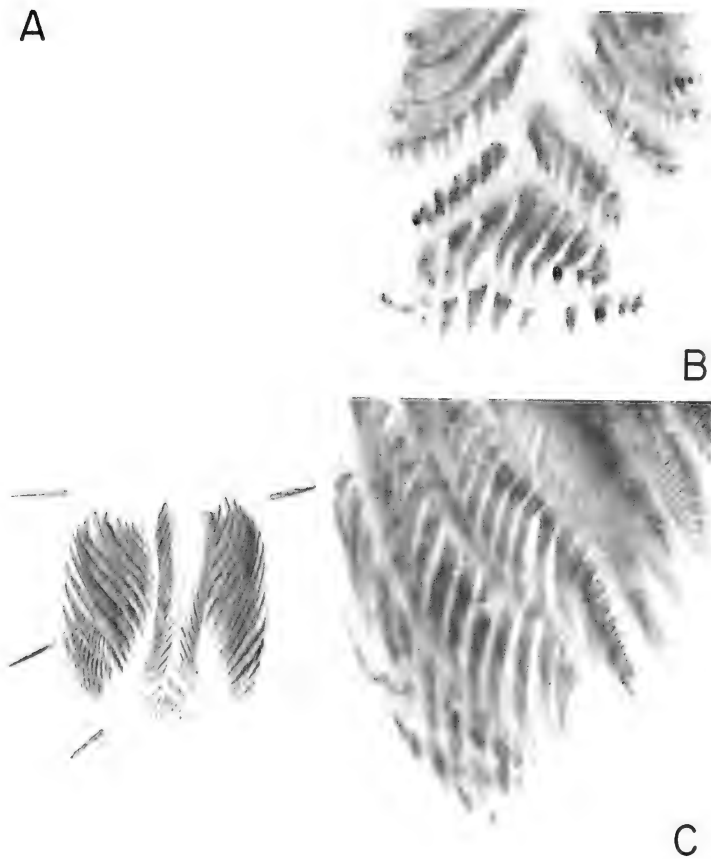


FIG. 20. Structure of the left hemipenis of *Pantodactylus schreibersii* (AMNH 101604). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing the general arrangement of the flounces in the lateral (left) and median (right) pockets. The chevron-shaped flounces, especially the basal ones, lack teeth at the apices.  $\times 9$ . B) Detail of the enlarged teeth on the lateral arms of the chevrons of the lateral pockets.  $\times 44$ . C) The large teeth in the short rows in the flounces that cross the base of the median welt.  $\times 44$ .

III. SPECIES REMOVED FROM THE GENUS *Prionodactylus*

Four species described as *Prionodactylus* do not belong in the genus as I define it. Three of these can appropriately be transferred to other genera.

*Prionodactylus spinalis* Boulenger

*Prionodactylus spinalis* Boulenger, 1911, Ann. Mag. Nat. Hist. ser. 8, 7: 23.

This species was described (Boulenger 1911) from BMNH 1911.12.13.33-46, reregistered as 1946.8.31.44-57. The type locality, Huancabamba, above 750 m, is certainly the central Peruvian town of that name in Pasco rather than the northern town in Piura. Although Boulenger indicated that the specimens may have come from Oxapampa (Barbour and Noble, 1921), I see no reason to doubt the original information; at most it is a matter of a few kilometers distance and a few meters in elevation.

I have examined the syntypes of *P. spinalis*. The absence of a double row of widened gular scales indicates that this species is not a *Prionodactylus*. *P. spinalis* shares most of the features by which I discriminate genera of teiid lizards in Group II with the type of the genus *Euspondylus*, *E. maculatus*. For this reason it seems appropriate to recognize this taxon as *Euspondylus spinalis* (cf. Peters and Donoso-Barros, 1970).

*Prionodactylus rahmi* Grijns

*Prionodactylus rahmi* Grijns, 1936, Zool. Anz. 116: 27.

This species was described from two specimens, a male and a female, numbered 5221 in the museum in Hamburg. The two syntypes appear to have been lost during World War II. The locality given by Grijns is Cuzco, Peru, 3000 m.

The quadrilateral rather than hexagonal dorsal scales and the absence of two median rows of conspicuously widened gular scales indicate that *rahmi* is not a member of the genus *Prionodactylus* as I define that genus. Presently, it seems best to recognize this taxon as *Euspondylus rahmi* (cf. Peters and Donoso-Barros, 1970). It is probably close to *Euspondylus spinalis*, as suggested by Grijns.

*Prionodactylus ocellifer* Werner

*Ecleopus (Aspidolaemus) affinis* Peters 1862, Abh. Akad. Wiss. Berlin: 199.  
*Prionodactylus ocellifer* Werner, 1901, Verh. Zool.-Bot. Ges. Wien, 51: 596.

*Prionodactylus ocellifer* was described (Werner, 1901) from a single specimen collected by Richard Haensch in Ecuador. Many of the labels for

Haensch's collection were illegible, however, and no specific locality is associated with the holotype. Other material in this collection came from both high and low elevations on both sides of the Andes, as well as from the inter-Andean valleys. No other examples of this taxon have been reported. I have examined the holotype of *P. ocellifer*, ZMB 16593. It is an adult female in poor condition. Werner's description is adequate, but the following points are worthy of note.

1. The loreal is large, in contact with the frontonasal, prefrontal, first superciliary, frenoocular, nasal, supralabial two (broadly) and three (narrowly; Fig. 23A, B.).

2. The first superciliary is large and expanded onto the dorsal surface of the head; the superciliary series is complete.

3. The prefrontals are ever so slightly separated by contact between the frontonasal and frontal.

4. Contact between supraoculars one and three at the superciliary series excludes supraocular two from the superciliaries (Fig. 23C, D).

5. The disc in the lower eyelid is divided into three pieces by vertical grooves.

6. There is a light-colored ring around the external ear opening; two or three larger tubercles project into the opening from the anterodorsal margin of the external ear opening (Fig. 23C, D).

The dorsal scales and the chin and throat scales are illustrated in Fig. 23E and 23F.

Most of these features (and many others) can be matched in the taxon usually called *Ecleopus affinis* (= *Aspidolaemus affinis*; Uzzell, 1969b). I have compared the holotype of *P. ocellifer* with some of these (MCZ 45666-67; FMNH 36714-22) and consider them to be conspecific, both on the basis of the characters described by Werner as well as those mentioned above; their general appearance also supports this conclusion, although the coloration is slightly different.<sup>5</sup> Much of the color difference may be due to the formalin-blackened condition of the specimens of *A. affinis* that I have examined, and to the poor condition and desquamation of the holotype of *P. ocellifer*.

I have examined the holotype of *Aspidolaemus affinis* (ZSM 644/O). It was carefully figured by Peters (1862); the specimen was labelled as type. Despite Peters' statement to the contrary, where epidermis persists, the dorsal scales have a distinct but weak keel. There is no wrinkling on the dorsals, however. I thus know of no trenchant differences between the holotypes of *P. ocellifer* and *A. affinis*.

Boulenger (1885) reported specimens of *E. (A.) affinis* in the British Museum from "western Ecuador" collected by Fraser, and from Intac (Imbabura Province), Ecuador, collected by Buckley. Others of Fraser's

<sup>5</sup>Benjamin Shreve made this identification without benefit of seeing the holotype.

specimens, for example, specimens of *Neusticurus ecpleopus* and *Euspondylus maculatus*, have erroneous locality data. Many specimens collected by Buckley reportedly both at Pallatanga and eastern Andean localities were apparently mislabelled (Peters 1955; Uzzell 1961). It is not unlikely that some other Buckley locality data are also incorrect. There is at present no reason to believe that *Aspidolaemus affinis*<sup>6</sup> occurs on the Pacific Andean slopes of Ecuador.

In view of the similarities of *Prionodactylus ocellifer* and *Aspidolaemus affinis*, I consider *P. ocellifer* to be a junior synonym of *A. affinis* (new synonymy)<sup>7</sup>. The name *P. ocellifer* is available, however, to designate a subpopulation within *A. affinis* should that prove useful.

#### IV. A NEW GENUS FOR *Prionodactylus leucostictus*

The only known specimen of *Prionodactylus leucostictus* Boulenger (1900) was collected by F. V. McConnell and J. J. Quelch on the summit of Mount Roraima (2150 m) in Guyana. I have examined the holotype (BMNH 99.3.25.4, reregistered as 1946.8.2.8). It is an adult female in relatively good condition. While it bears a superficial resemblance to other species of *Prionodactylus* because of its keeled, hexagonal dorsal scales, my observations convince me that it is unrelated to *Prionodactylus*, but instead belongs with *Leposoma* and its relatives (*Ecpleopus*, *Alopoglossus*, *Ptychoglossus*, *Arthro-saura*, and possibly *Amapasaurus*; Ruibal, 1952; Uzzell, 1969b; da Cunha, 1970). Because *P. leucostictus* differs from each of these genera in a variety of ways, I here erect a new genus for the taxon. The only known specimen shows some anomalies in scalation. I believe, however, that acquisition of additional material will reveal that most of the differences are real, and that *leucostictus* cannot readily be placed into any of the already established genera.

#### Riolama, new genus

TYPE SPECIES: *Prionodactylus leucostictus* Boulenger.

DESCRIPTION. Tongue with chevron-shaped plcae on anterior and posterior thirds, with imbricate scalelike papillae on middle third. Snout moderately long, blunt. Head scales without striations or rugosities. Single frontonasal and frontal; a relatively broad interparietal extending posterior to parietals; no median occipital (Fig. 24A). Paired prefrontals, frontoparietals, and

<sup>6</sup>A label with ZSM 644/0 indicates that it was collected in Pichincha by Wagler. The label is relatively recent, however, and Peters (1862) gave no such information.

<sup>7</sup>Richard R. Montanucci, who is revising the systematics of *Aspidolaemus* and *Pholidobolus*, concurs in this identification.



parietals; a pair of occipitals and postoccipitals behind interparietal. An enlarged temporal scale lateral to parietal and occipital. Nostril pierced in middle of nasal; no evidence of division above or below nostril although there is an indistinct groove between the nostril and the first upper labial. Nasals not in contact; on right side, nasal extended posteriorly almost to anterior angle of eye; a loreal incompletely divided from the nasal by a groove beginning near the posterior angle of the nasal. On left side, a loreal is present, separated from labials. A large frenoocular and a series of moderate infraoculars. Superciliary series complete; first superciliary short on right side; fused with first supraocular on left. Four supraoculars on each side, the first in contact with the prefrontals, separated from frontonasal. Eyelids well developed, the lower with a heavily pigmented central disc divided into three pieces by vertical grooves. Ear opening large; tympanum heavily pigmented, very shallowly recessed. A mental followed by one unpaired and four paired chin shields (Fig. 24B); the two anterior pairs form a median suture; the two posterior pairs are separated by small scales; the posteriormost pair is separated from the infralabials by small scales. Pregular (Ruibal, 1952) and gular scales are not clearly separated; collar fold very

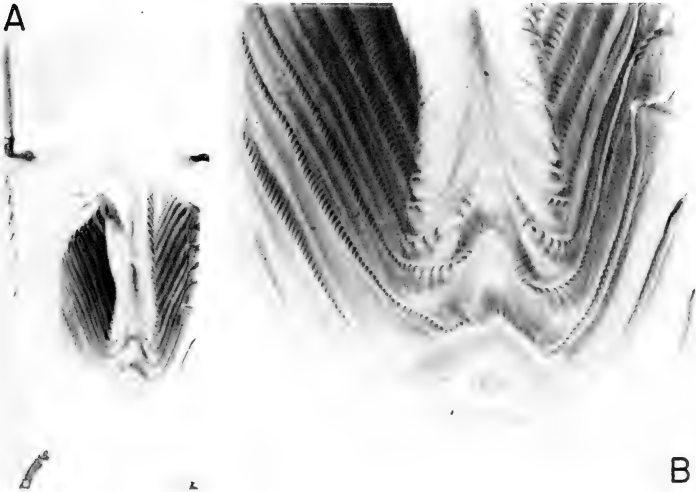


FIG. 21. Structure of the left hemipenis of *Cercosaura ocellata* (BMNH 1927.-8.1.150). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing the general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 10$ . B) Detail showing the teeth in the arms of the chevrons that join across the base of the median welt.  $\times 30$ .

well developed. Gulars flat, imbricate, irregular, large along midline, not forming pairs of large scales, rounded behind; collar scales flat, six in number including a large median scale, slightly rounded posteriorly. Limbs pentadactyl: digits much depressed except at tip; distalmost subdigital lamellae swollen (Fig. 25); digits clawed. Scales along inner margin of palm between thumb and wrist enlarged, with a free medial edge; 13 lamellae under fourth finger, the basal divided; 14 lamellae under fourth toe, the four basal ones divided, but not tuberculate. Dorsal scales keeled, bluntly hexagonal, in transverse rows. A zone of lateral scales four high, about half as large as dorsals, about  $\frac{2}{3}$  size of ventrals; one or two upper rows keeled. Ventral scales in transverse and longitudinal rows, smooth, rounded posteriorly. Anterior and posterior median preanal scales; each lateral preanal scale adjacent to both of these (Fig. 24C). Femoral pores well developed, 7 right, 6 left, none preanal.

DIAGNOSIS. The widely separated nasal scales, each surrounding a nostril, and the pentadactyl limbs with all digits clawed place *Riolama* in Boulenger's (1885) Group II of the Teiidae. The combination of uniformly keeled, hexagonal dorsal scales, slightly recessed tympanum, oblique plicae rather than papillae on the anterior part of the tongue, and depressed digits with swollen tips distinguish *Riolama* from all other genera in Group II.

RELATIONSHIPS. Several of the features of *leucostictus* distinguish it from the species I place in the genus *Prionodactylus*. In particular, the presence of oblique folds rather than papillae on the anterior part of the tongue, the large, nearly superficial heavily pigmented tympanum, and the markedly depressed toes are features not seen in *Prionodactylus*. The last pair of chin shields are widely separated from the infralabials, a condition that I have not noted in *Prionodactylus*, and the arrangement of the preanal scales with large anterior and posterior median scales, and large lateral scales that are neither anterior nor posterior adjacent to these also does not occur in *Prionodactylus*. Clearly, *leucostictus* is not a *Prionodactylus*.

The presence of plicae rather than papillae on the anterior as well as the posterior part of the tongue suggests that *Riolama* is close to *Alopoglossus*, *Ptychoglossus*, and *Ecleopus*, other genera of Group II that have plicae rather than papillae on the anterior part of the tongue. In fact, the arrangement of the plicae in *Ecleopus* (present on posterior part and usually on anterior part, but not the middle; Uzzell, 1969b) is an exact parallel for the condition seen in *Riolama leucosticta*.

Other characters also support this arrangement, albeit weakly. The posterior pair of chin shields are separated from the labials in several forms of *Leposoma*, *Alopoglossus*, and *Ptychoglossus* (Uzzell, 1969b). This condition is unusual in other genera of Group II. The arrangement of the prefrontals with respect to the supraoculars is reminiscent of the condition in *Ecleopus* (cf. Uzzell, 1969b, fig. 1; Boulenger, 1899, fig. 3a) except that in *Riolama*,

the prefrontals are relatively much farther forward. The digits in *Ecleopus* are also slightly depressed, but not markedly so as in *Riolama*. The arrangement of the preanal scales in *Riolama* is reminiscent of that seen in some species of *Arthrosaura* (cf. da Cunha, 1967, fig. 1). The location of the tympanum close to the surface of the head is also reminiscent of the condition in *Ecleopus*, although seen as well in such diverse genera as *Neusticurus*, *Placosoma*, *Anadia*, and *Echinosaura*. None of these similarities except the condition of the tongue, however, is more than suggestive.

On the other hand, it is easy to distinguish *Riolama* from *Leposoma* and its relatives. I made a detailed comparison of those genera except for *Amapasaurus* (Uzzell 1969b, table 2). On the basis of data provided in the generic diagnosis, I am not prepared to suggest that *Riolama* is closer to any one of those genera than to the others.

The only known species of the genus is *Riolama leucosticta* (Boulenger), new combination.

DERIVATION OF NAME. *Riolama* was the name and home of Rima, who inhabited another isolated mountain of northern South America in W. H. Hudson's *Green Mansions*. It is dedicated to a friend akin to Rima in spirit.



FIG. 22. Structure of the hemipenis of *Aspidolaemus affinis* (USNM 194382). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of the flounces in the lateral (left) and medial (right) pockets.  $\times 6.5$ . B) Detail of teeth in the short rows in the flounces that cross the base of the median welt and of the large tooth where two basal chevrons of the two pockets meet at the middle of the median welt.  $\times 18$ .

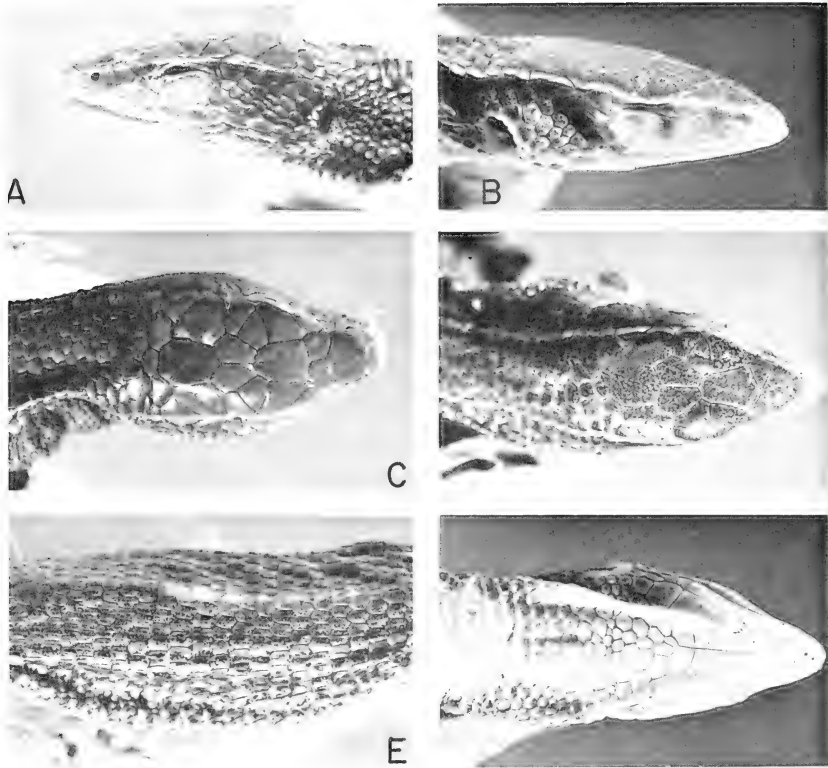


FIG. 23. Comparisons of the holotype of *Prionodactylus ocellifer* Werner (ZMB 16593) with recent specimens of *Aspidolaemus affinis* (FMNH 36720 and 36722) A-F,  $\times 5$ . A) Side of the head of *Aspidolaemus affinis* (FMNH 36720). B) Side of the head of *Prionodactylus ocellifer*  $\times 5$ . C) Top of head of *Aspidolaemus affinis* (FMNH 36722).  $\times 5$ . D) Top of head of *Prionodactylus ocellifer*  $\times 5$ . E) Dorsal scales of *Prionodactylus ocellifer*. F) Chin and throat scales of *Prionodactylus ocellifer*.

#### V. COMMENTS ON SPECIES OF THE GENUS *Euspondylus*

My work on *Prionodactylus* necessitated consideration of the forms of *Euspondylus* with which *Prionodactylus* has been long united (Burt and Burt, 1931). I record here observations of forms described in or referred to *Euspondylus* other than those discussed as *Prionodactylus*. These comments,

together with those on *Prionodactylus rahmi* and *P. spinalis*, provide a synopsis of the genus *Euspondylus*.

*Euspondylus maculatus* Tschudi

*Euspondylus maculatus* Tschudi, 1845, Arch. für Naturg. 11: 161.

*Ecleopus (Proctoporus) fraseri* O'Shaughnessy, 1881, Ann. Mag. Nat. Hist. (5) 4: 296.

This species, the type of the genus *Euspondylus*, was described by Tschudi in 1845; additional information was provided in 1846; the type locality was specified as Moyobamba in the front range of the Andes. This locality is at about 750 m above sea level in the valley of the Río Mayo, a tributary of the Río Huallaga in San Martín, Peru. There are two syntypes in the Musée d'Histoire Naturelle in Neuchâtel, Switzerland. Peters (1862) examined these, described them carefully, and figured the male. I have examined them also. Peters' description is excellent; the second syntype is a female. The male has about 42 scales around the midbody region, the female, 44. The female appears to have a single femoral pore on each side. The disc in the lower eyelid is divided into 2-3 parts by vertical grooves in the male, into 3-4 in the female. There are 5 posterior preanal scales in the female. According to Peters, the dorsal scales were slightly keeled in the sacral region.

I have seen other specimens that I believe are this species. They come from localities in southern and central Peru, on the Amazonian side of the Andes; elevations that are believable vary from about 500-1500 m above sea level.

*Ecleopus (Proctoporus) fraseri*, described by O'Shaughnessy on the basis of BMNH 58.7.25.14 (= 1946.8.2.48), a female, appears to be the same taxon, but lacks prefrontals. This synonymy, suggested by Boulenger (1885), appears to be correct; the type locality for *E. fraseri* (Guayaquil, Ecuador) almost certainly is incorrect. An alternative possibility is Gualaquiza, Morona-Santiago, Ecuador (600 m), where Fraser spent considerable time in 1857 and early 1858. Most of Fraser's collections of birds from Ecuador in 1857 and 1858 were reported by Sclater (Chapman, 1926). The localities for 1857 are all in eastern Ecuador. Fraser collected birds in western Ecuador in late 1858 (August-December) and in 1859. The holotype of *E. fraseri* was accessioned 25 July 1858 (A. F. Stimson, personal communication).

The large male in Brussels that Boulenger (1885) reported is MRHNB 951, I. G. 9422. Its locality is Chile. I believe that this is incorrect.

AMNH 1704, reportedly from Lake Aracona (= Lago de Aricoma), Juliaca, above 4000 m, certainly is incorrectly labelled. Dunn (1942) reported that Harvey Bassler suggested that American Museum material labelled Juliaca was sent there by a member of the Inca Mining Company

(apparently H. H. Keays), but was probably collected near the mine at Santo Domingo, at about 1200 m above sea level in Puno (cf. Uzzell 1970: 26).

Other specimens of *Euspondylus maculatus* that have satisfactory locality data include BMNH 1911.12.20.5-6 (Peru, Puno, Chaquimayo, 600-750 m) and FMNH 40584, 45474 and AMNH 56268 (Peru, Junín, Chanchamayo, 1200-1300 m). The valid locality records suggest an eastern Andean distribution at 500-1500 m throughout Peru and southern Ecuador, rather than the coastal areas of northern Peru and southern Ecuador suggested by Peters and Donoso-Barros (1970).

#### *Euspondylus simonsii* Boulenger

*Euspondylus simonsii* Boulenger, 1901, Ann. Mag. Nat. Hist. (7) 7: 549.

This species was described by Boulenger (1901) from a single female (BMNH 1900.11.27.34; reregistered as 1946. 8. 2. 3) collected at Puntoyacu, Río Perene, Peru, about 1250 m above sea level. No other specimens have been reported.

*Euspondylus simonsii* can be distinguished from *E. maculatus*, which it resembles, by the undivided disc in the lower eyelid and by the light line between the angle of the mouth and the forelimb insertion. It may also have a reduced number of scales around the midbody region. The palm of *E. simonsii* has no enlarged scales between the thumb and wrist. Enlarged scales with a projecting medial edge are present in *E. maculatus*.

#### *Euspondylus guentheri*

*Eupleopus (Euspondylus) guentheri* O'Shaughnessy, 1881, Proc. Zool. Soc. London 1881: 235.

This very distinct species, based on BMNH 80.12.8.18, reregistered as 1946.8.8.99, an adult female collected by Buckley near Sarayacu, Pastaza, Ecuador, has been reported from other localities in eastern Ecuador by Peters (1959).

#### *Euspondylus brevifrontalis* Boulenger

*Euspondylus brevifrontalis* Boulenger, 1903, Ann. Mag. Nat. Hist. (7) 12: 431.

The syntypes of *E. brevifrontalis* Boulenger (1903) include BMNH 1903.-6.30.34, reregistered as 1946.8.31.62, an adult female from Río Albireggas, Venezuela (about 2900 m), and BMNH 1903.10.30.1-2, reregistered as 1946.8.32-33, two adult males from about 2500 m at Escorial, Venezuela,

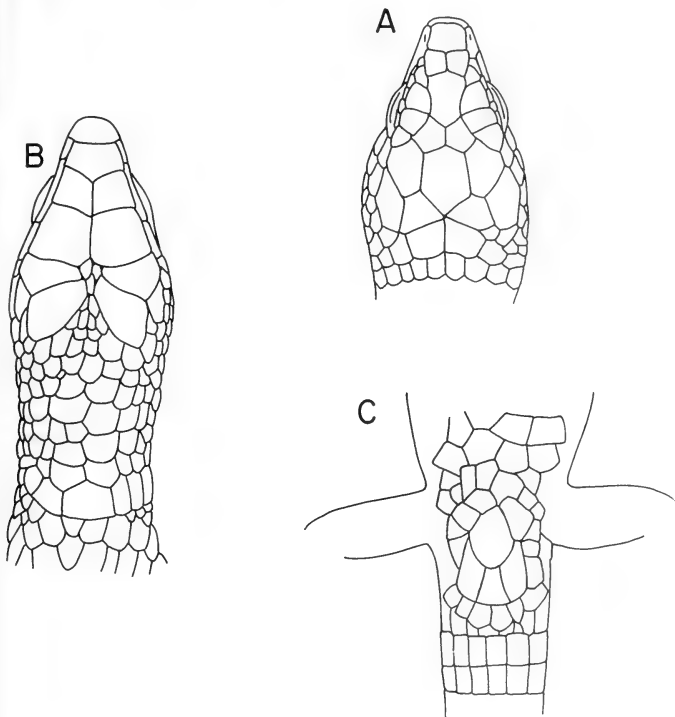


FIG. 24. Scale features of the holotype of *Riolama leucosticta* (BMNH 1946.-8.2.8.) A) Top of head  $\times 3.5$ . B) Chin and throat scales.  $\times 3.5$ . C) Scales of cloacal region.  $\times 3$ . Based on Boulenger, 1900.

collected by Briceño. As noted by Boulenger, these specimens are very similar to *Anadia bitaeniata*. Although this species perhaps should be transferred to the genus *Anadia* (Olav Oftedal and E. E. Williams, personal communication), minute differences between the taxa in arching of the distal phalanx of the toes, division of throat scales into two groups by a gular crease, and slightly smaller lateral scales may justify placing these two taxa on different sides of a generic boundary. An examination of features in addition to the scalation is needed to help place these two taxa correctly. At present I retain this form in *Euspondylus* but with no real conviction.



FIG. 25. Lateral view of the digits of the right forefoot of the holotype of *Riolama leucosticta* (BMNH 1946.8.2.8), showing the general depressed shape of the digit and the swollen digit tip.  $\times 25$ .

*Euspondylus acutirostris* (Peters)

*Ecleopos* (*Euspondylus*) *acutirostris* Peters, 1862 Abh. Akad. Wiss. Berlin 1862: 209.

The holotype of *Ecleopos* (*Euspondylus acutirostris*) Peters (1862) is ZMB 4597, an adult male from Venezuela. I have examined both the holotype and the small female (UMMZ 125769) reported by Test *et al.* (1966) from Rancho Grande, Aragua, Venezuela. I have compared the specimens directly, and I see no difficulty in their being conspecific. The arrangement of the subocular scales appears to be the same in both specimens.

The subdigital lamellae of the basal phalanges of the fore- and hind feet of *E. acutirostris* are somewhat widened and flattened; the subdigital lamellae of the distal phalanx on each toe are compressed. Although the distal phalanx is not arched, the arrangement is otherwise similar to that on the toes of arboreal species of *Anadia*, and supports the hypothesis that this may be an arboreal species (Test *et al.*, 1966).

Other specimens of this taxon have been reported by Lancini (1968) from the Cordillera de la Costa in Venezuela.

*Euspondylus phelpsi* Lancini

*Euspondylus phelpsi* Lancini, 1968, Pub. Ocas. Mus. Cienc. Nat., Zool. 12: 2.

I have seen no material of this recently described taxon (Lancini, (1968)). I am unable to determine whether it belongs in *Euspondylus*, *Prionodactylus*,



or some third genus. It is unusual among taxa referred to *Euspondylus* in having a light line beginning in the supralabial region behind the eye and passing above the forelimb insertion; such a light line is also present in *E. simonsii* and *E. acutirostris*.

*Euspondylus stenolepis* Boulenger

*Euspondylus stenolepis* Boulenger, 1908, Ann. Mag. Nat. Hist. Ser. 8, 2: 519.

*Euspondylus stenolepis* was described from an adult male (BMNH 1909.4.30.64, reregistered as 1946.8.2.39) collected by M. G. Palmer, who took it from the stomach of a bird shot at San Antonio, Valle del Cauca, Colombia at about 2200 m above sea level. Boulenger's (1908) description and figure are very good; most of the characters of *E. stenolepis* that argue for its generic placement can be seen in Boulenger's figure, which is reproduced here as Figure 26. There are four supraoculars, the anteriormost elongate; all are separated from the palpebrals by a complete row of superciliaries (Fig. 26A). The narrow interparietal and the parietals are almost coequal in posterior extension (Fig. 26A). The loreal is a diagonally placed scale, not reaching the supralabials, and extending dorsal to a line connecting the dorsal edge of the first superciliary and the nasal (Fig. 26B).

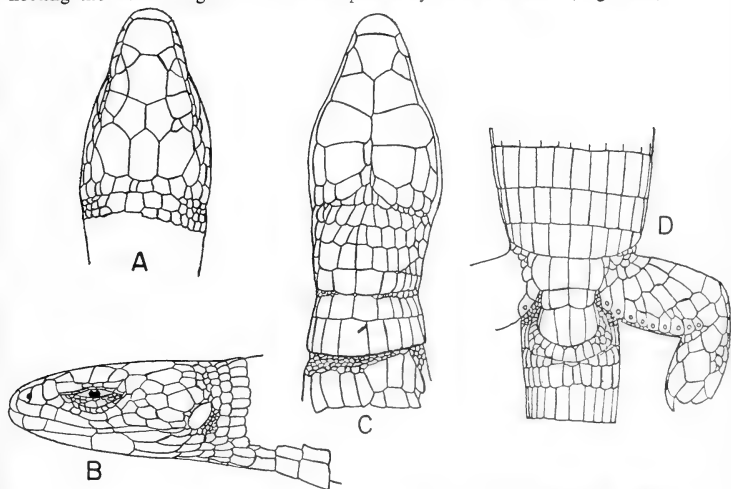


FIG. 26. Scale features of the holotype of *Euspondylus stenolepis* (BMNH 1946.-8.2.39).  $\times 3$ . A) Top of head. B) Side of head. C) Chin and throat. D) Cloacal region. After Boulenger, 1908.

The first superciliary is elongate (Fig. 26B). The fourth, posteriormost pair of chin shields is separated from the infralabials by a narrow, elongate scale (Fig. 26C). None of the median gular scales is widened; all are somewhat elongate rectangles (Fig. 26C). There are four elongate posterior preanal scales (Fig. 26D). There are no preanal pores (Fig. 26D).

Additional characters indicating the generic placement of *E. stenolepis* include the very narrow, obtusely keeled dorsal scales, the smooth gular, ventral, and preanal scales, and the elongate, rectangular shape of the ventrals.

I have examined the holotype of *E. stenolepis*. The most important feature to be added to Boulenger's description is the structure of the tongue, which has chevron-shaped plicae with the apices of the chevrons anterior. The scales on the upper and lower parts of the forelimb are smooth. In addition, the scales on the underside of the palm, between the base of the thumb and the wrist, are enlarged and have free medial edges. The subdigital lamellae at the bases of the third and fourth toes are divided, and the anterior member of each pair is swollen into a tubercle.

This collection of characters, especially the structure of the tongue, the elongate first superciliary and first supraocular, the coequal extension of the interparietal and parietals, the narrow, elongate dorsals and ventrals, the elongate posterior preanal scales, and the enlarged thenar scales on the palm of the forefeet clearly identify *stenolepis* as a member of the genus *Ptychoglossus* Boulenger (1890) and distinguish it from the type species of *Euspondylus*. This form must therefore stand as *Ptychoglossus stenolepis* (Boulenger), new combination.

## VI. A KEY TO THE SPECIES OF *Euspondylus*

The following key is modified from Peters and Donoso-Barros' (1970) key. It has not been tried on all species, and only on limited samples.

1. Either all dorsal scales smooth or wrinkled, or most smooth with some weakly keeled on posterior part of body ..... 2  
    All dorsal scales weakly to strongly keeled ..... 5
2. 40-50 scales from occiput to posterior edge of hind limbs; ventral surface uniform lead colored ..... *E. brevifrontalis*  
    39 or fewer dorsal scale rows; ventral surface often heavily marked with gray, but not uniform lead colored ..... 3
3. Infraorbitals smaller than upper labials ..... 4  
    Infraorbitals subequal to upper labials ..... *E. guentheri*
4. Transparent disc in lower eyelid divided; 40 scales around midbody region; no light line between tympanum and forelimb .... *E. maculatus*  
    Transparent disc in lower eyelid not divided; 35 or fewer scales

- around midbody region; a light line between tympanum and forelimb ..... *E. simonsii*
5. Fewer than 25 transverse rows of ventral scales between collar and preanal scales ..... *E. acutirostris*  
 More than 25 transverse rows of ventral scales between collar and preanal scales ..... 6
6. Four supraoculars, first of series smallest ..... *E. rahmi*  
 Three supraoculars ..... 7
7. No light lateral line on lip or above limb insertion ..... *E. spinalis*  
 A light lateral line on posterior supralabials, below ear opening, and above limb insertion ..... *E. phelpsi*

VII. STATUS OF TAXA PROPOSED IN OR REFERRED TO THE GENERA  
*Prionodactylus* AND *Euspondylus*

Some 19 taxa have been named in or referred to the genus *Prionodactylus*. Names preceded by asterisks have not been discussed in this paper.

- |                                       |   |
|---------------------------------------|---|
| * <i>albostrigatus</i> Griffin 1917   | <i>Pantodactylus schreibersii</i><br><i>albostrigatus</i> |
| <i>argulus</i> Peters 1862            | <i>Prionodactylus argulus</i>                             |
| <i>bolivianus</i> Werner 1899         | <i>Prionodactylus manicatus</i><br><i>bolivianus</i>      |
| * <i>champsonotus</i> Werner 1910     | <i>Placosoma cordylinum</i><br><i>champsonotus</i>        |
| <i>columbiensis</i> Werner 1916       | <i>Prionodactylus argulus</i>                             |
| <i>dicrus</i> , new species           | <i>Prionodactylus dicrus</i>                              |
| <i>eigenmanni</i> Griffin 1917        | <i>Prionodactylus eigenmanni</i>                          |
| <i>holmgreni</i> Andersson 1914       | <i>Prionodactylus argulus</i>                             |
| <i>leucostictus</i> Boulenger 1900    | <i>Riolama leucosticta</i>                                |
| <i>manicatus</i> O'Shaughnessy 1881   | <i>Prionodactylus manicatus</i><br><i>manicatus</i>       |
| <i>marianus</i> Ruthven 1921          | <i>Prionodactylus vertebralis</i>                         |
| <i>ocellifer</i> Werner 1910          | <i>Aspidolaemus affinis</i>                               |
| <i>okendeni</i> Boulenger 1907        | <i>Prionodactylus manicatus</i><br><i>bolivianus</i>      |
| <i>oshaughnessyi</i> Boulenger 1885   | <i>Prionodactylus argulus</i>                             |
| * <i>quadrilineatus</i> Boettger 1876 | <i>Pantodactylus quadrilineatus</i>                       |
| <i>palmeri</i> Boulenger 1908         | <i>Prionodactylus vertebralis</i>                         |
| <i>rahmi</i> Grijs 1936               | <i>Euspondylus rahmi</i>                                  |
| <i>spinalis</i> Boulenger 1911        | <i>Euspondylus spinalis</i>                               |
| <i>vertebralis</i> O'Shaughnessy 1879 | <i>Prionodactylus vertebralis</i>                         |

Some 14 forms have been named in or referred to *Euspondylus* in addition to the names above that were explicitly or implicitly treated as *Euspondylus* by Burt and Burt (1931). Names preceded by asterisks have not been discussed in this paper.

<i>acutirostris</i> Peters 1862	<i>Euspondylus acutirostris</i>
<i>ampuedae</i> Lancini 1968	(?) <i>Prionodactylus vertebralis</i>
<i>brevifrontalis</i> Boulenger 1903	<i>Euspondylus brevifrontalis</i>
* <i>cupreus</i> Andersson 1916	<i>Placosoma cordylinum</i> <i>champsonotus</i>
* <i>festae</i> Peracca 1897	<i>Neusticurus strangulatus</i>
<i>fraseri</i> O'Shaughnessy 1879	<i>Euspondylus maculatus</i>
<i>guentheri</i> O'Shaughnessy 1881	<i>Euspondylus guentheri</i>
<i>maculatus</i> Tschudi 1845	<i>Euspondylus maculatus</i>
* <i>ocellatus</i> Gray 1845	<i>Anadia ocellata</i>
<i>phelpsi</i> Lancini 1868	<i>Euspondylus phelpsi</i>
* <i>rhom bifera</i> Gunther 1859	<i>Anadia rhombifera</i>
<i>simonsii</i> Boulenger 1901	<i>Euspondylus simonsii</i>
<i>stenolepis</i> Boulenger 1908	<i>Ptychoglossus stenolepis</i>
* <i>strangulatus</i> Cope 1868	<i>Neusticurus strangulatus</i>

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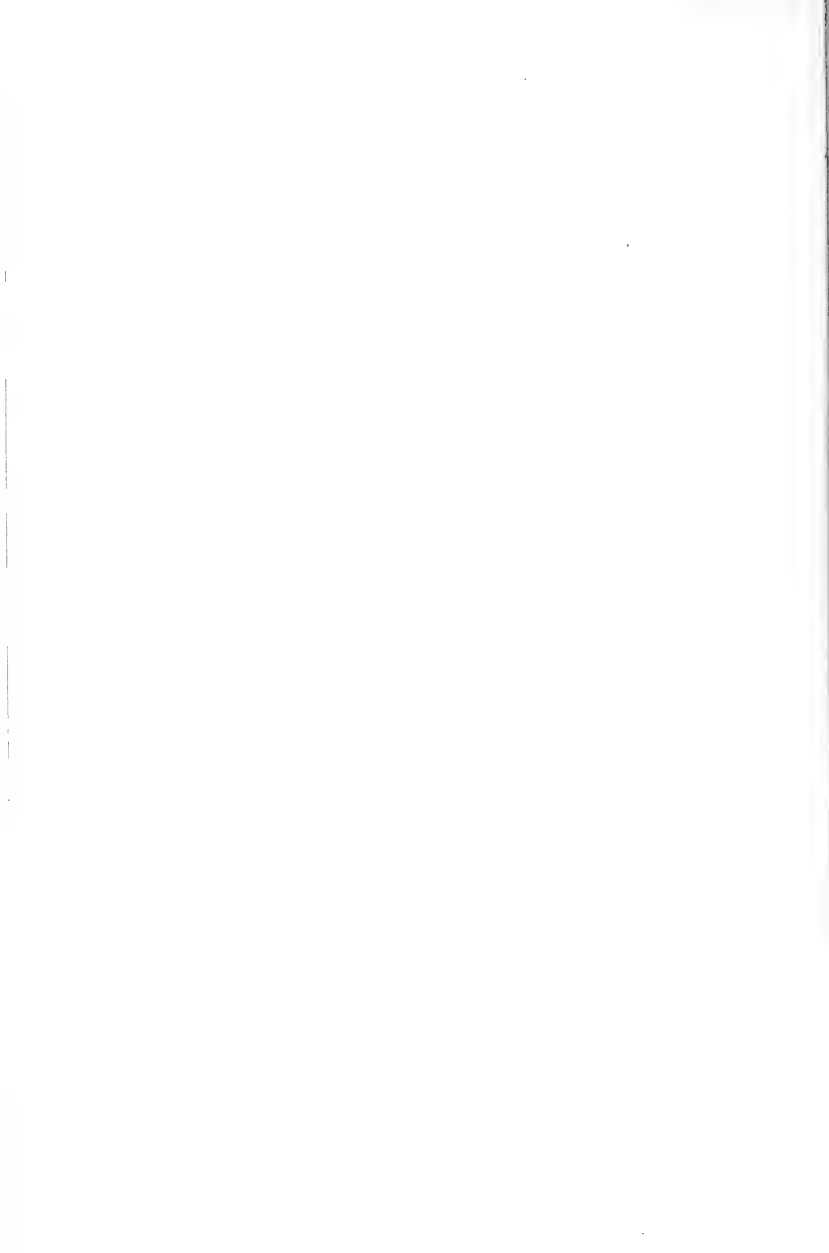
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