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VARIATION AND RELATIONSHIPS OF THE  
COLUBRID SNAKE *LEPTODEIRA FRENATA*

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INTRODUCTION

AMONG the herpetological specimens secured by Fernando Ferrari-Perez, chief naturalist of the Geographical and Exploring Commission of the Republic of Mexico, and put on display at the Exposition at New Orleans in 1885 was a small snake from Jalapa, Veracruz, Mexico. This snake, No. 298 in the collection of the Commission, was described as *Sibon frenatum* (= *Leptodeira frenata*) by Cope (*in* Ferrari-Perez, 1886: 184). For more than fifty years the name *Leptodeira frenata* persisted in the literature solely on the basis of Cope's description. In 1938 and 1939 Hobart M. Smith collected three specimens of this snake at Palma Sola, 10 miles east of San Juan de la Punta, in central Veracruz. Smith (1939: 192-95) compared his specimens with Cope's description and redescribed the species.

Thirteen specimens of *Leptodeira frenata* are now available. Seven of them were collected by the junior author and Jack Reid in the vicinity of Santiago Tuxtla in southern Veracruz. These have been made available to the senior author, who is undertaking a revision of the genus *Leptodeira*. We believe, on the basis of this material, that a more adequate description of the variation and a discussion of the relationships of *Leptodeira frenata* are now possible.

ACKNOWLEDGMENTS

During this study more than 70 specimens of snakes pertinent to the investigation have been examined. For the loan of specimens in their care we wish to thank Emmett R. Dunn, Academy of Natural Sciences of Philadelphia (ANSP); Charles M. Bogert, American Museum of Natural History (AMNH); J. C. Battersby, British Museum (Natural History) (BMNH); Robert F. Inger, Chicago

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Natural History Museum (CNHM); Edward H. Taylor, Edward H. Taylor-Hobart M. Smith Collection (EHT-HMS); Laurence M. Klauber (LMK); Arthur Loveridge, Museum of Comparative Zoology (MCZ); Doris M. Cochran, United States National Museum (USNM); and Hobart M. Smith, University of Illinois Museum of Natural History (UI). Dr. Norman Hartweg, University of Michigan Museum of Zoology (UMMZ) read the manuscript and we are grateful for his helpful suggestions. We are indebted to Ralph W. Axtell for a live specimen of *Leptodeira frenata*. We also wish to thank Donald M. Darling, who executed the drawings for Plate I, and Roger and Isabelle Hunt Conant, for the photograph for Plate II.

#### DESCRIPTION OF *Leptodeira frenata*

The following description is based on twelve specimens (7 males and 5 females). Ventrals 175-185 (av. 180) in females and 178-183 (av. 180.7) in males; caudals 61-70 (av. 65.6) in females and 71-80 (av. 75.8) in males. Upper labials 8-8 (4th and 5th in orbit); lower labials usually 10-10 (9-9 in one specimen); preoculars usually 2-2, but may be 1-1 or 3-3; postoculars 2-2; temporals 1+2+3. Rostral barely visible from above; prefrontals square, half again as long as internasals; frontal with sides parallel to point of posterior edge of supraocular. Upper preocular usually not in contact with frontal (in contact in one specimen). Anterior and posterior chinshields subequal in length; lower labials 1-5 in contact with anterior chinshield, and lower labials 5-6 in contact with posterior chinshield. One specimen with only 9 lower labials has 1-4 in contact with anterior chinshield and 4-5 in contact with posterior.

The dorsal scale rows are 21-21-15 (6 specimens), 19-21-15 (3), 21-21-17 (2), or 19-21-17 (1). Scale reduction formula based upon four males is:

$$19 + 10(16-28) - 21 \quad 9 + 10(110-113) - 19 \quad 8 + 9(120-123) - \\ 17 \quad 7 + 8(147-168) - 15 \quad (180-183)$$

Scale reduction formula for four females may be given as:

$$19 \quad 10(28) - 21 \quad 9 + 10(110-115) - 19 \quad 8 + 9 \quad (127-128) - \\ 17 \quad 7 + 8 \quad (167) - 15 \quad (177-185).$$

There is apparent sexual dimorphism in the place at which reduction from 19 to 17 scale rows occurs posteriorly, for this reduction is between ventrals 120 and 123 in males and between 127 and 128 in females. The dorsal scale rows drop to 15 posteriorly in all males, but in only 2 of 5 females.

The dorsal body pattern consists of 26-36 (av. 29.3) wide dark-

brown or black bands, 4–8 scales in length and 4–8 times as long as the light interspaces. The first body band is always longer than the succeeding ones. The bands may extend onto the edges of the ventrals or, especially posteriorly, only onto the second scale row, the first scale row being excluded. These bands may be entirely separate or, less frequently, the light interspaces alternate, so that the adjacent corners of the bands touch along the midline. In juveniles the bands are solid black, but in adults they are dark brown outlined in black. The light interspaces or ground color are white in juveniles and light tan or cream in adults. The interspaces are wider laterally than dorsally and contain a dark spot, which covers the edges of one or two ventrals and extends onto the second scale row. There are 11–17 (av. 13.6) dark bands on the tail.

The top of the head is grayish brown, with black or dark-brown flecks or dashes on the frontal, parietals, and temporals. There is a longitudinal dark spot on each parietal, a dark spot on the posteromedian corners of the parietals and adjacent postparietals, and sometimes a nearly round dark spot on the anterior part of the frontal. The snout is brown; the labial region, cream. A suffuse brown stripe extends from the nostril across the loreal and preoculars to the orbit. The posterior edges of upper labials 1–6 are dark brown, and each lower labial has a dark-brown stripe on its posterior edge. Beginning at the posterior edge of the orbit and extending across the postoculars, the dorsal part of the sixth upper labial, the middle of the seventh upper labial, the ventral part of the eighth upper labial, and onto the first four rows of dorsal body scales is a dark-brown or black stripe that connects with the first body band. The chin, ventrals, and caudals are immaculate creamish white.

The dentigerous bones were examined in three specimens. All have 10 subequal, recurved maxillary teeth followed by a space and two enlarged, grooved fangs. All have 8 palatine teeth; two have 21 and one has 20 pterygoid teeth. Of the two mandibles examined, one bears 14 and the other 16 teeth.

The hemipenis occupies the base of the tail for a length of eight caudals. It is capitate and has a single, unforked sulcus spermaticus. There are three primary longitudinal rows of hooked spines. These spines increase in size from the base to the distal part of the structure. In relation to the mid-line of the tail, one primary row lies lateral to the sulcus, and the other two lie median to the sulcus. The largest spines are those in the row just median to the sulcus. In this row there are five spines, the distal being twice the size of the distal spines in

the other primary rows. Secondary rows of small spines extend longitudinally for a short distance between the primary rows. The ventral part of the base is covered by small spines which merge to form the longitudinal rows, with exception of the large row just median to the sulcus. The dorsal side of the base is covered with spinules. The capitulum is set off from the rest of the organ by a deep fold and is finely papillose.

In general size and proportions, the head is broad and flat; it is quite distinct from the neck. Four adult females range 345–405 mm. (av. 381.3) in body length, 89–110 mm. (av. 96.0) in tail length, 434–515 mm. (av. 477.3) in total length, and 23.7–27.3 per cent (av. 25.2) in tail/body ratio. Six adult males range 243–425 mm. (av. 353.8) in body length, 66–127 mm. (av. 98.0) in tail length, 309–500 mm. (av. 437.6) in total length, and 27.2–31.6 per cent (av. 28.4) in tail/body ratio. One juvenile female has a total length of 242 mm., of which 45 mm. are tail.

Northern specimens from central Veracruz (Pl. I, A) tend to have broader body bands and narrower interspaces than do those from the southern part of that state (Pl. I, B). The bands in the northern specimens are dark and dense, are nearly as wide laterally as they are dorsally, and all extend onto the ventrals. In specimens from southern Veracruz the bands are brownish outlined with black, somewhat saddle-shaped, and leave wide interspaces laterally; many do not reach the ventrals or even the first scale row. In these southern individuals the lateral spots are larger than in the northern specimens and there may be dark streaks along the edges of the ventrals and on the first scale row.

One individual, UMMZ 112320, from 3–4 miles west-northwest of Acayucan, Veracruz, in life had a dorsal ground color of vivid salmon fading to creamish pink on the venter. The dorsal body bands were cocoa brown outlined with black; the black, in turn, bordered with pale yellow. The top of the head was light cocoa brown flecked with chocolate brown. The nape was pinkish gray. The labials and throat were white, the former barred with black. The iris was gray with suffuse salmon flecks. Another, UMMZ 111931, from 2.4 miles northwest of Santiago Tuxtla, had a similar coloration in life.

Although the data are limited, they suggest that minor differences exist between the populations of Palma Sola, Santiago Tuxtla, and Acayucan. The single male from Palma Sola has 183 ventrals and 78 caudals, the five males from Santiago Tuxtla have 179–182 (av. 180.8) ventrals and 71–80 (av. 76) caudals, and the single male from Acayu-

can has 178 ventrals and 72 caudals. Two females from Palma Sola have 177–180 (av. 178.5) ventrals and 66–70 (av. 68) caudals; two from Santiago Tuxtla have 175–183 (av. 179) and 61–66 (av. 63.5). Meager as they are the data indicate that there is a trend toward reduction of ventrals and caudals from northwest to southeast.

One specimen, LMK 40299, a banana-boat immigrant, is not included in the description and analysis of variation. The locality of origin is unknown and, although in all superficial appearances it closely resembles *Leptodeira frenata*, certain characters are at variance with those described. The individual is a small male which measures 303 mm. in total length and has 23 dorsal scale rows, a number recorded only for the type of *frenata*. The increase from 21 to 23 takes place by the splitting of the sixth scale row at the 50th ventral, and the reduction from 23 to 21 takes place by the fusion of the 10th and 11th scale rows at the 105th ventral. There are 195 ventrals and 82 caudals. This number of ventrals is ten higher than in any other *L. frenata* examined. There are 38 body bands; 20 on the tail. The head scutellation is normal except for the presence of 3 preoculars and 4 tertiary temporals.

#### RELATIONSHIPS OF *Leptodeira frenata*

The presence of the paired parietal spots, a dark spot on the postero-medial edges of the parietals, postorbital stripes connected with the first body band, wide body bands that reach or nearly reach the ventrals, and the dorsal scale formula suggest affinities with *Leptodeira yucatanensis* Cope and with *L. y. malleisi* Dunn and Stuart. The color-pattern characteristics are common to all. *Leptodeira frenata* usually has a maximum of 21, sometimes 23, scale rows. Of 20 specimens of *Leptodeira y. yucatanensis*, 17 have 21 rows, and 3 have 23 rows; of 38 *L. y. malleisi*, 33 have 21 and 5 have 23 rows. In the three forms the increase from 19 to 21 rows takes place by the splitting of the 9th row between the 16th and the 38th ventral, the greatest variation occurring in *L. y. malleisi* (18th to 38th). In all three the posterior reduction from 21 to 19 rows takes place by the fusion of the 9th and 10th rows between the 106th and the 121st ventral, and from 19 to 17 rows by the fusion of the 8th and 9th rows between the 117th and the 135th ventral. In those specimens that have only 15 rows posteriorly, reduction is accomplished by the fusion of the 7th and 8th rows.

The number of maxillary, palatine, pterygoid, and mandibular teeth in *Leptodeira frenata* is about the same as in *L. y. yucatanensis* and *L. y. malleisi*, but is much lower than in the widespread *Leptodeira*

*maculata* and *Leptodeira annulata* groups. *Leptodeira frenata*, *yucatanensis*, and *malleisi* all have the same kind of hemipenis. This type, with three enlarged distal spines and papillose capitulum, differs distinctly from the hemipenes of other groups of *Leptodeira*.

On the basis of the similarities and the closely approximated, although allopatric, ranges, *Leptodeira frenata* Cope (1886) and *Leptodeira yucatanensis* Cope (1887) may be considered conspecific.<sup>2</sup>

The specimens of *frenata* from southern Veracruz show trends toward *malleisi*. One from Acayucan, Veracruz, UMMZ 112320, (Pl. II) is considered to be an intergrade between *frenata* and *malleisi*. Chiapan specimens resemble those from southern Veracruz, but they have light-brown body bands, which extend only onto the third scale row (Pl. I, C). In general color pattern (solid-colored bands and bands that extend laterally to the ventrals) *frenata* more closely resembles *yucatanensis*, but in scutellation the three forms are similar (Table I).

From north to south on the Yucatán Peninsula there is a trend from a lower count of the large bands that extend onto the ventrals to a higher one of the smaller bands that are saddle-shaped and do not reach the ventrals. A similar trend is present in Veracruz. Specimens from the southern limits of the range of the species (northern Chiapas, Mexico; El Petén, Guatemala; and British Honduras), therefore, have the highest number of body bands and they also have lighter colored bands that are bordered with black and seldom extend laterally to the ventrals. These southern specimens are referable to the race *L. frenata malleisi* Dunn and Stuart (1935). Six specimens from Cozumel Island, Mexico, have low ventral counts, 170–179 (av. 174.3), and are variable in color pattern. The body bands range from 24 to 29, which is intermediate between the usual number in *yucatanensis* and in *malleisi*. In several aspects of coloration, notably the number and size of the bands in some specimens, they are similar to *yucatanensis* (Pl. I, D). Since a specimen from the adjacent mainland is referable to *malleisi*, for the present the specimens from Cozumel Island are considered to be *malleisi*.

*Leptodeira f. yucatanensis* ranges throughout the arid northern part of the Yucatán Peninsula and probably intergrades with *L. f. malleisi* to the south and east in the zone of the tropical evergreen forest. *Leptodeira f. malleisi* lives in tropical rain forest and tropical savanna

<sup>2</sup>Cope described the specimen that was later to be the type of *Leptodeira yucatanensis* in 1866 (Proc. Acad. Nat. Sci. Phila., p. 127) under the name *Leptodeira annulata* VAR., but he first applied the name *yucatanensis* to this description in 1887 (Bull. U. S. Nat. Mus., 32: 67).

in British Honduras; El Petén, Guatemala; and northern Chiapas northward through the southern and eastern parts of the Yucatán Peninsula to Cozumel Island. It intergrades with *L. f. frenata* in

TABLE I

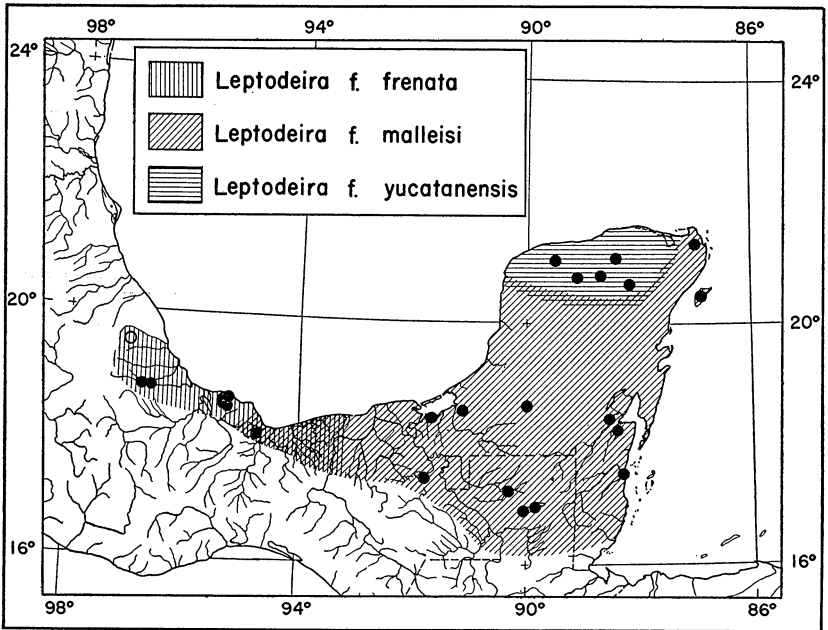
Comparison of Certain Characters in Three Subspecies of *Leptodeira frenata*

Ranges are given below the means. Number of specimens:  
*frenata* 7 ♂, 5 ♀    *malleisi* 19 ♂, 19 ♀;    *yucatanensis* 14 ♂, 7 ♀.

Character	Sex	<i>frenata</i>	<i>malleisi</i>	<i>yucatanensis</i>
Ventrals	♂	180.7 178-183	179.0 170-185	181.5 177-186
	♀	180.0 175-185	181.5 170-188	183.0 175-192
Caudals	♂	75.8 71-80	78.3 73-85	79.0 72-86
	♀	65.6 61-70	70.3 64-76	66.7 66-67
Ventrals + Caudals	♂	256.3 250-262	257.5 248-265	260.5 250-269
	♀	245.6 241-251	251.1 241-261	249.7 241-259
Body Bands	♂	28.7 26-32	30.9 24-39	20.5 18-23
	♀	30.2 28-36	29.9 26-39	22.0 19-26
Tail/Body Ratio	♂	28.4 27.2-31.6	29.9 28.3-31.3	30.5 27.8-32.2
	♀	25.2 23.7-27.2	27.1 24.4-29.9	24.7 22.6-26.2

extreme eastern Veracruz. *Leptodeira f. frenata* ranges southward and eastward from central Veracruz in tropical evergreen forest and rain forest (Map 1). All specimens from the Yucatán Peninsula are from low elevations, none over 200 meters. Specimens of *L. f. frenata* from the

vicinity of Santiago Tuxtla were collected at elevations from 150 to 430 meters. They were found during the dry season in large dry bromeliads growing in trees.



MAP 1. Distribution of the three subspecies of *Leptodeira frenata*. Solid dots represent localities from which specimens have been examined; open circle, the type locality of *L. f. frenata*, as recorded in the literature; different types of shading, the hypothetical ranges of the various races.

KEY TO SUBSPECIES OF *Leptodeira frenata*

The following key should be used with reservation, because there are geographical gradients in scutellation and color-pattern characters.

1. Body bands 24 or more (av. 30); bands brown, outlined with black and not extending onto ventrals; or, if extending onto ventrals, bands are solid black with light interspaces only one scale in width..... 2  
 Body bands 26 or less (av. 21); usually dark brown and not outlined with black; interspaces 2-3 scales in width..... *yucatanensis*
2. Body bands black with nearly straight edges and usually extending onto ventrals; interspaces only one scale in width..... *frenata*  
 Body bands usually brown, outlined with black and often saddle-shaped, usually not extending onto ventrals; interspaces usually more than one scale in width..... *malleisi*



## SPECIMENS EXAMINED

*Leptodeira f. frenata* (12): *no loc.*, LMK 40299; MEXICO: Veracruz: San Juan de la Punta, EHT-HMS 27679; Palma Sola, 10 mi. E of San Juan de la Punta, USNM 11193-94; 2 mi. NW of Santiago Tuxtla, UMMZ 111934; 2.4 mi. NW of Santiago Tuxtla, UMMZ 111931; 5 mi. NW of Santiago Tuxtla, UMMZ 111933; 3.3 mi. E of Santiago Tuxtla, UMMZ 111928-30; near Tula, UMMZ 111932; between Volcán San Martín and San Andrés Tuxtla, UI 33868.

*Leptodeira f. frenata* × *malleisi* (1): MEXICO: Veracruz: 3-4 mi. WNW of Acayucan, UMMZ 112320.

*Leptodeira f. malleisi* (38): BRITISH HONDURAS: Belize: Belize, USNM 24901, 24908, 26354, 52309, 56010-12; Corozal: Skate's Lagoon, CNHM 49343. GUATEMALA: El Petén: Flores, CNHM 43374; La Libertad, AMNH 69989, 69991, CNHM 43371-73, MCZ 46512, USNM 71367, 71369, UMMZ 74881, 74883, 74885-86; Río San Pedro at Paso Caballos, MCZ 38588-89. MEXICO: Campeche: Balchacah, UMMZ 81919; Pital, EHT-HMS 11619; Tuxpeña, UMMZ 73229-30; Chiapas: Palenque, USNM 111258-60; Quintana Roo: Colonia Santa María, UMMZ 76169; Isla de Cozumel, BMNH 86.4.15.23-24, UMMZ 76170, 78640-42; Río Hondo, AMNH 68611.

*Leptodeira f. yucatanensis* (22): MEXICO: Yucatán: USNM 24887; Chichén Itzá, ANSP 18259, AMNH 7867-71, CNHM 20604, 26983-84, 36361, MCZ 7242, 46889, USNM 46397, UMMZ 73027-28, 75589; Libre Unión, CNHM 36359; Mérida, CNHM 19421; Tekom, CNHM 49344; Yoktzonot, CNHM 36360, 36362.

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## PLATE I

Dorsal color pattern in *Leptodeira frenata* subsp.: (A) *L. f. frenata*, USNM 111993, from Palma Sola, Veracruz; (B) *L. f. frenata*, UMMZ 111929, from near Santiago Tuxtla, Veracruz (note tendency toward pattern of *malleisi*); (C) *L. f. malleisi*, USNM 111259, from Palenque, Chiapas; (D) *L. f. yucatanensis*, CNHM 49344, from Tekom, Yucatán. Drawings by Donald M. Darling.

PLATE I

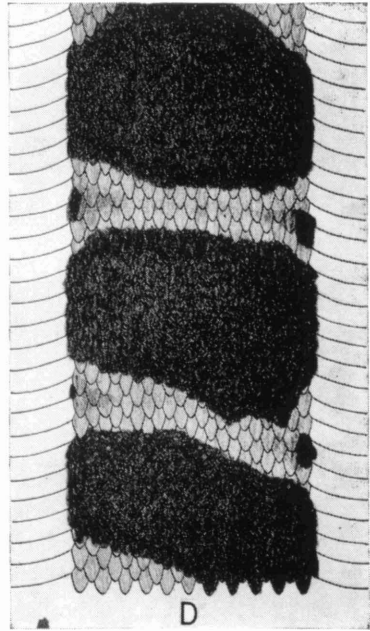
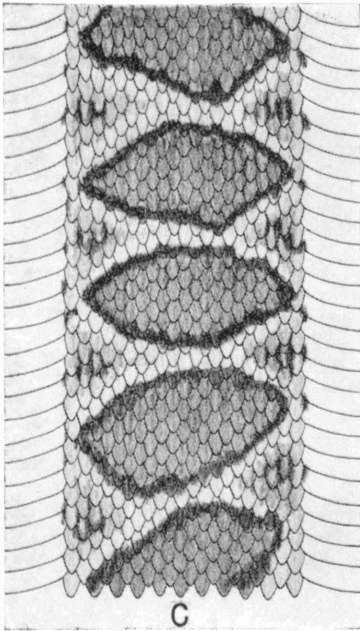
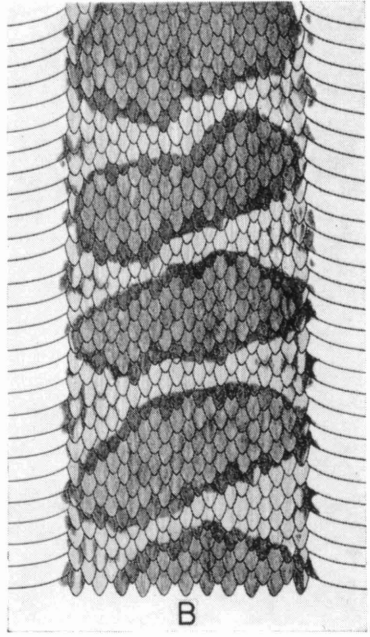
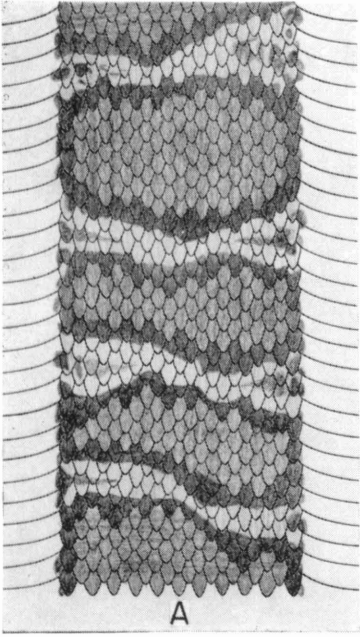


PLATE II

Intergrade (UMMZ 112320) between *Leptodeira frenata frenata* and *L. f. malleisi*,  
from Acayucan, Veracruz. Photograph by Isabelle Hunt Conant.

PLATE II

