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GEOGRAPHIC VARIATION IN THE MEXICAN PYGMY RATTLESNAKE, *SISTRURUS RAVUS*, WITH THE DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT: Geographic variation in the Mexican pygmy rattlesnake, *Sistrurus ravus*, is studied throughout its range. A new subspecies of *Sistrurus ravus* is described from the highlands of the Mexican state of Guerrero. This form is distinguished from the Oaxacan and nominate subspecies on the Altiplanicie Meridional by squamation, body proportions, color, and pattern. The distribution of *Sistrurus ravus* is of zoogeographical interest because it demonstrates the presence of disjunct populations restricted to widely separated highlands in central Mexico. The distribution is discussed in regard to climate, physiography, and sympatry with other crotaline species.

Key words: Reptilia; Serpentes; Viperidae; *Sistrurus*; Mexico; Subspecies

OF the diminutive rattlesnakes in the genus *Sistrurus*, the Mexican pygmy rattlesnake, *S. ravus* (Cope), is considered the most primitive (Klauber, 1972). The low rostral with a pointed apex, indistinct canthus rostralis, dorsal blotches that are usually longer than wide, and lateral series of vertically narrow blotches distinguish *S. ravus* from all other members of the genus. It is geographically remote from its congeners and is regarded as a relict confined to the Mexican central highlands (Gloyd, 1940).

While collecting in the Guerrero highlands in 1974, we obtained 7 specimens of *S. ravus* which had been previously unreported from the state. The specimens represent a considerable range extension of approximately 350 km west of Oaxacan localities and 175 km southward across the Río Balsas Depression from the nearest populations on the Mexican Plateau. In the summer of 1975, we secured additional material at our original locality near Omilteme and also from 2 localities west and southwest of Omilteme. These Guerreran individuals represent an isolated population that appears to be different from specimens we have collected elsewhere. The objective of the present study, therefore, is to examine intraspecific variation in *S. ravus*. We have studied specimens from Guerrero, 25 specimens from Oaxaca, and 60 specimens from the Mexican Plateau. In analyzing variation in this species previous authors suffered from a paucity of material from Oaxaca. Gloyd (1940) had only two specimens and Klauber (1952) only four. In a recent publication (Harris and Simmons, 1978), 13 specimens were reportedly examined, but the analysis of variation was incomplete and inaccurate.

We analyzed 15 scale and seven mensural characters and noted differences in pattern and coloration in preserved and in living animals from Morelos (9), Puebla (8), Oaxaca (1), and Guerrero (10). Palatine, pterygoid, and dentary teeth were usually counted on the right side only to minimize dissection of specimens. Tooth numbers are usually symmetrical in crotalines (Klauber, 1972). Comparisons of samples were made using Student's *t*-test. For purposes of analysis, paired characters (e.g., supralabials) were combined. Formulae for determining significance between linear regressions are found in Zar (1974). For many characters there is some overlap in ranges of variations; nevertheless, the differences are statistically significant. Most names used for physiographic areas follow those on the American Geographic Society map (1:1,000,000).

There are 3 widely disjunct populations of *S. ravus* in Mexico: one is isolated in

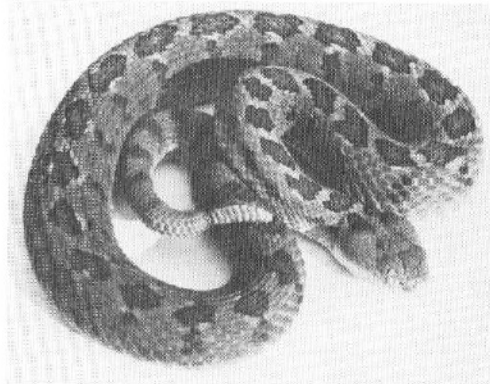

FIG. 1.—*Sistrurus ravus ravus*, adult female from near Huitzilac, Morelos.

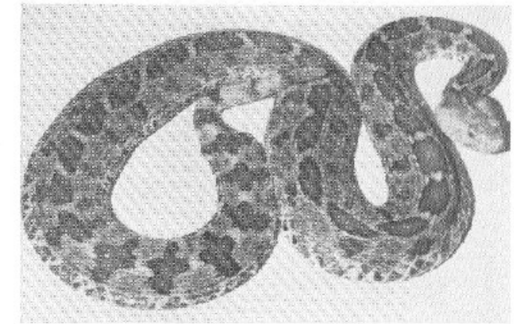

FIG 2.—*Sistrurus ravus ravus*, adult male, from 4.8 km southwest Zapotitlán, Puebla.

the Guerreran highlands, one is found in the central highlands of Oaxaca, and one ranges across the Altiplanicie Meridional from Mexico (state) to Veracruz and southward to Puebla. These populations are sufficiently distinct morphologically to warrant subspecific recognition. In addition to describing the new subspecies, we redefine the nominate and Oaxacan subspecies, and propose that *S. r. lutescens* Harris and Simmons be placed in synonymy of the nominate race.

Sistrurus ravus ravus (Cope)
Central Plateau pygmy rattlesnake

Crotalus ravus Cope, Proc. Acad. Nat. Sci. Philadelphia 17:191 (1865). Type locality: tableland of Mexico. Syntypes: USNM 25050–51, coll. C. Sartorius. Type locality subsequently restricted to Totalco, Veracruz, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull. 33, pt. 2(8):351.

Sistrurus ravus (Cope) Boulenger, Cat. Snakes British Mus. 3:571 (1896).

Sistrurus ravus (Cope) (part), Cloyd, Spec. Publ. Chicago Acad. Sci. 4:56 (1940).

Sistrurus ravus (Cope) (part), Klauber, Bull. Zool. Soc. San Diego 26:113 (1952).

Crotalus (Sistrurus) ravus (Cope) (part), Hoge, Mem. Inst. Butantan, Sao Paulo 32: 161 (1965).

Sistrurus ravus lutescens Harris and Simmons, Bull. Md. Herpetol. Soc. 14:136 (1978).

Sistrurus ravus ravus (Cope), Harris and Simmons, Bull. Md. Herpetol. Soc. 14:135 (1978).

Diagnosis.—A subspecies of *S. ravus* (Figs. 1, 2) distinguished from other races (Table 1) by normally having the dorsal scales in 21 rows at midbody, total prefoveals usually fewer than 3, a large rattle (dorsoventral width of proximal rattle segment usually exceeding 10% of tail length in males, 13% in females), and 2–4 tail bands in both sexes.

Variation.—The following variation observed in *S. r. ravus* is based on 60 specimens (including the syntypes) of which 34 are males and 26 are females. Where character ranges are given they are followed by the mean. The largest male and female examined measure 688 and 631 mm, respectively, in total length. The regressions of tail length against dorsoventral width of the proximal rattle segment (hereafter designated PRW) are given in Figs. 3 and 4. The number of palatine teeth is 3 in all but one specimen which has 2. Pterygoid teeth number 5 (2%), 6 (63%), 7 (30%), 8 (2%), or 9 (3%). Eight (30%), 9 (63%), or 10 (7%) teeth are present on the dentary. Dorsal scale rows at midbody are usually 21 (54 of 60 specimens). Reduction from 23 to 21 dorsal scale rows occurs anterior to ventral 20 in all but 3 specimens which have reduction between ventrals 20 and 30. Irregular addition of scale rows from 21 to 23 occurs anterior to ventral 80 in six specimens. Reduction from 21 to 19 scale rows occurs anterior to ventral 100 in all but four specimens which have reduction between ventrals 100 and 110. Posteriorly dorsal scale rows are reduced to 17 in all specimens. Ventrals range 138–150 ($\bar{x}$ = 143.3) in males, and 139–149 ($\bar{x}$ =

TABLE 1.—Comparison of samples of subspecies of *Sistrurus ravus*. When significant, the *P* value is given and is followed by the subspecies from which the sample differs.

	ravus				*exiguus*				*brunneus*			
Character	Mean ± SD	Range	$P <$	Subspecies	Mean ± SD	Range	$P <$	Subspecies	Mean ± SD	Range	$P <$	Subspecies
Prefoveals	2.8 ± 1.20	1–6	0.001	*brunneus* *exiguus*	4.4 ± 1.65	2–6	0.001	*ravus* *exiguus*	6.2 ± 0.94	4–9	0.001	*ravus* *brunneus*
Suboculars	4.7 ± 0.79	4–6	0.01	*exiguus*	4.6 ± 0.70	4–6	0.01	*exiguus*	5.3 ± 0.76	4–6	0.01	*ravus* *brunneus*
Supralabials	22.2 ± 1.30	19–25	0.01	*brunneus* *exiguus*	23.1 ± 1.20	20–25	0.01	*ravus*	23.4 ± 1.13	22–26	0.01	*ravus*
Infralabials	21.8 ± 1.17	18–24	0.001	*brunneus* *exiguus*	23.4 ± 1.02	21–26	0.001 0.05	*ravus* *exiguus*	24.1 ± 0.80	22–25	0.001 0.05	*ravus* *brunneus*
Parietals	highly variable			*exiguus*	usually undivided		0.001	*exiguus*	usually divided		0.001	*ravus* *brunneus*
Dorsal scale rows (midbody)	21.3 ± 0.70	21–23	0.001	*exiguus* *brunneus*	23.0 ± 1.08	21–25	0.001	*ravus*	23.0 ± 0.00	23	0.001	*ravus*
Ventrals:												
Males	143.3 ± 3.21	138–150			142.6 ± 3.94	136–150			144.1 ± 2.40	140–149		
Females	143.7 ± 2.87	139–149	0.05	*exiguus*	143.1 ± 2.64	140–147			145.2 ± 0.75	144–146	0.05	*ravus*
Subcaudals:												
Males	27.5 ± 1.69	25–30			28.3 ± 1.04	26–30	0.02	*exiguus*	27.2 ± 1.07	25–29	0.02	*ravus*
Females	23.0 ± 1.62	20–26	0.05	*exiguus*	22.7 ± 1.91	19–26			22.0 ± 0.63	21–23	0.05	*ravus*
Rattle-fringe scales	8.8 ± 0.87	8–10	0.05	*brunneus*	9.2 ± 0.86	8–10	0.05	*exiguus* *ravus*	8.6 ± 0.76	8–10	0.05	*brunneus*
Body blotches	29.5 ± 2.70	22–35	0.001	*brunneus*	37.1 ± 4.21	29–44	0.001	*exiguus* *ravus*	30.9 ± 3.43	24–35	0.001	*brunneus*
Tail bands:												
Males	3.7 ± 0.54	2–4	0.001	*brunneus*	6.4 ± 0.77	5–8	0.001	*exiguus* *ravus*	4.2 ± 0.90	3–6	0.001	*brunneus*
Females	2.8 ± 0.57	2–4	0.001	*brunneus*	5.0 ± 0.50	4–6	0.001	*exiguus* *ravus*	3.0 ± 0.63	2–4	0.001	*brunneus*
PRW % of TL:												
Males	11.6 ± 1.65	9.8–16.4	0.001	*brunneus* *exiguus*	9.4 ± 0.85	7.7–11.1	0.001 0.01	*ravus* *exiguus*	8.2 ± 0.89	7.1–9.6	0.001 0.01	*ravus* *brunneus*
Females	14.5 ± 1.48	12.0–17.1	0.001	*brunneus* *exiguus*	12.7 ± 1.01	11.7–14.4	0.001	*ravus*	11.6 ± 0.87	10.3–12.7	0.001	*ravus*

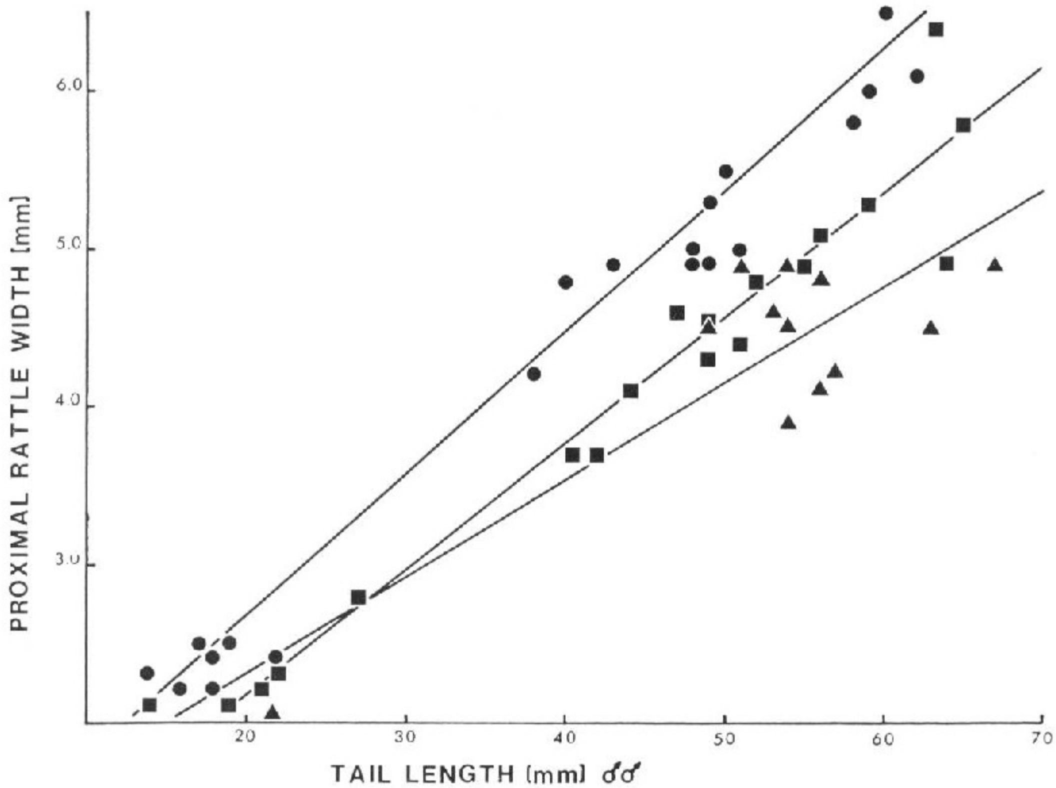

FIG. 3.—Regression of dorsoventral width of proximal rattle segment (PRW) on tail length (TL) for males of the subspecies of *Sistrurus ravus*. Circles represent *ravus*, squares *brunneus*, and triangles *exiguus*. Regression equations are: *ravus*, PRW = .841 TL + .091; *brunneus*, PRW = .553 TL + .080; *exiguus*, PRW = 1.068 TL + .061. The slope and elevation of the regression of *ravus* is significantly different ($P < 0.001$) from those of *brunneus* and *exiguus*, but the regressions of *brunneus* and *exiguus* are not significantly different from each other.

143.7) in females. The subcaudals vary from 25–30 ($\bar{x} = 27.5$) in males, and from 20–26 ($\bar{x} = 23.0$) in females. There are 8–10 rattle-fringe scales ($\bar{x} = 8.8$). Most individuals have a total (both sides) of 3 or fewer prefoveals (72%) but may occasionally have as many as 6. Two suboculars per side (total range = 4–6; $\bar{x} = 4.7$) tend to be more frequent (66%) than 3. In his definition of the genus *Sistrurus*, Gloyd (1940) gives the number of postoculars as 3–6, although in *S. r. ravus* as well as in the other subspecies two postoculars per side are generally present. Total supralabials number 19–25 ($\bar{x} = 22.2$) and infralabials 18–24 ($\bar{x} = 21.8$). This subspecies has the most variation in the condition of the parietals. Most frequently (38 of 60 specimens), the parietals are unsutured but specimens with incompletely (17) or completely (5) divided parietals do exist.

Distinctive differences in color occur between specimens from the high bunchgrass meadows along the Neovolcanic Axis and specimens from portions of Puebla and Veracruz where more xeric conditions prevail. The populations do not appear to be disjunct and gradation occurs from a relatively light greyish brown dorsum in snakes from the desert to a darker, usually brownish, dorsum in snakes from more mesic habitats at higher elevations. Specimens from Huitzilac, Morelos, are deep auburn with dark brown (almost black) dorsal blotches. Their labials are peach-colored with little or no stippling. The iris is copper-colored. Large adults tend to be darker than juveniles or smaller specimens, and strongly melanistic specimens are not rare. Snakes from near Cacaloapan and Zapotitlán, Puebla, have a light greyish brown

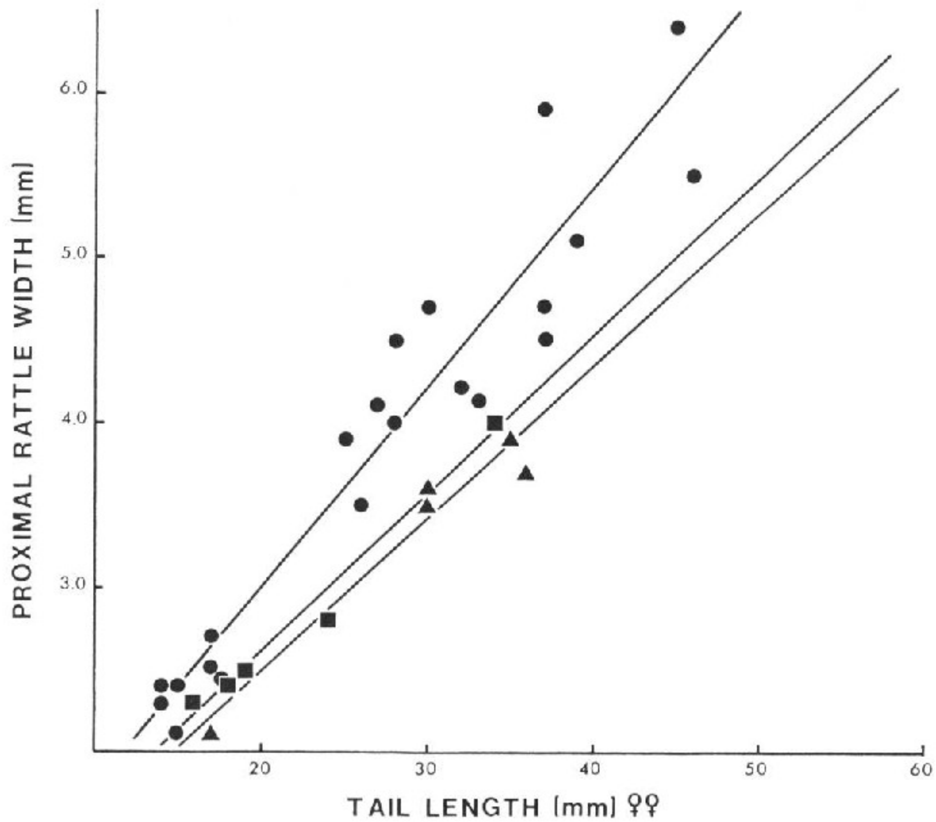

FIG. 4.—Regression of dorsoventral width of proximal rattle segment (PRW) on tail length (TL for females of the subspecies of *Sistrurus ravus*. Symbols are the same as in Fig. 3. Regression equations are: *ravus*, PRW = .563 TL + .122; *brunneus*, PRW = .700 TL −.096; *exiguus*, PRW = .665 TL + .092. The regression for *ravus* is significantly different for slope from *exiguus* ($P < 0.01$) and *brunneus* ($P < 0.05$).

dorsum, black bordered dark brown body blotches with tan interspaces, and a faint postocular stripe. In *S. r. ravus* dorsal body blotches range from 22–35 ($\bar{x} = 29.5$).

Harris and Simmons (1978) described *S. r. lutescens* from a series of 8 specimens from the vicinity of Huitzilac, Morelos. They relied heavily on coloration in distinguishing this population from other races of *S. ravus*. From their description it is impossible to ascertain what comparative material they used in selecting diagnostic characters for they gave no account of specimens examined. However, it is apparent they were unaware that *S. ravus* on the Altiplanicie Meridional varies greatly in coloration and that this variation is correlated in part with elevation and rainfall. Demes possessing coloration similar to specimens from Huitzilac exist on Volcán Toluca, Mexico, in the vicinity of Río Frío, Mexico-Puebla border, and on the lower slopes of Cerro La Malinche, Tlaxcala. These demes are isolated from one another, but are not isolated from other populations of *S. ravus* and a tremendous amount of color variation may be present in a 20 km (by air) transect (e.g., Sierra de Ajusco). Besides dorsal coloration, Harris and Simmons (1978) used the amount of pigmentation on the labials and ventrals to diagnose the Huitzilac population. These characters are so inconsistent from one region to the next they are of no use to distinguish this population, and males from this area often have extremely dark venters (Klauber, 1952: p. 114). The last two diagnostic characters given by Harris and Simmons (1978) similarly fail to survive scrutiny. Blotches in Huitzilac specimens are no "less squarish" than those observed in many other series from elsewhere (see Fig. 2 for typical specimen from near Zapoti-

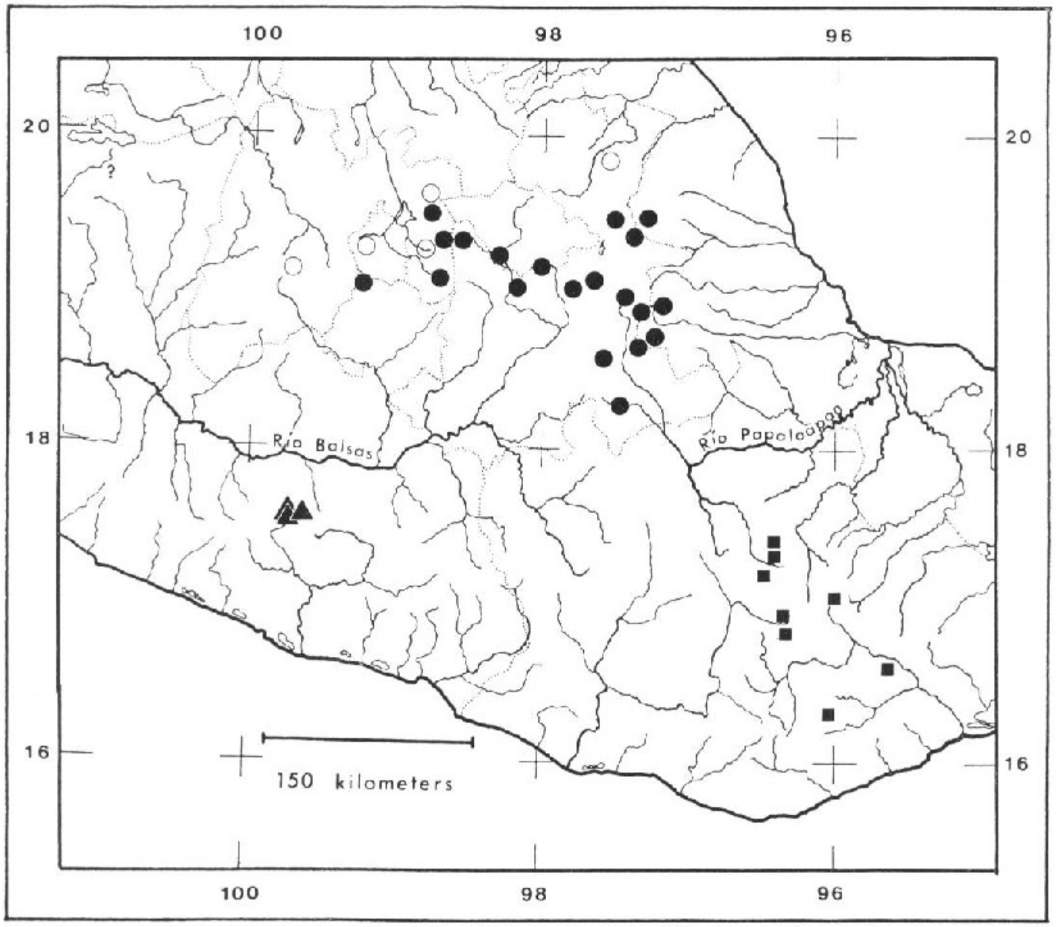

FIG. 5.—Geographic distribution of the Mexican pygmy rattlesnake, *Sistrurus ravus*, in Mexico. Symbols represent the following subspecies: circles *ravus*, squares *brunneus*, and triangles *exiguus*. Open symbols represent literature records. Multiple records in close proximity are plotted with a single symbol. Dotted lines are state boundaries.

tlán, Puebla) and examination of 54 specimens from across the Altiplanicie Meridional (but not from the vicinity of Huitzilac) reveals 28 of them possess 8 rattle-fringe scales. Therefore, the statement that the Huitzilac population may be separated by "having fewer rattle fringe scales, 8 instead of 10" is inaccurate and of no use diagnostically. For these reasons, we propose that *S. r. lutescens* Harris and Simmons be placed in the synonymy of *S. r. ravus* (Cope).

Range.—Across the Mexican Plateau from the Volcán de Toluca (Zinantecatl) in the state of Mexico to the highlands of west-central Veracruz southward through the Sierra de Acatepec in Puebla (Fig. 5) to extreme northern Oaxaca. Except for perhaps southern Puebla and northern Oaxaca, the range lies entirely within the Altiplanicie Meridional as delineated by West (1964). *Sistrurus ravus* has been reported from Hidalgo (Gloyd, 1940; Smith and Tayor, 1945) but we have been unable to find it there. We have seen several specimens in the Morelia Zoo (Parque Juárez) in Michoacán that reportedly were captured in mesquite-grassland on the outskirts of the city.

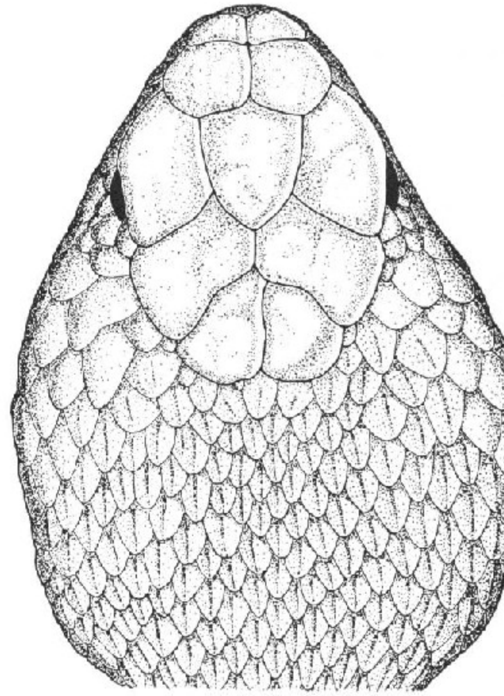

FIG. 6.—Dorsal aspect of head scalation of *Sistrurus ravus exiguus*, UTA R-4534, paratype, from 1.6 km east Omilteme, Guerrero. Note completely divided parietals.

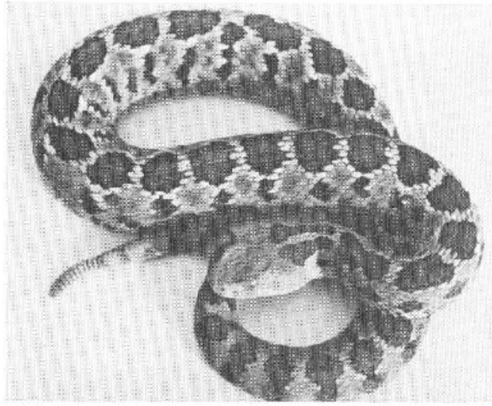

FIG. 7.—*Sistrurus ravus exiguus*, adult male paratype, UTA R-7221, from 1.6 km east Omilteme, Guerrero.

Sistrurus ravus **exiguus** subsp. nov.
Guerreran pygmy rattlesnake

Holotype.—UTA R-4533, an adult male from 1.6 km E Omilteme, Guerrero, elevation 2090 m, collected 18 May 1974 by J. A. Campbell and B. L. Armstrong. Original number JAC 814.

Paratypes.—Sixteen specimens: UTA R-4534 (Fig. 6) and 4535, same locality and date as holotype; 4488–89, two of a total of four offspring born to 4534; 6116–17 and 7221, Fig. 7 (29 May 1975), 6226 and 6256 (June 1975), topotypes; 4536, 0.8 km E Omilteme, 12 July 1974; 5623, immediate vicinity of Omilteme, 13 July 1974; 4912 and 5663, Ejido San Vicente, El Jazmín, 3 July 1975; 5664–65, Las Joyas, 3 July 1975 (all UTA nos. collected by JAC and BLA); KU 87763, 3.2 km E Omilteme, P. L. Clifton.

Diagnosis.—A subspecies of *S. ravus* distinguished from the other races (Table 1) by having the parietal scales divided transversely, the dorsal scales in 23 rows at midbody, total prefoveals usually numbering six or more, a small rattle (PRW usually less than 10% of tail length in males, 13% in females), 3 to 6 tail bands in males, and 2 to 4 tail bands in females.

Description of holotype.—Head length 28.1 mm; total length 510 mm; tail length 49 mm, comprising 9.6% of total; PRW 4.5 mm; straight line fang length from upper lumen to tip 5.2 mm; 3 palatine, 7 pterygoid, 9 dentary teeth; dorsal scale rows 25-23-17, 10 above tenth subcaudal; ventrals 140; subcaudals 26, undivided; anal entire; rattle-fringe scales 8; rostral 1.08 times broader than high, pointed at apex; nasals incompletely divided by vertical suture; loreal single; prefoveals 3/3; subfoveals and postfoveals lacking; preoculars 2/2; suboculars 2/2; postoculars 2/2; supralabials 11/11; interoculabial series incomplete; anterior subocular in contact with supralabials 4 and 5; infralabials 12/12, first pair in contact along midventral line, anterior 3/3 in contact with chin shields; mental 1.63 times broader than long; chin shields large; 7 gulars between chin shields and first ventral; parietals divided; 6 scales present in parietal area.

Dorsum in life pale reddish brown; top of head with paired rust-colored occipital blotches, otherwise without pattern; supralabials, infralabials, and gular area pale yellow with light stippling; 24 rust-colored dorsal body blotches coalescing posteriorly with lateral blotches; venter light yellow with fine stippling particularly toward outside of ventrals; tail with three dorsal crossbands; proximal subcaudals stippled, immaculate distally; proximal rattle segment yellow; iris copper-colored.

Variation.—The following data were obtained from the holotype, paratypes, a specimen lacking precise locality data (but from Guerrero), and three specimens presently alive. The sample consists of 14 males and 7 females. All specimens collected in the field were adults.

Adult males range in total length from 510–664 mm and adult females range from 413–481 mm. This subspecies possesses a relatively small rattle; variation of PRW is given for males (Fig. 3) and females (Fig. 4). Palatine teeth number 1 (12%), 2 (18%), or three (70%); pterygoid teeth number 5 (12%), 6 (70%), or 7 (18%); and dentary teeth number 8 (6%), 9 (59%), or 10 (35%). Dorsal scale rows are invariably 23 at midbody, and 25 or 27 at the level of ventral 10. The dorsal scale reduction from 27 or 25 to 23 occurs between ventrals 10 and 20; the reduction from 23 to 21 scale rows does not occur before ventral 80. In front of the vent the dorsal scale rows are reduced to 17 in 4 specimens and 19 in the rest. Ventrals range from 140–149 ($\bar{x} = 144.1$) in males, and from 144–146 ($\bar{x} = 145.2$) in females. Subcaudals vary from 25–29 ($\bar{x} = 27.2$) in males, and from 21–23 ($\bar{x} = 22.0$) in females. There are 8–10 ($\bar{x} = 8.6$) rattle-fringe scales. All except five specimens possess 3/3 prefoveals; three have a 3/4 combination, one has 5/4, and another has 2/2. There tend to be 3 suboculars per side (68%) more frequently than 2. Total supralabials number 22–26 ($\bar{x} = 23.4$); infralabials number 22–25 ($\bar{x} = 24.1$). The parietals are completely fragmented into at least four scales in 17 specimens; the suture is incomplete in four specimens.

Sistrurus r. exiguus is unique in having a high frequency (9 of 21) of individuals with a light rust-colored dorsum. These specimens had reddish-brown (in some cases dark-edged) dorsal blotches, and copper-colored irises. The labials and ventral surfaces were immaculate or lightly spotted with fine stippling.

Other snakes had a bluish grey or lavender ground color with burnt orange or dark brown dark-edged dorsal blotches. Their irises were grey. These snakes possess a moderate amount of stippling on the labials, gular area, ventrals, and subcaudals.

Subsequent to capture UTA R-4534 gave birth to four young (3 females and 1 male) on 4 June 1974. The young ranged from 184 to 190 mm ($\bar{x} = 186.3$) in total length at birth. The juveniles (born to a rust-colored female) had a light grey dorsum with brown blotches, a bright pink labial and gular area, and a yellow tail tip.

Range.—The Sierra Madre del Sur in Guerrero. Presently known from only three localities, all west of Chilpancingo and east of Río Yextla and Río Papagayo drainages (Fig. 5).

Etymology.—The trivial name is adjectival and derived from the Latin *exiguus*, meaning small, in reference to the size of the rattle.

Sistrurus ravus brunneus Harris and Simmons
Oaxacan pygmy rattlesnake

Sistrurus ravus (Cope) (part), Gloyd, Spec. Publ. Chicago Acad. Sci. 4:56 (1940).

Sistrurus ravus (Cope) (part), Klauber, Bull. Zool. Soc. San Diego 26:113 (1952).

Sistrurus (*Crotalus*) *ravus* (Cope) (part), Hoge, Mem. Inst. Butantan, Sao Paulo 32: 161 (1965).

Sistrurus ravus brunneus Harris and Simmons, Bull. Md. Herpetol. Soc. 14:135 (1978).

In the description of this form, Harris and Simmons (1978) gave only two diagnostic characters neither of which is diagnostic: (1) "being a reddish-brown color dorsally," and (2) "having ten rattle fringe scales (at least in males)." The name *brunneus* is singularly inappropriate. As we stated previously, *S. r. ravus* is subject to much variation in color and reddish brown specimens are not unusual. However, it would have been helpful if Harris and Simmons (1978) had stated the source of their information concerning the color of *S. r. brunneus* in life (by no stretch of the imagination can preserved specimens be called "reddish brown"). It should be noted that they did not collect the type specimens and in some instances the snakes were collected up to 84 years prior to the description. In the series of 25 specimens we examined, 7 snakes had 8 rattle-fringe scales, 5 had 9, and 13 had 10. The sample, when compared to *S. r. ravus*, is significantly different ($P < 0.05$), but this character serves to differentiate only slightly more than half (13/25) of the Oaxacan snakes, and the snakes from the Altiplanicie Meridional frequently have 10 rattle-fringe scales. The photograph pur-

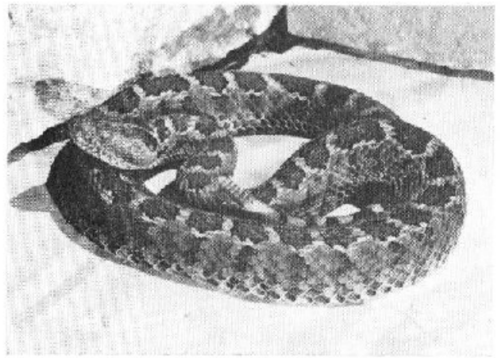

FIG. 8.—*Sistrurus ravus brunneus* from Cerro Guirone, west of San Lorenzo Albarradas, Oaxaca, México. Photograph courtesy of C. Bogert.

ported to be *S. r. brunneus* by Harris and Simmons (1978, Fig. 87) is obviously in error, and is actually *S. r. ravus*. This can be substantiated by taking locality data for the specimen and consulting their distribution map 31. In view of the inadequate and inaccurate diagnosis, and incomplete description provided by the authors of the Oaxacan pygmy rattlesnake, the following *Diagnosis* is necessary to distinguish it from the other subspecies. For precise locality data for the paratypic series (for which no locality data were given in the original description) see *Specimens Examined*.

Diagnosis.—A subspecies of *S. ravus* (Fig. 8) distinguished from the other races (Table 1) by having the parietals usually undivided, dorsal scales usually in 23 rows at midbody, total prefoveals usually exceeding 3 but not more than 6, a small rattle (PRW usually less than 10% of tail length in males, 13% in females), 5–8 tail bands in males, and 4–6 in females. The brief description of the holotype by Harris and Simmons (1978) contains two errors. There are 144 ventrals (not 148) and the total length is approximately 660 mm (not 640 mm).

Variation.—The following data are derived from 25 specimens including the holotype and paratypes. There are 18 males and 7 females in the sample. The greatest total lengths observed for males and females are 680 and 441 mm, respectively. The smallest juvenile is a male measuring 194 mm in over-all length. The rattles in *S. r. brunneus*, based on PRW, appear intermediate in size between those of *S. r. ravus* and *S. r. exiguus* but are closer to the latter (Figs. 3, 4). Palatine teeth number 1 (5%), 2 (5%), or 3 (90%); pterygoid teeth number 5 (5%), 6 (90%), or 7 (5%); and dentary teeth number 8 (10%), or 9 (90%). Dorsal scale rows at midbody are usually 23 (18 of 25 specimens), infrequently 24–25 (4), or 21 (3). At the level of ventral 10 the number of dorsal scale rows is 23–25. The reduction from 23 to 21 scale rows does not occur anterior to ventral 80. Specimens have either 17 or 19 scale rows immediately anterior to the vent except for 2 which have 15 and 16, respectively. Ventrals range from 136–150 ($\bar{x} = 142.6$) in males, and from 140–147 ($\bar{x} = 143.1$) in females. Subcaudals range from 26–30 ($\bar{x} = 28.3$) in males, and from 19–26 ($\bar{x} = 22.7$) in females. There are 8–10 ($\bar{x} = 9.2$) rattle-fringe scales. Prefoveals are more variable in this subspecies than in any other ranging from 2–6 ($\bar{x} = 4.4$). Specimens having 2 suboculars per side (total range 4–6; $\bar{x} =$ 4.6) outnumber specimens possessing 3 by about 2:1. Total supralabials number 20–25 ($\bar{x} = 28.1$) and infralabials 21–26 ($\bar{x} = 23.4$). The parietals are usually entire, but may be partially divided (4 of 25).

We have seen only one live specimen from Oaxaca (DMNH 4689) and it had a dark greyish-brown dorsum with black-edged dark brown body blotches. The labials and ventral surfaces were darkly mottled. Through the courtesy of C. M. Bogert, we have examined Kodachromes of 3 additional Oaxacan specimens including 2 of the paratypes. The ground color of a snake from Nueve Puntas (AMNH 89637) was light grey, lateral blotches were dark grey, and dorsal blotches were dark brown with narrow black borders. The pink labials were heavily stippled with grey. Two specimens from Cerro Guirone (including AMNH 100841) had a grey ground color, greyish-brown lateral blotches, dark brown dorsal blotches with narrow black edging, and pink labials strongly stippled with grey. Preserved specimens generally are dark ventrally but in a few specimens the distal subcaudals are light.

Range.—The Mesa del Sur in Oaxaca including the Sierra Juárez (Sierra de Ixtlán) and the mountains that extend northward from Cerro San Felipe (Sierra Aloapaneca) in the northwest; the Valley of Oaxaca; the Sierra Mixes and Cerro Zacatepec, highland masses flanking the Río Tehuantepec; and the coastal highlands, Cerro Neveria, the southernmost locality (Fig. 5). Further exploration may reveal its presence in localized areas west of the city of Oaxaca in the

Sierra de Cuatro Venados, Sierra Coicoyan, Cerro Yucuyacua, and Cerro Sartenejas.

Key to the Subspecies of *Sistrurus ravus*

1a Dorsal scale rows at midbody usually in 21 rows; rattle large, dorsoventral width of proximal rattle segment usually surpassing 10 and 13 percent of tail length in males and females, respectively .... *S. r. ravus*

b Dorsal scale rows at midbody usually in 23 rows; rattle smaller, dorsoventral width of proximal rattle segment usually less than 10 and 14 percent of tail length in males and females, respectively 2

2a Tail bands usually 5 or fewer in males, 4 or fewer in females; body blotches usually fewer than 34; parietals usually divided .... *S. r. exiguus*

b Tail bands usually 6 or more in males, 5 or more in females; body blotches usually exceeding 34; parietals usually undivided .... *S. r. brunneus*

Habitat

Sistrurus ravus inhabits temperate montane regions of moderate to high elevations. The lowest elevation from which we have taken the species is 1490 m in the Zapotitlán Basin of southern Puebla; the highest is from near Huitzilac, Morelos, at an elevation of nearly 3050 m. In the Sierra de Ajusco near Huitzilac the pygmy rattlesnake occurs in zacatón meadows surrounded by pine and fir forest (primarily *Pinus montezumae* with *Abies religiosa* occurring on the higher crests of 2800 m elevation or higher) interspersed with oaks and madroños. On an arid plain 1.6 km W of Cacaloapan, Puebla, at an elevation of 1950 m we found *S. r. ravus* in an area supporting xerophytic vegetation including yuccas, palmettos, agaves, and many species of cacti. Large clumps of *Ferocactus robustus* were the most conspicuous cacti. *Prosopis juliflora* and acacias were dominant trees. Near Ixtlán de Juárez in the Sierra Juárez, Oaxaca, at an elevation of 2195 m, *S. r. brunneus* is found in a temperate woodland of oaks, madroños (*Arbutus*), alders (*Alnus*), buckhorns (*Ceanothus*), and several species of pines (including *Pinus herrerai*). In the Sierra Madre del Sur of Guerrero near Omilteme *S. r. exiguus* occurs on floodplains overgrown with thick brush and *Baccharis*. The floodplains are flanked by hillsides supporting a pine-oak forest laden with a heavy epiphytic growth of *Tillandsia*.

Thus *S. ravus* inhabits areas of considerable ecological diversity and is not restricted to a single vegetation zone, biotic province, or life zone (sensu Leopold, 1950; Goldman and Moore, 1946; Smith, 1940; Stuart, 1964; or Goldman, 1951). Precipitation does not seem to be an important factor limiting distribution. The climate at Tehuacán, Puebla, differs little from the climate at Cacaloapan situated 27 km to the northwest. These localities are in the same rain shadow created by the southernmost extension of the Sierra Madre Oriental and receive approximately 478 mm annual rainfall. Although no precise data are available, the Zapotitlán Basin is located in a drier part of the rain shadow that probably receives less than half of this amount. In the vicinity of Ixtlán de Juárez a yearly mean of slightly over 1000 mm of precipitation falls and in the areas of the Sierra Madre del Sur where *S. r. exiguus* occurs precipitation may exceed 1500 mm per annum. Temperature is largely dependent on altitude and appears to be of some importance in determining distribution as *S. ravus* does not descend much below 1490 m and may occur slightly above 3000 m. Mean annual temperatures vary from near 10 C at 3000 m to more than 20 C at elevations of 1500 m and below (for data on precipitation and temperature see Contreras, 1942; and Page, 1930).

Perhaps the most important factors affecting local distribution are degree of slope and presence of open areas with a predominance of low vegetation such as grasses, desert scrub, or secondary growth on forest edges. Most snakes collected have been from plateaus, floodplains, alluvial fans or basins, or other areas of relatively little relief. The distribution of *S. r. ravus* appears to be less fragmented than either *S. r. brunneus* or *S. r. exiguus*. Only remnants of the former plateau surface occur over the Mesa del Sur and the Guerrero highlands are characterized by particularly rugged terrain.

The present ecological barriers between the races of *S. ravus* are not readily apparent from the literature. The highlands of Guerrero and parts of southern Oaxaca are collectively called the Sierra Madre del Sur. Most maps delineating vegetation of the region (Leopold, 1950; Wagner, 1964) give the impression of a continuous highland between the two states having a cover of temperate forest. However, low elevations are carved through the massif by the headwaters of the Río Balsas and Río Papagayo and in several places ridges are formed that do not exceed 1000 m elevation. Inhospitable conditions prevail on these ridges effectively isolating highland adapted forms to the east and west. Thus the range of *S. r. exiguus* does not appear to be continuous with that of *S. r. brunneus* due to the low intervening elevations and the extremely steep slopes of the Sierra Madre del Sur. Taylor (1942) emphasized the distinctness and high degree of endemism in reptiles and amphibians of the Guerreran and Oaxacan uplifts.

Due to elevational restrictions, any continuous distribution between *S. r. brunneus* and *S. r. ravus* could be along the Continental Divide (the ridge between the Río Balsas and Río Papaloapan). An intensive search in the area, particularly in the area of El Tejocote ("Tejocotes" on some maps), revealed the presence of 4 other crotalines, but not *S. ravus*. We believe the virtual absence of horizontal terrain in this rugged area excludes *S. ravus* from all but possibly a few small isolated localities. The present day disjunction between *S. r. ravus* and *S. r. brunneus* may mostly be due to erosion by the tributaries of the Río Balsas and Río Papaloapan.

Distribution of Sympatric Crotalines

Sistrurus ravus is sympatric with 3 crotaline species of similar length that are potential competitors for food. *Sistrurus ravus* is relatively heavy bodied and appears to be adapted to rather flat areas. It may be unable to compete on steep slopes with the more slender sympatric crotalines. In Guerrero *S. r. exiguus* was common on a floodplain of a small creek running eastward from Omilteme. *Bothrops undulatus* and *Crotalus intermedius omiltemanus* were frequently encountered on the steep slopes and ridges flanking the floodplain, but were rarely found on the floodplain proper. Conversely, *S. r. exiguus* was encountered only once on the slopes, and then only 10 m above the creek. *Sistrurus r. brunneus* inhabits river bottoms, regions of rolling hills (NE Mitla), and regions where small, flat, grassy areas occur in otherwise rugged terrain (near Ixtlán de Juárez). It is sympatric with the same two crotaline species that occur with *S. r. exiguus* in Guerrrero (as well as with the larger rattlesnake, *Crotalus basiliscus oaxacus*) and the same ecological separation appears to exist. Habitats in the Valley of Oaxaca have been so modified by over 2000 years of agriculture that assessment of the past distribution of *S. r. brunneus* is difficult. It probably was formerly widespread in the region and still occurs there sporadically. Usually it is found in rocky terrain untouched by the plow on the border of the Valley. *Sistrurus r. brunneus* also occurs in southeastern portions of the Valley where agriculture has not been as intense as elsewhere in the Valley. On the Altiplanicie Meridional, we invariably encountered *S. r. ravus* on relatively level or gently sloping areas. We found the species to be particularly abundant in the bunchgrass meadows north of Huitzilac. *Sistrurus r. ravus* appears to be absent from the conifer-bearing rocky slopes that surround this meadow, but *Crotalus t. triseriatus* and *C. transversus* were encountered in this area. The terrain south of the Neovolcanic Axis in Puebla becomes more rolling and less rugged. *Sistrurus r. ravus* was frequently taken in the broad, open valleys that characterize the northwestern headwaters of the Río Papaloapan. *Bothrops melanurus* is often sympatric with *S. r. ravus* in southern Puebla, but *B. melanurus* does not show any apparent affinity for a particular slope and was taken in a variety of situations. In the eastern portion of its range *S. r. ravus* is sympatric with *B. undulatus*, *C. i. intermedius*, and *C. t. triseriatus*, which are found on steep slopes.

Food and Behavior

Food habits.—Klauber (1972) reported 2 *Sistrurus ravus* containing mammal remains and one with a lizard of the genus *Mabuya*. He stated that the main food source for pygmy rattlesnakes is lizards. We found the primary food sources for juvenile *S. ravus* (under 300 mm) to be small rodents and crickets (Gryllacrididae). As the snakes mature, rodents constitute a greater percentage in both frequency and bulk.

The stomachs of 3 juvenile *S. r. ravus* contained 2 rodents and a cricket (*Stenopelmatus*). One adult contained a rodent and another an anguid (*Barisia imbricata*). Eight juvenile *S. r. brunneus* contained 5 rodents, 2 lizards (*Sceloporus* and *Eumeces*), 3 crickets (*Stenopelmatus*), and a small anuran. Scats from 7 adult *S. r. exiguus* all revealed rodent hair. Except for stenopelmatids, no more than a single prey item was present in a snake. The *Eumeces* and frog had been swallowed backwards; the other food items had been swallowed headfirst. In the laboratory, juvenile and adult *S. ravus* ate mice.

Other crotaline species sympatric with *S. ravus* prey on many of the same animals, but niche overlap is avoided because the former occupy steep slopes. In Guerrero, the scats of 18 *Crotalus i. omiltemanus* contained scales of *Sceloporus* and Klauber (1972) reported 12 additional specimens that had consumed lizards. The scats and stomach contents of 8 adult *Bothrops undulatus* from Guerrero contained the remains of rodents (mainly *Reithrodontomys*), and a juvenile regurgitated a *Barisia g. gadovii*. Stomach contents of several *C. i. gloydi* from El Tejocote and the Sierra de Juárez revealed the remains of *Sceloporus*. Klauber (1972) reported that 2 *C. i. intermedius* contained lizard scales. Adult *C. t. triseriatus* appear to prey on lizards and mammals with about equal frequency and often eat crickets (Klauber, 1972). Davis and Smith (1953) also reported specimens that contained a frog and wood rat (*Neotomodon alstoni*), and Klauber (1972) found a juvenile containing a salamander.

Activity patterns.—The activity patterns of *S. ravus*, like those of most reptiles, are strongly affected by seasonal climatic fluctuations. During the dry season (November–May) snakes were rarely found abroad. The first *S. r. exiguus* were found the day following the first rain of the season that fell the night of 17 May 1974. Previous collecting in the area for a week failed to produce any specimens. From our experience with these snakes we infer that they are diurnal foragers. Recently emerged specimens found early in the morning were usually coiled and basking in the sun. They made little attempt to escape and seemed incapable of rapid movement, being rendered inactive by the cool temperature. By late morning most snakes encountered were crawling and moved quickly when approached. In August 1973 we observed an individual crawling on the road between Tres Cumbres and Huitzilac in the rain at about 2200 hrs. Davis and Smith (1953) reported finding a specimen crawling in a field at night in Morelos.

Defensive behavior.—Like most rattlesnakes, *S. ravus* will rattle when annoyed. However, we feel that *S. r. ravus* is more easily provoked and aggressive than *S. r. exiguus* or *S. r. brunneus*. Specimens from Puebla would repeatedly coil and strike at moving objects placed in front of them. They also often bit and killed other snakes placed in the same collecting bag. On the other hand, snakes from Guerrero would usually rattle intermittently when pinned at midbody, but often would not turn and attempt to bite or even coil. D. A. Rossman (in litt.) described interesting escape behavior in a snake from Puebla. The specimen held its head at a sharp right angle to the long axis of its body so as to face its tormentors while it attempted to crawl away. We have noted that snakes from arid portions of Puebla (near Cacaloapan and Zapotitlán) tend to greatly compress their bodies dorsoventrally when defensively coiled but we have not observed this behavior in snakes from elsewhere.

Specimens Examined

Institutional abbreviations are listed in Edwards (1975). Distances originally given in miles have been converted to kilometers.

Sistrurus ravus ravus.—Distrito Federal: Lomas el Cristo, "Chapingo" (TCWC 46436). Mexico: 2.0 km E Amecameca (KU 85013); Río Frío (KU 26767–71). Morelos: 0.8 km W Huitzilac (TCWC 4135); 2.4 km SE Huitzilac (TCWC 7339); near Huitzilac (UTA R-4701, 5557, 5661); near Tres Marías (FMNH 113018). Tlaxcala: 27.2 km N Santa Ana, 20.8 km S Hueyotlipan (LACM 67177); 8.0 km SW Tlaxcala (TCWC 821. Puebla: Atzitzintla (FMNH 1513, SDSNH 657); 1.6 km W Cacaloapan (KU 157872, UTA R-5662); Cacaloapan (USNM 110594); Cerro Malinche, 5.0 km N Canoa (MVZ 112414); Chalchicomula (Cd. Serdán) (UIMNH 19185, USNM 46352); Hacienda Atlapaleca, Mpio. Libres (AMNH 114571, YPM 7795–98); Lago Salado (TCWC 862); 55 km E Mexico City (TCWC 861); Puebla (SDSNH 43745, UTA R-4537); 2.4 km S Puerto del Aire (LSU 11017); Rinconada (USNM 46351); 5.6 km S Zapotitlán (UTA R-4911); 4.8 km SW Zapotitlán (UTA R-5814, 6617–19). Veracruz: Acultzingo (FMNH 113011–16, UIMNH 19188–89); El Limón (UIMNH 48828, USNM 110595); 2.0 km W El Limón (KU 26478); 1.0 km NE Puente Colorada, Puebla (USNM 110596); Totalco (FMNH 113017, UIMNH 19187); South tableland (USNM 250–51, syntypes). Literature records.—Distrito Federal: Sante Fe (Gloyd, 1940, cites Richard); Contreras (Martín del Campo, 1942). Mexico: Chalco (Martín del Campo, 1935); San Juan Teotihuacán, Volcán de Toluca (Gloyd, 1940). Puebla: Sierra de Zacapoaxtla (Mocquard, 1909).

Sistrurus ravus exiguus.—Guerrero: near Chilpancingo (MVZ 45254); Ejido San Vicente, El Jazmín (UTA R-4912, 5663); Las Joyas (UTA R-5664–65); Omilteme (UTA R-5623); 0.8 km E Omilteme (UTA R-4536); 1.6 km E Omilteme (UTA R-4488–89, 4533 [holotype], 4534–35, 6116–17, 6226, 6256, 7221, Dallas Zoo—3 specimens); 3.2 km E Omilteme (KU 87763).

Sistrurus ravus brunneus.—Oaxaca: 16.8 km E Atepec (KU 137679); Cerro Guirone (AMNH 100842); 2.6 km E Ixtlán de Juárez (AMNH 104404); 2.7 km E Ixtlán de Juárez (AMNH 102916, holotype); 2.9 km E Ixtlán de Juárez (UNM 30762); 3.2 km E Ixtlán de Juárez (AMNH 93226–27, UNM 22748, 25526); 4.2 km E Ixtlán de Juárez (UNM 32097–101); Jilotepec (UIMNH 32553); 2.7 km SE Matatlán (AMNH 102915); 23.8 km N Mex. Hwy 190 on Mex. Hwy 175 (DMNH 4689); Mitla (AMNH 89636); 14.1 km NE Mitla (AMNH 100841); Nueve Puntas (AMNH 89637); 28.8 km NNE Oaxaca (LACM 64446); Quiegolani (AMNH 65174–75); Totontepec (USNM 46555, 46609).

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Resumen: Una nueva subespecie de *Sistrurus ravus* es descrita de tierra alta del estado Mexicano de Guerrero. Esta forma es distinguida de las otras dos subespecies por caracteres escamosos, proporciones del cuerpo, color, y diseño. La distribución de estos crotalinos es de interés zoogeográfico porque se demuestra la presencia de poblaciones descoyuntadas que son confinadas en tierras altas bastante separadas en México. Su distribución es considerado de acuerdo al clima, las fisiografía, y la simpatría con otras especies de crotalinos.

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