VARIATION AND DISTRIBUTION OF THE MIDDLE AMERICAN SNAKE GENUS, LOXOCEMUS COPE (BOIDAE?)

CRAIG E. NELSON AND JOHN R. MEYER

Department of Zoology, Indiana University and Department of Biological Sciences, University of Southern California

ABSTRACT. Taxonomy and distribution of *Loxocemus* are reviewed. All specimens are assigned to *L. bicolor*. This species is known on the Pacific versant from Nayarit, Mexico, to Costa Rica and on the Atlantic versant from Chiapas, Mexico, and Honduras. Sexual dimorphism exists in spurs. No other geographically consistent secondary sexual dimorphism is known. Georgraphic variation exists in several characters of scutellation and relative proportion. Previous authors have proposed dividing *Loxocemus* into two species, subspecies, or phases, primarily based on supposed dichromatism; these divisions do not correspond with the geographic variation demonstrated in scutellation. Variation in coloration is not dichromatic but gradational. Prior fixing of the type locality of one of the synonyms, *Plastoseryx bronni*, is untenable.

An examination of recently accumulated material of Loxocemus from Central America suggested that a re-evaluation of variation within the genus was advisable. This genus is usually placed in the Boidae but Romer (1956) placed it in the Aniliidae (sensu latu) and regarded it as structurally transitional to the Boidae. It differs from other New World boas in some characters that it shares with the Old World pythons (Romer, op. cit.). Although Bocourt (1882) and some other early workers considered all Loxocemus to be conspecific (summarized by Taylor, 1940), the recent trend, beginning with Taylor (op. cit.), has been to regard this genus as divisible into two forms which have been variously treated as species, subspecies (see synonomy) or dimorphic phases of one species (Zweifel, 1959; Duellman, 1961). The basis of this separation has been coloration, with or without other presumed differences. In both phases the dorsal surfaces of the head, body, and tail are usually uniform lavender-brown to grey-brown. Some specimens show irregular white spotting dorsally. In the dark or sumichrasti phase the venter is the same color as the dorsum, but is usually paler (Fig. 2). In the light or bicolor phase the supralabials and the ventral surface of the head, body and tail are immaculate white or cream (Fig. 3). Taylor (1940) proposed that three ratios of scale lengths would also separate the color phases. On the basis of 9 specimens, Woodbury and Woodbury (1944) suggested that these characters were invalid, an opinion with which H. M. Smith (in Woodbury and Woodbury, op. cit.) concurred. Duellman (1961) discussed six specimens all of which could be considered one phase on coloration and another on squamation.

METHODS. In order to evaluate previously proposed distinctions within *Loxocemus* and to check for possible sexual dimorphism and geographic variation, 13 characters, including sex and color, were examined. Characters selected had been emphasized by previous workers. Abdominal and subcaudal scute counts were recorded as were total length and snout-vent length. Four characters of head squamation were measured with a Bausch and Lomb "Measuring Magnifier" and recorded in tenths of a millimeter. These were length of suture between internasals, length of suture between prefrontals, length of left anterior chinshield, and length of scale bordering left anterior chinshield. When the length on the two sides of a suture, or of the scales on each side of



Fig. 1. Distribution of Loxocemus bicolor in Mexico and Central America.



Fig. 2. L. bicolor, ventral view. Venter entirely dark. (UMMZ 114492, Oaxaca).
Fig. 3. L. bicolor, ventral view. Venter unpigmented. (LBSC 1397, Nayarit).
Fig. 4. L. bicolor, ventral view. Venter with extensive mottling. (JV 38, Nicaragua).
Fig. 5. L. bicolor, ventral view. Venter grading from light anteriorly to very dark posteriorly. (USC cre 8211, Costa Rica).

the chin, differed more than 0.3 mm an average was recorded. These four measurements will be referred to respectively as internasal suture, prefrontal suture, chinshield length and border-scale length. As an explicit test of earlier statements (Taylor, 1940) attributing taxonomic significance to the relative size of certain scales, the comparative lengths of three pairs of measurements were coded with "1" indicating a ratio less than 1.0, "2" indicating the measurements were within 0.1 mm of being equal in length (neither scale appreciably larger), and "3" indicating a ratio greater than 1.0. The ratios coded in this manner are: prefrontal suture/internasal suture, chinshield length/borderscale length, and length from apex of chin to posterior corner of 2nd infralabial as measured parallel to body axis/the similar measurement

for 1st infralabial. Color was coded on a five point scale: "1"-supralabials and entire ventral surface of head, body and tail white or cream (Fig. 3); "2"—similar to "1" except that up to $\frac{1}{3}$ of ventral surface shows dark pigment; "3"-supralabials variable, ventral surface neither predominantly light or dark but with approximately equivalent portions of each, either blotched or grading smoothly from dark to light (Figs. 4 and 5); "4"-infralabials and ventral surfaces generally dark but showing light areas or with scales distinctly bordered with light; "5"-ventral surfaces and infralabials entirely pigmented (except for tip of terminal scale on tail) (Fig. 2). In addition to these 12 characters and ratios, sex was determined for most specimens. Some collections were examined before the criterion for sexing was established. Specimens with well developed spurs were considered males; those which lacked visible spurs or had only a rudimentary spur on one side were considered females. This sexing criterion was checked by dissection or by presence of everted hemipenes on more than 20 specimens of assorted sex. A computer program was used for calculating all ratios and correlation coefficients between these 13 characters as well as for calculation of mean, standard deviation, and standard error for each character and ratio. If differences between means exceeded twice the standard error of the larger samples significance was tested using the modifications of Student's t test recommended for small samples by Moroney (1956: 232-233). Unless otherwise stated, "significant" or "significantly" indicate a probability of chance occurrence of the observed difference of less than 0.05.

In order to separate other variation from geographic variation, the specimens were grouped into three samples: Central America; Oaxaca, Mexico; and Mexico north of Oaxaca. This separation was dictated by concentrations of specimens in various areas (see list of specimens). The two specimens examined from Chiapas, Mexico, are discussed in the consideration of geographic variation, but were omitted from calculations.

Range. Loxocemus occurs at low and moderate elevations on the Pacific versant of Mexico and Central America from northern Nayarit, Mexico, southward to northern Costa Rica. It is recorded on the Atlantic versant from the Grijalva Valley of Chiapas, Mexico, and from northeastern Honduras. These Caribbean versant specimens refute the contention that the genus is a strictly Pacific versant form (Stuart, 1963). The only definite localities previously recorded from south of Mexico are La Union, El Salvador, (Cope, 1862) and Comayagua and La Lima, Honduras (Meyer, 1966).

RESULTS AND DISCUSSION. Association of other characters with coloration: In order to examine the possibility that characters other than coloration might distinguish the two presumed color phases, samples within two geographic areas (Mexico north of Oaxaca and Oaxaca) were divided into light (color codes 1 and 2) and dark (color codes 3, 4 and 5) groups. As no predominantly dark specimens were examined from Central America, this sample was not divided on color. The result of the comparison of the two color groupings for the three ratios proposed by Taylor (1940) and for sex are summarized in Table 1. A significantly (p < .02) greater proportion of the light specimens are males in the Oaxacan sample. No other significant differences between the two color groups were found for any of the characters examined or for their ratios. In most cases the direction of the difference between the means of the dark and light samples is reversed between the two geographic samples. The lack of a taxonomically useful association, either between color and the coded ratios or among the ratios themselves, is confirmed by the absence of any consistent, significant correlation between these characters.

		Oaxaca 24 Light/17 Dark			North of Oaxaca 16 Light/15 Dark		
Character*	Color+	Range	Mean	Std. Dev.	Range	Mean	Std. Dev.
Internasal Suture Prefrontal Suture	Light Dark	0.56–1.87 0.69–1.42	0.92 1.00	0.276 0.213	0.44–1.62 0.44–1.36	0.77 0.77	0.350 0.277
Same Coded	Light Dark	1–3 1–3	1.67 1.76	0.865 0.903	1–3 1–3	1.44 1.40	0.814 0.737
Border Scale 1st Chinshield	Light Dark	0.55–1.13 0.37–1.22	0.80 0.76	0.029 0.054	0.48–1.11 0.48–1.44	0.70 0.81	0.158 0.284
Same Coded	Light Dark	1–3 1–3	1.58 1.76	0.830 0.529	1–3 1–3	1.25 1.40	0.683 0.737
Coded Comparison 1st & 2nd	Light	1–3	1.92	0.830	1–3	1.44	0.403
Infralabials	Dark	1–3	1.79	0.849	1–3	2.00	0.640
Sex ($\delta = 1, \varphi = 2$)	Light Dark	1–2 1–2	1.24 1.67*	0.436 *0.492	$1-2 \\ 1-2$	1.44 1.36	0.527 0.505

TABLE 1

Comparisons of Loxocemus with light+ and dark+ venters.

See text for definitions
Significant difference in means
Light = color codes 1 and 2; Dark = color codes 3, 4 and 5.

Sexual Dimorphism. Sexual dismorphism was analyzed in order to separate its effects from those of taxonomic significance and from geographic variation. The spurs are distinct in males and are usually not visible in females. This corresponds closely to differences noted in *Constrictor* (Hoge, 1947) and in *Enygrus* (Stickel and Stickel, 1946). The use of these spurs in courtship of various male boids is described by Davis (1936). No other geographically consistent significant differences between males and females were found for the characters or ratio examined. The absence of dimorphism in relative body length is confirmed by a high correlation (0.98–"1.000", p < .001) between total length and snout-vent length.

Those characters which differed significantly between the sexes in one or more of the samples are summarized in Table 2. A distinct difference exists in the total length of males and females in Central America (Table 2). This difference is reflected in all linear measurements for this sample. Such differences in this sample are omitted from Table 2 if they are not significant in either of the other samples. No significant differences between the sexes were found in the Central American sample for any size independent character, for the ratio of any two of these characters, or for the ratio of any two linear measurements. No geographically consistent differences between the sexes were found in the characters examined (Table 2). Some difference in color is indicated for the Oaxacan sample and some in head scales for the northern sample. Sumichrast (1880) proposed that specimens from near Tehuantepec were sexually dimorphic in coloration.

In the combined sample from all parts of the range the sex ratio is $46 \circ \delta : 30 \circ \circ$. This does not differ significantly from a 1:1 ratio.

Correlations. Analysis of the correlation coefficients between each of the 78 pairs of characters revealed no geographically consistent, significant correlation between any two characters except as a reflection of size. Thus, none of the characters which have been proposed as taxonomic criteria are correlated with one another, with sex, or with color. Combinations between linear measurements were the only correlations that were significant in all three samples, the only ones exceeding a coefficient value of 0.65, and the only ones which were very highly significant (p < .001) in any sample. These combinations reflect the fact that larger animals have larger scales.

Variation in coloration. In the material now available, coloration falls into a gradient. One extreme is an entirely light ventral surface. Successive stages are slightly darkened subcaudals, dark or mostly dark subcaudals and posterior abdominals, most ventral scales with an anterior dark edge with the amount of darkening increasing posterior-

TABLE 2

Character*	Area	Sex	Range	Mean S	td. Dev.
Color	North of Oaxaca	ð 9	1–5 1–4	2.83 2.50	1.528 1.195
	Oaxaca	8 9	1–5 1–5	1.25 3.23**	1.251 1.423
	Central America	ሪ የ	2–3 3–4	2.36 2.56	0.497 0.726
Coded Comparison of Infralabials	North of Oaxaca	රි ද	1–3 1	1.50 1**	0.636 0
	Oaxaca	රි ද	1–3 1–3	1.45 1.39	0.759 0.768
	Central America	රි ද	1–2 1–3	1.08 1.25	0.289 0.707
Chinshield Length Prefrontal Suture	North of Oaxaca	ð P	0.74–2.85 1.67–3.33	1.94 2.66**	0.663 0.537
	Oaxaca	රි ද	1.00–3.58 1.33–2.89	2.05 1.97	0.571 0.445
	Central America	රි ද	1.51–2.73 0.46–1.98	1.83 1.45	0.319 0.494
Border-Scale Lth. Prefrontal Suture	North of Oaxaca	ኛ የ	0.94–1.75 1.13–2.50	1.37 1.84	0.800 0.275
	Oaxaca	ሪ የ	1.00–2.33 1.03–2.31	1.53 1.46	0.352 0.358
	Central America	ô ያ	0.91–1.86 0.85–1.34	1.22 1.09	0.256 0.176
Total Length (mm)	North of Oaxaca	ô ያ	395–1071 350–1119	766.1 731.3	219.6 243.3
	Oaxaca	ଟ ହ	345–1309 510–842	692,2 685.7	270.5 096.2
	Central America	රි ද	382–1051 509–1247	632.4 869.6**	201.6 238.9

Sexual dimorphism in Loxocemus.

* See text for definitions. Numbers: North of Oaxaca 1233, 899; Oaxaca 2033, 1399; Central America 1433, 999. ** Significant difference between means for 33 and 99 (p < 0.05).

ly, and dark ventral surface with the more anterior scales having a posterior light margin. At the other extreme all of the ventral sruface is dark. This variation is illustrated in Figs. 2–5. Some of the intermediate specimens have the ventral surface irregularly mottled with dark and light blotches side by side (Fig. 4). No objective division of the gradient of coloration into dark and light phases is possible.

The localities from which dark or predominantly dark specimens come can be arranged in a geographic sequence from the Grijalva Valley of Chiapas; north and west through the Tehuantepec, Oaxaca, region; the coastal region of Guerrero; and the Michoacan section of the Balsas Basin; to the vicinity of Colima, Colima. Intermediate and/or light specimens are known from all these areas except coastal Guerrero. However, light specimens are known from coastal regions from near the Guerreran border in both Oaxaca and Michoacan. Light specimens are known in numbers without the presence of intermediate or dark associates only from the Nayarit region.

Geographic variation in squamation and proportion. The data for characters that show significant geographic variation are summarized in Table 3. There is no significant geographic variation in total length or coloration. The ratio of the snout-vent length/total length is significantly less in the Central American sample-in this sample the tails are relatively longer. This is reflected in a larger number of subcaudal scutes in this population. A cline is evident in the number of abdominal scutes: the minimum number and the mean both increase from north to south. The prefrontal suture is relatively larger and the internasal suture is relatively smaller in the Central American population. The ratio between these two sutures is consequently very different in this southern population as compared with the more northern ones. (A similarly significant difference occurs in the coded ratio but was not included in Table 3). In most characters for which the Central American and Oaxacan samples differ the sample from north of Oaxaca is intermediate. Of two specimens from Chiapas, one from Tuxtla Gutierrez is similar to the Oaxacan sample while one from Esquintla agrees with the Central American population.

Further analysis of the nature of geographic variation is currently impossible because of the lack of material from appropriate regions. Only nine widely scattered records are available for that third of the range lying between Oaxaca and Nicaragua. Further analysis of the variation north of Oaxaca was attempted by subdividing this sample, but the scattered nature of the records and the resultant small sample size for each area obscured any pattern that may exist. As can be seen

TABLE 3

Character*	Area	Range	Mean	Std. Dev.	Significance+
Abdominal Scutes	North of Oaxaca	234-270	251.3	7.49	p<0.01
	Oaxaca	243-267	256.1	4.78	0.001
	Central America	252-270	260.7	4.87	0.01
Subcaudal Scutes	North of Oaxaca	43–50	45.1	1.67	0.001
	Oaxaca	39-49	43.1	2.22	0.001
	Central America	44-52	48.1	2.07	0.001
Total length (mm)	North of Oaxaca	292-1119	682.4	256.24	not
	Oaxaca	333-1309	697.3	212.79	not
	Central America	382-1247	687.4	241.07	not
Snout-Vent length	North of Oaxaca	0.860-0.975	0.889	0.019	0.05
Total length	Oaxaca	0.838-0.934	0.898	0.015	not
-	Central America	0.871-0.930	0.884	0.011	0.001
Prefrontal Suture	North of Oaxaca	1.2-3.1	2.19	0.58	not
	Oaxaca	1.2-3.5	2.09	0.54	0.001
	Central America	2.0-4.3	2.92	0.75	0.001
Internasal Suture	North of Oaxaca	0.8-3.0	1.59	0.503	0.01
	Oaxaca	1.2 - 2.8	1.91	0.378	0.05
	Central America	0.8 - 2.2	1.32	0.384	0.001
Internasal Suture	North of Oaxaca	0.435-1.615	0.77	0.311	0.02
Prefrontal Suture	Oaxaca	0.560-1.867	0.94	0.252	0.001
	Central America	0.279-0.739	0.46	0.117	0.001
Color	North of Oaxaca	1–5	2.48	1.484	not
	Oaxaca	1–5	2.70	1.365	not
	North of Oaxaca	2–3	2.37	0.572	not

Geographic variation in Loxocemus.

* See text for definitions. Numbers: North of Oaxaca—31, Oaxaca—41, Central America—27. † Comparisons listed in order: N. of Oaxaca with Oaxaca, N. of Oaxaca with Central America, and Oaxaca with Central America.

from the map (Fig. 1) the records are very strongly clustered—mainly along the subhumid portions of major highways.

Habitat. In Michoacan Loxocemus inhabits arid scrub forest at low elevations, which is composed of thorny, deciduous trees that are often stunted and widely spaced (Duellman, 1961). Similar vegetationscrub or thorny open forest-occurs through most of the range of Loxocemus (Carr, 1950; Duellman, 1960; Holdridge, references in Tosi, 1964; Leopold, 1950; Shelford, 1963; Stuart, 1954; Wagner, 1964).

The vegetation of the Grijalva Valley (Chiapas) and of the Balsas Basin (Guerrero) is continuous with and of the same semi-arid nature as that of the adjacent Pacific lowlands. Holdridge's (cited in Tosi, 1964) large scale vegetation maps of Central America show that the dry tropical forest (Bosque Tropical Seco) includes all of the Central American records for Loxocemus with the exception of Tela. Honduras. Tela lies within the wet tropical forest (Bosque Tropical Humedo=poor tropical rain forest of Shelford, op. cit.) but is only 15 km. (9 mi.) from the edge of the dry tropical forest. Thus the specimen recorded from Tela may have acutally come either from the main body of the dry tropical forest or from some local subhumid situation. No gross difference in the vegetation is apparent that would account for the concentration of the darker specimens in the mid-portion of the range. Neither are any differences in the soils of the area where darker specimens occur evident from Stevens' (1964) maps of the soils of Mexico and Central America.

Loxocemus has been collected from rock piles (Taylor, 1940); holes in the ground (Oliver, 1937); under leaf litter, logs and the bark of logs (Woodbury and Woodbury, 1944); and crawling on the ground and highway (Schmidt and Shannon, 1947; Fouquette and Rossman, 1963; Meyer, 1966; D. C. Carter, *pers. comm.*, Costa Rica; CEN, *pers. obs.*, Guerrero and Honduras). Woodbury and Woodbury (op. cit.) noted no ecological differences between the color extremes where they occur together in the Tehuantepec region and no such differences are evident in the very limited available information.

CONCLUSIONS. Loxocemus has generally been separated into two species, subspecies, or phases. These separations were based primarily on supposed color dimorphism but sometimes included differences in head scutellation. No scutellation characters are known that would support a division on color. The range of the darker specimens is entirely enclosed by that of the lighter specimens, and the darker specimens almost invariably occur in association with intermediate or light specimens. Coloration in the specimens now available grades continuously from light to dark and cannot be objectively separated into light and dark phases. Thus Loxocemus does not seem to offer an appropriate parallel to the discontinuous variation present in the California Kingsnakes (Klauber, 1936) with which it has been previously compared (Woodbury and Woodbury, 1944). No habitat differences are evident that would account for the differences in color. No basis was found for dividing Loxocemus into two or more species. Consequently all specimens are referred to L. bicolor. This agrees with the formal

treatment by Duellman (1961) and some pre-1910 workers, and with the suggestion of Zweifel (1959). An abbreviate synonomy, including primarily those references not cited by Taylor (1940) or Mertens (1951), is given below.

The Central American and, to a lesser extent, the more northern Mexican populations are significantly different from the Oaxacan population in some characters of scutellation. A cline of increasing mean and minimum number of abdominal scutes occurs from north to south. In contrast, for other characters the northern and southern populations both tend to diverge in a similar fashion from the Oaxacan population. Due to inadequate material it is presently impossible to determine whether the clines connecting these populations are stepped or gradual. Any attempt to distinguish subspecies at this time would thus be premature.

Plastosteryx bronni Jan 1862, lacks a definite type locality. It has usually been considered a synonym of L. bicolor (type locality at La Union, El Salvador) with which it agrees in coloration (Mertens, 1951). The other characters of the type as given by Mertens (1951), are matched only in the population from north of Oaxaca. The number of abdominal scutes (242) excludes an origin from Central America (where 251 is the minimum known number of abdominals). The characters of the type of bronni thus are such as to invalidate the fixing of the type locality at La Union, El Salvador (Smith and Taylor, 1950), thereby supporting suggestions by Dunn and Stuart (1951) and Mertens (1951, 1952) that fixing was premature. P. bronni may be a senior synonym of L. sumichrasti (type locality at Tehuantepec, Oaxaca).

SYNONOMY

Loxocemus bicolor Cope

Loxocemus bicolor Cope, Proc. Acad. Nat. Sci. Phila. 1862:77 (Type locality: La Union, El Salvador). Oliver, J. A., Occ. Pap. Mus. Zool. Univ. Mich., 360:18, 1937. Taylor, E. H. and H. M. Smith, Univ. Kans. Sci. Bull. 25(13):239-240, 1939 (1938). Taylor, E. H., *Ibid.* 26(14):445-447, 1940 (1939) (includes synonomy and previous records). Smith, H. M., Proc. U. S. Nat. Mus. 93(3169):445, 1943. Smith, H. M. and E. H. Taylor, Bull. U. S. Nat. Mus. 187:27 (summarize Mexican localities, give range south to Costa Rica). Mertens, R. R., Abh. Senckenb. Naturf. Ges. 487:60, 1952. Peters, J. A., Occ. Pap. Mus. Zool., Univ. Mich. 554:21, 1954. Taylor, E. H., Univ. Kans. Sci. Bull. 36(pt. 2, no. 11):681, 1954. Zweifel, R. G., Amer. Mus. Novitates No. 1953:5, 1959. Duellman, W. E., Univ. Kans. Pub. Mus. Nat. Hist. 15(1):89-90, 1961.

Plastoserxy bronni Jan, Arch. Für Naturgesch. 28, vol. 1: 242, 244-6, 1862 (Type locality unknown). Taylor, E. H., Univ. Kans. Sci. Bull. 26(14):446 (Questions conspecificity with L. bicolor). Mertens, R. R., Senckenbergiana 32(3):205-6 (Dem-

onstrates conspecificity with *L. bicolor*; reviews past history to which should be added Taylor op. cit.).

Loxocemus sumichrasti Bocourt, Ann. Sci. Nat. Ser. 6, vol. 4(7): 1, 1876 (Type locality: Tehuantepec). Taylor, E. H., Univ. Kans. Sci. Bull. 26(14):447-448, 1940 (1939) (Reviews earlier synonomy and records). Schmidt, K. P. and F. A. Shannon, Fieldiana: Zoology 31(9):76, 1947. Alvarez del Toro, M. and H. M. Smith, Herp. 12(1):12, 1956. Davis, W. B. and J. R. Dixon, Proc. Biol. Soc. Wash. 72:82, 1959. Pianka, E. R. and H. M. Smith, Herp. 15(3):119, 1959.

Loxocemus bronni Boucourt, Etude sur les Reptiles, Miss. Sci. au Mexique et dans l'Amer. Cent. Livr. 8:516, 1882 (*Fide* Taylor, 1940).

Loxocemus bicolor bicolor, Woodbury, A. M. and D. M. Woodbury, J. Wash. Acad. Sci. 34(11):360, 1944.

Loxocemus bicolor sumichrasti, Woodbury, A. M. and D. M. Woodbury, J. Wash. Acad. Sci. 34(11): 360-364, 1944.

SPECIMENS EXAMINED

Total of 108. Specimens enclosed in brackets were not used in the statistical analyses. Abbreviations for collections are listed in acknowledgments. MÉXICO: [no specific locality, USNM 86639, 89387.] Navarit: 17 mi S Acaponeta, LBSC 1399; 129.2 mi S Mazatlán (ca. 53 mi NW Tepic), DH 63-39; 18.3 mi S Tuxpan turnoff on M15, LBSC 1400; between San Blas and Tuxpan turnoffs, LBSC 1397-98; south of Río Santiago, SU 23062; 0.2 mi W jct. M15 & M54 on M15, SU 23787; [21 mi E San Blas, EAL 136]; 21.8 mi E San Blas, LBSC 1401; 15 mi NE San Blas, AMNH 8251; 160.5 mi S Mazatlán (ca. 23 mi NW Tepic), DH 63-32. Colima: no specific locality, USNM 61924; 3 mi SE Cihuatlán, LSU 7891; 23.8 mi E jct. M80 & M200, LSU 7890; vicinity of Colima, SDZS 40362, 42312; between Coquimatlán and Villa Alvarez, UMMZ 80184. Michoacán: Apatzingán, CNHM 39075; 1.1 mi S Lombardia, UMMZ 125566; 3.8 mi E Apatzingán, UMMZ 114492; 4.2 mi E Apatzingán, UMMZ 112562; 10.2 mi E Apatzingán, UMMZ 112563. Morelos: Km. 98 on Mexico-Taxco road (=near Puente de Ixtla), USNM 140089. Guerrero: south of Agua Bendita, CNHM 105157; 3 mi S Iguala, TNHC 28435; Km. 208 south of Mexico City, CNHM 105156; 2.5 mi N Milpillas, AMNH 71373; 1 mi W Acahuitzotla, TCWC 7412; 64 mi S Chilpancingo (=2 mi N Xaltianguis), UIMNH 31686; Coyuca (de Benitez), UIMNH 25958; near Coyuca (de Benitez), USNM 110323; El Limoncito (near Acapulco), CNHM 104799; [0.9 mi ESE El Marques, UF 11264]. Oaxaca 16-25 mi W Pinotepa Nacional, UIMNH 53023; [8 mi W Pinotepa Nacional, EAL 1120]; 1 km E Tequisistlán, UMMZ 124756; cerro Arenal (16 mi W Tehuantepec), AMNH 68068; [Escurano (15 mi WNW Tehuantepec), CNHM 104800]; between (?) Quiengola Mt. north of Tehuantepec (=Cerro Guengola, 10 mi WNW Tehuantepec), UMMZ 82455; [Mixtequilla, CAS 73652]; near Tehuantepec, AMNH 68066-67, LSU 8451; Tehuantepec, AMNH 66787-88, 66791, UIMNH 37328, 56126, UU 2507, 2522, 2526, 2530, 2707, 2717, 2718, 2737, USNM 110324; Río Pozo, near Tehuantepec, UIMNH 6131, CNHM 71852; Hierba Santa, near Tehuantepec, UIMNH 6133; San Pablo, near Tehuantepec, AMNH 66790; Oscurances, near Tehuantepec, AMNH 68069; Isla Laguna Superior. Tehuantepec, AMNH 68881; 4 mi W Tehuantepec, UU 2800; 3.5 mi W Tehuantepec, UKMNH 68898; Nisa Pipi, 8 km NW Tehuantepec, UMMZ 82456; Ranchero Poso Río, 6 km S Tehuantepec, UMMZ 82458-59; Tecaune, 3 leagues S Tehuantepec, UMMZ 82460-62; 6.5 mi W Tehuantepec, UMMZ 114491; 6.4 km E Tehuantepec, UMMZ

124755; 7 km NW Reforma, UKMNH 87438; 20 mi W Zanatepec, TNHC 28596; 2 mi E Zanatepec, AMNH 88823; 4 mi E. Tapanatepec, TCWC 21537. *Chiapas:* [Teran, Tuxtla Gutierrez, AMNH 71392]; [6 km NE Escuintla, Dist. Soconusco, UMMZ 87700].

GUATEMALA: Jutiapa: Ferica La Gloria, 6 km SE Casa Grande, UMMZ 107373.

HONDURAS: Atlantida: Tela, MCZ 31654. Cortes: 5 mi NW La Lima, TCWC 19229. Comayagua: 4 mi N Comayagua, TCWC 19228. Choluteca: 6 mi N Perspire, TNHC 31315.

NICARAGUA: no specific locality, USNM 16131. Chinandega: Rancho San Isidro, Río San Isidro, UU FVN520. Matagalpa: 2 km N Dario, UKMNH 86170. León: 8 km SE León, UKMNH 86172. Managua: 5 mi NW Managua, UKMNH, 42301, 42303; 5 km E Managua, JV 038; 1 km S Tipitapa, UKMNH 86169; 2 km S Tipitapa, UKMNH 86171; Los Robles, 3 km SE Managua, JV 166, 268; 3 mi SW Managua, UKMNH 42302. Carazo: Las Jinotepes, 11 km S Managua, UF 471. Masaya: near Masaya, JV 167.

COSTA RICA: *Guanacaste*: 11.9 mi N Liberia, USC CRE8106; 3.1 mi W Liberia on road to Sardinal, USC CRE8211; 10 mi W Liberia, USC CRE8212; 27.1 mi S Liberia, USC CRE8174; 10 mi NW Cañas, UCR 172; 6 mi NW Cañas, TCWC 19248; 5.1 mi N Cañas, USC CRE8182; 20 km S Cañas, USC CRE250.

Additional Records: MEXICO: Nayarit: Rosamorada, AMNH 19393 (Zweifel, 1959). Michoacán: La Orilla, BMNH 1914.1.28.124 (Gadow 1930, fide Duellman, 1961). Guerrero: 92 km NW of Acapulco on M200, E. Pianka, Private Coll. (Pianka and Smith, 1956). Chiapas: Finca La Valdiviano, 16 km SW Cintalapa, MZTG 2 (Alvarez del Toro and Smith, 1956). EI SALAVADOR: La Unión, USNM 4948 (Type of L. bicolor, specimen now missing, fide Smith and Taylor, 1945; Stuart, 1963:84).

We thank the following for allowing us to examine specimens in their care (abbreviations are those used in the paper to indicate the various collections): Charles E. Bogart, American Museum of Natural History (AMNH); (BMNH below); Alan E. Leviton, California Academy of Sciences (CAS); Robert F. Inger and Hymen Marx, Chicago Natural History Museum (CNHM); Don Hunsaker II, private collection, San Diego State College (DH); Ernest A. Liner, private collection, Houma, Louisiana (EAL); Jamie Villa, University of Costa Rica, San Jose (UCR) and private collection (JV); Richard B. Loomis, Long Beach State College, (LBSC); Douglas A. Rossman, Louisiana State University (LSU); Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ); (MZTG below); Allen J. Sloan, San Diego Zoological Society (SDZS); George S. Meyers, Stanford University Natural History Collection (SU); Richard J. Baldauf, Texas Cooperative Wildlife Collection, Texas A & M University (TCWC); Gerald G. Raun, Texas Natural History Collection, University of Texas (TNHC); (UCR, above); Walter Auffenberg, Florida State Museum, University of Florida (UF); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); William E. Duellman, University of Kansas Museum of Natural History (UKMNH); Donald W. Tinkle, University of Michigan Museum of Zoology (UMMZ); Jay M. Savage, University of Southern California (USC); Doris Cochran and James A. Peters, United States National Museum (USNM); and John M. Legler, University of Utah (UU). Other abbreviations used for specimens cited in the literature but not examined are British Museum of Natural History (BMNH) and Museum of Zoology at Tuxtla Gutierrez, Chiapas, Mexico, (MZTG).

We are indebted to Dr. W. Frank Blair and Dr. William B. Davis for advice and assistance.

This research was conducted at the Department of Zoology, University of Texas (Nelson) and the Department of Wildlife Science, Texas A&M University (Meyer).

LITERATURE CITED

ALVAREZ DEL TORO and H. M. SMITH. 1956. Notulae Herpetologicae Chiapasiae I. Herpetologica. 12: 3–17.

BOCOURT, M. F. 1882. Etude sur les Reptiles: Miss. Sci. Mex. et l'Amer. Cent. 1-1021 pp. (1870-1909) (Not seen).

CARR, A. F., JR. 1950. Outline for a Classification of Animal Habitats in Honduras. Bull. Amer. Mus. Nat. Hist. 94: 567–594.

COPE, E. D. 1862. Some Remarks Defining the Following Species of Reptilia Squamata. Proc. Acad. Nat. Sci. Philadelphia 1861: 75–77.

DAVIS, D. D. 1936. Courtship and Mating Behavior in Snakes. Zool. Ser. Field Mus. Nat. Hist. 20: 257–290.

DUELLMAN, W. E. 1960. A Distributional Study of the Amphibians of the Isthmus of Tehuantepec, México. Univ. Kansas Publ. Mus. Nat. Hist. 13: 19-72.

————. 1961. The Amphibians and Reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist. 15: 1–48.

DUNN, E. R. and L. C. STUART. 1951. Comments on some Recent Restrictions of Type Localities of Certain South and Central American Amphibians and Reptiles. Copeia 1951: 55–61.

FOUQUETTE, M. J., JR. and D. A. ROSSMAN. 1963. Noteworthy Records of Mexican Amphibians and Reptiles in the Florida State Museum and the Texas Natural History Collection. Herpetologica 19: 185–201.

HOGE, A. R. 1947. Notas erpetologicas. 2. Dimorfismo nos Boideos. Memorias, Instituto Butantan, 20: 181–187.

KLAUBER, L. M. 1936. The California King Snake, A Case of Pattern Dimorphism. Herpetologica 1: 18–27.

LEOPOLD, S. A. 1950. Vegetation Zones of Mexico. Ecol. 31: 507-518.

MEYER, J. R. 1966. Records and Observations on Some Amphibians and Reptiles from Honduras. Herpetologica 22: 172–181.

MERTENS, R. R. 1951. Über den Boiden-Typus Plastoseryx bronni. Senckenbergiana 32: 205-206.

------. 1952. Die Amphibien und Reptilien von El Salvador. Abh. Senckenb. Naturf. Ges. 487: 1–120.

MORONEY, J. M. 1956. Facts from Figures. 3rd. ed. Penguin Books, 472 pp.

PIANKA, E. and H. M. SMITH. 1956. Distributional Records for Certain Mexican and Guatemalan Reptiles. Herpetologica 15: 119–120.

OLIVER, J. A. 1937. Notes on a Collection of Amphibians and Reptiles from the State of Colima, México. Occas. Papers Mus. Zool. Univ. Michigan 360: 1–28.

ROMER, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago. 772 pp.

SCHMIDT, K. P. and F. A. SHANNON. 1947. Notes on Amphibians and Reptiles of Michoacán, México. Fieldiana: Zool. 31: 63–85.

SHELFORD, V. E. 1963. The Ecology of North America, University of Illinois Press Urabana. 610 pp.

SMITH, H. M. and E. H. TAYLOR. 1945. An Annotated Checklist and Key to the Snakes of Mexico. U.S. Nat. Mus. Bull. 187:iv + 239 pp.

-----. 1950. Type Localities of Mexican Reptiles and Amphibians. Univ. Kansas Sci. Bull. 33: 313–380.

STEVENS, R. L. 1964. The Soils of Middle America and Their Relation to Indian Peoples and Cultures. p. 265–315 *In* R. C. West (ed) Natural Environment and Early Cultures, Vol. I of R. Wauchope (ed) Handbook of Middle American Indians, University of Texas Press.

STICKEL, W. H. and L. F. STICKEL. 1946. Sexual Dimorphism in the Pelvic Spurs of *Enygrus*. Copeia 1946: 10-12.

STUART, L. C. 1954. A Description of a Subhumid Corridor Across Northern Central America, With Comments on its Herpetofaunal Indicators. Contrib. Lab. Vert. Biol. Univ. Michigan 65: 26 pp.

———. 1963. A Checklist of the Herpetofauna of Guatemala. Misc. Pub. Mus. Zool. Univ. Michigan 122: 1–150.

SUMICHRAST, F. 1880. Contribution a l'histoire naturelle du Mexique I. Notes sur une collection de Reptiles et de Batraciens de la partie occidentale de l'Isthme de Tehuantepec. Société Zoologique de France (Paris), Bull. 5: 162–190.

TAYLOR, E. H. 1940 (1939). Some Mexican Serpents. Univ. Kansas Sci. Bull. 26: 445-487.

------. 1954. Further Studies on the Serpents of Costa Rica. Univ. Kansas Sci. Bull 36: 673–801.

TOSI, J. A., JR. 1964. Climatic Control of Terrestrial Ecosystems: A Report on the Holdridge Model. Economic Geography 40: 173-181.

WAGNER, P. L. 1964. Natural Vegetation of Middle America p. 216–264. In R. C. West (ed) Natural Environment and Early Cultures, Vol. 1 of R. Wauchope (ed) Handbook of Middle American Indians, University of Texas Press.

WOODBURY, A. M. and D. M. WOODBURY. 1944. Notes on Mexican Snakes from Oaxaca. J. Washington Acad. Sci. 34: 360–373.

ZWEIFEL, R. G. 1959. Additions to the Herpetofauna of Nayarit Mexico. Amer. Mus. Novitates 1953: 1–13.