

# B R E V I O R A

## Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS.

30 JUNE 1982

NUMBER 466

### SYSTEMATICS OF THE *MEXICANA* SPECIES GROUP OF THE COLUBRID GENUS *LAMPROPELTIS*, WITH AN HYPOTHESIS MIMICRY

WILLIAM R. GARSTKA<sup>1</sup>

**ABSTRACT.** Variation within the *mexicana* group of kingsnakes, genus *Lampropeltis* (Fitzinger), is discussed. Three species are recognized: *L. mexicana* (Garman), *L. alterna* (Brown), and *L. ruthveni* (Blanchard), which is added to the species group. *L. leonis* (Gunther) is placed in the synonymy of *L. mexicana*. Qualitative and quantitative characters of external and internal morphology are used to diagnose the taxa. Outgroup comparisons with other *Lampropeltis* and other colubrids indicate that *L. mexicana* is primitive relative to *L. alterna*. Evolution within the group and an hypothesis of mimicry to explain pattern polymorphisms are discussed.

*L. alterna* as interpreted here is restricted to areas north of the Anticline of Arteaga, Mexico and occurs throughout the Bolsón de Mapimí and north to the foot of the Guadalupe Mountains. *L. mexicana* is a montane and plateau form occurring on and to the south of the Anticline of Arteaga. *L. ruthveni* has been found in northwestern Michoacán and adjacent Querétaro in the transverse volcanic region. Sympatry is not recorded for the taxa.

### INTRODUCTION

The kingsnakes allied with *Lampropeltis mexicana* (Garman) are relatively small (less than one meter) little-known snakes which inhabit the Chihuahuan Desert and adjacent areas. They occur from

<sup>1</sup>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present address: Department of Biological Sciences, University of Alabama in Huntsville, Huntsville, Alabama 35899.

northern Michoacán, Mexico, north to perhaps southern New Mexico. The taxa have been considered closely related and have been called variously a species group (Smith, 1942, 1944; Webb, 1961) or a species complex (Gehlbach and Baker, 1962; Gehlbach and McCoy, 1965; Gehlbach, 1967; Tanzer, 1970). The nominal taxa are *L. mexicana* (Garman), *L. thayeri* Loveridge, *L. greeri* Webb, *L. leonis* Gunther, *L. alterna* (Brown), and *L. blairi* Flury. These species have been considered as a unit because of the following shared characteristics: a light-edged red-centered black blotch, mottled speckling, distinct head, and long tail (Gehlbach and Baker, 1962). I also include in this group *L. ruthveni* (Blanchard) because it clearly fits these criteria, and is sympatric with *L. triangulum*.

The findings reported here suggest that the *mexicana* group consists of three species-level taxa which are distinctive in several character suites: *L. alterna* (including *L. alterna* and *L. blairi*), *L. mexicana* (including *L. mexicana*, *L. thayeri*, *L. greeri*, and *L. leonis*), and *L. ruthveni* (removed from the synonymy of *L. t. arcifera*).

The *mexicana* group is related closely to *L. triangulum* on the basis of shared hemipenial characters (Smith, 1942) and may also show close relationship to *L. pyromelana* and *L. zonata* when pertinent characters are more closely examined in those species. The *mexicana* group has been considered both as ancestral to the remaining species of *Lampropeltis* (Webb, 1961) and as the most derived species (Blanchard, 1921; Smith, 1942, 1944; Tanner, 1953). Data will be presented demonstrating that *L. alterna* is the most derived species in the group, and that both it and *L. ruthveni* are closely related to *L. mexicana*. Although the distribution of all three species appears to be presently patchy and perhaps relictual, this is not sufficient justification for considering them ancestral.

Four specimens of *Lampropeltis*, seemingly related to *L. mexicana*, were collected by the author in Coahuila and Nuevo León, Mexico, during 1975 and 1976. It was not possible to refer three of the four specimens to any presently recognized taxon when compared to the key in Webb (1961) and the descriptions in Gehlbach (1967). Comparison with reference material did not clarify the situation. Of the four specimens previously known from the vicinity of Galeana, Nuevo León (Gehlbach and McCoy, 1965; Gehlbach, 1967), one was identified as *L. mexicana thayeri*, one as *L.m. alterna*, and two as *L.m. thayeri*  $\times$  *L.m. mexicana* intergrades. The only additional specimen from Nuevo León was the holotype of the obviously closely

related *L. leonis*. It was clear then that a revision of the group and reidentification of the reference material was necessary.

One of the above specimens collected by the author (from San Lazaro, Coahuila) has a series of 24 laterally truncated body rings; thus it should have been classed as *L.m. thayeri* (Webb, 1961). However, in comparison with the type specimen of *thayeri* and a living specimen quite like the type, this Coahuila specimen was clearly different. The head was much more triangular, as has been noted for *alterna* (Brown, 1901; Gehlbach, 1967); the number of ventral scales was nearly 20% greater than reported for *thayeri*, and the iris was silver-grey, like specimens from Texas and unlike the gold-brown iris of animals collected in the mountains of Nuevo León. Living specimens collected in the mountains of Durango, Mexico, were similar in these three characters with those from Nuevo León, and were likewise similar to specimens from Querétaro, except in ventral scale number.

The specimens recently collected in Querétaro, Mexico, posed another problem, as they closely resembled the single previous specimen identified as *L. ruthveni* (Blanchard, 1921), which had been synonymized (Williams, 1978) with *L.t. arcifera*. These specimens share many of the same features of *L. mexicana*, and indeed are distinguishable only on ventral scale number from some *L. mexicana* from Nuevo León. They are clearly not *L. triangulum nelsoni* nor *L.t. arcifera*, with which they are sympatric; both subspecies of *L. triangulum* have been collected (Williams, 1978) in the valleys that surround the montane area where the *ruthveni* were collected. Therefore an initial hypothesis of three valid taxa, *alterna*, *mexicana*, and *ruthveni*, was considered, and characters were analyzed within that framework.

The most striking feature of kingsnakes is their often brilliant color and pattern. Color and pattern have been relied upon exclusively in diagnoses of the species of *Lampropeltis* (Blanchard, 1920, 1921; Gehlbach, 1967; Smith, 1942; Webb, 1961) and the subspecies of *L. triangulum* (Williams, 1978). The extreme variability of color and pattern among individuals in the *mexicana* group and the similarity of the patterns of *ruthveni* and some *mexicana* with some subspecies of *triangulum* makes using only this character untenable.

Color and pattern variability is also well documented in Texas *alterna* (Gehlbach and Baker, 1962; Gehlbach and McCoy, 1965; Gehlbach, 1967; Tanzer, 1970; Miller, 1979). There is a gradation of

patterns from extremes of more than 17 narrow rings with alternating dots (*alterna*) to a low number (9–17) of major bands with no alternating reduced markings (*blairi*). Tanzer (1970) reported a brood from an *alterna* female which contained both *blairi* and *alterna* offspring. Melanism is also known in both *alterna* (Miller, 1979) and *mexicana*.

The morphological characters examined in this study are: 1) lepidosis, 2) color and pattern, including color of the iris, 3) osteology of the skull and vertebrae, and 4) hemipenes. The variation in these characters is analyzed in *mexicana*, *ruthveni*, and *alterna*, and each taxon is compared with its respective sympatric *triangulum* population. The three taxa are redefined, and a hypothesis of relationship and of selection pressures leading to evolution within the group is presented.

## MATERIALS AND METHODS

### *Specimens*

Both preserved and living specimens including all age classes were examined. Embryo and hatchling specimens were examined and used in ontogenetic comparisons with adults. Living snakes were sexed by the method of Laszlo (1975) using probes manufactured by J & M Specialty Parts. All living specimens in the author's collection will be deposited in the Museum of Comparative Zoology. Wild caught specimens only were used in the character analysis as captive bred animals cannot be considered as statistically independent samples.

### *External Morphology*

Scale counts recorded included ventrals (method of Dowling, 1951), subcaudals, infralabials, supralabials, temporals, and dorsal scale rows at mid-body (V method of Peters, 1964). The location of the umbilical scar on hatchling specimens was noted. Dissected and everted hemipenes of each taxon were examined. Statistical analysis of data used methods from Sokal and Rohlf (1969). All sample means indicated in the text are followed by  $\pm$  one standard error of the mean.

### *X-Rays*

Radiographs of preserved specimens were taken on an F.E. Faxitron X-ray machine using Kodak Industrex R film. Measurements of

five thoracic vertebrae posterior to #20 were taken from each specimen radiographed. Coiling of preserved specimens prevented examination of the same five vertebrae on every animal. Measurements and terminology of the vertebrae are from Johnson (1955a, 1955b) and Auffenberg (1963). Comparisons were made between replicate radiographs of the same vertebrae, and between measurements from a prepared skeleton and radiographs of the same vertebrae to be confident of accuracy and precision. Differences were less than 3%. Dorsoventral radiographs of heads and measurements of the length and width of the skull at various levels were also taken. Individual osteological elements of the skull were not examined. Comparisons were again made of three sets of duplicate radiographs, and the differences were less than 2%.

### *Field Work*

During 1972, 1973, and 1975 trips were made to the Chihuahuan Desert areas of Texas, principally to Brewster, Presidio, and Val Verde counties. During 1974, 1975, 1976, 1979, and 1980 trips were made to various localities in Mexico. Collection of living specimens provided information on the ecology and extent of distribution of the group.

## ANALYSIS OF CHARACTERS

### *Lepidosis*

There is a marked difference in the numbers of ventral scales of the three taxa (see Table 1 and Fig. 1). A one-way ANOVA shows that there is significant heterogeneity of mean ventral scale number among taxa ( $F = 85.3$  at  $2/83$  df,  $p < 0.005$ ). In a Student-Newman-Keuls test of differences between ranked pairs of means, all differences are significant at the 1% level. In order to be assured that distinct populations were sampled, the distributions were tested for normality. The individual taxon distributions are not different from normal by the Kolmogorov-Smirnov cumulative test ( $D$  [*alterna*] = 0.09, critical value = 0.29,  $\alpha = 0.01$ ;  $D$  [*mexicana*] = 0.07, critical value = 0.30,  $\alpha = 0.01$ ;  $D$  [*ruthveni*] = 0.13, critical value = 0.30,  $\alpha = 0.01$ ). The total distribution was tested for normality and was found to be significantly different from normal ( $D = 0.27$ , critical value = 0.18).

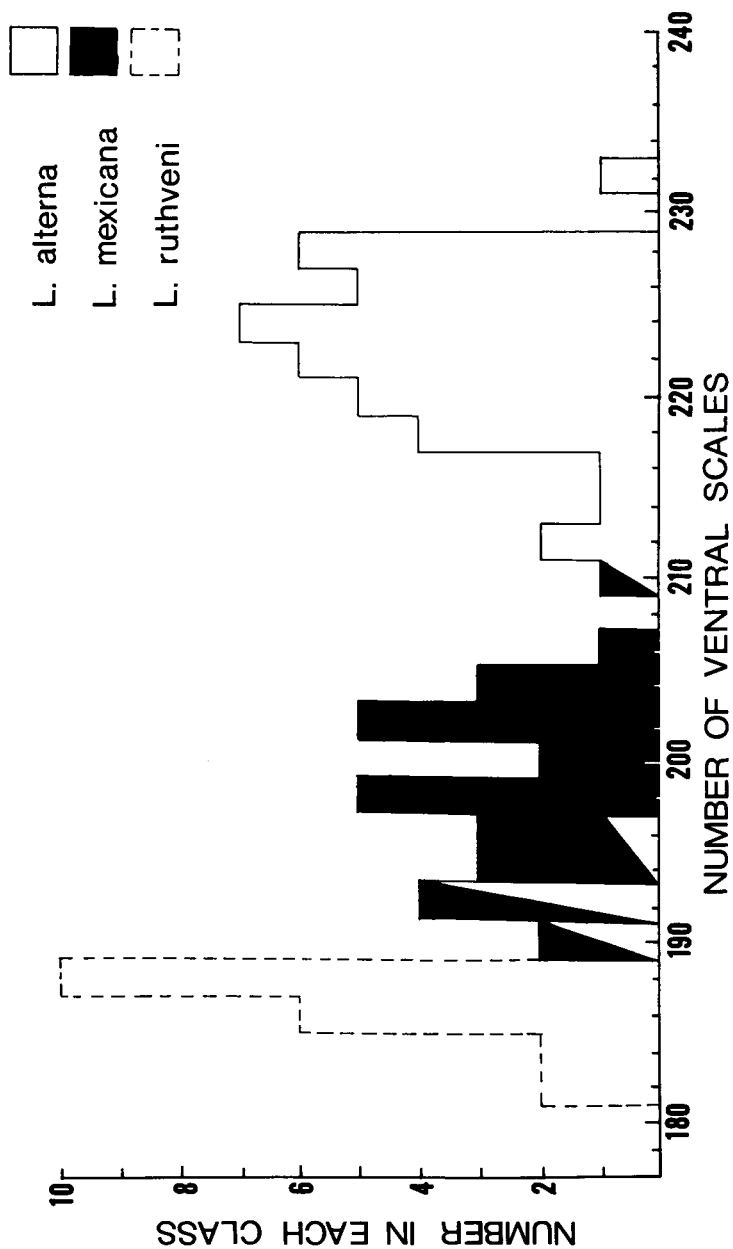


Figure 1. Ventral scale counts of the three species in the *mexicana* group.

The variation among the ventral scale means of *alterna*, *mexicana*, and *ruthveni* appears as a north to south cline. This variation, however, is not clinal within a taxon, and the differences among taxa are stable in captive-bred animals. Clinal variation in ventral scale number has been documented for *Coluber constrictor* (Auffenberg, 1955) and *Lampropeltis triangulum* (Williams, 1978). In both taxa the change is gradual, with counts high in the south, low in the north. The effects of differing temperatures of incubation on scale counts (Fox *et al.*, 1961) could explain that situation, although no experimental evidence was given for either species.

The geographic distribution of ventral scale numbers within each taxon appears random (Table 2). The southernmost specimens of *alterna* from just north of Saltillo, Coahuila (USNM 110819) and from near San Antonio, Durango (TCWC 36892), have 223 and 218 ventrals, respectively. The northernmost *mexicana* specimens, three from the Rio Mimbres area of Durango (UCM 21061 and 2 Garstka collection) and one from the Anticline of Arteaga near Los Lirios, Coahuila (ITESM uncataloged), have 203, 202, 204, and 190, respectively. The Los Lirios *mexicana* has the lowest ventral number of any *mexicana* examined.

The hypothesis that the north to south cline in ventral scale counts may be a result of differing incubation temperatures was examined by incubating two clutches of *mexicana* eggs and one clutch of *alterna* eggs in the same container at the same time (*alterna*: 3 August–23 October; *mexicana*: 14 July–25 September; 28 June–18 September 1977). The same means of ventral counts are *alterna* =  $218.5 \pm 2.50$  (N=2); *mexicana* =  $204.6 \pm 1.45$  (N=10), and the difference is significant ( $t = 8.47$ ,  $p < 0.001$ ). In an additional sample of captive-bred *alterna* ( $218.8 \pm 0.38$ , N=40) and captive-bred *mexicana* ( $201.6 \pm 7.87$ , N=7), the difference is also significant ( $t = 18.28$ ,  $p < 0.001$ ). The conditions and dates of incubation for the latter sample are not known.

Juvenile specimens usually possess an umbilical scar. The number of ventral scales anterior to the scar is  $170.9 \pm 1.48$  for 11 *mexicana* and  $190.0 \pm 1.69$  for 12 *alterna* ( $t = 12.98$ ,  $p < 0.001$ ). The length of the scar is the same in both taxa; the mean lengths in the samples are  $4.5 \pm 0.25$  scales for *mexicana* and  $5.0 \pm 0.37$  scales for *alterna* ( $t = 1.25$ ,  $0.3 > p > 0.2$ ). No sex differences were noted. The single juvenile *ruthveni* (KU 155528) had no visible scar.

Table 1. Diagnostic characters of the *mexicana* group and sympatric subspecies of *Lampropeltis triangulum*.

Taxon	Character				
	ventrals		body rings		
	N	range	$\bar{X} \pm SE$	range	$\bar{X}$
<i>L. alterna</i>	30	211-230	221.3 $\pm$ 0.8	9-32	16
<i>L. mexicana</i>	29	190-211	198.5 $\pm$ 1.0	23-46	32
<i>L. ruthveni</i>	28	182-196	188.6 $\pm$ 0.6	23-34	29
					black to posterior of parietals, or with some red or white flecks
<i>L. t. annulata</i> <sup>1</sup>	40	181-207	194.7 $\pm$ 1.1	14-22	18
<i>L. t. arcifera</i> <sup>1,2</sup>	18	196-220	210.1 $\pm$ 1.6	17-27*	24
<i>L. t. cetaenops</i> <sup>1</sup>	12	170-194	183.4 $\pm$ 2.6	17-25	22
					black to center of parietals or with white flecks
<i>L. t. nelsoni</i> <sup>1,2</sup>	23	203-221	215.0 $\pm$ 2.4	13-18*	16
					white to posterior of prefrontals, then black, or with black flecks
<i>L. t. ssp. nov.</i> <sup>2</sup>	6	189-201	196.2 $\pm$ 1.7	14-22**	21
					black to posterior of parietals, or with white flecks

<sup>1</sup>data from Williams (1978)<sup>2</sup>data from H. Quinn (personal communication)

\*some red rings split with black mid-dorsally

\*\*most red rings split with black mid-dorsally



Table 2. The relationship between latitude and number of ventral scales in the *mexicana* group.

Degrees North Latitude	Number of Ventral Scales		
	<i>alterna</i>	<i>mexicana</i>	<i>ruthveni</i>
30-32	221.5 $\pm$ 1.7 (N=8)		
28-30	222.3 $\pm$ 1.1 (18)		
26-28	214.0 $\pm$ 1.0 (2)		
24-26	220.5 $\pm$ 2.5 (2)	200.9 $\pm$ 1.6 (11)	
22-24		196.3 $\pm$ 1.0 (18)	
20-22			188.6 $\pm$ 0.7 (26)
18-20			188.0 $\pm$ 0.0 (2)

The pattern of ventral scale counts in these taxa is clearly different from that of each sympatric *triangulum* variety (Williams, 1978). *L. triangulum celaenops* and *L.t. annulata* are sympatric with *alterna*, *L.t. nelsoni* and *L.t. arcifera* with *ruthveni*, and there is apparently no *triangulum* sympatric with the montane *mexicana*. The ventral scale counts of Williams' (1978) and Quinn's (in preparation) samples of *celaenops*, *annulata*, *arcifera*, *nelsoni*, and a new subspecies can serve to distinguish each species of the *mexicana* group from its sympatric *L. triangulum* subspecies (Table 1.)

There is no clear separation of the taxa in other scale characters. The uppermost preoculars in most *mexicana* and *ruthveni* extend onto the top of the head to or nearly to the frontal, whereas in *alterna* they rarely do so. There is much variability and overlap between taxa in the number and arrangement of the temporal scales. There is also no differences among taxa in numbers of labial scales, subcaudals, or dorsal scale rows, and all specimens examined possess a loreal (Table 3).

### Color Pattern

The variable head and snout markings of this group can be grouped into four categories: I) asymmetric spot or blotch markings without red, II) snout evenly black to the middle or posterior of the parietals, with or without a red infusion, III) a red-centered, three-lobed cloverlike marking with the anterior lobe across the frontal or usually the prefrontals, and IV) a similar three-lobed marking, without red, that can have the anterior lobe either split to form a double Y, detached, or enlarged and subrectangular (Fig. 2). None of these categories is exclusive to any taxon, but most *ruthveni* are category II, and most *alterna* are category I. The head markings connect to the nuchal blotch only in some *mexicana*. The nuchal blotch of *mexicana* and *alterna* is usually light-centered and can be split longitudinally. Postocular stripes are usually present in all taxa (absent in UCM 21061, a *mexicana*), but may be reduced or obscured, as occurs in category II.

All living specimens examined of *alterna* have a distinctive silver-grey iris; *mexicana* and *ruthveni* have a golden-brown iris. Other *Lampropeltis* (*getulus*, *triangulum*, *pyromelana*, and *zonata*) examined also have a golden-brown iris.

Table 3. Scale count variation in the *mexicana* group.

Scale Character	Range of Scale Counts		
	<i>alterna</i>	<i>mexicana</i>	<i>ruthveni</i>
ventrals	211-230	190-211	182-196
subcaudals	56-67	51-65	49-57
dorsal scale rows	23-27	21-25	21-25
temporal scale rows	2-4	2-4	2-4
number of scales in anterior temporal row	2-3	1-3	1-2
number of scales in posterior temporal row	3-5	3-5	3-5
supralabials	7-8	7-8	6-8
infralabials	9-11	8-11	8-9

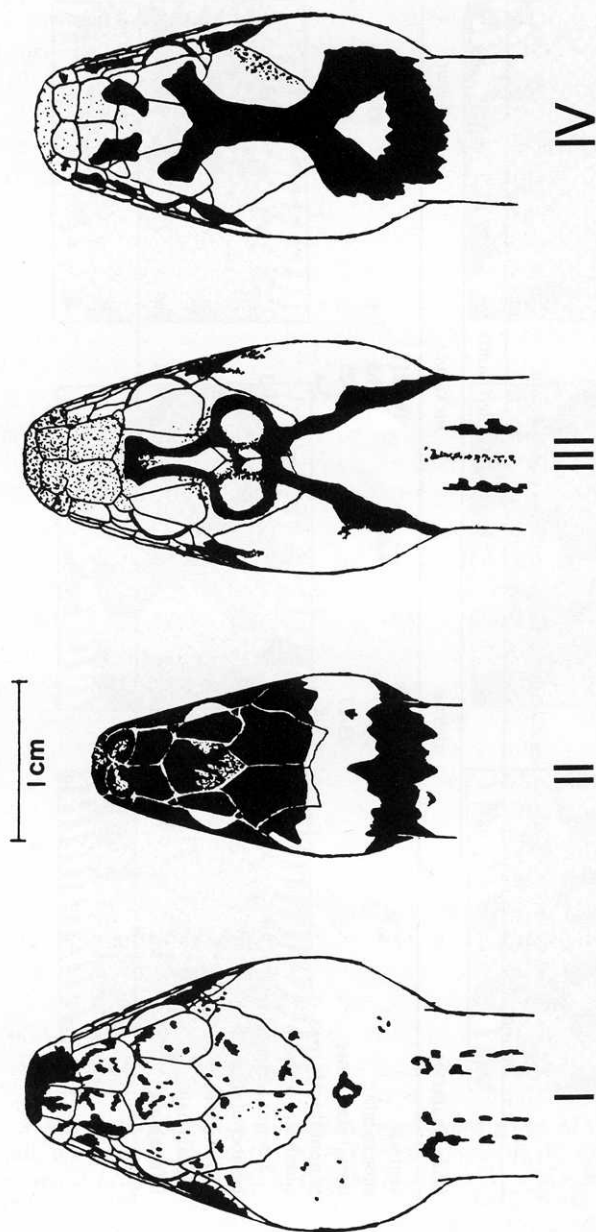


Figure 2. Categories of head and snout markings in the *mexicana* group. I) *L. alterna* (USNM 110819); II) *L. ruhveni* (in Garska collection); III) *L. mexicana* (MCZ24976); IV) *L. mexicana* (in Garska collection).

The number of primary, usually red-centered, body markings varies considerably and is not by itself indicative of any taxon (Table 1). The *blairi* form of *alterna* has the fewest primary markings (9–17).

The 47 offspring produced in ten broods by one male and two female *mexicana* collected from a single site near San Juanito, Nuevo León, are variously ringed, blotched, or spotted. All possible variants of the dorsal head pattern occur in these offspring, and ground color ranges from lemon-yellow through various shades of brown, orange, and grey. The blotches vary in number from fewer than 20 to more than 40, and in shape from spots to rings extending around the body. The number of body bands falls within the ranges of all the forms except *blairi*. In some, alternating reduced markings occur in one or several rows. One specimen has red only in the nuchal blotch. Thus, neither number, level of truncation (Webb, 1961) or alternating reduction (Blanchard, 1920, 1921; Smith, 1942) of body bands are diagnostic characters. The local variability characteristic of *mexicana* and *alterna* is not present in any *triangulum* subspecies, nor are alternating reduced markings recorded for any *L. triangulum*.

Ventral pigmentation ranges from nearly entirely black to nearly entirely background color in *alterna* and *mexicana*. The *ruthveni* examined most commonly have rings which extend around the body; this also occurs with the anterior rings in some *mexicana*. The venter of *alterna* and *mexicana* can also be checkered in black and background color as in *L.t. triangulum* and *Elaphe guttata* (see figure in Smith, 1942, pp. 202–203), and some *ruthveni* have a checkered red pattern ventrally.

A ventrolateral expansion of the first (anteriormost) tail blotch with red extending onto (usually across) the subcaudals is characteristic of *mexicana*. This character is not evident in any of the *alterna* examined. The underside of the tail of one specimen of *mexicana* (BMNH 1946-1-4-10) has red infused anteriorly in a longitudinal black line. The tails of the *ruthveni* examined have a ringed condition similar to *mexicana*; however, the first tail ring is not usually widened ventrolaterally. The anterior tail rings are not different from body rings in any of the *L. triangulum* subspecies.

The *L. triangulum* subspecies sympatric with each taxon can be distinguished by a combination of color patterns and scale characters from the sympatric member of the *mexicana* group (Table 1).

The snout color and symmetric body annuli of *ruthveni* make these animals easily distinguishable from the sympatric *nelsoni*. Similarly, the high number of annuli of *celanops* and *annulata* are different from the usually few annuli of the ringed or saddled *blairi* form of *alterna*. In the other cases, some combination of color pattern with ventral scale number serves to diagnose members of the *mexicana* group.

### Skull

Data from dorsoventral radiographs of similarly sized, adult *alterna* (N = 7) and *mexicana* (N = 12) were compared to quantify the observation of a more triangular head shape in *alterna*. The premaxilla to occipital condyle length, the width of the maxilla at

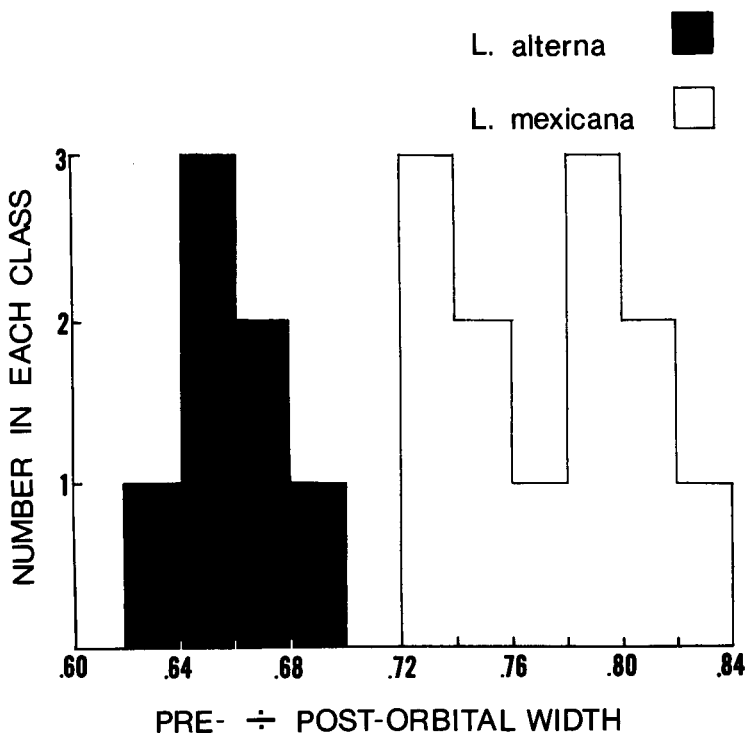


Figure 3. The ratio of pre-orbital and post-orbital width of *L. alterna* and *L. mexicana* adults.

the prefrontals, the least width of the frontals, the maximum widths across the post-orbitals, across the supratemporals, and across the quadrates were measured. The ratio of preorbital to postorbital width was used to quantify triangularity of the skull, as that should be least influenced by kinesis. The mean ratio of the *alterna* sampled is  $0.66 \pm 0.007$  and of the *mexicana* sampled is  $0.77 \pm 0.010$ . They are significantly different ( $t = 7.343$ ,  $p < 0.001$ ) (Fig. 3). The single *ruthveni* adult examined for this character (USNM 46558) has a ratio of 0.74.

Additionally, ten juveniles each of *alterna* and *mexicana* were compared for this character. The mean ratio of the sample of *mexicana* juveniles is  $0.74 \pm 0.007$ , with one specimen outside the range of variation of the adults, in the direction of *alterna*. In the sample of juvenile *alterna*, five are outside the variational range of adult *alterna* in the direction of *mexicana*, and the mean is  $0.69 \pm 0.008$ . Thus the two taxa are more similar as juveniles, and, importantly, are more like *mexicana* than *alterna* as juveniles. This indicates that there is differential growth to the adult stage in *alterna*.

Adults of other species of *Lampropeltis* were also examined in outgroup comparison for this character. *L. triangulum amaura* and *L. t. polyzona* both had a preorbital to postorbital ratio of 0.77, a single *L. pyromelana* had a ratio of 0.73, and a single *L. calligaster* had a ratio of 0.73. Thus, it appears that the lesser triangularity of the skull in the *mexicana* condition is not only the common condition for juveniles, but also for other *Lampropeltis*.

### *Vertebrae*

Eight or more individual thoracic vertebrae (Johnson, 1955a, 1955b; = first precaudal series, Auffenberg, 1963; = lumbar series, Bullock and Tanner, 1966) prepared from each of eight adult specimens of *alterna* and four adult *mexicana* were examined. X-rays in lateral and dorsoventral aspect of an additional three adult and five juvenile *alterna* and six adult and nine juvenile *mexicana* were also examined. No *ruthveni* vertebrae were available. None of the commonly used measures (Johnson, 1955a, 1955b) or ratios (Auffenberg, 1963) showed any significant difference between adults of the two taxa. The amount of individual variation in qualitative appearance of the vertebrae is substantial, however, even in the small sample examined; because of the lack of descriptions of the range of

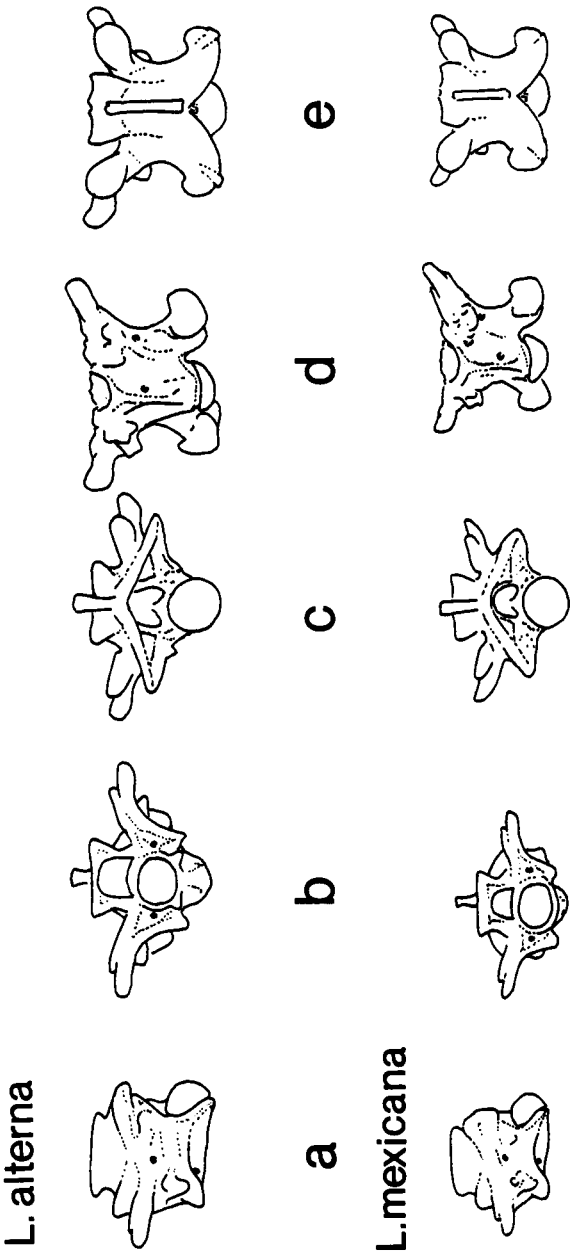


Figure 4. Vertebrae of *L. alterna* (MCZ 157764) and *L. mexicana* (MCZ 157766). a) left lateral; b) anterior; c) posterior; d) ventral (angled to right); and e) dorsal aspects.



individual variation of colubrid vertebrae, and the importance of vertebral characters in the systematics of fossil forms, an analysis of the vertebrae follows (Fig. 4).

The neural spine may be blunt or pointed, and in all individuals of *mexicana* examined it overhangs both anteriorly and posteriorly. In lateral X-ray the neural spine of a single *alterna*, USNM 110819, appears to not overhang anteriorly. The zygosphenes are crenate to convex from above and usually have a broad shallow notch. In anterior aspect the dorsum of the neural arch is flattened or slightly arched and is thinned centrally; the sides are obtusely angled, forming a dorsolateral articulating surface. The dorsal articulating surfaces of the anterior zygapophyses are ovoid to reniform and their lateral accessory processes can be blunted or pointed, directed laterally or upward, and if upward, may be curved. The processes may be rounded to dorsoventrally compressed, and if compressed, may be tilted to be parallel to the centrum. The cotyle may be round to ovoid and if ovoid, may have accessory flanges or fillets, usually ventrally, that make it appear rectangular. The parapophyses may or may not project ventral to the cotyle and may be projected anteriorly. The paradiapophysial articulating surfaces are in the form of a figure-8 with the upper portion larger and directed anteriorly, and the lower surface directed laterally to posteriorly. There is a small foramen on the parapophyses lateral to the cotyle on each side approximately at its midline. The haemal keel is usually ridgelike, though it may be flattened or absent. The subcentrum ridges are straight to slightly concave. There are two pairs of subcentrum foramina, one pair on either side of the haemal keel and the other more lateral and dorsal, just ventral to the lateral flange of the body. The condyle is oblique. In posterior view, the neural arch is rounded dorsally and flattened ventrally with a central ventral ridge. There are also lateral minor ridges extending the length of the canal on either side approximately one third of the distance superior to the base. The ventral exterior articulating surfaces of the posterior zygapophyses are ovoid to reniform with the long axis perpendicular to the centrum. The medial articulations that match the dorsal zygosphenes corners, the zygantra, appear as enlarged triangular holes lateral to the neural arch. There are small projections posterior and lateral to the posterior zygapophyses just dorsal to the ventral articulating surfaces.

Juvenile vertebrae present quite a different appearance from those of adults, which is most noticeable in the proportionally larger neural canal. The ratio of length of the centrum to width of the neural canal in a sample of three adult *mexicana* is  $2.1 \pm 0.10$ , of three adult *alterna* is  $2.3 \pm 0.08$ , and of eight juvenile *mexicana* is  $1.2 \pm 0.03$ . The neural spine is also proportionally higher. The ratio of length to height of the neural spine of a sample of three *mexicana* adults is  $2.4 \pm 0.34$  and of three juvenile *mexicana* is  $1.5 \pm 0.09$ . The juvenile *alterna* sampled had vertebrae insufficiently ossified to obtain the measurements for comparison. Since nervous tissues have grown most in relation to other tissues at birth, and since ossification is incomplete then, these differences are to be expected.

The thoracic vertebrae of *L. triangulum* differ from *alterna* and *mexicana* in the form of the zygosphenes which is arched rather than flattened (Brattstrom, 1955; Auffenberg, 1963). All of the tricolored kingsnakes examined (*L. triangulum*, *L. pyromelana*, *L. zonata*, *L. alterna*, and *L. mexicana*) share the single foramina lateral to the cotyle and the two pairs of subcentrum foramina. *L. getulus* and *L. calligaster*, however, have two pair of foramina adjacent to the haemal keel and a pair of foramina on each side of the cotyle.

### *Hemipenes*

Previous workers (Smith, 1942; Gehlbach and Baker, 1962) have reported on the hemipenes of *alterna* and *mexicana*, and allied the taxa with *L. triangulum* on the basis of overall similarity of gross structure. The hemipenes of three adult *mexicana*, five adult *alterna*, and two subadult *ruthveni* have been examined. They are uniformly longitudinally flounced proximally, then abruptly spinulate, quickly grading into slightly spinulate fringed calyces. The sulcus is single and terminates laterally on the very slightly bilobed organ. This morphology is similar to that of *L. triangulum*.

The spination on the hemipenes is clearly different among the *mexicana* group, however (Fig. 5). The spines of *mexicana* are very slightly recurved and are about 0.4 mm long. They appear diamond-shaped in cross section and are tightly packed on the organ. The spines of *alterna* and *ruthveni* are also recurved but are longer, to approximately 0.8 mm in *alterna* and 0.6 mm in *ruthveni*, and the supporting tissue makes them appear more ovoid or flattened in cross section. The spines also appear to be fewer in number in these

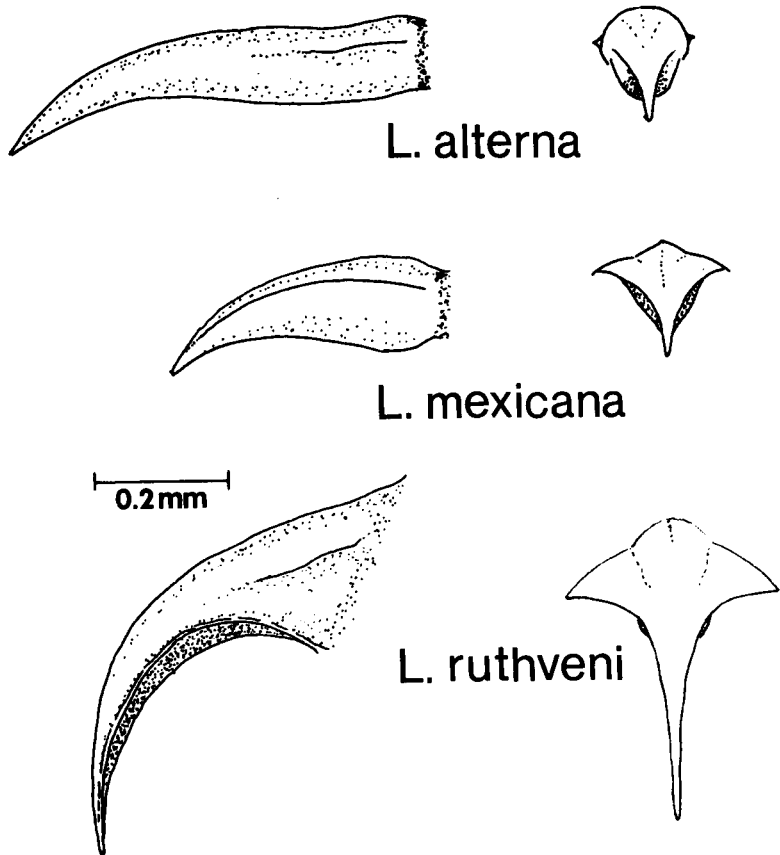


Figure 5. Hemipenial spines of *L. alterna*, *L. mexicana*, and *L. ruthveni*. Lateral (L) and distal (R) aspects.

taxa than in *mexicana*. The spines of both *ruthveni* examined are more strongly recurved than those of both *mexicana* and *alterna*.

### *Ecology*

The distribution of the entire *mexicana* group has been characterized as xeric to subhumid (Gehlbach and Baker, 1962) and roughly corresponds to the limits of the Chihuahuan Desert as described by Morafka (1977) (Fig. 6).

*L. alterna* is found within the Chihuahuan Desert, usually in association with typically desert floral elements such as *Prosopis* and *Larrea* (Jameson and Flury, 1949; Mecham and Milstead, 1949; Worthington, 1974). All known localities are within or north of the Bolsón de Mapimí. Specimens collected in the Chisos Mountains, Brewster County, Texas (Murray, 1939) and near Saltillo, Coahuila, Mexico (Smith, 1941) were found in rock crevices, though the species appears to be primarily nocturnal (Miller, 1979).

*L. mexicana* seems to be limited, except for CM 59980, to forested mesic areas peripheral to the desert, but with xerophytic vegetation such as *Echinocactus* and *Ariocarpus*. At *mexicana* localities in Nuevo León, San Luis Potosí, and Durango, Mexico, the vegetation may be termed "mesic to arid oak-pine forest" (J. Henrickson, personal communication), with the following dominant plants in common at the three localities: *Pinus cembroides*, *Quercus* sp., *Juniperus* sp., *Buddleja cordata*, and *Bouvardia ternifolia*. The author has collected specimens in rock crevices, under stones in an arroyo, and active on the road at night.

*L. ruthveni* is presently known from the northeastern portion of the trans-volcanic region in a habitat very similar to *mexicana*. In the vicinity of Amealco, Querétaro, Mexico, *ruthveni* are locally abundant in areas with scattered patches of *Quercus*-dominated woodland along arroyos and on hilltops. *Bouvardia* is common here as well. All recent collections have been of animals either in crevices or diurnally active.

Both *mexicana* and *ruthveni* appear to be more mesic species than *alterna*, occurring in more temperate forested areas. However, CM 59980 was collected in a desert area with stunted *Larrea*, cacti, and short grasses (D. Morafka, personal communication). The elevation of this rocky area is over 2,000 m, and while it is surrounded by a sandy plain, it is also closely adjacent to mesic upland areas. Many similar hilly areas in the vicinity have been deforested in recent times (T. Wendt, personal communication) and the area may have been woodland as recently as 100 years ago. *L. alterna* may also occupy upland (Worthington, 1974) or riparian habitats within the desert; however, it appears to be primarily a desert species. The higher ventral scale numbers of *alterna* may indicate adaptation to a desert environment, as Klauber (1941) found a correlation of higher ventral counts in desert habitats and lower counts in more humid coastal habitats in 12 of 13 taxa tested.

## DISCUSSION

*Phylogeny*

Underwood (1967) considered *Lampropeltis* as derived from *Elaphe* on the basis of similarity of a long intrapulmonary bronchus, a series of skull characters, presence of similar scale tubercles, similar arrangement of pits on the head, and similar paired pits on trunk scales. The characters that define *Lampropeltis* as a group distinct from *Elaphe* are the entire anal scale and the unkeeled dorsal scales. Minton (1976) and Minton and Salanitro (1972) discussed the phylogeny of colubrids, based on the immunoelectrophoretic analysis of serum proteins and found that both *E. guttata* and *L. getulus* have the same degree of difference from *E. obsoleta*. Karyological evidence also demonstrates this similarity to *Elaphe*. A karyotype of  $2N = 36$  (16 macrochromosomes and 20 microchromosomes) has been reported for *L. getulus*, *calligaster*, and *alterna*, as well as for most *Elaphe* (*E. subocularis* is an exception) (Bury, *et al.* 1970; Baker, *et al.* 1972). This close relationship between *Lampropeltis* and *Elaphe* is also substantiated by vertebral morphology. The form of the neural spine and the arrangement of the vertebral foramina are similar in *L. getulus*, *L. calligaster*, and *Elaphe*.

All of the tricolored kingsnakes (*alterna*, *mexicana*, *pyromelana*, *ruthveni*, *triangulum*, *zonata*) share grossly similar derived hemipenial (Smith, 1942) and vertebral character states that are unlike those of the remaining species in the genus, *L. calligaster* and *L. getulus*, which are in turn similar to each other and to *Elaphe* (Cope, 1898).

Captive-breeding experiments (Miller, 1979; Tryon and Garstka, in preparation) have produced *alterna*  $\times$  *mexicana*, *pyromelana*  $\times$  *alterna*, and *pyromelana*  $\times$  *zonata* hybrids. None of these species will mate with any *triangulum* subspecies tested in captivity. This can be taken as tentative evidence of their relationships. Therefore, it appears that all the tricolored kingsnakes share a common ancestor, and that the *mexicana* group forms a logical unit within that lineage, perhaps most closely related to *pyromelana* and *zonata*. Within the *mexicana* group, *alterna* is the most derived species, as shown by its iris color and head shape. These characters suggest that *alterna* is the most derived species within the genus as well (Fig. 6).

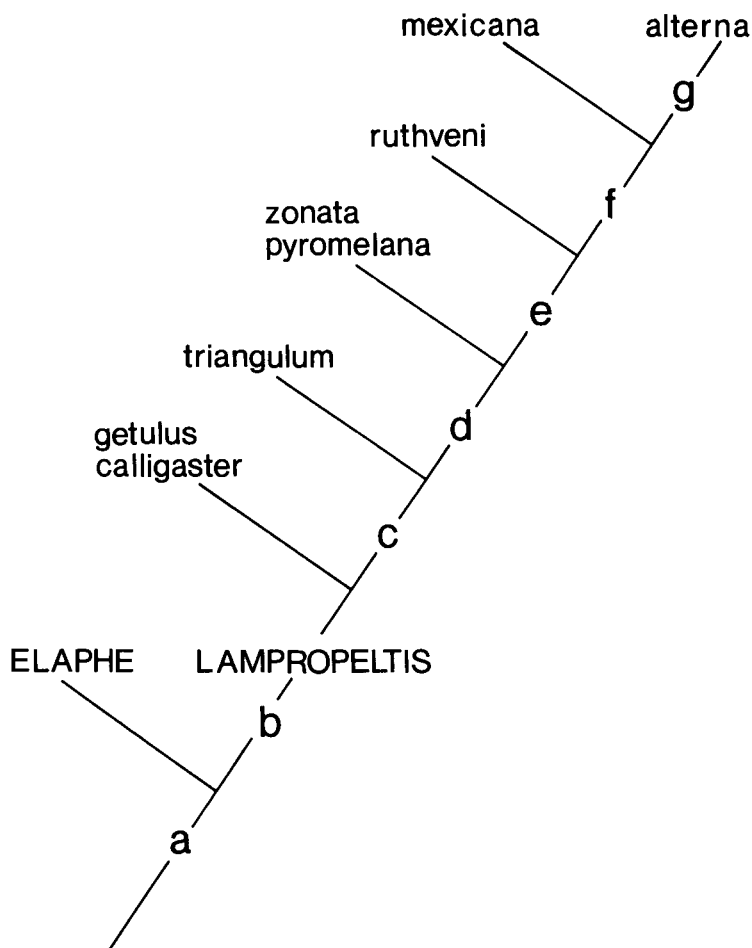


Figure 6. Hypothesis of relationship within the genus *Lampropeltis*. Derived character states uniting the taxa are: a) paired pits on trunk scales, long intrapulmonary bronchus; b) entire anal scale, unkeeled dorsal scales; c) single paired foramina lateral to hemal keel and cotyle, hemipenes flounced proximally and spinulate distally, pattern in three colors including red; d) behavioral traits in male aggression and reproduction; e) light-edged, red-centered blotch; f) alternating reduced markings possible; and g) grey iris, "triangular" skull.

The data presented here suggest that the three taxa hypothesized, *L. mexicana*, *L. alterna*, and *L. ruthveni*, are distinct morphological species. However, the taxa are allopatric, as are the two apparently most closely related species, *L. pyromelana* and *L. zonata*. Therefore the allocation of species status must still be regarded as an hypothesis until appropriate species borders or contact zones are established.

The species borders of *mexicana* and *alterna*, that is, the Anticline of Arteaga and the uplands of central Durango at the periphery of the desert, should be further collected. The presence of *alterna* at the base (USNM 110819) and *mexicana* (ITESM uncataloged) at the top of the Anticline of Arteaga indicate a high probability of a contact zone. Southern San Luis Potosí, Guanajuato, and northern Michoacán including the Sierra de Santa Rosa (Duges, 1897) and the escarpment of the basin of the Río Lerma should be explored as well for a species boundary or area of intergradation as this is between the localities of *mexicana* and *ruthveni*. Finally, the mountainous area of northern Durango north of Otinapa and west of Santiago Papasquiaro and the upper reaches of the Ríos San Juan and Verde need investigation. There are no kingsnakes known from that large area between the localities of *mexicana* and *pyromelana* (Taylor, 1940).

In addition, small sample sizes of some of the Mexican Plateau subspecies of *triangulum* make it difficult to determine the extent of sympatry, especially with *ruthveni*, and make comparisons difficult. More collections from that area, and revision of the genus or at least of the tricolored group, are necessary before the relationships among the various taxa can be better understood.

### *Variation and Selection of Color and Pattern*

Many explanations of the significance of color and pattern in snakes have been proposed (see review by Jackson *et al.*, 1976). Aposematism, to warn potential predators, has been proposed as an explanation of bright colors on venomous snakes (Goodman and Goodman, 1976; Gehlbach, 1972; Smith, 1969). Mimicry of coral snakes by nonvenomous forms has been discussed extensively (Smith, 1969; Gehlbach, 1972; Greene and Pyburn, 1973; Echternacht, 1973; Hecht and Marien, 1956) as an explanation for the brightly colored rings on many snakes. Crypsis on broken back-

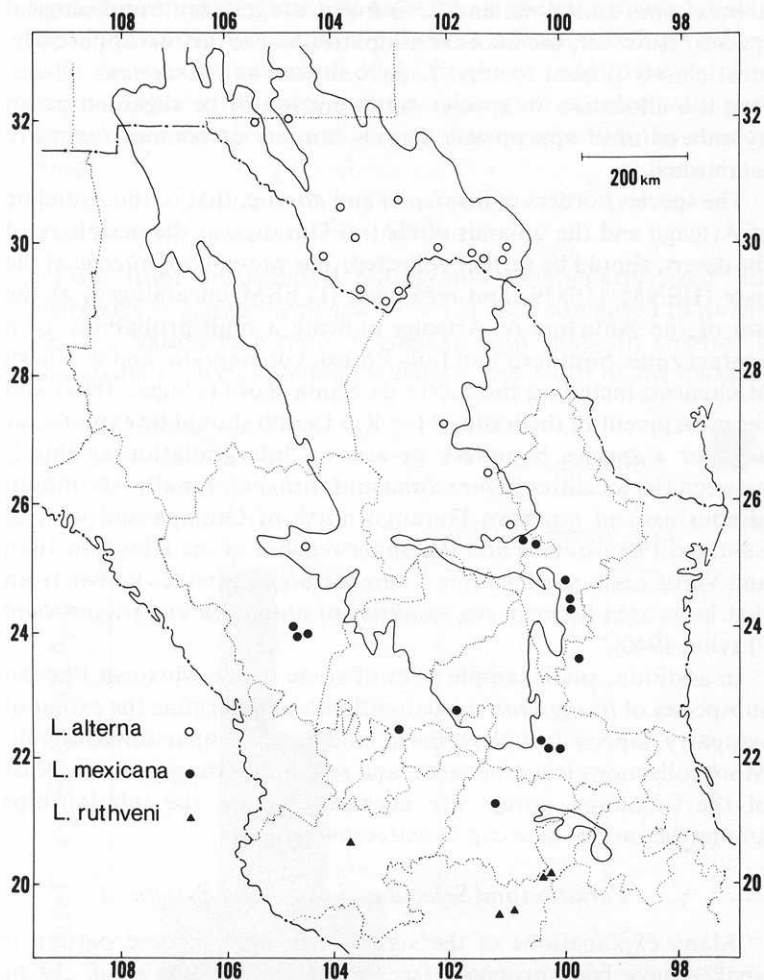


Figure 7. Distribution of the species in the *mexicana* group. State boundaries are shown as a dotted line, national borders as a broken line, and the extent of the Chihuahuan Desert (after Morafka, 1977) as a solid line. The Anticline of Arteaga is the band of mountains extending into the desert across southern Coahuila at about latitude 25°N. North of that is the Mapimian portion of the desert, and south of the Anticline is the Saladan portion of the desert (Morafka, 1977). Symbols denote only localities and not numbers of specimens.



grounds (Pough, 1976; Brattstrom, 1955), or lack of crypsis on a unicolored background (Camin and Erhlich, 1958) have also been cited to explain the presence or absence of a ringed or blotched pattern.

Gehlbach (1972) reported experimental evidence that self-mimicry, that is, the coral snake behavior of flipping the tail over, thwarted predation by coatimundis (*Nasua*) and peccaries (*Tayassu*). This effect was enhanced if the rubber models were painted aposematically. Evidence of the effectiveness of coral snake mimicry has been provided by experiments offering striped and ringed stick models to naive captive-raised motmots (*Eumomota superciliosa*) (Smith, 1975). The birds responded to red and yellow ringed models by avoidance and, in some cases, alarm notes.

*L. mexicana* and *L. alterna*, even though they may be brightly colored, do not look very much like coral snakes. Gans (1961) discussed an hypothesis of mimicry in *Dasypeltis*, a small nonvenomous snake that eats eggs of birds large enough to eat it. He demonstrated a correspondence of pattern between *Dasypeltis* and the local possible viperid models over its entire range. The pattern of the particular similar-sized viper in its range was mimicked. Therefore, the distribution of venomous snakes of the same general size and habits as *Lampropeltis*, and occurring within the range of the *mexicana* group, was examined. Crotaline models were considered, as the fine dark speckling on the scales lends an illusion of texture to the smooth-scaled *Lampropeltis*.

*Agkistrodon mokeson pictigaster* occurs in Texas west through the Big Bend region, but west of Val Verde County occurs only in the vicinity of permanent water sources. *Crotalus lepidus* is found throughout the range of *alterna* and is present in the same microhabitat. *Crotalus lepidus*, with its alternating broken pattern, can easily be mistaken for *alterna*. A similar pattern is also seen on *Trimorphodon* from west Texas. *Micrurus fulvius* is found in Texas west to Val Verde County.

The variation in Texas *alterna* could be a function of multiple models, the *blairi* form of *alterna* being a mimic of *Agkistrodon*. The relative constancy of pattern in *alterna* outside of the range of *Agkistrodon* could be due to having a single available model in those areas, *C. lepidus*. In recent years Val Verde County, Texas, has had increased rainfall, and the *blairi* form, first collected in 1948

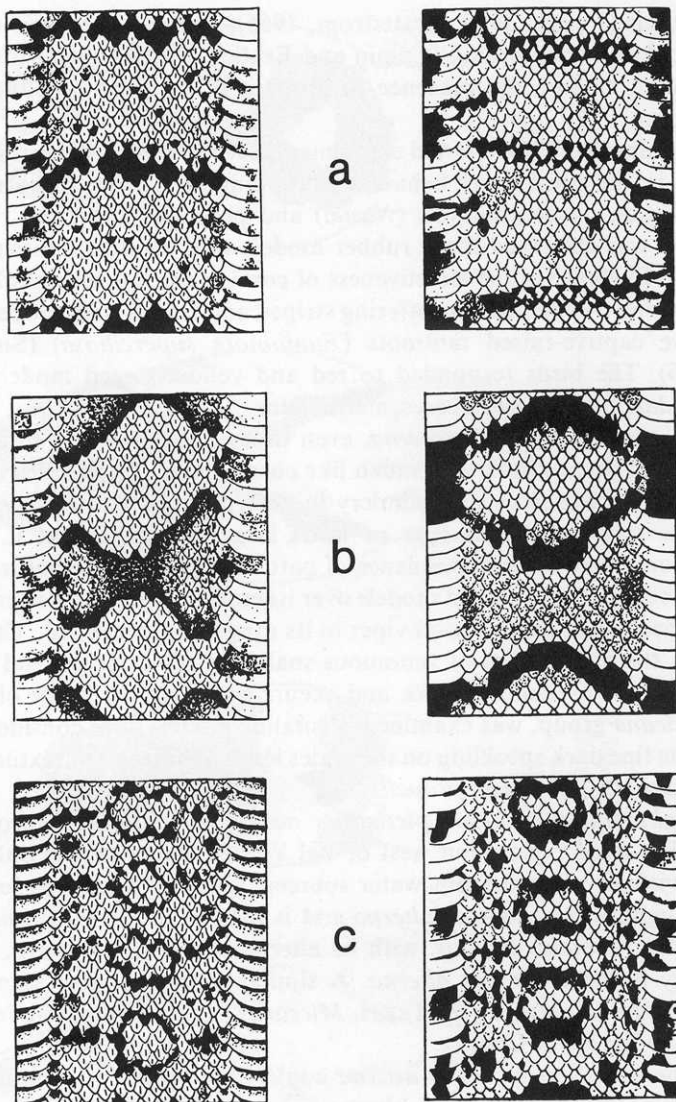


Figure 8. Hypothesis of mimicry in the *mexicana* group. a) *Crotalus lepidus* (L) with sympatric *L. alterna* (R); b) *Agkistrodon mokeson* (L) with sympatric *blairi* morph of *L. alterna* (R); and c) *Crotalus triseriatus* (L) with sympatric *L. mexicana* (R).

(Axtell, 1951), is today quite commonly found. *Agkistrodon* are common along the Devil's and Pecos river drainages as well, in similar habitat with *blairi*; *Micrurus fulvius* is found there as well. The sporadic appearance of *blairi*-like animals in Presidio and Brewster counties in the Big Bend region is correlated with the distribution of *Agkistrodon*. Both *A.m. pictigaster* and *M. fulvius* are very conspicuous, brightly colored animals, and though *C. lepidus* is also sympatric in Val Verde County, its dull appearance may make it a less efficient model. The increased red in the *blairi* morph may be a result of stimulus generalization by predators.

In San Luis Potosí *Crotalus triseriatus aquilis* shares the range and habitat of *mexicana*. The pattern match of these animals is quite remarkable. In life, *C.t. aquilis* is gray-brown with black speckling and a mid-dorsal row of 28 to 40 (mean = 34.5, Klauber, 1952) almost rectangular red-brown irregular blotches. Ventrolateral black blotches are also present. The W.W. Brown 1923 collection at Alvarez for the MCZ contained 10 *mexicana* and 20 *C.t. aquilis*.

The color variability of *mexicana* in the Nuevo León population sampled could reflect the local variability of the model, *Crotalus lepidus*, or a multiple model system. In that area *C. lepidus* varies from ochre to blue in background color, with deep reddish-orange on the ventral side of the tail, which is also apparent in *C.t. aquilis*. Some *mexicana* from Nuevo León are clearly ringed, like *Micrurus*. *Micrurus fulvius* is present on the Atlantic versant of the Sierra Madre. The mobility of predatory birds, as well as the relative rarity of the crotaline model, could affect the occurrence of mimicry in *mexicana*.

There are two situations in which the mimicry hypothesis is less certain. The population of *mexicana* in Durango, Mexico, is rather uniform in appearance and not clearly like any other snake found there. Possible models which share the same canyons with *mexicana* are *C. lepidus*, *C. pricei*, and *C. willardi*. The *mexicana* are most like male *C. lepidus* in that both are yellow-green to gray-green in background color with contrasting narrow dark crossbands. The *mexicana*, however, have many more bands and the bands are usually red-centered. The second situation concerns *ruthveni*. On the same hills in southwestern Querétaro where *ruthveni* is locally abundant, *C. triseriatus* is also abundant, yet *ruthveni* is a brightly ringed animal. *Micrurus fitzingeri* is sympatric with *ruthveni* over much of

its range, but appears not to be present at those localities. *M. fitzingeri* is ringed similarly to *ruthveni*, with up to 28 triads of more or less equal annuli (Smith and Taylor, 1966). Again, the conspicuousness of the red color may contribute to its stimulus value.

An alternate prediction can be made (Levene, 1953) that the areas showing polymorphism are in some way spatially patchy. The habitat of *mexicana* in Nuevo León could be considered patchy in that there are, in close proximity, areas of pine forest, chaparral, open desert, and natural and man-made meadows. There is, however, no correlation of observed morph to microhabitat. There is some spatial heterogeneity in *alterna* habitat also, with *alterna* found in both riparian and desert situations. However, this does not correlate with the distribution of the *blairi* and *alterna* morphs.

Parallel selection processes for crypsis in both the "model" and "mimic" could also explain the similarity of pattern in each situation. The *blairi* case, however, with the change of color pattern of *alterna* to the more abundant and conspicuous model *Agkistrodon*, even in the presence of *C. lepidus*, argues strongly for something other than parallel selection.

## DESCRIPTIONS AND DIAGNOSES OF THE TAXA

### *Lampropeltis alterna* (Brown)

*Ophibolus alternus* Brown 1901

*Lampropeltis alterna*, Stejneger and Barbour 1917

*Lampropeltis blairi* Flury 1950

*Lampropeltis mexicana blairi*, Gehlbach and Baker 1962

*Lampropeltis mexicana alterna*, Gehlbach and Baker 1962

*Type specimen* (holotype): Acad. Nat. Sci. Phil. 14977

*Type locality*: Davis Mountains, Jeff Davis County, Texas

*Description and Diagnosis*: A moderately sized (to about 1 m) snake with a very distinct head and overall mottled grey color. The pattern is a series of white-edged black blotches or saddles that may be red-centered. Alternating reduced markings may be present between major markings. The iris of the relatively large eye is silver-grey in color. The number of ventral scales is 210–232. The proximate spines on the hemipenes are ovoid in cross section and approximately 0.7 mm long.

*Distribution:* Specimens have been collected over the entire Mapimian portion of the Chihuahuan Desert (Morafka, 1977). These localities range from latitude 32° N (Worthington, 1974) south to latitude 25° N (Tanzer, 1970).

*Lampropeltis mexicana* (Garman)

*Ophibolus triangulus* var. *mexicanus* Garman 1884

*Oreophis boulengeri* Duges 1897

*Coronella mexicana*, Gunther 1900

*Coronella leonis* Gunther 1900

*Lampropeltis mexicana*, Blanchard 1921

*Lampropeltis leonis*, Blanchard 1921

*Lampropeltis leonis*, Loveridge 1924

*Lampropeltis thayeri* Loveridge 1924

*Lampropeltis greeri* Webb 1961

*Lampropeltis mexicana greeri*, Gehlbach and Baker 1962

*Lampropeltis mexicana thayeri*, Gehlbach and Baker 1962

*Lampropeltis mexicana mexicana*, Gehlbach and Baker 1962

*Type specimen* (syntypes): MCZ 4652, 4653

*Type locality:* near Ciudad San Luis Potosí, Mexico

*Description and Diagnosis:* A moderately sized (to about 1 m) snake with a slightly distinct head and overall mottled grey to yellow or brown color. The pattern is a series of white-edged black blotches, saddles or rings that may be red-centered. Alternating reduced markings may be present, usually ventrolaterally, between major markings. The anterior tail blotch is enlarged ventrolaterally and red extends onto or usually across the subcaudals. The iris of the relatively large eye is yellow-brown in color. The number of ventral scales falls between 190 and 212. The proximate spines of the hemipenes are rhomboidal in cross section and are approximately 0.4 mm long.

*Distribution:* Specimens have been collected mainly from the mountains surrounding the Saladan portion of the Chihuahuan Desert (Morafka, 1977). The localities have ranged from about latitude 25° N in the Sierra Madre Oriental (P. Bartlett, personal communication) south to 21° N (Duges 1897). A single desert locality (D. Morafka, personal communication) may be a result of recent man-altered changes in the habitat.

*Lampropeltis ruthveni* Blanchard*Lampropeltis ruthveni* Blanchard 1921*Lampropeltis triangulum arcifera*, Williams 1978 (in part)

Type specimen (holotype): USNM 46558

Type locality: Potrenaro = Patzcuaro?, Michoacán, Mexico

**Description and Diagnosis:** A moderately sized (to about 0.8 m) snake with a slightly distinct black head and a uniformly ringed pattern. The black rings are light-edged and red-centered and extend entirely around the body. The small amount of background color is a mottled tan to lime green. The iris is yellow-brown in color. The number of ventral scales falls between 182 and 196.

*L. ruthveni* can be distinguished from the central Mexican milk snakes *L.t. nelsoni* and *L.t. arcifera* on several features of external morphology. First, the head of *L. ruthveni* is distinct from the neck, as in *L. mexicana*. Second, the ringed pattern of *L. ruthveni* is uniform; the red is not much broader nor is the background color much narrower than the black as in *L.t. nelsoni*. Third, there is no tendency in any of the *L. ruthveni* examined for the black to extend along the dorsal midline through the red, as is the case in both *L.t. nelsoni* and *L.t. arcifera* (Smith, 1942; Williams, 1978). Fourth, the black rings of *L. ruthveni* are bordered with a lighter color, usually a pale lime green; this is similar to *L. mexicana* and is distinct from *L. triangulum*. Finally, the ventral scales of the *L. ruthveni* examined were never greater than 196 (mean = 188), while the range of ventrals of *L.t. nelsoni* is 203–231 and of *L.t. arcifera* is 197–217.

**Distribution:** The type locality is cited (Blanchard, 1921) as Pátzcuaro, Michoacán, but this may be incorrect. The locality with the specimen is Potrenaro, Michoacán. The base camp of the collector, W.E. Nelson, in August 1892 was Pátzcuaro (F. McCullough, personal communication). Recent collections have been in the vicinity of La Piedad, Querétaro (C. Lieb, J. Dixon, E. Wagner, personal communication and personal observation), Morelia (UMSNH) and Contepec, Michoacán (D. Armstrong and J. Campbell, personal communication) and Tapalpa, Jalisco. All of the recent collections have been in rocky, wooded uplands. The range of this species may extend entirely across the Mexican Plateau.

## SPECIMENS EXAMINED

*Lampropeltis alterna*. MEXICO: *Coahuila*: Cuatrociénegas (FMNH 47090); Cruz Verde Mt. c. Saltillo (USNM 110819); Puente de la Muralla c. Monclova (Garstka coll., 1 spec.). *Durango*: 26 mi. N San Juan del Río (TCWC 36892). UNITED STATES, TEXAS: *Brewster Co.*: hills N of Study Butte (MCZ 157763). *Jeff Davis Co.*: 17.7 mi. N Fort Davis (TCWC 26181). *Presidio Co.*: 25 mi. W Lajitas (UTA 7875). *Val Verde Co.*: W of Comstock (UTA 2633); 8 mi. W of Comstock (UTA 2941); 8.5 mi. N of Comstock (UTA 8690); 32 mi. NW of Comstock (TCWC 33759); 2 mi. W of Comstock (TCWC 30515); N of Comstock (MCZ 157764, 157765; Garstka coll., 1 spec.); 15 mi. NE Del Río (TCWC 26179); 1.5 mi. E of Langtry (UTA 6680); 7.5 mi. E of Langtry (UTA 6681); N of Langtry (UTA 7188); 6 mi. N of Langtry (UTA 8671); Langtry Loop Road (MCZ 156175); 1 mi. E of Langtry (Garstka coll., 1 spec.); 11 mi. N of Loma Alta (UTA 8668); c. 10 mi. S of Loma Alta (UTA 7874); 0.5 mi. E of Pecos River on US 90 (UTA 8095); Roadside rest c. Pecos River (UTA 8568); Pecos River overlook (TCWC 26180). NO SPECIFIC LOCALITY: (UTA 7969, 8179); (Wagner coll., no. 19). CAPTIVE-HATCHED: Gravid female collected 8.7 mi. N of Comstock (TCWC 33761–33763). CAPTIVE-BRED: *Male parent* collected Brewster Co., Christmas Mts.; *Female parent* collected Val Verde Co., c. Langtry (MCZ 156271–156273); *Both parents* collected Val Verde Co., c. Langtry (MCZ 157724–157728; 156173, 156174; Garstka coll., 10 spec.); *Both parents* collected no specific locality (Texas) (MCZ 156259–156270, 157755–157758, 157760–157762, 158326–158335; Garstka coll., 1 spec., UTA 8126–8129, 7873; Wagner coll., 1, 5, 7, 19, 21–25, 34, 44).

*Lampropeltis mexicana*. MEXICO: *Durango*: 42 mi. S of Cd. Dgo. (UCM 21061); 23 mi. S of Cd. Dgo. (Wagner coll., G1, G2); Canyon of the Río Tunal (Garstka coll., 2 spec.); Highway 40 at the Río Chico (LACM 107230, 107231); Rancho Sta. Barbara (Houston Zoo, 1 spec.); no specific locality (San Diego Zoo, 9 spec.). *Nuevo León*: c. Galeana, Linares-San Roberto highway (ITESM 2507, 2508); Galeana (TCWC 56823); 5 mi. SE of Galeana (TU 16483); c. Los Lirios (ITESM uncataloged); Ojo de Agua c. Galeana (FMNH 30819–30821); c. La Angostura (Garstka coll., 3 spec.); no specific locality (BMNH 146–1–4–10). *San Luis Potosí*: Alvarez

(MCZ 19022–19025, 24976–24979; AMNH 77602; USNM 120823); c. Armadillo de los Infantes (Wagner coll., 1 spec.); c. Rioverde (KU 85010); c. Cd. San Luis Potosí (MCZ 4652, 4653); 52 mi. WNW of Cd. San Luis Potosí (CM 59980). *Tamaulipas*: Miquihuana (MCZ 19551). CAPTIVE-BRED: *Both parents* collected Mexico, Durango, no specific locality (MCZ 157754; Garstka coll., 1 spec.; Wagner coll., G3, G5). *Both parents* collected Mexico, Nuevo León, c. La Angostura (MCZ 156274–156277, 157766; also Garstka coll.)

*Lampropeltis ruthveni*. MEXICO: *Michoacán*: Club Campestre at Morelia (UMSNH uncataloged); Potrenaro = Patzcuaro? (USNM 46558). *Querétaro*: Canyon of the Río Galindo c. Amealco (MCZ 161010–161012; Mexican govt. coll., Agencia Forestal y de la Fauna Z-06586, Z-06587; Garstka coll., 5 spec.; Wagner coll., 9 spec.; 5 spec. released at site of capture). *Jalisco*: Mts. W Zacualco (KU 155528); Tapalpa (SDMNH 46093); 6.5 mi. E Tapalpa (LACM 37307).

### ACKNOWLEDGMENTS

I would most like to thank E. E. Williams for his patience and presence throughout this study. T. Fritts was instrumental in the early stages of the study, as were many discussions with D. F. Retes, E. Wagner, and others. G. C. Mayer criticized several drafts. D. Crews, J. Dixon, M. Scott, and two reviewers also commented on the manuscript. Access to specimens was provided by: J. Alvarado, Universidad Michoacana de San Nicolas Hidalgo, Morelia, Michoacán, Mexico (UMSNH); P. Bartlett, Instituto Tecnológico y Escuela Superior de Monterrey, Monterrey, Nuevo León, Mexico (ITESM); R. Bezy & J. Wright, Los Angeles County Museum (LACM); J. Dixon, Texas Cooperative Wildlife Collection (TCWC); W. Duellman, University of Kansas (KU); H. Dundee, Tulane University (TU); T. Fritts, San Diego Museum of Natural History (SDMNH); A. G. C. Grandison, British Museum (Natural History) (BMNH); W. R. Heyer, United States National Museum (USNM); D. Hoffmeister, University of Illinois Museum of Natural History (UIMNH); P. Maslin, University of Colorado Museum (UCM); C. J. McCoy, Carnegie Museum (CM); W. Pyburn, University of Texas at Arlington (UTA); T. Van Devender, University of Arizona (UA); and R. Zweifel, American Museum of Natural History (AMNH). Access to specimens was also provided by numerous zoo



and private collections, especially J. Bacon (Zool. Soc. San Diego), J. Murphy (Zool. Soc. Dallas), H. Quinn, and B. Tryon (Zool. Soc. Houston), E. Wagner (Zool. Soc. Seattle) and D. F. Retes. Botanical material was identified by J. Henrickson, T. Wendt, and M. Donaghue.

Permission to collect in Mexico was issued by Lic. M. L. Cossio-Gabucio, Lic. I. Ibarrola-Bejar, and Lic. M. Gonzalez-Escamilla, all of the Agencia Forestal y de la Fauna.

### LITERATURE CITED

- AUFFENBERG, W. 1955. A reconsideration of the racer, *Coluber constrictor*, in the eastern United States. *Tulane Stud. Zool.*, **2**(6): 89-155.
- . 1963. The fossil snakes of Florida. *Tulane Std. Zool.*, **10**(3): 132-216.
- AXTELL, R. W. 1951. An additional specimen of *Lampropeltis blairi* from Texas. *Copeia*, **1951**(4): 313-314.
- BAKER, R. S., G. A. MENGDEN, AND J. J. BULL. 1972. Karyotypic studies of thirty-eight species of North American snakes. *Copeia*, **1972**(2): 257-265.
- BLANCHARD, F. N. 1920. A synopsis of the kingsnakes: genus *Lampropeltis* Fitzinger. *Occas. Pap. Mus. Zool. U. Mich.* No. 87, pp. 1-8.
- . 1921. A revision of the kingsnakes, genus *Lampropeltis*. *Bull. U.S. Nat. Mus.* No. 114, vi+260 pp.
- BRATTSTROM, B. H. 1955. The coral snake mimic problem and protective coloration. *Evolution*, **9**(2): 217-219.
- BROWN, A. E. 1901. A new species of *Ophibolus* from western Texas. *Proc. Acad. Nat. Sci. Phil.*, **53**(3): 612-613.
- BULLOCK, R. E., AND W. W. TANNER. 1966. A comparative osteological study of two species of colubridae (*Pituophis* and *Thamnophis*). *BYU Sci. Bull.*, **8**(3): 1-29.
- BURY, R. B., F. GRESS, AND G. C. GORMAN. 1970. Karyotypic survey of some colubrid snakes from western North America. *Herpetologica*, **26**(4): 461-466.
- CAMIN, J. H., AND P. R. EHRLICH. 1958. Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. *Evolution*, **12**(4): 504-511.
- COPE, E. D. 1898. The crocodilians, lizards and snakes of North America. *Ann. Rep. USNM*, **1898**: 153-1270.
- DOWLING, H. G. 1951. A proposed standard system of counting ventrals in snakes. *Brit. J. Herpetol.*, **1**(5): 97-98.
- DUGES, A. 1897. Description d'un ophidien nouveau de Mexique, *Oreophis boulengeri* (g. et sp. nn.) *Proc. Zool. Soc. Lond.*, **1897**: 284-285.
- ECHTERNACHT, A. C. 1973. The color pattern of *Sonora michoacensis* (Duges) (Serpentes, Colubridae) and its bearing on the origin of the species. *Breviora Mus. Comp. Zool.* No. 410, pp. 1-18.
- FLURY, A. 1950. A new kingsnake from trans-Pecos Texas. *Copeia*, **1950**(3): 215-217.

- FOX, W., G. GORDON, AND M. H. FOX. 1961. Morphological effects of low temperature during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica*, **46**(5): 57-71.
- GANS, C. 1961. Mimicry in procryptically colored snakes of the genus *Dasypeltis*. *Evolution*, **15**(1): 72-91.
- GARMAN, S. 1884. The reptiles and batracians of North America, part 1. Ophidia. *Memoirs Mus. Comp. Zool.*, **8**(3): xxxi + 185.
- GEHLBACH, F. R. 1967. *Lampropeltis mexicana* (Garman) pp. 55.1-55.2. In H. G. Dowling (ed.), *Catalogue of American Amphibians and Reptiles*. Soc. Study of Amphib. Rept.
- . 1972. Coral snake mimicry reconsidered: the strategy of self-mimicry. *Forma et Functio*, **5**(4): 311-320.
- GEHLBACH, F. R., AND J. BAKER. 1962. Kingsnakes allied with *Lampropeltis mexicana*: taxonomy and natural history. *Copeia*, **1962**(2): 291-300.
- GEHLBACH, F. R., AND C. MCCOY. 1965. Additional observations on variation and distribution of the gray-banded kingsnake, *L. mexicana* (Garman). *Herpetologica*, **21**(1): 35-38.
- GOODMAN, J. D., AND J. M. GOODMAN. 1976. Contrasting color and pattern as enticement display in snakes. *Herpetologica*, **32**(2): 145-148.
- GREENE, H. W., AND W. F. PYBURN. 1973. Comments on aposematism and mimicry among coral snakes. *Biologist*, **55**(4): 144-148.
- GUNTHER, A. 1900. *Biologia Centrali-Americana: Reptilia and Batrachia*. London, Bernard Quaritch.
- HECHT, M. K., AND D. MARIEN. 1956. The coral snake mimic problem: a reinterpretation. *J. Morphol.*, **98**(2): 335-365.
- JACKSON, J. F., W. INGRAM, AND H. W. CAMPBELL. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *Am. Nat.*, **110**: 1029-1953.
- JAMESON, D. L., AND A. G. FLURY. 1949. The reptiles and amphibians of the Sierra Vieja range of southwestern Texas. *Texas J. Sci.*, **1**(2): 54-79.
- JOHNSON, R. G. 1955a. The application of X-rays to the study of small reptiles and amphibians. *Copeia*, **1955**(3): 259-261.
- . 1955b. The adaptive and phylogenetic significance of vertebral form in snakes. *Evolution*, **9**(4): 367-388.
- KLAUBER, L. 1941. The correlation between scalation and life zones in San Diego County snakes. *Bull. Zool. Soc. San Diego* No. 17, pp. 73-79.
- . 1952. Taxonomic studies of the rattlesnakes of mainland Mexico. *Bull. Zool. Soc. San Diego* No. 26, pp. 1-143.
- LASZLO, J. 1975. Probing as a practical method of sex recognition in snakes. *Int. Zoo Year Book*, **15**: 178-179.
- LEVENE, H. 1953. Genetic equilibrium when more than one ecological niche is available. *Am. Nat.*, **87**: 311-313.
- LOVERIDGE, A. 1924. A new snake of the genus *Lampropeltis*. *Occas. Pap. Boston Soc. Nat. Hist.*, **5**: 137-139.
- MECHAM, J., AND W. MILSTEAD. 1949. *Lampropeltis alterna* from Pecos County, Texas. *Herpetologica*, **5**(6): 140.

- MILLER, D. J. 1979. A life history study of the gray-banded kingsnake, *Lampropeltis mexicana alterna* in Texas. Chihuahuan Desert Research Institute, Contrib. No. 87, pp. 1-48.
- MINTON, S. A. 1976. Serological relationships among some congeneric North American and Eurasian colubrid snakes. *Copeia*, 1976(4): 672-678.
- MINTON, S. A., AND S. K. SALANITRO. 1972. Serological relationships among some colubrid snakes. *Copeia*, 1972 (2): 246-252.
- MORAFKA, D. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica vol. 9. The Hague, Junk, vi + 313 pp.
- MURRAY, L. J. 1939. Annotated list of amphibians and reptiles from the Chisos Mountains. Contrib. Baylor Mus., 24: 4-16.
- PETERS, J. 1964. Dictionary of Herpetology. N.Y., Hafner, vii + 427 pp.
- POUGH, F. H. 1976. Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia*, 1976(4): 834-836.
- SMITH, H. M. 1941. *Lampropeltis alterna* from Mexico. *Copeia*, 1941(2): 112.
- . 1942. Remarks on the Mexican kingsnakes of the *triangulum* group. Proc. Roch. Acad. Sci., 8: 196-207.
- . 1944. Snakes of the Hoogstraal expeditions to Northern Mexico. Field Mus. Nat. Hist. Ser. Zool., 29: 135-152.
- SMITH, H. M., AND E. H. TAYLOR. 1966. The Herpetology of Mexico. Ashton, MD., Lundberg, 610 pp.
- SMITH, N. G. 1969. Avian predation of coral snakes. *Copeia*, 1969(2): 402-404.
- SMITH, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. Science, 187(4178): 759-760.
- SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman, xxi + 776 pp.
- STEJNEGER, L., AND T. BARBOUR. 1917. A checklist of North American Amphibians and Reptiles. Harvard, Cambridge, Ma.
- TANNER, W. W. 1953. A study of the taxonomy and phylogeny of *Lampropeltis pyromelana* (Cope). Great Basin Nat., 13(1,2): 47-66.
- TANZER, E. 1970. Polymorphism in the *mexicana* complex of kingsnakes with notes on their natural history. Herpetologica, 26(4): 419-428.
- TAYLOR, E. H. 1940. A new *Lampropeltis* from western Mexico. *Copeia* 1940(4): 253-255.
- UNDERWOOD, G. 1967. A contribution to the classification of snakes. BMNH Pub. 654, x + 179 pp.
- WEBB, R. 1961. A new kingsnake from Mexico with remarks on the *mexicana* group of the genus *Lampropeltis*. *Copeia*, 1961(3): 326-333.
- WILLIAMS, K. 1978. Systematics and natural history of the American milk snake *Lampropeltis triangulum*. Pub. Biol. Geol. Milwaukee Pub. Mus. No. 2, 258 pp.
- WORTHINGTON, R. D. 1974. Western records of the Davis Mountain kingsnake, *L.m. alterna* in Texas. SW Nat., 19(3): 330-331.