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A REVISION OF THE KING SNAKES: GENUS LAMPROPELTIS

BY

FRANK N. BLANCHARD
Instructor in Zoology, University of Michigan, Ann Arbor

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LAMPROPELTIS LEONIS (Günther).

1893. *Coronella leonis* GÜNTHER, Biol. Cent. Amer., Rept. and Batr., p. 110, pl. 39, fig. A (type locality, Nuevo Leon, Mexico; type in British Museum; W. Taylor, collector).—BOULENGER, Cat. Snakes Brit. Mus., vol. 2, 1894, p. 199.

Description.—As this form is known only from the type specimen, the original description is here quoted in full:

Scales in 23 rows, without pit, smooth; head similar to that of *Coronella laevis*; anterior frontals not quite half the size of posterior; vertical 5-sided, with the lateral margins convergent; 1 praeocular not reaching the vertical; 2 postoculars; loreal longer than deep; 7 upper labials, the third and fourth entering the orbit; temporals 2+3, of the 2 anterior only the upper one is in contact with the postoculars. Ventrals 200; anal entire; subcaudals 50. Body pale olive-color on the back, with 27 salmon-colored incompletely black-edged spots, some being of a transversely oval shape, but the majority presenting the appearance of being formed of 2 rounded portions. On the tail the spots lose their light center and appear merely as brown spots. The lateral spots which are so conspicuous in most variations of *Coronella triangulum* are here nearly entirely absent. Vertical and each occipital with a black spot, red in the center; abdomen with only a few blackish blotches irregularly scattered. A black band along the middle of the lower part of the tail. The single specimen measured 23½ inches, the tail 3¾ inches. This snake may be considered to be one of the aberrant forms of *Coronella triangulum*.

Remarks.—The description is incomplete in some respects, and the type specimen has not been available for examination. If, as stated above, scale pits are actually absent, in which case other distinctive differences will almost certainly be found, the specimen can hardly be a *Lampropeltis*, but an error may easily have been made on this point. Further examples must be obtained before the status of this form can be stated with assurance. But from the description and excellent figure, it appears to be a distinct form closely allied to the other members of the *calligaster* group. Further discussion, however, is hardly profitable at present.

SUMMARY.

The handicap of insufficient material has been more than usually acute in the study of this group.

The intimate relationship existing between *rhombomaculata* and *calligaster* and the fact that the former is a derivative by reduction of the latter need not here be more than recalled, after the discussions already given under Variation and Affinities of these forms.

That *leonis* is a member of the group must be allowed, pending further knowledge of the form.

We may therefore express the relations of the forms of the *calligaster* group, diagramatically, as follows:

leonis——*calligaster*——→*rhombomaculata*

The Atlantic States—the "Southeast"—may therefore be excluded from consideration as a possible center of origin or dispersal of this group.

LAMPROPELTIS RUTHVENI Blanchard.

Fig. 74.

1920. *Lampropeltis ruthveni* BLANCHARD, Occ. Pap., Univ. Mich., no. 81, p. 8, pl. 1, fig. 2 (type locality, Patzcuaro, Michoacan, Mexico; type specimen, U. S. Nat. Mus., no. 46558; collected by E. W. Nelson, Aug. 2, 1892).

Since the type specimen is the only one known, the original description is quoted in full:

Diagnosis.—A ringed form similar in coloration to *L. polyzona* Cope, *L. triangulum nelsoni* Blanchard, and *L. multicincta* (Yarrow). From *L. polyzona* it differs in the complete absence of black tips on the red and whitish scales, in the completely black head, and in the low number of ventral plates, 189. From *nelsoni* it differs principally in the higher number of annuli, 30, and the much narrower red rings, 2 to 3 scales in width. From *L. multicincta* it is distinguished by the low numbers of ventrals and annuli, by the fact that the black rings show scant, if any, tendency to overspread the red areas dorsally, and by the mottling of the yellow rings with darker, particularly on the sides.

Range.—Patzcuaro, Michoacan, Mexico.

Type Specimen.—United States National Museum No. 46558 (skin and head only); Patzcuaro, Michoacan, Mexico; collected by E. W. Nelson, August 2, 1892.

Description of type specimen.—Ventrals, 189; anal single and entire; caudal scutes 50 plus, divided (tip of tail missing); dorsal scale rows, 21 anteriorly, 23 on middle of of body, and 19 posteriorly (formula therefore 21–23–21–19); upper labials 8 on left side, 7 on right; lower labials 9; 1 preocular, 2 postoculars; temporals somewhat irregular, about 2+3+4, the upper left anterior temporals much reduced; loreal longer than high; nasals injured on each side; anterior chin shields in contact with each other and with the first four lower labials; posterior chin shields shorter than the anterior and separated from each other by 2 or 3 small scales; other head shields normal for the genus.

Total length (tip of tail missing), about 745 mm., tail length 112 mm.

The dentition is as follows: Maxillary teeth, 14 on the left side, 15 on the right, the last two distinctly enlarged; mandibular teeth, 14 on the left side 13 on the right, decreasing slightly in size; palatine teeth, 13 on the left, 11 on the right; pterygoid teeth, 21 on the right side.

The color pattern is composed of 24 whitish rings on the body and 6 on the tail. These rings are about 1½ scales wide on the middorsal line and 2 scales wide on the first row of scales; on the sides and on the belly, posteriorly, they are mottled with darker. Bordering the whitish rings are black annuli about 2 scales wide dorsally and 1 scale wide on the belly. The black rings are separated by red rings, 2 to 3 scales in width. The actual colors can not be determined from so old a specimen, but there are indications that the whitish rings may have been suffused with pink.

The head is black nearly to the tips of the parietal shields, except for flecks of whitish on the lower portions of some of the upper labials. The chin is whitish except for some black on the first 5 or 6 of the lower labials. The first black ring begins about 2 scales behind the parietals and is continuous across the throat.

Remarks.—The status and significance of this form, represented as it is by only a single specimen, must remain in doubt for the present. It appears, however, to be more closely allied to *L. multicincta* than to any other form in the genus.

2. *Elapsoides* is a derivative of *amaura*, or of the form that represented it in the Texas region before the appearance of *syspila* and *triangulum*. In the northeastern portion of its range it has given rise to the color pattern variety, *virginiana*.

3. The subspecies of *triangulum* may all be traced to a center of dispersal in the plateau region of Mexico.

4. The relationships of *pyrrhomelaena* and *multicincta* are doubtful, but there seems to be the least difficulty in regarding *pyrrhomelaena*

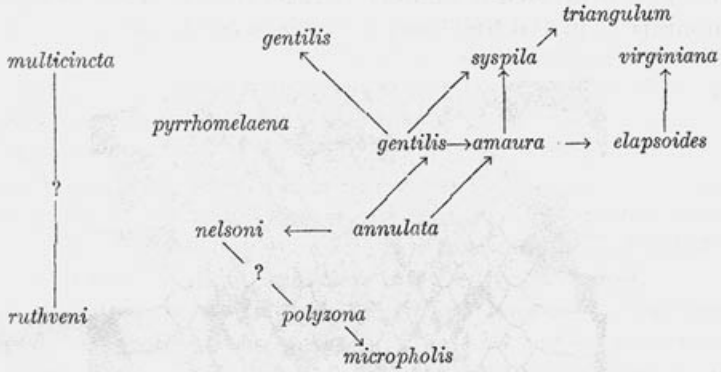

FIG. 76.—A DIAGRAMMATIC PRESENTATION OF THE RELATIONSHIPS OF THE FORMS OF THE TRIANGULUM GROUP.

as a specialized and isolated form, much older than the subspecies of *triangulum*, and *multicincta* as the west coast representative of the rest of the *triangulum* group.

ISOLATED FORMS.

LAMPROPELTIS MEXICANA (Garman).

Fig. 77.

1883. *Ophibolus triangulus*, var. *mexicanus* GARMAN, S., Mem. Mus. Comp. Zool., vol. 7, no. 3, p. 66 (type locality, Mexico, near San Luis Potosi; cotypes, probably numbers 4652 and 4653 of the collection of the Museum of Comparative Zoology at Cambridge, Massachusetts).

1902. *Coronella mexicana* GÜNTHER, Biol. Cent.-Amer., p. 110.

No type was designated in the original description of *mexicana*, and no specimens were listed. The description shows, however, that there were at least two specimens, and it fits remarkably well for two from that locality in the collection of the Museum of Comparative Zoology. The scales of both are in 23 rows; the ventral plates are exactly 193 and 199, as in the original description; the head is "much swollen at the temples;" and the pattern and coloration answer well. According to the description, the caudals are 56–58 pairs, and the dorsal blotches are 38–40; these specimens seem to have 55 pairs each of caudals, and about 39 blotches each. These differences when compared with the coincidences are too

slight to render it improbable that these are the specimens from which the original description of *mexicana* was prepared, and their numbers have therefore been given above as the cotypes of this form.

Description.—Since the original description is somewhat incomplete, the following is offered in its stead: Ventrals, 193 and 199; caudals, 55, in two rows (both specimens females); supralabials, 7; infralabials 10, fifth largest, 5 under the last 3 upper labials; preocular single except that it is divided in number 4652 on the left side; postoculars, 2; temporals, 2 in the first row, 3 in the second, and 4 or 5 in the

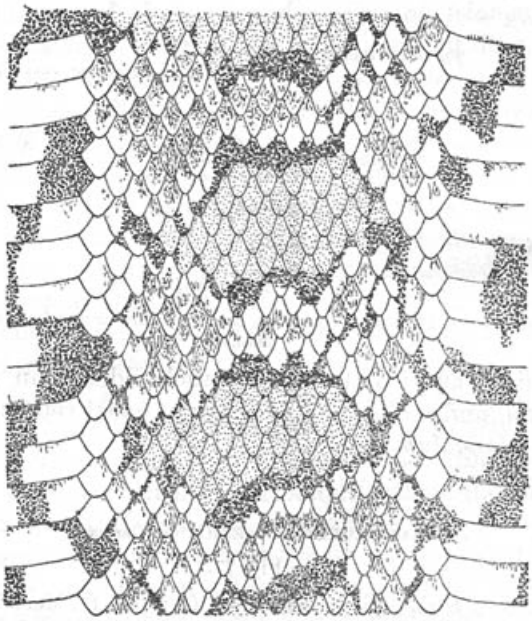

FIG. 77.—LAMPROPELTIS MEXICANA (M.C.Z., SCALE PATTERN FROM NO. 4653, COLOR PATTERN FROM NO. 652, SAN LUIS POTOSI, MEXICO). ABOUT 1¼ × NAT. SIZE. SHOWING COLOR PATTERN.

third; posterior chin shields shorter than the anterior, and separated from each other by 2 small scales; loreal about twice as long as high; anal plate entire; scales smooth, with 2 apical pits; dorsal scale rows, 23–21–19.

Body moderately slender, tapering slightly toward the tail; belly flat, meeting the sides in a rather distinct angle; head flat, distinct from the neck, swollen at the temples, tapering anteriorly, snout truncate; tail, 0.16 to 0.17 of the total length; eye large, its diameter nearly twice the height of the third upper labials. One of the specimens measures 803 millimeters, the other 452.

The pattern of the body (fig. 77) recalls that of *triangulum*. There are about 39 transversely oblong red blotches on head and tail

bordered with black, and separated by narrower grayish mottled spaces. The red blotches are about 2 to 3½ scales long, and they maintain this length through a width of about 8 scales across the back, then narrowing, they extend down on the sides to about the second or third row of scales. These downward extensions are sometimes nearly or quite isolated from the dorsal blotches. The black borders are ½ to 1 scale in width dorsally, becoming narrower on the sides. The spaces between the blotches are whitish, and strongly but minutely mottled with dark, except close to the black borders. The belly is heavily blotched with black; the tendency is for narrow transverse bands to cross the belly and end on the first row of scales in alternation with the dorsal blotches, but these are often broken in the middle and obscured by large black patches between them and opposite to the dorsal blotches. On the head of the small specimen are two red V-shaped marks black-bordered, opening forward, the larger chiefly on the parietals, the smaller chiefly on the frontal. Behind the eye is a large black blotch. Rest of head, chin, and throat whitish, minutely mottled with darker.

The dentition is as follows: Maxillary teeth, 13, the last two enlarged, not grooved nor separated from the rest by an interspace; mandibular teeth, 14 in one specimen (number 4652) and 16 and 17 in the other, the third, fourth, and fifth large, the last small; palatines, 13 in each instance; pterygoids, 22 (only one set counted).

Remarks.—If, as is entirely probable, the two specimens described above are the originals, then they are the only specimens of the form known. That they belong to the genus *Lampropeltis* as at present defined, must be conceded. They can not, however, be closely related to any other form in the genus; the head pattern is unique, and, although the body pattern bears a superficial resemblance to *triangulum* and to the members of the *calligaster* group, it yet bears a distinct stamp of originality; the 10 lower labials, long tail, swollen temples, and high number of palatine teeth are all features that mark it as specialized. It is doubtless more closely allied to the *triangulum* group than to either of the other two.

LAMPROPELTIS ALTERNA (Brown).

Fig. 78.

1902. *Ophibolus alternus* Brown, Proc. Acad. Nat. Sci. Philadelphia for 1901 (Feb. 6, 1902), p. 612, pl. 34 (type locality, Davis Mountains, Jeff Davis County, Texas; type specimen, number 14977, Acad. Nat. Sci., Philadelphia, E. Meyenberg, collector); same, 1903, p. 550.—Ditmars, Reptile Book, 1907, p. 356.—Strecker, Baylor Bull., vol. 18, no. 4, 1915, p. 39.—*Lampropeltis alterna* Stejneger and Barbour, Check List, 1917, p. 87.

This name rests upon a single specimen, received alive at the Zoological Gardens in Philadelphia, and said to have been found in

bordered with black, and separated by narrower grayish mottled spaces. The red blotches are about 2 to 3½ scales long, and they maintain this length through a width of about 8 scales across the back, then narrowing, they extend down on the sides to about the second or third row of scales. These downward extensions are sometimes nearly or quite isolated from the dorsal blotches. The black borders are ½ to 1 scale in width dorsally, becoming narrower on the sides. The spaces between the blotches are whitish, and strongly but minutely mottled with dark, except close to the black borders. The belly is heavily blotched with black; the tendency is for narrow transverse bands to cross the belly and end on the first row of scales in alternation with the dorsal blotches, but these are often broken in the middle and obscured by large black patches between them and opposite to the dorsal blotches. On the head of the small specimen are two red V-shaped marks black-bordered, opening forward, the larger chiefly on the parietals, the smaller chiefly on the frontal. Behind the eye is a large black blotch. Rest of head, chin, and throat whitish, minutely mottled with darker.

The dentition is as follows: Maxillary teeth, 13, the last two enlarged, not grooved nor separated from the rest by an interspace; mandibular teeth, 14 in one specimen (number 4652) and 16 and 17 in the other, the third, fourth, and fifth large, the last small; palatines, 13 in each instance; pterygoids, 22 (only one set counted).

Remarks.—If, as is entirely probable, the two specimens described above are the originals, then they are the only specimens of the form known. That they belong to the genus *Lampropeltis* as at present defined, must be conceded. They can not, however, be closely related to any other form in the genus; the head pattern is unique, and, although the body pattern bears a superficial resemblance to *triangulum* and to the members of the *calligaster* group, it yet bears a distinct stamp of originality; the 10 lower labials, long tail, swollen temples, and high number of palatine teeth are all features that mark it as specialized. It is doubtless more closely allied to the *triangulum* group than to either of the other two.

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1902. *Ophibolus alternus* Brown, Proc. Acad. Nat. Sci. Philadelphia for 1901 (Feb. 6, 1902), p. 612, pl. 34 (type locality, Davis Mountains, Jeff Davis County, Texas; type specimen, number 14977, Acad. Nat. Sci., Philadelphia, E. Meyenberg, collector); same, 1903, p. 550.—Ditmars, Reptile Book, 1907, p. 356.—Strecker, Baylor Bull., vol. 18, no. 4, 1915, p. 39.—*Lampropeltis alterna* Stejneger and Barbour, Check List, 1917, p. 87.

This name rests upon a single specimen, received alive at the Zoological Gardens in Philadelphia, and said to have been found in

the Davis Mountains, Texas. It answers so closely in structural features to the genus *Lampropeltis* that, in spite of its unique type of pattern, and lesser structural peculiarities, it must be included here until further specimens make possible a determination of its true status.

Description.—Since the original description is very accurate it is quoted in entirety:

Maxillary teeth 13; mandibular 14–15. Body moderately slender; head distinct, muzzle contracted; eye rather large. Rostral low and broad, barely visible from

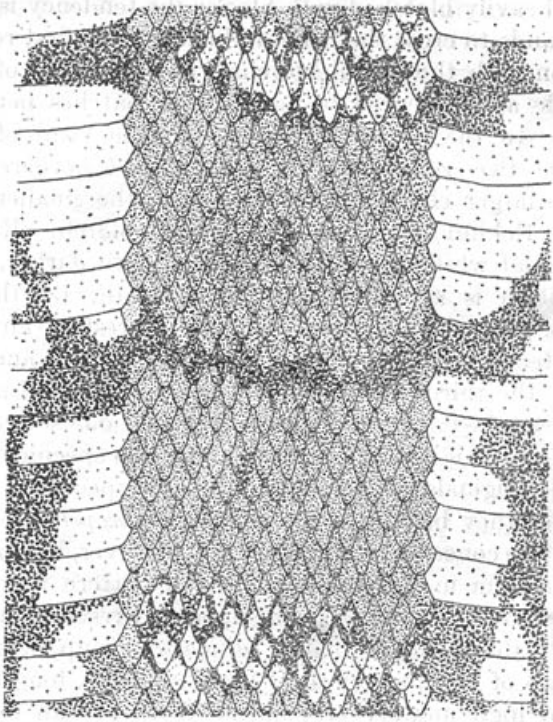

FIG. 78.—LAMPROPELTIS ALTERNA (ACAD. NAT. SCI., PHILADELPHIA, NO. 14977, TYPE, DAVIS MOUNTAINS, TEXAS). 2 × NAT. SIZE. SHOWING STYLE OF COLOR PATTERN.

above; internasals about half the length of prefrontals; frontal a little longer than the suture between parietals, longer than the snout; parietals large, wide in front, narrow behind; nasals 2, the nostril between them; loreal small, longer than high; preocular 1; postoculars, 2 on one side, 3 on the other; temporals, 2+3 on one side, 3+4 on the other; upper labials 7, third and fourth in orbit; lower labials 11. Posterior chin shields a little shorter than the anterior, not separated by scales. Scales smooth, with two inconspicuous pits, in 25 rows. Ventrals 217; anal entire; subcaudals 60 pairs. Total length 710 mm. (tail 115).

The ground color is slate gray, crossed on the back, at intervals of 3 to 5 scales, by bands of black which are alternately wider and narrower, the wide ones covering from 2 to 3 scales on the middle of the back, and more or less divided transversely on their centers with scarlet. The narrow bands are about 1 scale wide and wholly black, occasionally broken through by the ground color. On the neck the bands are narrower

and less defined, while the red is more pronounced on the posterior part of the body. There are 19 red and black bands on the body, and an equal number of the intermediate black ones. On the tail there are 5 bands, which form quite distinct rings, on the last two of which the red is absent. The head, including the labials, is dark gray with small dark mottlings, not well defined, and a narrow black streak from the postoculars to the angle of the mouth. Ventral surface grayish white, heavily blotched with black, into which the black portion of the cross bands runs.

By way of correction and addition to the above it may be noted that the temporals are 3+4+5 on each side; the left lower labials are 11, the right, 10; the third postocular is on the left side and is a derivative of the fourth supralabial; the last two maxillary teeth are slightly enlarged, and the palatines are 12 on each side; the dorsal scale formula is 25–23–25–23–21–19–20, and the changes in the number of rows take place in the manner usual for this genus; the tail is about 0.17 of the total length.

Remarks.—It will be evident from the above description that this specimen is about as far removed in its structural features from the normal forms of the genus as is *pyrrhomelaena*. Like the latter it has a long tail, wide head, high numbers of ventrals, caudals, scale rows, temporals, infralabials, and a long, narrow loreal. Its style of coloration is, however, quite different from anything else in the genus, but knowing how easily one pattern may be changed into another radically different in appearance, we can not assign great importance to that fact alone. The writer would agree with Brown (1901, 613) in placing it nearer to *pyrrhomelaena* in structural features than to any other form of the genus, but it does not appear to lie at all near to *leonis*, as that author suggested. It would seem best to await the finding of more specimens before making any definite statement as to its status.

CONCLUSION.

The preceding descriptions and discussions have brought out the fact that the genus *Lampropeltis* is naturally divided into three main groups, of closely related forms (exclusive of two forms of doubtful relationships, *mexicana* and *alterna*). Two (the **GETULUS** and **CALLIGASTER** groups) are more closely allied to each other than either to the third, and the latter (the **TRIANGULUM** group) is composed of at least three minor groups, representing different degrees and kinds of differentiation, and different periods of dispersal. On account of these facts and because the most primitive forms of the groups are apparently very far from being directly related, each group has been treated very nearly independently in searching for its center of dispersal, for it is conceivable that the groups as now known may have started from different centers without affecting the propriety of uniting them all in a single genus. This treatment has resulted in showing that in all probability each of these groups origi-

nated in some portion of the region between Texas and Nicaragua. This, together with the fact that the only forms of doubtful relationships are located in this region, indicates that the center of dispersal of the entire genus is in the Southwest.

Let us now consider how the genus as a whole answers to the criteria for determination of centers of dispersal, as formulated by Adams (1902, 122). There are 10 of these criteria, as follows:

1. Location of greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms (Allen).
4. Location of maximum size of individuals (Ridgway-Allen).
5. Location of greatest productiveness and its relative stability, in crops (Hyde).
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
9. Direction indicated by biogeographical affinities.
10. Direction indicated by the annual migration routes, in birds (Palmen).

Some of these criteria are of only limited value, and the fifth, ninth, and tenth can not be used at all in the present instance. The others will be discussed in order.

1. *Location of greatest differentiation of a type.*—In the Southwest we have *polyzona, nelsoni, annulata, leonis, calligaster, splendida, pyrrhomelaena, ruthveni,* and *alterna.* The only region at all comparable with this in diversity of type is the Southeast. Here we have four forms, all specialized, and two of them (*elapsoides* and *rhombomaculata*) obvious derivatives of western types; but there is no representative of *pyrrhomelaena* in the Southeast, nor of *mexicana,* nor of *alterna.* The greatest differentiation is therefore unquestionably in the Southwest.

2. *Location of dominance or great abundance of individuals.*—This criterion is of only minor value; exceptions may be readily called to mind. It is valueless in this case, however, since, in the present unsatisfactory state of our knowledge, there is as much to be said on one side as on the other.

3. *Location of synthetic or closely related forms.*—It has been noted frequently that those forms of this genus to which the groups trace their origin are more closely allied in structure with each other than with any of the other forms in the genus. For example, the southwestern types, *calligaster* and *leonis* may, much more readily than the specialized *rhombomaculata* of the Southeast, be associated with the **GETULUS** group, and it is with the western representatives of

the latter rather than with the eastern that the closest relationship lies. Of the **TRIANGULUM** group the outlying types, *micropholis, elapsoides, virginiana,* and *triangulum,* are much more differentiated from the other groups than its southwestern representatives, *polyzona* and *annulata.* This criterion is therefore admirably fulfilled by the Southwest, and by this region only, and its value as a criterion may be regarded as second only to the sixth.

4. *Location of maximum size of individuals.*—Apparently no greater size is obtained by any forms than that reached by the southwestern representatives of all the groups, with the exception of the purely peninsular and derived forms, *floridana* and *brooksi;* and it will be remembered that the forms which are most reduced in size and scutellation occupy regions most distant from the southwest, namely *conjuncta* of the Cape region of Lower California, and *elapsoides,* and *rhombomaculata* of the southeastern States. Of *nelsoni* and *annulata* we have too few specimens to know what the normal or the maximum size may be but *polyzona* of southern Mexico may properly be compared with *triangulum* of the northeastern States. Of 300 specimens of the latter the largest measured 1,085 mm., and of 61 of the former the largest measured 1,610 and the next largest 1,580 mm., a decided difference in favor of the Southwest. The forms of the **GETULUS** group are of approximately equal size; of the two well-known forms of the **CALLIGASTER** group, the western representative is decidedly the larger. This criterion therefore points definitely to the Southwest.

6. *Continuity and convergence of lines of dispersal.*—Both the **GETULUS** and **CALLIGASTER** groups are represented in the Southwest, and the isolated types, *mexicana, alterna,* and *pyrrhomelaena,* are not represented outside of the Southwest. But it is the **TRIANGULUM** group that illustrates this most admirably. In this we see the convergence toward Mexico of the *polyzonamicropholis* line from the south, the *annulata-gentilis* line from the north, the *annulata-elapsoides* line from the east, and the *annulata-triangulum* line from the northeast.

All genetic lines in the genus, therefore, either converge to the Southwest, or are represented in the Southwest as well as elsewhere, or are not represented outside of the Southwest, and no genetic lines converge to any region other than the Southwest. Thus this most dependable of all criteria is satisfied only by the Southwest.

7. *Location of least dependence upon a restricted habitat.*—Too little is known of the habitat relations of these snakes to discuss this criterion profitably, but it may be noted that the only burrowing forms (*elapsoides, virginiana,* and *rhombomaculata*) are located in the Southeast.

8. *Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.*—Lengthy demonstration of this criterion is not necessary here, since the descriptions and summaries demonstrate conclusively its direct applicability to the Southwest.

It will be evident that although these criteria are not of equal value, all point to the Southwest, and that the most dependable of these, the third, sixth, and eighth, are especially definite in this respect. The argument for the Southwest is not expected to rest upon any single piece or line of evidence, but it is believed that the weight of positive and the lack of negative evidence, as brought out in the summaries of the separate groups and in the discussion of the preceding criteria, amount to a demonstration that the center of dispersal of the genus *Lampropeltis* is in the southwestern portion of the North American continent.

Before concluding, a few remarks on the relation between the environment and the distribution of species and subspecies, as exhibited by the genus *Lampropeltis*, may not be out of place. It is noticeable that each form inhabits a region of rather definite environmental conditions, and that, within any such region, a group of directly related forms has but a single representative. Thus, restricted to the southeastern States, we have three forms, each representing a different line of descent. Each of these forms is replaced west of the Alabama-Mississippi region by a closely allied form, and the different environmental conditions of southern Florida are reflected in these forms as follows: One apparently does not extend south of the northern portion of the State, one is replaced by a closely allied form derived from it, and the third expresses an extreme reduction that may yet lead to subspecific differentiation. The prairie region is characterized by two forms (*calligaster* and *syspila*), the lower Mississippi Valley by one (*amaura*), and another (*holbrooki*) ranges over both of these areas, but does not extend to any adjacent region. Two characterize the northeastern deciduous forest province; one of these (*niger*) is confined to the southern section, west of the Alleghenies, the other (*triangulum*) inhabits the whole province, but has developed most successfully in the north. At the western limit of forests in Texas, both *holbrooki* and *amaura* are replaced by their close relatives, *splendida* and *gentilis*, respectively. In Mexico the major environments are represented by *polyzona* in the lowlands of the east and south, *nelsoni* on the west coast, and *annulata* in the plateau region. Whatever may be the cause of speciation, or the breaking up into subspecies, it is a fact that when a form has migrated into a region of decidedly different environment it has become altered, and the alteration has remained constant in its main features

throughout that environment. Thus it has come about that the direct relative of any form is found in an adjacent environment. The peculiar exception offered by *californiae* (p. 94), where speciation by mutation is indicated, affords opportunity for a most interesting investigation. But in general, the oft emphasized rule holds for this genus; namely, the occurrence of two different forms of the same genus in the same locality is prima facie evidence that they belong to different lines of descent, and, conversely, directly related forms are not found in the same locality.

The preceding might be detailed more fully, and more complete information on the little known forms would doubtless result in added illustrations of the fact that the environment seems to exert a circumscribing influence on the species, that is, the range of the species is determined by the environment, and, that when the latter changes, the species is altered or dies out.

The obvious differences in the relative ages of certain forms and groups of forms in the genus *Lampropeltis*, as shown by specialization, structural isolation and diversification, geographic position, etc., leads naturally to speculation as to the time relations of their spread from the Southwest. Since *triangulum* is typically developed only north of the southern limit of glaciers, we may assign it to a post-Pleistocene migration. The range of *syspila* and the northern portion of the range of *gentilis* were doubtless likewise largely uninhabitable during the glacial epoch, and this together with the perfect intergradation between these forms indicates that they belong to the same "wave" of dispersal. The high specialization of *elapsoides* and its distinctness from its nearest relative argues for isolation, and greater age than that of *triangulum* and *syspila*. These demands are satisfied by assuming it to have reached the Southeast at some favorable time during or before the ice age, and to have been isolated by an embayment of the lower Mississippi Valley during the Pleistocene (see map in Willis and Salisbury, 1910, 277). The high degree of specialization and structural isolation of *pyrrhomelaena* suggests that it is as old as any form in the genus. As it certainly has no relatives outside of the Southwest, it may be regarded as indigenous to this region, and its structural isolation is doubtless due to an early differentiation from the primitive stock. In the **CALLIGASTER** group the apparently sharp separation and the specialization of its eastern representative, make natural an assignment to a period similar to that when *elapsoides* reached the Southeast. Consequent separation during a greater or less portion of the Glacial Epoch induced divergent differentiation. The **GETULUS** group may be considered nearly or quite as recent as the varieties of *triangulum*, with, perhaps, greater age indicated for the western representatives

to allow them to reach Cape San Lucas and Santa Catalina Island. The Central American forms are less easy to account for. *Nelsoni* assumed its specific identity before the Tres Marias Islands were separated from the mainland. This is likely to have been pre-Pleistocene. *Polyzona* shows too great variability to be easily regarded as an ancient type, but it is old enough to have produced the well-marked *micropholis* in Colombia and Ecuador, and is therefore without doubt older than the northern varieties of *triangulum*.

The preceding paragraph may be summarized as follows: The genus *Lampropeltis* underwent a differentiation in the southwestern portion of the North American continent in the late Tertiary, producing a type that favored the mountains and uplands, the ancestor of the **TRIANGULUM** group, and another type that favored the lowlands, ancestor of the **GETULUS** and **CALLIGASTER** groups. The latter early differentiated into the progenitors of the two last groups, and of these it was the **CALLIGASTER** section that first spread northeast and east. This must have occurred previous to the Pleistocene, and at about the same time that the migration took place which brought the progenitor of *elapsoides* to the southeast. During the Pleistocene, the latter and the ancestral type of *rhombomaculata* suffered an isolation from their direct relatives west of the present position of the Mississippi River and were thus free to undergo considerable differentiation. Following the Pleistocene, *elapsoides* extended its range south into Florida, there undergoing still further specialization during the Recent Epoch, and west to Louisiana, here meeting the form *amaura*, the post-Pleistocene representative of its ancestral stock. If *rhombomaculata* extended its range into southern Florida, it is yet to be found there. *Calligaster*, after the retreat of the glaciers, was able to extend its range throughout the prairie region northeastward, and north to the limit of its endurance of cold. The western section of the **GETULUS** group may have begun its evolution during or perhaps preceding the Pleistocene, but it was only following that period that the spread east and northeast occurred. And it was following the Ice Age, also, that the latest forms of the **TRIANGULUM** group reached their present ranges (*amaura*, *syspila*, *triangulum*, and at least the northern section of *gentilis*).

This historical outline corresponds with the present distribution and structural relations of the king snakes, and with probable Pleistocene geography. The genus as a whole seems to be relatively recent, but the question of its origin is beyond the limits of the present study. In this connection, however, we may say that there are apparently no nearly related genera in South America, in the West Indies, nor in Asia, and that it is entirely likely that its nearest relatives are to be found in the genus *Coronella* of Europe and northern Africa.