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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 49

STUDIES OF NEOTROPICAL
COLUBRINAE

VIII. A REVISION OF THE GENUS
DRYADOPHIS STUART, 1939

BY
L. C. STUART

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS
MARCH 19, 1941

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FREDERICK M. GAIGE
Director of the Museum of Zoology

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STUDIES OF NEOTROPICAL COLUBRINAE. VIII. A REVISION OF THE GENUS *DRYADOPHIS* STUART, 1939*

INTRODUCTION

FOR the past ten years I have been engaged in an investigation of the neotropical ophidian genus *Drymobius* Fitzinger, 1843, as defined by Boulenger (1894: 8). Within that period several papers have appeared in which various phases of the problem were discussed (Stuart, 1932; 1933*a*; 1933*b*; 1938; and 1939). Of these, the first, second, fourth, and fifth are of the most importance to the problem at hand. In the first, Boulenger's *Drymobius* complex was broken down into 4 separate genera: *Drymobius*, *Eudryas* (= *Dryadophis*), and *Dendrophidion*, all of Fitzinger, 1843, and *Drymoluber* Amaral, 1929. In the second, new species of *Eudryas* were described, and a check list of the *boddaerti* complex was presented. In the fourth, another form of *Eudryas* was named, and in the last, *Dryadophis* replaced the preoccupied name *Eudryas*.

Since the publication of the first and second papers, new and additional material has been available, so that, although in the main the conclusions presented still hold, many minor changes must be made. It is the purpose of this paper, therefore, to present my now completed investigations on the genus *Dryadophis*.

A word should be said concerning the organization of the paper. To the "catalogue" type of mind the presentation of the various points may appear to be entirely wanting in organization. Such phases as pattern and scutellation evolution and the laws of variation are presented before the material upon which the principles are based is described. This has been done to facilitate description and in order that remarks on the origin and affinities of each group might conclude my discussion of each group of forms. If the reader finds it difficult to accept certain statements which are based upon a description not yet given, he should refer to the specific description in order to satisfy himself that I am correct.

It should be clearly stated that I have no illusions as to the permanency of my conclusions. To revise so large and so widespread a group on the basis of the few available specimens makes it impossible to achieve even an approach to completeness. In some instances only 2 or 3 specimens of a form have been examined, and, therefore, any attempt to fit them into the whole scheme of the genus must be based not only on the scientific data which they present but also, to some extent, on that intuitive feeling vernacularly known as "hunch." Most systematists are familiar with those

* Part of a dissertation submitted in partial fulfillment of the requirements for the degree of doctor of philosophy in the University of Michigan.

occasional instances in which 2 forms, though alike in all measurable characters, show very few resemblances when viewed as a whole. Thus, those who are thoroughly familiar with *Thamnophis butleri*, for instance, find no difficulty in separating that form at a glance from *Thamnophis s. sirtalis*. Others, to whom the former is something of a rarity, however, could accomplish the same end only through a detailed examination. In the situation at hand, *bruesi* has been placed in the *pleei* group rather than in the *boddaerti* group, in spite of the fact that, on the basis of measurable characters, the form might fit equally well into either group. Yet, when *bruesi* is seen in its entirety, it simply "looks like" a *pleei* rather than like a *boddaerti* relative. There is a certain angularity and delicateness in the forms of the *pleei* group which the *boddaerti* forms do not have. Though such a practice is not to be condoned in general systematic procedure, I am of the opinion that in certain instances, such as those cited above, an investigator's "feeling for" laboriously accumulated data, should not be criticized too seriously when, in the absence of measurable characters, it is utilized in an attempt to further our knowledge.

ACKNOWLEDGMENTS

A host of friends and colleagues have, during the past 8 years, given their time, attention, and aid to me, and I take this opportunity to acknowledge help and to thank them for their many kindnesses. I am indebted primarily to Dr. A. G. Ruthven, of the University of Michigan. It was he who first suggested the problem and directed it through its many painful stages of development. Mrs. Helen T. Gaige, of the Museum of Zoology, University of Michigan, has been a source of constant aid and encouragement throughout my studies, and I sincerely appreciate her interest and advice. To others of my colleagues at the University of Michigan, Dr. N. E. Hartweg, Dr. C. L. Hubbs, Dr. L. R. Dice, Dr. P. E. James, Dr. Joseph Bailey, and Mr. James Oliver, I wish to extend my sincere thanks for their patience in considering my problems and in aiding in their solution.

For the loan and description of materials and many other courtesies, I am indebted to Dr. Thomas Barbour, Mr. Arthur Loveridge, and Mr. Benjamin Shreve, of the Museum of Comparative Zoology, Harvard University; Dr. G. K. Noble, of the American Museum of Natural History; Dr. Doris M. Cochran and Dr. Leonhard Stejneger, of the United States National Museum; Mr. M. Graham Netting, of the Carnegie Museum; Mr. K. P. Schmidt, of the Field Museum of Natural History; Mr. J. R. Slevin, of the California Academy of Sciences; the authorities of the Academy of Natural Sciences of Philadelphia; Dr. Edward H. Taylor, of the University of Kansas; Mr. H. W. Parker and Mr. J. C. Battersby, of the British Museum (Natural History); Dr. Afranio do Amaral, of the Instituto Butantán; and Brother Nicéforo Maria, of the Instituto La Salle. I wish finally to thank my friend

Dr. E. R. Dunn, of Haverford College, for his advice, interest, and constructive criticisms.

For stenographic aid I take this opportunity to acknowledge the help of Miss Geneva Smithe and Miss Helen Johnson, and for the care and effort expended on the drawings I am greatly indebted to Miss Grace Eager, of the Museum of Zoology.

MATERIALS AND METHODS

The revision in this paper is based upon an examination of approximately 650 specimens,¹ the distribution of which, according to the several forms, is set forth in Table I.

TABLE I

Form	Number of Specimens
<i>bifossatus</i>	59
<i>triseriatus</i>	9
<i>striatus</i>	5
Intergrades	61
<i>boddaerti</i>	163
<i>ruthveni</i>	30
<i>dunni</i>	2
<i>heathii</i>	3
Intergrades	33
<i>pleei</i>	38
<i>amarali</i>	7
<i>bruesi</i>	31
<i>alternatus</i>	83
<i>laevis</i>	12
<i>dorsalis</i>	16
<i>melanolomus</i>	14
<i>veracruzis</i>	19
<i>slevini</i>	19
Intergrades	21
<i>pulchriccps</i>	13

Although such forms as *alternatus*, *boddaerti*, and *bifossatus* are well represented in collections, some, like *dunni* and *heathii*, are known from only a few specimens. It is unfortunate that material in the European museums could not be examined, as in many instances it would fill important gaps. But, despite this poor representation of some forms, I have been able to see at least 2 specimens of each species. Of the type specimens I have seen but few, yet this has not been a serious drawback. In most instances the type descriptions have proven adequate, and these have often been supplemented with further notes and photographs furnished by those in charge of the various collections.

¹ Of these 97 are in the British Museum (Natural History) and have not been handled. Mr. Battersby of that institution has, however, supplied me with such excellent descriptions of each specimen that it is possible to include them with those which I have seen personally.

The institutions which have made their material available to me are: the Museum of Zoology, University of Michigan (U.M.M.Z.); the Museum of Comparative Zoology, Harvard University (M.C.Z.); the American Museum of Natural History (A.M.N.H.); the United States National Museum (U.S.N.M.); the Field Museum of Natural History (F.M.N.H.); the California Academy of Science (C.A.S.); the Carnegie Museum (C.M.); the British Museum (Natural History) (B.M.); Instituto Butantán (I.B.); Instituto La Salle (I.L.); and the personal collection of Dr. E. H. Taylor, of the University of Kansas (E.H.T.).

No new methods have been developed in this study, and no new characters of taxonomic significance have been utilized. Statistical methods have been applied in some instances only, for my satisfaction, and these are not presented in this paper. Inasmuch as a statistical analysis of many of the forms is impossible, it would be useless to present coefficients of variation, standard deviations, standard errors, and the like, for the few forms for which I have worked out these various functions.

The descriptions of the various forms may appear inadequate to many of the more systematically-minded herpetologists in that they lack completeness with reference to such items as size and shape of head scales. I have long felt that the continual repetition of generic characters is unwarranted. For this reason many features are described only in the generic diagnosis, and variations in those characters are also discussed only in that diagnosis, whereas the specific descriptions are limited to the diagnostic characters of pattern and ventral scutellation.

Certain other features relevant to the specific descriptions should be mentioned. Although I have at hand synonymies of each form which I consider more than 95 per cent complete, they have not been included in this paper, because, in many instances, particularly in the work of Europeans, I have not had access to the specimens mentioned or described and, therefore, cannot be certain as to what species are represented. For example, it is impossible to say whether Boettger (1895: 45), in mentioning several specimens of "*Drymobius boddaerti*" from Tobago, was referring to *amarali* or to *dunni*. References to Venezuelan *boddaerti* may be based upon *amarali*, *pleei*, or *ruthveni-boddaerti* intergrades. Sometimes certain species have been allocated to genera to which they do not belong. Atkinson, for example (1907: 156), refers to *Drymobius caeruleus* in Guatemala and gives ventral counts of the same, erroneously allocating to "*Drymobius*" a species of another genus. In the face of such confusion it seems best to omit all but original descriptions in the synonymies, for in the majority of instances it is difficult to say what form is being considered.

I have listed only those specimens which I have examined, and these alone have been included on the maps. Unfortunately, the scale of the maps

used has been so small that some few localities have had to be omitted. The reason for having plotted only specimens examined is made obvious in the foregoing paragraph. In the outer limits of the ranges, however, some reliable records have been taken into account. In plotting these limits I have also drawn upon physiographic, climatic, and vegetational maps.

The procedure followed here, in instances of composite descriptions involving several species, should perhaps be explained. I believe that the best extant description of any form is the one which causes the least confusion and that it should, therefore, be used if possible. In *Drymobius rappii* Günther, 2—possibly 3—species are involved (Günther was describing the juvenile pattern of *ruthveni-boddaerti* intergrades and possibly of some typical *boddaerti* and *pleei*). I believe that a fair description of *pleei* exists. Thus, although some of the cotypes of *rappii* could be selected as representative of this form, the *ruthveni-boddaerti* intergrades are also representative, and there is a good description of *ruthveni*. I have, therefore, chosen to bury *rappii* in the synonymy of *boddaerti* and to utilize the later, but more certain, name, *ruthveni*. Similarly, in *Dromicus pleii* Duméril and Bibron, several forms are included in the description, but, since they were all described at a later date, the name *pleii* had to be allocated to one.

The pattern drawings are all the work of Miss Grace Eager, staff artist of the Museum of Zoology. Each drawing was made not from one specimen but from several specimens. Age, state of preservation, and other factors produce considerable variation in such features as intensity of color and minor scale markings. For this reason Miss Eager was directed to portray the primary pattern of one specimen, but to intensify or lighten the markings of that specimen so that a mean of all the specimens might be the result. The drawings are, therefore, not schematic in any sense, but are an actual portrayal of a single specimen so shaded as to represent a more average condition.

DRYADOPHIS STUART, 1939

Eudryas, Fitzinger, *Systema Reptilium*, 1843: 26 (type *boddaerti* Sentzen, 1796).

Dryadophis, Stuart, *Copeia*, 1939: 55 (new name for *Eudryas* Fitzinger preoccupied by *Eudryas* Boisduval, 1836).

The synonymic history of *Dryadophis* offers few complications. Named *Eudryas* by Fitzinger in 1843, with *Coluber boddaerti* Sentzen designated as the type, it had received no other name until Brongersma (1937: 4-5) pointed out that the name was preoccupied by the lepidopteran genus *Eudryas* Boisduval (1836), and hence the new name *Dryadophis* was proposed by me (1939: 55). Since Fitzinger's work, the genus has been recognized as an entity but once, and even then only in subgeneric rank (Duméril and Bocourt, 1870-1909). It is true that species in this genus have been allocated to other genera by various workers and that in the older studies

several different species have been frequently placed in different genera. The species have often been allocated to *Herpetodryas*, *Coryphodon*, *Ptyas*, *Alsophis*, and *Dromicus*.

DESCRIPTION.—Head scutellation normal. The upper surface with 2 internasals which are shorter than the following 2 prefrontals; a single frontal and 2 supraoculars lying behind the prefrontals and followed by a pair of parietals. The snout is rounded, with a normal rostral which is visible from above. Laterally, there are 2 nasals (between which the nostril is located), a loreal, 1 preocular (occasionally 2 on but 1 side), 2 postoculars, and a varying number of temporals (typically probably 2 + 2). There are 8 or 9, and atypically 10, supralabials and 9, 10, or 11 infralabials. Of the infralabials, 1 pair is in contact behind the mental plate, and 5 pairs are in contact with the anterior pair of chin shields, which are shorter than the posterior ones. The majority of the cephalic plates, while specifically constant, are variable in size and proportions throughout the genus.

The dorsal scales are smooth, with 2 apical pits, in 17 or 15 longitudinal series anteriorly and 15 just in front of the anus. Abdominal² scutes, 159–206; subcaudals, 79–136; total ventrals, 238–332. Anal divided, tail comprising between one-fourth and one-third of the total length. Maximum size, about 2 meters.

The maxillary teeth are 18–26 in number, are subequal or slightly enlarged posteriorly, and may or may not have a diastema in front of the last 2 or 3. The mandibular teeth are subequal.

The hemipenis is not capitate, the sulcus is single, and the organ may be slightly bilobed. The proximal one-fourth is bare. On the next one-fourth are long, slender spines, arranged in about 11 rows around the organ and graded little by little into the calyces which cover the distal half of the penis. The calyces are arranged in 15–20 rows around the structure and often form a compact mass along the sulcus.

The pattern is variable. The majority of the juveniles are banded; the adults may be banded, striped, or unicolor.

RANGE.—Generally distributed throughout the neotropical region from Mexico south to the Argentine Republic.

HABITS AND HABITATS.—So little is known of the habits and habitats of the forms of this genus that any discussion of them is rendered impossible. In some instances the localities from which specimens have been derived have been suggestive of the general habitats which a form inhabits. For example, from a comparison of climatic records and vegetational types at various localities it appears that *pleei* prefers arid habitats, whereas *ruth-*

² The terms "abdominals," "subcaudals," and "total ventrals" refer to the gastrosteges, urosteges, and gastrosteges with urosteges, respectively. Means are given throughout in parentheses.

veni and *ruthveni-boddaerti* intergrades in the same general region seem to concentrate in the more humid areas. Beyond occasional conclusions based on such flimsy data, I am unable to make any statements as to habitat preference of the various forms.

VARIATION WITHIN THE GENUS

Although there is so much interspecific variation as to render a generic description difficult, intraspecific variation is not great. Variation within the species is included in the discussion of each species, so that only the broader phases of variation need to be considered here.

CEPHALIC SCUTELLATION (Pl. I, Figs. 1-4).—The rostral plate is always broader than high in all forms except those of the *bifossatus* group, in which forms the reverse is true. Considerable variation in the degree of widening or heightening exists in the various species, but it seems to have no taxonomic significance. The internasals and prefrontals do not vary either in proportions or shape, although the prefrontals are always longer than the internasals. The frontal is longer than its distance from the end of the snout in all but the *bifossatus* group, and the supraoculars are of about the same length as the frontal. The parietals vary little and are at least as long as, and generally longer than, the frontal.

Laterally, the nasals do not vary, but in the *bifossatus* group the loreal, which is generally about twice as long as it is high and which is rectangular in the *boddaerti*-like groups, is as high as, or higher than, it is long and has a trapezoid shape. The preoculars number 1 on each side except in 2 specimens of *slevini*, of which 1 has a small subocular on one side only and the other a subocular on both sides. The postoculars on each side are likewise remarkably constant in numbering 2, but an occasional specimen has 3. The upper postocular is always 2 to 3 times as large as the lower postocular. The temporals are the most variable set of scales in the genus. The task of plotting the numerous variations would be extremely difficult, and, moreover, these variations apparently have no taxonomic significance. However, the formula 2 + 2, which I believe to be typical, is found most frequently in the *bifossatus* group.

The supralabials number 8, 9, or 10, but are typically 9 in the *boddaerti*-like forms and 8 in the *bifossatus* group and in *pulchriceps*. In the former, labials 4, 5, and 6 enter the orbit (4 just touching it), whereas only 4 and 5 enter the orbit in the latter. It is difficult to determine, from the position of the labial plates, whether a plate has been added to produce 9 or has been lost to produce 8. I am unable to explain just how this loss or addition is accomplished, but the change takes place around the plate just anterior to the orbit (at the third in the forms with 8 labials and at the fourth in the others). In some instances forms of the *bifossatus* group have 9 supra-

labials, and species which normally have 9 may possess 10. A small scale beyond the last typical scale comprises every such addition to the typical number of supralabials. Occasionally, one of the *boddaerti*-like species has specimens with but 8 supralabials—a reduction which results from the dropping of a scute or from the fusion of 2 scutes anterior to the orbit. The infralabials are extremely variable in all forms and, like the temporals, almost defy description. The typical number is 9 in all those species which have 8 supralabials and 10 in those which have 9 supralabials. They vary indiscriminately, however, from 9 to 11. There is no significant variation in the chin shields.

In the variation in head scutes, a definite law seems to be apparent. Ruthven (1908: 31) has shown that the loss of supralabials may take place either in front of or posterior to the orbit and that such losses result in a shortening of the head toward the eye. Inasmuch as loss of labials in *Dryadophis* is always anterior to the orbit, the head is always shortened from snout to orbit. The shortening of the head is reflected in other characters as well. For instance, the loreal is so compressed as to become at least as high as it is long in the *bifossatus* group, which has but 8 supralabials. Similarly, the shortening of the snout in this same group is evident in that the frontal is always at least as long as it is distant from the end of the snout, whereas in other forms with 9 supralabials the distance between the frontal and the end of the snout exceeds the length of the frontal. Although this rule holds in *pulchriceps* with reference to the shape of the loreal, it does not apply to the frontal character. It is unfortunate that I have not had access to skulls of these various species in order to take exact measurements to test the validity of the law of shortening of the head.

DORSAL SCUTELLATION.—There is almost no variation in dorsal scutellation. There are only 2 dorsal scale formulae in the genus. The one, found in the *bifossatus* group only, consists of 15 rows of dorsal scutes from neck to anus. Reduction in this group does not take place anteriorly to the tail. In all other species, however, the scale formula is 17–15. The reduction from 17 to 15 rows of scales is brought about by loss of the fourth row of scales on either side in the immediate vicinity of the pyloric valve, as described by Proctor (1920: 361–63). Occasionally, the reduction is the result of the loss of the third or fifth row of scales on either side. The point at which reduction takes place may be computed mathematically by dividing the number of abdominal scutes into the number of the scute at which reduction occurs. The position so computed varies from .52 to .66. Although superficially some specific correlation seems to be apparent, my data are too few to test the results statistically and are hardly worth presenting at this time.

VENTRAL SCUTELLATION.—In the ventral scutellation sexual dimorphism,

genetically lethal characters (see p. 18), and the normally great variability of this character combine to make it the most unstable feature of the genus. Interspecific variability in *Dryadophis* is such that the number of ventral scutes becomes a taxonomic character of considerable importance. As already noted, the abdominals vary from 159 to 206, the subcaudals from 79 to 136, and the total ventrals from 238 to 332—variations of 47, 57, and 94, respectively. According to Ortenburger (1928) the closely related genera *Masticophis* and *Coluber* vary in abdominals from 31 to 35, respectively, and in subcaudals from 66 to 54. No counts on total ventrals are given. Although *Dryadophis* exceeds these 2 genera in abdominal scutellation, it compares very favorably in subcaudal scutellation. In other words, variation in the genus is not excessive. It is, in fact, considerably less than that in the wholly unrelated genus *Lampropeltis*, in which the abdominals and subcaudals vary to the extent of 102 and 52, respectively (*vide* Blanchard, 1921).

The discussion of interspecific variation is rendered difficult by the possibility of confusing the influence of the number of available specimens of each form with the influence of the size of range of the forms. With an increasingly greater number of specimens, an increase in variation is the normal expectancy. But greater variability would also be expected in those forms which have the greater range. In *boddaerti*, for example, it is impossible to determine whether the great variation is caused by the extensive range, or whether the greater number of specimens which have been available makes its variation appear larger than that of some other form actually similar in this respect but imperfectly known. From comparable material, however, it appears likely that the greater the range of a species is, the greater is its variability. The variation in total ventrals (Table II) bears out this statement.

TABLE II

Form	Specimens	Variation in Total Ventrals
<i>ruthveni</i>	30	20
<i>bruesi</i>	31	25
<i>pleei</i>	38	32
<i>alternatus</i>	83	35
<i>boddaerti</i>	162	71

Each of the first 2 forms in Table II, *ruthveni* and *bruesi*, has only a limited range: *pleei* and *alternatus* are more extensively distributed; and *boddaerti* is the most widespread form in the genus. The variation of *pleei* and that of *alternatus*, despite the discrepancy in number of specimens, is about the same. It may be inferred from this that, within limits, variability is dependent more upon the size of the range of a species than upon the number of specimens available, but further data must be obtained before the validity of this conclusion can be completely tested.

With respect to ventral scutes, the interpretation of intraspecific variation is further complicated by the fact that some species show considerable sexual dimorphism (see Fig. 2) and others show but little. Still further complications lie in the extent of the range of each form. Incipient speciation is evident within wide-ranging forms, such as *boddaerti* or *alternatus*, and this has a considerable effect upon the variability of a single species. Other features, such as the peripheral reduction in ventral scutes (see p. 32) and the complexity of physical features throughout the range of a form, render the discussion of intraspecific variation even more difficult. As a result, any general laws based on the scanty material at hand would be so poorly supported that they are not worthy of statement. Discussion of this variation is, therefore, deferred and is given with each individual form.

One rather significant feature should, however, be indicated. In the process of studying the variation in *boddaerti* I noted that certain juvenile specimens increased variation greatly and thus produced means which did not appear when adults alone were considered. In the course of plotting the number of total ventral scutes with relation to the length of the specimens (as an indication of age), it was discovered that at 1 locality a few juvenile specimens made up the lower 35 per cent of the entire range of variation. Thus, plotting the total ventral scutes against the length of the snake for a series of *boddaerti* from the vicinity of Medellín, Colombia, gives the result portrayed in Figure 1. This indicates that some juveniles with very few ventral scutes never reach maturity (whether because of the direct lethal effect of this deficiency or because of the importance of the small number of ventral scutes as a survival character in conjunction with some other character, such as speed) and may, therefore, be excluded from discussions of variation, since their own characters are never passed on. This feature is noticeable in *boddaerti*, but not in *alternatus*. Therefore, in the consideration of intraspecific variation, if the atypical condition of some juveniles would detract from the correctness of the conclusions with regard to inherited variation, the data on juveniles are excluded. Variation in scutellation between the sexes is discussed in conjunction with sexual dimorphism.

The conclusions with reference to variation in scutellation in the genus which seem most important are as follows: (1) Variation in cephalic scutellation is not great. Variation in the number of labials, in the shape of the loreal, and in the length of the frontal is of taxonomic significance and is correlated with the length of the snout. (2) Variation in dorsal scutellation results in 2 scale formulae, 15 and 17-15. This is of taxonomic importance and intraspecifically is very stable. (3) The variation in ventral scutellation is not excessive in comparison with that of closely related genera. Interspecific variation shows some correlation with range, in direct proportion. Intraspecific variation is generally correlated with incipient speciation and in some instances with age.

TAIL LENGTH.—The variation in tail length (tail length to total length) ranges from .20 to .36 in adults, and it is about the same in juveniles. This variability is expressed primarily as sexual dimorphism (see p. 24). Inter-specific variation is slight, and, perhaps because the material is rather scanty, no evolutionary or geographic trends in this respect are evident.

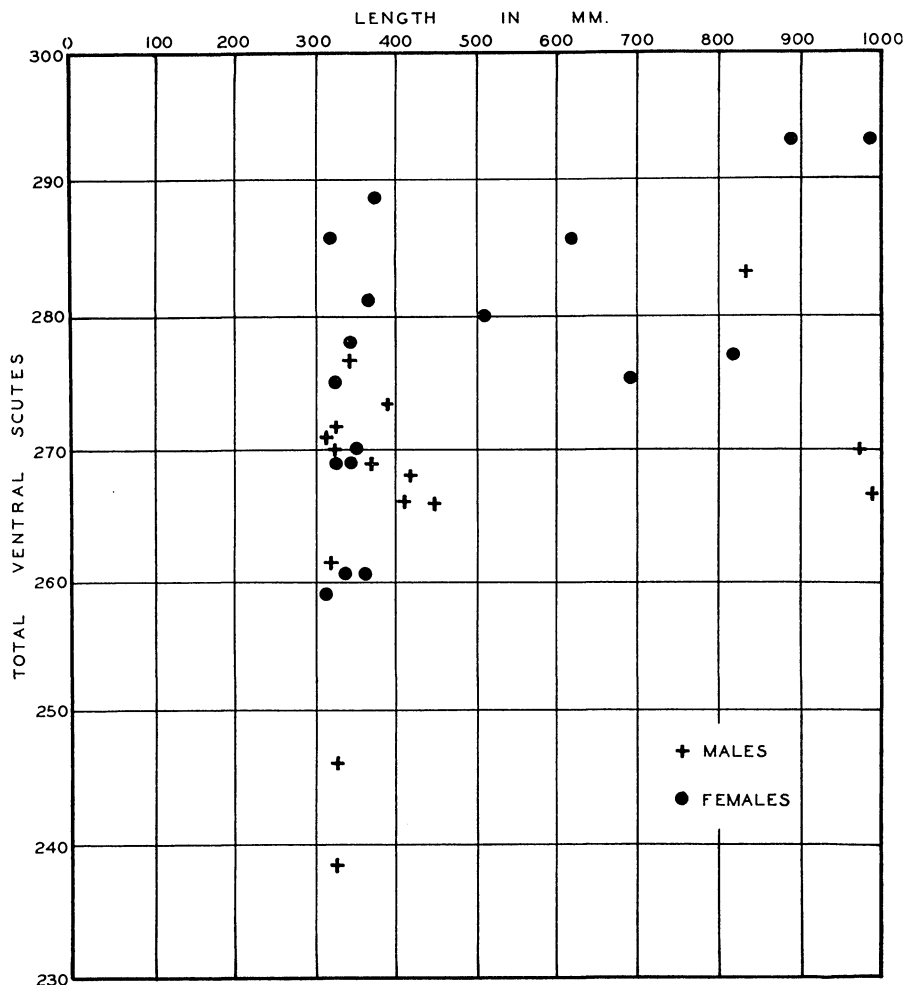


FIG. 1. Supposed lethal character of a reduced number of total ventral scutes. No adult individuals, male or female, have so few total ventrals as some juveniles have. This population was all from the vicinity of Medellín, Colombia.

In Table III are listed some of the species of 3 groups in evolutionary sequence, with the range and the means of tail lengths in the males.

It will be noted that variation follows no trends; it is "hit or miss"

TABLE III

<i>boddaerti</i>	<i>melanolomus</i>	<i>pleei</i>
<i>ruthveni</i>	<i>alternatus</i>	<i>pleei</i>
.258-.302 (.288)	.267-.329 (.290)	.201-.295 (.255)
<i>boddaerti</i>	<i>melanolomus</i>	<i>bruesi</i>
.243-.300 (.276)	.309-.356 (.326)	.288-.308 (.298)
	<i>veraccrucis</i>	
	.299-.336 (.315)	

throughout. Generally speaking, there is a direct correlation between the number of subcaudals and the tail length. This is not true in all instances, however, since in some species the number of abdominals is greater in forms in which the number of subcaudal scutes also is greater. When adults and juveniles are compared it is found that they coincide very closely as to length of tail.

TEETH.—Variation in teeth is not great, either generically, interspecifically, or intraspecifically. In all species of the *boddaerti*-like groups, except *bruesi*, the average number of maxillary teeth is about 20, whereas in the *bifossatus* group it is 24. In *bruesi* the number of maxillary teeth averages 23. Unless this is the retention of a "primitive" character, I can offer no explanation for this condition.

PATTERN.—It is difficult to discuss pattern without making a few observations as to evolutionary trends. Since these are fully discussed elsewhere in this paper (p. 32), the following discussion is limited to description. There are in the genus 2 general dorsal pattern types. The one, a striped pattern (which fades until it becomes unicolor in 2 end forms), is characteristic of all adults except those of the *bifossatus* group and of *pulchriceps*. A complete description of the adult pattern is given in the description of each species. The second is the "banded" pattern of all juveniles and of the adults of members of the *bifossatus* group and of *pulchriceps*.³

The banded pattern, as I have chosen to call it, though the name is misleading, may be 1 of 2 types. The first type consists of a series of broad dark bands extending from ventral to ventral across the back, and separated by narrow white bands of the same width (Pl. I, Fig. 6). These vary in number from 54 to 65 (59), but my data are too few to indicate whether or not there is any interspecific variation of taxonomic significance. Although less marked than in the second banded type, as will be seen, there is a tendency for the length of both black and white bands to decrease posteriorly, as is indicated in Table IV (lengths in terms of scales).

The pattern on the tail is the same as that immediately in front of the

³ Inasmuch as there is no difference between the juveniles and adults of members of the *bifossatus* group and *pulchriceps*, they will not be considered in the following discussion. For a full treatment of these see the species descriptions.

TABLE IV

Position	Black	White
Neck	3.0-3.5 (3.3)	0.75-1.0 (0.85)
Mid-body	2.5 (2.5)	0.5 (0.5)
Preanal	2.0-3.0 (2.4)	0.5 (0.5)

anus. In some instances the pattern on the tail is irregular and broken up. This type is limited to the juveniles of *dorsalis*, *melanolomus*, and *verae-crucis*. In the last-named species there is a perplexing variation, an occasional specimen showing evidences of a lateral light stripe. A discussion of the significance of this feature is to be found in the specific description. Although all forms of the *bifossatus* group, in both the adult and the juvenile stages, possess this type of pattern (Pl. II, Figs. 4-6), *triseriatus* and *bifossatus* show a lateral constriction of the dark bands, which in *triseriatus* is carried to the extent of producing a pattern of dorsal blotches opposite to and separated from a lateral series.

The second type of banded pattern is actually not banded at all; it consists of a series of black lateral blotches that extend from the ventrals to the fourth row of scales and are separated from each other by a narrow white band of the same vertical extent (Pl. I, Fig. 5). Alternating with the lateral blotches are similar dorsal blotches which extend from scale row 5 on one side to scale row 5 on the other side. Occasionally, especially on the anterior part and in juveniles just beginning to mature, these 2 series of blotches become separated through the appearance of a light line on scale rows 4 and 5. The blotches on the body vary in number from 40 to 75 and show some specific correlation, as is indicated in Table V.

TABLE V

Form	Blotches on Body
<i>boddaerti</i> (11)	49-74 (61)
<i>alternatus</i> (9)	42-54 (47)

It is unfortunate that there has not been sufficient material available so that this variation could be worked out in other forms. Conceivably, the number of bands in the juveniles might be not only of considerable taxonomic importance but also of phylogenetic significance.

There is apparently no correlation between the number of blotches and the number of abdominal scutes, as indicated in Table VI showing the condition in five males of *boddaerti* from Bolivia.

TABLE VI

Abdominal Scutes	Dorsal Blotches
175	58
179	55
181	60
184	49
185	55

As in the other banded pattern, the blotches, both black and white, shorten posteriorly (Table VII).

TABLE VII

Position	Black	White
Neck	2.0-3.5 (2.7)	0.8-2.5 (1.6)
Mid-body	2.0-3.0 (2.5)	1.0-2.0 (1.2)
Preanal	1.5-3.5 (2.4)	0.5-1.0 (0.7)

On the tail the alternating blotches tend to become opposite to produce the true banded condition. This pattern exists in the adults of *pulchriceps*, in the juveniles of members of the *boddaerti* and *pleei* groups (so far as they are known), and in *alternatus* and *slevini* in the *alternatus* group. Table VIII is a summary of the distribution of the 2 banded types of pattern in the genus.

TABLE VIII

Pattern Type	Adults	Juveniles
Continuous crossbands	<i>bifossatus</i> <i>triseriatus</i> <i>striatus</i>	<i>bifossatus</i> <i>triseriatus</i> <i>striatus</i> <i>dorsalis</i> <i>melanolomus</i> <i>veraecrucis</i>
Alternating pattern	<i>pulchriceps</i>	<i>pulchriceps</i> <i>boddaerti</i> <i>ruthveni</i> <i>alternatus</i> <i>slevini</i> <i>pleei</i> <i>amarali</i> <i>?bruesi</i> <i>?dunni</i> <i>?heathii</i>

At present there is no way in which the juveniles may be identified except in the general groups noted above.

As the juvenile pattern breaks down to produce the adult pattern, the half-grown specimens assume numerous patterns, which causes much confusion. As a rule, the juvenile pattern gradually fades, and the adult pattern slowly becomes evident, yet neither dominates the other. At this stage the specimen is marked here and there with irregular, vertical black streaks and faint white flecks, through which the adult pattern is evident but not conspicuous. The breaking up of the juvenile pattern begins on the tail and progresses forward, and even when the adult pattern is fully evident, traces of the juvenile pattern often persist on the neck.

The adult patterns, which are reported in detail under each specific description, may, like the juvenile pattern, be classified into several groups. The first forms to be considered are those which have a banded adult pattern. These have been noted briefly and are discussed in detail under the

specific descriptions. In general, the variations in this pattern resolve themselves into groups according to the degree to which the bands break up to produce a spotted pattern. To go further into this matter at this point would merely be to repeat. Only those species in which the adults are striped or unicolor are considered here.

Two types of striped patterns exist in this genus. These 2 types are based not upon the number of lateral stripes, which basis would result in an unnatural classification (because the single-striped pattern has arisen independently in all 3 of the *boddaerti*-like groups), but upon the position of the lateral stripes. The 2 types consist, first, of those forms in which the upper lateral stripe involves the third, fourth, and fifth scale rows anteriorly (Pl. III, Fig. 3), and second, of those in which only the fourth and fifth scale rows are involved (Pl. III, Fig. 5).

Two groups, *melanolomus* and *boddaerti*, possess the latter type of pattern. The stem form of both these groups has, in addition to this upper stripe, another on scale rows 1 and 2, as is described farther on. Inasmuch as there is no variability in this lower stripe, it need not be considered here. It should be noted, however, that in more specialized forms this lower stripe is lacking, and that in some end forms even the upper stripe disappears and a unicolor condition is thereby produced.

As is pointed out elsewhere in this paper, the *melanolomus* and *boddaerti* groups are very closely related. The basis of my argument for this relationship is primarily the position of the upper lateral stripe. On the anterior part of typical specimens it apparently covers the upper half of scale row 4 and the lower half of row 5. In many instances of minor variation, however, either more or less of these 2 scale rows may carry the stripe. Variations in this feature show no correlations, in either geographical, sexual, or any other relation. The extent of this stripe along the length of the body is also subject to considerable variation. Much of this apparent variation may be caused by the relative states of preservation, for, in those specimens which have been obviously well preserved in alcohol, it is visible almost to the vent. Similarly, there is variability in the intensity of the narrow black border which is often present. In *alternatus* the presence or absence of this border shows geographic correlation, which will be noted later, but in *ruthveni* and *boddaerti* there is every indication that the state of preservation accounts for much of the variability in this character.

Variation in the position of the stripe in this pattern type is negligible. Ruthven (1908: 36-37) showed that although in some species of *Thamnophis* the lateral stripe was associated with the dorsal scales, in the majority it was not. In other words, in but 1 species (*radix*) did he find that when a scale row containing a stripe was dropped the stripe became narrower. He showed that in the other forms the stripe either moved upward or descended

1 row of scales, and thus retained its original width. In all species in which the stripe is restricted to the fourth and fifth scale rows (the *melanolomus* and *boddaerti* groups—except *heathii*), the lateral stripe continues on the original fifth scale row when the fourth is lost, thus causing a narrowing of the stripe.

The second striped pattern is found only in the forms of the *pleei* group. In this group the upper lateral stripe is on scale rows 3, 4, and 5, except in the end form *bruesi*, in which it is restricted to rows 4 and 5 (this problem is discussed farther on). In both *pleei* and *amarali* no variation in the position is found, but in *pleei* alone the stripe extends to the vent. This type of lateral stripe is quite different from that already discussed, in that when the fourth scale row is dropped the lateral stripe ascends to cover the original scale rows 3, 5, and 6. This general situation is paralleled in *heathii*. Here the stripe occurs on scale rows 4, 5, and 6 anteriorly, and when 4 is dropped the stripe moves down to occupy original scale rows 3, 5, and 6.

Variations in the lower lateral stripe (on scale rows 1 and 2) beyond the narrow black borders, which in some instances at least are caused by differences in the state of preservation, are slight. This lower stripe is rarely persistent beyond the middle of the body, except in *pleei*. Other variations in pattern, such as the 3 anterior dorsal stripes in *pleei*, are discussed under the specific descriptions, and the significance of the above-noted variations will be discussed presently.

Variations in other features of the pattern are extensive, but frequently result from differences in the state of preservation, from the persistence of juvenile markings in the adults, and from similar causes. On the basis of the scanty material at hand they do not warrant a full discussion, but it should be pointed out that one of the most striking features of the pattern in this genus is the lateral dark smudge on the side of the head. This smudge is so constant as to be of generic significance.

SEXUAL DIMORPHISM.—Sexual dimorphism in the genus *Dryadophis* is not great. Cephalic and dorsal scutellation, pattern, number of teeth, size, and similar characters show no sexual variability. The ventral scutellation, on the other hand, varies considerably in the sexes. In Figure 2 is indicated the sexual dimorphism existing in the abdominals, subcaudals, and total ventrals in representative forms of 3 of the 4 species groups. In all instances the female has a greater number of abdominal scutes than the male has. The same condition was found in *Masticophis* by Ortenburger (1928: 12–13) and in *Lampropeltis* by Blanchard (1921: 15). The amount of sexual difference in this character varies in the several species. In *alternatus*, for example, it is slight, but in *pleei* the males and females barely overlap.

The number of subcaudals in the 2 sexes is generally about the same, but occasionally a male having a slightly greater number is discovered. This is

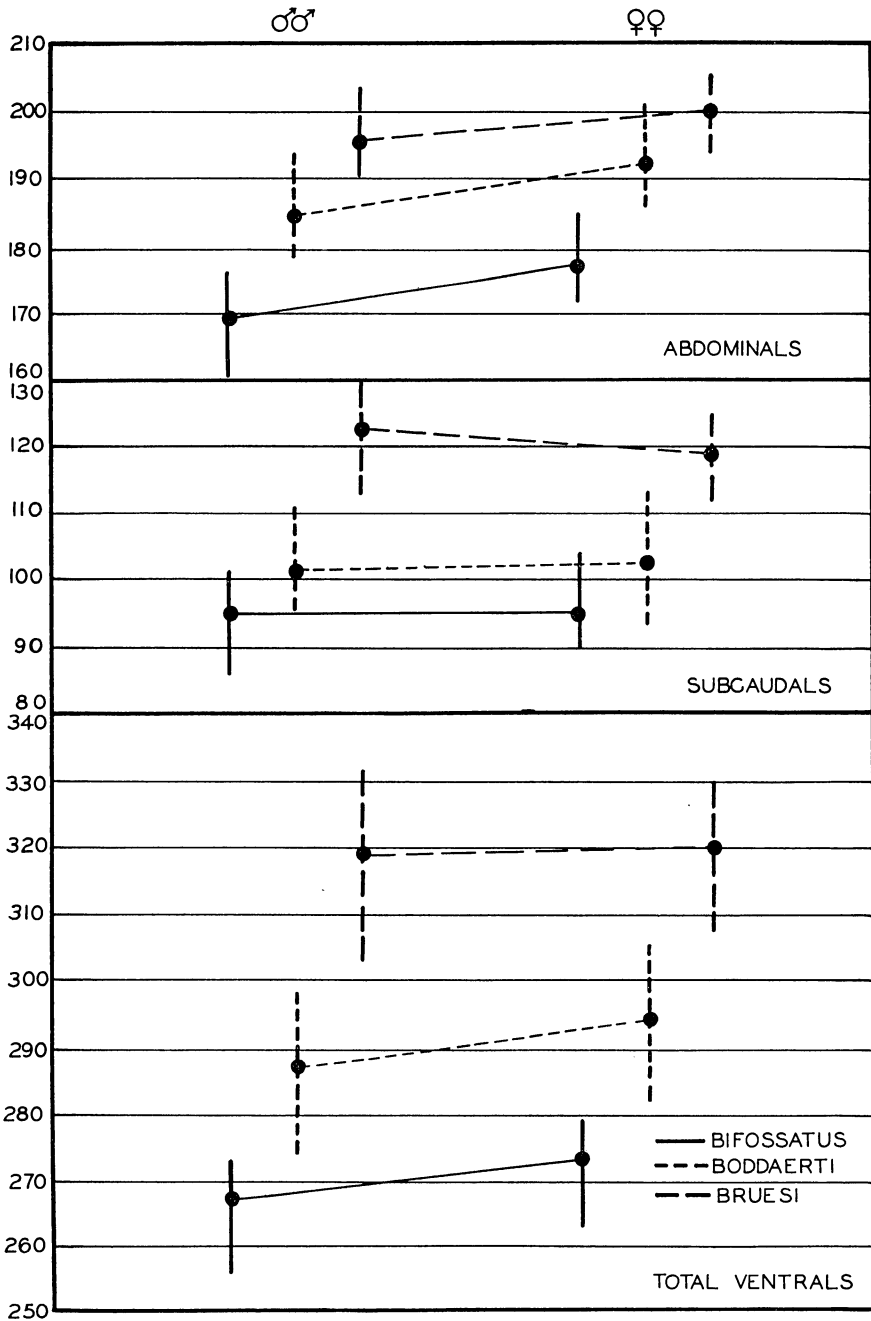


FIG. 2. Sexual dimorphism in ventral scutellation in 3 forms representing 3 different species groups. The subcaudals are about equal in the 2 sexes, and the total ventrals parallel the condition in the abdominals.

contrary to the condition found by various investigators in other genera, as there is usually a distinct tendency for the males to have a greater number of subcaudals than the females have. The fact that the males have fewer abdominals than, and about the same number of subcaudals as, the females have naturally results in a greater number of total ventrals in the females. This difference in the number of total ventrals is about the same as, or slightly less than, the difference in the number of abdominal scutes.

Because of these discrepancies in ventral scutellation between males and females, any study of geographic variability must be corrected for differences in the numbers in the 2 sexes. For this reason, and also because one sex or the other in the species may be better represented, each of my discussions of geographic variation is limited to either one sex or the other; only occasionally are both sexes represented well enough to be discussed together.

Sexual dimorphism in tail length is obviously dependent upon the relation between the number of total ventral scutes and subcaudals. Thus, inasmuch as the female has a greater number of total ventrals and approximately the same number of subcaudals, it follows that it would have a comparatively shorter tail than the male. Such is the case, but in many instances this difference is so slight as to fall within the limits of personal error. In the Panama population of *alternatus* the difference is marked. The mean tail length (tail length to total length) is .256 in the females and .280 in the males. In *bruesi* the mean tail length is .290 in the females and .299 in the males.

In a summary of the significant variations, the following observations may well be regarded as having taxonomic and phylogenetic importance: (1) Variation in cephalic scutellation is the result of a shortening of the snout. (2) Variation in dorsal scutellation is the result of the loss of scale row number 4. (3) Variation in pattern is most pronounced in juvenile-adult dimorphism in all but the *bifossatus* group and *pulchriceps*. Juvenile pattern may be of 2 types, but is always banded. Adult pattern may be either banded or striped. There are 2 types of striped pattern, one in which the stripe is intimately associated with the dorsal scale rows and the other in which it is not. (4) Sexual dimorphism is slight. In general, the females possess more abdominals and total ventral scutes than do the males and have slightly shorter tails.

COMPOSITION OF THE GENUS

From the foregoing discussion of variation within the genus it is evident that 2 major groups are readily separable. The *bifossatus* group (1) has a banded adult pattern, 8 supralabials, a shorter snout and the characters accompanying this condition, and 15 series of dorsal scale rows. In contrast to this group are (2) the *boddaerti*-like species with a striped or uni-

color adult pattern, 9 supralabials, a longer snout, and 17 dorsal scale rows situated anteriorly. Connecting these groups is *pulchriceps*, which in some characters resembles the *bifossatus* group and in others is more *boddaerti*-like; it resembles the former in having the banded adult pattern and 8 supralabials, but its 17 rows of dorsal scales place it nearer the *boddaerti* group.

The *boddaerti*-like forms may be otherwise arranged in 2 sections—the *melanolomus* and *boddaerti* groups, in which the lateral light stripe is associated with the dorsal scale rows (except in *heathii*), and the *pleei* group, in which the stripe is independent of the scales. Whether or not the *melanolomus* and *boddaerti* groups should be united I am unable to say, but on the basis of morphological characters they cannot be separated. The reasons for not regarding them as one are considered elsewhere in this paper; it is sufficient here to point out that evolutionary trends and the apparently long isolation of these groups from each other preclude any but a remote chance of their union.

The composition of the genus may be outlined as follows:

Genus *Dryadophis*

bifossatus complex⁴

pulchriceps complex

boddaerti complex

pleei series

boddaerti series

melanolomus group

boddaerti group

The genus, then, is made up of a number of series of species which arrange themselves into aggregations of varying degrees of differentiation. For example, the *bifossatus*, *melanolomus*, *boddaerti*, and *pleei* aggregates each represent "species groups" in the taxonomic sense, and are all of equal taxonomic value as entities which together compose the genus *Dryadophis*. And yet the same 4 groups show considerable differences in their degrees of differentiation. In other words, the *melanolomus*, *boddaerti*, and *pleei* groups are more closely related to each other than are any of the 3 to the *bifossatus* group. The genus *Dryadophis* might well be regarded as being made up of 2 subgenera, the *bifossatus* complex and the *boddaerti* complex. The use of this taxonomic category, however, has few advantages and can do little more than increase taxonomic confusion. Furthermore, to be consistent, the use of subgenera would require the selection of some category (for which there is no name) by which the separation of the *boddaerti* series from the *pleei* series could be emphasized. For these reasons, although I discuss the degree of differentiation between the various groups, I have not

⁴ The terms "complex," "series," and "group" are used here for convenience only and are not taxonomically significant.

designated any taxonomic category for the purpose of distinguishing between the genus and the 4 species groups, which may be listed as follows:

Genus *Dryadophis*

bifossatus group

pleei group

boddaerti group

melanolomus group

(*pulchriceps* group in intermediate position)

These larger units are, in turn, composed of species and subspecies, which, like the larger groups, have varying degrees of differentiation. For example, there is far greater similarity between the subspecies *striatus* and *bifossatus* than exists between the several local populations of *boddaerti*. This difference in degree of differentiation is of considerable importance in the naming of island forms, as will be made evident. But the species and subspecies offer few difficulties in comparison with certain local populations in which there is incipient differentiation. It is always difficult to determine to what extent "splitting" should be carried, and *Dryadophis* offers an excellent example of this problem. For instance, in *alternatus* the populations of Saboga Island and of the Panama-Costa Rica highlands are different in several minor respects from typical *alternatus*. The problem arises, then, as to whether or not they should be named. The Colombian population of *boddaerti* presents a similar problem. If *alternatus* and *boddaerti* are of subspecific status there is no category available which would include these slightly different populations within a subspecies except by the utilization of a quadrinomial system, as advocated by some of the European systematists. Although such a step would prove of tremendous value in discussions of variation, evolutionary trends, and other problems, it would only cause confusion and further burden already overburdened synonymies with a profusion of names to be rearranged by each succeeding investigator. It seems best, therefore, to recognize these smaller units but to refrain from according them taxonomic status.

In summing up this discussion of the composition of the genus we are confronted with a series of increasingly smaller units. These are based not only upon group relationships but upon degree of differentiation. The various degrees of differentiation may be listed as follows:

1. Generic differentiation.
2. Subgeneric differentiation, as between the *bifossatus* group and the *boddaerti*-like series.
3. Group differentiation, as between the various groups of the *boddaerti*-like series.
4. Specific differentiation, such as occurs between *boddaerti* and its subspecies and *heathii*.

5. Subspecific variation, as in the several subspecies of *melanolomus*.

6. Local variation, or variation within a subspecies, as represented by the Colombian population of *boddaerti*.

From the above it is evident that the present nomenclatorial system is inadequate, since it affords no way by which both phylogenetic relationships and extent of differentiation may be expressed. This problem becomes increasingly complex when the smaller categories of the genus are considered. Thus, although relationships form the primary basis for according certain forms their taxonomic status, tremendous differences in the degree of differentiation may exist within a single group. Merriam (1919: 6-9) realized that taxonomic status, when based on relationship, as indicated by intergradation, does not always present the facts clearly. For this reason he suggested that specific or subspecific status be accorded forms on the basis of degree of differentiation and even went so far as to hold that 2 forms with slight differences be given subspecific rank even if they were known not to intergrade (Merriam, 1897: 753-58). In commenting upon this concept Taverner (1920: 124-27) and more recently Grinnell and Hill (1936: 9) hold that only proven intergradation should be the criterion of subspecific rank.

I have been confronted by these 2 conflicting concepts and have attempted to utilize our taxonomic system for the double purpose of indicating both the closeness of relationship and the degree of differentiation. In consequence, my application of specific and subspecific status to the various forms may often seem devoid of reason. Apparent discrepancies are the result of my attempts to render more elastic a system which cannot, in my judgment, adequately cope with 2 conflicting concepts.⁵

For example, 2 island forms, *bruesi* and *dunni*, have been accorded different taxonomic rank, the former specific and the latter subspecific. The reason for so doing is based purely upon the greater degree of differentiation which *bruesi* shows. On the other hand, I have been consistent in according subspecific status in all cases in which intergradation is known to exist regardless of degree of differentiation. It is apparent that the genus *Dryadophis* is difficult to deal with taxonomically because it is composed of so many different categories which are based in some instances on relationships and in other instances upon degree of differentiation. I have attempted to take a conservative stand, and for this reason may be accused of inconsistency. As I see it, the genus resolves itself into the following:

Genus *Dryadophis*

bifossatus group

bifossatus bifossatus

bifossatus triseriatus

bifossatus striatus

⁵ Since this was written, the problem has been commented on at length; see Henry Fitch, "A Biogeographical Study of the *Ordinoides* Artenkreis of Garter Snakes (Genus *Thamnophis*)," *Univ. Calif. Publ. Zool.*, 44 (1940), 1: 4-6.

pleei group*pleei**amarali**bruesi**melanolomus* group*melanolomus alternatus**melanolomus laevis**melanolomus melanolomus**melanolomus veraecrucis**melanolomus slevini**dorsalis**boddaerti* group*boddaerti boddaerti**boddaerti ruthveni**boddaerti dunni**heathii**pulchriceps* (position uncertain)

A word upon the relationships of *Dryadophis* is pertinent to this discussion of the composition of the genus. In a previous paper (Stuart, 1932) I attempted to show that *Dryadophis* sprang from *Drymobius*, which in turn could be traced back to *Dendrophidion*. Whether or not this conclusion is tenable, I am unable to say definitely. It has been suggested that *Dryadophis* should occupy the stem position, but, on the basis of the data which were presented (Stuart, 1932), I judge that such a view of the relationship of *Dryadophis* would prove rather unsatisfactory. Whatever the early history of the genus in South America may have been, all lines of evidence (as is pointed out further on in this paper) indicate that the progenitors of the genus entered that continent and then differentiated there to form a considerable number of colubrine genera which secondarily reinvaded North America. The later history of *Dryadophis* has been one of group, species, and subspecific differentiation, and at various times certain of the "primitive" members of the genus have undoubtedly given rise to such closely related genera as *Drymoluber* and *Salvadora*. Whatever their relationship may be, it cannot be denied that *Drymobius*, *Salvadora*, and *Drymoluber* are the genera most closely allied to *Dryadophis*.

EVOLUTIONARY TRENDS

Any discussion of evolutionary trends must of necessity be largely hypothetical. Although some characters, such as temporals, are too variable to warrant any conclusions, in other characters there appear definite trends which are highly significant in the task of unravelling the history of the genus.

SCUTELLATION.—Only 3 scutellation characters offer any clues as to the trends within the genus. These are the supralabials (and the associated infralabials), the dorsals, and the ventrals. Within the genus 2 labial formulae are found. The first is that of *pulchriceps* and the *bifossatus* group, which have 8 supralabials and 9 infralabials; the second is found in all those other forms which typically have 9 supralabials and 10 infralabials. It is particularly significant that there is little variability in this character, and that there is a general tendency for the number to be higher in the variant specimens than in the typical specimens. Within the genus it is difficult to indicate which is the "primitive" condition, but, as previously pointed out (Stuart, 1932: 9), there is a tendency for the number of labials to decrease through the *Dryadophis-Salvadora-Masticophis-Coluber* series. It seems evident, therefore, that the presence of 8 supralabials indicates a specialized condition, and that the variant specimens represent throwbacks in this character.

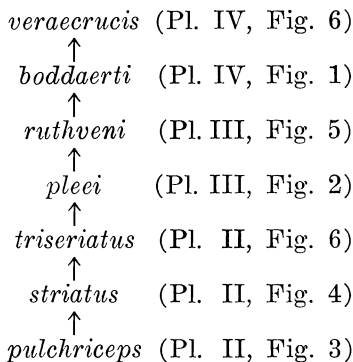
The number of dorsal scale rows appears to parallel the condition in the labials, in that reduction appears to be the trend. The basis for this assumption is again found in the evolutionary line described above, in which there is a tendency for the dorsal scale rows to decrease in number. This does not bear out the conclusions of Ortenburger, who discovered in *Masticophis* a tendency to increase the dorsal scutellation (Ortenburger, 1928: 12). With reference to Ruthven's law of reduction in dorsal scale rows as related to dwarfing, the genus *Dryadophis* parallels *Masticophis* in apparently having no such correlation. In fact, the opposite is true, since the *bifossatus* group, the largest species in the genus, has but 15 rows of dorsal scutes. Any attempt to harmonize these conflicting viewpoints on the trends in labials and dorsals must await further studies. Possibly the difference of opinion arises from the fact that Ortenburger, by selecting a genus of so much greater variability, as is exhibited by *Masticophis*, was able to base his conclusions on data within a single genus, whereas my assumptions are based primarily on trends through a series of related genera.

Trends in ventral scutellation are somewhat difficult to understand. It is possible that 2 conflicting factors are at work in controlling the number of ventral scutes. There may be an orthogenetic trend within the species which is tending to increase the number of scutes. At the same time there may be a tendency for the environment to select those with a small number of scutes. It is certainly clear that, except for a few generalizations, there is no definite law applicable to the genus as a whole. In *Masticophis*, Ortenburger (1928: 13) found that in one group the tendency was toward increase in the number of ventrals at the outer limits of the group and that in the other group the reverse was true. In general, there is a marked tendency for the number of ventral scutes to increase with distance from the center of the group (see Figs. 5 and 11). This general law holds, however, only in

those groups which have moved away from the center of origin, viz., *melanolomus* and *pleei*. As this migration has for the most part been northward, it might be assumed that the increase is intimately related to the environment. If such were the case, however, it would be expected that altitude might produce the same results as latitude. In the cases of *ruthveni* and *dorsalis* (both mountain forms) this conclusion is borne out, but in *boddaerti*, from the mountains of Colombia, and in *alternatus*, from the highlands of Panama and Costa Rica, there is reduction rather than the expected addition.

Aside from this tendency toward an increase in ventral scutes in the peripheral forms of the group, only 1 trend is significant. In such lines as *alternatus-veraegrucis* or *pleei-bruesi*, the increase in subcaudal scutes reaches a maximum point beyond which reduction is the rule. This peripheral reduction is brought out in the 3 forms shown in Figure 3. In these the reduction is progressive in a northerly direction, and it may be the result of conditions associated with latitude. More likely it merely indicates the stunted condition that is to be expected in the individuals that exist at the extremities of the range of the form, under a most unfavorable environment, the form having reached, in the northern region, the limits of its tolerance.

PATTERN.—The pattern in *Dryadophis* offers one of the most interesting problems presented by the genus, and presents, in addition, the basis for the unravelling of the phylogenic history. In general, the pattern has passed from the banded type through the striped condition and has in 2 instances progressed to the unicolor form. The "primitive" pattern was of the alternating blotched type which is now found in *pulchriceps*. This pattern gave way to the banded type, as in *striatus*, which eventually broke down into the spotted pattern of *triseriatus*. Eventually, the spotted pattern assumed the striped condition of *pleei*, and finally the lateral stripes were restricted to form the *ruthveni* pattern. Continued loss of the lateral stripes produced the unicolor phase of *veraegrucis*. In outline, the progression has been as follows (as illustrated with living forms):



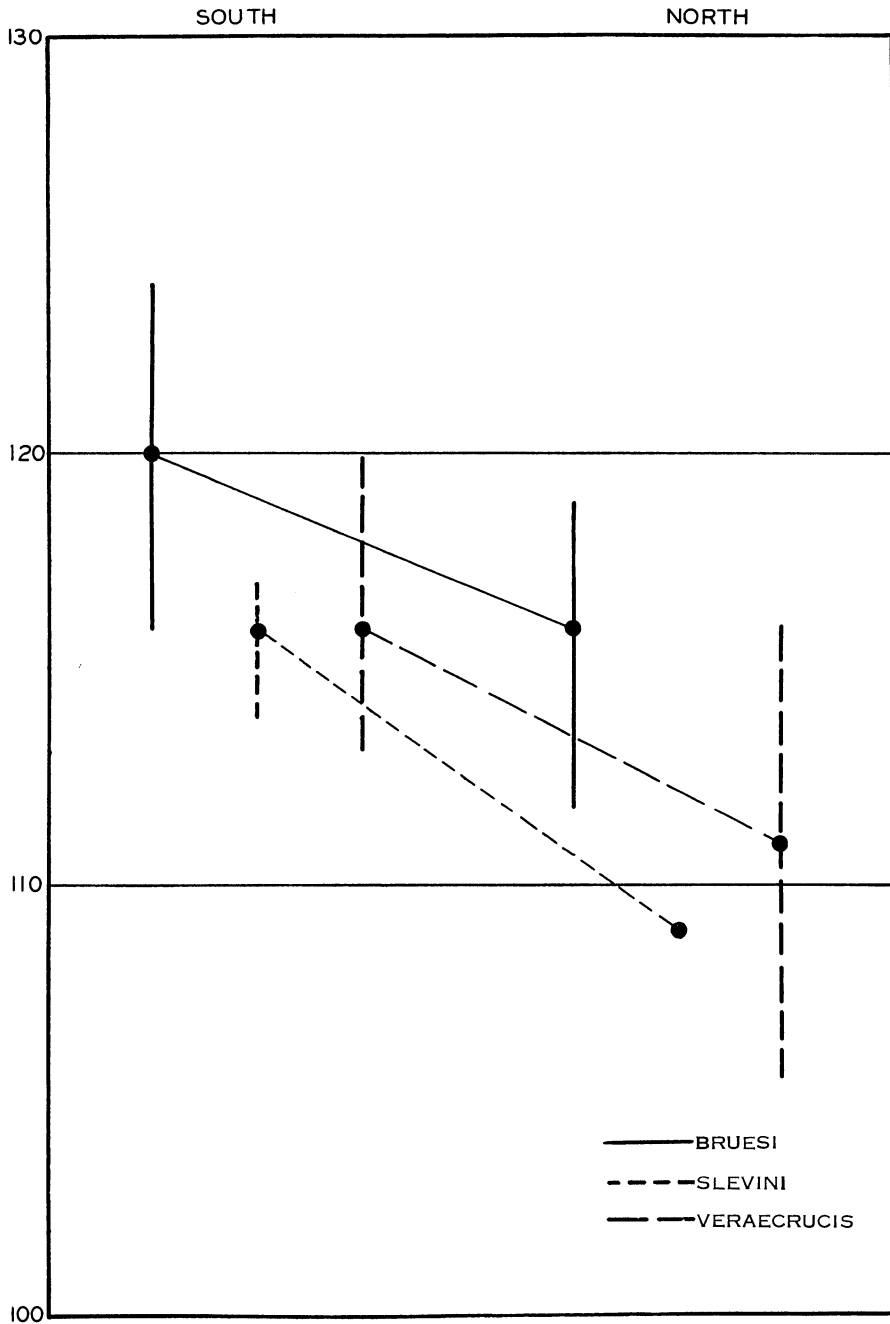


FIG. 3. Peripheral reduction in subcaudals in 3 forms which occupy a peripheral position in the distribution of the genus. Note that in all instances the northern population shows a decided reduction in the number of subcaudal scutes. Only 3 specimens of northern *slevini* were available, and all had 109 subcaudals.

The basis for the above argument is complex, largely because some forms, though they have retained "primitive" characters, are specialized along certain lines. Thus, as pointed out further on in this paper, the juveniles of such forms as *ruthveni* and *boddaerti* have the "primitive" pattern of alternating dorsal and lateral blotches. Yet these are specialized in that the lateral and dorsal blotches tend to separate on scale rows 4 and 5 rather than on rows 3, 4, and 5.

The prototype of the genus undoubtedly was similar in pattern to *pulchriceps* in all respects excepting constriction of the blotches, which was probably on scale rows 3, 4, and 5. These blotches eventually evolved into continuous bands constricted at the same place. The evidence for this change from the alternate blotched pattern to the banded condition is the presence of a banded pattern in the juveniles of the more specialized members of the *melanolomus* group, similar to that in the adults of the *bifossatus* group. The conclusion that constriction of the bands occurred on scale rows 3, 4, and 5 is derived from the fact that as the banded pattern broke down to produce a pattern of dorsal spots opposite to and separated from a series of lateral spots (as in *triseriatus*), scale rows 3, 4, and 5 were left devoid of color. In *triseriatus* scale rows 3 and 4 present this condition, but it must be remembered that this form has but 15 rows of dorsal scales and that scale row 4 has been lost, so that the break is on original scale rows 3 and 5. It is evident, therefore, that the break in the prototypic form, with 17 scale rows, was on scale rows 3, 4, and 5 (scale row 4 in forms with but 15 series of dorsal scutes being equivalent to scale row 5 in the others).

It should be noted here that this "primitive" stripe was probably not associated with the scales, and that the tendency in the genus is to develop such an association. Thus, the *bifossatus* group, despite its "primitive" pattern is specialized in this feature. The *pleei* group, on the other hand, has retained the "primitive" condition, and it was not until the *boddaerti* and *melanolomus* groups developed that this specialization took place in the striped forms. In *heathii*, a species apparently closest to the *boddaerti* group, there has been a retention of this "primitive" character despite a specialization of the pattern.

Further evolution resulted in the disappearance of the spots and in their replacement by a lateral stripe on scale rows 1 and 2 and by another on rows 3, 4, and 5. It is difficult to determine the nature of the dorsal pattern, but it may possibly have resembled *pleei*. This early striped pattern, unassociated with the scale rows, finally became fixed, and the upper stripe became restricted to scale rows 4 and 5. This stage is represented today in *ruthveni* and *alternatus*, but *amarali* offers an example of a pattern intermediate between their pattern and that of *pleei*. Continued evolution produced the single-striped design of *boddaerti*; this pattern eventually faded still more

in the lateral stripe and produced the *bruesi* condition, which may fade completely to become unicolor.

In the foregoing remarks on pattern evolution, pattern alone has been considered. It has been necessary to omit characters of scutellation from illustrations of the various evolutionary steps, and the evolutionary sequence has been presented without regard to actual relationships of the living forms.

In the more specialized types such as *laevis* and *melanolomus* the juveniles have specialized further by developing a banded pattern rather than one of alternating blotches, although the juvenile pattern of *slevini* has not entirely reached that stage. The most specialized in pattern, *verae-crucis*, has progressed so far that today some of the juveniles tend toward the striped rather than the banded pattern.

This parallel evolution of pattern in the several groups, especially in the *boddaerti* and *melanolomus* groups, leads to considerable confusion in identification of the various forms. Thus *ruthveni*, *dunni*, *alternatus*, *laevis*, and occasionally *slevini* all have a pattern of 2 light, lateral stripes. In *ruthveni* the upper stripe is bordered with black, thus differentiating it from the unbordered stripe of *dunni* (Pl. III, Figs. 5 and 6). In *alternatus* (Pl. IV, Fig. 3), on the other hand, the upper light stripe may or may not be bordered with black, and on the basis of pattern alone the form resembles either *ruthveni* or *dunni*. Similarly, *laevis* and *slevini* often have faint traces of 2 light lateral stripes, and since they overlap each other as well as *dunni* in scutellation, a most confusing situation may result when identification is attempted.

This simplification of dorsal pattern has been accompanied by loss of color on the ventrum; *pulchriceps* is extremely dark ventrally, *striatus* is somewhat lighter, and *triseriatus* is the first in the evolutionary series to have an immaculate or almost immaculate belly. In the later forms ventral markings, if present, are only on the chin and throat and are faintly visible on the lateral edges of the abdominals.

Some forms, such as *dorsalis*, *melanolomus*, and *heathii*, do not fit into the evolutionary scheme indicated above. For these I can offer no explanation other than what may be indicated by the facts set forth in the species discussion. Instances such as these which have been inconsiderate enough to break up a fairly logical picture bring home again and again the hypothetical nature of our feeble gropings and the futility of our naive attempts to regiment the works of nature.

The evolution of pattern in *Dryadophis* has progressed anteriorly along the animal body in this genus. In the forms in which the alternate pattern is on the body, the pattern on the tail is characterized by a more advanced banded condition. The change from the juvenile pattern, which gradually fades to that of the adult, is initiated on the posterior part of the body, and

proceeds forward. So striking is this feature that occasionally one finds fully developed adults that still retain on the fore part of the body evidences of the juvenile pattern.

The change from the banded condition of the juvenile pattern to the striped condition of the adult pattern is brought about by the loss of color, the black blotches or bands fading to the shade of the intervening ground color. Likewise, the evolution from the banded to the unicolor state proceeds through the further fading of the dorsal ground color to that of the stripes. In the progress from *ruthveni* to *boddaerti*, the black edges along the upper lateral stripe disappear in the intergrades and the sides lighten, obliterating the lower stripe. Continued fading would, of course, produce a unicolor form.

OTHER CHARACTERS.—Evolutionary trends in other features are not conspicuous. The greater number of maxillary teeth in *bruesi* and the *bifossatus* group is apparently an example of the retention of a "primitive" condition. The steady decrease in the number of teeth in the series of *Dryadophis* to *Coluber* constitutes the basis for this argument.

Trends in tail length accord with the suggestion, already made, that tail length and number of subcaudals may be correlated directly. My data are too few to enable me to discuss evolutionary trends in such variable features as proportionate sizes of the several structures.

I see in this genus all the various stages of evolution through which such end forms as *bruesi* or *veraecrucis* have passed. It would at first appear likely that the more central forms such as *alternatus* or *bifossatus* have remained static over a long period of time. Such, however, has not been the situation. The prototype of this genus was probably a species of moderate size, with a pattern of alternating dorsal and lateral black blotches, 17 dorsal scale rows, 9 supralabials, and possibly about 175 abdominals and 90 subcaudals. No living form in the genus answers this description. The species *pulchriceps* most closely approaches this hypothetical prototype, but even it has evolved by way of reduction in the number of supralabials. Subspecies of the *bifossatus* group stand next in the evolutionary line, and these are followed by the *pleei*, *boddaerti*, and *melanolomus* groups respectively.

It will be noted that, with the exception of *pulchriceps*, about which nothing is known, the least specialized groups, *bifossatus* and *pleei*, are restricted to the more arid regions, and the *boddaerti* and *melanolomus* groups have invaded more humid areas (though some of them, *heathii* and *slevini*, for example, have secondarily re-entered arid localities). From this it may be assumed that the more arid regions of northern South America (see the summary of the genus) constituted the ancestral home of the genus. In the forms which have invaded humid regions, specialization has been

greatest. In other words, evolution has been retarded at the ancient center of origin and has been accelerated in all directions away from this center. This is evident even when forms within a single group are considered. Thus, in the *boddaerti* group, which probably had its inception at the time when it left the arid habitats and invaded the more humid ones, *heathii* has apparently returned to the arid habitats, and, in consequence, is most peculiarly specialized. Similarly, on the relatively arid highlands of Guatemala, *dorsalis*, in the *melanolomus* group, has evolved a unique pattern. For this reason, such stem forms as *alternatus* and *pleei*, inhabiting the ancestral homes of their respective groups, have evolved less than have the end forms such as *veraacruzis* or *bruesi*.

This does not necessarily mean that these stem forms have been static. I prefer, rather, to interpret their "primitiveness" in other terms. The following argument can be built up, if it is assumed that selection is an active agent in evolution, and that the characters diagnostic of the forms of this genus, such as a simplified pattern and the reduced number of supralabials and of dorsal scale rows, are of survival value. (It must be borne in mind that merely because, from an anthropocentric viewpoint, we cannot see the survival value in many characters, those characters are not necessarily proven to be of no benefit to the animal.) If mutation has been as active in a stem form as it has been in an end form, it seems reasonable that, other things being equal, both should change at about the same rate. Unfortunately, others things have not been equal. In the instances in which one form is subjected to the environment under which the group had its origin (and to which it is already adapted) and another is coming into contact with a new environment, it should follow that selection would tend to destroy many new mutations in the former and preserve them in the latter. This has already been demonstrated in *Dryadophis*.

"Orthomodification" has characterized the trends of evolution of the various forms. By "orthomodification" I wish to denote modification along certain definite lines; I refrain from the use of the terms "orthogenesis" and "orthoselection" because of their implications. The fact that evolutionary trends in this genus have been along lines of orthomodification is indicated in several ways—in the development of the dorsal pattern from the banded to the unicolor condition, in the reduction of labials, and in the increase in number of ventral scutes. These trends have, except in peripheral forms, diverged from the center of origin and have, in general, been associated with the amount of difference rather than the type of difference in environment. The evolutionary history of the individual forms, of the groups, and of the genus is discussed under each species, under the group summary, and under the generic summary.

KEY TO THE IDENTIFICATION OF THE ADULTS OF
*DRYADOPHIS*⁶

- A. Dorsal scales in 15 longitudinal rows at mid-body B
 B. Body pattern of continuous, narrow, dark crossbands (Pl. II, Fig. 4); total ventrals, more than 279 *striatus* (p. 46)
 BB. Body pattern of constricted, broad, dark crossbands or series of dark dorsal and lateral blotches; total ventrals, less than 279 C
 C. Body pattern of laterally constricted, dark crossbands (Pl. II, Fig. 5)
 bifossatus (p. 39)
 CC. Body pattern of series of dark, dorsal blotches separated from an opposite series of similar lateral blotches (Pl. II, Fig. 6) *triseriatus* (p. 43)
 AA. Dorsal scales in 17 longitudinal rows at mid-body D
 D. Supralabials, normally 8; body pattern of alternating dorsal and lateral dark blotches (Pl. II, Fig. 3) *pulchriceps* (p. 50)
 DD. Supralabials, normally 9; body pattern, striped, unicolor, or narrowly banded (occasionally in *laevis*) E
 E. Body pattern anteriorly with at least 1 narrow, dark middorsal stripe F
 F. Body pattern anteriorly with 3 narrow, dark dorsal stripes (which merge into a single broad band posteriorly) and a dark lateral stripe (Pl. III, Figs. 1 and 2) *pleei* (p. 53)
 FF. Body pattern anteriorly with a single, narrow, dark middorsal stripe and occasionally a similar stripe on either side (Pl. IV, Fig. 5) *dorsalis* (p. 95)
 EE. Body pattern anteriorly lacking a middorsal stripe G
 G. Body pattern, reticulate, caused by prominent black border on each scale; often 2 lateral light stripes apparent (Pl. IV, Fig. 4)
 melanolomus (p. 88)
 GG. Body pattern not reticulate, though scales often with faint, narrow black border H
 H. Body pattern of at least 1 lateral light stripe J
 J. Two lateral light stripes K
 K. Upper lateral light stripe on scale rows 3, 4, and 5 anteriorly (Pl. III, Fig. 3) *amarali* (p. 57)
 KK. Upper lateral light stripe on scale rows 4 and 5 only L
 L. Subcaudals, less than 110 (Pl. IV, Fig. 3) *alternatus* (p. 81)
 LL. Subcaudals, more than 110 M
 M. Upper light stripe with prominent dark borders (Pl. III, Fig. 5) *ruthveni* (p. 64)
 MM. Upper light stripe unbordered N
 N. Lateral light stripes prominent, well differentiated from ground color (Pl. III, Fig. 6) *dunni* (p. 76)
 NN. Lateral light stripes obscure
 laevis (p. 86) or *slevini* (p. 93)⁷
 JJ. A single light lateral stripe O
 O. Light lateral stripe on scale rows 4, 5, and 6 (Pl. IV, Fig. 2)
 heathii (p. 77)
 OO. Light lateral stripe involving only scale rows 4 and 5 P

⁶ I and Q are purposely omitted in order that confusion may be avoided.

⁷ Parallelism makes it difficult to separate certain specimens of *laevis* and *slevini* from each other or from *dunni*. For discussion, refer to p. 35.

- P. Stripe narrow and zigzag in appearance; total ventrals more than 308 (Pl. III, Fig. 4) *bruesi* (p. 59)
- PP. Stripe broader and straight; total ventrals less than 308 (Pl. IV, Fig. 1) *boddaerti* (p. 66)
- HH. No lateral light stripes (occasionally present posteriorly in banded phase of *laevis*, see p. 86) R
- R. Body pattern of narrow, light crossbars anteriorly *laevis* (p. 86)
- RR. Body pattern lacking; unicolor S
- S. Abdominals, usually less than 180 T
- T. Total ventrals less than 297 *veraecrucis* (p. 91)
- TT. Total ventrals more than 297 *laevis* (p. 86)
- SS. Abdominals usually more than 180
laevis (p. 86) or *slevini* (p. 93)

THE BIFOSSATUS GROUP

Dryadophis bifossatus bifossatus (Raddi)

Coluber bifossatus Raddi, 1820: 33 (type locality, Brazil; type, Museo Reale, Florence, number unknown).

Coluber capistratus Lichtenstein, 1823: 104 (type locality, Brazil; type, probably in the Museum für Naturkunde, Berlin).

Coluber lichtensteini Wied, 1825: 493 (type locality, Brazil; type, location of type unknown).

Coluber pantherinus (non Daudin) Schlegel, 1837: 143, Pl. V, Figs. 13 and 14 (type locality, St. Paul [São Paulo], Brazil; type, location of type unknown).

DESCRIPTION.—At mid-body, where the dorsal pattern is most typical, the ground color (*stratum corneum* lacking) is yellow to white. Superimposed upon this light ground color is a series (31–47, nape to vent) of dark-margined, gray crossbands varying (middorsally) from 3 to 5 scales in length. The scales included in these dark crossbands are heavily stippled or flecked with black or dark gray. Middorsally the crossbands are separated by $\frac{1}{2}$ – $2\frac{1}{2}$ scales (average .8 scales). Laterally, these crossbands are strongly constricted on the upper half of scale row 3 and the lower half of scale row 4. Ventrally from this point the dark bands are somewhat narrower than they are middorsally, and they extend broadly on the belly, where they become irregular in shape and are often broken up into dark blotches. Posteriorly from mid-body the crossbands become somewhat shorter and darker, owing to the increased dark stippings on the involved scales, and the degree of lateral constriction decreases and may be entirely lacking. On the tail the dark crossbands are closer together and gradually pinch out the light ground color, to leave, toward the end of the tail, a dorsal color of dark gray, irregularly flecked with light. Anteriorly from mid-body the dark crossbands lengthen slightly and become oblique in shape. The lateral constrictions are more and more emphasized, until, on the fore part of the body and on the neck, the dorsal ground color breaks through to produce a pattern of 3 dark-edged, gray blotches, 1 dorsally and 1 laterally on either side. These are

separated by a clear-cut streak of ground color on the upper half of scale row 3 and the lower half of scale row 4. The lateral spots are somewhat shorter than the corresponding dorsal spot, and on the neck all break up and become irregular (Pl. II, Fig. 5).

The ground color of the head is slightly darker than that of the body. The rostral is outlined with dark gray or black, leaving a light spot in the center. A dark gray crossband extends across the posterior half of the internasals, and another across the posterior half of the prefrontals. A dark interorbital band covers three-fourths of the supraoculars and frontal. The parietals are dark gray except around the anterior, medial, and lateral margins, where the ground color persists. This dark color extends posteriorly on the neck to produce 2 paraventral dark stripes (which fuse to form the first dorsal blotch behind the neck), 3-4 scale rows in width and separated middorsally by a light stripe of ground color; a second branch extends obliquely laterally across the posterior temporals and on the undersurface of the neck. These dorsal head markings may or may not have a very narrow light border outside the dark borders. On the head, laterally, the nostrils are mottled with gray. The posterior half of the loreal is dark, and this vertical stripe joins the prefrontal stripe on the upper surface of the head. The supralabials are light, with dark posterior margins. A broad dark gray stripe extends obliquely from the eye to the angle of the mouth. The infra-labials have dark margins; the chin and throat are cream or white, irregularly margined or flecked with black (Pl. I, Figs. 1 and 2).

The ground color of the undersurfaces is cream to white. Laterally, the belly is broadly infringed upon by the dorsal crossbands, which here often break up into large irregular blotches with light centers. The dark markings on the belly are extremely irregular and variable, rendering description almost impossible. Posteriorly, the dark blotches break up into black flecks or stipplings and cover more and more of the undersurface. On the tail the light ground color is almost completely obscured with black or gray and remains only in the form of numerous white flecks.

In specimens in which the *stratum corneum* is in place, the dorsal ground color is brown, the posterior part of each scale being somewhat darker than the anterior. The dorsal crossbands are of a darker hue, each scale flecked with gray or black. The belly color varies from yellow to cream.

The ventral scutellation is as follows: abdominals, 161-85 (174); sub-caudals, 86-102 (95); total ventrals, 254-79 (269).

RANGE.—This subspecies is found along the humid east coast of Brazil from Bahia southward to Rio Grande do Sul. Along its northern and western boundaries it intergrades little by little, over a wide belt, with *triscrivatus* (Map 1).



MAP 1

MATERIAL EXAMINED

Locality (and Museum Number)

Brazil (U.M.M.Z. 62678-83)

Minas Geraes

Brejauba (I.B. 8365)
 Cedoderta (I.B. 638)
 Entre Rios (C.M. 329)
 Sereno (U.S.N.M. 100677)
 Simplicio (I.B. 9816)

Rio Grande do Sul

Porto Alegre (B.M. 86.10.4.11)

Rio de Janeiro (B.M. 55.10.16.281; M.C.Z. 570, 843 [2], 1387[3])

Barra Mansa (I.B. 9814)
 Friburgo (I.B. 948)
 Manguinhos (I.B. 726)
 Monte Serrat (Serro do Itatayia) (A.M.N.H. 23044)
 Porto Real (B.M. 87.12.29.8, 87.12.29.19-20)
 Uruably (C.M. 381)
 Vargeur Alegre (I.B. 259)
 Volte Redonde (I.B. 258)

São Paulo (A.M.N.H. 25516-18; B.M. 1908.5.22.3; F.M.N.H. 19393; M.C.Z. 16689, 17788, 17968-70; U.M.M.Z. 62720-23)

Bento Carvalho (I.B. 9780)
 Bocaina (I.B. 9800)
 Butantán (M.C.Z. 62808)
 Casa Branca (U.M.M.Z. 79644)
 Colina (I.B. 9791)
 Crystaes (I.B. 9813)
 Gallia (I.B. 9779)
 Guararema (U.S.N.M. 100732)
 Guaxinduva (U.S.N.M. 100743)
 Jafa (U.M.M.Z. 79643)
 Jundiáí (I.B. 9817)
 Luis (I.B. 9818)
 Novo Horizonte (I.B. 9812)
 Pantellão (I.B. 7250)
 Taipas (I.B. 2161)
 Vallinhos (I.B. 9789)

VARIATION.—Practically all the material at hand originated in the state of São Paulo or in that of Rio de Janeiro. As a result, any discussion of geographic variation in this species is impossible. Individual variation is most noticeable in the ventral pattern, where there is a tremendous variation in frequency and intensity of the dark blotching, which could be adequately shown only through illustration. With increased age (as determined through length) the dark belly markings become more regular—that is, the blotches become more closely associated with the lateral spots—and the

black, very intense in juveniles, fades to gray. Variation in scutellation and in other characters shows no geographic correlation and is very slight.

AFFINITIES.—The affinities of this form are taken up in the discussion of *triseriatus*, and its origin is treated under the discussion of the group.

Dryadophis bifossatus triseriatus (Amaral)

Drymobius bifossatus triseriatus Amaral, 1931: 86 (type locality, Taunay, Mato Grosso; type, I.B., No. 5395).

DESCRIPTION.—At mid-body the dorsal ground color (*stratum corneum* lacking) is gray, stippled with black. Typically, the pattern consists of a series of somewhat darker, black-edged, dorsal rhombs (35, neck, to 47, vent), varying in shape from squarish to almost round. Middorsally these spots are 3 to 5 scale rows in length and are separated by 1–2 (average, 1.2) scales of ground color. Corresponding to, and considerably shorter than, these dorsal spots is a lateral blotch on either side. Like the dorsal rhombs these are dark gray with a narrow black border. They are separated from the dorsal spot by ground color on the upper half of scale row 3 and on the lower half of scale row 4. The separation of the dorsal and lateral blotches is not in all instances complete, and may resolve into a pattern similar to that in *bifossatus*, but with the lateral constriction of the crossbands more pronounced. The lateral spots barely extend on the belly and in some instances are evidenced only by stippings on the outer ends of the ventrals. Posteriorly, the dorsal blotches are somewhat shorter and their separation from the lateral ones is less complete. The dark stippling on the ground color also increases and in some instances becomes so intense that both dorsal and lateral spots are completely obliterated. On the tail the stippling is progressively more dense and toward the end is solid black. No traces of the pattern of rhombs or crossbands exists, and the tail presents an irregular pattern of light flecks or spots on a black ground color. Anteriorly, the dorsal spots lengthen slightly and become oblique in shape. A narrow light margin appears outside the broader dark margin of some of the spots. Separation between dorsal and lateral spots is complete (Pl. II, Fig. 6).

The ground color of the upper surface of the head and neck is dark gray, in some instances so intense as to obliterate all traces of pattern. Typically, the pattern consists of a series of dark crossbands similar to those in *bifossatus* (one on the posterior half of the internasals, another on the posterior half of the prefrontals, and a third forming an interorbital band). Darker spots occupy most of the parietals, and in lighter-colored specimens these spots extend posteriorly on the neck as 2 longitudinal dark stripes (separated middorsally), which fuse to form the first dorsal blotch. The second branch of each of these lines, which extends posteriorly in an oblique direction across the sides of the neck in *bifossatus*, is barely discernible in this

form. The ground color of the sides of the head is cream or yellow, all the scales being heavily flecked with brown. A trace of a dark stripe extends from the eye to the angle of the mouth, but it is irregular and not distinct. The supralabials possess a dark posterior border which may widen to include most of each labial. The infralabials are yellow or cream, each with a black posterior border.

The chin, throat, and undersurface of the belly are cream, either immaculate or lightly stippled with gray. Laterally, the ventrals are slightly infringed upon by the lateral spots. Posteriorly, the dark stippling increases, and the undersurface of the tail becomes black, heavily flecked with cream.

In specimens in which the *stratum corneum* is in place, the dorsal color and pattern consist of shades of brown rather than of gray, and the undersurfaces are cream or yellow.

The ventral scutellation is as follows: abdominals, 169–81 (175); subcaudals, 88–99 (92); total ventrals, 263–78 (269).

RANGE.—The range of this subspecies extends throughout the dry lands of central and western Brazil and eastern Bolivia, from Ceará and Parahyba, southward to the Argentine. Through Bahia and eastern Goyaz, Minas Geraes, and Mato Grosso it intergrades broadly with *bifossatus*. To the north, through the isolated savanna areas of the Amazon basin, it merges into *striatus* (Map 1).

MATERIAL EXAMINED

Locality (and Museum Number)

Argentina (A.M.N.H. 17576)

Bolivia

Buena Vista (U.M.M.Z. 60726, 64161, 69376)

Ixiamas (A.M.N.H. 22464)

Brazil

Baturité (Ceará) (B.M. 97.12.29.18)

Mato Grosso (I.B. 3432)

Santa Philomena (I.B. 1697)

Therezina (I.B. 511)

I have also examined the following *bifossatus-triseriatus* intergrades:

Brazil

Bahia (A.M.N.H. 36152; B.M. 61.3.23.10; M.C.Z. 1184 [2])

Santa Luzia (I.B. 3208)

Goyaz (M.C.Z. 9883)

Campinas (I.B. 4478, 6177, 6490)

Mato Grosso

Agachi (I.B. 7746, 8809)

Albuquerque (I.B. 4535–36, 4630)

Aquidauana (I.B. 5579, 6222, 6225, 6544)

Arapuá (I.B. 5496, 5631)

- Campo Grande (I.B. 8456)
 Correntes (I.B. 7327)
 Corumbá (B.M. 92.4.20.12; I.B. 5500, 7888, 8161-62)
 Guaicurus (I.B. 9815)
 Jaragua (I.B. 7781)
 Miranda (I.B. 6133)
 Mutúm (I.B. 3612)
 Porto Esperança (I.B. 8019, 8281)
 Ribeiro Claro (I.B. 7740)
 Taunay (I.B. 5843, 6262, 6489, 6533, 6554, 6612, 6902, 7791)
 Teneros (I.B. 7741, 9069)
 Tres Lagoas (I.B. 5970)
 Urucum (F.M.N.H. 9243)
 Victoriano (I.B. 7667, 7815)
 Minas Geraes (M.C.Z. 3024)
 Montes Claros (I.B. 5985)
 Pernambuco (B.M. 44.1.9.22, 44.7.20.11, 44.7.20.16)
 Sergipe
 Pacatuba (I.B. 7491)
 Paraguay
 Asunción (B.M. 94.30.14.33, 1930.11.27.188-90)

VARIATION.—Only 9 specimens of this form, from widely separated localities, were available, and hence any discussion of its variation is impossible.

AFFINITIES.—The relationship between *triseriatus* and *bifossatus* is one of the closest of any in the entire genus, and the region of intergradation between the two extends over a very large area. The conclusions as to intermediates are based largely on the very fine series of specimens collected at different points along the railway from Tres Lagoas to Corumbá, Mato Grosso. The first specimen with the typical pattern of *triseriatus* is from Mutúm, Mato Grosso; from that point westward to Corumbá, where several typical specimens of *bifossatus* appear, the entire population displays all the characters of intergradation typical of the genus. There are 3 types of specimens found: typical *bifossatus*, typical *triseriatus*, and others which represent an intermediate condition. Although *triseriatus*-like specimens make up the greater part of this population, it is suspected that if more material were available from the region of Tres Lagoas, Arapuá, and Mutúm, where *bifossatus* would be expected to predominate, the number of specimens of each type might well balance.

Because the majority of the intergrades are from localities near the *triseriatus* border, it is necessary to divide the population into an eastern group and a western group so that comparisons along the line of intergradation may be made. Assuming that the intergrading population extends from Victoriano to a point west of Corumbá, one may draw the dividing line through Correntes as the approximate mid-point. The specimens, divided into the 3 classes referred to above, may be charted as in Table IX (number of specimens followed by per cent of total in parentheses).

TABLE IX

LOCALITY	TOTAL NUMBER OF SPECIMENS	NUMBER OF SPECIMENS IN EACH OF THE 3 GROUPS		
		<i>bifossatus</i> (per cent)	intermediates (per cent)	<i>triseriatus</i> (per cent)
East	9	6 (67)	2 (22)	1 (11)
West	26	3 (11)	7 (27)	16 (62)

It should be noted that in each locality specimens similar to the adjacent form predominate, whereas typical intermediates and specimens similar to the other form make up only about one-fourth of the entire population.

Because it seems clear that the band of intergradation is broad, rather than on the basis of actual material, of which there is little, the specimens from Goyaz, Bahia, Pernambuco, and Sergipe are considered intergrades. It should be reiterated at this point that *bifossatus* is apparently restricted to the rain forest of the plateau slopes and narrow lowlands, and that *triseriatus* inhabits the dryer *campos* and *catingas* to the west and north. It should also be pointed out that the type locality of *triseriatus* is Taunay, Mato Grosso, a locality in which the population, although made up of intergrades, is like *triseriatus* in pattern.

A discussion of the relationship of these 2 forms to *striatus* is included in the discussion of *striatus*.

Dryadophis bifossatus striatus (Amaral)

Drymobius bifossatus striatus Amaral, 1931: 86 (type locality, Villavicencio [Colombia]; type, I. L., number unknown).

DESCRIPTION.—The ground color of the dorsal surface (*stratum corneum* lacking) is white with a rufous tinge, each scale being slightly stippled or flecked with black. At mid-body the pattern consists of a series of black-margined crossbands (50–62, neck to vent) produced by the irregular black marking on the scales involved. These crossbands are 2–2½ scales long mid-dorsally and gradually narrow down, at the fourth scale row, to about 1 scale in length. Below this point the bands retain that length and infringe rather strongly on the ventral surface. The crossbands are separated by ½–1 scale. Posteriorly, the ground color becomes darker, because of an increase in the dark stipplings on the scales, and the crossbands become somewhat obscure. The crossbands are slightly narrower than at mid-body and are somewhat more closely placed. On the tail the ground color becomes progressively darker and is eventually pinched out by the darker crossbands, so that the color near the end of the tail is a solid black, touched in some specimens with occasional lighter flecks. Anteriorly, from mid-body, the

dark crossbands become slightly broader and oblique in shape and are broken into 3 segments—one middorsally and one on either side, where the ground color breaks through on either side of the upper half of scale row 3 and on the lower half of scale row 4. On the neck the ground color is dark gray and the dorsal pattern is extremely irregular and broken up (Pl. II, Fig. 4).

Above, the ground color of the head is dark gray, and upon this ground color is superimposed a pattern similar in all respects to that of *bifossatus*. Briefly, this consists of a dark internasal band, another band across the posterior half of the prefrontals, and a third which is interorbital. The whole central part of each parietal is dark; this color extends posteriorly on the neck to form 2 dark paraventral stripes, which soon fuse to form the first dorsal blotch. Another streak of this darker shade extends from the parietals posteriorly in an oblique direction across the posterior temporals and on the undersurface of the neck, where it breaks up. Laterally, the head is dark gray, and all the scales have irregular dark markings. The anterior supralabials are pale pink, with black posterior margins. A dark streak extends from the eye to the angle of the mouth. The infralabials are pink, with dark posterior margins; the chin and throat are of the same color with irregular dark fleckings.

The belly is pinkish, with irregular gray blotches (less extensive than in *bifossatus*), and is laterally infringed upon by the dorsal crossbands. Posteriorly, the belly is progressively more heavily stippled with black to the tail, on which the ground color is black with numerous light flecks and stipplings.

In specimens which retain the *stratum corneum*, the dorsal ground color is reddish brown, that of the crossbands is darker brown, and the color of the upper surface of the head is a very dark brown. The labials and undersurfaces have a pinkish ground color.

The ventral scutellation is as follows: abdominals, 173–89 (180); subcaudals, 92–105 (100); total ventrals, 279–81 (280).

RANGE.—This form probably is widespread throughout the savannas of eastern Colombia, southern Venezuela and the Guianas, and northern Brazil (north of the Amazon). It probably intergrades broadly with *triseriatus* through the isolated savannas of the Amazon basin (Map 1).

MATERIAL EXAMINED

Locality (and Museum Number)

Colombia

Villavicencio (I.L. 25, 26; M.C.Z. 19200, 31908–9; U.M.M.Z. [not catalogued—locality in doubt])

The following *striatus-triseriatus* intergrades have been examined:

Venezuela

Arabupu (A.M.N.H. 36059–60; U.M.M.Z. 85271)

VARIATION.—Inasmuch as I have had access to only 6 specimens of this species, representing but a single locality, it is impossible to present any discussion of variation in this form. It should be noted that, on the basis of the material available, there is a marked indication of tremendous sexual dimorphism with respect to the number of abdominal scutes, as indicated in Table X.

TABLE X

Sex	Specimens	Range	Mean
Male	3	173-79	175
Female	2	185-89	187

AFFINITIES.—Only the relationships of this species to the other 2 members of the group need to be mentioned here. Although *bifossatus* and *triseriatus* differ from each other in pattern alone, *striatus* may be separated from them on the basis of scutellation (total ventrals) as well as on the basis of pattern. In other words, this form seems better differentiated and has apparently been isolated from the other 2 for a considerable period of time. In Table XI differences in ventral scutellation are indicated.

TABLE XI

Form	Number of Specimens	Abdominals	Subcaudals	Total Ventrals
<i>striatus</i>	6	173-89 (180)	92-105 (100)	279-81 (280)
<i>bifossatus</i>	61	161-85 (174)	86-102 (95)	254-79 (269)
<i>triseriatus</i>	9	169-81 (175)	88- 99 (92)	263-78 (269)

Intergradation between *striatus* and *triseriatus* is indicated in specimens from Arabupu, Venezuela. Scattered throughout the Amazonian forest are local patches of savannas which, in all probability, form a broken chain from the *campos* of the Guianas to those of Pará, and further collecting in those areas may reveal that there is a gradual transition between *triseriatus* and *striatus*.

It is difficult to say which of the other 2 subspecies *striatus* most closely resembles. The completeness of the crossbands indicates a close relationship to *bifossatus*, but the slightly greater number of crossbands and the black tail indicate a *triseriatus* relationship. On the basis of the belly pattern it is intermediate. Geographically, it is closer to *triseriatus*. This problem is more adequately discussed in the following section.

ORIGIN AND AFFINITIES OF THE *BIFOSSATUS* GROUP

The *bifossatus* group, with its banded adult pattern, lower number of dorsal scale rows, and greater number of maxillary teeth, appears to contain

the most "primitive" forms in the entire genus. Little or no specialization is evident in the group, but the pattern has progressed from the prototypic alternating series of dorsal and lateral blotches to the more advanced continuous dorsal bands or derivatives thereof. In this respect it has paralleled the condition existing in the juveniles of *dorsalis*, *laevis*, *melanolomus*, and *veracrucis* in the *melanolomus* group. Because of its having retained this "primitiveness," the *bifossatus* group may be assumed to be the most ancient in the genus; its evolution may have been retarded by its having existed, throughout its history, under conditions similar to those in which the prototype had its inception. Its increase in size (it is one of the largest of the few colubrids existing in South America) may possibly be the result of a favorable habitat, which has enabled it to prosper in the almost complete absence of competing colubrids.

The history of the *bifossatus* group has been relatively uneventful as compared with that of other groups in the genus. The areas inhabited by the various forms have been fairly stable geologically over a long period. The Archiguayan shield and the Plano Alto, which form the greater part of its range, have remained almost unchanged throughout the Cenozoic, though much of the Amazon basin has been covered by fresh-water lakes of considerable size during the same era. Since it is thus restricted in its range, an explanation of its present distribution is relatively simple.

The prototype of the group apparently had its inception on the Guiana highlands of southern Venezuela, the Guianas, and northern Brazil, sometime during the early Cenozoic, from a form which invaded South America from North America prior to the mid-Eocene. That this region was the ancestral home of the generic prototype is evident. The reasons for this assertion are discussed elsewhere in this paper. This *bifossatus* prototype was probably very similar in pattern and scutellation to *pulchriceps*, except that it possessed 17 rows of dorsal scales. From the Guiana highlands the form spread southward on the Plano Alto and invaded most of South America east of the region now covered by the Andes and south to Paraguay. The reversal of the Amazon River during the Miocene and the subsequent development of the Amazonian lowlands, with their luxuriant rain forest, split this wide-ranging form into 2 populations, one to the north of the Amazon and the other to the south. With this effective barrier between the 2 populations, differentiation was inaugurated. This first differentiation probably took the form of a reduction in the number of ventral scutes, which might be interpreted as peripheral reduction such as that in *slevini*, *veracrucis* and *bruesi*. It is possible that while this was taking place the pattern of alternating dorsal and lateral blotches changed to one of continuous bands. After the split into 2 populations, some of the southern population appears to have invaded the more humid regions of the plateau slope, while

in the west, on the dry lands, the original type persisted. In these 2 diverse localities, the original southern type gradually differentiated into 2 different forms, *bifossatus* and *triseriatus*, but so slightly that a broad region of intergradation persists even today. The northern population, on the other hand, gave rise to *striatus*.

Thus, although apparently there was differentiation, it had not progressed far enough to preclude interbreeding between *striatus* and *triseriatus* when interbreeding became geographically possible. In the final stage 3 subspecies have been produced; of these 2 are extremely close to each other, but the third is a well-differentiated form which has joined the other 2 secondarily. The phylogenetic outline of Figure 4 indicates the relationships of the forms as I conceive them.

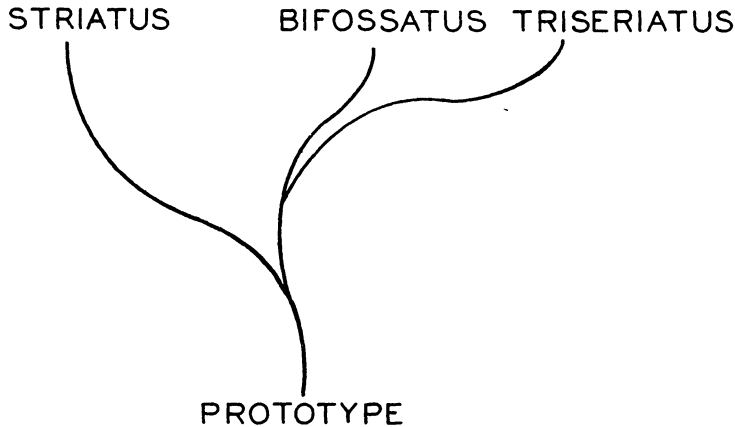


FIG. 4. Relationships of the forms of the *bifossatus* group.

POSITION UNCERTAIN

Dryadophis pulchriceps (Cope)

Masticophis pulchriceps Cope, 1868: 105 (type locality, Plateau Valley of Quito [Ecuador]; type, U.S.N.M. No. 6704 [existence doubtful]).

Coluber fasciatus Rosen, 1905: 172, Pl. XI, Fig. 2 (type locality, Ecuador; type, Lund Museum, number unknown).

DESCRIPTION.—This poorly understood species appears to have the combined characters of the *bifossatus* and *boddaerti*-like groups. In possessing but 8 supralabials and a banded adult pattern, it resembles the *bifossatus* group, but its 17 rows of dorsal scales indicate a relationship to the *boddaerti* series.

In alcohol (*stratum corneum* lacking) the dorsal pattern to the vent consists of a series of 30–50 dark gray, black-edged, rectangular blotches which extend from scale row 5 on one side to scale row 5 on the other. Laterally,

and alternating with these dorsal blotches, is a series of spots similar in color and shape to the dorsal ones and extending from the ventral scutes to dorsal scale row 4. Although these lateral and dorsal blotches are generally fused, there is a distinct tendency for them to be separated by a narrow, light lateral line formed by white fleckings on scale rows 4 and 5. These series of blotches, both dorsal and lateral, are separated one from another by light crossbands formed by a white border and a gray center on each scale in the band. At mid-body the dark blotches are 3-4 scales in length and the intervening light bands are 1-2 scales long. Posteriorly on the body the light bands are progressively somewhat shorter, and there is a distinct tendency for the dorsal and lateral black blotches to be opposite rather than to alternate. On the tail, the latter condition is typical, and the pattern becomes a series of long dorsal bands separated (except along the lower scale rows on either side) by short, light bands. Anteriorly on the body, both the light bands and the dark blotches become slightly longer, and the latter tend to become irregular and often obliquely placed. On the neck and extreme fore part of the body the lateral line mentioned above becomes intensified on scale rows 4 and 5 and generally produces complete separation of dorsal and lateral dark blotches.

The head pattern is variable, but has certain general, stable characteristics. The rostral is black with a small median light spot or narrow vertical line and with a light superior border. The internasals and prefrontals are light, with a narrow black border and a dark median spot. The frontal and supraoculars are mottled black and gray, and all have a narrow white border. The parietals are black, with a narrow white border which medially combines with its neighbor to produce a median white stripe on the posterior part of the head. Laterally, the nasals, loreal, lower half of the preocular, lower postocular, and lower temporals are black, a black stripe being thereby produced. This stripe divides on the posterior labials and sends one branch to the angle of the mouth and another to the first dorsal blotch, which is divided by a white line medially. This light line on the nape extends forward and splits at the parietals, to send one branch forward on either side across the upper temporals to produce a V-shaped, white figure. The supralabials are white, mottled, or flecked with black. A dark stripe extends obliquely from the base of the orbit across labials 4, 5, and 6 to the mouth. The infralabials are black, with white median spots which in some instances extend to the mouth. The chin and throat are black, flecked with white. The belly is black or of a mottled pattern of black, gray, and white, and the majority of the ventral scutes have, on either side, a lateral white spot. These spots tend to disappear posteriorly. The undersurface of the tail is black or gray (Pl. II, Figs. 1-3).

The ventral scutellation of this form is as follows: abdominals, 171-85 (180); subcaudals, 84-99 (93); total ventrals, 264-84 (275).

RANGE.—So far as is known, this species is restricted to the Guaymas basin and the more humid habitats of west central Ecuador (Map 1).

MATERIAL EXAMINED

Locality (and Museum Number)

Ecuador

- Balzapamba (A.M.N.H. 35952)
- Guayaquil (U.S.N.M. 62803-7)
- Hulgra, Río Chiquancy (A.N.S. 18124, 18126)
- Pasage (A.M.N.H. 22098)
- Penaherrera (U.M.M.Z. 83712)
- West Ecuador (B.M. 60.6.16.57, 60.6.16.64-65)

VARIATION.—Too few specimens of this perplexing species have been available to afford a very complete discussion of variation. Not only does *pulchriceps* need further study, but also, *boddaerti* in western Ecuador is not satisfactorily known. It is most difficult to distinguish between juvenile *boddaerti* and *pulchriceps* in this region, but *pulchriceps* is readily identified by the possession of only 8 supralabials. Unfortunately, there are occasional specimens with 9 supralabials and a few *boddaerti* with but 8. In these instances one must rely upon the very dark ventrum of *pulchriceps* for identification.

AFFINITIES.—As previously indicated, *pulchriceps* probably is very like the prototype of the entire genus, and has apparently specialized only in the reduction of the number of maxillary teeth and of the number of supralabials. It has been pointed out above that this form is intermediate between the *bifossatus* group and the *boddaerti*-like species, though neither of these has sprung directly from it. *D. pulchriceps* probably represents, rather, a slightly specialized offshoot of the prototype. It therefore seems fairly certain that the form is a relict which has in some manner become isolated in western Ecuador. This isolation was undoubtedly brought about by the elevation of the Andes, possibly during the Miocene. Geological evidence indicates that the Andes were first folded during the Cretaceous and that peneplanation took place throughout the early Cenozoic. In the Miocene were begun the elevation and subsequent erosion which produced mature land forms, and further elevation took place during the Pliocene and Pleistocene. It must be assumed that the early folding resulted in sufficient elevation to produce fairly arid conditions along the west coast of South America, since the prototype of the genus seems to have occupied arid, but not desert, habitats. The bird distribution along western South America indicates that such climatic conditions prevailed (Chapman, 1926: 73).

The prototype of *pulchriceps* was distributed over most of northern South America and, by means of the elevation of the Andes, was separated into eastern and western populations; later evolution caused the replacement

of the prototype in the east, but the more "primitive" characters were retained in the west (Ecuador). This is substantiated by Chapman's discovery of a parallel condition in birds (Chapman, 1926: 62-74). Apparently, *pulchriceps* has not spread southward on account of the very arid Peruvian coast, and it has not spread northward because of the humid Choco.

THE PLEEI GROUP

Dryadophis pleei^s (Duméril and Bibron)

- Dromicus pleei* Duméril and Bibron, 1854: 661 (type locality, Martinique [undoubtedly an error]; types, Museum National d'Histoire Naturelle, Nos. 1255, 3549, and 7355).
Herpetodryas quinquelineatus Steindachner, 1870: 346 (type locality, Rio Vaupés [Brazil or Colombia]; type, Zoologisches Institut der Universität Wien, number unknown).
Dromicus (Alsophis) maculivittis Peters, 1877: 458 (type locality, Calabozo [Venezuela]; type, probably in Zoologische Museum, Berlin, number unknown).
Alsophis pulcher Garman, 1887: 283 (type locality, Testigos Island; type, M.C.Z. No. 6146).

DESCRIPTION.—An adequate description of this species would require a separate discussion of each individual. Examination of numerous specimens indicates, however, that all individual variations are merely slight departures from a basic pattern type. This basic type is produced by a darkening of various parts of the scales with varying shades of gray or brown, depending on the state of preservation. The typical form may be described as follows: scale row 9 (middorsal row) is light. The upper half of scale row 8 on each side is black; there is, therefore, a dorsal dark stripe with a light center. The lower half of scale row 8 and the upper half of scale row 7 are light. Scale row 6, like scale row 9, is light and is bordered on either side by a black stripe, caused by the darkening of the lower half of scale row 7 and of the upper half of scale row 5. So striking is the black, and so flecked with gray or black are the light scales (with the exception of the upper half of scale row 7 and the lower half of scale row 8, which remain very light), that a pattern of 3 dark dorsal stripes is formed. These appear to be located on scale rows 5, 6, and 7 on each side, and middorsally on scale rows 8, 9, and 8. These dark dorsal stripes all have lighter centers. Laterally, the lower half of scale row 5, all of scale row 4, and the upper half of scale row 3 are light, thus producing a broad, light lateral stripe. The lower half of scale row 3 and the upper half of scale row 2 are black, producing a narrow dark stripe; the lower half of scale row 2 and all of scale row 1 are light.

About a third of the distance posteriorly on the body the 3 dark dorsal

^s As I have been unable to examine the types of this form, it is with some hesitancy that I use the name. My friend, E. R. Dunn, informs me that there is, in the Academy of Natural Sciences of Philadelphia, a specimen which he believes to be one of the cotypes. Dunn's description leaves little doubt as to the identity of that specimen.

stripes fuse to produce a pattern more like that found in the *boddaerti* and *alternatus* groups. This may be described as a dark dorsal ground color with 2 lateral light stripes—the upper on scale rows 3, 4, and 5, bordered above and below by a narrow dark line, and the other on scale rows 1 and 2, and bordered above by a narrow dark band.

The upper surface of the head has the dorsal ground color and is heavily mottled with darker shades. Laterally, the head is somewhat lighter, but bears a broad dark streak which extends from the nostril through the eye and across the temporals. In many specimens this is continuous with the more lateral of the dorsal dark stripes. The supralabials are light, with a very dark inferior border which in some cases extends upward and enters the orbit. The infralabials, chin, and throat are light, very heavily mottled with dark gray. This mottling may extend posteriorly to the belly, which is light, and there produce a mid-ventral smudge. The undersurface of the tail is of the same color as is the belly. Laterally, the belly and underside of the tail are infringed upon by the dorsal ground color, the limits of which are never definite. In living specimens the lighter shades appear to be yellow or cream and the darker parts are either black or very dark brown (Pl. I, Figs. 3 and 4, Pl. III, Figs. 1 and 2).

The ventral scutellation of this species is as follows: abdominals, 171–91 (183); subcaudals, 83–105 (94); total ventrals, 263–94 (277).

RANGE.—This species ranges over the more arid parts of Colombia and Venezuela, and is known from Margarita and Testigos Islands. It has also invaded Central America along the Pacific coast to as far north as Panama City (Map 2).

MATERIAL EXAMINED

Locality (and Museum Number)

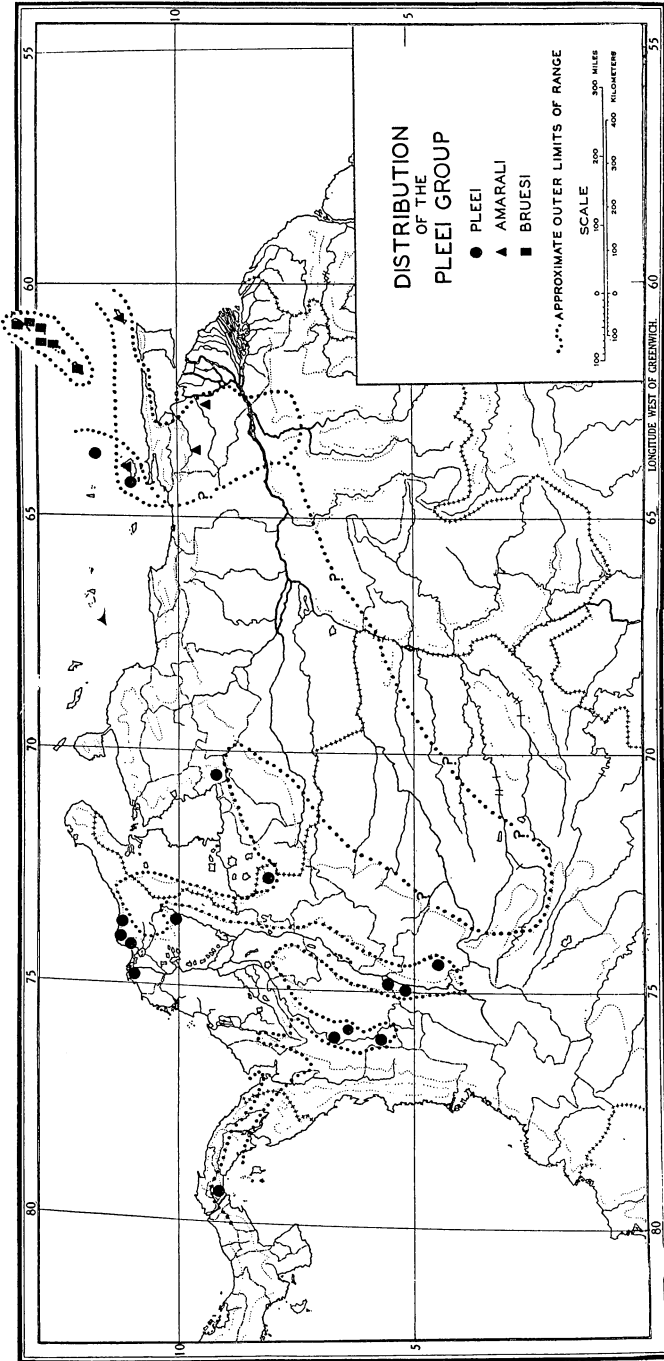
Central America (U.S.N.M. 12474)

Colombia

- Barranquilla (I.L. 5)
- Bonda (C.M. 177–82, 186)
- Ciénaga (B.M. 1922.6.16.24–27)
- Cúcuta (I.L. 5)
- Honda (I.L. 3; U.M.M.Z., uncatalogued)
- Jericó (I.L. 2)
- La Mesa (I.L. 7)
- Rosario de Cúcuta (B.M. 89.8.23.8)
- Sabanalarga (A.M.N.H. 35791)
- San Pedro (A.M.N.H. 35747, 35750, 35791)
- Valencia (U.M.M.Z. 54956)
- Valparaiso (C.M. 202)

Panama

- Cloche Province (U.M.M.Z. 83514)
- Isthmus of Panama (B.M. 1905.7.10.3)
- Savannas of Panama (U.M.M.Z., uncatalogued)



- Testigos Island (M.C.Z. 6146 [type, *Alsophis pulcher*])
Venezuela (A.N.S. 5604; B.M. 46.7.23.— [one of types of *rappii*])
Cacaguileto (C.M. 2009, 2020)
Margarita Island (B.M. 1906.8.14.34; F.M.N.H. 2678; U.S.N.M. 22533, 79225)
Mendoza (U.M.M.Z. 57396)

VARIATION.—A complete discussion of the variation found in the pattern of *pleei* would require a detailed description of each individual specimen. As has been pointed out, the variations may all be considered as departures from the basic pattern type previously described. Although the majority of these departures are brought about by slight variations in the color of but a few individual scales, the few variations can produce an effect of having altered the pattern completely. To illustrate, one of the most common variants is caused by the change in certain scales above the broad, lateral light stripe, these scales having taken on a much lighter color or having light borders. In many instances these scales are arranged in rows across the dorsum, and the effect is a banded pattern, since the 3 dorsal dark stripes seem to have been obliterated. Actually, the dorsal dark stripes remain and are merely interrupted at intervals by these lighter bands, but the eye subordinates the longitudinal stripes to the white crossbands.

Another pattern variation of considerable frequency is produced by the reduction of the black stripe separating the 2 light lateral stripes. It often happens that this dark stripe is reduced to a mere narrow streak in the center of scale row 3, and occasionally it is lacking and scale rows 1, 2, 3, 4, and the lower half of 5 are left light, except for dark fleckings on some of the scales. There are other variations—too numerous and too complex to describe—which are produced by white or black scale margins, by various dark streakings on other scales, and by remnants of juvenile pattern, and which have neither geographic or phylogenetic significance.

Variations in scutellation and in pattern are for the most part without significance. It should be reiterated, however, with reference to the number of abdominal scutes, that sexual dimorphism is greater in *pleei* than in any other form in the genus. Geographic variation is slight and is entirely lacking in trends. Specimens from the Bogotá region are almost identical with those from the lower Magdalena Valley, though both groups have a slightly greater number of abdominal and total ventral scutes than have the Margarita Island specimens. There is no such variation, however, as is found in *alternatus* (discussed below).

AFFINITIES.—Although the identity of derivatives of *pleei* is more or less obvious, the progenitor of this species is lost in oblivion, and the character of the prototype from which it developed is open to conjecture. The clear differentiation of all members of this group and the fact that 1 species has reached Grenada, the Grenadines, and St. Vincent, its range thus exceeding

the ranges of the other groups in the Antilles, may possibly be taken as indications of a history somewhat longer than that of either the *melanolomus* or the *boddaerti* group. With the exception of the peculiar *heathii*, no other group of the genus has a pattern in which 3 scale rows are involved in the production of the upper light lateral stripe. Furthermore, the 3 dark dorsal stripes present a condition which does not, on the basis of available material, lend itself to interpretation.

With reference to pattern it should be noted, however, that in species of closely related genera, i.e., *Salvadora pulcherrimus* and *Masticophis t. girardi*, 3 scale rows are involved in the upper light lateral stripe, whereas in other species of the same genera no more than 2 scale rows enter into that same stripe. In the genus *Salvadora*, in particular, the lateral light stripe of the basic form of the *mexicanus* group involves the same 3 scale rows. Furthermore, this species, *pulcherrimus*, has a more southerly range than has any other form of the entire genus. Since *Salvadora* probably came from the same protostock that *Dryadophis* is derived from, it does not seem illogical to assume that the transition from the previously described banded pattern to the striped condition passed through a stage in which scale rows 3, 4, and 5 made up the dominant light lateral stripe. Unfortunately, none of the species of *Dryadophis* which have retained the "primitive" pattern show any indication of a lateral light stripe involving more than 2 scale rows, for scale row 4 has been lost.

The *pleei* group, whatever its prototype may have been, apparently had its origin in northern South America, and the indications are that physiological mutations caused it to be restricted to the more arid regions while the *boddaerti* group was developing in the more humid habitats. For this reason *pleei* has been prohibited from southward movement by the Amazonian forest. That it did not move southward with the *bifossatus* group when conditions might well have permitted that migration (see discussion of *bifossatus* group) may be explained by the likelihood that other genera were already in possession of the ecological niches which *pleei* otherwise might have occupied. Beyond these few suggestions, discussion of the origin and affinities of *pleei* is rendered impossible both by the lack of material and by a lack of knowledge of the early history of the species.

Dryadophis amarali (Stuart)

Eudryas amarali Stuart, 1938: 7 (type locality, Margarita Island; type, U.S.N.M. No. 22534).

DESCRIPTION.—The very few specimens which have been available indicate that this form is remarkably constant in pattern. In alcohol (*stratum corneum* lacking) the dorsal ground color is a bluish gray. In some specimens each scale is finely dusted with a darker shade, particularly on the

posterior half of the scale. A very narrow dark posterior border on each scale is an almost constant character. Anteriorly there is a light lateral stripe on scale rows 3, 4, and 5. This stripe includes the upper half of scale row 3, all of scale row 4, and the lower half of scale row 5. The lower half of scale row 3 and the upper half of scale row 5 are darkened somewhat, so that a narrow dark border on the lateral stripe is formed. Both the light stripe and its dark border gradually fade posteriorly and disappear at about one-third of the way back on the body. Below this stripe, in some specimens, there is evidence of a narrower light stripe on the extreme upper part of scale row 1 and the lower margin of scale row 2. The upper surface of the head is of the same color as is the dorsum. Laterally, this color becomes lighter, leaving the supralabials white or cream. A faint dark smudge extends from the nostril through the eye and across the temporals. The infra-labials, chin, throat, and entire under parts are cream or white, generally immaculate or lightly dusted with gray. Laterally the belly and underside of the tail are infringed upon by the dorsal ground color, the limits of which are demarked by a narrow light line (Pl. III, Fig. 3).

The ventral scutellation is as follows: abdominals, 183-96 (189); sub-caudals, 110-19 (115); total ventrals, 300-312 (306).

RANGE.—Although this species is imperfectly known there is a reasonable probability that it inhabits the dry lands of northeastern Venezuela and the islands off the north coast, with the exception of Trinidad, to Tobago (Map 2).

MATERIAL EXAMINED

Locality (and Museum Number)

Tobago Island (U.S.N.M. 10137 [paratype of *amarali*])

Venezuela

Cariquito (A.N.S. 18286-87 [paratype of *amarali*])

Margarita Island (U.S.N.M. 22534 [holotype of *amarali*])

San Antonio de Maturín (M.C.Z. 9988-90 [paratypes of *amarali*])

VARIATION.—The available specimens of this species are too few to serve as the basis of adequate discussion of variation.

AFFINITIES.—As stated in the description of this form, there can be no doubt but that it has been derived either directly from *pleei* or from a *pleei*-like ancestor (Stuart, 1938: 8). The pattern is readily recognized as having been derived from that of *pleei* through a loss of throat mottling and through the fusion of the 3 middorsal stripes. In fact, so close is the pattern of *amarali* to that which covers the posterior part of the body in *pleei* that the 2 are almost identical. An increase in the number of ventral scutes in *amarali* has accompanied the simplification of pattern. Similarly, scutellation increase has accompanied pattern simplification in the forms which have

developed from *alternatus*. It seems probable that from a *pleei*-like stock *amarali* developed on the outer parts of the Parian land mass when that part of Paria was still connected with the mainland, or later on one of the islands off the northern coast (Tobago, most probably) while *pleei* was developing farther to the south and west on continental South America. *D. amarali* reinvaded the mainland (possibly as a waif) when separation had been completed and now exists with *pleei* on the mainland and on some of the coastal islands.

Dryadophis bruesi (Barbour)

Alsophis bruesi Barbour, 1914: 337 (type locality, near St. George's, Grenada, B. W. I.; type, M.C.Z. No. 7792).

DESCRIPTION.—Although variable in detail, a condition possibly resulting from differences in the states of preservation, this species exhibits a basically fundamental pattern throughout. The dorsal ground color is probably light blue-gray, but so heavily is each scale powdered with darker hues that the ground color appears to be very dark blue-gray. A light lateral stripe is present on scale rows 4 and 5, or, occasionally, only on row 4. If the former condition prevails, the upper posterior margin of scale row 4 and the lower anterior margin of scale row 5 are lightened, and the result is a zigzag appearance. Occasional specimens have only a narrow light posterior border on row 4. The upper half of scale row 5 and the lower half of scale row 4 are darkened, a dark border of the lighter lateral stripe being thereby produced. Scale rows 1, 2, and 3 generally have darker centers, and the borders are somewhat lightened. This is especially noticeable on scale row 1 and often produces a lower lateral light stripe. All traces of stripes disappear about halfway back on the body. The upper surface of the head is of the same color as is the dorsum. This color becomes lighter laterally, and is entirely lacking on the labials. A dark smudge extends from the nostril through the eye and across the temporals and upper portion of the posterior supralabials. The supralabials and infralabials are cream or white, many of the scales possessing a narrow darker border. The chin and throat are white, as is the underside of the body and tail. The under parts are in some instances immaculate, but more generally they are dusted with gray. Laterally, on the belly and underside of the tail the ground color of the dorsum is strongly evident, and its limits are demarked by a conspicuous light line. In living specimens the dorsal ground color appears to be dark olive brown, whereas the under parts are cream (Pl. III, Fig. 4).

The ventral scutellation is as follows: abdominals, 191–206 (199); subcaudals, 112–30 (122); total ventrals, 308–32 (321).

RANGE.—This species is known only from Grenada, the Grenadine Islands, and St. Vincent, British West Indies (Map 2).

MATERIAL EXAMINED

Locality (and Museum Number)

- Grenada Island (B.M. 88.2.13.54; U.S.N.M. 79191)
 St. George's (M.C.Z. 4509 [5], 6120 [6], 7792 [7] [types of *bruesi*])
- Grenadines
 Caille Island (U.S.N.M. 79161)
 Moustique (B.M. 91.5.12.5)
 Quatre Island (U.S.N.M. 79099)
 Union Island (U.S.N.M. 79166)
- St. Vincent Island (B.M. 88.2.13.55, 90.11.25.19-20; M.C.Z. 6142 [3])
- Trinidad (undoubtedly an error) (B.M. 97.7.23.51)

VARIATION.—There is little to be said concerning the variation in the species. As pointed out previously, this form is unique among all the forms in the *boddaerti*-like groups in that it has a slightly greater number of maxillary teeth. I am unable to offer an interpretation of this peculiarity at this time, unless it indicates "primitiveness," as previously discussed.

The most conspicuous variant character in this form is the number of ventral scales. There is a tendency for the peripheral populations of peripheral forms to have a smaller number of ventral scutes. This species is no exception, as indicated in Table XII (based on female specimens only).

TABLE XII

Locality	Number of Specimens	Abdominals	Subcaudals	Total Ventrals
Grenada Isl.	6	197-206 (202)	116-24 (120)	313-29 (322)
St. Vincent Isl.	4	196-204 (201)	112-19 (116)	308-21 (317)

Variations in other characters are so negligible as not to warrant discussion.

AFFINITIES.—I feel that, to be intellectually honest, I must admit that the conclusions in accordance with which I assign this species to the *pleei* group have been drawn from a very slight amount of scientific evidence. That this form may be a member of the *boddaerti* group is by no means impossible, but I believe that the little (and extremely weak) evidence which exists points toward a *pleei* relationship. The *pleei* group as a whole is made up of species neither so large nor so robust as those of the *boddaerti* group, and *bruesi* is, with the exception of *pulchriceps*, the smallest and most slender form in the entire genus. The members of the *pleei* group are well differentiated one from another (to a specific degree in the case of *pleei* and *amarali*), whereas *boddaerti*, *ruthveni*, and *dunni* are very closely related, and the mainland forms intergrade with one another. This degree of differentiation may be taken as an indication of age, and it therefore seems only

logical to conjecture that the older group would be more likely to have reached the more distant islands. Furthermore, the sequence of pattern from *pleei* to *bruesi* forms a far more logical chain than does that from *ruthveni* to *bruesi*. For example, *amarali* has a reduced *pleei* pattern (fusion of dorsal stripes), but *bruesi* has an *amarali* pattern even further reduced and approaching—what I believe to be the end pattern throughout the genus as a whole—the unicolor condition. In some specimens of *amarali* the dorsal scales have a definite dusting of gray or black, and in *bruesi* this dusting is greatly intensified. If *bruesi* were a member of the *boddaerti* group, on the other hand, its pattern would represent a radical change from *dunni*, which is very like *ruthveni*. With reference to ventral scutellation, this species might well be a member of either group. It is therefore to be suggested on this evidence, meager though it is, that *bruesi* fits logically into the *pleei* line.

If the above conclusions are correct, the closest relative of *bruesi* is *amarali*. This view is supported by morphological as well as geographical evidence. Morphologically, with reference to ventral scutellation, bodily proportions, and pattern, *bruesi* presents one end of a *pleei-amarali-bruesi* line, as previously pointed out. Evidence indicates that *bruesi* has developed from an *amarali*-like progenitor rather than directly from a *pleei*-like type. Geographically, moreover, there is ample support for the view that *bruesi* is an offshoot of *amarali*. As has been shown, *amarali* very probably developed either on the outer extension of the ancient Parian land mass while it was still joined to South America, or later, on one of the coastal islands after they had become separated from South America. At any rate, it seems very probable that an *amarali* prototype or *amarali* itself entered Grenada as a waif (ocean currents in this region flow northwesterly along the coast and hence from Tobago toward the Grenadines) and from it developed *bruesi*, which later spread through the Grenadines and to St. Vincent. It is far more logical to assume that Grenada was populated from the nearer islands than that it was populated from the mainland.

ORIGIN AND AFFINITIES OF THE PLEEI GROUP

If the previous conclusions as to the composition of the *pleei* group are correct, the task of explaining the origin and distribution of the various forms offers few difficulties. An examination of biological data and of the resultant reconstruction of the history of this group, based entirely upon this evidence, coincides perfectly with the geological history of the region which the group inhabits. This geological history, which has been treated in detail by Schuchert (1935), may well be summarized at this point.

The history of the *pleei* group is laid primarily on the ancient land mass of Paria and in the region directly to the south of it. Paria extended north and east into the Caribbean Sea from what is now northern Venezuela to

Barbados. This land mass began to break down during the late Cretaceous, but land connections existed to Tobago until the upper Miocene or possibly until the early Pliocene. Barbados, on the other hand, was subjected to tremendous oscillatory movement during the entire Cenozoic and did not finally emerge from the sea until the late Pliocene. The southern Caribbees, Grenada to St. Vincent inclusive, have a more obscure history. By some authorities it is held that there may have been connections between the mainland and this chain up to the Pliocene, although others deny that such a bridge existed. It should be noted, however, that the assumption that this land connection existed is not the only possible way of explaining the entrance of *bruesi* into the island chain. The species could—and very probably, did—enter the island chain as a waif. Finally, it is important to understand that no land connection existed between Tobago, the southern Caribbees, and the coastal islands after the lower Pliocene, and that these islands were never connected one with another after that date.

Another physical feature of this region to which attention should be called is the South Atlantic equatorial current. This current strikes the continent at Cape de São Roque, Brazil, and one branch swings northward along the Brazilian and Guianan coasts. Its main body passes between Tobago and Trinidad, and it washes the shores of the islands off the north coast of Venezuela. This current, depending on the intensity of the trade winds, moves northward and southward, so that at times it flows past the southern Caribbees and at other times moves southward to wash the Venezuelan mainland.

The only biological data of importance in an examination of the origin of the *pleei* group are those of pattern and ventral scutellation. Progressing from *pleei*, *amarali* represents the first stage in the loss of pattern through a fusion of the 3 dark dorsal stripes and a reduction of the lower lateral light stripe; *bruesi* represents a still further reduction in pattern through the almost complete loss of the lower lateral stripe and a considerably reduced upper lateral stripe. Although the unicolor condition considered as the end result in the genus has not been attained in this group, there is a marked tendency in that direction. The ventral scutellation shows a distinct increase from *pleei* through *amarali* to *bruesi* and parallels the situation found in the *melanolomus* group. In Figure 5 this gradual increase in the number of ventral scutes is indicated graphically. On the basis of both pattern and ventral scutellation, therefore, it appears that a distinct orthoëvolutionary trend exists from *pleei* to *bruesi*.

On the basis of these geological and biological data it seems probable that the *Dryadophis* prototype entered South America from North America prior to the mid-Eocene and gave rise to the ancestral *Dryadophis* which eventually formed the *pleei* prototype. Although it is difficult to visualize

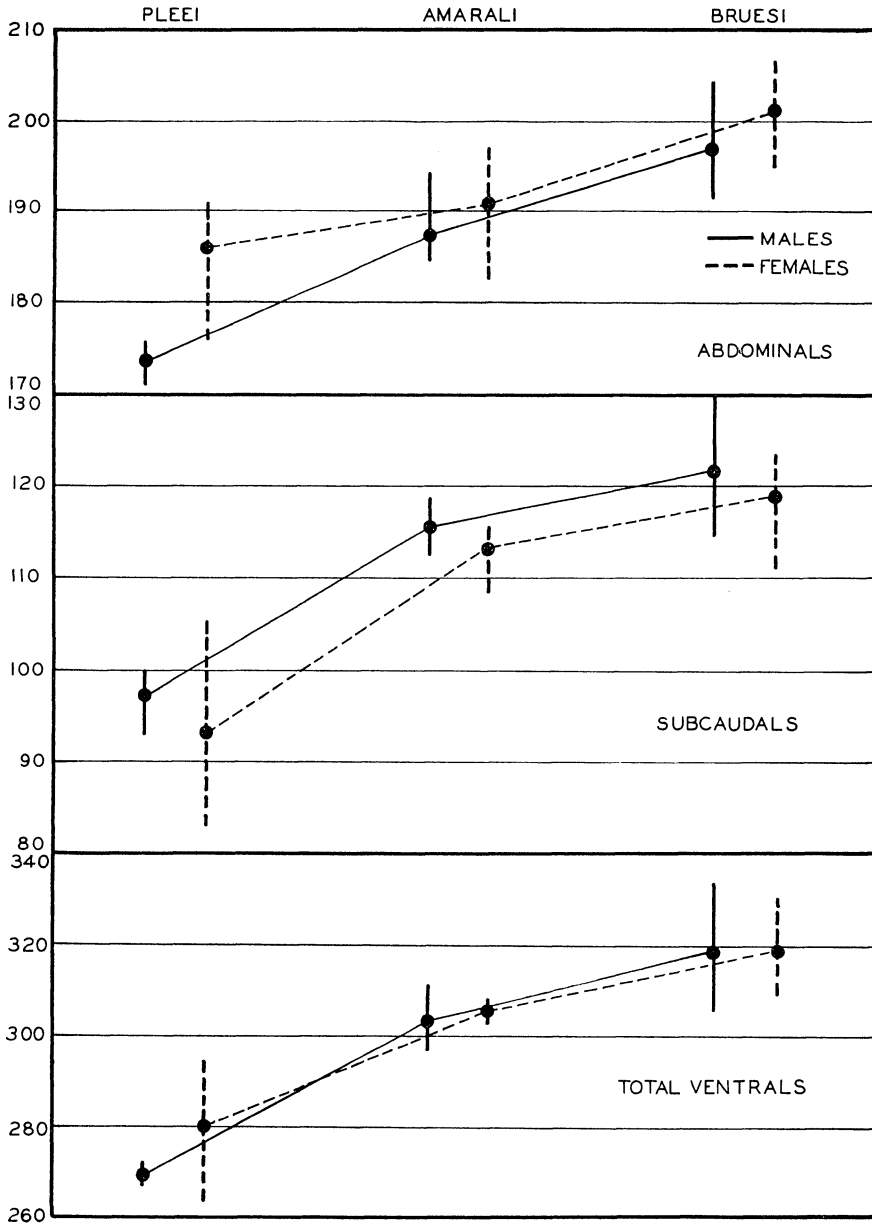


FIG. 5. Trends in ventral scutellation in the *pleei* group. Compare this with the trend in subcaudals in the *melanolomus* group (Fig. 11). There is great sexual dimorphism in the abdominals of *pleei*.

the prototype of the group, that it resembled *pleei* appears fairly evident. The ancestral home of the group was undoubtedly Paria and the area to the immediate south. On the outer end of this land mass a form similar to *amarali* developed, whereas to the west the prototype probably was changing but little under the ancestral environment. When the connection between the mainland and Tobago was severed (probably in the lower Pliocene), the *amarali* ancestor was isolated, and eventually it became true *amarali*. Two explanations may be offered to account for *bruesi*. Either the *amarali* ancestor reached the southern Caribbees by way of a land bridge which may have existed prior to the Pliocene, or, more probably, it entered those islands as a waif from Tobago after a more *amarali*-like form had evolved there and subsequently became *bruesi* on the southern Caribbees. At any rate, 3 forms appear to have developed serially: *pleei* on the mainland, *amarali* on Tobago, and *bruesi* on the southern Caribbees. Later currents account for the re-invasion of the mainland and of the coastal islands by *amarali* as a waif and for the re-invasion of the coastal islands in the same manner by *pleei*. The reason why *bruesi* has never entered the coastal islands or the mainland may be that no ocean currents wash the shores of both the lower Caribbees and the northern coast of South America. The absence of *amarali* from Trinidad is not explicable in the light of present knowledge of the group, but it may be due to some ecological factor. My concept of the relationships of the forms of this group is presented in Figure 6.

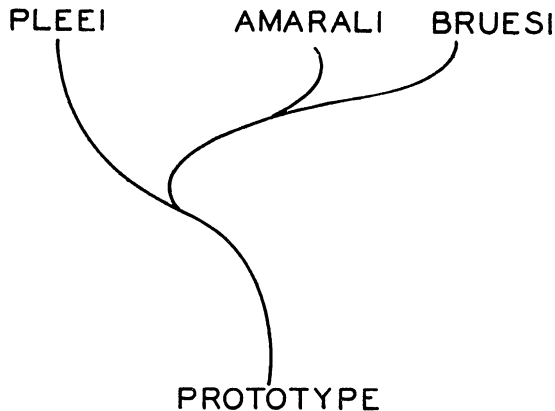


FIG. 6. Relationships of the forms of the *pleei* group.

THE *BODDAERTI* GROUP

Dryadophis boddaerti ruthveni (Stuart)

Eudryas ruthveni Stuart, 1933a: 4 (type locality, slopes of San Lorenzo in the Sierra Nevada de Santa Marta, Colombia, altitude about 5500 feet; type, U.M.M.Z. No. 54954).

DESCRIPTION.—The dorsal ground color (*stratum corneum* lacking) of this form is blue-gray. Laterally, on each side, a light line is present on

scale rows 4 and 5. This line is produced by an intense lightening of the upper half of scale row 4 and of the lower half of scale row 5. The lower half of scale row 4 and the upper half of row 5 are black; there are therefore dark upper and lower margins along the light line. Below this dark-margined, light stripe is a second light line on scale rows 1 and 2. This lower stripe is variable in width and intensity, but typically it is the result of a lightening of the lower anterior part of scale row 2 and of the upper posterior part of scale row 1, these giving this lower stripe a chainlike appearance. Above and below, this stripe also may have a narrow dark margin, though the lower margin is usually lacking. The lower stripe generally disappears by mid-body, but the upper one is often continuous, though frequently very inconspicuously, to the vent. The surface of the head is of the same color as is the dorsum. Laterally, the ground color becomes increasingly lighter, leaving the supralabials a dirty white. An indication of a slightly darker smudge extends from the nostril through the eye and across the lower temporals and upper portions of the posterior supralabials. The infralabials, chin, and throat are immaculate white, though they may occasionally be flecked with gray. The belly and undersurface of the tail are white, sometimes slightly mottled with light gray. Laterally, the dorsal ground color infringes upon the underside; the limits of this infringement may or may not be marked by a narrow light line. In specimens in which the *stratum corneum* is in place, the dorsal ground color is olive brown, the labials, chin, and throat, cream, and the belly and underside of the tail, pale yellow (Pl. III, Fig. 5).

The ventral scutellation is as follows: abdominals, 181-99 (191); subcaudals, 114-22 (118); total ventrals, 300-319 (309).

RANGE.—Restricted to the Sierra Nevada de Santa Marta, Colombia (Map 3), at altitudes above 2200 feet (Ruthven, 1922: 65).⁹

MATERIAL EXAMINED

Locality (and Museum Number)

Colombia

Bonda (C.M. 176, 183)

La Concepción (M.C.Z. 6521, 6544-47 [paratypes of *ruthveni*])

Palomina (M.C.Z. 6554-55, 6575, 6577 [paratypes of *ruthveni*])

San Lorenzo, Sierra Nevada de Santa Marta (U.M.M.Z. 55674 [paratype of *ruthveni*])

Sierra Nevada de Santa Marta (various elevations) (C.M. 1873; U.M.M.Z. 45591-97, 54949-53, 54955 [paratypes of *ruthveni*], 54954 [holotype of *ruthveni*])

Valparaiso (C.M. 203)

Vista Nieve (U.M.M.Z. 63775)

South America (C.M. 1872)

⁹ The specimen referred to by Ruthven as collected on the flood-plain forest at Valencia proves to be *pleei*.

VARIATION.—Aside from the variations in pattern already noted, and which may be the result of the state of preservation, this form appears to be remarkably constant. Variations in scutellation are negligible. The restricted range of *ruthveni* undoubtedly accounts for its constancy (see p. 17).

AFFINITIES.—In certain features *ruthveni* may be looked upon as the “primitive” form of the *boddaerti* group. As has been pointed out, the generalized pattern of the prototypes of the *boddaerti*, *melanolomus*, and *pleei* groups consisted of 2 lateral, light stripes. It should be noted that in pattern *ruthveni* does not differ greatly from *alternatus*, especially the population on the Pacific coast. It is believed that the prototype of both the *melanolomus* and *boddaerti* groups occupied northern South America sometime prior to the middle Miocene when the Panamanian–Costa Rican portal finally allowed it to enter Central America.

From that time on *boddaerti* probably began to develop in South America and to replace the *ruthveni*-like prototype. In the meantime Paria was fast breaking up, and the Maracaibo embayment may have isolated a part of that prototypic-like stock on the peninsular arm in northern Colombia the northern limit of which was marked by the Sierra Nevada de Santa Marta. It seems probable, therefore, that, although *boddaerti* developed in northern South America, there remained in the Santa Martas a relict population of the ancient stock which, although increasing its ventral scutellation, retained its “primitive” pattern and became *ruthveni*. The affinity between *ruthveni* and *boddaerti* will be discussed under *boddaerti*; *ruthveni* is here conceived of as a relict form, isolated at a fairly early date in the Sierra Nevada de Santa Marta.

Dryadophis boddaerti boddaerti (Sentzen)

Coluber Boddaerti Sentzen, 1796: 59 (type locality, unknown;¹⁰ type, location of type unknown).

Coluber fuscus Hallowell, 1845: 241 (type locality, within 200 miles of Caracas, Republic of Colombia [Venezuela]; type, location of type unknown).

Herpetodryas rappii Günther, 1858: 116 (type locality, many localities in South America; type, many cotypes in British Museum [Natural History]).

?*Herpetodryas reticulata* Peters, 1863: 285 (type locality, Guayaquil [Ecuador]; type, possibly in Zoologische Museum, Berlin).

DESCRIPTION.—The very large series of this form which has been available indicates that considerable variation in pattern exists within the race. Whether the apparent variation is merely the result of varied states of preservation or actually exists in the living specimens it is impossible to

¹⁰ Merrem (1820: 110) seems to have been the first definitely to allocate this name. His remark “Aufenthalt: Südamerika, vorzüglich Surinam” suggests Dutch Guiana as the type locality. I have, therefore, restricted *boddaerti* to this widespread South American form.

say; but, despite the seemingly tremendous variability, the pattern of *boddaerti* (just as in *pleei* and in *alternatus*) is basically uniform throughout. The dorsal ground color (*stratum corneum* lacking) ranges from pale gray to very dark gun-metal blue, depending on the state of preservation. Laterally, there is a light longitudinal stripe on scale rows 4 and 5 or varying parts thereof. In very large specimens and in those which are dark in color, this stripe is often either very faint or occasionally entirely obliterated. This stripe, which may or may not have narrow, dark borders, generally extends more than three-fourths of the length of the body. The top and sides of the head are of the same color as is the dorsal surface of the body. A dark smudge extends from the nostril through the eye and across the anterior temporals and posterior supralabials. The supralabials are considerably lighter than are the sides of the head and are irregularly mottled with light gray. The infralabials, chin, and throat are white, either immaculate or mottled with gray. The belly and undersurface of the tail vary from white to gray, with or without darker flecks or mottlings. Laterally, the belly is infringed upon by the dorsal ground color, the limits of which are generally demarked by a narrow, light line. Fresh, well-preserved material indicates that in life the ground color of the dorsum, top, and sides of the head varies from green to olive brown, and that the labials and under parts are cream or yellow (Pl. IV, Fig. 1).

The ventral scutellation of this race is as follows: abdominals, 159–201 (184); subcaudals, 79–113 (101); total ventrals, 238–308 (285).

RANGE.—With the exception of Venezuela and the Santa Marta region of Colombia, this form inhabits the more humid areas of northern South America south to the limits of the Amazon basin. It is known from the Andes, from Bolivia to Colombia, but is present along the west coast of South America only from Ecuador northward. The occurrence of specimens from Bahia, Brazil, indicates that an isolated colony exists around Bahia and possibly as far southward as Espirito Santo (Map 3).

MATERIAL EXAMINED

Locality (and Museum Number)

Bolivia

- Beni River (A.M.N.H. 22271)
- Buenavista (B.M. 1927.8.1.199; U.M.M.Z. 67924, 67925 [2])
- Espía, Bopi River (A.M.N.H. 21249–50)
- Ivón (A.M.N.H. 22490, 22500)
- La Paz region (A.M.N.H. 32995)
- Río Madre de Dios (U.M.M.Z. 59773)
- Rurrenabaque (A.M.N.H. 22476)
- Santa Cruz (U.M.M.Z. 60793, 63921, 64010–12, 63923)

Brazil (B.M. i C [type of *rappii*])

- Bahia (M.C.Z. 2953, 3281)



MAP 3

- Cametá (I.B. 2190, 2199, 2223)
 Jatuarana (M.C.Z. 2571)
 Manáos (I.B. 1566-67)
 Marajó Island (B.M. 1923.11.9.103-6)
 Obidos (I.B. 1256, 1258)
 Pará (Belém) (B.M. 51.2.3.4; I.B. 3107, 3144; M.C.Z. 5670)
 Parintins (I.B. 1290)
 Porto Velho (A.M.N.H. 22252-53)
 Santarém (M.C.Z. 2586, 2800, 3292, 3339; U.M.M.Z. 56312)
 São Luiz de Cáceres (I.B. 1390)
 Tajipura River (M.C.Z. 2565)
- British Guiana (B.M. 86.4.21.3-4)
 Berbice (B.M. 53.4.6.66, h C [types of *rappii*])
 Dunoon (U.M.M.Z. 53941-42, 53974)
 Georgetown (Demerara) (A.N.S. 20818; B.M. 55.8.28.20, 78.12.13.8-9; A.M.N.H. 2666, 8568-69)
 Groets Creek, Essequibo River (A.M.N.H. 8092)
 Kartabo (A.M.N.H. 14252, 15148-49, 18166-68, 21273, 21334; U.M.M.Z. 65164)
 Lena Creek, Demerara River (A.M.N.H. 36112)
 Santa Rosa Island, Monica River (U.M.M.Z. 55872)
- Colombia
 Aprilo (I.L. 9)
 Gorgona Island (B.M. 1927.9.2.5)
 Medellín (A.M.N.H. 35612-17, 35620, 35638, 35640, 35648-49, 35652-57, 35659-61, 35663-67, 35695-97, 35699-702, 35709)
 Murzo (I.L. 14)
 Pena Liza (B.M. 1914.5.21.28)
 Pueblo Rico (B.M. 1910.7.11.23)
 San Pedro (A.M.N.H. 35746)
 Sonsón (I.L. 8; M.C.Z. 21986)
 Tolima Province (M.C.Z. 15933)
 Villavicencio (I.L. 10)
- Dutch Guiana (Surinam) (A.N.S. 5649-50; B.M. 58.10.22.3-4; M.C.Z. 841; U.S.N.M. 11151)
 Paramaribo (M.C.Z. 15548)
 Port Groningen (A.M.N.H. 8675)
- Ecuador (A.N.S. 5711)
 Bulum (A.M.N.H. 13590)
 Chan Chan Valley (M.C.Z. 17089)
 Chaquarapata (A.M.N.H. 23031)
 Parumba (A.M.N.H. 13433; B.M. 98.4.28.57)
 Playas Montalva (U.M.M.Z. 83950)
 Portovelo (A.M.N.H. 18321)
 San Nicolás (U.M.M.Z. 83705, 83707)
 Santa Elena (A.M.N.H. 22099)
 Santa Javier (B.M. 1901.3.29.27)
- French Guiana
 Cayenne (B.M. 1920.1.20.411; M.C.Z. 1957)
- Peru
 Chyavetas (B.M. 67.6.13.16)

- Huaraz (B.M. 1900.6.20.25)
 Perene (B.M. 1900.11.7.36)
 Río Ucayali (U.M.M.Z. 71615)
 San Fernando (Río Casireni) (U.S.N.M. 60716)
 Yurimaguas (B.M. 67.6.13.10)
 Trinidad (A.M.N.H. 2943, 3511; B.M. 93.4.22.8, 97.7.23.52-55, 1917.9.27.24; M.C.Z. 6145
 [3]; U.S.N.M. 452, 5577-78, 17752-53, 17755-56)
 Patas Island (A.M.N.H. 8724)

The following *boddaerti-ruthveni* intergrades have also been examined:

Colombia

Bucaramanga (I.L. 6)

Venezuela (B.M. 46.7.23?, 47.7.18.19 [types of *rappii*])

Arabupu (Mount Roraima) (A.M.N.H. 36058, 36063; U.M.M.Z. 85272-73)

Boquerón (U.M.M.Z. 55898)

Caracas (A.N.S. 5491-92, 5601; U.S.N.M. 16831)

Elvecia (Sucre) (C.M. 7996)

La Fria (Puebla Nueva) (U.M.M.Z. 57061)

La Guaira (U.S.N.M. 22535)

Macuto (U.S.N.M. 27822)

Maracaibo (B.M. 43.10.12.26)

Mérida (A.M.N.H. 13591-94; U.M.M.Z. 46622)

Milla (A.M.N.H. 13434, 13436)

Mount Tumuriquire (F.M.N.H. 17837)

Puerto La Cruz, Federal District (C.M. 7285, 7334, 7341)

Santa Estebán (U.M.M.Z. 55885-86)

Santa Lucía, Mirada (C.M. 7459)

Sucre (F.M.N.H. 17838)

VARIATION.—As already stated, the comparatively large series of this form to which I have had access and its extensive range indicate that variation in *boddaerti* is considerable. Whether this variation is real or merely apparent and caused by differences in states of preservation it is impossible to say, but in some instances, at least, it is certain that the method of preservation utilized has had a considerable effect upon the pattern of some specimens. Unaffected by the state of preservation, and therefore of greater importance as an indication of actual differences, is the variation in the ventral scutellation.

It has been found that both the age of any particular specimen and the method of preservation produce apparent pattern variability in *boddaerti*. Juvenile specimens can, of course, be readily recognized and show no variation which is not easily interpreted. The variations of pattern in half-grown specimens and in very large adults, on the other hand, should be more thoroughly explained. The former, especially those which have completely lost the juvenile pattern and on which the adult pattern is plainly visible, often present an atypical appearance because of the retention of irregular dark markings over the body and of especially dark mottlings on the chin

and throat. The latter are merely remnants of the juvenile ventral markings, which are retained long after the juvenile dorsal pattern has been lost. The former are likewise the last remains of the dorsal bands, which in some instances, through their irregular arrangement, tend to obliterate to the eye the primary pattern of the single lateral stripe. In occasional specimens, which, judged by their size, are fully adult, the juvenile pattern is retained. This is probably because of retarded development of the pattern, or possibly may be explained as a "sport." In very large specimens another variation is often noticed, that is, the complete obliteration of the lateral stripes through such a lightening of the ground color that a unicolor condition is produced. It is possible that the comparative state of preservation may contribute to this obliteration of the lateral stripes.

Even in the typical adult pattern (a light lateral stripe on scale rows 4 and 5), minor variations are numerous. The greatest variability in the lateral stripe is its width. I am inclined to believe that typically this stripe occupies the upper half of scale row 4 and the lower half of 5. In types of variation which are not unusual, however, this stripe occupies scale rows 4 and 5 in their entirety, all of one scale row and only part of the other, or only about one-fourth of each scale row. A very narrow black border above and below the lateral stripe constitutes a frequent variation. It is to be understood that none of the above-mentioned variations have any correlation with geographic area or with sex, and, on the basis of the material available, they appear to be of no taxonomic significance. Phylogenetically, however, they are suggestive. Most striking is the tendency of the pattern in large adults to approach the unicolor condition, which, as has been indicated, seems to be the ultimate pattern throughout the genus. The purpose of the above discussion is to describe variations which might prove confusing to one unfamiliar with the genus.

Although the above variations are of minor importance, there is one of pattern which appears to be of no little significance. This is the very dark and often unicolor condition found in specimens from the Colombian Andes. In all these specimens, regardless of method of preservation, the dorsal color (*stratum corneum* lacking) is a very dark gun-metal blue. In many, the lateral stripe is entirely obliterated, or at best very faint. The chin, throat, and undersurfaces of body and tail are heavily mottled with light gray. If the very dark dorsal color is the result of the method of preservation, this population may be slightly different physiologically from the other populations of the form. This geographical variant takes on further significance when it is noted that it is coupled with scale variation.

Variation in scutellation at any one locality is apparently no greater than is found in a single population of any other form in the genus. With a single exception, the lack of variability between various populations over

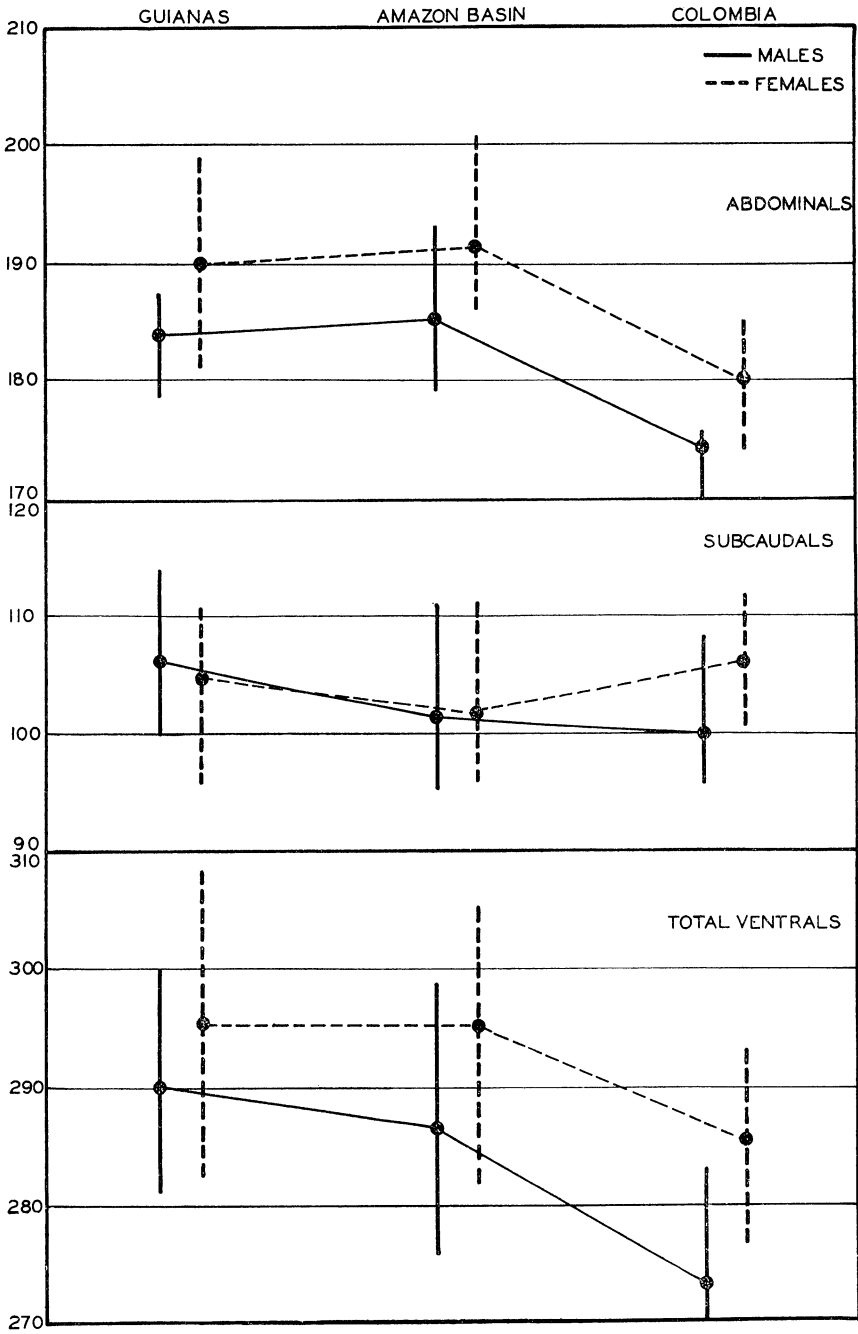


FIG. 7. Local differentiation in the Colombian population of *boddaerti*. Note the decrease in abdominals and total ventrals (controlled by the abdominals).

the form's extensive range is most surprising. Material from Trinidad, the Guianas, and various parts of the great Amazon basin shows little or no variation in ventral scutellation, as is indicated in Figure 7. Unfortunately, *boddaerti* is not without its complexities, for, in the Colombian Andes, there is a pronounced reduction in the number of ventral scutes. Scanty material from the Andes of Bolivia and Peru compares favorably with that of the Amazon basin. In Ecuador, however, reduction is initiated, and finally becomes very noticeable in the Colombian highlands. This gradual decrease in the number of ventral scutes in the females is indicated in Table XIII. (Because of the few available specimens from the Andes south of Colombia, these figures are not included in Figure 7.)

TABLE XIII

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Bolivia-Peru	3	191-93 (192)	105-8 (107)	298-99 (299)
Ecuador	6	180-91 (184)	97-110 (102)	277-92 (284)
Colombia	7	174-85 (180)	101- 12 (106)	275-93 (285)

This reduction is centered primarily around the abdominals. When the Colombian population is compared with specimens from the Guianas and from the Amazon basin, the reduction is seen to be extremely well marked and statistically significant. Figure 7, showing the condition existing in adult females (juveniles being excluded for reasons previously discussed), brings out this striking feature.

The significance of this variant Colombian population is only too evident. Throughout its tremendous range (with the exception of Colombia and Ecuador) *boddaerti* does not vary geographically either in pattern or in scutellation. In Colombia and to a lesser degree in Ecuador, however, there exists a population which has a definite average difference from all other populations in both pattern and scutellation. It seems apparent, therefore, that in Colombia, particularly, incipient speciation is present and a new race is evolving. A similar situation is discussed further on under *alternatus*, the Saboga Island and Costa Rican highland populations of which also give every indication of race formation.

AFFINITIES.—As already suggested, *boddaerti* is the derivative of a *ruthveni*-like ancestor, and, although *ruthveni* and *boddaerti* developed in different areas, they retained some connection in Venezuela, where there is an extensive intergrading population. Since these 2 subspecies differ so greatly in both pattern and scutellation, this intergrading population is naturally very complex genetically. Its condition is similar to that found in *alternatus-laevis* intergrades (discussed later) and far more complex than is the situation found in the intermediate *bifossatus-triseriatus* population already noted.

It is found that there are 3 pattern types among the intergrades. First, there is the *ruthveni* pattern, or a slight modification of it, produced by a slight fading in the narrow dark margins of the light lateral bands; second, a pattern intermediate between *ruthveni* and *boddaerti* (identical with the pattern of *dunni*, as will presently be pointed out); and finally, the *boddaerti* pattern, which is often modified to such an extent that it has a very distinct black margin along the light lateral stripe. It is unfortunate that my material is too scanty to indicate the distribution of these 3 patterns over the range of the intergrading population, as it was possible to do in the case of *bifossatus-triseriatus* intermediates. The majority of the specimens, however, present the intermediate condition.

With reference to ventral scutellation, Figure 8 indicates the gradual decrease in the number of subcaudals and total ventrals from *ruthveni* to *boddaerti*. (The abdominals are constant.) The range of variation of the intermediates in their entirety almost completely spans the range of both *ruthveni* and *boddaerti*—an indication of the genetical complexity of that population.

In both pattern and scutellation, the entire population assumes an intermediate character. In other words, the majority of individuals could never be mistaken for either typical *boddaerti* or typical *ruthveni*, since they may be intermediate in all characters, or they may possess the pattern of one form and the scutellation of the other. To illustrate, a female from Bucaramanga, Colombia (I.L. No. 6), has the typical *ruthveni* pattern, but possesses only 109 subcaudals and 293 total ventrals—well below the lower limits of these 2 characters in female *ruthveni*, which are 114 and 305, respectively. Again, a male from Mérida, Venezuela (U.M.M.Z. No. 46622), with *boddaerti* pattern, has 114 subcaudals and 304 total ventrals, whereas male *boddaerti* never exceed 113 subcaudals and 300 total ventrals.

One of the most striking features of the *ruthveni-boddaerti* relationship is the absence of any intergradation between *ruthveni* and the populations south of it, as typified by the Medellín population. Intergradation, in other words, is found only to the east of *ruthveni*. The reason for this lack of intergradation to the south may be explained on the basis of the very arid conditions prevailing in that region. The *boddaerti* group is restricted primarily to humid habitats, and *pleei* replaces it in the more arid regions. Thus the Medellín population is completely isolated from *ruthveni*, and therefore there is intergradation between *ruthveni* and the Guiana populations only.

Intergradation between the *boddaerti* and *alternatus* groups may eventually be found and thus necessitate the combining of the 2. Intermediates must be sought in eastern Panama. Although it is possible that there may be such intergradation, there is no indication of such conditions either in

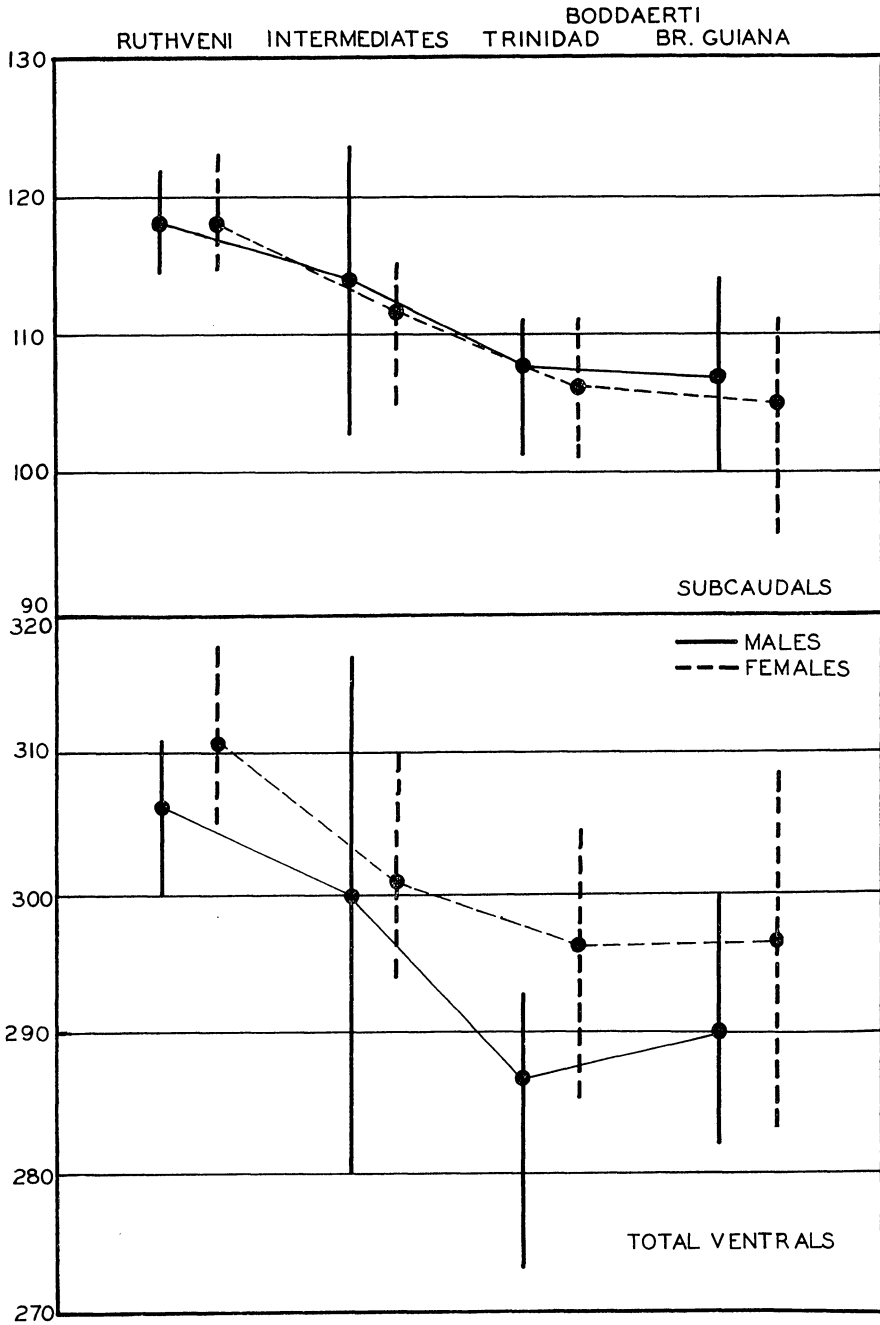


FIG. 8. The nature of intergradation between *ruthveni* and *boddaerti*. The abdominal scutes show little variation and were not plotted. Compare with the *alternatus-laevis* intergrades illustrated in Figure 10.

the Panamanian population of *alternatus* or in the Medellín and Choco populations of *boddaerti*.

As to the origin of *boddaerti*, it is impossible to state whether it developed from the same stock that later became *ruthveni*, and changed as it moved eastward, or whether it developed in the east while *ruthveni* was developing in the west and the 2 later hybridized. On the basis of geological history, the latter condition is most strongly indicated (as discussed under *ruthveni*). At any rate, this differentiation has taken place since the Miocene and was probably initiated in Venezuela.

The occurrence of an isolated colony in eastern Brazil is not surprising. This same distributional pattern is found in other groups, notably the monkeys, and is probably the result of postglacial recession of the forests in northeastern Brazil which separated the 2 populations of the humid-land subspecies.

Dryadophis boddaerti dunni (Stuart)

Eudryas dunni Stuart, 1933a: 5 (type locality, Tobago Island, British West Indies; type, M.C.Z. No. 12071).

DESCRIPTION.—Dorsally the ground color (*stratum corneum* lacking) is blue-gray. A part of scale rows 1 and 2 is slightly lighter, and this results in a very faint lateral line, which is visible only at the anterior extreme. A distinct lateral stripe occupies the upper half of scale row 4 and the lower half of row 5. This upper stripe is visible over most of the length of the body. The top of the head (*stratum corneum* in place) is olive brown. Laterally, this color becomes somewhat lighter; it is even lighter on the supralabials. An indefinite dark smudge extends from the nostril through the eye and across the temporals and posterior supralabials. The infralabials, chin, and throat are dirty white, heavily mottled with gray. The undersurface of the body is pinkish white, blotched with gray-blue and infringed upon laterally by the dorsal ground color, the limits of which are not clearly defined. The underside of the tail is cream, slightly flecked with gray (Pl. III, Fig. 6).

The ventral scutellation is as follows: abdominals, 184–96 (190); subcaudals, 119–22 (121); total ventrals, 303–18 (311).

RANGE.—This subspecies is known only from Tobago, British West Indies.

VARIATION.—As the only specimens of this race are the type and paratype, nothing is known of its variation (Map 3).

MATERIAL EXAMINED

Locality (and Museum Number)

Tobago Island (M.C.Z. 12071–72 [holotype and paratype of *dunni*])

AFFINITIES.—In according this insular form only subspecific rank, I have

attempted to indicate its very close relationship to both *ruthveni* and *boddaerti*. In an earlier paper (Stuart, 1933a: 5-7) I suggested that *dunni* was intermediate between *boddaerti* and *bruesi*, but since I have removed *bruesi* from the *boddaerti* group, this suggestion becomes untenable. It is now my opinion that *dunni* has been derived from an intermediate *boddaerti-ruthveni* stock. In fact, there are among the *boddaerti-ruthveni* intergrades some specimens which might well pass as *dunni*. I have already shown, however, that the former represent a mixed population, and I believe that *dunni* will eventually prove to be a pure strain. This argument is based on the fact that the single available female (the paratype) exceeds in number of abdominals, subcaudals, and ventrals the limits found in the females of the *boddaerti-ruthveni* intergrades. Isolated as *dunni* is, this parallelism between an intergrading population and a distinct race is reminiscent of the condition which I have described (Stuart, 1935: 4-6) as having been found in intergrades between *Lampropeltis t. nelsoni* and *L. t. polyzona* and *L. t. blanchardi*.

It is my opinion that *dunni* has reached Tobago and developed there in a manner similar to that in which *amarali* has developed. It seems probable that while the *pleei* group was developing in the more arid habitats of ancient Venezuela and the Parian land mass, the *boddaerti* group was inhabiting the humid areas in the same region. This protostock of the *boddaerti* group was at this time evolving from the double-striped type (*ruthveni*) to the single-striped form (*boddaerti*). Possibly during the late Miocene or early Pliocene, when Tobago was severed from the mainland, a portion of that stock was isolated on Tobago, and *dunni* subsequently developed. It is not surprising, therefore, to find that, in pattern and scutellation, *dunni* closely resembles intergrades between *ruthveni* and *boddaerti* and yet has had a history of isolation. That *dunni* is more restricted in its range than is *amarali*, which has had a similar history, must be laid to the fact that suitable habitats have apparently been wanting.

Dryadophis heathii (Cope)

Drymobius heathii Cope, 1875: 179 (type locality, Valley of Jequetepeque, Peru; type, possibly in the A.N.S.P.).

DESCRIPTION.—Despite the fact that this species is abundantly represented in European museums, it is exceedingly rare in American collections, and I have had access to but 3 specimens. These, however, indicate that the form is fairly constant in pattern. Above (*stratum corneum* lacking), depending on the state of preservation, the ground color varies from light gray to gun-metal blue. At mid-body each scale (except those involved in the lateral stripe) has a black anterior border and a black apical spot. Both anteriorly and posteriorly these darker markings become much re-

duced or disappear entirely. On each side is a light stripe occupying scale rows 4, 5, and 6 anteriorly. Posteriorly, this stripe becomes less evident, and when the number of dorsal scutes is reduced it drops down to occupy scale rows 3, 4, and 5. The surface and sides of the head are colored as is the dorsum. A narrow dark smudge just above the supralabials extends from the nostril through the eye and across the lower temporals. The supralabials are either immaculate or mottled with gray. The infralabials, chin, and throat are white and may or may not be slightly mottled with gray. The belly and undersurface of the tail are immaculate white. Laterally, the belly is infringed upon by the dorsal ground color, the limits of which, although distinct, are not demarked by the narrow white line so frequent in other forms of the genus. When the *stratum corneum* is preserved, the dorsal ground color is probably pale yellowish green and the under parts are pale yellow or white (Pl. IV, Fig. 2).

The ventral scutellation is as follows: abdominals, 191-97 (195); subcaudals, 108-15 (112); total ventrals, 299-310 (305).

RANGE.—This species is apparently restricted to the very arid coastal desert from Ecuador possibly to as far south as Chile (Map 3).

MATERIAL EXAMINED

Locality (and Museum Number)

Peru (U.S.N.M. 38557)

Lima (Verrugus Cañon) (U.S.N.M. 51513)

Pacasmayo (F.M.N.H. 5706)

VARIATION.—The presence of only 3 specimens (all females) of this species renders a discussion of variation impossible.

AFFINITIES.—It is with considerable hesitancy that I place this form in the *boddaerti* group. The similarity to *pleei*, in that 3 scale rows are involved in the lateral stripe, the independence of that stripe from the scale rows, and its distribution along the arid west coast of South America speak against its inclusion. But, unless *heathii* represents an isolated relict, it is too far removed, geographically, to fit the *pleei* picture. I prefer to look upon it as a somewhat specialized species retaining a "primitive" character, originating *in situ* from pre-*boddaerti* under conditions of extreme aridity.

ORIGIN AND AFFINITIES OF THE *BODDAERTI* GROUP

Inasmuch as the evolution of the *boddaerti* group took place in northern South America, it may be well to glance briefly at the historical geology of that region. Of greatest importance is the history of the Panamanian-Costa Rican portal, since it was across that region that the progenitors of the South American colubines made their way from North America. It is now generally agreed that this portal was closed from the Cretaceous

through the lower Eocene and was open from middle Eocene times to the middle Miocene, after which it was permanently closed (Schuchert, 1929: 341-43; and 1935: 568-79). Next in importance is the history of Paria, also adequately discussed by Schuchert (1935). Briefly, this land mass, which included northern Venezuela and extended into the Caribbean to Barbados, began to break up during the Cretaceous, but land connections existed to Tobago possibly until the lower Pliocene. After Oligocene times the remnants of Paria and the Archiguayan shield were broadly joined to form a land mass upon which the history of the genus *Dryadophis* was unfolded. A third significant feature is the fact that the Sierra Nevada de Santa Marta formed a peninsula end to the Pliocene, since much of northern Colombia was flooded during the Cenozoic and the Maracaibo basin was far more extensive than it is at present. This left an arm of land, connected only to the south, jutting out into the Caribbean. The significance of the peninsula-like piece of land is seen in the history of *ruthveni*, and has already been noted briefly. On these 3 geological features rests the explanation of the present distributional pattern of the *boddaerti* group.

Biological evidence of importance in the history of the group is displayed by the patterns of the various forms. As previously noted, it is believed that the pattern of 2 lateral light stripes is a "primitive condition," and that the end point of specialization is the unicolor condition. It seems evident, therefore, that *boddaerti* with a single lateral stripe is the most specialized of the group insofar as pattern is concerned, that *ruthveni* is the most generalized, and that *dunni* is intermediate between them.

An increase in abdominals and subcaudals indicates specialization in scutellation. In this respect *boddaerti* and *ruthveni* reverse the condition found in the pattern, whereas *dunni* again occupies an intermediate position. With these remarks serving as an introduction, the history of the *boddaerti* group may be outlined.

As indicated in the discussion of the *bifossatus* group, the ancestor of *Dryadophis* entered South America from Central America sometime prior to the middle Eocene. During the period from middle Eocene to middle Miocene the genus developed in northern South America and gave rise to the *boddaerti*, the *pleei*, and the *bifossatus* groups. In northern Venezuela the former 2 groups developed together, but at some early date became physiologically distinct, so that *boddaerti* probably occupied the more humid areas while *pleei* moved into more arid regions. The prototype of the *boddaerti* group was undoubtedly *ruthveni*-like in pattern and possibly occupied most of northern South America. At some time prior to the Pliocene (when *dunni* was cut off) a *boddaerti*-like form began to develop and to replace the two-striped *ruthveni* type. With the breaking up of the Parian borderland, *dunni*, in which the lower lateral stripe had already

faded to a considerable degree, was isolated with *amarali* on Tobago during the lower Pliocene and here specialized by increasing its number of ventral scutes while retaining a more "primitive" pattern.

It seems certain that in the meantime a part of the prototypic stock became more or less isolated on the peninsula in northern Colombia (already noted) and took refuge in the Sierra Nevada de Santa Marta. In northern Venezuela and in the Amazon basin, and possibly also in the rising Andes, *boddaerti* developed through a simplification of pattern. When South America assumed its present form *boddaerti* and *ruthveni* met along their western and eastern boundaries, respectively, and by hybridization produced the great intermediate population now found in Venezuela.

Finally, the Andes, in rising to their present level, cut off in Colombia, through the Knot of Pasto, a part of the early *boddaerti* population which is slowly evolving into the variant population already discussed. As previously indicated, *heathii* developed *in situ* from *boddaerti* on the arid west coast. The absence of the group from Grenada and the islands to the north (where *bruesi* of the *pleei* group is found) must be explained on the basis of unsuitable habitats at the time when the entrance of *boddaerti* to those islands was possible through land connections.

The outline of the history of these forms as here given may be far different from their actual history, but it is strongly indicated by the morphological features of the group and by what is known of the geological history of the region. My concept of the relationships of the 3 forms of the *boddaerti* group is illustrated in Figure 9.

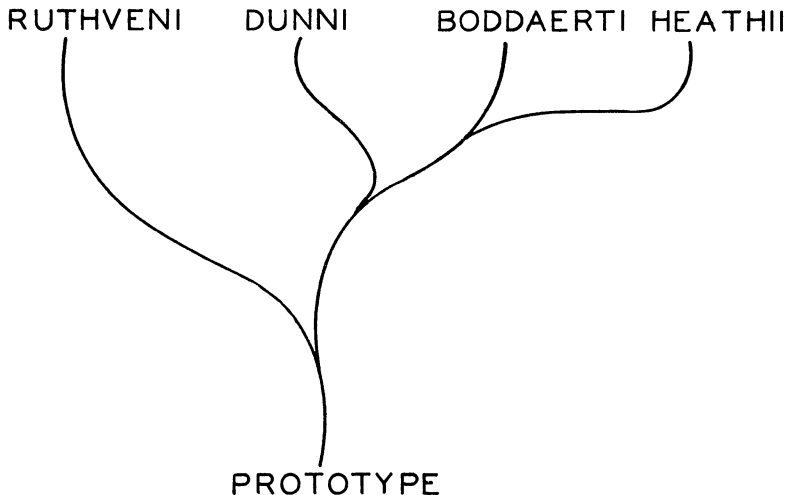


FIG. 9. Relationships of the forms of the *boddaerti* group.

THE *MELANOLOMUS* GROUP*Dryadophis melanolomus alternatus* (Bocourt)

Coryphodon alternatus Bocourt, 1884: 133 (type locality, Isthmus de Darien; type, Museum National d'Histoire Naturelle, No. 6202).

Eudryas boddaerti gaigeae Stuart, 1933a: 7 (type locality, Wright's Ranch, Boquete, Chiriquí Province, Panama (type, U.M.M.Z. No. 57917).

DESCRIPTION.—Because so many specimens of this form have been available from so many localities, *alternatus* appears to exhibit considerable variation. Certain populations, as those of the Pearl Islands or of the Chiriquí and Costa Rican highlands, definitely indicate that new subspecies are in the making, but, at present, differentiation has not progressed far enough to warrant naming. A study of all the minor variations in pattern indicates that they may be reduced to 1 basic type. In alcohol (*stratum corneum* lacking), the dorsal ground color consists of varying hues of gray or blue. Laterally, scale row 1 and the lower half of scale row 2 are somewhat lighter, as are the upper half of scale row 4 and the lower half of scale row 5. The extent to which these scale rows are lightened is extremely variable, but they always produce a pattern of 2 light lateral stripes, which may or may not have a narrow black edge. These lateral stripes gradually fade posteriorly and disappear at the vent. The surface of the head is colored the same as is the dorsum and is often flecked or blotched with black. Laterally, the head becomes lighter, leaving the supralabials white. A dark smudge extends from the nostril through the eye and across the temporals. The infralabials, chin, and throat are white, often lightly mottled with gray, or with a narrow, dark margin on each scale. The belly and underside of the tail are white, infringed upon laterally by the dorsal ground color, the limits of which are often demarked by a narrow light line. Fresh specimens indicate that in life the dorsal ground color consists of various shades of brown; the undersurfaces are cream or yellow (Pl. IV, Fig. 3).

The ventral scutellation is as follows: abdominals, 163–95 (181); subcaudals, 85–110 (100); total ventrals, 263–97 (281).

RANGE.—This form extends throughout Panama and Costa Rica and is found on the islands off the coast and northward on the Caribbean slope of Nicaragua and Honduras. Its distribution in Honduras is unknown, but the form is probably limited to the low Caribbean coastal plain as far as the region of Tela, where it intergrades with *laevis* (Map 4).

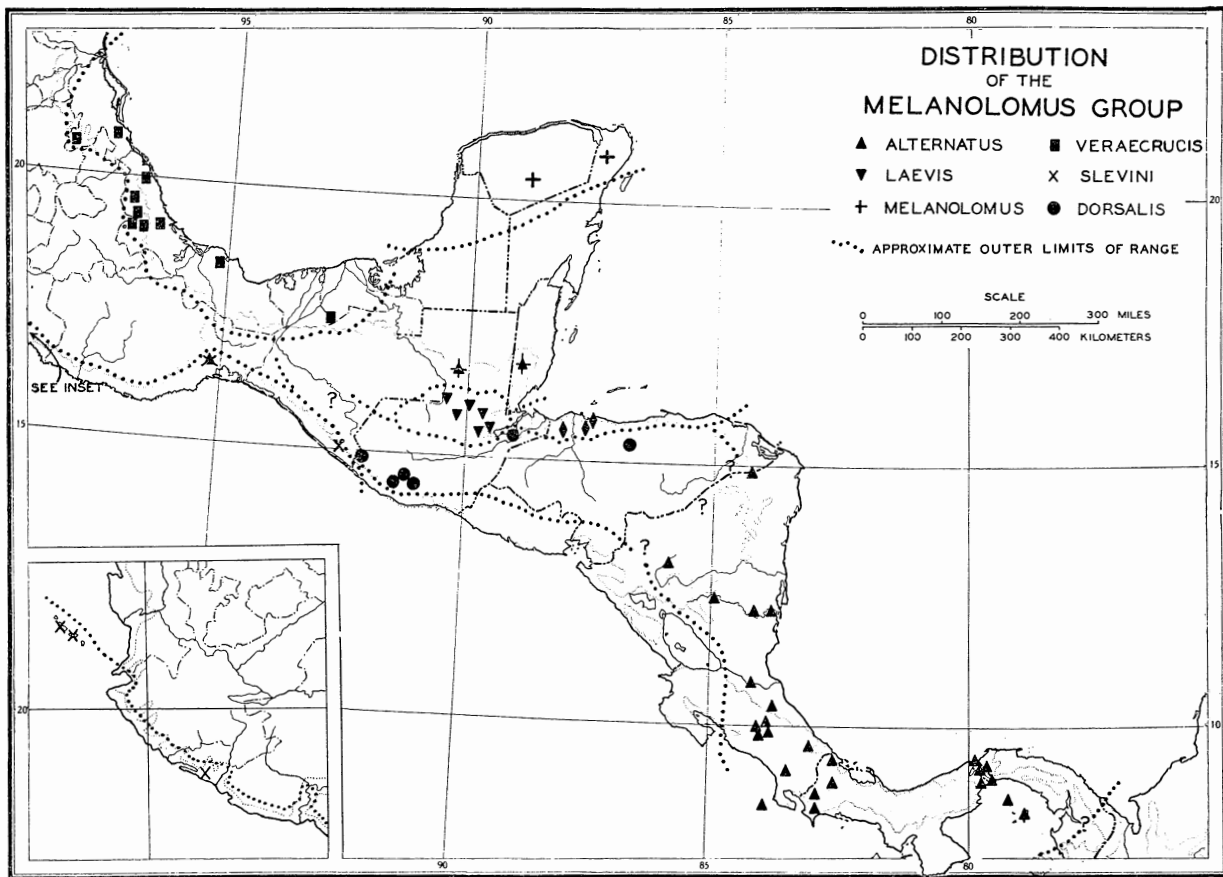
MATERIAL EXAMINED

Locality (and Museum Number)

Costa Rica (A.M.N.H. 17269, 17310; U.S.N.M. 14065, 32609–11)

Arriba¹¹ (U.S.N.M. 6353 [3])

¹¹ Referring to the highlands of Costa Rica; probably from the vicinity of San José.



MAP 4

- Boruca (A.M.N.H. 17304)
 Guapiles (M.C.Z. 15324)
 Irazú (A.M.N.H. 17343)
 Monte Redondo (B.M. 95.7.13.14)
 Navarro (M.C.Z. 15325)
 San José (U.S.N.M. 13539)
 Talamanca (M.C.Z. 19350)
- Honduras
- Segovia River (U.S.N.M. 24530)
- Nicaragua (U.S.N.M. 15195)
- Bluefields (A.M.N.H. 12648)
 Chontalez (B.M. 94.10.1.16)
 Cupitna (A.M.N.H. 12647)
 Metagalpa (U.S.N.M. 56499)
 Recero (U.M.M.Z. 79763)
 Río San Juan (U.S.N.M. 19559)
- Panama (U.S.N.M. 13504, 14117)
- Bocas del Toro (U.S.N.M. 38673)
 Boquete (U.M.M.Z. 57912-13, 57918-22, 57932 [paratypes of *gaigeae*], 57917 [holotype of *gaigeae*]; U.S.N.M. 51967, 51978)
 Progreso (U.M.M.Z. 57916)
 Rabo de Puerco (U.M.M.Z. 57911)
 Saboga Island (M.C.Z. 9339-46)
 San Miguel Island (M.C.Z. 9338)
 Canal Zone (U.S.N.M. 38505)
- Ancon (M.C.Z. 13299-300, 16400, 20574, 24001; U.S.N.M. 59869, 65870)
 Balboa (M.C.Z. 25114-15)
 Barro Colorado Island (U.M.M.Z. 63763-65)
 Bruja Point (M.C.Z. 25095-96)
 Colón (M.C.Z. 22216)
 Empire (U.S.N.M. 54265)
 Fort Clayton (M.C.Z. 22270, 26772)
 Fort Davis (M.C.Z. 25131; U.S.N.M. 65855-56)
 Gatun (U.M.M.Z. 56230; U.S.N.M. 54013-14, 54156)
 Juan Mina (M.C.Z. 26639-44)
 Tabernilla (U.S.N.M. 54158)
 Toro Point (M.C.Z. 22232, 22235, 22237)

VARIATION.—In pattern, the most conspicuous variation in *alternatus* is the presence or absence of the black borders on the lateral light stripes. These black margins are best developed in specimens from Chiriquí Province, Panama, and to a lesser extent in the specimens from the Pacific coast of lower Panama. On the Caribbean coast of Panama, on the other hand, these dark margins are much less intense and are not found at all from Bocas del Toro, Panama, northward. Thus, 2 geographic trends in this particular character are evident: (1) the variations existing between populations of the Pacific and the Caribbean coasts, and (2) the northward fading of the dark margins.

There is a second striking variation in pattern in the Pearl Island popu-

lation. Here, contrary to expectations, the lateral stripes are not margined with black. The lateral stripes are, moreover, almost completely obscured, owing to the dark fleckings on the scales involved in producing the lateral stripes.

Variations in ventral scutellation, although showing some differences between various populations, are of rather minor importance except in 1 or 2 instances. As already noted, there exists a slight difference in pattern between the Caribbean-slope and Pacific-slope populations. Although a slight difference exists in scutellation between these 2 localities, it is of no significance, taxonomically speaking. The variation in ventral scutellation of females from the 2 sides of the Panama Canal Zone is shown in Table XIV.

TABLE XIV

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Caribbean Coast	8	181-90 (187)	93-102 (98)	274-92 (284)
Pacific Coast	7	175-92 (182)	92-106 (98)	272-86 (278)

In the males this same slight reduction in the number of abdominals and total ventrals on the Pacific coast is present in about the same degree. A comparison of the very few specimens available from both sides of Costa Rica shows this same variation, so that it may be concluded that the Pacific-coast population has a lower average number of abdominals and total ventrals than has the Caribbean population. No such south-to-north trend in the number of ventral scutes as was noted in the pattern is apparent. Table XV, containing comparisons of females in three given localities on the Caribbean slope, indicates that although slight variation exists it is of little consequence.

TABLE XV

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Canal Zone	8	181-90 (187)	93-102 (98)	274-92 (284)
Costa Rica	3	182-91 (187)	93- 94 (94)	276-84 (280)
Nicaragua	3	190-91 (190)	85-105 (97)	275-95 (287)

In the populations from the highlands of Costa Rica and Panama are variations in scutellation of slightly more significance. The highland populations, although different from one another in the number of subcaudals and total ventrals, when combined are quite different from all the other specimens on the lowlands, especially in the number of abdominals. Table XVI indicates the differences in the males of these 2 populations.

In Table XVII these 2 populations combined are compared with males from the lowlands of Panama, Costa Rica, and Nicaragua (recalling again that slight differences exist between the Caribbean and Pacific populations).

TABLE XVI

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Boquete, Panama	5	168-76 (172)	100-108 (105)	271-84 (278)
San José, Costa Rica	5	169-75 (172)	91-101 (96)	263-79 (270)

Although, as noted earlier, the Pearl Island population differs somewhat in pattern, it does not vary in scutellation from the lowland population on

TABLE XVII

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Lowlands	22	175-93 (181)	92-109 (101)	272-93 (281)
Highlands	10	168-76 (172)	91-108 (100)	263-84 (274)

the mainland. In Table XVIII the males from Saboga Island are compared with those on the entire mainland, except the highland specimens.

TABLE XVIII

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Saboga Isl.	5	178-84 (180)	101- 10 (105)	280-89 (285)
Mainland	22	175-93 (181)	92-109 (101)	272-93 (281)

The variation in *alternatus*, although much of it has a geographic correlation, is too slight and too overlapping to warrant taxonomic recognition. It seems evident, however, that a number of races are now in the process of differentiating, and that if we were to utilize a quadrinomial system they would be recognizable. If differentiation proceeds uninterruptedly, 4 races may be the end result. These incipient forms at present appear to include a Pearl Island race, recognizable through a distinctive pattern; a Pacific-slope race with dark-margined stripes; a Caribbean-slope race with unmargined stripes; and a highland Panamanian-Costa Rican race with a reduced number of abdominal scutes.

AFFINITIES.—As will be shown later, it is believed that *alternatus* or an *alternatus*-like ancestor represents the original *Dryadophis* stock in Central America. This conclusion is largely based on the fact that the ancestral pattern of the *boddaerti*, *pleei*, and *alternatus* groups was of 2 lateral light stripes. The origin of the Central American forms will be taken up later, but it should be pointed out that, at present, the *alternatus* group has severed all connections with the South American groups—a condition the interpretation of which lies in the geological history of Panama. Thus, the original connections between *alternatus* and the South American forms have

now disappeared, and the Central American group has dispersed and differentiated in almost complete isolation from the rest of the genus.

As to *alternatus* itself, it has probably differentiated *in situ* from the original stock, which sent off a number of forms to the north, while retaining many of the original characters in Panama, Costa Rica, Nicaragua, and Honduras. In this last-named country, *alternatus* now intergrades with *laevis*; this feature will be considered under *laevis*.

Dryadophis melanolomus laevis (Fischer)

Herpetodryas laevis Fischer, 1881: 227 (type locality, Guatemala; type, Naturalien-Kabinet, Stuttgart, No. 2032).

Dromicus coeruleus Fischer, 1885: 103, Pl. IV, Fig. 7 (type locality, Cobán, Guatemala; type, location of type unknown).

Drymobius boddaerti var. *modesta* Werner, 1903: 346 (type locality, Cobán, Guatemala; type, Zoologische Sammlung des Bayerischen Staates, München, No. 1627/o).

DESCRIPTION.—This form, because of the few specimens available and because of the variation in pattern, is the most poorly understood of the *alternatus* group. Material at hand indicates that this subspecies may retain the juvenile pattern until fully grown, at which stage it may lose its banded condition for a faint striped pattern and may eventually become unicolor.

When the banded pattern predominates, the dorsal ground color (*stratum corneum* lacking) appears as a series of narrow (1 scale row wide), gray-blue bands which number about 60 on the body. These light bands are separated by broad bands (3 scale rows wide) which are much darker and are narrowly bordered anteriorly and posteriorly by black. That the light bands and not the dark represent the ground color is inferred from our knowledge of the development of the adult pattern from the juvenile. What is apparently a later stage in the reduction of these evidences of the juvenile pattern is the striped phase. In specimens of this type, the dorsal ground color is gray-blue, and the first, second, fourth, and fifth scale rows are somewhat lighter. This gives the appearance of a faded *alternatus* pattern. That this is a later stage of pattern development is indicated by the fact that several of the specimens at hand, although definitely banded, have evidences of lateral stripes, apparently representing the transition from the banded to the striped phase. When the uniform pattern is present, the ground color is like that of the other 2 phases. Whether or not a uniform condition actually exists is open to question. The state of preservation may well be the reason for the obliteration of all traces of a faint pattern of lateral stripes. Aside from this variation in dorsal body pattern the characters of specimens in all 3 phases are uniform. The unicolor phase (which in life may have been striped) has been named *laevis* and *modesta*, and *coeruleus* has been applied to the banded type.

Above, the color of the head is the same as the ground color of the dorsum. Laterally this color becomes lighter and may leave the supralabials cream or white, mottled, or bordered with gray. An indication of a dark smudge, extending from the nostril through the eye and across the temporals, is present. The infralabials, chin, throat, belly, and undersurface of the tail are white. Anteriorly, on the chin, throat, and fore part of the belly, there are heavy mottlings of gray. Laterally the belly and underside of the tail are infringed upon by the dorsal ground color, the limits of which are demarked by a narrow, light line.

In life, 2 distinct color phases were observed in specimens which I collected in Alta Verapaz, Guatemala. The one has a ground color of olive brown on the upper surfaces, while in the other the dorsal ground color is a brilliant, reddish orange.

The ventral scutellation of this form is as follows: abdominals, 171-86 (180); subcaudals, 114-36 (124); total ventrals, 296-317 (306).

RANGE.—This subspecies is apparently restricted to the highlands of Alta Verapaz, possibly the Cuchumatanes, and the adjacent lowlands (Map 4).

MATERIAL EXAMINED

Locality (and Museum Number)

Guatemala (U.S.N.M. 6764)

- Chamá (U.M.M.Z. Field Nos. 154, 291, 709)
- Panzamala (U.M.M.Z. Field Nos. 31, 1052)
- Quiriguá (F.M.N.H. 20552; U.S.N.M. 56284)
- Semicoch, above Panzos (U.S.N.M. 35903)
- Senahú (U.S.N.M. 35912)
- Sepacuité (M.C.Z. 24945)
- Vera Paz, low forest (B.M. 64.1.26.20)

I have also had access to the following *alternatus-laevis* intergrades:

Honduras

- Lancetilla (M.C.Z. 28040)
- Santa Ana, 3 miles northwest of San Pedro Sula (F.M.N.H. 5284-89)
- Tela (M.C.Z. 27255, 32009; U.S.N.M. 82161, 82169)

VARIATION.—No other form in the entire genus shows such striking variation as the dichromatism in *laevis*. The several patterns and color phases previously described show no consistent sexual or size correlation. Of 4 adult females, 3 are banded and 1 is striped, whereas in the same number of males only 1 is banded, 1 is striped, and the other 2 are unicolor. It is quite possible that these variations may be loosely associated with age, in which case the expected series would progress as follows: banded → stripes and bands → bands → unicolor.

Another possibility, of course, is that pattern dimorphism, such as that described by Klauber (1939) in *Lampropeltis getulus californiae*, may exist.

Whatever the significance may be, the problem can certainly not be solved on the basis of such scanty material.

Discussion of variation in scutellation is impossible because of the lack of material. It is interesting to note, however, that sexual dimorphism appears to be considerable with respect to subcaudals and total ventrals, as indicated by the figures in Table XIX.

TABLE XIX

Sex	Specimens	Abdominals	Subcaudals	Total Ventrals
♂	5	171-86 (180)	127-36 (131)	313-17 (315)
♀	6	175-83 (180)	115-25 (121)	293-306 (300)

AFFINITIES.—Although several possibilities present themselves as explanations as to the affinities of *laevis*, the available material indicates that this form has arisen from an *alternatus*-like ancestor. Specimens from Tela, Honduras, and vicinity represent ideal intergrades. In pattern much the same condition exists as has been noted with respect to *ruthveni-boddaerti* intergrades. Some specimens are unicolor (perhaps because of the method of preservation); others show very faint lateral stripes arranged as in *alternatus*; and still others exhibit the typical *alternatus* pattern. Accompanying all 3 types of dorsal pattern, however, is a mottled condition on the chin and throat. This mottling is much less intense than in typical *laevis* and represents, therefore, a condition intermediate between *laevis* and *alternatus* in which mottling, if present, is always very faint.

The scutellation of this Honduran population is that which would be expected in intermediate specimens. Figure 10 depicts graphically the increase in scutellation from typical *alternatus* in Nicaragua to *laevis* in Guatemala.

As will be discussed later, it is not impossible that, from a population similar to the one found about Tela, Honduras, which at a former period may have evolved in northern Honduras, *laevis* may have developed in the south while *veraecrucis* and *melanolomus* were developing in the north. After differentiation, *laevis* may have spread along the coast of Honduras and may have hybridized with *alternatus*; hence the apparent relationship between *alternatus* and *laevis* may well be secondary. Direct relationship between *laevis* and either *veraecrucis* or *melanolomus* seems improbable.

Dryadophis melanolomus melanolomus (Cope)

Masticophis melanolomus Cope, 1868: 134 (type locality, Yucatán; type, U.S.N.M. No. 24985).

DESCRIPTION.—This subspecies, because of its distinctive pattern, cannot be confused with any other form in the genus. The ground color of the dorsum (*stratum corneum* lacking) is bluish gray. The anterior half of

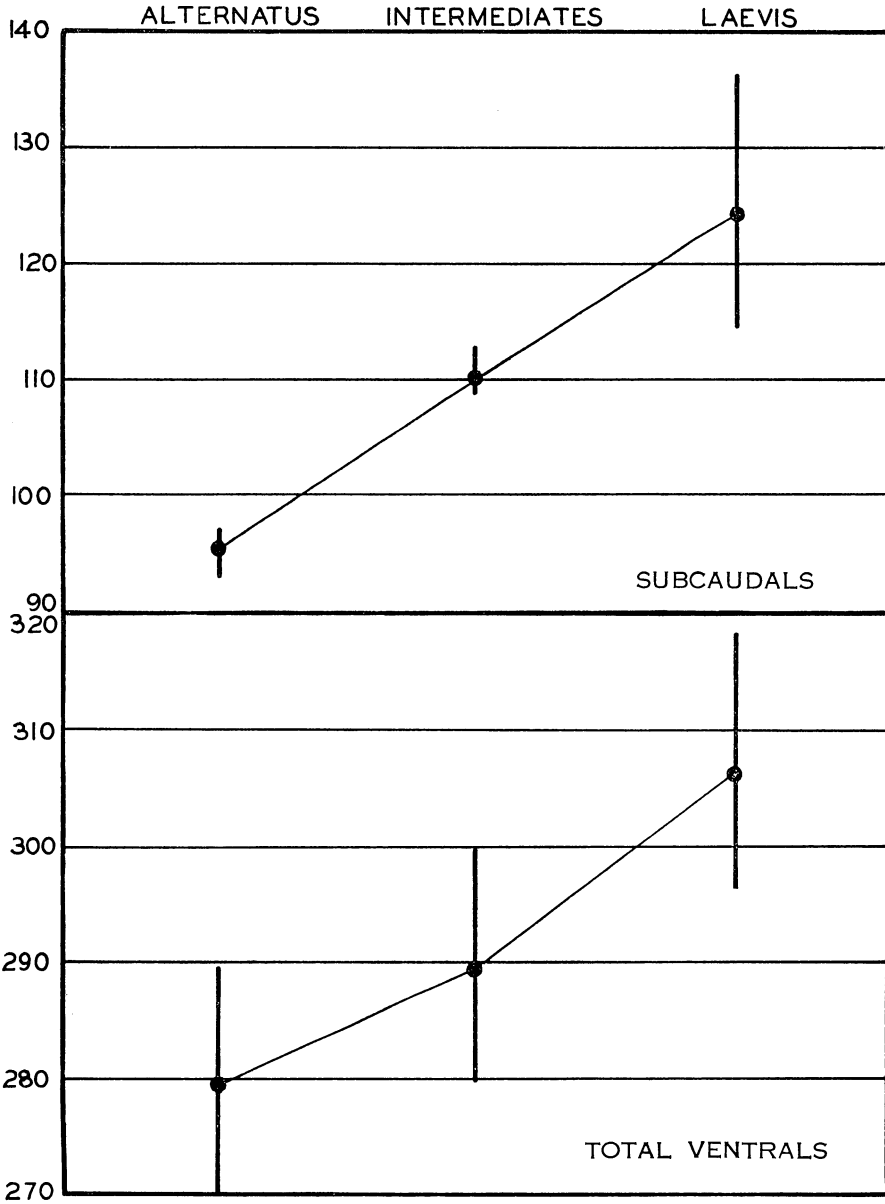


FIG. 10. Intergradation between *alternatus* and *laevis*, as illustrated in a comparison of 3 male populations—Nicaraguan *alternatus*, Honduran intergrades, and the total *laevis* population.

each scale has a narrow black edge, and thus is produced an illusion of a series of narrow black stripes on the ground color. This black edging is reduced on scale rows 1 and 2, and 4 and 5 except on the upper half of scale row 2 and the lower half of scale row 3, where it is often somewhat wider and gives the effect of 2 lateral light stripes separated by a darker one. This condition may well be interpreted as the holdover of the lateral striping typical of *alternatus*. The top of the head is colored as is the dorsum; laterally the color gradually fades to white or cream. A faint black smudge may extend from the nostril through the eye and across the temporals. The supralabials are white, often flecked with gray. The infralabials, chin, throat, and under parts of the body and tail are white. Laterally, the dorsal ground color infringes upon the belly and tail, the limits of this infringement being demarked by the narrow light line.

In living specimens the dorsal ground color is brown. The labials, chin, throat, and fore part of the belly are cream, and the posterior third of the belly and underside of the tail are brilliant pink (Pl. IV, Fig. 4).

The ventral scutellation of this form is as follows: abdominals, 173-88 (181); subcaudals, 116-30 (123); total ventrals, 294-307 (301).

RANGE.—Although known from only 2 exact localities, this race probably is widespread throughout the semiarid northern part of the Yucatán Peninsula (Map 4).

MATERIAL EXAMINED

Locality (and Museum Number)

Mexico

Yucatán (B.M. 80.7.13.9-10; U.S.N.M. 10302, 24986)

Chichen Itzá (M.C.Z. 26839-41; U.M.M.Z. 68233, 73076-78, Field Nos. 3, 21)

Colonia Santa Maria (U.M.M.Z. 76164)

The following *alternatus-melanolomus* intergrades have also been available:

British Honduras

San Augustine (U.M.M.Z. 80714)

Guatemala

Petén (B.M. 64.1.26.19)

La Libertad (El Petén) (U.M.M.Z. 74897)

VARIATION.—Because there were very few specimens and they were from only 2 localities, any discussion of variation in this form is impossible. It is important to reiterate, however, that the majority of the specimens have an indication of the 2 light lateral stripes which are evident in the typical pattern of *alternatus*.

AFFINITIES.—Like most of the Yucatán fauna, this subspecies is of fairly recent origin and its affinities are fairly clear. From El Petén, Guatemala, and from British Honduras, specimens which are evidently intergrades be-

tween *melanolomus* and *alternatus* have been available. Although these specimens are almost unicolor, there is distinct evidence of the black anterior edging on the scales. In scutellation, moreover, they are also intermediate. From this population, or more probably an earlier, yet similar, population, inhabiting the central portion of the Yucatán Peninsula, has also developed *veraecrucis*. Because of the difference in scutellation it is not logical to assume that *melanolomus* is related to *laevis*. It appears that from an *alternatus*-like ancestor or a population similar to *laevis-alternatus* intergrades (previously discussed) *laevis* has developed in one direction while *melanolomus* and *veraecrucis* have developed in another.

Dryadophis melanolomus veraecrucis, new name¹²

Eudryas boddaerti mexicanus Stuart, 1933a: 8 (type locality, Zacuapán (=Zacualpán?), Mexico; type, B.M. [Natural History] No. A, b in Boulenger, 1894: 12, under *Drymobius boddaerti*).

DESCRIPTION.—The pattern typical of this form is somewhat confusing, since it appears to change with age or to be of 2 different types. In the very large adults the dorsal surface is probably unicolor gray-blue (*stratum corneum* lacking). In smaller adults there is frequently a light lateral stripe on scale rows 4 and 5 which extends only over the anterior one-fourth of the body and is often confined to the neck alone. The surface of the head is of the same color as is the dorsum, and in smaller adults irregular lighter markings may be present on the nape. A dark smudge extends from the nostril through the eye and across the temporals, occasionally extending posteriorly on the body, where it may form a dark superior border to the lateral light stripe (if present). The supralabials are light, mottled with gray. The infralabials, chin, and throat are white, mottled in varying degrees with gray (the larger adults are generally immaculate). The undersurface of the body and tail is cream or white, infringed upon laterally by the dorsal ground color, the limits of which are demarked by a narrow light line. The undersurface of the tail may be mottled with gray.

The juveniles display 3 different patterns. One is the banded phase, similar to the juvenile pattern of *laevis*. The second type lacks all traces of banding but has a narrow light line on scale rows 4 and 5. The third is a combination of the 2. Only a single specimen with the third type has been found among the material available, while the others are about equally divided between the banded and the striped types. The undersurfaces display the typical mottled condition, although there is a tendency for the outer end of each ventral scute to be spotted and a third irregular spot is found on the center of each ventral scute, thus producing what appears to be 3 dark ventral stripes (Pl. IV, Fig. 6).

¹² The name *mexicanus* is preoccupied by *Herpetodryas mexicanus* Bocourt (1890: 722); this author placed under *Drymobius (Eudryas) laevis* a specimen so labeled by Jan.

The ventral scutellation is as follows: abdominals, 166-82 (175); subcaudals, 106-20 (111); total ventrals, 276-97 (287).

RANGE.—Generally distributed on the humid lowlands and east slopes of the plateau of eastern Mexico from Tabasco to Tamaulipas (Map 4).

MATERIAL EXAMINED

Locality (and Museum Number)

Mexico (B.M. 61.1.8.11)

Tabasco

Teapa (B.M. 94.3.1.11-12; U.S.N.M. 46592)

Vera Cruz

Catemaco (U.S.N.M. 46478-79)

Hacienda del Hobo (B.M. (80.4.7.55)

Huatuzeo (B.M. 93.4.26.32-33)

Jalapa (M.C.Z. 16102; U.S.N.M. 5346)

Mirador (U.S.N.M. 25007)

Orizaba (U.S.N.M. 30357)

Potrero (A.M.N.H. 19831; U.M.M.Z. 80944)

San Rafael (U.S.N.M. 32162)

Texola (A.N.S. 15337)

Tuxpan (U.S.N.M. 25194)

Zacuapán (= Zacualpán?) (B.M. b A [In Boulenger, 1894; type of *mexicanus*])

VARIATION.—Most perplexing is the variation in the juvenile and adult patterns in this race. It is suggested that here is a form which is actively differentiating. As has been noted, evolution in the genus as a whole has tended toward loss of pattern, and *veraecrucis* is apparently now in the process of assuming a unicolor condition. This suggestion is based on the fact that, although many of the smaller adults are unicolor, the very large adults are always unicolor. With the exception of this significant correlation with size, there appears to be no connection of pattern with sex, geographical position, or any morphological feature.

Variation in scutellation is very similar to that already discussed under *bruesi* and that to be noted later in *slevini*. There is a definite peripheral decrease (in this case northward) in the number of subcaudal and total ventral scutes. As is indicated in Table XX, this condition exists in the males.

TABLE XX

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
South	4	175-82 (178)	113-20 (116)	292-97 (295)
North	10	168-78 (174)	106-16 (111)	278-91 (280)

AFFINITIES.—The affinities of *veraecrucis* must be looked for in the central portion of the Yucatán Peninsula. From that region I have seen specimens (already noted) which might well be intergrades between *veraecrucis*,

melanolomus, and *alternatus*. It seems fairly evident that this intergrading population has developed from another population very like the *laevis-alternatus* intergrades of Honduras, and that subsequent differentiation has given rise to *melanolomus* in one direction and *veraecrucis* in the other. The El Petén population is, however, most like *melanolomus*. This concept of relationship is based primarily on the relationship lines indicated by the ventral scutellation, and will be taken up in greater detail later.

Dryadophis melanolomus slevini (Stuart)

Eudryas slevini Stuart, 1933a: 9 (type locality, Maria Madre Island, Tres Marias Islands, Mexico; type, C.A.S. No. 58679).

DESCRIPTION.—Because of the lack of material and because of the tremendous variation existing within the material at hand, this form, as here recognized, is extremely complex and may represent a composite of as many as 3 distinct races. In alcohol (*stratum corneum* lacking) the dorsal ground color is generally gray-blue. In many specimens the interstitial skin is black, and, especially in Tres Marias Islands specimens, the dorsal scales may be powdered or streaked with darker shades. In several instances there is a faint indication of 2 light lateral stripes, as in *alternatus*. The head is colored as is the dorsum and likewise may be streaked with black. A dark smudge extends from the nostril through the eye and across the posterior supralabials and temporals. The supralabials are white or cream, mottled with gray or black. The infralabials, chin, and throat are light and mottled, in varying degrees of intensity, with gray or black. The belly and underside of the tail are white, infringed upon laterally by the dorsal ground color, the limits of which are not definitely demarked. The underside of the tail may be lightly mottled with gray.

In living specimens the dorsal ground color varies from olive green to olive brown. The dorsal part of the head is of the same color as is the dorsum, while the under parts are white or cream (Pl. IV, Fig. 6).

It should be reiterated that the juveniles of this form have the same pattern as *alternatus* has, not that of *laevis*, *melanolomus*, and *veraecrucis*.

The following is the ventral scutellation: abdominals, 179–95 (186); subcaudals, 108–18 (113); total abdominals, 292–310 (300).

RANGE.—This form, as here recognized, extends along the Pacific slopes from Guatemala northward to Colima, Mexico, and on the Tres Marias Islands (Map 4).

MATERIAL EXAMINED

Locality (and Museum Number)

Guatemala

Volcán Zunil (C.A.S. 66946)

Mexico (A.M.N.H. 19571)

Acapulco (E.H.T. 10094)

Chiapas

- Finca Juárez, 30 kilometers northeast of Esquintla (U.M.M.Z. Field Nos. 1018, 1062, 1137)
 Colima Province (U.S.N.M. 56283)
 Colima, city (C.M. 7253; U.M.M.Z. 80202)
 Tres Marias Islands (B.M. 81.10.1.103, 81.10.1.108, 82.11.15.41)
 Maria Madre Island (C.A.S. 58679 [type]; U.S.N.M. 24674-78)
 Maria Magdalena Island (U.S.N.M. 24679)

I have also seen the following *alternatus-slevini* intergrades:

Tehuantepec, Mexico

Tehuantepec (U.M.M.Z. Field Nos. 430, 653, 741, 1068, 1108, 1439, 1448)

VARIATION.—Because of the scanty material, the task of interpreting the variation in this form is difficult. Most striking is the difference between the mainland and island populations in scutellation. In Table XXI this condition in the males is clearly indicated. No such comparison of the females was possible because too few female specimens were available.

TABLE XXI

Locality	Specimens	Abdominals	Subcaudals	Total Ventrals
Mainland	5	179-95 (186)	114-17 (115)	294-310 (301)
Tres Marias Isls.	6	181-86 (184)	109	292- 96 (294)

In pattern the most striking feature lies in the very intense mottling on the chin and throat in the island populations as compared with the very faint mottling in the Colima specimens. Were more material available, it is not improbable that a name should have to be applied to the mainland specimens. With this material lacking, however, it appears that, since variation in *slevini* parallels that in *veraecrucis* (i.e., decreasing northward), a name is unwarranted. It is impossible to distinguish any differences whatsoever between the Colima and Chiapas material. The significance of this point is brought out further on in this paper.

AFFINITIES.—The affinities of *slevini* are complex in the extreme. The Museum of Zoology has a series of *Dryadophis* from the Isthmus of Tehuantepec which cannot be distinguished from the intergrades between *alternatus* and *laevis* in northern Honduras. This Tehuantepec population undoubtedly represents an isolated colony of relicts which were at a former date distributed from western Mexico southward throughout Central America. The opening of the Tehuantepec portal separated the 2 populations and isolated the former. From this point *slevini* probably differentiated (though it retained in the juvenile pattern a remnant of the prototype), spread northward, and later moved southward, taking on the same characters in both directions. That the same pattern should develop in both directions is to be expected, since there were no new lines open for pattern evolution unless an evolutionary reversal were to take place.

If this explanation of the discontinuity of the distribution of *slevini* is correct, there is no reason to suspect that the Chiapas and Colima populations are genetically identical. If the 2 populations are only superficially identical but physiologically distinct (and I have reason to believe that they are),¹³ they warrant a name, but herpetological systematics has not yet become involved in the naming of physiological races. As has already been suggested, *slevini* may in the future be broken into 3 separate races, namely, the Chiapas population, the Colima (and probably Guerrero, Michoacán, and northern Oaxaca) population, and, finally, the Tres Marias Islands population.

It may well be argued that further exploration in Salvador, western Nicaragua, and western Guatemala may result in the discovery of an unknown link connecting *alternatus* and the Chiapas populations directly. For the present it seems best to consider *slevini* as a direct affinity of *alternatus*, and as having arisen from an isolated population of an *alternatus*-like ancestor.

Dryadophis dorsalis (Bocourt)

Drymobius (*Eudryas*) *dorsalis* Bocourt, 1890: 724, Pl. LI, Fig. 2 (type locality, Guatemala; type Museum National d'Histoire Naturelle, Nos. 7391 and 91-257).

DESCRIPTION.—The ground color of the dorsum (*stratum corneum* lacking) is composed of shades of bluish gray. Some of the dorsal scales may be flecked with white at the edges or may have a narrow white anterior border, usually concealed by the posterior part of the preceding scale. A middorsal, longitudinal, dark stripe extends from the nape to the end of the tail and is formed by the darkening of scale row 9 and of the upper half of scale rows 8 and 10. In some specimens there is an indication of a lateral dark stripe on scale row 3 over the fore part of the body. The upper surface of the head is of the same color as is the dorsum, and the sides of the head are somewhat lighter. A slight dark smudge extends from the nostril through the eye and across the temporals. The supralabials are white, sometimes narrowly margined with gray. The infralabials, chin, and throat are immaculate white. The belly and undersurface of the tail are white, heavily mottled or flecked with gray. Laterally, the dorsal ground color infringes upon the belly and ventral surface of the tail and is delimited by a narrow white line. Fresh specimens have not been available, but Bocourt stated (1870-1909: 725) that the dorsal ground color is olive, and I have seen specimens in the zoological gardens in Guatemala City which bear out this statement (Pl. IV, Fig. 5).

The scutellation of *dorsalis* is as follows: abdominals, 177-96 (183); subcaudals, 109-31 (121); total ventrals, 286-316 (302).

¹³ The Chiapas specimens were taken on the very humid west slopes of the mountains, and the Colima specimens are from the arid coast typical of western Mexico.

RANGE.—This species is known only from the highlands of western and southern Guatemala and the Honduran uplands. The exact limits of its range are at present unknown (Map 4).

MATERIAL EXAMINED

Locality (and Museum Number)

- Guatemala (F.M.N.H. 25226)
 Central Guatemala (A.N.S. 5520)
 Atitlán (F.M.N.H. 1965)
 Duenas (B.M. 60.12.1.30, 64.1.26.14 [2], 64.1.26.25)
 El Porvenir, San Marcos (F.M.N.H. 20332)
 Olas de Moca, Sololá (F.M.N.H. 20416)
 Panajachel (M.C.Z. 22440)
 Quiriguá (F.M.N.H. 20554–55)
 Volcán St. Lucas (M.C.Z. 25215)
- Honduras
 Subirana Valley, Yoro (M.C.Z. Field Nos. B 278, B 291, B 319)

VARIATION.—Although a fair series of this species has been available, the majority of the specimens are from the vicinity of Lake Atitlán, Guatemala, and the remainder from localities too scattered to permit any discussion of variation. The variation in pattern (the presence or absence of the dark lateral stripes) may in all probability be attributed to the state of preservation. As to scutellation, however, 2 specimens (a male and a female) from lower altitudes on the Pacific slope of Guatemala have fewer subcaudals than highland specimens have. Whether or not this altitudinal correlation with number of subcaudals actually exists can only be determined when more material is available.

AFFINITIES.—The affinities of this species are the most obscure of any in the *alternatus* group. The juvenile pattern indicates that the species is to be associated with *veraecrucis*, *laevis*, and *melanolomus* and that it has arisen from the same ancestry. True intergrades between *dorsalis* and any other form are lacking.

It should be noted that the pattern of *dorsalis* is not too difficult to derive from an *alternatus*-like pattern. Throughout the genus as a whole, well-preserved adults tend to be dark middorsally, though this darker shade fades gradually into the lighter shade laterally and is often imperceptible. If we were to assume that an *alternatus*-like pattern were to fade to such an extent that the upper and lower lateral light stripes became the same shade as is the rest of the body while scale rows 3 and 9 retained their original shade, the pattern of *dorsalis* would be the result. That this has actually happened seems to offer the only logical explanation of the *dorsalis* pattern.

It appears, therefore, that *dorsalis* probably had the same type of, or even the very same, ancestor as *laevis*, *melanolomus*, and *veraecrucis*, but, in moving to the highlands of Guatemala, became sufficiently isolated to sever all

connection with these. So far has differentiation progressed that, if no intergrades are known from Honduras, it seems very probable that they do not exist elsewhere. There is, moreover, no evidence of intergradation between *dorsalis* and *slevini* in a specimen of the latter from western Guatemala. This statement is based on the fact that the juvenile patterns of the 2 are of different types (discussed more fully below) and on the conclusion that, if *dorsalis* does not intergrade with either *alternatus* or *laevis*, it would not be expected to intergrade with *slevini*, which has had a rather peculiar and isolated history.

ORIGIN AND AFFINITIES OF THE *MELANOLOMUS* GROUP

The key to the present distribution of the *melanolomus* group in Central America is to be found in the geological history of the Panamanian-Costa Rican and the Tehuantepec portals. These have been adequately discussed by Schuchert (1929: 341-42; and 1935: 568-79) and are outlined in this paper under *boddaerti*. Briefly stated, the Panamanian-Costa Rican portal was apparently closed during the late Cretaceous and lower Eocene. From the middle Eocene to the middle Miocene, with the possible exception of a short period in the lower Oligocene, this portal was open, and from the upper Miocene to the present it has remained closed. The Tehuantepec portal, on the other hand, remained closed until the Pliocene, or possibly until the late Miocene, when it was open; and it remained open until the upper Pliocene. Of some importance to the history of the *melanolomus* group is the fact that eastern Mexico (lowlands) and the Yucatán Peninsula were widely flooded during the Pliocene and Pleistocene and that the highlands of Guatemala and Honduras were never flooded during the Cenozoic.

The biological evidence upon which the history of this group rests consists of the pattern types of the various forms and the ventral scutellation. It should be noted that, as already discussed in the introduction, the pattern of *alternatus*, with its 2 lateral light stripes, probably most closely approaches the ancestral type of the group. Furthermore, *laevis*, *melanolomus*, *veraecrucis*, and the Oaxaca population all retain traces of this prototypic pattern. Well differentiated, on the other hand, are *dorsalis*, with its peculiar pattern of a dorsal stripe (the possible origin of which has already been discussed), and the unicolor *slevini*. Finally, it should be emphasized again that *dorsalis*, *laevis*, *melanolomus*, and *veraecrucis* have a juvenile pattern quite different from that of *alternatus* and *slevini*. In scutellation, there is a tendency for the subcaudal scutes to increase in number in all directions from *alternatus* except, as already noted, in peripheral populations of *slevini* and *veraecrucis*. These geological and biological facts form the basis for my conception of the origin and distribution of the several forms of the *alternatus* group.

A fairly clear evolutionary history of the *melanolomus* group may be based entirely upon the geological history of Central America. The genus *Dryadophis* probably had its origin in northern South America. It is generally conceded that the colubrids originated in the Holarctic region. If this is true, it is probable that some colubrids invaded South America by way of Central America at some period between the Upper Cretaceous and the beginning of the middle Eocene. Isolation in South America from that time until the middle Miocene, caused by the open portal in Panama and Costa Rica, probably resulted in considerable generic differentiation, and, as has already been pointed out, such genera as *Dendrophidion*, *Dryadophis*, *Chironius*, and possibly *Leptophis* arose during that interval. When this portal was finally closed, these genera invaded Central America; among them was the prototype of the *melanolomus* group. This prototype probably spread northward through Central America, on the highlands of Honduras and Guatemala, and into western Mexico. (Eastern Mexico and the entire Yucatán Peninsula were submerged at that time.) As the Miocene drew to a close, or possibly early in the Pliocene, the Tehuantepec portal appeared, which isolated in western Mexico a part of the protostock in much the same way as that in which *Cnemidophorus gularis* was isolated (Burt, 1931: 73-74). During the Pliocene differentiation proceeded in southern Central America, in the Honduran and Guatemalan highlands, and in western Mexico. The Tehuantepec portal was again closed in the upper Pliocene, whereupon the western Mexican population migrated southward into Chiapas. Later, the Yucatán Peninsula and eastern Mexico emerged, permitting the spread of the Central American type into these newly formed regions.

This history is borne out by the biological evidence, especially with reference to pattern. As indicated previously, the prototype of the *melanolomus* group which entered Central America during the Miocene was probably very similar in pattern to the living *alternatus*. From this original type differentiation has taken place in 3 directions: (1) the development of the *alternatus* pattern—this form, despite its long history, very probably has not changed greatly from the prototype, since it has always inhabited an environment similar to that in which it had its origin; (2) the great amount of differentiation which has taken place in *dorsalis* and *slevini*—these 2 forms, although their history is no more ancient than that of *alternatus*, have been subjected to environments radically different from their ancestral home, *dorsalis* on the highlands and *slevini* on the arid west Mexican coast; (3) the rather recently differentiated forms, *laevis*, *melanolomus*, and *veraecrucis*, all of which still retain traces of the prototypic pattern.

After the ancestor of the *alternatus* group had entered Central America, it spread over all of Central America and into western Mexico. When the

Tehuantepec portal had been opened, differentiation began in lower Central America, on the highlands of Honduras and Guatemala, in western Mexico, and possibly on the lowlands of northern Honduras. In lower Central America differentiation was slight. On the highlands of northern Central America it must have been fairly rapid to produce the bizarre pattern of *dorsalis* and to change this form so thoroughly in physiological respects as to preclude any chance of later hybridization. In western Mexico the striped pattern gradually faded to the unicolor condition (except in Oaxaca, where it retained traces of the original), but at the same time the form did not completely sever its connection with the prototype, as it retained the original juvenile pattern. On the lowlands of northern Honduras, on the other hand, differentiation probably proceeded slowly, yet rapidly enough to produce a new type of juvenile pattern, and it may have been from this ancestry that *dorsalis* was derived. When the Tehuantepec portal was finally closed, the Oaxaca population was able to spread southward along the coast. There it produced a form which paralleled *slevini* in the north and which today cannot be distinguished from it. Finally, it remained only for the Yucatán Peninsula and the lowlands of eastern Mexico to emerge and open new territory into which the slightly differentiated population of northern Honduras, with its distinctive type of juvenile pattern, could move. When this occurred, toward the close of the Pleistocene, *laevis* developed at the base of the Yucatán Peninsula and invaded the upland of Alta Verapaz, *melanolomus* differentiated in northern Yucatán, and *veraecrucis* evolved on the lowlands of eastern Mexico. As previously stated, these 3 all retain remnants of the prototypic pattern, as evidenced in the indication of lateral light stripes, and are to be considered the most recently differentiated of the *melanolomus* group. They have, however, progressed well along the line toward the unicolor condition, which at present is found only in *slevini*.

Evolutionary evidence presented by scutellation parallels that of the pattern and fits the scheme of origin already presented. The number of abdominals shows very little differentiation; they are somewhat erratic in their variation from one locality to another within a single form as well as between the various forms, so that no definite trends are discernible.

With reference to the interspecific trends in the number of abdominals, there appears to be a slight decrease in all directions from *alternatus*, though more noticeable in *melanolomus* and *veraecrucis* than in the others. This decrease is so slight, however, that it is apparently without significance. Further comment on this character or a table of variations and means does not seem warranted.

The number of subcaudal scutes, on the other hand, offers an excellent phylogenetic clew and fits exactly into the history already drawn up, which is based on geological development and pattern. Evolution, except in the

peripheral positions already noted, has produced an increase in subcaudals. The trends in subcaudals of the total population of *alternatus* (6 forms) are set forth in Figure 11, the mean number of subcaudals being considered as indicative of the trends.

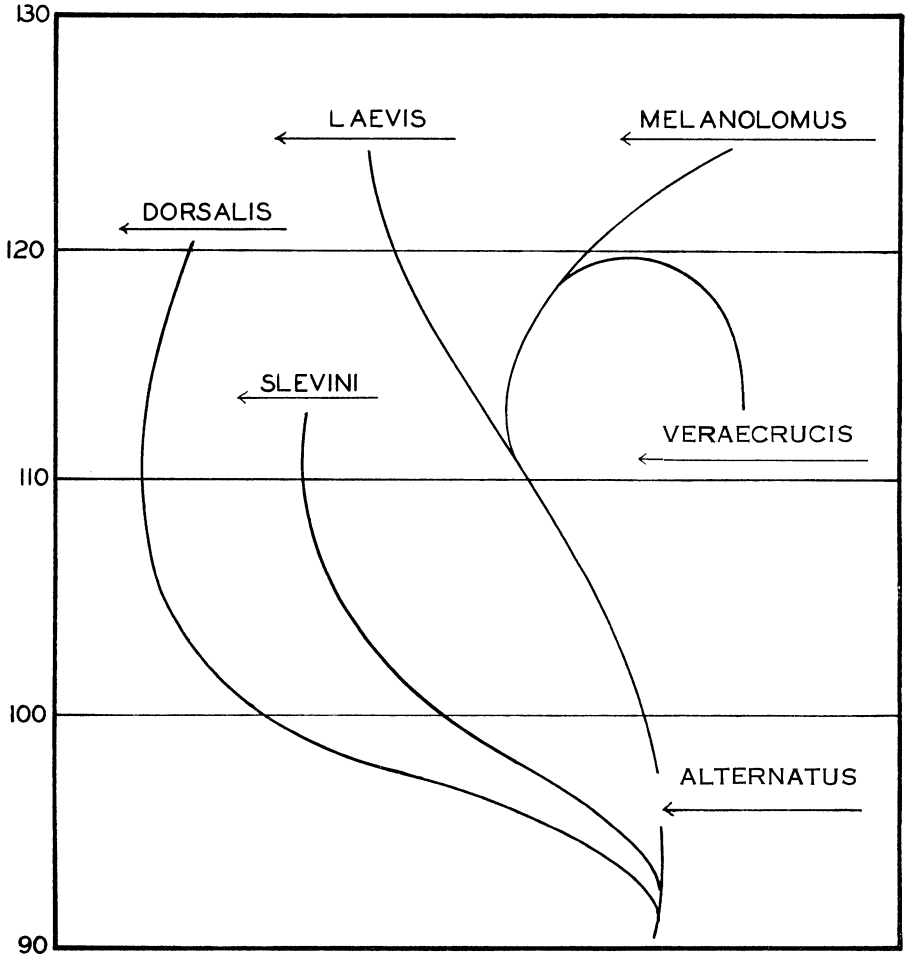


FIG. 11. Trends in subcaudals in the total population (averages only plotted) of the 6 forms of *alternatus*. Note the tendency toward increase in peripheral forms. The low number of subcaudals in *slevini* and *veraecrucis* (end forms) is the result of intra-specific peripheral reduction illustrated in Figure 3. Compare this figure with Figure 5.

In both *slevini* and *veraecrucis* the increase is not comparable to that of *laevis*, *dorsalis*, and *melanolomus*, partly because the peripheral decrease in subcaudals in specimens from the northern part of their ranges has had a

marked effect on the means. As in pattern, the Oaxaca population is similar to the Honduran intergrades—a similarity which is further evidence of the close relationship of the 2 populations. The slightly greater mean number of subcaudals in the latter may be explained on the basis of secondary *laevis* influence.

A chart of the increase in total ventral scutes would present much the same picture. The increase, however, would be less marked than in the subcaudals, because, as previously noted, the abdominal scutes decrease slightly in number in all directions from *alternatus* and would, therefore, counteract to some extent the increase in subcaudal scutes.

All evidence points to the following history of the *alternatus* group: a protostock entered Central America from South America prior to the middle Eocene. Here it spread over the entire area and north into western Mexico, but remained isolated from South American groups because of the open Panamanian–Costa Rican portal. In late Miocene times the Tehuantepec portal opened and isolated the population in western Mexico. Here developed *slevini*; meanwhile *dorsalis* evolved on the Guatemalan and Honduran highlands, and the original prototype changed but little to form *alternatus* in southern Central America. At the end of the Pliocene, emergence began, and opened for colonization the east coast of Mexico and the Yucatán Peninsula. The *alternatus* stock in Honduras then spread northward and became *veraecrucis* in eastern Mexico, *melanolomus* at the outer end of the Yucatán Peninsula, and *laevis* at the base and on the adjacent highlands. The relationships of the forms of the *melanolomus* group, as I conceive them to be, are indicated in Figure 12.

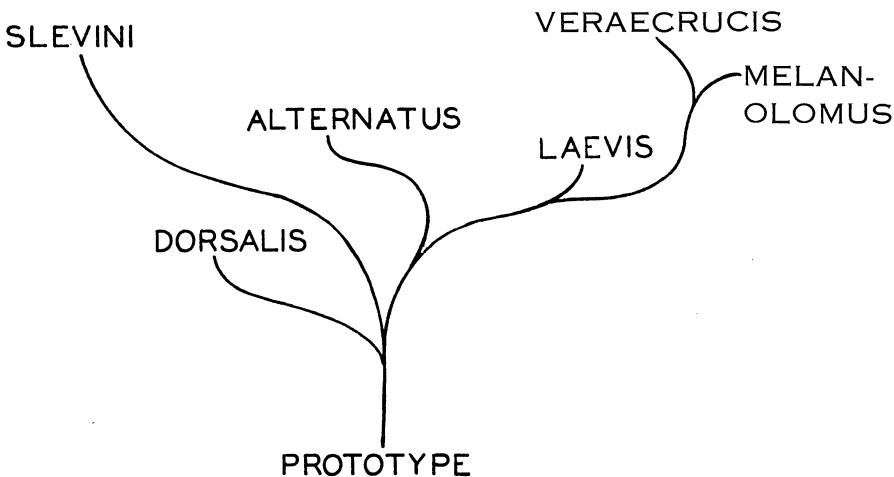


FIG. 12. Relationships of the forms of the *melanolomus* group.

ORIGIN AND AFFINITIES OF THE SPECIES GROUPS

Inasmuch as the history of the various species comprising each species group has been covered in some detail it remains only to show how they have arisen and have become distributed since the prototype of the genus had its inception. Previous investigators, the most famous of whom are Matthew and Adams, have listed criteria by which they suggested the manner of determining the center of origin. Matthew's concept has never, so far as I know, received any support from so ephemeral a category as a genus, though for larger units his conclusions are now generally accepted. Adams' criteria, on the other hand, when applied to smaller taxonomic categories, are most useful. His 10 criteria may be reclassified in 2 major groups, (1) those dealing with the location of generalized types, such as location of living generalized forms and location of least dependence upon restricted habitat, and (2) the place of contact of evolutionary lines, such as the continuity and convergence of lines of dispersal and the location of greatest differentiation of type.

When these 2 general criteria and their implications are applied to the genus *Dryadophis*, it becomes evident that generalized types are situated in northern South America, where such forms as *striatus* and *pleei* are found. (The occurrence of the most generalized form, *pulchriceps*, in Ecuador has already been discussed.) This same region is the place of contact of evolutionary lines, as the *melanolomus*, *pleei*, and *bifossatus* groups all converge on this region and the *boddaerti* group is centered in the same area. It is evident, therefore, that northern South America represents the center of the genus.

The early history of the genus, then, was enacted upon the Parian land mass, which had already begun to break up in the Cretaceous, but persisted as a borderland until the Pliocene, and upon the very ancient and stable continental block to the south which is known as the Archiguayanan shield. Later, a part of the genus entered Central America and in this region underwent evolution which paralleled the changes which were taking place in South America at the same time.

It is indicated that the progenitor or progenitors of the neotropical colubrids entered South America prior to the Eocene break across Panama and Costa Rica. Isolated from the middle Eocene to the Miocene, a number of genera developed in South America, and in the north the *Dryadophis* prototype came into being in the more arid habitats. Prior to the Miocene this prototype was well developed, and the rising Andes isolated in western Ecuador a population destined to become *pulchriceps*. In the meantime this same prototypic population was giving rise to the *bifossatus* group on the Archiguayanan shield, while in the north on Paria a *boddaerti*-like form was developing. By the middle Miocene this *boddaerti*-like form had divided

into 2 populations, one, in the arid habitats, which was destined to become the prototype of the *pleei* group, and, in the more humid areas, the population which was to give rise to the *boddaerti* and *melanolomus* groups.

When the Panamanian–Costa Rican portal closed at the middle Miocene, a part of this latter population invaded Central America and subsequently passed through the evolutionary stages already discussed. The remaining part of that population in South America developed along parallel lines and produced the *boddaerti* group. These 2 populations had little chance to intergrade, since, being essentially humid-land forms, they were separated by the arid region of northern Colombia. The *pleei* group remained restricted to the arid regions of northern South America and evolved as has already been discussed. Farther to the south the *bifossatus* group was evolving and spreading southward.

The genus evolved from a colubrine ancestor which entered South America from North America prior to middle Eocene times. It is evident that between the middle Eocene and lower Miocene the prototypes of the 4 groups were developed, and that since the middle Miocene these groups have differentiated along parallel lines into the 17 forms which now make up the genus *Dryadophis*. My concept of the relationship of the various groups is depicted in Figure 13.

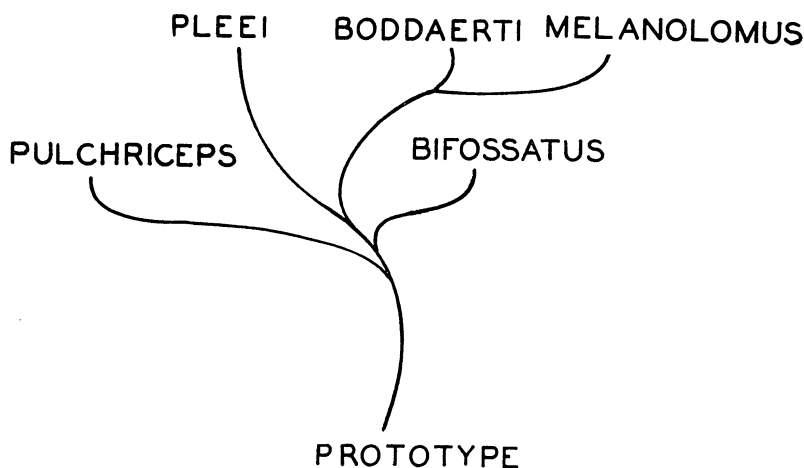


FIG. 13. Relationships of the various forms.

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PLATES I-IV

PLATE I

FIGS. 1 and 2. Side and dorsal surface of head in *bifossatus*, the short-snouted type.

FIGS. 3 and 4. Side and dorsal surface of head in *pleei*, the long-snouted type.

FIG. 5. Juvenile pattern of *alternatus*, illustrating the juvenile pattern of alternating dorsal and lateral blotches.

FIG. 6. Juvenile pattern of *dorsalis*, depicting the juvenile pattern of the banded type.

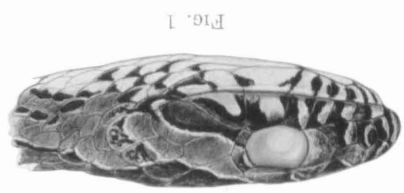


FIG. 1



FIG. 2



FIG. 3

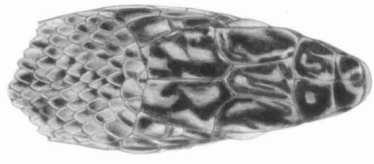


FIG. 4

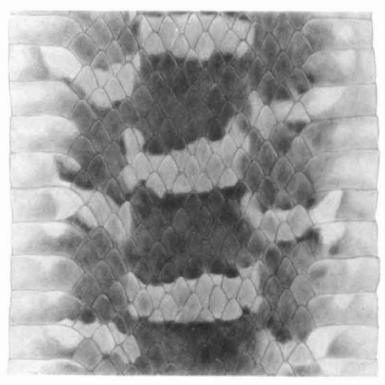


FIG. 5

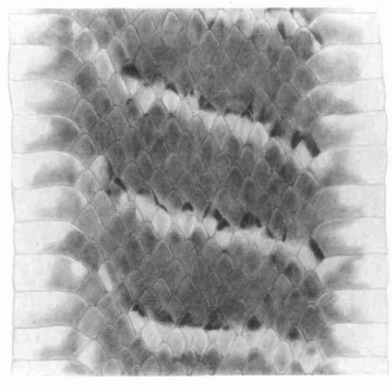


FIG. 6

PLATE II

FIGS. 1 and 2. Side and lateral view of head in *pulchriceps*. Note the very dark head and throat.

FIG. 3. Dorsal pattern of *pulchriceps*.

FIG. 4. Dorsal pattern of *striatus*. Note the shortness of the crossbands.

FIG. 5. Dorsal pattern of *bifossatus*.

FIG. 6. Dorsal pattern of *triseriatus*. Note the light ventrals.

PLATE II



FIG. 1

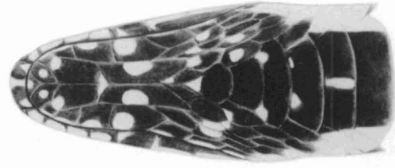


FIG. 2

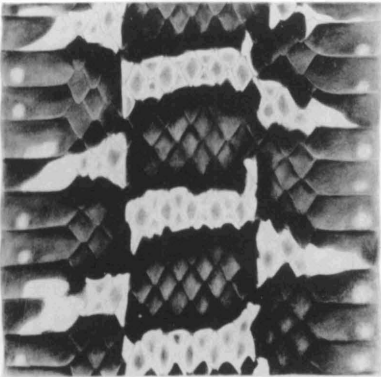


FIG. 3

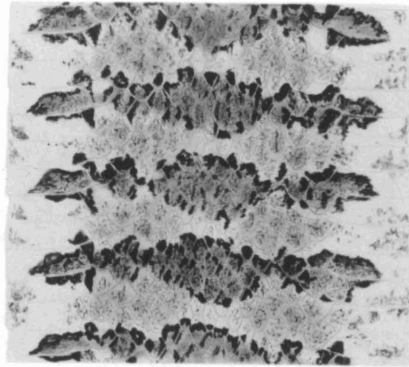


FIG. 4

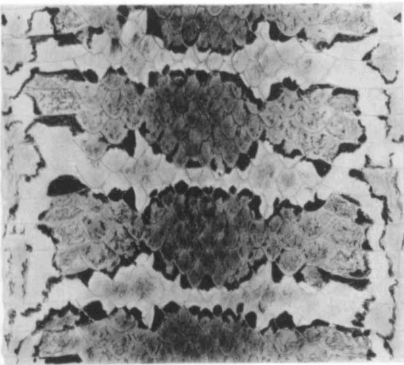


FIG. 5

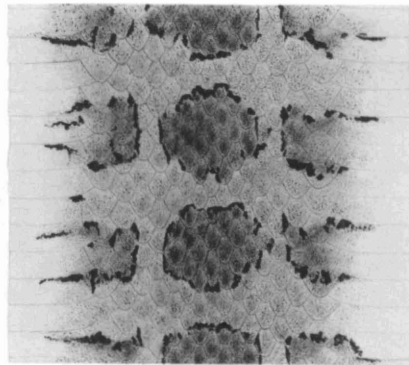


FIG. 6

PLATE III

FIG. 1. Dorsal pattern of *pleei*, anteriorly. Note the 3 dorsal dark stripes.

FIG. 2. Dorsal pattern of *pleei* beyond mid-body. The 3 middorsal stripes have fused to form a single dorsal band.

FIG. 3. Dorsal pattern of *amarali*. Note the similarity to the posterior pattern of *pleei*.

FIG. 4. Dorsal pattern of *bruesi*.

FIG. 5. Dorsal pattern of *ruthveni*. Compare this pattern with that of *alternatus* (Pl. IV, Fig. 3).

FIG. 6. Dorsal pattern of *dunni*. The dark margins on the upper lateral light stripe have been lost.

PLATE III

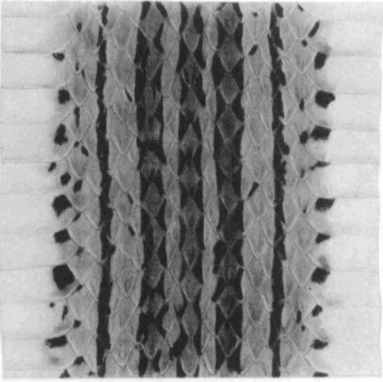


FIG. 1

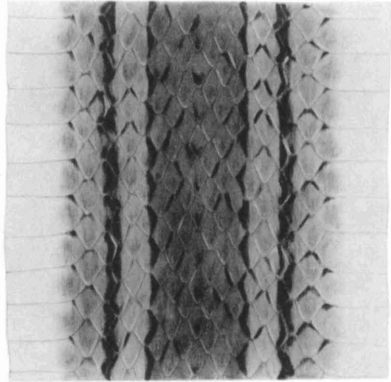


FIG. 2

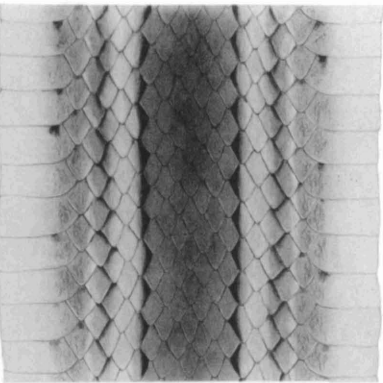


FIG. 3

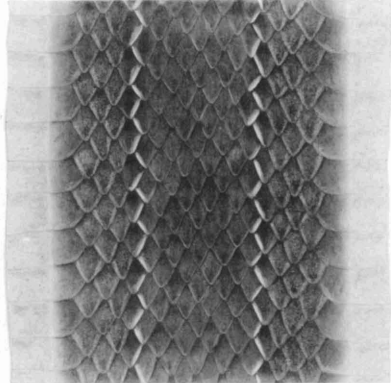


FIG. 4

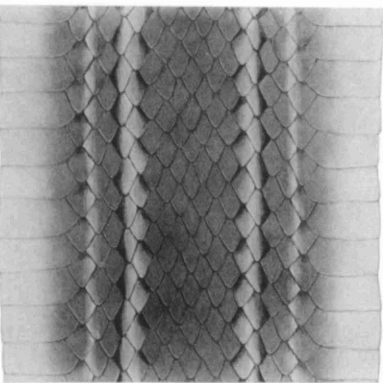


FIG. 5

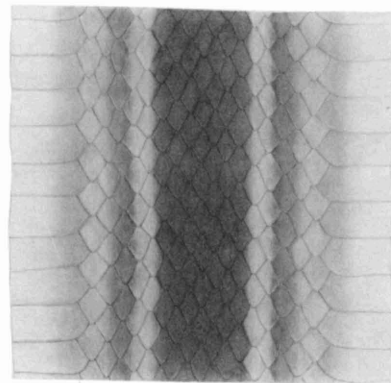


FIG. 6

PLATE IV

- FIG. 1. Dorsal pattern of *boddaerti*.
FIG. 2. Dorsal pattern of *heathii*. Note the position of the lateral light stripe.
FIG. 3. Dorsal pattern of *alternatus*.
FIG. 4. Dorsal pattern of *melanolomus*.
FIG. 5. Dorsal pattern of *dorsalis*.
FIG. 6. Dorsal pattern of *slevini*. The same pattern is found in *veraecrucis* and in the unicolor *laevis*.

PLATE IV

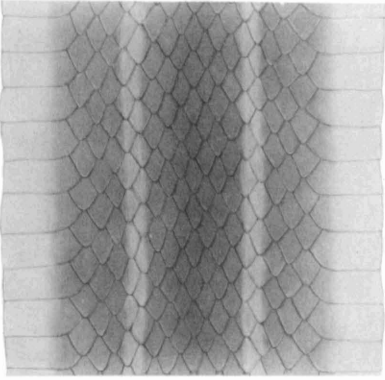


FIG. 1

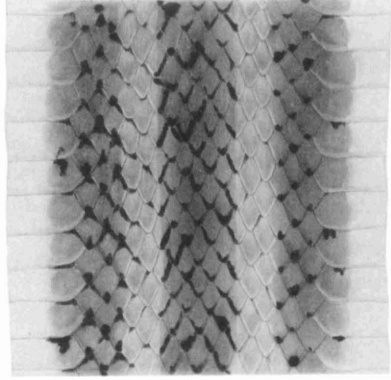


FIG. 2

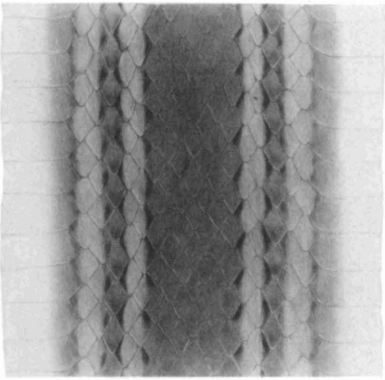


FIG. 3

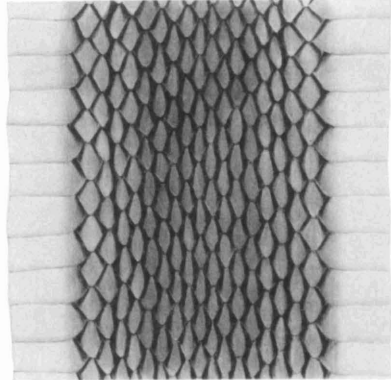


FIG. 4

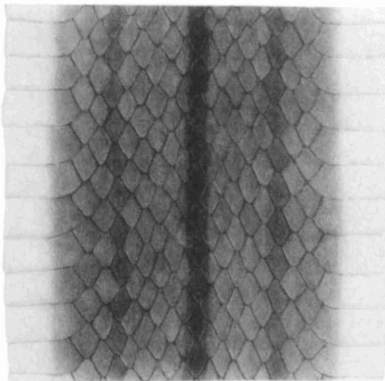


FIG. 5

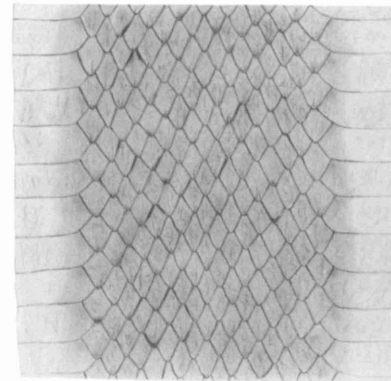


FIG. 6

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