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STUDIES ON NEOTROPICAL COLUBRINAE

I. THE TAXONOMIC STATUS OF THE GENUS *Drymobius* FITZINGER

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INTRODUCTION

IN the light of present day herpetological investigations, which have tended towards a breaking up of larger genera into smaller groups by the use of finer differential characters, it is somewhat remarkable that the genus *Drymobius* has existed in its present form for so long a time. Although both Ortenburger and Amaral have shown that great differences exist between various groups of forms of both the nearctic and neotropical races, which have long been considered as a single genus, the most obviously heterogeneous group has remained untouched. Thus species such as *Drymarchon corais corais* and *Drymoluber dichrous,* two forms of great superficial similarity, were split apart, while *Drymobius boddaertii* and *Drymobius rhombifer* were retained within the same genus.

Fitzinger as early as 1843 recognized differences within this group and assigned the known species to separate genera. As recognized at the present time, the genus *Drymobius* is one of a group of genera, which might well be referred to as a tribe,

including *Drymoluber, Drymarchon, Masticophis, Coluber,* and *Salvadora.* As a whole they may be characterized as having an attenuated body form, a rather long, narrow head, which is distinct from the neck, 15 or 17 rows of dorsal scales with apical pits, 2 postoculars, and a reduction in the number of scale rows brought about by the dropping of the fourth row on each side of the body.

It is to be further noted that within each of the above mentioned genera, except *Drymobius,* there is a consistency of characters. The scales are either keeled or smooth, the anal plate is either divided or single, the dentition is a single type, and the hemipenis is always of the same character. In *Drymobius* some forms have keeled scales and others have smooth, the anal plate is single in some and double in others, there are several types of dentition, and vast differences in the hemipenial characters.

It seems evident then, that, as now recognized, the genus *Drymobius* departs from the laws which govern the group, and that if it can be broken up into several genera, each of which is consistent within itself, such a division is not only logical but necessary. In the present paper my efforts will be confined to demonstrating this fact.

Systematic Discussion

In the following discussion four genera only, *i.e.,* those which make up what has heretofore been known as *Drymobius,* will be considered. The following key shows how easily we may break up this single group.

A. Scales smooth ..... B
  B. Anal single ..... *Drymoluber*
  BB. Anal divided ..... *Eudryas*
AA. Some or all dorsal scales keeled C
  C. Maxillary teeth generally more than 33
    Hemipenis simple with few spines and unflounced calyces
    ..... *Dendrophidion*
  CC. Maxillary teeth generally less than 33
    Hemipenis more complex with numerous spines and flounced calyces ..... *Drymobius*

Since three of the above genera have lain in more or less neglect since Fitzinger first referred to them, and the fourth was not fully understood by its author, a redescription of each is necessary. No attempt will be made in this paper to give a full synonomy, since, at the present time, a revision of each of the above genera is under way and will appear in the near future.

Drymoluber Amaral

1929 *Drymoluber* Amaral, Mem. Inst. Butantan, IV: 335.

Type.—*dichrous* Peters, Mon. Berl. Ac., 1863: 284.

Description.—Body attenuated. Dorsal scales in 15 to 17 rows, smooth, with apical pits. Ventrals 160–194, subcaudals in two rows, 87–123 in number. Anal single, rarely divided. Head scutellation normal; supralabials 8, fourth and fifth typically entering the orbit. One prae- and two postoculars, temporals typically 2 + 2, though great variation exists. Maxillary teeth 18–24, generally 22 or 23, subequal or posterior one slightly enlarged. Hemipenis not capitate. Sulcus undivided, with a corrugated fold devoid of spines along the proximal portion. Proximal one-fourth bare, spines stout, often with distal hook and extending to about one-half the distance to the distal end of the organ. Calyces numerous and deep; making obscure the nature of the calyces are long, flouncing spines which grade into basal spines (Plate I, fig. 3).

Range.—This genus appears to be limited to the area east of the Andes, and extending from the Guianas to southern Brazil.

Discussion.—A careful study of the characters of this genus has brought me to the conclusion that Dr. do Amaral had justifiable grounds for his recognition of a new genus. In fact I anticipated such a step following my examination of *Drymobius brazili*, although unaware of the fact that *Drymoluber dichrous* entered into the complex. So characteristic is the structure of the hemipenis of these two forms, that, coupled with the identical number of supralabials and single anal plate together with a range confined to the region east of the

Andes (to be commented upon later), it would prove a difficult task to show that *Drymoluber* is not a distinct genus. Thus my proposal is that the genus *Drymoluber* no longer be considered monotypic, but should include both *dichrous* and *brazili.*

In the light of Dr. do Amaral's recent study,[1] *dichrous* needs no further comment, and *brazili* has so recently been described[2] that a redescription is not necessary. A simple key will show the status of the forms included:

A. Dorsal scales in 15 rows ..... *D. dichrous*
AA. Dorsal scales in 17 rows ..... *D. brazili*

It might be added that while Gomes believed that the anal plate in *brazili* was both single and divided, I have found only a single specimen, that recorded by Gomes, in which the divided condition exists.

Eudryas Fitzinger

1843 *Eudryas* Fitzinger, Syst. Rep.: 26.
1870 *Drymobius* (*Eudryas*) Duméril et Bocourt, Miss. Sci. Mex.: 720–730.
1894 *Drymobius* Boulenger, Cat. Sn. Brit. Mus., II: 10–11.
1931 *Drymobius* Amaral, Mem. Inst. Butantan, IV, 1929: 81, 154.

Type.—*boddaertii* Setzen, Myer's Zool. Arch, ii, 1796: 59.

Description.—Body attenuated. Dorsal scales smooth, in 15–17 rows, with apical pits. Ventrals 159–206; subcaudals in two rows, 79–132 in number. Anal divided. Head scutellation normal; supralabials typically 8 or 9, fourth and fifth, or fourth, fifth, and sixth entering orbit. One prae- and two postoculars; temporals typically 2 + 2, with great variation. Maxillary teeth 18–29, subequal, with a more or less distinct space before the posterior three or four. Hemipenis not capitate, sulcus single. Proximal one-fourth bare, distal to this are long slender spines in about 11 rows, totalling between 50 and 60 and grading into calyces at about the middle of the

[1] do Amaral, A., Mem. Inst. But., IV, 1929: 333–337.
[2] Gomes, J. F., Mem. Inst. But., I, 1918: 81–83, pl. XIV, fig. 2.

organ. Distal to the spines are deep calyces, flounced with spinelike projections in 15–20 rows. Occasionally several rows forming a compact mass on border of sulcus, number of calyces variable (Plate III, figs. 1 and 2).

Range.—This genus ranges throughout the Neotropics from southern Mexico through Central America and southward to Argentine on both sides of the Andes.

Discussion.—The genus is, perhaps, the most complex of the entire group. Into it fall two forms, *boddaertii* and *bifossatus*. The vast range of the former has led me to make a thorough investigation of the forms, and the results of this study are to appear shortly. It is sufficient to say at this time that distinct subspecies exist, all of which, with the possible exception of one, have long since been named. So complex is the synonomy that the proper nomenclature to be applied to the various subspecies cannot be presented at this time. Likewise, *bifossatus* may probably be broken up into several varieties. Dr. do Amaral has recently named two subspecies,[3] but as yet a careful check of the material has not been made.

Dendrophidion Fitzinger

1843 *Dendrophidion* Fitzinger, Sys. Rep.: 26.
1860 ?*Dendrophidium* Cope, Proc. Acad. Nat. Sci. Philad.: 561.
1870 *Dendrophidion* Duméril et Bocourt, Miss. Sci. Mex.: 730.
1894 *Drymobius* Boulenger, Cat. Sn. Brit. Mus., II: 15.
1895 *Cacocalyx* Cope, Tran. Am. Phil. Soc., XVII: 205, pl. XIX, 1.
1931 *Drymobius* Amaral, Mem. Inst. But., IV, 1929: 82, 154.

Type.—*dendrophis* Schlegel, Phys. Serp., 1837: 196.

Description.—Body attenuated. Dorsal scales keeled, in 17 rows, with apical pits. Ventrals 145–172; subcaudals in two rows, 94–158 in number. Anal single or divided. Head scutellation normal; supralabials typically 9, fourth, fifth, and sixth entering orbit. One prae- and two postoculars; temporals typically 2 + 2, with great variation. Maxillary teeth 33–50 in continuous series and subequal. Hemipenis very simple; sulcus undivided; proximal portion bare, distal one-

[3] do Amaral, A., Bull. Ant. Inst. Am., IV, 4, 1931: 86.

fourth with 10–15 shallow calyces which are unflounced and beneath which lie a very few short spines in about eight poorly defined longitudinal rows (Plate I, figs. 1 and 2).

Range.—Northern South America and Central America.

Discussion.—This genus, so similar in appearance to the other genera, shows a great departure from the others in the hemipenial form. The organ in this genus represents what is either the most primitive or most degenerate type in the Colubrinae. Although the hemipenes of numerous supposedly related genera have been examined, I have been unable to find anything even remotely resembling that of *Dendrophidion.* The structure of the organ is the same in both species referred to the genus, *dendrophis* and *bivittatus,* but is more primitive in the latter.

With reference to the synonomy of this genus, Cope first described it and properly noted Fitzinger as its author.[4] The former, however, noted that it was to be split from *Drymobius* on the basis of keeled scales and *two praeoculars.* In all the material examined, I have been unable to find any specimen with two praeoculars. Cope further changed the Greek ending *ion* to the Latin *ium.* Duméril and Bocourt offered the first accurate description of the genus in 1870.[5] In 1895 Cope designated a new genus, *Cacocalyx,*[6] assigning as its type *percarinatus.* Unfortunately the description of *percarinatus* is poor, but the excellent figure of the hemipenis leaves no doubt that *Cacocalyx* should be referred to *Dendrophidion.*

Drymobius Fitzinger

1843 *Drymobius* Fitzinger, Sys. Rep.: 26.
1894 *Drymobius* Boulenger, Cat. Sn. Brit. Mus., II: 14, 17.
1931 *Drymobius* Amaral, Mem. Inst. But., IV: 154–155.

Type.—*margaritiferus* Schlegel, Phys. Serp., 1837: 184.

Description.—Body attenuated. Dorsal scales keeled, in 17 rows, with apical pits. Ventrals 142–168; subcaudals 85–126,

[4] Cope, E. D., Proc. Acad. Nat. Sci. Philad., 1860: 561.
[5] Duméril, M. A. and Bocourt, M., Miss. Sci. Mex., 1870: 730.
[6] Cope, E. D., Trans. Am. Phil. Soc., XVII, 1895: 205, pl. XIX, 1.

in two rows. Anal divided. Head scutellation normal; supralabials typically 9, fourth, fifth, and sixth entering orbit. One prae- and two postoculars; temporals typically 2+2. Maxillary teeth 22–34, noticeably enlarged posteriorly. Hemipenis similar to that of *Eudryas* except that the basal spines are shorter (resembling those in *Dendrophidion*) and are generally in 12 or 13 longitudinal rows with the calyces in more than 20 rows, whereas in *Eudryas* the spines are in 11 rows and the calyces are usually in less than 20 rows (Plate II, figs. 1 and 2).

Range.—This genus is confined to northern and western South America, and is the only one which enters the Nearctic Region to any great extent.

Discussion.—To this genus have been assigned two forms, *margaritiferus* and *rhombifer*. The very distinct keels on the scales make it easily recognizable from all forms except the genus *Dendrophidion,* from which it differs in penial structure. A revision of the two species is at present under way.

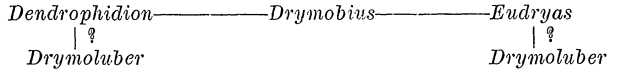
Origin and Affinities of Group

In any discussion relating to the origin and affinities of a group of genera or species, the conclusions arrived at must necessarily remain, at best, highly problematic. That certain conditions exist which appear to point towards orthogenetic development can be stated as a fact, but the interpretation of the conditions is ever open to question. In the following discussion the interpretation of the data which I have before me will be presented, but I do not mean to imply that the conclusions set forth are any more than a highly speculative explanation of what might have occurred within the group.

In attempting to follow the trend of the development of this group a number of characters must be considered. Most important among these are the structure of the hemipenis, the number of teeth, the number and type of scales, the tail length, and, a very important factor, the geographical distribution.

In examining the first of these we are at once given a very definite clue. In *Dendrophidion* there is a very simple type of hemipenis. The calyces are few and the spines are short and limited in number. Thus it can be placed at one end of an orthogenetic line. An examination of the genital organ of *Drymobius* shows the same type of spine occurring in greater numbers and an increase in complexity of the calyces. In *Eudryas,* the basal spines have lengthened and are much better developed, while the calyces remain similar to those in *Drymobius. Drymoluber* has a hemipenis different from any of the other forms, since the spines are heavy and have developed to some extent on the fringe of the calyces. Thus it may be concluded that *Drymoluber* has sprung from a different line; possibly directly from *Dendrophidion,* or an overdevelopment of spines may indicate a close relationship to *Eudryas.*

Thus, considering hemipenial structure, the following relationship may exist:



It is impossible to state in which direction this progression has proceeded, but, because of the very simple structure in *Dendrophidion,* it may logically be assumed that this is the primitive form. To this list might be added *Drymarchon,* in which the calyces have developed in complexity at the expense of the spines; *Drymarchon* may have a direct connection with *Eudryas.* It is further to be noted that the step between *Dendrophidion* and *Drymobius* is so great that there should be an intermediate form. This intermediate may have occurred and become extinct, or it may remain as yet undescribed. But the lack of a similar connection between either *Dendrophidion* or *Eudryas* and *Drymoluber* has led me to believe that the two steps were probably made without an intermediate form. (Plate IV shows the generic types of hemipenes.)

Turning next to the tooth number in the groups the following condition exists:

	Dendrophidion	*Drymobius*	*Eudryas*	*Drymoluber*
Range	33–50	22–34	18–29	18–24
Average ...	37	28	25	22

This again indicates that the line is *Dendrophidion* to *Drymobius* to *Eudryas*. *Drymoluber* appears to be related directly to *Eudryas* on the basis of this character, so that the assumption that it was derived from it on penial structure is strengthened. *Drymarchon* has fewer teeth than *Drymoluber*.

An examination of the anal plate shows that in *Dendrophidion* this plate is both single and double. It is single in *Drymoluber* and divided in both *Drymobius* and *Eudryas*. In as much as both conditions exist in *Dendrophidion*, it may be possible to place the latter at one end of the line. The single anal plate in *Drymoluber* seems to indicate a closer relationship to *Dendrophidion* than to *Eudryas*.

The dorsal scales again give some clue to relationships. In *Dendrophidion* and *Drymobius* they are keeled, while in *Eudryas* and *Drymoluber* they are smooth. In both the former genera the scales are in 17 rows, while in the latter two they are in 15 or 17 rows. Here again *Dendrophidion* and *Drymobius* are grouped, as are *Eudryas* and *Drymoluber*.

An examination of the number of supralabials shows this same condition. They number 9 in both *Dendrophidion* and *Drymobius*, 8 or 9 in *Eudryas*, and 8 in *Drymoluber*. Thus *Eudryas* lies between the former two genera and *Drymoluber*.

The average tail length in the group is as follows:

Dendrophidion	*Drymobius*	*Eudryas*	*Drymoluber*
.38	.32	.28	about .22

Again an orthogenetic line seems to have been established. Taking into consideration all the characters, it is possible to indicate the following relationship:

Dendrophidion———*Drymobius*———*Eudryas*———*Drymoluber*

It might further be mentioned that in *Dendrophidion dendrophis* the adult coloration, a banded condition, is similar to the juvenile coloration of the other forms. This might possibly be looked upon as a case of phylogenetic primitiveness.

To discover in which direction this development has progressed, it is necessary to turn to a discussion of the origin of the South American Colubrinae and to the geographical range of the group.

It is to be noted first that all the genera of Colubrinae in South America, with the exception of the *Spilotes—Phrynonax—Chironius* complex (a group of forms which are members of what might possibly be referred to as another tribe), belong to the *Drymobius—Coluber—Masticophis* tribe already noted. Thus a connection between these nearctic and neotropical forms must be established.

An examination of the nearctic forms shows that such a connection possibly does exist in living forms. The hemipenis of *Coluber, Masticophis,* and *Salvadora* is remarkably constant in spine structure, in that there is in all three genera one or more large basal spines. This character does not occur in any neotropical genera, so that another gap in the line is present. Here again it is possible that the mutation was made in a single step, or the intermediate genus is either unknown up to the present or has been exterminated. In other characters, however, the genera are obviously closely related to *Eudryas.* The tail continues to shorten, the teeth decrease in number, the dorsals are in 15 or 17 longitudinal series, and the supralabials range from 7 to 9. Thus there is a continuation of the *Dendrophidion—Drymobius—Eudryas* line in the Nearctic Realm. The entire group seems to have progressed through the following series:

Coluber
↑
Masticophis
↑
Salvadora
↑
Drymoluber
↑
Eudryas
↑
Drymobius
↑
Dendrophidion

In discussing the direction of progression two possible explanations present themselves:

(1) *Dendrophidion* represents the most primitive form of the group, and from it or a pro-*Dendrophidion* stock has been derived all neogaeic (or possibly all) colubrines; or

(2) The subfamily Colubrinae had its origin from some other form, and *Dendrophidion* represents a highly specialized or secondarily degenerate form.

In making a critical examination of the first possibility several considerations seem to dispose of this argument. Dunn,[7] on a purely statistical basis, points with some confidence to North America as the ancestral home of the neogaeic colubrines. This seems to me a wholly unwarranted conclusion. The mere fact that the Colubrinae have found Nearctica a more favorable area for differentiation than Neotropica, does not, from my viewpoint at least, offer sufficient grounds for assuming that area as the center of dispersal. The fact that the ophiines are the colubrid representative of the neotropical ophidian fauna suggests that an earlier colubrine group, of which the *Drymobius* and *Spilotes* complexes remain as relicts, has been crowded out or exterminated. If the nearctic colubrines were thus crowded from South America, this peripheral group has become highly successful in a new habitat. That this is a very plausible explanation of what has actually occurred seems evident on the basis of two lines of evidence:

(1) The supposition that the simple hemipenis is a primitive type is strengthened by the fact that the probable primitive type of coloration occurs with it; the simultaneous occurrence of these two factors does not seem wholly coincidental; and

(2) The decreasing number of other characters following the increasing complexity of the hemipenis indicates a specialization, since evolution seems to be accompanied throughout the Ophidia by a decrease in number of characters such as teeth, tail length, etc. (compare the aglyphs with the proteroglyphs and selenoglyphs). That this point offers a new field

[7] Dunn, E. R., Copeia, III, 1931: 116.

for study, is suggested; as a generalization it appears to be true superficially.

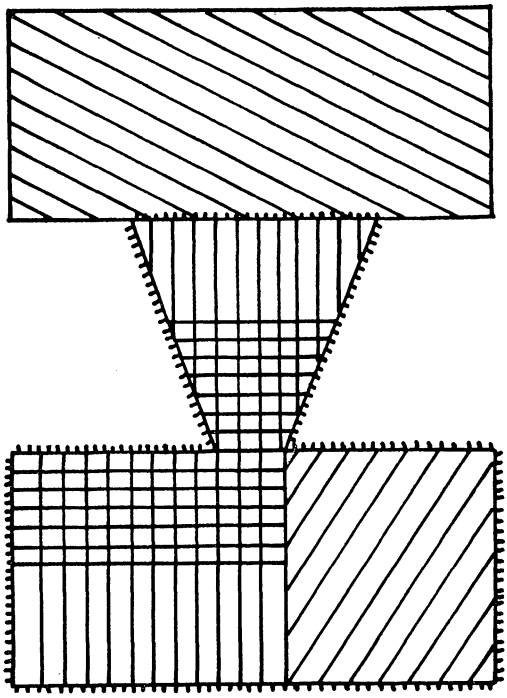
There is yet another way in which the presence of what might be considered the primitive form in the neotropics may be explained if we follow the principle of Matthew;[8] *i.e.*, to assume that the primitive form is to be found on the periphery of the range of the group. Let us suppose that *Dendrophidion* or pro-*Dendrophidion* actually existed in North America. At the point of origin it is possible that it gave rise to a form more successful than itself and was crowded by it to the periphery of the range or northern South America. At this point the unfavorable environment would cause modifications until the several genera were established in South America. Thus *Dendrophidion* might still be considered the primitive form and at the same time occur on the periphery of the range of the entire subfamily.

Turning now to an examination of the second argument, its plausibility is somewhat more difficult to establish and calls for a more fantastic explanation of the presence of *Dendrophidion* in Neotropica. If it is assumed that evolution has proceeded toward a seemingly degenerate hemipenis and an increase in the number of other characters, a direct line (already referred to) is established, but the occurrence of the primitive type of coloration along with the very simple hemipenis cannot be explained unless evolution has repeated itself or unless this character is completely disregarded.

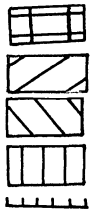
Summing up the plausible possibilities it can be said that *Dendrophidion* represents either a primitive form at the point of origin or a primitive form on the periphery. That *Dendrophidion* represents a specialized form does not seem logical in the face of the data presented.

Thus far we have considered only the morphological characters in seeking an explanation of the presence of *Dendrophidion* in South America. Let us now turn to an examination of its distribution with reference to the other members of its group. The following diagram gives the ideal distribution of the group, the actual ranges being shown in Plate V:

[8] Matthew, W. D., N. Y. Acad. Sci., XXIV, 1915: 171–318.



Schematic representation of the ranges of the several genera under discussion. The lower quadrangle represents South America, the upper, North America, while the intervening polygon is equivalent to Central America. Key to the ranges:



Dendrophidion

Drymoluber

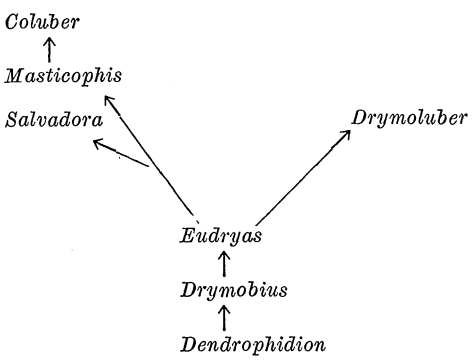
Coluber, Masticophis, and *Salvadora*

Drymobius

Eudryas

It is to be noted that *Dendrophidion* occupies the very center of the range of the group in South America. If we apply the distribution to the first morphological explanation, a very credible scheme results. *Dendrophidion,* the parent form, inhabited northern South America. At this point it gave rise to a more plastic form, *Drymobius,* which was able to spread

out and occupy the surrounding area as well as the region at the point of origin. Likewise *Drymobius* gave rise to *Eudryas,* which was able to spread over most of South and Central America. Next in the morphological line is *Drymoluber,* followed by *Salvadora.* From its geographic position it is improbable that the latter was derived from the former. It is to be noted, however, that the gap between *Eudryas* and *Salvadora* with respect to teeth, supralabials, oculars, dorsals, etc., is not large. The hemipenis of *Salvadora,* moreover, represents a possible intermediate between *Eudryas* and *Masticophis.* It seems logical, therefore, to assume that *Eudryas* gave rise separately to *Salvadora* in northern Mexico and to *Drymoluber* in South America east of the Andes, producing the following line:



Considering both geographic and morphologic characters, it is very probable that *Dendrophidion* represents a primitive form at the point of origin.

If we attempt to fit together the geographic factors with the morphologic in an effort to show that *Dendrophidion* represents a primitive form on the periphery, a result is produced which is too illogical to accept. If *Dendrophidion* were crowded into South America and there gave rise first to *Drymobius* which in turn produced *Eudryas,* the distribution would be acceptable; but to assume that in North America it gave rise to a *Salvadora—Masticophis—Coluber* group in a

single long step and later in South America filled in the intervening gap is beyond the limits of my imagination. If, on the other hand, we were to suppose that, having given rise to the North American group, the latter were to give rise to *Eudryas* and *Drymobius* respectively, both of which were crowded into South America, it is probable that the stem form would lie on the periphery of the range of the entire group rather than remain surrounded by the other forms.

Thus I believe that all evidence, both morphological and geographical, points to *Dendrophidion* as the primitive form lying at the point of origin.

Summary

1. The genus *Drymobius* should, because of its diverse nature, be split into several genera in order to conform to the laws of the group of which it is a part.

2. It is proposed to split this genus into the genera *Dendrophidion, Drymobius, Eudryas,* and *Drymoluber.*

3. Because of its morphological and geographical peculiarities it is believed that *Dendrophidion* represents the primitive form of the group and that the other genera successively were derived from each other in the order noted.

Acknowledgments

In the preparation of this paper much aid from numerous sources has been received, and I wish to take this opportunity to express my sincere thanks to all those who assisted in the work.

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PLATE I

FIG. 1. Hemipenis of *Dendrophidion dendrophis*, U. of M., Mus. Zool. No. 67927.

FIG. 2. Hemipenis of *Dendrophidion bivittatus*, M. C. Z., No. 21984.

FIG. 3. Hemipenis of *Drymoluber brazili*, M. C. Z., No. 20707.

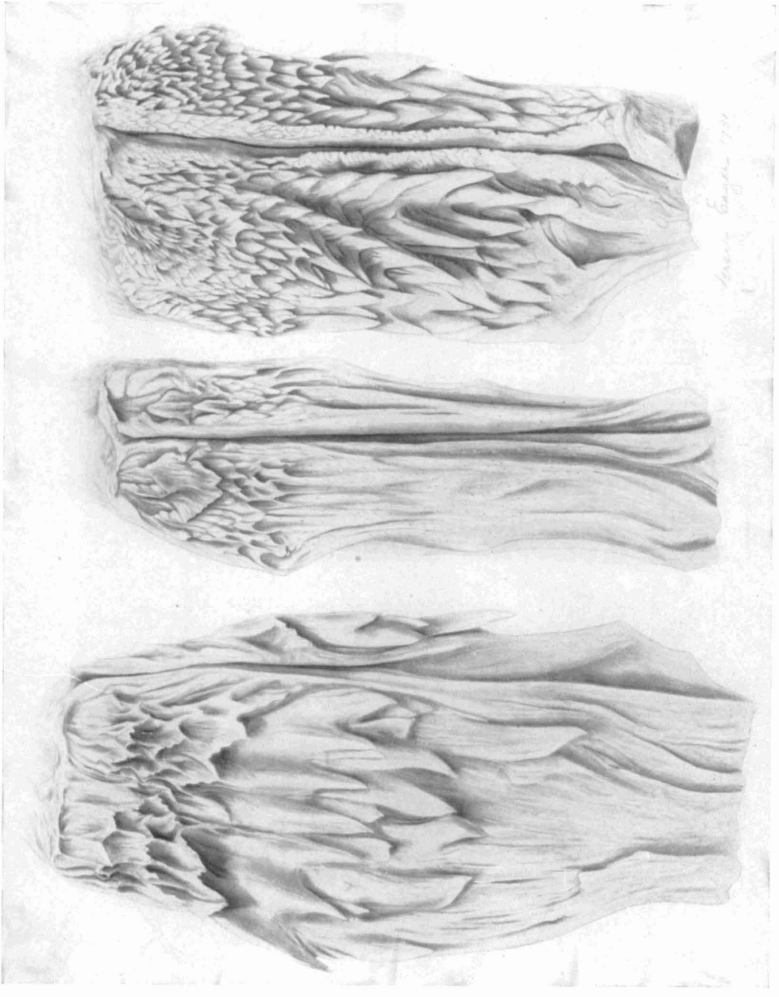


PLATE II

FIG. 1. Hemipenis of *Drymobius rhombifer,* U. of M., Mus. Zool., No. 54959.

FIG. 2. Hemipenis of *Drymobius margaritiferus,* U. of M., Mus. Zool., No. 63365.

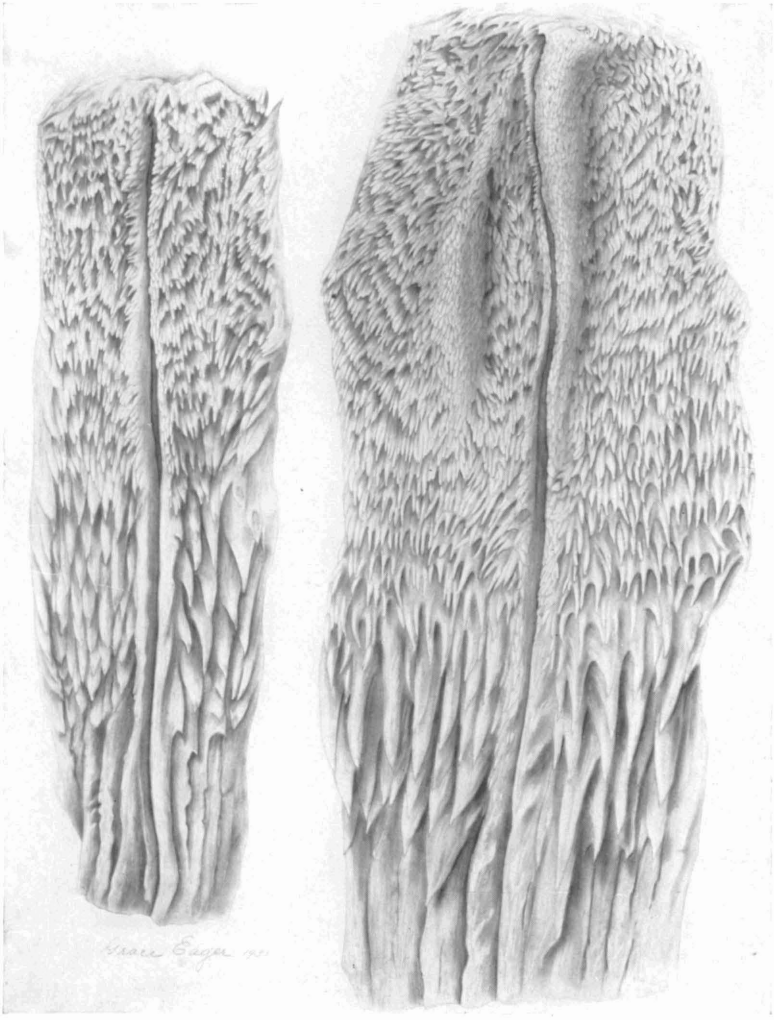


PLATE III

FIG. 1. Hemipenis of *Eudryas boddaertii,* U. of M., Mus. Zool., No. 45597.

FIG. 2. Hemipenis of *Eudryas biffosatus,* M. C. Z., No. 16689.

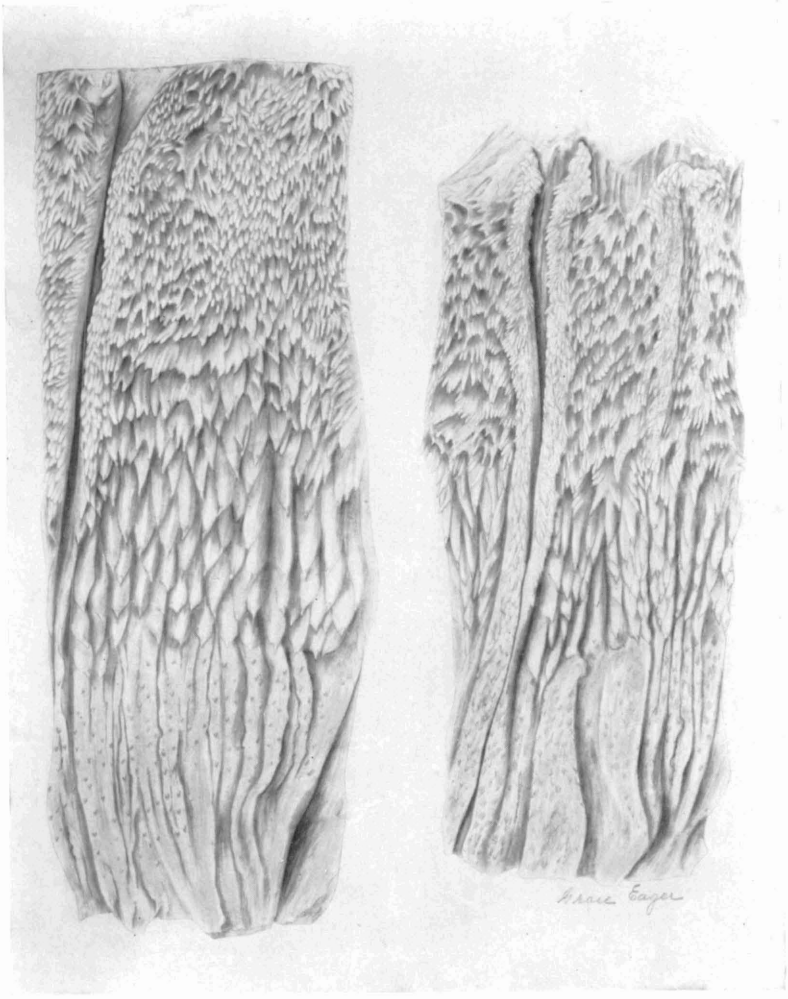

Bruce Eager

PLATE IV

Plate showing the orthogenetic development of the hemipenis through the several genera.

FIG. 1. *Dendrophidion dendrophis*, U. of M., Mus. Zool., No. 67927.

FIG. 2. *Drymobius rhombifer*, U. of M., Mus. Zool., No. 54959.

FIG. 3. *Eudryas biffosatus*, M. C. Z., No. 16689.

FIG. 4. *Drymoluber brazili*, M. C. Z., No. 20707.

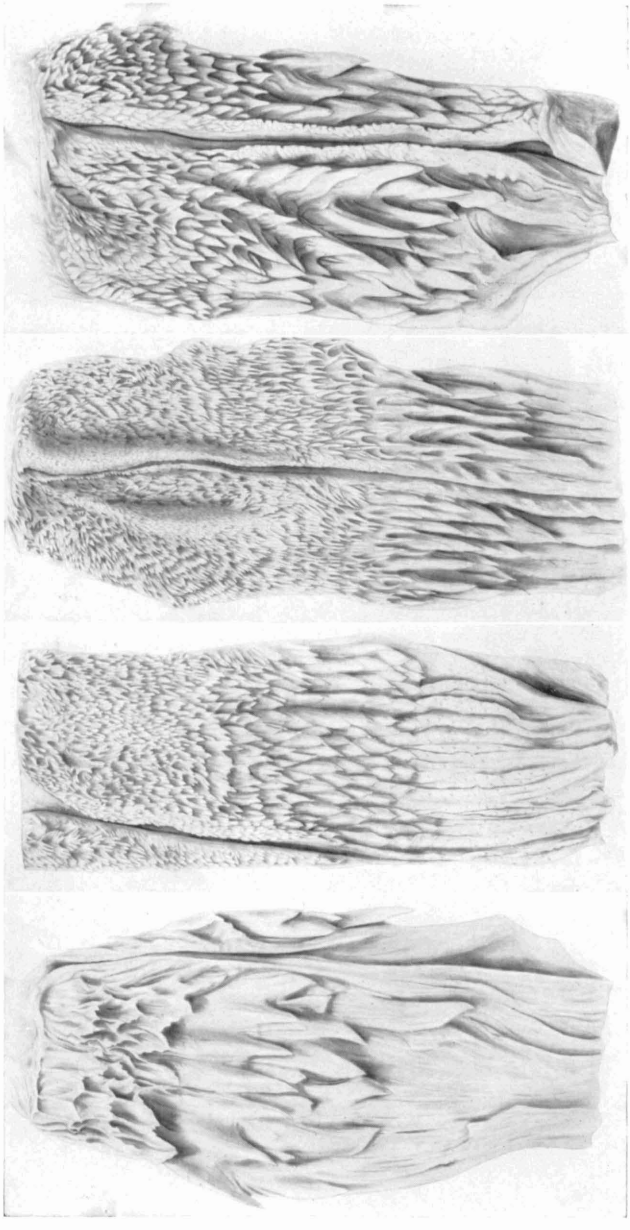
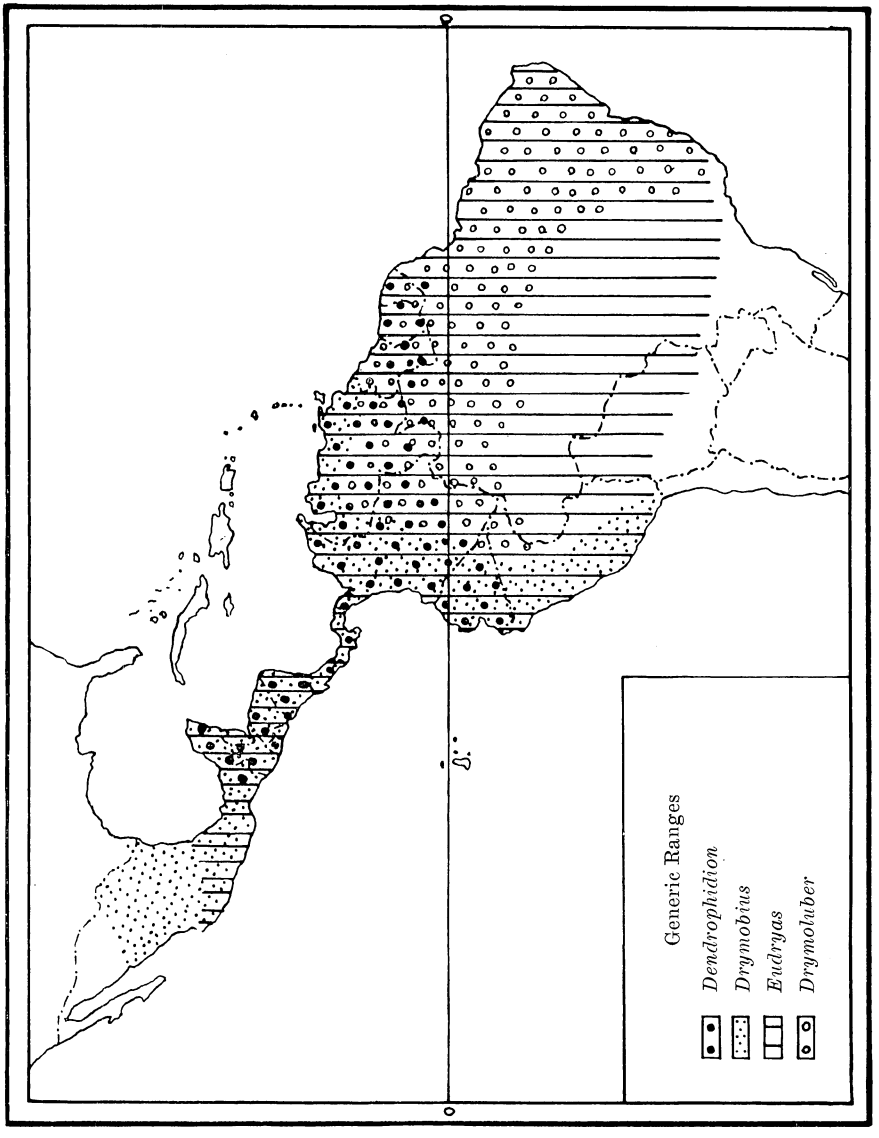


PLATE V

Map showing the generic ranges of the forms discussed. The range of *Dendrophidion* should be shown as extending into Bolivia.


Generic Ranges
Dendrophidion
Drymobius
Eudryas
Drymoluber