

THE RELATIONSHIPS AND
ZOOGEOGRAPHY
OF THE
GENUS *THALEROPHIS* OLIVER

JAMES A. OLIVER

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PREFACE

THIS STUDY was suggested by Laurence C. Stuart in the fall of 1937. At that time he believed that sufficient material was available in museum collections to permit an analysis of the major evolutionary trends and phylogenetic relationships within the genus. The problem was undertaken with the intention of submitting it as a doctoral dissertation. The study was carried out at the Museum of Zoology, the University of Michigan, under the capable direction of Alexander G. Ruthven. During the years 1938-1939 and 1939-1940 the work was done under the tenure of a University Fellowship, while in 1940-1941 it was completed under a Hinsdale Scholarship at the Museum of Zoology. I wish to express my sincere gratitude to the authorities of the University of Michigan for rendering this financial assistance.

Throughout my entire association with the Museum of Zoology I have come under the endearing influence of Helen T. and Frederick M. Gaige, and I wish to express a gratitude to them for far more than professional guidance and inspiration.

All of the material available in the collections of the museums in the United States as of 1940 was examined, and a report of the study was submitted in 1941 to the Graduate School of the University of Michigan in partial fulfillment of the requirements of the degree of Doctor of Philosophy in zoology.

The advent of World War II necessitated a temporary interruption of the project, but a check list of the members of the genus as recognized by me, including the descriptions of new forms, was published (Oliver, 1942). At this time it was recognized that the generic name *Leptophis* Bell was of questionable validity as applied to a group of American snakes. However, it was believed desirable for reasons of nomenclatorial stability to retain this name that had been in use for nearly 100 years. Malcolm Smith (1943), in his study of the snakes of British India, showed that the type species of Bell's *Leptophis* was the type of an Asiatic snake genus as the result of action that preceded the erection of Bell's genus. Thus a new name was required for the American snake genus

that had been called *Leptophis*. In 1947 I proposed the name *Thalerophis* for this genus (Oliver, 1947a).

The earlier portion of the study has been expanded and revised at the American Museum of Natural History. Additional material has been received from museums in the United States since 1940, and pertinent material in several foreign collections also has been made available. During the period that this project has been under consideration, I have become indebted to a great number of persons for numerous kindnesses and encouragement of both a material and a spiritual nature. Neither space nor words permit the adequate acknowledgment of these important contributions. Nor is it possible merely to list the names of those to whom I owe real appreciation. Often valuable contributions have been garnered from casual conversation, from formal lectures, or from scientific reports without a later awareness of the source. This is especially true of informal discussions with other students and colleagues.

My wife, Elizabeth Kimball Oliver, has been a continual source of encouragement throughout the study and has offered innumerable helpful suggestions, including the formation of the generic name *Thalerophis*. Charles M. Bogert has generously proffered his time and extensive herpetological knowledge in discussing all aspects of the problem, offering many improvements, and making it possible for me to bring this study to completion. Ernst Mayr has been an important influence and a continual source of stimulation. Laurence Stuart critically discussed many of the early aspects of the study and carefully read the dissertation, offering many helpful suggestions. Joseph R. Bailey, Norman Hartweg, and Charles Walker have offered considerable assistance or advice. I am especially indebted to Joseph R. Bailey for data on nearly 30 specimens that he examined in the collections of museums in South America and for his first-hand observations pertinent to many of the perplexing problems concerning the genus in South America. Emmett R. Dunn has given me much of

value from his incomparable store of knowledge on Neotropical herpetology. Arnold Grobman and Mont Cazier have provided assistance and advice concerning statistical procedures. Harvey Bassler has kindly permitted me to examine the specimens of the genus in his large Peruvian collection and has given me valuable information about the material.

Marcos Freiberg of Buenos Aires, Argentina, has been most gracious in his efforts to enable me to study specimens in the collections of Argentine museums. H. W. Parker of the British Museum (Natural History) has kindly provided me with detailed information on the type specimens in the collections of his institution, as well as sending me the material from South America for my personal examination. Hobart M. Smith has offered detailed field observations from his wide experience in Mexico, has furnished data for Mexican specimens, and provided me with data for several type specimens in the early stages of the study.

Several artists have contributed their skill to preparing the illustrations, but most of these were obtained through the kindness of the Illustrators Corps of the American Museum of Natural History. The late Grace Eager executed the four drawings of the hemipenes shown in plates 16 and 17. These are used through the courtesy of the Museum of Zoology, the University of Michigan. Barbara Kurtz did all of the drawings of the maxillae, the side and dorsal head drawings, and the dorsal body patterns in plate 19 and text figure 6. Grace Orton prepared the two dorsal body patterns in text figure 5. Alma Froderstrom made the drawings for text figures 11 and 12.

I wish to express my appreciation to Ruth Tyler, Editor of Scientific Publications of the American Museum of Natural History, for

her helpful advice and careful editorial supervision.

Finally, I am deeply indebted to the following individuals for the loan of specimens in their care: Charles M. Bogert of the American Museum of Natural History (A.M.N.H.)¹; Emmett R. Dunn of the Academy of Natural Sciences of Philadelphia (A.N.S.P.); William Beebe of the New York Zoological Society (Beebe Coll.); H. W. Parker of the British Museum (Natural History) (B.M.N.H.); Joseph Slevin of the California Academy of Sciences (C.A.S.); Graham Netting of the Carnegie Museum (C.M.); Karl P. Schmidt and Clifford Pope of the Chicago Natural History Museum (C.N.H.M.); Edward H. Taylor of the University of Kansas, for specimens from his personal collection (E.H.T.); D. C. Geijskes of the Agricultural Experimental Station, Paramaribo, Dutch Guiana (Geijskes Coll.); Brother Niceforo Maria of the Institute de la Salle, Bogota, Colombia (I.L.S.); Laurence M. Klauber of San Diego, California (L.M.K.); the late Thomas Barbour and Arthur Loveridge of the Museum of Comparative Zoölogy (M.C.Z.); Victor M. Badano of the Museu de Entre Rios, Parana, Argentina (M.E.R.); Helen T. Gaige and Norman Hartweg of the Museum of Zoology of the University of Michigan (U.M.M.Z.); and Doris Cochran of the United States National Museum (U.S.N.M.).

In addition to material in these collections, I have utilized the data furnished me by Joseph R. Bailey for specimens from Instituto Butantan in São Paulo, Brazil (I.B.); Museu Nacional, Rio de Janeiro, Brazil (M.N.R.); Museu Paulista (M.P.), São Paulo, Brazil.

¹ The alphabetical abbreviations in parentheses are those that will be used in the lists of material to indicate specimens from the respective institutions.

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INTRODUCTION

THE GENUS *Thalerophis* comprises a group of snakes that in the past have been a poorly understood assemblage of species, partly because of the small number of specimens available in museum collections and chiefly because of the marked superficial similarity between many of the arboreal and semi-arboreal colubrine snakes of the Old and New Worlds. The similarity of attributes of these snakes has caused disarray, from the time of Linnaeus up to recent years, in respect to both interspecific and intergeneric classification. Many forms have been assigned to the genus that we now know belong elsewhere, while forms that rightly belong to this genus have been allocated to other genera. Even in recent years the species belonging to the genus have received such varied treatment that scarcely any two workers have been in complete accord as to their proper disposition.

Since the beginning of the present century the accumulation of specimens belonging to this genus has been substantial. In so far as was feasible, I have examined the bulk of the available material with the exception of the collections in the continental European museums. From the results of this examination the most useful systematic characters have been determined, the geographic distribution of these characters has been plotted and considered in relation to its genetic implications, the nature of the populations that comprise the genus have been inferred and are discussed in connection with our present knowledge of their bionomics, and, finally, the relationships, phylogeny, and evolution of these populations have been outlined. The restrictions of the available material and of our present knowledge limit the results of this study primarily to those of analysis rather than synthesis. The former must always precede the latter, and it is only in the more completely understood groups of animals that major contributions can be derived from synthesis. It is hoped that the results presented herein will form a basis upon which to formulate the future work on this genus when more material is at hand. Most of the conclusions derived from the present study must

be considered as tentative, based on our present knowledge of the genus and subject to alteration as new data accumulate. Nothing is to be gained by awaiting the slow process of the accumulation of more material before presenting the results that are now apparent, despite the certainty that these results will be modified.

In the analysis of characters, new characters have been sought to replace some of those that had been used by earlier workers but that were found to be of little or no value. I have endeavored to determine the limits, trends, and distribution of the individual, geographic, and sexual variation in all of the characters considered. The evolution of these characters has been inferred and traced as far as possible despite the lack of knowledge concerning the genetic basis of the characters. Much of value had been obtained concerning gene dispersions through the conservative consideration of the available phenotypes represented within populations.

In this study I have been guided by the consideration of populations rather than the consideration of specimens. Inferences concerning these populations have been based upon the individuals represented in museum collections, and the accuracy of the inferences about a particular population is in direct proportion to the number of specimens available. The consideration of populations provides a better basis for the study of phylogenies and speciation phenomena, and will cause concern only to those who believe that a taxonomic category is a Procrustean bed for use of the classifier.

The species concept employed in the present work is that of the "biological species" as described and defined by Mayr (1940, 1942). Mayr (1942, p. 121) states that "The application of a biological species definition is possible only in well-studied taxonomic groups, since it is based on a rather exact knowledge of geographical distribution and on the certainty of the absence of interbreeding with other similar species." Few genera of snakes, especially those inhabiting the tropics, can be called "well-studied taxonomic groups." Despite the imperfections that may

result, the biological species concept appears to afford the best basis for a "natural" arrangement within a genus and a nomenclature indicative of relationships and phylogeny. This concept requires the consideration of more than morphological attributes in arriving at conclusions related to specific and subspecific allocations.

Since a system of classification founded on phylogenetic relationships manifestly provides the best basis for a natural arrangement of organisms and since isolation is a primary prerequisite of vertebrate evolution, it appears to me to be more logical in the absence of definite proof of intergradation or reproductive isolation between closely related allopatric or geographically vicarious forms to consider them as subspecies rather than species. Or, to put it another way, in the case of closely related allopatric forms it is more logical to place the burden of proof on showing that reproductive isolation has been established rather than on proving the existence of intergradation. Mayr (1942) has ably and fully elaborated the applications and ramifications of the concept of the biological species, and there is therefore no need to discuss them further here.¹

The adoption of such a concept has necessitated a change in the status of several members of the genus from that presented in my check list of these snakes (Oliver, 1942). Whereas formerly the 18 recognized forms were placed in 11 species, they now comprise six species. In this arrangement there are some apparent inconsistencies since all forms are not treated in the same way. For example, included as subspecies of *richardi* are several forms that at present are not known to intergrade with any adjacent populations. However, from the available data it is inferred that they are capable of interbreeding with one or more of the adjacent populations. On the other hand, *diplotropis* and *mexicanus* are considered as allopatric species. The two are related, but on the basis of the available

information I infer that the two are reproductively, as well as geographically, isolated.

There is no doubt that additional forms, primarily subspecies of biological species although they may not be so called when proposed, will be recognized within the genus. When additional material has been assembled to delimit adequately critical local populations, the following populations will probably merit recognition: a northern race of *diplotropis* (occurring on, but not restricted to, the Tres Marias Islands); an upland and northern race of *mexicanus*; a Pacific slope race separated from *occidentalis* in lower Central America; restriction of the typical race of *occidentalis* to northwestern Ecuador with a new name for the remainder of the present subspecies; recognition of northern and southern races of *depressirostris*; probably several new Brazilian races of *richardi*; and the division of *marginatus* into a northern and a southern race. It is almost possible roughly to define some of these populations at present, and names are available for several of these. However, there are problems requiring solutions and geographic gaps that require partial bridging before an adequate basis can be obtained for an understanding of these populations. As Dunn (1936, p. 555) has aptly said, "I do not believe in naming animals on the basis of what the future may show."

Several usages in the present paper possibly need a word of explanation. The generic synonymy presents in chronological order the different generic names to which members of the genus *Thalerophis* have been referred at one time or another, together with an indication of a species synonymy under which one such detailed citation can be found. The terms "normally" and "usually" are used to describe conditions that exist in 75 per cent or more of a population. Thus "temporals normally 1-2" means that in that particular population the observed temporal formula was 1-2 on both sides of the head in 75 per cent or more of the specimens examined. This is an arbitrary usage of these terms that neither conforms to nor violates any standard of which I am aware.

¹ While the present paper was in press, Mayr (1948) published an article that discusses at length the subject, "Subspecies versus Allopatric Species."

NOMENCLATORIAL HISTORY OF THE GENUS

WITH THE BEGINNING of the binomial system of nomenclature in 1758, *Coluber ahaetulla* Linnaeus included individuals of the genus *Thalerophis* as well as specimens of an Asiatic genus. In the tenth edition of the "Systema naturae," Linnaeus presented no characters that are conclusively diagnostic of either species, and the habitat, "in Asia, America," is of no aid in restricting the application of the name. Because of the bitypic nature of the species and the fact that no types were designated by Linnaeus much nomenclatorial confusion has resulted. Recently Smith (1930, 1943), Meise and Hennig (1932, 1935), Stejneger (1933), and Mertens (1934) have endeavored to achieve stability in the application of this name and in the generic designations based on it, but these authorities have not reached agreement.

Linnaeus associated specimens with the name *ahaetulla* three times prior to the publication of the tenth edition of the "Systema naturae": 1745, 1748, and 1754. The word "ahaetulla," as shown by Wall (1910), is a Singhalese name used for one or more of the green arboreal snakes of Ceylon. The word implies "eyeplucker." Linnaeus, in the first use of the term in 1745, listed such descriptive references as "Serpens Ceylonica," "Anguis Borneocus," "Serpens indicus," and "Ahaetulla Ceilonensibus, i.e. oculis infestus." No mention of America or references to snakes originating in America are to be found under this first description. In this first account Linnaeus specifically states that the scales are smooth, without raised keels. This condition is characteristic of the Asiatic form involved but not of the American, although it has been incorrectly attributed to several members of the genus *Thalerophis*. American specimens were definitely placed under this name in 1748 when Linnaeus reported on material from Surinam.

Following the publication of the tenth edition of the "Systema naturae," authors of herpetological works perpetuated the Linnaean concept of *Coluber ahaetulla*. Daubenton (1784) applied the vernacular name "boiga" and presented a virtual repetition in French of Linnaeus' first (1745) description,

including the attribute of smooth scales. He added the habitat, in Asia and in America, given in Linnaeus' later (1758) account. Lacépède (1789) referred specifically only to specimens from India and Borneo, but contrary to the statement of Smith (1943, p. 241) he did not limit the application of the name to the Asiatic species: "On doit regretter que l'espèce du Boiga ait besoin, pour subsister, d'une chaleur plus forte que celle de nos contrées & qu'elle ne se trouve que vers l'équateur, tant dans l'ancien que dans le nouveau continent."¹ Bechstein (1801), closely following Lacépède's arrangement and description, mentioned specifically only Old World localities while stating that it "nur in die Gegend um den Aequator eingeschränkt ist." Shaw (1802) was the first to assign but a single locality, India, to the species. Daudin (1803) used the name to include only the American species and commented on the confusion in earlier writings: "Les naturalistes ont confondu jusqu'à présent, comme une même espèce de boiga, plusieurs couleuvres également élégantes, . . . cette erreur fut principalement occasionnée par Seba, qui a représenté dans son ouvrage plusieurs espèces comme autant de variétés l'une de l'autre: Linnaeus, Gmelin, etc., ont réuni sous ce même nom des serpents de l'Asie, de l'Inde, et des diverses parties de l'Amérique, et cependant tous les boigas que j'ai observés jusqu'à présent ont été trouvés sur le continent dans l'Amérique méridionale, principalement à Cayenne et à Surinam."

Subsequent to 1803 some writers have followed the concept of Shaw, whereas others have agreed with Daudin. From 1843 to 1943 the *Coluber ahaetulla* of Linnaeus usually has been associated with the South American species as limited by Daudin (*supra cit.*).

Link (1807) proposed the genus *Ahaetulla* to include two species of snakes that he called *fasciata* from India and *mycterizans* from America. The two species were based on

¹ Meise and Hennig (1935) and Smith (1943) have pointed out that there is no such name as *Coluber boiga* Lacépède. Rather, Lacépède followed Daubenton's (1784) usage of the vernacular name "boiga" for *Coluber ahaetulla* Linnaeus.

descriptions taken from Bechstein (1801). Bechstein's specimen upon which Link's *fasciata* was based was designated *Coluber ahaetulla* and is obviously the source for the generic name. Smith (1943) has suggested that Link changed the specific name from *ahaetulla* to *fasciata* to avoid tautonymy.

Bell (1825) proposed the generic name *Leptophis* to include the species *purpurascens*, *ahaetulla*, *aestivus*, and *mancas*. This author, like Link, considered *ahaetulla* as an Indian species, and the only species in Bell's genus that came from the New World, the species *aestivus*, does not belong to the genus *Thalerophis*.

In 1825 J. E. Gray presented a genus "*Ahaetulla*, Gray" that included four species: *decorus*, *caeruleus*, *sagittalis*, and *punctulatus*, all of which are Old World forms. This generic name is preoccupied by *Ahaetulla* Link, 1807. In 1827 Gray stated that his *Ahaetulla* was synonymous with *Leptophis* Bell and he used this latter name. In 1826 the name *Dendrophis* H. Boie¹ was used by Fitzinger (1826a) for the species *ahaetulla* Linnaeus, considered as an American form. Later the same year, Fitzinger (1826b) included three species in the same genus: *decorus*, *pelias*, and *ahaetulla*. The first two are indicated as Old World species, whereas the latter is "Ex America, Brasilia." In the text it is stated that the genus is based on *Coluber ahaetulla* Linnaeus and is the same as *Ahaetulla* Gray, 1825. The nomenclature became more confusing in 1837 when Gray proposed the name *Ahoetula* (*sic*) as a substitute for the name *Leptophis*.

Meise and Hennig (1932) incorrectly considered *Ahaetulla fasciata* as indeterminable and designated *mycterizans* the type of *Ahae-*

tulla Link. Malcolm Smith (1943) quite correctly points out that "*Ahaetulla fasciata* . . . based on the *Coluber ahaetulla* (in part) of Linnaeus, becomes the type of the genus *Ahaetulla* by absolute tautonymy (Art. 30,d)."

Fitzinger (1843), considering the species *ahaetulla* as an American form, designated it the type of *Leptophis* Bell. In so doing he disregarded the earlier designation of this species as the type of *Dendrophis* H. Boie. This was further complicated by his designation of a different species, *picta*, as the type of this latter genus. As Mertens (1934) has pointed out and as shown herein, the type of *Dendrophis* is *Coluber ahaetulla* Linnaeus. When the name was first published it contained but a single species, *ahaetulla*. In the next use of the name, later in the same year (1826), the genus contained three species, but a statement in the text specifically says that the genus is based on *Coluber ahaetulla* Linnaeus. Furthermore, in 1827 F. Boie discussed his brother's systematic arrangements and concerning the genus *Dendrophis* he states, "Typus: *Col. ahaetulla* Linn."

From the foregoing it is clear that *Leptophis* Bell cannot be used for an American genus of snakes while *Dendrophis* H. Boie is applied to an Asiatic snake genus. The two names are synonymous, and both are synonyms of *Ahaetulla* Link. The correct application of this latter name depends upon the status of *Coluber ahaetulla* Linnaeus, whether it is Asiatic or American.

The derivation of the name "*ahaetulla*" and the earliest references listed by Linnaeus under his first use of the term clearly indicate an original concept of an Asiatic snake. Daubenton (1784) is the first author subsequent to 1758 to provide a diagnostic character by which the name can be restricted to either of the forms. His statement that *Coluber ahaetulla* possesses smooth scales without elevated keels correctly indicates an Asiatic snake. Moreover, the first author to attribute but a single locale for the species was Shaw (*supra cit.*) who considered it an Asiatic species. Stejneger (1933) concluded that the name should be applied to the South American snake rather than the Asiatic. His most cogent argument in support of this conclusion was that four of the five extant Linnaean

¹ This name is usually cited in the literature as "*Dendrophis* Fitzinger." However, Fitzinger clearly indicated (1826a, 1826b) that it is H. Boie's name. Later in the same year, Schlegel (1826) also discussed the generic arrangements and names of H. Boie and made a specific statement concerning Fitzinger's use of H. Boie's names. The manuscript of H. Boie, in which his new names and arrangements appeared, was apparently never published, although Fitzinger (*supra cit.*), Schlegel (*supra cit.*), F. Boie (1827), and others utilized portions of it. In accordance with Article 21 of the International Rules of Zoological Nomenclature, it would appear that the name should be cited "*Dendrophis* H. Boie, 1826" since "it is clear from the contents of the publication that some other person is responsible for said name. . . ."

specimens examined by Lönnberg (1896) and Andersson (1899) were identified by them as the South American species; the fifth specimen was referred to the Asiatic species. However, this is not equivalent to a type designation and does not invalidate the evidence presented above.

Stejneger utilized the number of ventral plates in an endeavor to determine the identity of the Linnaean specimens. The validity of this argument is open to question because of the overlap in ventral number between the Asiatic and American species. It is interesting to note that the counts listed by Linnaeus (1745, 1748, 1754, and 1758), namely, 162–166, are below the minimum of 167 given by Smith (1943) for the species to which he assigns the name *ahaetulla*.

Whether *Coluber ahaetulla* Linnaeus is to be associated with an Asiatic or an American species can always be a potential source of disagreement unless a ruling on its status is obtained from the International Committee on Zoological Nomenclature. Arguments can be mustered in support of the application of the name to either species. As stated above, the best evidence indicates that the name should be used for an Asiatic species rather than an American, and it will be so considered herein.

In the earlier literature snakes of this genus have been assigned to several genera: *Coluber* Linnaeus, *Ahaetulla* Gray, *Dendrophis* H. Boie, *Hapsidophrys* Fischer, *Leptophis* Bell, *Philothamnus* Smith, and *Thrasops* Hallowell. None of these names is available for the American species. *Diplotropis* Günther, 1872, was based on his species *bilineata* which is a synonym of *depressirostris* Cope, 1860. This name is preoccupied by *Diplotropis* Boheman, 1857, for a genus of Coleoptera. In the absence of any available name, I have proposed the name *Thalerophis* (Oliver, 1947a).

The South American species hitherto known as *ahaetulla* must be assigned another name. The next name appearing in the synonymy of this species is *Coluber filiformis* Linnaeus, 1758. The status of this name has been in doubt. Linnaeus (*supra cit.*) gave the habitat as "in Indiis." Lacépède (1789) and Bechstein (1801) indicated that it occurred in both the East and West Indies, whereas

Shaw (1802) stated that it was a "native of India." None of the early authors provided diagnostic characters, and the illustrations do not enable one to make an accurate allocation. Boulenger (1894) did not list the name anywhere. The name has been placed in the synonymy of the South American species primarily on the basis of Andersson's (1899) statement, "This Linnaean type has not been identified by the authors. One specimen from Mus. Ad. Frid. is preserved in the Royal Museum, which *evidently* [italics mine] was the type for Linnaeus's description of *Col. filiformis* in Mus. Ad. Frid. It is a young *Leptophis liocercus* (Wied) or *Leptophis ahaetulla* (L.)." The species is indeterminable on the basis of the original description (Linnaeus, 1758) and figure given by Linnaeus (1754), the type locality is uncertain, and even the identity of the type specimen is uncertain. In consideration of these facts, the utilization of the name *filiformis* for the South American species formerly known as *Leptophis ahaetulla* would merely be substituting one uncertainty for another. Consequently I consider the species *filiformis* unidentifiable. The earliest recognizable name available for the species is *richardi* Bory St. Vincent, 1823. Thus the species formerly known as *Leptophis ahaetulla* (Linnaeus) should now be called *Thalerophis richardi* (Bory St. Vincent). This is the type species of the genus.

Names proposed for the forms now comprising the genus *Thalerophis* are listed below in alphabetical order, with the author's name, the date of publication, the type locality, and the present status of the name:

- aeruginosus* Cope, 1876; type locality: Costa Rica; synonym of *depressirostris* (Cope)
- affinis* Steindachner, 1870; type locality: Brazil; synonym of *richardi marginatus* (Cope)
- ahaetulla* Linnaeus, 1758 (in part); type locality: Asia, America; synonym of *richardi richardi* (Bory St. Vincent)
- argentinus* Werner, 1903; type locality: Rosario, Argentina; synonym of *richardi marginatus* (Cope)
- bilineata* Günther, 1872; type locality: Costa Rica; synonym of *depressirostris* (Cope)
- bocourti* Boulenger, 1898; type locality: Paramba and Cachabe, Ecuador; *richardi bocourti* (Boulenger)
- bolivianus* Oliver, 1942; type locality: Buena-

- vista, Department of Santa Cruz, Bolivia; *richardi bolivianus* (Oliver)
- brevior* Boulenger, 1914; type locality: Pena Lisa, Condote, Choco, Colombia; synonym of *riveti* (Despax)
- chocoensis* Oliver, 1942; type locality: El Rio Condote, Camp Penalisa, Choco, Colombia; *richardi chocoensis* (Oliver)
- coeruleodorsus* Oliver, 1942; type locality: Trinidad, British West Indies; *richardi coeruleodorsus* (Oliver)
- copei* Oliver, 1942; type locality: Salto do Hua, Brazilian-Venezuelan boundary; *richardi copei* (Oliver)
- depressirostris* Cope, 1860; type locality: Cocuyas de Veraguas, New Grenada; *depressirostris* (Cope)
- diplotropis* Günther, 1872; type locality: Tehuantepec, Mexico; *diplotropis* (Günther)
- flagellum* Andersson, 1901; type locality: Rio de Janeiro, Brazil; synonym of (?) *richardi liocercus* (Wied)
- forreri* Smith, 1943; type locality: Tres Marias Islands, Mexico; synonym of *diplotropis* (Günther)
- insularis* Barbour, 1905; type locality: Gorgona Island, Colombia; synonym of *richardi bocourti* (Boulenger)
- linnei* Gray, 1831; substitute name for *ahaetulla* Linnaeus; synonym of *richardi richardi* (Bory St. Vincent)
- liocercus* Wied, 1824, type locality: Brazil; *richardi liocercus* (Wied)
- marginatus* Cope, 1862; type locality: Paraguay; *richardi marginatus* (Cope)
- maximus* Weller, 1930; type locality: unknown; synonym of *richardi praestans* (Cope)
- mexicanus* Dumeril and Bibron, 1854; type locality: Mexico; *mexicanus mexicanus* (Dumeril and Bibron)
- modesta* Günther, 1872; type locality: Rio Chisoy, near Cubulco, Guatemala; synonym of *mexicanus mexicanus* (Dumeril and Bibron)
- nebulosus* Oliver, 1942; type locality: Cariblanca, Costa Rica; *nebulosus* (Oliver)
- nigromarginatus* Günther, 1866; type locality: upper Amazon; *richardi nigromarginatus* (Günther)
- occidentalis* Günther, 1859; type locality: Guayaquil and western Ecuador; *richardi occidentalis* (Günther)
- ortoni* Cope, 1876; type locality: middle Amazon; *richardi ortoni* (Cope)
- praestans* Cope, 1868; type locality: Peten, Guatemala; *richardi praestans* (Cope)
- richardii* Bory St. Vincent, 1823; type locality: Guiana; *richardi richardi* (Bory St. Vincent)
- riveti* Despax, 1911; type locality: Gualaquiza, Ecuador; *riveti* (Despax)
- rostralis* Lönnberg, 1902; type locality: San Miguel, Chaco; synonym of *richardi marginatus* (Cope)
- sargii* Fischer, 1881; type locality: Guatemala; synonym of *richardi praestans* (Cope)
- saturatus* Cope, 1876; type locality: Sipurio, Costa Rica; synonym of *depressirostris* (Cope)
- ultramarinus* Cope, 1894; type locality: Pozo Azul, Costa Rica; synonym of *richardi occidentalis* (Günther)
- urosticta* Peters, 1873; type locality: Bogota, Colombia (*vide* Dunn, 1944); synonym of *richardi occidentalis* (Günther)
- vertebralis* Werner, 1909; type locality: Petropolis, Brazil; synonym of *richardi liocercus* (Wied)
- yucatanensis* Oliver, 1942; type locality: Coba, Quintana Roo, Mexico; *mexicanus yucatanensis* (Oliver)

GENERIC SYNONYMY AND DESCRIPTION

GENUS *THALEROPHIS* OLIVER

Coluber LINNAEUS, 1758, (in part), *Systema naturae*, ed. 10, vol. 1, p. 225. Genotype; *constrictor* Linnaeus (for *richardi* Bory St. Vincent).

Ahaetulla LINK, 1807, (in part), *Beschreibung der Naturalien-Sammlung der Universität zu Rostock*, vol. 2, p. 73. Genotype: *ahaetulla* Linnaeus (for *ahaetulla* Linnaeus, in part = *richardi richardi* Bory St. Vincent).

Leptophis BELL, 1825, (in part), *Zool. Jour.*, vol. 2, p. 328. Genotype: *ahaetulla* Linnaeus (for *ahaetulla* Linnaeus, in part = *richardi richardi* Bory St. Vincent).

Ahaetulla GRAY, 1825, (in part), *Ann. Phil.*, new ser., vol. 10, p. 208 (*nec* Link, 1807). Genotype: *decorus* Shaw (for *diplotropis* Günther).

Dendrophis H. BOIE, in Fitzinger, 1826, (in part), *Isis*, vol. 19, p. 884. Genotype: *ahaetulla* Linnaeus (for *ahaetulla* Linnaeus, in part = *richardi richardi* Bory St. Vincent).

Herpetodryas H. BOIE, in Schlegel, 1826, *Bull. Sci. Nat. Geol. Paris*, vol. 9, p. 237. Genotype: *bicarinatus* Wied (for *affinis* Steindachner = *richardi marginatus* Cope).

Ahaetula GRAY, in Griffith, 1831, (in part), *The animal kingdom*, vol. 9, p. 93 (*nec* Link, 1807; *nec* Gray, 1825). Substitute name for *Leptophis* (for *linnei* Gray, in part = *richardi richardi* Bory St. Vincent).

Philothamnus SMITH, 1849, (in part), *Illustrations of the zoology of South Africa*, reptiles, pls. 49–60, 64–65 and accompanying pages of text. Genotype: *semivariiegatus* Smith (for *depressirostris* Cope).

Hapsidophrys FISCHER, 1856, (in part), *Abhandl. Naturwiss. Ver. Hamburg*, vol. 3, p. 110. Genotype: *lineatus* Fischer (for *saturatus* Cope = *depressirostris* Cope).

Thrasops HALLOWELL, 1857, (in part), *Proc. Acad. Nat. Sci. Philadelphia*, vol. 9, p. 67. Genotype: *flavicularis* Hallowell (for *praestans* Cope = *richardi praestans* Cope).

Diplotropis GÜNTHER, 1872, *Ann. Mag. Nat. Hist.*, ser. 4, vol. 9, p. 24. Genotype: *bilineata* Günther (for *bilineata* Günther = *depressirostris* Cope).

Thalerophis OLIVER, 1947, *Copeia*, p. 64. Genotype: *richardi* Bory St. Vincent.

The maxillary teeth are long and slender, varying in number from 18 to 36, increasing in size posteriorly, with the last two to four teeth enlarged but not grooved and normally not separated from the preceding teeth by a

diastema. The mandibular teeth are long and slender anteriorly, decreasing in size posteriorly, ranging in number from 20 to 36. The palatine teeth are long and slender, subequal, varying in number from 11 to 22. The pterygoid teeth vary in number from 21 to 40, are long and slender, decreasing in length posteriorly.

Hypapophyses are not present on the posterior body vertebrae.

The hemipenis is five to nine subcaudals in length, simple or slightly bilobed, with a single sulcus, non-capitate and without a terminal awn, with or without enlarged basal spines. Spines are always present on the proximal portion of the organ, whereas the distal portion is calyculate, with the calyces sometimes obscured by fringing papillae.

The dorsal scales are arranged in oblique transverse rows, with 15 longitudinal rows present on the anterior two-thirds of the body and 11 rows on the posterior one-third of the body. The dorsal scales on the tail are reduced from six to four longitudinal rows opposite caudals 2 to 38. Keels are always present, although they may be restricted to the scales of the paravertebral rows on the posterior third of the body in at least two species. The dorsal scales normally possess a single apical pit.

The ventral plates vary from 133 to 184 in number, occasionally angulate with a slight to moderate lateral keel. The anal plate is normally divided; the subcaudals range in number from 134 to 189.

The head scutellation is characteristically colubrine. The rostral is broader than high, visible from above. The paired internasals are shorter than the paired prefrontals and narrowed anteriorly. The prefrontals may (in forms lacking a loreal) or may not (in forms with a loreal) be in contact with the upper labials. The single frontal and the single supraocular on each side are large and prominent, followed posteriorly by the large paired parietals. The nasal is normally divided, with the nostril located between the anterior and posterior portions. The loreal may be present or absent; when present it is longer than high. There is a single preocular

and normally two postoculars. There is a single anterior temporal and normally two posterior temporals. The upper labials number eight (fourth and fifth in contact with the orbit) or nine (fifth and sixth in contact with the orbit); the lower labials number 10 (six in contact with chin shields) or 11 (seven in contact with the chin shields). The anterior chin shields are normally shorter than the posterior.

The form is slender and elongate, with the head distinct from the neck. The head length

is contained in the head-body length 17 to 32 times. The tail length varies from 47 to 75 per cent of the head-body length. The maximum size recorded is 2243 mm. (7 feet, 4 inches). The eye is large with a round pupil.

The coloration is predominantly green or light brown, either unicolored or with a pattern of longitudinal stripes or narrow transverse bands. Species may exhibit an ontogenetic change in pattern, or the juveniles may possess the same pattern as the adults.

CHARACTER ANALYSIS

THE CHARACTERS customarily employed in ophidian systematics have been utilized as far as practicable in the study of the genus *Thalerophis*. These have been analyzed to determine the extent of individual, sexual, geographical, and phylogenetic variation. The following section contains a résumé of

the more elementary statistical procedures have been used. The model studies of Klauber (1936, 1937, 1938, 1939, 1940, 1941, 1943, 1945) have clearly indicated the desirability of detailed statistical treatment of the characters currently employed in herpetology, and the results of his painstaking character

TABLE 1
Thalerophis MATERIAL STUDIED

Species	Number of Specimens	Number of Males	Number of Females	Ratio of Males/Females ^a
<i>depressirostris</i>	34	16	18	.89
<i>diplotropis</i>	60	37	23	1.61
<i>mexicanus mexicanus</i>	144	72	72	1.00
<i>mexicanus yucatanensis</i>	18	9	9	1.00
<i>nebulosus</i>	5	4	1	4.00
<i>richardi richardi</i>	87	48	39	1.23
<i>richardi bocourti</i>	7	4	3	1.33
<i>richardi bolivianus</i>	26	9	17	.53
<i>richardi chocoensis</i>	7	4	3	1.33
<i>richardi coeruleodorsus</i>	35	19	16	1.19
<i>richardi copei</i>	6	5	1	5.00
<i>richardi liocercus</i>	21	14	7	2.00
<i>richardi marginatus</i>	24	13	11	1.18
<i>richardi nigromarginatus</i>	194	83	111	.75
<i>richardi occidentalis</i>	126	68	58	1.17
<i>richardi ortonii</i>	33	10	23	.43
<i>richardi praestans</i>	31	19	12	1.58
<i>riveti</i>	12	11	1	11.00
Total	870	445	425	1.05
Specimens not included above because of lack of data	22			
Total of all specimens	892			

^a A ratio greater than 1.00 indicates a preponderance of males, whereas one less than 1.00 denotes a larger number of females in the sample.

the characters that have been found to be the most important in this work. In several instances attention is called to the potential value of characters, or different aspects of characters, that are normally not used in such studies. Detailed analysis of these has not always been made. A regrettable handicap has been the lack of adequate material for the broad application of statistical methods of evaluation. Consequently only

analyses will be referred to frequently in the following discussion.

Klauber (1941), Simpson (1941), and Stuart (1941), as well as many others, have indicated the relationship between the size of the sample analyzed and the scope of variation observed. Stuart was dealing with a group of colubrine snakes that are related to *Thalerophis*, and the difficulty expressed by him also pertains to *Thalerophis*. He states

that, "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 greater variation is caused by the extensive range, or whether the greater number of

although not ranked in the same order. For example, on the basis of the maximum variation in the number of ventral plates the males are ranked in decreasing order from the top down according to the numeral on the left side of the name. The numeral on the right hand side indicates the rank according to the material available, with number 1

TABLE 2
NUMBER OF MANDIBULAR, MAXILLARY, PALATINE, AND PTERYGOID TEETH
(Data from prepared skulls)

Species	Number	Mandibular	Maxillary	Palatine	Pterygoid
<i>depressirostris</i>	1	36-36	34-35	21-22	39-40
<i>diplotropis</i>	2	20-22	18-20	11-11	21-24
<i>mexicanus mexicanus</i>	3	23-25	20-21	13-14	25-29
<i>mexicanus yucatanensis</i>	1	23-23	20-21	13-14	29-30
<i>richardi richardi</i>	1	26-26	26-27	15-16	26-27
<i>richardi bocourti</i>	1	26-?	22-23	14-14	25-26
<i>richardi chocoensis</i>	1	27-27	22-23	14-14	27-29
<i>richardi marginatus</i>	1	22-?	22-23	12-13	21-22
<i>richardi nigromarginatus</i>	1	24-24	25-27	14-?	24-?
<i>richardi occidentalis</i>	2	24-25	23-23	13-13	24-25
<i>richardi praestans</i>	1	24-26	23-25	13-13	21-22

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 increased variability associated with a larger geographic range is related to population size and the greater number of different genotypes available in larger populations as compared to smaller and geographically more circumscribed populations.

In the material studied in the genus *Thalerophis* (see table 1) the relationship between size of the sample and the scope of variation can be demonstrated simply by arranging the species and subspecies in order according to the number of specimens representing each and comparing this order with that obtained on a basis of variation for a particular character. This provides only a crude method of comparison, but in every character for which this was done the five most variable were nearly always the five that were represented by the most material,

being represented by the highest number of individuals and number 5 by the lowest number of individuals among the first five forms.

1. *occidentalis* 3
2. *mexicanus* 2
3. *richardi* 4
4. *nigromarginatus* 1
5. *diplotropis* 5

If the number of specimens in a given form is plotted on a graph against the range of variation observed in the form, the proportional increase in the range of variation is slight in those forms represented by more than 20 specimens. In regard to the males of *Thalerophis*, only the first five forms indicated above are represented by more than 20 specimens each. Thus in this genus any form represented by fewer than 20 individuals for each sex appears to be inadequately represented for a useful understanding of its variation. The size of the geographic range, as Stuart suggests, has an important influence on the variability of a species. This factor is not easily evaluated on a comparative basis.

DENTITION

In all species of the genus teeth are present on the dentary (mandibular teeth), the maxillary, the palatine, and the pterygoid bones. Those on the maxillary bone provide the most useful qualitative and quantitative indications of differentiation and are relatively easily examined, in contrast to the other dentitional series. The teeth on the dentary, the palatine, and the pterygoid bones can be analyzed accurately only by the study of cleaned skulls or by the removal and study of the individual dentigerous bones. This makes their use impractical in most

teeth on the other bones, and vice versa. This proportional relationship is not constant, however, and the number of teeth on these bones may provide a useful basis for separating related forms, as, for example, the number of pterygoid teeth in *occidentalis* and *praestans*. The data suggest, but are inadequate to establish the fact, that important differences may exist in respect to the relative numbers of teeth on the different dentigerous bones. Thus *depressirostris*, *yucatanensis*, and *chocoensis* possess a markedly higher number of pterygoid teeth than maxillary teeth;

TABLE 3
NUMBER OF MAXILLARY TEETH

Species	Number of Specimens	Extremes	Mean
<i>depressirostris</i> ^a	23	33-36	34.9
<i>diplotropis</i> ^a	19	17-21	18.5
<i>mexicanus mexicanus</i> ^a	26	20-25	21.2
<i>mexicanus yucatanensis</i>	6	20-21	20.7
<i>nebulosus</i>	2	27-28	—
<i>richardi richardi</i> ^a	18	23-28	25.3
<i>richardi bocourti</i>	6	22-25	23.3
<i>richardi bolivianus</i>	10	21-26	23.7
<i>richardi chocoensis</i>	9	22-23	22.3
<i>richardi coeruleodorsus</i> ^a	8	21-23	22.2
<i>richardi copei</i> ^a	6	26-28	27.0
<i>richardi liocercus</i>	10	22-24	23.0
<i>richardi marginatus</i> ^a	9	21-23	22.3
<i>richardi nigromarginatus</i>	45	23-28	25.4
<i>richardi occidentalis</i> ^a	47	18-25	21.6
<i>richardi ortonii</i> ^a	15	24-28	25.9
<i>richardi praestans</i>	17	23-25	23.8
<i>riveti</i> ^a	11	26-29	27.8

^a Illustrated in figure 1.

systematic studies because of the time and the labor involved in the preparation of each skull.

A series of 15 skulls, representing 11 forms, was cleaned for examination, and from these skulls were obtained the data for the palatine, pterygoid, and mandibular teeth shown in table 2. The variation in number of these teeth in general is similar to that observed in the number of maxillary teeth to the extent that forms with the highest number of maxillary teeth also have the greatest number of

chocoensis has a higher number of mandibular teeth than maxillary teeth; *depressirostris* and *yucatanensis* exhibit a higher number of pterygoid teeth than mandibular teeth.

The variation in number of maxillary teeth is shown in table 3, and 10 sample maxillae are illustrated in figure 1. In all forms the maxillary teeth increase in size posteriorly, and at least the two posterior teeth are pronouncedly enlarged, as in *mexicanus* and *diplotropis*. The remaining species have three or four enlarged posterior teeth. These en-

larged teeth may be sharply differentiated in size from the teeth anterior to them, as in *mexicanus*, or the increase in size may be a gradual process, as in *ortoni*. Normally there is no diastema to separate the enlarged posterior teeth, although a slight gap may be present, as illustrated in *richardi*.

nation and low magnification the illusion of a groove can be obtained, but in every case observed in this study higher magnification and better light have dispelled the illusion.

In view of the small variety of organisms recorded as food items for members of the genus, there would appear to be no correla-

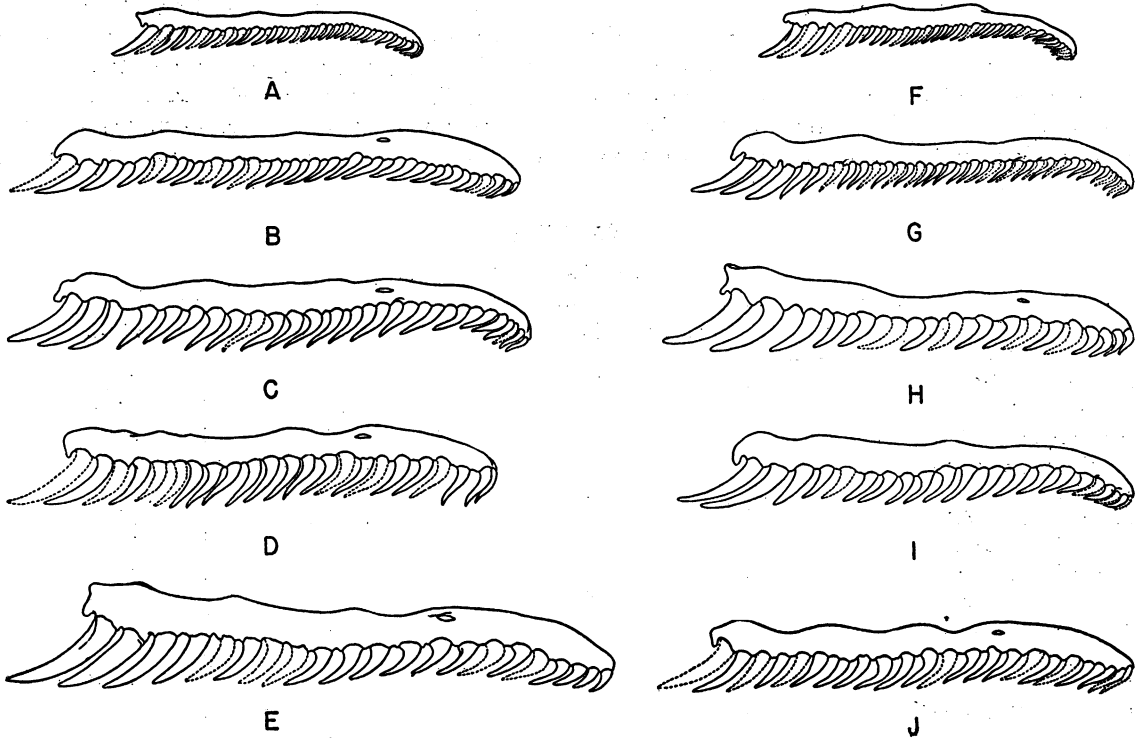


FIG. 1. Lateral view of the right maxillae of 10 forms of the genus *Thalerophis*, illustrating representative variations in the maxillary dentition. Note enlargement of the posterior teeth in the different forms illustrated. A. *richardi ortoni*. B. *richardi copei*. C. *richardi richardi*. D. *richardi coeruleodorsus*. E. *richardi occidentalis*. F. *riveti*. G. *depressirostris*. H. *diplotropis*. I. *mexicanus mexicanus*. J. *richardi marginatus*.

The enlarged maxillary teeth are laterally compressed, tear shaped in cross section, with a slight anterolateral ridge. No specimens have been examined that possessed grooved teeth such as are characteristic of opisthophous snakes. Under inadequate illumi-

tion between the total number of maxillary teeth and food. Clinal variation in total number of maxillary teeth has been observed for several forms and will be discussed in more detail later.

HEMIPENIS

The male hemipenis has not been employed as a taxonomic character by previous workers dealing with this genus. This organ shows

considerable interspecific differentiation and intraspecific constancy, affording a useful taxonomic character and one of the best in-

dicators of phylogenetic history. The hemipenes have been thought by some to be the best indicators of phylogenetic history because of the assumption that they show more conservatism in their evolution than do other characters. This assumption is not entirely supported by fact. Dunn (1928, p. 20) states that "wide peneal variation in closely related snakes is found chiefly among arboreal and among burrowing forms." Bogert (1940, p. 9) cites several cases in which adaption to specialized habitats has been accompanied by modifications of the penis. Because of the high frequency of incomplete tails the data from *Thalerophis* are few, but they lend support to Bogert's (*loc. cit.*) statement "that the evolution of a slender tail is coupled with a shortening of the hemipenis."

The reluctant recognition of the potential adaptive modification in the hemipenes has somewhat minimized their evolutionary significance. Such knowledge has produced an attitude of healthy conservatism and scepti-

cism among most herpetologists so that the hemipenial characters are utilized with appropriate reserve.

In the genus *Thalerophis* these organs vary from relatively short, generalized colubrine hemipenes, five to six subcaudals long, with little or no specialized structural modification, to a more elongate organ nine subcaudals long with enlarged basal spines¹ and the calyces almost completely obscured by papillae.

Plates 16 and 17 show four representative types of hemipenes found in the genus. The hemipenis of *riveti*, shown in plate 16, is the most generalized type observed in the genus. That of *depressirostris* (pl. 16) shows a slight increase in structural modification over the condition observed in *riveti*. The hemipenes of *praestans* and *mexicanus* (pl. 17) show still further modifications in respect to this character, with *mexicanus* being the most complex. The remaining forms of the genus are intermediate or similar to these four types.

SCUTELLATION

In ophidian systematics the most important morphological characters for the diagnosis of lower taxonomic categories are those of the scutellation. These differ and are treated according to the part of the animal on which they occur: (1) the dorsal scales on the body and tail; (2) the ventral plates covering the under side of the body; (3) the anal plate covering the anal opening; (4) the subcaudal plates covering the under side of the tail; and (5) the head plates, including the labials and chin shields. For most of these types of scales both qualitative and quantitative attributes are present, although the latter have been most frequently employed because of their more objective nature.

DORSAL SCALES

The number of dorsal scale rows on the body is constant throughout the genus, 15-15-11. One form, *urosticta* Peters, 1873, was described as possessing a maximum of 13 dorsal scale rows. This name is assigned to the synonymy of *occidentalis*; it is based on an aberrant specimen, is the result of erroneous

counting, or is an error in recording the number (*vide* Dunn, 1944). A count of 13 dorsal scale rows can be obtained only within a limited area of the body in the region of the point of reduction in the number of dorsal scales.

A raised longitudinal keel is present on the scales of two or more rows of dorsal scales, at least on the posterior one-fourth of the body. Much individual, sexual, geographic, and interspecific variation is exhibited in respect to the number of rows keeled, the prominence of the keels, and the distribution of the keels over the body. Large adult males have the keels best developed, whereas juvenile females have them least developed or, rarely, absent entirely. The species *depressirostris* and *diplotropis* are characterized in part by having keels present only on the paravertebral rows of the body. The species *riveti* is the most heavily keeled member of the genus, with well-developed keels normally present on all of the dorsal scale rows on the body and

¹ Contrary to the statement of Stuart (1932, p. 10) that "This character [one or more enlarged basal spines] does not occur in any neotropical genera" of Colubrinae.

extending onto the tail. The remaining forms exhibit conditions between these extremes. A number of forms have keels present on only the median three to seven rows, with females and juveniles in such forms occasionally exhibiting only the paravertebral scales keeled.

In lower Central America there is a notable difference in the number of dorsal rows keeled in the populations of *occidentalis* from the Atlantic and Pacific drainages. Specimens from the drier Pacific slope possess keels on all of the dorsal rows except row I. Specimens from the more humid Atlantic slope usually have keels only on rows V, VI, VII, IX, X, and XI. Row VIII may or may not be keeled. If a keel is present on this row, it is always less pronounced than the keels on the adjacent paravertebral rows and disappears anterior to the anal region.

The presence or absence of and the number of apical or scale pits when present are frequently used in ophidian systematics. In the genus *Thalerophis* these pits are highly constant in number and distribution. This latter factor is one that has not been emphasized.

The characteristic distribution pattern in this genus consists of a single apical pit on the posterior tip of the dorsal scales of every row except row I. On the posterior one-third of the body a single pit is regularly present on the scales of rows III-V, with row V occasionally having two pits.

There is greater variation in the distribution of the pits on the posterior third of the body than there is on the anterior third, and those of the latter region are larger and more prominent than those on the former. The two outstanding exceptions to the above-described pattern are *diplotropis*, which usually has two pits on the scales of the paravertebral rows throughout the body, and *mexicanus*, which frequently has no pits on the scales of the two lower and two upper dorsal rows at midbody.

A thorough survey of the distribution of the apical pits in other snake genera has not been made in the course of this study, but casual comparisons indicate that marked differences do exist in this character, as well as in the number of pits, among colubrine snakes. In contrast to *Thalerophis* in which the distribution of the pits is reduced poste-

riorly, members of some genera (*Dryadophis*, *Elaphe*, *Leptodrymus*, and *Opheodrys*) retain a constant distribution throughout the length of the body, whereas others (*Drymarchon*) increase in distribution and number posteriorly. An additional difference that appears to be generically constant is that in some genera (*Coluber*, *Drymobius*, and *Thalerophis*) the pits are first reduced or suppressed on the lowermost rows of the dorsal scales, whereas in others (*Rhinocheilus*, *fide* Klauber, 1941) the scales of the lowermost rows have more pits per scale. These distributions seem to merit further study from a phylogenetic point of view.

An important qualitative attribute of the dorsal scales that has been neglected is that of shape and size. As Malcolm Smith (1943) points out, "Very little attention has been paid to the size and shape of the dorsal scales, and they are worth a closer study." Later in the same paper, however, he notes that the difficulty of expressing these qualitative characters is a deterrent to their use in taxonomy. Under the section on the generic relationships of *Thalerophis* some intergeneric differences in shape and size will be pointed out and are illustrated in figure 13. Within this genus interspecific differences also can be observed, although these revolve around a limited generic pattern. A few forms, e.g. *diplotropis*, have the vertebral scales somewhat enlarged, and in some forms the scale rows are more obliquely arranged than in others. In all members of this genus the scales of the first and vertebral rows are larger than the scales of rows III to V. When the dorsals, other than the vertebral scales, are modified they are narrowed and elongated, yet retain the symmetry of unmodified scales.

The reduction in number of dorsal scales on the body from 15 rows to 11 rows is brought about by the suppression of two upper rows, V and VI, or VI and VII, and two lower rows, II and III, or III and IV. These suppressions take place in a relatively restricted area, opposite ventrals 84 to 118 within this genus, in the vicinity of the pyloric sphincter (as pointed out by Procter, 1920). In a given form there is a general consistency regarding the rows involved in reduction, but in no

form is this character sufficiently constant to be of diagnostic value.

In most instances it is not possible to determine with accuracy the exact row that disappears. In this genus the reduction appears to be brought about not by the loss of a definite row of scales, but by the fusion of two adjacent rows of dorsal scales. This is shown in many cases by the increase in size of the single scale that occupies the position immediately posterior to the point where the two rows fuse and in some instances by the presence of two keels on this enlarged scale.

The point at which the reduction in number of dorsal scale rows takes place has been used in other genera (Hartweg, 1940; Smith, 1941) as an additional taxonomic character. This character has been determined for all the forms of *Thalerophis*, and the data are included under the specific descriptions. Originally I labored under the illusion that in this genus the character was correlated with the total number of ventral scales. As a result of plotting these data and determining the coefficient of correlation for *mexicanus* a positive correlation was obtained of +.67. However, Klauber (1945) has clearly pointed out that such a correlation is spurious because of the heterogeneous nature of the material and states, "correlation is to be expected in collections representing entire species." Analyzing data from a homogeneous series of *diplotropis*, Klauber (*loc. cit.*) found a marked correlation in respect to bilateral symmetry of the point of reduction for the same dorsal rows on the two sides of the body and a significant positive correlation between the two points of suppression involved in the reduction from 15 to 11 dorsal rows, but, he says, "there seems to be no correlation between points of suppression and total ventrals." He states further that spurious correlations such as that obtained for *mexicanus* demonstrate "the existence of correlated territorial trends or clines."

A minor difference is apparent between the sexes in respect to the average position of the dorsal scale reduction, even though no difference has been observed in respect to the total number of ventrals in the two sexes. For example, the average number of ventrals is virtually identical for males and females in

depressirostris (150.47 for the males and 150.33 for the females), but the average point of reduction occurs farther posteriorly in the females than in the males (on the average opposite ventral 90 in the males and ventral 95 in the females). The difference is slight, but appears to be consistent in most of the forms that have been studied. An exception to this is presented by *yucatanensis* in which the males average 107.70 and 106.90 compared to 105.37 and 103.75 in the females. This exception may be the result of inadequate material for this subspecies.

An investigation was made of the reduction in the number of dorsal scales on the tail. The major reduction that takes place in colubrine snakes involves the change from six to four rows of scales on the dorsal surface of the tail. The point at which reduction occurs, measured in terms of the number of the subcaudal scale opposite the point of reduction, varies considerably in some forms, whereas others show slight variation (see fig. 2). Two of the forms here treated, *mexicanus* and *richardi*, exhibit a significant sexual dimorphism in this respect. Large homogeneous samples adequate for statistical analysis of the observed variations are lacking, so that the significance of this character is not understood fully. It warrants further investigation as a possible additional indication of phylogenetic differentiation. From the observations made during this study those forms characterized by marked variations in this respect, e.g., *diplotropis* and *mexicanus*, show a tendency towards a positive correlation between length of tail and the point at which reduction takes place. Whether this correlation is significant or not, I do not know.

Drymobius chloroticus closely resembles *occidentalis* and *praestans* superficially, although differing in several important details. During the course of this study eight specimens of *Drymobius chloroticus* were sent to me for examination as specimens of "*Leptophis occidentalis*." All eight specimens can be distinguished from all specimens of the genus *Thalerophis* on the basis of the point of reduction of the dorsal scales on the tail.

Klauber (1940) has utilized the number of scales around the tail as a valuable diagnostic character in the genus *Leptotyphlops*.

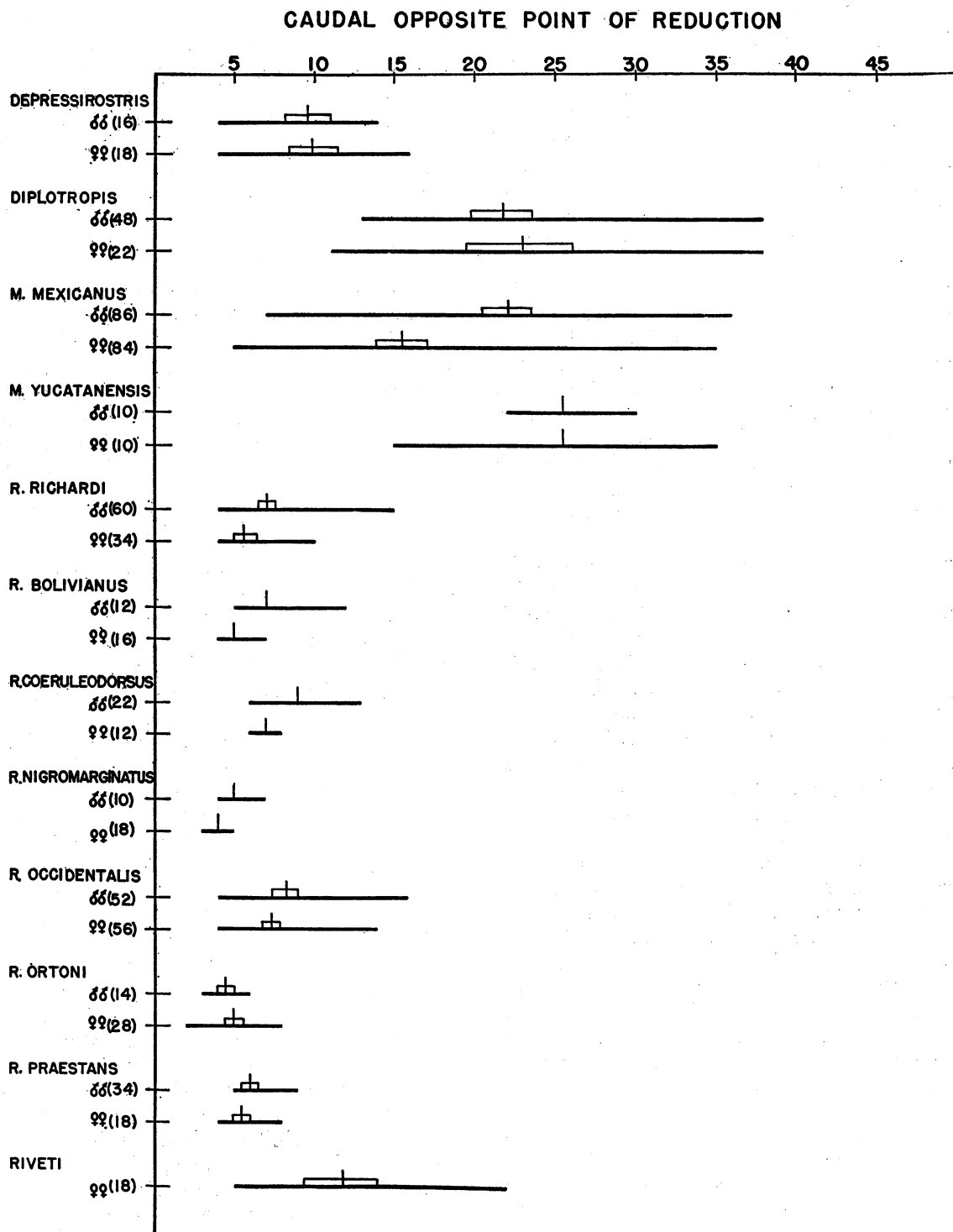


FIG. 2. Graph illustrating variation in the point of reduction in the number of dorsal scales on the tail (with extremes, mean, and twice the standard error of the mean on each side where sufficient data are present).

Balli (1939), in a variational study of the European *Tropidonotus natrix*, recorded a marked sexual dimorphism in the number of transverse dorsal scales (four, five, or six) at the middle of the tail. I believe that the differences observed by Balli could have been more accurately defined in terms of the point at which the reduction from six to four rows occurs. Aside from these two studies, I know of no others that have utilized this character in ophidian systematics.

VENTRAL PLATES

The number of ventral plates varies within the genus from a minimum number of 133 in

of Iquitos, Peru. A calculation of the data from these specimens yields a coefficient of variation of 2.53 for 27 males and 2.01 for 46 females, indicating that the ventrals comprise a highly stable taxonomic character in the population analyzed.

In the majority of forms the females have a higher maximum and a greater average number of ventral plates than are observed in the males. A few forms, such as *depressirostris*, have virtually identical numbers of ventrals in the two sexes. No member of the genus exhibits complete segregation of the sexes in this character.

Joseph R. Bailey, in his study of the genus

TABLE 4
NUMBER OF VENTRAL PLATES

Species	Males		Females	
	Extremes	Mean	Extremes	Mean
<i>depressirostris</i>	144-157	150.47	145-158	150.33
<i>diplotropis</i>	167-184	174.44	172-184	178.04
<i>mexicanus mexicanus</i>	148-169	157.30	154-174	161.15
<i>mexicanus yucatanensis</i>	164-172	168.11	165-174	169.22
<i>nebulosus</i>	150-160	153.00	158	
<i>richardi richardi</i>	156-176	162.55	159-178	164.91
<i>richardi bocourti</i>	160-166	163.25	164, 165	
<i>richardi bolivianus</i>	156-169	162.00	162-173	167.70
<i>richardi chocoensis</i>	161-168	164.50	165, 165, 167	
<i>richardi coeruleodorsus</i>	158-166	160.79	158-172	164.75
<i>richardi copei</i>	173-179	177.00	176	
<i>richardi liocercus</i>	151-164	156.46	156-166	161.42
<i>richardi marginatus</i>	157-170	161.85	162-172	167.27
<i>richardi nigromarginatus</i>	147-165	152.28	150-166	156.91
<i>richardi occidentalis</i>	152-177	167.89	161-182	171.39
<i>richardi ortonii</i>	153-169	175.22	152-168	161.54
<i>richardi praestans</i>	166-182	174.89	174-183	179.27
<i>riveti</i>	133-149	141.18	147	

riveti to a maximum of 184 in *diplotropis*. The observed variation is shown in table 4. The individual, sexual, territorial, and population variation in the number of these plates is such as to make them one of the most valuable morphological attributes utilized in this study. An indication of the variability of the ventrals was obtained from the large homogeneous series of *nigromarginatus* collected by Dr. Harvey Bassler in the vicinity

Pseudoboa (unpublished), and Grobman (1941), investigating the bionomics of *Opheodrys vernalis*, have both observed a tendency towards a positive correlation between maximum number of ventrals and large size within a population. Klauber (1945, pp. 83-89), in his meticulous study of herpetological correlations, analyzed this phenomenon carefully and concluded "that, in a homogeneous series of snakes of approximately the same

age, correlation is not generally evident between size and number of ventral scales, but the largest individuals do tend to have an above-average number of ventrals." This is illustrated within the genus *Thalerophis* by the series of *nigromarginatus* from Iquitos, Peru, collected by Dr. Harvey Bassler:

tirely through linkage of the genes controlling the separate characteristics.

There is no conclusive evidence to show what the correct explanation might be. It has not been shown definitely that the larger females that possess higher ventral counts produce young that likewise have higher

	MALES (30)		FEMALES (45)	
	Head-Body Length	Ventrals	Head-Body Length	Ventrals
Five largest specimens	807	159	680	160
	714	153	670	158
	703	153	668	160
	702	156	650	165
	698	157	642	162

Mean number of ventrals for all males, 153.00; for all females, 157.02

The same general tendency is suggested by the observed interspecific variation. The form that obtains the maximum recorded size for the genus also has the highest average number of ventrals observed in the genus, and, conversely, the form with the lowest number of ventrals has the smallest maximum size in the genus. Between these extremes there are a number of exceptions, and more evidence is required before this can be accepted as an established trend.

A number of herpetologists (Klauber, 1936; Stuart, 1941; Dunn, 1942; Inger, 1942, 1943) have presented data illustrating a difference in scutellation between juvenile and adult populations of the same species, indicating a differential survival of snakes within particular limits of variation in respect to scutellation. It is significant to note that in those examples involving a difference in number of ventrals, the juveniles possessed the lower average number. A further point of interest is that within a species the larger snakes usually produce more young (Blanchard, 1937; Klauber, 1936). These phenomena suggest a phylogenetic increase in size and number of ventrals. On the other hand, they may be related to a simple mechanical phenomenon in that a greater number of ventrals allows greater growth and larger size, consequently more young, or that some increased survival value is obtained through an increase in locomotor ability associated with the increased number of ventrals. Furthermore, the phenomena may be explained en-

ventral counts. The data from the studies mentioned above on juvenile and adult populations of the same species suggest that other factors operate to produce a higher mean number of ventrals in the adult population. It has not been shown that a higher number of ventrals necessarily allows for greater growth. Perhaps all of these factors contribute some influence.

Territorial variation in the number of ventral plates is exhibited in all forms that occur over a wide geographic area and that are represented by more than a few specimens from several localities. In the material from the Northern Hemisphere, clines (fig. 3) are more apparent than in specimens from the Southern Hemisphere. This is due doubtless to the greater number of species and specimens of this genus available from localities in the Northern Hemisphere.

In lower Central America the populations of *occidentalis* from the Pacific and Atlantic slopes differ in the average number of ventrals. The number for the population from the drier Pacific side is lower (average 165.21 in the males, 165.33 in the females) than that of the specimens from the more humid Atlantic side (average 172.87 in the males, 176.20 in the females). In *coeruleodorsus* the average number of ventrals appears to be higher in the population from Tobago Island than in the populations from Trinidad and the mainland of Venezuela. Where island populations exist in this genus, the tendency is towards an increase in the average number

of ventrals as compared to specimens from the adjoining mainland (*vide* Mertens, 1934).

The quantitative variation in the ventral plates is the attribute of these particular scales that has proved most useful in the study of the genus *Thalerophis*. There are also qualitative variations that seem to be of value as indicators of differentiation. Two

Thalerophis have the keel well developed, although many have the notch.

ANAL PLATE

The anal plate is normally divided in all species of the genus. There is a slight amount of variation from the normal condition, and this variation exhibits an interesting distribution within the genus. In *depressirostris*

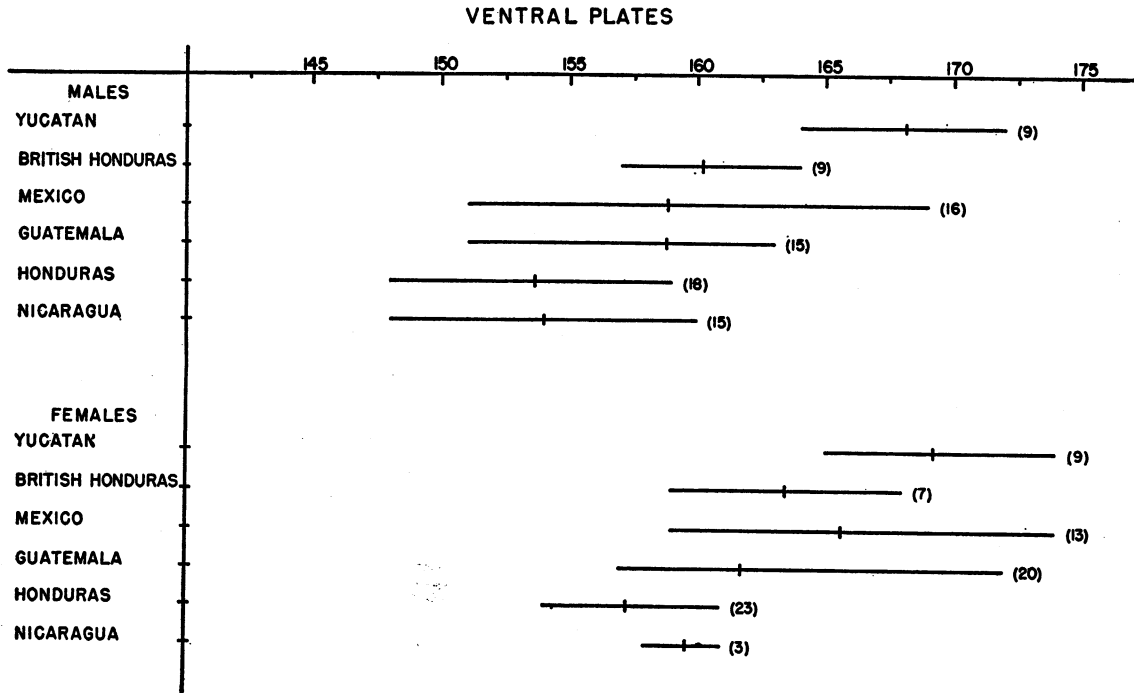


FIG. 3. Geographic variation in the number of ventral plates in *Thalerophis mexicanus*, including *m. mexicanus* and *m. yucatanensis*.

of these that have been noted in the specimens examined are the shape of the individual ventral plates and the presence or absence of a lateral keel. There is marked subspecific and interspecific variation in respect to these two qualitative features of the ventral plates, but because of the difficulty of accurately recording and expressing such variation, these characters have not been used extensively. Extremes of variation are illustrated in figure 13. The presence of a well-developed lateral keel and of a lateral notch appears to be associated with an arboreal habit. No members of the genus

one male has a single anal plate; the remaining 33 specimens examined have the divided or double anal plate. In *diplotrophis* two males, among 60 specimens examined, have the anal plate partly divided; all other specimens have the plate completely divided. In *mexicanus* the variants in a series of 160 specimens include two males with undivided anal plates, five males with partly divided anal plates, and a single female with a partly divided anal plate. One male *riveti* has a partly divided anal plate, whereas the remainder of the specimens of that species have the divided plate.

Local populations within the species *richardi* exhibit the maximum amount of variation observed within the genus. North of Panama and south of Bolivia and Brazil only the normal condition has been observed in this species. In Panama a single male *occidentalis* has been noted with a partly divided anal plate. The geographical distribution of this variation in South America, except Argentina and Paraguay, can best be illustrated in tabular form.

has not been of great value in the present study. The reason for this is that so few specimens (35.3 per cent of all males and 37.7 per cent of all females) possessed a definitely complete tail (see table 6). In many instances it is impossible to tell accurately whether the tail has been damaged or not; data for such specimens were recorded with a question mark but have not been used in the species diagnoses or descriptions unless no other data were available.

	UNDIVIDED	PARTLY DIVIDED	COMPLETELY DIVIDED
Bolivia	0	2 males	9 males
Brazil	4 males	6 males	15 males
		2 females	27 females
Colombia	3 males	3 males	19 males
	1 female	1 female	25 females
Guianas	1 male	9 males	18 males
		1 female	18 females
Peru	16 males	16 males	46 males
	1 female		102 females
Venezuela	2 males	3 males	17 males
(including Trinidad and Tabago)		1 female	17 females
	26 males	40 males	194 males
	2 females	5 females	261 females

The majority of these variants tabulated above are from the Amazon Valley, with the eastern area of Peru being the region with greatest variation. In the material from Peru 41 per cent of the males lack the completely divided anal plate, whereas fewer than 1 per cent of the females from the same area are so characterized. The genetic basis for the character of the anal plate in the genus *Thalerophis* appears to be sex influenced, with a predominance of males among the observed variants. In the population from eastern Peru the condition of variation observed approaches one of partial sexual dimorphism. The genetics of this variation would prove a profitable investigation since the condition of the anal plate is frequently used in generic diagnoses and because of the conditions discussed by Dunn (1943) in *Chironius* and *Dendrophidion*.

SUBCAUDAL PLATES

The number of subcaudal plates has not been adequately analyzed for the genus, and consequently this character, as noted earlier,

The subcaudals are paired in *Thalerophis*, with one row on each side of the ventral surface of the tail. The known variation within the genus is from a minimum of 135 (recorded for a female of *riveti* and a female of *diplotropis*) to a maximum of 189 (recorded in a male *occidentalis*). The observed variation in the subcaudals is shown in table 5. In 12 of the 18 forms recognized the number of subcaudal plates equals or exceeds the number of ventral plates. The greatest difference in relation to these two is in *chocoensis* where the observed maximum number of subcaudal plates exceeds the observed maximum number of ventrals by 15 scales. In two forms the number of subcaudals in both males and females exceeds the number of ventrals; in six forms only the males possess a higher maximum number for the subcaudals; in two forms only the number recorded for females exceeds the maximum number of ventrals; and in two forms the maximum subcaudal count in the females equals that of the ventrals. However, from the small number of specimens now available

TABLE 5
NUMBER OF SUBCAUDAL PLATES

Species	Males		Females	
	Extremes	Mean	Extremes	Mean
<i>depressirostris</i>	163, 169		158-170	163.00
<i>diplotropis</i>	138-161	148.93	135-150	142.09
<i>mexicanus mexicanus</i>	144-175	157.80	140-173	156.31
<i>mexicanus yucatanensis</i>	171-181	174.71	160-169	164.60
<i>nebulosus</i>	145-151	147.66	—	
<i>richardi richardi</i>	146-178	160.75	144-174	160.37
<i>richardi bocouti</i>	163+		163, 165	
<i>richardi bolivianus</i>	147, 151		147-158	149.26
<i>richardi chocoensis</i>	172-183	177.75	175, 178	
<i>richardi coeruleodorsus</i>	152-172	163.33	160-167	163.80
<i>richardi copei</i>	178, 184		—	
<i>richardi liocercus</i>	151, 157		163	
<i>richardi marginatus</i>	138		144	
<i>richardi nigromarginatus</i>	139-160	150.76	137-166	150.57
<i>richardi ortonii</i>	144, 161		144-169	157.90
<i>richardi praestans</i>	153, 172, 175		170-185	177.00
<i>riveti</i>	140-145	142.00	135	

TABLE 6
TAIL/BODY RATIO AND NUMBER OF SPECIMENS WITH COMPLETE TAILS
(Per cent in parentheses)

Species	Tail/Body Ratio				Number with Complete Tails	
	Males		Females		Males	Females
	Extremes	Mean	Extremes	Mean		
<i>depressirostris</i>	.72, .75		.66-.75	.718	2(13%)	5(27%)
<i>diplotropis</i>	.55-.60	.555	.47-.59	.540	15(44%)	11(50%)
<i>mexicanus mexicanus</i>	.57-.75	.670	.56-.70	.639	40(63%)	35(53%)
<i>m. yucatanensis</i>	.62-.70	.675	.59, .60		7(78%)	5(55%)
<i>nebulosus</i>	.62-.70	.666	—		3(75%)	—
<i>richardi richardi</i>	.60-.71	.640	.61-.72	.655	16(33%)	16(35%)
<i>r. bocourti</i>	.62		.66		1(25%)	1
<i>r. bolivianus</i>	.59, .60		.59, .61		2(25%)	6(35%)
<i>r. chocoensis</i>	.54-.67	.615	.62, .66		3(75%)	2(66%)
<i>r. coeruleodorsus</i>	.58-.71	.668	.65-.68	.667	6(32%)	5(31%)
<i>r. copei</i>	.68		—		2(40%)	—
<i>r. liocercus</i>	.65		.63		1(7.7%)	1(14%)
<i>r. marginatus</i>	.60		.61		1(7.7%)	1(9%)
<i>r. nigromarginatus</i>	.58-.69	.648	.60-.71	.613	27(33%)	40(36%)
<i>r. occidentalis</i>	.55-.65	.608	.59-.66	.617	15(24%)	8(15%)
<i>r. ortonii</i>	.66, .69		.64-.70	.660	2(22%)	10(77%)
<i>r. praestans</i>	.61, .63		.56-.68	.602		4(36%)
<i>riveti</i>	.69-.72	.702	.65		4(36%)	1

with complete tails it is manifestly certain that the true condition with respect to the subcaudals in this genus is not known.

HEAD PLATES

The cephalic scutellation in the genus *Thalerophis* exhibits few modifications from a generalized colubrine condition, and only a few characters are of diagnostic value in specific or subspecific differentiation.

The loreal plate is perhaps the most im-

sequently of little significance. My findings in respect to this character are that it is characterized by a high degree of constancy and therefore is a useful character. In the species that normally possess a loreal, four individuals, or 1.6 per cent of the specimens examined (258 in total), lacked the plate on one or both sides; whereas in the species that normally do not possess a loreal, 24 individuals, or 4.1 per cent of those studied (627 in total), had a loreal on one or both sides of

TABLE 7
OBSERVED FREQUENCIES IN UPPER AND LOWER LABIALS

Species	Upper Labials								Lower Labials											
	7/7	7/8	7/9	8/8	8/9	9/9	9/10	10/10	7/9	8/9	9/9	8/10	9/10	9/11	10/10	10/11	10/12	11/11	11/12	12/12
<i>depressirostris</i>			1	2	1	29	1				1		4		19	7		1		
<i>diplotropis</i>				53	3	3				1	3		5		46	3		1		
<i>m. mexicanus</i>				125	6	1					4		5		107	7		8		
<i>m. yucatanensis</i>				17	1										15	2		1		
<i>nebulosus</i>				4		1									4	1				
<i>r. richardi</i>				10	7	63	3						2		10	10		52	4	4
<i>r. bocourti</i>				2		4	1								3			4		
<i>r. bolivianus</i>				25									4		11	7		2	1	
<i>r. chocoensis</i>					1	6				1		1			1			3	1	
<i>r. coeruleodorsus</i>		1	1	20	1	12	1			1			2		19	9		3		
<i>r. copei</i>						4	1	1							1			3	2	
<i>r. liocercus</i>	1			12	3	4							4		11	3		1		
<i>r. marginatus</i>				22	1	1				1					16	2		3		
<i>r. nigromarginatus</i>	1	4		63	36	88	4		1	2	1		11		43	44		81	6	1
<i>r. occidentalis</i>		1		44	24	46	3	1		1			10	1	70	14		18	1	
<i>r. ortoni</i>				8	3	20				1	1		1	1	4	6		16		
<i>r. praestans</i>		2		11	9	6					1		2		18	3	1	3		
<i>riveti</i>				13							2		1	1	8	1				
Total	2	8	2	431	96	288	14	2	1	8	13	1	51	3	404	121	1	200	15	5

portant of the head shields from a historical standpoint, for its presence or absence has been used in the past (Cope, 1886, 1887) to segregate species of this genus into two genera. Three of the currently recognized species normally possess a single loreal plate on each side of the head. These are *depressirostris*, *diplotropis*, and *mexicanus*. The remaining species in the genus normally lack the loreal plate. The presence or absence of the loreal in this genus has been considered by some herpetologists to be highly variable and con-

the head. In passing, it is interesting to note that the forms that show the greatest variation in the loreal also show the maximum variation in the anal plate.

One factor that has contributed to the view that the loreal plate was a highly variable character has been the confusion regarding the identity of various forms of the genus. For example, *nebulosus* does not possess a loreal plate, but all specimens of that species have been allocated in collections to *mexicanus* which does have a loreal.

After the loreal plate, the number of labials has been the most useful of the head shields in indicating relationships and differentiation. The number of these plates, especially of those on the lower jaw, represents a variable character that is more useful in illustrating trends of differentiation than in providing a clear-cut indicator of speciation. The number is usually either eight or nine upper labials and 10 or 11 lower labials, but

number of eight upper labials results from fusion of the second and third or the third and fourth of nine upper labials.

When the number of lower labials is 10, there are normally six labial plates in contact with the chin shields, whereas the number in contact with the chin shields is seven when the total number of lower labials is 11. The increase from 10 to 11 lower labials most frequently is brought about by the division of

TABLE 8
OBSERVED VARIATION IN OCULAR SCALES

Species	Preoculars			Postoculars					
	1-1	1-2	2-2	1-1	1-2	2-2	2-3	3-3	2-4
<i>depressirostris</i>	34			2		33			
<i>diploptropis</i>	60					60			
<i>m. mexicanus</i>	135	1	2			136		1	
<i>m. yucatanensis</i>	18				1	17			
<i>nebulosus</i>	5				1	4			
<i>r. richardi</i>	80	1	4			84	1		
<i>r. bocourti</i>	7					7			
<i>r. bolivianus</i>	24	1			1	22	1	1	
<i>r. chocoensis</i>	7					6		1	
<i>r. coeruleodorsus</i>	29	3	3		1	36			
<i>r. copei</i>	6					6			
<i>r. liocercus</i>	20				1	9	2	6	1
<i>r. marginatus</i>	23	1		2		22			
<i>r. nigromarginatus</i>	202	2	1	2	1	188	4	2	
<i>r. occidentalis</i>	118	2	4	1	1	115	7	2	
<i>r. ortonii</i>	31					31			
<i>r. praestans</i>	29			1		28	1	1	
<i>riveti</i>	13			2	2	9			
Total	841	11	14	10	9	813	14	14	1

other numbers occasionally occur. The numbers observed and their respective frequencies in the different forms of the genus are shown in table 7. When the number of upper labials is eight, the fourth and fifth plates are in contact with the orbit; when the number is nine, the fifth and sixth plates are in contact with the eye. Thus it is apparent that the difference in number of these plates involves the area anterior to the eye rather than that behind the eye. Observation reveals that the number of nine upper labials results from division of the second or third of eight upper labials, or, conversely, that the

the third or fourth lower labial, or, conversely through the fusion of the second and third or of the third and fourth labials the number is changed from 11 to 10.

It might be expected that the higher number of labials would be associated with an elongation of the anterior portion of the head. Data to establish any such relationship are lacking at the present time. There are definite indications, however, that a high number of upper labials is not always associated with a high number of lower labials. For example, the majority of specimens of *depressirostris* have nine upper labials but only 10 lower

labials. Moreover, there is no apparent relationship between a high number of labials and a high number of maxillary teeth. Geographic clines in the proportionate variation in the labials are illustrated in several instances; for example, there is a progressive increase in number of labials from eastern Peru to the mouth of the Amazon and the Guianas. On the other hand, the wide-ranging *occidentalis* has an approximately equal number of individuals with eight and nine upper labials throughout its distribution without any apparent geographic or sexual differentiation.

The remaining head shields, either because of marked constancy or erratic variability, have been of little value in the present study. The data for the ocular shields are shown in table 8. The condition of a single preocular is slightly more constant (97.1 per cent of all specimens examined) than that of two postoculars (94 per cent of all specimens examined). In respect to the postoculars two trends of variation are worthy of mention: four of the nine *riveti* studied have the postocular fused to a single plate on one or both sides, and nine of the 20 *liocercus* have more than two postoculars on one or both sides.

The various formulas observed in the temporal shields are shown in table 9 with their relative frequencies. Seventy-five per cent of the individuals studied have one anterior temporal and two posterior temporals. The main variation from this formula was in the direction of a reduction in the number of posterior temporals to only one shield. Thus 7 per cent of the specimens had only one posterior temporal on both sides, while 8 per cent had two posterior temporals on one side and only one on the opposite side. In respect to this trend, *marginatus* exhibits the most pronounced variation, for 15 of the 24 specimens have but a single posterior temporal on one or both sides, with nine specimens possessing a formula of 1-1/1-1.

In the early stages of this study data were recorded on the shape, proportion, and spatial relationships of most of the head shields. This procedure proved impractical because of the additional time required to record such observations, the difficulty of expressing the conditions observed, and the little value gained from such data. In only a few instances was an additional indicator of differentiation obtained. These characters are detailed in the species descriptions.

SIZE AND PROPORTIONS

Real differences in size between distinct species are readily apparent but are difficult to delimit with precision. Such variation is obviously based on the genetic make-up of the species involved. One of the drawbacks to the utilization of size as a characteristic of an ophidian population is the incompleteness of our knowledge of growth in snakes. In most snakes the growth increments are reduced progressively with age and may stop entirely after a particular adult size is reached, or growth may continue throughout the life of the individual, although at a much slower rate after maturity is reached. It has been suggested (Smith, 1943) that the Boidae may differ from other snakes in continuing to grow throughout life. Klauber (1937), in his detailed study of growth in the rattlesnakes, was unable to determine "whether growth ceases entirely, as in birds and mammals, or whether there is a continued but

proportionately slower growth thereafter."

Indications of interspecific differences in size can be obtained from the analysis of broods, the maximum size observed in large samples, and the age at which individuals became sexually mature. These sources of data provide an approximate method of comparing various species in regard to size. Few data are available for broods in *Thalerophis*. The data for the observed maximum size are presented in table 10, together with the available information on the minimum size of females that contained developing eggs. These data are incomplete and give only the known potentialities for each form. From these observations *nebulosus* and *riveti* appear to be the smallest members of the genus, whereas *occidentalis* and *praestans* seem to obtain the maximum length recorded for the genus. The maximum observed length in *nebulosus* is below that of *riveti*, but only

TABLE 9
TEMPORAL FORMULA OBSERVED IN *Thalerophis*

	<i>depressirostris</i>	<i>diplotropis</i>	<i>mexicanus mexicanus</i>	<i>m. yucatanensis</i>	<i>nebulosus</i>	<i>richardi richardi</i>	<i>r. bocourti</i>	<i>r. bolivianus</i>	<i>r. chocoensis</i>	<i>r. coeruleodorsus</i>	<i>r. copei</i>	<i>r. liocercus</i>	<i>r. marginalus</i>	<i>r. nigromarginalus</i>	<i>r. occidentalis</i>	<i>r. ortonii</i>	<i>r. praestans</i>	<i>riveti</i>	Totals
1/1-1								1					1						1
1/1-2								3											1
1-1/1-1		4	1			2		1					9	31	5	4	1	1	61
1-1/1-2	2	4	3					1		1	1	2	6	33	8	6	1		68
1-1/1-2-1								1						2					2
1-1-1/1-2								2											1
1-1-2/1-1-2		2	7			4				1	1	2	1		3	1	1	1	26
1-1-2/1-1-1-2		1	2																3
1-1-2/1-1-3															1				1
1-1-2/1-2		4	2	2								1		1	4	1	1	1	17
1-1-2/2-1-2			1																1
1-1-2/2-1-2-1													1						1
1-1-2/2-2						1										1			2
1-1-2/2-2-2			1								1								2
1-1-2-/1-2-1			1																
1-1-3/2-1-2				1															1
1-2/1-2	31	45	113	15	5	73	7	16	7	34	4	12	7	120	99	17	23	9	637
1-2/1-3	1		1			1								2		2			7
1-2/2						1													1
1-2/2-2			1			2								1	1		1		6
1-2/2-2-1														1					1
1-2-1/1-2-2																1			1
1-2-2/2-2-2														1					1
1-2-2/1-2-2						1													1
1-2-2/1-3-2															1				1
2-1-2/2-2-3														1					1
2-2/2-2												2							2
Total																			848

three adults are known for the former. The largest specimen measured by me was a male *praestans* that had a head-body length of 1470 mm., plus an incomplete tail length of 773+ mm., giving an over-all total length of 2243 mm. (7 feet, 4 inches). The largest female specimen studied also was a representative of *praestans*, with a head-body length of 1240 mm., plus an incomplete tail length of 644+ mm., with a total over-all length of 1884 mm. (6 feet, 2 inches). Dr. Emmett R. Dunn of Haverford College has shown me the head of the largest specimen of *occidentalis* among 450 individuals examined by him from Panama. This specimen had a head length of 46

mm. which is exactly the same as the head length of the largest male *praestans* mentioned above.

The data presented in table 10 indicate that males appear to attain a larger size than females. In only three of the 18 forms did the females exceed the males in observed length. It is well to repeat that the maximum size shown in this table merely indicates the known size potential for the species or race. This figure may be misleading where few specimens have been available.

Characters of shape and proportion in respect to structures of the head, the body, the tail, and scutellation are frequently of great

TABLE 10

MAXIMUM SIZE IN MILLIMETERS

(Data for the head-body length on the left and the tail length on the right in the column. Minimum size of females with developing eggs)

Species	Males	Females	Females with Eggs
<i>depressirostris</i>	835, 550 +	827, 405 +	548 (3 observations)
<i>diplotropis</i>	897, 512	731, 368 +	
<i>m. mexicanus</i>	879, 336	776, 399 +	505 (5 observations)
<i>m. yucatanensis</i>	753, 516	764, 384 +	588 (1 observation)
<i>nebulosus</i>	502, 352	433, +	
<i>r. richardi</i>	940, 523 +	943, 588 +	466 (3 observations)
<i>r. bocourti</i>	939, 582 +	672, 458	
<i>r. bolivianus</i>	757, 376 +	625, 361 +	
<i>r. chocoensis</i>	1104, 697 +	950, 485 +	
<i>r. coeruleodorsus</i>	860, 534 +	963, 588 +	746 (2 observations)
<i>r. copei</i>	1008, 622 +	762, 490 +	
<i>r. liocercus</i>	1073, 646 +	848, 529 +	723 (1 observation)
<i>r. marginatus</i>	995, 523 +	932, +	
<i>r. nigromarginatus</i>	823, 480	746, 472 +	471 (35 observations)
<i>r. occidentalis</i>	1161, 660 +	907, 538 +	798 (3 observations)
<i>r. ortonii</i>	794, 527	617, 388 +	556 (3 observations)
<i>r. praestans</i>	1470, 773 +	1240, 644 +	
<i>riveti</i>	512, 362	459, 298	459 (1 observation)

TABLE 11

PROPORTIONAL SIZE OF THE EYE (DIAMETER OF EYE/HEAD LENGTH)

(Figures in parentheses indicate the number of specimens in each class)

Size Group (Body Length)	<i>mexicanus</i>	<i>diplotropis</i>	<i>depressirostris</i>	<i>occidentalis</i>	<i>nigromarginatus</i>
1- 300 mm.	25.66 (3)	—	—	25.7 (1)	22.31 (6)
300- 600 mm.	20.47 (7)	18.98 (5)	23.90 (3)	20.67 (4)	21.71 (15)
600- 900 mm.	20.21 (7)	17.66 (13)	22.02 (4)	20.53 (8)	20.07 (16)
900-1200 mm.	—	—	—	20.6 (1)	—

TABLE 12

PROPORTIONAL HEAD LENGTH (BODY LENGTH/HEAD LENGTH)

(Figures in parentheses indicate the number of specimens in each class)

Size Group (Body Length)	<i>mexicanus</i>	<i>diplotropis</i>	<i>depressirostris</i>	<i>occidentalis</i>	<i>nigromarginatus</i>
1- 300 mm.	19.06 (3)	—	—	—	18.86 (5)
300- 600 mm.	20.70 (7)	24.94 (5)	26.90 (3)	21.30 (1)	26.99 (13)
600- 900 mm.	25.44 (7)	27.03 (13)	29.00 (4)	26.77 (4)	29.06 (10)
900-1200 mm.	—	—	—	29.26 (8)	—
1200-1300 mm.	—	—	—	31.00 (1)	—

value in indicating degrees of similarity and divergence, in denoting different ontogenetic stages, and in attesting to habits and habitat preferences through analogy with species of known habits. The limitations in the analysis and use of these characters are the result of a lack of large homogeneous samples. The proportional characters exhibit both ontogenetic and phylogenetic differences that are the result of both heterauxesis (ontogenetic allometry) and allomorphosis (absolute-size allometry).¹ This can be seen most readily in the genus *Thalerophis* in the proportional size of the eye and in the relative length of the head, as compared to the head length and the body length, respectively. A few data for these two characters are presented in tables 11 and 12. Both the head and eye appear to decrease in size in relation to increase in the size of the body and head, respectively, with the most rapid change occurring early in life.

A proportionally large eye is often associated with arboreal habits. If the proportional size of the eye is accepted as an indicator of the degree of adaption to an arboreal existence, the data presented in table 11 attest that *depressirostris* leads a more arboreal life than do the other three forms for which data are presented. Such an assumption is supported by other observations.

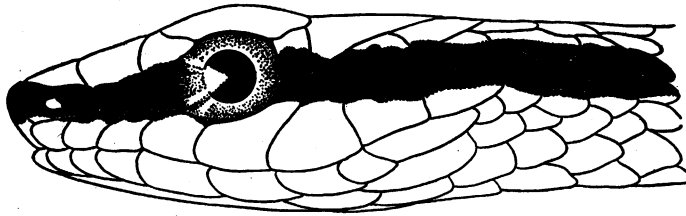
One of the proportional measurements most frequently used in ophidian taxonomy is the tail/body ratio. This character has been of little use in the present study because of the already mentioned high percentages of specimens with an incomplete tail. Interspecific differences are apparent in regard to this proportional character, but the scope and significance of its variation cannot be fully analyzed. Within a small homogeneous series of eight adult male *diplotropis* with complete tails a significant positive coefficient of correlation is obtained between this character and the total number of subcaudal plates

($r = +.8387$; P less than .01). A similar relationship is found in a small series of male *m. mexicanus* from Tela, Honduras. No such relationship exists in several instances where different species are compared. For example, four male *riveti* have an average number of subcaudals equal to 142.00 and a tail/body ratio average of .702, whereas four male *chocoensis* have an average number of subcaudals of 177.75 but an average tail/body ratio of .615.

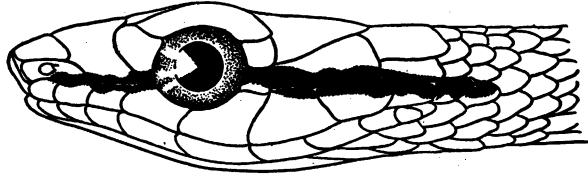
Klauber (1943), in his thorough analyses of tail-length differences in snakes, found that an ontogenetic variation in tail-length proportionality of considerable degree is usually present, but he remarks that "the change in proportionality—its direction and degree—seems to be a generic and even a species character without any widely applicable uniform rule of variation." The only data for *Thalerophis* that have been analyzed in this connection are inadequate to determine the condition that exists within the genus, but they suggest that the ontogenetic change is relatively slight. My observations on *Thalerophis* corroborate Klauber's findings that slim snakes tend to have long tails and that long-tailed snakes do tend to have low sexual dimorphism in respect to tail-length proportionality.

A serious drawback to the more extensive use of characters of shape proportions lies in the fact that many of them are largely qualitative and hence difficult to describe, and are often subject to variation under different conditions of preservation. An endeavor to develop cephalic indices for the purpose of expressing differences in the shape of the head and to develop a quantitative expression for differences in the thickness of the body produced unsatisfactory results. A further difficulty in the use of such characters is created by the already mentioned ontogenetic variation, necessitating comparison of similar size groups. The available material is inadequate for accurate interspecific and intraspecific comparisons on the basis of similar size groups.

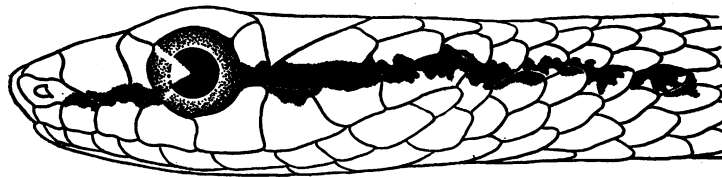
¹ See Reeve and Huxley, 1945, for a discussion of the phenomena related to allometric growth.



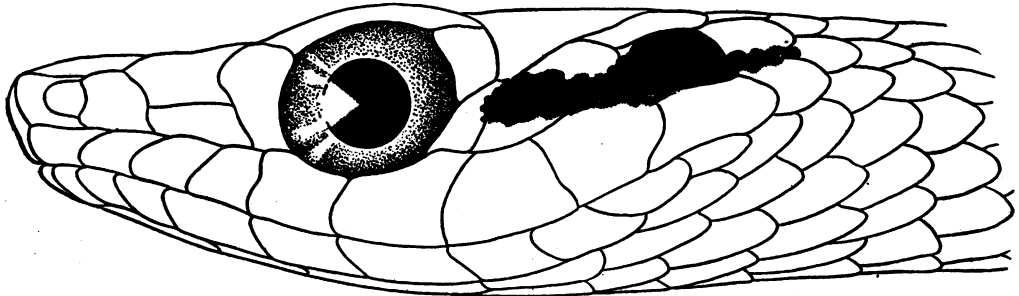
MEXICANUS MEXICANUS



NEBULOSUS

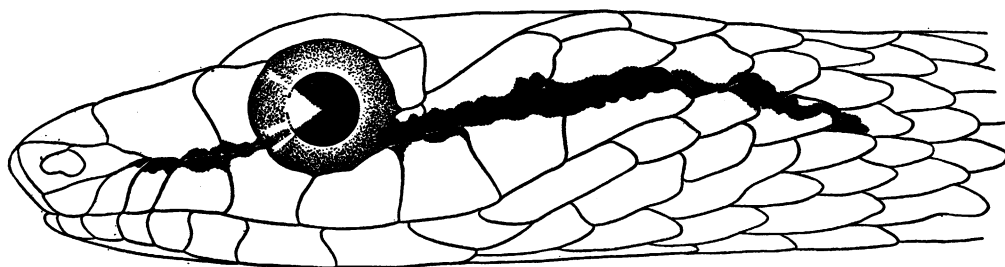


RIVETI

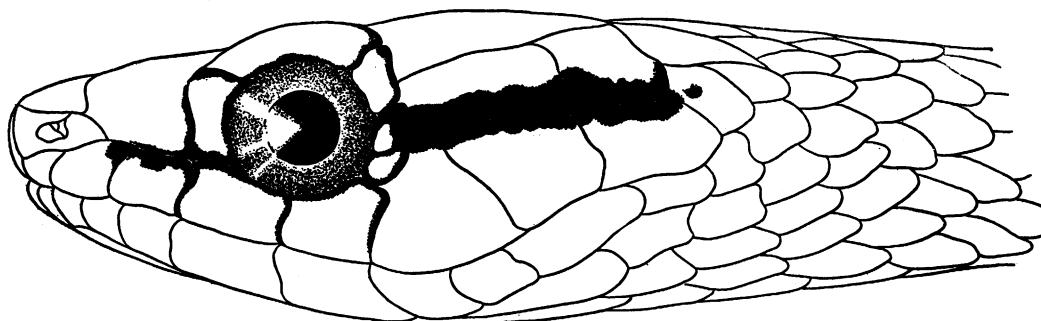


DEPRESSIROSTRIS

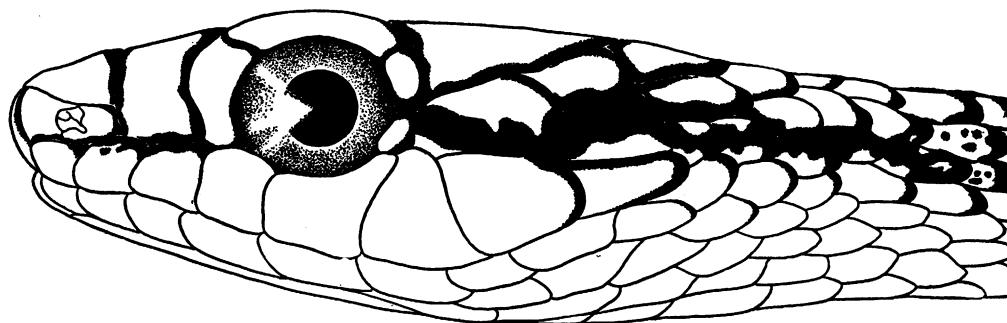
FIG. 4 (THIS PAGE AND OPPOSITE). Lateral view of heads of eight forms of *Thalerophis*, indicating variation in the black ocular stripe and the distribution of black pigment on the head.



RICHARDI RICHARDI



RICHARDI LIOCERCUS



RICHARDI MARGINATUS



RICHARDI NIGROMARGINATUS

COLOR PATTERN¹

Previous workers, in dealing with the members of this genus, have placed all or most of the emphasis on purely morphological structures. Color descriptions have been given when new forms have been proposed, but the color pattern has not been utilized as a diagnostic character. This may be due in part to the marked similarity in color pattern that exists among the elongate arboreal and semi-arboreal snakes of both the Tropical and Neotropical regions. Within the genus *Thalerophis* there is marked variation in the details of the color pattern, with a high degree of intraracial or intraspecific constancy. In many cases the pattern is the most distinct indication of differentiation, whereas a similarity in pattern has occurred in only a few forms that are not closely related on morphological grounds. Further there is a segregation of forms on the basis of the presence or absence of ontogenetic color change.

The pattern characters that have been of most value in the present study have been those of the dorsal body coloration, although others have been used where feasible. On the head, the dark postocular stripe has proved of diagnostic importance in many forms (see fig. 4). In *bocourti*, *bolivianus*, *nigromarginatus*, and *marginatus* the distribution of black pigment on the top and side of the head serves as a useful mark of differentiation (see pls. 18, 19). The pattern on the dorsal surface of the tail could be used in only a few forms.

The adult color patterns may be grouped arbitrarily into three principal categories: a pattern of dark transverse bands, a pattern of longitudinal stripes, or a predominantly unicolored green or greenish blue dorsum. Sharp delimitation of these categories cannot be made because marked minor variations occur, and one type may pass gradually into another.

Only one species, *riveti*, normally exhibits an adult pattern of prominent dark transverse bands on the body and the tail (see fig. 5). At least two predominantly unicolored forms possess minor scale ornamentations

that are arranged in the thin oblique transverse bands. In one of these, *praestans*, the transverse markings are white and are seen most readily when the scales are spread apart, exposing the usually concealed portions of the scales and skin. These marks extend downward and backward from the middorsal line. In the second of these, *nigromarginatus*, the superimposed pattern is of thin oblique black lines formed by black pigment on the posterior tips of the scales. These lines extend downward and forward from the middorsal line.

The species *mexicanus* (fig. 7) and *nebulosus* possess an adult pattern of a pair of dark longitudinal stripes on the body and the tail. The dark stripes are separated by a lighter middorsal area. The subspecies *richardi* has a similar striped adult pattern consisting of a pair of dark stripes separated by a lighter area, although in a few specimens the stripes are not continuous for the entire length of the body. In these three forms the light ventral coloration extends up onto the lower dorsal scale rows I–II, or I–IV.

The third pattern is that of a predominantly uniform dorsal ground color of green or greenish blue. As stated above, minor scale ornamentation may or may not be present, but the appearance is that of a uniform predominant color occupying all of the dorsal rows. Forms placed in this category are *bocourti*, *bolivianus*, *chocoensis*, *depressirostris*, *nigromarginatus*, *occidentalis*, and *praestans*. Black margins on the individual dorsal scales and head plates, as well as black on the keels of the dorsal scales, are frequently present in these forms (text figs. 4, 6; pls. 18, 19). In fact, *bocourti*, *bolivianus*, *chocoensis*, and *nigromarginatus* exhibit the most pronounced melanistic tendencies found in the genus and are characterized in part by the distribution of their black pigment. These forms occur in warm and humid regions, and this melanism is doubtless correlated with the environmental conditions prevailing in such habitats (Hesse, Allee, and Schmidt, 1937, p. 379).

The following forms exhibit various intermediate patterns between the striped and uniform: *coeruleodorsus*, *copei*, *diplotropis*, *liocercus*, *marginatus*, and *ortoni*. In *diplo-*

¹ In the species and subspecies descriptions the colors given in parentheses are from Ridgway, 1912.

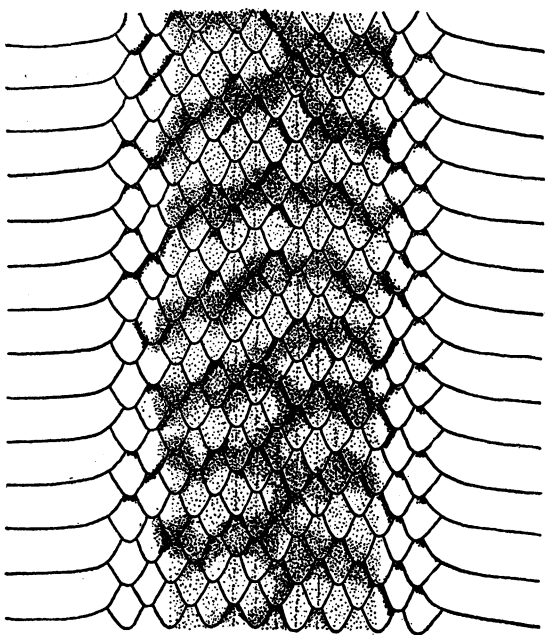
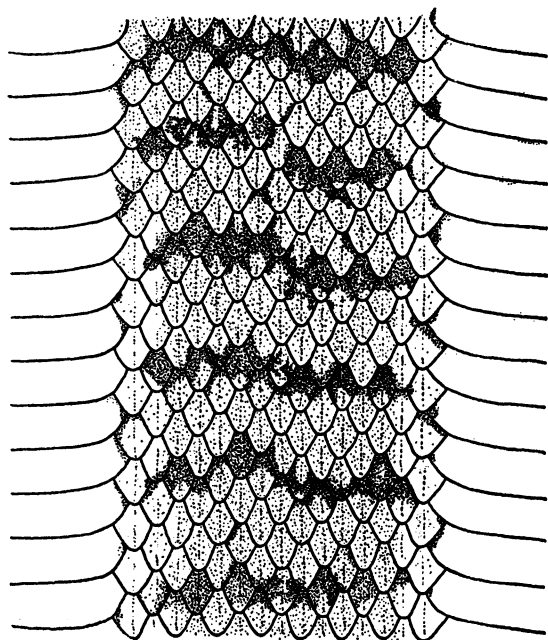


FIG. 5. Midbody pattern of adult *Thalerophis riveti* (upper) and of juvenile *richardi praestans* (lower).

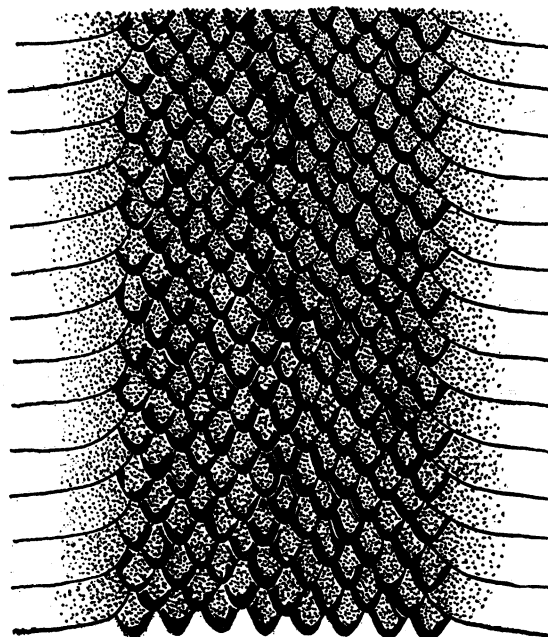
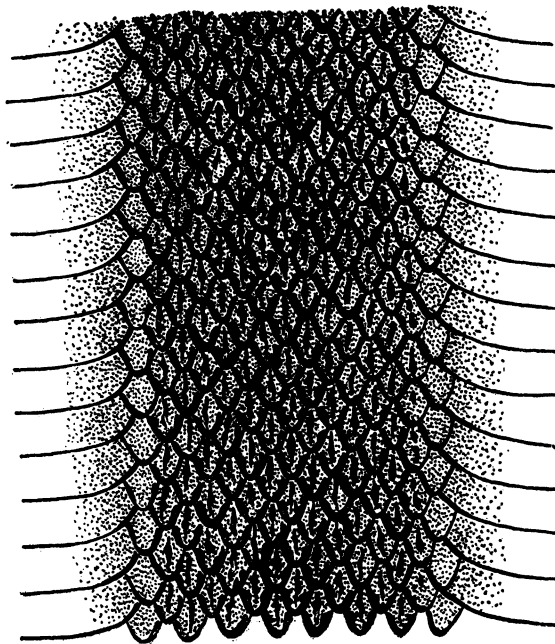


FIG. 6. Midbody pattern of *Thalerophis richardi bolivianus* (upper) and of *richardi nigromarginatus* (lower), illustrating the difference in distribution of black pigment on dorsal scales of body.

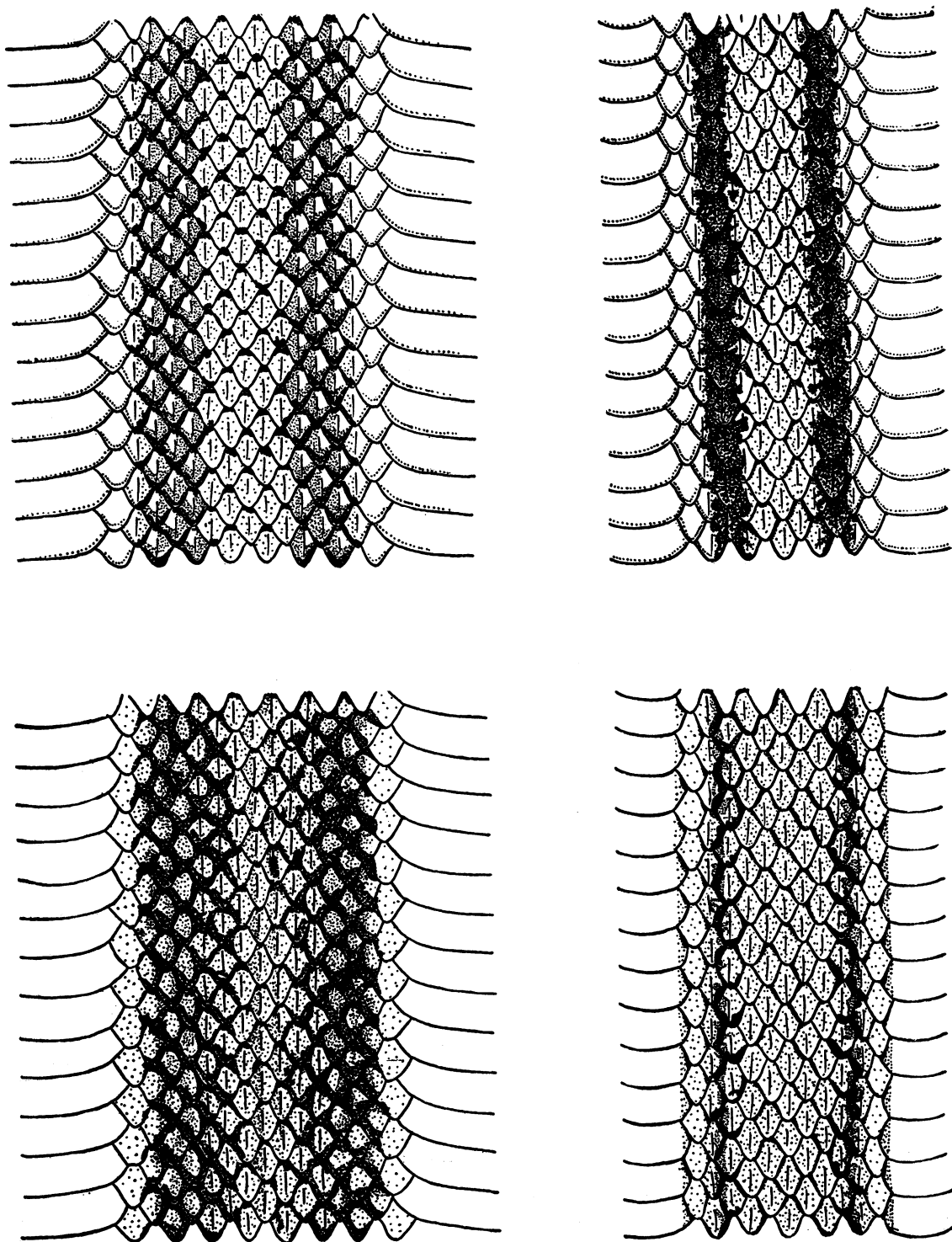


FIG. 7. Anterior (left) and posterior (right) dorsal pattern of *Thalerophis mexicanus yucatanensis* (upper) and of *mexicanus mexicanus* (lower), illustrating differences in the striped pattern of the two subspecies.

tropis the uniformity of the green dorsal color is broken by a light vertebral stripe and a broad black lateral stripe on the anterior fourth of the body. In *copei*, *liocercus*, and *marginatus* the anterior body coloration differs from that on the posterior part of the body. The coloration on the dorsal surface of the head and on the anterior portion of the body is greenish blue; the body coloration does not occupy all of the dorsal scale rows. This coloration usually persists for only a short distance posterior to the head in *liocercus* and *marginatus*, but in *copei* it does not disappear until about midbody. The posterior coloration in these forms is light gray to dark metallic bronze.

In *coeruleodorsus* and *ortoni* the lower rows of dorsal scales on the anterior one-third of the body, rows II-IV, are light colored like the ventrals. The remaining dorsal rows are uniformly colored dark green to greenish blue. In *ortoni* the dorsal coloration occupies relatively the same width on the body for the entire length. In *coeruleodorsus* the dorsal color becomes restricted in distribution posteriorly, forming a single, narrow, dark mid-dorsal stripe on the posterior one-fourth of the body.

In all forms the ventral coloration is uniform, varying from white to a lighter green or greenish blue than the dorsum, without any contrasting pattern except that in some forms the anterior and lateral margins are speckled or marked with dark green or black.

The juveniles exhibit the same pattern as the adults in the species *riveti*, *nebulosus*, *mexicanus*, *diplotropis*, and possibly *depres-*

sirostris. No very young individuals of this latter species have been studied except for the poorly preserved types of Cope's *aeruginosus* in which the color pattern is no longer discernible. Cope (1876, p. 132) indicates no essential difference in this character other than the fact that the juvenile is lighter than the adult. Two subadult females from the Choco of Colombia possess a coloration unlike that of any other specimens of this species examined. They are described in detail in the section on *depressirostris* but are mentioned here because both exhibit narrow, oblique, transverse, black lines when the scales are spread apart. This may be indicative of a banded juvenile pattern. Young have not been examined in all the races of *richardi*, but in every case save one the young have possessed a pattern of oblique dark bands, at least anteriorly (see fig. 5). The single exception is the subspecies *richardi* in which two juveniles possessed a striped pattern like that of the adults, whereas a third juvenile has a pattern of oblique bands superimposed on the striped pattern.

Unfortunately, only a few juveniles have been available for examination, and the state of preservation of these in most cases has been such that the variation in respect to the number of transverse bands could not be determined. Additional data regarding this juvenile pattern might yield information of considerable taxonomic and phylogenetic importance.

No marked sexual dimorphism in coloration has been noted, except that females are occasionally lighter in color than the males.

CHARACTER CLINES

CHARACTER GRADIENTS or, as Huxley (1939) termed them, clines have long been known in zoology and constitute one of the most interesting phenomena of variation. Mayr (1942) has stressed the fact that the observed morphological and pigmentary clines run parallel to climatic gradients with which they are correlated. Ruthven (1908), in his excellent monographic study of the garter snakes, has shown that these gradients may progress in different directions in an independent manner. This important point has been further elaborated by Huxley and Mayr. Numerous clines are indicated in the genus *Thalerophis*, and doubtless additional ones exist that are not apparent now because of inadequate material. Exact knowledge of these clines in *Thalerophis* is not attainable now, but probable causes can be suggested in several instances.

Clinal variation is most readily discernible in *Thalerophis* in the number of ventral plates. The same type of gradient is suggested in the number of subcaudal plates, but because of the more limited data for them, clines are not so clearly indicated as in the ventrals. In reality variation in both of these scales is an expression of variation in the number of vertebrae. In *diplotropis*, *mexicanus*, *richardi occidentalis*, and *richardi praestans* in Central America there is an increase in the average number of ventrals from south to north. This is illustrated for *mexicanus* in figure 3.

The nature of the cline in the number of ventrals suggests a causal relation with thermal factors of the environment. It is a well-known phenomenon in fishes that the number of vertebrae is increased or decreased by development at temperatures above or below the normal temperatures. In most of the studies on fish, an increase in the number of vertebrae is usually observed with a decrease in developmental temperature, but a decrease in the number of vertebrae usually results from high developmental temperatures. In trout an increase in the number of vertebrae has been observed with both high and low temperatures during development. An excellent summary of the recent works treat-

ing this subject can be found in Tåning (1944).

It might appear at first that the increase in the number of ventral plates from south to north in Central America was the result of development in a progressively cooler environment. However, while the average annual temperature and the temperature of the coldest month of the year decreases from south to north the temperature of the hottest month of the year increases. Therefore in the absence of experimental evidence it is impossible to say what the precise causal factor of the environment is. Sufficient data are not available to analyze the difference in ventrals between lowland and upland populations of the same species. In *mexicanus* a green color phase, upon which the name *modesta* was based, has been collected at the maximum altitude recorded for the species. These specimens all possess a number of ventral plates that is above the average for the rest of the species, and in some cases above the maximum observed in the species. These observations lend support to an increase in the number of ventrals with a decrease in environmental temperatures.

Ventral clines in the South American populations are not so readily apparent as in the Central American forms, partly because of the more limited material. There is a cline in the number of ventrals in the populations in the Amazon Valley, with an increase in number of ventrals from west to east or from the upper to the lower Amazon. This trend can be seen by comparing the average number of ventrals for *nigromarginatus*, *ortoni*, and *richardi*.

	<i>nigromarginatus</i>	<i>ortoni</i>	<i>richardi</i>
Ventrals			
Males	152.28 (82)	157.22(9)	162.55(49)
Females	156.91(111)	161.54(13)	164.91(34)

A possible clinal increase from north to south in the Southern Hemisphere is suggested by comparing the average number of ventrals for *nigromarginatus* and *bolivianus*.

	<i>nigromarginatus</i>	<i>bolivianus</i>
Ventrals		
Males	152.28(82)	162.00(8)
Females	156.91(111)	167.70(17)

Another character that exhibits marked clinal variation is coloration. In the Amazon Valley there is a pronounced decrease in the amount and distribution of black pigment from the upper to the lower Amazon. Thus *nigromarginatus*, as its name implies, is heavily ornamented with black pigment (pl. 18; text fig. 4); *ortoni* of the middle Amazon frequently has black borders on the head shields and narrow black borders on many of the dorsal scales; *richardi* (text fig. 4) of the lower Amazon lacks black borders on the head shields and has much reduced, frequently absent, black tips on some of the dorsal scales. This cline is probably related to a progressive change in temperature and humidity, although the exact relationship is not clear. In the hot humid regions of the Colombian Choco and northwestern Ecuador two races of *richardi* occur that are characterized in part by a profuse amount of black ornamentation. These are *bocourti* and *chocoensis*. From these forms through *occidentalis* to *praestans* there is a progressive decrease in the amount of black pigment on the head and body, from south to north. This cline also seems to be correlated with a change in temperature and humidity. The increase in black pigment seems most pronounced in those forms occurring in the warmer and more humid areas occupied by the genus, and this increase is doubtless due to the environmental conditions that prevail in such habitats (Hesse, Allee, and Schmidt, 1937).

A number of other clines are apparent in coloration within the genus but are less easily assessed. For example, there is a gradual change in the Amazon Valley from west to east, parallel to the cline in black pigmentation, from a nearly uniform coloration to a pattern of dark blue lateral stripes such as is characteristic of *richardi*.

Gradients in size and proportion most certainly exist in the genus, but the data are

too limited for them to be defined. Clines in the number of maxillary teeth are apparent in *diplotropis* where the number of teeth decreases from south to north, and in *occidentalis* and *praestans* that increase the number of maxillary teeth from south to north. No possible correlation between these gradients and climatic factors is now apparent. The data on food habits are inadequate for the relation between diet and number of maxillary teeth to be analyzed.

Clinal trends are also apparent in regard to the number of labials in some forms. For example, in the Amazon Valley from west to east there is a progressive increase in the number of specimens with nine upper labials as compared with eight upper labials. This is seen by comparing the percentages of each in the populations of *nigromarginatus*, *ortoni*, and *richardi*.

	<i>nigro-</i> <i>marginatus</i>	<i>ortoni</i>	<i>richardi</i>
Per cent of specimens with 8 upper labials	32.1	25.8	12.0
Per cent of specimens with 9 upper labials	44.9	64.5	75.9

There appears to be no readily discernible correlation between the number of upper labials and climatic factors. This variation is not related to a similar change in the number of maxillary teeth, for all three have nearly identical average numbers of maxillary teeth.

Numerous other character clines doubtless exist in the genus and can be clearly analyzed when more material is available. When adequate material is at hand, most characters appear to exhibit clinal variation. The above examples are by no means all of the characters that exhibit clines, but they serve to illustrate the types and the direction of the gradients that have been studied.

COMPOSITION OF THE GENUS AND IDENTIFICATION OF SPECIES AND SUBSPECIES

FROM AN ANALYSIS of the available populations in relation to their characters and their geographic distribution, 18 forms, comprising six species, are here recognized. These are readily separable into two groups on the basis of the presence or absence of the loreal plate. At one time those forms possessing a loreal were placed in a separate genus from those without a loreal (Cope, 1886, 1887). Such a separation does not provide a satisfactory grouping when viewed in the light of other characters.

The three species that possess a loreal plate are *depressirostris*, *diplotropis*, and *mexicanus*. It has already been noted that *mexicanus* and *diplotropis* differ from all the other forms of the genus in possessing two strongly enlarged posterior maxillary teeth. Likewise these two forms differ from the rest of the genus in the point of reduction of the dorsal scales on the tail. From *depressirostris* they differ in having fewer maxillary teeth, fewer upper labials, more ventrals, and structural differences in the skull.

In two morphological attributes *diplotropis* resembles *depressirostris* more closely than *mexicanus*. Both species have keels only on the scales of the paravertebral rows, and in regard to the hemipenial structure, although differences are apparent, *diplotropis* and *depressirostris* are more similar than either is to *mexicanus*. On the basis of other characters the three forms that possess a loreal plate are not closely related, and any grouping based on this character alone does not provide a "natural" assemblage of species and scarcely warrants further consideration.

The six species of the genus can be separated into groups on the basis of a number of single attributes other than the presence or absence of a loreal, but no separation provides compact compartmentalization of the genus into satisfactory subgeneric groups. Too little is known of the life histories of the species to formulate groups on the basis of behavioral or physiological traits. Separation on the basis of known geographical distribution is not satisfactory, although it probably

provides the best method of combining the species into subgeneric groups: the predominantly Central American species *depressirostris*, *diplotropis*, *mexicanus*, and *nebulosus*, and the predominantly South American *richardi* and *riveti*. In this arrangement *depressirostris* and *riveti* provide a broad overlapping of the two groups.

On the basis of evolutionary plasticity or genetic variability *richardi* is clearly set off from the other species in the genus as a more widely distributed, more variable, probably younger, and apparently more progressive species than the rest of the genus. The remaining species seem to be more stable, less widely distributed, more conservative, probably older, and of more uncertain relationships than *richardi*. Thus while the members of the genus *Thalerophis* are not readily separable into subgeneric groups on the basis of morphological or geographical characters, the species differ in the stage of the evolutionary development that they have attained and in their genetic plasticity.

Provision for the identification of specimens is a desirable by-product of taxonomic or systematic studies. The construction of keys to serve this function is often a difficult task because of the nature of the material treated and the concern with populations rather than individuals. The utilization of "key characters" may produce a distorted concept of the relations of the various entities treated.

The keys that appear below will permit 96 per cent of the specimens studied to be allocated to their respective species, and approximately 90 per cent of the adults can be correctly assigned to the subspecies to which they belong. In the case of poorly preserved specimens, these keys may be of little value. Specimens that cannot be allocated satisfactorily through the use of the keys can be identified only by a careful comparison with the specific and subspecific descriptions of forms occurring in their general geographic province. In the identification of any member of the genus, it must be remembered that the

geographic locality from which the snake was collected is an important datum pertaining to the diagnosis of each form.

KEY 1. KEY TO THE SPECIES OF *Thalerophis*

1. Loreal present 2
Loreal absent 4
2. Keels present on scales of all rows of dorsal scales on body except outer row; distinct keels on dorsal scales on tail for most of length *mexicanus* (see Key 2)
Keels present only on scales of paravertebral rows on body, occasionally low keels on adjacent lower row also; no keels on dorsal scales on tail 3
3. Ventrals 144 to 158; maxillary teeth 33 to 36; last 3 or 4 enlarged (see fig. 1G); upper labials 9 in number *depressirostris*
Ventrals 167 to 184; maxillary teeth 17 to 21, last 2 enlarged (see fig. 1H); upper labials 8 in number *diplotropis*
4. Ventrals 133 to 149, adults with a color pattern of dark oblique bands (see fig. 5); keels present on the scales of all dorsal rows *riveti*
Ventrals usually more than 149, adults not with a color pattern of dark oblique bands; no keels on scales of first row of dorsals 5
5. Adult color pattern consisting of a broad greenish blue or blue dorsolateral stripe anteriorly on rows III-IV or III-V; Central America *nebulosus*
Adult color pattern not as above; if greenish blue or dark blue dorsolateral stripe is present anteriorly it covers more than rows III-V; Central and South America, but striped forms only in latter *richardi* (see Key 3)

KEY 2. KEY TO THE SUBSPECIES OF *mexicanus*

1. Lateral dark stripe on posterior third of body normally occupying upper edge of scales in row II, all of scales in row III, and lower edge of scales in row IV (see fig. 7); ventrals in males 164-172, average 168, in females 165-174, average 169.22 *mexicanus yucatanensis*
Lateral dark stripe on posterior third of body normally occupying only upper edge of scales of row II and lower edge of scales in row III (see fig. 7); ventrals in males 148-169, average 157.30, in females 154-174, average 161.15 *mexicanus mexicanus*

KEY 3. KEY TO THE SUBSPECIES OF *richardi*

1. Adult color pattern consisting of a broad greenish blue or dark blue dorsolateral stripe anteriorly on scales of rows III-VII, separated by a light vertebral stripe on scales of row VIII. *richardi richardi*
Adult pattern not of two dark dorsolateral stripes separated by a light vertebral stripe 2
2. Adult color pattern of a predominantly uniform greenish blue occupying scales of all dorsal rows 3
Adult color pattern not as above or, if of a predominantly uniform greenish blue, not occupying scales of all dorsal rows 8
3. No black postocular stripe; dorsal body pattern with narrow, white, chevron-shaped, transverse bands that may not be apparent until dorsal scales have been spread apart. *richardi praestans*
Black postocular stripe present; dorsal body pattern without narrow, white, chevron-shaped bands 4
4. Black postocular stripe very broad, occupying all or nearly all of anterior temporal and lower posterior temporal; heavy, irregularly defined black marks on keels of scales on median dorsal rows *richardi chocoensis*
Black postocular stripe narrow, occupying only lower edges of anterior temporal and lower posterior temporal; if black marks are present on keels of dorsal scales, marks are narrow and well defined 5
5. Head plates rarely margined with black; if narrow black margin is present, head plates are never marked with numerous small black spots or with a prominent large black spot on each parietal and supraocular shield *richardi occidentalis*
Head plates margined with black and with numerous small black spots or with a prominent large black spot on each parietal and supraocular plate 6
6. Head plates and dorsal scales with numerous small, irregularly shaped black spots, also present on extreme outer edge of ventrals anteriorly (see pl. 19) *richardi bocourti*
Head plates and dorsal scales not marked as above, but with a prominent large spot on each parietal and supraocular plate (see pl. 18) 7
7. Dorsal scales without, or with only a narrow black margin, but with a distinct narrow black line along the keel of each dorsal

- scale (see fig. 6); ventrals in males 156–169, average 162.00, in females 162–173, average 167.70 . . . *richardi bolivianus*
- Dorsal scales with heavy prominent black margins, no black on keels (see fig. 6); ventrals in males 147–165, average 152.28, in females 150–166, average 156.91
 *richardi nigromarginatus*
8. Ventrals more than 172. . . . *richardi copei*
 Ventrals fewer than 172 9
9. Dorsal coloration of head and anterior body region persisting throughout length of body although sometimes reduced in distribution; north and central South America 10
- Dorsal coloration of head and anterior body distinctly different from that of posterior half of body; southern South America. 11
10. Dorsal coloration on body occupies proportionately the same width throughout entire body length; ventral plates margined anteriorly and laterally with dark greenish blue; maxillary teeth 24–28, average 25.9 *richardi ortonii*
- Dorsal coloration on body reduced in distribution posteriorly; ventrals not margined; maxillary teeth 21–23, average 22.2 *richardi coeruleodorsus*
11. Plates on top of head heavily margined with black, postparietal scales 5–8, average 6.07; temporals frequently 1-1
 *richardi marginatus*
- Plates on top of head not or but slightly margined with black; postparietal scales 7–11, average 8.62; temporals typically 1-2 *richardi liocercus*

SPECIES ACCOUNTS

Thalerophis depressirostris Cope

Philothamnus depressirostris COPE, 1860, Proc. Acad. Nat. Sci. Philadelphia, vol. 12, p. 557; Cocuyas de Veraguas, New Grenada.

Diplotropis bilineata GÜNTHER, 1872, Ann. Mag. Nat. Hist., ser. 4, vol. 9, p. 24; Costa Rica.

Leptophis aeruginosus COPE, 1876, Jour. Acad. Nat. Sci. Philadelphia, vol. 8, art. 4, p. 132; Costa Rica.

Leptophis saturatus COPE, 1876, *ibid.*, vol. 8, art. 4, p. 133; Sipurio, Costa Rica.

Hapsidophrys saturatus COPE, 1886, Proc. Amer. Phil. Soc., vol. 23, p. 271.

Leptophis mexicanus SCHMIDT, 1933, Smithsonian Misc. Coll., vol. 89, no. 1, p. 16.

Leptophis depressirostris GAIGE, HARTWEG, AND STUART, 1937, Occas. Papers Mus. Zool. Univ. Michigan, no. 357, p. 14.

TYPE LOCALITY: Cocuyas de Veraguas, New Grenada (=Cocuyas de Veraguas, Panama).

RANGE: From Nicaragua south in the Caribbean drainage to Panama, the Choco region of Colombia south to northwestern Ecuador, (?) and northern Peru. Except for the questionable Peruvian locality, this species is known at present in South America only from the Pacific drainage of the northwestern portion of the country (fig. 8).

DESCRIPTION: The maxillary teeth number 33–36; the average for 23 counts is 34.9. The last three teeth are strongly enlarged and the fourth from the posterior end is usually partly enlarged, representing an intermediate condition (fig. 1); occasionally this fourth posterior tooth is equally enlarged in comparison with the last three. The hemipenis is six subcaudals long, with no enlarged basal spines; six to seven transverse rows of small spines occur opposite the posterior half of subcaudal 2 and all of subcaudal 3; the spines pass gradually into calyces with long spinous papillae that obscure the structure of the calyces. The papillae decrease in length and spinosity distally while becoming increasingly fleshy; the tip of the organ, opposite the posterior half of subcaudal 5 and all of subcaudal 6, is covered with calyces with short, fleshy papillae (see pl. 16).

Keels are present only on the scales of rows VII and IX anteriorly; they are much

reduced in the anal region and disappear completely at the point of reduction in the number of dorsal scales on the tail from six to four rows. The transverse rows of dorsal scales are arranged in markedly oblique rows on the anterior third of the body; the scales of rows III–V, occasionally row VI, are smaller than those of the remaining rows.

Reduction in the number of dorsal scales on the body involving rows V–VI occurs opposite ventrals 85–96, average 90.25, in the males; 85–103, average 94.75, in the females. That involving rows II–III, or occasionally III–IV, occurs opposite ventrals 88–97, average 92.55, in the males; 89–106, average 94.79, in the females. The reduction in the number of dorsal scale rows on the tail from six to four rows takes place opposite subcaudals 4–14, average 8.25, in the males; 4–16, average 9.68, in the females.

The ventral plates in the males vary from 144 to 157, average 150.47; in the females from 145 to 158, average 150.33. Two males have complete tails with subcaudal counts of 163 and 169. Two additional males possess tails that have been injured near the tip; these have subcaudal counts of 167+ and 169+. Five female specimens with complete tails have 158–170 subcaudals, with an average of 163.00. A single male from Nicaragua has an undivided anal plate; all other specimens have a completely divided anal plate.

The upper labials usually are nine in number, and the majority of specimens have 10 lower labials. All specimens examined possessed a loreal plate on both sides of the head with the exception of one female that lacked this plate on one side of the head. All have one preocular on both sides of the head and, except for two individuals, two postoculars on each side of the head. The two variants possessed only one postocular on each side of the head. The lower postocular is usually equal to, or larger than, the upper postocular. The preocular is not in contact with the frontal. The parietal is slightly longer than broad and in contact with the lower postocular; the parietal may be truncate or acuminate posteriorly and may or may not be notched by the upper posterior temporal.

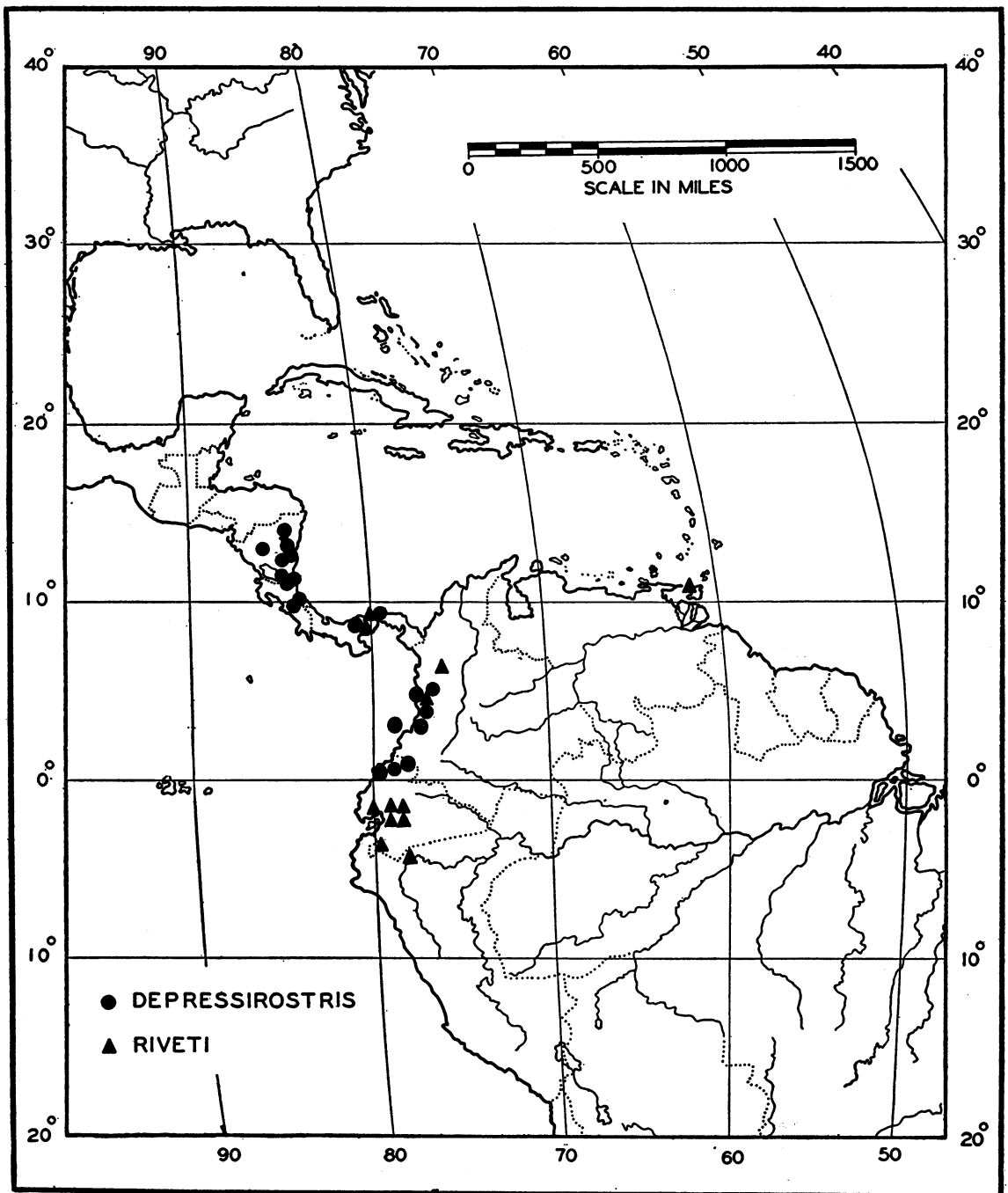
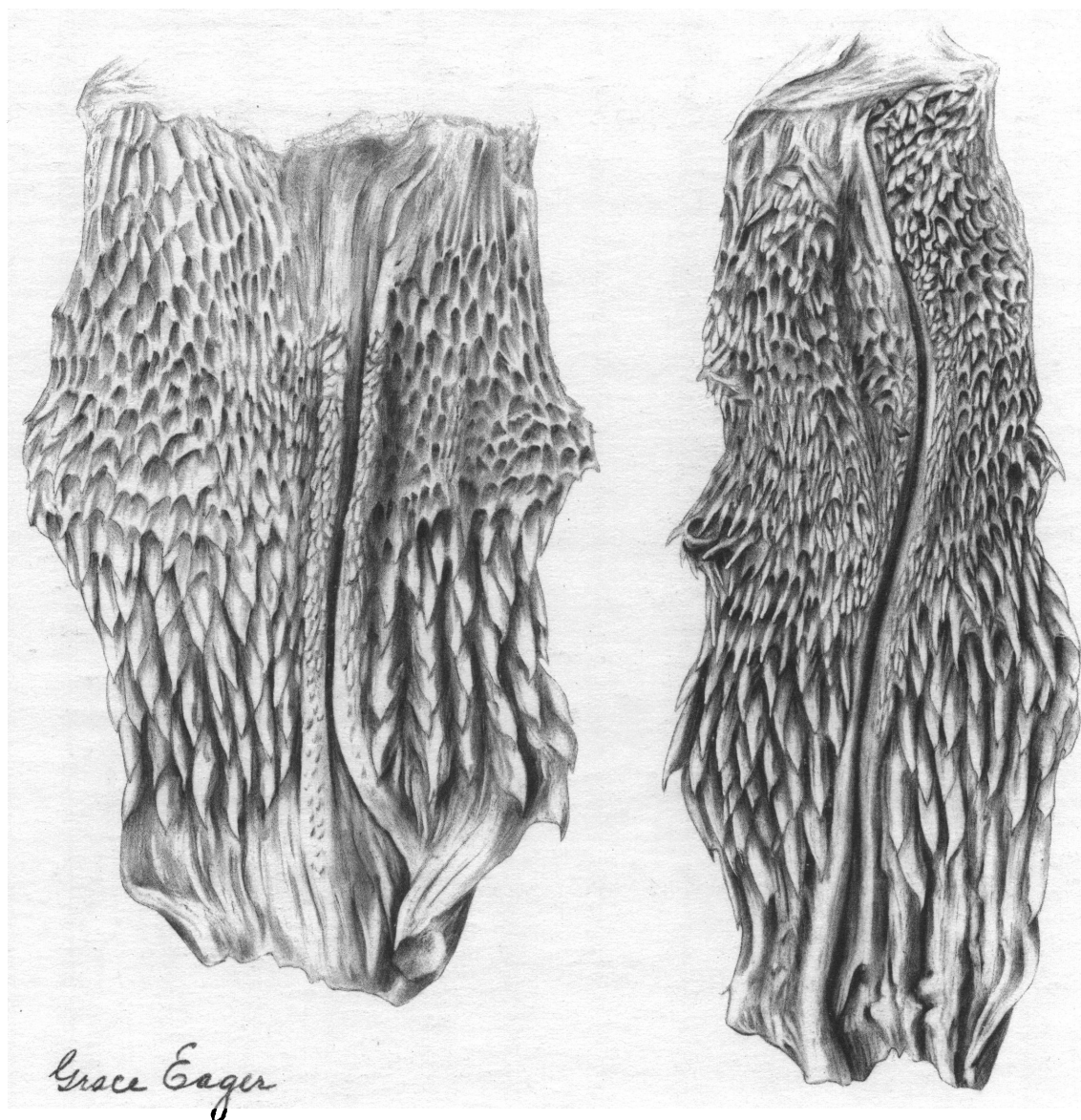


FIG. 8. Distribution of *Thalerophis depressirostris* and *riveti* based on the locality data of the specimens examined.



Grace Eager

Hemipenes of *Thalerophis riveti* (left) and *depressirostris* (right). Drawn from the organs in the retracted position, slit down the dorsal aspect and laid open. Note the absence of enlarged basal spines



Hemipenes of *Thalerophis riveti* (left) and *depressirostris* (right). Drawn from the organs in the retracted position, slit down the dorsal aspect and laid open. Note the absence of enlarged basal spines

The length of the frontal is greater than that of the interparietal suture. All but three individuals have one anterior and two posterior temporals on both sides of the head. The eye is large, with the diameter greater than the distance from its anterior border to the posterior tip of the nostril.

The largest male examined has a head-body length of 835 mm., plus a tail length of 550+ mm.; the largest female had a head-body length of 827+ mm., plus a tail length of 405+ mm. Two males with entire tails have tail/body ratios of .72 and .75; five females have tail/body ratios of .66-.75, with an average of .718.

The coloration (in alcohol) is: top of head dark blue (Dark Orient Blue) to dark greenish blue (Sea Green); a black postocular stripe on lower postocular, anterior temporal, lower posterior temporal, and upper edges of last two upper labials; this stripe disappears one to three scales posterior to last upper labials. Upper labials light greenish blue (Pale Nile Blue) to dirty white; those directly under eye lightest in color.

Dorsal surface of body and tail dark blue (Dark Orient Blue) to dark greenish blue (Sea Green), outer row or outer two rows lightest in color. Chin white; ventrals bluish white or light greenish blue (Pale Nile Blue) with posterior margin narrowly bordered, at least laterally, by greenish blue dorsal coloring. Under side of tail anteriorly colored like ventrals, becoming darker posteriorly. Keels on scales of paravertebral rows black, forming two narrow longitudinal black lines.

VARIATION: Considerable variation exists in respect to the prominence of the keels on the scales of the paravertebral rows. The observed variation appears to lack any geographical correlation but exhibits a pronounced correlation with sex and ontogeny. In juvenile and immature specimens the keels are difficult to discern or may be absent entirely. The females have the keels less well developed than the males, and occasionally require close examination for their presence to be determined. In all adult specimens that I have examined keels were present on the scales of the paravertebral rows at least on the posterior one-fourth of the body. I have been unable to determine definitely the pres-

ence of keels on a poorly preserved juvenile with a head-body length of less than 300 mm. In regard to the upper labials, 29 specimens have 9/9, two have 8/8, and one each has 7/9, 8/9, and 9/10. Nineteen have 10/10 lower labials, seven have the lower labials 10/11, four have 9/10, and one each has 9/9 and 11/11.

The most pronounced variation observed is in the coloration of individuals from the Choco region of Colombia. Boulenger (1913, p. 1034) has described this variation, under the name *Leptophis bilineatus* Günther, as follows: "a metallic bronze on the back and sides, the head dark green, the sides of the neck green, the lower parts pale green." The interesting feature of this variation is the metallic bronze appearance on the dorsal surface of the posterior two-thirds to three-fourths of the body and tail. The individual dorsal scales have a dark blue, occasionally black, anterior and ventral border, whereas the posterior-dorsal portion of the scale (approximately one-third of the total area) is of a metallic bronze color. The extent of the bronze coloration increases posteriorly. Under normal circumstances the darker portion of the scale is concealed, so that the appearance is that of a nearly uniform color. When the scales are spread apart, exposing the concealed surface of the scales, a pattern of narrow, dark, oblique bands somewhat like that of *riveti* is apparent. This variation has been observed in two specimens among 11 studied from the Choco, both females, and in a single adult female from northwestern Ecuador.

Some variation has been observed also in respect to the black postocular stripe. The stripe may extend from anterior to the orbit through the eye and posteriorly onto the neck as a sharply defined black streak, or it may be reduced to irregular, elongate black spots on the anterior and lower posterior temporals. Too few specimens are available for this variation to be properly evaluated.

REMARKS: The type of Cope's *depressirostris* is an adult female with a head-body length of 681 mm. In Cope's original description the dorsal scales are described as smooth. Examination of the type reveals that keels are present on the scales of the paravertebral

rows. In 1876 Cope again described a member of this species as possessing smooth dorsal scales. On this occasion he proposed the names *aeruginosus*. The type of this species is a juvenile. At present it is in such a poor state of preservation that little diagnostic data can be obtained from it. Except for the reputedly smooth scales, Cope's description indicates that *aeruginosus* is conspecific with *depressirostris*. In the same publication in which he described *aeruginosus*, Cope proposed another species in the same genus, *saturatus*. The type of this proposed species is an adult female of which Cope states in the description, "one [scale row] on each side of the median vertebral, weakly keeled." Farther on in the same account he says of *saturatus*, "The wide and depressed head as well as the smooth scales and color, distinguished this species from the *L. mexicanus* D. & B." The type has keels on the scales of the paravertebral rows, and the species is clearly conspecific with *depressirostris*.

Günther's *bilineata* is based on an adult specimen from Costa Rica. The type is extant in the collections of the British Museum (Natural History) but has not been examined by me. Günther's detailed description leaves no doubt as to the status of this name. It is curious that these synonyms of *depressirostris* should all be based on specimens from Costa Rica. Actually the names are the result of sexual and ontogenetic differences in the development of the dorsal keels, in the proportions of the head, and perhaps in coloration.

The relationships of *depressirostris* are not readily discernible. It seems scarcely more closely related to one species than to another. In the total of its structural attributes it is one of the most generalized members of the genus. In geographic distribution its range broadly overlaps that of another generalized species, *riveti*, although there is some indication that the two species are separated ecologically.

The two species *riveti* and *depressirostris* have a number of similar structural attributes. Both have a relatively high number of maxillary teeth, a relatively low number of ventrals, similar generalized hemipenial structures, and similar tail/body ratios. De-

spite these similarities several prominent morphological differences are readily noticed: *depressirostris* possesses a loreal, *riveti* lacks this plate; *depressirostris* has keels on only the scales of the paravertebral rows and none on the tail, *riveti* has keels on the scales of all dorsal rows and well-developed keels on the tail; *depressirostris* normally has nine upper labials, *riveti* has eight; and *depressirostris* is uniformly colored with a narrow black longitudinal stripe on either side of the paravertebral rows, while *riveti* has a conspicuous pattern of dark oblique bands.

In 1929 Amaral suggested that *depressirostris* and *diplotropis*, along with several other forms, should be referred to the synonymy of *mexicanus* which appeared to be subdivided into several races. This species *diplotropis* has a marked superficial similarity to *depressirostris*. This resemblance is due primarily to the fact that both possess a loreal shield and prominent keels on the scales of the paravertebral rows, and that only those two rows are normally keeled. There is, in addition, a general similarity in coloration, although minor differences are readily apparent. The resemblance between these two is only superficial, and pronounced differences exist in the dentition (see fig. 1G and H), the hemipenial structures, the number of ventral and subcaudal plates, the number of upper labials, the point of reduction in the number of transverse rows of dorsal scales on the body and on the tail, and the tail/body ratio. Most of the differences that are noted between *diplotropis* and *depressirostris* exist between the latter and *mexicanus*.

Geographically *diplotropis* and *depressirostris* are separated by a wide area from southern Mexico to northern Nicaragua. Whereas *diplotropis* is an inhabitant of the scrub forests of the semi-arid Pacific coastal area in Mexico, *depressirostris* typically occurs in the hot and humid lowland forests of lower Central America and northwestern South America. In the latter region *depressirostris* occurs in the wettest area of the Western Hemisphere, the Choco of Colombia. The ranges of *mexicanus* and *depressirostris* overlap geographically in Nicaragua and Costa Rica. Whether the two species are ecologically segregated in that area cannot be stated with authority, although inferences

drawn from other regions indicate that they are.

At the present time the precise relationship of *depressirostris* cannot be indicated. It appears to occupy a position close to the ancestral stock from which the genus has been derived and to lie between *riveti* on one hand and *diplotropis-mexicanus* on the other. It is probably more closely related to the former than to the latter two species.

The distribution of *depressirostris* follows a well-known zoogeographic pattern in lower Central America and northern South America (Dunn, 1940). In this distribution the faunal elements of the tropical rain forest of the Atlantic slope of Central America cross over in Panama and continue along the hot and exceedingly wet Choco region of Colombia to northwestern Ecuador. The faunal elements of the drier Pacific slope of Central America also cross over and continue into northern Colombia and Venezuela along the Atlantic slope. This pattern has been noted by zoogeographers for many groups of animals and has been especially well demonstrated in birds (Chapman, 1917, 1926).

SPECIMENS EXAMINED (34)

COLOMBIA. Choco: Andagoya, M.C.Z. Nos. 32729, 32730; Pena Lisa (=Penalisa), B.M.N.H. Nos. 1913.11.12.43-1913.11.12.45; Pizarro, C.N.H.M. No. 43736; Rio San Juan, U.S.N.M. Nos. 72350, 73299. El Valle: Buenaventura, B.M.N.H. No. 95.11.16.21. Narino: Gorgona Island, A.M.N.H. No. 63565, B.M.N.H. No. 1927.9.2.4.

COSTA RICA. La Castilla, A.N.S.P. No. 22362; San Jose, U.S.N.M. No. 11266; "Costa Rica," U.S.N.M. No. 32563 (type of *saturatus* Cope).

ECUADOR. Charchi: Paramba, B.M.N.H. No. 1901.3.29.107. Esmeraldas: Pambelar, A.M.N.H. Nos. 13583, 13584; St. Javier, B.M.N.H. No. 1901.3.29.39.

NICARAGUA. Cupitna Camp, A.M.N.H. Nos. 12659-12661; Eden Mine, A.N.S.P. No. 22798; Greytown, U.S.N.M. No. 19743; Machuca, A.N.S.P. No. 5287; Matagalpa, M.C.Z. No. 9586; Rama, Rio Sigüia, U.M.M.Z. Nos. 79782, 79783; Recero, Rio Mico, U.M.M.Z., No. 79781; "Nicaragua," U.S.N.M. No. 14216.

PANAMA. Cocuyas de Veraguas (=Veraguas), A.N.S.P. No. 5207 (type); Colon, M.C.Z. No. 4809; Porto Bello, U.S.N.M. Nos. 54082, 54083.

(?) PERU. Junin: Chanchamayo, B.M.N.H. No. 1915.3.9.3.

Thalerophis diplotropis Günther

Ahaetulla diplotropis GÜNTHER, 1872, Ann. Mag. Nat. Hist., ser. 4, vol. 9, p. 25; Tehuantepec, Mexico.

Leptophis diplotropis (sic) SUMICHRIST, 1882, La Naturaleza, vol. 5, p. 286.

Hapsidophrys diplotropis COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 69.

Leptophis diplotropis var. *aeneus* BOCOURT, 1897, in Duméril, Bocourt, and Mocquard, Mission scientifique au Mexique et dans l'Amerique Centrale, Etude sur les reptiles, p. 837; Mexico.

Diplotropis diplotropis STEJNEGER, 1899, North American Fauna, no. 14, p. 63.

Leptophis diplotropis forreri SMITH, 1943, Proc. U. S. Natl. Mus., vol. 93, p. 443; Tres Marias Islands.

TYPE LOCALITY: Tehuantepec, Oaxaca, Mexico.

RANGE: From southwestern Chihuahua and southern Sonora south along the Pacific slope to southeastern Oaxaca, Mexico (fig. 9). The Tres Marias Islands.

DESCRIPTION: The maxillary teeth are 17-21; the average for 19 counts is 18.5. The last two maxillary teeth are strongly enlarged (fig. 1H). The hemipenis is eight to nine subcaudals long; the base of the organ opposite subcaudals 1 and 2 is bare except for numerous tiny spines opposite subcaudals 2; there are no enlarged basal spines, although the eight spines of the proximal row are larger than the remaining spines. There are five to six transverse rows of small spines opposite subcaudals 3 and 4, and the anterior third of subcaudal 5; these pass immediately (opposite subcaudal 5) into calyces with fringing papillae that nearly obscure the structure of the calyces. The papillae are relatively long proximally but not spinous; they decrease in length distally, leaving the distal third of the organ typically calyculate. In a specimen with the hemipenis fully everted the proximal one-fourth of the organ is bare or covered only with minute spines; this is followed distally by five to six transverse rows of spines occupying one-fourth of the total length; the distal half is calyculate with the proximal calyces bearing long fringing papillae.

Keels are present only on the scales of the paravertebral rows, although rarely a male specimen may possess an occasional low keel on the scales of rows VI and X. The keels disappear in the vicinity of the anal region. The

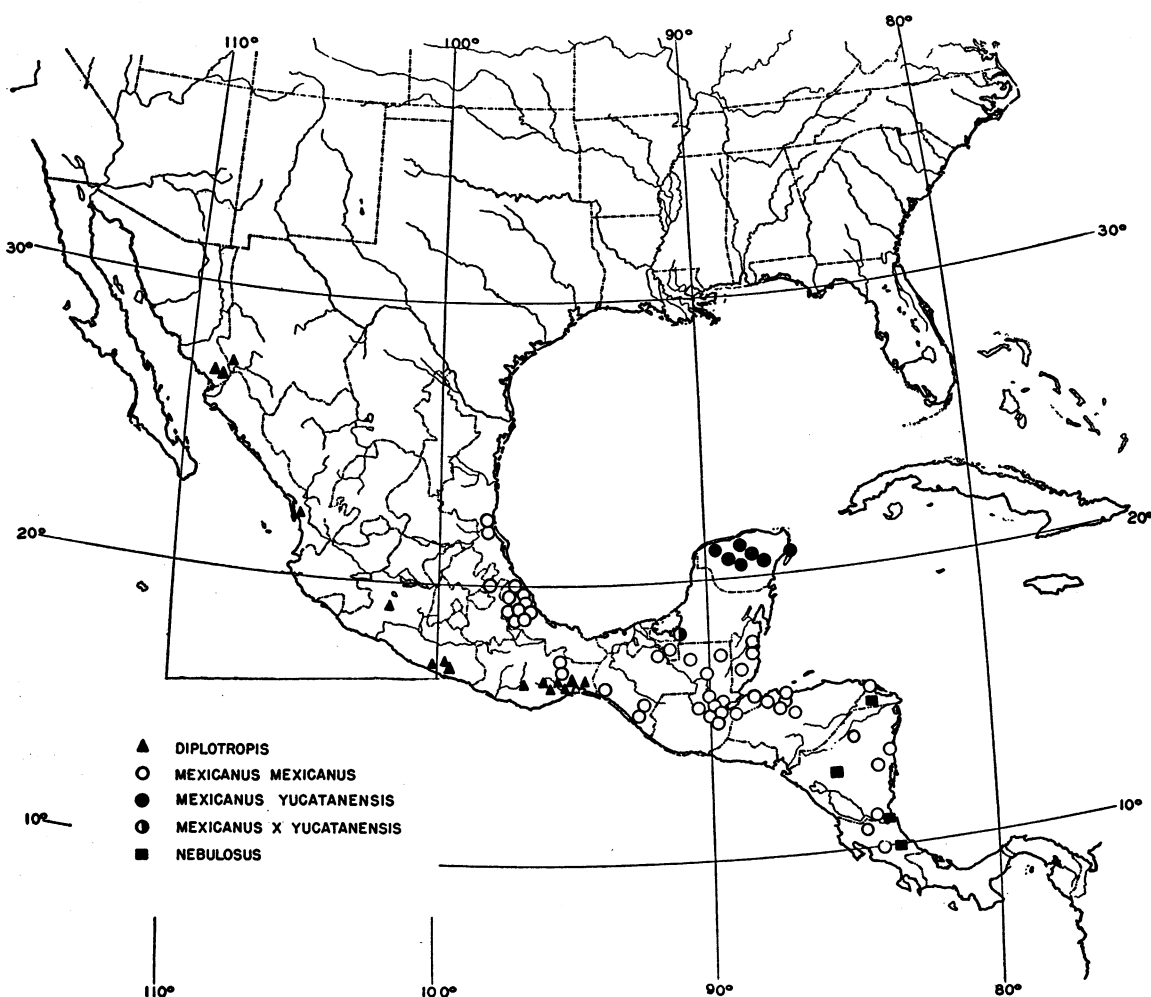


FIG. 9. Distribution of *Thalerophis diplotropis*, *mexicanus*, and *nebulosus* based on the locality data of the specimens examined.

scales of the vertebral row are slightly enlarged.

The reduction in the number of rows of dorsal scales on the body, involving rows V–VI, takes place opposite ventrals 94–111, average 102.35, in the males; opposite ventrals 102–112, average 105.50, in the females. That involving rows III–IV takes place opposite ventrals 95–110, average 103.52, in the males; opposite ventrals 98–114, average 106.45, in the females. The reduction of the dorsal scales on the tail from six to four rows occurs opposite subcaudals 13–38, average 21.60, in the males; 11–38, average 22.81, in the females.

The ventral plates number 167–184, average 174.44, in the males; 172–184, average 178.04, in the females. The subcaudals are 138–161, average 148.93, in the males; 135–150, average 142.09, in the females. Two males have been examined with partly divided anal plates; all others have the anal plate completely divided.

The upper labials are normally eight and the lower labials are normally 10. All specimens possess a loreal plate on both sides of the head except a female that lacks this plate on one side of the head. All specimens have one preocular and two postoculars on both sides of the head. The lower postocular is

equal in size to the upper. The preocular is not in contact with the frontal. The parietal is longer than broad, truncate posteriorly, and not, or but slightly, notched by the upper posterior temporal. The parietal is usually in contact with the lower postocular. The length of the frontal is equal to, or slightly less than, the length of the interparietal suture. The temporals are normally 1-2. The eye is moderately small; its diameter is less than the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 897 mm., plus a tail length of 512 mm.; the largest female had a head-body length of 731 mm., plus a tail length of 368 mm. The tail/body ratio observed in the males is .53-.60, average .555; in the females .47-.49, average .540.

The coloration in alcohol is: top of head bluish-slate (Greenish Glaucon Blue to Parula Blue), a black ocular stripe commences on lower edge of nasal plate, passes posteriorly along upper edge of first four upper labials, lower edge of loreal, and lower edge of preocular. Posterior to orbit this stripe widens out, covering all of lower postocular, lower edge of upper postocular, and lower edge of parietal, lower half of anterior temporal, lower half to two-thirds of lower posterior temporal, and upper edges of last four upper labials.

This stripe continues onto body anteriorly on rows III-VII; at a point opposite ventral 18-23 stripe breaks up, forming short oblique black bands one and a quarter to two scales wide and separated from one another by one scale row; bands persist for distance approximately equal to that of uninterrupted black stripe and gradually disappear as black color is reduced in distribution. Scales of rows III-VII between oblique black bands have white anteroventral spot, while remainder of scale is blue (Parula Blue). At midbody black has all disappeared but white anteroventral

spots continue posteriorly to point of body scale reduction.

Widened vertebral scale row nearly all white anteriorly with only a narrow light blue (Bluish Glaucon) posterior margin; margin increases in size posteriorly so that at point of scale reduction on body only small anterior white spot is present on scales; spot may persist as faint light spot as far caudad as anal region.

Two upper labials in contact with orbit pure white, remainder pale light blue to dirty white below black upper edges. Rows I and II on anterior one-fourth of the body white with pale blue (Bluish Glaucon) posterior margin; posterior to this they acquire same blue coloration as possessed by remaining dorsal scales. Outer edges of ventrals light blue (Bluish Glaucon) to light bluish green (Pale Nile Blue); center of ventrals, throat, and chin pure white. Keels on paravertebral scales black on middle and posterior third of body.

VARIATION: Aside from the variation already indicated, three specimens have nine upper labials on both sides and three have nine on one side and eight on the other. In regard to the lower labials five specimens have the formula 9/10; three have 9/9; three have 10/11; and one each has 8/9 and 11/11. Seventy-five per cent of the specimens studied have the temporal formula 1-2. Of the remaining specimens four have the formula 1-1/1-1, four have the formula 1-1/1-2, four have the formula 1-1-2/1-2, two have 1-1-2/1-1-2, and one has 1-1-2/1-1-1-2.

Clinical variations in respect to two structural attributes, the average number of ventral plates and the average number of maxillary teeth, are suggested by the variation observed from Tehuantepec in the south to Sonora and Chihuahua in the north. Clear definition of this variation is not apparent now because of a scarcity of material from the middle and northern parts of the range.

	VENTRALS		MAXILLARY TEETH
	Males	Females	(Both Sexes)
Chihuahua	182, 184	181, 182	18-19, av. 18.4(4)
Sonora	177-179, av. 178(4)	180, 183	17-18, av. 17.8(5)
Tehuantepec	167-178, av. 173(18)	175-184, av. 179(10)	18-21, av. 19.3(8)

A female from Guerrero exhibits a number of peculiarities. This individual is not believed to represent an aberrant specimen such as Stuart (1941, p. 18) discusses among juveniles in the genus *Dryadophis*. The female has a head-body length of 455 mm. which is approaching subadult size. It has the loreal plate lacking on one side, the apical pits reduced in distribution, poorly developed keels, and the lowest ventral count recorded for any female—167. Because of the over-all peculiarities of the specimen, data from it have not been included in the ventral counts for the species.

There is little variation from the coloration described above. Some individuals have the ocular stripe reduced anterior to the orbit to a thin line along the upper edge of labials 2, 3, and 4.

REMARKS: The three cotypes upon which Günther based his *diplotropis* are all females, to judge by the ventral counts recorded for them and as stated by Boulenger (1894). The types are still extant in the collections of the British Museum (Natural History) but have not been studied by me. There is no question in relation to the status of this name. Bocourt's variety (1897, p. 837) *aeneus* is based on a juvenile without specific locality data, but, as suggested by Smith and Taylor (1945, p. 90), probably from Michoacan or Jalisco. There is no apparent basis for recognition of the name as valid.

Smith (1943, p. 443) has proposed nomenclatorial recognition of the population of *diplotropis* from the Tres Marias Islands on the basis of the high ventral counts reported by Boulenger (1894, p. 111) for specimens from these islands. Smith has examined no specimens from mainland Mexico farther north than Nayarit. In support of the argument for nomenclatorial recognition of the specimens from the Tres Marias Islands Smith states, "This corresponds with the differences found between mainland *Drymarchon corais rubidus* and the islands *D. m. cleofae*; between *Constrictor c. imperator* and *C. c. sigma*; *Dryadophis melanolomus stuarti* and *D. m. slevini*; *Lampropeltis triangulum blanchardi* and *L. t. schmidtii*; *Masticophis flagellum striolatus* and *M. f. variolosus*." In all of the examples cited by Smith the insular specimens have a slightly higher number of ventrals and in

some cases a higher number of subcaudals. In at least two of the examples additional differences are indicated, and doubtless some of these examples merit nomenclatorial recognition. However, arguments against the acceptance of classification predicated solely on the basis of minor average differences in ventral and subcaudal counts already have been presented (Bogert and Oliver, 1945, p. 361).

As pointed out above, there appears to be a clinal trend towards an increase in the number of ventrals from south to north. The maximum ventral count for males from the northern part of the range on the mainland (Chihuahua) differs from that for the insular specimens by two ventrals. As stated elsewhere in the present paper, insular populations of *Thalerophis* support the usual trend noted by Mertens (1934) that insular populations of snakes are generally larger and usually have more vertebrae (consequently more ventrals and subcaudals) than related populations from the adjacent mainland. In view of these considerations I see no basis at present for recognition of the population to which Smith has applied a name but for which he has presented no diagnostic characters.

With the availability of additional material, northern (not restricted to the Tres Marias Islands) and southern races of *diplotropis* can doubtless be defined, but the material now available does not permit these races to be diagnosed adequately. Differences other than the average number of ventrals and subcaudals that may prove to be of diagnostic value in differentiating these populations are the number of maxillary teeth, the tail/body ratio, and minor details of coloration.

Morphologically this species possesses attributes in common with, and different from, those of both *mexicanus* and *depressirostris*. Geographically it is widely separated from *depressirostris*, whereas its range adjoins without overlapping that of *mexicanus*. There is no indication of any genetic exchange between *mexicanus* and *diplotropis*, but the former doubtless represents the closest living relative of the latter. The two have a number of structural attributes in common, as well as several significant morphological differences. At the present time *diplotropis* is re-

productively isolated from all other members of the genus.

The present distribution of *diplotropis* coincides for the most part with the areas of tropical scrub forest on the Pacific coast of Mexico. The northern limit of this forest on the west coast of Mexico corresponds with the northern limit of the tropical climate in the vicinity of Mazatlan, Sinaloa (Ward and Brooks, 1936, fig. 10). Ochoterena (1937, pp. 463-597) and others have pointed out that north of this boundary there occur isolated areas of the scrub forest in the humid barrancas. H. S. Gentry, who collected the specimens from Chihuahua, has stated (*in litt.*) that they were collected "up river (Rio Mayo) in the subtropical barrancas."

SPECIMENS EXAMINED (60)

MEXICO. Chihuahua: Guasaremos, M.C.Z. Nos. 43268-43271. Guerrero: Acapulco, A.M.N.H. No. 63935; Chilpancingo, C.N.H.M. Nos. 38352-38355; Laguna Coyuca, U.M.M.Z. No. 80940; Ocotito, E.H.T. No. 4573; "Guerrero," M.C.Z. No. 28647. Michoacan: Uruapan, E.H.T. Nos. 5345-5349. Nayarit: Acaponeta, U.S.N.M. No. 46458. Oaxaca: Escurana, U.S.N.M. No. 110550; Guiengola, A.M.N.H. No. 66820; La Concepcion, U.S.N.M. No. 110552; San Blas, A.M.N.H. No. 66822; San Mateo del Mar, A.M.N.H. No. 65939; San Pedro Quiechapa, U.S.N.M. No. 110551; Tapanatepec, M.C.Z. No. 27826; Tehuantepec, A.M.N.H. No. 64579, M.C.Z. Nos. 46404, 46457, 46480; U.M.M.Z. Nos. 82571-82590; U.S.N.M. Nos. 30175, 30176; Tres Cruces, A.M.N.H. No. 66821. Sonora: Alamos, A.M.N.H. No. 64233; Guirocoba, A.M.N.H. Nos. 63726-63731. "Mexico," A.M.N.H. No. 19766.

Thalerophis mexicanus mexicanus Duméril and Bibron

Leptophis mexicanus DUMÉRIL AND BIBRON, 1854, *Erpétologie générale*, vol. 7, pt. 1, p. 536; Mexico.

Ahaetulla mexicana GÜNTHER, 1858, *Catalogue of the colubrine snakes in the . . . British Museum*, p. 154.

Thrasops mexicanus COPE, 1860, *Proc. Acad. Nat. Sci. Philadelphia*, vol. 12, p. 557.

Ahaetulla modesta GÜNTHER, 1872, *Ann. Mag. Nat. Hist.*, ser. 4, vol. 9, p. 26; Rio Chisoy, near Cubulco, Guatemala.

Hapsidophrys mexicanus COPE, 1885, *Proc. Amer. Phil. Soc.*, vol. 22, p. 379.

Philothamnus modestus COPE, 1887, *Bull. U. S. Natl. Mus.*, no. 32, p. 69.

Leptophis mexicanus SLEVIN, 1939, *Proc. California Acad. Sci.*, vol. 23, no. 26, p. 401.

TYPE LOCALITY: Mexico.

RANGE: From extreme southern Tamaulipas, Mexico, south through the Mexican states of Vera Cruz, Tabasco, eastern Oaxaca, Chiapas, and Campeche, south along the Caribbean drainage in British Honduras, Guatemala, Honduras, Nicaragua, and Costa Rica. Known from the Pacific slope only in Chiapas and extreme eastern Oaxaca, Mexico. (Fig. 9.)

DESCRIPTION: The maxillary teeth are 20-25; the average of 26 observations is 21.2. The last two maxillary teeth are strongly enlarged (fig. 11). The hemipenis is eight subcaudals long, with four enlarged basal spines, approximately equal in length, attached opposite subcaudal 2. The spine on the inner side of the sulcus is slightly longer than the others. These are followed distally by three to four transverse rows of smaller spines, opposite subcaudals 3 and 4; the spines decrease in size distally. In the proximal row of these smaller spines the spine on the outer side and adjacent to the sulcus is nearly as long as the four basal spines. These spines gradually pass into calyces with fringing spinous papillae that obscure the structure of the calyces. The papillae decrease in length and spinosity distally, so that the distal portion opposite subcaudal 8 is typically calyculate. Many specimens possess numerous tiny spines about the base of the hemipenis, above and below, between and on the four basal spines (see pl. 17).

Keels are present on the scales of rows II-XIV; row VI is distinctly keeled above the anus. There are prominent keels on the two median rows of dorsal scales on the tail for most of its length; rarely in juveniles and females only the scales on the anterior one-third of the tail are keeled.

Dorsal scale reduction on the body involving rows VI-VII, occasionally rows V-VI, takes place opposite ventrals 89-107, average 97.43, in the males; opposite ventrals 93-109, average 100.14, in the females. That involving rows III-IV occurs opposite ventrals 88-105, average 97.74, in the males; opposite ventrals 92-108, average 100.55, in the females. Reduction of the dorsal scales on the tail occurs opposite subcaudals 7-36, average

22.09, in the males; opposite subcaudals 5–35, average 15.59, in the females.

The ventral plates in the males are 148–169, average 157.30; 154–174, average 161.15, in the females. The subcaudals in the male are 144–175, average 157.80; in the females 140–173, average 156.31. The anal plate is normally divided.

The upper labials normally are eight and the lower labials are typically 10 in number. The loreal plate is normally present. There is slight variation from the normal condition of one preocular and two postoculars. The lower postocular is smaller than the upper. The preocular is not in contact with the frontal. The parietal is much longer than broad, truncate posteriorly, not or but slightly notched by the upper posterior temporal. The length of the frontal is approximately equal to the length of the interparietal suture. The temporals are usually 1–2. The eye is moderate; its diameter is equal to the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 879 mm., plus a tail length of 336 mm.; the largest female examined had a head-body length of 776 mm., plus a tail length of 399+ mm. The tail/body ratio observed in the males is .57–.75, average .670; in the females .56–.70, average .639.

The coloration in alcohol is: top of head dark greenish blue (Sea Green to Dark Orient Blue), a black stripe across the upper portion of rostral, passing posteriorly across nasal, loreal, and lower portion of preocular scales; on upper edge of first four labials. Posterior to eye this stripe broadens and involves upper edge of labials 5, 6, 7, and 8, all of lower postocular, lower half of upper postocular, antero-ventral edge of parietal, lower two-thirds of anterior temporal, and all of lower posterior temporal.

Stripe continues onto body, anteriorly on scale rows II–VI; on rows II and VI only on upper and lower margins, respectively. On rows III–V stripe interrupted by antero-ventral spot of bluish white (Pale Nile Blue) or bluish green (Pale Sulphate Green). Light spots increase in size posteriorly while black is reduced in size and distribution. Posterior to point of scale reduction on body stripe is limited to common border of rows II and III,

becomes diffuse and interrupted on the tail where it is present only on upper edge of lower dorsal row.

On dorsal surface of body and tail between dark lateral stripes color is pale to dark bronzy brown (Olive-Ocher to Isabella Color) when stratum corneum is present; when absent it is light greenish blue to light greenish brown. Head, body, and tail below lateral stripes pure white to dirty white. This pattern is shown in figure 7.

VARIATION: One specimen has nine upper labials on both sides of the head, and six have nine on one side and eight on the other. More variation is apparent in the lower labials than in the upper. Eight specimens have 11 lower labials on both sides, whereas four have only nine on each side. Seven have the asymmetrical arrangement of 10 on one side and 11 on the other, and five have nine on one side and 10 on the other. Two specimens fail to exhibit the normal condition of a single loreal on each side of the head. One of these variants lacks a loreal on both sides, while the other lacks the shield on only one side of the head. Two specimens have two preoculars on each side of the head, and one specimen has two on one side and the normal one plate on the other. A single individual varies from the typical condition in respect to the postoculars. This specimen has three postoculars on each side of the head. The temporals exhibit a number of variations from the usual condition of one anterior and two posterior shields. The observed variations include: seven with the formula 1-1-2; three with 1-1/1-2; two with 1-1-2/1-2; two with 1-1-2/1-1-2; one with 1-1; one with 1-1-2/2-1-2; one with 1-1-2/2-2-2; one with 1-1-2-1/1-2-1; one with 1-2/1-3; and one with 1-2/2-2.

The geographic variation observed in the ventral plates is shown in figure 3. There is an increase in the average number of these scales from south to north. The subcaudals indicate the same south-north trend, but because of the low number of specimens with complete tails it is not so clearly defined. There are more fully discussed under the section on character clines.

In respect to coloration there is considerable variation in the tint of the observed

color. Whether this is due to preservation, is related to ecdysis, or is an indication of genetic differences is not known at the present time. The pattern described above is highly constant, with one exception that will be noted below. An occasional individual from Mexico and Guatemala exhibits a tendency towards reduction in the amount of black pigment on the dorsal scales. Thus the black margin of the scales may be reduced at midbody to an anterior and posterior black spot. The portion of the scale above and posterior to the anteroventral light spot is dark blue. Posterior to the point of scale reduction the black is present only as a narrow upper margin on the scales of row II, while all or only the lower half of the scales of row III is dark blue. Thus the posterior lateral stripe is dark blue and on the scales of row III, rather than a narrow black stripe along the common borders of the scales of rows II and III. This condition is an approach to that found in the population of the Yucatan Peninsula and is only occasionally observed outside of that form.

A striking type of color variation has been observed in individuals from several scattered localities. These have a broad, black, postocular stripe continuing onto the anterior third of the body and breaking up to form the margins of the scales of rows II-VI. The stripe is much reduced on the head anterior to the orbit where it is present only on the upper edge of the second to fourth upper labials. The black margins on the dorsal scales are reduced so that at midbody, or slightly anterior to that point, only the anterior and posterior tips of the scales are black. Posterior to the point of reduction in the number of rows of dorsal scales the black pigment disappears completely. The dorsal surface is uniformly dark green in color except for the black tips on the dorsal scales indicated above. The anteroventral light spots on the lateral dorsal scales normally found in *mexicanus* are completely lacking or are so reduced as to be visible only when the scales are spread apart. Anteriorly the dorsal green color extends ventrally below the black-edged scales onto row I and the outer edge of the ventral plates. The ventrals, except for the outer edges, are silvery white to dirty white. At midbody the

ventral color encroaches onto the scales of row I, and the greenish color is present on the ventrals and the scales of the outer dorsal row as minute green stippling. On the posterior third of the body the ventral color extends dorsally onto the lower half of row II.

The number of ventrals in these color variants is higher than the average observed in the normal colored specimens. The data for these have not been included in computing the average for the other populations. In all other observed characters these individuals resemble the conditions found in typical *mexicanus*.

REMARKS: Of the 10 species assigned to the genus *Leptophis* by Duméril and Bibron (1854), two are referable to the genus *Thalerophis*: *liocercus* and *mexicanus*. The former of these two included more than one currently recognized form. The latter appears to have included only the form now called *mexicanus mexicanus*. The types have not been studied by me, and I do not know whether they are still in the Paris Museum or not.

Elsewhere (Oliver, 1942, p. 17) I have indicated that Günther's *Ahaetulla modesta* is probably a synonym of *mexicanus*. This name appears to have been based on a green color phase of *mexicanus* that may or may not warrant nomenclatorial recognition when it has been fully analyzed. The limited locality data available for these green specimens suggest that they may represent a subspecies that replaces the typical race at higher elevations and at the northernmost end of the range.

A specimen collected in Chiapas, Mexico, at an elevation of 3500 feet exhibits a coloration virtually intermediate between that of *m. mexicanus* and the green phase. This specimen has the high ventral count that is characteristic of the green phase. At present the limited data available on the green phase make it inadvisable to recognize *modesta* as a valid subspecies of *mexicanus*. The majority of specimens available lack precise locality or ecological data. Boulenger (1894, pp. 108-109) referred this variation to his variety D, of which he had seen seven specimens, but only one had definite locality data. This problem clearly illustrates the necessity of exact

locality and ecological data before we can adequately evaluate the variation observed and arrive at a correct analysis of the forms with which we are dealing.

The type locality of *modesta* is "Rio Chisoy, near Cubulco, Guatemala." Two members of the genus *Thalerophis* are known to occur in Guatemala: *mexicanus mexicanus* and *richardi praestans*. The latter is a nearly uniform green snake that superficially resembles the figure (Günther, 1902, pl. 48) of *modesta*. The possibility that Günther's new form was based on a specimen of *praestans* with the loreal plate atypically present seems extremely doubtful. The number of ventrals reported for *modesta* is below the minimum recorded for Guatemalan specimens of *praestans*; *modesta* has a distinct black postocular stripe, whereas *praestans* lacks the black postocular stripe; the keels on the dorsal scales of *modesta* are well developed on the scales of rows II–XIV and are without black lines, whereas *praestans* frequently lacks keels on the scales of the lower dorsal rows and has distinct black lines on the keels at least on the paravertebral rows of dorsal scales.

The relationships of *mexicanus* are not clearly discernible. It shares the largest number of its structural attributes with *diplotropis* to which its distributional range is geographically adjacent. Like *diplotropis* it has a loreal shield, eight upper and 10 lower labials, a similar number of maxillary teeth with the two posteriormost teeth strongly enlarged, similar variation in respect to the point of reduction in the number of dorsal scales on the tail, and overlapping counts in the number of ventral plates. The two species differ in the average numbers of maxillary teeth and ventral plates, the distribution of keels on the dorsal scales, the hemipenial structure, and the color pattern.

Previous workers in dealing with members of this genus have placed considerable weight on the presence or absence of a loreal shield in denoting relationships. I do not believe that this character is as important in indicating phylogeny as are several other morphological features, such as the maxillary teeth and the hemipenial structure. Therefore I do not believe that the presence of a loreal shield in

both *depressirostris* and *mexicanus* is necessarily an indication of close relationships. These two species differ in so many respects that the relationship between them appears to be a rather distant one.

Intergradation between *m. mexicanus* and *m. yucatanensis* apparently occurs in two geographic areas where the two forms are in contact. The populations of *m. mexicanus* from British Honduras and the Peten region of Guatemala exhibit high ventral counts similar to those observed in *yucatanensis*. The ventral counts of these populations represent a part of the south-north cline already mentioned in *mexicanus*. The British Honduran and Peten populations are not designated as intergrades, although they show an approach to the conditions of *yucatanensis*.

Three specimens from Campeche, Mexico, are considered as intergrades between *mexicanus* and *yucatanensis*. These have the general color pattern of *yucatanensis* with the number of ventral plates characteristic of *mexicanus*. It appears that two clines exist within the species *mexicanus* and provide the most easily recognized basis for diagnosing the subspecies *yucatanensis*. One of these clines is more limited geographically than the other and pertains to coloration, with a change from west to east in southern Mexico; the second involves the number of ventral plates, with an increase from south to north throughout the species range.

Boulenger (*loc. cit.*) records a specimen of *mexicanus* from Amula, Guerrero, under his variety A which includes in addition to this specimen only representatives of the subspecies *mexicanus*. Under his variety C he lists three specimens from Guerrero and Jalisco. In spite of the recently increased intensity of collecting in Mexico, no specimens of *mexicanus* have been obtained from the Pacific drainage in Mexico north of the Isthmus of Tehuantepec. The only member of the genus known from western Mexico north of the isthmus is *diplotropis*. The data given for the specimens by Boulenger allocate them with *mexicanus* rather than *diplotropis*. On the basis of all other information concerning the two species, the Guerrero and Jalisco records of Boulenger are considered to be in error.

The distribution of *mexicanus* in Mexico (fig. 9) follows a prominent geographic pattern that is exhibited by many Neotropical animals that attain the northern limit of their distribution in Mexico. In this pattern the animals occur in the lowlands on both coasts south and east of the Isthmus of Tehuantepec in Mexico: in Chiapas on the Pacific side; Campeche and Tabasco on the Atlantic side. On the Pacific side these forms occur near the coast north to approximately Tonala, Chiapas, thence inland on the higher slopes and across the isthmus to the Atlantic side, where they extend northward into northern Vera Cruz and southern Tamaulipas. These forms are usually either absent entirely from the Pacific side north of the isthmus or are replaced by a related species or subspecies. This pattern is correlated with climatic factors, primarily moisture, and is reflected in the vegetation so that the distribution pattern for the animals corresponds closely to that of the wet tropical forest in Mexico.

SPECIMENS EXAMINED (142)

BRITISH HONDURAS. Belize, C.N.H.M. No. 6931, U.S.N.M. Nos. 24907, 26056, 26356, 65149; Cohune Ridge, U.M.M.Z. No. 80709; Manatee, C.N.H.M. Nos. 4219-4227.

COSTA RICA. "Costa Rica," U.S.N.M. No. 9783; San Jose, A.M.N.H. No. 17371; "Tunjical, Sonora Farm, (?) Costa Rica," M.C.Z. No. 20485.

GUATEMALA. Caballo Blanco, C.N.H.M. No. 1959; Chama, Alta Verapaz, M.C.Z. No. 28094, U.M.M.Z. Nos. 91024, 91025; Chejel, Baja Verapaz, U.M.M.Z. No. 89977; "Guatemala," C.N.H.M. No. 188; La Libertad, Peten, C.N.H.M. Nos. 43381-43383; U.M.M.Z. Nos. 74850, 74852-74858, U.S.N.M. Nos. 71364, 71365; Los Alpes, U.M.M.Z. No. 89975; Peten, U.S.N.M. No. 71782; Puerto Barrio, Izabal, U.M.M.Z. No. 79052; Quiriagua, C.A.S. No. 67008, C.N.H.M. Nos. 20556-20558; Samanzana, U.M.M.Z. No. 91026; San Pedro River, M.C.Z. No. 38650; Senchu, U.S.N.M. No. 35911; Sepacuite, M.C.Z. No. 24947; Treces Aguas, U.S.N.M. No. 115504; Uaxactun, U.M.M.Z. Nos. 70454-70456; Volcan, Alta Verapaz, U.M.M.Z. No. 89976.

HONDURAS. Garcia Plantation, M.C.Z. Nos. 21182, 21195, U.M.M.Z. No. 62533; Guaymas District, U.M.M.Z. No. 62526 (2); Hicaque (=Micaque?) Farm, U.M.M.Z. Nos. 62524, 63362 (3); "Honduras," A.M.N.H. Nos. 32342, 32813, 32850, U.M.M.Z. No. 63364, U.S.N.M. No. 17810; Lancetilla, A.M.N.H. No. 46976,

M.C.Z. No. 27256, U.M.M.Z. No. 70785; Matederes (?) Mountains, M.C.Z. No. 38736; Omoa, A.N.S.P. No. 5198; Patuca, U.S.N.M. No. 20267-20269; Progreso, M.C.Z. No. 26856; Puerto Arturo, U.M.M.Z. No. 63363 (2), Subirana Valley, M.C.Z. No. 38735; Tela, A.M.N.H. Nos. 46975, 59110, M.C.Z. Nos. 19943, 19944, 20212, 21168-21171, 22810, U.M.M.Z. No. 62517 (4), U.S.N.M. Nos. 82160, 82162; Yoro, C.N.H.M. No. 21885.

MEXICO. Campeche: Balchacaj, E.H.T. Nos. 11624-11626. Chiapas: Aguacate, U.S.N.M. No. 110555; Cruz de Piedra, U.M.M.Z. No. 87695, U.S.N.M. No. 110556; Esperanza, northwest of Escuintla, U.M.M.Z. No. 87693; Juarez, northeast of Escuintla, U.M.M.Z. No. 87694; Tonala, U.S.N.M. No. 110554. "Mexico," A.M.N.H. Nos. 19591, 63630, C.N.H.M. No. 40828, U.M.M.Z. No. 67215. Oaxaca: Chivela, M.C.Z. No. 25219; Matias Romero, A.M.N.H. No. 65924; San Geronimo, C.N.H.M. No. 1460. Puebla: Necaxa, U.M.M.Z. No. 85965. Tabasco: Tenosique, U.S.N.M. No. 110553. Tamaulipas: Altamira, U.S.N.M. No. 46524; Padilla, M.C.Z. No. 46372. Vera Cruz: Cameron, U.M.M.Z. No. 89978; Jicaltepec, A.N.S.P. No. 11707; La Malmilla, Jalacingo, A.M.N.H. No. 4289; Mata de Cana, U.S.N.M. No. 110557; Nuevo, A.M.N.H. No. 19834; Orizaba, U.S.N.M. No. 30493; Paraje Nuevo, U.M.M.Z. No. 85320; Paso de Macho, U.M.M.Z. No. 85321; Potrero, U.M.M.Z. No. 80941; Potrero Viejo, U.M.M.Z. No. 89979, U.S.N.M. No. 110559; San Juan de la Punta, U.S.N.M. No. 110558; Terminal Camp, near Tampico, A.M.N.H. No. 43360; "Vera Cruz," A.N.S.P. Nos. 4875, 4876.

NICARAGUA. Canal Zone area, M.C.Z. No. 32044; Machuca, A.N.S.P. No. 5197; (?) Matagalpa, U.M.M.Z. (uncatalogued); "Nicaragua," M.C.Z. No. 6248, U.S.N.M. No. 16126; Rio Grande, U.S.N.M. No. 12662-12665; Wounta Haulover, Mosquite coast, A.N.S.P. No. 15433.

Thalerophis mexicanus yucatanensis

Oliver

Leptophis mexicanus var. B. BOULENGER, 1894, Catalogue of the snakes in the British Museum, vol. 2, p. 109; Yucatan.

Leptophis mexicanus yucatanensis OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 10; Coba, Quintana Roo, Mexico.

TYPE LOCALITY: Coba, Quintana Roo, Mexico.

RANGE: Known only from the Yucatan Peninsula, Mexico (fig. 9).

DESCRIPTION: The maxillary teeth number

20–21, average 20.7 for six observations. The last two maxillary teeth are strongly enlarged. There are no constant differences in hemipenial structure from that of *mexicanus mexicanus*. The hemipenis is eight to nine subcaudals long, with four enlarged basal spines, approximately equal in size, attached opposite to subcaudal 2. The longest of the basal spines is on the inner side of and adjacent to the sulcus. These are followed distally by three to four transverse rows of smaller spines opposite subcaudals 3 and 4. The spines decrease in size distally and gradually merge into calyces with spinous fringing papillae that obscure the structure of the calyces. The papillae decrease in length and spinosity distally, so that the distal portion, opposite subcaudal 8, is typically calyculate.

Keels are present on the scales of rows II–XIV; row VI is distinctly keeled above the anus. There are prominent keels on the two median rows of dorsal scales on the tail posterior to the point of dorsal scale reduction from six to four rows.

Dorsal scale reduction on the body involving rows VI–VII occurs opposite ventrals 101–115, average 107.70, in the males; opposite ventrals 99–111, average 105.37, in the females. That involving rows III–IV takes place opposite ventrals 101–115, average 106.90, in the males; opposite 99–108, average 103.75, in the females. Reduction of the dorsal scales on the tail occurs opposite subcaudals 22–30, average 25.62, in the males; opposite subcaudals 14–35, average 25.83, in the females.

The ventrals in the males are 164–172, average 168.11; in the females 165–174, average 169.15. Seven males have complete tails with subcaudal counts of 171–181, average 174.71; five females with complete tails have subcaudals 160–169, average 164.60. All have the anal plate divided.

The upper labials are eight in all except one specimen that has 8/9; the lower labials are 10 in 15 specimens, 10/11 in two, and 11 in one. All specimens have a single preocular and two postoculars except one specimen that has a single postocular on one side. The lower postocular is smaller than the upper. The preocular is not in contact with the frontal. The loreal plate is present in all specimens.

The parietal is much longer than broad, truncate posteriorly, not or but slightly notched by the upper posterior temporal. The length of the frontal is approximately equal to the length of the interparietal suture. The temporals are 1-2 in all but three specimens, two of which have 1-1-2/1-2, and the third has 1-1-3/2-1-2. The eye is moderate; its diameter is equal to the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 753 mm., plus a tail length of 516 mm.; the largest female had a head-body length of 764 mm., plus a tail length of 384+ mm. Four males with complete tails have tail/body ratios of .62–.70, average .675; two females have ratios of .59 and .60.

The coloration in alcohol is: top of head dark greenish blue (Sea Green to Dusky Bluish Green); a narrow, diffuse black stripe across upper third of rostral, passing posteriorly across lower half of nasal, lower portion of loreal and preocular, onto upper edges of first four upper labials; posterior to orbit stripe broadens out, covering all of lower postocular, lower edge of upper postocular, lower half of anterior temporal, all of lower posterior temporal, lower edge of upper posterior temporal, and forming a broad upper black margin on last three upper labials.

Black stripe continues onto body, anteriorly on scales of rows II–VI and X–XIV forming an anterior and posterior black tip, rarely a complete margin connecting tips. Anterioventral light spot of bluish white (Pale Nile Blue) or bluish green (Pale Sulphate Green), small, bordered above and posteriorly by dark blue (Venetian Blue) or dark greenish blue (Sea Green). Anterioventral light spots and black margins and tips decrease in size posteriorly, while dark greenish blue or dark blue color increases in area; thus at mid-body there is a nearly uniform lateral band of dark blue approximately three scales wide (fig. 7).

Posterior to point of scale reduction on body, row II retains prominent upper black margin, while rows III and IV have only irregular, diffuse black tips. Dark lateral band occupies upper edge of row II, all of row III, all or only lower half of row IV, and occasionally lower edge of row V. Lateral stripe con-

tinues on tail, occupying upper one-third of row I and lower half of row II posterior to point of reduction from six to four dorsal scale rows.

Dorsal coloration between lateral stripes light gray (Pale Gull Gray) to light brown (Drab). Ventrals, tail, body, chin, and upper labials below lateral stripe pure white.

VARIATION: The only variation not already indicated that merits mention is the ocular stripe and the dark lateral coloration. One specimen has the ocular stripe reduced anterior to the orbit to a margin on the upper edges of the first four upper labials. Two additional specimens approach this extreme in reduction of the black pigment anterior to the orbit. Three specimens have the dark blue lateral coloration on the entire scales of row VI on the anterior one-fourth of the body. The width of the dark lateral stripe on the posterior third of the body varies in the specimens examined from one and a half scale rows to two and a half scale rows wide.

REMARKS: Since the description of this subspecies (Oliver, 1942) there has been no new data to necessitate any modification of its taxonomic status.

The closest relationships of *yucatanensis* are with *mexicanus*, and the two apparently intergrade in both Campeche and southern Yucatan, Mexico. Specimens from the former area have been considered as intergrades. No specimens have been seen from southern Yucatan that were classed as intergrades, but individuals from British Honduras and the Peten region of Guatemala exhibit a tendency towards the high ventral and subcaudal counts of *yucatanensis*. Thus it seems highly probable that the two do intergrade somewhere in southern Yucatan.

Lundell (1934, pp. 253–321) has pointed out the close relationship that exists between the flora of Yucatan and that of the British Honduras-Peten, Guatemala, region. Stuart (1935, pp. 18–25) has shown the same relationship between the herpetofauna of the two regions. Stuart suggests three possible explanations for the origin of the endemic Yucatan fauna. The first of these, origin *in situ*, seems to be the most plausible explanation of the origin of *yucatanensis*, known only from the dry scrub forest of the Yucatan Peninsula. It

is this portion of the peninsula, covered with scrub forest, that is characterized by a high degree of endemism. In commenting on this Stuart states, "It is only to be expected that a species of wide distribution through tropical forests would differentiate in such an area of comparative aridity."

SPECIMENS EXAMINED (18)

MEXICO. Quintana Roo: Coba, U.M.M.Z. No. 83940 (type), No. 83941. Yucatan: Chichen Itza, C.N.H.M. No. 26982, M.C.Z. Nos. 15550, 22063, 22064, U.M.M.Z. No. 73035, U.S.N.M. No. 46567; Kantunil, C.N.H.M. (uncatalogued: E. W. Andrews field no. 655), No. 36436; Libre Union, C.N.H.M. No. 36434; Merida, C.N.H.M. No. 36435; Mujeres Island, C.N.H.M. No. 34637; Xkichmook, C.N.H.M. No. 40746; Yokdzonot, C.N.H.M. Nos. 36433, 36437; "Yucatan," U.S.-N.M. Nos. 24884, 24885.

Thalerophis nebulosus Oliver

Leptophis nebulosus OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 12; Cariblanca, Costa Rica.

TYPE LOCALITY: Cariblanca, Costa Rica.

RANGE: From Patuca, Honduras, south to Cariblanca, Costa Rica (fig. 9).

DESCRIPTION: The maxillary teeth in two specimens are 27 and 28, with the last three teeth enlarged. The hemipenis is seven subcaudals long, the proximal portion opposite subcaudal 1 and the anterior half of subcaudal 2 is bare; this is followed distally by seven to eight transverse rows of small spines opposite the posterior half of subcaudal 2, all of subcaudal 3, and the anterior half of subcaudal 4; no enlarged basal spines present, those of proximal row largest; the spines pass gradually into calyces with fringing papillae; the posterior portion opposite the posterior half of subcaudal 5, and all of subcaudals 6 and 7 are typically calyculate.

Keels usually present on the dorsal scales of rows II–XIV on the body; well-developed keels present on the tail posterior to the point of reduction from six to four rows.

The reduction of dorsal scales on the body involving rows VI–VII occurs opposite ventrals 93–104, average 99.87, in males; opposite ventrals 99–100 in the single female. That involving rows III–IV takes place opposite ventrals 95–104, average 99.62, in the males;

opposite ventrals 103 and 104 in the female. The reduction of dorsal scales on the tail takes place opposite subcaudals 7-9, 18-22, in two males and opposite subcaudals 6 in the female.

The observed variation in the number of ventral plates is 150-160, average 152.77, in the males, and 158 in the single female. Two males have undamaged tails with 145 and 151 subcaudals. The female has an incomplete tail. All specimens have a divided anal plate.

Four specimens have eight upper and 10 lower labials, while one individual has nine upper and 10 to 11 lower labials. The loreal is absent in all specimens. All have a single preocular; four have two postoculars on both sides of the head, while one specimen has one postocular on the left side of the head and two on the right. The lower postocular is small. The preocular is in, or barely missing, contact with the frontal. The parietal is longer than broad, not in contact with the lower postocular. The frontal is large, its length approximately equal to that of the interparietal suture. The temporals are one to two in all specimens. The eye is moderate in size; the diameter is equal to the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 502 mm., plus a tail length of 352 mm.; the female has a head-body length of 433 mm. The tail/body ratios of the two males with complete tails are .62 and .70.

The coloration (in alcohol) is: top of head bluish green (Sea Green); a narrow black stripe beginning on upper posterior edge of first or second upper labial and passing posteriorly along upper edge of upper labials and extreme lower edge of prefrontal and preocular; posterior to orbit stripe is on lower edge of upper postocular and upper edge of lower postocular, lower edge of anterior temporal and lower posterior temporal and upper margin of last two upper labials. Stripe continues onto body for a short distance, not greater than length of the head.

Dorsal body coloration on anterior one-half of body white to light cream (Cream Color) on rows I and II; on rows III, IV, and occasionally row V, bright blue (Mathew's Blue) with stratum corneum absent or dusky greenish blue (Sea Green) with stratum corneum present; rows VI, VII, and VIII

light gray (Pale Olive-Gray) when stratum corneum is absent or light metallic bronze (Old Gold) when stratum corneum is present.

Posterior coloration essentially the same except that blue lateral stripe is reduced in distribution, a short distance anterior to point of dorsal scale reduction blue color is present only on all of row IV and upper edge of row III; posterior to point of scale reduction blue is present only on row III. Blue coloration persists to end of tail, becoming reduced posteriorly.

Upper labials below black upper margin, lower edge of small postocular and frequently anterior lower edge of anterior temporal, lower labials, chin shields, ventrals, and subcaudals all uniformly white to light cream (Cream Color).

VARIATION: The five specimens available as representatives of this species exhibit slight variation aside from that indicated above. The width of the blue lateral stripe varies on individual specimens with an occasional blue upper margin on the scales of row II or a blue lower margin on the scales of row VI.

REMARKS: No new specimens of this species have been studied since its description (Oliver, 1942), and consequently nothing further can be stated concerning its status.

The limited material available representing this species makes it the least known member of the genus *Thalerophis*. The specimens in museum collections have usually been identified as *mexicanus*, the common striped species of the genus in central America. The two cannot be considered conspecific on the basis of our present knowledge. The details of the striped patterns in the two species exhibit a number of small differences. In addition to the difference in color pattern, the maxillary teeth in *nebulosus* number 27-28, with the last three teeth enlarged, whereas *mexicanus* has 20-25, average 21.2, with the last two teeth strongly enlarged. The hemipenes in the two are vastly different in structure, with the organ of *nebulosus* lacking enlarged basal spines. The loreal shield is present in *mexicanus* and lacking in *nebulosus*. The geographic range of *mexicanus* overlaps that of *nebulosus*, but the ecology of the two species is not known. In the sum total of its attributes *nebulosus* represents a more generalized form than *mexicanus*, and in part serves to

bridge the gap between *mexicanus* and *riveti*. In most of the structural attributes in which *nebulosus* differs from *mexicanus* it resembles *riveti*: 27–28 maxillary teeth with the last three teeth enlarged; hemipenis without enlarged basal spines; and the absence of a loreal plate. Differences between *nebulosus* and *riveti* include pronounced differences in color pattern, distribution of the keels on the dorsal scales, and number of ventral plates. The two species are allopatric in their geographic distribution.

SPECIMENS EXAMINED (5)

COSTA RICA. Cariblanca, M.C.Z. No. 15287 (type).

HONDURAS. Patuca, U.S.N.M. No. 20270.

NICARAGUA. Greytown, U.S.N.M. No. 19568; Matagalpa, M.C.Z. No. 17094; "Nicaragua," U.S.N.M. No. 20683.

Thalerophis richardi richardi Bory St. Vincent

Coluber ahaetulla LINNAEUS, 1758, (in part), *Systema naturae*, ed. 10, vol. 1, p. 225; Asia, America.

Coluber richardi BORY ST. VINCENT, 1823, in *Dictionnaire classique d'histoire naturelle*, Paris, vol. 4, p. 588; Guianas.

Coluber linnei GRAY, 1831, (in part), in Griffith, *The animal kingdom*, p. 93; substitute name for *Coluber ahaetulla* Linnaeus.

Dendrophis liocercus SCHLEGEL, 1837, (in part), *Essai sur la physionomie des serpens*, vol. 2, p. 224.

Leptophis ahaetulla FITZINGER, 1843, *Systema reptilium*, vol. 1, p. 26.

Leptophis liocercus DEPLANCHE, 1858, *Bull. Soc. Linnéenne Normandie*, vol. 3, p. 13.

Leptophis ahaetulla PARKER, 1935, *Proc. Zool. Soc. London*, vol. 2, pt. 3, p. 520.

Leptophis ahaetulla ahaetulla OLIVER, 1942, *Occas. Papers Mus. Zool. Univ. Michigan*, no. 462, p. 1.

Thalerophis richardi OLIVER, 1947, *Copeia*, p. 64.

TYPE LOCALITY: The Guianas.

RANGE: From British Guiana south along the Atlantic coast to the state of Bahia, Brazil (fig. 10).

DESCRIPTION: The maxillary teeth are 23–28, average 25.3 for 18 observations; the last three maxillary teeth are enlarged (fig. 1C). The hemipenis is six subcaudals long, bare opposite subcaudal 1. There are five to six somewhat enlarged spines at the base oppo-

site the common boundary of subcaudals 1 and 2. These are followed distally by five to six transverse rows of smaller spines opposite subcaudals 2 and 3. The spines pass immediately into calyces with long fringing papillae; the papillae decrease in length and number distally, becoming more fleshy towards the tip. The distal half of the organ opposite subcaudals 4, 5, and 6 is calyculate.

Keels are usually present on the scales of rows II–XIV, but occasionally only on the scales of rows VI–X; the keel is absent or reduced on the scales of the vertebral row. There is no keel on the scales of row VI above the anus, and there are no keels on the dorsal scales of the tail. The scales of the vertebral row are slightly enlarged. The transverse rows of dorsal scales on the anterior part of the body are arranged in distinctly oblique rows.

The reduction in number of rows of dorsal scales involving rows V–VI or VI–VII occurs opposite ventrals 92–107, average 99.42, in the males; 95–109, average 103.03, in the females. That involving rows III–IV occurs opposite ventrals 89–108, average 98.75, in the males; 100–110, average 104.80, in the females. Reduction in the number of dorsal scales on the tail from six to four rows occurs opposite subcaudals 4–15, average 7.08, in the males; opposite subcaudals 3–10, average 5.61, in the females.

The ventral plates are 156–176, average 162.55, in the males; 159–178, average 164.91, in the females. The subcaudals are 146–178, average 160.75, in the males; 144–174, average 160.37, in the females. The anal plate is usually divided.

The labials are variable but most frequently are nine upper and 11 lower. The loreal shield is normally absent. The oculars consist of one preocular and two postocular shields. The lower postocular plate is less than half the size of the upper. The preocular is normally not in contact with the frontal. The parietal is longer than broad, not or but slightly notched by the upper posterior temporal, and rounded posteriorly. The parietal is not in contact with the lower postocular. The length of the frontal is greater than the length of the interparietal suture. The temporals are typically one to two. The eye is moderate in size; its diameter is equal to, or

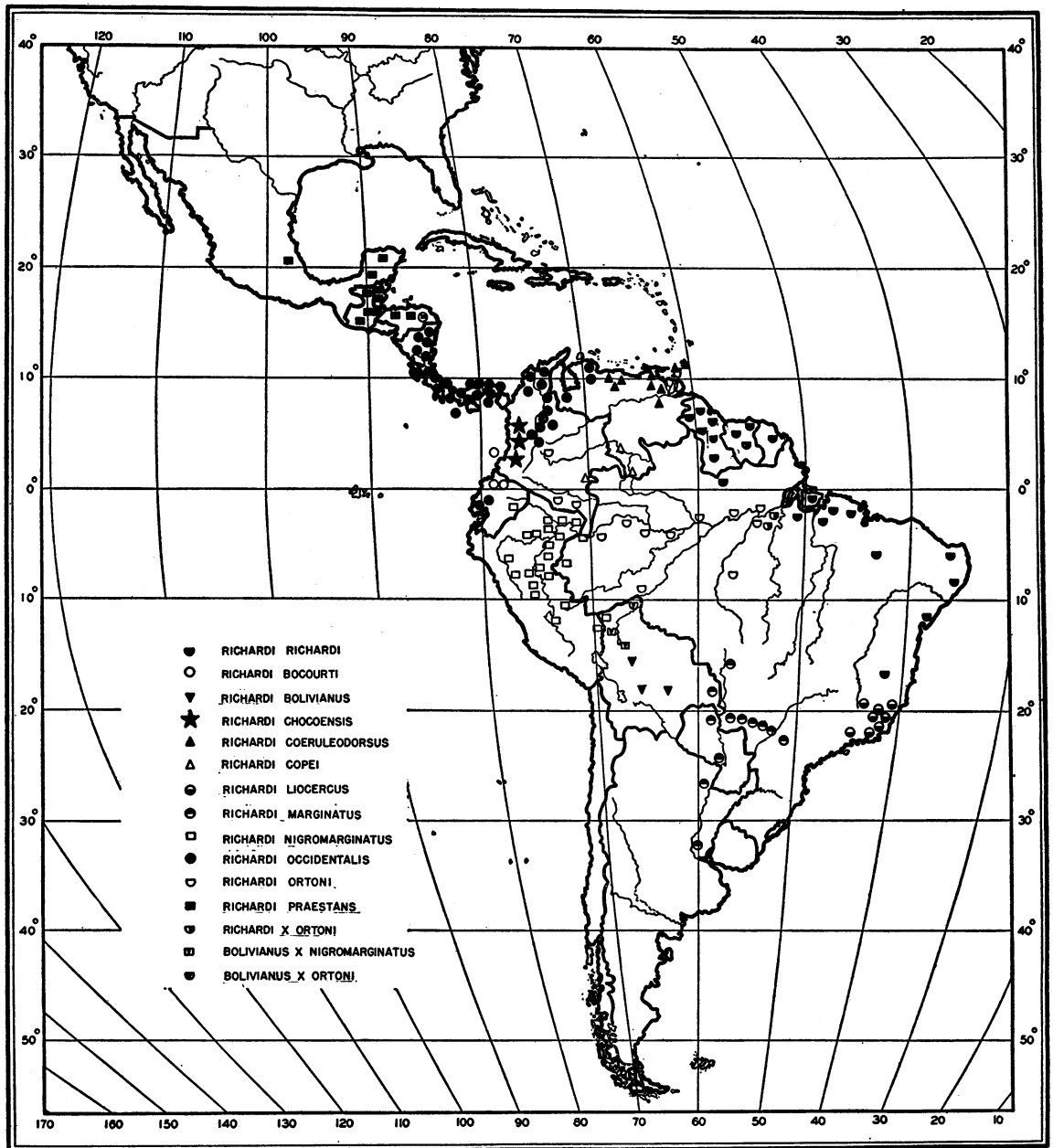


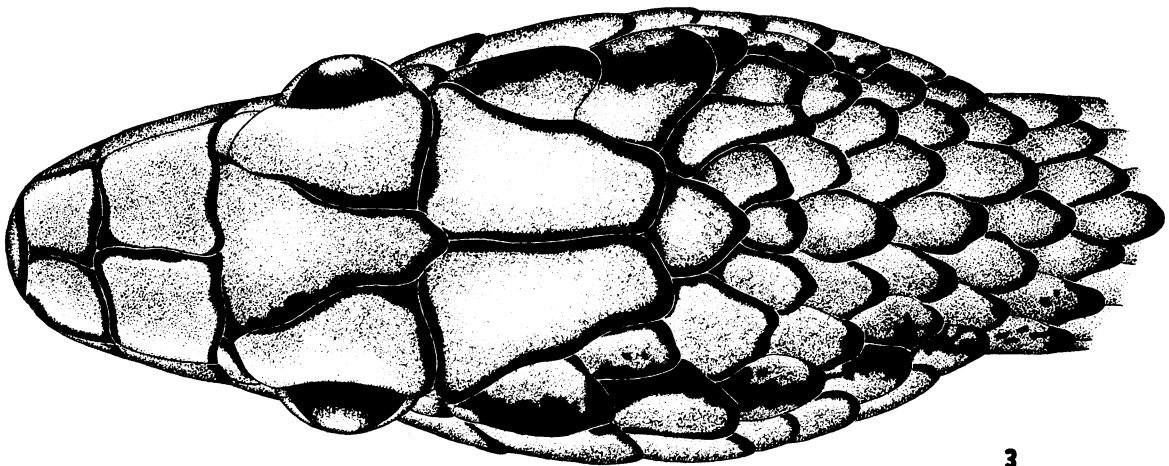
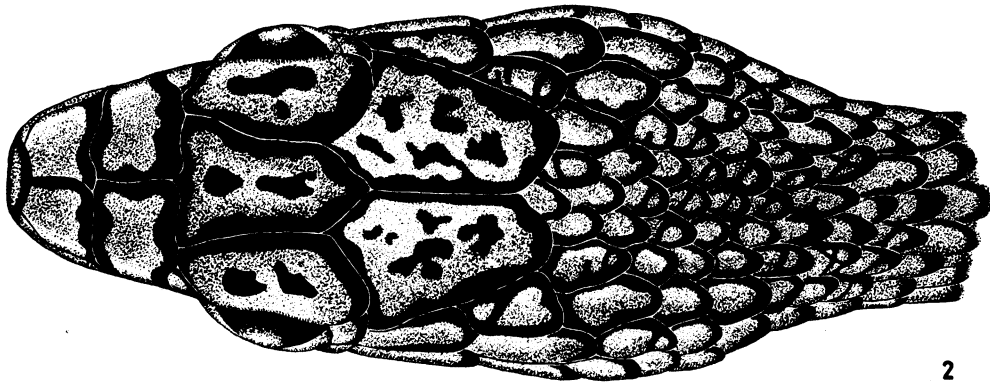
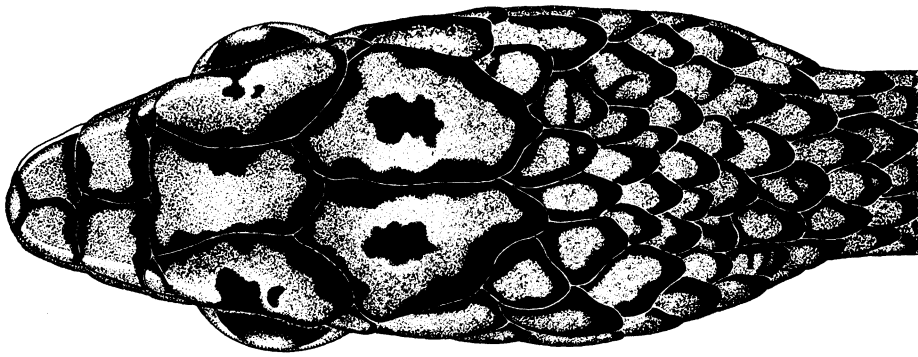
FIG. 10. Distribution of *Thalerophis richardi* based on the locality data of the specimens examined.

slightly less than, the distance from its anterior border to the nostril.

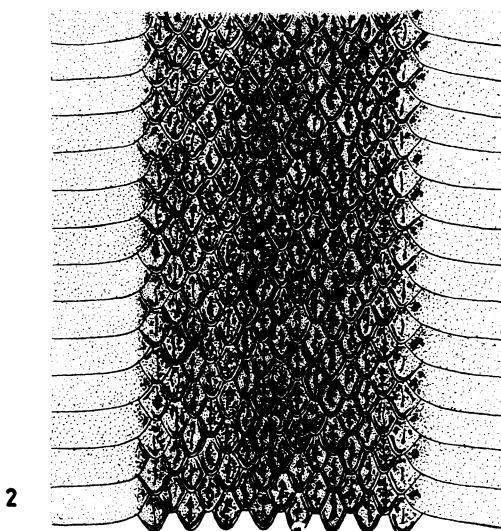
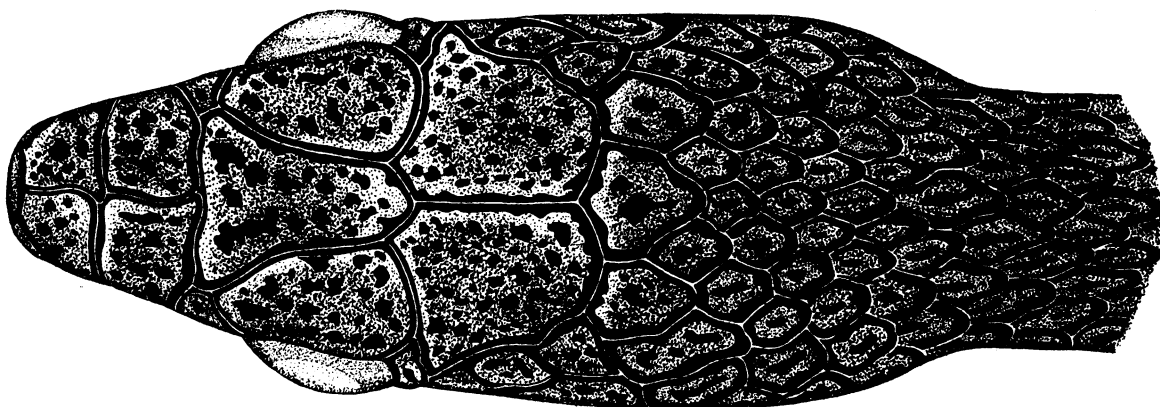
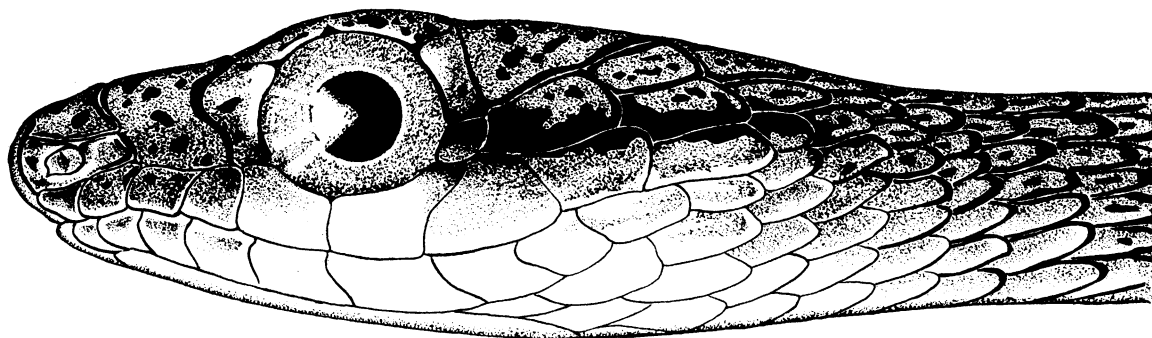
The largest male specimen had a head-body length of 940 mm., plus a tail length of 523+ mm.; the largest female had a head-body length of 943 mm., plus a tail length of 588+ mm. The tail/body ratio in 12 males with complete tail is .60-.71, average .640; in

14 females this ratio is .61-.72, average .655.

The coloration in alcohol is: top of head dark blue (Dark Orient Blue) to dark bluish green (Sea Green); narrow black ocular stripe commences on lower posterior edge of nasal plate and extends posteriorly along upper edges of upper labials 2, 3, 4, and 5, not or but rarely on lower edge of prefrontal and pre-



Dorsal view of heads of three subspecies of *richardi*, illustrating the distribution of black pigment on the head shields. 1. *nigromarginatus*. 2. *bolivianus*. 3. *marginatus*



1. Lateral and dorsal views of head of *Thalerophis richardi bocourti*, illustrating distribution of black pigment on the head shields. 2. Midbody pattern of the same subspecies

ocular. Posterior to orbit stripe broadens out, covering all or nearly all of lower postocular, occasionally lower edge of upper postocular, passing posteriorly along common suture of upper labials and temporal shields, almost equally distributed on the plates involved. Stripe may continue onto body for short distance or may disappear two scales posterior to last upper labial.

Dark blue or bluish green coloration of head continues onto body, anteriorly on rows II–XIV where it is present only on upper edge of scales of rows II and XIV, or rarely only on rows IV–XII. Dorsal scales narrowly margined with black above and with black tips to scales. A short distance posterior to head the scales of vertebral row become light in coloration, light metallic bronze (Old Gold) with stratum corneum present, or light gray (Pale Gull Gray) when stratum corneum is absent, forming a longitudinal light vertebral stripe characteristic of this subspecies. Posteriorly the light coloration of vertebral stripe spreads out laterally, occupying the scales of the paravertebral rows, while light ventral coloration encroaches dorsally on lateral rows so that dark blue or greenish blue lateral coloration is reduced in distribution.

On posterior third of body the bluish coloration is reduced to a stripe on upper half of row III, all of row IV, and lower half of row V, or further reduced to a narrow stripe along common borders of rows IV and V. Two lateral stripes normally continue onto tail where they become indistinct and are present only along middle of two median rows posterior to point of reduction from six to four rows of scales.

Upper labials below black upper edges, chin, and anterior ventrals pure white to dirty white; ventral color extends dorsally onto lower rows of dorsals where it is adulterated by minute stippling of a metallic bronze color. Posteriorly ventrals become somewhat darker in color through presence of minute stippling of brown. Where stratum corneum is present on posterior third of body, ventrals and row I and lower half of row II are light brown (Olive Lake), whereas rows above with exception of those involved in lateral blue stripe are dark golden brown (Isabella Color) with metallic luster.

A color description of a living specimen has

been given by Beebe (1946, p. 33): "Color in Life: Coll. No. 609, Kartabo, Color Plate 398, June 10, 1922, total length 1030 mm., weight 27.6 grams. Head grass green with an indistinct, oval, dark grayish blotch on top, between and slightly back of orbits. Back generally grass green with a median dorsal line of cadmium yellow, beginning narrowly on the back of the neck and widening and shading to old gold on tail. All the back scales are shaded on the outer edges with black and are turquoise green on the inner edges, giving a brilliant blue green tinge to the general color. Side of head tinged with chrysophrase and paling to light green above the superorbitals. There is a narrow, lateral, preocular line of black faintly shaded below with gold, running through the base of eye. Behind the eye this becomes wider and stronger and the gold almost covers the eighth labial. The upper labials below this lateral line are bluish-white. The lateral line becomes indistinct black and gold stippling on the side of the neck, widening and becoming light cadmium on anterior sides, widening and deepening again to a broad line of bronze on posterior body and tail. Chin and under neck white with pinkish tinge, becoming more and more heavily shaded with pale pinkish lavender and deepening through buff to dull brownish-lilac on posterior ventrals and tail.

"Iris strongly empire yellow around pupil, becoming lighter and greenish toward periphery. Two patches of olive green stippled with darker, small and barely touching iris on left, larger and wider on right, both sides fraying out downward in bright crescents. These dark marks continue the black, lateral head line through the orbit.

"The colors of this specimen after twenty-four years of preservation have all gone. It is now dark brownish-black above, leaden blue below, labials, chin and throat pale pink."

VARIATION: Among 39 males of this subspecies, two have undivided anal plates and 12 have the anal plate only partly divided; a single female out of 28 specimens has a partly divided anal plate, the remainder have the normal divided plate. These variants are discussed under the section on the anal plate. Ten individuals have eight upper labials on both sides of the head; seven have eight on one side and nine on the other; three have

nine on one side and 10 on the other side. In regard to the lower labials 10 have 10 on both sides, 10 have 10 on one side and 11 on the other, four have 11 on one side and 12 on the other, four have 12 on both sides, and two have nine on one side and 10 on the other. One specimen has a single preocular on one side but two on the opposite side, and four specimens have two preoculars on both sides. Only a single specimen varies from the normal condition of two postoculars, having three on one side. Two specimens have a single atypical loreal shield present on one side of the head only. The most common variation from the normal temporal formula is that of 1-1-2 which has been seen in four specimens. Two have the formula 1-1, two have 1-2/2-2, and one each has 1-1-2/2-2, 1-2/1-3, 1-2/2, and 1-2-2.

A slight average difference in the number of ventrals is apparent when the population of *richardi* from Brazil is compared with that from the Guianas.

BRAZIL	GUIANAS
Ventrals	
Males	
158-176, av. 165.69	156-170, av. 161.03
Females	
160-175, av. 166.30	159-171, av. 164.33

One aberrant subadult male has a ventral count of only 148 plates. Data for this specimen have not been included in the observed range for the subspecies.

There is considerable variation in the extent and distribution of the dorsal greenish blue coloration. Except for intergrades with *ortoni*, all specimens examined have the dorsal pattern of two dorsolateral blue stripes, at least anteriorly. The width of these stripes varies, and in a few specimens the stripes disappear completely on the middle and posterior thirds of the body so that these regions are uniform light to dark golden brown with the keels darker than the remainder of the scales.

Two juveniles, with head-body lengths of 206 mm. and 220 mm., exhibit a color pattern that is exactly like that of the adults except for being slightly lighter. But the pattern is striped rather than banded. Another juvenile, slightly larger than the previous one with a head-body length of 279 mm.,

has a color pattern that is striped like that of the adult, but also has a pattern of dark oblique bands superimposed on the striped pattern.

REMARKS: The pertinent details relating to the taxonomy of this subspecies have been presented in the discussion of the generic nomenclature and require no further mention here.

The relationships of this subspecies appear to be closest with *ortoni*. This is the only race with which it is known to intergrade, although it is doubtless capable of fertile interbreeding with one or more of the other subspecies to which it is geographically adjacent. The details of its relations to the other races are not known. On the basis of its color characters and morphological attributes it is also closely related to *coeruleodorsus*, *copei*, and *liocercus*. Intergradation with *ortoni* takes place in the vicinity of Santarem, Brazil, as indicated by a number of specimens from that locality.

The variation in regard to the extent and distribution of the dorsolateral greenish blue coloration in this form suggests the possibility of determining a correlation between habitat and coloration if precise ecological data were available for the specimens. The distribution of this subspecies is primarily the same as that of the tropical rain forest in the Guianas and the lower Amazon, but there are also scattered areas of savanna in the region from which specimens are known. It is possible that the observed variations in color may be associated with these different habitats.

The presence of two different types of juvenile color pattern in this race creates a number of speculations: (1) Is the banded specimen correctly identified; (2) is it an aberrant juvenile; (3) is this race in the process of developing a different juvenile pattern than the one observed in most other subspecies of this species; (4) is the race as now recognized a composite form? The banded juvenile specimen seems to be correctly identified on the basis of all other attributes and closely resembles adult specimens from the same locality. The locality is at the southern end of the geographic range, but the adults from the same locality are readily allocated with this race. As already mentioned, several authors have called attention to the

frequency of aberrant juveniles, and this banded individual may represent such a variant, but in respect to its other attributes it is not aberrant. More data are required to determine the problem of the two juvenile patterns. I do not feel that this is any indication that *richardi* as now recognized is a composite race.

All specimens of this subspecies examined by me have come from near the Atlantic coast from British Guiana to the southern border of the state of Bahia, Brazil. Joseph R. Bailey, who has furnished me with detailed data on some 30 specimens of the genus from South America, reports a specimen in the Instituto Butantan that was collected at Guaycurus, Matto Grosso, Brazil, by a reliable collector for that institution. Bailey states in correspondence that he sees no reason to doubt the locality data. In a later letter he mentions examining another specimen of *richardi* from "near the Serra de Parecis in western Matto Grosso." The specimens are definitely not *marginatus*, the only race known from Matto Grosso, and the data allocate the specimens with *richardi*. Whether the range of this form extends westward and south to Matto Grosso, whether these specimens represent an isolated population of *richardi*, whether they represent still another race of this subspecies, or just what their status is I cannot say.

SPECIMENS EXAMINED (87)

BRAZIL. Bahia: Bahia, B.M.N.H. (no reg. number), M.C.Z. No. 2944. Para: Baraja Island, B.M.N.H. No. 1923.11.9.115; Cameta, I.B. No. 2225; Javary, M.C.Z. No. 2977; Marajo Island, M.C.Z. No. 22448; Maranhao, M.C.Z. No. 5616; "Para," A.M.N.H. No. 56157, B.M.N.H. No. 95.3.29.9, M.C.Z. Nos. 894, 1173, 2881, 3294; Santa Clara, M.C.Z. No. 2989; Tapajos, M.C.Z. No. 3288. Pernambuco: M.C.Z. Nos. 1450, 5618. Piahy: I.B. No. 482; Therezina, I.B. No. 503. Rio Grande do Norte: U.M.M.Z. No. 56305. "Brazil," A.M.N.H. (no number), No. 37937, A.N.S.P. Nos. 5180, 5190, 5191, M.C.Z. Nos. 2973, 3004; Lago Alexo, M.C.Z. No. 2579.

BRITISH GUIANA. Aremu River, U.M.M.Z. No. 56427; Berbice, B.M.N.H. Nos. 53.4.6.73-53.4.6.76; Demerara, B.M.N.H. (no reg. number); Dunoon, U.M.M.Z. Nos. 47762, 47763; Essequibo River, C.N.H.M. Nos. 26661, 26662; Georgetown, A.M.N.H. No. 9624, U.M.M.Z. No. 80502; Kartabo, A.M.N.H. Nos. 15152, 15153; 18176-18178; 21281, 44906, Beebe Coll. Nos. 245, 609, 783,

C.N.H.M. No. 14839; McTurks, A.M.N.H. No. 60792; Pomeroon, U.S.N.M. Nos. 84516, 84518; Rupenuni Savannah, B.M.N.H. Nos. 1933.6-19.55, 1933.6.19.56; Wismar, A.M.N.H. No. 61559; "British Guiana," A.M.N.H. Nos. 2315, 36126, A.N.S.P. Nos. 5187-5189, B.M.N.H. Nos. 1929.4.29.8, 1929.4.29.9, U.S.N.M. No. 56440.

DUTCH GUIANA (SURINAM). Moengo, U.S.N.M. No. 64625; Paramaribo, A.M.N.H. Nos. 4425, 4427, 8131, 8147, 8687, 8688, B.M.N.H. Nos. 1946.4.16-1946.4.18, Geijkes Coll. Nos. 7 and 8-DG; "Surinam," A.N.S.P. Nos. 5183-5185. Geijkes Coll. Nos. 19, 20, U.S.N.M. No. 6116 (2); Border of Dutch Guiana and Venezuela, A.M.N.H. No. 4415.

FRENCH GUIANA. Cayenne, B.M.N.H. No. 1920.1.20.1413, M.C.Z. No. 1980, U.S.N.M. No. 451.

Thalerophis richardi bocourti Boulenger

Leptophis bocourti BOULENGER, 1898, Proc. Zool. Soc. London, p. 116; Paramba and Cachabe, Ecuador.

Leptophis occidentalis insularis BARBOUR, 1905, Bull. Mus. Comp. Zool., vol. 46, no. 5, p. 101; Gorgona Island, Colombia.

Leptophis occidentalis bocourti OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 15.

TYPE LOCALITY: Paramba and Cachabe, Ecuador.

RANGE: Known only from northwestern Ecuador and Gorgona Island, Colombia (fig. 10).

DESCRIPTION: The maxillary teeth number 22-25; the average for six observations is 23.3; the last three are enlarged. The hemipenis is seven subcaudals long with six basal spines opposite subcaudal 2; there are five to six transverse rows of smaller, stouter spines opposite subcaudals 3 and 4. These decrease in size distally, passing immediately into calyces with fringing papillae; the papillae decrease in length and number distally, while the calyces increase in size. The distal three-sevenths of the organ is typically calyculate.

Keels are present on the scales of rows II-XIV; these are strongly developed in males, less pronounced in females. The keel on the vertebral scales is less distinct than that on the scales of the paravertebral rows. The scales of row VI have a distinct but low keel above the anus; the two median rows of dor-

sal scales on the tail are keeled for most of the length of the tail.

Reduction in the number of rows of dorsal scales involving rows V-VI or VI-VII occurs opposite ventrals 94-100 in the males; opposite ventrals 99-100 in one female. That involving rows III-IV takes place opposite ventrals 96-98 in the males; opposite ventral 98 in one female. The reduction in the number of dorsal scales on the tail from six to four rows occurs opposite subcaudals 7-9 in the males; opposite subcaudal 5 in the female.

Ventrals in four males are 160-166; in two females 164 and 165. None of the males has a complete tail, but one has a subcaudal count of 163+. The two females have complete tails with 163 and 165 subcaudals. All have the anal plate completely divided.

Four specimens have nine upper labials, two have eight, and one has nine to 10. Four have 11 lower labials and three have 10. All lack a loreal plate and have the normal arrangement of oculars: one preocular and two postoculars. The preocular is not in contact with the frontal; the lower postocular is much smaller than the upper. The parietal is slightly longer than broad, notched by the upper posterior temporal, and not in contact with the lower postocular. The frontal is large; its length is greater than that of the interparietal suture. In all specimens the temporals are 1-2. The eye is moderate in size; its diameter is slightly less than the distance from its anterior edge to the nostril.

The largest male examined had a head-body length of 939 mm., plus a tail length of 582+ mm.; the largest female had a head-body length of 672 mm., plus a tail length of 458 mm. The male with 163+ subcaudals has a tail/body ratio of .62+; one female with a complete tail has a tail/body ratio of .66.

The specimens at hand are in a poor state of preservation and make a color description difficult. They are all dark slate gray in their present condition. The dark reticulations and streaks characteristic of this subspecies are plainly visible. These consist of a distinct, narrow, black, postocular stripe on the anterior temporal and the lower posterior temporal; all of the head shields possess a black margin, and numerous small black dots or streaks are present on the upper head shields (see pl. 19).

On the dorsal scales the keels and margins of the scales are black with numerous small black spots and streaks between the scale margins and the black keels. Several small circular black spots are present on the lateral edge of each ventral except at the extreme anterior end of the body (see pl. 19).

Boulenger (1898, p. 116) gives the color of this snake as follows: "Bright green above, closely speckled all over with black; the keels on the scales black; a black streak behind the eye; upper lip and lower parts pale green."

VARIATION: There is little variation apparent from the material at hand. Only a single male has been examined from Gorgona Island, so that no insular differentiation is apparent. The most distinctive feature of this subspecies is the nature and distribution of the black pigment over the head and body. This pattern is remarkably constant in all the specimens examined.

REMARKS: Boulenger (1898) described *bocourti* on the basis of two specimens from northwestern Ecuador, and referred a specimen described by Bocourt (1895) from Peru to the synonymy of his new species. Bocourt's specimen appears to be the same as *bocourti*, but the locality data are apparently in error. Boulenger's types are in the collections of the British Museum (Natural History), but have not been studied by me.

Barbour (1905) proposed the name *insularis* for a race of *Leptophis occidentalis* inhabiting Gorgona Island off the coast of Colombia. The population named by Barbour from Gorgona Island is identical with *bocourti*, although Barbour was correct in assigning it subspecific status. I have examined the type of *insularis* which is in the collections of the Museum of Comparative Zoölogy at Harvard College.

As indicated by Barbour (*loc. cit.*), the relationships of *bocourti* are with *richardi occidentalis*. However, the precise relation between the two is not known, and no intergrades between them have been studied. It is assumed that the two are not reproductively isolated and are capable of genetic exchange. Where the two subspecies are in contact is not definitely known, although the most probable area is in northwestern Ecuador. The population of *occidentalis* now known to occur in northwestern Ecuador exhibits greater differ-

ences from *bocourti* than do the specimens from the interior valleys of Colombia. The latter population is now well isolated geographically from *bocourti*. No specimens of *occidentalis* are known from the Choco of Colombia. This subspecies is replaced in that region by *chocoensis*. It seems unlikely but not impossible that the connection is through *chocoensis* to a more northern and, morphologically, more similar, population of *occidentalis*. At present there is no evidence to indicate the precise nature of the relationships between the subspecies *bocourti*, *chocoensis*, and *occidentalis*.

The only localities from which *bocourti* is known are in dense, humid, tropical forest.

SPECIMENS EXAMINED (7)

COLOMBIA. Narino: Gorgona Island, M.C.Z. No. 6985 (type of *occidentalis insularis* Barbour).

ECUADOR. Esmeraldas: Saint Javier, B.M.N.H. No. 1901.3.29.30; San Mateo, C.N.H.M. Nos. 28054, 28056. Imbabura: Carolina, Ibarra, U.M.-M.Z. Nos. 83709-83711.

Thalerophis richardi bolivianus Oliver

Leptophis ahaetulla bolivianus OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 1; Buenavista, Department of Santa Cruz, Bolivia.

TYPE LOCALITY: Buenavista, Department of Santa Cruz, Bolivia.

RANGE: Known only from the departments of Beni and Santa Cruz in Bolivia (fig. 10).

DESCRIPTION: The maxillary teeth are 21-26, with an average of 23.7 for 10 observations. The last three maxillary teeth are enlarged. The hemipenis is six subcaudals long, with no enlarged basal spines; there are five to six transverse rows of small spines opposite subcaudals 2 and 3, the seven spines of proximal row largest; the spines decrease in length distally, passing opposite the posterior end of subcaudal 3 into calyces with long fringing papillae that obscure the structure of the calyces. The papillae decrease in length distally and become more fleshy; the distal portion is typically calyculate opposite the posterior half of subcaudal 4, all of caudals 5 and 6.

Keels are present on the scales of rows II-XIV; row VI is usually keeled above the anus, and there are short but distinct keels on the dorsal scales of the tail posterior to the point

of reduction from six to four rows for at least a short distance posterior to that point, frequently for most of the tail length.

Reduction in the number of rows of dorsal scales involving rows VI-VII takes place opposite ventrals 93-97, average 94.75, in the males; opposite ventrals 87-108, average 99.50, in the females. That involving rows II-III or III-IV occurs opposite ventrals 96-103, average 99.37, in the males; opposite ventrals 98-112, average 102.80, in the females. The reduction in the number of dorsal scales on the tail from six to four rows occurs opposite subcaudals 5-12, average 7.87, in the males; opposite subcaudals 4-7, average 5.10, in the females.

The ventral plates in the males are 156-169, average 162.00; in the females 162-173, average 167.70. Two males have complete tails with subcaudal counts of 147 and 151; six females with complete tails have 147-158 subcaudals with an average of 149.26. One male has a partly divided anal plate; all others studied have the anal plate completely divided.

The upper labials are eight in all specimens examined. The number of lower labials is variable, but individuals with 10 on both sides are more frequent than those with other numbers. The loreal plate is normally absent. The oculars are typically one preocular and two postoculars. The lower postocular is smaller than the upper. The preocular normally is not in contact with the frontal. The parietal is longer than broad, not or but slightly notched by the upper posterior temporal, usually rounded posteriorly. The parietal is not in contact with the lower postocular. The length of the frontal is greater than the length of the interparietal suture. The temporals are 1-2 in the majority of specimens. The eye is moderate in size with the diameter equal to, or slightly less than, the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 757 mm., plus a tail length of 376+ mm.; the largest female individual had a head-body length of 625 mm., plus a tail length of 361+ mm. The tail/body ratio in two males with complete tails is .59 and .60. Two females with complete tails have head/body ratios of .59 and .61.

The coloration in alcohol is: top of head greenish blue (Sea Green), head scales narrowly but distinctly margined with black, usually a poorly defined, diffuse black spot on each parietal and a distinct, elongate black spot on each supraocular plate (pl. 18). Greenish blue coloration of head passes posteriorly onto body and tail, occupying all of scales of rows I–XV on body. Dorsal body scales not or but slightly margined with black, but keels of these scales black (fig. 6). Anteriorly dorsal coloration is present on outer edges of ventrals; ventrals not margined anteriorly with dark greenish blue or blue and dirty white in color between outer edges.

Posteriorly lateral coloration spreads out on median portion of ventral plates so that short distance anterior to anus ventral coloration is uniform pale green (Glaucous Green to Deep Glaucous Green). This coloration continues posteriorly onto tail, becoming somewhat darker towards tip. Upper labials pale green to dirty white; chin and gular region white.

VARIATION: Seven individuals have the asymmetrical lower labial formula of 10/11, one has 11/12, and four have 9/10, whereas 11 have 10/10 and two have 11/11. Only one specimen varies from the typical condition of a single preocular on both sides of the head; it has one on one side and two on the other side. One specimen has three postoculars on both sides, one has three on one side and two on the other, and one individual has a single postocular on one side and two on the other. The variation in respect to the number of temporal shields is mostly in the direction of a reduction in the number of temporals. Three specimens have the formula 1-1 on both sides, one has 1-1/1-2, one has 1/1-2, two have 1-1-2 on both sides, and one has 1-1-2/1-2.

Two specimens have a loreal plate present on both sides of the head, and two have this plate atypically present on one side of the head only. The remaining specimens examined lack this shield on both sides of the head.

A juvenile, with head-body length 331 mm., has a pattern of narrow black oblique bands on the anterior third of the body resembling that observed in other forms that

characteristically have a banded juvenile pattern. Variation in adult coloration consists primarily of differences in the prominence of the black marks on the keels and the extent of the black spots on the dorsal surface of the head. The specimen illustrated in plate 18 shows an extreme extent of the black pigment on the head and in this respect indicates an approach to the condition found in *nigromarginatus*. Most specimens of *bolivianus* do not have such prominent parietal spots as shown in the plate.

REMARKS: No changes in the taxonomic status of this form have been necessitated since its description (Oliver, 1942).

This subspecies most closely resembles *nigromarginatus* to the northwest in most of its characters; intergradation is indicated not only with that subspecies but also with *ortoni* to the north and probably with *marginatus* to the east. The primary diagnostic differences between those forms are in the color pattern, although average differences in morphological attributes are also apparent. Intergradation with *nigromarginatus* is indicated by a specimen (A.M.N.H. No. 22446) from Rurrenabaque, Beni, Bolivia. The color pattern of this specimen (pl. 18) is intermediate in some details between that which characterizes the separate subspecies, although it most closely resembles *bolivianus* in this respect (fig. 6). The ventral count is that of *nigromarginatus*.

Intergradation with *ortoni* is indicated by two specimens (A.M.N.H. Nos. 22267–22268) from northern Bolivia, collected along the Beni River. These specimens are more like *ortoni* in the total of their characters, but the color pattern indicates an approach to the coloration of *bolivianus* in the small head spots and the fine black lines on the keels of the dorsal scales. No specimens from specific geographic areas have been examined that suggest intergradation between *bolivianus* and *marginatus*. One specimen without locality data combines some of the color characters of the two races, suggesting the possibility of genetic exchange between the two forms. However, little can be denoted by a single specimen that is of unknown origin.

In distribution *bolivianus* is known at present from the lowland tropical rain forest that occupies a narrow strip along the eastern edge

of the Andes in central and northern Bolivia.

SPECIMENS EXAMINED (26)

BOLIVIA. Beni: Rurrenabaque, A.M.N.H. No. 22446; upper Beni River, A.N.S.P. No. 11335. Santa Cruz: Buena Vista, B.M.N.H. Nos. 1928-8.1.183, 1928.8.1.184, C.M. No. 2702, C.N.M.H. Nos. 35614-35621, M.C.Z. No. 27553, U.M.M.Z. Nos. 60701, 60702, 60709, 67973 (type), 67974, 67975, 67976 (2), 67977 (2); Santa Cruz de la Siema, B.M.N.H. No. 1904.10.29/53; Las Yuntas (=Las Yungas?), C.M. No. 23.

Thalerophis richardi chocoensis Oliver

Leptophis occidentalis chocoensis OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 15; Penalisa, Rio Condote, Choco, Colombia.

TYPE LOCALITY: Penalisa, Choco, Colombia.

RANGE: Known only from the Choco region of Colombia (fig. 10).

DESCRIPTION: The maxillary teeth are 22-23; the average for nine observations is 22.3; the last three are enlarged. The hemipenis is seven subcaudals long, with six moderately enlarged spines at the base of the organ opposite the suture between subcaudals 2 and 3. The longest of these is adjacent to, and on the inner side of, the sulcus; there are six transverse rows of smaller, stouter spines following distally. These decrease in size towards the tip, opposite caudals 3 and the anterior one-third of subcaudal 4. The spines gradually merge into calyces with fringing papillae. The papillae decrease in number and length distally, becoming fleshy. The distal half of the organ is typically calyculate.

Keels are present on the scales of rows II-XIV, with an occasional keel on the scales of rows I and XV in adult males. The keel on the vertebral scales is not so prominent as those on the paravertebrals, disappearing a short distance anterior to the anus. Low but distinct keels are present on the tail posterior to the point of reduction from six to four rows.

Dorsal scale reduction involving rows VI-VII takes place opposite ventrals 96-102 in males and 102-103 in the only female for which this information was recorded. That involving rows III-IV takes place opposite ventrals 98-101 in males and opposite ventrals 103-104 in the female. Reduction of the

dorsal scales on the tail from six to four occurs opposite subcaudals 6-8 in the males, opposite subcaudal 5 in the female.

The ventrals are 161-168, average 164.50, for four males; 165, 165, and 167 in the three females. The males have 172+ to 183 subcaudals, with an average of 177.75; two females with complete tails have 175 and 178 subcaudals. All specimens studied have the anal plate divided.

The labials are usually nine upper and 11 lower, with the lower labials the more variable. The loreal plate is absent in all specimens. The oculars are normally one preocular and two postoculars; the lower postocular is slightly smaller than the upper. The preocular is normally in contact with the frontal. The parietal is slightly longer than broad, notched by the upper posterior temporal, and not in contact with the lower postocular. The frontal is very broad in front, its width equal to four-fifths of its length. The temporals in all specimens are one anterior and two posterior. The eye is large, its diameter is greater than the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 1104 mm., plus a tail length of 697+ mm.; the largest female examined had a head-body length of 950 mm., plus a tail length of 485+ mm. The tail/body ratio in the males varies from .54 to .67, average .615. In the two females with complete tails the ratios are .62 and .66.

The coloration in alcohol is: top of head greenish brown (Light Brownish Olive) with stratum corneum, (Light Grayish Olive) without stratum corneum. A broad black postocular stripe present on lower one-half of upper postocular, upper one-third of lower postocular, virtually all of anterior temporal, all of lower and lower one-third of upper posterior temporal, and upper edge of labials 8 and 9. Stripe continues onto neck for a distance of two scales posterior to last labial. Upper labials are light olive green (Bluish Gray-Green).

Color of head extends onto neck for a distance approximately equal to half length of head. Color of median dorsal region, including upper half of rows V and XI, and all of rows VI-X greenish blue (Sea Green) with faint metallic copper reflection; scales of

lower dorsal rows bluish (Orient Blue). Median coloration much reduced on tail which is mostly of a bluish color (Orient Blue).

Ventral surface of head, body, and tail pale blue to light bluish green (Light Glaucous Blue), somewhat lighter on throat and chin. Keels of all dorsal scales broadly and distinctly marked with black; marking on keels of rows VI, VII, IX, and X broadest, forming two black lines on each side of vertebral row.

VARIATION: One specimen had eight upper labials on one side of the head and nine on the other. Four of the seven specimens studied have asymmetrical lower labial formulas with one each having 8/9, 8/10, 10/11, and 11/12; the remaining three individuals have 11 on both sides. One specimen has three postoculars on both sides of the head.

One subadult female retains traces of a banded juvenile pattern. This specimen is lighter than the others, with the lower row of dorsals on each side much lighter than the other dorsal rows. The ventral coloration and that of the lower edge of the upper labials are nearly white, although there are outer margins of blue on the anteriolateral edges of the ventrals.

REMARKS: Little has been added to our knowledge of this form since it was described (Oliver, 1942), and its taxonomic status is little modified, although the generic and specific nomenclature has changed.

The relationships of *chocoensis* are with *occidentalis* and *bocourti*. It more closely resembles the former than the latter in morphological attributes, but it seems unlikely that it is reproductively isolated from either form. At present no evidence of intergradation between any of these three has been studied.

Both *chocoensis* and *bocourti* occupy essentially similar climatic regions, characterized by a hot, humid climate. Both are inhabitants of dense forest. Both differ from *occidentalis* in part by a marked increase in black pigment, and they differ in part from each other in the distribution of this black pigment. It is this differentiation in regard to the dispersion of the black pigment in two closely related forms occupying similar and adjacent geographic regions that constitutes one of the most interesting problems of speciation in the genus.

SPECIMENS EXAMINED (7)

COLOMBIA. Choco: Pena Lisa (= Penalisa), Rio Condoto, B.M.N.H. Nos. 1919.11.12.46–1919.11.12.47, 1914.5.21.38, U.M.M.Z. No. 55528 (type), Pizarro, C.N.H.M. No. 43737; "Choco," A.M.-N.H. No. 8062, M.C.Z. No. 13298.

Thalerophis richardi coeruleodorsus Oliver

Ahaetulla liocercus MOLE AND URICH, 1894, Proc. Zool. Soc. London, p. 510.

Leptophis coeruleodorsus OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 4; Trinidad, British West Indies.

Leptophis ahaetulla ortoni BEEBE, 1946, Zoologica, vol. 31, pt. 1, p. 34.

TYPE LOCALITY: Trinidad, British West Indies.

RANGE: The northeastern coastal region of Venezuela, the islands of Trinidad and Tobago in the British West Indies (fig. 10).

DESCRIPTION: The maxillary teeth number 21–23, with an average of 22.2 for eight observations; the last three are enlarged (fig. 1D). The hemipenis is seven subcaudals long, with six to eight small basal spines attached opposite the suture between subcaudals 2 and 3; the longest of these spines is adjacent to, and on the inner side of, the sulcus. These are followed distally by five to seven transverse rows of small, stout spines opposite subcaudals 3 and 4. The spines decrease in size distally and merge into calyces with spinous fringing papillae that obscure the structure of the calyces. The papillae decrease in length and number distally, becoming more fleshy and exposing the structure of the calyces. The distal end of the organ, opposite the posterior half of subcaudal 6 and all of subcaudal 7, is typically calyculate.

Keels are present on the scales of rows II–XIV; those on rows VI–X are the strongest. Row VI may or may not be keeled directly above the anus; keels are usually absent on the dorsal scales of the tail.

Reduction in the number of rows of dorsal scales on the body involving rows VI–VII, occasionally rows V–VI, occurs opposite ventrals 91–103, average 96.92, in the males; opposite ventrals 96–111, average 102.55, in the females. That involving rows III–IV occurs opposite ventrals 93–108, average 100, in the males; opposite ventrals 93–113, average 105.22, in the females. Reduction of the dorsal scales on the tail from six to four rows

occurs opposite subcaudals 6–13, average 9.70, in the males; opposite subcaudals 6–8, average 6.42, in the females.

The ventrals are 158–166, average 160.79, in the males; 158–172, average 164.75, in the females. The subcaudals are 152–172, average 163.33, in the males; 160–167, average 163.80, in the females. Four specimens exhibit atypical variation in the condition of the anal plate; the remainder have the normal divided plate.

The upper labials are normally either eight or nine; the lower labials are most frequently 10. All specimens studied lack the loreal shield. The oculars are usually one preocular and two postoculars. The lower postocular is much smaller than the upper; the preocular is not in contact with the frontal. Parietal much longer than broad, distinctly notched by upper posterior temporal. Frontal large, its length greater than the length of the interparietal suture. Temporals are 1-2 except in two specimens that have 1-1/1-2 and 1-1-2. The eye is moderate in size, its diameter less than the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 860 mm., plus a tail length of 534+ mm.; the largest female had a head-body length of 963 mm., plus a tail length of 588+ mm. Five males have tail/body ratios of .58–.71, average .668; three females have tail/body ratios of .65–.68, average .667.

The coloration in alcohol is: top of head dark blue (Orient Blue); a distinct rather broad black postocular stripe occupying all of lower postocular, occasionally lower one-fourth of upper postocular, lower half of anterior temporal, lower one-half to two-thirds of lower posterior temporal, upper edges of last three upper labials, and extending onto neck a distance of two to eight scales posterior to last labial. Anterior to orbit stripe is indicated by black upper margin on all labials except first; upper labials white except for blue upper margin of those included in ocular stripe. Anterior lower margin of nasal and lower one-half to two-thirds of rostral white.

Blue coloration of head extends onto body where it is limited in distribution to five median dorsal scale rows; five lower rows on each side are dirty white on anterior one-half

of body. All of dorsal scales with a narrow blue margin, at least on posterior half of scale many with blue posterior tip. Scales of median five rows have irregular scattered light spots diluting blue coloration; posteriorly light spots on median scale rows increase in size, restricting blue coloration to three median scale rows at midbody. Farther posterior, blue coloration may be reduced still more, so that only vertebral row may be blue, although usual condition is a blue vertebral stripe formed from blue coloration on paravertebrals and vertebral row. Blue coloration never completely restricted or obliterated on posterior third of body, and in all specimens examined it extends onto tail for most of tail length.

Color below blue median stripe grades from light metallic bronze (Light Old Gold) dorsally to dirty white on ventrals. Keels of dorsal scales dark brown on middle and posterior thirds of body. When stratum corneum is present posterior two-thirds of body light brown (Isabella Color to Old Gold) with fine longitudinal dark brown stripes formed by color of keels.

A color description of a living specimen has been given by Beebe (1946, p. 34) for an individual from Caripito, Venezuela: "In general color above it was turquoise blue from snout to tail tip. The lowermost two or three scales throughout the body, from the gape to the vent, were bright orange, while the labials, chin, throat and ventral to vent were white. The orange spreads across all subcaudals as well as the sides of the tail. A narrow, preocular black line is continued pigmentally through the iris itself, and on to a stronger black line along the side of the head to the last upper labial. The top and bottom of the iris are bright yellow.

"In this specimen, after four years in preservative, all color is lost, the dorsal scales being brown, and ventrals steel blue."

VARIATION: Twenty specimens have eight upper labials, 12 have nine, and one each has 7/8, 7/9, 8/9, and 9/10. Variation in lower labials includes nine with 10/11, three with 11, two with 9/10, and one with 8/9. Three have two preoculars on both sides, while three also have one on one side and two on the opposite side. Only a single specimen varies from the typical condition of two post-

oculars, with one on one side and two on the other. The only variations observed in the temporals are one with 1-1/1-2 and one with 1-1-2.

A slightly higher number of ventrals appears in the population from Tobago, as indicated by the data for females.

and *coeruleodorsus* in northwestern Venezuela. The separation in the east between *coeruleodorsus* and *richardi* is not so apparent. The area between the known ranges of these two has not been explored extensively from a herpetological standpoint. The distribution of *richardi* probably coincides with the areas

	VENEZUELA	TRINIDAD	TOBAGO
Ventrals			
Males	158-164, av. 160.83(6)	158-164, av. 160.33(12)	166
Females	158-164, av. 161.33(3)	160-167, av. 163.66(9)	167-172, av. 169.75(5)

As pointed out above there is noticeable variation in respect to the width of the mid-dorsal blue stripe and the amount of light coloring on the median dorsal scales. Although very much reduced in two specimens, the blue coloration is always present. In three specimens the lateral light area is light green with an iridescent sheen. Two of the specimens from Tobago Island are nearly black from preservation, and the median dorsal blue band is scarcely discernible.

REMARKS: Until its recognition as a distinct entity, this form was included under the most widely known South American species, *richardi* (variously termed *ahaetulla* or *liocercus*). The form is here considered as a subspecies of *richardi*.

This subspecies occurs in a geographic area that is between *occidentalis* and *richardi*. It is not surprising to find that it also represents an intermediate condition between these two races in regard to many structural attributes. Morphologically it is somewhat more like *occidentalis* than *richardi*, whereas in coloration it is more like the latter than the former. These intermediate populations, here called *coeruleodorsus*, might be labeled as intergrades between *occidentalis* and *richardi*. However, they are distinct populations that maintain a high degree of constancy in virtually all characters that have been analyzed throughout a sizable geographic area that includes two large islands.

There is no indication at present where intergradation takes place between the subspecies mentioned above. The northern continuation of the Cordillera de los Andes, the Venezuelan extension of the eastern Andes of Colombia, appears to separate *occidentalis*

of tropical rain forest in the Guianas and eastern Venezuela, whereas *coeruleodorsus* appears to occupy the scrub or tropical deciduous forest. Thus the two races are probably in contact in the vicinity of the mouth of the Orinoco River where the two types of forest occur together.

It is possible with the examination of additional material that the population on Tobago Island may warrant nomenclatorial recognition as distinct from the Trinidad and Venezuelan populations. At present the available material is inadequate for a clear analysis of these various populations.

SPECIMENS EXAMINED (35)

BRITISH WEST INDIES. Tobago: B.M.N.H. (no reg. number); Milford Bay, M.C.Z. Nos. 1194, 1195, 12026, 12027.

TRINIDAD. Mt. St. Benedict, St. George Co., C. M. Nos. 6491, 6540; Port of Spain, B.M.N.H. No. 1940.3.11.83, M.C.Z. No. 6740; "Trinidad," A.M.N.H. Nos. 8718, 8719, 9022 (type), 9023, 9024, B.M.N.H. Nos. 71.5.6.4, 94.4.6.15-94.4.6.16, U.S.N.M. Nos. 5587, 15235, 17746, 59931-59933, 60598; Tucker Valley, A.M.N.H. No. 64478 (2).

VENEZUELA. Aragua: Limon, Beebe Coll. No. 30613. Bolivar: Cariquita, A.N.S.P. No. 18288. Distrito Federal: Macuto, U.S.N.M. No. 27821. Miranda: Rio Chico, U.S.N.M. No. 27831; Santa Lucia, C.M. No. 7433. Monagas: Caripito, Beebe Coll. Nos. 30163, 30280; Sotillo, near Uracoa, C.M. No. 17387.

Thalerophis richardi copei Oliver

Leptophis copei OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 7; Salto do Hua, Brazil-Venezuela boundary.

TYPE LOCALITY: Salto do Hua, Brazil-Venezuela boundary.

RANGE: Known only from the area of the

divide between the Orinoco and Negro rivers (fig. 10).

DESCRIPTION: The maxillary teeth number 26–28, the average of six counts is 27.0; the last three teeth are enlarged (fig. 1B). The hemipenis is seven subcaudals long; the proximal portion is bare, with five enlarged basal spines opposite the posterior half of subcaudal 2. The two largest spines are adjacent to the sulcus. These are followed distally by six to seven transverse rows of spines opposite subcaudal 3 and the anterior one-third of subcaudal 4; the spines gradually pass distally into calyces with long fringing papillae that obscure the structure of the calyces. The papillae decrease in length distally, becoming increasingly fleshy. The distal portion opposite subcaudals 6 and 7 is typically calyculate.

Keels are present on rows II–XIV; those of rows VI, VII, IX, and X are the strongest; row VI is normally not keeled above the anus; there are no keels on the scales of the tail posterior to the point of reduction from six to four rows. The scales of the vertebral and paravertebral rows are somewhat larger than those of the adjacent rows.

Dorsal scale reduction involving rows V–VI occurs opposite ventrals 107–116, average 110.75, in the males; opposite ventral 118 in the single female specimen. That involving rows III–IV occurs opposite ventrals 107–118, average 112.00, in the males; opposite ventrals 119–120 in the female. The reduction of dorsal scale rows on the tail from six to four rows occurs opposite subcaudals 4–9, average 6.00, in the males; opposite subcaudal 4 in the female.

The ventrals are 173–179, average 176.60, in the males; and 176 in the female. Two males have complete tails with 178 and 182 subcaudals. The female specimen has a damaged tail. Three of the five males have divided anal plates; the single female has the anal plate divided.

The upper labials are normally nine and the lower labials 11. All lack the loreal plate and have the normal generic condition in respect to the oculars: one preocular and two postoculars. The postoculars are approximately equal in size. The preocular may or may not be in contact with the frontal. The

parietal is much longer than broad, is not in contact with the lower postocular, and is usually notched by the upper posterior temporal. The frontal is large; its length is slightly greater than that of the interparietal suture. The majority of specimens have the temporals 1–2. The eye is moderate to large in size; its diameter is equal to, or slightly less than, the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 1008 mm., plus a tail length of 622+ mm.; the female has a head-body length of 762 mm., plus a tail length of 490+ mm. One male with a complete tail has a tail/body ratio of .68.

The coloration in alcohol is: top of head dark greenish blue (Sea Green); black postocular stripe on upper two-thirds of lower postocular and posteriorly along common border to posterior upper labials and temporals, terminating on last upper labial. Ocular stripe not present anterior to orbit or indicated only by an irregular suffusion of black on upper edge of upper labials.

Greenish blue coloration of top of head extends posteriorly onto anterior portion of body, where it is present on scales of rows III–XIII. Scales of rows II–XIV all tipped with black posteriorly and many with anterior tip of black as well as narrow dorsal margin of black. Greenish blue coloration reduced in distribution by a light—white to light blue—anterioventral spot on scales. Light spots appear a short distance posterior to head and increase in size posteriorly. Light areas on scales of vertebral row and lower dorsal rows III and IV expand more rapidly than on rows V, VI, and VII so that at midbody a light vertebral stripe is present and greenish blue lateral area is reduced to a narrow stripe occupying only rows VI and VII.

Posterior to midbody greenish blue coloration may be completely obliterated except for irregular spots on concealed portions of scales. Dorsal coloration then a light grayish (Light Olive-Gray) with stratum corneum absent or light to dark metallic bronze (Old Gold) with stratum corneum present. If greenish blue coloration is not completely obliterated, it persists as a narrow, diffuse,

dorsolateral stripe occupying paravertebral scale rows.

Upper labials below dark upper margins white to light cream (Cream Color). Lower labials, chin shields, ventrals, and subcaudals white to light cream (Cream Color).

VARIATION: One male has an undivided anal plate, and another has this plate only partly divided. One specimen has 10 upper labials on both sides of the head, while another has 10 on one side and nine on the other. Two have upper labials 11/12, and another specimen has 10/11. The following atypical temporal conditions have been observed: 1-1/1-2 in one individual, 1-1-2 in one specimen, and 1-1-2/2-2-2 in one specimen.

Most of the observed variation in this subspecies is in coloration. The specimen from San Antonio, Venezuela, has very little of the greenish blue coloration remaining on the exposed portion of the dorsal scales on the posterior five-sixths of the body. The stratum corneum is still present, and the predominant dorsal coloration is a dark metallic bronze (Old Gold). The light anterioventral spots are quite prominent.

One of the two specimens from Salto do Hua on the Brazil-Venezuela border has the dorsolateral greenish blue stripe continuous for the entire length. In the other specimen from this locality this stripe is obscured at midbody.

REMARKS: This form was described originally as a full species (Oliver, 1942) but is here assigned as a subspecies of *richardi*. This is in accord with the principles set forth in the introduction to this study.

In the total of its morphological characters *copei* appears to be closely allied to *richardi*. At the same time it exhibits a number of similarities to *ortoni*. Geographically it occupies a somewhat intermediate position but is closer to *ortoni* than to *richardi*. Too few specimens of *copei* are available for its variation to be analyzed adequately, and therefore it cannot be stated to which form it is most closely related. It differs from *ortoni* and *richardi* in the same way in regard to morphological attributes, e.g., a higher average number of maxillary teeth and ventral plates than either, and is different from both in

respect to color pattern. No intergradation has been observed between *copei* and either *richardi* or *ortoni*.

SPECIMENS EXAMINED (6)

BRAZIL. Amazonas: Salto do Hua, Brazil-Venezuela border, U.S.N.M. No. 83564 (type), 83570; Sao Isabel, A.M.N.H. No. 38097.

COLOMBIA: Vaupes: Caruru, A.M.N.H. Nos. 4463, 4464.

VENEZUELA: Amazonas: San Antonio, upper Orinoco River, U.S.N.M. No. 83617.

Thalerophis richardi liocercus Wied

Coluber liocercus WIED, Abbildungen zur Naturgeschichte von Brasilien, p. 665; Brazil.

Dendrophis liocercus SCHLEGEL, 1837, (in part), Essai sur la physionomie des serpens, vol. 2, p. 224.

(?) *Leptophis flagellum* ANDERSSON, 1901, Bi-hang till Handl. K. Svenska Vetensk. Akad., vol. 27, abd. 4, no. 5, p. 13; Rio de Janeiro, Brazil.

Leptophis liocercus DE WITTE, 1930, Une mission biologique Belge au Brésil, vol. 2, p. 3.

TYPE LOCALITY: Brazil.

RANGE: The littoral zone of southeastern Brazil (fig. 10).

DESCRIPTION: The maxillary teeth number 22-24; the average in 10 specimens is 23.0. The last three, occasionally four, teeth on the maxillary bone are enlarged, and usually the tips are laterally compressed on these enlarged teeth. The hemipenis is six subcaudals long, with four enlarged basal spines; the two on either side of the sulcus are the largest. These enlarged basal spines are followed distally by five to six transverse rows of short, stout spines opposite subcaudals 2 and 3. The spines decrease in length distally, passing into distinct calyces with fringing papillae. The papillae decrease in length and number towards the tip so that the distal half of the organ opposite subcaudals 4, 5, and 6 is calyculate.

Keels are present on the scales of rows II-XIV; usually there is no keel on the scales of row VI above the anus, and there are no keels on the dorsal scales of the tail. The scales of the vertebral row are occasionally slightly enlarged.

The reduction in number of rows of dorsal scales involving rows VI-VII occurs opposite ventrals 87-93, average 89.90, in males;

opposite ventrals 92-95, average 93.25, in the females. That involving rows III-IV takes place opposite ventrals 89-94, average 91.10, in the males; opposite ventrals 96-98, average 97.50, in the females. The reduction of the dorsal scales on the tail from six to four occurs opposite subcaudals 5-9, average 6.80, in the males; opposite subcaudals 5-6, average 5.25, in the females.

The ventrals vary from 151 to 164, average 156.46, in the males; from 156 to 166, average 161.75, in the females. A single male has a complete tail with 151 subcaudals; another male with an incomplete tail has 157+ subcaudals. No females are available with unquestionably complete tails; one with a questionably complete tail has 163 subcaudals. The anal plate is divided in a majority of the specimens examined, but nearly half of the males exhibit atypical variations.

Eight upper and 10 lower labials is the condition most commonly observed. The loreal plate is absent in all specimens seen. All have one preocular, but more than half of the specimens vary from the generic condition of two postoculars on each side of the head. When more than one postocular is present the upper is usually larger. The preocular is not in contact with the frontal. The parietal is longer than broad, slightly notched by the upper temporal, rounded posteriorly. The parietal is not in contact with the lower postocular. The length of the frontal is greater than the length of the interparietal suture. Most specimens have one anterior and two posterior temporals. The eye is moderate; its diameter is equal to the distance from its anterior border to the nostril.

The largest male examined had a head-body measurement of 1073 mm., plus a tail length of 646+ mm.; the largest female had a head-body length of 848 mm., plus 529+ mm. The single male with a complete tail has a tail/body ratio of .65, whereas the female with the questionably complete tail has a tail/body ratio of .63.

The coloration in alcohol is: top of head dark bluish green (Sea Green) to brownish green (Serpentine Green); black ocular stripe on lower postocular, posteriorly along common borders of last three upper labials and temporals, ending on last upper labial or one

scale posterior to last labial. Anterior to orbit, stripe occasionally present as narrow margin on upper edge of labials 2, 3, and sometimes 4.

Coloration of top of head extends posteriorly onto body where it is present on exposed portions of scales of rows II-XIV or III-XIII anteriorly. Same color is present on concealed portions of ventral plates and scales of rows I and XV. On anterior one-fourth of body greenish color prominently present in well-preserved specimens; even in this region of body it is adulterated with irregular areas of light brown (Sulphine Yellow) or light metallic bronze.

On posterior three-fourths of body dorsal coloration is light brown (Old Gold) to darker brown (Isabella Color), keels and margins of dorsal scales darker than remaining exposed portion, whereas concealed portions of scales usually retain bluish green coloration of anterior body and head. Posterior dorsal color continues onto tail. Upper labials below portions involved in ocular stripe are minutely colored with greenish blue and light metallic bronze, giving a dirty appearance. Chin and ventral plates light yellowish brown (Naples Yellow) to pure white; ventrals occasionally with narrow posterior dark margins, especially on outer edge.

VARIATION: All females have the anal plate divided, as do four males; two males have single anal plates and one has the plate only partly divided. Four specimens have nine upper labials on both sides of the head, three have 8/9, and one has seven on both sides. Four have 9/10 lower labials, three have 10/11, and one has 11 on both sides. The variation of greatest frequency in respect to the postoculars is the condition of three shields on both sides of the head, which is found in six of the specimens studied; two have 2-3 and one each has 1-2 and 2-4. In regard to the temporals two have the formula 1-1/1-2, two have 1-1-2, one has 1-1-2/1-2, and two have 2-2.

There is little indication of geographic variation in this race, largely because of the limited material. Joseph R. Bailey (*in litt.*) has called my attention to potential differences between the population from the Federal District as compared with the populations from other areas.

	FEDERAL DISTRICT	REMAINDER OF BRAZIL
Ventrals		
Males	152-155, av. 153.25(4)	155-164, av. 159.83(6)
Females	156, 160	158-166, av. 162.80(5)

There is relatively little variation in coloration exhibited in the material studied. The extent of the dorsal greenish blue color varies slightly. No juveniles have been seen, but a specimen with a head-body length of 512 mm. exhibits a faint pattern of narrow, black, oblique bands that is suggestive of the banded juvenile pattern seen in other members of this species.

REMARKS: Wied's (1824) original description was based on a snake from an unspecified locality in eastern Brazil, but the author stated that he had seen the form frequently in the meridional provinces of Brazil, near Cabo Frio, at Marica, Saquarema, Araruama, Lagoa Feia, on the Parahyba and the Espirito Santo, but not farther north. These localities are all in the "Southeast corner of Brazil," in the coastal area to the east and north of Rio de Janeiro. Since these are the only localities mentioned by Wied, it seems probable that the type specimen came from one of them. In the following year, Wied (1825) presented a more detailed description of *liocercus*, using the same specimen as the basis for this description. Here the ventrals are given as 159 plates and the subcaudals as 147.

In the collections of the American Museum of Natural History there is a specimen, A.M.N.H. No. 3531, labeled "*Leptophis liocercus* Wied, Brazil, Maximilian." This specimen was included in the material that was purchased by the American Museum in 1870 from the collection of Prince Alexander Maximilian of Wied. Many of Wied's type specimens were included in this material, and it seems highly probable that this specimen represents the type of *liocercus*. The ventral and subcaudal counts for this specimen are identical with those recorded by Wied, the other details of scutellation are the same, and the measurements, allowing for some change due to the long period of preservation, are extremely similar. The coloration is not like that shown in Wied's color plate, but the specimen has lost all of the stratum corneum and cannot be expected to have retained all

details of coloration.

Andersson's *Leptophis flagellum* is placed in the synonymy of this subspecies with a question mark because the description does not permit an accurate allocation of the form. The number of maxillary teeth is greater than that observed in *liocercus*, the two posterior teeth are said to be enlarged and separated by a short space from the other teeth, the number of mandibular teeth is higher than that observed in *liocercus*, and *flagellum* has a loreal shield. The color and geographic locality suggest that this form is the same as *liocercus*, but unless an error was made in the observations on the teeth, it seems unlikely that the two are the same. Amaral (1930b) assigned *flagellum* to the synonymy of *occidentalis* as recognized by him.

Leptophis vertebralis Werner (1909) is a homonym of *Leptophis vertebralis* Duméril and Bibron (1854). The latter does not belong to the genus *Thalerophis*. Werner's description omits a number of pertinent details for the proper identification of his form. It may prove that his description was based on an aberrant juvenile. Amaral (*loc. cit.*) stated that he examined the type of *vertebralis*, that it has keeled scales instead of smooth scales as indicated by Werner, and that he considers it a synonym of "*L. ahaetulla*" that is known from the state of Rio de Janeiro.

The name *liocercus* Wied has often been used to include most members of the genus that occurred east of the Andes in South America, or has been assigned to the synonymy of *ahaetulla* when that name was used for the populations west of the Andes. Virtually no author has restricted its application to the populations from the littoral zone of southeastern Brazil.

This subspecies is closely related to both *marginatus* and *richardi*. It probably intergrades with both of these races, but where intergradation takes place is not known at the present time. It is possible that the geographic ranges of *marginatus* and *liocercus* are not now in contact.

The distribution records for *liocercus* do

not seem to correspond to a given major vegetational type. This is owing in part to the lack of precise ecological data for the specimens available, as well as to incomplete phytogeographic data for much of South America. The precise relations of *liocercus* to *marginatus* and *richardi* cannot be determined until more is known of the ecology of these forms.

Two of the specimens studied are reported from Goyaz, Brazil. Except for these individuals, the remaining specimens come from localities in the Atlantic drainage of southeastern Brazil. The specimens in question are in the collections of the Museum of Comparative Zoölogy and were received originally as a gift from the Instituto Butantan in Brazil. The vast number of snakes received in the serpentarium of the latter institution seem to have caused occasional errors in locality data recorded for individual specimens. Consequently until further material is obtained to substantiate the record from the interior, I believe it is wiser to limit the known range of this subspecies to the coastal area.

SPECIMENS EXAMINED (21)

BRAZIL. Bahia: Caravellas, I.B. No. 966. Distrito Federal: Cascadura, I.B. No. 9019; Santíssimo, I.B. No. 278. Espírito Santo: Araguaia, I.B. No. 8403; Baixo Grandis, I. B. No. 8271; Ita, I.B. Nos. 8987, 8989, 8971; Victoria, M.C.Z. No. 2975. Minas Gerais: Pedra Corrida, I.B. Nos. 9477, 9612. Rio de Janeiro: Rio de Janeiro, M.C.Z. Nos. 1379 (2), 2675 (2), U.S.N.M. No. 120830. "Brazil," A.M.N.H. No. 3531 (type), B.M.N.H. (no reg. number), U.M.M.Z. No. 56306.

Thalerophis richardi marginatus Cope

Thrasops marginatus COPE, 1862, Proc. Acad. Nat. Sci. Philadelphia, vol. 14, p. 349; Paraguay.

Herpetodryas affinis STEINDACHNER, 1870, Sitzber. Akad. Wiss. Wien, vol. 62, p. 348; Brazil.

Leptophis rostralis LÖNNBERG, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 10, p. 458; San Miguel (Chaco), Argentina.

Leptophis argentinus WERNER, 1903, Abhandl. K. Bayerischen Akad. Wiss., vol. 22, div. 2, p. 384; Rosario, Argentina.

Leptophis liocercus SERIE, 1915, Bol. Soc. Physis, vol. 1, p. 573.

Leptophis nigromarginatus AMARAL, 1925, Com. Lin. Tele. Est. do Matto Grosso ao Amazonas, Publ. No. 84, vol. 5, p. 1-29.

Leptophis ahaetulla FREIBERG, 1939, Mem. Mus. Entre Rios, no. 11, pp. 1-28.

Leptophis marginatus OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 10.

TYPE LOCALITY: Paraguay.

RANGE: From extreme southeastern Bolivia across Matto Grosso to western São Paulo in Brazil, southward through Paraguay into northern Argentina (fig. 10).

DESCRIPTION: The maxillary teeth are 21-23; the average of nine observations is 22.3. The last three maxillary teeth are enlarged and frequently compressed laterally at the tips (fig. 1J). The fourth tooth from the posterior end of the maxillary is usually partly enlarged, representing an intermediate condition between the teeth anterior to it and the three enlarged teeth that follow it. The hemipenis is seven subcaudals long, with five enlarged basal spines opposite the posterior end of subcaudal 2; the two largest spines are on either side of the sulcus. Following the enlarged basal spines distally are six to seven transverse rows of smaller spines opposite subcaudals 3 and 4. These spines decrease in length distally, passing into calyces with long, non-spinous papillae. The papillae opposite subcaudal 5 obscure the structure of the calyces but decrease in length distally, becoming fleshy towards the tip. The distal portion opposite subcaudals 6 and 7 is typically calyculate.

Keels are present on the scales of rows II-XIV, that on the vertebral row equal in prominence to those on the adjacent rows. The scales of row VI are not, or only weakly, keeled above the anus. The scales of the vertebral row are not enlarged.

The reduction in the number of rows of dorsal scales involving rows VI-VII takes place opposite ventrals 94-98, average 96.37, in males; opposite ventrals 107-107 in the single female for which these data were recorded. That involving rows III-IV occurs opposite ventrals 93-101, average 96.25, in the males; opposite ventrals 105-106 in the female. Reduction of the dorsal scale rows on the tail from six to four occurs opposite subcaudals 7-10, average 7.87, in males and opposite subcaudals 10-11 in the single female for which these data were registered.

The ventrals in the male are 157-170, average 161.85; in the females 162-172,

average 167.27. Only a single male, with 138 subcaudals, and a single female, with 144 subcaudals, have complete tails. All specimens have the anal plate divided.

Normally the upper labials are eight and the lower labials 10 on both sides of the head. With the exception of one male that has a loreal on both sides of the head, this plate is absent. The typical condition is one preocular and two postoculars. The lower postocular is much smaller than the upper. The preocular usually is not in contact with the frontal. The parietal is longer than broad, somewhat acuminate posteriorly, not notched by the upper posterior temporal. The parietal is not in contact with the lower postocular. The length of the frontal is greater than that of the interparietal suture. Temporals 1-1 or 1-2. The eye is moderate to small; its diameter is less than the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 995 mm., plus a tail length of 523+mm.; the largest female had a head-body length of 932 mm. The tail/body ratio in the single male with a complete tail is .60; that of the single female with complete tail is .61.

The coloration in alcohol is: top of head dark blue (Dark Orient Blue) to dark greenish blue (Sea Green), most of shields on top and side of head prominently margined with black (pl. 18). Typically a distinct small black spot approximately in center of each parietal plate and on outer side of each supra-ocular shield. Broad black postocular stripe from posterior edge of orbit along common borders of postocular shields, but not on lower edge of lower postocular; passing posteriorly on most of anterior temporal, most of lower posterior temporal, and upper edges of last three upper labials. Anteriorly stripe indicated by a prominent upper margin on upper labials 2, 3, and 4.

Postocular stripe continues onto body, breaking up after a distance approximately equal to one-half the length of the head. Dorsal scales on anterior third of body margined with black except those of outer row.

Dark blue or greenish blue coloration of head extends onto body for a short distance, not on outer two rows of dorsal scales; coloration decreased in distribution posteriorly

and replaced by bronze or light brown (Old Gold). Point at which greenish blue coloration disappears varies considerably in specimens examined. On one specimen it disappears completely on anterior one-fifth of body; on another it is retained on anterior edges of scales of median dorsal rows for entire length of body. With but one exception all specimens examined have predominant dorsal body color bronze or metallic brownish (Old Gold) coloration. Upper labials below black upper edges clear white; chin and ventrals also clear white.

VARIATION: One specimen has nine upper labials on both sides, another has nine on one side and eight on the other. Three specimens have 11 lower labials, on both sides of the head, and two have 10 on one side and 11 on the other. One variant from the typical condition of a single preocular has been observed; this specimen has two preoculars on one side. Two specimens have only one postocular on both sides of the head. The most interesting variation in respect to scutellation characters in this race is that in the temporals. Nine specimens have the formula 1-1 on both sides, six have 1-1/1-2, seven have 1-2, while one each has 1-1-2 and 1-1-2/2-1-2-1.

There is considerable variation, as indicated above, in regard to the coloration, primarily in respect to the distribution of the dorsal greenish blue pigment. One specimen, collected in Argentina over 50 years ago, is pale uniform green on the body and tail. The head shields are typically marked with black. The sides of the body are lighter in shade than the median dorsal region and are the same color as the ventrals. In all other specimens studied the ventrals are clear white, and the sides are much lighter than the median dorsal region. Very little material has been studied from Argentina, and differences in color between populations from that country and those from the northern part of the range have been indicated by literature references (Berg, 1898).

No juvenile specimens have been seen by me. That the juvenile pattern is that of dark oblique bands is indicated by Lönnberg's (1902) description of his proposed new species, *rostralis*. He states, "On the anterior part of the body a series of oblique dark stripes are seen running from the back and

sloping down the sides in a backward direction. These stripes are regularly arranged and are formed in such a manner that the tip of every third scale is blackish. Posteriorly the body and the tail are uniformly bronzy." The specimen described by Lönnberg had a total length of 360 mm.

REMARKS: Cope's species was based on an adult male specimen collected in Paraguay and now in the collections of the Academy of Natural Sciences of Philadelphia. The type has been examined and is in a good state of preservation. The color pattern is essentially that given in the subspecies description. If future material necessitates the recognition of two races instead of the one now called *marginatus*, this name will be applicable to the northernmost race.

Amaral (1930a) has pointed out that Steindachner's *Herpetodryas affinis* is referable to the genus *Thalerophis*. After examination of the type of this species, Amaral stated that there was no doubt in his mind "as to the absolute identity of this form with *Leptophis occidentalis* (Günther) . . ." Later in the same year Amaral (1930b) reiterated this opinion regarding the status of *Herpetodryas affinis* and added that it properly was a synonym of the race *nigromarginatus* (considered by Amaral as a race of *occidentalis*). According to Amaral the type of *affinis* is a specimen collected in Matto Grosso. At present the only representative of the genus studied from Matto Grosso is *marginatus* and on geographical grounds the name *affinis* should be referred to the synonymy of this form. All of the characters reported for *affinis* by Steindachner permit its allocation with *marginatus*, despite the presence of an atypical loreal shield. Amaral has pointed out the atypical nature of the loreal shield and stated that it was present on one side only (the side figured by Steindachner). Amaral is the only author to provide data on the number of ventral and subcaudal plates for *affinis*, 173 and 181, respectively. The ventral count exceeds by one plate the maximum observed by me for *marginatus*, but the subcaudal count reported for *affinis* is 37 plates more than the observed maximum for *marginatus*. However, of the specimens of this subspecies examined by me, only 8 per cent have complete tails

and thus complete subcaudal counts. As noted under the remarks about *richardi*, Joseph R. Bailey has examined two specimens from Matto Grosso that he believes are referable to *richardi*. It is possible, but not very probable, that *affinis* belongs in the synonymy of *richardi*.

Lönnberg's (1902) species *rostralis* was based on a juvenile from San Miguel in northern Argentina. At the time of his description, Lönnberg stated that his proposed species "might perhaps turn out to be the young stage of some other species . . ." There seems to be no doubt that it does represent the juvenile of *marginatus*, and indicates that the juvenile pattern consists of transverse oblique dark bands.

Werner (1903) described a *Leptophis argentinus* from Rosario, Argentina, detailing the differences between his proposed species and *nigromarginatus*. The reported ventral counts for *argentinus* is one plate below the minimum observed by me, and the subcaudal count was obviously obtained from a specimen with an incomplete tail. The characters pointed out for *argentinus* as points of difference from *nigromarginatus* are all within the variation observed in *marginatus*.

The distribution of *marginatus* appears to conform closely to the area of tropical deciduous forest in eastern Bolivia, Paraguay, south central Brazil, and northern Argentina as indicated in Smith and Johnston's (1945) "Generalized phytogeographic map of Latin America." Intergradation with *bolivianus* probably occurs in eastern Bolivia where the two races meet. As to the precise relationships of *liocercus* and *marginatus* little can be said. They are closely related, but whether their respective geographic ranges are now in contact or not is unknown.

SPECIMENS EXAMINED (24)

ARGENTINA. Chaco: Colonia Resistencia, B.M.N.H. No. 1919.9.10.21. Entre Rios: Parana, M.E.R. No. 632. "Argentina," A.M.N.H. No. 17566.

BOLIVIA. Santa Cruz: Puerto Suarez, C.M. No. 314.

BRAZIL. Matto Grosso: Camisao, I.B. No. 9894; Corrientes, I.B. Nos. 7620, 7890; Guaycurus, I.B. No. 3219; Miranda, I.B. Nos. 3267, 9107, 9265, 9485, U.S.N.M. No. 100748; San Luis de Caceres, M.N.R. (no number); Taunay, I.B.

No. 6629. São Paulo: Cesario Motla, I.B. No. 3094; Presidente Prudente, I.B. No. 5772; "São Paulo," U.M.M.Z. No. 62803.

PARAGUAY. Asuncion, B.M.N.H. Nos. 94.3.14.46, 1930.11.27.211; Pedro Juan Caballero, M.C.Z. No. 46997; Puerto Bahia Negra, B.M.N.H. No. 98.6.3.4; "Paraguay," A.N.S.P. Nos. 5514 (type), 6288.

***Thalerophis richardi nigromarginatus* Günther**

Ahaetulla nigromarginata GÜNTHER, 1866, Ann. Mag. Nat. Hist., ser. 3, vol. 18, p. 28; "Upper Amazons."

Leptophis nigromarginatus GRIFFIN, 1915, (in part), Mem. Carnegie Mus., vol. 7, no. 3, p. 184.

Leptophis occidentalis nigromarginatus AMARAL, 1929, Mem. Inst. Butantan, vol. 4, p. 162.

Leptophis ahaetulla nigromarginatus OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 4.

TYPE LOCALITY: "Upper Amazons."

RANGE: Extreme southeastern Colombia, western Brazil, eastern Ecuador, and eastern Peru (fig. 10).

DESCRIPTION: The maxillary teeth are 23–28, the average for 45 observations is 25.4; the last three teeth are enlarged. The hemipenis is six subcaudals long, with five to six moderate-sized spines in the basal row opposite the posterior half of subcaudal 2; the two spines on the inner side of, and adjacent to, the sulcus are somewhat enlarged. These are followed distally by five to six rows of transverse smaller spines opposite subcaudals 3 and 4; the spines merge into calyces with long fringing papillae that obscure the structure of the calyces. The papillae decrease in length, becoming more fleshy towards the tip, leaving the distal portion, opposite the posterior half of subcaudal 5 and all of subcaudal 6, typically calyculate.

Keels are present on the scales of rows II–XIV in the males, usually only on the scales of rows VI–X in females; row VI is not keeled above the anus, and there are no keels on the dorsal scales on the tail posterior to the point of reduction from six to four rows. The scales of the vertebral row sometimes are slightly enlarged; the transverse rows of dorsal scales are six to four rows. The scales of the vertebral row sometimes are slightly enlarged; the transverse rows of dorsal scales are quite oblique in arrangement on the anterior one-third of the body.

The reduction in the number of rows of dorsal scales involving rows VI–VII or V–VI occurs opposite ventrals 89–99, average 95.16, in the males; opposite ventrals 93–106, average 99.06, in the females. That involving rows III–IV occurs opposite ventrals 90–98, average 94.83, in the males; opposite ventrals 92–109, average 100.37, in the females. Reduction of the dorsal scales on the tail from six to four rows occurs opposite subcaudals 4–7, average 5.16, in the males; opposite subcaudals 3–5, average 4.50, in the females.

The ventrals in the males are 147–165, average 152.28; in the females, 150–166, average 156.91. The subcaudals are 139–160, average 150.76, in the males; 137–166, average 150.57, in the females. This subspecies exhibits the maximum variation observed in the character of the anal plate; the anal is normally divided in females, but in the males it may be completely divided, partly divided, or undivided.

The upper labials are either eight or nine, and the lower labials are 10 or 11. The loreal shield is normally absent. The oculars are normally one preocular and two postoculars. The lower postocular plate is less than half the size of the upper; the preocular is normally not in contact with the frontal. The parietal is longer than broad, not or but slightly notched by the upper posterior temporal, rounded posteriorly, and not in contact with the lower postocular. The length of the frontal is greater than the length of the interparietal suture. The temporals are usually 1–2, although there is a noticeable trend towards fusion of the posterior temporals resulting in the formula 1–1. The eye is small to moderate in size; its diameter is less than the distance from the anterior border of the orbit to the nostril.

The largest male examined had a head-body length of 823 mm., plus a tail length of 480+ mm.; the largest female had a head-body length of 746 mm., plus a tail length of 472+ mm. The tail/body ratio in males is .58–.69, average .648; in the females .60–.71, average .613.

The coloration in alcohol is: top of head dark blue (Orient Blue) to greenish blue (Sea Green), all of shields on dorsal surface of head heavily margined with black and a large black spot in center of each supraocular

shield and on each parietal shield (pl. 18). Spot on parietal usually elongate in shape. Greenish blue or dark blue coloration on top of head extends posteriorly onto body and tail, occupying dorsal scales of rows I–XV as well as outer portions of ventrals and most of subcaudals. All of dorsal scales of body and tail margined with black, median dorsal rows have broadest black margins (fig. 6). Keels of dorsal scales not black. Black markings on dorsal scales frequently form pattern of narrow black oblique lines across back.

Upper labials lighter blue or greenish blue than dorsal coloration; chin dirty white; throat and ventrals pale greenish blue (Pale Dull Glauous Blue). Ventrals with irregular dark outer and anterior margin virtually same color as on dorsal scales. Subcaudals of same color as dorsal scales.

VARIATION: Among 82 males of this subspecies, 35 exhibit an atypical variation from the normal generic condition of a divided anal plate; 18 of these males have the anal plate only partly divided, while 17 have the anal plate undivided. Among 112 females only four exhibit any variation in respect to the anal; three have the plate only partly divided, while one has the plate undivided. Variation in this character within the species has been discussed in a preceding section.

The following conditions have been observed in respect to the upper labial variation: 88 have 9, 63 have 8, 36 have 8/9, four have 7/8, four have 9/10, and one has 7/7. The variation in the lower labials is: 81 have 11, 44 have 10/11, 43 have 10, 11 have 9/10, six have 11/12, two have 8/9, one has 7/9, one has 9/9, and one has 12/12. Four specimens have a loreal shield on both sides of the head; four have a loreal shield present only on one side of the head; the remaining specimens studied all lack the loreal. One specimen has two preoculars on both sides of the head, while two specimens have one on one side and two on the other. Four have the postoculars 2/3; two have 1/1; two have 3/3; and one has 1/2. In respect to the temporal variation 33 specimens have the formula 1-1/1-2, 31 have 1-1, two have 1-1/1-2-1, two have 1-2/1-3, one each has 1/1-1, 1-1-2/1-2, 1-2/2-2, 1-2/2-2-1, 1-2-1/2-2-2, 2-1-2/2-2-3.

There is little evidence of geographic variation in the number of ventral plates in this

subspecies. Through the kindness of Harvey Bassler the large series of specimens of this race collected by him in Peru has been made available for this study. Bassler's material provides the largest homogeneous sample available for the genus, and consequently this race is better known in respect to its bionomics than the other members of the genus. In most of the physical attributes that have been employed as diagnostic characters within the genus this subspecies is highly variable. A notable exception to this statement is found in the ventral plates; these are highly constant in the populations observed. Coefficients of variation have been calculated for a sample obtained by Bassler in the vicinity of Iquitos, Peru. The males have a coefficient of variation of 2.53 in a sample of 27 specimens; the females have a coefficient of variation of 2.01 in a sample of 46 females.

One of the most pronounced variations observed in the subspecies, and one that has been most perplexing in the systematic treatment of this form, is that of the coloration and color pattern. This has been a puzzling type of variation because the race is most readily diagnosed on the basis of its color pattern. The essential features of the coloration are the amount and distribution of the black pigment, the ventral extent of the dark dorsal coloration, and the coloration of the ventral plates. On the basis of these features of the color pattern four color categories have been recognized:

1. This is essentially the color pattern described in the subspecies description above and is the color phase that is usually associated with the name *nigromarginatus*.

2. The second category is similar to number 1 except that the ventrals and the scales of the two lowest rows of dorsal scales on each side of the body are light cream color, and the ventrals have a prominent anterior and lateral margin of dark blue.

3. This is the same as number 2 except that the black spots on the head shields are smaller in size and are present on either the supraoculars or the parietals but not on both. The margins of the other head shields are less prominent, but this feature is not noticeable unless a large series is studied.

4. This category includes specimens with the same color pattern as is noticed in speci-

mens of *ortoni* from the western part of the latter's range, with black borders on the head shields and many of the dorsal scales, without black spots on the head shields, with light ventral and lower dorsal coloration.

In the Peruvian populations these four categories are represented by the following frequencies:

	I	II	III	IV
Males	43	6	12	3
Females	44	24	18	9
Total	87(54.7%)	30(18.9%)	39(18.9%)	12(7.5%)

Three-fourths of the specimens in category IV are from the locality in Peru that is closest to the range of *ortoni*, and the proportional representation of the last three categories decreases with an increase in the distance away from *ortoni*. All individuals of these populations with heavy black margins on the head shields and with one or more pairs of spots on the head shields are referred to *nigromarginatus*. Thus 92.5 per cent of the Peruvian specimens are readily allocated to *nigromarginatus* on the basis of color pattern. It is interesting to note that in categories II, III, and IV the females are more numerous than the males in each category, suggesting a possible sex influence on the genetic mechanisms that determine the coloration.

REMARKS: With the recognition of additional related subspecies in geographic regions adjacent to the form called *nigromarginatus*, the correct application of Günther's name has been somewhat uncertain. When *bolivianus* was described (Oliver, 1942), I endeavored to restrict the application of *nigromarginatus* to the populations that best fitted Günther's description and geographic locality, "Upper Amazons." H. W. Parker has generously sent me detailed data for the type specimen, and it is gratifying to learn that the name was applied correctly. This subspecies has most frequently been referred to as a race of *occidentalis*, although there is no evidence at the present time of interbreeding with that form. In 1942, I classified it as a race of *ahaetulla* because of a continuous gene flow from *nigromarginatus* through *ortoni* to *ahaetulla*. Both *occidentalis* and

nigromarginatus are here considered races of *richardi* (= *ahaetulla* auct.).

Intergradation is known to take place between *nigromarginatus* and the two races with which it is known to be in geographic contact, *bolivianus* and *ortoni*. Intergradation with *bolivianus* is indicated by a specimen (A.M.N.H. No. 22446) from northwestern

Bolivia, and intergradation with *ortoni* is indicated by two specimens (A.M.N.H. Nos. 22258, 22259) from northern Bolivia, as well as a number of specimens from the Amazon River near the Peru-Brazil border. That there is a genetic exchange between *nigromarginatus* and *ortoni* in a fairly wide area is suggested by the variation mentioned above in the color pattern observed in specimens from northeastern Peru.

There is no evidence that *nigromarginatus* and *occidentalis* interbreed in any region. They seem to be effectively separated by the Andes Mountains, although this separation may have existed for a relatively short period of time to judge by the number of similar attributes exhibited by the two forms. These, however, may be the result of parallel development.

This is one of the most variable members of the genus. Amaral (1926) commented on this some years ago, "Quando se examinam comparativamente muitos exemplares de *L. nigromarginatus* (Guenther), fica-se surpreso diante das variações que muitos delles mostram." This variation may be due in part to the amount of material available, but this does not appear to be the only factor. The proportional variation within the subspecies was not greatly increased in most characters by the addition of more than 160 specimens, although the variation could be analyzed much more accurately. The geographic area occupied by the subspecies is not latitudinally great, but it is an area of marked climatic and vegetational variation within short horizontal distances. Whatever the external factors related to this variation may be, it is obvious

that *nigromarginatus* is characterized by a high degree of genetic plasticity in most of its characters. One of the few characters that does not exhibit pronounced variation is the number of ventral plates.

SPECIMENS EXAMINED (193)

BRAZIL. Criniaea, Pranguina, C.M. Nos. 2007, 2008.

COLOMBIA. Amazonas: Leticia, M.C.Z. Nos. 48981-48985.

ECUADOR. Oriente: Mapoto, U.M.M.Z. No. 88913; Pastaza River, M.C.Z. No. 36967; Sarayacu, B.M.N.H. No. 81.5.13.58.

PERU. Amazonas: Upper Rio Marañon, B.M.N.H. No. 1913.6.4.7. Junin: Mouth of Rio Tambo, A.M.N.H. No. 52900. Loreto: Contamana, A.M.N.H. Nos. 52165, 52296, 52885, 53008, 53010, 53564; Cushabatay, A.M.N.H. Nos. 52345, 53234, 53235, 55954; Iquitos, A.M.N.H. Nos. 52044, 52045, 52049, 52121, 52137, 52153, 52230, 52258, 52320, 52419, 52421, 52501, 52508, 52518, 52520, 52529, 52530, 52597, 52598, 52629, 52647, 52653, 52669, 52723, 52732, 52733, 53047, 53074, 53154, 53225, 53226, 53271, 53391, 53396, 53397, 53402, 53411, 53412, 53610, 53648, 53684, 53685, 53711, 53759, 53829, 54084, 54116, 54134, 54153, 54210, 54216, 54225, 54233, 54335, 54345, 54644, 54715, 54810, 54865, 54894, 54940, 54976, 54980, 54984, 55076, 55080, 55125, 55140, 55211, 55246, 55273, 55278, 55313, 55908, 56037, 56092, 56093; Loreto, C.N.H.M. No. 11184; lower Rio Napo, A.M.N.H. No. 53299; lower Rio Tigre, A.M.N.H. No. 53185; Orellana, A.M.N.H. Nos. 52903, 52904, 54575, 54580, 54588, 54614, 55672; Pampa Hermosa, A.M.N.H. Nos. 52028, 53380-53382, 53430, 53504, 53513, 53518, 55349, 55384, 55430, 55431, 55436, 55454, 55461 (2), 55479, 55480, 55727, 55728, 55734, 55742, 55745, 55751, 55755, 55762, 55799, 55803, 55962, 55964, 56007, 56013, 56015; Pebas, B.M.N.H. Nos. 67.9.17.26, 67.9.17.27, M.C.Z. No. 12433; Peru-Brazil border on Rio Tapiche, A.M.N.H. No. 52192; Peruvian Amazon, B.M.N.H. Nos. 69.5.21.23, 69.5.21.24; Punga, Rio Tapiche, A.M.N.H. Nos. 52080, 52082, 52084; Requena, A.M.N.H. Nos. 55512, 55515, 55574, 55604, 55612, 55621, 55623, 55637, 55644, 56036; Rio Nanay, A.M.N.H. No. 56079; Rio Tamaya, A.M.N.H. Nos. 52334, 55326; Rio Ucayali, A.M.N.H. No. 53206, B.M.N.H. No. 95.3.29.13, M.C.Z. Nos. 3789, 3796; Roaboya, A.M.N.H. Nos. 52231, 52233, 52544, 52559, 52892, 53088, 53443, 54421, 54430, 54436, 54443, 54444, 55697. Madre de Dios: C.N.H.M. Nos. 40031, 40032; Maldonado, A.M.N.H. Nos. 56140, 56141. San Martin: Moyobamba, A.M.N.H. No. 52961, B.M.N.H. Nos. 74.8.4.57, 74.8.4.58; Pachisa, A.M.N.H. Nos. 52564, 52567. "Peru,"

A.M.N.H. No. 17615, A.N.S.P. Nos. 111350, 111351.

Thalerophis richardi occidentalis Günther

Ahaetulla occidentalis GÜNTHER, 1859, Proc. Zool. Soc. London, p. 412; Guayaquil and western Ecuador.

Thrasops occidentalis COPE, 1860, Proc. Acad. Nat. Sci. Philadelphia, vol. 12, p. 552.

Ahaetulla urosticta PETERS, 1873, Monatsber. K. Akad. Wiss. Berlin, p. 603; Bogota, Colombia (vide Dunn, 1944).

Leptophis ultramarinus COPE, 1894, Proc. Acad. Nat. Sci. Philadelphia, vol. 46, p. 204; Pozo Azul, Costa Rica.

Leptophis ahaetulla MARIA, 1933, Libro conmemorativo del segundo centenario de Don Jose Celestino Bruno Mutis y Bosio, Bogota, p. 48.

Leptophis occidentalis SCHMIDT, 1933, Smithsonian Misc. Coll., vol. 89, no. 1, p. 16.

Leptophis occidentalis occidentalis OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 14.

TYPE LOCALITY: Guayaquil and western Ecuador.

RANGE: Both coasts of Central America from Nicaragua on the Caribbean coast, Costa Rica on the Pacific, southward to northern Colombia, eastward along the Caribbean coast of western Venezuela, southward in the interior valleys of Colombia, to northwestern Ecuador. Unknown from the Choco region of Colombia (fig. 10).

DESCRIPTION: The maxillary teeth are 18-25; the average for 47 observations is 21.6; the last three teeth are enlarged (fig. 1E). The hemipenis is eight subcaudals long, with five to six enlarged basal spines opposite the suture between subcaudals 2 and 3. The longest spine is adjacent to, and on the inner side of, the sulcus; the two or three spines opposite the sulcus (on the "back side") are smaller. These are followed distally by four to six transverse rows of smaller, stouter spines opposite subcaudals 3 and 4; these pass immediately into well-defined calyces with short fringing papillae. The papillae decrease in number and size, becoming more fleshy distally, while the calyces increase in size. The distal half of the organ is typically calyculate.

Keels are usually present on the scales of rows II-XIV, or only on rows VI-X; they are absent or reduced on the scales of the

vertebral row. Scales of row VI may or may not be keeled above the anus. Keels may be present or absent on the dorsal scales of the tail posterior to the point of reduction from six to four rows; when present they are weakly developed and not prominent.

The reduction in the number of rows of dorsal scales involving rows V-VI or VI-VII occurs opposite ventrals 93-110, average 99.85 in the males; opposite ventrals 92-115, average 103.60, in the females. That involving rows III-IV or II-III takes place opposite ventrals 94-111, average 101.70, in the males; opposite ventrals 95-125, average 105.77, in the females. Dorsal scale reduction on the tail from six to four rows occurs opposite subcaudals 4-16, average 8.25, in the males; opposite subcaudals 4-14, average 7.28, in the females.

The ventrals in the males are 152-177, average 167.89; in the females, 161-182, average 171.39. Fifteen males with complete tails have subcaudals 153-189, average 171.47; eight females with complete tails have 161-175, average 168.20. With the exception of three specimens from Colombia and one from Ecuador, all have the anal plate divided.

The upper labials may be either eight or nine, but the lower labials are most frequently 10. The loreal shield is normally absent. The oculars are normally one preocular and two postoculars. The lower postocular is smaller than the upper. The preocular normally is not in contact with the frontal. The parietal is as long as, or slightly longer than, broad, it may or may not be in contact with the lower postocular, and it is usually notched by the upper posterior temporal. The frontal is large, and its length is greater than that of the interparietal suture. The temporals are normally 1-2. The eye is moderate to large in size, its diameter approximately equal to the distance from its anterior border to the nostril.

The largest specimen examined had a head-body length of 1161 mm., plus a tail length of 660+ mm.; the largest female had a head-body length of 907 mm., plus a tail length of 538+ mm. The tail/body ratio in males is .55-.65, average .608; in females .59-.66, average .617.

The coloration in alcohol is: top of head dark blue (Deep Orient Blue) to greenish

blue (Sea Green); black postocular stripe covers lower postocular, anterior temporal, lower posterior temporal and upper edges of last three upper labials. Anterior to orbit ocular stripe either absent or reduced to narrow black margin on upper edge of two labial plates immediately anterior to orbit. Upper labials lighter in color than top of head, being light greenish blue (Glaucous Blue).

Coloration of top of head extends posteriorly onto body and tail; on body it covers dorsal scale rows I-XV and is present on outer edges of ventrals. Keels on scales of median dorsal rows rarely marked with black. Lower labials, chin, and ventrals pale greenish blue (Light Glaucous Blue) to yellowish white, except outer edges of ventrals. Subcaudals uniformly pale greenish blue (Light Glaucous Blue).

VARIATION: Approximately equal numbers of individuals possess eight or nine upper labials; and over 20 per cent of those examined had eight on one side and nine on the other. In addition to these, three have nine on one side and 10 on the other, and one each has 7/8 and 10/10 upper labials. Ten is the most frequent number of lower labials, but 18 specimens have been observed with 11, 14 have been observed with 10/11, 10 have been recorded with 9/10, one each with 8/9, 9/11, and 11/12. There seems to be no geographic correlation or localization in the observed labial variation, and the same relative frequencies are maintained throughout the range of the subspecies. Three specimens have a loreal plate on both sides of the head, four have this plate present on only one side of the head. Four specimens have two preoculars on both sides of the head, and two have two plates only on one side of the head. Seven have two postoculars on one side and three on the other, two have three shields on both sides of the head, one each has 1/1 and 1/2.

The temporals normally are 1-2, but many variations from this formula have been noted: eight have 1-1/1-2; five have 1-1; four have 1-1-2/1-2; three have 1-1-2; one has 1-1-2/1-1-3; one has 1-2/2-2.

Variation in respect to the distribution and prominence of keels on the dorsal scales exhibits geographic, as well as sexual and ontogenetic, variation. Specimens from the At-

lantic side of Central America usually have only the scales of rows VI, VII, IX, and X with prominent keels at midbody, and there is no keel on the scales of row VI above the anus. Also in the Atlantic populations there are no keels on the dorsal scales on the tail posterior to the point of reduction from six to four rows. In the populations from the Pacific side of Central America the scales of rows II–XIV are usually keeled, and the scales of row VI are keeled above the anus. Occasionally the dorsal scales on the tail are keeled posterior to the point of reduction from six to four rows of scales. Populations from Colombia appear to exhibit both conditions in respect to the keels, without any noticeable geographic localization. The Ecuadorian population resembles that from the Pacific side in Central America.

In lower Central America the Atlantic and Pacific populations exhibit several additional differences that appear to be well segregated between them but that seem to be intermixed in a random fashion in the Colombian, Ecuadorian, and Venezuelan populations. In the Pacific forms the parietal is usually in contact with the lower postocular, the parietal is usually notched by the upper posterior temporal, and the postocular stripe is more clearly defined and not covering the lower half of the postocular. The Atlantic populations have the parietal rarely in contact with the lower postocular, the parietal is typically notched by the upper posterior temporal, and black postocular stripe is irregular in outline and normally covers all of the lower postocular. Further differences are seen in the average number of ventrals:

Two individuals are available from Coiba Island. One, a male, has 174 ventrals, whereas the other, a female, has 175 ventrals. Six specimens have been studied from San Miguel Island. Four of these are males with ventrals 171–179, average 176.00; two are females with 172 and 174 ventrals. In respect to the other attributes mentioned above these specimens cannot be allocated precisely with either the Atlantic or the Pacific populations, exhibiting features found in both. These two islands are off the Pacific coast of Panama; Coiba is in the Gulf of Chiriqui several hundred miles southwest of the Canal Zone, and San Miguel is a short distance southeast of the Canal Zone in the Gulf of Panama.

Aside from the variation in ventrals already mentioned, there is a general but not clearly defined trend towards an increase in the number of ventrals from the south to the north. The lowest ventral counts recorded in the subspecies are from Ecuador, next are the populations from the Pacific side of lower central America, the specimens from the interior valleys of Colombia, and the highest are from those on the Atlantic coasts of Central America, Colombia, and Venezuela.

In respect to the number of maxillary teeth the Ecuadorian population has the lowest average number in the subspecies, 19 for six specimens; the Colombian and Venezuelan specimens have 20–22, average 20.66 in six specimens; the Atlantic Central American population has 20–23, average 21.62 in eight specimens; and the Pacific Central American population has 22–24, average 22.60 in five specimens.

Juveniles have a color pattern of dark

	ATLANTIC	PACIFIC
Ventrals		
Males	163–177, av. 171.36(11)	158–173, av. 164.89(19)
Females	166–181, av. 174.83(6)	161–170, av. 165.37(14)

Virtually all of the overlapping counts indicated above are from specimens collected in the Panama Canal Zone, suggesting that the genetic interchange between these populations occurs in that area. West and north of the Canal Zone the populations seem to be isolated from each other and appear to maintain several distinctive attributes.

oblique bands similar to that of *riveti*. Too few juveniles have been available for study to determine the variation in this banded pattern. Several subadults exhibit traces of the banded pattern and have the two lower rows of dorsal scales on either side of the body lighter in color than the remainder of the dorsal surface.

REMARKS: Günther's types are two adult males from Guayaquil and western Ecuador. The specimens are in the collections of the British Museum (Natural History). H. W. Parker has kindly provided me with detailed data for these specimens. The data supplied by Parker conform closely to those provided by the other Ecuadorian specimens examined by me. His data for the ventral plates agree more closely than do those recorded by Günther and indicate that the latter made an error. The ventral counts given by Parker are 154 and 162 as compared with Günther's counts of 160 and 172, respectively. Boulenger (1894) gives these counts as 152 and 165, respectively. I feel certain that with the acquisition of more material from Ecuador, Colombia, and lower Central America the subspecies *occidentalis* as herein recognized will be subdivided further into additional races. This will restrict the application of Günther's name, *occidentalis*, to what I believe will prove to be an isolated population in western Ecuador. However, that is purely speculation.

Amaral (1930b) and Dunn (1944) have both suggested that Peters' *urosticta* was based on an aberrant specimen of *occidentalis*, or an error in counting, or in recording the number of dorsal scales. Dunn has pointed out that the type locality is probably an error since no member of the genus is known from the elevation of Bogota. I am in complete agreement with my predecessors in regarding this name as a synonym of *occidentalis*.

Cope's *ultramarinus* was based on an adult male from Pozo Azul, Costa Rica. This specimen is now in the collections of the American Museum of Natural History. Should the name *occidentalis* be restricted to the population in western Ecuador, this name is available for the subspecies in Central America.

As already stated, I feel that the subspecies as treated here is a complex of local variants that are either incipient races, already differentiated but at present unrecognizable races, or marked local ecological variants. With more material from critical areas, with more accurate and detailed locality and ecological data, I believe that several of these populations may be recognizable as distinct races.

The relationships of *occidentalis* with sev-

eral geographically adjacent races of the species are fairly obvious. However, intergradation is definitely known to occur with only one other race, *praestans*. These two intergrade in the vicinity of the Segovia River in Honduras. It seems probable that *occidentalis* interbreeds with *bocourti*, *chocoensis*, and *coeruleodorsus* where their respective ranges come in contact. But the details of these relationships are not known. On the other hand it is highly improbable that there is any genetic exchange between *occidentalis* and *nigromarginatus* or *ortoni*. These forms are separated by the Andes, which appear to form an effective barrier to them. That *occidentalis* and *nigromarginatus* have not been separated for a relatively long period of time is suggested by a number of attributes held in common; this is reflected in the synonymy of *nigromarginatus*.

The distribution, as indicated by the available records, exhibits a number of anomalies. For example, as pointed out by Dunn (1940) most forms that occupy the lowland rain forest of the Caribbean coast of lower Central America cross over to the Pacific side in Colombia. The cross over of Pacific side lower Central American forms to the Caribbean coast of Colombia is less pronounced but commonly occurs. In *Thalerophis* the species *depressirostris* follows the first of these distribution patterns. Despite a fair representation of specimens from the region, *occidentalis* is unknown from the Pacific slope of Colombia, being replaced in the Choco by a closely related subspecies, *chocoensis*. The population of *occidentalis* from the Caribbean coast of Colombia resembles that occurring on the Caribbean coast of lower Central America in possessing a higher number of ventral plates, but is like the form on the Pacific side of Central America in regard to the distribution of the keels on the dorsal scales. The population in northwestern Ecuador more closely resembles the form on the Pacific side of Central America than it does that from the Caribbean side. The most critical area from which material is badly needed is that of Colombia and northwestern Ecuador.

The specimens from Coiba and San Miguel Islands off the Pacific coast of Panama are of interest because the number of ventral plates is similar to that of the population from the

Caribbean side of Panama, but the other attributes are similar to those of both Caribbean and Pacific populations. These islands are continental islands (Schuchert, 1935) that have been separated from the mainland for a relatively short period of time. The most likely explanation for the differences observed in these insular specimens is that they represent a population that became separated from the mainland population prior to the fixation of the differences that have or are becoming established through genetic drift in the respective mainland populations.

SPECIMENS EXAMINED (126)

COLOMBIA. Atlantico: Barranquilla, I.L.S. No. 161. Antioquia: Medellin, A.M.N.H. Nos. 35703, 35704; 37936; Sonson, M.C.Z. No. 21981. Bolivar: Cartagena, B.M.N.H. Nos. 59.12.28.13, 59.12.28.15, 59.12.28.27; Los Mangos, B.M.N.H. No. 1908.5.29.52. Boyaca: Muzo, C.N.H.M. No. 28327, I.L.S. No. 160. Cundinamarca: Sasaima, I.L.S. No. 154. Magdalena: Aracataca, A.N.S.P. No. 19784; Bonda, C.M. Nos. 141, 1095, M.C.Z. No. 11859; Cacagualito, C.M. No. 2011; Rio Frio, M.C.Z. Nos. 25046 (6 heads), 32764. Norte de Santander: Cucuta, I.L.S. (two specimens, uncatalogued). Tolima: Apulo, U.M.M.Z. No. 78275; Guamo, B.M.N.H. No. 1919.3.6.19. "Bogota," M.C.Z. No. 19202. "Colombia," A.M.N.H. Nos. 10100, 17501, 17507, 17512, I.L.S. No. 153.

COSTA RICA. Barranca, C.N.H.M. No. 35893; Buenos Aires, C.N.H.M. No. 2527; Colorado Bar, A.M.N.H. No. 12670; Limon, M.C.Z. No. 19737; Pozo Azul, A.M.N.H. No. 17363 (type of *ultramarinus* Cope); Siquirres, Limon Prov., U.S.N.M. No. 68859; "Costa Rica," U.S.N.M. No. 32647.

ECUADOR. Guayas: Colonche, B.M.N.H. No. 1931.10.21.12; Guayaquil, U.S.N.M. Nos. 12269, 12272, 12352; Rosedelia Plant, U.S.N.M. No. 60524. "Ecuador," U.S.N.M. Nos. 14031, 14039.

NICARAGUA. Chontales, San Miguelito, A.M.N.H. No. 12666; Cukra, A.M.N.H. Nos. 12667, 12668; Cupitna Camp, A.M.N.H. Nos. 12669, 12718; Greytown, U.S.N.M. No. 19570; Machuca, A.N.S.P. No. 5288; Rama, Rio Sigüia, U.M.M.Z. No. 79768; Rio San Juan, U.S.N.M. No. 19569; San Juan del Norte, U.S.N.M. No. 15626; Topaz Mine, 90 miles northwest of Bluefields, U.S.N.M. No. 37344; Tunkey, A.N.S.P. No. 22799; Waunta Haulover, Mosquito Coast, A.N.S.P. No. 15434.

PANAMA. Agua Dulce, A.M.N.H. No. 67060; Albrook Field, C.Z., L.M.K. No. 25281; Ancon, M.C.Z. Nos. 16392, 16393, U.S.N.M. No. 51909; Barro Colorado Island, C.N.H.M. No. 3413, U.S.N.M. No. 89401; Blanco District, Chiriqui,

M.C.Z. No. 31953; Bocas del Toro, Punta de Pina, U.S.N.M. No. 38671; Boquete, C.A.S. Nos. 78911-78921, 79034, 79035; Bruja Point, M.C.Z. No. 31952; "Canal Zone," U.S.N.M. No. 38506; Chagras River, M.C.Z. No. 31528; Chepo, U.S.N.M. No. 48958; Chilibre, C.Z., U.M.M.Z. No. 95337; Chorrea, C.N.H.M. No. 16742, M.C.Z. Nos. 37148, 37149 Corozal, C.Z., M.C.Z. No. 37121; Culebra, U.M.M.Z. No. 61285; Darien ("Atlantic Side"), U.S.N.M. No. 24504; El Valle, A.M.N.H. (uncatalogued); Empire, C.Z., U.S.N.M. No. 59928; Fort Davis, C.Z., M.C.Z. No. 22254; Fort Sherman, Toro Point, M.C.Z. No. 22234; Gamboa, A.M.N.H. No. 32816; Gatun, C.N.H.M. Nos. 16743, 16744, U.S.N.M. No. 50106; Juan Mina, M.C.Z. Nos. 26636-26638; Los Santos Province, U.S.N.M. No. 51910; Obispo Sta., M.C.Z. No. 2719; "Panama," A.N.S.P. No. 5204; Panama City, M.C.Z. Nos. 22219, 38225, U.S.N.M. No. 50124; Pedro Miguel, C.Z., M.C.Z. No. 23985; Progreso, Chiriqui, U.M.M.Z. No. 57907; Punta Paitilla, M.C.Z. No. 18891; Punto Armuelles, Chiriqui, M.C.Z. No. 31652; San Miguel Island, M.C.Z. Nos. 9347-9352.

VENEZUELA. Falcon: Pauji, Acosta District, M.C.Z. No. 48757; Rio Caraperro, San Feliz, U.M.M.Z. No. 55895; Rucito, Acosta District, M.C.Z. No. 49041. Tachira: Drope (= Orohe?), C.N.H.M. No. 2588. Yaracuy: Aroa, U.M.M.Z. No. 55896.

Thalerophis richarei orton Cope

Leptophis orton COPE, 1876, Jour. Acad. Nat. Sci. Philadelphia, vol. 8, p. 177; Solmoens or middle Amazon.

Leptophis occidentalis nigromarginatus AMARAL, 1935, Mem. Inst. Butantan, vol. 9, p. 9.

Leptophis ahaetulla orton OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 4.

TYPE LOCALITY: Solmoens (= Solimoes) or middle Amazon.

RANGE: The Amazon Valley of southeastern Colombia, the middle Amazon region of Brazil, and extreme northern Bolivia (fig. 10).

DESCRIPTION: The maxillary teeth number 24-28; the average for 15 is 25.9; the last three teeth are enlarged (fig. 1A). The hemipenis is five subcaudals long, with no large basal spines; the spine of the proximal row on the inner side of and adjacent to the sulcus is much larger than the others. There are six to seven transverse rows of spines opposite subcaudals 2 and 3; those of the proximal row are the largest. The spines decrease in size distally, passing immediately into calyces with elongate fringing papillae that decrease

in length towards the tip. The distal two-fifths of the organ is typically calyculate opposite subcaudals 4 and 5.

Keels are normally present on the scales of rows VI–X, occasionally on rows II–XIV in males, occasionally only rows VII and IX in females; the scales of row VI are not keeled above the anus. There are no keels on the dorsal scales on the tail posterior to the point of reduction from six to four rows. The scales of the vertebral row are frequently slightly enlarged.

Reduction in the number of rows of dorsal scales involving rows VI–VII takes place opposite ventrals 91–104, average 97.75, in the males; opposite ventrals 95–112, average 101.57, in the females. That involving rows III–IV takes place opposite ventrals 93–107, average 98.37, in the males; opposite ventrals 95–111, average 102.32, in the females. Reduction of the dorsal scales on the tail from six to four rows takes place opposite subcaudals 3–15, average 5.93, in the males; opposite subcaudals 2–8, average 5.00, in the females.

The ventrals are 153–169, average 157.22, in the males; 152–168, average 161.54, in the females. The subcaudals are 144 and 161 in two males with complete tails; 144–169, average 157.90, in 10 females with complete tails. All but five specimens have the normally divided anal plate.

The labials are highly variable, but most frequently are nine upper and 11 lower labials. With the exception of one specimen that has an atypical loreal present on one side of the head, all specimens examined lack the loreal plate. All have one preocular and two postoculars. The preocular is normally not in contact with the frontal; the lower postocular is much smaller than the upper. The parietal is longer than broad, not or but slightly notched by the upper posterior temporal, and not in contact with the lower postocular. The length of the frontal is greater than that of the interparietal suture. The temporals are variable but most commonly 1-2. The eye is moderate in size; its diameter is equal to, or slightly less than, the distance from its anterior border to the nostril.

The largest male had a head-body length of 794 mm., plus a tail length of 527+ mm.; the largest female had a head-body length of

617 mm., plus 388+ mm. The tail/body ratio in two males with complete tails is .66 and .69; in nine females with complete tails the tail/body ratio is .64–.70, average .660.

The coloration in alcohol is: top of head dark blue (Dark Orient Blue) to dark greenish blue (Sea Green); narrow black postocular stripe usually present on lower edge of lower postocular, posteriorly along common margins of temporals and last three upper labials, stopping at posterior end of upper labials. Stripe not present anterior to orbit. Head shields are usually narrowly margined with black.

Dark blue or greenish blue coloration of head continues onto body, anteriorly present on exposed portions of scales of rows III–XIII and concealed portion of scales of rows I, II, XIV, and XV; without light vertebral stripe. Dorsal scales of all rows normally possess black tips and black upper margins, at least anteriorly. Posteriorly greenish blue coloration reduced dorsally, replaced ventrally by upward extension of ventral coloration. On posterior third of body darker coloration present on exposed portion of scales of rows IV–VIII, reduction continues on tail.

First three upper labials with upper edges of greenish blue or same blue coloration as top of head, below this color labials yellowish white (Sea-Foam Yellow); upper labials below eye clear yellowish white. Posterior upper labials below black upper margins yellowish white with some irregular minute specks of greenish blue on upper portions. Chin and ventrals yellowish white; ventrals with prominent bluish green or dark blue anterior and outer margins. Caudals margined with dark blue anteriorly and laterally, as well as along median edge of scales; latter margin tends to form an irregular longitudinal blue line down center of under surface of tail.

VARIATION: The upper labial formulas observed are nine in 20 specimens; eight in eight specimens; and 8/9 in three specimens. The lower labial formulas are: 11 in 16 specimens; 10/11 in six specimens; 10 in four specimens; 9/10 in one; and 9/11 in one. The observed temporal formulas are: 1-2 in 17 specimens; 1-1/1-2 in six specimens; 1-1 in four specimens; 1-2/1-3 in two specimens; and one each has 1-1-2, 1-1-2/1-2, 1-1-2/2-2, 1-2-1/1-2-2, 1-2-2/1-3-2.

There is a suggestion of a west to east cline in ventral variation, with a gradual increase towards the east. There is a geographic trend in respect to the black pigment on the scales, with a decrease from west to east. Four out of 13 eastern specimens lack a black postocular stripe and have scarcely discernible black margins on the head shields. In the western part of the range all specimens have heavy black margins on the head shields and on the dorsal scales. Every stage in color pattern change has been observed from *nigromarginatus* in eastern Peru and *bolivianus* in Bolivia to the eastern specimens with no black markings.

A single juvenile has a pattern of oblique dark bands similar to that noted on other juveniles of this species. There is no light vertebral stripe in the juvenile, and the juvenile lacks the dark anterior and outer margins of dark blue on the ventrals.

REMARKS: The cotypes of *ortoni* are in the collections of the Academy of Natural Sci-

terpret *ortoni* as representing merely populations of intergrades between *richardi* and *nigromarginatus*, with intergradation over a rather broad geographic area. The problem of whether to consider these populations intergrades or to grant them nomenclatorial recognition as a distinct race is a difficult one and one that recurs frequently in systematics where clinal variation is involved. There is no doubt that *ortoni* represents a series of populations intermediate between *richardi* and *nigromarginatus* in characters, but populations that exhibit sufficient local consistency to enable more than 75 per cent of the individuals over a wide geographic area to be definitely identified.

Two clines are particularly prominent in populations occurring in the Amazon Valley, involving *nigromarginatus*, *ortoni*, and *richardi*. From *nigromarginatus* to *ortoni* to *richardi*, i.e., from west to east, there is a gradual increase in the average number of ventral plates.

	<i>nigromarginatus</i>	<i>ortoni</i>	<i>richardi</i>
Ventrals			
Males	152.28 (82)	157.22 (9)	162.55 (49)
Females	156.91 (111)	161.54 (13)	164.91 (34)

ences of Philadelphia but are in a very poor state of preservation. These specimens have been examined in the course of this study but little data of diagnostic value can be obtained from them. Cope's (1876) description clearly associates the name *ortoni* with the population of *Thalerophis* from the region of the middle Amazon Valley, despite his statement that the scales are smooth.

This subspecies has usually been allocated to the synonymy of *nigromarginatus*.

This subspecies is known to intergrade in the eastern edge of its geographic range with *richardi* in the vicinity of Santarem, Brazil; in the western edge of its range with *nigromarginatus*, in the Amazon Valley near the Peru-Brazil border; and in the southern part of its range with *bolivianus* in northern Bolivia. Geographically *ortoni* occupies an area between the three races with which it is known to interbreed. In most of its characters it is intermediate between *richardi* and *nigromarginatus*. Another herpetologist might in-

From *nigromarginatus* to *ortoni* to *richardi* i.e., from west to east, there is a gradual decrease in black pigment on the head shields and dorsal scales. This cannot be expressed quantitatively, but can be appreciated in part by comparing the head drawings in text figure 4 of *richardi* and *nigromarginatus*. In the eastern end of its range *ortoni*, in the coloration of the head, is virtually identical to *richardi*, yet in the western part of its range where it comes in contact with *nigromarginatus* it is very similar to that form in head coloration. This latter statement is not true of the population of *ortoni* from eastern Colombia, for, although in these the head shields may be bordered with black, none has been seen that exhibited a tendency towards prominent spots on any of the head shields.

Whether *ortoni* is in genetic contact with either *occidentalis* or *copei* is not known. The eastern Andes of Colombia seem to be an effective barrier separating *ortoni* and *occidentalis*. There appears to be no marked physio-

graphic barrier to separate *ortoni* from *copei*; however, there are pronounced differences in vegetation in the area where their ranges are adjacent, and it seems likely that they are effectively separated ecologically.

SPECIMENS EXAMINED (33)

BOLIVIA. Beni: Beni River, A.M.N.H. Nos. 22267, 22268; Riberalta, A.M.N.H. Nos. 22258, 22259; Villa Bella, C.M. No. 366.

BRAZIL. Amazonas: Abuna, U.M.M.Z. No. 56898; Ayapua, Rio Purus, Solimoes, B.M.N.H. No. 1926.4130.16; Manaus, B.M.N.H. Nos. 97.12.29.15, 97.12.29.16; Porto Velho, A.M.N.H. No. 22254; Sao Paulo de Olivenca, A.M.N.H. No. 56160; Solimoes, middle Amazon, A.N.S.P. Nos. 25774-75 (cotypes): Tefte, M.C.Z. Nos. 2958, 2980. Para: Obidos, M.C.Z. No. 2584, U.M.M.Z. No. 56304(2); Oyapock River, A.M.N.H. No. 58205; Santarem, M.C.Z. Nos. 2573 (3), 2792, 2808, U.M.M.Z. No. 65861, Taparinha, M.C.Z. No. 2938, U.S.N.M. Nos. 120828, 120829.

COLOMBIA. Amazonas: La Pedrera, I.L.S. No. 158. Caqueta: Morelia, upper Rio Caqueta, A.N.S.P. Nos. 25646, 25647; Rio Caqueta, I.L.S. Nos. 157, 159. Meta: Villavicencio, I.L.S. Nos. 155, 156.

Thalerophis richardi praestans Cope

Thrasops praestans COPE, 1868, Proc. Acad. Nat. Sci. Philadelphia, vol. 20, p. 309; Peten, Guatemala.

Thrasops (Ahaetulla) sargii FISCHER, 1881, Arch. Naturgesch., vol. 47, no. 1, p. 229; Guatemala.

Leptophis maximus WELLER, 1930, Proc. Jr. Soc. Nat. Sci. Cincinnati, vol. 1, p. 1; unknown.

Leptophis occidentalis occidentalis STUART, 1934, Occas. Papers Mus. Zool. Univ. Michigan, no. 292, p. 15.

Leptophis occidentalis praestans OLIVER, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 16.

TYPE LOCALITY: Peten, Guatemala.

RANGE: From central Vera Cruz, Mexico, east to Yucatan, southward through British Honduras, central and eastern Guatemala, to and including Honduras (fig. 10).

DESCRIPTION: The maxillary teeth are 23-25, the average for 17 observations is 23.8; the last three teeth are strongly enlarged. Hemipenis eight subcaudals long, with five enlarged basal spines opposite subcaudal 2; the longest spine is adjacent to, and on the inner side of, the sulcus; four to five trans-

verse rows of smaller spines occur opposite subcaudals 3 and 4. These spines gradually merge into calyces with long, spiny, fringing papillae that obscure the structure of the calyces; papillae decrease in length distally, becoming more fleshy and leaving the distal portion typically calyculate opposite subcaudal 8. (See pl. 17.)

Keels are present on the scales of rows V-XI, occasionally on those of rows II-XIV. The keels on the scales of the vertebral row are weak and indistinct; those on the scales of the paravertebral rows are the strongest and most distinct of all. Scales of row VI are not keeled above the anus, and there are no keels on the dorsal scales on the tail posterior to the point of reduction from six to four rows.

The reduction in the number of rows of dorsal scales involving rows V-VI or VI-VII occurs opposite ventrals 96-104, average 98.79, in the males; opposite ventrals 101-110, average 105.68, in the females. That involving rows III-IV, occasionally rows II-III, occurs opposite ventrals 95-105, average 100.29, in the males; opposite ventrals 101-114, average 106.87, in the females. Reduction of the dorsal scales on the tail from six to four rows takes place opposite subcaudals 5-9, average 6.29, in the males; opposite subcaudals 4-8, average 5.33, in the females.

The ventral plates are 166-182, average 174.89, in the males; 174-183, average 179.27, in the females. Two males have complete tails with 153 and 172 subcaudals; another male has the tail incomplete but has 175 subcaudals. Four females with complete tails have 170-185, average 177.00, subcaudals. All specimens have the anal plate completely divided.

The upper labials are either eight or nine in number; the lower labials are most frequently 10 in number. The loreal is absent in all specimens examined except one female which has the shield present on both sides of the head. The preocular is single in all specimens studied, whereas there are three variants from the normal two postoculars: 1/1, 2/3, and 3/3. The lower postocular is much smaller than the upper. The preocular occasionally is in contact with the frontal. The parietal is as broad as, or broader than, long, deeply notched by the upper posterior tem-

poral, and may or may not be in contact with the lower postocular. The frontal is large, bell shaped, and its length is equal to, or greater than, the length of the interparietal suture. The temporals are normally 1-2. The eye is large in size, and its diameter is greater than the distance from its anterior border to the nostril.

The largest male examined had a head-body length of 1470 mm., plus a tail length of 773+ mm., and is the largest specimen examined in the genus; the largest female studied had a head-body length of 1240 mm., plus a tail length of 644+ mm. One male with a complete tail has a tail/body ratio of .61, while one with an incomplete tail has a ratio of .63. Four females with complete tails have ratios of .56-.68, average .602.

The coloration in alcohol is: top of head dark blue (Deep Orient Blue to Indigo Blue); dorsal region of body and tail of same color; no black ocular stripe. Upper labials lighter than top of head (Light Glaucous Blue); lower labials, chin shields, and anterior ventrals of same color as upper labials. Ventrals darker posteriorly than anteriorly; posterior third of body and subcaudals darker blue (Glaucous Blue) than anterior third of body.

Keels of scales of dorsal rows V, VI, VII, IX, X, and XI, frequently black; black on paravertebral rows most prominent and most widely dispersed on scales, forming prominent longitudinal black line along each side of vertebral scale row.

On anterior two-thirds of body usually a series of distinct oblique bands of white, forming chevrons; less than one scale row in width and formed by white spots on edges of dorsal scales and by regular white chevrons on skin between scales. White marks separated from one another by distance equal to one or two scales, and most clearly seen when scales are spread apart slightly.

VARIATION: Eleven specimens have eight upper labials, nine have 8/9, six have nine, and two have 7/8. The lower labials are 10 in 18 specimens, three have 11, three have 10/11, two have 9/10, one has nine, and one has 10/12. One specimen each has the following temporal formula: 1-1, 1-1/1-2, 1-1-2, 1-1-2/1-2, and 1-2/2-2.

There is considerable variation in the number of dorsal scale rows that are keeled and

in the distinctness of the keels. The keels on rows V, VI, VII, IX, X, and XI are the most pronounced. The adult males are more prominently and distinctly keeled than the adult females, and it is in the former that keels are most frequently observed on rows II-XIV. When keels are present on the scales on the vertebral row, they are usually weak and only present for a short distance.

There is a good deal of variation in respect to the amount and distinctness of the white areas on the dorsal surface. In some individuals only irregular, scattered white spots are visible without spreading the scales apart. No representative of this subspecies has been examined in which these white chevrons could not be seen by spreading the scales apart. A juvenile from Guatemala with a head-body length of 373 mm. exhibits the banded juvenile pattern. (See fig. 5.)

The data are too few for the geographical variation in the number of ventral plates to be analyzed precisely. There appears to be a clinal trend with an increase from south to north, but this cannot be clearly shown with the material available.

REMARKS: Cope, in his description (1868) of this form, called attention to its large size and the distinctive features of the dorsal keels, especially those of the scales of the paravertebral rows. He failed to mention the pattern of white chevron-shaped marks and the absence of a black postocular stripe that are characteristic features of this subspecies. Cope's types are extant and have been examined during this study. Both exhibit the white chevron marks and both lack a postocular stripe.

On the basis of one specimen from Guatemala, Fischer (1881) proposed the species *sargii* and stated that it was closely related to Cope's *praestans*. Fischer's very detailed description leaves no doubt of the identity of his species, and all of the differences that he cites between *praestans* and *sargii* are included in the variation of the former.

Weller (1930) described a specimen of unknown origin, proposing the name *maximus* for it. The type is supposedly in the collection of the Cincinnati Society of Natural History, but could not be located in 1937 by Ralph Dury, the director of that institution. I am grateful to Dury for sending me a typewritten

copy of Weller's original description. In 1931 Weller published a brief note assigning *maximus* to the synonymy of *occidentalis*, but from the description the name appears to be a synonym of *praestans* rather than *occidentalis*.

The relationships of *praestans* are clear-cut since it represents the end form of a chain of subspecies. Its closest relative, geographically and morphologically, is *occidentalis*, with which it is known to intergrade in the vicinity of the Segovia River in southeastern Honduras. Two specimens (U.S.N.M. Nos. 24531, 24532), a male and a female, from that area exhibit a mixture of the characters that have been employed in diagnosing the two races.

SPECIMENS EXAMINED (31)

BRITISH HONDURAS. Cocquericot, U.M.M.Z. No. 74905; Cohune Ridge, U.M.M.Z. No. 80713.

GUATEMALA. Izabal, C.N.H.M. No. 20089; La Libertad, U.M.M.Z. Nos. 74904, 79053; Nueva Agua, U.S.N.M. No. 71366; Pacala, west of Chama, U.M.M.Z. No. 89974; "near Peten," U.S.N.M. No. 6754 (2 cotypes); Quebradas, C.N.H.M. No. 20489; Santa Teresa, U.M.M.Z. No. 74851.

HONDURAS. Chameleon, San Pedro Sula, M.C.Z. No. 28043; Lancetilla, A.M.N.H. Nos. 46973, 46974, M.C.Z. Nos. 28045, 29409; Progreso District, U.S.N.M. No. 21714; San Pedro, C.N.H.M. Nos. 5292-5294; Segovia River, U.S.N.M. Nos. 24531, 24532; Tela, M.C.Z. Nos. 33339, 33554, U.S.N.M. No. 84259; Taloa Creek, M.C.Z. No. 21194; "Honduras," A.M.N.H. No. 32341.

MEXICO. Quintana Roo: Xkanha, A.M.N.H. No. 7861. Vera Cruz: Montzorongo, M.C.Z. Nos. 21071, 21072. Yucatan: Colonia Santa Maria, U.M.M.Z. No. 76165.

Thalerophis riveti Despax

Leptophis riveti DESPAX, 1911, Mission du service géographique de l'armée pour la mesure d'un arc méridien Equatorial en Amérique du Sud, Paris, vol. 9, no. 2, p. 26; Gualaquiza, Ecuador.

Leptophis occidentalis FOWLER, 1913, Proc. Acad. Nat. Sci. Philadelphia, vol. 65, p. 153.

Leptophis brevior BOULENGER, 1914, Proc. Zool. Soc. London, vol. 2, p. 815; near Pena Lisa, Choco, Colombia.

Leptophis riveti AMARAL, 1925, Proc. U. S. Natl. Mus., vol. 67, art. 24, p. 1.

TYPE LOCALITY: Gualaquiza, Ecuador.

RANGE: From central Panama south through western Colombia to southwestern

Ecuador and north central Peru; Trinidad, British West Indies (fig. 8).

DESCRIPTION: The maxillary teeth number from 26 to 29; the average for 11 counts is 27.8. The last three teeth are enlarged (fig. 1F). The hemipenis is six subcaudals long, without enlarged basal spines; there are six to seven transverse rows of small spines opposite the posterior half of subcaudal 2 and all of subcaudal 3; the spines decrease in size distally and merge into calyces with long spinous papillae, opposite the anterior half of subcaudal 4; the papillae decrease in length distally, leaving the distal third of the organ, opposite subcaudals 5 and 6, calyculate with the walls of the calyces denticulate. (See pl. 16.)

Keels are normally present on the scales of all dorsal rows but are strongest on rows II-XIV. Pronounced keels are present on the scales of the two median rows on the tail for nearly its entire length.

The reduction in the number of rows of dorsal scales on the body involving rows VI-VII occurs opposite ventrals 84-106, average 92.90, in the males; 89-90 in the single female. That involving rows III-IV occurs opposite ventrals 84-97, average 91.20, in the males; 88-90 in the female. The reduction of the dorsal scales on the tail from six to four rows takes place opposite subcaudals 5-22, average 11.66, in the males; opposite subcaudals 11-13 in the female.

The ventral plates vary in the males from 133-149, average 141.18; in the single female there are 147 ventrals. The subcaudals are 140-145, average for four specimens 142.00; the female has 135 subcaudals. All specimens examined have the anal plate divided, except that in one male the plate is only partly divided.

The upper labials are eight in number with the fourth and fifth in contact with the orbit; the majority of specimens have 10 lower labials with the first six in contact with the chin shields. The loreal is absent in all specimens examined. All have a single preocular scale, and most have two postoculars. The lower postocular is small. The preocular is not in contact with the frontal. The parietal is much longer than broad, truncate posteriorly or but slightly notched by the upper posterior temporal, usually in contact with

the lower postocular. The length of the frontal is less than that of the interparietal suture. Temporals are usually 1-2. Eye small to moderate in size, its diameter less than the distance from the anterior border of the orbit to nostril.

The largest male examined had a head-body length of 512 mm., plus tail length of 362+ mm.; the single female, an adult with developing eggs, had a head-body length of 459 mm., plus tail length of 298 mm. The tail/body ratios of four males with complete tails are .69-.72, average .702; for the female, .65.

The coloration (in alcohol) is: top of head light brown (Buffy Citrine) with stratum corneum present, light greenish blue (Greenish Glauous-Blue) when absent; black stripe on posterior edge of nasal plate, posteriorly along upper margins of first four upper labials, sometimes on lower edge of prefrontal and preocular; posterior to orbit, black stripe on upper margins of last four upper labials, lower postocular, lower margins of anterior temporal and lower posterior temporal, stopping on last scale or continuing posteriorly onto neck for short distance. Upper labials below stripe pure white.

Body above light golden brown (Old Gold) with stratum corneum present, light gray (Pale Smoke Gray) to light green (Niagara Green) when outer layer is absent, with narrow oblique bands of dark blue (Orient Blue). Blue bands approximately one scale row wide and separated by interspace one and one-half to two and one-half scales wide; anterior third of body, blue bands on all scale rows except outermost rows, posteriorly blue coloration of oblique bands present as narrow anterior margin of scales of two outer rows. Two specimens with 60 and 61 bands, respectively, on body.

Oblique bands continue onto tail where they become irregular and interrupted, forming more or less scattered spots of blue. Chin and ventrals of anterior one-fourth of body pure white. Posterior to this, dark blue of oblique bands appears on outer edge of every other ventral scale. The amount and distribution of the blue coloration on the ventrals increase posteriorly so that on posterior third of body every ventral plate has a prominent outer blue margin. Blue margins of ventrals

together with anteroventral blue margin of scale row I form irregular longitudinal blue stripe along outer edge of ventrals with appearance of light stripe above on upper two-thirds of scales of row I and lower two-thirds of scales of row II.

Approximately at midbody ventrals acquire minute brown stippling that increases posteriorly, making posterior ventrals much darker than anterior plates. Coloration continues onto tail where, in addition to lateral blue edges of caudal scales, there is small amount of blue coloration on inner edge of plates, forming narrow, irregular stripe down center of tail. Banded pattern is illustrated in figure 5.

VARIATION: Aside from the observed variation indicated above in the description, a slight amount of variation has been noted in several of the head shields. Eight specimens have 10 lower labials on both sides of the head, whereas two have the formula 9/9 and one each has 9/10, 9/11, and 10/11. Nine individuals have two postoculars on each side of the head, two have one postocular on each side, and two have one on one side and two on the other. Nine have the normal temporal formula of 1-2, whereas one each has the formulas 1-1, 1-1-2, and 1-1-2/1-2. All but three specimens have the outer row of dorsal scales keeled. The single adult female has the oblique bands less pronounced and narrower than in the males that have been studied, and at midbody the bands break up, forming lateral spots. The dorsal ground color of this specimen is darker than in the males examined. The two specimens from Panama and the one from Trinidad are somewhat more elongate and slender in appearance than the remaining specimens, and the ventrals in these are somewhat more angulate.

The variations observed do not appear to be correlated geographically or ecologically, but this species is represented by so few specimens that no trends can be determined. The variation in respect to the head shields is suggestive in that the majority of the variants exhibit a reduction in the number of plates. In this connection it is worthy of note that the shape of the other head plates, e.g., the low, elongate anterior temporal, and the general appearance of the head all give the impression of a trend towards a flattening of

the head. Such a modification is not generally characteristic of arboreal adaptations but is more common among burrowing snakes. However, the available field observations indicate that the species is arboreal.

REMARKS: Despax's (1911) description of *riveti* was based on an adult specimen from the eastern side of the Andes in Ecuador. I have no information regarding the present status of the type specimen. The meticulous description presented by Despax leaves no doubt concerning the identity of his species. Boulenger (1914) proposed a new species, *brevior*, on the basis of an adult female from the Choco of Colombia. This name can be readily allocated to the synonymy of *riveti*.

This is one of the most distinct species in the genus and yet it has seldom been accorded recognition as a valid form. Most of the specimens in museum collections have been catalogued as *occidentalis*. The two do share a number of similar attributes but are readily separable. Interbreeding between *riveti* and other representatives of the genus is unknown and seems improbable.

Its relationships to the other species of the genus are difficult to determine with any degree of confidence. It seems almost equally close, or distant, to *depressirostris*, *mexicanus*, *nebulosus*, and *richardi*. Geographically the known range of *riveti* is not in contact with that of *mexicanus* or *nebulosus*, but it is in part sympatric with *depressirostris* and *richardi*. It appears to resemble *nebulosus* most closely in structural characters, although the color pattern of *riveti* is similar to that seen in the juveniles of most races of *richardi*.

The geographic records for *riveti* present several interesting distributional problems and suggest an early differentiation of this species in comparison with the other members of the genus. It is the only species in the genus that is found on both sides of the Andes in an undifferentiated form, i.e., not subdivided into races that are separated by the mountains. Only the species *richardi* occurs on both sides of the Andes, but it is represented by different races on the two sides. Parker (1938), in his distributional study of reptiles and amphibians in Ecuador, found that only one snake, *Dryadophis b. boddaerti*, out of the 28 studied occurred in the "Humid Tropical Zone" on both sides of the Andes.

Chapman (1926, pp. 33-61) has pointed out the similarity in many instances between the avifauna of western Ecuador and that of the Amazon Valley. He states, "The elevation of the Andes has not only separated tropical eastern, from tropical western Ecuador, but has divided the humid tropical zone of South America into apparently disconnected cis- and trans-Andean areas, and hence has severed the ranges of the identical and representative forms common to these areas."

In southern Ecuador the pass near Loja is one of the lowest in the central Andes, with an elevation of about 9000 feet. Another farther south in Peru is about 7000 feet and is one of the lowest passes in the entire Andean system. These passes may have provided a path of migration at some earlier date during a lower stage of Andean elevation. The passes of necessity would have to have been of a lower elevation than they are at present to be traversed by snakes of the warm tropical forests. Both of these passes open onto an arid portion of the Pacific slope, but according to Chapman (1926, frontispiece) there is a narrow extension of the Humid Tropical Zone along the Pacific slope just above the lower arid region and extending southward nearly to the pass at Loja.

It seems unlikely that the distribution of *riveti* in Ecuador can be explained satisfactorily through utilization of the two passes discussed above. The passes may have served as possible routes for avian migration, but they seem unsuitable for snakes inhabiting warm, humid tropical forests. The only evidence for this theory is a specimen (A.M.N.H. No. 22234) from Alamor, Ecuador, a locality nearly 5000 feet in elevation, at the extreme southern tip of the narrow strip of the "Humid Tropical Zone" that extends along the western slope of the Andes in southwestern Ecuador in the vicinity of Loja Pass.

Another possible explanation is suggested by the known distribution of a number of tropical mammals (unpublished information from Philip Hershkovitz). Among the mammals identical forms are present in the tropical forest on both sides of the Andes in Ecuador. The Amazonian forest of eastern Ecuador extends northward along the eastern slope of the Andes in Ecuador nearly to the

Lake Maracaibo region, and thence westward in a narrow strip that connects with the forest region of the Choco in western Colombia (Veatch, 1917). The collecting localities suggest that the mammals followed this forest around the northern flanks of the Andes rather than actually crossing the main divide in Ecuador. The exact route across northern Colombia is not certain, but several possible routes are suggested in Veatch (*loc. cit.*) and in Chapman (1917).

The available locality records for *riveti* are inadequate to cast much light on this distributional problem, but they suggest that the latter explanation is the more probable of the two discussed above. Specimens are known from northwestern Ecuador, the Choco of Colombia, Medellin between the western and eastern Andes of Colombia, and a locality on the eastern side of the Andes in both Ecuador and Peru. In Colombia there are no locality records east of the eastern Andes. However, this is a rare species in collections, and much more material will be necessary before the distributional problems can be settled satisfactorily.

A single specimen of this species in the collections of the British Museum (Natural History) is labeled from Trinidad, British West Indies. The specimen was collected by Ivan Sanderson in 1937 on Mount Aripo. I questioned the correctness of the locality data, and J. C. Battersby of the British Museum kindly provided me with additional details relating to the collection of the specimens, stating that he saw no reason to believe

that the locality was not correct. The specimen was taken from foliage at the top of a tree and was collected at an elevation of about 3000 feet. Shortly after I had received Battersby's letter, I saw Sanderson and questioned him about the specimen. He did not remember the particular individual but verified the identification of his field tag which was on the specimen. On the basis of the field number, he assured me that the specimen could have come from nowhere but Trinidad. This specimen presents a further distributional problem concerning which I can offer no information at the present time.

In connection with the distributional problems it is interesting to note that wherever altitudinal data are available for this species, it has been collected at altitudes of 3000–5000 feet which represent the known maximum elevations recorded for the genus.

SPECIMENS EXAMINED (12)

BRITISH WEST INDIES. Trinidad: Mount Aripo, B.M.N.H. No. 1940.3.11.84.

COLOMBIA. Antioquia: Medellin, A.M.N.H. No. 35705. Choco: Andagoya, M.C.Z. No. 32728.

ECUADOR. Canar: Rio Chanchan Valley, U.M.M.Z. No. 85102. Guayas: Guayaquil, U.S.N.M. No. 62791. Loja: Alamor, A.M.N.H. No. 22234. Los Rios: Balzapamba, A.M.N.H. No. 24203; Playa de Montalvo, U.M.M.Z. Nos. 83952, 83953. Haigra to Rio Chiquancay, A.N.S.P. No. 20895.

PANAMA. Agua Clara, A.N.S.P. No. 21766; Cerro Campana, A.N.S.P. No. 21589.

PERU. Amazonas: Rio Ceupa, Rio Maranon, A.M.N.H. No. 52545.

HABITS

FEW OBSERVATIONS ARE AVAILABLE regarding the habits of these snakes. In the past they have been considered to be strictly arboreal, as indicated by the generally applied name of "tree snake." A few of the forms can rightly be termed arboreal, but most appear to be more properly considered as semi-arboreal. This view is based in part on the differences in the development of attributes associated with an arboreal existence and in part on field observations recorded for the different species. Much more information about these snakes in the wild is needed to indicate the true habits of the different species and subspecies. Our knowledge at present is the result of a few casual observations in the field and inferences based on morphological characters.

All members of the genus are comparatively long, slender snakes capable of agile, active movements. The food habits, as indicated from analysis of stomach contents, consists primarily of arboreal or semi-arboreal frogs of the family Hylidae, suggesting that most of the snakes forage in bushes, shrubs, and trees. Whether encountered on the ground or in foliage, the snakes habitually endeavor to elude pursuit by escaping through the foliage. The round pupil is suggestive of diurnal habits; field observations confirm the diurnal nature of the activity of these snakes.

That the snakes are diurnal is an interesting factor in relation to their known food habits, for nearly all of the organisms that make up the diet of these snakes are nocturnal or crepuscular in habits. There may be possible advantages to a predator in locating its prey at a time when the latter is in a quiescent state and from which it emerges under a relative disadvantage in sensory efficiency as compared with that of the active predator. Whether this is true or not, I cannot say. A study of the detailed relationship and adaptations of predator and prey would be a valuable and interesting undertaking.

The detailed observations on food habits are presented in table 13. In many of the older accounts, and even in some recent semi-popular ones (Röhl, 1942), these snakes are

credited with a diet that consists only of birds and bird eggs. The observations based on the examination of stomach contents suggest that such statements are the result of pure supposition or are based on one or two observations.

All of the species are oviparous. The number of developing eggs observed in females varies from one to 10. In the case of those with but a single egg it is probable that other eggs had been laid shortly before capture. The actual minimum appears to be three eggs. Seven or more eggs appear to be an exceptional number. In a large series of female *nigromarginatus* from Peru the most frequently observed numbers of eggs per female were five (35 per cent), four (23 per cent), and three (23 per cent). The data for *nigromarginatus* suggest that in a fairly uniform climate, such as that of eastern Peru, reproduction may take place throughout the year, although more females with developing eggs were collected in the month of March than during any other month. Nothing is known about where the eggs are deposited or of the time required for incubation.

In his interesting paper on the warning reactions in reptiles, Mertens (1946) has pointed out that at least some members of the genus *Thalerophis* inflate the neck sufficiently to expose the skin between the scales, that the skin may have a color that enhances the threatening appearance of the snake, and that the mouth is widely opened when in a warning posture. He states that *mexicanus* is among the snakes that do not hiss when exhibiting the warning reaction. I know of no reports for hissing in *Thalerophis*.

The following passage from Mole and Urich (1894) provides information about the reactions in *coeruleodorsus*: "Locally known as 'Lora,' a Spanish word for parrot, because the sheeny iridescent greenish gold on the neck and anterior portion when inflated is thought to be like the hues of the feathers on the neck of the yellow-crested green parrot. Ordinarily, this snake has a common-place grey colour. Its head is of a dark greenish-brown colour, with an under surface of white. When caught, it opens its enormous

TABLE 13

OBSERVED STOMACH CONTENTS

(Figures indicate the actual number of each organism observed in the stomachs)

Species	Food Items
<i>depressirostris</i>	Hylid frog, ^a 1; <i>Anolis</i> sp., 1
<i>diplotropis</i>	<i>Agalychnis dacnicolor</i> , 1; frog ^a 1; <i>Rana pipiens</i> , 1
<i>m. mexicanus</i>	<i>Hyla baudinii</i> , 1; hylid frog, 5; <i>Thecadactylus rapicaudus</i> , 1
<i>m. yucatanensis</i>	Hylid frog, 2
<i>nebulosus</i>	Frog, 1
<i>r. richardi</i>	Frog, 2; hylid frog, 6
<i>r. bolivianus</i>	Hylid frog, 2
<i>r. chocoensis</i>	Hylid frog, 1
<i>r. coeruleodorsus</i>	<i>Dryadophis b. boddaerti</i> , 1; nestling bird, 1
<i>r. nigromarginatus</i>	Bird egg, 1; gecko, 1; hylid frog, 58; young bird, 1
<i>r. occidentalis</i>	<i>Agalychnis</i> sp., 1; bird egg, 1; frog, 1; hylid frog, 5; <i>Thecadactylus</i> sp., 1; young bird, 1
<i>r. ortoni</i>	Gecko, 1; hylid frog, 3
<i>r. praestans</i>	<i>Hyla baudinii</i> , 1
<i>riveti</i>	Hylid frog, 1
Summary: Hylid frog, 88; frog, 6; gecko, 4; bird, 3; bird egg, 3; <i>Anolis</i> , 1; snake, 1	

^a Many of the remains could not be identified in detail. All members of the family Hylidae that could not be identified generically were recorded as "hylid frog"; all other salientians that could not be identified generically were recorded as "frog."

mouth to its fullest extent and threatens in a most ferocious, but at the same time somewhat absurd, manner. It rarely bites, but when it does it is apt to inflict small wounds with the two long teeth which are placed one on each side in the posterior parts of the upper jaw-bones. They are exceedingly slender reptiles and their heads at first sight appear large and disproportioned to the rest of their bodies. They frequently reach a length of $3\frac{1}{2}$ and even 4 feet. They feed on frogs and lizards. On several occasions lizards which have been partially swallowed by these snakes and have escaped have died soon afterwards. The Lora is swift in its movements, and when rushing along on a level surface the outside portions of its curves do not appear to touch the earth."

Through the courtesy of Brayton Eddy of the New York Zoological Society I have recently had the opportunity to observe a live specimen of *occidentalis* from Colombia. This individual opened its mouth and spread the jaws apart to make the mouth appear much larger than was expected from the size of the snake. This seemed to be accomplished by extending the quadrates out laterally to

where they were almost in a horizontal position and perpendicular in relation to the long axis of the skull; thus the mouth opening seemed to be distorted in a lateral direction while being almost normal in a vertical direction. This was unquestionably the gaping reaction mentioned by Mertens, as well as by Mole and Urich. The specimen inflated the neck for only a short distance posterior to the hind part of the head. One of the most interesting observations that I noted on this specimen was the bright dark green color of the tongue which was flicked in and out both when the mouth was gaped and when it was closed. When the specimen was in its cage and was disturbed it maneuvered its head in order to look straight at an intruder in such a fashion as to indicate that it was employing binocular vision.

The specimens of *diplotropis* collected by Norman Hartweg and myself in Oaxaca, Mexico, were not observed to exhibit any such reactions and none of them seemed to make any effort to bite. This may be indicative of individual peculiarities or of a species difference in temperament.

An interesting problem centers around the

question of whether or not members of this genus have or employ a venom. Phisalix (1922) has stated that it ("*Leptophis*") is considered a venomous aglyphous snake. Certainly none examined by me had a groove on the posterior teeth, yet all have the posterior teeth enlarged in varying degrees. Afra-nio Amaral has told me in personal conversation that he believes these snakes have a venom that is capable of killing small lizards. In the above quotation from Mole and Urich it will be noted that they state that "On several occasions lizards which have been partially swallowed by these snakes and have escaped have died soon afterwards."

The problem probably originates from the fact that the genus represents a somewhat intermediate stage in the transition from an aglyphous harmless snake to an opisthoglyphous venomous snake. Smith and Belairs (1947) have discussed the changes in the parotid gland and in the posterior teeth that take place in the development and evolution of the opisthoglyphous condition. They state, "In general, the differentiation of the gland precedes the grooving of the teeth, but not always their enlargement." *Thalerophis* appears to be in a stage of development where the glands and the teeth are enlarged, but in which no grooves have been developed on the teeth. From some of the observations cited above, this stage of development seems to function effectively in killing small prey.

The seasonal incidence of the collection of one member of the genus, *nigromarginatus*, in a climate characterized by slight monthly fluctuations has already been discussed (Oliver, 1947b). The data for this form indicate that more (29 per cent of the total) specimens were collected in March than in any other month. The greater number collected in March seems to be correlated with factors dependent on rainfall: the abundance of the frogs that make up the diet and the restriction of the available dry-land area as a result of widespread flooding. Members of the genus occurring in regions that have greater seasonal fluctuations in the climatic factors probably exhibit a more pronounced seasonal variation in the numbers observed or collected.

Bates (1928) analyzed a collection of 1564 snakes from the Panama Canal Zone. The

eight most common species comprised 72 per cent of the total number of specimens. The eighth species in order of abundance in this collection was *Thalerophis richardi occidentalis*. It was represented by 62 specimens or 4 per cent of the total collection. Dunn has made the most complete and extensive faunal analysis of Panama, based on more than 9500 specimens. I do not have his figures for the relative abundance of *Thalerophis*, but he has presented a summary (Dunn, 1940) of pertinent observations from this analysis. He states that "the dominant snake species differ from area to area, although the areas may have similar conditions and a similar list of species. In each area a few forms are abundant and the rest are rare. Roughly 10% of the species make up half the population; while half of the species make up 5% of the population." Where data are available, no *Thalerophis* is among the abundant 10 per cent of the species that make up half of the local population. Some species of the genus, e.g., *nebulosus* and *riveti*, are definitely rare, while others may be common locally, e.g., *diplotropis*, *mexicanus*, *richardi richardi*, *r. nigromarginatus*, and *r. occidentalis*.

Stuart (1935) states that in Guatemala *mexicanus* "was most generally found in the branches of the bushes and only occasionally was it seen on the ground. When alarmed it attempts to escape in the bushes rather than across the forest floor. One (U.M.M.Z. No. 75854) was found six feet from the ground part way down a hole in a stump. It was trying to secure a specimen of *Triprion petesatus* (sic)."

Slevin (1939) records a specimen of the same species in Guatemala "crawling about the edge of a pile of rotting banana leaves near Quirigua." He suggests that "Probably the excellent type of cover the banana plantation affords made this more or less common species difficult to find, as only a single specimen was seen during twelve days intensive hunting." In relation to this observation of Slevin's it is worth mentioning that the only members of the genus that have been reported from or found in bananas shipped to the United States were *mexicanus mexicanus*. I have examined three such individuals.

Most of the specimens of *diplotropis* collected by Hartweg and me in southern Mex-

ico were found on the ground in the vicinity of water. The natives state that the species congregate in large numbers for the purpose of mating in the bushes surrounding a semi-permanent pond. But they were rather vague as to the time of this occurrence.

Slevin (1942) describes *occidentalis* in western Panama as "One of the commoner species about Boquete, where thirteen specimens were taken. Strictly confined to the heavy-growth areas in close proximity to water it was found on the floor of the Caldera Valley, islets in the Caldera River, and along the edge of streams in the mountainous sections above the valley floor. This snake is striking in color, so intense that it is conspicuous even against the luxuriant tropical foliage."

Emmett R. Dunn (*in litt.*) describes capturing in Panama a specimen of *riveti* that was in a tree about 15 feet above ground. Another was found by him in the grass, but it started to climb a bush. Ivan Sanderson collected a specimen of *riveti* "in the foliage at the top of a tree."

William Beebe (1946) has recorded a number of interesting observations on *richardi richardi* in British Guiana: "These snakes are excellent climbers and often rest quietly for hours draped over branches and twigs. Six of those taken at Kartabo, however, were hunting on the ground. One had just caught a leopard *Hyla*. It relinquished its hold on the frog in the excitement of being captured, but

ten minutes later when placed in a wire cage with the still unhurt frog, it again attacked and this time swallowed the unfortunate amphibian. Two were caught in the laboratory when they dropped from the rafters to the floor.

"The small Kartabo specimens were nervous and bit at every opportunity. No. 245, with a total length of 975 mm., when set at liberty for an hour in the laboratory compound, made straight for the nearest bamboo stem and would not be turned aside. It climbed the stem, which was six inches thick and exceedingly smooth, ascending rapidly by throwing S-shaped coils around half the circumference, and holding on by pressure on opposite sides of the stem. It soon shifted to an adjoining shrub, climbing easily among the slender branches, holding the head and neck raised stiffly, and occasionally swaying them from side to side.

"This head-rearing seems to be a habit. From a level of foliage in a bush-covered clearing a single object projected, and closer examination showed this to be six inches of head and neck of a brilliant green and white whip snake. It permitted me to approach and actually grasp its neck, but instantly the little serpent became a fiend, seized my finger and so jerked its head from side to side that its teeth tore the flesh and caused a few drops of blood to escape. Unlike the boas it fought until I shut it tightly in a bag."

DISTRIBUTION

PARKER (1935) HAS STATED that "any attempt to plot the distribution of a species from the published records is much more likely to result in a map of the distribution of herpetological collectors than to give a picture of its range." This is equally true in plotting unpublished records based on museum collections. Much material has been accumulated in the collections of museums, and many geographical gaps have been filled since the date of Parker's statement, but unfortunately there is still a large measure of truth in the observation as can be seen by the plotted records for *richardi marginatus* in Brazil (fig. 10). The straight line of localities for the subspecies across southern Brazil does not indicate a sharp faunal break in that region, but marks rather clearly the Sao Paulo-Porto Esperance railway.

Thalerophis occurs in the lowlands, usually below 3000 feet, from northern Mexico to northern Argentina, occupying virtually all of the Neotropical realm on the mainland except the west coast deserts of South America south of the equator and the west coast of Central America from northern Costa Rica to the southern Mexican border. The genus is unknown from the West Indies except on the two continental islands of Trinidad and Tobago, off the coast of Venezuela. The known distribution of the genus follows closely the distribution of the tropical and subtropical rain forest and the tropical deciduous forest as indicated on the "Generalized phytogeographic map of Latin America" (Smith and Johnston, 1945). A few records for the genus occur within or close to areas indicated as savanna, thorn forest, or palm forest. Whether members of the genus normally occur within these vegetation types or in small "islands" of the rain forest and deciduous forests within these vegetation types is not known. In one area, the northwestern coast of Mexico, indicated as thorn forest on this map, *diplotropis* occurs in a vegetational type that Gentry (1942) recognized as distinct from the thorn forest, the "Short-tree Forest." Gentry says that this type is "a heterogeneous deciduous forest with a strong infusion of tropical elements" and occurs in the

humid barrancas. It is probable that the occurrence of *Thalerophis* in the savannas and palm forest is to be explained by a similar infusion of vegetational types. For example, it is well known that in many savanna areas forests occur along the larger streams. In such situations *Thalerophis* may occur. It is, of course, also possible that some of the forms of the genus have invaded the savanna area and are a part of the savanna fauna. It is possible that *copei* and *marginatus*, in the northern part of its range, represent savanna-inhabiting races of the species *richardi*. Unfortunately very little information is available on the ecology of the species. Our present meager knowledge indicates that all members of the genus are inhabitants of the tropical and subtropical rain forest, the tropical deciduous forest, or the scrub forest; and consequently the distribution of the genus corresponds roughly to the distribution of these vegetational types.

The arid Pacific slope of Central America from the northern border of Costa Rica to the southern border of Mexico has been poorly explored from a herpetological standpoint. Whether the genus *Thalerophis* is entirely absent from this region or what species may occur there is not known at present. It seems likely that some member of the genus occurs in the area, to judge from the conditions in the adjoining geographic areas. In the west coast deserts of South America south of the equator it appears that the genus is absent. This area is better known herpetologically than the one mentioned above and is characterized by a small fauna that is adapted to conditions of pronounced aridity. Schlegel (1837) recorded "*Dendrophis liocercus*" from Chile. Gay (1858) likewise lists a "*Dendrophis liocercus*" from Chile, but states that he is not certain that it occurs within the boundaries of the country. It is extremely doubtful that any representative of the genus *Thalerophis* occurs in Chile at the present time.

Schlegel (*loc. cit.*) also listed his "*Dendrophis liocercus*" from the island of Martinique in the West Indies. Reinhardt and Lütken (1862) list "*Ahaetulla liocercus*" from the

same island, probably on the basis of Schlegel's earlier report. Barbour (1914) has pointed out the error of these records.

In addition to the mainland localities, the genus is known from the following larger islands: (1) the Tres Marias Islands (*diplo-trophis*); (2) Coiba and San Miguel Islands (*richardi occidentalis*); (3) Gorgona Island (*depressirostris*, *richardi bocourti*); (4) Tobago (*richardi coeruleodorsus*); and (5) Trinidad (*richardi coeruleodorsus*, *riveti*).

The known distribution of *Thalerophis* in the countries of Latin America is presented in the list that appears below. The countries are arranged in alphabetical order and the species are listed in alphabetical order following the name of the country.

Argentina: *richardi marginatus*

Bolivia: *richardi bolivianus*, *r. marginatus*, *r. nigromarginatus*, *r. ortonii*

Brazil: *richardi copei*, *r. liocercus*, *r. marginatus*, *r. nigromarginatus*, *r. ortonii*, *r. richardi*

British Guiana: *richardi richardi*

British Honduras: *mexicanus mexicanus*, *richardi praestans*

Chile: None known. Schlegel (1837) reports an all green variety of "*Dendrophis liocercus*" from Chile, but the record appears to be erroneous

Colombia: *depressirostris*, *richardi bocourti*, *r. cho-coensis*, *r. copei*, *r. nigromarginatus*, *r. occidentalis*, *r. ortonii*, *riveti*

Costa Rica: *depressirostris*, *mexicanus mexicanus*, *nebulosus*, *richardi occidentalis*

Dutch Guiana: *richardi richardi*

Ecuador: *depressirostris*, *richardi bocourti*, *r. nigromarginatus*, *r. occidentalis*, *riveti*

French Guiana: *richardi richardi*

Guatemala: *mexicanus mexicanus*, *richardi praestans*

Honduras: *mexicanus mexicanus*, *nebulosus*, *richardi praestans*

Mexico: *diplo-trophis*, *mexicanus mexicanus*, *m. yucatanensis*, *richardi praestans*

Nicaragua: *depressirostris*, *mexicanus mexicanus*, *nebulosus*, *richardi occidentalis*

Panama: *depressirostris*, *richardi occidentalis*, *riveti*

Paraguay: *richardi marginatus*

Peru: (?) *depressirostris*, *richardi nigromarginatus*, *riveti*

El Salvador: None known

Uruguay: None known

Venezuela: *richardi coeruleodorsus*, *r. copei*, *r. occidentalis*

West Indies: *richardi coeruleodorsus* from Trinidad and Tobago, *riveti* from Trinidad. Under the name *liocercus*, the genus has been reported from Martinique (Schlegel, 1837), but Barbour (1914) has shown that this was an error

EVOLUTIONARY TRENDS

THE CHARACTERS AND DISTRIBUTION of this genus suggest that it evolved from an ancestral stock in lower Central America and had a secondary center of dispersal in northwestern South America. By analysis of the character distribution and variation, certain conditions of character development can be inferred as more or less primitive and other conditions as more or less advanced or specialized. If it can be assumed that the ancestral form had characters similar to those that are considered primitive, a hypothetical ancestral form can be visualized on the basis of these characters.

The most generalized condition in regard to the maxillary teeth appears to be that of a large number of teeth, 33–36, with three, four, or more of the posterior teeth larger than those preceding them. The generalized condition for the genus in the hemipenis is an organ approximately eight or nine subcaudals long with no enlarged basal spines, with the proximal half to one-third of the organ covered with small spines and the distal half to two-thirds covered with calyces that have denticulate borders.

The generalized dorsal scales have no keels or keels only on the scales of the paravertebral rows, with no keels on the scales of the tail. The scales of the vertebral row are not enlarged. The ventrals have no lateral keel or lateral notch. The number of ventrals probably averages about 141 in both sexes. The subcaudal plates average about the same in number as the ventrals.

The head shields, with the exception of the loreal, are of little value in indicating clear-cut evolutionary trends. The tendency appears to be towards a reduction in the total number of head shields. Thus in the generalized condition the upper labials are probably nine and the lower labials are probably 11 in number. The loreal is present. The oculars consist of one preocular and two postoculars. The temporals are 1–2.

The size is small to moderate with a head-body length of approximately 500 mm. The primitive coloration is probably that of a uniform green with no pattern other than a black postocular stripe and possibly longi-

tudinal black streaks on the keels of the scales in the paravertebral rows.

The conditions of character development described above represent the generalized or primitive stage. A snake possessing these characters is believed to be similar to the ancestral stock from which the genus has evolved towards a more advanced state indicated by character development of an opposite nature to that of the primitive condition. In the development of the maxillary teeth, *diplotropis* appears to be the most advanced in the genus, with an average number of teeth of 18.5 and with only the last two posterior teeth strongly enlarged (fig. 1H).

The trend in development of the hemipenis is towards an organ with enlarged basal spines, followed distally by several transverse rows of smaller spines that merge distally into calyces with spinous fringing papillae, and only a small distal portion that appears typically calyculate. In this trend *mexicanus* appears to be the most advanced member of the genus (see pl. 17).

The trend in regard to the dorsal scales is towards keels on the scales of all dorsal rows. This trend is entirely independent of that concerning enlargement of the scales of the vertebral row. In development of keels on the dorsals, *riveti* represents the most advanced condition with keels on the scales of all dorsal rows and prominent keels on the dorsal scales of the tail. In enlargement of the vertebrae either *diplotropis* or *richardi* *richardi* represents the most modified condition. In relation to the number of ventrals *diplotropis* exhibits the maximum number observed in the genus, 184, but *richardi* *praestans* has a nearly equal number. A male of *richardi occidentalis* exhibits the highest number of subcaudals observed in the genus—189.

Several forms normally have eight upper and 10 lower labials with little or no variation from this condition, but *riveti* exhibits only eight upper labials, and the variation in the lower labials is towards further reduction. In the number of oculars all specimens of *riveti* have a single preocular, and the only variation from the normal two postoculars is to-

wards the condition of a single postocular. In relation to the condition of the temporals only *richardi marginatus* exhibits a pronounced trend towards reduction in the number of these shields.

In size *richardi praestans* is the largest known member of the genus. The most advanced coloration is the striped pattern observed in *mexicanus*, *nebulosus*, and *richardi richardi*.

To summarize, the main evolutionary trends in the genus involve: (1) a reduction in the number of maxillary teeth, with fewer posterior teeth enlarged, but these are relatively larger than the other maxillary teeth; (2) an increase in the size of the spines at the base of the hemipenis, and an increase in the area covered by spines with a consequent decrease in the apparent calyces; (3) an increase in the number of rows of dorsal scales with keels; (4) a proportionate enlargement of the scales of the vertebral row; (5) an increase in the number of ventral and subcaudal plates, i.e., an increase in the number of vertebrae; (6) a reduction in the number of head shields through fusion of adjacent shields; (7) an increase in size; (8) the development of a striped pattern.

It will be readily apparent that a number of characters are not considered in these evolutionary trends. These have been omitted because of the inadequacy of the data available to permit the deduction of the trends.

In regard to two of the trends that are listed above, the distribution of keels on the dorsals and the number of labials, the conclusions concerning them are highly tentative in relation to the direction of the trends. The presence of keels on the scales of only two dorsal rows might appear as a specialized condition following a secondary reduction in the distribution of the keels. Stuart (1932), in his study of a group of genera closely related to *Thalerophis*, implies that the presence of keels is a more generalized condition than the absence of keels. The primary evidence upon which I base the view that the condition with keels only on the scales of the paravertebrals represents a primitive or generalized condition is based on the postembryonic ontogenetic change that occurs in the distribution of the keels. In forms that typically have keels on the scales of rows II–XIV

in the adults, juveniles have been studied that had no keels, or keels only on the scales of the paravertebral rows. Subadult males and occasional adult females of the same forms have keels on the scales of rows VI–X.

As noted earlier, the distribution and development of the keels are sex influenced, being more widely distributed and better developed in males than in females. The trend from no keels to keels on the scales of most rows seems to parallel the phylogenetic development of keels in snakes as a whole. The earliest known and most primitive snakes (on the basis of the total of their characters) have smooth scales without keels, whereas some of the most advanced snakes, such as the Crotalidae and Viperidae, have keels on most of the dorsal scales. Whether or not a secondary reduction in the keels has taken place in some genera, I do not know. I am aware of no published work on the embryonic development of keels on the dorsal scales of snakes.

The number of labial shields and the geographic distribution of the various numbers exhibit so much variation in some forms that it is difficult to evaluate the evolutionary trend in these shields. The supposition that nine upper and 11 lower labials represent the primitive condition is supported by little evidence within the genus, except the general trend towards a reduction in the number of head shields. A majority of peripheral forms that are specialized in other attributes have eight upper and 10 lower labials. On the other hand, *riveti* represents a more or less generalized condition in the majority of its structural characters but has only eight upper labials and 10 or fewer lower labials. The bulk of the evidence from other characters indicates an evolutionary line of development down the Amazon Valley from west to east, but in the same populations there is a gradual increase in the number of labials from west to east.

In so far as can be determined without detailed genetic analysis, most of the evolutionary trends indicated for the characters considered in the preceding section vary independently of the trend for any other character. Still, a number of these trends may be distributed geographically in a parallel manner and thus facilitate the determination of phylogenetic lines. No single character can be employed to determine the relationships of

any form nor can a single character be used to determine the most primitive or most advanced member of the genus. The systematist must analyze as many characters as possible in order to arrive at the most accurate arrangement possible with the material at hand. There are practical limits to the number of characters that should or can be employed, and the complexity of the problem increases with the number of characters used. As stated by Bogert (1947), "The basic difficulty, of course, lies in knowing which char-

acters in any species can be given the most weight in setting up a natural classification."

In endeavoring to determine the phylogeny of the species comprising the genus, I have relied mostly upon the characters of the maxillary teeth, the hemipenis, the number of ventrals, the present geographic distribution, the distribution of keels on the dorsal scales, the presence or absence of a loreal shield, and the color pattern. These are listed in order of the approximate relative importance assumed for the different characters.

PHYLOGENY

A DISCUSSION of the phylogeny of this genus based upon the data available must be considered as a tentative presentation of probabilities that are to a large degree speculative. Bogert (1947), in his study of the status of the monotypic genus *Leptodrymus*, has reviewed the attributes and composition of eight colubrine genera that are closely related to *Thalerophis*. He concludes, "The state of our knowledge at present does not permit us to set up a phylogenetic arrangement that is very meaningful." Despite the limitations in the knowledge about these snakes and the imperfections that may result from any attempts to deduce phylogenies, some probable and some improbable relationships can be indicated. If such action does no more than stimulate the accumulation of data for the subsequent refutation of the hypotheses, it will be of value.

One of the biggest handicaps to the neontologist, in making phylogenetic deductions, is the absence of any fossil record to provide either a clue to the age of the animals with which he is dealing or an indication of the

past condition and distribution of the characters that are used in differentiating the groups under consideration. The fossil record of snakes as a whole is poorly known. Gilmore (1938) has reviewed the known fossil snake material from North America. The oldest fossil form that is congeneric with any recent genus is *Crotalus* from the Lower Pliocene. The only fossil species that are the same as recent species are known from the Pleistocene. In Europe the fossil history of at least two living genera (*Elaphe* and *Vipera*) has been traced back to the Miocene (Romer, 1945). The most closely related genus to *Thalerophis* that is known from the fossil record is *Coluber* which has been found in the Pleistocene of North America. Thus in the entire fossil record of the snakes there is little that can be used in deducing phylogenetic relationships except for a few relatively old and primitive families. Therefore any attempts to associate the phylogenetic history of this genus with past geological events is purely speculative, although interesting and perhaps instructive.

INTERSPECIFIC RELATIONSHIPS

A study of the genus to determine its phylogenetic history reveals at once that the species comprising the genus are not readily comparable. They represent strikingly different stages of evolutionary development. Four of the six recognized species are monotypic: *depressirostris*, *diplotropis*, *nebulosus*, and *riveti*. One of the two remaining species, *mexicanus*, is composed of two subspecies, whereas the other, *richardi*, has 12 subspecies. The geographic areas occupied by these various species differ tremendously in size. Four of the six species are considered as the basic stock of the genus. These are *depressirostris*, *diplotropis*, *mexicanus*, and *riveti*. From a prototype similar to *riveti* the most progressive and widespread species in the genus, *richardi*, has developed. That the four basic species are old species is indicated by the marked morphological differences between them. In the total of its characters *depressi-*

rostris exhibits a condition more like that of the hypothetical ancestor than any other member of the genus. Among the four species of the basic stock, *depressirostris* has the same generalized condition as the hypothetical ancestral form in the characters listed above, except for the hemipenis and the number of ventrals. In regard to these characters *riveti* exhibits a slightly more generalized condition than *depressirostris*, but the latter is more primitive in these characters than either *diplotropis* or *mexicanus*.

The species *riveti* represents a stage similar to, but slightly more advanced than, *depressirostris*. It exhibits the most generalized condition found in the genus in hemipenial structure and in the number of ventrals, but is the most advanced in regard to distribution and development of keels on the dorsal scales and in the condition of some of the head shields. It possesses an adult color pattern

that is unique among adult members of the genus but that is found in the juveniles of most subspecies of *richardi*.

The species *diplotropis* and *mexicanus* represent more advanced stages of development in most characters than either *depressirostris* or *riveti*, but the two have developed along different lines and both retain some generalized character conditions. It is difficult to say which has progressed furthest, but *mexicanus* seems to be the more advanced of the two.

The species *nebulosus* is poorly known, and in consequence its relationship to the other species is based on less satisfactory clues. It appears to be less advanced than *mexicanus* but has apparently developed along somewhat similar lines. In most characters it occupies a position intermediate between *mexicanus* and *riveti*. The species *richardi* will be discussed more fully below, but it appears to be more closely related to *riveti* than to any of the other species. On the basis of the foregoing remarks a diagram can be constructed to indicate the probable phylogenetic relationship of the species comprising the genus (fig. 11).

In regard to geographic distribution, *depressirostris* occupies virtually a central position in relation to the other species, since its geographic range is in contact with or partly overlaps the ranges of the other species except *diplotropis*. This centralized geographic position, associated with the primitive condition in regard to character development, is in accord with the common observation that the reverse of Matthew's (1915) rule generally is true for species. The northern part of the geographic range of *depressirostris*, i.e., lower Central America, appears to be the most likely center of origin of the genus.

Dunn (1926) and Stuart (1941) have presented analyses of the criteria (Adams, 1902; Matthew, 1915) for determining the point of origin of a group of animals from the standpoint of their application to herpetological studies. Dunn concludes that Matthew's criteria that are of value in indicating the point of origin are those based on the continuity and convergence of lines of dispersal, continuity and directions of individual variations or modifications radiating from the center of origin along the highways of dispersal, and direction indicated by the biogeographical affinities.

Stuart summarizes the applicable criteria of Adams as the location of the generalized types and the place of contact of the evolutionary lines. The location of the generalized type or types may or may not provide a valid criterion for determining the point of origin. The generalized type at the present time may have a much more restricted distribution than it did formerly and may represent a relict form that has been able to exist in a secluded area far removed from the point of origin.

On the basis of the criteria considered applicable to herpetological problems by Dunn and by Stuart, the most probable point of origin for the genus appears to be in lower Central America in the vicinity of southern Nicaragua and northern Costa Rica. The next most likely region, on the basis of these criteria, is in northern South America in the vicinity of southwestern Colombia and northwestern Ecuador. The former locality appears to be the more likely of the two from the standpoint of the criteria of convergence of lines of dispersal, convergence of lines of modification (evolutionary lines), and biogeographical affinities. On the criterion of location of generalized types it could be either area, although more probably the latter of the two localities.

Four of the six species have been recorded from southern Nicaragua and northern Costa Rica. A fifth species, *riveti*, which is rare in collections, is known from as close to this area as the Panama Canal Zone. The sixth species, *diplotropis*, is known only from a restricted area along the west coast of Mexico. Three of the six species occur at present in southwestern Colombia and northwestern Ecuador: *depressirostris*, *richardi*, and *riveti*. It is unfortunate that so little is known of the ecological characteristics of the different species. Differences certainly exist, at least in those species that are in parts of their range sympatric, but the scope and nature of the differences are not known. Lack (1944) has shown in birds that ecological segregation is the rule in closely related sympatric species. Is the geographic separation of *diplotropis* and *mexicanus* the result of a similarity in ecological requirements? Is the slight geographical overlap in the ranges of *depressirostris* and *mexicanus* attributable to competition between the two species?

The phylogeny of the species would be more clearly understood if precise knowledge concerning their respective ecological relationships was available. The biogeographical affinities of the species are indicated roughly in the diagram of probable phylogenetic relationships (fig. 11), since this is in part a somewhat schematic diagram of geographic distribution. Three species, *diplotropis*, *mexicanus*, and *nebulosus*, are confined to Central America, while the other three species (*depressirostris*, *richardi*, and *riveti*) are primarily inhabitants of South America or occur in both Central and South America.

So far in this discussion of phylogeny little has been said about the species *richardi*. This is the only species in the genus that has undergone a second phase of rapid evolution that has accompanied vigorous colonization of an enormous geographic area. During this second phase of successful evolution *richardi* has produced 12 subspecies and occupied a geographic area including virtually all of the region occupied by the other five species and many times larger than that area. That the evolutionary development of the subspecies of *richardi* has been rapid and recent is indicated by the incomplete segregation of attributes in geographically adjacent populations of the species.

The success of this widespread species appears to be due in part to its possession of a high degree of genetic variation that has permitted relatively rapid adaptation to a variety of situations. The genetic plasticity that characterizes this species makes it difficult to relate it to the other species of the genus. Obviously some of the subspecies of *richardi* are morphologically, geographically, and phylogenetically more closely related to the other species of the genus than are the remaining subspecies. The races of *richardi* in their evolutionary development have in many instances paralleled the evolutionary trends observed in the other species of the genus, while in a few lines of development they have reversed the trends noted in other species. For example, the trend in most of the species, and in the development of many of the subspecies of *richardi*, is towards a reduction in the number of maxillary teeth. In the developmental line from the more generalized *occidentalis* in northwestern Ecuador through the more advanced *occidentalis* populations of lower

Central America to the end form, *praestans*, in upper Central America there has been a gradual increase in the number of teeth. That the direction of development in this line was actually the reverse of that indicated above appears to be entirely impossible since it would run counter to virtually all of the other data for the forms and would produce an utterly illogical phylogeny.

The center of radiation of *richardi* appears to have been in northwestern South America

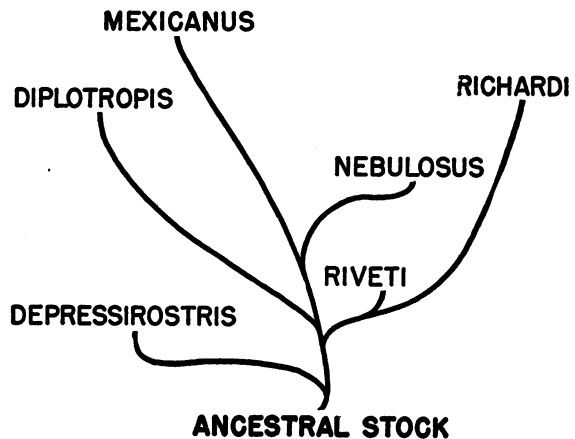


FIG. 11. Diagram indicating the probable phylogenetic relationships of the species of *Thalerophis*. The diagram also provides a rough approximation of the respective geographic ranges of the species, except for *richardi* which is the most widely distributed form in the genus. The species *depressirostris* and *riveti* are considered the most generalized members of the genus, whereas *mexicanus* appears to possess the greatest number of specialized attributes.

in the vicinity of southwestern Colombia and northwestern Ecuador. This is indicated by application of the criteria for determining the point of origin to the subspecies of *richardi*. The lines of dispersal, the lines of evolutionary development, and the biogeographic affinities clearly indicate this region. In addition it is the region in which the more generalized members of the genus are located.

To summarize the probable history of the genus as inferred from the available data, an ancestral prototype spread northward and southward from lower Central America, most likely from the region of present-day southern Nicaragua and northern Costa Rica. As the ancestral prototype moved northward and southward it began to differentiate *in situ*

along the evolutionary lines that have been indicated above. The development of these trends in character modification, of course, was not the same in all of the species nor did it proceed at a similar rate in the species. During this period of differentiation and territorial expansion of the ancestral stock it must have become separated into several completely isolated populations.

As to how and where this isolation of populations came about, I have no direct evidence. A possibility that is in agreement with the known facts about the genus and that has been indicated as an important factor in the history of other groups of animals (see discussion in Mayr, 1946) is the fact that the land connection between North and South America was broken into a series of isolated islands between the Middle Eocene and the Upper Pliocene (Mayr, *ibid.*, fig. 1). The separate land masses resulting from the water gaps indicated by the geological record are so located as to fit well the facts of the geographical distribution of the four basic species. Thus the ancestral population that was to give rise to *riveti* may have been isolated in northwestern South America by the Panamanian-Colombian water gap; the prototype of *depressirostris* may have been isolated in Costa Rica and Panama by the Nicaraguan and Panamanian-Colombian water gaps. The Nicaraguan gap possibly isolated the ancestral stock of *diplotropis* and *mexicanus* from the southern stock, and at a later period (Lower Miocene to Upper Pliocene) the Tehuantepec gap may have isolated the prototype of *diplotropis* from the *mexicanus* stock.

This association of the possible phylogenetic history of the genus with the geological record for the region in which the genus apparently developed is purely speculative. There is no fossil record for the genus to lend support either for or against such a hypothesis. Such an association would require a great age for the species and a period of isolation that is sufficient for differentiation on a generic level. On the basis of our present knowledge of the genus it is the most probable phylogenetic history that can be inferred without violation of the observed developmental trends. Such a history still leaves many unsolved problems. For example, why

is *diplotropis* restricted to the lowlands of only the Pacific coast of Mexico if its prototype became isolated in that area prior to the arrival of ancestral *mexicanus*? Or did it, too, arrive after the Tehuantepec gap was closed? How and where did *nebulosus* develop?

To pursue the above speculation further, since the water gaps have closed it appears that *riveti* has had little success in entering Central America, as it is known there only from Panama. On the other hand, *depressirostris* has spread southward into South America along the humid west coast of Colombia to northwestern Ecuador. It was in or close to the latter area by Pleistocene times when Gorgona Island became separated from the mainland of Colombia. Its expansion north of Nicaragua may have been prevented by the presence of *mexicanus* in a similar ecological niche, and the latter has managed to spread only a little distance south of the former Nicaraguan water gap. To the north *mexicanus* has invaded the lowlands of eastern Mexico, and has developed a subspecies on the Yucatan Peninsula since the beginning of Pleistocene times. It is not known whether the competition from *mexicanus*, an inhospitable environment, or what factor has prevented *diplotropis* from spreading beyond the former Tehuantepec water gap.

During the isolation in South America of the prototype of *riveti* the ancestral stock of *richardi* became differentiated, and this stock in contrast to that of *riveti* underwent rapid territorial expansion and evolution in South America. It invaded virtually all of the Neotropical realm on the continent, with populations separated from the mainland populations in Pleistocene times on the continental islands of Gorgona (*richardi bocourti*), Tobago (*richardi coeruleodorsus*), and Trinidad (*richardi coeruleodorsus*). None of these three insular populations is racially distinct from the populations on the adjacent mainland.

With the closing of the water gaps part of the *richardi* stock has invaded Central America and a northern subspecies has been developed in upper Central America. The races of *richardi* appear to have developed *in situ* as the ancestral stock spread throughout the humid lowlands of South America. The

most generalized members of the species are found today in Ecuador and northeastern Peru, with *occidentalis* on the west side of the Andes representing the most generalized member of one developmental line, whereas *nigromarginatus* on the east side of the Andes appears to be the most generalized member in another developmental line. The two generalized subspecies exhibit a number of common

structural attributes and probably represent closely related but at present completely isolated forms. They have probably developed from a common ancestral population that became isolated during the later stages of Andean elevation. The most probable present day genetic link between the two developmental lines is through *coeruleodorsus*, or possibly *ortoni*.

INTERGENERIC RELATIONSHIPS

Bogert (*loc. cit.*) suggests that "From some standpoints it would be preferable to place the eight New World genera (and perhaps others) in a single genus (*Coluber*), recognizing subgenera as well as species groups." I think that this will prove to be desirable when an increase in knowledge is attained concerning the genera involved, but at the present time, as Bogert indicates, our knowledge is far too limited to permit an adequate definition of such an inclusive genus.

Stuart (1932) reviewed the relationships of the genera discussed by Bogert, except *Leptodrymus* and *Thalerophis*. Stuart arranged the genera in series based on the progression of particular character gradients. Virtually all of the gradients recognized by Stuart within these genera are represented in *Thalerophis*. This may be the result of parallel modification, but from the large number of similar attributes shared by some of the genera I believe it indicates a close phylogenetic relationship.

The characters presented by Stuart indicate that *Thalerophis* represents a condition similar to that of *Drymobius* and *Dryadophis* but closer to the latter, as indicated by three of the characters presented below.

be readily perceived between these three genera, but on the basis of our present knowledge *Drymobius* and *Dryadophis* are probably the closest living relatives of the genus *Thalerophis*.

Affinities between *Thalerophis* and other living colubrine genera are easily noted, but the evidence does not permit a closer allocation than that indicated above. This allocation is sufficient to designate with a high degree of certainty the faunal element, Old Northern, to which the genus belongs and consequently to indicate in a general way its phylogenetic history.

Another proposal concerning the relationships of the genus *Thalerophis* has been made by Meise and Hennig (1932, 1935), who suggest that it be included under a single generic name with *Ahaetulla* (*Dendrophis* auct., of the Indo-Australian region) and *Philothamnus* (of Africa). This is quite a different proposal from that of Bogert and would involve drastic geological changes. The three genera are superficially similar and have been confused with one another in the past (see discussion of nomenclatorial history of *Thalerophis*). The confusion concerning the status of the genera is largely due to a convergence of char-

	<i>Drymobius</i>	<i>Dryadophis</i>	<i>Thalerophis</i>
Maxillary teeth	22-34, average 28	18-29, average 25	17-36, average 24
Dorsal scales	17 rows, keeled	17 or 15 rows, smooth	15 rows, keeled
Supralabials	9	8 or 9	8 or 9

This similarity is also indicated by comparison of the hemipenes of the generalized species of *Thalerophis*, *depressirostris* and *riveti*, with those figured by Stuart for *Drymobius* and *Dryadophis*. Differences can

acter development in snakes of a similar ancient lineage developing along similar lines in different geographical areas but in similar habitats and with similar habits. A comment of Cope's (1900) is pertinent to this state of

confusion about these snakes, "The tendency of some authors to neglect characters and to depend on 'physiognomy' . . . destroys precision and explains nothing, besides rendering the identification of species more laborious."

A consideration of characters that appear as common features among the semi-arboreal and arboreal colubrids is of value in attempting to analyze the relationships of these snakes. Such characters may represent adaptations to the arboreal habitat, or their adaptive significance may not be understood fully at present. Two principal morphological types are found among the arboreal colubrids and these two types may be used to establish two arbitrary categories: (1) the blunt-headed tree snakes and (2) the long-headed tree snakes. Members of the two categories have some features in common yet exhibit differences in morphology, general color pattern, and habits. It is the category of the long-headed tree snakes that includes the genera of present interest, and the discussion that follows pertains only to them.

In the long-headed tree snakes the characters listed below are commonly present and appear to be similar structural attributes representing adaptive responses to an arboreal existence. The characters included here are: (1) the long, narrow, frequently pointed head; (2) the long, slender, often laterally compressed body and tail; (3) the proportionately large eyes; (4) the pronounced oblique pattern of the transverse rows of dorsal scales with the accompanying modification in the shape of the individual scales of the longitudinal rows, including enlargement of the scales of the vertebral and first rows; (5) the lateral keel and notch on the ventral and subcaudal plates; (6) the proportionately short hemipenis in relation to the tail length; and (7) the predominantly green, gray, or brown coloration in which three principal pattern conditions predominate: longitudinal stripes, oblique bands, or no pattern, resulting in a uniformly colored snake. Another pattern character that is frequently present with any of the three preceding patterns is that of an anterioventral light spot on the individual dorsal scales. These characters are largely qualitative, and the degree of development of the characters is ap-

parently correlated with the extent of the arboreal habits. Thus, for example, the genera *Oxybelis*, *Theletornis*, *Dryophis*, and *Chrysopelea* are among the most arboreal colubrids, and they in turn have attained the highest development of these characters. It is interesting to note that these four genera are opisthoglyphs and that two of them have attained the highest development of binocular vision found among snakes.

Sixteen genera enter into the problem under consideration and share, in varying degrees, most of the characters listed above. In trying to determine the validity of Meise and Hennig's proposal only three of the genera need to be considered further at this time: *Ahaetulla* (*Dendrophis* auct.), *Philothamnus*, and *Thalerophis* (*Leptophis* auct.). In 1935 Meise and Hennig, in explaining the similarity of the three genera, postulated a Cretaceous land connection between the continents of the Southern Hemisphere with a circumtropic distribution of "*Leptophis*-like" snakes from which the three genera have developed either monophyletically or diphyletically.

In diagnosing *Ahaetulla* they state that the same characters used by them to define that genus are of equal value in defining *Philothamnus* and *Thalerophis*. They add that *Philothamnus* is distinguished from most *Ahaetulla* species in lacking enlarged vertebrae, while *Thalerophis* is distinguished from *Ahaetulla* in possessing elongated anterior mandibular teeth and elongated posterior maxillary teeth. No further differences between the genera are mentioned by them. Except for the number and character of the maxillary teeth, which overlap in the three genera, all of the characters given by Meise and Hennig may be found in the list given above of characters commonly shared by arboreal snakes, or else they are characters common throughout the Colubrinae. Thus the similarity in the genera that caused these authors to suggest that they be combined into a single genus is based on a group of characters commonly associated with arboreal colubrids.

Valid differences do exist between the three genera, as will be shown below, but the total of differentiation is expressed in differ-

ent combinations of characters and different degrees of character prominence that seem to be correlated with the extent of the arboreal habit. Of the three genera, *Ahaetulla* has these characters most prominently developed: a pronounced keel and notch on the ventrals; enlarged scales of the first and vertebral rows, with marked modification of the scales of the other dorsal rows; and great elongation of the body and tail. The literature dealing with the habits of this genus indicates that it is highly arboreal. Malcolm Smith (1943) states, "They live entirely among bushes and on trees." From both literature accounts and character development *Thalerophis* is the least arboreal of these three genera, whereas *Philothamnus* represents an intermediate condition. Some members of *Thalerophis* (for example, *richardi richardi*) exhibit an approach to the character modifications seen in *Ahaetulla*, but most do not.

Representatives of the three genera have been studied in an endeavor to evaluate the proposals of Meise and Hennig. These include six species of *Ahaetulla*, one of *Philothamnus*, and all of the species of *Thalerophis*. Two additional characters have been studied that appear to be of diagnostic value. These are the hemipenis and the modifications found in the dorsal scales. The reviewers of the genus *Ahaetulla*, with the exception of Malcolm Smith, have overlooked the hemipenial structure as a diagnostic character. It is possible that he failed to consider one of the most important structures on these organs in that genus, namely, the terminal awn. The only positive mention in the literature of this character in this genus is that of Dunn in 1927, whereas Cope (1895) and Pope (1935) have reproduced figures of this organ without the awn. This structure is easily overlooked in an examination of the organ *in situ* in some species of the genus. The terminal awn is a constant feature of the hemipenis in all of the species of the genus *Ahaetulla* that have been examined, though it exhibits marked variation between different species of the genus. Another characteristic of the hemipenis in this genus is the absence of enlarged basal spines and the presence of the transverse distal fold of tissue or capitum. On the basis of the hemipenial structure alone, *Ahaetulla* is

sharply set off from both *Thalerophis* and *Philothamnus*. The latter genus is similar in this respect to species of *Thalerophis* that possess enlarged basal spines (fig. 12).

Malcolm Smith, in criticizing Meise and Hennig's arrangement of the oriental species of *Ahaetulla*, says, "The affinities of the species must, I believe, be sought for in the comparative enlargement of the vertebral scales rather than in the teeth; the difficulty of adequately expressing that enlargement in measurable terms, prevents its use as a major key character." This same author in the general discussion of the characters found in the snakes of British India states, "Very little attention has been paid to the size and shape of the dorsal scales, and they are worth a closer study." In the present survey of arboreal genera, a pronounced difference in the nature of the dorsal scales was noted and suggests that the character may be useful as an additional indicator of phylogenetic relations. As Smith points out, the difficulty is to express adequately the condition that exists (fig. 13).

On the basis of scalation alone the three genera are readily separable, on qualitative characters. The genus *Ahaetulla* differs in having the vertebral scales strongly enlarged in such a fashion that the anterior and posterior edges of the scales are rounded or truncate rather than acuminate. *Philothamnus* does not have the vertebrals enlarged, and whereas some species of *Thalerophis* have these scales slightly enlarged, the scales are never truncate. In the genus *Ahaetulla* the transverse dorsal scales are arranged in conspicuously oblique rows with an accompanying modification in the scales of the rows other than the first and vertebral rows. In general this modification consists of a broadening of the scale dorsally with loss of the anterioventral portion. This type of modification in the shape of the dorsal scales is not found in either *Thalerophis* or *Philothamnus* but is characteristic of the forms of *Ahaetulla* that have been studied. *Philothamnus* has dorsal scales that are only slightly modified, without apical pits. In *Thalerophis* the dorsal scales, when modified, are narrowed and elongated, yet retain the symmetry of unmodified scales. Apical pits are present in all

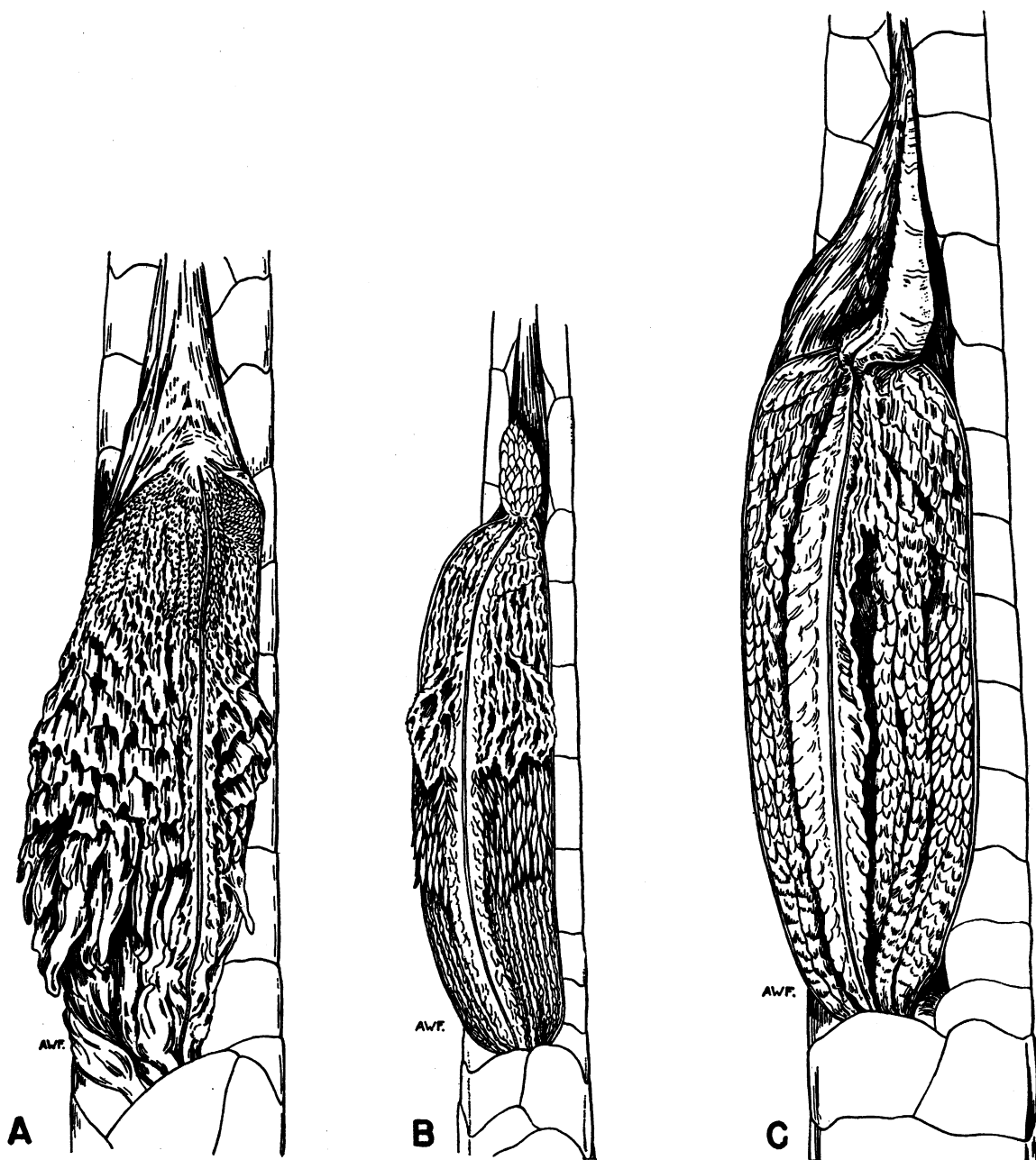


FIG. 12. Hemipenes of representatives of the genera *Philothamnus* and *Ahaetulla*, illustrating structural differences in the organs depicted and differences from the hemipenial structure observed in *Thalerophis*. Note the terminal awn in the hemipenis of *Ahaetulla*. A. *Philothamnus* s. *semivariatus*. B. *Ahaetulla ahaetulla*. C. *Ahaetulla calligaster*.

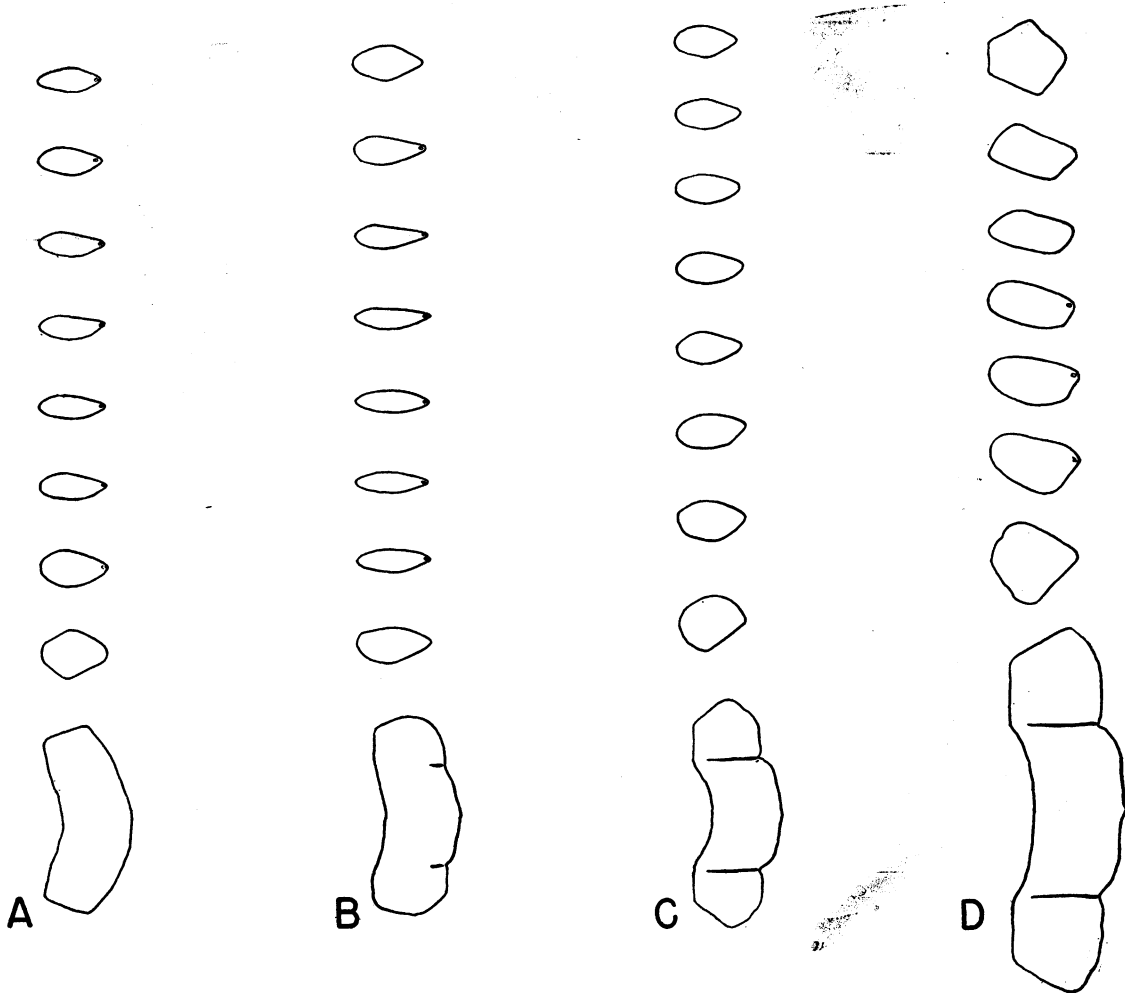


FIG. 13. Outline drawings showing differences in the shape of the dorsal scales and ventral plates in two members of the genus *Thalerophis* and in representatives of the genera *Ahaetulla* and *Philothamnus*. A. *Thalerophis depressirostris*. B. *Thalerophis richardi richardi*. C. *Philothamnus s. semivariegatus*. D. *Ahaetulla punctulata*.

species of this genus. *Thalerophis* lacks the well-developed ventral keels and notches that are found in both of the other genera, although a few forms exhibit these characters in a poorly developed stage.

From the foregoing account of differences that occur between these three genera, I believe that the proposal to combine them into a single genus is ill advised and completely unwarranted from the data available. The closest relative of each of the three genera is not to be found in the other two genera on adjacent continents, but rather each of the genera finds its closest relative on the same

continent that it occupies. Thus, for example the closest relative of *Thalerophis* is to be found in the Neotropical region in the genera *Drymobius* and *Dryadophis*.

As already mentioned, the fossil record of snakes throws little light on their past history, but the scanty information available from the fossil record for other reptiles contradicts the proposal of Meise and Hennig concerning the origin of these arboreal snakes. The recent studies of Dunn (1931), Simpson (1943), and Schmidt (1943) have elaborated the evidence derived from reptilian data in support of the distribution principles of

Matthew. They have stressed the fact that the dispersal routes for the existing reptilian groups having no fossil record can readily be interpreted in such a manner that they conform to the routes of those groups whose paleontological history is known. Similar faunal elements in the tropical regions of different parts of the world whose fossil history is well known show an earlier wide northern distribution, followed by extinction in the north and survival in the south, and

there is no necessity to alter continental outlines to explain their distribution. It is not necessary to assume a different history for those lacking any fossil record. Both the morphological and geological evidence indicate that the three genera of snakes considered here have developed polyphyletically from Old Northern racer-like colubrines that have entered Central and South America, Africa, and Asia from the northern continents.

SUMMARY AND CONCLUSIONS

THE GENUS *Thalerophis* Oliver is composed of six species; four of these are monotypic, one embraces two subspecies, and another contains 12 subspecies. All have the posteriormost maxillary teeth enlarged but not grooved; the hemipenis may or may not have enlarged basal spines; the dorsal scale formula is 15-15-11, and keels are present on the scales of at least two rows; the ventrals vary in number from 133 to 184 plates; the upper labials are eight or nine in number, with two shields in contact with the orbit; the loreal shield is present or absent; the oculars are one preocular and two postoculars; the temporals normally consist of one anterior and two posterior shields; and all have some green in the coloration, which in the adults is usually a uniform green or with dark longitudinal stripes, but one species has an adult color pattern of narrow, dark transverse bands.

The genus occurs in the warm, relatively

humid lowlands of the mainland of Latin America from northern Mexico to northern Argentina. The members of the genus are semi-arboreal or arboreal inhabitants of the forested areas: the tropical and subtropical rain forest, the tropical deciduous forest, and the scrub forests of the Neotropical realm. They are oviparous and feed principally on frogs of the family Hylidae.

The genus is a part of the Old Northern colubrine stock that has entered Middle and South America from the north and has undergone subsequent evolution in these areas. It appears to be most closely related to the genera *Drymobius* and *Dryadophis* which are also inhabitants of the Neotropical region. *Thalerophis* probably originated in lower Central America from which region it has spread northward into upper Central America and southward into virtually all of the warm, humid, lowland, forest areas.

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