

A MONOGRAPHIC STUDY OF  
THE COLUBRID SNAKE  
GENUS *LEPTODEIRA*

WILLIAM E. DUELLMAN

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## INTRODUCTION

SEVERAL YEARS AGO I ventured into the American tropics for the first time. This occasion opened for me a new sphere of biological investigation, for in comparison with the northeastern United States, the rich and varied herpetofauna offers endless opportunities for the study of reptiles and amphibians, their relationships with one another and with their environment, their life histories, and their distributions. However, I soon realized that many of these fields of investigation could not be pursued. The reason was a paucity of knowledge concerning the systematics of the fauna. The ecologist or zoogeographer is greatly handicapped by the many ill-defined species of questionable or unknown relationships, often by few numbers of specimens originating from widely scattered localities, and by the unwarranted lumping and splitting of species and genera by investigators who have worked with only a part of the entire problem. To change these chaotic conditions it will be necessary to carry out thorough systematic studies on every group in the herpetofauna. During the last two decades herpetologists have been chipping away at the wall that confronts them; several revisionary studies, such as Bogert and Del Campo (1956), Klauber (1952), Oliver (1948), Smith (1939), and Stuart (1940), have appeared. To these may be added another.

For a study of distribution and speciation in the American tropics the colubrid snake genus *Leptodeira* was chosen. These snakes are well represented in museum collections, and members of the genus range throughout the tropics of the Americas. Therefore, *Leptodeira* seems to be well fitted for this kind of study.

Most of the work was with series of pre-

served specimens lent to me by various individuals and institutions. Especially valuable was the large series from the vicinity of Iquitos, Peru. These specimens, collected by Dr. Harvey Bassler for the American Museum of Natural History and lent to me by Mr. Charles M. Bogert, provided sufficient material for statistical analysis of variation within a given population, as well as data on growth and seasonal incidence.

I was fortunate in being able to spend about 12 months in México, an experience that provided me with first-hand knowledge of the environmental conditions in the country where *Leptodeira* shows the greatest diversity. Equally important was the knowledge gained concerning the living snakes and their behavior. In order to obtain information on the habitats and behavior of the species with which I have had no field experience, I have found it useful to practice the art of "brain-picking" in order to secure the necessary information from a wide variety of sources.

Of necessity, the basis of this study has been systematic in nature. I have included all the available information on habits, habitat, life history, and other non-systematic data. The time and effort expended in the collecting and analyzing of the data have resulted, I hope, in a sound interpretation of the systematics. Whether or not the systematic arrangement presented here is correct will be proved only in time. The taxonomy and phylogenetic relationships are the foundations for the more synthetic aspects, e.g., ecology and zoogeography. Without a knowledge of the former any conclusions concerning the latter that are not, at least in part, erroneous cannot be expected.

## ACKNOWLEDGMENTS

During the course of my work on this group of snakes I have built up a debt of gratitude to many people who have provided me with data on specimens or localities, or who have offered advice or criticism in one way or another. Each has helped to make this study more nearly complete. For their

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Hooper, Dr. Theodore H. Hubbell, Dr. Laurence M. Klauber, Dr. Paul S. Martin, Dr. James E. Mosimann, Dr. James A. Peters, Dr. George B. Rabb, Dr. Janis A. Roze, the late Dr. Karl P. Schmidt, Dr. Edward H. Taylor, Mr. Fred G. Thompson, Mr. Thomas M. Uzzell, Jr., and Dr. Richard G. Zweifel.

Through the courtesy of museum curators and owners of private collections, I have received on loan over 2000 specimens from 25 collections in this country, six in Europe, and five in Latin America. Without the help of these people a study of this nature would be impossible. For their cooperation I wish to thank Sr. Miguel Alvarez del Toro, Mr. Ralph Axtell, Mr. J. C. Battersby, Mr. Charles M. Bogert, Mr. Bayard H. Brattstrom, Dr. Bryce C. Brown, Dr. Fred R. Cagle, Dr. Doris M. Cochran, Dr. William B. Davis, Mr. James R. Dixon, the late Dr. Emmett R. Dunn, Dr. Josef Eiselt, Mr. Carl Gans, Dr. Howard K. Gloyd, Dr. Coleman J. Goin, Dr. Jean Guibé, Dr. Walter Hellmich, Dr. Robert F. Inger, Dr. Laurence M. Klauber, Sr. Anterño Leitão de Carvalho, Mr. Arthur Loveridge, Dr. George H. Lowery, Mr. Hymen Marx, Dr. Robert Mertens, Dr. George S. Myers, Sr. Gustavo Orces V., Dr. James A. Peters, Mr. Neil D. Richmond, Sr. Janis A. Roze, Dr. Frederick A. Shannon, Dr. Joseph R. Slevin, Dr. Hobart M. Smith, Dr. Robert C. Stebbins, Dr. Edward H. Taylor, Dr. Paulo E. Vanzolini, Dr. Heinz Weremuth, and Dr. Richard G. Zweifel.

I am particularly indebted to Mr. Charles M. Bogert and Dr. Richard G. Zweifel for permission to study the specimens collected by Dr. Harvey Bassler for the American Museum of Natural History.

Many of the photographs used in this paper were donated for this particular use. For supplying me with the needed prints I wish to thank Dr. Stanley A. Cain, Mr. Carl Gans, Dr. Emmet T. Hooper, Dr. Charles F. Walker, and Dr. Richard G. Zweifel.

Through his knowledge of Central American biogeography and ophidian systematics, Dr. Laurence C. Stuart has contributed much to this study, and for this he has my heart-

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My greatest debt of gratitude is to my wife, Ann S. Duellman, who, besides computing all the data used in the character analysis and in the species accounts, has patiently edited and typed the manuscript. She accompanied me for seven months in México on a search for *Leptodeira* and other herpetological material. Most of all she has offered encouragement when my own enthusiasm was faltering. Such indebtedness, I fear, can never be repaid.

The plates are the work of Mr. William L. Brudon, staff artist of the Museum of Zoology, University of Michigan. His fine work was accomplished through far more time and effort than he realized financially. I shall always be proud of his work.

I also wish to express my gratitude to Dr. Norman Hartweg, Dr. Theodore H. Hubbell, the late Dr. J. Speed Rogers, and Dr. Charles F. Walker for placing at my disposal the facilities of the Museum of Zoology at the University of Michigan. Field work in México in 1955 was financed in part by a grant from the Horace H. Rackham School of Graduate Studies, University of Michigan; that in 1956 was supported in part by a grant from the Penrose Fund of the American Philosophical Society and in part by the Museum of Zoology, University of Michigan.

I wish to express my thanks to the authorities of the American Museum of Natural History for the publication of this study.

#### MATERIALS AND METHODS

During the course of this study I have examined 2531 specimens that I refer to the ge-

nus *Leptodeira*; of these, detailed scale counts, measurements, and notes on color pattern



were made on 2355 individuals.

Scale counts were made according to usual practices. Ventrals were counted by the method proposed by Dowling (1951a); the anal plate was not included. In the count of the caudals (=subcaudals) the terminal spine was not included. The formula for showing reduction in the dorsal scale rows has been modified from that proposed by Dowling (1951b) in order to express variation in a given sample. For example, the following formula, based on 10 males,

$$19+10(35-41)-219+10(106-118)-19(160-167)$$

shows that in these 10 specimens there is an increase from 19 to 21 rows anteriorly by the addition of the tenth row between ventrals 35 and 41, a reduction from 21 to 19 rows by the fusion of the ninth and tenth rows between ventrals 106 and 118, and that the total number of ventrals varies from 160 to 167. All scales that border the anterior edge of the orbit between the supraocular and the labials are called preoculars; no distinction is made between preoculars and presuboculars.

Measurements were taken to the nearest millimeter with a meter stick. Body length is the distance from the tip of the snout to the posterior edge of the anal plate; total length, to the tip of the tail.

Unless otherwise indicated, color descriptions are based on preserved specimens. Dorsal body blotches were counted on one side; only those that include the vertebral row of scales were counted. The term "lateral intercalary spots" refers to those spots on the sides of the body between the dorsal blotches. The length of a blotch is its longitudinal extent and is given as the number of scales in the vertebral row that are included. The width of the blotch is its transverse extent expressed in the number of scale rows covered; e.g., blotches extend laterally to third scale row. Nape stripe refers to a median longitudinal stripe extending posteriorly from the posteromedian corner of the parietals. Postorbital stripe refers to a dark stripe extending posteriorly from the eye. (See fig. 1.)

The dentigerous bones were removed from 108 specimens and cleaned in a 50 per cent solution of commercial Chlorox. As the teeth are sometimes missing, more accuracy can be obtained by counting the sockets. The

maxillary count is always given as the number of maxillary teeth anterior to the diastema plus the two enlarged posterior maxillary teeth; e.g., 18 +II.

I have used the term "form" to mean species and subspecies. I have followed Oliver's (1948) usage of "usually" in referring to 75 per cent or more of the specimens in any one group. "Normally" also has the same quantitative meaning, but I have used the term in reference to a normal condition as against one in which the condition is abnormal.

In the tables in the accounts of the species the number in parentheses is the number of specimens in the sample, that below it is the mean, and the hyphenated number below the mean is the observed range. Throughout the text I have given the observed range of variation followed by the mean in parentheses, for example, 65-84 (73.2).

Each synonymy includes, so far as I have found, all the generic and specific combinations, with the exception of emendations, that have been used for that form. Aside from these references I have also included revisionary studies, catalogues, and check lists. These references, as well as those in the text, are given in full in the bibliography.

The locality records for the various species have been plotted on maps. Hollow symbols are literature records; these have been used only when the identification of the specimen is known to be correct, and then only if the locality extends the range of the form. All localities that could be found have been plotted; the American Geographical Society's Map of Hispanic America (scale 1:1,000,000) has been the primary source, but other maps and atlases have been consulted. In the list of specimens examined the localities and specimens are given in the following order: country (United States, México, and alphabetically in Central America and South America); states in alphabetical order in each country; localities in alphabetical order in each state; museum abbreviations in alphabetical order as given below; museum numbers in numerical order after the abbreviations. When more than one specimen is included on a single number, the number of specimens is given in parentheses following the museum number. Localities that have not been located to state follow the country.

Specimens with data giving only the country or state are listed first in that political unit under "No specific locality."

The abbreviations for the museum collections are:

A.M.N.H., the American Museum of Natural History  
 A.N.S.P., Academy of Natural Sciences of Philadelphia  
 B.C.B., Bryce C. Brown, Waco, Texas  
 B.M.N.H., British Museum (Natural History)  
 C.A.S., California Academy of Sciences  
 C.M., Carnegie Museum  
 C.N.H.M., Chicago Natural History Museum  
 Ch.A.S., Chicago Academy of Sciences  
 D.Z., Departamento de Zoologia, São Paulo, Brazil  
 E.H.T.-H.M.S., Edward H. Taylor-Hobart M. Smith, Lawrence, Kansas  
 E.P.N., Escuela Polytechnica Nacional, Quito, Ecuador  
 F.A.S., Frederick A. Shannon, Wickenburg, Arizona  
 J.A.P., James A. Peters, Providence, Rhode Island  
 L.M.K., Laurence M. Klauber, San Diego, California  
 L.S.U., Louisiana State University  
 M.B.U.C.V., Museo de Biología, Universidad Central de Venezuela, Caracas  
 M.C.Z., Museum of Comparative Zoology

M.N.H.N., Museum National d'Histoire Naturelle, Paris  
 M.N.R., Museu Nacional, Rio de Janeiro, Brazil  
 M.V.Z., Museum of Vertebrate Zoology, University of California  
 M.Z.T.G., Museo Zoológico de Tuxtla Gutierrez, Chiapas, México  
 N.M.W., Naturhistorischen Museums Wien, Vienna  
 S.N.M., Senckenbergische Natur-Museum, Frankfurt  
 S.U., Stanford University Natural History Museum  
 T.C.W.C., Texas Cooperative Wildlife Collection, Agricultural and Mechanical College of Texas  
 T.U., Tulane University  
 U.C.L.A., University of California at Los Angeles  
 U.F., University of Florida Department of Biology  
 U.I., University of Illinois Museum of Natural History  
 U.K., University of Kansas Museum of Natural History  
 U.M.I., University of Minnesota  
 U.M.M.Z., University of Michigan Museum of Zoology  
 U.O., University of Oklahoma  
 U.S.N.M., United States National Museum  
 Z.M.B., Zoologisches Museum, Berlin  
 Z.S.B.S., Zoologische Sammlung der Bayerischen Staates, Munich

## SYSTEMATICS

### GENUS LEPTODEIRA FITZINGER

*Coluber* LINNAEUS, 1758, (in part), *Systema naturae*, ed. 10, vol. 1, p. 224 (*annulatus*). LACÉPÈDE, 1789, *Histoire naturelle serpens*, vol. 2, p. 94 (*albofuscus*, substitute name for *annulatus*). HALLOWELL, 1845, *Proc. Acad. Nat. Sci. Philadelphia*, vol. 2, p. 244 (*ashmeadi*).

*Leptodeira*<sup>1</sup> FITZINGER, 1843, *Systema reptilium*, p. 27 (type, *Coluber annulatus* Linnaeus, by monotypy). GÜNTHER, 1858, (in part), *Catalogue of the colubrine snakes in the . . . British Museum*, p. 165; 1868, *Ann. Mag. Nat. Hist.*, ser. 4, vol. 1, p. 425 (*nigrofasciata*). COPE, 1869, *Proc. Acad. Nat. Sci. Philadelphia*, vol. 20, p. 310 (*pacifica* and *personata*); 1869, *Proc. Amer. Phil. Soc.*, vol. 11, p. 151 (*mystacina*). GÜNTHER, 1872, *Ann. Mag. Nat. Hist.*, ser. 4, vol. 9, p. 32 (*rhombifera*); 1895, *Biologia Centrali-Americana, Reptilia*, pp. 170-173 (*affinis*, *ocellata*, *polysticta*, and *splendida*). BOULENGER, 1896, (in part), *Catalogue of the snakes in the British Museum*, vol. 3, pp. 88-89. WERNER, 1901, *Verhandl. Zool.-Bot. Gesell. Wien*, pp. 598-599 (*nycthemera*); 1913, *Mitt. Nat. Hist. Mus. Hamburg*, vol. 30, pp. 28-29 (*dunckeri*). BARBOUR AND AMARAL, 1927, *Bull. Antivenin Inst. Amer.*, vol. 1, no. 1, pp. 25-27. DUNN, 1936, (in part), *Proc. Natl. Acad. Sci.*, vol. 22, pp. 689-698. TAYLOR, 1938, *Univ. Kansas Sci. Bull.*, vol. 25, no. 15, pp. 315-355.

*Dipsas*, KENNICOTT, 1859, (in part), *in Baird, Reptiles of the Boundary*, vol. 2, p. 16 (*septentrionalis*). GÜNTHER, 1872, (in part), *Ann. Mag. Nat. Hist.*, ser. 4, vol. 9, pp. 32-33 (*approximans*).

*Megalops* HALLOWELL, 1861, *Proc. Acad. Nat. Sci. Philadelphia*, for 1860, p. 488 (type, *Megalops maculatus* Hallowell, by monotypy).

*Eteirodipsas*, JAN, 1863, (in part), *Elenco sistematico ophidi*, p. 105 (*rhomboidalis*). SAUVAGE, 1884, *Bull. Soc. Philom. Paris*, ser. 7, vol. 8, p. 146 (*weineri*).

*Crotaphopeltis*, PETERS, 1867, (in part), *Monnatsber. Akad. Wiss. Berlin*, for 1866, pp. 93-94 (*punctata*).

*Comastes*, BOCOURT, 1884, (in part), *Bull. Soc. Philom. Paris*, ser. 7, vol. 8, p. 141 (*ornata*).

*Sibon*, COPE, 1866, (in part), *in Ferrari-Perez, Proc. U. S. Natl. Mus.*, vol. 9, p. 184 (*frenatum*); 1887, (in part), *Bull. U. S. Natl. Mus.*, no. 32, p. 67 (*yucatanensis*); 1893, (in part), *Proc. Amer. Phil. Soc.*, vol. 31, p. 347 (*rubricatum*); 1895, (in part), *Trans. Amer. Phil. Soc.*, vol. 18, p. 209.

*Anoplophallus* COPE, 1893, *Amer. Nat.*, vol. 27, p. 480 (substitute name for *Megalops* Hallowell, preoccupied; type, *Megalops maculatus* Hallowell, 1861).

*Hypsiglena*, GÜNTHER, 1894, (in part), *Biologia*

*Centrali-Americana, Reptilia*, p. 138, pl. 49, fig. B (*latifasciata*). BOULENGER, 1894, (in part), *Catalogue of the snakes in the British Museum*, vol. 2, p. 211. MOCQUARD, 1908, (in part), *in Duméril and Bibron, Mission scientifique au Mexique et dans l'Amerique Centrale*, vol. 3, p. 870, pl. 70, fig. 2.

*Pseudoleptodeira* TAYLOR, 1938, *Univ. Kansas Sci. Bull.*, vol. 25, no. 15, pp. 343-344 (type, *Hypsiglena latifasciata* Günther, by original designation). TANNER, 1944, (in part), *Great Basin Nat.*, vol. 5, nos. 3 and 4, p. 31.

### HISTORICAL SUMMARY

In 1754 Linnaeus figured and in 1758 described *Coluber annulatus* from America. Lacépède proposed the name *Coluber albofuscus* in 1789. Both of these specific names were widely used in the literature until the early part of the twentieth century, when Griffin (1917) showed that *albofuscus* was intended to be a substitute name for *annulatus*. Fitzinger (1843) proposed the generic name *Leptodeira* (Greek *leptos*, meaning slender; Greek *deire*, meaning neck), with *Coluber annulatus* Linnaeus as the type species. Günther (1858) synonymized *Crotaphopeltis* Fitzinger, 1843 (type species, *Coronella rufescens* Schlegel), with *Leptodeira*, thus including in one genus a species from Africa, *Crotaphopeltis rufescens*, and one from South America, *Leptodeira annulata*. Boulenger (1896) and others followed Günther in assigning both American and African species to *Leptodeira*. Barbour and Amaral (1927) discussed the differences between the African and American species and concluded that they should be recognized as two genera, *Crotaphopeltis* in Africa and *Leptodeira* in the Americas.

Various species now referred to *Leptodeira* have been described as *Dipsas*, *Eteirodipsas*, *Megalops*, *Comastes*, and *Sibon*. During the latter part of the nineteenth century Cope considered *Leptodeira* as a synonym of *Sibon*, and during that time *frenata*, *rubricata*, and *yucatanensis* were described by him as *Sibon*. The status and history of the name *Megalops maculatus* are discussed under *Leptodeira maculata* in the present paper. The species *punctata* from western México was described as a *Crotaphopeltis*, the description being based on a specimen purported to be from South Africa.

In his survey of the genus *Leptodeira*, Dunn (1936) included all the American spe-

<sup>1</sup> The emendation "*Leptodira*" is combined under *Leptodeira* throughout.

cies formerly referred to that genus along with those referred to *Hypsiglena*. However, this combination has not been accepted, and most workers today consider the two groups to be distinct, but closely related, genera. Taylor (1938) proposed the genus *Pseudo-leptodeira* for *Hypsiglena latifasciata* Günther. He also referred *Leptodeira discolor* Günther to this genus. In the present paper *latifasciata* is placed in the genus *Leptodeira*, whereas the poorly known *discolor* is relegated to *incerta sedis*.

All the trivial names proposed for *Leptodeira* in the Americas and other names that are now referred to that genus are here listed, with their nomenclatural status as recognized in this paper:

*Leptodira affinis* Günther  
*Coluber albofuscus* Lacépède  
*Coluber annulatus* Linnaeus  
*Eteirodipsas annulata* var. *rhomboidalis* Jan  
*Leptodeira annulata taylori* Smith  
*Sibon annulatum yucatanensis* Cope  
*Dipsas approximans* Günther  
*Coluber ashmeadi* Hallowell  
*Leptodeira bakeri* Ruthven  
*Leptodeira bressoni* Taylor  
*Leptodeira discolor* Günther  
*Leptodeira duellmani* Peters  
*Leptodira dunckeri* Werner  
*Leptodeira ephippiata* Smith and Tanner  
*Sibon frenatum* Cope  
*Leptodira guilleni* Boulenger  
*Leptodeira larcorum* Schmidt and Walker  
*Hypsiglena latifasciata* Günther  
*Leptodira leucocephala* Günther  
*Megalops maculatus* Hallowell  
*Leptodira mystacina* Cope  
*Leptodira nigrofasciata* Günther  
*Leptodira nycthemera* Werner  
*Leptodira ocellata* Günther  
*Comastes ornata* Bocourt  
*Leptodira pacifica* Cope  
*Leptodira personata* Cope  
*Leptodira polysticta* Günther  
*Crotaphopeltis punctatus* Peters  
*Leptodira rhombifera* Günther  
*Leptodeira rhombifera kugleri* Shreve  
*Dipsas septentrionalis* Kennicott  
*Sibon septentrionalis rubricatum* Cope  
*Leptodeira smithi* Taylor  
*Leptodira splendida* Günther  
*Eteirodipsas weineri* Sauvage  
*Leptodeira weiseri* Müller  
*Leptodeira yucatanensis malleisi* Dunn and Stuart

#### DESCRIPTION OF THE GENUS

The genus *Leptodeira* is a member of the family Colubridae; because the hemipenis has an unforked sulcus spermaticus, and hypapophyses are absent from posterior body vertebrae, it is placed in the subfamily Colubrinae.

In *Leptodeira* the hemipenis is capitate and provided with large spines. The maxillary teeth vary in number from eight to 18, increase in length posteriorly, and are followed by a diastema and two enlarged, grooved fangs. The palatine teeth vary from seven to 12 in number; pterygoid, 16 to 32; dentary, 14 to 28. There is a large parotid (venom)

*L. septentrionalis ornata*  
*L. annulata annulata*  
*L. annulata annulata*  
*L. annulata annulata*  
*L. septentrionalis polysticta*  
*L. frenata yucatanensis*  
*L. annulata annulata*  
*L. annulata ashmeadi*  
*L. bakeri*  
*L. splendida bressoni*  
*Incerta sedis*  
*L. splendida bressoni*  
*L. septentrionalis ornata*  
*L. splendida ephippiata*  
*L. frenata frenata*  
*L. latifasciata*  
*L. septentrionalis larcorum*  
*L. latifasciata*  
*Lycognathus rhombeatus* Peters  
*L. maculata*  
*L. nigrofasciata*  
*L. nigrofasciata*  
*L. annulata annulata*  
*L. annulata rhombifera*  
*L. septentrionalis ornata*  
*L. punctata*  
*L. maculata*  
*L. septentrionalis polysticta*  
*L. punctata*  
*L. annulata rhombifera*  
*L. annulata ashmeadi*  
*L. septentrionalis septentrionalis*  
*L. annulata rhombifera*  
*L. maculata*  
*L. splendida splendida*  
*L. annulata annulata*  
*Oxyrhopus bachmani inaequifasciatus* Werner  
*L. frenata malleisi*

gland on either side of the head in the temporal region.

The head shields are of an unmodified colubrid type, with a short rostral, paired internasals and prefrontals, divided nasals, and a single loreal. The snout is blunt and not protruding. The preoculars are one to four; postoculars, one to four; upper labials, seven to nine, usually eight; lower labials, eight to 12, usually 10; temporals normally one plus two plus three; chin shields subequal in length; ventrals, 150 to 208, rounded and overlapping; caudals, 54 to 107, paired and imbricate; anal divided; dorsal scales smooth and in 17 to 25 rows at midbody with two apical pits and keels, rarely present, in anal region only; scale reduction normally involving the paravertebral row; tail length more than 20 per cent of body length; maximum total length slightly exceeding 1 meter.

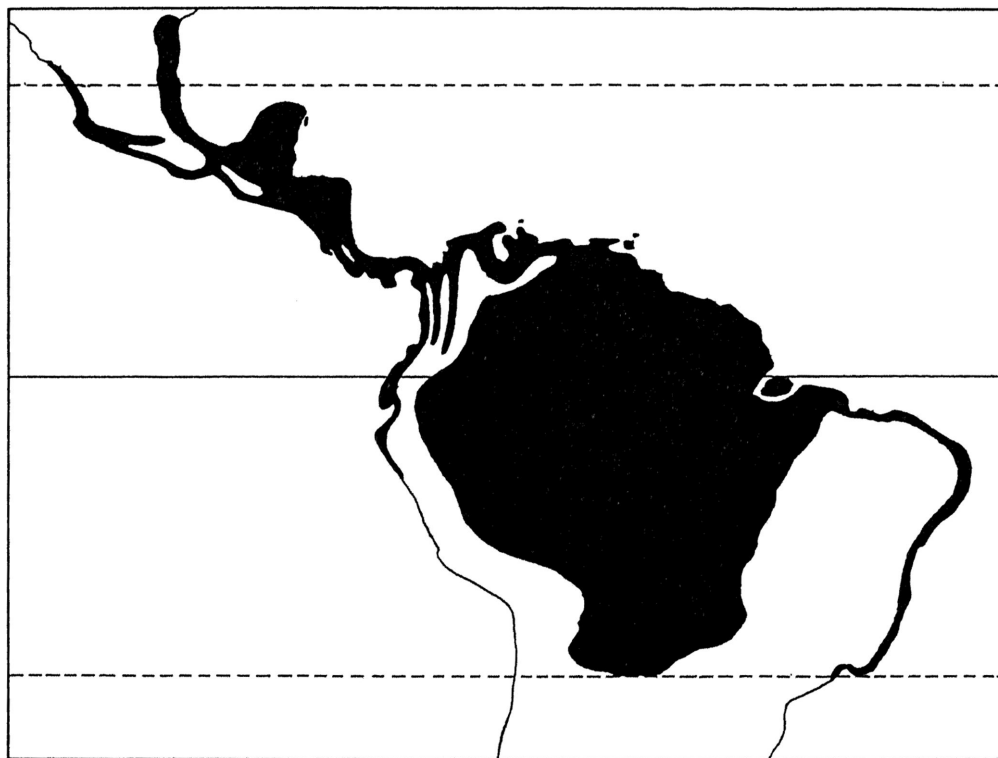
The dorsal color pattern consists of dark spots, blotches, or bands on a lighter ground color; the ventral surfaces are immaculate cream-white or with only scattered dark flecks.

These snakes have an elliptical pupil; they are nocturnal and feed primarily upon frogs and toads, sometimes upon small lizards.

#### DISTRIBUTION OF THE GENUS

The range of the genus *Leptodeira* is essentially that of the tropics in the Neotropical Realm. The genus occurs at low and moderate elevations, usually not exceeding 2000 meters, and is distributed from southern Sonora, México, and the Rio Grande Embayment in southern Texas to northern Argentina and Paraguay, with the exception of the high Andes and the coastal deserts of Peru and Chile; in the West Indies it is known from four continental islands—Aruba, Margarita, Tobago, and Trinidad, which lie off the coast of Venezuela. (See map 1.)

Six species are more or less restricted to dry environments within the region; *bakeri* is found only on the arid island of Aruba; *latifasciata*, *maculata*, *punctata*, and *splendida* occur in semi-arid habitats in western México; *nigrofasciata* occurs in dry habitats from southern México to Costa Rica. The other



MAP. 1. Geographical distribution of the genus *Leptodeira*.

three species are found in both wet and dry habitats in different parts of their ranges; *annulata* lives in dry habitats in México, Central America, and northern South America, but in the Amazon Basin inhabits wet forests; *frenata* ranges from tropical rain forest in southeastern México and northern Guatemala to arid scrub forest in the tip of the Yucatán Peninsula; *septentrionalis* lives in semi-arid habitats in northeastern México and in northern Peru, but in wet forests in southern México, Central America, and northwestern South America.

A detailed description of the range of each species and subspecies is given in the systematic accounts, and locality records are shown on the accompanying maps.

The known distribution of *Leptodeira* in the countries of the Americas is presented in the list below. The countries are arranged in alphabetical order, and the species are listed in alphabetical order following the name of the country.

ARGENTINA: *annulata pulchriceps*

BOLIVIA: *annulata annulata*, *annulata annulata* × *pulchriceps*, *annulata pulchriceps*

BRAZIL: *annulata annulata*, *annulata pulchriceps*

BRITISH GUIANA: *annulata annulata*, *annulata annulata* × *ashmeadi*

BRITISH HONDURAS: *frenata malleisi*, *septentrionalis polysticta*

BRITISH WEST INDIES (TOBAGO AND TRINIDAD): *annulata ashmeadi*

COLOMBIA: *annulata annulata*, *annulata ashmeadi*, *annulata ashmeadi* × *rhomboifera*, *septentrionalis ornata*

COSTA RICA: *annulata rhombifera*, *nigrofasciata*, *septentrionalis ornata*, *septentrionalis ornata* × *polysticta*, *septentrionalis polysticta*

DUTCH WEST INDIES (ARUBA): *bakeri*

ECUADOR: *annulata annulata*, *septentrionalis larcorum* × *ornata*, *septentrionalis ornata*

EL SALVADOR: *annulata rhombifera*, *septentrionalis polysticta*

FRENCH GUIANA: *annulata annulata*

GUATEMALA: *annulata rhombifera*, *frenata malleisi*, *nigrofasciata*, *septentrionalis polysticta*

HONDURAS: *annulata rhombifera*, *nigrofasciata*, *septentrionalis polysticta*

MÉXICO: *annulata cussiliris*, *frenata frenata*, *frenata frenata* × *malleisi*, *frenata malleisi*, *frenata yucatanensis*, *latifasciata*, *maculata*, *nigrofasciata*, *punctata*, *septentrionalis septentrionalis*, *septentrionalis septentrionalis* × *polysticta*, *septentrionalis polysticta*, *splendida bressoni*, *splendida bressoni* × *ephippiata*, *splendida ephippiata*, *splendida splendida*

NICARAGUA: *annulata rhombifera*, *nigrofasciata*, *septentrionalis polysticta*

PANAMÁ: *annulata ashmeadi* × *rhomboifera*, *annulata rhombifera*, *septentrionalis ornata*

PARAGUAY: *annulata pulchriceps*

PERU: *annulata annulata*, *septentrionalis larcorum*

SURINAM: *annulata annulata*

UNITED STATES: *septentrionalis septentrionalis*

VENEZUELA: *annulata annulata*, *annulata ashmeadi*

## COMPOSITION OF THE GENUS

From an analysis of the populations in relation to their morphological characters, ecology, and geographical distribution, nine species comprising 20 forms are recognized herein. These are readily separated into three groups on the basis of scutellation and coloration. There are two divergent groups, *punctata* and the *nigrofasciata* group including *latifasciata*. Of the other six species, *annulata*, *bakeri*, *maculata*, and *frenata* may be grouped together and at the same time separated from *septentrionalis* and *splendida* on the basis of the hemipenis.

The following key makes no pretense of showing phylogenetic relationships; it is entirely artificial. Certain forms, because of their variability, cannot be distinguished readily from some others on the basis of one set of characters; consequently, they have

been brought out in the key in more than one couplet. The key should be used in connection with the tables in the character analysis. If the key fails to place a specimen satisfactorily, the text should be consulted. Care has been exercised to avoid the use of characters that are dependent on sex or the tail; individuals of either sex, with or without complete tails, can be keyed with equal ease.

### KEY TO THE SPECIES AND SUBSPECIES OF *Leptodeira*

1. Scales in 17 or 19 rows at midbody . . . . 2  
Scales in more than 19 rows at midbody . . . . 9
2. Scales in 19 rows at midbody and in 15 rows posteriorly; upper labials usually seven; lower labials usually nine; ventrals 150-153 in males, 156-167 in females; five to six longitudinal rows of dark spots on yellowish ground color; maximum body length 422

- mm. . . . . *punctata*  
 Not so . . . . . 3
3. Body blotches large, 10–27 in number, extending to or nearly to the ventrals . . . . . 4  
 Body blotches 25 or more, extending only to scale rows 3 or 4 . . . . . 6
4. Body bands 10–21, long, with straight edges extending to ventrals; no lateral intercalary spots; no ornate head pattern on frontal and parietals; two preoculars; usually 17 scale rows posteriorly . . . . . *nigrofasciata*  
 Dorsal body blotches 14–27, with rounded lateral edges; lateral intercalary spots present . . . . . 5
5. Preoculars one or two; dorsal blotches often with light centers; no ornate head pattern; usually 15 scale rows posteriorly . . . . . *bakeri*  
 Preoculars three; dorsal blotches without light centers; ornate head pattern on frontal and parietals; usually 17 scale rows posteriorly . . . . . *splendida ehippiata*
6. Vertebral and paravertebral scale rows noticeably enlarged; body laterally compressed; no longitudinal nape bars . . . . . 7  
 Vertebral and paravertebral scale rows not noticeably enlarged; body rounded; two longitudinal nape bars usually present . . . . . 8
7. Preoculars usually one; no dark, well-defined, lateral, intercalary spots; dorsal blotches ovoid, usually longer than wide. . . . .  
 . . . . . *annulata annulata*  
 Preoculars usually two; lateral intercalary spots well defined; dorsal blotches more rectangular, often wider than long. . . . .  
 . . . . . *septentrionalis ornata*
8. Two wide, longitudinal, dark bars on nape; no longitudinal stripes on parietals or temporals or Y-shaped mark on parietals . . . . .  
 . . . . . *annulata ashmeadi*  
 Two wide, longitudinal, dark bars usually present on nape; longitudinal dark stripes on parietals or temporals or a Y-shaped mark on parietals . . . . . *annulata pulchriceps*
9. Seven to 10 long dark bands on body; a light occipital region . . . . . *latifasciata*  
 More than 10 body bands or blotches . . . . . 10
10. A dark postorbital stripe usually in broad contact with first body blotch; a single dark spot or longitudinal stripe in the center of each parietal; a brown spot on, or a short nape stripe beginning on, posteromedian corner of parietals; no ornate dorsal head pattern . . . . . 11  
 No dark postorbital stripe; or, if so, usually not in broad contact with first body blotch; no single dark spot in the center of each parietal . . . . . 13
11. Body blotches 26 or less (average 21); blotches usually dark brown and not outlined with black; dorsal interspaces two or three scales in length. . . . . *frenata yucatanensis*  
 Body blotches 24 or more (average 30); blotches brown and outlined with black and usually not extending to ventrals; or, if extending to ventrals, blotches are solid black, with the dorsal interspaces only one scale in length . . . . . 12
12. Body blotches black, with nearly straight edges and usually extending onto ventrals; dorsal interspaces one scale in length . . . . . *frenata frenata*  
 Body blotches usually brown, outlined with black, often saddle-shaped, and usually not extending to the ventrals; dorsal interspaces usually more than one scale in length . . . . . *frenata malleisi*
13. A nape stripe usually present; postorbital stripe present; dorsal head pattern ornate, usually consisting of a Y- to an 8-shaped mark on frontals and parietals; usually three preoculars . . . . . 14  
 Nape stripe absent; or, if present, no ornate dorsal head pattern of a Y- to an 8-shaped mark, although other head markings may be present; one to three preoculars . . . . . 16
14. Dorsal body blotches 28 or more, narrow, never longer than interspaces; ground color grayish brown; two rows of lateral spots, one on scale rows 2–6 in lateral interspaces and one on scale rows 2–4 below the mid-dorsal blotches . . . . . *splendida bressoni*  
 Dorsal body blotches fewer than 28, longer than interspaces; ground color cream to tan; small, elongate, lateral, intercalary spots . . . . . 15
15. More than 170 ventrals; dorsal blotches more than twice the length of dorsal light interspaces and extending onto scale rows 1 or 2 . . . . . *splendida ehippiata*  
 Less than 170 ventrals; dorsal blotches only slightly longer than middorsal interspaces and extending onto scale rows 3 and 4. . . . . *splendida splendida*
16. Dorsal scales in 21 rows, with vertebral and paravertebral rows noticeably enlarged; body laterally compressed . . . . . 17  
 Dorsal scales in 21–25 rows, with vertebral and paravertebral rows not noticeably enlarged; body rounded or only slightly compressed . . . . . 18
17. Preoculars usually one; no dark, well-defined, lateral, intercalary spots; dorsal blotches ovoid; usually longer than wide. . . . .  
 . . . . . *annulata annulata*  
 Preoculars usually two; lateral intercalary spots well defined; dorsal blotches more rectangular, often wider than long . . . . .  
 . . . . . *septentrionalis ornata*

18. Dorsal blotches large, twice the length of mid-dorsal light interspaces, extending to scale row 2 or to ventrals . . . . . 19  
Dorsal blotches smaller; if twice the length of dorsal light interspaces, then not extending to second scale row . . . . . 23
19. Lateral intercalary spots present, large or reduced . . . . . 20  
Lateral intercalary spots absent. . . . . 22
20. Dorsal blotches with light centers; lateral intercalary spots sometimes with dark streaks dorsally into light interspaces; 14-27 dorsal blotches; ventrals less than 180. . . *bakeri*  
Dorsal blotches without light centers; no dark streaks in light interspaces . . . . . 21
21. Preoculars three; ventrals 181-199 in males, 185-208 in females; nape stripe usually present; 20-35 black or dark brown blotches on a cream to light tan ground color . . . . . *septentrionalis septentrionalis*  
Preoculars usually two; ventrals 162-185 in males, 158-189 in females; no nape stripe; 21-48 brown or black blotches on grayish brown ground color . . . *annulata cussiliris*
22. Preoculars two; ventrals less than 180; body blotches 12 to 28 . . . . . *maculata*  
Preoculars three; ventrals more than 180; body blotches 20-35. . . . . *septentrionalis septentrionalis*
23. A single median nape stripe . . . . . 24  
No median nape stripe; or, if so, bordered by a longitudinal bar on either side . . . . . 26
24. Ventrals 186 or more; body slender; two lateral nuchal blotches that may be fused to form a U-shaped blotch; nape stripe not touching nuchal blotch; 38-70 (average 54) small dorsal blotches as wide as or wider than long; usually three preoculars . . . . . *septentrionalis polysticta*  
Ventrals fewer than 186; body rounded; no paired nuchal blotches; nape stripe touching first body blotch or not; blotches larger; 56 or fewer in number, longer than interspaces; usually two preoculars . . . . . 25
25. Nape stripe laterally expanded anteriorly to form a butterfly-shaped mark on postparietals and posttemporals; 34-49 (average 42) dorsal blotches . . . *septentrionalis larcorum*  
Nape stripe not expanded to form butterfly pattern; 23-56 (average 36) dorsal blotches . . . . . *annulata rhombifera*
26. Two wide, longitudinal, dark bars on nape; no longitudinal stripes on parietals or temporals or Y-shaped mark on parietals . . . . . *annulata ashmeadi*  
Two wide, longitudinal, dark bars usually present on nape; longitudinal dark stripes on parietals or temporals or a Y-shaped mark on parietals . . . *annulata pulchriceps*

#### CHARACTER ANALYSIS

All the morphological characters usually employed in ophidian systematics have been used as far as possible in this study of the genus *Leptodeira*. These have been analyzed (statistically, when possible) to determine the extent of individual, sexual, and geographical variation. The following section contains a synopsis of the characters that have been used in the systematic revision of the genus. Characters with little variation, such as head scales, or based on relatively few observations, such as the dentition, have been presented only as frequency distribution tables. Characters with a wide range of variation and based on large numbers of observations have been analyzed statistically, and the range, mean (*M*), standard deviation (*S.D.*), and coefficient of variability (*C.V.*) are given. For those characters showing sexual dimorphism the coefficient of difference (*C.D.*) between the sexes has been calculated. The statistical terms and formulas have been

adopted from Mayr, Linsley, and Usinger (1953).

The dorsal head shields were found to be of no taxonomic value in *Leptodeira*. In some species the ratio of the length of the parietal suture to the length of the frontal shows slight geographical variation; the proportionate length of the prefrontals and internasals is also slightly different in certain species. Most of the variation in proportions and connections of the dorsal head shields is individual and of no taxonomic importance; consequently, they have been omitted in the following discussion.

Variation is greatest in those forms that have the most extensive geographical ranges. In these the variation in a given character at any one locality is only a part of the total variation of that character over the entire range. For example, the variation in ventrals in male *annulata* from over the entire range of the subspecies in the Amazon Basin is 180-



200, whereas 21 males from a rather limited area in eastern Ecuador vary from 180 to 189. Likewise, forms in which the whole taxon has a rather restricted range show less variation in any given character than does a form with an extensive range; *yucatanensis*, restricted to the arid tip of the Yucatán Peninsula, México, has 177–186 ventrals in the males. Steep geographical gradients in a character may show a great variation over a rather limited geographical area. In *nigrofasciata*, with a range from southern México to Costa Rica, the males have 161–196 ventrals. Males from Oaxaca, México, have 187–196, and those from Nicaragua have 161–173. Therefore, when considering the variation in any specific character, one must take into account the extent of the geographical range and the presence of geographical gradients to compare fairly the character in two or more forms.

#### DENTITION

Snakes of the genus *Leptodeira* bear teeth on the maxillary, palatine, pterygoid, and dentary (mandible). The maxillo-ptyergopalatine arch and the dentary bones were removed from more than 100 specimens representing every species of the genus. Differences noted between species in the character or the number of teeth on one bone were always accompanied by similar differences in the teeth on the other bones. For example, *frenata* differs from *annulata* in having fewer teeth on the maxillary, palatine, pterygoid, and dentary.

The maxillary teeth are long and sharply curved backward. The anterior series consists

of eight to 18 teeth slightly increasing in size posteriorly, followed by a diastema and two enlarged, grooved teeth. These are situated nearly side by side on the posterior edge of the maxillary, which is considerably widened posteriorly. The two enlarged teeth point almost directly backward. The enlarged posterior teeth in *latifasciata* have only a faint groove, whereas in other species the groove is deep.

The palatine teeth are stout, curved backward, and of subequal length; the pterygoid and dentary teeth are stout, slightly curved and decrease in size posteriorly.

The dentition characters have been analyzed by species, and the results are given in tables 1–4.

#### HEMIPENIS

The hemipenes are typically colubrine, with an unforked sulcus, enlarged spines, and crenulate capitulum. They show interspecific differences as well as intraspecific variation. The extent of the hemipenis *in situ* varies from six to nine caudals. Usually opposite the sulcus are one or more longitudinal rows of enlarged spines, which in some species increase in size distally. The capitulum may be spinous or crenulate and may have a cup-shaped depression. Representative types of hemipenes are shown in plates 26 and 27.

#### SCUTELLATION

On the specific and subspecific levels of ophidian systematics, the most important and most frequently utilized morphological characters are those of scutellation. These discrete characters are easily treated quanti-

TABLE 1  
VARIATION IN THE NUMBER OF MAXILLARY TEETH ANTERIOR TO THE DIASTEMA

Species	N	No. of Maxillary Teeth										
		8	9	10	11	12	13	14	15	16	17	18
<i>annulata</i>	47	—	—	—	—	—	—	—	7	28	9	3
<i>bakeri</i>	4	—	—	—	—	—	—	1	1	2	—	—
<i>frenata</i>	11	4	2	5	—	—	—	—	—	—	—	—
<i>latifasciata</i>	3	—	—	—	—	2	1	—	—	—	—	—
<i>maculata</i>	10	—	—	—	—	—	—	—	—	5	4	1
<i>nigrofasciata</i>	10	—	—	2	1	7	—	—	—	—	—	—
<i>punctata</i>	7	—	—	—	—	—	—	3	4	—	—	—
<i>septentrionalis</i>	11	—	—	—	—	—	1	1	3	4	1	1
<i>splendida</i>	7	—	—	—	—	—	—	—	3	4	—	—

TABLE 2  
VARIATION IN THE NUMBER OF PALATINE TEETH

Species	N	No of Palatine Teeth					
		7	8	9	10	11	12
<i>annulata</i>	46	—	—	—	20	25	1
<i>bakeri</i>	4	—	—	—	4	—	—
<i>frenata</i>	11	—	10	1	—	—	—
<i>latifasciata</i>	3	—	3	—	—	—	—
<i>maculata</i>	10	—	—	—	2	8	—
<i>nigrofasciata</i>	9	6	3	—	—	—	—
<i>punctata</i>	7	—	—	—	4	3	—
<i>septentrionalis</i>	11	—	—	3	7	1	—
<i>splendida</i>	7	—	—	—	6	1	—

tatively and analyzed statistically. Those that have been found to be the most useful in the study of *Leptodeira* are: oculars, labials, dorsals, ventrals, and caudals.

OCULARS: The number of preocular scales

varies from one to four. The upper scale of the series is always the largest; it may be in contact with the anterolateral corner of the frontal. The lower preocular is on the anteroventral edge of the orbit and might be called a presubocular; however, I find it more convenient to consider all the series as preoculars. (See fig. 1.) The presence or absence of the lower preocular usually determines the number of upper labials that enter the orbit. Normally, the lower preocular, when present, is small and separates the posterodorsal corner of the third upper labial from the orbit. The distribution frequency of preoculars is given in table 5. The postoculars also vary in number from one to four, but there is little interspecific difference; the variation is mostly individual. (See table 6.)

LABIALS: There are usually eight upper labials in all species, except *punctata*, in which there are seven. In *punctata* labials 3 and 4

TABLE 3  
VARIATION IN THE NUMBER OF PTERYGOID TEETH

Species	N	No. of Pterygoid Teeth																
		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>annulata</i>	42	—	—	—	—	—	—	—	1	2	3	6	4	10	10	1	3	2
<i>bakeri</i>	4	—	—	—	—	—	—	—	—	—	2	1	—	1	—	—	—	—
<i>frenata</i>	9	—	—	—	1	4	2	1	1	—	—	—	—	—	—	—	—	—
<i>latifasciata</i>	3	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>maculata</i>	10	—	—	—	—	—	—	—	—	—	2	4	1	1	1	—	—	1
<i>nigrofasciata</i>	10	2	4	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>punctata</i>	7	—	—	—	—	—	—	—	—	3	—	1	1	1	—	1	—	—
<i>septentrionalis</i>	11	—	—	—	—	—	—	—	1	3	2	1	2	2	—	—	—	—
<i>splendida</i>	7	—	—	—	—	—	—	—	—	—	—	2	1	—	1	2	1	—

TABLE 4  
VARIATION IN THE NUMBER OF DENTARY TEETH

Species	N	No. of Dentary Teeth														
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>annulata</i>	46	—	—	—	—	—	—	2	2	4	7	12	7	9	2	1
<i>bakeri</i>	4	—	—	—	—	—	—	—	1	1	—	2	—	—	—	—
<i>frenata</i>	10	7	2	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>latifasciata</i>	2	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
<i>maculata</i>	8	—	—	—	—	—	—	—	—	1	1	—	4	2	—	—
<i>nigrofasciata</i>	10	4	4	—	2	—	—	—	—	—	—	—	—	—	—	—
<i>punctata</i>	7	—	—	—	—	—	1	3	—	3	—	—	—	—	—	—
<i>septentrionalis</i>	9	—	—	—	—	—	1	1	—	1	1	2	2	1	—	—
<i>splendida</i>	7	—	—	—	—	—	—	1	—	2	2	1	1	—	—	—

TABLE 5  
VARIATION IN THE NUMBER OF PREOCULAR SCALES

Form	No. of Preocular Scales						Total	
	1-1	1-2	2-2	2-3	3-3	3-4		
<i>a. annulata</i>	319	18	38	—	—	—	1	376
<i>a. ashmeadi</i>	15	2	47	—	2	—	—	66
<i>a. cussiliris</i>	9	13	402	15	10	—	—	449
<i>a. pulchriceps</i>	2	2	16	3	—	—	—	23
<i>a. rhombifera</i>	11	12	279	25	27	1	1	356
<i>bakeri</i>	3	1	11	—	—	—	—	15
<i>f. frenata</i>	1	1	8	1	1	—	—	12
<i>f. malleisi</i>	1	3	31	1	4	—	—	40
<i>f. yucatanensis</i>	—	2	14	3	1	—	—	20
<i>latifasciata</i>	—	—	8	—	—	—	—	8
<i>maculata</i>	16	4	134	3	1	—	—	158
<i>nigrofasciata</i>	—	1	57	1	—	—	—	59
<i>punctata</i>	7	3	15	—	—	—	—	25
<i>s. septentrionalis</i>	—	—	—	—	70	—	—	70
<i>s. larcorum</i>	5	2	14	—	2	—	—	23
<i>s. ornata</i>	9	4	75	3	6	—	—	97
<i>s. polysticta</i>	1	3	35	19	143	2	—	203
<i>s. splendida</i>	—	—	—	—	11	3	1	15
<i>s. bressoni</i>	—	—	2	1	4	—	—	7
<i>s. ephippiata</i>	—	—	—	1	5	—	—	6

TABLE 6  
VARIATION IN THE NUMBER OF POSTOCULAR SCALES

Form	No. of Postocular Scales					Total	
	1-1	1-2	2-2	2-3	2-4		
<i>a. annulata</i>	1	1	371	2	—	1	376
<i>a. ashmeadi</i>	—	—	64	2	—	—	66
<i>a. cussiliris</i>	—	—	440	7	1	1	449
<i>a. pulchriceps</i>	—	—	17	4	—	2	23
<i>a. rhombifera</i>	1	2	345	5	—	3	356
<i>bakeri</i>	—	—	14	1	—	—	15
<i>f. frenata</i>	—	—	12	—	—	—	12
<i>f. malleisi</i>	2	1	35	1	—	1	40
<i>f. yucatanensis</i>	—	—	20	—	—	—	20
<i>latifasciata</i>	—	—	8	—	—	—	8
<i>maculata</i>	1	—	157	—	—	—	158
<i>nigrofasciata</i>	6	5	48	—	—	—	59
<i>punctata</i>	—	—	24	1	—	—	25
<i>s. septentrionalis</i>	—	—	69	1	—	—	70
<i>s. larcorum</i>	—	—	21	1	—	1	23
<i>s. ornata</i>	—	1	90	4	—	2	97
<i>s. polysticta</i>	—	1	198	2	—	2	203
<i>s. splendida</i>	—	—	15	—	—	—	15
<i>s. bressoni</i>	—	—	7	—	—	—	7
<i>s. ephippiata</i>	—	—	6	—	—	—	6

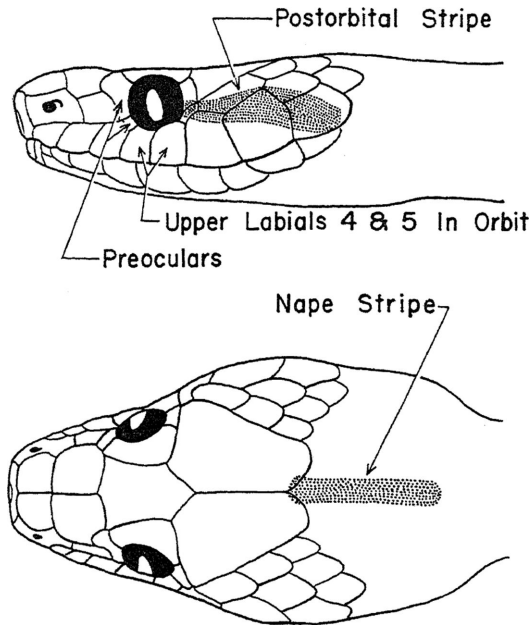


FIG. 1. Head of *Leptodeira* showing typical scutellation and characters used in the systematic study of the genus.

normally enter the orbit; in the other species the fourth and fifth, or the third, fourth, and fifth, usually enter the orbit; the sixth and seventh are the largest and are in contact with the anterior temporal. The frequency distribution of upper labials and labials entering the orbit is given in tables 7 and 8. Usually there are 10 lower labials and sometimes 11 or 12; in *punctata* there are nine. Lower labials 1 through 5 are in contact with the anterior chin shield, and lower labials 5 and 6 are in contact with the posterior one. In *punctata* lower labials 1 through 4 are in contact with the anterior, 4 and 5 with the posterior, chin shield. The distribution of lower labials is given in table 9.

**TEMPORALS:** Normally there are a single primary, two secondary, and three tertiary temporals. The tertiary row is the most variable. I have found them to be of no taxonomic significance; the frequency distribution of temporals is given in table 10.

**CHIN SHIELDS:** The chin shields are nearly equal in length, except in *bakeri*, in which the anterior is three-fourths of the length of the posterior. In all species except *punctata* lower labials 1 through 5 are in contact with

the anterior chin shield, and 5 and 6 are in contact with the posterior; in *punctata* 1 through 4 are in contact with the anterior, 4 and 5 with the posterior, chin shield.

**DORSALS:** The dorsal scales are usually smooth, somewhat elongate, and with two apical pits. Those in the anal region in some *bressoni* and *annulata* are weakly keeled. The maximum number of rows is approximately at midbody; this number varies interspecifically and intraspecifically, the entire range of variation being from 17 to 25; anterior to the anus the number of rows is reduced, there being 11 to 19 rows. (See table 11.) Scale reduction normally involves the paravertebral row. Addition of one or two rows on the anterior part of the body takes place by the splitting of the paravertebral row to form two rows. The reduction takes place either by the fusion of the paravertebral and vertebral rows or by the fusion of the paravertebral and the adjacent lateral row. (See fig. 2.) The place of scale reduction in relation to ventral number is highly variable and of little taxonomic importance.

In the species *annulata* and *septentrionalis* there are populations having a marked reduction in the number of dorsal scale rows (to 17

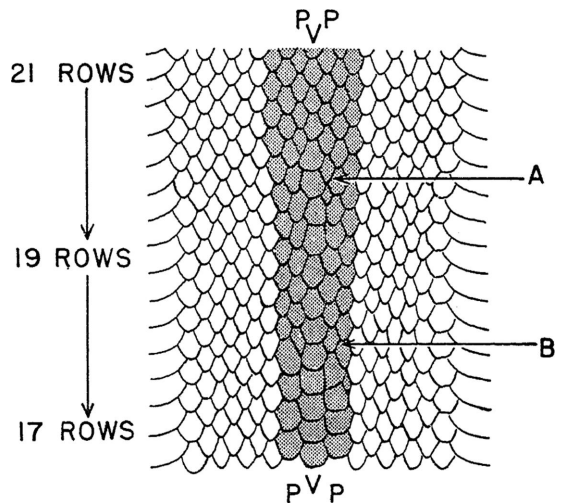


FIG. 2. Dorsal body scales of *Leptodeira* showing method of posterior scale reduction, which may take place by the fusion of the paravertebral row with the vertebral row (A) or by fusion of the paravertebral row with the adjacent lateral row (B). Abbreviations: V, vertebral row; P, paravertebral row. The scale rows involved in the scale reduction are shaded.

TABLE 7  
 VARIATION IN THE NUMBER OF UPPER LABIALS

Form	No. of Upper Labials						Total
	7-7	7-8	8-8	8-9	9-9	Other	
<i>a. annulata</i>	1	6	360	—	—	3	376
<i>a. ashmeadi</i>	—	—	65	—	1	—	66
<i>a. cussiliris</i>	—	—	446	3	—	—	449
<i>a. pulchriceps</i>	1	2	18	1	1	—	23
<i>a. rhombifera</i>	—	—	349	7	—	—	356
<i>bakeri</i>	—	—	15	—	—	—	15
<i>f. frenata</i>	—	—	12	—	—	—	12
<i>f. malleisi</i>	—	—	40	—	—	—	40
<i>f. yucatanensis</i>	—	—	20	—	—	—	20
<i>latifasciata</i>	—	—	8	—	—	—	8
<i>maculata</i>	—	—	158	—	—	—	158
<i>nigrofasciata</i>	—	1	56	2	—	—	59
<i>punctata</i>	21	2	2	—	—	—	25
<i>s. septentrionalis</i>	—	—	70	—	—	—	70
<i>s. larcorum</i>	—	—	22	1	—	—	23
<i>s. ornata</i>	—	—	97	—	—	—	97
<i>s. polysticta</i>	—	—	201	2	—	—	203
<i>s. splendida</i>	—	—	15	—	—	—	15
<i>s. bressoni</i>	—	—	7	—	—	—	7
<i>s. ephippiata</i>	—	—	6	—	—	—	6

TABLE 8  
 VARIATION IN THE NUMBER OF UPPER LABIALS ENTERING ORBIT

Form	Labials Entering Orbit							Other	Total
	3-4	3-4	3-4-5	3-4-5	4-5	4-5	4-5		
	3-4	4-5	3-4-5	4-5	4-5	4-5-6	5-6		
<i>a. annulata</i>	1	2	232	31	103	1	1	5	376
<i>a. ashmeadi</i>	—	—	11	2	52	—	—	1	66
<i>a. cussiliris</i>	—	—	—	2	446	—	1	—	449
<i>a. pulchriceps</i>	1	1	1	—	18	—	1	1	23
<i>a. rhombifera</i>	—	—	—	—	352	3	—	1	356
<i>bakeri</i>	—	—	1	—	14	—	—	—	15
<i>f. frenata</i>	—	—	—	—	12	—	—	—	12
<i>f. malleisi</i>	—	—	2	2	36	—	—	—	40
<i>f. yucatanensis</i>	—	—	—	2	18	—	—	—	20
<i>latifasciata</i>	—	—	—	—	8	—	—	—	8
<i>maculata</i>	—	—	—	—	158	—	—	—	158
<i>nigrofasciata</i>	—	1	—	2	55	—	1	—	59
<i>punctata</i>	23	—	—	—	1	—	—	1	25
<i>s. septentrionalis</i>	—	—	—	—	70	—	—	—	70
<i>s. larcorum</i>	—	—	4	2	16	1	—	—	23
<i>s. ornata</i>	—	—	11	3	83	—	—	—	97
<i>s. polysticta</i>	—	—	9	5	188	—	1	—	203
<i>s. splendida</i>	—	—	—	—	15	—	—	—	15
<i>s. bressoni</i>	—	—	—	—	7	—	—	—	7
<i>s. ephippiata</i>	—	—	—	—	6	—	—	—	6

TABLE 9  
VARIATION IN THE NUMBER OF LOWER LABIALS

Form	No. of Lower Labials							Other	Total
	9-9	9-10	10-10	10-11	11-11	11-12	12-12		
<i>a. annulata</i>	5	5	220	83	55	5	1	2	376
<i>a. ashmeadi</i>	1	4	58	2	1	—	—	—	66
<i>a. cussiliris</i>	6	13	400	24	5	—	—	1	449
<i>a. pulchriceps</i>	—	—	18	1	3	—	—	1	23
<i>a. rhombifera</i>	2	9	313	24	8	—	—	—	356
<i>bakeri</i>	1	1	13	—	—	—	—	—	15
<i>f. frenata</i>	1	—	11	—	—	—	—	—	12
<i>f. malleisi</i>	—	—	38	2	—	—	—	—	40
<i>f. yucatanensis</i>	1	1	17	1	—	—	—	—	20
<i>latifasciata</i>	—	—	8	—	—	—	—	—	8
<i>maculata</i>	7	11	137	2	1	—	—	—	158
<i>nigrofasciata</i>	4	7	46	2	—	—	—	—	59
<i>punctata</i>	23	2	—	—	—	—	—	—	25
<i>s. septentrionalis</i>	2	3	63	1	1	—	—	—	70
<i>s. larcorum</i>	—	—	22	1	—	—	—	—	23
<i>s. ornata</i>	1	—	48	11	28	4	5	—	97
<i>s. polysticta</i>	7	6	166	11	10	2	1	—	203
<i>s. splendida</i>	—	—	15	—	—	—	—	—	15
<i>s. bressoni</i>	—	—	7	—	—	—	—	—	7
<i>s. ephippiata</i>	—	1	4	1	—	—	—	—	6

TABLE 10  
VARIATION IN THE NUMBER OF SCALES IN THE TEMPORAL SERIES

Form	No. of Primary, Secondary, and Tertiary Temporals								Other	Total
	1-1-2	1-2-2	1-2-2	1-2-3	1-2-3	1-2-4	1-3-3	1-3-4		
	1-1-2	1-2-2	1-2-3	1-2-3	1-2-4	1-2-4	1-3-3	1-3-4		
<i>a. annulata</i>	2	—	2	346	3	1	2	1	19	376
<i>a. ashmeadi</i>	—	1	—	60	—	1	2	—	2	66
<i>a. cussiliris</i>	—	3	17	396	16	9	—	—	8	449
<i>a. pulchriceps</i>	—	—	1	19	—	—	1	1	1	23
<i>a. rhombifera</i>	—	—	2	316	14	11	—	—	13	346
<i>bakeri</i>	—	—	—	15	—	—	—	—	—	15
<i>f. frenata</i>	—	—	—	10	—	1	—	—	1	12
<i>f. malleisi</i>	—	—	—	39	—	1	—	—	—	40
<i>f. yucatanensis</i>	—	—	—	20	—	—	—	—	—	20
<i>latifasciata</i>	—	—	—	8	—	—	—	—	—	8
<i>maculata</i>	1	—	—	150	1	1	—	—	5	158
<i>nigrofasciata</i>	1	—	—	57	—	—	—	—	1	59
<i>punctata</i>	—	—	1	21	1	—	1	—	1	25
<i>s. septentrionalis</i>	—	—	1	54	9	3	—	—	3	70
<i>s. larcorum</i>	—	—	—	22	—	—	—	—	1	23
<i>s. ornata</i>	—	1	2	83	3	1	—	2	5	97
<i>s. polysticta</i>	—	3	2	184	5	3	—	—	6	203
<i>s. splendida</i>	1	—	—	14	—	—	—	—	—	15
<i>s. bressoni</i>	—	—	—	7	—	—	—	—	—	7
<i>s. ephippiata</i>	—	—	—	6	—	—	—	—	—	6

TABLE 11  
VARIATION IN THE NUMBER OF DORSAL SCALE ROWS

Form	Maximum					Minimum Posteriorly					Total
	17	19	21	23	25	11	13	15	17	19	
<i>a. annulata</i>	10	330	36	—	—	6	206	162	2	—	376
<i>a. ashmeadi</i>	—	19	46	1	—	—	1	57	8	—	66
<i>a. cussiliris</i>	—	—	6	407	36	—	—	41	405	3	449
<i>a. pulchriceps</i>	—	5	18	—	—	—	1	20	2	—	23
<i>a. rhombifera</i>	—	—	103	231	22	—	—	34	321	1	356
<i>bakeri</i>	—	14	1	—	—	—	—	13	2	—	15
<i>f. frenata</i>	—	—	11	1	—	—	—	9	3	—	12
<i>f. malleisi</i>	—	—	35	5	—	—	1	33	6	—	40
<i>f. yucatanensis</i>	—	—	17	3	—	—	2	16	2	—	20
<i>latifasciata</i>	—	—	5	4	—	—	—	2	6	1	9
<i>maculata</i>	—	—	33	122	3	—	—	23	131	4	158
<i>nigrofasciata</i>	—	59	—	—	—	—	—	2	57	—	59
<i>punctata</i>	—	25	—	—	—	—	—	21	4	—	25
<i>s. septentrionalis</i>	—	—	9	61	—	—	—	26	43	1	70
<i>s. larcorum</i>	—	—	21	2	—	—	—	16	7	—	23
<i>s. ornata</i>	—	15	77	5	—	—	7	87	3	—	97
<i>s. polysticta</i>	—	—	35	167	1	1	—	156	45	1	203
<i>s. splendida</i>	—	—	15	—	—	—	—	1	14	—	15
<i>s. bressoni</i>	—	—	7	—	—	—	—	1	6	—	7
<i>s. ephippiata</i>	—	1	5	—	—	—	—	1	5	—	6

at midbody and to 11 posteriorly) and a corresponding enlargement of the vertebral and paravertebral rows. These scutellation characters, with the accompanying lateral compression of the body, indicate morphological adaptation to an arboreal existence.

**VENTRALS:** The number of ventral scutes ranges from a minimum of 150 in *punctata* to 211 in *polysticta*. The greatest variation in one species is 151 to 200, in *annulata*. Numerous geographical gradients in this character are present. A statistical analysis of the variation in ventrals is given in table 12.

**ANAL PLATE:** Normally the anal plate is completely divided; in occasional individuals it is only partially divided or creased.

**CAUDALS:** The number of caudal scutes varies from a minimum of 54 in *maculata* to a maximum of 107 in *polysticta*. The character also shows geographical gradients. There is considerable sexual dimorphism in the number of caudals; in some populations there is no overlap in the variation in the males and females. A statistical analysis of the variation in caudals is given in table 13.

#### SIZE AND PROPORTIONS

Although size differences do exist between the species of *Leptodeira*, the character is a difficult one to use, for continued growth does not permit the ready age grouping and systematic sorting that is possible in many groups of animals. Females usually average somewhat larger than males. The smallest species appears to be *punctata*, whereas the largest specimens examined were *rhombifera* and *polysticta*. The longest individual, a female *polysticta*, has a body length of 820 mm. and a total length of 1055 mm. The maximum size observed in each species is given in table 14.

More useful than the actual measurements in snakes are the proportions; of these, the tail/body proportion is the most easily used. The length of the tail is controlled by the number of caudal vertebrae (therefore, caudal scutes), and the differences that exist between species in caudal number are similar to the differences existing in tail/body ratio. The character is sexually dimorphic, the males having the longer tails. The forms of *Leptodeira* that are arboreal have relatively

TABLE 12  
VARIATION IN THE NUMBER OF VENTRALS

Form	Males					Females					
	N	Range	M	S.D.	C.V.	N	Range	M	S.D.	C.V.	C.D.
<i>a. annulata</i>	166	180-200	189.0	3.95	2.09	194	174-199	186.0	13.74	7.39	0.170
<i>a. ashmeadi</i>	33	174-192	181.9	4.57	2.52	31	171-194	181.5	5.09	2.80	0.041
<i>a. cussiliris</i>	204	160-185	171.2	3.66	2.14	236	158-181	172.4	4.43	2.56	0.148
<i>a. pulchriceps</i>	11	186-204	193.6	4.47	2.31	12	184-198	189.8	4.08	2.15	0.444
<i>a. rhombifera</i>	168	151-181	167.6	3.10	1.85	180	156-177	167.8	3.62	2.16	0.030
<i>bakeri</i>	5	171-174	172.2	1.12	0.65	9	167-179	169.9	1.77	1.04	0.796
<i>f. frenata</i>	6	179-183	181.2	1.48	0.82	5	175-185	180.0	4.12	2.29	0.214
<i>f. malleisi</i>	18	170-185	179.0	3.84	2.15	19	170-188	181.5	4.87	2.68	0.287
<i>f. yucatanensis</i>	14	177-186	181.5	2.63	1.45	7	175-192	183.0	4.96	2.71	0.198
<i>latifasciata</i>	4	176-186	181.3	4.28	2.36	5	176-192	187.0	4.36	2.33	0.660
<i>maculata</i>	68	160-176	166.0	3.20	1.93	87	159-175	168.0	1.62	1.56	0.344
<i>nigrofasciata</i>	26	161-196	176.2	10.13	5.75	33	169-196	183.7	8.68	4.73	0.399
<i>punctata</i>	13	150-156	153.0	1.75	1.14	11	151-167	157.9	4.06	2.57	0.843
<i>s. septentrionalis</i>	28	181-199	190.8	5.27	2.76	43	185-208	194.7	5.11	2.62	0.376
<i>s. larcorum</i>	9	176-184	178.4	2.52	1.41	14	170-185	178.1	4.01	2.25	0.046
<i>s. ornata</i>	51	175-201	187.0	6.22	3.33	56	174-194	185.5	1.41	0.76	0.197
<i>s. polysticta</i>	114	186-208	197.8	19.13	9.67	97	186-211	198.9	5.50	2.77	0.045
<i>s. splendida</i>	8	160-168	163.0	2.51	1.54	6	160-168	164.0	3.03	1.85	0.181
<i>s. bressoni</i>	5	165-170	166.0	5.48	3.30	2	165-169	167.0	—	—	—
<i>s. ephippiata</i>	2	175-177	176.0	—	—	4	180-184	181.5	1.91	1.05	—

TABLE 13  
VARIATION IN THE NUMBER OF CAUDALS

Form	Males					Females					
	N	Range	M	S.D.	C.V.	N	Range	M	S.D.	C.V.	C.D.
<i>a. annulata</i>	140	74-102	94.1	16.85	17.91	157	72-100	84.1	12.41	14.76	0.342
<i>a. ashmeadi</i>	25	79-98	88.9	5.18	5.83	20	71-90	80.6	5.17	6.41	0.802
<i>a. cussiliris</i>	170	59-84	71.0	4.74	6.68	199	54-74	64.2	4.82	7.51	0.711
<i>a. pulchriceps</i>	10	71-91	83.4	6.38	7.65	10	72-82	76.2	3.17	4.16	0.754
<i>a. rhombifera</i>	128	65-89	78.0	8.12	10.41	135	59-82	70.4	3.84	5.45	0.635
<i>bakeri</i>	3	70-74	71.3	—	—	3	63-71	67.0	—	—	—
<i>f. frenata</i>	5	71-80	76.6	4.00	5.22	5	61-70	65.6	3.24	4.94	1.519
<i>f. malleisi</i>	15	73-85	78.3	3.59	4.58	14	64-76	70.3	3.54	5.04	1.122
<i>f. yucatanensis</i>	13	72-86	79.0	4.32	5.47	7	66-67	66.7	0.54	0.81	2.531
<i>latifasciata</i>	4	76-82	78.5	2.64	3.36	5	64-71	69.0	3.08	4.46	1.836
<i>maculata</i>	56	67-82	73.8	3.35	4.54	69	54-75	67.9	3.88	5.71	0.816
<i>nigrofasciata</i>	22	63-76	68.1	3.47	5.10	25	54-68	62.6	3.72	5.94	0.765
<i>punctata</i>	12	59-69	65.7	3.07	4.64	9	54-62	58.7	2.64	4.50	1.230
<i>s. septentrionalis</i>	26	66-94	78.7	5.27	6.69	34	60-81	70.5	5.11	7.40	0.790
<i>s. larcorum</i>	8	86-93	90.1	2.17	2.41	12	72-84	79.3	3.47	4.38	1.915
<i>s. ornata</i>	38	72-104	94.7	4.96	5.24	48	78-98	86.0	4.18	4.86	0.952
<i>s. polysticta</i>	103	84-106	95.0	4.98	5.24	75	73-107	85.4	5.56	6.51	0.911
<i>s. splendida</i>	8	76-84	80.5	2.73	3.39	6	70-76	74.0	2.19	2.96	1.321
<i>s. bressoni</i>	3	82-87	84.3	—	—	1	—	71.0	—	—	—
<i>s. ephippiata</i>	2	78-85	81.5	—	—	3	77-81	78.7	—	—	—



TABLE 14

MAXIMUM BODY AND TOTAL LENGTHS IN THE FORMS OF *Leptodeira*

(The measurements are in millimeters. If the largest specimen has an incomplete tail, the total length given in parentheses was calculated for that specimen with the use of the mean tail/body ratio for that sex of the form.)

Form	Males		Females	
	Body	Total	Body	Total
<i>a. annulata</i>	601	838	660	870
<i>a. ashmeadi</i>	525	(713)	640	(845)
<i>a. cussiliris</i>	510	638	670	(893)
<i>a. pulchriceps</i>	575	735	610	(788)
<i>a. rhombifera</i>	510	(681)	820	1038
<i>bakeri</i>	410	(542)	535	(691)
<i>f. frenata</i>	425	(547)	405	515
<i>f. malleisi</i>	464	609	577	(736)
<i>f. yucatanensis</i>	550	714	565	705
<i>latifasciata</i>	401	526	555	688
<i>maculata</i>	508	659	673	(843)
<i>nigrofasciata</i>	430	(551)	473	581
<i>punctata</i>	410	539	445	(621)
<i>s. septentrionalis</i>	595	774	810	985
<i>s. larcorum</i>	450	619	680	882
<i>s. ornata</i>	550	745	665	865
<i>s. polysticta</i>	700	965	820	1055
<i>s. splendida</i>	402	550	473	619
<i>s. bressoni</i>	430	(587)	567	(730)
<i>s. ephippiata</i>	440	605	441	571

TABLE 15

## VARIATION IN TAIL/BODY RATIO (GIVEN IN PER CENT)

Form	N	Range	Males			N	Range	Females			
			M	C.D.	C.V.			M	S.D.	C.V.	C.D.
<i>a. annulata</i>	139	29.3-41.6	37.0	2.14	5.78	158	26.3-38.4	32.9	1.78	5.41	1.046
<i>a. ashmeadi</i>	25	30.6-41.7	35.9	2.81	7.83	22	27.5-35.5	32.1	2.34	7.29	0.737
<i>a. cussiliris</i>	166	20.1-32.6	28.3	1.81	6.39	192	20.8-29.4	25.0	1.87	7.48	0.896
<i>a. pulchriceps</i>	9	27.8-34.3	32.3	0.61	1.90	10	26.8-32.6	29.0	1.05	3.62	1.964
<i>a. rhombifera</i>	127	27.7-39.0	33.6	2.26	6.73	130	25.6-37.8	29.6	2.28	7.70	0.881
<i>bakeri</i>	3	29.5-34.2	32.1	—	—	3	27.7-30.8	29.1	—	—	—
<i>f. frenata</i>	5	27.2-31.6	28.6	1.73	6.05	5	22.8-27.2	24.7	1.55	6.28	1.189
<i>f. malleisi</i>	14	28.3-31.3	29.9	0.87	2.91	11	24.4-29.9	27.5	1.85	6.73	0.882
<i>f. yucatanensis</i>	11	27.8-32.2	30.6	1.26	4.12	5	22.6-26.6	24.7	1.18	4.78	2.418
<i>latifasciata</i>	3	28.7-32.9	30.9	—	—	5	25.0-25.5	25.2	2.18	8.65	—
<i>maculata</i>	53	24.9-35.6	30.7	2.37	7.72	66	22.7-32.6	27.5	1.71	6.22	0.784
<i>nigrofasciata</i>	21	23.0-32.7	28.2	2.62	9.29	25	22.8-27.0	24.9	1.14	4.58	0.878
<i>punctata</i>	12	31.2-35.1	32.9	1.24	3.77	8	25.8-31.8	28.4	2.20	7.75	1.304
<i>s. septentrionalis</i>	24	23.8-34.9	28.5	3.86	13.54	33	20.7-28.3	24.6	1.73	7.03	0.689
<i>s. larcorum</i>	8	34.1-39.6	36.6	3.57	9.75	11	29.7-34.0	32.1	1.16	3.61	0.951
<i>s. ornata</i>	39	28.1-40.5	36.8	2.30	6.28	48	28.2-36.2	32.6	1.86	5.71	1.010
<i>s. polysticta</i>	88	27.1-37.9	33.5	4.07	12.15	58	26.6-37.6	29.9	2.07	6.92	0.586
<i>s. splendida</i>	8	32.7-37.8	36.2	1.46	2.48	5	30.0-33.6	32.4	1.52	4.63	1.419
<i>s. bressoni</i>	3	35.4-38.0	36.5	—	—	1	—	28.8	—	—	—
<i>s. ephippiata</i>	1	—	37.5	—	—	3	29.5-32.0	31.2	—	—	—

longer tails than the terrestrial ones; in the arboreal *annulata* the males have a maximum tail/body ratio of 0.416, whereas in the terrestrial *cussiliris* the range is from 0.201 to 0.326. A statistical analysis of the tail/body ratios is given in table 15.

#### COLOR PATTERN

The color pattern consists of spots, blotches, or bands of dark color on a lighter ground color. In all species except *punctata* there is a longitudinal series of dorsal body blotches of varying size and color. There may be as few as seven blotches in *latifasciata* and as many as 70 in *polysticta*; these may extend to the ventrals, as in *maculata*, *frenata*, *yucatanensis*, *latifasciata*, *nigrofasciata*, and *septentrionalis*, or be restricted to a comparatively narrow area on the dorsum, as in *bressoni* and *polysticta*. In *annulata annulata* they may be fused to form a dorsal stripe anteriorly. The longitudinal extent of the blotches is considered to be the length and is expressed in the number of dorsal scales included within them. The transverse extent of the blotches is considered to be the width and is expressed in the number of included scale rows. Although the number of body blotches is highly variable, I have found them to be a valuable

taxonomic character. A statistical analysis of the number of dorsal body blotches is given in table 16. The color pattern of *punctata* consists of five or six longitudinal rows of small dark spots on the dorsum. This species has not been included in table 16. In many forms there are also lateral spots. These are situated on the lateral rows of dorsal scales between the edges of the larger dorsal blotches and are referred to as lateral intercalary spots. The head and nape patterns are of great importance. The head pattern may consist of any one of several ornate markings on the parietals and frontal, longitudinal stripes on the parietals and temporals, a series of spots on the parietals and frontal, or it may be unicolorous. A dark postorbital stripe is present in many forms. The nape may be unmarked or marked with a single longitudinal nape stripe, or with a longitudinal bar on each side. (See fig. 1.)

There is little ontogenetic change in color pattern. All juvenile specimens examined showed the same color pattern as the adults. Often the ground color is lighter in the juveniles. The darkening with age begins on the lateral parts of the body and proceeds dorsally. This is especially true in *rhomboifera* and in the *cussiliris* from southern México. In the

TABLE 16  
VARIATION IN THE NUMBER OF BODY BLOTCHES

Form	N	Range	M	S.D.	C.V.
<i>a. annulata</i>	293	25-50	33.4	3.72	11.14
<i>a. ashmeadi</i>	67	31-51	39.0	4.26	10.92
<i>a. cussiliris</i>	460	21-48	29.2	4.43	15.17
<i>a. pulchriceps</i>	23	33-46	39.2	3.92	10.00
<i>a. rhombifera</i>	355	23-56	35.7	5.44	15.23
<i>bakeri</i>	14	14-27	21.1	1.15	5.45
<i>f. frenata</i>	11	26-36	29.1	2.74	9.42
<i>f. malleisi</i>	38	24-39	30.4	1.11	3.65
<i>f. yucatanensis</i>	21	18-26	21.0	2.21	10.52
<i>latifasciata</i>	10	7-9	7.9	0.75	9.49
<i>maculata</i>	155	12-28	18.1	4.32	23.87
<i>nigrofasciata</i>	59	10-21	14.5	2.54	17.52
<i>s. septentrionalis</i>	72	20-35	26.2	4.03	15.38
<i>s. larcorum</i>	23	34-49	42.1	3.76	8.93
<i>s. ornata</i>	109	30-52	39.9	5.68	14.24
<i>s. polysticta</i>	199	38-70	53.6	7.60	14.18
<i>s. splendida</i>	14	18-25	20.8	2.40	11.54
<i>s. bressoni</i>	7	32-38	35.3	2.89	8.19
<i>s. ephippiata</i>	5	22-25	23.6	1.58	6.69

latter the darkening may not include the dorsomedian scale rows, so that in the adults these are lighter than the lateral rows. The juveniles of *annulata annulata* and *septentrionalis ornata* have a pure white occipital region; with age this darkens to the dorsal ground color of the adults.

#### SEXUAL DIMORPHISM

In any given population of a species there are differences of a greater or lesser degree between the males and females. These differences are always present in the number of caudal scutes and in the tail/body ratio; males consistently have more caudals and a relatively longer tail than do the females. (See tables 13 and 15.) Females usually attain a greater size than do the males. (See table 14.) In other characters the sexual dimorphism is less pronounced. There are sometimes slight differences in the number of ventral scutes. (See table 12.) Females often have more dorsal scale rows; females of *maculata*, for example, more often have 25 rows than do males. There is often sexual dimorphism in the scale reduction. In *macu-*

*lata* from the Balsas Basin the sexual difference in scale reduction is particularly noticeable; all females have 17 rows posteriorly, whereas 36 per cent of the males have 15 rows; the others have 17. The position of dorsal scale reduction also shows slight sexual differences; in females the addition of dorsal rows takes place more anteriorly and the reduction of dorsal rows more posteriorly than in males. The females have a stockier body and a greater length of the body, with the maximum number of dorsal scale rows. In *maculata*, for example, the average position of the splitting of the tenth scale row to give 23 rows is opposite the thirty-second ventral in females; in males it is opposite the forty-first. The average position of reduction from 23 to 21, from 21 to 19, and from 19 to 17 rows is opposite ventrals 96, 106, and 131 in females, and 94, 101, and 116 in males.

I have been unable to detect sexual dimorphism in head scales and body pattern. In some forms there is a slight average difference in the number of tail blotches, the males having more than the females.

#### SYSTEMATIC ACCOUNT OF THE SPECIES

In the following section are presented the systematic data based on the examination of the specimens available to me, together with information concerning the variation, ecology, and distribution of the forms considered to belong to the genus *Leptodeira*. Each of the nine species is taken as a unit; in the polytypic species, each subspecies is individually delimited and described. Under each form I have organized the discussion as follows; synonymy, types, description, sexual dimorphism, variation, remarks, range, and specimens examined. The species are arranged in four groups; subspecies are given in geographical order from north to south.

Although working primarily with preserved material and for the most part relying on morphological characters, I have tried to realize a biological concept of the species as defined by Mayr (1942). Individuals and series of specimens are considered to be only samples of the natural populations, and individual variation is assigned secondary importance as compared to the variation within

and between the populations. Differences between populations that can be shown to represent a continuous cline or internal cline (Huxley, 1942) are not considered as valid standards for the recognition of subspecies. Discontinuous variation and external clines (Huxley, *op. cit.*) that represent distinct differentiation between populations that still maintain genetic contact are used as criteria for the recognition of subspecies.

Of the 35 names referable to *Leptodeira*, I have examined the type specimens of 16 and had available detailed data on 14 of the others. The types of *nycthemera* and *dunckeri*, both of Werner, have not been located.

#### *Annulata* GROUP

This group, composed of four species—*annulata* with five subspecies, *maculata*, *bakeri*, and *frenata* with three subspecies—is characterized by a hemipenis that usually has a cup-shaped depression in the capitulum which is set off from the rest of the organ by a fold, maxillary teeth normal or reduced in

number, and a dorsal body pattern consisting of dark blotches on a light ground color.

Members of this group range from southern Tamaulipas and southern Sinaloa, México, to northern Argentina and Paraguay, exclusive of the Pacific coast of South America.

*Leptodeira annulata* Linnaeus

*Coluber annulatus* LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 224.

**DISTRIBUTION:** The range of *Leptodeira annulata* extends from southern Tamaulipas and Guerrero southward at low and moderate elevations along both coasts of México, excluding the wet forests of southern Veracruz and the Yucatán Peninsula, through the central plateaus and along the Pacific coast of Central America to Panamá, thence through the interior valleys of Darien to northern Colombia, Venezuela, and the Guianas, including Isla de Margarita, Tobago, and Trinidad, and throughout the Amazon Basin, southward into the Chaco of Paraguay and northern Argentina, and along the Atlantic coast of Brazil southward to São Paulo. (See maps 2 and 3.)

**DESCRIPTION:** Head distinct from neck; rostral barely visible from above; prefrontal square or slightly longer than broad, half again as long as the internasals; upper preocular in contact with frontal or not; frontal slightly longer than suture between parietals; preoculars usually one or two, sometimes three, the upper much larger than the lower; postoculars normally two, occasionally three; temporals normally one plus two plus three; upper labials normally eight, with fourth and fifth, or third, fourth, and fifth, entering the orbit; lower labials usually 10, sometimes 11; chin shields subequal in length; lower labials 1 to 5 in contact with anterior chin shield, 5 and 6 in contact with posterior one.

Dorsal scales smooth; vertebral and paravertebral rows enlarged or not; scales in 17 to 25 rows at midbody. Males sometimes show weak keels on dorsal scales in anal region. Dorsal scale reduction is accomplished by the fusion of the paravertebral row with adjacent lateral row or with vertebral row.

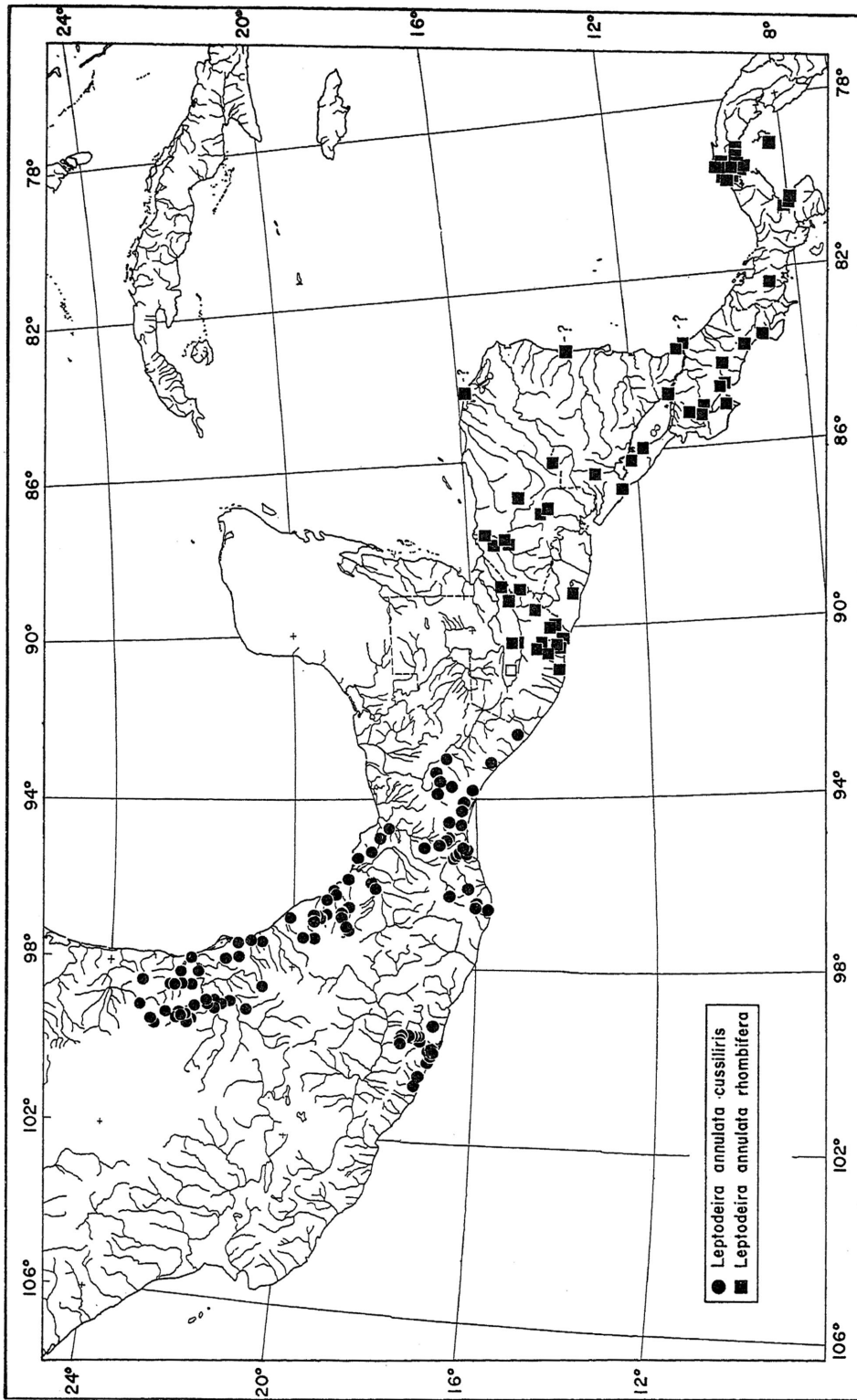
The ranges and means of tooth counts based on 53 specimens are: maxillary, 15-18+II (16.3); palatine, 10-12 (10.6); pterygoid, 23-32 (27.7); and dentary, 20-28 (24.3).

The hemipenis is seven to nine caudals in length. There is a primary row of four large spines, of which the middle ones are the largest and the distal the smallest. Median to the primary row are three longitudinal rows of small spines. There is a deep cup in the capitulum, which is finely crenulated and set off from the rest of the hemipenis by a deep fold. The sulcus is opposite the primary row of spines. The base is covered with spinules.

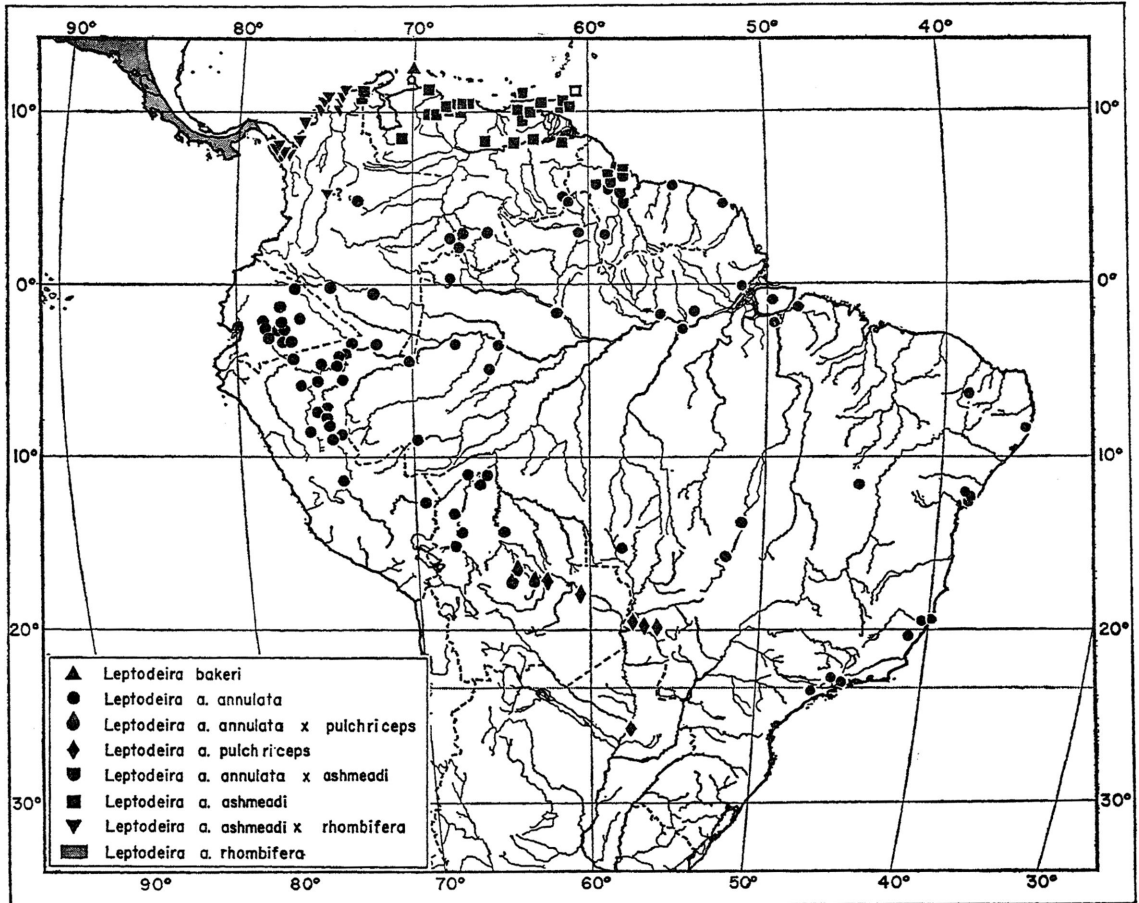
The color pattern consists of a cream to grayish brown ground color, with dark brown or black dorsal blotches. There may or may not be dark, lateral, intercalary spots. The head may be unicolorous brown or black, or it may be light brown with dark mottling. A nape stripe may be present.

The total length seldom exceeds 850 mm.; the tail/body ratio varies from 21 to 42 percent.

**GEOGRAPHICAL VARIATION:** This highly variable, widespread species shows numerous geographical gradients. In general there is an increase in the number of body blotches, ventrals, caudals, and tail/body ratio, and there is a decrease in the number of dorsal scale rows and in the total number of teeth from north to south in México and Central America. (See table 17.) In South America the picture is somewhat more complicated. North of the Andes and the Río Orinoco in Colombia and Venezuela, and on the islands of Margarita, Tobago, and Trinidad, the population continues the trend from lower Central America. A disjunct population in southeastern Bolivia, northern Argentina, Paraguay, and Mato Grosso, Brazil, is very similar to the populations in northern South America. All these snakes, including those in México and Central America, are terrestrial, with rounded bodies, the vertebral scale row not enlarged, and 21 to 25 dorsal scale rows at midbody; they show a preference for dry habitats. Throughout the Amazon Basin the population is strikingly different. The snakes there have laterally compressed bodies, enlarged vertebral scale rows, and usually 19 dorsal scale rows at midbody; they are arboreal and live in rain forests. In eastern Brazil there are some populations that show differences from those mentioned in South America; however, so little material is available from these areas that only suggestions can be made concerning their relationships. The ar-



MAP 2. Locality records for *Leptodeira annulata* in México and Central America.



MAP 3. Locality records for *Leptodeira annulata* and *bakeri* in South America.

TABLE 17

GEOGRAPHICAL VARIATION IN *Leptodeira annulata* IN MÉXICO AND CENTRAL AMERICA

(The mean counts are listed; those for body blotches and teeth are both sexes; the others, males only.)

Region	Body Blotches	Ventrals	Caudals	Tail/Body	Teeth (Total)
San Luis Potosí and Tamaulipas	23	169	65	27	82
Veracruz	26	172	67	27	82
Guerrero	32	172	75	29	—
Oaxaca and Chiapas	29	171	72	29	84
Guatemala	29	165	72	33	84
Honduras	32	166	80	34	—
Nicaragua	34	164	71	33	—
Costa Rica	35	167	82	34	—
Panamá: Canal Zone	29	170	78	35	81
Panamá: Darien	35	168	78	33	—

TABLE 18

DIAGNOSTIC CHARACTERS OF THE FIVE SUBSPECIES OF *Leptodeira annulata*

(Numbers in parentheses are not the usual condition, but occur often enough to be present in more than 10 per cent, but less than 25 per cent, of the population.)

Subspecies	Body Shape	Vertebral Row	Preoculars	Body Blotches (Mean)	Lateral Intercalary Spots	Nape Pattern
<i>annulata</i>	Compressed	Enlarged	1 (2)	33.4	No	None
<i>ashmeadi</i>	Rounded	Normal	2	38.9	Yes	2 bars
<i>cussiliris</i>	Rounded	Normal	2	29.2	Yes	None
<i>pulchriceps</i>	Rounded	Normal	2 (1)	39.2	Yes	2 bars
<i>rhomboifera</i>	Rounded	Normal	2	35.6	Yes	1 stripe

boreal form with a compressed body of the Amazon Basin intergrades with the southern terrestrial form in southeastern Bolivia and with the northern terrestrial form in British Guiana, thus tying together the two morphological types in a single species.

On the basis of the morphological types (rounded as compared with compressed body), the scutellation, and coloration characters *Leptodeira annulata* may be divided into five subspecies. (See table 18.)

*Leptodeira annulata* is the most successful species in the genus. It has the greatest geographical and ecological range. As a highly plastic species it has become adapted to diverse habitats; the two morphological types, i.e., laterally compressed and rounded bodies, are the reflection of the two main habitats in which the species has become established. The round-bodied type is more or less typical of terrestrial, non-burrowing colubrids; the compressed-bodied type is indicative of a forest environment for a species with arboreal habits. The laterally compressed body and enlarged vertebral and paravertebral scale rows in *Leptodeira annulata annulata* are not so well developed as those found in *Imantodes* and *Dipsas*. However, this seems to be a recent innovation in *Leptodeira*, whereas there may have been a longer evolutionary history of the arboreal adaptations in *Imantodes* and *Dipsas*.

*Leptodeira annulata cussiliris*,<sup>1</sup> new subspecies

*Leptodeira personata*, GÜNTHER, 1895, (in part),

<sup>1</sup> The subspecific name *cussiliris* is from the Latin word meaning cowardly and alludes to the timid nature of these snakes.

Biologia Centrali-Americana, Reptilia, pp. 171-172, pl. 54, figs. a, b. BOULENGER, 1896, (in part), Catalogue of the snakes in the British Museum, vol. 3, pp. 93-94. MOCQUARD, 1908, (in part), in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, pp. 903-904, pl. 73, fig. 1.

*Leptodeira albofusca*, BOULENGER, 1896, (in part), Catalogue of the snakes in the British Museum, vol. 3, pp. 95-97. STEJNEGER, 1926, (in part), Proc. U. S. Natl. Mus., vol. 69, pp. 1-3.

*Leptodeira annulata annulata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 204.

*Leptodeira annulata personata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 204.

*Leptodeira septentrionalis maculata*, DUNN, 1936, (in part), Proc. Natl. Acad. Sci., vol. 22, p. 697.

*Leptodeira maculata*, TAYLOR, 1938, (in part), Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 337-342, figs. 6-7, pls. 31-33. SMITH AND TAYLOR, 1945, (in part), Bull. U. S. Natl. Mus., no. 187, p. 88; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 348.

DIAGNOSIS: A subspecies of *Leptodeira annulata* having a low number of ventrals (average 171.8) and caudals (average 71.0 in males and 64.2 in females), a relatively short tail, relatively few body blotches (average 29.2), lateral intercalary spots, no nape stripe, and usually a maximum of 23 and a minimum of 17 dorsal scale rows. It differs from *rhomboifera* in lacking a nape stripe, from *annulata* in having more dorsal scale rows and in not having the vertebral row enlarged, from *ashmeadi* and *pulchriceps* in lacking the broad nape bars, and further from *pulchriceps* in the much lower number of ventrals and in lacking the ornate head pattern.

HOLOTYPE: Number 82617 in the collection

of the University of Michigan Museum of Zoology, an adult male, collected at Rancho Poso Río, 6 kilometers south of Tehuantepec, Oaxaca, México, by Norman Hartweg and James A. Oliver, August 20, 1936. Sixteen specimens (U.M.M.Z. Nos. 82606-82616 and 82618-82623) collected in the vicinity of Tehuantepec by Hartweg and Oliver during the summer of 1936 are here designated paratypes.

**DESCRIPTION OF HOLOTYPE:** An adult male with 172 ventrals, 76 caudals, two preoculars, two postoculars, one plus two plus three temporals, eight upper labials, the fourth and fifth entering the orbit, 10 lower labials, body length 394 mm., tail length 122 mm., and tail/body ratio 0.310. Dorsal scales in 21-23-17 rows; scale-reduction formula:

$$21 \frac{+11 (28)}{+11 (28)} \quad 23 \frac{10+11 (97)}{10+11 (95)} \quad 21 \frac{9+10 (109)}{9+10 (106)}$$

$$19 \frac{9+V (127)}{9+V (127)} \quad 17 (172)$$

The dorsal ground color is light grayish tan. There are 28 dark brown body blotches that are three to four scales in length and extend laterally onto the fourth scale row. The blotches are outlined with a pale cream color. Lateral intercalary spots are present on scale rows 2-4, and the ventral edges of scales in rows 4 and 5 between the dorsal blotches are edged with dark brown. There are 12 dark brown blotches on the dorsal surface of the tail. The ventral surfaces are an immaculate cream-white color. (See pl. 1.)

The top of the head is dark brown mottled with light cream, the light color being most prominent on the edges of the head shields. The dark brown postorbital stripe is continuous with the dark color of the temporals. The labials are cream; upper labials 1-5 and lower labials 1-3 are smudged with gray. (See pl. 1.)

**DESCRIPTION OF SUBSPECIES:** Males with 160-185 (171.2) ventrals and females with 158-181 (172.4) ventrals. Caudals in males 59-84 (71.0) and in females 54-74 (64.2). The dorsal scales are smooth and usually in 23 rows at midbody, occasionally there are 25 and rarely 21; these usually are reduced to 17 rows posteriorly, rarely to 19 or 15. Scale-reduction formula in eight males with a maximum of 23 rows:

$$21 +11 (28-37) - 23 10+11 (95-104) - 21 9+10$$

$$\text{or } 10+V (103-113) - 19 8+9, \text{ or } 9+V (122-136) - 17 (164-176)$$

Reduction in eight females with a maximum of 23 rows:

$$21 +11 (18-44) - 23 10+11 (93-106) - 21 9+10$$

$$\text{or } 10+V (106-120) - 19 8+9, \text{ or } 9+V (123-155) - 17 (160-176)$$

A female (U.M.M.Z. No. 82618) with a maximum of 25 rows shows the following reduction:

$$21 \frac{+11 (28)}{+11 (25)} \quad 23 \frac{+12 (59)}{+12 (59)} \quad 25 \frac{11+12 (92)}{11+12 (89)}$$

$$23 \frac{10+11 (104)}{10+11 (104)} \quad 21 \frac{9+10 (116)}{9+10 (116)} \quad 19 \frac{8+9 (140)}{8+9 (140)}$$

$$17 (176)$$

The dorsal ground color varies from cream to grayish brown; often the lighter color is on the back, the darker on the sides. There are 21 to 48 dark brown to black dorsal body blotches. These are normally one and one-half to three times the length of the dorsal interspaces. The blotches usually extend laterally onto scale rows 1 to 5. The blotches are rounded laterally. In the lateral interspaces there are dark spots present on scale rows 1 to 3 or 2 to 4. These may be distinct and dark or appear as indistinct smudges. The dorsal blotches are often outlined with black and bordered by cream. (See pls. 1 and 2.) There are seven to 21 tail blotches, which decrease in size posteriorly. The venter is an immaculate white to cream color.

The top of the head is dark brown to black. In many specimens the dark color of the head is fragmented by light cream or tan. In these specimens the head plates are often outlined with the light color, leaving their centers dark. In some there is a dark, V-shaped mark on each parietal. A postorbital dark stripe begins on the lower postocular and passes over the anterior part of the primary temporal, the top of the sixth upper labial, and the middle of the seventh and eighth to the corner of the mouth. In those specimens with a mottled head pattern the postorbital dark stripe is usually bordered above by light tan or cream. In those with a solid dark head pattern there is no light stripe, and the dark color of the head is continuous with the postorbital dark stripe, so that the stripe as such



is not present. There may be a dark stripe from the nostril across the loreal and lower part of the upper preocular to the orbit. The labials are light tan or cream. Usually there are vertical dark bars on the labials, but in some the lower labials are immaculate. (See pls. 1 and 2.)

Males range in body length from 200 to 510 mm. (382 mm.) and from 252 to 638 mm. (483 mm.) in total length; females range from 200 to 670 mm. (427 mm.) and from 248 to 810 mm. (505 mm.). The smallest juvenile examined was a male with a body length of 135 mm. and an incomplete tail. The smallest specimen with a complete tail, also a male, had a body length of 145 mm. and a total length of 188 mm.

**SEXUAL DIMORPHISM:** Males characteristically differ from females in having more

ventrals and proportionately longer tails. Males have an average of 71.0 caudals; females, 64.2. The tail/body ratio in males ranges from 0.201 to 0.326 (0.283) and in females from 0.208 to 0.294 (0.250). The numbers of caudals and ventrals for a population of these snakes in Oaxaca are shown in figure 3.

**VARIATION:** Although relatively uniform in its scutellation and body proportions, *L. a. cussiliris* is highly variable in its coloration. In general there is a cline for an increase in the number of dorsal body blotches from north to south in eastern México (see fig. 4); snakes from the Pacific coastal regions of Guerrero and Oaxaca have the highest number of body blotches. Specimens from eastern México are characterized by a dark brown head, indistinctly set off by a dark preorbital

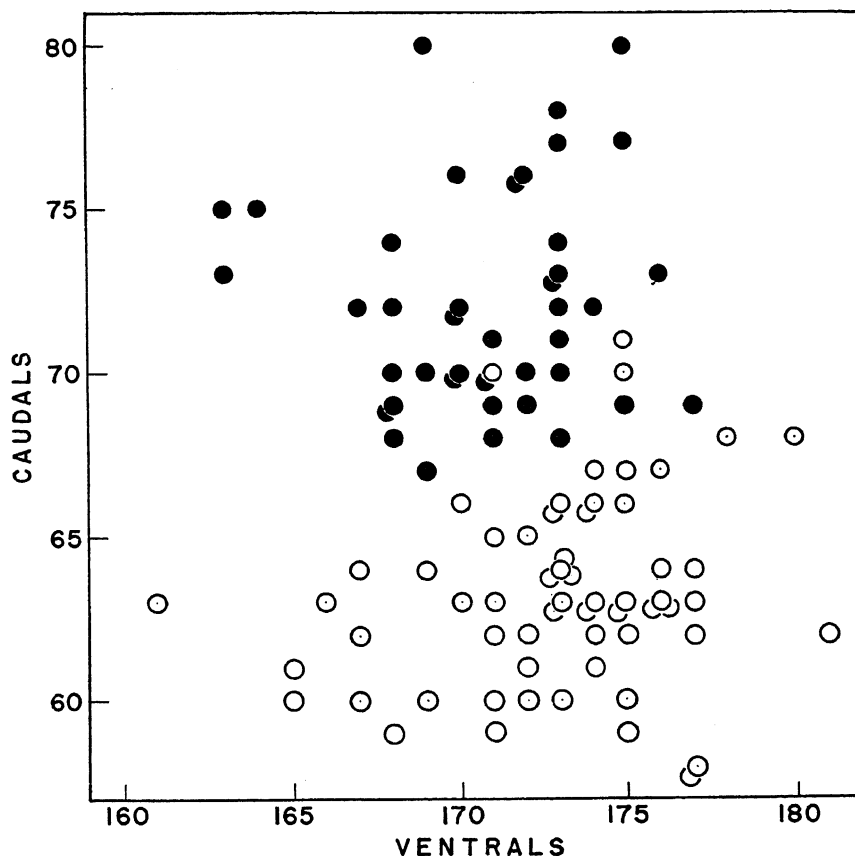


FIG. 3. Sexual dimorphism in the numbers of ventrals and caudals in *Leptodeira annulata cussiliris* from southeastern Oaxaca. Solid dots are males; open circles are females.

and postorbital stripe. The dorsal blotches vary in number from 21 to 34; there are slightly fewer body blotches in specimens from Tamaulipas and San Luis Potosí than in those from Veracruz. Individuals from north-eastern México often lack the lateral intercalary dark spots; when present they are dirty smudges on scale rows 1 and 2. In southern Veracruz the lateral intercalary spots are better developed than in the north. In northern specimens the dorsal dark blotches are two or three times the length of the light interspaces and extend laterally to scale rows 1 or 2. Farther south the blotches are slightly smaller and extend laterally to scale rows 2 or 3.

Snakes from Guerrero and Oaxaca are highly variable, and many individuals are strikingly different from those in the rest of the range. In some specimens the dorsal blotches are two to three times the length of the dorsal light interspaces and may extend laterally onto scale rows 3 or 4. In others the blotches are considerably shorter and equal in length to the light interspaces; in these the blotches extend laterally only onto rows 5 and 6. Lateral intercalary dark spots usually are present on scale rows 2 to 4. However, in some specimens these are lacking; three individuals (U.I. Nos. 17792-17794) from Totolapam, Oaxaca, have the lateral intercalary spots absent or reduced to a thin dark line on the edges of scale rows 2 and 3. Several specimens from the lowlands of Guerrero (e.g., U.I. No. 17820 from El Limoncito) show an extreme reduction of the dorsal blotches. In this individual there are 46 dorsal body blotches reduced to small brown spots on the vertebral and paravertebral rows; most of the blotches are only one scale in length and one-half of the length of the light interspaces. Minute lateral intercalary spots are present on scale rows 4 and 5. A nuchal blotch four scales in length extends laterally nearly to the ventrals. (See pl. 3, fig. 1.) That this does not represent a distinct species is attested by the fact that in the series available from the lowlands of Guerrero, the color pattern varies from a few large blotches to a large number of reduced ones. Many individuals from Oaxaca and some from Guerrero have a dorsal head coloration differing from that encountered elsewhere in the

range. In these the dorsal head plates are outlined with cream or light tan, and their centers are dark brown. Also, there may be a dark, V-shaped mark on each parietal. This mottled type of head pattern is not consistent within any one population and shows all degrees of differentiation from the solid-colored dark head. Two specimens from Tonolá, Chiapas, have a dark nape stripe; in this respect they approach *L. a. rhombifera* in Guatemala. The Chiapas specimens have 25 to 33 body blotches that are half again as long as the light interspaces and extend laterally to scale rows 2 to 4. There are large lateral intercalary spots on scale rows 1 to 3.

The following color descriptions are based on living specimens from various parts of the range of the subspecies in México:

An adult from Xicoténcatl, Tamaulipas (U.M.M.Z. No. S-1755), had a dorsal ground color of light brown; the dorsal blotches were black flecked with light brown and outlined with a cream-tan; the venter was cream-white. The nape was a cream-tan. The iris was light grayish brown.

An adult from Tehuantepec, Oaxaca (U.M.M.Z. No. 114569), had a dark brown ground color; the dorsal blotches were black and outlined with yellowish tan. The labials were yellowish cream barred with black. The venter was a cream color, and the iris was grayish brown.

Another adult from southern Oaxaca, near Chivela (U.M.M.Z. No. 114574), had a reddish brown dorsal ground color, with a dusty cream-colored nape band.

An adult from Tuxtla Gutierrez, Chiapas (U.M.M.Z. No. 114568), had a reddish brown ground color, with grayish brown dorsal blotches that were outlined with pinkish tan. On the anterior third of the body the first scale row was lemon yellow.

A juvenile from Matlapa, San Luis Potosí (U.M.M.Z. No. 114429), had an orange-tan dorsal ground color, black dorsal blotches, a cream-colored nape band, and a white venter.

The scutellation in *cussiliris* is less variable. The specimens from northeastern México have slightly fewer ventrals than do those from southern México; a similar but greater difference is apparent in the number of caudals and in the tail/body ratio. (See table 19.)

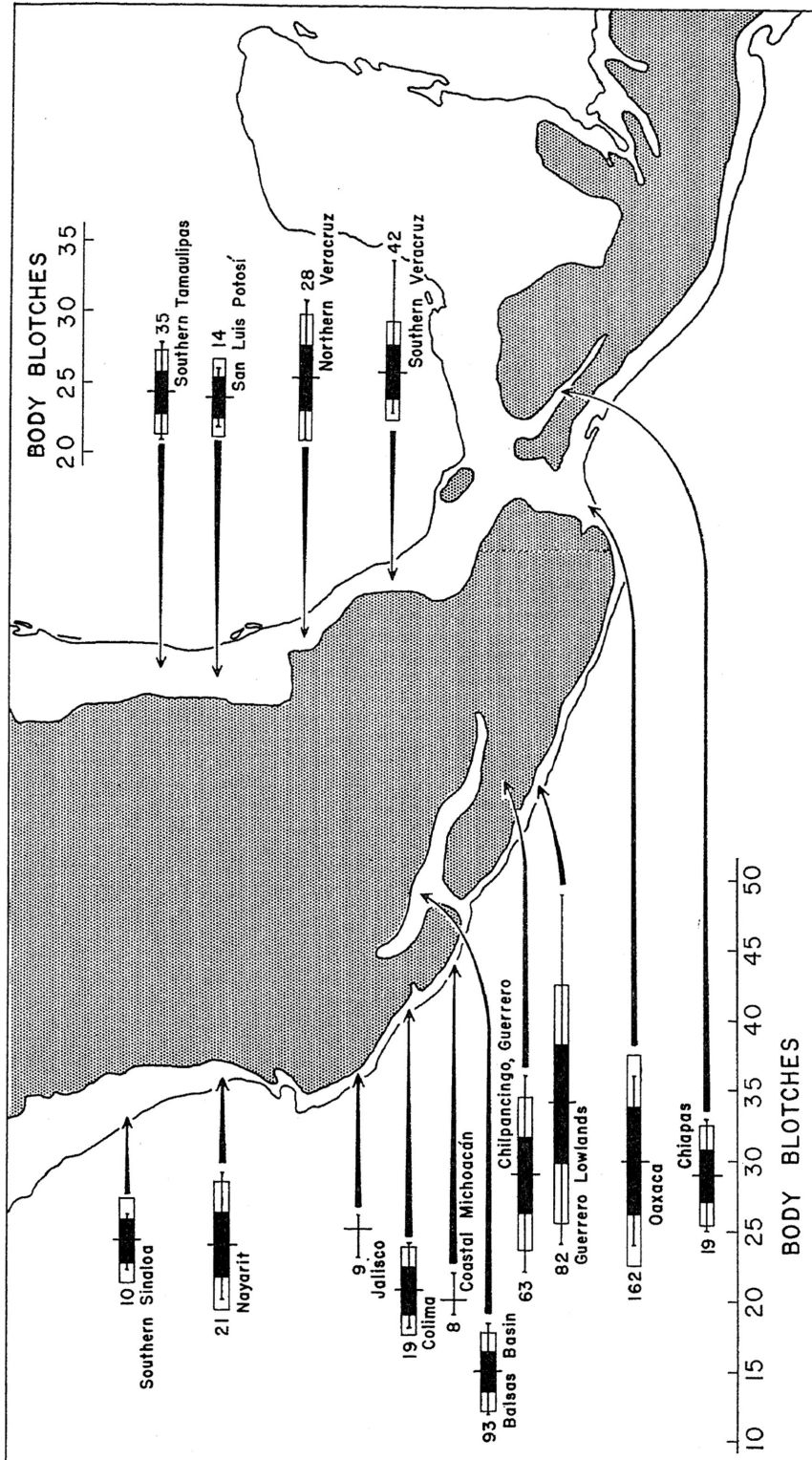


FIG. 4. Geographical variation in the number of body blotches in *Leptodeira annulata cussiviris* and *L. maculata*. The population in the Balsas Basin and northward on the Pacific coast is *maculata*. Vertical line, mean; horizontal line, observed range; box includes one and two standard deviations on either side of the mean; the number of specimens is given for each sample. The shaded area is above the 1000-meter contour.

TABLE 19  
COMPARISON OF FOUR CHARACTERS IN *Leptodeira annulata cussiliris*  
FROM EASTERN AND SOUTHERN MÉXICO

Region	Ventrals	Caudals	Tail/Body	Body Blotches
Eastern				
Males				
<i>N</i>	(54)	(45)	(42)	—
<i>M</i>	171.0	65.9	0.265	—
<i>O.R.</i>	164–179	59–69	0.241–0.283	—
Females				
<i>N</i>	(63)	(50)	(47)	—
<i>M</i>	170.8	59.4	0.238	—
<i>O.R.</i>	158–189	54–70	0.211–0.282	—
Males and females				
<i>N</i>	—	—	—	(119)
<i>M</i>	—	—	—	25.1
<i>O.R.</i>	—	—	—	21–34
Southern				
Males				
<i>N</i>	(137)	(112)	(111)	—
<i>M</i>	171.2	73.5	0.290	—
<i>O.R.</i>	160–185	65–84	0.260–0.326	—
Females				
<i>N</i>	(165)	(137)	(134)	—
<i>M</i>	173.0	66.3	0.256	—
<i>O.R.</i>	161–181	58–74	0.214–0.312	—
Males and females				
<i>N</i>	—	—	—	(307)
<i>M</i>	—	—	—	30.9
<i>O.R.</i>	—	—	—	22–48

There is some evidence of altitudinal variation in the number of body blotches. Although few specimens are accompanied by altitudinal data, the number of body blotches has been plotted against the approximate altitude of the collection sites for a series of 129 specimens taken along a transect from Chilpancingo to Acapulco, Guerrero. (See fig. 5.) The trend from a lower number of body blotches at higher altitudes to a higher number at lower altitudes indicates that the same factors may be responsible for both the altitudinal and latitudinal responses. Specimens from northern México have fewer body blotches than do those from southern México. (See fig. 4.) On the other hand the great variation displayed by these snakes from lowland Guerrero may be due to other factors, such as influx of genes from another population.

REMARKS: Previous workers have considered *cussiliris* (= *maculata* auct.) and *rhombifera* to be distinct species. However, Stu-

art (1954a) hinted that there may be a genetic relationship between the two forms. Although no new evidence has come to light, I am convinced that the two forms should be treated as subspecies. *Leptodeira a. cussiliris* in Chiapas has an average of 29 dorsal body blotches, and the males have 172 ventrals and 69 caudals, as compared with 29 body blotches, 165 ventrals, and 72 caudals in Guatemalan specimens of *rhombifera*. The presence of a nape stripe in two Chiapan specimens and its absence in five Guatemalan individuals indicate that there may be genetic interchange between the two populations. A comparison between northern populations of *L. a. rhombifera* and southern ones of *L. a. cussiliris* is given in table 20. The reasons for my considering the population in the Balsas Basin and on the Pacific coast of México north of the Río Balsas, *Leptodeira maculata*, a distinct species are given in the discussion of that form.

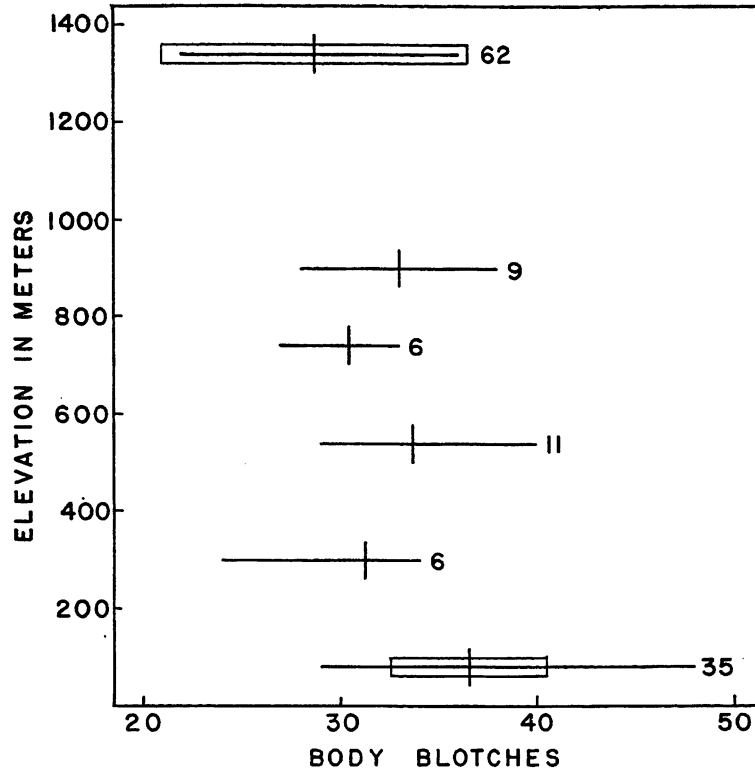


FIG. 5. Altitudinal variation in the number of body blotches in *Leptodeira annulata cussiliris* in Guerrero, México. Vertical line, mean; horizontal line, observed range; box includes one standard deviation on either side of the mean.

TABLE 20

COMPARISON OF POPULATIONS OF *Leptodeira annulata* FROM CHIAPAS AND GUATEMALA  
(Twelve males and seven females from Chiapas and 21 of each sex from Guatemala.)

Character	Sex	Chiapas	Guatemala
Ventrals	♂	166-176 (171.9)	155-173 (165.3)
	♀	168-177 (171.1)	163-177 (168.0)
Caudals	♂	63-75 (69.4)	65-85 (72.1)
	♀	60-66 (63.0)	62-75 (67.8)
Tail/body	♂	0.266-0.301 (0.279)	0.278-0.360 (0.329)
	♀	0.240-0.262 (0.252)	0.260-0.329 (0.284)
Body blotches	♂ + ♀	25-33 (28.8)	23-35 (29.3)
Nape stripe	♂ + ♀	10%	88%
Lateral spots	♂ + ♀	Small	Large
Lateral extent of body blotches	♂ + ♀	Rows 2-4	Rows 3-6

RANGE: The subspecies *cussiliris* ranges in the coastal lowlands and low foothills of the Sierra Madre from southern Tamaulipas, México, southeastward to the Isthmus of Tehuantepec, and thence westward along the Pacific lowlands to the Río Balsas, southeastward along the Pacific coast to southeastern Chiapas, and through the Grijalva Valley of Chiapas. This subspecies apparently is partial to semi-arid conditions; it is not found in areas of tropical rain forest or cloud forest. In the wet forests of southeastern México and in the Yucatán Peninsula it is replaced by another terrestrial species, *frenata*. Altitudinally, the "scaredy-cat-eyed" snake ranges from sea level to about 2000 meters. The highest records are in the southern part of its range in Guerrero and Oaxaca; the highest locality in the northern part is 510 meters at Santa Barbara, Tamaulipas.

The locality records for the 517 specimens examined are:

México: *Chiapas*: Near Asunción, E.H.T.-H.M.S. No. 4642, U.I. No. 17805; Cintalapa, A.M.N.H. No. 71390; Huixtla, A.M.N.H. Nos. 66452-66454; between Ocozacoautla and San Ricardo, E.H.T.-H.M.S. No. 4643; Pijijiapan, A.M.N.H. No. 64575; Rancho San Bartola, U.I. No. 6184; San Ricardo, E.H.T.-H.M.S. Nos. 4644, 4651; Tonolá, E.H.T.-H.M.S. Nos. 4648-4649, U.S.N.M. Nos. 111216-111218, U.I. No. 17804; Tuxtla Gutierrez, M.C.Z. Nos. 54342-54347, M.Z.T.G. Nos. 52-53, 144, 146, 148-149, 152-153, 199, 293, 295, 299, 305-306, U.M.M.Z. No. 114568 (3); 6 miles east of Tuxtla Gutierrez, U.I. No. 6185. *Guerrero*: Acahuitzotla, T.C.W.C. Nos. 9501-9505, 7442, 7446-7447; 1 mile west of Acahuitzotla, T.C.W.C. No. 7443; Acapulco, A.M.N.H. Nos. 66163-66165, L.M.K. Nos. 36271, 36286, 36424, S.U. No. 9478, U.S.N.M. No. 46403; Agua del Obispo, U.S.N.M. No. 111206, U.I. Nos. 17807, 17811; Ayutla, B.M.N.H. No. 1906.6.1.226; Buena Vista, E.H.T.-H.M.S. No. 16151; Chilpancingo, A.M.N.H. Nos. 72483-72484, C.N.H.M. Nos. 38474-38490, M.C.Z. Nos. 33653-33662, M.V.Z. Nos. 45139-45164, U.K. No. 23786, U.M.M.Z. Nos. 85699-85702, 85714, 73934 (3); 4 miles west of Chilpancingo, T.C.W.C. No. 9506; 12 miles south of Chilpancingo, E.H.T.-H.M.S. Nos. 4652-4653; El Limoncito, near Acapulco, E.H.T.-H.M.S. Nos. 16156-16157, 16159, 16162, 16166, 16168-16169, 16174-16175, U.I. Nos. 17812-17822; El Treinte, E.H.T.-H.M.S. Nos. 5183 (2), 5184, U.I. No. 17808; 2 miles north of Garrapatas, E.H.T.-H.M.S. No. 4627, U.I. No. 17800; 2 miles south of Garrapatas, E.H.T.-

H.M.S. Nos. 4634, 4654; Laguna Coyuca, U.S.N.M. Nos. 46344, 111201-111203; 1 mile north of Los Organos, E.H.T.-H.M.S. Nos. 4629, 4655, U.I. Nos. 17801-17802; Morijonaros, 7 kilometers north of Tierra Colorado, U.I. No. 25955; Omilteme, M.C.Z. Nos. 42673-42674; 6.5 miles west of Pie de la Cuesta, U.M.M.Z. No. 104618; Rincón, T.C.W.C. Nos. 7441, 7445; 8 miles south of Tecpan, U.I. No. 25957; 15 miles east of Tecpan, U.M.M.Z. Nos. 104616-104617; Tierra Colorado, A.M.N.H. Nos. 66157-66158, U.S.N.M. Nos. 111204-111205, U.I. Nos. 17791, 25956, 28022; 5 miles southwest of Tierra Colorado, T.C.W.C. No. 7444; near Xaltianguis, U.I. Nos. 17795-17798, 17810. *Hidalgo*: Zacualtipan, A.N.S.P. No. 15774. *Oaxaca*: Arenal, near Tehuantepec, U.I. Nos. 6191-6194; Bisilana, near Tehuantepec, A.M.N.H. Nos. 67988-67989; Caba, Cerro Arenal, A.M.N.H. Nos. 67995-67999; Cerro Arenal, near Tenango, A.M.N.H. Nos. 67990-67993, U.S.N.M. No. 111214; Cerro Calderona, U.I. No. 3786; Cerro Quiengola, U.S.N.M. No. 111215; Cerro Santa Lucia, U.I. No. 3785; 2.5 miles north of Chivela, U.M.M.Z. Nos. 114573-114574; 7.4 miles south of Chivela, U.M.M.Z. No. 114576; Dami Liesa, near Tehuantepec, A.M.N.H. No. 66843; El Palmas, Cerro Atravesado, A.M.N.H. No. 66842; Escuranos, A.M.N.H. No. 65895; between Huilotepec and Tehuantepec, U.M.M.Z. No. 82614; 1 mile west of Humor, U.I. No. 6190; Las Tejas, near Tehuantepec, U.M.M.Z. Nos. 82620-82621, U.I. Nos. 6181-6182; 4 miles south of Matías Romero, U.M.M.Z. Nos. 114570-114572; 20 miles south of Matías Romero, T.C.W.C. Nos. 12587-12589; Mixtequilla, A.M.N.H. No. 19574; Nizabibi, U.I. Nos. 3779-3780; Ocatita, near Tehuantepec, A.M.N.H. No. 65124; Pochutla, U.I. Nos. 6177-6180; between Quiengola and Tehuantepec, U.M.M.Z. Nos. 82618-82619; Rancho Poso Río, 6 kilometers south of Tehuantepec, U.M.M.Z. Nos. 82616-82617; Río Hondo, north of Cerro Quiengola, U.I. No. 27562; Salazar, near Tehuantepec, A.M.N.H. No. 66841; 1.3 miles north of Salina Cruz, U.M.M.Z. No. 114575; San Antonio, near Tehuantepec, A.M.N.H. Nos. 65123, 65893-65894, 67987; San Juan Guichicovi, U.I. No. 17790; Santa María, near Tehuantepec, A.M.N.H. No. 67986; Tapanatepec, M.C.Z. Nos. 27732-27798, U.M.M.Z. No. 84485 (5); Tecuane, U.M.M.Z. Nos. 82622-82623; Tehuantepec, A.M.N.H. Nos. 64594, 64596, 65122, 65938, 66844, 67985, U.S.N.M. Nos. 30306-30307, 30480, 111207-111213, U.I. Nos. 3781-3784; U.M.M.Z. Nos. 82606-82613; 1 mile north of Tehuantepec, U.I. No. 6183; 1 mile east of Tehuantepec, U.I. Nos. 6187-6189; 3.2 miles east of Tehuantepec, U.M.M.Z. No. 114569; 6 miles east of Tehuan-

tepec, U.M.M.Z. No. 112508; 1-2 leagues south-southeast of Tehuantepec, U.M.M.Z. No. 82615; near Totolapam, U.I. Nos. 17792-17794; Zamutepec, U.S.N.M. Nos. 46497-46498; 3.4 miles west-northwest of Zanatepec, U.M.M.Z. No. 114577; 4.5 miles west-northwest of Zanatepec, U.M.M.Z. No. 114578. *Puebla*: San Antonio, Limón, Totalco, U.I. No. 17823. *San Luis Potosí*: El Nacimiento del Coy, L.S.U. No. 4201; El Pujal, C.N.H.M. No. 34272; 3.5 miles west of El Pujal, T.U. No. 16006; El Salto, L.S.U. No. 5381; Huichihuayan, U.S.N.M. Nos. 111219-111220; Los Sabinas, 7 miles north of Valles, A.M.N.H. No. 67000; 3.8 miles north of Matlapa, U.M.M.Z. No. 114429; Palictla, A.M.N.H. Nos. 67311-67313; Rancho Sabinal, L.S.U. No. 4873; Río Axtla, near Axtla, A.M.N.H. Nos. 67334-67335; T.C.W.C. No. 844; 6.3 miles northeast of Sabanito, L.S.U. No. 299; Salto de Agua, T.C.W.C. No. 6975; Tamazunchale, L.M.K. No. 38061, U.I. No. 25954; 2.7 miles east of Tamuín, U.M.M.Z. No. 114428. *Tamaulipas*: Fourteen miles north of Antiguo Morelos, U.I. No. 19282; 1 mile north of Chamal, U.M.M.Z. No. 109740; 1 mile east of Chamal, U.M.M.Z. Nos. 109739, 109741; 5 miles east of Chamal, U.M.M.Z. No. 109730; 6 miles east of Chamal, U.M.M.Z. No. 109731; 4 kilometers northwest of Chamal, T.U. Nos. 15520 (4), 15529; 15 miles north of Ciudad Mante, U.I. No. 3843; 22 miles north of Ciudad Mante, U.I. No. 19283; 29 miles north of Ciudad Mante, T.C.W.C. No. 12582; 8 miles south of Ciudad Mante, T.C.W.C. No. 12583; 5 miles northeast of Gómez Farías, U.M.M.Z. Nos. 104068-104072, 105486, 109733-109734; 12 miles southeast of Gómez Farías, U.M.M.Z. No. 109729; Hacienda La Clementina, near Forlón, E.H.T.-H.M.S. Nos. 4638-4640; La Unión, 9.5 kilometers north of Gómez Farías, T.U. No. 15461; Kilometer 609, north of Limón, U.I. No. 17806; Magiscatzin, T.C.W.C. Nos. 6976, 7003; Río Guayalejo, near Magiscatzin, M.C.Z. Nos. 45560-45562, U.M.M.Z. No. 88241; Santa Barbara, foothills of Sierra de Tamaulipas, U.M.M.Z. Nos. 109735-109738; Tampico, B.M.N.H. Nos. 94.12.28.7-94.12.28.15, 1936.6.6.9; 2 miles southeast of Xicoténcatl, U.M.M.Z. No. 109732. *Veracruz*: Alvarado, U.K. No. 26477; 2 miles southeast of Angel Carbada, U.M.M.Z. No. 114431; 1 mile northwest of Ciudad Alemán, U.M.M.Z. No. 114434; 5 miles southwest of Ciudad Alemán, U.M.M.Z. No. 114433; Cuautlapan, B.C.B. Nos. 2598, 2607; Cuautotlapam, U.M.M.Z. No. 41568; El Chico, 7 miles south-southeast of Jalapa, C.N.H.M. 70748; 4 miles east of Encero, E.H.T.-H.M.S. Nos. 4632, 4635, 4637; Jalacingo, Las Palmillas, A.M.N.H. Nos. 4284-4288; Jalapa, A.N.S.P. No. 10288, M.C.Z. Nos. 16104-16107; 5 miles east of

Jalapa, E.H.T.-H.M.S. No. 4631; 1 mile north of La Laja, U.I. No. 3844; Minatitlan, A.M.N.H. No. 65937; Mirador, U.S.N.M. Nos. 6376, 25040, 61990-61992; Orizaba, U.S.N.M. Nos. 6324, 7095; Paso del Macho, U.M.M.Z. Nos. 85357, 88681; Posa Rica, U.I. Nos. 3845-3846; Potrero, C.N.H.M. No. 25877, M.C.Z. No. 45680, U.M.M.Z. Nos. 85358, 88680 (2), 88684, 89376 (3); Potrero Viejo, E.H.T.-H.M.S. Nos. 16150, 27909, U.S.N.M. Nos. 111195-111197, U.I. No. 17890, U.K. Nos. 26475-26476, U.M.M.Z. Nos. 88682-88683, 89375; Puente Nacional, U.I. No. 21827; 1.8 miles west-northwest of Remundadero, U.M.M.Z. No. 114430; 1.5 miles north of Reventadero, T.U. No. 15981; 5 miles southeast of Rincondada, T.C.W.C. Nos. 12584-12586; 10 miles east of San Juan de la Punta, U.S.N.M. Nos. 111198-111200; 1.4 miles north of San Juan Sugar, U.M.M.Z. No. 114432; 3 miles southwest of San Marcos, U.K. No. 23908; Veracruz, A.M.N.H. No. 19717; west of Veracruz, U.S.N.M. No. 5317; 15 miles west of Veracruz, E.H.T.-H.M.S. No. 5176; Vivero Forestal, A.M.N.H. 19578.

#### *Leptodeira annulata rhombifera* Günther

*Leptodeira rhombifera* GÜNTHER, 1872, Ann. Mag. Nat. Hist., ser. 4, vol. 9, p. 32; 1895, Biologia Centrali-Americana, Reptilia, p. 173, pl. 54, fig. C. DUNN, 1936, (in part), Proc. Natl. Acad. Sci., vol. 22, pp. 693-694. TAYLOR, 1951, Univ. Kansas Sci. Bull., vol. 34, no. 1, p. 126; 1954, *ibid.*, vol. 36, no. 11, pp. 748-750.

*Sibon rhombiferum*, COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 87; 1891, Proc. U. S. Natl. Mus., vol. 14, p. 677; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Sibon septentrionale rubricatum* COPE, 1893, Proc. Amer. Phil. Soc., vol. 31, p. 347.

*Leptodeira ocellata* GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, pp. 172-173; pl. 55, fig. B. BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, pp. 94-95. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amerique Central, vol. 3, pp. 904-905, pl. 73, fig. 6. WERNER, 1924, Arch. Naturgesch., vol. 12, p. 125. TAYLOR, 1951, Univ. Kansas Sci. Bull., vol. 34, no. 1, p. 125; 1954, *ibid.*, vol. 36, no. 1, p. 748.

*Leptodeira rubricata*, TAYLOR, 1951, Univ. Kansas Sci. Bull., vol. 34, no. 1, p. 122.

HOLOTYPE: Number 1946.1.9.92 in the collection of the British Museum (Natural History) from Río Chisoy, near Cubulco, Guatemala; Osbert Salvin collector.

DESCRIPTION: Males with 151-181 (167.6) ventrals; females with 156-177 (169.7); caudals in males 65-89 (78.0) and in females 59-

82 (70.5). Dorsal scales in a maximum of 21, 23, or 25 rows, usually reducing to 17 posteriorly, but sometimes reducing to 15. Dorsal scale reduction in four males from Guatemala:

21 +11 (31-36) - 23 10+11 (92-101) - 21 9+10 (104-110) - 19 8+9 (121-131) - 17 (161-170)

Reduction in five females from Guatemala:

21 +11 (23-48) - 23 10+11 (96-102) - 21 9+10 (107-113) - 19 8+9 (127-135) - 17 (163-173)

Reduction in a female with 25 scale rows (U.M.M.Z. No. 106716):

21  $\frac{+11 (13)}{+11 (13)}$  23  $\frac{+12 (53)}{+12 (51)}$  25  $\frac{11+12 (88)}{11+12 (89)}$   
 23  $\frac{10+11 (100)}{10+11 (100)}$  21  $\frac{9+10 (116)}{9+10 (113)}$  19  $\frac{8+9 (131)}{8+9 (130)}$   
 17 (163)

The dorsal ground color is cream to grayish or yellowish tan. There are 23 to 51 (35.6) rounded, middorsal, dark brown to black blotches on the body. The edges of the blotches are often darker than the middle, and the blotches are usually outlined with a cream color. The blotches are two to five scales in length and may be equal to, or as much as twice the length of, the dorsal light interspaces; the blotches extend laterally onto scale rows 2 to 6. Large, dark, usually squarish, lateral intercalary spots are on scale rows 1 to 3 or 3 to 6. There usually are small dark spots below the lateral edge of the dorsal blotches on scale row 1 and on the edges of the ventrals. The first dorsal blotch may have a straight anterior transverse edge, or it may be U-shaped, with the arms of the U extending anteriorly on the sides of the neck. (See pls. 4 and 5, and pl. 6, fig. 3.) There are 10 to 29 dark tail blotches decreasing in size posteriorly.

The top of the head may be a light or dark brown color. In those that are dark brown it is unmarked; in the others there is usually a dark spot in the middle of each head plate. On the parietals there may be two spots, one long spot, or an inverted V-shaped mark formed by the fusion of the parietal spots with that of the frontal. A dark brown post-orbital stripe begins on the lower postocular and continues posteriorly across the anterior part of the primary temporal, the lower part

of the lower secondary temporal, the tops of the sixth and seventh upper labials, and nearly all of the eighth labial to terminate at the angle of the mouth. In some individuals there is a dark mark from the parietals across the tertiary temporals to the corner of the mouth. A dark nape stripe begins on the posteromedian corners of the parietals and extends posteriorly, usually to connect with the first body blotch. (See pls. 4 and 5.) The labials and ventral surfaces are a cream color; usually the posterior edges of the upper labials are tinted with brown.

Males range from 200 to 515 mm. (355 mm.) in body length and 270 to 790 mm. (470 mm.) in total length; females range from 205 to 630 mm. (395 mm.) and from 264 to 740 mm. (503 mm.). The smallest juvenile is a female with a body length of 138 mm. and a total length of 179 mm. The smallest male has a body length of 151 mm. and a total length of 204 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes occur in the number of caudals and the tail/body ratio. Males average 78.0 caudals; females, 70.5. The tail/body ratio in males ranges from 0.287 to 0.390 (0.340), and in females from 0.233 to 0.378 (0.298).

**VARIATION:** The variation in scutellation in this subspecies is negligible. There is a slight increase in the numbers of caudals and ventrals from Guatemala to Panamá. In males the change is from an average of 165 ventrals and 72 caudals in Guatemala to 170 and 78 in Panamá. The greatest difference in scutellation is in the number of dorsal scale rows; these are always at least in 23 rows and sometimes 25 in Guatemala and Honduras, whereas in Costa Rica and Panamá the majority of the snakes have only 21.

There is a geographical gradient from northwest to southeast in the number of body blotches. (See fig. 6.) A corresponding change in the size of the blotches also takes place; in specimens from Guatemala the blotches extend laterally onto the second or third scale rows. In Panamá the blotches extend only onto the fourth or fifth scale rows. The anterior transverse edge of the first body blotch is straight in Guatemalan specimens; to the southeast towards Panamá there is a clinal tendency for the anterior edge of the blotch to be indented in the middle, accompanied by



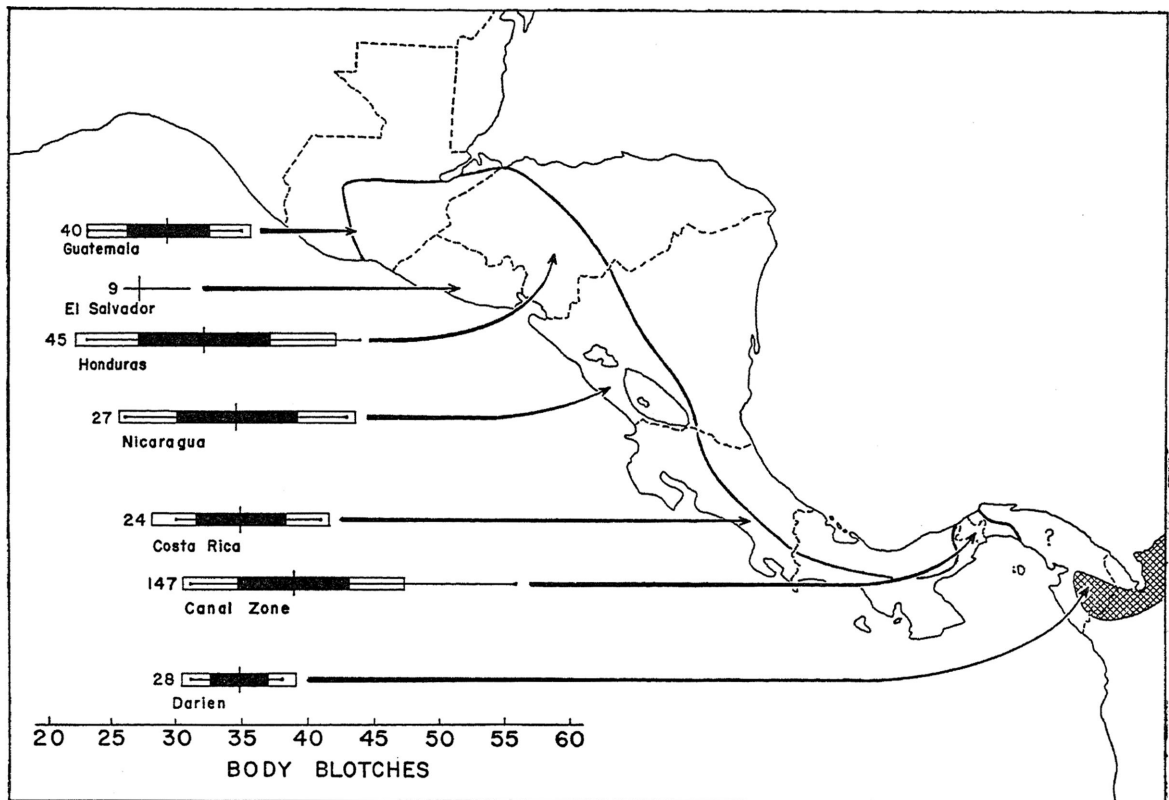


FIG. 6. Geographical variation in the number of body blotches in *Leptodeira annulata rhombifera*. Vertical line, mean; horizontal line, observed range; box includes one and two standard deviations on either side of the mean; the number of specimens in each sample is given. The range of *L. a. rhombifera* is shown by the heavy solid line; the cross-hatched area represents the eastern part of the region of intergradation between *rhombifera* and *ashmeadi*. (Compare with fig. 4.)

a corresponding forward extension of the arms, until, in Panamá, the blotch becomes U-shaped.

Two specimens from Guatemala are significantly different in their color pattern. In both there is an increased number of body blotches. One (U.M.M.Z. No. 107256) has 51 solid dark brown body blotches two or three scales in length and twice the length of the interspaces. At midbody the blotches extend laterally onto the seventh scale row; on scale rows 3 to 6 are large, round, intercalary spots, and on scale rows 1 to 4 below the lateral edges of the dorsal blotches are round brown spots. On the first scale row and on the edges of the ventrals are dark brown flecks. (See pl. 6, fig. 1.) The other (U.M.M.Z. No. 98104) has 44 squarish body blotches of dark chocolate brown color outlined with black. Most of

the blotches are divided medially by a mid-dorsal cream stripe. The blotches are three to four scales in length; the interspaces, one scale. At midbody the blotches extend onto the sixth scale row. On scale rows 2 to 4 are squarish intercalary spots. Small, irregular, dark spots are aligned on the edges of the ventrals and on the first scale row. (See pl. 6, fig. 2.) I believe that these specimens merely show an extreme condition of pattern variation and do not represent specific entities.

Five Guatemalan specimens (one from Finca la Trinidad, one from Lago de Amatitlan, and three from Esquipulas) have no nape stripe; in this respect they show affinities to *L. a. cussiliris* in México. (See table 20.) Specimens from Darien, Panamá, often have the first dorsal body blotch almost completely

divided along the midline and not connected with the dark nape stripe. In this respect they show affinities towards the northern South American populations of *annulata*.

REMARKS: The type of *L. rhombifera* is from Cubulco, Guatemala. From the description given by Günther in 1872 and the specimen illustrated in 1895, I believe that this is the correct name for the population of *annulata* in northern Central America. The name *ocellata* was applied to specimens of *annulata* from Nicaragua and Costa Rica. The description and illustration (Günther, 1895) are of a snake with slightly more body blotches than in Guatemalan *rhombifera*. Also, the somewhat U-shaped first body blotch is visible. If the southern Central American population can be shown to warrant a name, *ocellata* is applicable. The type of *L. rubricata* Cope (A.M.N.H. No. 17367, from Boca Mala, Costa Rica) is an unusual variant of *L. a. rhombifera*. It is normal in its scutellation. The ground color is cream-brown; the blotches are black and number 50. The dorsal head coloration consists of a faint, X-shaped mark on the frontal and a U-shaped mark on the parietals. The latter is connected to the first body blotch by the nape stripe.

Specimens from northern Colombia and from Darien, Panamá, are intermediate between *rhombifera* and *ashmeadi*. The two wide longitudinal nape bars in *ashmeadi* apparently represent the lateral parts and the forward arms of the first body blotch as found in lower Central American *rhombifera*. The complete division of the first blotch is accompanied by the loss of the nape stripe. Individuals that have a nearly divided blotch and a nape stripe are here considered to be intergrades between *rhombifera* and *ashmeadi*.

RANGE: *Leptodeira annulata rhombifera* ranges from central and southeastern Guatemala east and south in xeric habitats to Panamá. In lower Central America the species occurs on the central plateaus and the arid Pacific coast; it is found throughout the Panama Canal Zone. Its range extends eastward in Panamá along the Pacific coast to the Río Chepo; then there is a break in the distribution to the interior valleys of Darien. The subspecies also occurs on the islands of the Archipiélago de las Perlas in the Golfo de Panamá. Records for this form from along

the Caribbean coast of Central America are from ports and are of questionable validity. (See map 2.) The subspecies has been found from sea level to elevations of about 1000 meters.

The locality records for the 368 specimens examined are:

COSTA RICA: No specific locality, M.C.Z. No. 15331, U.K. Nos. 34015, 34018-34019; San Antonio de Bellina, M.C.Z. Nos. 31779-31780. *Guanacaste*: Bebedero, N.M.W. No. 14406 (5); Cañas, A.N.S.P. No. 22372; Las Huecas, U.M.M.Z. No. 71202; Tenorio, U.K. Nos. 34020-34023. *Limón*: Colorado, A.M.N.H. Nos. 12685-12686. *Puntarenas*: Barranca, Finca San Miguel, C.N.H.M. Nos. 37229-37230, 61140; Boca Mala, A.M.N.H. No. 17367; Miramar, U.S.N.M. No. 75037; mouth of Río Barranca, U.K. Nos. 34016-34017. Palmar, U.K. Nos. 34012-34014. *San José*: San Isidro del General, M.V.Z. No. 36452; San José, A.M.N.H. No. 17344.

EL SALVADOR: *San Salvador*: San Salvador, A.N.S.P. Nos. 10102-10103, C.N.H.M. Nos. 64957-64963; 6 miles east of San Salvador, U.K. No. 41544.

GUATEMALA: No specific locality, C.N.H.M. No. 194. *Amatitlan*: Lago Amatitlan, U.M.M.Z. No. 79061. *Baja Verapaz*: Salamá, C.N.H.M. Nos. 20664-20665. *Chiquimula*: Esquipulas, U.M.M.Z. Nos. 106715, 106716 (3). *Escuintla*: U.S.N.M. No. 12692; Río Guacalate near Masagua, U.S.N.M. No. 125238. *Guatemala*: Near Guatemala, M.C.Z. Nos. 49641-49643. *Izabel*: Los Amates, U.M.M.Z. No. 56425. *Jutiapa*: Finca El Carnero, 7 miles west of Jutiapa, C.N.H.M. Nos. 68613-68614, 69113; Finca La Trinidad, U.M.M.Z. Nos. 107253-107260; Jutiapa, U.M.M.Z. Nos. 98104, 98105; 1 mile southeast of Monogoy, U.K. No. 41548. *Progreso*: Finca Los Leones, U.M.M.Z. No. 106717. *Sacatepequez*: Lago San Antonio, near Dueñas, M.C.Z. No. 49640. *Santa Rosa*: Finca La Cachuito, U.M.M.Z. No. 107079; Finca La Gloria, U.M.M.Z. No. 106718; Finca Las Sabanetas, M.C.Z. Nos. 31930-31933; Lago Ayarza, U.S.N.M. Nos. 125341-125348. *Zacapa*: Zacapa, U.S.N.M. No. 123662.

HONDURAS: No specific locality, A.N.S.P. Nos. 10218-10219, U.S.N.M. No. 25858; Sonora Farm, M.C.Z. Nos. 20486-20489. *Colon*: Patuca (? = Río Patuca), U.S.N.M. Nos. 20277-20281. *Copan*: Copan, U.M.M.Z. Nos. 83039-83040. *Cortez*: Agua Azul, A.M.N.H. Nos. 70250-70252, 70626, M.C.Z. Nos. 49970-49973; Río Chameleon, U.S.N.M. No. 128099; Río Lindo, A.M.N.H. No. 70249; San Pedro Sula, M.C.Z. No. 27253; U.M.M.Z. Nos. 68696, 70786. *Francisco Morazon*:

El Zamorano, A.M.N.H. Nos. 70199-70200; Montaña de Guaimaca, A.M.N.H. Nos. 70254; Tegucigalpa, M.C.Z. Nos. 49827-49835, 49988. Yoro: Subirana Valley, C.N.H.M. No. 21778, M.C.Z. Nos. 38753-38755.

NICARAGUA: No specific locality, U.S.N.M. Nos. 16109-16116, 20679-20681. *Esteli*: Esteli, U.S.N.M. No. 89477. *Granada*: Volcan Mombacho, U.C.L.A. No. 6161. *Leon*: Polvón, M.C.Z. Nos. 3803, 5655, 5718. *Nueva Segovia*: El Cororo, 12 kilometers northeast of Jalapa, U.C.L.A. No. 7471. *Managua*: Managua, U.S.N.M. No. 79973. *Río San Juan*: Río San Juan, A.N.S.P. No. 10209; San Juan del Norte (Greytown), B.M.N.H. No. 1900.9.21.3, U.S.N.M. Nos. 15631-15632, 24479, 32227; San Carlos, U.S.N.M. No. 19560. *Rivas*: Three miles southeast of San Pablo, U.K. Nos. 41545-41547. *Zelaya*: Huaunta, A.N.S.P. Nos. 15445-15447.

PANAMÁ: *Archipiélago de las Perlas*: Isla San José, U.S.N.M. No. 120676-120678. *Canal Zone*: Agua Clara, A.N.S.P. No. 25713, M.C.Z. Nos. 45369-45370; Albrook Field, M.C.Z. No. 33889; Ancon, M.C.Z. Nos. 16333-16336, 23893; Balboa, A.M.N.H. No. 36171, M.C.Z. No. 23890, U.S.N.M. No. 102879, U.M.M.Z. No. 64336; Barro Colorado, A.N.S.P. No. 22880; Bella Vista, M.C.Z. No. 23892; Coco Sole, U.S.N.M. No. 65863; Corozal, C.N.H.M. No. 6114, M.C.Z. Nos. 18846, 22266, 26774; Corozal Road, M.C.Z. Nos. 23899-23900; Cristobal, A.N.S.P. Nos. 10216, 22817; Culebra, M.C.Z. No. 23888, U.M.M.Z. No. 61292; Darien, M.C.Z. No. 2703 (2), U.S.N.M. No. 51968; Empire, C.N.H.M. No. 16750, U.S.N.M. No. 60027; Fort Clayton, M.C.Z. Nos. 20562, 22271-22272, 26775, U.S.N.M. Nos. 65849-65852; Fort Davis, C.M. Nos. 22966, 22972, M.C.Z. Nos. 22247-22251, U.S.N.M. Nos. 65853-65854; Fort Randolph, M.C.Z. Nos. 20559-20561, U.S.N.M. Nos. 65859-65861; France Field, M.C.Z. Nos. 18847, 37889, U.S.N.M. Nos. 65873-65874; Frijoles, C.N.H.M. No. 6114, M.C.Z. Nos. 17617, 23896; Gamboa, A.M.N.H. No. 71679, M.C.Z. Nos. 23895, 23973, U.M.M.Z. 95490; Gatun, C.N.H.M. Nos. 16747-16749, M.C.Z. Nos. 18825, 23894, U.S.N.M. No. 54078; Juan Mina, A.M.N.H. No. 71678, M.C.Z. Nos. 24950-24951, 26634-26635; La Joya, A.N.S.P. No. 25077; La Venta, U.S.N.M. No. 103482; Madden Dam, M.C.Z. Nos. 39747-39748, 45368; Madden Highway, A.N.S.P. No. 24760; Miraflores, M.C.Z. Nos. 23930-23934; Monté Lirio, M.C.Z. No. 23897; Naval Ammunition Depot, C.N.H.M. No. 57613; Obispo Station, M.C.Z. Nos. 2714, 2716; Paraiso, M.C.Z. Nos. 23905-23908, U.M.M.Z. No. 64335; Pedro Miguel, M.C.Z. Nos. 23909-23910, U.M.M.Z. Nos. 64334, 64355; Punta Bruja, M.C.Z. No. 25110; Red Tank, M.C.Z. No. 23898;

Río Chagres, A.N.S.P. No. 22295, U.M.M.Z. No. 76718 (2); Río Juan Franco, M.C.Z. Nos. 23886-23887; San Pablo Station, M.C.Z. No. 3939. *Chiriqui*: Boquete, U.M.M.Z. No. 57954. *Cocle*: U.M.M.Z. Nos. 83521-83522; Chitre, C.N.H.M. No. 68084; Río Santa María, M.C.Z. No. 24283. *Colon*: Nombre de Dios, M.C.Z. No. 24926; Puerto Pilón, A.N.S.P. Nos. 25709-25712. *Herrera*: Parita Province, U.S.N.M. Nos. 127303-127304. *Los Santos*: U.S.N.M. Nos. 51913-51914. *Panamá*: Alhajuela, M.C.Z. No. 31460, U.S.N.M. No. 48957; Chepo, N.M.W. No. 14402 (4); Gatuncillo, M.C.Z. No. 25125; Isla Gorgona, M.C.Z. No. 6990; Juan Díaz, C.N.H.M. No. 68082; mouth of Río Pequeni, M.C.Z. Nos. 37102-37104; Pacora District, M.C.Z. Nos. 42821-42829; Panamá, A.N.S.P. No. 22599, M.C.Z. Nos. 7298 (2), 17616, 23901-23902, 31548, 32050-32051, U.S.N.M. Nos. 52492-52493, 65871, U.M.M.Z. No. 86201 (7); Panamá Vieja, A.M.N.H. Nos. 67054, 71676-71677; Punta Paitilla, M.C.Z. No. 51802; Río Abajo, C.N.H.M. No. 68083, M.C.Z. No. 23891; Sabañas, A.N.S.P. Nos. 23898-23899, 24715-24716, 24754, M.C.Z. Nos. 45360-45363, U.M.M.Z. Nos. 83158 (8), 83169 (8); Sabañas-Pacora area, M.C.Z. Nos. 39763-39769; Sabanita, A.M.N.H. No. 67062; Salomas, U.M.M.Z. No. 76712 (4).

Locality records for 72 specimens considered to be intergrades between *L. a. rhombifera* and *ashmeadi* are:

PANAMÁ: *Darien*: A.M.N.H. Nos. 36191, 36193-36195, 36198, 36202, 36204; Cana, A.N.S.P. Nos. 22300-22301, 23873; El Real de Santa María, M.C.Z. Nos. 31555-31557, S.U. No. 12477, U.M.M.Z. No. 76705 (3); Pinogana, A.N.S.P. No. 24758; Río Aruza, U.S.N.M. No. 54227; Yavissa, M.C.Z. Nos. 37864-37886, 42743-42746, 51803-51805, U.M.M.Z. No. 113031 (3); fork of Río Pihuila and Río Jucuti, M.C.Z. Nos. 51806-51809. COLOMBIA: *Antioquia*: Turbo, M.C.Z. No. 2700. *Atlántico*: Barranquilla, D.Z. Nos. 2117, 2136; Guaimaral, U.S.N.M. No. 117504; Villanueva, U.S.N.M. No. 117508. *Bolívar*: Arjona, U.S.N.M. No. 61673; Isla Fuerte, C.N.H.M. Nos. 74926-74933. *Chocó*: Río Atrato, Sautata, C.N.H.M. Nos. 74904-74905. *Cundinamarca*: ? Honda, B.M.N.H. 1909.7.23.27. *Magdalena*: Bolívar, U.M.M.Z. No. 54942; Bonda, C.M. Nos. 191-192, 194, 205, M.C.Z. No. 11858; Cacagnalito, C.M. No. 2023; Ciénega, A.M.N.H. No. 20396; Fundación, U.M.M.Z. Nos. 45598-45604; Río Frio, M.C.Z. Nos. 25054, 32761-32763.

*Leptodeira annulata ashmeadi* Hallowell

*Coluber ashmeadii* HALLOWELL, 1845, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, p. 244.

*Leptodeira annulata*, BARBOUR, 1916, Proc.

Biol. Soc. Washington, vol. 29, p. 224.

*Leptodeira albofusca*, RUTHVEN, 1922, Misc. Publ. Univ. Michigan Mus. Zool., no. 8, p. 67.

*Leptodeira rhombifera*, DUNN, 1944, *Caldasia*, vol. 3, no. 12, p. 207.

*Leptodeira rhombifera kugleri* SHREVE, 1947, Bull. Mus. Comp. Zoöl., vol. 99, no. 5, pp. 531-532.

*Leptodeira annulata annulata*, MARCUZZI, 1950, *Novedades Cien., zool. ser.*, vol. 3, p. 12. ROZE, 1952, *Acta Biol. Venezuelica*, vol. 1, no. 5, pp. 105-107; 1953, *Bol. Soc. Venezuela Cien. Nat.*, vol. 14, no. 79, p. 208.

**HOLOTYPE:** Although Hallowell did not designate a type specimen, there are five specimens of this snake in the collection of the Academy of Natural Sciences of Philadelphia (Nos. 10090-10094) collected within 200 miles of Caracas, Venezuela, by Samuel Ashmead. Of the five specimens, No. 10093 best fits the description given by Hallowell. There is only one discrepancy; the specimen has 93 caudals, whereas the description lists 113. This number certainly is in error, for no *Leptodeira* has that many caudals. Therefore, I here designate A.N.S.P. No. 10093 as lectotype and restrict the type locality to the vicinity of Caracas, Distrito Federal, Venezuela. I am indebted to Dr. Janis A. Roze of Caracas who called my attention to the identity of this name.

**DESCRIPTION:** Ventrals in males 174-192 (181.6), in females 171-194 (181.5); caudals in males 79-98 (88.7), in females 71-90 (80.6). Maximum number of dorsal scale rows at midbody 21 in 48 specimens, 23 in one, and 19 in 19. Dorsal-scale reduction in five males:

19 +10 (14-35) - 21 9+10 (104-119) - 19 8+9 (118-135) - 17 7+8, or 8+V (147-175) - 15 (182-192)

One female has the following scale-reduction formula:

19 +10 (25) - 21 9+10 (116-114) - 19 8+9 (126)-17 (162) - 15 (190)

The dorsal color pattern consists of 29-51 (38.9) dark brown body blotches outlined with a darker brown or black. The blotches are three to four scales in length, twice the length of the interspaces of cream color or light tan ground color. At midbody the

blotches extend laterally onto scale rows 4 to 6. Dark brown, lateral, intercalary spots are present on scale rows 2 to 4; these spots usually are no more than two scales in length. There may be small dark spots indistinctly arranged in a row on scale rows 1 and 2. (See pl. 7.) The dorsal blotches sometimes alternate, one lateral half being offset anteriorly or posteriorly from the other half; occasionally the blotches are interconnected, but not so as to form a long, continuous, zigzag band. There are 10 to 25 dorsal tail blotches, which become smaller towards the tip of the tail. The venter is an immaculate cream color.

The first body blotch is divided along the midline by a stripe of ground color. In some individuals the separation is not complete, so that either the posterior or the anterior end of the blotch, or both, may be in contact. This blotch extends anteriorly on the nape to the postparietals or the posterior edge of the parietals. The dorsal surface of the head is light brown, with irregular dark brown spots on the prefrontals, frontal, and parietals. These spots may be small and scattered or may be larger and centered in the middle of each plate. There may be a dark brown stripe along the lateral edge of the parietal and connecting with the nape blotches on the posteromedian border of the parietal. There is a dark brown preorbital stripe from the nostril across the loreal to the orbit and a postorbital stripe that begins on the postoculars and passes over the lower part of the primary temporal, upper posterior corner of the sixth upper labial, top of the seventh, and middle of the eighth. The stripe may terminate on the eighth upper labial or continue posteriorly for a short distance on the third scale row. The labials are a cream color; the posterior edges of the upper labials are light brown. (See pl. 7.)

Males range from 295 to 525 mm. (410 mm.) in body length and from 390 to 693 mm. (542 mm.) in total length; females range from 265 to 615 mm. (462 mm.) in body length and from 355 to 797 mm. (577 mm.) in total length. The smallest juvenile available is a female with a body length of 158 mm. and a total length of 213 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals, the relation of tail length to body length, and

in the number of blotches on the tail. Males have 79-98 (88.7) caudals; females, 71-90 (80.6). Tail/body ratio in males is 0.307-0.417 (0.360) and in females 0.275-0.375 (0.321). Males have an average of 21.1 tail blotches; females, 18.2.

VARIATION: There are minor differences between the various populations studied. Specimens from Trinidad have slightly fewer ventrals and caudals than the mainland specimens. Those from Colombia have lower ventral and caudal counts, and there is a

slight trend for an increase in the number of these scutes from west to east; however, lack of material from western Venezuela prohibits any definite conclusions at this time. Males from the Orinoco Basin have a low number of caudals; the decrease from the more northern specimens is much greater in the males than in the females. Geographical variation in this race is summarized in table 21.

Individuals from Trinidad are smaller than those from the mainland. Males from the

TABLE 21  
GEOGRAPHICAL VARIATION IN FOUR CHARACTERS IN *Leptodeira annulata ashmeadi*

Character and Sex	Northeastern Colombia	North-central Venezuela	Orinoco Basin	Paria Peninsula	Trinidad	Isla de Margarita
<b>Ventrals</b>						
<b>Males</b>						
<i>N</i>	(2)	(13)	(7)		(12)	(1)
<i>M</i>	177.0	184.2	182.3	—	179.8	175
<i>O.R.</i>	175-179	177-192	177-186		174-189	175
<b>Females</b>						
<i>N</i>		(9)	(3)	(5)	(13)	(1)
<i>M</i>	—	182.7	182.0	185.8	178.9	180
<i>O.R.</i>		173-186	179-187	177-194	171-186	180
<b>Caudals</b>						
<b>Males</b>						
<i>N</i>	(2)	(9)	(6)		(9)	(1)
<i>M</i>	86.5	92.6	83.0	—	89.4	87
<i>O.R.</i>	81-92	87-98	79-86		85-89	87
<b>Females</b>						
<i>N</i>		(6)	(3)	(2)	(8)	(1)
<i>M</i>	—	79-7	77.0	84.0	82.6	74
<i>O.R.</i>		71-86	74-82	82-86	76-90	74
<b>Tail/body</b>						
<b>Males</b>						
<i>N</i>	(2)	(8)	(5)		(9)	(1)
<i>M</i>	0.384	0.370	0.335	—	0.369	0.370
<i>O.R.</i>	0.383-0.385	0.346-0.417	0.326-0.346		0.320-0.394	0.370
<b>Females</b>						
<i>N</i>		(7)	(2)	(2)	(9)	(1)
<i>M</i>	—	0.312	0.291	0.330	0.335	0.280
<i>O.R.</i>		0.275-0.343	0.280-0.301	0.328-0.332	0.321-0.355	0.280
<b>Body length</b>						
<b>Males</b>						
<i>N</i>	(1)	(11)	(6)		(10)	(1)
<i>M</i>	350	443	418	—	355	405
<i>O.R.</i>	350	285-525	383-460		295-435	405
<b>Females</b>						
<i>N</i>		(10)	(2)	(5)	(12)	(1)
<i>M</i>	—	511	425	532	392	445
<i>O.R.</i>		402-603	375-475	355-640	265-462	445

mainland average 88 mm. longer in body length; females, 119 mm. The two individuals from Isla de Margarita are only slightly smaller than the means for the mainland specimens.

REMARKS: In comparison with the series from Venezuela, specimens from west of the Sierra Santa Marta in northern Colombia have slightly fewer ventrals, caudals, and body blotches, and a relatively shorter tail. Furthermore, the nape blotch usually is not completely divided as is typical of *ashmeadi*, and there is often a nape stripe. The males have 173–188 (179.4) ventrals and 81–100 (87.4) caudals; females have 174–187 (180.8) ventrals and 74–85 (78.9) caudals. The tail/body ratio in males ranges from 0.341 to 0.402 (0.366) and in females from 0.275 to 0.360 (0.314). The number of body blotches varies from 29 to 53 (38.5). Usually the blotches extend farther laterally than in the Venezuelan and Trinidad populations of *ashmeadi*. As stated in the discussion of the subspecies *rhomgifera*, the population in northwestern Colombia, together with that in Darien, Panamá, is intermediate between *L. a. rhomgifera* in Panamá and *L. a. ashmeadi* in Venezuela.

One specimen from the vicinity of Honda on the Río Magdalena, Colombia (B.M.N.H. No. 1909.7.23.27), is tentatively referred to this race. The specimen is a male with 180 ventrals, 73 caudals, and 54 body blotches that are three times the length of the interspaces. It is from beyond the geographical range of other South American *annulata*. However, little material is available from Colombia, and it is possible that the species does range southward in the north-south inter-Andean valleys.

The population in northern British Guiana is here considered to be intermediate between *ashmeadi* in Venezuela and Colombia and typical *annulata* to the south and east. This is the connecting link between the populations formerly considered to be distinct species. Of the 50 specimens examined from British Guiana, 40 have 21 scale rows, one has 23, and nine have 19. Usually there are two preoculars, sometimes one; normally labials 4 and 5 enter the orbit. Males have 179–199 (189.4) ventrals and 77–100 (88.6) caudals; females

have 177–192 (186.6) ventrals and 70–93 (81.6) caudals. The tail/body ratio in males ranges from 0.298 to 0.376 (0.347); in females, from 0.268 to 0.350 (0.308). The body is rounded or only slightly compressed; usually the vertebral scale row is not enlarged. The dorsal ground color is tan to light grayish brown. There are 31 to 52 (41.1) dorsal body blotches that are brown to black, three to five scales in length, twice or nearly equal to the length of the dorsal interspaces, and extending laterally to scale rows 4 to 6. Some individuals have no lateral intercalary spots; most have the spots on rows 3 and 4, and sometimes small spots on rows 1 and 2. The top of the head is grayish brown, unmarked or with scattered dark brown flecks. The first body blotch may be longitudinally divided along the midline, with arms extending nearly to the parietals. In those in which the first body blotch is not divided there may be a short nape stripe. In some individuals there is a wide brown spot on the posterior edge of the parietals and adjacent postparietals. The labials are a cream or tan color; often their posterior edges are brown.

The intermediate status of this population is most clearly shown by the color pattern of the nape. Some specimens have a light, unmarked nape typical of *annulata*; others have the two longitudinal nape bars characteristic of *ashmeadi*; whereas in some individuals the intermediate condition, a single nape stripe, is present.

*Leptodeira rhomgifera kugleri* described by Shreve (1947) from Riecito, Departamento Falcón, Venezuela, is an absolute synonym of *L. annulata ashmeadi*.

RANGE: *Leptodeira annulata ashmeadi* is known from northeastern Colombia (east of the Sierra Santa Marta) eastward through northern Venezuela in mountain valleys and along the Caribbean coast, southward to the Río Orinoco. This race also occurs on the islands of Tobago and Trinidad, British West Indies, and Isla de Margarita, Venezuela. (See map 3.) The subspecies has been collected from stations situated near sea level to 1000 meters. Apparently it is distributed along the dry Caribbean coast and in the valleys of Caracas and Valencia in the Cordillera Central in Venezuela. Although it inhabits

the semi-arid coastal regions, it also lives in the Orinoco llanos, an area of alternating extremes of wet and dry seasons.

The locality records for the 74 specimens examined are:

COLOMBIA: *Magdalena*: Río Barbacoa, U.M.M.Z. No. 54944; Río Rancheria, Fonseca, U.M.M.Z. No. 54943.

VENEZUELA: *Aragua*: Maracay, U.M.M.Z. No. 56902. *Bolívar*: Ciudad Bolívar, U.S.N.M. No. 56005; Río Orinoco below Ciudad Bolívar, M.C.Z. No. 38531. *Carabobo*: Borburata, M.B.U.C.V.; Milagro, M.B.U.C.V. *Delta Amacuro*: Manoa, N.M.W. No. 14401 (2). *Distrito Federal*: Camurí Chico, M.B.U.C.V. (2); Caracas, A.N.S.P. Nos. 10090-10094, 10104, B.M.N.H. Nos. 51.7.17.134, 51.7.17.140, S.N.M. No. 19798, U.S.N.M. No. 55333; El Valle, A.M.N.H. No. 59417; Naiguata, Los Canales, C.M. No. 22777. *Falcón*: Riecito, M.C.Z. Nos. 49044, 49046, U.M.M.Z. No. 111307. *Gudricó*: Espino, M.B.U.C.V. (6); Sosa, M.B.U.C.V., S.U. No. 16302. *Merida*: Merida, Z.M.B. No. 25920. *Miranda*: Cumaya, M.B.U.C.V.; Los Chorros, M.B.U.C.V.; Miranda, A.M.N.H. Nos. 59453, 73928-73929; Santa Lucia, C.M. No. 7465. *Monagas*: Caicara, A.M.N.H. No. 38092; Caripito, M.B.U.C.V. *Nueva Esparta*: Isla de Margarita, C.N.H.M. 2677 (2). *Sucre*: Cumanacoa, La Florida, C.M. Nos. 7890, 7939; Guira, M.C.Z. No. 43889. *Yaracuy*: Nirgua, M.B.U.C.V.

BRITISH WEST INDIES: *Tobago*: (Barbour, 1916). *Trinidad*: A.M.N.H. No. 73190, C.N.H.M. 49967, M.C.Z. 6150, S.U. 12509; Brickfield, C.N.H.M. 49965; Cedros, A.M.N.H. Nos. 73104-73105; Churchill-Roosevelt Highway, A.M.N.H. 73112; Freeman Road, A.M.N.H. No. 73111; Mayaro, A.M.N.H., No. 73110, U.F. No. 3629; Mount Saint Benedict, C.M. Nos. 8014-8015; Port of Spain, U.F. No. 3630; San Raphael, C.N.H.M. No. 49966; Saint Augustine, A.M.N.H. No. 73108; Saint Joseph, A.M.N.H. No. 73107; south coast, S.N.M. No. 19785; Tucker Valley, A.M.N.H. Nos. 64476 (5), 74539.

Locality records for 50 specimens considered to be intergrades between *L. a. ashmeadi* and *L. a. annulata* are:

BRITISH GUIANA: Aremu River, U.M.M.Z. No. 56429; 5-8 miles from Bartica, M.C.Z. No. 39975; Demerara, B.M.N.H. Nos. 1929.7.13.30-1929.7.-13.32; Demerara River, U.M.M.Z. Nos. 53897-53899, 53917, 53920, 53929-53931, 53973; Georgetown, B.M.N.H. No. 1931.3.26.1, U.M.M.Z. No. 82864; Ishearton, A.M.N.H. Nos. 60784-60787; Kartabo, A.M.N.H. Nos. 14253, 18155-18157, 21282, 67879-67880, C.N.H.M. Nos. 14843-

14845; Kulacoon, A.M.N.H. Nos. 8093, 8163; Kurupung, U.M.M.Z. No. 83615; Kuyuwini River, A.M.N.H. No. 60780; Lama Creek, Demerara River, A.M.N.H. No. 36111, Mackenzie, B.M.N.H. No. 1934.11.1.134; Parabam, A.M.N.H. Nos. 60802, 60818-60819; Wismar, A.M.N.H. No. 61558, U.M.M.Z. Nos. 76694 (3), 77503 (3), 77525, 80420.

#### *Leptodeira annulata annulata* Linnaeus

*Coluber annulatus* LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 224. DAUDIN, 1803, *Histoire naturelle . . . des reptiles*, vol. 6, pp. 369-373. LATREILLE, 1830, in Sonnini and Latreille, *Histoire naturelle des reptiles*, vol. 4, pp. 127-128.

*Coluber albofuscus* LACÉPÈDE, 1789, *Histoire naturelle . . . des serpens*, vol. 2, pp. 94, 312.

*Dipsas annulata*, DUMÉRIL AND BIBRON, 1854, *Erpetologie générale*, vol. 7, pt. 2, pp. 1141-1146.

*Leptodeira annulata*, FITZINGER, 1843, *Systema reptilium*, vol. 1, p. 27. GÜNTHER, 1858, *Catalogue of the colubrine snakes in the . . . British Museum*, pp. 166-167. BOULENGER, 1896, *Catalogue of the snakes in the British Museum*, vol. 3, pp. 97-98. GRIFFIN, 1917, *Ann. Carnegie Mus.*, vol. 11, pp. 321-326. WERNER, 1924, *Arch. Naturgesch.*, vol. 12, p. 126.

*Eteirodipsas annulata* var. *rhomboidalis* JAN, 1863, *Elenco sistematico degli ofidi*, p. 105.

*Dipsas approximans* GÜNTHER, 1872, *Ann. Mag. Nat. Hist.*, ser. 4, vol. 9, pp. 32-33.

*Eteirodipsas wieneri* SAUVAGE, 1884, *Bull. Soc. Philom. Paris*, ser. 7, vol. 8, p. 146.

*Sibon annulatum*, COPE, 1891, *Proc. U. S. Natl. Mus.*, no. 14, p. 677; 1900, *Rept. U. S. Natl. Mus.*, for 1898, p. 1107.

*Leptodeira albofusca*, BOULENGER, 1896, *Catalogue of the snakes in the British Museum*, vol. 3, pp. 95-97. WERNER, 1924, *Arch. Naturgesch.*, vol. 12, p. 125.

*Leptodeira nycthemera* WERNER, 1901, *Verhandl. Zool.-Bot. Gesell. Wien*, for 1901, pp. 598-599; 1924, *Arch. Naturgesch.*, vol. 12, p. 125.

*Leptodeira annulata annulata*, AMARAL, 1929, (in part), *Mem. Inst. Butantan*, vol. 4, p. 78. DUNN, 1936, *Proc. Natl. Acad. Sci.*, vol. 22, pp. 692-693.

HOLOTYPE: Number 9 in the Zoologiska Institutionen Uppsala. Dr. Hyddmark has provided me with the scale counts of the type specimen. It is a male with 190 ventrals, 98 caudals, 19 scale rows at midbody, and one and two preoculars. Through the courtesy of Dr. L. M. Klauber I have been able to examine copies of a figure of this specimen published by Linnaeus in 1754. The coloration,

as well as the scutellation, agrees with that of the subspecies of *annulata* found in the Amazon Basin. This specimen was part of a collection belonging to Adolf Frederick, King of Sweden; there is no record of a locality. Because the specimen agrees well with those found in the lower Amazon Basin, I propose that the type locality be restricted to the lower Rio Amazon, Pará, Brazil.

**DESCRIPTION:** Preoculars usually one, sometimes two; upper labials 3, 4, and 5 or 4 and 5 in orbit. Males with 180–200 (189.0) ventrals, and females with 174–199 (186.0); caudals in males 74–102 (94.0) and in females 72–100 (84.1). Body laterally compressed; vertebral and paravertebral scale rows noticeably enlarged. Dorsal scales usually in a maximum of 19 rows, rarely 21 or 17, and reducing posteriorly to 15 or 13, rarely 17 or 11. Dorsal scale reduction in six males:

*19* 8+9, or 9+V (115–131) – *17* 7+8, or 8+V (129–165) – *15* (185–194)

Reduction in six females:

*19* 8+9, or 9+V (111–127) – *17* 7+8, or 8+V (122–155) – *15* (185–193)

The dorsal ground color varies from cream-tan to gray-brown. There are from 25 to 50 (33.4) chocolate brown, saddle-shaped body blotches that are four or five scales in length, three to four times the length of the middorsal interspaces, extending laterally onto scale rows 5 to 7. Sometimes the dorsal blotches are interconnected and form a zigzag stripe down the back. In a few individuals the zigzag band may be straight and narrow, giving the appearance of a dark brown middorsal stripe. Lateral intercalary spots are absent or exist only as darkened scale borders on rows 1 to 3. There are 10 to 21 (15.4) dark brown tail blotches; the ventral surfaces are an immaculate cream color. (See pls. 8 and 9.)

The color of the top of the head varies from a light brown to a dull grayish brown. It is usually unmarked, but sometimes there is a faint stripe along the lateral edge of each parietal. In a few individuals there is an indistinct dark stripe on each side of the neck diverging from the posterior edge of the parietals, sometimes extending posteriorly to the first body blotch. A dark brown post-orbital stripe begins on the postoculars and extends posteriorly across the anterior part

of the primary temporal, the bottom of the lower secondary temporal, and the top of upper labials 6 and 7, to terminate on the posteroventral corner of upper labial 8. The labials are cream, their posterior edges tinted with brown. (See pl. 8.)

The juveniles have a striking coloration. The nape region from the posterior edge of the parietals and including the temporals to the first body blotch is a pure, glossy white. With age the white color fades so that in the adults the area is much the same as the ground color. Juveniles often have a lighter ground color than do the adults from the same locality. (See pl. 9.)

Males range from 250 to 601 mm. (459 mm.) in body length and from 342 to 838 mm. (623 mm.) in total length; females range from 275 to 660 mm. (482 mm.) in body length and from 362 to 870 mm. (636 mm.) in total length. The smallest juvenile examined is a female with a body length of 159 mm. and a total length of 210 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in three characters involving the tail. Males average 94.0 caudals; females average 84.1. The tail/body ratio in males is 0.293–0.416 (0.370) and in females 0.263–0.384 (0.328). There is a slight difference in the average number of tail blotches, 16.3 in males and 14.4 in females.

**VARIATION:** In scutellation and coloration the population of *L. annulata* that inhabits the large area comprising the Amazon Basin shows little variation. There is a slight trend in the number of body blotches; those individuals from eastern Brazil and the Guianas have slightly more blotches than do those from the upper reaches of the Amazon in Peru and Ecuador. The presence of two preoculars is more common in specimens from the Guianas than in those from the rest of the range.

Although *annulata* appears to be a uniform population in the Amazon Basin, the snakes from outside the basin are often considerably different. This is especially true in extreme northern South America and in southern Brazil and adjacent Bolivia and Paraguay. In these areas the populations are considered distinct on the subspecific level; *annulata* intergrades with *pulchriceps* in Departamento Santa Cruz, Bolivia, and with *ashmeadi* in



northern British Guiana. However, there are still other populations of *annulata*-like snakes to be defined. There is too little material available to enable one to delimit the ranges of the snakes accurately and to describe the variation. Consequently, I am considering these as populations of *Leptodeira annulata* and am not assigning subspecific names at this time.

**SÃO FRANCISCO FORM:** (Four specimens from Aruanã, Goiás, and from Barreiras, Bahia, Brazil). These snakes have one, two, or three preoculars, and usually have upper labials 4 and 5 entering the orbit. Two have a maximum of 21 dorsal scale rows, and two have 19. The body is rounded, and the vertebral row is not noticeably enlarged. Three males have 187–198 ventrals; one female has 186. Males have 94–101 (97.5) caudals, and the female has 83. The males have a tail/body ratio of 0.369, the female 0.331. The dorsal body blotches are chocolate brown and vary in number from 42 to 48 (44.5). In the Goiás specimens the blotches are nearly twice the length of the light dorsal interspaces and extend laterally onto scale rows 4 or 5. The specimen from Barreiras, Rio São Francisco, has lighter brown blotches that extend laterally to scale rows 3 or 4. The ground color in all the specimens is creamish tan; there are lateral intercalary spots on rows 1 and 2. In the Goiás individuals some of the spots may extend onto scale row 3.

**NORTHERN COASTAL FORM:** (Seven specimens from the vicinity of Salvador, Bahia, from Souza, Paraiba, and from Recife, Pernambuco, Brazil). These snakes have two or three preoculars and labials 4 and 5 entering the orbit. The body is only slightly compressed, and the vertebral scale row is not noticeably enlarged. Six individuals have a maximum of 21 scale rows; one has 19. Four males have 180–201 (190.0) ventrals; two females have 190–203 (196.5) ventrals. Caudals in males range from 87 to 91 (89.7), and a single female has 83. The tail/body ratio ranges from 0.266 to 0.405 (0.333) in males, whereas the single female has a ratio of 0.306. The dorsal ground color is grayish brown; there are 32 to 42 (38.3) dark brown body blotches outlined with black that are three to four scales in length, twice the length of the light interspaces, and extend laterally to

scale rows 4 to 6. There are large, lateral, intercalary spots on rows 2 to 5. The head is grayish brown above, with a dark stripe along the lateral edge of each parietal; these stripes fuse on the posterior edge of the parietals to form a nape stripe. The postocular stripe extends to the corner of the mouth; the labials are a cream color smudged with brown.

**SOUTHERN COASTAL FORM:** (Thirteen specimens from the states of Espírito Santo, Rio de Janeiro, and São Paulo). Preoculars are one, two, or three; usually labials 4 and 5 enter the orbit. The body is only slightly compressed, with a moderately enlarged vertebral scale row. There are 21 scale rows in five specimens, and 19 in three. Ventrals in four males range from 186 to 200 (193.3) and in four females from 182 to 196 (188.8); caudals in males, 87–93 (90.0), in females, 82–90 (86.0); tail/body ratio in males, 0.321–0.357 (0.338), in females, 0.327–0.364 (0.339). The dorsal ground color is light tan. There are 29–39 (34.9) dark brown dorsal body blotches that are three or four scales in length, two or three times the length of the dorsal light interspaces, and extend laterally onto scale rows 4 to 6. The lateral intercalary spots are small and are on rows 2 to 3. The top of the head is brown, with a dark stripe along the lateral edge of each parietal, the stripes fusing on the posterior edge of the parietals to form a nape stripe. The postocular stripe terminates in the middle of the eighth upper labial. A specimen from Emas, São Paulo (D.Z. No. 1892), has a light brown head with scattered dark marks on the frontal and parietals. This form closely approaches typical *annulata* from the Amazon Basin.

**REMARKS:** Specimens from the Andean foothills in the Departamento Santa Cruz, Bolivia, are intergrades between typical *annulata* and *pulchriceps* to the south and east. They differ from the *annulata* to the north in Ecuador, Peru, and northern Bolivia in having more body blotches, fewer ventrals, and a relatively shorter tail. The body is only moderately compressed, and the vertebral scale row only slightly enlarged. There are dark stripes present on the parietals; there is a nape stripe.

The development of the enlarged vertebral and paravertebral scale rows is correlated

with the reduction in the number of dorsal scale rows; these and the development of a laterally compressed body seem to be correlated with the forest environment of these snakes. The forms of *annulata* that are terrestrial and live in scrub forest and savanna country have rounded bodies without enlarged vertebral scale rows. The development of the enlarged scale rows and compressed body in *L. septentrionalis ornata* on the Pacific coast of South America, *annulata annulata* in the Amazon Basin, and an *annulata*-like form on the coast of Brazil points to a close association between the environment and the morphological characteristics of the snakes.

**RANGE:** *Leptodeira annulata annulata* ranges the Amazon Basin of South America to elevations slightly exceeding 1000 meters on the eastern slopes of the Andes in Ecuador, Peru, and Bolivia, and along the Atlantic coast of Brazil southward to São Paulo. (See map 3.) It lives in tropical rain forests and by its laterally compressed body and enlarged vertebral and paravertebral scale rows is well adapted to an arboreal existence.

The locality records for the 480 specimens examined are:

**BOLIVIA:** Charobamba, B.M.N.H. No. 95.11.21.-29; Manoa, U.M.M.Z. Nos. 56898-56899. *Beni:* A.M.N.H. Nos. 2965-2969; Cachuela Esperanza, A.M.N.H. No. 22496; Ivón, A.M.N.H. No. 22492; Riberalta, A.M.N.H. No. 22266, U.M.M.Z. Nos. 63224-63228, 63229 (2), 63230-63231; Río Beni, M.C.Z. No. 6322; Río Mamore, Trinidad, B.M.N.H. No. 1923.11.7.13; Rurrenabaque, A.M.N.H. Nos. 22471, 22474. *La Paz:* Ixiamas, A.M.N.H. No. 22452; Sorata, Z.S.B.S. No. 2013/-0. *Pando:* Río Madre de Dios, B.M.N.H. No. 95.11.21.28, U.M.M.Z. Nos. 59767-59770.

**BRAZIL:** No specific locality, A.M.N.H. Nos. 3852-3858; Chofrada, A.N.S.P. Nos. 11120-11121; São João, A.N.S.P. Nos. 11117-11119; Vianna, A.M.N.H. No. 27350; Viranduba, M.C.Z. No. 2576. *Acre:* Placido de Castro, D.Z. No. 2564; Río Purus, D.Z. No. 2495. *Amapá:* Macapá, D.Z. No. 2812. *Amazonas:* M.C.Z. Nos. 4773-4774; Ayapua, Río Purus, B.M.N.H. No. 1926.4.30.19; Boca de Río Téffe, M.N.H.N. No. 00-466-8; Borba, M.N.R. No. 3007; Carvoeira, A.M.N.H. No. 36165; Manaos, M.N.R. Nos. 453-457; Paraná de Fonte Boa, M.N.R. No. 458; Pari-Cachoeira, Río Tiquié, M.N.R. No. 3019; Rio Livramento, A.M.N.H. No. 56151; Roraima, M.N.R. No. 464. *Bahia:* M.C.Z. Nos. 1360, 2949, 3280, M.N.H.N.

No. 6882; Barreiras, U.M.M.Z. No. 108814; 30 kilometers southwest of Feira de Santana, U.K. No. 29441; Salvador, D.Z. No. 2817, U.M.M.Z. No. 113756; São Gonçalo, U.K. Nos. 29442-29443. *Distrito Federal:* Rio de Janeiro, M.C.Z. Nos. 1096 (3), 6854, U.S.N.M. No. 98639; Jacarepaguá, D.Z. No. 2020. *Espirito Santo:* Linhares (Refugio Sooretama), D.Z. No. 2461; Rio Doce, D.Z. No. 405; Santa Leopoldina, M.N.R. No. 463. *Goias:* Aruanã, D.Z. Nos. 2152, 2161. *Maranhão:* Z.M.B. No. 10855. *Mato Grosso:* M.N.R. Nos. 222, 225, 346-348; Alto Araguaia, M.N.H.N. Nos. 46-47; Rio Matsaua, tributary of Rio Xingú, M.N.R. No. 2950; San Luiz de Cáceres, M.N.R. No. 461. *Pará:* A.M.N.H. No. 49221, M.N.R. No. 462; Cameté, N.M.W. No. 14400; Isla de Marajo, M.C.Z. No. 22445; Obidos, M.C.Z. Nos. 1215 (3), 2581; Santarem, B.M.N.H. No. 56.3.25.9, M.C.Z. No. 2577 (3), N.M.W. No. 14413; Serra de Eraré, M.N.R. No. 459. *Paraíba:* Fazenda do Acanã Souza, M.N.R. Nos. 1953, 1973. *Pernambuco:* Recife, C.N.H.M. No. 42198. *Rio Branco:* Boa Vista, N.M.W. Nos. 14403 (2), 14404. *Rio de Janeiro:* Meninas Caxias, M.N.R. Nos. 2655, 2971. *São Paulo:* Emas, D.Z. No. 1892; São Paulo, U.M.M.Z. No. 62719.

**BRITISH GUIANA:** Dadanawa, Rupununi River, A.M.N.H. Nos. 60843-60844.

**COLOMBIA:** *Amazonas:* Ginogojé, M.C.Z. Nos. 53226-53227; Leticia, M.C.Z. No. 48995; mouth of Río Loreto-yacu, M.C.Z. No. 50235. *Caquetá:* Río Caquetá, La Taqua, Tres Troncos, C.N.H.M. No. 69656. *Meta:* Villavicenci, A.N.S.P. No. 24140, A.M.N.H. No. 62229, M.C.Z. No. 22005. *Putumayo:* Río Putumayo, C.N.H.M. No. 37441. *Vaupés:* San Felipe de Río Negros, M.C.Z. No. 53228.

**ECUADOR:** No specific locality, A.M.N.H. Nos. 61580, 61593, 61789-61790, M.N.H.N. No. 6142 (type of *Eteirodipsas weineri*); Turula, A.M.N.H. No. 35964. *Chimborazo:* Huigra, U.S.N.M. No. 60754; Pallatanga, A.M.N.H. No. 23027; Riobamba, A.M.N.H. Nos. 15212, 15220, 23256, 23269, 23284, 23308-23310, 23539. *Napo-Pastaza:* Andoas, A.M.N.H. Nos. 49075-49076, 49083, 49150, C.N.H.M. No. 27591; Avila, U.M.M.Z. No. 92013; Canelos, C.N.H.M. No. 4063, E.P.N. No. 781; Canelos-Baños region, A.M.N.H. No. 35878; Cavercas del Río Bobonaza, J.A.P. Nos. 2275, 2552-2554; Chichirota, E.P.N. Nos. 777, 786-787, 819; Loreta, E.P.N. Nos. 766, 791, 805; Palanda, Río Bobonaza, E.P.N. Nos. 756-757; Puerto Napo, E.P.N. No. 784; near Puto, E.P.N. Nos. 778-780; 1 kilometer north of Puyo, J.A.P. No. 2264; between Puyo and Canelos, E.P.N. Nos. 764-765; Río Cotopino, E.P.N. No. 758, U.M.M.Z. No. 92012; Río Copotaza, E.P.N. Nos. 753-754; Río Curaray, mouth of Río Villana,

C.N.H.M. No. 23481; Río Napo, M.N.H.N. Nos. 6170-6171, U.M.M.Z. No. 88912; Río Oglán, E.P.N. No. 767; Río Pastaza, U.M.M.Z. No. 88911; Rocofuerte, C.N.H.M. No. 36621; Sarayacu, E.P.N. No. 755; near Shell Mera, E.P.N. No. 774; near Tena, U.M.M.Z. No. 84760. *Santiago Zamora*: U.M.M.Z. No. 82888; Macas, A.M.N.H. Nos. 28822, 35837, 35851, 35856, U.S.N.M. No. 65486; Macuma, E.P.N. Nos. 768-773.

FRENCH GUIANA: Cayenne, M.C.Z. No. 5701.

PERU: No specific locality, A.M.N.H. Nos. 17533, 17621, 20394, 52467, 56059. *Huanuco*: Tingo María, C.N.H.M. No. 5596. *Loreto*: C.N.H.M. Nos. 11187-11188; Achinamisa, Río Huallaga, A.M.N.H. Nos. 52443, 52759; Armenia, Río Coengua, A.M.N.H. No. 52459; Cashiboya, Río Ucayali, A.M.N.H. Nos. 53126, 53128; Chanchamayo, A.M.N.H. Nos. 52062, 52149, 52186, M.N.H.N. No. 05-297; Chiogana, Río Huallaga, A.M.N.H. No. 52252; Chipurana, Río Huallaga, A.M.N.H. Nos. 52214, 52220; vicinity of Contamana, Río Ucayali, A.M.N.H. Nos. 52167, 52857, 53006, 53012, 53211, 53565; Iquitos, A.M.N.H. Nos. 17484, 52021, 52043, 52074, 52092, 52157, 52250, 52259, 52376-52377, 52420, 52450, 52488, 52493, 52582, 52632, 52651, 52657, 52668, 52685, 52708, 52754, 52765, 52960, 52967-52968, 53004, 53052, 53079, 53081-53082, 53147, 53151, 53261, 53227, 53280, 53333, 53340, 53393, 53700, 53707, 53783, 54012, 54043, 54066-54067, 54072, 54091, 54249, 54266, 54484, 54494, 54510, 54514, 54569, 54642, 54722, 54763-54764, 54838, 54864, 55122, 55165, 55283, 55285, 55297, 55318, 55321, 55875-55876, 55883-55884, 55906, 56032, 56038-56039, 56046, 56048, 56089, 56099, 56101, C.N.H.M. Nos. 45561-45562, U.S.N.M. Nos. 28295-28296; Isla Cedro, A.M.N.H. No. 52379; Juanjui, Río Huallaga, A.M.N.H. No. 52720; Lagunas, Río Huallaga, C.N.H.M. No. 5668; lower Río Napo, A.M.N.H. No. 53300; Monte Carmelo, near Isla Cedro, Río Ucayali, A.M.N.H. Nos. 55510, 55624, 55630-55631, 55639, 55916, 56028, 56040, 56051; mouth of Río Cushabatay, A.M.N.H. No. 55955; mouth of Río Santiago, Río Marañón, A.M.N.H. Nos. 53243, 53464, 55703; mouth of Río Tambo, Río Ucayali, A.M.N.H. No. 52898; mouth of Río Tigre, lower Río Marañón, A.M.N.H. No. 53485; Orellana, A.M.N.H. Nos. 54577, 54589-54590, 54594, 54606, 54613, 54621, 54623, 54626-54628, U.S.N.M. No. 127119; Pampa Hermosa, Río Cushabatay, A.M.N.H. Nos. 53383, 53385-53386, 53389, 53394, 53553-53554, 55438-55439, 55445, 55457, 55462, 55465, 55478, 55710-55711, 55735, 55741, 55750, 55756, 55767, 55773, 55775, 55784, 55790, 55805, 55807, 55814, 55816, 55819, 55829, 55839, 55852, 55893, 55959, 55975-55976, 55979, 55981, 55996-55997,

56000, 56002, 56011; Panya, Río Cushabatay, A.M.N.H. No. 52352; Pebas, M.C.Z. Nos. 12435-12436, S.U. Nos. 8722, 12491-12493, Z.M.B. No. 7156; west-southwest of Pucallpa, M.C.Z. No. 45921; Puesto Carachana, lower Río Tigre, A.M.N.H. Nos. 53184, 53193; Punga, Río Tapiche, A.M.N.H. No. 53481; Puritania, Río Amazonas, A.M.N.H. No. 52287; Río Cenipa, Río Marañón, A.M.N.H. No. 52728; Río Cushabatay, A.M.N.H. Nos. 52113, 52115, 53236; Río Dos de Mayo, Río Ucayali, A.M.N.H. No. 52380; Río Marañón, A.M.N.H. No. 52465; Río Samiria, A.M.N.H. Nos. 57270, 57281-57284; Río Santa Ana, Río Huallaga, A.M.N.H. No. 53594; Río Tamaya, Río Ucayali, A.M.N.H. Nos. 55327, 55339; Río Ucayali, A.M.N.H. Nos. 71116-71120, B.M.N.H. Nos. 95.2.29.17-95.2.29.19, C.N.H.M. No. 4064, U.M.M.Z. No. 48212; Roaboya, Río Ucayali, A.M.N.H. Nos. 52088-52089, 53479, 52798, 52887, 52893, 53087, 54446, 55693; Santa Rosa, Río Tigre, A.M.N.H. No. 49166; Santa Teresa, lower Río Tigre, A.M.N.H. Nos. 53175, 53179; Utuquinia, A.M.N.H. No. 52453; Yarina-cocha, C.N.H.M. Nos. 45563-45564. *Madre de Dios*: Río Pambopata, M.C.Z. No. 26622. *San Martín*: Moyobamba, B.M.N.H. Nos. 74.8.4.60-74.8.4.61, 74.8.4.78-74.8.4.82, 74.8.4.120.

SURINAM: No specific locality, S.N.M. No. 19805, Z.S.B.S. Nos. 2012/0 (2), 2014/0; Alkmaar, M.C.Z. Nos. 19241-19242; Paramaribo, A.M.N.H. Nos. 8133, 8136, 8138, 8668, 8680-8681, B.M.N.H. No. 1946.4.4.57.

VENEZUELA: San Antonio, U.S.N.M. No. 83616. *Amazonas*: Casiquiare, M.C.Z. No. 51474; Esmerelda, A.M.N.H. Nos. 36604-36605, M.B.U.C.V. No. 0-41 (5); Maroa, M.B.U.C.V. No. 0-12; Cerro Duida, A.M.N.H. Nos. 36621, 36624. *Bolívar*: Arabupu, U.M.M.Z. No. 85291; Paulo, near Roraima, A.M.N.H. No. 36048, U.M.M.Z. No. 85290.

Locality records for 38 specimens considered to be intergrades between *L. a. annulata* and *pulchriceps* are:

BOLIVIA: *Santa Cruz*: Buenavista, C.M. No. 2753, C.N.H.M. Nos. 16792, 35630-35635, U.M.M.Z. Nos. 60648 (3), 60698-60699, 60775, 63222-53223, 63232-63233, 67898-67900, 113063; Río Colorado, C.M. No. 2863; Santa Cruz de la Sierra, A.M.N.H. No. 8792, C.M. Nos. 70-71, 73-74, 76, 78-82, M.C.Z. No. 11853; Sara, B.M.N.H. No. 1907.10.31.54, C.M. Nos. 9, 37.

*Leptodeira annulata pulchriceps*,<sup>1</sup> new subspecies  
*Leptodeira albofusca*, BOULENGER, 1896, (in

<sup>1</sup> The subspecific name is derived from the Latin *pulchra*, meaning "pretty," and the Greek *kephale*, meaning "head," and refers to the ornate head pattern.

part), Catalogue of the snakes in the British Museum, vol. 3, pp. 95-97.

**DIAGNOSIS:** A race of *Leptodeira annulata* that resembles *L. a. ashmeadi* of northern South America, but differs from it in having a higher number of ventrals and a lower number of caudals; it differs from all other *annulata* in having two dark, longitudinal stripes on top of the head.

**HOLOTYPE:** Number 2578 in the collection of the Departamento de Zoologia, São Paulo, Brazil, from Bodoquena, Mato Grosso, Brazil; J. D. Frisch, collector. The following specimens from southern Mato Grosso are designated as paratypes: D.Z. No. 2577, U.M.M.Z. Nos. 108813, 113757-113758, and U.S.N.M. Nos. 76335-76336.

**DESCRIPTION OF HOLOTYPE:** An adult female with a body length of 510 mm. and a total length of 650 mm.; 194 ventrals, 72 caudals, two preoculars, two postoculars, one plus two plus three temporals, eight upper labials (fourth and fifth in orbit), 10 lower labials (1-5 in contact with anterior chin shield, 5 and 6 with posterior), chin shields subequal in length. Dorsal scales in 19-21-15 rows, showing the following reduction:

$$19 \frac{+10 (41)}{+10 (38)} \quad 21 \frac{10+V (111)}{10+V (109)} \quad 19 \frac{8+9 (126)}{8+9 (125)}$$

$$17 \frac{8+V (153)}{8+V (158)} \quad 15 (194)$$

The dorsal ground color is light brown. There are 37 rounded dark brown blotches on the back. These are three to three and one-half scales in length along the midline and are separated by interspaces of ground color one and one-half to two scales in length. At midbody the blotches extend laterally onto the fifth or sixth scale row where they are one and one-half to two scales in length. The edges of the blotches are black and are bordered by a cream color. In the lateral interspaces are dark brown spots on scale rows 1 to 4 which extend two or three scales in length. Small brown spots are present on scale rows 1 and 2 below the dorsal body blotches. A thin row of dark brown dashes extends the length of the body on the scale row below the lateral edges of the dorsal blotches. (See pl. 10.) There are 12 dark brown blotches on the dorsal surface of the tail; the under surfaces are an immaculate cream color.

The top of the head is grayish brown. There is a large dark brown spot on the common suture of the prefrontals, one on the anterolateral part of the prefrontal that connects with a dark stripe from the nostril to the eye, and a pair of spots on the frontal. Also there are scattered small dark spots on the parietals. A dark brown stripe begins on the anterolateral part of the parietal and extends posteriorly along the lateral edge of the parietal and adjacent parts of the secondary and tertiary temporals to the posterior edge of the parietal where it meets a transverse dark bar on the postparietals and posterior edges of the parietals. Continuing posteriorly from this bar are two dark bars two or three scales in width and separated by a light area the width of two scales. These bars connect with the first body blotch. The postorbital stripe begins on the postoculars and passes over the lower half of the primary temporal and lower secondary temporal, the tops of the sixth and seventh upper labials, all of the eighth labial, and onto the tenth lower labial, the postlabial, and the adjacent gulars. From there it continues posteriorly as a poorly defined stripe on scale rows 1 and 2 to the level of the fourth ventral. (See pl. 10.) The labials are a cream color smudged with brown.

**DESCRIPTION OF SUBSPECIES:** Males with 186-204 (193.6) and females with 184-198 (189.8) ventrals; caudals in males 71-91 (83.4) and in females 72-82 (76.2). Maximum number of dorsal scale rows 21 in 18 specimens and 19 in five. Two individuals have 17 scale rows posteriorly, one has 13, and the rest have 15. The scale-reduction formula for four males is:

$$19 +10 (45-56) - 21 9+10, \text{ or } 10+V (110-113) - 19 8+9, \text{ or } 9+V (112-126) - 17 7+8, \text{ or } 8+V (138-153) - 15 (193-196)$$

Scale-reduction formula for four females:

$$19 +10 (37-50) - 21 9+10, \text{ or } 10+V (101-111) - 19 8+9, \text{ or } 9+V (114-126) - 17 8+V (141-185) - 15 (184-194)$$

In one male with 196 ventrals scale rows 2 and 3 fuse at ventrals 187 and 191 to give only 13 rows in front of the anus.

There are 33 to 46 (39.2) dorsal body blotches and 12 to 20 (16.6) tail blotches. For the most part the condition of the dorsal blotches and the lateral intercalary spots is as described for the type specimen. In some

individuals the right and left halves of the blotches are offset longitudinally, and in some the left half of one blotch may be connected with the right half of the next blotch.

Males range from 434 to 575 mm. (474 mm.) in body length and from 574 to 735 mm. (648 mm.) in total length; females, from 415 to 610 mm. (515 mm.) and from 532 to 715 mm. (645 mm.). A juvenile male measures 190 mm. in body length and 249 mm. in total length.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals and in the tail/body ratio. Males have an average of 83.4 caudals as compared with 76.2 in females. In tail/body ratio males vary from 0.278 to 0.343 (0.323), and females from 0.268 to 0.326 (0.290).

**VARIATION:** There is considerable variation in the head pattern. The presence of two broad, longitudinal, dark bars on the nape is constant. Of the 23 available specimens, nine have the head pattern as described for the type specimen. Of the other 14, one has no dorsal head stripes, and in two the dorsal head stripes are not connected with the transverse dark bar on the posterior edge of the parietals. In the other 11 specimens the transverse parietal bar is absent; of these, in three individuals the dorsal head stripes are in contact with the longitudinal bars of the nape; in five others they are not. Another specimen has a median nape stripe extending from the posteromedian corners of the parietals posteriorly for a length of five scales, and short, broad, dorsal head stripes not connected to the longitudinal nape bars. In the two remaining individuals the dorsal head stripes are broken into spots, and the parietals and frontal are heavily spotted with brown.

**REMARKS:** *Leptodeira annulata pulchriceps* represents a relict population closely resembling *L. a. ashmeadi* in northern South America. At one time an *ashmeadi-pulchriceps* stock probably extended from northern South America to Paraguay and northern Argentina in a savanna or mixed forest and savanna habitat. The round-bodied individuals from Goias, Bahia, and Paraiba, Brazil, mentioned in the discussion of the subspecies *annulata* may represent isolated populations of this ancient stock in that region. The only real evidence of intergradation between *pul-*

*chriceps* and *annulata* is found in those snakes from the Departamento de Santa Cruz in Bolivia.

**RANGE:** This subspecies ranges from southern Mato Grosso, Brazil, westward to the vicinity of Santa Cruz de la Sierra, Bolivia, and southward to Asunción, Paraguay; one specimen is from an unknown locality in Argentina. (See map 3.) Apparently *L. a. pulchriceps* is an inhabitant of the scrub forest called *cerrado*, from the foothills of the Andes in Bolivia to central Mato Grosso, and then south into the Chaco region of northern Argentina and Paraguay, possibly south to the Río Parana.

Locality records for the 23 specimens examined are:

**ARGENTINA:** No specific locality, Z.M.B. No. 20631.

**BOLIVIA:** No specific locality, C.M. No. 2940. *Santa Cruz:* San José de Chiquitos, C.M. Nos. 34103-34104; vicinity of Santa Cruz de la Sierra, C.M. Nos. 72, 77, 2757, 2793-2794.

**BRAZIL:** *Mato Grosso:* Aquidauana, M.N.R. Nos. 1480-1483; Bodquena, D.Z. Nos. 2577-2578, U.M.M.Z. Nos. 113757-113758; Porto Esperanza, U.S.N.M. Nos. 76335-76336; Salobra, M.N.R. No. 1484, U.M.M.Z. No. 108813.

**PARAGUAY:** No specific locality, Z.M.B. No. 2652. *La Cordillera:* Asunción, B.M.N.H. No. 94.3.14.63.

#### *Leptodeira maculata* Hallowell

*Megalops maculatus* HALLOWELL, 1861, Proc. Acad. Nat. Sci. Philadelphia, for 1860, p. 488.

*Leptodeira personata* COPE, 1869, Proc. Acad. Nat. Sci. Philadelphia, vol. 20, p. 310. GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, pp. 171-172, pl. 54, figs. a, b. BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, pp. 93-94. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, pp. 903-904, pl. 73, fig. 1.

*Sibon personatum* COPE, 1887, Bull. U. S. Natl. Mus., no 21, p. 67; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Leptodeira albofusca*, STEJNEGER, 1926, Proc. U. S. Natl. Mus., vol. 69, pp. 1-3.

*Leptodeira annulata personata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 204.

*Leptodeira septentrionalis maculata*, DUNN, 1936, (in part), Proc. Natl. Acad. Sci., vol. 22, p. 697.

*Leptodeira maculata*, TAYLOR, 1938, (in part), Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 337-342, pl. 33, figs. 3, 3a. SMITH AND TAYLOR, 1945, (in part), Bull. U. S. Natl. Mus., no. 187, p. 88.

*Leptodeira smithi* TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 334-336, pl. 31, fig. 5. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 89. SCHMIDT AND SHANNON, 1947, Fieldiana, zool. ser., vol. 31, no. 9, p. 82. DUELLMAN, 1954, Occas. Papers Mus. Zool. Univ. Michigan, no. 560, p. 15.

HOLOTYPE: Number 7367 in the collection of the United States National Museum from "Tahiti" (in error), collected by Mr. Adams.

Because there has been so much confusion regarding the name *Megalops* (= *Leptodeira maculatus*) and the type locality of the species I feel that the following remarks are not out of place.

The early history of the name has been reviewed by Stejneger (1926), who rediscovered the type specimen in the United States National Museum and correctly placed it in the genus *Leptodeira*, assigning the name to the synonymy of *L. albofusca*. Stejneger gave the locality as probably Nicaragua. The type specimen was labeled "Tahiti," and Mr. Adams was listed as the collector. This specimen was one in an assemblage of material purportedly collected by the United States Navy North Pacific Exploring Expedition under the command of Captain John Rogers. Upon returning from the Pacific, the vessel docked at San Francisco. At that time Mr. Adams left for Nicaragua; hence the reason for Stejneger's assuming that the specimen probably originated in Nicaragua.

The type specimen of *L. maculata* has 19 body blotches and no nape stripe. Of the 27 specimens of *L. annulata rhombifera* from Nicaragua that I have studied, all have a nape stripe, and the body blotches range from 26 to 43. Certainly, the type of *L. maculata* did not come from Nicaragua. Dunn (1936) reported six specimens of *L. maculata* in the collection of the Museo Nacional de Costa Rica and presumed the snakes to be from that country. Since then Taylor (1951) and Stuart (1954) have shown reason to doubt the authenticity of the origin of the Museo Nacional specimens and of the Nicaraguan type locality. The late Dr. E. R. Dunn has provided me with data on the six snakes in the Museo Nacional. They have 23 to 25 body blotches and no nape stripe. The 24 *L. annulata rhombifera* from Costa Rica that I have examined have 30 to 50 body blotches,

and all have a nape stripe. Consequently I concur with Taylor and Stuart in the belief that the six specimens in question probably did not come from Costa Rica.

The elimination of lower Central America as a possible type locality of *L. maculata* necessitates the selection of a locality within the known range of the subspecies in México. Smith and Taylor (1950) restricted the type locality to 5 miles east of Jalapa, Veracruz, México. For reasons given below I believe this restriction to be unjustified. As the type specimen was part of a collection sent to the United States National Museum by the Rogers expedition, it is not unreasonable to assume that the specimen was collected by Adams, as reported. The ship sailed from San Francisco to Nicaragua, so that it is necessary to consider only the ports that he may have visited during that voyage. In 1860, the Mexican ports of Mazatlán, Manzanillo, Acapulco, and Salina Cruz were stopping places for ocean-going vessels.

When the type specimen with 19 body blotches and 170 ventrals is compared with series from the areas of the above-mentioned ports, it is found to agree best with those from the coastal region of Colima, near Manzanillo. Nineteen individuals have 18-24 body blotches and 165-175 ventrals. Only in Colima, the adjacent coastal regions of Michoacán, and in the Balsas Basin are found specimens with as few as 19 body blotches. Even at the present time there are no ports on the coast of Michoacán.

On the basis of the close agreement of the type specimen with individuals from Colima, and the probability that the port of Manzanillo was a stopping place during Adams' voyage to Nicaragua, I hereby restrict the type locality of *Leptodeira maculata* to Manzanillo, Colima, México. Smith and Taylor's (1950) arbitrary restriction should be disregarded.

The type locality of *Leptodeira personata* is Mazatlán, Sinaloa, and that of *Leptodeira smithi* is near Uruapan, Michoacán; both of these are within the range of *Leptodeira maculata*, and both names properly belong in the synonymy of *L. maculata*.

DESCRIPTION: Head distinct from neck; rostral barely visible from above; prefrontals square, half again as long as internasals; up-

per preocular in contact with frontal or not; frontal slightly longer than suture between parietals; normally two preoculars and two postoculars; temporals normally one plus two plus three; eight upper labials, the fourth and fifth entering the orbit; usually 10 lower labials, of which the first through the fifth are in contact with the anterior chin shield, and the fifth and sixth are in contact with the posterior chin shield; chin shields subequal in length.

The body is rounded, and the tail is relatively short. The dorsal scales are smooth; the paravertebral and vertebral rows are not enlarged.

The ranges and means for tooth counts in 10 specimens are: maxillary, 16-18+II (16.6); palatine, 10-11 (10.8); pterygoid, 25-32 (26.9); and dentary, 22-26 (24.6).

The hemipenis *in situ* is seven or eight caudals in length. Opposite the sulcus is a primary row of four large spines; of these the middle ones are the longest and the distal the shortest. Median to the primary row are three longitudinal rows of small spines. There is a deep cup in the finely crenulate capitulum, which is set off from the rest of the organ by a deep fold. The base is covered with spinules.

Males with 160-176 (166.0) ventrals; females with 159-175 (168.0); caudals in males 67-82 (73.8) and in females 54-75 (67.9). Dorsal scales usually in a maximum of 23 rows at midbody, sometimes 21 and rarely 25, and usually 17 rows posteriorly, sometimes 15 or rarely 19. Scale-reduction formula for seven males with 21 rows:

$21\ 9+10\ (96-105) - 19\ 8+9$ , or  $9+V\ (108-122) - 17\ 7+8$ , or  $8+V\ (140-163) - 15\ (164-168)$

Scale reduction in two males with 23 scale rows:

$21\ +11\ (30-54) - 23\ 10+11\ (90-97) - 21\ 9+10\ (105-108) - 19\ 9+V\ (121-128) - 17\ 8+V\ (159-161) - 15\ (163-167)$

Scale reduction in two males with 19 scale rows anteriorly and 21 rows at midbody:

$19\ +10\ (24-28) - 21\ 9+10\ (95-103) - 19\ 8+9\ (108-115) - 17\ 8+V\ (146-153) - 15\ (162-166)$

Scale reduction in 10 females:

$21\ +11\ (27-38) - 23\ 10+11\ (89-101) - 21\ 9+10\ (100-112) - 19\ 8+9\ (120-147) - 17\ (164-171)$

The dorsal ground color is a cream to yellowish tan with 12-28 (18.1) dark brown to black, saddle-shaped, dorsal blotches. The blotches are five to 15 scales in length, two to three times the length of the dorsal light interspaces, and they extend laterally onto scale rows 1 to 3. Lateral intercalary spots are usually absent; if present, they are small, indistinct, and confined to scale rows 1 and 2. Usually the dorsal blotches are narrower laterally than dorsally, and in certain individuals some of the blotches are connected along the midline. (See pl. 11.) There are from three to 14 dark brown blotches on the dorsal surface of the tail.

The top of the head is a dark brown to black color. Sometimes the edges of the head shields are outlined with light brown or cream. The dark color extends onto the sides of the head to a line passing from the lower edge of the nostril to that of the orbit and thence across the middle of the upper labials to the corner of the mouth. Posteriorly the dark brown stops on a line from the corner of the mouth to the posterior edge of the parietal. The labials are a cream color; upper labials 1-5 are often smudged with brown. (See pl. 11.) The ventral surfaces are cream-white.

Males range from 313 to 508 mm. (400 mm.) in body length and from 413 to 659 mm. (514 mm.) in total length; females range from 308 to 673 mm. (420 mm.) and from 398 to 783 mm. (544 mm.). The smallest specimen examined, a female, has a body length of 145 mm. and a total length of 185 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals, the tail/body ratio, the number of tail blotches, and in dorsal-scale reduction. Males have an average of 73.8 caudals; females, 67.9. The tail/body ratio in males ranges from 0.249 to 0.356 (0.307), and in females, from 0.227 to 0.326 (0.275). Males have slightly more tail blotches than females do. Dorsal-scale reduction from 19 to 17 rows takes place farther anteriorly in males than in females; the average point of reduction for 11 males is at the 116th ventral, and for 10 females, at the 130th ventral.

**VARIATION:** There is little variation in scutellation. The number of body blotches is

higher in those specimens from Sinaloa and Nayarit than in those from the Balsas Basin; 10 specimens from southern Sinaloa have an average of 23.6 body blotches, and 93 from the Balsas Basin in Michoacán have an average of 15.0. The occurrence of lateral intercalary spots is more frequent in specimens from the northern coastal regions than it is in individuals from the interior basin. Also, the blotches in the northern specimens are not so long as those from the Basin.

Juveniles usually have a lighter ground color than the adults. Young specimens are pale cream above and white below. Adults from the vicinity of Apatzingán, Michoacán, in life had a yellowish tan ground color and dark chocolate brown blotches; in a few individuals the blotches were black.

REMARKS: *Leptodeira maculata* is similar to *L. annulata cussiliris* in most characters of scutellation, size, and proportions. Individuals of the latter form from northeastern México closely resemble *maculata* in color pattern. The principal criterion for the recognition of these forms as two species is the nature of the geographical gradients in the number of body blotches. In *L. a. cussiliris* there is an increase in the number of body blotches from north to south in eastern México and across the Isthmus of Tehuantepec to Oaxaca and Guerrero, the highest number of blotches being found in specimens from these last two states. Conversely, in *maculata* the number of blotches decreases from north to south along the coastal regions of western México and into the Balsas Basin. Individuals from coastal Michoacán have an average of 20.2 blotches, whereas those from the coastal regions of Guerrero have an average of 34.0 blotches. (See fig. 4.) Apparently the break between the ranges of the two forms is the Río Balsas. No intermediate specimens are known, and there is no indication that the two species are sympatric in any area. If intergrades between *maculata* and *annulata cussiliris* do occur, they might be sought in the Cañon del Zopilote between Chilpancingo and Mexcala, Guerrero.

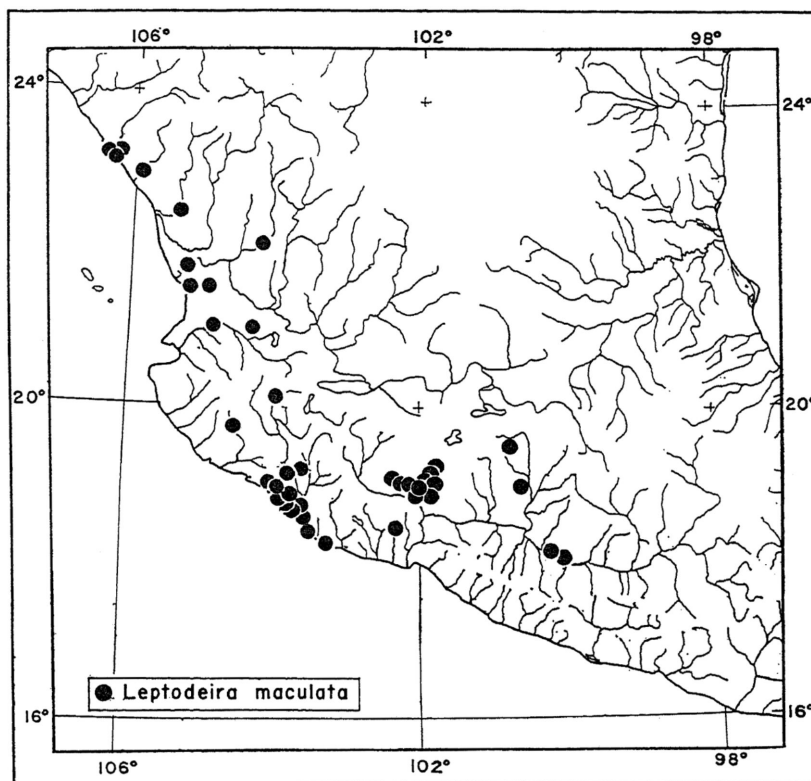
RANGE: *Leptodeira maculata* occurs in the Pacific coastal lowlands and adjacent slopes of the Sierra Madre Occidental from southern Sinaloa southeastward to the Río Balsas, and inland in the Balsas Basin in Michoacán and

Guerrero to elevations of about 2000 meters. (See map 4.)

The locality records for the 173 specimens examined are:

MÉXICO: *Colima*: Colima, A.M.N.H. Nos. 19576, 19581, U.S.N.M. Nos. 31426, 31485-31490; 3 miles southwest of Colima, U.M.M.Z. No. 114435; Manzanillo (?), U.S.N.M. No. 7367; Orolata, U.S.N.M. No. 56344; Paso del Río, E.H.T.-H.M.S. Nos. 4621, 4623, U.I. No. 17799; Periquillo, U.M.M.Z. Nos. 80218, 80219 (2); Pueblo Juárez, U.M.M.Z. Nos. 115578-115580; near Queseria, E.H.T.-H.M.S. No. 4641; Río Salada, U.M.M.Z. No. 80217; 8 kilometers southwest of Tecomán, U.M.M.Z. No. 80216. *Guerrero*: Balsas, C.N.H.M. No. 985; Río Balsas, B.M.N.H. No. 1906.6.1.225. *Jalisco*: Two miles north of La Resolana, U.M.M.Z. No. 101917 (4); Ocotlan, A.M.N.H. No. 19577; Santa Domingo de Guzmán, B.M.N.H. No. 90.10.10.86; Hacienda Santa Gertrudie, B.M.N.H. Nos. 90.10.31.64-90.10.31.66. *Michoacán*: Apatzingán, C.N.H.M. Nos. 37033-37035, 37037, 39085-39091, U.S.N.M. Nos. 111255-111256; 2.3 miles east of Apatzingán, U.M.M.Z. No. 112447; 3.3 miles east of Apatzingán, U.M.M.Z. Nos. 112448-112449; 4.6 miles east of Apatzingán, U.M.M.Z. No. 112440; 5 miles east of Apatzingán, U.M.M.Z. Nos. 112445-112446; 6.6 miles east of Apatzingán, U.M.M.Z. Nos. 112441-112442; 7 miles east of Apatzingán, U.M.M.Z. No. 114438; 15.3 miles east of Apatzingán, U.M.M.Z. No. 114436; Arteaga, N.M.W. Nos. 14398-14399; 3.5 miles north of Capirio, U.M.M.Z. Nos. 114441-114442; 4.2 miles north of Capirio, U.M.M.Z. No. 114439; 1.2 miles south of Charapendo, U.M.M.Z. Nos. 112438-112439; Coahuayana, U.M.M.Z. No. 104613; 4 kilometers west of Coahuayana, U.M.M.Z. Nos. 104497, 104609; Cofradía, B.M.N.H. No. 1914.1.28.137; 2.3 miles west of Cuatros Caminos, U.M.M.Z. No. 114440; Estopilas de Salitre, U.M.M.Z. No. 104614; Jorullo, B.M.N.H. No. 1914.1.28.138; La Placita, U.M.M.Z. Nos. 104610-104611; 0.5 mile northeast of La Placita, U.M.M.Z. No. 104612; 0.6 mile north of Lombardia, U.M.M.Z. No. 112497; 1.4 miles south of Lombardia, U.M.M.Z. No. 112502; 3-5 miles south of Lombardia, U.M.M.Z. Nos. 112469-112496, 112498-112500, 112507; 5-7 miles south of Lombardia, U.M.M.Z. Nos. 112458-112468; 1-3 miles north of Nueva Italia, U.M.M.Z. Nos. 112503-112506; 2.5 miles south of Nueva Italia, U.M.M.Z. Nos. 112450-112455; 6.6 miles southwest of Nueva Italia, U.M.M.Z. No. 112444; 8.5 miles southwest of Nueva Italia, U.M.M.Z. No. 112443; 8 miles southeast of Nueva Italia, U.M.M.Z. No. 114437; 1 mile east of Pómaro, U.M.M.Z. 104615; Para-





MAP 4. Locality records for *Leptodeira maculata*.

cuaro Station, U.M.M.Z. Nos. 112456-112457; Río Cupatitzio, 6.5 miles south of Lombardia, U.M.M.Z. No. 112501; 10 miles north of Tafetan, U.I. Nos. 17827-17828; Tierra Caliente, N.M.W. No. 14396 (2). *Nayarit*: Acaponeta, A.M.N.H. Nos. 62269-62274; 1 mile east of Ixtlan, U.M.M.Z. No. 101919 (4); Jalisco, near Tepic, A.M.N.H. No. 69698; Moramar, U.S.N.M. Nos. 51471-51477; San Blas, U.S.N.M. No. 51478; 12-16 miles east of San Blas, F.A.S. No. 11368; 1 mile southwest of San José de Conde, U.M.M.Z. No. 101918; Santiago Ixcuintla, A.M.N.H. No. 19575; 23 miles northwest of Tepic, T.C.W.C. No. 12590. *Sinaloa*: Chele, U.M.M.Z. Nos. 110906-110908; Mazatlán, N.M.W. No. 14397, U.S.N.M. No. 6836 (type of *L. personata*); Presidio, B.M.N.H. Nos. 83.4.5.52-83.4.5.53, E.H.T.-H.M.S. Nos. 4656-4657; Rosario, U.S.N.M. 62201.

***Leptodeira bakeri* Ruthven**

*Dipsas annulata*, LIDTH DE JEUDE, 1887, Notes Leyden Mus., vol. 9, p. 133.

*Leptodeira annulata*, RUTHVEN, 1923, Occas. Papers Mus. Zool. Univ. Michigan, no. 143, p. 9.

*Leptodeira bakeri* RUTHVEN, 1936, Occas. Papers Mus. Zool. Univ. Michigan, no. 330, pp. 1-2.

**HOLOTYPE**: Number 57130 in the collection of the University of Michigan Museum of Zoology from Aruba Island, Dutch West Indies; H. B. Baker, collector.

**DESCRIPTION**: Head distinct from neck; rostral barely visible from above; prefrontals pentagonal, twice the length of the internasals; frontal slightly longer than suture between parietals; upper preocular in contact with frontal or not; preoculars usually two, sometimes one; postoculars two; temporals one plus two plus three; lower labials usually 10, sometimes nine; labials 1-5 in contact with anterior chin shield and fifth and sixth in contact with posterior chin shield; anterior chin shield three-fourths of the length of posterior.

Ventrals in males 171-174 (172.2) and in females 167-179 (170.8); caudals in males 70-74 (71.3) and in females 63-71 (67.0). Dorsal scales usually in a maximum of 19 rows (one has 21) and reducing to 15 posteriorly. Scale-reduction formula for two males:

19 8+9 or 9+V (108-112) - 17 7+8, or 8+V (132-137) - 15 (171-172)

Scale-reduction formula for four females:

19 8+9 (103-118) - 17 7+8, or 8+V (140-150)-15 (170-171)

The ranges and means for tooth counts in four specimens are: maxillary, 14-16+II (15.2); palatine, 10; pterygoid, 25-28 (26.0); and dentary, 21-24 (22.8).

The hemipenis *in situ* extends posteriorly for the length of seven caudals. Opposite the sulcus are six longitudinal rows of large spines, three to five spines in each row, the distal ones the largest. There is a cup in the finely crenulated capitulum which is set off from the rest of the hemipenis by a deep fold.

The dorsal ground color is light tan. There are 14-27 (21.1) chocolate brown dorsal body blotches three to eight scales in length, twice the length of the interspaces, and extending laterally onto scale rows 2 or 3. The centers of the blotches are light brown. Dark, lateral, intercalary spots usually are present on rows 1 and 2. Often these are elongate; usually there is a dorsal extension of this dark color into the lateral light interspaces between the dark dorsal blotches. (See pl. 12.) There are seven to 10 dark tail blotches; the ventral surfaces are an immaculate cream color.

The top of the head is light brown, sometimes with scattered small dark flecks on the frontal and parietals. There is a dark brown transverse bar on the postparietals and posterior edge of the parietals. Sometimes extending posteriorly from this for a length of two or three scales is a dark nape stripe, thus forming a T-shaped mark on the neck. A dark stripe extends from the nostril across the loreal and upper preocular to the orbit, and a postorbital stripe begins on the postoculars and extends across the anterior part of the primary temporal, the tops of the sixth and seventh upper labials, and the middle of the eighth to terminate at the corner of the mouth. (See pl. 12.) The labials are tan, sometimes smudged with brown.

Males range from 234 to 410 mm. (336 mm.) in body length and from 303 to 510 mm. (412 mm.) in total length; females range from 410 to 535 mm. (451 mm.) and from 562 to 595 mm. (579 mm.). The smallest

juvenile is a female with a body length of 156 mm. and a total length of 201 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals and in the tail/body ratio. Males have an average of 71.3 caudals; females, 67.0. In tail/body ratio males range from 0.295 to 0.342 (0.321), and females, from 0.277 to 0.308 (0.291).

**VARIATION:** One specimen (A.M.N.H. No. 73256) has dorsal blotches that are alternating and connected. In a few individuals the lateral intercalary spots on rows 1 and 2 are elongated and form a dark streak on the side of the body.

**REMARKS:** The character of the hemipenis is the best clue to the relationships of this species. The cup in the capitulum is characteristic of the *annulata* group. As *bakeri* does not differ strikingly in any other basic morphological characters from the species in the *annulata* group, it should be considered as a member of that group. *Leptodeira bakeri* has fewer dorsal scale rows, body blotches, ventrals, and caudals than any terrestrial *annulata* from South America. It is most closely approached in scutellation by *L. a. cussiliris* from México. Because it is distinct from mainland specimens of *annulata*, and because it possesses such a distinctive color pattern, *bakeri* here is accorded specific rank.

**RANGE:** This species is definitely known only from Aruba Island, Dutch West Indies. (See map 3.) A specimen alleged to be from Surinam (Z.S.B.S. No. 2026/0) is believed to have erroneous locality data. Aruba Island is arid, with sandy soil and columniferous cacti (Hummelinck, 1940). Thus the habitat of *bakeri* is in keeping with that of the terrestrial forms of *annulata*.

The locality records for the 15 specimens examined are:

**DUTCH WEST INDIES:** *Aruba Island:* A.M.N.H. Nos. 57959, 69124, 70915, 73256; *Bubali,* M.C.Z. No. 46511, U.M.M.Z. Nos. 57129-57131, 57133-57134; *Lago Col,* A.M.N.H. No. 73254; *Oranjestad,* A.M.N.H. Nos. 73258, 73388; *San Nicolaas,* A.M.N.H. No. 73255.

**SURINAM:** No specific locality (?), Z.S.B.S. No. 2026/0.

***Leptodeira frenata* Cope**

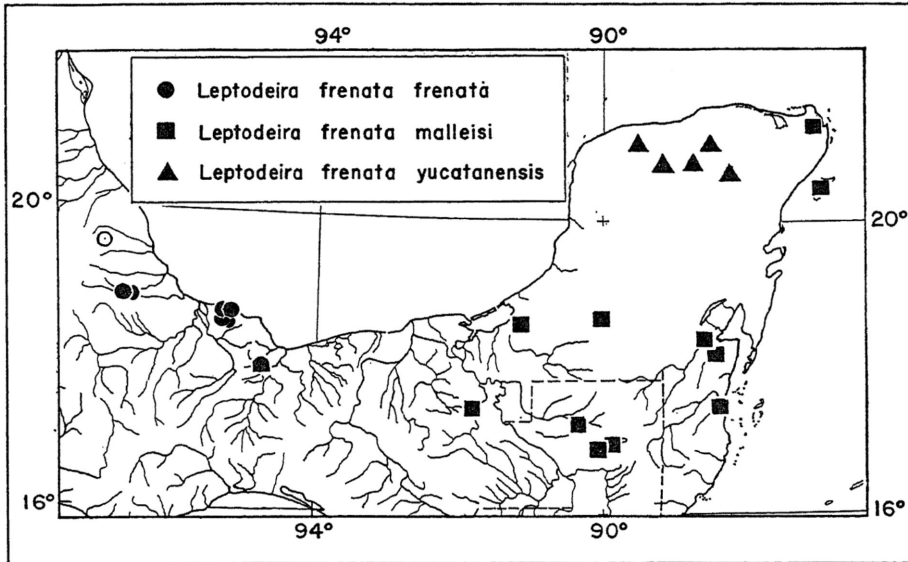
*Sibon frenatum* COPE, 1886, in Ferrari-Perez, Proc. U. S. Natl. Mus., vol. 9, p. 184.

**DISTRIBUTION:** *Leptodeira frenata* ranges from central Veracruz southward and eastward through southern México in the states of Tabasco and Chiapas, throughout the Yucatán Peninsula, in El Petén in Guatemala, and British Honduras. The species occurs on Isla de Cozumel off the east coast of the Yucatán Peninsula. (See map 5.)

**DESCRIPTION:** Head broad and flat, distinct from neck; rostral barely visible from above; prefrontals square, half again as long

the tenth row between ventrals 16 and 38. The posterior reduction from 21 to 19 rows takes place by the fusion of the ninth and tenth rows between ventrals 106 and 121; from 19 to 17 rows by the fusion of the eighth and ninth rows between ventrals 117 and 135. In individuals having only 15 scale rows posteriorly the reduction from 17 to 15 rows is accomplished by the fusion of the seventh and eighth rows.

The ranges and means of tooth counts



MAP 5. Locality records for *Leptodeira frenata*.

as the internasals; frontal with parallel sides to the point of the posterior edge of the supraocular; upper preocular usually not in contact with frontal; preoculars usually two, sometimes one or three; postoculars usually two, sometimes one or three; upper labials eight, normally with only the fourth and fifth entering the orbit, but sometimes when only one preocular is present the third also may enter the orbit; chin shields subequal in length; lower labials usually 10, sometimes nine or 11, with labials 1 to 5 in contact with anterior chin shield, and labials 5 and 6 in contact with posterior one.

All the dorsal scales are smooth, with the vertebral and paravertebral rows not enlarged, and usually in a maximum of 21 rows, sometimes 23. The increase anteriorly from 19 to 21 rows takes place by the addition of

based on 11 specimens are: maxillary, 8–10 +II (9.1); palatine, 8–9 (8.1); pterygoid, 19–23 (20.7); and dentary, 14–16 (14.4).

The hemipenis *in situ* is seven or eight caudals in length. There are three primary longitudinal rows of large, hooked spines; the spines of the primary rows increase in size from the base to the distal part. The largest spines are in the middle row, the latter with five spines, and the distal one twice as large as its counterpart in the other rows. Secondary rows of small spines extend longitudinally for a short distance between primary rows. The ventral part of the base is covered with small spines that merge to form the primary longitudinal rows. The dorsal side of the base is covered with spinules. The capitulum is finely crenulated and set off from the rest of the hemipenis by a deep fold.

The dorsal and ventral ground color is cream or light tan; the dorsal body blotches are brown or black and four to eight times the length of the interspaces, reaching or nearly reaching the ventrals. The first body blotch is considerably longer than those farther posteriorly. Dark, lateral, intercalary spots are present. There are paired dark parietal spots and a dark spot on the posteromedian edges of the parietals. Usually the postorbital stripe connects with the first body blotch.

whether they are uniformly dark or are light and outlined with black, also show some geographical variation. Again, in specimens from the tip of the Yucatán Peninsula and central Veracruz the blotches are a solid color; towards the south, in Chiapas, Guatemala, and British Honduras, they are always light with dark outlines.

On the sole basis of these differences in color pattern in the various parts of the range, this species may be divided into three races.

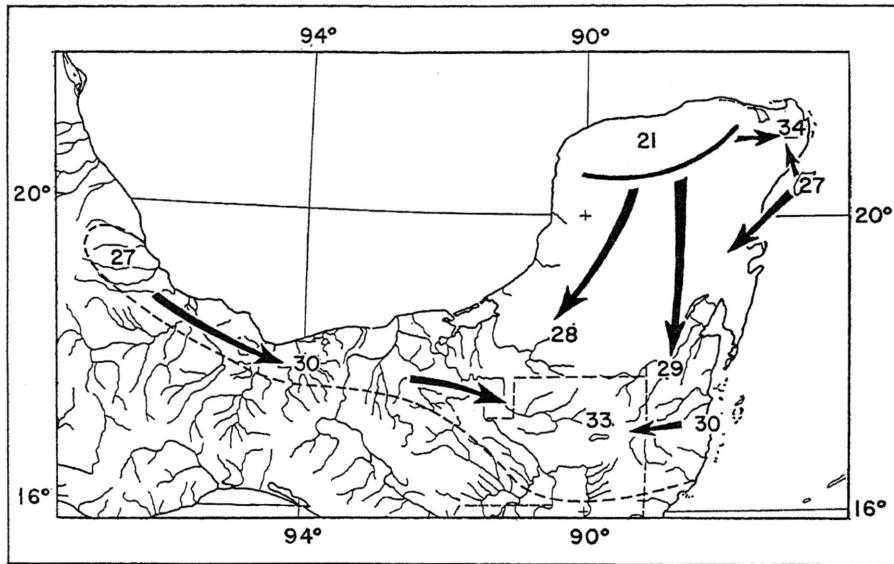


FIG. 7. Geographical variation in the number of body blotches in *Leptodeira frenata*. Arrows point from areas in which specimens have few blotches to areas in which they have more.

The total length seldom exceeds 700 mm.; the tail/body ratio ranges from 0.25 to 0.30.

**GEOGRAPHICAL VARIATION:** The most striking character gradient is in the number of body blotches; these increase in number from north to south, both in the Yucatán Peninsula and along the northwest-southeast axis of Veracruz. (See fig. 7.) When the number of body blotches per specimen from the mainland of the Yucatán Peninsula is plotted against latitude, a definite, although moderate, cline is evident. (See fig. 8.) As the blotches become more numerous, they tend to become somewhat more saddle-shaped and do not extend laterally to the ventrals. The intensity of the color in the body blotches, and

#### *Leptodeira frenata frenata* Cope

*Sibon frenatum* COPE, 1886, in Ferrari-Perez, Proc. U. S. Natl. Mus., vol. 9, p. 184; 1887, Bull. U. S. Natl. Mus., vol. 32, p. 67; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Leptodeira frenatum* COPE, 1891, Proc. U. S. Natl. Mus., vol. 14, p. 677.

*Leptodeira frenata*, GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 173. BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 92. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, p. 906. WERNER, 1924, Arch. Naturgesch., vol. 12, p. 125. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 696. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 333-334. SMITH, 1939, Proc. Biol. Soc.

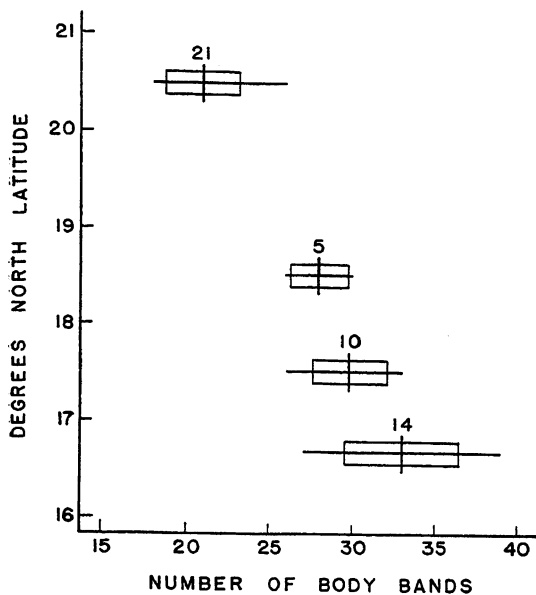


FIG. 8. Geographical gradient in the number of body blotches in *Leptodeira frenata* in the Yucatán Peninsula. Vertical line, mean; horizontal line, observed range; box includes one standard deviation on either side of the mean.

Washington, vol. 52, pp. 192–195, fig. 8, pl. 2. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 88; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 348.

*Leptodeira annulata personata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 204.

*Leptodeira frenata frenata*, DUELLMAN AND WERLER, 1955, Occas. Papers Mus. Zool. Univ. Michigan, no. 570, pp. 1–9, pls. 1–2.

**HOLOTYPE:** The type specimen is lost; it was Number 298 in the collection of the Geographical Exploring Commission of México, from Jalapa, Veracruz, México; Fernando Ferrari-Perez, collector.

**DESCRIPTION:** Males with 179–183 (181.2) ventrals and females with 175–185 (180.0) ventrals; caudals in males 71–80 (76.6) and in females 61–70 (65.6). Dorsal scales in a maximum of 21 rows; scale-reduction formula for four males:

19 +10 (16–28) – 21 9+10 (110–113) – 19 8+9 (120–123) – 17 7+8 (147–168) – 15 (180–183)

Scale reduction for four females:

19 +10 (28) – 21 9+10 (110–115) – 19 8+9 (127–128) – 17 7+8 (167) – 15 (180–183)

The dorsal color pattern consists of 26 to 36 long, dark brown or black blotches four to eight times the length of the light interspaces. These blotches may be entirely separate, or, less frequently, the light interspaces may alternate, so that the blotches are connected along the midline. In juveniles the blotches are solid black, but in larger individuals they are dark brown or light brown outlined with black. The blotches may extend onto the edges of the ventrals, or sometimes, especially posteriorly, reach only to the second scale row. The interspaces are white in the young to light tan in large individuals and are slightly longer laterally than they are dorsally, where they are usually one scale in length. The lateral intercalary spots usually involve the edges of one or more ventrals and may extend dorsally onto the third scale row. (See pl. 13.) There are 11 to 17 dark blotches on the tail.

The top of the head is brown. Black or brown flecks or dashes may occur on the frontal, parietals, and temporals. There is a dark longitudinal mark on each parietal, and sometimes there is a nearly round dark spot on the anterior part of the frontal. A dark spot is always present on the posteromedian edges of the parietals and adjacent postparietals. The snout is brown; the labial region is a cream color. Passing from the nostril across the loreal and preoculars to the orbit is a suffuse dark brown bar. The posterior edges of upper labials 1 to 6 are dark brown, and all lower labials have dark brown stripes along the posterior edge. A dark brown or black stripe that connects with the first body blotch begins on the postoculars and passes over the dorsal part of the sixth upper labial, through the middle of the seventh, across the lower part of the eighth, and onto the first four rows of dorsal body scales. (See pl. 13.) The ventral surfaces are an immaculate cream-white color.

Males range from 243 to 425 mm. (353 mm.) in body length and from 309 to 507 mm. (438 mm.) in total length; females range from 345 to 405 mm. (381 mm.) in body length and from 434 to 515 mm. (477 mm.) in total length. One juvenile female has a body length of 197 mm. and a total length of 242 mm.

**SEXUAL DIMORPHISM:** Differences between

the sexes are found in the length, scutellation, and coloration of the tail, and in the dorsal scale reduction on the body. The number of caudals in males varies from 71 to 80, in females from 61 to 70; the number of dark blotches on the tail varies in males from 13 to 17 and in females from 11 to 15; the tail/body ratio in males varies from 0.272 to 0.316 (0.286) and in females from 0.237 to 0.272 (0.247). The reduction from 19 to 17 rows posteriorly takes place between ventrals 120 and 123 in males and at 127 or 128 in females.

**VARIATION:** Specimens from central Veracruz tend to have longer dark blotches that are more dense in color than those from southern Veracruz. Also, the blotches are nearly as long laterally as they are dorsally, and they always extend to the ventrals. Specimens from southern Veracruz tend to have a few more blotches that are brownish in color and outlined with black; these are often saddle-shaped, leaving long interspaces laterally, and often do not extend onto the ventrals or even to the first scale row. The lateral intercalary spots are larger than those in more northern specimens, and there may be dark streaks along the edges of the ventrals and on the first scale row.

One individual (U.M.M.Z. No. 112320) in life had a dorsal ground color of vivid salmon fading to a creamy pink on the venter. The dorsal body blotches were cocoa brown outlined with black, in turn bordered by pale yellow. The top of the head was light cocoa brown flecked with chocolate brown. The nape was pinkish gray; the labials and throat were white, the former barred with black. The iris was gray, with suffuse salmon flecks.

A specimen without locality data (L.M.K. No. 40299) is a male with 195 ventrals and 82 caudals. This individual was discussed by Duellman and Werler (1955) and has not been included in the analysis of variation here.

**REMARKS:** Duellman and Werler (*loc. cit.*) have shown that *frenata* intergrades with *malleisi* in southern Veracruz. Intermediate specimens also probably occur in Tabasco. The closest records for *malleisi* are in Chiapas, more than 150 miles to the east of the easternmost record for *frenata*.

Specimens of *Leptodeira f. frenata* have been collected at elevations ranging from 150 to 450 meters. Several individuals, found in southern Veracruz during the dry season, were taken from bromeliads growing in trees.

**RANGE:** At the present time *L. f. frenata* is known only from a few scattered localities in tropical evergreen forest and tropical rain forest from central Veracruz southward and eastward to the vicinity of San Andrés Tuxtla. (See map 5.)

The locality records for the 13 specimens examined are:

No specific locality, L.M.K. No. 40299.

**MÉXICO: Veracruz:** Three to 4 miles west-northwest of Acayucan, U.M.M.Z. No. 112320 (intergrade with *malleisi*); San Juan de la Punta, E.H.T.-H.M.S. No. 27679; 10 miles east of San Juan de la Punta, U.S.N.M. Nos. 111193-111194; 2 miles northwest of Santiago Tuxtla, U.M.M.Z. No. 111931; 5 miles northwest of Santiago Tuxtla, U.M.M.Z. Nos. 111928-111930; near Tula, U.M.M.Z. No. 111932; between Volcán San Martín and San Andrés Tuxtla, U.I. No. 33868.

***Leptodeira frenata malleisi* Dunn and Stuart**

*Leptodeira yucatanensis malleisi* DUNN AND STUART, 1935, Occas. Papers Mus. Zool. Univ. Michigan, no. 313, pp. 1-3. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 696. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 327-328. SCHMIDT, 1941, Publ. Field Mus. Nat. Hist., zool. ser., vol. 22, no. 8, pp. 505-506. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 90; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 325.

*Leptodeira frenata malleisi*, DUELLMAN AND WERLER, 1955, Occas. Papers Mus. Zool. Univ. Michigan, no. 570, pp. 1-9, pl. 1.

**HOLOTYPE:** Number 73230 in the collection of the Museum of Zoology, University of Michigan, from Tuxpeña, Campeche, México; C. L. Lundell, collector.

**DESCRIPTION:** Males with 170-185 (179.0) ventrals and females with 170-188 (181.5) ventrals. Caudals in males 73-85 (78.3) and in females 64-76 (70.3). Maximum number of dorsal scale rows 21 in 33 specimens and 23 in five. Scale-reduction formula for four males:

19 +10 (26-36) - 21 9+10 (107-113) - 19 8+9 (118-125) - 17 7+8 (137-152) - 15 (174-181)

Scale-reduction formula for four females:

19 +10 (32-35) - 21 9+10 (106-121) - 19 8+9 (117-135) - 17 7+8 (146-158) - 15 (174-187)

The dorsal ground color is cream-brown to gray-brown, with 26 to 39 dark to medium brown blotches on the body. The blotches are outlined with dark brown or black. Dorsally the blotches are three to seven scales in length, but laterally they often cover only one or two. The blotches usually extend to the second or third scale row, although in some snakes they reach the first and in others do not reach the third. The interspaces, varying from one to three scales in length dorsally, are considerably longer laterally. The dark brown or black lateral intercalary spots extend from the edges of the ventrals onto the second and often the third scale row and may be two or three scales in length. Along the edges of the ventrals and on the first row of body scales is a row of irregular small brown spots. In some individuals these spots are fused to form irregular lines. (See pl. 14.) There are 11 to 20 dark tail blotches.

The top of the head is dark grayish brown as far back as the anterior edge of the parietals; this fades into the lighter ground color on the nape. One or two brown spots are present on each parietal. A nape stripe begins on the posteromedian edges of the parietals and usually extends posteriorly for three to five scales, but sometimes nearly reaches the first body blotch. The postorbital stripe extends posteriorly from the orbit, covering the lower postocular, the anterior part of the primary temporal, the dorsal part of the sixth upper labial, the middle of the seventh, and the ventral part of the eighth. In some specimens (40%) the stripe terminates there; in the rest it continues on the tenth lower labial, from whence it passes over dorsal body scale rows 2 to 6 and merges with the first body blotch. The lower posterior edge of the upper labials and the upper posterior edge of the lower labials are brown or black. The rest of the labials, the chin, and ventral surfaces are cream. (See pl. 14.)

Adult males range from 212 to 464 mm. (325 mm.) in body length and from 272 to 609 mm. (408 mm.) in total length; females range from 320 to 576 mm. (417 mm.) in body length and from 405 to 717 mm. (515 mm.) in total length. The smallest juvenile

available has a body length of 155 mm. and a total length of 203 mm.

**SEXUAL DIMORPHISM:** The number of caudals, the tail/body ratio, and the number of tail blotches show sexual dimorphism. The number of caudals in males averages 78.3 as opposed to 70.3 in females. The males have more tail blotches, an average of 16.7 as opposed to 13.5 in females. The tail/body ratio in males is 0.283-0.313 (0.299) and in females 0.244-0.299 (0.271).

**VARIATION:** There is an increase in the number and a corresponding decrease in size of the body blotches from Campeche south to Chiapas and Guatemala. Three specimens from Palenque, Chiapas, have light brown blotches edged with black. The one specimen from northeastern Quintana Roo has 34 solid brown body blotches that nearly reach the ventrals. On the basis of this specimen and of the similarity of the type of habitat with that of the lower part of the peninsula, that is, tropical forest, as contrasted with the more arid thorn forest of northwestern Yucatán, it may be postulated that the range of *L. f. malleisi* extends to the northeastern tip of the peninsula. (See map 5.) Six specimens are available from Isla de Cozumel; of these, four are males with ventral counts of 170-176 (174), and two are females with 170 and 179 (174.5). These averages are considerably lower than those for the race as a whole (179.0 and 181.5, respectively). Also, the color pattern is slightly different from that of more typical, southern mainland, *malleisi*. The number of body blotches varies from 24 to 29 (17). The blotches are solid brown in four specimens, and in the other two they are noticeably outlined with black. The blotches extend nearly to the ventrals; the lateral interspaces are only slightly shorter than the dorsal interspaces. In many respects these specimens resemble *L. f. yucatanensis*, but in the number of body blotches they are more like *malleisi*. Furthermore, the ventral counts more closely approach those of *malleisi* than those of *yucatanensis*. At the present time there is inadequate material for the populations of the northeastern part of the Yucatán Peninsula and Isla de Cozumel to be defined accurately. The apparent intermediate condition of the Cozumel population in

regard to the populations to the west and south may indicate that the Cozumel population became isolated when it was a part of an earlier, undifferentiated, *malleisi-yucatanensis* stock.

REMARKS: Intergradation with *L. f. yucatanensis* probably occurs in the zone of the tropical deciduous forest to the east and south of the arid scrub forest, a formation to which *yucatanensis* appears to be restricted. *Leptodeira f. malleisi* apparently thrives in the tropical rain forest and tropical savannas. Smith (1943a) collected this snake in bromeliads at Palenque, Chiapas, and Stuart (1935) found it around water holes near La Libertad, Guatemala.

RANGE: This subspecies occurs in the rain forests and tropical savannas from northern Chiapas, El Petén in Guatemala, and British Honduras northward through the Yucatán Peninsula with the exception of the arid northern part; Isla de Cozumel. (See map 5.)

Locality records for the 38 specimens examined are:

MÉXICO: *Campeche*: Balchacas, U.M.M.Z. No. 81919; Pital, E.H.T.-H.M.S. No. 11619; Tuxpeña, U.M.M.Z. Nos. 73229-73230. *Chiapas*: Palenque, U.S.N.M. Nos. 111258-111260. *Quintana Roo*: Colonia Santa María, U.M.M.Z. No. 76169; Isla de Cozumel, B.M.N.H. Nos. 86.4.15.23-86.4.15.24, U.M.M.Z. Nos. 76170, 78640-78642; Río Hondo, A.M.N.H. No. 68611.

BRITISH HONDURAS: *Belize*: Belize, U.S.N.M. Nos. 24901, 24908, 26354, 52309, 56010-56012; *Corozal*: Skate's Lagoon, C.N.H.M. No. 49343.

GUATEMALA: *El Petén*: Flores, C.N.H.M. No. 43374; La Libertad, A.M.N.H. Nos. 69989, 69991, C.N.H.M. Nos. 43371-43373, M.C.Z. No. 46512, U.S.N.M. Nos. 71367, 71369, U.M.M.Z. Nos. 74881, 74883, 74885-74886; Río San Pedro at Paso Caballos, M.C.Z. Nos. 38588-38589.

#### *Leptodeira frenata yucatanensis* Cope

*Leptodeira annulata* var. COPE, 1866, Proc. Acad. Nat. Sci. Philadelphia, p. 127 (original description of specimen from Yucatán).

*Sibon annulatum yucatanensis* COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 67 (name applied to description given in 1866).

*Sibon yucatanense* COPE, 1891, Proc. U. S. Natl. Mus., vol. 14, p. 677; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Leptodeira septentrionalis yucatanensis*, SCHMIDT AND ANDREWS, 1936, Publ. Field Mus. Nat. Hist., zool. ser., vol. 20, no. 18, p. 176.

*Leptodeira yucatanensis yucatanensis*, DUNN AND STUART, 1935, Occas. Papers Mus. Zool. Univ. Michigan, no. 313, pp. 1-3. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, pp. 695-696. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, p. 329. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, pp. 89-90; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 352.

*Leptodeira frenata yucatanensis*, DUELLMAN AND WERLER, 1955, Occas. Papers Mus. Zool. Univ. Michigan, no. 570, pp. 1-9, pl. 1.

HOLOTYPE: Number 24887 in the collection of the United States National Museum from Yucatán; A. Schott, collector. Smith and Taylor (1950) restricted the type locality to Chichén Itzá, Yucatán, México.

DESCRIPTION: Ventrals in males 177-186 (181.5), in females 175-192 (183.0); caudals in males 72-86 (79.0), in females 66-67 (66.7). Maximum number of dorsal scale rows 21 in 17 specimens and 23 in three. Scale-reduction formula for three males with counts of 19-21-15:

19 +10 (18-38) - 21 9+10 (111-118) - 19 8+9 (121-127) - 17 7+8 (143-154) - 15 (177-184)

Reduction in two females with 19-21-15 rows:

19 +10 (25-33) - 21 9+10 (112-114) - 19 8+9 (123-125) - 17 7+8 (165-184) - 15 (184-192)

Reduction in two specimens with 13 scale rows posteriorly:

Male: 19 +10 (40) - 21 9+10 (103) - 19 8+9 (115) - 17 7+8 (135) - 15 3+4 (169-174) - 13 (181)

Female: 19 +10 (33) - 21 9+10 (114) - 19 8+9 (125) - 17 7+8 (165) - 15 2+3 (178-180) - 13 (184)

Reduction in a female with 23 scale rows:

21 +11 (68) - 23 10+11 (108) - 21 9+10 (121)-19 8+9 (140) - 17 (183)

The dorsal body pattern consists of 18 to 26 dark brown blotches that extend to the first scale row or onto the edges of the ventrals. These blotches occupy five to eight scales dorsally and three to five laterally. The light tan or cream interspaces occupy two scales dorsally and three to five laterally. Dark brown lateral intercalary spots are present on the edges of the ventrals, the first, and sometimes the second, scale rows in the light



interspaces. There are eight to 16 dark blotches on the tail. The body blotches are usually a solid brown, but in a few individuals they are bordered with a darker brown or black. The edges of the blotches are wavy and uneven. (See pl. 15.) In juveniles the blotches are very dark, almost black, and the ground color is light cream, presenting a more contrastive pattern than in the adults.

The top of the head anterior to the eyes is brown; this fades posteriorly to the light tan or cream ground color on the nape. Dark brown or black flecks on the head may be fused into spots in the middle of the plates. There is a large dark spot in the middle of each parietal. Beginning on the postero-medial corners of the parietals and extending posteriorly for the length of three to five mid-dorsal scales is a dark nape stripe. This stripe does not touch the first body blotch. The parietal spots are usually not connected with the nape stripe. The loreal region is light brown or cream, and there may be an indistinct dark stripe anterior to the orbit. A dark brown postorbital stripe covers the lower postocular, lower part of the primary temporal, dorsal part of the sixth upper labial, entire seventh, and most of the eighth. It continues onto body scale rows 3 to 5 and connects with the first body blotch. (See pl. 15.) The labials are light tan or cream; the posterior edge of the upper labials and the upper part of the lower labials are banded with brown or black. The under surfaces are white or cream. In about one-third of the specimens examined there are small brown spots near the lateral edges of the gulars and ventrals 1 to 5.

Adult males range from 225 to 533 mm. (461 mm.) in body length and from 296 to 688 mm. (593 mm.) in total length; females range from 274 to 565 mm. (483 mm.) and from 336 to 705 mm. (547 mm.). The smallest juvenile, a male, measured 160 mm. in body length and 209 mm. in total length.

**SEXUAL DIMORPHISM:** As in the other forms of *L. frenata*, this subspecies shows strong sexual dimorphism in the number of caudals and in the tail/body ratio; however, the number of blotches is not significantly different, and there are insufficient data from which to determine whether or not the place of reduction from 19 to 17 dorsal body scale rows is

different in the sexes. Males have an average of 79.0 caudals, as opposed to 66.7 in females. The tail/body ratio in males is 0.278–0.322 (0.302), and in females, 0.226–0.262 (0.247).

**VARIATION:** In color pattern this race is quite uniform. The length of the light lateral interspaces is the most variable part of the color pattern. In some individuals the blotches are nearly straight-edged, not narrowing laterally so as to form saddle-shaped blotches.

**REMARKS:** In general appearance *yucatanensis* more closely resembles *frenata* than *malleisi*. The number of body blotches is much lower than in *frenata*, but the more or less uniform color of the blotches, the relatively short interspaces laterally, and the flecking on the head are similar.

**RANGE:** The nominal subspecies is found in the arid scrub forest and parts of the tropical deciduous forest zone of the northwestern part of the Yucatán Peninsula. (See map 5.)

Locality records for the 22 specimens examined are:

MÉXICO: *Yucatán*: U.S.N.M. No. 24887; Chichén Itzá, A.N.S.P. No. 18259, A.M.N.H. Nos. 7867–7871, C.H.N.M. Nos. 20604; 26983–26984, 36361, M.C.Z. Nos. 7242, 46889, U.S.N.M. No. 46397, U.M.M.Z. Nos. 73027–73028, 75589; Libre Unión, C.N.H.M. No. 36359; Mérida, C.N.H.M. No. 19421; Tekom, C.N.H.M. No. 49344; Yokt-zonot, C.N.H.M. Nos. 36360, 36362.

#### *Septentrionalis* GROUP

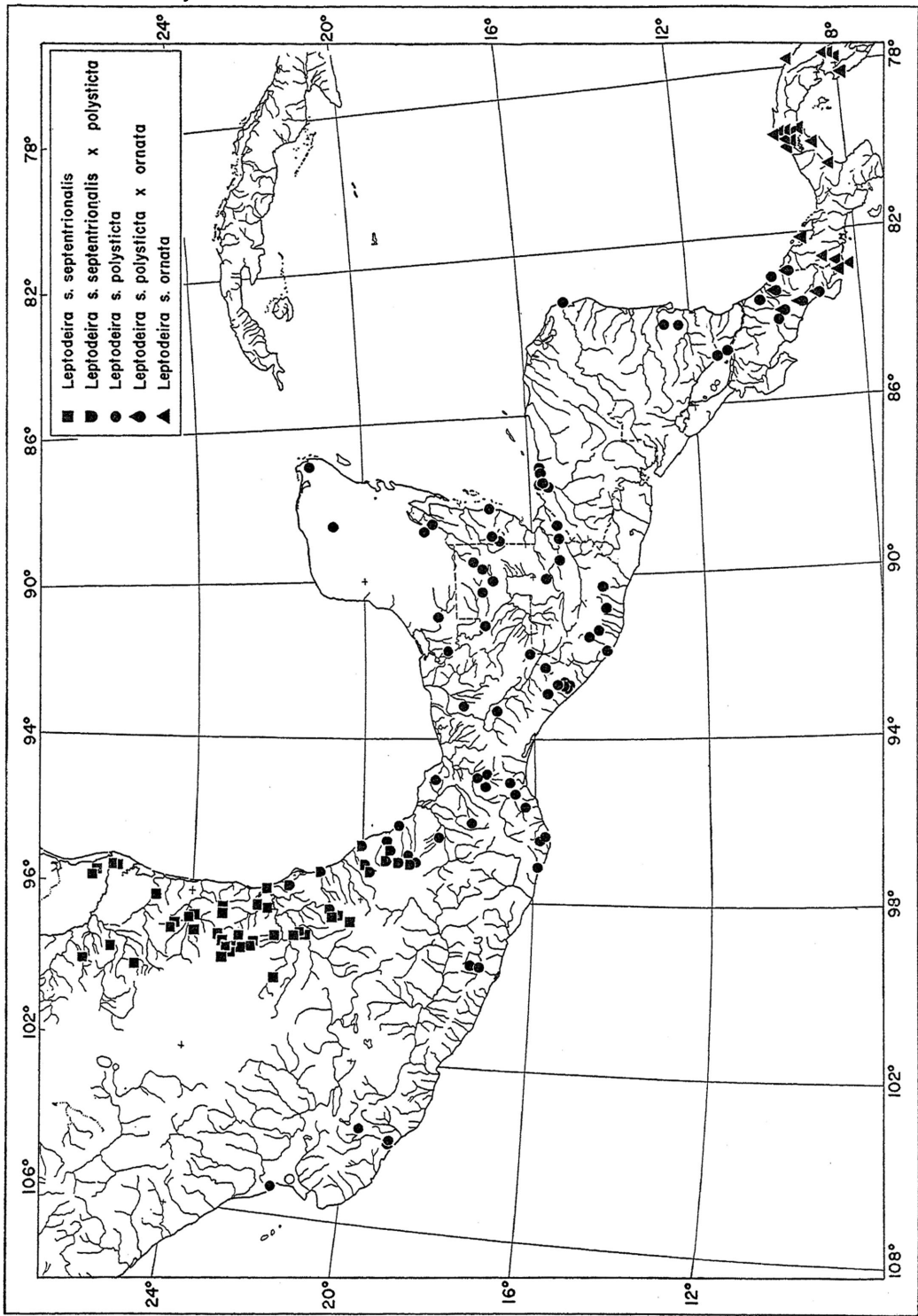
This group, composed of the species *septentrionalis*, with four subspecies, and *splendida*, with three subspecies, is characterized by a hemipenis with many spines and without a deep fold around the base of the capitulum, and a high number of maxillary teeth.

The species range from northern México to northern Peru on the west coast of South America.

#### *Leptodeira septentrionalis* Kennicott

*Dipsas septentrionalis* KENNICOTT, 1859, in Baird, Reptiles of the Boundary, vol. 2, p. 16, pl. 8, fig. 1.

**DISTRIBUTION:** This species is found in lowlands to elevations of about 2000 meters from the Rio Grande Embayment in Texas and northeastern México on the east and cen-



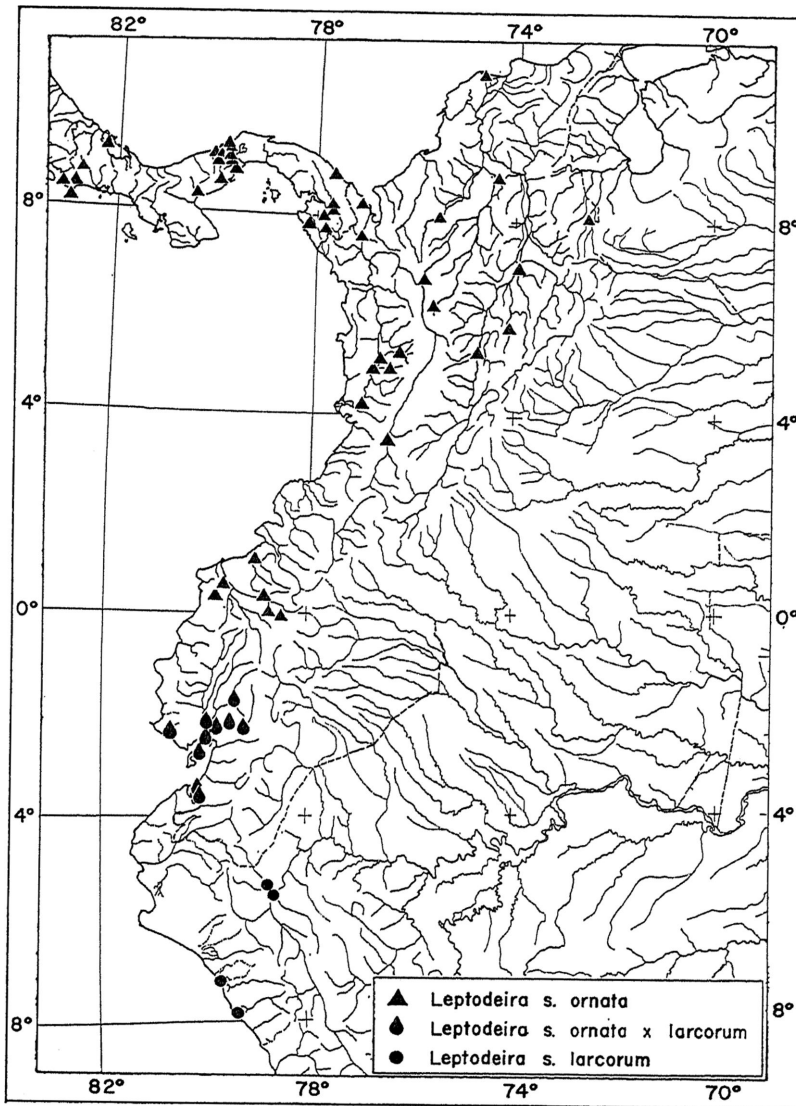
MAP 6. Locality records for *Leptodeira septentrionalis* in México and Central America.

tral Nayarit on the west, southward and eastward along both coasts of México and Central America, including the Yucatán Peninsula, but excluding the Balsas Basin, to the valleys of the Río Magdalena and Río Cauca in Colombia, along the Pacific slopes and coast of South America southward to northern Peru, and in the upper Río Marañón valley in Peru. (See maps 6 and 7.)

DESCRIPTION: Head distinct from neck; rostral barely visible from above; prefrontals square, half again as long as the internasals; upper preocular in contact with frontal or

not; preoculars usually two or three, sometimes one; postoculars normally two; temporals normally one plus two plus three; upper labials normally eight, with fourth and fifth entering orbit; lower labials usually 10, often 11, sometimes 12; chin shields subequal in length; lower labials 1 to 5 in contact with anterior chin shield, 5 and 6 in contact with posterior one.

Dorsal scales smooth; vertebral and paravertebral rows enlarged or not; scales usually in 21 or 23 rows, sometimes 19 at midbody, and reducing to 17 or 15 rows posteriorly.



MAP 7. Locality records for *Leptodeira septentrionalis* in South America.

Dorsal-scale reduction takes place by the fusion of the paravertebral row with the adjacent lateral row or with the vertebral row. The body may be rounded or laterally compressed.

The ranges and means of tooth counts based upon seven specimens are: maxillary, 14-18+II (15.9); palatine, 9-11 (9.9); pterygoid, 23-28 (25.6); and dentary, 20-26 (23.7).

The hemipenis has a length *in situ* of seven to nine caudals. There are two primary longitudinal rows of five spines of which the proximal ones are the largest. These rows are bordered by four longitudinal rows of smaller spines. The capitulum is rounded and finely crenulated. The base is covered with spinules.

The dorsal color pattern consists of dark brown or black blotches on a cream to grayish brown ground color. These blotches may be large, few in number, and extend to the ventrals, or they may be small and confined to the dorsal part of the body. Lateral intercalary spots may be present. The head is brown, with or without dark markings. A nape stripe may be present.

The total length may exceed 1000 mm. The tail/body ratio ranges from 0.207 to 0.405.

**GEOGRAPHICAL VARIATION:** There is considerable variation in the color pattern, scutellation, and body form in this species. The specimens from southern Texas and northeastern México are rather robust and round-bodied; those from southern México and northern Central America are more slender; those from southern Central America, Colombia, and Ecuador are laterally compressed; in Peru they are again round-bodied.

In color pattern, those from northeastern México and southern Texas are unique in having few large blotches that reach the ventrals and in not having lateral intercalary spots. The individuals from southern México, Yucatán Peninsula, and northern Central America have a high number of blotches, large lateral intercalary spots, and a nape stripe. The South American specimens, with the exception of those from Peru, have fewer blotches than do individuals from southern México and may or may not have a nape stripe. The snakes from Peru have a dark, butterfly-shaped mark on the nape, large, lateral, intercalary spots, and fewer body blotches than those from Colombia and

Panamá. Geographical trends in this species are shown in figure 9.

*Leptodeira septentrionalis* has become adapted to a terrestrial life in semi-arid regions as well as to an arboreal one in rain forests. The enlarged vertebral scale row and laterally compressed body of the specimens from the wet forests of the Pacific slopes of Colombia and northern Ecuador and from lower Central America are parallel adaptations to those shown in *L. annulata*.

The populations in northwestern South America and lower Central America, here regarded as *septentrionalis*, have been considered by other workers to be conspecific with *annulata*, and most herpetologists have referred those populations to *L. a. annulata*. I have been unable to find any direct geographical connection between the populations of *annulata* in the Amazon Basin and those that I call *septentrionalis* in lower Central America and northwestern South America. Furthermore, it is now evident that *L. a. annulata* is conspecific with *rhombifera*, the range of which broadly overlaps that of *septentrionalis*.

On the basis of characters previously mentioned, four geographic races of *septentrionalis* are recognized. The diagnostic characters of the four subspecies are given in table 22.

***Leptodeira septentrionalis septentrionalis***  
Kennicott

*Dipsas septentrionalis* KENNICOTT, 1859, in Baird, Reptiles of the Boundary, vol. 2, p. 16, pl. 8, fig. 1.

*Eteirodipsas annulata* var. *septentrionalis*, JAN AND SORDELLI, 1870, Iconographie général ophiidiens, pt. 1, fig. 2.

*Sibon annulatum septentrionale*, COPE, 1875, Bull. U. S. Natl. Mus., no. 1, p. 38. YARROW, 1882, Bull. U. S. Natl. Mus., no. 24, p. 98. COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 67.

*Sibon septentrionale*, COPE, 1891, Proc. U. S. Natl. Mus., vol. 14, pp. 677-678; 1900, Rept. U. S. Natl. Mus., for 1898, pp. 1107-1108.

*Leptodeira annulata*, GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 170.

*Leptodeira septentrionalis*, STEJNEGER, 1891, Proc. U. S. Natl. Mus., vol. 14, p. 505. BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 93. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, p.

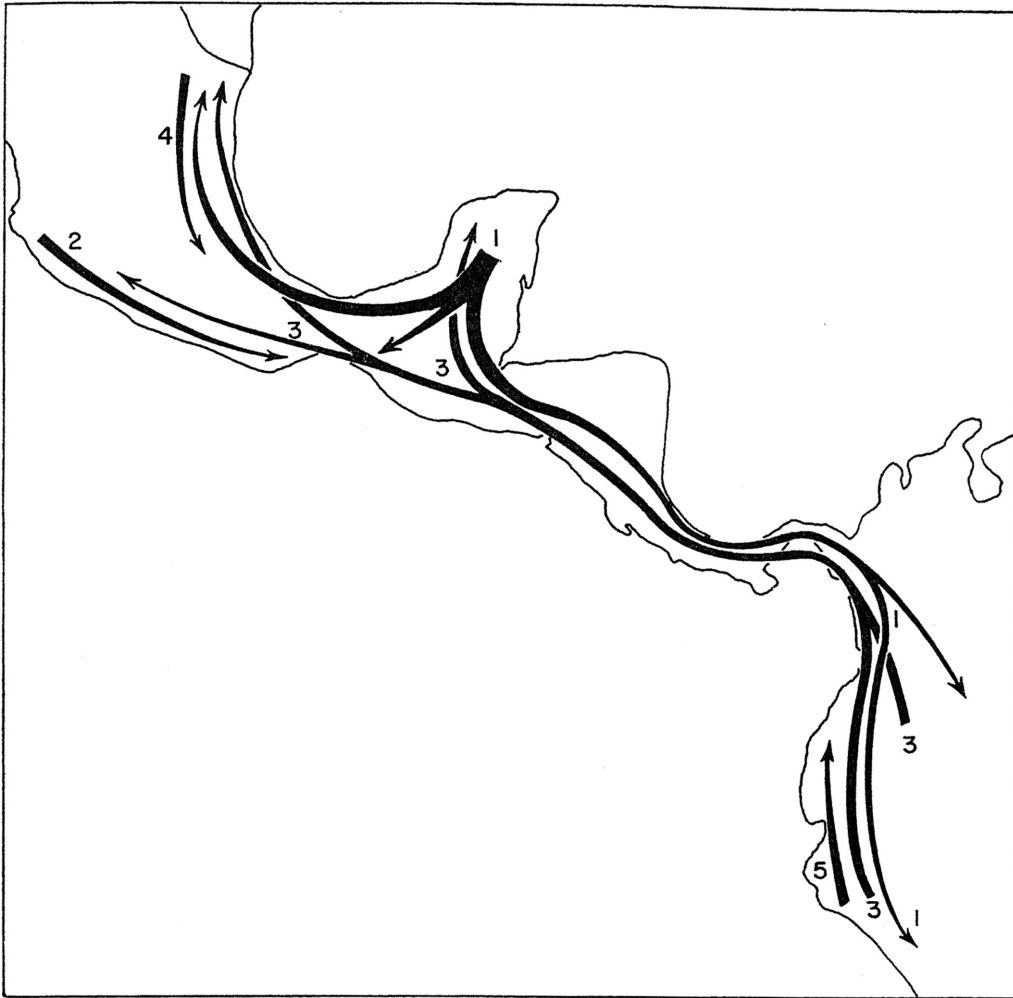


FIG. 9. Geographical gradients in *Leptodeira septentrionalis*. Arrows represent the various geographical trends: 1, a gradient for a decrease in the numbers of body blotches, ventrals, and caudals; 2, a trend similar to 1 on the Pacific coast of México; 3, a trend for an increase in the number of dorsal scale rows and the number of preoculars; 4 and 5, trends from a snake with a round body to one with a laterally compressed body. The arrows indicate only character gradients and not evolutionary trends.

902, pl. 73, fig. 5. WERNER, 1924, Arch. Naturgesch., vol. 12, p. 125. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 329-331, pl. 31, fig. 3.

*Leptodeira annulata septentrionalis*, AMARAL, 1929, Mem. Inst. Butantan, vol. 4, p. 78. SMITH, 1941, Proc. Biol. Soc. Washington, vol. 54, p. 117; 1943, Proc. U. S. Natl. Mus., vol. 93, p. 439. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 87; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 361. BROWN, 1950, An annotated checklist of the reptiles and amphibians of Texas, p. 166. SCHMIDT, 1953, A check-list of North

American amphibians and reptiles, ed. 6, p. 218.

*Leptodeira septentrionalis septentrionalis*, DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 697.

**HOLOTYPE:** Kennicott designated three syntypes, two (U.S.N.M. No. 4267) from Matamoras, Tamaulipas, México, collected by Lieutenant Couch, and one (U.S.N.M. No. 2288) from Brownsville, Cameron County, Texas, collected by Captain S. Van Vliet. Smith and Taylor (1950) restricted the type locality to Brownsville, and by so doing desig-

TABLE 22

COMPARISON OF DIAGNOSTIC CHARACTERS OF THE FOUR SUBSPECIES OF *Leptodeira septentrionalis*  
(Counts in parentheses occur in more than 10 per cent of the population, but never in more than 25 per cent.)

Subspecies	Body Shape	Scale Rows	Preoculars	Body Blotches (Mean)	Lateral Intercalary Spots
<i>larcorum</i>	Rounded	21 (23)	2 (1 or 3)	42.0	Present
<i>ornata</i>	Compressed	21 (19 or 23)	2 (1 or 3)	39.6	Present
<i>polysticta</i>	Slightly compressed	23 (21)	3 (2)	53.6	Present
<i>septentrionalis</i>	Rounded	23	3	26.2	Absent

nated U.S.N.M. No. 2288 as the lectotype. This specimen was lost for many years, but it recently was found and recatalogued as U.S.N.M. No. 131739.

DESCRIPTION: Preoculars three; fourth and fifth labials entering the orbit; males with 181-199 (190.8) ventrals, and females with 185-208 (194.7) ventrals; caudals in males 66-94 (78.7) and in females 60-81 (70.5). Body rounded, not laterally compressed; vertebral and paravertebral scale rows not or only slightly enlarged. Dorsal scales smooth and usually in 21-23-17 rows in females and 21-23-15 rows in males. A few individuals have a maximum of 21 rows at midbody. Scale-reduction formula for six males:

21 +11 (41-76) - 23 10+11 (106-117) - 21 9+10 (120-128) - 19 8+9 (133-139) - 17 7+8 (159-186) - 15 (189-197)

Reduction formula for six females:

21 +11 (32-45) - 23 10+11 (105-117) - 21 9+10 (118-127) - 19 8+9 (136-143) - 17 (191-201)

The dorsal ground color is cream to reddish tan. There are 20-35 (26.2) dark brown to black dorsal body blotches that usually extend onto the first scale row but sometimes onto the edges of the ventrals or only to scale rows 2 or 3. The blotches are five to nine scales in length, three to four times the length of the dorsal light interspaces. Usually the blotches are almost as long laterally as dorsally; however, in some individuals the blotches are saddle-shaped, leaving wider interspaces laterally. In these individuals there may be small, dark brown, lateral, intercalary spots on the first and second scale rows. The anterior body blotch is always no-

ticeably longer than the others. (See pl. 16.) There are eight to 19 dark tail blotches. The ventral surfaces are cream; there may be brown flecks on the edge of the ventrals.

The dorsal surface of the head is grayish brown. An indistinct and highly variable pattern of dark brown or black markings on the head usually consists of a group of one to three small spots on the frontal and a longitudinal dark dash or series of spots on each parietal. These are often fused with the spots on the frontal. There may be a dark brown border on the lateral edge of each parietal. There is always a short nape stripe that begins on the postparietals and extends posteriorly for two or three scales. In a few individuals the stripe extends for four or five scales and sometimes comes in contact with the first body blotch. The temporal region is brown to grayish brown; the upper secondary and tertiary temporals may be dark brown or black. A dark postorbital stripe begins on the postoculars or anterior temporal and passes over the lower secondary temporal, the top of the seventh upper labial, and the middle of the eighth to the corner of the mouth. The upper labials are brown or gray, with their anterior edges cream; the lower labials are cream, the anterior three or four usually smudged with gray. (See pl. 16.)

Males range from 270 to 595 mm. (444 mm.) in body length and from 345 to 810 mm. (532 mm.) in total length; females range from 392 to 774 mm. (583 mm.) in body length and from 430 to 985 mm. (654 mm.) in total length. The smallest specimen examined is a male with a body length of 166 mm. and a total length of 216 mm.

**SEXUAL DIMORPHISM:** Males differ significantly from females in the number of caudals and in the tail/body ratio. Caudals in males average 78.7, in females, 70.5. In males the tail/body ratio ranges from 0.238 to 0.349 (0.285), in females, from 0.207 to 0.283 (0.246). There is an average difference in the number of tail blotches, 13.1 in males as compared with 11.6 in females. The number of dorsal scale rows posteriorly in males usually is 15, whereas in females the minimum number usually is 17.

A juvenile from Tamazunchale, San Luis Potosí (U.M.M.Z. No. 114580), in life had a light tan dorsum with dark brown blotches and a pale cream venter; the iris was reddish brown.

**REMARKS:** Specimens from northern and central Veracruz are intermediate between *polysticta* and *septentrionalis* in that they have body blotches of an intermediate size and a partially developed nape stripe. This is the population that was named *L. annulata taylori* by Smith. The type specimen is much

TABLE 23  
GEOGRAPHICAL VARIATION IN DORSAL BODY PATTERN IN *Leptodeira septentrionalis septentrionalis*

Locality	Body Blotches	Lateral Extent of Blotches	Intercalary Spots
Nuevo Leon	(7)		
	22.6	Ventrals	Absent
Texas and northern Tamaulipas	20-27		
	(14)	Ventrals	Absent
Southern Tamaulipas	24.0		
	21-27		
San Luis Potosí	(28)		
	25.9	Scale row 1	Absent
Hidalgo	20-34		
	(10)	Scale row 2 or 3	Present
Hidalgo	28.9		
	24-34	Scale row 2 or 3	Present
Hidalgo	(6)		
	28.7		
	23-34		

**VARIATION:** There is a latitudinal gradient in the number and shape of the body blotches. (See table 23.) In specimens from the northern part of the range the blotches have straight edges and extend to or onto the edges of the ventrals, and there are no lateral intercalary spots. Towards the southern part of the range in San Luis Potosí and Hidalgo the blotches are saddle-shaped and extend laterally only to the second or third scale row. In these the lateral intercalary spots are usually present on the first and second scale rows. The specimens from the vicinity of Sabinas Hidalgo, and Santiago, Nuevo Leon, have a pale cream ground color that is noticeably lighter than that in individuals from other parts of the range. This may be a response to the arid environment in that part of Nuevo Leon, an area that is perhaps drier than any other inhabited by this form.

closer to *polysticta* than *septentrionalis*; consequently, *taylori* is synonymized with *polysticta*.

**RANGE:** *Leptodeira s. septentrionalis* occurs in the Rio Grande Embayment in southern Texas, the lowlands of northeastern México southward to the Río Panuco, and in the Sierra Madre Oriental from southern Tamaulipas southward to Hidalgo. (See map 6.) It has been found from elevations near sea level to about 2000 meters; it inhabits scrub forest and tropical deciduous forest, and has been found in cleared areas within cloud forest.

The locality records for the 79 specimens examined are:

**UNITED STATES:** *Texas:* Cameron County, U.S.N.M. No. 17066; Cameron County, Brownsville, A.N.S.P. No. 22242, C.N.H.M. No. 38055, M.C.Z. No. 5864, U.S.N.M. Nos. 1312, 131739; Hidalgo County, 2 miles northwest of Edinburg,

Ch.A.S. No. 6349; Hidalgo County, 19 miles north of McAllen, U.T. No. 14194.

México: *Hidalgo*: Near San Francisco, E.H.T.-H.M.S. No. 16146; Zacualtipan, A.N.S.P. Nos. 11662-11663, 14775; 5 miles south of Zacualtipan, E.H.T.-H.M.S. No. 23995. *Nuevo Leon*: Sabinas Hidalgo, C.N.H.M. Nos. 34418, 34420; Santiago, Horsetail Falls, C.N.H.M. Nos. 30823, 34419; Santiago, Las Adjuntas, C.N.H.M. No. 37030; Santiago, Vista Hermosa, C.N.H.M. Nos. 37028-37029. *San Luis Potosí*: L.S.U. Nos. 303, 5872, M.C.Z. No. 4516; Ebano, L.S.U. No. 300; Huichihuayan, B.C.B. No. 2602; La Joya, 5 kilometers west of Aquismón, L.S.U. No. 4872; Luna Media, L.S.U. No. 5380; 4 miles north-northwest of Tamazunchale, U.M.M.Z. No. 114580; Valles, A.M.N.H. No. 67314, C.N.H.M. Nos. 37031-37032, T.U. No. 16006 (2); 13 miles northeast of Valles, U.F. No. 3447; Xilitla region, L.S.U. No. 304, U.K. Nos. 24020-24021; Xilitla region, Apetsco, L.S.U. No. 592. *Tamaulipas*: Aserrado del Paraiso, 10 miles north-northwest of Chamal, U.M.M.Z. No. 109728; Cerro Gordo, 8 miles south-southwest of Llera, U.M.M.Z. No. 110788; Gómez Farías, U.M.M.Z. Nos. 109718-109719; 5 miles northwest of Gómez Farías, U.M.I., U.M.M.Z. Nos. 102897, 102984, 108790, 109721-109722, 109726-109727; Hacienda La Clementina, E.H.T.-H.M.S. No. 4616; La Joya de Salas, U.M.M.Z. Nos. 101268, 109725; La Unión, 9.5 kilometers north of Gómez Farías, T.U. Nos. 15464 (2), 15485, 15513; Las Flores, near Morón, U.O.; Marmolejo, U.M.M.Z. No. 69250; Matamoros, A.N.S.P. No. 10085, M.C.Z. No. 415, U.S.N.M. Nos. 4267 (2), 4273, U.M.M.Z. No. 3791; Pano Ayuctle, 5 miles northeast of Gómez Farías, U.M.M.Z. No. 109720; Rancho Santa Ana, 8 miles southeast of Padilla, M.C.Z. Nos. 46325-46327; Río Corona at Victoria, Jiménez road, M.C.Z. No. 46324; Río Guayalejo near Magiscatzin, M.C.Z. No. 45559; Río Purificación at Padilla, T.U. No. 15975; Río Sabinas, 3 miles northeast of Gómez Farías, U.M.M.Z. No. 109723; San Fernando, B.C.B. No. 2601; Santa Barbara, foothills of Sierra de Tamaulipas, U.M.M.Z. No. 109724; Santa María, Sierra de Tamaulipas, U.M.M.Z. No. 102896; Tamaulipeca, U.M.M.Z. No. 69249; Tampico, B.M.N.H. No. 94.12.28.16; 7 miles west of Victoria, U.I. No. 17826.

Locality records for 24 specimens considered to be intergrades between *L. s. septentrionalis* and *polysticta* are:

México: *Hidalgo*: Tianguistengo, E.H.T.-H.M.S. No. 16147. *Veracruz*: Coscomatepec, U.K. No. 26474; Cuautlapan, B.C.B. Nos. 2608, 2930; Huatusco, B.M.N.H. No. 94.12.28.19; Jalacingo, A.M.N.H. No. 4286; Jalapa, B.M.N.H.

No. 81.10.31.54, M.C.Z. Nos. 2842, 16103; Jiclatepec, A.N.S.P. Nos. 11695, 11717; Jico, C.N.H.M. No. 1346; Mirador, M.C.Z. No. 46859, U.S.N.M. No. 12113 (5); 39 miles south of Tampico, U.I. No. 33865; 4 kilometers west of Tlapacoyan, U.K. No. 23914; Tuxpan, U.S.N.M. Nos. 25206-25207, 25209-25211.

***Leptodeira septentrionalis polysticta* Günther**

*Leptodeira polysticta* GÜNTHER, 1895, *Biologia Centrali-Americana*, Reptilia, p. 172, pl. 55.

*Leptodeira albofusca*, BOULENGER, 1896, (in part), *Catalogue of the snakes in the British Museum*, vol. 3, pp. 95-97. MOCQUARD, 1908, (in part), *in* Duméril and Bocour, *Mission scientifique au Mexique et dans l'Amérique Centrale*, vol. 3, pp. 905-906.

*Leptodeira annulata polysticta*, DUNN, 1936, *Proc. Natl. Acad. Sci.*, vol. 22, p. 693. TAYLOR, 1938, *Univ. Kansas Sci. Bull.*, vol. 25, no. 15, pp. 331-333, pl. 30, fig. 3. SMITH AND TAYLOR, 1945, *Bull. U. S. Natl. Mus.*, no. 187, p. 87; 1950, *Univ. Kansas Sci. Bull.*, vol. 33, no. 8, p. 316.

*Leptodeira annulata taylori* SMITH, 1941, *Proc. Biol. Soc. Washington*, vol. 54, pp. 115-117. SMITH AND TAYLOR, 1945, *Bull. U. S. Natl. Mus.*, no. 187, p. 87.

HOLOTYPE: Eight specimens from México and Central America are syntypes. Smith and Taylor (1950) restricted the type locality to Belize, British Honduras. This action designated a specimen numbered 1946.1.8.45 in the collection of the British Museum (Natural History) as the lectotype; Frederick Godman, collector.

DESCRIPTION: Preoculars usually three, sometimes two, rarely one or four; fourth and fifth upper labials normally enter the orbit, occasionally the third also. The body is slender and slightly laterally compressed; the vertebral and paravertebral scale rows may be slightly enlarged. Males have 186-208 (197.6) ventrals, and females have 186-211 (199.7); caudals in males 84-106 (95.0), in females 73, 107 (91.4). Dorsal scales usually in a maximum of 23 rows; sometimes there are only 21. Posteriorly the scales are usually in 15 rows, and sometimes in 17. Scale-reduction formula for six males:

$$21 + 11 (51-53) - 23 10 + 11 (121-124) - 21 9 + 10 (122-135) - 19 8 + 9, \text{ or } 9 + V (134-151) - 17 8 + V (147-180) - 15 (197-201)$$

Reduction formula for six females:

$$21 + 11 (43-49) - 23 10 + 11 (116-124) - 21 9 + 10$$



(123-234) - 19 8+9, or 9+V (134-155) - 17 (199-206)

The dorsal ground color is yellowish to grayish tan. There are 38 to 70 (53.6) brown dorsal body blotches that are equal to or shorter than the light dorsal interspaces. At midbody the blotches are from one to three scales in length and extend laterally onto scale rows 5 to 7. Brown lateral intercalary spots. (See pl. 17.) The paired nuchal blotches are four to six scales in length; the posterior edges of the nuchal blotches may fuse to form a U-shaped mark. There is an irregular row of dark spots on the dorsal surface of the tail. The ventral surfaces are a cream color.

The top of the head is yellowish to grayish brown. There are scattered, irregular, dark brown spots on the prefrontals, frontal, and parietals. Often some of these spots are fused to form short stripes. A dark brown nape stripe begins on the posteromedian edges of the parietals and extends posteriorly for the length of four or five scales, sometimes to connect with the fused nuchal blotches. A thin, brown, postorbital stripe begins on the postoculars and passes over the anterior edge of the primary temporal, the bottom of the lower secondary temporal, the top of the sixth upper labial, and the middle of the eighth to the corner of the mouth. The labials are cream, sometimes smudged with gray or brown. (See pl. 17.)

Males range from 257 to 700 mm. (467 mm.) in body length and from 340 to 965 mm. (624 mm.) in total length; females range from 272 to 820 mm. (505 mm.) in body length and from 346 to 1055 mm. (666 mm.) in total length. The smallest juvenile examined is a female with a body length of 164 mm. and a total length of 205 mm.

**SEXUAL DIMORPHISM:** There are slight differences between the sexes in the number of caudals and the relation of tail to body length. Caudals in males average 95.0 and in females 91.4. The tail/body ratio in males is 0.271-0.379 (0.335), and in females, 0.266-0.376 (0.299). Males usually have 15 scale rows posteriorly, whereas only about half of the females have that number.

**VARIATION:** Specimens from México, British Honduras, Guatemala, and Honduras usually have a yellowish tan ground color; those from Nicaragua and northern Costa

Rica have a slightly darker ground color, making the dark spots less distinct. There is considerable geographic variation in the number of body blotches. Individuals from southern Veracruz have an average of 45 blotches, thus showing a trend towards *septentrionalis* in northeastern México. The populations in the Yucatán Peninsula and on the Pacific coast of México west of the Isthmus of Tehuantepec have an average of 52 blotches. The highest number of blotches is found in individuals from the Pacific coast of Chiapas where the range is 47 to 67 (57); the average number of body blotches in specimens from Guatemala, Honduras, Nicaragua, and northern Costa Rica is 54, 52, 47, and 44, respectively.

Individuals from the northern part of the range of *polysticta* have the highest number of ventrals; males from Yucatán have an average of 203, and males from Colima and Jalisco, 205. There is a gradual decline in the average number of ventrals southeastward through Central America; males from Costa Rica have an average of 194.

Usually there are three preoculars in Mexican and Guatemalan specimens; in Nicaragua and Costa Rica usually there are only two. The maximum number of dorsal scale rows shows a similar pattern of variation; specimens from México and Guatemala usually have 23 rows; those from the southern part of the range have 21 rows.

A specimen from Catemaco, Veracruz (U.M.M.Z. No. 114583), in life had a dirty yellowish tan dorsum fading to pale yellow below; the blotches were dark brown, and the iris was pale yellowish gray.

**REMARKS:** In northeastern México *polysticta* is replaced by *septentrionalis*. The geographical gradients in scutellation and color pattern culminate in an intergrading population between *polysticta* and *ornata* in Costa Rica. Typical *polysticta* have body blotches that are only one to three scales in length and extend laterally to scale rows 5 to 7. In Costa Rica the condition changes; there the body blotches are three to five scales in length and extend laterally to scale rows 4 to 6. Thus a more ovoid blotch replaces the cross-bar type found in *polysticta*.

*Leptodeira s. polysticta* is an inhabitant of forested areas. It has been collected from 150

to 1800 meters on the Pacific slopes in Chiapas. Stuart (1954b) reported a specimen from 2200 meters in southeastern Guatemala.

RANGE: *Leptodeira s. polysticta* occurs in the lowlands and to elevations slightly in excess of 2000 meters from Nayarit and southern Veracruz, México, including the Yucatán Peninsula, southward and eastward to central Costa Rica, being found only in local mesic habitats on the dry Pacific coast from El Salvador to Costa Rica. (See map 6.)

The locality records for the 230 specimens examined are:

MÉXICO: *Campeche*: Encarnación, U.I. No. 17789; Pital, E.H.T.-H.M.S. No. 11617; Río Candelaria, Pacaytún, C.N.H.M. No. 36325. *Chiapas*: Berriozabál, M.C.Z. No. 54359; Cerro Ovando, U.M.M.Z. Nos. 87690-87692; Chicomuselo, U.M.M.Z. No. 94602; 7.5 miles southeast of Comitán, U.M.M.Z. No. 94603; near Escuintla, U.M.M.Z. Nos. 88249 (2), 88301, 88306; 6 kilometers northeast of Escuintla, U.M.M.Z. Nos. 87672-87684, 87689; 30 kilometers northeast of Escuintla, U.M.M.Z. Nos. 87685, 87687-87688; Finca Juarez, U.S.N.M. Nos. 111245-111254; Finca Prussia, U.M.M.Z. No. 95154; La Esperanza, U.S.N.M. Nos. 111239-111241, U.M.M.Z. Nos. 94601, 98012; La Magnolia, U.S.N.M. No. 111244; 4.6 miles south of La Trinitaria, U.M.M.Z. No. 114582; Las Nubes, Cerro Ovando, U.S.N.M. Nos. 111228-111230; 15 miles south of Pichucalco, U.I. No. 6176; Rancho Las Gradass, U.S.N.M. Nos. 111242-111243; Salto de Agua, U.S.N.M. Nos. 111231-111238. *Colima*: Hacienda Paso del Río, E.H.T.-H.M.S. No. 4620, 2 kilometers west of Hacienda Paso del Río, U.M.M.Z. No. 80020. *Guerrero*: Acahuitzotla, T.C.W.C. Nos. 7440, 8577, 9500; Agua del Obispo, E.H.T.-H.M.S. No. 23514, T.C.W.C. No. 7448, U.S.N.M. No. 111224; Malinoltepec, Z.M.B. No. 34293. *Jalisco*: Nevado de Colima, B.M.N.H. No. 1906.6.1.223, N.M.W. No. 14408. *Nayarit*: Compostela (Smith, 1943b); 4 miles east of San Blas, U.M.M.Z. No. 114584. *Oaxaca*: Camotlan, U.S.N.M. Nos. 120952, 120954; El Soledad, U.I. Nos. 6164-6175; 25 miles southeast of Jesús Carranza (Veracruz), U.K. No. 27561; 30 kilometers southeast of Jesús Carranza (Veracruz), A.M.N.H. No. 62275; Lachigiuri, U.S.N.M. No. 111225; La Concepción, U.S.N.M. No. 111226; Lagartero, U.I. Nos. 6162-6163; Río Sarabia, 2.8 miles north of Sarabia, U.M.M.Z. No. 114581; Pluma Hidalgo, A.M.N.H. No. 19725; Quiengola, A.M.N.H. No. 65125; San Felipe Lachillo, E.H.T.-H.M.S. No. 27515; Soyaltepec, Tuxtepec, U.C.L.A. No. 5009; Zavaleta Cañon, B.M.N.H. No. 98.3.7.1. *Quintana Roo*: Colonia Santa María, U.M.M.Z. No. 76168;

Felipe Carillo Puerto, U.M.M.Z. Nos. 113559-113560; Laguna Chacanbacab, M.C.Z. No. 53120; Xcopen, M.C.Z. No. 9596. *Veracruz*: 1.5-2 miles east of Acultzingo, E.H.T.-H.M.S. No. 4618; 6.4 miles south of Catemaco, U.M.M.Z. No. 114583; Cerro Gordo, U.S.N.M. No. 111257; Orizaba, U.S.N.M. Nos. 7088, 30207-20308; Veracruz, U.S.N.M. No. 30508; west of Veracruz, U.S.N.M. No. 65154. *Yucatán*: Chichén Itzá, C.N.H.M. Nos. 20620, 36325, M.C.Z. No. 26838, U.M.M.Z. Nos. 68230, 73036.

BRITISH HONDURAS: No specific locality, B.M.N.H. Nos. 1924.2.18.8, 1935.2.4.1, C.N.H.M. Nos. 4250-4253. *Cayo*: Cohune Ridge, U.M.M.Z. Nos. 80715-80717; San Augustine, U.M.M.Z. No. 80718. *Stann Creek*: Stann Creek, M.V.Z. No. 45490, U.S.N.M. No. 26058.

COSTA RICA: No specific locality, A.M.N.H. Nos. 60458, 62114, U.K. No. 34031. *Limón*: Limón, A.M.N.H. No. 6755, M.C.Z. Nos. 12561, 22370; Los Diamantes, 2.5 miles south of Guápiles, U.K. No. 25473; Suretka, U.K. Nos. 39003-39004.

GUATEMALA: No specific locality, A.M.N.H. Nos. 17305, 17360-17361. *Alta Verapaz*: Cobán, Z.S.B.S. No. 2019/0; Finca Chama, Río Negro, U.M.M.Z. Nos. 91056-91057; Panzos, U.M.M.Z. No. 91058; Río Polochic, near Panzos, U.S.N.M. No. 115503. *Chimaltenango*: Finca Recreo, U.M.M.Z. Nos. 107263-107264, 107266; Finca Victoria, U.M.M.Z. No. 107265; Yepocapa, U.M.M.Z. Nos. 107027-107033, 107261. *El Petén*: La Libertad, C.N.H.M. Nos. 43375-43376, U.S.N.M. Nos. 71788-71790, U.M.M.Z. Nos. 74872-74880; Paso Caballos, Río San Pedro, M.C.Z. No. 38590; Piedras Negras, U.S.N.M. No. 111227; Tikal, U.M.M.Z. Nos. 115661-115666, 115668-115669; Uaxactun, A.M.N.H. No. 70943. *Guatemala*: Lago Ayarza, U.S.N.M. No. 125340. *Izabal*: Quirigua, C.N.H.M. Nos. 20548-20551; Río Bobos, near Playitas, C.N.H.M. No. 20119. *Jalapa*: Aserradero San Lorenzo, U.M.M.Z. No. 106720. *Quezaltenango*: Volcan Zunil, C.A.S. Nos. 66937-66938. *Retalhuleu*: S.U. No. 4068; Hacienda Casa Blanca, U.M.M.Z. No. 107268. *San Marcos*: Finca La Paz, 2 kilometers northwest of La Reforma, U.M.M.Z. Nos. 98318, 106721 (2), 115667. *Santa Rosa*: Finca La Gloria, U.M.M.Z. Nos. 106719, 107267. *Sololá*: Finca Monte del Oro, U.M.M.Z. No. 107262; Mocá, C.N.H.M. No. 20169; Río Mocá, A.M.N.H. No. 38091.

HONDURAS: No specific locality, A.M.N.H. Nos. 58806, 58844; Subirana Valley, M.C.Z. Nos. 38751-38752. *Atlántida*: Hicaque, M.C.Z. Nos. 22019-22022; Lancetilla, A.M.N.H. No. 70235; Río Ulúa, M.C.Z. Nos. 20227, 21183; Tela, M.C.Z. Nos. 19953, 29610, U.S.N.M. No. 64683; Toloa, M.C.Z. No. 21196. *Cortez*: San Pedro Sula,

M.C.Z. No. 27254; west of San Pedro Sula, C.N.H.M. No. 5310. *Yoro*: Portillo Grande, C.N.H.M. Nos. 38228, 41048.

NICARAGUA: No specific locality, C.M. No. 2059. *Cabo Gracias a Dios*: Cabo Gracias a Dios, U.S.N.M. Nos. 15308-15309. *Chontales*: Río San Juan (Colorado Junction), U.S.N.M. Nos. 19573-19574; San Miguelito, A.M.N.H. No. 12687. *Zelaya*: Pichinga, A.M.N.H. No. 70253; Santa Ana, Río Huahuashan, A.M.N.H. No. 70255.

Locality records for 17 specimens considered to be intergrades between *L. s. polyistica* and *ornata* are:

COSTA RICA: No specific locality, A.M.N.H. Nos. 58954, 61049, 61578, 61791. *Cartago*: Orosi, N.M.W. No. 14409 (2). *Limón*: Cairo, S.N.M. No. 19783; Finca Morehouse, U.K. No. 25742; Salvadora Farm, Río Parismina, A.N.S.P. Nos. 22885-22887; Santa Clara, M.C.Z. No. 15289; Surubres, M.C.Z. Nos. 15290-15291. *San José*: San Isidro el General, U.K. No. 31930; 15 miles south of San Isidro el General, U.K. No. 34024; *San José*, A.M.N.H. No. 64556.

*Leptodeira septentrionalis ornata* Bocourt

*Sibon annulatum*, COPE, 1875, Jour. Acad. Nat. Sci. Philadelphia, for 1874, p. 131; 1887, Bull. U. S. Natl. Mus., no. 32, p. 67.

*Eteirodipsas annulata*, GARMAN, 1875, Proc. Boston Soc. Nat. Hist., vol. 18, p. 205; 1876, *ibid.*, p. 408.

*Comastes ornatus* BOCOURT, 1884, Bull. Soc. Philom. Paris, ser. 7, vol. 8, pp. 141-142.

*Hypsiglena ornata*, GÜNTHER, 1894, Biologia Centrali-Americana, Reptilia, p. 139.

*Leptodeira affinis* GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 170.

*Leptodeira albofusca*, BOULENGER, 1896, (in part), Catalogue of the snakes in the British Museum, vol. 3, pp. 95-97. MOCQUARD, 1908, (in part), in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, pp. 905-906. BOULENGER, 1913, Proc. Zool. Soc. London, p. 1035.

*Leptodeira annulata*, MOCQUARD, 1908, (in part), in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, pp. 901-902. AMARAL, 1927, Bull. Antivenin Inst. Amer., vol. 1, no. 2, p. 46.

? *Leptodeira dunckeri* WERNER, 1913, Mitt. Nat. Hist. Mus. Hamburg, vol. 30, pp. 28-29.

*Leptodeira annulata annulata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 78. DUNN, 1936, (in part), Proc. Natl. Acad. Sci., vol. 22, pp. 692-693. TAYLOR, 1951, Univ. Kansas Sci. Bull., vol. 34, no. 1, pp. 122-125; 1954, *ibid.*, vol. 36, no. 11, pp. 712-713.

*Pseudoleptodeira ornata*, TANNER, 1944, Great Basin Nat., vol. 5, nos. 3, 4, p. 31.

*Hypsiglena torquata torquata*, TAYLOR, 1954, Univ. Kansas Sci. Bull., vol. 36, no. 11, pp. 712-713.

HOLOTYPE: Number 6201 (two syntypes) in the collection of the Museum National d'Histoire Naturelle, Paris, from the Isthmus of Darien, Panamá; Dr. Viguiet, collector.

DESCRIPTION: Body laterally compressed; vertebral and paravertebral scale rows noticeably enlarged; preoculars usually two, sometimes one or three; normally with the fourth and fifth upper labials entering the orbit; lower labials 10, 11, or 12, rarely nine. Ventrals in males 175-201 (186.5), in females 174-194 (185.5); caudals in males 72-104 (94.0), in females 78-98 (85.9). Dorsal scales usually in 21 rows at midbody, sometimes 19 or 23, and usually reducing to 15 rows, sometimes 13 or 17 posteriorly. Dorsal scale-reduction formula for two males with 19 rows:

19 9+V (114-125) - 17 8+V (124-150) - 15 (179-186)

Reduction formula for two males with 21 rows:

19 +10 (46-52) - 21 10+V (116-121) - 19 9+V (126-128) - 17 8+V (134-144) - 15 (185-187)

Reduction formula for four females with 21 rows:

19 +10 (41-47) - 21 10+V (107-118) - 19 8+9, or 9+V (116-126) - 17 8+V (128-162) - 15 (179-184)

The dorsal ground color is cream-tan to grayish tan. There are 30 to 52 (39.6) dark brown dorsal body blotches that are three to four scales in length, twice the length or equal to the length of the dorsal light interspaces, and extend laterally to scale rows 4 to 6. There are dark, lateral, intercalary spots on rows 2 to 5. The dorsal blotches may be rounded or saddle-shaped, but more often are in the shape of cross bands. (See pl. 3, fig. 3, and pl. 18.) There are 15 to 29 dark tail blotches. The ventral surfaces are an immaculate cream color.

The top of the head is grayish brown; sometimes there are scattered dark brown spots on the frontal and parietals. In some there is a thin, often indistinct, nape stripe extending posteriorly from the posterior margins of the

parietals for the length of three to five scales. A postorbital stripe begins on the postoculars and passes across the anterior edge of the primary temporal, the bottom of the lower secondary temporal, the top of the sixth and seventh upper labials, and the middle of the eighth to terminate at the corner of the mouth. (See pl. 18.) The labials are cream, with their posterior edges usually smudged with brown.

Males range from 266 to 500 mm. (426 mm.) in body length and from 361 to 745 mm. (581 mm.) in total length; females, from 255 to 665 mm. (462 mm.) in body length and from 339 to 865 mm. (611 mm.) in total length. The two smallest juveniles, a male and a female, each have body lengths of 137 mm. and total lengths of 181 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals and in the tail/body ratios. Caudals in males average 94.0 and in females 85.9. The tail/body ratio in males varies from 0.281 to 0.405 (0.367), in females, from 0.282 to 0.362 (0.325).

**VARIATION:** This subspecies is naturally divided into three populations: one in lower Central America, one on the Pacific coast of South America, and one in the inter-Andean valleys in Colombia. There are minor differences between these populations. Perhaps the most distinct is the one in the inter-Andean valleys. In these snakes, usually the nape stripe is present, and it may be connected to the first body blotch. In some individuals there is a lateral expansion of the nape stripe anteriorly to form a T-shaped mark, with the arms of the T extending laterally onto the postparietals. The dorsal body blotches are short and equal to the length of the dorsal interspaces.

The snakes from Chocó, Colombia, also have rather short body blotches, but usually have an indistinct nape stripe. Those from northwestern Ecuador usually have no nape stripe, and the blotches are noticeably longer than in those individuals from Chocó. A comparison between these populations is given in table 24.

Juveniles have a white nape band; the white color includes the posterior temporals, postparietals, and dorsal scale rows to the first body blotch. The color darkens with age,

so that in adults that of the nape is the same as the ground color. The juvenile nape coloration is identical with that found in *L. a. annulata*.

Color notes taken on living young from a banana boat import show that the dorsal ground color was orange-tan; the blotches were dark brown, and the venter was cream. The occipital region was an immaculate white, and the iris was reddish tan.

**REMARKS:** To the north in Costa Rica *ornata* intergrades with *polysticta*; to the south in southwestern Ecuador it intergrades with *larcorum*. Individuals from southern Ecuador run the gamut from typical *larcorum* to typical *ornata*. Some have only moderately compressed or rounded bodies and have a butterfly-shaped nape mark, characteristic of *L. s. larcorum*, whereas others have noticeably compressed bodies and no nape mark.

The complex geography of northwestern South America and the absence of large series of specimens from many parts of the range of *ornata* create the possibility that more than one form may be included in this subspecies. Analysis of additional material may show that the populations of the Río Magdalena and Río Cauca valleys are different from those inhabiting the coastal regions of Colombia and Panamá. However, until the zoogeography of the region and the populations of *Leptodeira* are better known, I believe they should be considered as a single subspecies.

No connection between the populations of *annulata* in the Amazon Basin and *ornata* in the Caribbean and Pacific drainages has been found. Although in many superficial respects the two forms closely resemble each other, they can be separated easily. In *L. a. annulata* there are usually no lateral intercalary spots and only one preocular, whereas in *L. s. ornata* there are large lateral intercalary spots and usually two preoculars. The laterally compressed body and enlarged vertebral and paravertebral scale rows, characters that previously have been used to unite the two forms, are parallel adaptations for arboreal life in wet forests.

*Leptodeira dunckeri* Werner, 1913, is questionably included in the synonymy of *ornata*. The type specimen cannot be located, and the original description gives few clues to the identity of the specimen Werner described;

it may not be a *Leptodeira*.

RANGE: *Leptodeira septentrionalis ornata* ranges in the lowlands to an elevation of 1000 meters, from southern Costa Rica along both coasts of Panamá to Colombia and thence southward along the Pacific slopes to northwestern Ecuador, also in the valleys of the Río Magdalena and Río Cauca in Colombia. (See maps 6 and 7.)

The locality records for the 124 specimens examined are:

COSTA RICA: *Puntarenas*: Palmar, U.K. Nos. 34025-34030.

PANAMÁ: *Bocas del Toro*: U.S.N.M. No. 56006. *Canal Zone*: L.M.K. No. 25275; Agua Clara, M.C.Z. No. 45383; Barro Colorado, A.N.S.P. No. 63597, C.M. Nos. 7682, 7685, M.C.Z. No. 25087 (2), U.M.M.Z. Nos. 64460, 69535; Cana Mines, M.C.Z. No. 45399; Chagres, U.M.M.Z. No. 76719 (2); Madden Dam, M.C.Z. No. 38232, U.M.M.Z. No. 76726; Río Chagres, M.C.Z. No. 34192. *Chiriquí*: M.C.Z. Nos. 28209-28210; 16 miles west of Potrerillos, M.V.Z. No. 35561. *Cocle*: Valle de Anton, Finca Arce, C.N.H.M. Nos. 57614, 68075-68076. *Colon*: Portobelo, U.S.N.M. No. 45567. *Comarca del Barú*: Progreso, U.M.M.Z. No. 57953; Río Corotú, near Puerto Armuelles, C.N.H.M. No. 68077; Puerto Armuelles, M.V.Z. No. 17984. *Darien*: A.M.N.H. No. 36197; Cana, A.N.S.P. No. 23872; El Real, Río Tuira, U.M.M.Z. No. 76704; fork of Pihuila-Jucuti branch of Río Tuira, M.C.Z. Nos. 37077-37079; Serrania del Sapo, Río Jeanito, M.C.Z. Nos. 17176, 17188; Yavisa, M.C.Z. Nos. 37135-37137, 42740-42742, U.M.M.Z. Nos. 76701 (2), 79917. *Panamá*: Cerro Campana, C.N.H.M. No. 68078; Esperanza-Pequini Ridge, M.C.Z. No. 42784; Punta Paitilla, M.C.Z. No. 51802. *San Blas*: Bahía de Caledonia, L.M.K. No. 34979.

COLOMBIA: Puerto Bay, U.M.M.Z. No. 78271; Río Magdalena, Z.S.B.S. No. 98/1926; Villa Arteaga, C.N.H.M. No. 65323. *Antioquia*: Medellín, A.M.N.H. Nos. 35611, 35635-35636, 35645-35646, 35685-35689, 35691-35694, 35722, 37934, B.M.N.H. No. 97.11.12.13; Nechi, Río Cauca, C.N.H.M. No. 54923; Sabanalarga, Río Cauca, A.M.N.H. No. 37935; Valdivia, C.N.H.M. No. 69657; 8 kilometers south of Valdivia, C.N.H.M. No. 63769. *Atlántico*: Barranquilla, D.Z. Nos. 2118-2119. *Caldas*: Pueblo Rico, Station Cecilia, C.N.H.M. Nos. 54919-54922. *Chocó*: M.C.Z. No. 13297; Andagoya, M.C.Z. Nos. 32736-32738, U.S.N.M. No. 124254; Boca de la Raspadura, upper Río Quito, A.M.N.H. No. 18296; Peña Lisa, Condoto, B.M.N.H. Nos. 1913.-11.12.56-1913.11.12.57, 1935.2.3.3; Río Atrato,

A.N.S.P. No. 10215, A.M.N.H. No. 18297; Río San Juan, U.S.N.M. No. 72351; Unguia, C.N.H.M. Nos. 63770-63771; upper Río Jiradó, A.N.S.P. No. 25583. *Cundinamarca*: Honda, B.M.N.H. Nos. 1909.7.23.25-1909.7.23.26. *Norte de Santander*: Cucutá, B.M.N.H. Nos. 98.8.23.10-98.8.23.11. *Santander*: Barrancabermeja, C.N.-H.M. Nos. 27578-27579. *Valle*: Cali, B.M.N.H. No. 95.11.16.23, N.M.W. No. 14414 (2).

ECUADOR: *Esmeraldas*: Quinde, E.P.N. No. 792; Río Caoní, tributary to Río Blanco, E.P.N. Nos. 759-760; San Xavier, A.M.N.H. Nos. 5255, 13541, Z.M.B. No. 16453. *Imbabura*: Paramba, B.M.N.H. No. 98.4.28.77. *Pichincha*: Chiriboga, E.P.N. No. 775; Santo Domingo de los Colorados, A.M.N.H. Nos. 28727-28728, E.P.N. Nos. 739, 763, 782, N.M.W. No. 14410; 9 kilometers west of Santo Domingo de los Colorados, S.U. Nos. 13308-13310.

Locality records for 24 specimens considered to be intergrades between *L. s. ornata* and *larcorum* are:

ECUADOR: No specific locality, U.S.N.M. Nos. 14024, 14027, 14042-14043, 14045. *Bolívar*: Balzapamba, A.M.N.H. Nos. 35948, 35954. *E. Oro*: Machala, E.P.N. Nos. 761-762, 783, 785; Río Puyango, A.M.N.H. No. 22097. *Guayas*: Bucay, A.M.N.H. Nos. 22093, 24334; Colonche, B.M.N.H. No. 1931.10.-21.13-1931.10.21.14; Duran, A.N.S.P. No. 18116, J.A.P. No. 2275; Guayaquil, B.M.N.H. No. 58.9.20.2; Copping, E.P.N. No. 752, L.M.K. No. 22115, M.C.Z. No. 8390, Z.M.B. No. 6213 (2); Isla Puna, S.U. No. 8803; Milagro, E.P.N. Nos. 788-790; Río Daule, M.C.Z. Nos. 3560-3563, 3567-3568. *Los Ríos*: Babahoya, Z.S.B.S. No. 37/1926 (2).

*Leptodeira septentrionalis larcorum*  
Schmidt and Walker

*Leptodeira annulata*, DUNN, 1923, Proc. Biol. Soc. Washington, vol. 33, p. 186.

*Leptodeira larcorum* SCHMIDT AND WALKER, 1943, Publ. Field Mus. Nat. Hist., zool. ser., vol. 24, no. 27, pp. 311-312.

*Leptodeira rhombifera larcorum*, SHREVE, 1947, Bull. Mus. Comp. Zool., vol. 99, no. 5, p. 531.

HOLOTYPE: Number 34302 in the collection of the Chicago Natural History Museum from Chiclin, Libertad, Peru; Constante Larco Hoyle, collector.

DESCRIPTION: Body slightly laterally compressed or not; vertebral scale row not noticeably enlarged. Preoculars usually two, sometimes one or three; usually fourth and fifth upper labials entering the orbit, sometimes

TABLE 24  
GEOGRAPHICAL VARIATION OF FOUR CHARACTERS IN SIX POPULATIONS  
OF *Leptodeira septentrionalis ornata*

Locality and Sex	Ventral	Caudals	Tail/Body	Blotches
Costa Rica and eastern Panamá				
Males				
<i>N</i>	(5)	(3)	(3)	—
<i>M</i>	194.2	94.0	0.342	—
<i>O.R.</i>	188-201	89-90	0.321-0.366	—
Females				
<i>N</i>	(4)	(4)	(4)	—
<i>M</i>	187.3	87.5	0.323	—
<i>O.R.</i>	185-189	87-88	0.302-0.347	—
Males and females				
<i>N</i>	—	—	—	(9)
<i>M</i>	—	—	—	43.9
<i>O.R.</i>	—	—	—	39-50
Panamá: Canal Zone				
Males				
<i>N</i>	(10)	(8)	(8)	—
<i>M</i>	192.6	96.0	0.365	—
<i>O.R.</i>	187-201	89-013	0.335-0.386	—
Females				
<i>N</i>	(12)	(12)	(12)	—
<i>M</i>	188.3	85.1	0.316	—
<i>O.R.</i>	181-194	78-84	0.282-0.362	—
Males and females				
<i>N</i>	—	—	—	(25)
<i>M</i>	—	—	—	38.0
<i>O.R.</i>	—	—	—	34-48
Panamá: Darien				
Males				
<i>N</i>	(9)	(6)	(6)	—
<i>M</i>	188.9	95.2	0.360	—
<i>O.R.</i>	180-197	92-102	0.335-0.370	—
Females				
<i>N</i>	(9)	(8)	(8)	—
<i>M</i>	188.6	85.0	0.318	—
<i>O.R.</i>	182-194	78-91	0.282-0.346	—
Males and females				
<i>N</i>	—	—	—	(18)
<i>M</i>	—	—	—	41.4
<i>O.R.</i>	—	—	—	35-52
Colombia: valleys				
Males				
<i>N</i>	(17)	(14)	(14)	—
<i>M</i>	182.7	93.8	0.377	—
<i>O.R.</i>	175-193	85-104	0.331-0.405	—
Females				
<i>N</i>	(14)	(9)	(8)	—
<i>M</i>	184.5	86.3	0.329	—
<i>O.R.</i>	179-191	85-91	0.300-0.345	—
Males and females				
<i>N</i>	—	—	—	(29)
<i>M</i>	—	—	—	40.7
<i>O.R.</i>	—	—	—	33-52

TABLE 24—(Continued)

Locality and Sex	Ventral	Caudals	Tail/Body	Blotches
Colombia: Chocó				
Males				
<i>N</i>	(4)	(3)	(4)	—
<i>M</i>	184.3	96.7	0.377	—
<i>O.R.</i>	179–187	96–98	0.369–0.382	—
Females				
<i>N</i>	(6)	(5)	(5)	—
<i>M</i>	182.7	92.0	0.332	—
<i>O.R.</i>	179–186	79–91	0.315–0.341	—
Males and females				
<i>N</i>	—	—	—	(10)
<i>M</i>	—	—	—	38.7
<i>O.R.</i>	—	—	—	34–44
Ecuador				
Males				
<i>N</i>	(5)	(3)	(3)	—
<i>M</i>	183.4	92.0	0.358	—
<i>O.R.</i>	180–187	84–97	0.321–0.377	—
Females				
<i>N</i>	(7)	(6)	(6)	—
<i>M</i>	181.0	88.0	0.343	—
<i>O.R.</i>	174–186	83–98	0.315–0.362	—
Males and females				
<i>N</i>	—	—	—	(13)
<i>M</i>	—	—	—	38.8
<i>O.R.</i>	—	—	—	30–47

third labial also. Males with 176–184 (178.4) ventrals, females with 170–185 (178.1); caudals in males 86–93 (90.1), in females 72–84 (79.3). Dorsal scales in 21 rows, sometimes 23, and reducing to 17 or 15 posteriorly. Scale-reduction formula for two males:  $21\ 9+10$  (110–121) –  $19\ 8+9$  (123–125) –  $17$  (176–184)

Reduction formula for four females:

$21\ 9+10$  (95–108) –  $19\ 8+9$ , or  $9+V$  (118–129) –  $17$  (175–182)

The dorsal ground color is cream-brown to light grayish brown. There are 34 to 49 (42) dark brown dorsal body blotches that are two to four scales in length, twice the length of the dorsal light interspaces, and extend laterally onto scale rows 4 to 6. The dorsal blotches may be partially fused along the midline to form a zigzag band. On rows 2 to 4 are lateral intercalary spots. (See pl. 19.) There are 16 to 25 dark brown tail blotches; the ventral surfaces are a cream color.

The top of the head is grayish brown. There is a dark brown stripe from the nostril across the loreal and upper preocular to the orbit. The postorbital stripe begins on the postoculars and passes over the anterior edge of the primary temporal, the bottom of the lower secondary temporal, the top of the sixth and seventh upper labials, and the middle of the eighth to terminate at the corner of the mouth. Above the postorbital stripe is a light tan or cream stripe that fades into the ground color dorsally. A dark brown nape stripe flares laterally on the posttemporals and postparietals to form a butterfly-shaped pattern. The nape stripe may or may not be in contact with the first body blotch. (See pl. 19.) The labials are cream, the posterior edges of the upper ones being tinged with brown.

Males range from 280 to 450 mm. (392 mm.) in body length and from 380 to 619 mm. (536 mm.) in total length; females range from 285 to 610 mm. (410 mm.) in body

length and from 375 to 882 mm. (525 mm.) in total length. The smallest juvenile examined is a male with a body length of 163 mm. and a total length of 222 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals and in the tail/body ratio. Males average 90.1 caudals; females, 79.3. The tail/body ratio in males ranges from 0.341 to 0.396 (0.366) and in females from 0.297 to 0.340 (0.321).

**VARIATION:** Specimens from the coast of Peru differ only slightly from those from the upper Río Marañón. (See table 25.) Usually the butterfly-shaped pattern on the nape is present; however, in some individuals it may fade into the ground color, or one of the wings may be absent. Juveniles have a cream ground color that is considerably lighter than that found in the adults.

**REMARKS:** This subspecies occurs in semi-arid habitats. It is present in both the coastal region and in the dry upper Marañón Valley and is the only form of *Leptodeira* that straddles the Andes. Although there are passes across the Andes in northern Peru at elevations of little more than 2000 meters, it is doubtful that the two populations are connected at the present time. The genetic continuity that must have existed in the past may have been interrupted either by the altitudinal fluctuation of the climate during the Pleistocene or by geological uplift during Pleistocene or Recent times.

In southern coastal Ecuador *larcorum* intergrades with *ornata*, which occurs in the wet forests in northern Ecuador, coastal Colombia, and lower Central America.

**RANGE:** Northern coastal Peru and the valley of the upper Río Marañón, Peru. (See map 7.)

Locality records for the 24 specimens examined are:

PERU: *Cajamarca*: Bellavista, M.C.Z. Nos. 17454-17465; Perico, M.C.Z. Nos. 17412-17414, 17416, U.M.M.Z. No. 111308. *Libertad*: Chiclin, C.N.H.M. Nos. 34302, 34306-34311; Pacasmayo, S.N.M. No. 19792.

#### *Leptodeira splendida* Günther

*Leptodeira splendida* GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 171, pl. 53, fig. B.

TABLE 25

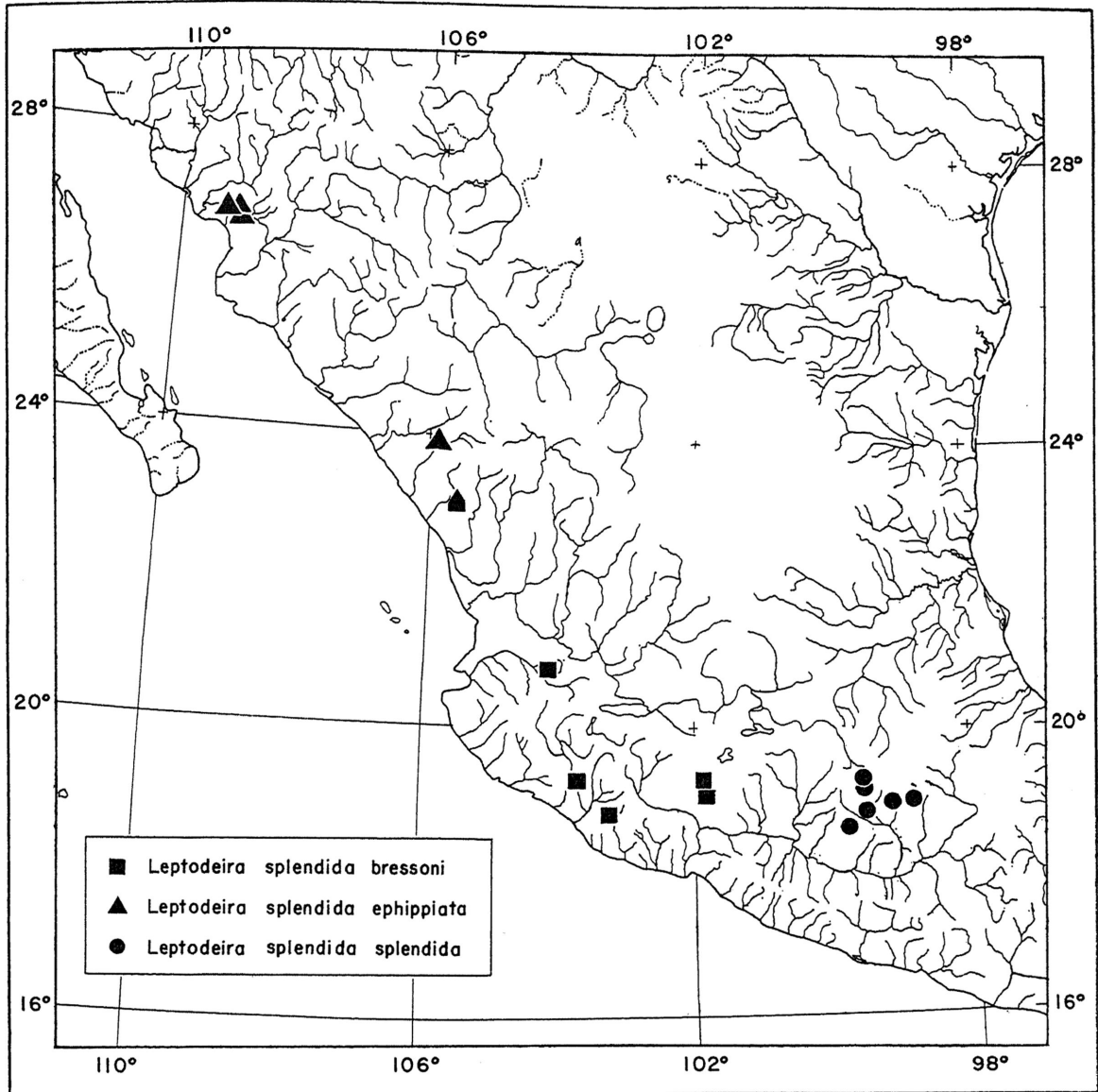
COMPARISON OF A SERIES OF *Leptodeira septentrionalis larcorum* FROM THE COAST OF PERU WITH A SERIES FROM THE UPPER MARAÑÓN VALLEY OF PERU

Character and Sex	Coastal	Marañón
Body blotches		
Males and females		
<i>N</i>	(6)	(17)
<i>M</i>	39.0	43.1
<i>O.R.</i>	34-46	37-49
Ventrals		
Males		
<i>N</i>	(4)	(5)
<i>M</i>	178.8	178.3
<i>O.R.</i>	176-184	176-179
Females		
<i>N</i>	(2)	(10)
<i>M</i>	181.0	177.6
<i>O.R.</i>	179-183	170-185
Caudals		
Males		
<i>N</i>	(4)	(4)
<i>M</i>	89.0	91.3
<i>O.R.</i>	86-91	89-93
Females		
<i>N</i>	(2)	(10)
<i>M</i>	73.5	80.4
<i>O.R.</i>	72-75	77-84
Tail/body		
Males		
<i>N</i>	(4)	(4)
<i>M</i>	0.369	0.364
<i>O.R.</i>	0.341-0.396	0.344-0.360
Females		
<i>N</i>	(2)	(9)
<i>M</i>	0.306	0.325
<i>O.R.</i>	0.297-0.314	0.308-0.340

**DISTRIBUTION:** The range of *Leptodeira splendida* extends from southern Sonora southward along the foothills and Pacific slopes of the Mexican Plateau to the coastal sierra of Michoacán and thence inland in the Balsas Basin to southwestern Puebla. (See map 8.)

**DESCRIPTION:** Head broad and flat, distinct from neck; rostral barely visible from above; prefrontals pentagonal, half again as long as the internasals; frontal wider across anterior border than at point of contact with the posterior corner of the supraocular; upper preocular seldom in contact with frontal





MAP 8. Locality records for *Leptodeira splendida*.

(27%); preoculars usually three, sometimes two or four; postoculars two; upper labials eight, with the fourth and fifth entering the orbit; anterior and posterior chin shields subequal in length; lower labials normally 10, sometimes nine or 11; lower labials 1 to 5 in contact with anterior chin shield, and 5 and 6 in contact with posterior one.

Dorsal scales smooth, with the exception of a few specimens in which the posterior body

scales are weakly keeled in both sexes. The keels appear first on the vertebral row from the level of the ninety-ninth to the 153d ventral. Posteriorly the lateral scale rows may be progressively more keeled; however, keels are never present on rows 1 to 3. Posteriorly the keels disappear between caudals 5 and 8. There are usually 21 dorsal scale rows anteriorly and always 21 at midbody, dropping to 17 posteriorly; reduction from 21 to

19 rows takes place by the fusion of the ninth and tenth rows between ventrals 84 and 111, and from 19 to 17 by the fusion of the eighth and ninth rows between ventrals 93 and 132. A few specimens are at variance with part of the above description. In one individual the reduction from 21 to 19 rows is accomplished by the fusion of the third and fourth rows on one side; the other side is normal. In another specimen the sixth and seventh rows fuse on one side. One specimen has only 19 rows anteriorly; the increase from 19 to 21 rows takes place by the addition of the fourth scale row at ventrals 36 and 38. One individual shows a reduction to 15 scale rows immediately anterior to the anus.

The ranges and means of tooth counts based on seven specimens are: maxillary, 15-16+II (15.6); palatine, 10-11 (10.1); pterygoid, 26-31 (28.4); and dentary, 20-25 (22.7).

The hemipenis *in situ* is six to eight caudals in extent. There are two primary longitudinal rows of spines; lateral to the primary row on either side of the sulcus are two secondary rows. The three rows converge at the end of the sulcus where there is a large spine on each side. These spines give way laterally to four spines of decreasing size. The proximal half of the hemipenis is covered with spinules. The capitulum is crenulated.

The dorsal color pattern is dull grayish brown to creamish tan, with dark brown or black blotches; the body blotches may or may not reach the ventrals. Lateral intercalary spots are present. There is a well-defined nape stripe, as often as not connected with the first body blotch; ornate markings are usually present on top of the head; most often these originate as two arms of a Y on the lateral edges of the frontal and extend posteriorly to form a nape stripe on the posterior part of the parietals; a postorbital stripe usually connects the first body blotch. The ventral surfaces are an immaculate cream color.

The total length seldom exceeds 600 mm.; the tail/body ratio ranges from 29 to 38 per cent.

**GEOGRAPHICAL VARIATION:** In *Leptodeira splendida* there is a latitudinal gradient in the number of ventrals, a greater number to the north in Sonora and Sinaloa than in the

south in Morelos and Guerrero. (See fig. 10.) Specimens from the northern part of the range and from Morelos, Guerrero, and Puebla have large body blotches and small lateral intercalary spots; individuals from Colima, Jalisco, and Michoacán have a greater number of body blotches (32 to 38, as compared with 18 to 25 in Morelos and 22 to 25 in Sonora) and larger, lateral, intercalary spots. The typical dorsal head pattern is often fragmentary in specimens from Colima, Jalisco, and Michoacán.

On the basis of these differences in color pattern, combined with the difference in the number of ventrals, this species is divided into three easily recognizable subspecies.

***Leptodeira splendida ephippiata***  
Smith and Tanner

*Leptodeira ephippiata* SMITH AND TANNER, 1944, Copeia, no. 3, pp. 131-136, fig. 1. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 88.

**HOLOTYPE:** Number 28931 in the collection of the Museum of Vertebrate Zoology, University of California, from 8.3 miles west-northwest of Álamos, Sonora, México; C. Sibley, collector.

**DESCRIPTION:** Males with 175-177 (176.0) ventrals and females with 180-184 (181.5) ventrals; caudals in males 78-85 (81.5) and in females 77-81 (78.7). Dorsal scales in 21-21-17 rows; scale-reduction formula for one male:

21 9+10 (95) - 19 8+9 (110-112) - 17 (175)

Reduction formula for three females:

21 9+10 (105-111) - 19 8+9 (125-132) - 17 (180-182)

The dorsal ground color is cream-tan, not noticeably darker on the sides. There are 22 to 25 dark brown body bands that are faintly outlined with black, which, in turn, is indistinctly bordered with pale cream. The body bands are five or six scales in length, twice the length of the light interspaces. The bands are nearly as long laterally as dorsally, and they reach the first or second scale rows. On the edges of the ventrals, the first, and sometimes the second, scale row are elongate brown spots. (See pl. 20.) There are 13 to 16 dark tail bands, each about equal in length to

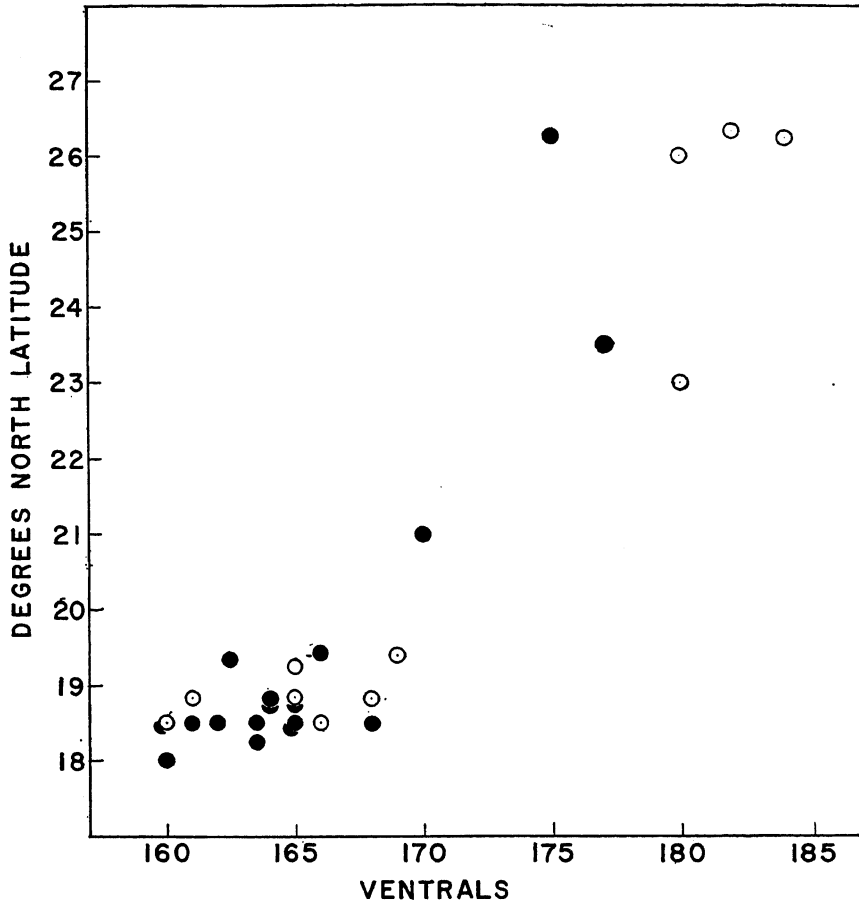


FIG. 10. Geographical gradient in the number of ventrals in *Leptodeira splendida*. Solid dots are males; open circles are females.

the adjacent light areas. The venter is pale cream-white.

The snout and top of the head to the anterior edge of the parietals are grayish brown. There are dark brown spots on the prefrontals. A dark mark begins on each side of the frontal and extends posteriorly across the parietal to meet either the nape stripe or a dorsal extension of the postorbital stripe on the tertiary temporals, or both. The nape stripe begins on the posteromedian corners of the parietals and may or may not meet the first body band. The postorbital stripe is broad; extending posteriorly from the eye, it passes over the postoculars, the lateral corner of the parietal, the entire primary temporal, the lower secondary and tertiary temporals, the upper half of the seventh upper labial, and the entire eighth upper labial

to the angle of the mouth, from where it continues posteriorly on scale rows 4 and 5 to connect with the first body band. There is a dark mark on the tertiary temporals and the posttemporals that may or may not be connected to the postorbital and the parietal markings. The posterior borders of upper labials 1, 2, and 3 are brown, and brown flecks are present on all upper labials, lower labials 1, 2, and 3, and the mental. (See pl. 20.)

One adult male has a body length of 440 mm. and a total length of 605 mm. Three adult females range from 337 to 441 mm. (396 mm.) in body length, and two range from 540 to 571 mm. (556 mm.) in total length. There are no juveniles available.

**SEXUAL DIMORPHISM:** Although the number of specimens is inadequate for an analysis

to be made of the differences between the sexes, it may be pointed out that the single male has a tail/body ratio of 0.375, and that two males have an average of 81.5 caudals, as compared with the variation from 0.295 to 0.320 (0.310) in tail/body ratio and an average of 78.7 caudals in three females. Noteworthy also is the higher number of ventrals in females, 180 to 184, as compared with 175 to 177 in males.

**REMARKS:** A female from Plomosas, Sinaloa (U.S.N.M. No. 46459), has been referred to this form by Smith and Tanner (1944) and to *bressoni* by Taylor (1938). In general appearances the specimen resembles *ephippiata*, but in the number of body bands (32) it closely approaches *bressoni*. I consider the specimen to be an intergrade between *bressoni* and *ephippiata*.

**RANGE:** This subspecies is known from the foothills of the Sierra Madre Occidental from southern Sonora to southern Sinaloa. (See map 8.) *Leptodeira s. ephippiata* ranges farther north on the Pacific coast of México than any other species in the genus. Apparently it does not extend northward beyond Guirocoba and Álamos in the region of the northern limits of the arid tropical scrub forest. This area is the northern terminus for several genera of Neotropical snakes, such as *Leptophis* and *Drymobius*.

The locality records for the six specimens examined are:

**MÉXICO:** *Sinaloa:* Fourteen miles southwest of El Batel, A.M.N.H. No. 75882; Plomosas, U.S.N.M. No. 46459 (intergrade with *bressoni*). *Sonora:* Agua Marín, 8.3 miles west-northwest of Álamos, M.V.Z. No. 28931; 7 miles southeast of Álamos, L.M.K. No. 41181; Guirocoba, M.V.Z. Nos. 50835-50836.

*Leptodeira splendida bressoni* Taylor

*Leptodeira bressoni* TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 321-325, fig. 2, pl. 31, fig. 4, pl. 33, fig. 4. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, pp. 87-88.

*Leptodeira duellmani* PETERS, 1954, Occas. Papers Mus. Zool. Univ. Michigan, no. 554, pp. 25-28.

**HOLOTYPE:** Number 5172 in the Taylor-Smith collection from Hacienda El Sabino, 20 miles south of Uruapan, Michoacán, México; J. R. Bresson, collector.

**DESCRIPTION:** Males with 165-170 (166.5) ventrals and females with 165-169 (167.0) ventrals; caudals in males 82-87 (84.3) and in females 71. Dorsal scales normally in 21-21-17 rows; scale-reduction formula for two males:

21 9+10 (99-102) - 19 8+9 (116-126) - 17 (166-170)

Scale-reduction formula for two females:

21 9+10 (92-96) - 19 8+9 (114-123) - 17 (165-169)

The dorsal ground color is grayish brown, with 32 to 38 (35.3) dark, chocolate brown, middorsal spots three to four scales in length, as long as the interspaces. Usually the spots extend laterally only to the fifth or sixth scale rows and are outlined with an indistinct, light gray border. Often the spots are divided along the midline and alternate with one another, so that the posterior edge of the right half of a given blotch may touch the anterior edge of the left half of the next blotch. There are two or three rows of lateral spots. The primary row consists of round spots incorporating two or three scale lengths on scale rows 2 to 6 in the lateral interspaces between the middorsal spots. The secondary row consists of irregular splotches of dark brown on scale rows 2 to 4 just lateral to the edges of the dorsal spots. The tertiary row, when present, consists of small brown spots on the first scale row and on the edges of the ventrals. The dark grayish brown of the dorsum fades to a somewhat lighter color on the sides of the body. The gray suffuses onto the edges of the ventrals. (See pl. 21.) There are 10 or more distinct dark brown spots on the dorsal surface of the tail; the spots are reduced to flecks on the distal part of the tail. The venter is cream.

The ground color of the head is grayish brown or grayish tan, being darkest anterior to the eye. The dorsal head pattern consists of two or three dark brown spots on the prefrontals, usually a spot in the middle of each scale and sometimes one on their common border. On each side from the posterolateral corner of the frontal begins a dark wavy band that extends nearly the length of the parietal. These bands do not merge with the nape stripe, which begins on the postero-

median edges of the parietals and extends posteriorly for the length of six or seven scales. The nape stripe does not meet the first body blotch. There is a faint, incomplete, preorbital stripe from the nostril to the eye. A chocolate brown postorbital stripe, usually outlined with black, extends posteriorly from the eye across the lower postocular, lower part of the upper postocular, lower part of the primary temporal, lower secondary temporal, and the upper parts of upper labials 7 and 8 to a point just posterior to the angle of the mouth. There it may be met by a forward extension of the first body blotch, which, because of its anterior projections, is roughly U-shaped. Between the postorbital stripe and the parietal markings and the nape stripe may be a dark mark from the posterolateral border of the parietal onto the tertiary temporals and thence posteriorly onto the nape. Also present on top of the head are numerous dark brown flecks. The gray dorsal ground color extends onto the anterior upper labials, the mental, and lower labials 1, 2, and 3, and sometimes onto the anterior chin shields. The other labials are a dusty cream. (See pl. 21.)

Color notes based on a living specimen from Uruapan, Michoacán, indicate that there is little change in the dorsal coloration through preservation. The venter, however, was white anteriorly and a pale salmon-pink posteriorly. The iris was a brilliant copper color.

Four adult males range from 308 to 430 mm. in body length, and two females are 372 mm. and 567 mm. Three males have a range in total length from 425 mm. to 505 mm. The largest individuals of both sexes have incomplete tails. There are no juveniles available.

**SEXUAL DIMORPHISM:** The small number of specimens does not permit an analysis of differences between the sexes. Of three males with complete tails, the variation in tail/body ratio is 0.354 to 0.380 (0.365). The single female with a complete tail has a tail/body ratio of 0.288. This is probably indicative of a sexual difference. Also, the three males have an average of 84.0 caudals, as compared to 71 in the single female.

**VARIATION:** There is considerable individual variation in the head pattern. In some the parietal markings are broken down into a

series of small dark flecks. In others the markings on the tertiary temporals are absent, while those on the nape are retained. In all specimens the postorbital and nape stripes are present and distinct.

Two specimens, both males, show the following abnormal scale reductions:

U.M.M.Z. No. 104620 19  $\frac{+4 (36)}{+4 (38)}$  21  $\frac{9+10 (92)}{3+4 (91)}$   
 19  $\frac{8+9 (107)}{8+9 (93)}$  17  $\frac{7+8 (109)}{7+8 (109)}$  16  $\frac{7+8 (163)}{7+8 (163)}$   
 15 (165)

U.M.M.Z. No. 104490 21  $\frac{9+10 (96)}{9+10 (94)}$   
 19  $\frac{9+V (112)}{9+V (114)}$  17 (164)

One specimen (U.M.M.Z. No. 104490, the type of *L. duellmani*) has the color pattern reduced to a series of spots on the vertebral and paravertebral rows. The lateral spots are reduced to short dashes on the second and third scale rows at midbody. (See pl. 3, fig. 2.)

One male from the Sierra de Ixtlan in north-central Jalisco has 170 ventrals, four more than any from Michoacán. In this respect this specimen approaches the higher counts found in *L. splendida ephippiata* in Sinaloa and Sonora.

**REMARKS:** Peters (1954) described *Leptodeira duellmani* on the basis of a single specimen (U.M.M.Z. 104490) from Coalcomán, Michoacán. In the description Peters stated that the specimen may be an aberrant individual of *L. bressoni*. The fact that typical *bressoni* was found at the same locality eliminates the possibility of an almost unicolored race of *splendida* in the Coalcomán region. Peters believed that the unusual coloration, with the difference in scale reduction (reduction from 19 to 17 rows by the fusion of the ninth row with the vertebral instead of with the eighth row), was a sufficient basis for the recognition of a distinct species. However, the method and place of scale reduction in *Leptodeira* are highly variable and are hardly sufficient evidence in themselves for the recognition of species. The color pattern of *duellmani* is different only in the reduction of the size of the dorsal and lateral spots. The number of spots (38) is within the normal range of *bressoni*, and the complicated head pattern is essentially the same. The reduction of color

pattern in this form parallels that found in *L. annulata cussiliris* in the lowlands of Guerrero. Consequently, I believe that *duellmani* is nothing more than an aberrant individual of *L. splendida bressoni* and that the name should be synonymized with *bressoni*.

**RANGE:** *Leptodeira splendida bressoni* is known only from scattered localities in the states of Colima, Jalisco, and Michoacán in southwestern México. It has been collected at elevations ranging from 500 to 1500 meters. At Uruapan, Michoacán, it has been found above the lower limits of the pine forest in that area (1100 meters). (See map 8.)

The locality records for the eight specimens examined are:

**México:** *Colima:* Colima, M.C.Z. No. 11411. *Jalisco:* Rancho El Rodeo, Sierra de Ixtlan near San Marcos, M.V.Z. No. 56319. *Michoacán:* Coalcomán, U.M.M.Z. Nos. 104619-104620, 104490; Hacienda El Sabino, 20 miles south of Uruapan, U.I. No. 27385; Uruapan, U.M.M.Z. Nos. 112436-112437.

*Leptodeira splendida splendida* Günther

*Leptodeira splendida* GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 171, pl. 53, fig. B. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 320-321, pl. 30, fig. 1. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 89.

*Leptodeira personata*, BOULENGER, 1896, (in part), Catalogue of the snakes in the British Museum, vol. 3, p. 93. MOCQUARD, 1908, (in part), in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, p. 903.

*Leptodeira rhombifera*, DUNN, 1936, (in part), Proc. Natl. Acad. Sci., vol. 22, p. 693.

**HOLOTYPE:** Numbers 1946.1.9.94 and 1946.1.9.95 (two syntypes) in the collection of the British Museum (Natural History) from Izucar de Matamoras, Puebla, México; Adolphe Boucard, collector.

**DESCRIPTION:** Males with 160-168 (162.7) ventrals and females with 160-168 (164.0) ventrals; caudals in males 76-84 (80.9) and in females 70-76 (74.0). Dorsal scales in 21-21-17 rows; scale-reduction formula for four males:

21 9+10 (84-98) - 19 8+9 (108-124) - 17 (160-168)

Scale-reduction formula for four females:

21 9+10 (87-102) - 19 8+9 (114-128) - 17 (161-168)

The dorsal color pattern consists of 18 to 25 (20.8) dark brown or black, rounded body blotches on a ground color that is usually yellowish brown or cream dorsally, blending to a grayish brown laterally. The blotches are irregular in shape; sometimes they are interconnected, but usually they are discrete, with their sides not parallel. They are four to seven scales in length and only slightly longer than the light interspaces. The first body blotch is somewhat longer than the others. The blotches extend laterally onto the third or fourth scale row. The lateral intercalary spots are narrow and elongate and may be four scales in length. These spots occur on the second and third scale row. Elongated lateral spots also may be present just below the lateral edges of the body blotches. (See pl. 22.) There are nine to 18 tail blotches; these are the same color as those on the body. The under surfaces are an immaculate cream color.

The ground color of the head from the snout to the posterior edge of the temporals is a medium brown to grayish brown. Upper labials 1 through 6, lower labials 1, 2, and 3, mental, and anterior parts of the anterior chin shields are smudged with gray. The nape, chin, and other labials are a cream color. The head pattern is ornate. There are dark brown or black spots on the internasals, prefrontals, and anterior part of the frontal. On the posterolateral borders of the frontal originate the arms of a dark-colored Y. These arms extend posteriorly across the parietals, merging near their posteromedian border to form a well-defined nape stripe, which extends to or nearly to the first body blotch. There is a poorly defined dark stripe from the nostril to the orbit. A heavy, dark, postorbital stripe extends from the eye across the lower postocular, the lower part of the upper postocular, the upper parts of upper labials 6, 7, and 8, and the lower temporals to the angle of the mouth, where it may be met by an anterior extension of the first body blotch on scale rows 3, 4, and 5. Usually there is a more or less distinct dorsomedian extension of the postorbital stripe across the tertiary temporals and the posterior parts of the secondary temporals to or nearly to the

arms of the Y on the parietals just anterior to the place of mergence to form the nape stripe. (See pl. 22.)

Six adult males range from 338 to 402 mm. (365 mm.) in body length and from 460 to 550 mm. (499 mm.) in total length; four adult females range from 393 to 473 mm. (436 mm.) in body length and from 523 to 619 mm. (576 mm.) in total length. The smallest juvenile, a male, has a body length of 155 mm. and a total length of 211 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes exist in the number of tail bands, the number of caudals, the relative length of the tail, and in the place of reduction of the dorsal scale rows. Tail bands in males average 13.7 and in females 10.7. The number of caudals in males averages 80.9 and in females 74.0. The tail/body ratio in males ranges from 0.327 to 0.378 (0.363) and in females from 0.300 to 0.336 (0.321). Reduction from 19 to 17 dorsal scale rows takes place between ventrals 108 and 124 (114) in males and between 114 and 128 (120) in females.

**VARIATION:** The greatest degree of individual variation is in the shape of the body blotches and the development of the ornate head pattern. In approximately half of the specimens examined some of the body blotches are fused to one another. In two specimens the dark markings on the frontal and parietals are in the shape of an 8, with the nape stripe connected to the posterior loop of the 8. In most the markings are Y-shaped, but in some there are two dots or dashes, which represent the tips of the arms of the Y, and a nape stripe.

There is a change in the dorsal ground color with age. In juveniles the entire ground color of the dorsum is cream. In small adults there is a slight darkening on the lateral part of the body. In large individuals the sides are gray, but the dorsal part of the body remains a cream or light tan color.

**REMARKS:** No intergrading specimens between *splendida* and *bressoni* have been found; two specimens from 12 miles south of Puente de Ixtla, Morelos (U.I. Nos. 27386-27387), show a slight tendency towards *bressoni* in certain characters. They have 23 and 25 dorsal body blotches that are somewhat reduced in size. The lateral intercalary spots are more rounded than is normal in

*splendida*. They do, however, possess the typical head pattern of *splendida* and resemble that form more closely than *bressoni*. Intergrades between *splendida* and *bressoni* may be expected in the area of the lower slopes of the Mexican Plateau in the state of México.

**RANGE:** *Leptodeira splendida splendida* is found in the semi-arid upper Balsas Basin and adjacent slopes of the Mexican Plateau at elevations ranging from 900 to 1700 meters in southern Morelos, northern Guerrero, and western Puebla. (See map 8.)

The locality records for the 16 specimens examined are:

MÉXICO: *Guerrero*: Five kilometers south of Taxco, E.H.T.-H.M.S. No. 5596. *Morelos*: Twelve kilometers northwest of Axochiapan, U.I. No. 25926, T.C.W.C. Nos. 4115, 7314-7317; Cuernavaca, A.M.N.H. No. 75931, E.H.T.-H.M.S. No. 29830, N.M.W. No. 14395 (2); 4 miles north of Cuernavaca, U.M.M.Z. No. 95099; Progreso, U.I. No. 26072; 12 miles south of Puente de Ixtla, E.H.T.-H.M.S. No. 5178, U.I. Nos. 27386-27387.

#### *Nigrofasciata* GROUP

Apart from all other members of the genus are two relatively small species, *nigrofasciata* and *latifasciata*, characterized by long dark bands on the body, hemipenis with spinous capitulum, somewhat elongated and flattened heads, and reduced numbers of teeth on all dentigerous bones.

These snakes live in the arid and semi-arid portions of the Pacific coastal region and Balsas Basin of México southward to Costa Rica.

#### *Leptodeira nigrofasciata* Günther

*Leptodeira nigrofasciata* GÜNTHER, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 425; 1895, Biologia Centrali-Americana, Reptilia, p. 169. BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 92. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amerique Centrale, vol. 3, pp. 900-901. WERNER, 1909, Mitt. Nat. Hist. Mus. Hamburg, vol. 26, p. 230; 1924, Arch. Naturgesch., vol. 12, p. 125. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 698. TAYLOR, 1954, Univ. Kansas Sci. Bull., vol. 36, no. 11, pp. 744-746.

*Leptodeira mystacina* COPE, 1869, Proc. Amer. Phil. Soc., vol. 11, p. 151. GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, pp. 169-170. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 698.

TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, pp. 325-326. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, pp. 88-89; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 340. WERLER AND SMITH, 1952, Texas Jour. Sci., vol. 4, no. 4, pp. 568-570.

*Sibon nigrofasciatum*, COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 67; 1891, Proc. U. S. Natl. Mus., vol. 14, p. 678; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Sibon mystacina* COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 67.

*Leptodeira annulata punctata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 204.

HOLOTYPE: Number 1946.1.8.37 in the collection of the British Museum (Natural History) from Nicaragua; Dr. Seemann, collector.

DESCRIPTION: Head long, flattened; rostral barely visible from above; prefrontals pentagonal, twice as long as internasals; frontal longer than its distance from the snout and longer than the common suture between parietals; frontal wider anteriorly than at point of contact with parietals, with a long posterior projection between anterior parts of parietals; upper preocular in broad contact with anterolateral corner of frontal; preoculars usually two, sometimes one or three; postoculars usually two, sometimes one; temporals normally one plus two plus three; upper labials usually eight, sometimes seven or nine, normally with the fourth and fifth entering orbit; lower labials usually 10, sometimes nine or 11; posterior chin shields slightly longer than anterior; lower labials 1 to 5 in contact with anterior chin shield, and 5 and 6 in contact with posterior one.

Males with 161-196 (176.2) ventrals, females with 169-196 (183.6); caudals in males 63-76 (68.1), in females 54-68 (62.6). Dorsal scales smooth and normally in 19-19-17 rows; scale reduction in 12 males:

$$19 \ 8+9 \ (115-139) - 17 \ (161-196)$$

Scale reduction in 10 females:

$$19 \ 8+9 \ (112-138) - 17 \ (169-193)$$

Scale reduction in two males with 15 rows posteriorly:

$$19 \ \frac{8+9 \ (127)}{8+9 \ (127)} \ 17 \ \frac{2+3 \ (167)}{2+3 \ (159)} \ 15 \ (173)$$

$$19 \ \frac{8+9 \ (117)}{8+9 \ (117)} \ 17 \ \frac{7+8 \ (121)}{7+8 \ (121)} \ 15 \ (171)$$

The dorsal body pattern consists of 10 to 19 long, dark brown to black cross bands varying from five to 14 scales in length and separated from one another by cream to grayish tan interspaces varying from one to seven scales in length. The dark bands are straight-edged and extend onto the tips of the ventrals. (See pl. 23.) In some instances the bands are divided along the midline for part of their lengths, thus giving a zigzag appearance. There are no lateral intercalary spots. From three to 10 dark bands are found on the tail. The venter is cream to light grayish tan.

The top of the head is dark brown or black to the posterior edges of the parietals, where the dark color is interrupted by a straight-edged, transverse, cream, nape band from two to four scales in length. The first dark body band extends onto the nape within three to five scale lengths of the parietals. In some individuals the dark brown color of the top of the head includes the sides of the head and labials. In other specimens a dark stripe passes from the nostril to the eye and another from the orbit across the lower postocular, lower half of the upper postocular, and tops of the sixth and seventh upper labials to terminate on the eighth upper labial. Also, in some specimens, there is a continuous or interrupted brown stripe extending posteroventrally from the lower edge of the orbit across upper labials 4 to 6, or only 5 and 6; in these the upper and lower labials are usually cream and may be heavily smudged with brown. (See pl. 23.) The chin and throat may be cream or grayish tan, or, as in many, the dark color of the head extends onto the lower labials, chin shields, and gulars.

The ranges and means of tooth counts of 10 specimens are: maxillary, 10-12+II (11.5); palatine, 7-8 (7.3); pterygoid, 16-20 (17.4); and dentary, 14-17 (15.0).

The hemipenis extends for eight or nine caudals. The dorsal surface of the hemipenis is covered with nine longitudinal rows of spines; those on the sides are more irregular and smaller than the median ones. The spines increase in size distally, the middle row consisting of four large spines, with many small ones leading from these to the spinous capitulum. The base is covered with small spines.

Adult males range from 162 to 430 mm.



(284 mm.) in body length; females, from 195 to 473 mm. (328 mm.). In total length males range from 202 to 486 mm. (358 mm.); females, from 240 to 581 mm. (410 mm.). The smallest juvenile is a male with a body length of 133 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are found in the number of caudals (63–76 in males and 54–68 in females) and in the relative length of the tail. The tail/body

A parallel situation is encountered in the number of ventral scutes; these are highest in México and lowest in Honduras or Nicaragua (depending upon the sex) with a slight reversal of the trend in Nicaragua and Costa Rica. (See table 26.) With the difference in the number of ventral scutes there is a corresponding change in the place of reduction from 19 to 17 scale rows. In males from Oaxaca this reduction takes place between

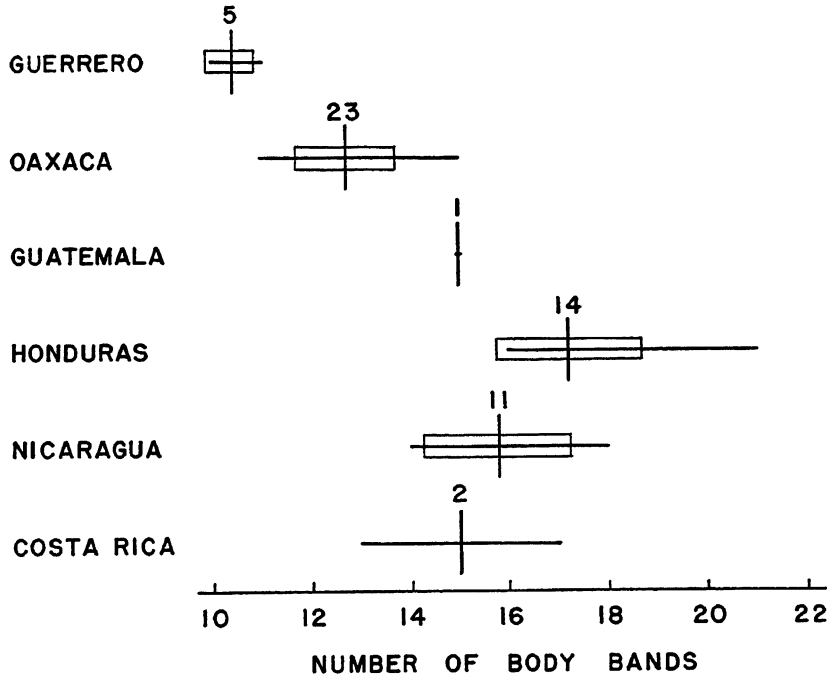


FIG. 11. Geographical variation in the number of body bands in *Leptodeira nigrofasciata*. Vertical line, mean; horizontal line, observed range; box includes one standard deviation on either side of the mean.

ratio in males is 0.247–0.382 (0.287); in females, 0.228–0.270 (0.249).

**VARIATION:** Specimens from the extremes of the range are quite different in color pattern, size, and in certain scale counts. The most obvious difference is in the number and length of the body bands. Individuals from Guerrero and Oaxaca have a low number of relatively long bands; those from Guatemala and Honduras have a greater number of bands, but these are much shorter. Individuals from Nicaragua and Costa Rica have fewer body bands than those from Honduras, but more than those from México. (See fig. 11.)

ventrals 117 and 139 (127), and in females, between 119 and 138 (128.5); in males from Honduras between ventrals 115 and 129 (119.8), and in females, between 112 and 119 (115.2). These data are based on counts of five males and five females from Oaxaca and seven males and four females from Honduras. In size 15 females from Oaxaca average 365 mm. in body length; six females from Honduras average 305 mm.

**REMARKS:** Most workers have regarded *mystacina* and *nigrofasciata* as distinct species (Smith and Taylor, 1945; Taylor, 1954). The differences between the populations from México (*mystacina*) and those from Central

TABLE 26  
GEOGRAPHICAL VARIATION IN THE NUMBERS OF VENTRALS AND CAUDALS  
IN *Leptodeira nigrofasciata*

	Ventrols		Ventrols+ Caudals	
	Males	Females	Males	Females
Guerrero				
<i>N</i>	(2)	(4)	(2)	(4)
<i>M</i>	185.0	192.5	255.0	258.3
<i>O.R.</i>	185	189-196	252-258	254-260
Oaxaca				
<i>N</i>	(6)	(16)	(5)	(12)
<i>M</i>	190.8	189.6	257.4	253.8
<i>O.R.</i>	187-196	185-195	252-263	245-261
Guatemala				
<i>N</i>	(1)	—	(1)	—
<i>M</i>	175	—	249	—
<i>O.R.</i>	175	—	249	—
Honduras				
<i>N</i>	(8)	(6)	(6)	(4)
<i>M</i>	171.1	172.6	241.1	234.5
<i>O.R.</i>	167-173	169-176	234-250	232-237
Nicaragua				
<i>N</i>	(7)	(4)	(6)	(4)
<i>M</i>	167.7	175.0	236.0	231.8
<i>O.R.</i>	161-173	172-180	230-249	226-236
Costa Rica				
<i>N</i>	(2)	—	(2)	—
<i>M</i>	174.0	—	241.5	—
<i>O.R.</i>	169-179	—	238-245	—

America (*nigrofasciata*) are ones of scutellation and color pattern that show geographical gradients. The characters common to the two populations place them together, yet apart from most other species in the genus. Differences between the Mexican population and the lower Central American population are minimized by a character gradient apparently diverging from Honduras to the northwest as far as Guerrero and to the southeast as far as Costa Rica. As the populations blend into one another and there are no basic color pattern differences or structural differences between the populations, there is little cause to recognize them as subspecies.

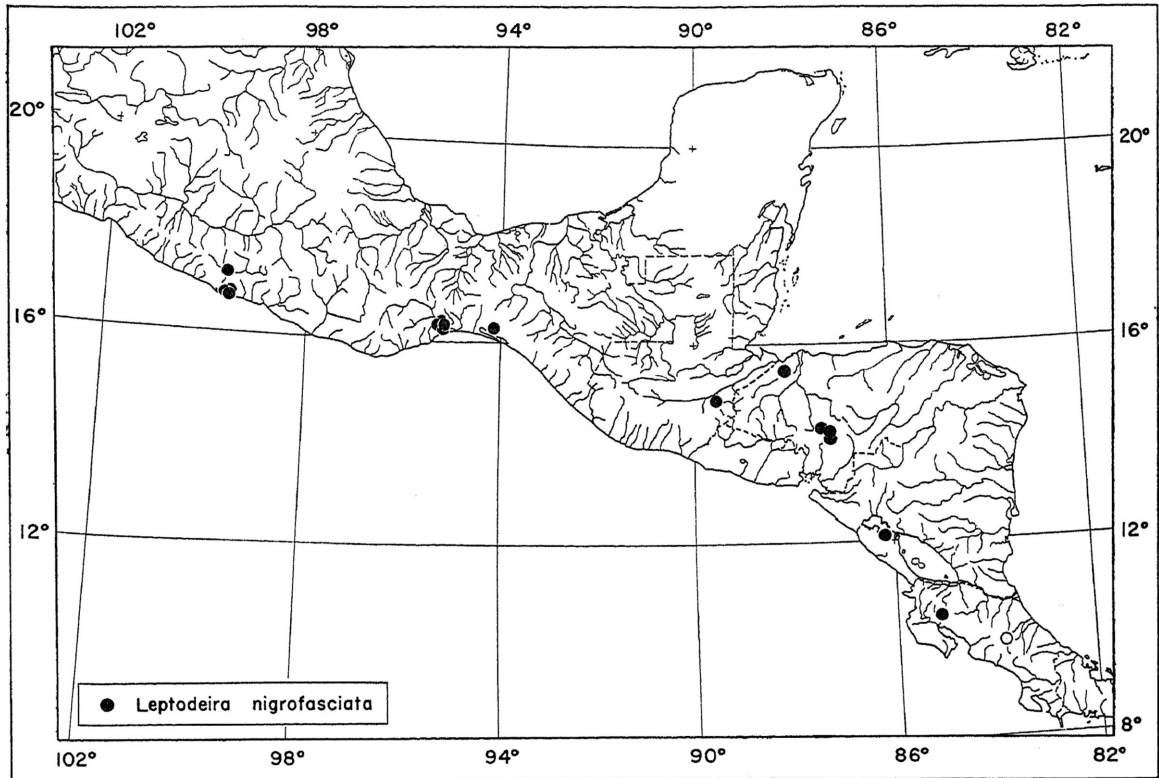
RANGE: *Leptodeira nigrofasciata* is found in the Pacific lowlands of México from south-central Guerrero to the Isthmus of Tehuantepec, thence presumably eastward through the Grijalva Valley of Chiapas and Guatemala to the central plateau of Honduras, Nicaragua, and Costa Rica. (See map 9.)

The localities from which *Leptodeira nigro-*

*fasciata* has been collected are in the Pacific drainage. In México the species inhabits semi-arid situations in the narrow Pacific coastal strip. It has been found in dry inland plateau country to elevations of 1000 meters in Central America and along the dry Pacific coastal area of Nicaragua and Costa Rica. Although no direct connection between the Mexican and Central American populations has been discovered, it is not unreasonable to assume that this species follows the sub-humid corridor across northern Central America described by Stuart (1954a).

Locality records for the 59 specimens examined are:

México: *Guerrero*: Acapulco, L.M.K. No. 36283, U.S.N.M. No. 46551; 3 miles north of Acapulco, U.S.N.M. No. 111221; Laguna Coyuca, A.M.N.H. No. 66147; Tierra Colorado, E.H.T.-H.M.S. No. 21400. *Oaxaca*: Cerro Quinegola, A.M.N.H. Nos. 64592, 65126, U.S.N.M. No. 111223; Escurano, U.I. No. 3787; La Concepción, U.I. No. 3788; Tapanatepec, B.M.N.H. No. 81.

MAP 9. Locality records for *Leptodeira nigrofasciata*.

10.29.7, M.C.Z. Nos. 27835–27836; Tecuane, U.M.M.Z. Nos. 82604–82605; Tehuantepec, A.M.N.H. Nos. 62646, 65127, 65885, 68044–68045, B.M.N.H. No. 90.10.10.85, E.H.T.-H.M.S. No. 27560, U.I. Nos. 6195–6197, U.S.N.M. Nos. 30339–30340, 111222; 19 kilometers east of Tehuantepec, U.I. Nos. 27563–27564.

COSTA RICA: No specific locality, A.M.N.H. No. 17268. *Guanacaste*: Tenorio, U.K. No. 31932.

GUATEMALA: *Chiquimula*: Chiquimula, C.N.-H.M. No. 68612.

HONDURAS: *Cortez*: Between San Pedro Sula and Cofradia, C.N.H.M. No. 11371. *Francisco Morazan*: El Zamorano, A.M.N.H. Nos. 70201–70202; Tegucigalpa, M.C.Z. Nos. 49819–49826; Yeguaré River Valley, M.C.Z. Nos. 48695–48697.

NICARAGUA: No specific locality, U.S.N.M. Nos. 16117–16122, 25240. *Managua*: Managua, U.S.N.M. Nos. 79967–79970.

#### *Leptodeira latifasciata* Günther

*Hypsiglena latifasciata* GÜNTHER, 1894, *Biologia Centrali-Americana*, Reptilia, p. 138, pl. 49, fig. B. BOULENGER, 1894, *Catalogue of the snakes in the British Museum*, vol. 2, p. 211. MOCQUARD, 1908, *in* Duméril and Bibron, *Mission scientifique*

au Mexique et dans l'Amérique Centrale, vol. 3, p. 870, pl. 70, fig. 2.

*Leptodeira guilleni* BOULENGER, 1905, *Proc. Zool. Soc. London*, p. 247, pl. 7, fig. 2. MOCQUARD, 1908, *in* Duméril and Bibron, *Mission scientifique au Mexique et dans l'Amérique Centrale*, vol. 3, p. 903. WERNER, 1924, *Arch. Naturgesch.*, vol. 12, p. 125.

*Leptodeira latifasciata*, DUNN, 1936, *Proc. Natl. Acad. Sci.*, vol. 22, pp. 696–697.

*Pseudoleptodeira latifasciata*, TAYLOR, 1938, *Univ. Kansas Sci. Bull.*, vol. 25, no. 15, pp. 343–344; 1940, *ibid.*, vol. 26, no. 14, p. 467. TANNER, 1944, *Great Basin Nat.*, vol. 5, nos. 3, 4, pp. 31–32. SMITH AND TAYLOR, 1945, *Bull. U. S. Natl. Mus.*, no. 187, p. 113. SCHMIDT AND SHANNON, 1947, *Fieldiana, zool. ser.*, vol. 31, no. 9, p. 81. SMITH AND TAYLOR, 1950, *Univ. Kansas Sci. Bull.*, vol. 33, no. 8, p. 331. DUELLMAN, 1954, *Occas. Papers Mus. Zool. Univ. Michigan*, no. 560, p. 16.

HOLOTYPE: Number 1946.1.2.44 in the collection of the British Museum (Natural History) from "southern México"; Frederick du Cane Godman and Osbert Salvin, collectors. Smith and Taylor (1950) restricted the

type locality to Huajintlán, Morelos.

**DESCRIPTION:** Head elongate and flattened; rostral barely visible from above; prefrontals pentagonal, half again as long as the internasals; upper preocular normally not in contact with frontal; frontal not so long as common suture between parietals; preoculars two; postoculars two; temporals one plus two plus three; eight upper labials, fourth and fifth entering orbit; 10 lower labials, 1 to 5 in contact with anterior chin shield and 5 and 6 in contact with posterior; posterior chin shields slightly longer than anterior ones.

Ventrals in males 176–186 (181.3) and in females 176–192 (187.0); caudals in males 76–82 (78.5) and in females 64–71 (69.0). Dorsal scales smooth and in 21 (five specimens) or 23 rows (four specimens) at mid-body, reducing to 17 rows or, rarely, 15 rows posteriorly. Scale-reduction formulas are:

$$\begin{array}{l} \text{Female (A.N.S.P. No. 25065)} \quad 21 \frac{+7 (32)}{+7 (34)} \\ 23 \frac{6+7 (100)}{6+7 (104)} \quad 21 \frac{5+6 (122)}{5+6 (118)} \quad 19 \frac{4+5 (144)}{4+5 (149)} \\ 17 (187) \end{array}$$

$$\begin{array}{l} \text{Female (U.S.N.M. No. 46550)} \quad 21 \frac{+7 (32)}{+7 (35)} \\ 23 \frac{5+6 (97)}{5+6 (97)} \quad 21 \frac{4+5 (106)}{4+5 (106)} \quad 19 \frac{5+6 (123)}{5+6 (129)} \\ 17 (176) \end{array}$$

The dorsal ground color is light grayish tan to light brown. There are seven to nine (7.9) dark chocolate brown bands with relatively straight edges that extend onto the edges of the ventrals; the bands are 14 to 28 scales in length, four to six times the length of the light interspaces. There are no lateral intercalary spots. On the tail are three dark chocolate brown bands. The venter is cream-tan; in large specimens the anterior edge of each ventral scute is smudged with brown. (See pl. 24.)

Anterior to the orbit the top of the head is dark brown, with the individual head shields edged in light cream or tan. The posterior part of the frontal, the supraoculars, parietals, and the temporals above the postorbital stripe are cream. The supraoculars and frontals are mottled with dark brown; there may be a dark diagonal bar or two or more dark spots on each parietal. From the postero-

median corners of the parietals a dark brown nape stripe extends posteriorly for three to five scale lengths. There is a broad, dark brown stripe from the nostril to the eye. A postorbital stripe envelops the lower half of the upper postoculars, the lower postocular, and the top corner of the fifth upper labial to pass posteriorly across the lateral corner of the parietal, the primary and secondary temporals, upper parts of the sixth and seventh upper labials, and all the eighth upper labial, thence extending posteriorly on scale rows 2 to 6 to connect with the dark nape band. The nape band is five or six scales in length and with the posterior extensions of the postorbital stripes encloses the light area of the parietals and anterior part of the nape. The upper and lower labials are cream, spotted with dark brown; there may be a dark spot on each anterior chin shield. (See pl. 24.)

The ranges and means of tooth counts based on three specimens are: maxillary, 12–13+II (12.3); palatine, 8; pterygoid, 18–20 (19.0); and dentary, 18–20 (19.0). The two enlarged maxillary teeth posterior to the diastema have only a faint groove.

The hemipenis is seven or eight caudals in length. One primary row of four large spines, of which the distal one is the largest, is bordered on each side by four rows of spines of diminishing size. The primary row merges into a row of small, needle-like spines that extends to the spinous capitulum. The base is covered with small spines.

Two adult males vary from 364 to 401 mm. (383 mm.) in body length and from 484 to 526 mm. (505 mm.) in total length; two adult females vary from 360 to 550 mm. (455 mm.) in body length and from 450 to 688 mm. (569 mm.) in total length. The smallest juvenile is a male with a body length of 181 mm. and a total length of 233.

**SEXUAL DIMORPHISM:** Differences between the sexes are noted in the number of caudals and in the tail/body ratio. Males have an average of 78.5 caudals, and females 69.0. The tail/body ratio in males varies from 0.287 to 0.329 (0.309) and in females from 0.250 to 0.255 (0.252). All males examined have a maximum of 21 dorsal scale rows; half of the females have 23 rows. The examination of additional material may reveal a dimorphism in this character.

**VARIATION:** The small number of available specimens shows no significant variation in scutellation. The characteristic light area on the parietals and nape varies in size but is always present. In some individuals the head pattern is reduced to a series of dark spots in the light field. Two juveniles have only a small nape spot. One specimen (U.I. No. 18721) has a narrow and indistinct post-orbital stripe.

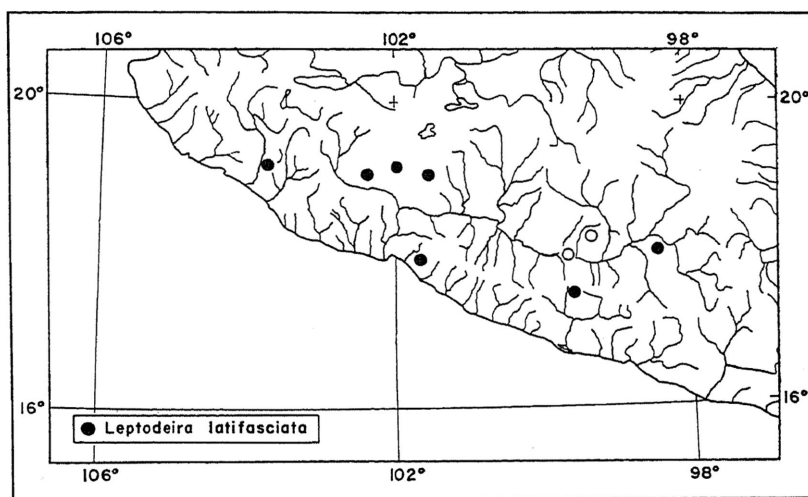
A specimen from La Union, Guerrero (A.N.S.P. No. 25065), in life had light grayish white interspaces and dark chocolate

is allopatric, it is conceivable that they are conspecific.

**RANGE:** *Leptodeira latifasciata* is known from the lowland plateau region of Colima, eastward through the Balsas Basin to western Puebla. (See map 10.) It has been collected at elevations ranging from 100 to 1300 meters.

Locality records for the nine specimens examined and literature records are:

México: No specific locality, A.M.N.H. No. 66148. Colima: La Salada, U.M.M.Z. No. 114458. Guerrero: Acahuitzotla, T.C.W.C. Nos. 7488, 11588; El Naranjo (Taylor, 1938, p. 343); La



MAP 10. Locality records for *Leptodeira latifasciata*.

brown bands that were somewhat lighter laterally. The light area on the head was orange-salmon, and the iris was grayish tan. A specimen from La Salada, Colima (U.M.M.Z. No. 114458), in life had a brick-red head.

**REMARKS:** The character of the color pattern, the hemipenis, the maxillary, and the dentition place this species close to *L. nigrofasciata*. On the other hand it has more scale rows and different scale reduction than *nigrofasciata*, and it differs from all other *Leptodeira* in having only a faint groove in each of the enlarged posterior maxillary teeth. Additional specimens of this species and of *nigrofasciata* may show that the two are more closely related than I have indicated. Because the known distribution of the two forms

Unión, A.N.S.P. No. 25065; Río Balsas (Boulenger, 1905, p. 247). Michoacán: Apatzingán, C.N.H.M. No. 37036; Hacienda El Sabino, 20 miles south of Uruapan, U.I. No. 18721; La Playa, Volcán Jorullo, U.M.M.Z. No. 105158. Morelos: Huajintlán (Taylor, 1940, p. 467). Puebla: Piaxtla, U.S.N.M. No. 46550.

#### *Punctata* GROUP

*Leptodeira punctata* is distinct from all other species of *Leptodeira* not only in general body appearance and color pattern, but in the reduced numbers of ventrals, caudals, labials, and teeth. In general physiognomy it approaches snakes of the genus *Hypsiglena*.

The single monotypic species occurs in the arid portions of western México.

*Leptodeira punctata* Peters

*Crotaphopeltis punctata* PETERS, 1867, Monatsber. Akad. Wiss. Berlin, for 1866, pp. 93-94.

*Leptodeira pacifica* COPE, 1869, Proc. Acad. Nat. Sci. Philadelphia, vol. 20, p. 310. GÜNTHER, 1895, Biologia Centrali-Americana, Reptilia, p. 169. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, p. 694.

*Sibon pacificum* COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 67; 1891, Proc. U. S. Natl. Mus., vol. 14, p. 678; 1900, Rept. U. S. Natl. Mus., for 1898, p. 1107.

*Leptodeira punctata*, BOULENGER, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 91. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, pp. 899-900. WERNER, 1924, Arch. Naturgesch., vol. 12, p. 125. TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, p. 319, pl. 30, fig. 1. SMITH AND TAYLOR, 1945, Bull. U. S. Natl. Mus., no. 187, p. 89; 1950, Univ. Kansas Sci. Bull., vol. 33, no. 8, p. 343.

*Leptodeira annulata punctata*, AMARAL, 1929, (in part), Mem. Inst. Butantan, vol. 4, p. 78.

HOLOTYPE: Number 5378 in the Zoologisches Museum Berlin, supposedly purchased in South Africa by Mr. Godeffroy. I have examined the type specimens of both *punctata* and *pacifica* (U.S.N.M. No. 6833); there is no doubt that they are the same species. The type of *punctata* must have been collected in México and later transported to South Africa from a seaport on the west coast of México, probably Mazatlán. Smith and Taylor (1950) have restricted the type locality of *punctata* to Mazatlán, Sinaloa, México, a restriction that is reasonable. The type locality of *pacifica* also is Mazatlán.

DESCRIPTION: Head distinct from neck, not noticeably flattened; rostral barely visible from above; internasals half of the length of prefrontals with their posterior edges rounded; upper preocular in contact with frontal or not; length of frontal less than that of the interparietal suture; posterior edge of each head shield slightly overlapping adjacent posterior shield. Preoculars usually two (sometimes one); postoculars two; temporals normally one plus two plus three; upper labials usually seven (sometimes eight), and normally with the third and fourth entering the orbit; usually nine lower labials (sometimes 10), with labials 1 to 4 in contact with the anterior chin shield, and 4 and 5 in con-

tact with posterior chin shield. The chin shields are subequal in length.

Ventrals in males 150-156 (153.0), in females 151-167 (157.9); caudals in males 59-69 (65.7), in females 54-62 (58.7); dorsal scales in 19 rows at midbody and usually in 15 rows posteriorly. Scale-reduction formula for seven males:

19 8+9 (93-104) - 17 7+8 (113-139) - 15 (150-156)

Reduction in five females:

19 8+9 (94-112) - 17 7+8 (130-144) - 15 (156-160)

Ranges and means for tooth counts based on seven specimens are: maxillary, 14-15 +II (14.6); palatine, 10-11 (10.4); pterygoid, 24-30 (26.1); and dentary, 19-22 (20.7).

The hemipenis *in situ* extends for a length of six caudals. There is a median row of three large spines, the distal spine being the largest. On each side there are two rows of smaller spines, four or five spines in each row, which converge distally; the distal spine is common to both rows. The sulcus is opposite the primary row of spines and extends to the middle of the capitulum. The capitulum is disc-shaped, finely crenulated, and set off from the rest of the organ by a deep fold.

The dorsal ground color is yellowish tan to light brown. There are five or six longitudinal rows of black or dark brown spots on the dorsum. The largest spots are on scale rows 7 and 8; in some individuals these are fused across the vertebral scale row to form a series of transverse bars. The second row of spots is on scale rows 3 and 4; these spots are smaller than the dorsal ones and are often indistinct. The lowermost row of spots is on scale rows 1 and 2. These often are reduced to a dark area on the edges of the scales. (See pl. 25.) There is a black nuchal blotch four to six scales in length and extending laterally to the third scale row. This blotch may be divided along the midline. The tail is marked dorsally with three to five rows of small dark spots. The venter is an immaculate cream color.

The top of the head is cream-yellow to tan; there may be an ornate head pattern consisting of an 8-shaped mark on the frontal and parietals, with an anterior Y-shaped projection on the frontal and prefrontals, and a nape

stripe extending posteriorly from the parietals for the length of three or four dorsal scales. There also may be a dark mark on the temporals. A dark postorbital stripe begins on the common borders of the postoculars and extends across the anterior part of the primary temporal, the top of the seventh upper labial, and sometimes across the eighth upper labial to the corner of the mouth. The dorsal head pattern usually is fragmentary and may consist solely of the nape stripe and a pair of dark spots on each parietal. (See pl. 25.)

An adult from near Mazatlán, Sinaloa (U.M.M.Z. No. 115383), in life had a yellowish brown dorsum fading to yellowish tan on the venter. The dorsal spots were black; the throat and chin were white; the iris was a light grayish yellow. A juvenile from the same locality (U.M.M.Z. No. 114469) differs from the adult in having a yellowish tan dorsum and a pale lemon-yellow venter.

Males range from 313 to 410 mm. (369 mm.) in body length and from 414 to 538 mm. (489 mm.) in total length; females, from 302 to 445 mm. (401 mm.) in body length and from 398 to 563 mm. (501 mm.) in total length. The smallest juvenile examined was a female with a body length of 162 mm. and a total length of 204 mm.

**SEXUAL DIMORPHISM:** Differences between the sexes are apparent in the number of caudals, the tail/body ratio, and in the place of dorsal scale reduction. Males have an average of 65.7 caudals and females have 58.7. In tail/body ratio males range from 0.312 to 0.351 (0.329), and females range from 0.258 to 0.318 (0.284). Of 11 females available, only seven have 15 rows of dorsal scales posteriorly; all males have 15 rows. The average place of reduction from 17 to 15 rows is at ventral 124 in males and at ventral 137 in females.

**VARIATION:** Aside from the differences already noted in the dorsal color pattern of the head, there are few noteworthy variations apparent in the sample of specimens. There are no evident geographical gradients in either scutellation or color pattern.

**REMARKS:** This species has been collected in the arid Pacific coastal region and in the low western part of the Mexican Plateau; it is the only member of the genus that invades the Plateau, although other species

have been taken at higher elevations.

**RANGE:** *Leptodeira punctata* ranges from the lowlands of north-central Sinaloa south-eastward to Lago de Chapala, Jalisco (1500 meters), México. (See map 11.)

Locality records for the 25 specimens examined are:

No specific locality, Z.M.B. No. 5378.

México: *Jalisco*: Mouth of Río Lerma, Lago de Chapala, A.M.N.H. No. 19854. *Nayarit*: Acajoneta, A.M.N.H. Nos. 62265-62266; Peñitas, A.M.N.H. Nos. 75586, 75592. *Sinaloa*: Six miles north of Caitime, F.A.S. No. 8505; 10.9 miles south of Caitime, F.A.S. No. 8503; Mazatlán, S.U. No. 4086, U.S.N.M. No. 6833; 2-4 miles north-northwest of Mazatlán, A.M.N.H. No. 19853, U.M.M.Z. Nos. 114469, 114471-114476, 115383; 5 miles north-northwest of Mazatlán, A.M.N.H. No. 75883; 6 miles north-northwest of Mazatlán, T.C.W.C. No. 12580; 19 miles north-northwest of Mazatlán, U.M.M.Z. No. 114470; 2 miles east of Mazatlán, E.H.T.-H.M.S. No. 4614; 3 miles east of Mazatlán, T.C.W.C. No. 12581; Presidio, B.M.N.H. No. 82.11.15.47.

#### INCERTA SEDIS

One species described as a *Leptodeira* is unassignable to generic or specific designation at this time. For completeness of the record a description from the literature sources and a discussion of this name are appended.<sup>1</sup>

#### *Leptodeira* (?) *discolor* Günther

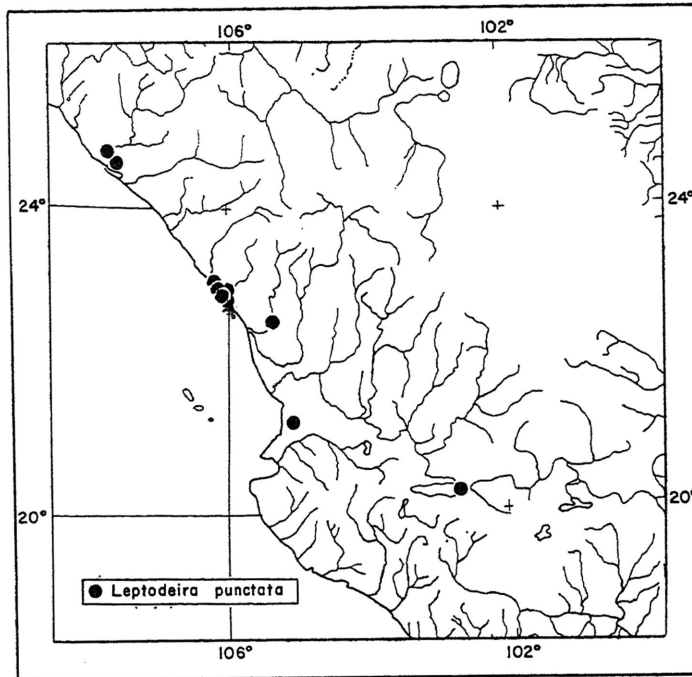
*Leptodeira discolor* GÜNTHER, 1860, Proc. Zool. Soc. London, pp. 317-318. GARMAN, 1884, Bull. Essex Inst., vol. 16, p. 23. DUNN, 1936, Proc. Natl. Acad. Sci., vol. 22, pp. 697-698.

*Hypsiglena discolor*, COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 78. GÜNTHER, 1894, Biologia Centrali-Americana, Reptilia, pp. 137-138, pl. 49, fig. A. BOULENGER, 1894, Catalogue of the snakes in the British Museum, vol. 2, p. 211. MOCQUARD, 1908, in Duméril and Bocourt, Mission scientifique au Mexique et dans l'Amérique Centrale, vol. 3, p. 871, pl. 70, fig. 1. AMARAL, 1929, Mem. Inst. Butantan, vol. 4, p. 183.

*Pseudoleptodeira discolor*, TAYLOR, 1938, Univ. Kansas Sci. Bull., vol. 25, no. 15, p. 343.

**HOLOTYPE:** Two specimens (syntypes) numbered 1946.1.23.67 and 1946.1.23.68 in the collection of the British Museum (Nat-

<sup>1</sup> While the present paper was in press, a specimen of this snake became available for study. A discussion of it will appear at a later date.



MAP 11. Locality records for *Leptodeira punctata*.

ural History) from "Oaxaca" (?), México; Auguste Sallé, collector.

**DESCRIPTION:** The following description is based on that given by Günther, together with additional information forwarded to me by Mr. J. C. Battersby of the British Museum (Natural History).

The syntypes are males; there are two apical pits in the dorsal scales, 16 maxillary teeth plus two enlarged posterior teeth without a noticeable groove (jaws were not removed and cleaned), and hemipenis unknown.

The ventrals are 175 and 180 in number, caudals 88 and 89, preoculars one, postoculars two, temporals one plus two plus three, upper labials seven and eight, with the third and fourth or fourth and fifth entering the orbit, lower labials nine; dorsal scales in 19 rows at midbody and 17 rows posteriorly; body lengths, 365 and 402 mm.; total lengths, 509 and 555 mm.; tail/body ratio, 0.380 and

0.394.

Günther (1894) described the color pattern as follows: "The ground-colour of the upper parts is dirty white, the upper part of the head is brown; there is a whitish collar behind the occipitals. Fifty-one or fifty-four black bands cross the trunk and extend onto the edge of the belly; they are broader than the interspaces between and become interrupted and spot-like on the tail."

**REMARKS:** The combination of characters given in the description and shown in Günther's figure (1894, pl. 49, fig. A) do not apply to any known species of *Leptodeira* or *Hypsiglena*. Although dissimilar in scutellation, the color pattern of *discolor* superficially resembles that of *Hypsiglena torquata*. The designation of this name must await the discovery and study of additional specimens. Possibly *discolor* represents an early divergent species, such as *latifasciata* and *nigrofasciata*, from a primitive *Leptodeira* stock.



## ANALYSIS OF CLINAL VARIATION

CLINAL VARIATION, as defined by Huxley (1942), has been extensively utilized by herpetologists during the last decade. Recently Auffenberg (1955) studied the geographical variation of *Coluber constrictor* and presented a very precise picture of clinal trends in that species, although there was no attempt to

correlate morphological characteristics of the snakes with the environmental factors. Numerous workers have mentioned clinal variation, but little has been offered in the way of correlation between the animals and their environments.

### DESCRIPTION AND COMPARISON OF CLINES

The geographical character gradients shown by the six species of which there is sufficient material for this kind of study are diverse and necessitate individual description. The gradients are most easily recognized in Central America and México, where the lowlands of both coasts lie roughly on a northwest to southeast axis. Descriptions of the character gradients follow:

#### 1. *annulata*

From northwest to southeast in México and Central America there is an increase in the number of dorsal body blotches accompanied by a decrease in their size and by an increase in the size of the lateral intercalary spots; there is a decrease from 23 to 21 scale rows and a slight decrease in the relative tail length. From northern South America into the Amazon Basin there is a decrease in the number of dorsal body blotches, a reduction of the lateral intercalary spots, an increase in the numbers of ventrals and caudals and in the relative tail length, and a reduction from two to one preocular and from 21 to 19 or 17 dorsal scale rows accompanied by an enlargement of the vertebral and paravertebral rows. In southern Brazil and Paraguay there is a reversal in the gradients of all characters with the exception of the number of ventrals.

#### 2. *maculata*

From north to south along the Pacific coast of México and into the Balsas Basin there is a decrease in the numbers of body blotches and ventrals and a slight increase in the relative tail length.

#### 3. *frenata*

From north to south in the Yucatán Peninsula and from northwest to southeast in

eastern México there is an increase in the number of dorsal body blotches accompanied by a reduction in their size and the development of lateral intercalary spots.

#### 4. *septentrionalis*

From northeastern to southern México there is a slight decrease in the numbers of ventrals and caudals and an increase in the number of dorsal body blotches accompanied by a reduction in their size and a development of lateral intercalary spots. From southern México to the Pacific slopes of South America there is a decrease in the numbers of body blotches, ventrals, caudals, and preoculars. The number of dorsal scale rows drops from 23 to 21 or 19, accompanied by an enlargement of the vertebral and paravertebral rows in lower Central America and northwestern South America.

#### 5. *splendida*

From northwestern México into the Balsas Basin there is a decrease in the numbers of ventrals and caudals. Along the coastal regions from north to south there is an increase in the number of body blotches, and from the coastal regions inland into the Balsas Basin there is a decrease in the number of body blotches.

#### 6. *nigrofasciata*

From southern México to Costa Rica there is an increase in the number of body bands and a decrease in the numbers of ventrals and caudals.

The clinal variation displayed by *Leptodeira* is of the nature noted by Mayr (1942, p. 96) in that the clines represent means of a fluctuating trend. Two kinds of clines are apparent, the internal cline (Huxley, 1939 and

1942) being a continuous geographical gradient, and the external cline (Huxley, *op. cit.*) representing discontinuous geographical variation. The designation of these character gradients as ecoclines or geoclines is difficult. Radical changes in environmental conditions from place to place in tropical America may be reflected in the sometimes abrupt changes of the character gradients. Throughout the range of *Leptodeira* the only large area of rather uniform environment is the Amazon Basin. In that area there are few detectable trends in the morphological characters of the snakes; however, on the periphery on the Basin there are many. Under the circumstances in *Leptodeira* it is necessary to consider most of the internal clines and all the external ones to be ecoclines.

In figure 12 are plotted the mean numbers of ventrals and dorsal body blotches for three species of *Leptodeira* from southern México to Panamá. Although the gradients are in some cases rather erratic, the general trends are visible and represent continuous variation. On the sole basis of these characters the recognition of subspecies in this area would not be valid. However, in *annulata* other differences exist between the population in Oaxaca and that in Guatemala. Specimens from Oaxaca are characterized by the presence of small, lateral, intercalary spots and the absence of a nape stripe, whereas those from Guatemala possess large, lateral, intercalary spots and a well-defined nape stripe. In this region there is a rather abrupt discontinuity separating the two populations. A similar but more striking situation is found in South American *annulata*. In the northeastern part of the continent there is a trend towards a gradual increase in the numbers of ventrals and caudals and a decrease in the number of body blotches. Along with these gradients there is an abrupt change from a round-bodied form with two preoculars, normal vertebral and paravertebral scale rows, and two dark nape bars to one with a laterally compressed body, one preocular, enlarged vertebral and paravertebral scale rows, and an unmarked nape.

Another type of discontinuous variation is found in *Leptodeira splendida* in western México. (See fig. 13.) There is a continuous gradient from northwest to southeast in the

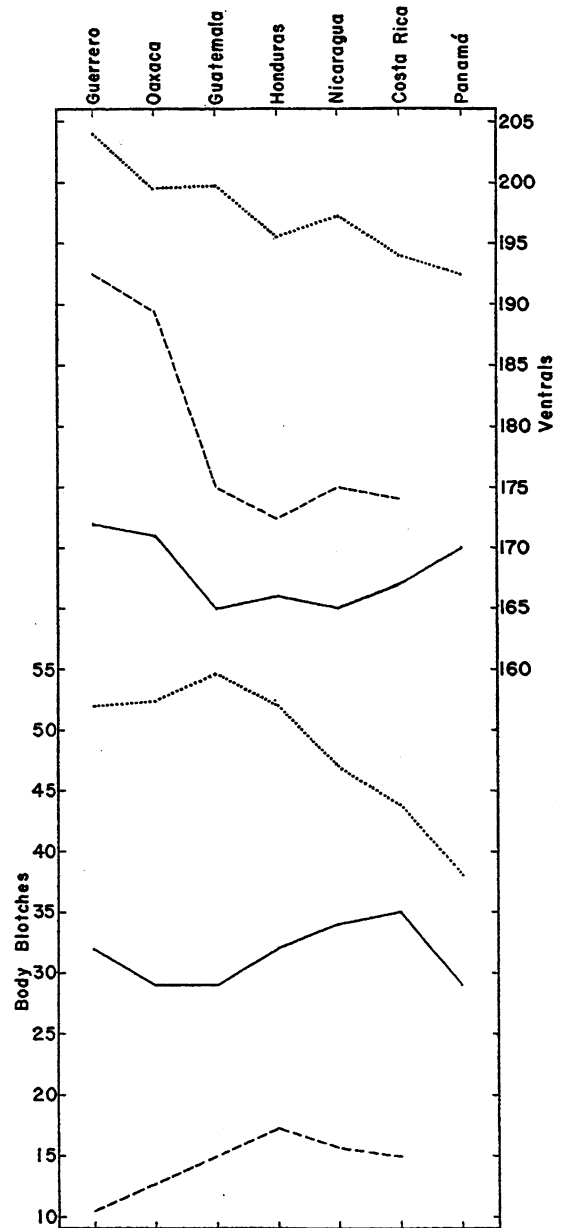


FIG. 12. Comparison of character gradients in three species of *Leptodeira* from southern México and Central America. The mean counts for each character are plotted for each locality. The solid line is *L. annulata*; the broken line, *nigrofasciata*; and the dotted line, *septentrionalis*.

tail/body ratio and in the number of ventrals. However, there is discordant variation displayed by the dorsal color pattern. In the extremes of the geographical range of the spe-

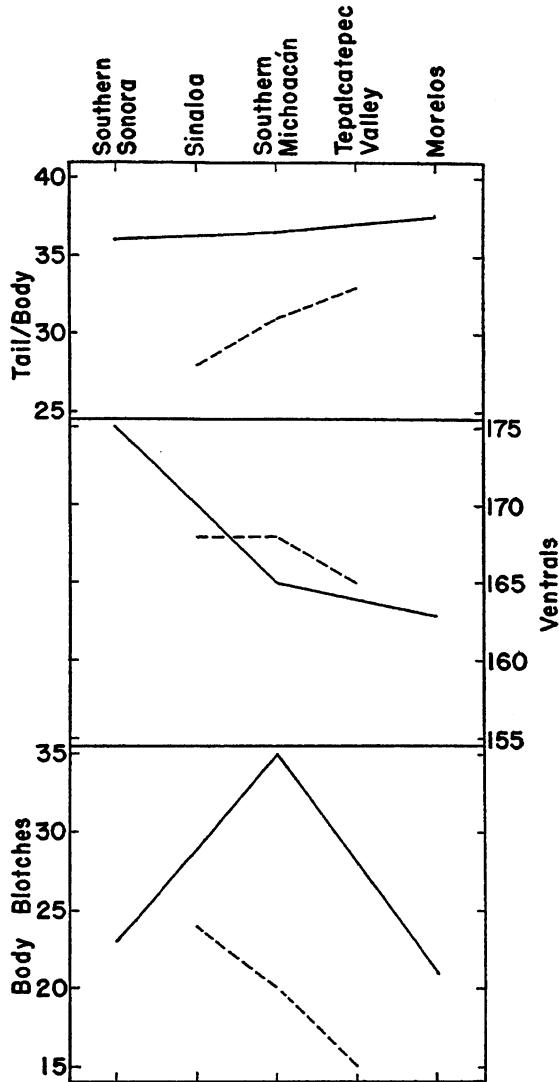


FIG. 13. Comparison of character gradients in *Leptodeira maculata* (broken line) and *L. splendida* (solid line). The means for each species in the various areas are plotted.

cies there are few dorsal body blotches and small lateral intercalary spots, whereas in the middle the dorsal blotches are small and numerous, and the lateral intercalary spots are large. Although these discordant variants are often abrupt, they represent only partial discontinuities in the clinal variation. When certain characters of *Leptodeira maculata* and *annulata* from western México are plotted, geographical gradients are apparent, but these gradients are opposed to one another.

(See fig. 14.) Such drastic discordance or complete discontinuity is indicative of complete genetic isolation and evidence for the treatment of the two populations as species. (See Huxley, 1942, p. 209.)

When the geographical character gradients in different species of *Leptodeira* are compared, three phenomena are apparent. First, two or more characters may vary independently of one another. Second, species inhabiting the same region do not necessarily show parallel gradients. (See figs. 12 and 13.) Third, there may be similar gradients in widely separated geographical areas; these parallel trends may take place in one species, or they may be present in two or more species. The first point is well illustrated by the varia-

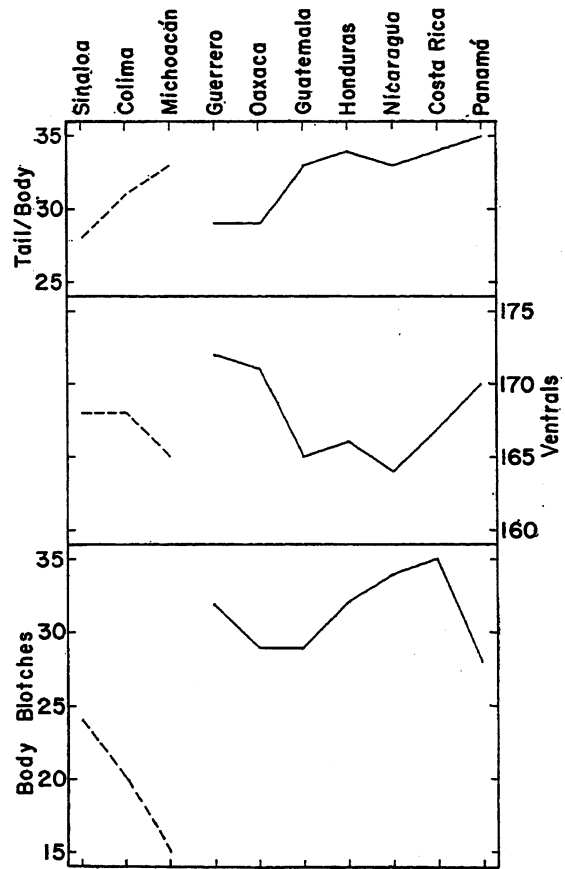


FIG. 14. Discontinuous variation in *Leptodeira annulata* (solid line) and *L. maculata* (broken line) in western México and Central America. The means for each species in the various areas are plotted.

tion displayed by *Leptodeira splendida*, in which species there is a gradient from northwest to southeast for the reduction in numbers of ventrals, for an increase in the relative tail length, and for a sharp increase followed by an equally sharp decrease in the number of body blotches. The second phenomenon applies to sympatric species such as *annulata*, *nigrofasciata*, and *septentrionalis* in Central America, where there is an increase in the number of body blotches from northwest to southeast in *nigrofasciata*, a decrease in *septentrionalis*, and a seemingly uncorrelated variation in *annulata*. In the numbers of ventrals there is a decrease in *nigrofasciata* and *septentrionalis* and no definite trend in *annulata*. The third point is best shown by *annulata* and *septentrionalis*. In the latter species in the northern third of Veracruz there is an ex-

ternal cline involving the change from snakes with round bodies and with a low number of body blotches to snakes with laterally compressed bodies and a high number of body blotches. The number of body blotches is again reduced in an internal cline in lower Central America. The body shape changes from laterally compressed to rounded in an external cline from north to south in the lowlands of Ecuador. Similar external clines are present in the change from a round-bodied terrestrial form to a compressed-bodied arboreal form in *annulata* and *septentrionalis*. These external clines are found in different geographical regions; in *annulata* they occur on the periphery of the Amazon Basin, and in *septentrionalis* in Ecuador and more gradually in México and Central America.

#### CORRELATION OF CLINAL VARIATION WITH ENVIRONMENTAL FACTORS

There have been few attempts to correlate the geographical variation in animals with change in environmental factors. Klauber (1941) presented evidence showing that in 13 species of snakes in southern California there is an almost universal tendency towards a higher number of ventrals in specimens from the desert than in those from the coast. Klauber stated that the outstanding difference between the two regions is that of humidity; however, he did not outlaw the possibility that temperature was a controlling factor. Fitch (1940) reported that in *Gerrhonotus multicarinatus* and *G. coeruleus* northern specimens differ from southern ones by having shorter tails, fewer caudal whorls, and smaller size. Through his studies of the plethodontid salamander *Ensatina eschscholtzi*, Stebbins (1949) found evidence that indicated coloration in these animals was influenced by humidity, temperature, and light. Fox (1948) presented the only experimental evidence concerning environmental effect on morphological characters in snakes. His results show that gravid female *Thamnophis elegans atratus* kept at cool temperatures produced young having fewer ventrals, caudals, dorsal scale rows, labials, and lateral dark spots than those born to females kept at warm temperatures. Although his results are based on small samples, they give a strong indica-

tion of the influence of temperature on the developing *Thamnophis* embryo. Investigations on the correlation of water temperature and the number of vertebrae in fishes have been carried out in the field by Hubbs (1922) and Schultz (1926) and experimentally by Gabriel (1944) and others. Their results show that the number of vertebrae varies inversely with the temperature (Jordan's Rule). Such variation is not always solely the reflection of the temperature, for other environmental factors are known to play an important role, e.g., salinity.

To determine the possible correlation between certain environmental factors and morphological characters of *Leptodeira* two rather localized series of each of three species were selected. Temperature and rainfall data for the localities were taken from Contreras (1942) and Clayton and Clayton (1947). Because the experimental work of Fox (*supra cit.*) indicates that the environment affects the developing embryo, only the mean temperatures and rainfall for the presumed period of development, July, August, and September, were used. The results show that there is no consistent correlation between the characters used and the amount of rainfall or the mean temperatures for the months of June, July, and August. (See table 27.) For example, in *L. maculata* there is an increase

TABLE 27

COMPARISON OF CERTAIN ENVIRONMENTAL FACTORS WITH MORPHOLOGICAL CHARACTERS IN THREE SPECIES OF *Leptodeira*

(The counts given are the means for the males from each locality, with the exception of body blotches which are the means for both sexes. The temperatures are in degrees Centigrade, and the rainfall is in millimeters. The temperature data are means for the months of July, August, and September; the rainfall is the total for the same months.)

	<i>annulata</i>		<i>maculata</i>		<i>nigrofasciata</i>	
	Mante, Tamaulipas	Veracruz, Veracruz	Mazatlán, Sinaloa	Apatzingán, Michoacán	Tehuantepec, Oaxaca	Tegucigalpa, Honduras
Temperature	27°	27°	28°	28°	27°	28°
Rainfall	680	992	678	528	522	394
Body blotches	24	26	24	15	13	17
Ventrals	169	174	168	165	191	171
Caudals	65	67	70	72	66	70
Tail/body ratio	26	26	28	33	26	31

in the number of caudals and in the relative tail length and a decrease in the numbers of ventrals and body blotches from Mazatlán, Sinaloa, to Apatzingán, Michoacán; the mean temperature is the same and the amount of rainfall is higher at Apatzingán. In some species there is a positive correlation between the mean temperature and certain morphological characteristics; in others the same morphological characters may vary inversely with the mean temperature.

Altitudinal variation in the number of body blotches in *Leptodeira annulata cussiliris* from Guerrero is shown in figure 5. The average number of blotches in individuals from Chilpancingo at an elevation of 1350 meters is 28; that at Acapulco at sea level, 38. Climatic data for Chilpancingo are not available, but it is assumed that the mean temperature there is less than at Acapulco. If environmental factors, such as temperature and humidity, have an effect on the developing embryos so as to produce differences in

scutellation and color pattern in different geographical areas, presumably the same factors are in operation with respect to altitudinal gradients.

The lack of precise knowledge concerning the microenvironments of areas does not permit an accurate analysis or interpretation of the correlation between environment and morphological characters. To ascertain correctly the relationships between environmental factors and such morphological characteristics as scutellation, body proportions, and color pattern, it is necessary to carry out further experimental studies such as those of Fox (*supra cit.*). Only in this manner can the effect of certain environmental factors on the expression of genes responsible for the morphological characters be determined. Data such as those presented here may only indicate the possibility of a relationship between the environment and the manner of genetic expression.

## MORPHOLOGY OF *LEPTODEIRA* AND RELATED GENERA

THE FOLLOWING DISCUSSION of morphology deals primarily with *Leptodeira*. Included in the description and general discussion are the genera *Hypsiglena* and *Trimorphodon*, which were grouped with *Leptodeira* by Dunn in his arrangement of American colubrids (1928). There is a paucity of information concerning the morphology of snakes; it is hoped that this brief discussion will be of value to other

workers who may have the misfortune of becoming involved in working out the morphology of other colubrid snakes. The morphological descriptions are not intended to be complete; aside from the cranial osteology, I have emphasized only those structures that are known or thought to be of significance in the interpretation of phylogenetic relationships.

### OSTEOLOGY

For osteological studies of the genus *Leptodeira* I have had available for examination eight dried and one cleared and stained complete skeletons representing five species; 17 skulls representing all species of the genus; and more than 100 sets of dentigerous bones from all forms of the genus. I have examined two complete skeletons, one additional skull, and three sets of dentigerous bones of *Hypsiglena*, and one complete skeleton and an additional skull of *Trimorphodon*. In the terminology of skull elements, for the most part I have followed Parker (1878), Radovanović (1937), and Szunyoghy (1932); for vertebral

terminology I have followed Sood (1948), Gadow (1933), and Romer (1956).

#### THE SKULL OF *Leptodeira*

The skull of *Leptodeira* is typically that of a generalized colubrid snake. The following description is based on two specimens of *Leptodeira maculata* (U.M.M.Z. Nos. S-1796 and S-1799). (See fig. 15.)

**NASAL REGION:** The premaxillary is relatively small, with the lateral processes sloping posteroventrally at an angle of about 45 degrees. The dorsal spine curves posteriorly almost to the common suture between the

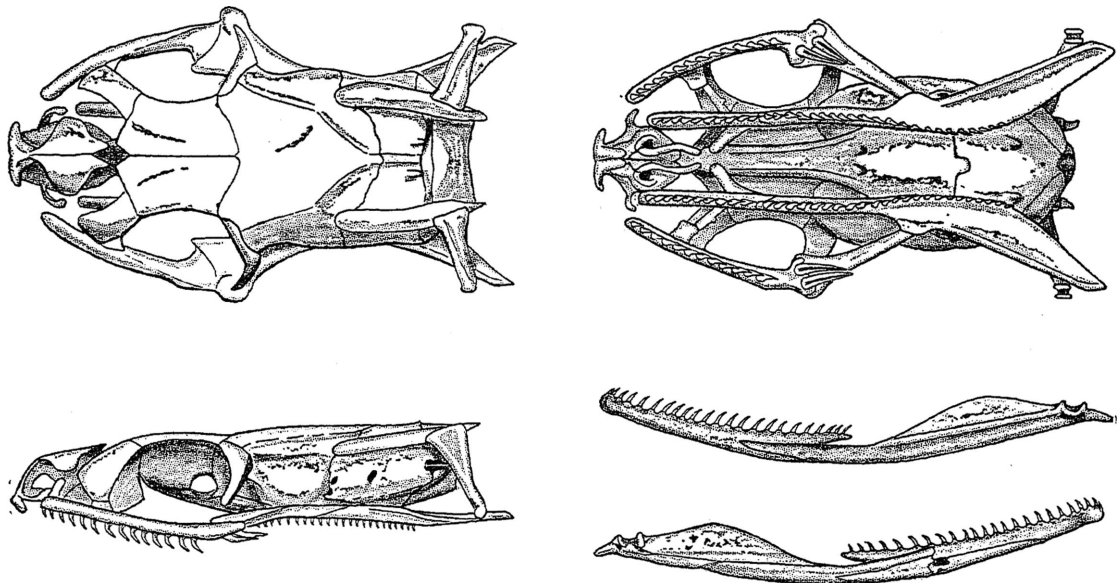


FIG. 15. Skull of *Leptodeira maculata* (U.M.M.Z. No. S-1799) showing dorsal, ventral, and lateral views of the skull, and lateral and lingual views of the left mandible.  $\times 2.5$ .

nasals. The posterior processes of the premaxillary are robust and bluntly rounded posteriorly below their articulations with the anterior processes of the septomaxillaries; the latter lie below the nasals and border the ventral edge of the nasal septum for its entire length. A lateral wing extends in an arch from the lateral edge of the septomaxillary to a point lateral to the nasal plate. The wide, median part of the septomaxillary forms the roof and anterior border of the vacuity of Jacobson's organ; the posterior and lateral boundaries of the vacuity are encompassed by the vomer, the anterior part of which forms the main part of the capsule in which the organ is located. The thin postero-inferior process of the vomer encloses the vomerine foramen. The posterosuperior process of the vomer is a thin sheet of bone lying medially to the heavy posterior process of the septomaxillary, which articulates with the heavy septomaxillary process of the frontal. The length of the nasal plate is twice its width; it is flat above and curved downward laterally and medially to fuse into the median nasal septum.

**CRANIUM AND ASSOCIATED ELEMENTS:** The length of the frontal is more than twice its width; it is flat above, with emarginate lateral edges. From the dorsolateral edges the frontal slopes gradually ventrally and medially to articulate with the parasphenoid. The frontal forms the anterior border of the optic foramen, and the roof of the frontal together with its septomaxillary process encompasses the large olfactory fenestra. The prefrontal is sutured to the anterolateral corner of the frontal; it provides partial roofing for the nasal cavity and forms the posterior boundary of that cavity and the anterior edge of the orbit. A curved nasal process consisting of a narrow spine of bone extends dorsomedially from the anteroventral edge of the prefrontal. The prefrontal bears the large orbital-nasalis foramen. The parietals are fused into a large bone that forms the roof and sides of the middle part of the cranial cavity. The dorsal surface of the parietal is flat, this area being delimited by the parietal crests extending from near the anterolateral corners to a median point near the posterior border of the parietal. Posterior to this point is a median supratemporal crest on the posterior part

of the parietal and on the supraoccipital. On the anterolateral corner of the parietal is the postfrontal process supporting the rather narrow postfrontal, which curves laterally and ventrally to form the posterior rim of the orbit. Dorsally to ventrally the posterior edge of the parietal is sutured with the supraoccipital, the prootic, and the basisphenoid. Extending posteriorly from the anterior part of the frontal and forming the floor of the anterior part of the cranial cavity is a narrow parasphenoid. Posterior to the optic foramen it is sutured with the parietal and fused with the basisphenoid, the latter forming the floor of the middle part of the cranial cavity and the ventral covering of the median pituitary capsule. Posterolateral to the parietal and dorsal to the posterior part of the basisphenoid is the prootic. This bone is deeply emarginate posteriorly, forming the major part of the otic notch, through which protrudes the columella. On the dorsolateral surface of the prootic is a short, heavy crest forming the lateral boundary of the squamosal articulation. The lateral facet of the prootic bears many foramina. Near the anterior edge of the bone are two anteriorly directed foramina through which pass two branches of the trigeminal nerve—the ophthalmicus profundus and the maxillaris. Posteroventrally is the foramen for the mandibularis branch of the trigeminal nerve. Posterior to these is the facial foramen. The posterior part of the cranium consists of a median ventral basioccipital, a median dorsal supraoccipital, and paired dorsolateral exoccipitals. Prominent on the ventral surface of the basioccipital are two pairs of posteriorly projecting tubercles, the pterygoid processes. Posteriorly the basioccipital forms the ventral third of the occipital condyle. Dorsolateral to the lateralmost pterygoid process is the flat plate of the exoccipital forming the posteroventral border of the otic notch. Immediately posterior to this plate and just lateral to the foramen magnum is a triangular depression containing the glossopharyngeal and vagus foramina. Within the otic fenestra is the auditory foramen. Posteroventrally to the lateral plate of the exoccipital the median portion of that bone makes up the lateral third of the occipital condyle. The exoccipitals bear high occipital crests extending posterolaterally from the

posterior corners of the supraoccipital. Median to the crests and posterior to the supraoccipital the exoccipitals form a thin dorsal covering for the foramen magnum. Lateral to the supratemporal crest on the supraoccipital is a slightly raised crest extending posteriorly beyond the posterior edge of the supraoccipital. The squamosal articulates with the posterior edge of the dorsolateral surface of the parietal, the dorsolateral surface of the protic, and the lateral part of the exoccipital, as well as the lateral surface of the supraoccipital. This thin bone terminates in a point considerably posterior to the hind edge of the brain case. The quadrate articulates with the dorsolateral surface of the posterior part of the squamosal. The quadrate has a rather high anterior flange. About midway in its length on the posteromedian surface is the columellar process, the point of fusion of the columella. Dorsal to this process there is a crest on the posteromedian surface of the quadrate. Ventrally there is a narrow neck in the quadrate before it expands into the articulating process.

**MAXILLO-PALATAL-PTERYGOID ARCH:** Anteriorly the maxillary begins just posterior to the tip of the lateral process of the premaxillary. The robust maxillary curves slightly laterally. On the anterior third of its lateral surface are two foramina. Issuing from the dorsomedian surface at about one-third of its distance from the anterior end is a broad, thin, median process that extends towards, but does not articulate with, the lateral process of the palatine. The maxillary teeth are set in sockets on the ventral edge of the bone. At the level of the last prediastemal tooth is a median trans-palatine process that articulates with the anteromedian part of the trans-palatine. Posterior to this point the maxillary narrows and then expands into a posterior knob, on the posteroventral surface of which are located the two enlarged posterior maxillary teeth. The anterolateral part of the trans-palatine articulates with the dorsal surface of the posterior knob of the maxillary. The palatine is rounded and extends anteriorly to the level of the posterior edge of the vacuity of Jacobson's organ. Posteriorly it is sutured with the anterior end of the pterygoid; from the median face of the palatine is a posterior pterygoid process

which overlaps the anterior end of the pterygoid. About midway in the length of the palatine is a lateral process which curves ventrolaterally to terminate in a spine. The large palatal foramen is located at the base of this process. Immediately posterior to the lateral process is a thin sphenoid process which issues from the dorsomedian surface of the palatine and extends to the position of the anterior end of the parasphenoid. The palatine teeth are set in shallow sockets on the ventromedian edge of the bone. From its articulation with the posterior knob of the maxillary the trans-palatine extends posteromedially to suture with the lateral surface of the pterygoid. Posterior to this suture is a deep pterygoid groove in the dorsolateral edge of the pterygoid. The dorsal surface of the pterygoid is rounded anteriorly and flattened posteriorly. Anterior to the lateral process articulating with the trans-palatine the pterygoid is narrow and rounded, with a slight lateral shelf along the dorsolateral edge. The teeth, decreasing in size posteriorly, are situated in sockets on a high median crest, which is a posterior extension of the rounded anterior part of the pterygoid. Lateral to this crest is a shallow, thin plate, bounded by a lateral pterygoid crest extending posteriorly from the trans-palatine suture to the hind tip of the pterygoid.

**MANDIBLE:** The dentary is laterally compressed, rounded below, and with a narrow dorsolateral crest bearing teeth on the median side. The posterior half of the dentary overlies the anterior part of the fused surangular-prearticular. In the middle of the broad lateral surface of the dentary is the large mental foramen. The splenial lies in a trench in the median surface of the dentary. Near the posterior end of their common dorsal suture is the large anterior inferior alveolar foramen; posteroventrally and lying entirely within the splenial is the smaller anterior mylohyoid foramen. Posterior to the splenial is the blunt anterior edge of the angular, a wedge-shaped bone lying between the dorsomedian part of the prearticular and the ventromedian part of the surangular. Near the anterior edge of the angular is the small posterior mylohyoid foramen. The articular, prearticular, and surangular are fused. The prearticular portion forms the high median wall of Meckel's



canal. Along the posterior part of the ventromedian surface is a low crest extending to the posterior end of the articular. Just posterior to the end of the dentary in the surangular portion is the large surangular foramen. Meckel's canal separates the surangular and prearticular through the posterior two-thirds of their length. The canal terminates at the articular condyle, which is followed by a short tympanic crest of the articular.

#### DENTITION

In *Leptodeira* the maxillary teeth are directed ventrally from the socket and then curve sharply backward. The teeth on the maxillary, pterygoid, and dentary decrease in size posteriorly; those on the palatine are subequal in size. The most posterior teeth on the pterygoid are small, only about one-third of the length of those on the anterior part. The posterior enlarged and grooved maxillary teeth are located on the posterior knob of the maxillary; they sit in shallow sockets on a posteroventral facet of the anterior part of

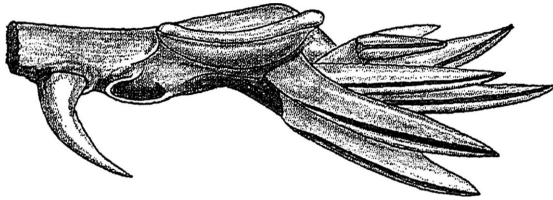


FIG. 16. Lingual view of the posterior part of maxillary of *Leptodeira frenata malleisi* (U.M.M.Z. No. 74885) showing position of replacement teeth of the enlarged posterior maxillary fangs.  $\times 10$ .

the knob and extend posteriorly. The grooves are on the ventrolateral surface of the tooth. Tooth replacement takes place from behind and from the side. On the maxillary and dentary the replacement teeth lie in the buccal tissue medial to the bone; on the pterygoid and palatine they lie lateral to it. The enlarged posterior maxillary teeth are replaced from teeth lying in a position dorsal to them. Several sets of replacement teeth are found at one time in the thick mass of tissue at the posterior end of the maxillary. (See fig. 16.)

Aside from the differences in the number of teeth on the four dentigerous bones (see sec-

tion on Character Analysis), there are few minor differences in shape. The maxillary teeth of the *septentrionalis* group, especially those of *splendida*, are somewhat more elongate, slender, and more gradually curved backward than in the other species groups. The enlarged posterior maxillary teeth of *Leptodeira latifasciata* have only a faint groove. This groove has been overlooked by previous workers and has been used as a character to separate this species on the generic level.

#### INTRAGENERIC VARIATION IN SKULL ELEMENTS

For a comparison of the skulls of the species of *Leptodeira* five elements that show distinctive interspecific differences were studied. These are discussed individually.

**QUADRATE:** The diagnostic features of this bone are the relative size and shape of the columellar process, the development of the supracolumellar crest, and the degree of depression in either the lateral or medial surfaces.

In the *annulata* group the columellar process is elliptical, with its long axis from anterodorsal to posteroventral. The interior supracolumellar crest is well developed but not particularly robust. On the lateral surface the anterior flange is well defined in most species, being least so in *maculata*. There is a median depression in the lateral surface; the dorsal articulating surface is directed anteriorly. The median process of the articulating condyle is thin and larger than the lateral process.

Snakes of the *septentrionalis* group have a columellar process as in the *annulata* group; the interior supracolumellar crest also is similar. There is a slight depression in the medial surface and a deep one in the lateral surface producing a strong anterior flange. The leading edge of the dorsal articulating surface is strongly directed anteriorly. The median process of the articulating condyle is large and thin.

The two species in the *nigrofasciata* group have a large, elliptical, columellar process that has a nearly straight anterior edge. The interior supracolumellar crest is heavy and curved somewhat more posteriorly than in the *annulata* and *septentrionalis* groups.

There is a shallow depression in the lateral surface; the anterior flange is not high but has a sharp leading edge. The anterior corner of the dorsal articulating surface is blunt and directed anteriorly. The median process of the articulating condyle is large and thin.

In *Leptodeira punctata* the columellar process is large, subtriangular, and with a nearly straight anterior edge. The interior supra-columellar process is low and curved somewhat posteriorly. The depression in the lateral surface is deeper than in species of the *nigrofasciata* group; the anterior flange is low and has a sharp leading edge. The anterior corner of the dorsal articulating surface sharply projects anteriorly. The median process of the articulating condyle is only slightly larger than the lateral process.

VOMER: Szunyoghy (1932) found the shape of the postero-inferior vomerine process and that of the vomerine fenestra to be of systematic value at the generic and specific levels. These structures in the species of *Leptodeira* are strikingly different, particularly so in the species groups. The postero-inferior vomerine process usually lies on a longitudinal axis, but in some specimens it is curved as shown in figure 15. This may be an artifact of preparation. The various shapes of the postero-inferior vomerine process and vomerine fenestra as found in *Leptodeira* are shown in figure 17.

Of the *annulata* group, in *annulata* and *maculata* the ventral part of the process is horizontal; at the posterior end it curves sharply anterodorsally, enclosing an elliptical fenestra. In *bakeri* the process is similar in shape, but the fenestra is nearly round. In *frenata* the process extends posterodorsally and then curves sharply anterodorsally, enclosing a triangular fenestra.

In the *septentrionalis* group the ventral part of the process is horizontal; there is a slight posterior projection after the process curves anterodorsally, enclosing a trapezoidal fenestra, in which the dorsal horizontal border is the shortest. This border is straight in *septentrionalis* and curved in *splendida*.

The process is curved posterodorsally and then strongly anterodorsally to enclose an elliptical fenestra in the *nigrofasciata* group.

In *punctata* the process extends posteriorly along the horizontal axis and then directly

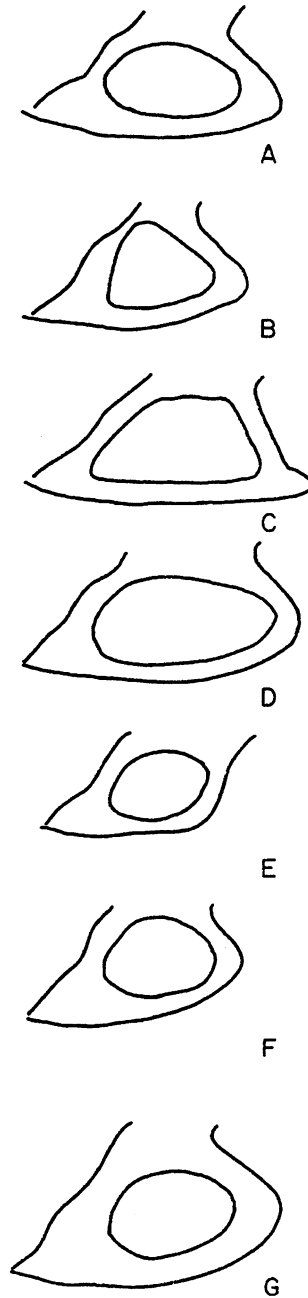


FIG. 17. Variation in the structure and size of the postero-inferior vomerine process and the vomerine fenestra in *Leptodeira* and related genera. The anterior part of the vomer is to the left. A. *Leptodeira annulata cussiliris*. B. *L. f. malleisi*. C. *L. s. septentrionalis*. D. *L. latifasciata*. E. *L. punctata*. F. *Hypsiglena o. ochrorhyncha*. G. *Trimorphodon b. biscutatus*.

dorsally to enclose a nearly round fenestra.

**PREMAXILLARY:** Bogert (1947) has shown the value of the shape of the premaxillary in studies of colubrid systematics and evolution. In *Leptodeira* the dorsal spine does not touch the nasals; the lateral processes are not robust, and there is no shelf of bone connecting them to the posterior processes.

In the *annulata* group the dorsal spine is high; the lateral processes are medium in weight and length. The lateral processes slope posterolaterally at an angle of about 60 degrees in *annulata annulata* and somewhat less so in the other forms. In *frenata* the dorsal spine has a straight anterior edge; the lateral processes are heavier at the base than in the other species in this group.

Species in the *septentrionalis* group have a high dorsal spine. In *septentrionalis* the lateral processes are long, heavy at the base, with a thin distal portion, and slope posteroventrally; in *splendida* they are shorter and heavier, but with the same slope.

In the *nigrofasciata* group the lateral processes curve backward only slightly; from the midline they slope ventrally and then extend laterally on a horizontal plane. The tips of the processes are pointed.

In *punctata* the dorsal spine is high; the lateral processes are thick, curve downward at an angle of about 45 degrees, and are not noticeably pointed. The posterior edge of the lateral process is perpendicular to the body axis; the anterior edge slopes backward.

**PTERYGOID:** Although there are no significant differences in the over-all shape of this element, the bulk of the lateral crest and the depth of the ventral depression vary between the groups of species.

In the *annulata* group the lateral trans-palatine articulating process is rounded; the lateral crest is heavy, and the ventral depression is deep.

In the *septentrionalis* group the lateral trans-palatine articulating process is angular and not so thick as in the *annulata* group. The lateral pterygoid crest is high but not robust, and the ventral depression is moderate in depth.

In the *nigrofasciata* group the lateral trans-palatine articulating process is thin and rounded; there are a slight lateral crest and a shallow ventral depression.

In *punctata* the lateral trans-palatine articulating process is elongate and thin; the lateral crest is rounded and not particularly heavy; the ventral depression is shallow.

**MAXILLARY:** There are few differences in the shape of the maxillary; these are the degree of compression of the element and the shape of the posterior knob. The number and position of the maxillary foramina are variable within the species groups and even within the species. The maxillaries of several forms are shown in figure 18.

In the *annulata* group the maxillary is robust, with a heavy posterior knob; in the *septentrionalis* group it is somewhat laterally compressed, and the posterior knob is not so heavy as in the former group. The maxillary of *nigrofasciata* resembles that of *septentrionalis*. That of *punctata* is not robust and is compressed posteriorly; the posterior knob is horizontally flattened and has a curving, antero-medial process.

#### THE VERTEBRAE OF *Leptodeira*

The following description is based on a specimen of *Leptodeira annulata cussiliris* (U.M.M.Z. No. S-1760). Hypapophyses are present on the first 31 vertebrae (including the atlas and axis). With the exception of the atlas, axis, and following three vertebrae, the neural spines are low, with long, horizontal, dorsal edges. These remain unchanged in shape throughout the column, even to the end of the tail.

The fiftieth vertebra is described in detail as follows. (See fig. 19.) The neural spine is elongate and thin, with the posterior edge more emarginate than the anterior. The zygosphene is roughly triangular in mid-sagittal section; laterally the zygosphene terminates in a slightly raised metapophysis, the flat surface of which faces ventrolaterally. The prezygapophyses extend laterally beyond the terminal articulating processes of the post-zygapophyses. A lateral crest connects the bases of the zygapophyses. The zygantrum is broad and shallow. On the ventral part of the base of the prezygapophysis is the region of rib articulation, the posterior part of which protrudes from the centrum and terminates in a rounded process, the parapophysis. The anteroventral part of the parapophysis, lying at the anterior edge of the base of the pre-

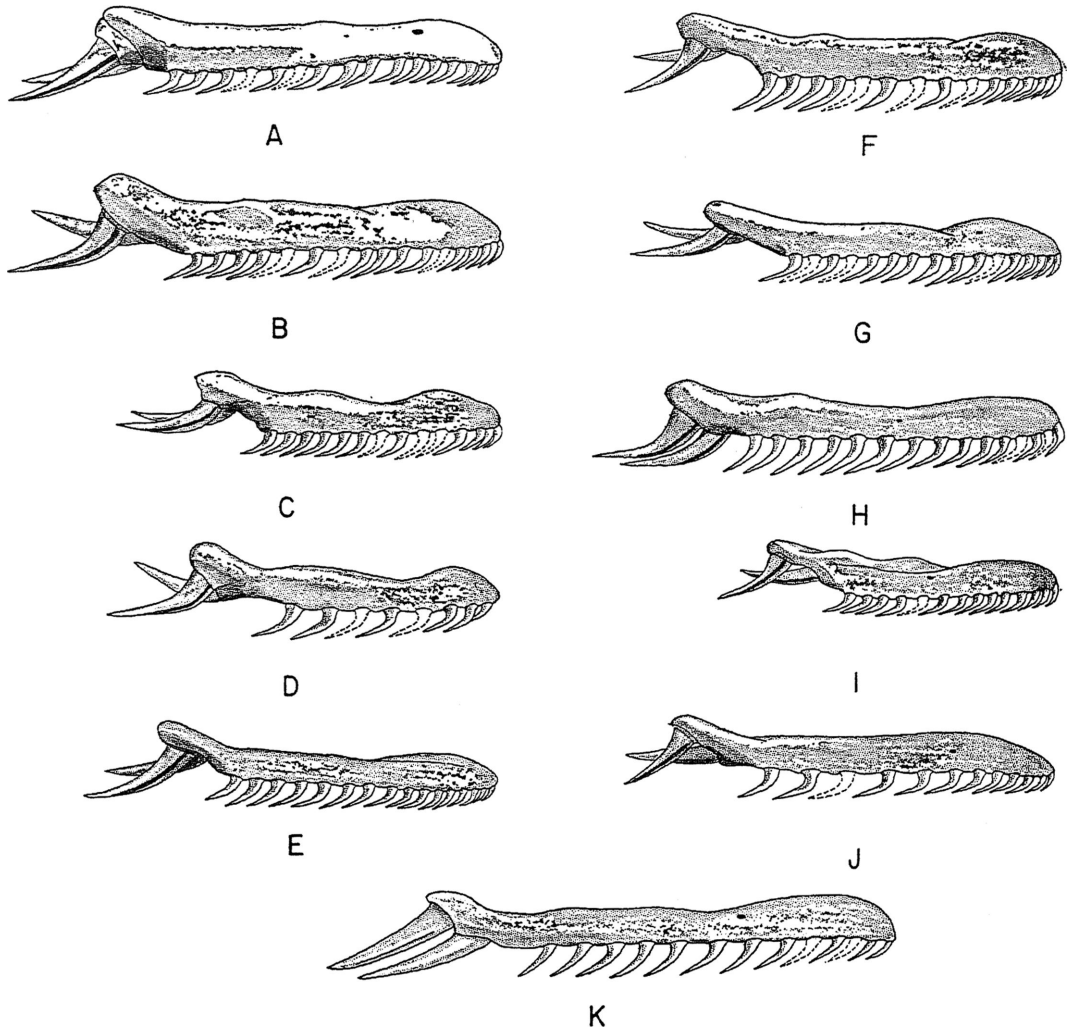


FIG. 18. Lateral view of the right maxillaries of 11 forms of *Leptodeira* showing characteristic shape of the bone and nature of dentition. A. *L. annulata annulata*. B. *L. annulata cussiliris*. C. *L. bakeri*. D. *L. frenata malleisi*. E. *L. maculata*. F. *L. septentrionalis septentrionalis*. G. *L. septentrionalis ornata*. H. *L. splendida splendida*. I. *L. punctata*. J. *L. nigrofasciata*. K. *L. latifasciata*.

zygapophysis, presents a flattened articulating surface. The ventral spinal foramen is formed by a small notch in the posterior margin of the pedicel immediately above the base of the ball; the dorsal, by a posteriorly directed groove in the neural arch between the bases of the metapophysis and the prezygapophysis. On the ventral surface of the centrum is a robust longitudinal crest.

The capitulum and tuberculum of the rib are fused; however, there are two distinct points of articulation with the vertebra, one

on the anteroventral articulating surface at the base of the prezygapophysis and the other posterodorsally on the rounded part of the parapophysis. Near the base of the rib is a short, posterodorsally projecting, costal process. With the exception of the posterior three pairs, these processes are present on all ribs.

Little intrageneric variation in the vertebral column was found. In *L. s. polysticta* hypapophyses were present on the first 32 vertebrae; in *punctata* they were found on the

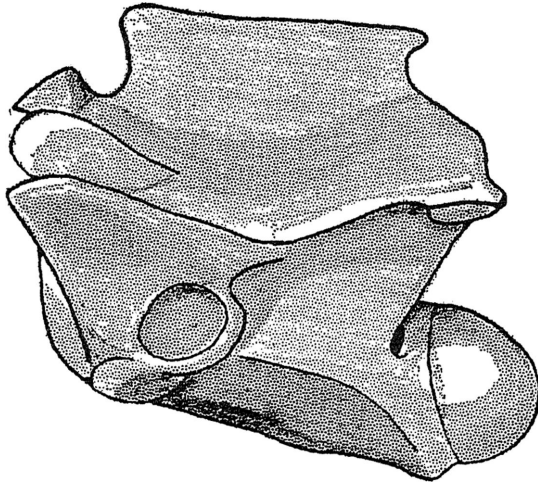


FIG. 19. Lateral view of the fiftieth vertebra of *Leptodeira annulata cussiliris*.  $\times 11$ .

first 28. In the latter species the rounded, protruding part of the parapophysis lies almost directly dorsal to the flattened, anterior, articulating surface. The costal processes of the ribs are situated closer to the proximal end of the ribs and touch the lateral crest of the centrum.

COMPARISON OF OSTEOLOGICAL CHARACTERS IN *Leptodeira* AND RELATED GENERA

The skull of *Trimorphodon biscutatus* (U.M.M.Z. No. S-1779), in comparison with the skull of *Leptodeira*, presents many striking differences. In the latter species the premaxillary has broad, wing-shaped, lateral processes; the septomaxillary is broad and thin anteriorly, and the lateral wing of the septomaxillary is shorter and has a broader base than in species of *Leptodeira*. The dorsal roof of the nasals extends anteriorly to fuse with the dorsal spine of the premaxillary;

however, the nasal septum is short and limited to the posterior part of the nasal area. The postero-inferior process of the vomer is robust and encloses a relatively small and nearly round vomerine fenestra. (See fig. 17.) The post-frontal is heavy, relatively small, and triangular. The supra-temporal crest is very high and fuses with the high, transverse, supraoccipital crest, which flares posteriorly. The squamosals are heavier and more rounded than in *Leptodeira*; the quadrate has a mid-lateral keel and a shallow depression on the median surface. In comparison with any of the species of *Leptodeira* the pterygoid bears fewer teeth and is much narrower posteriorly; also the maxillary bears fewer teeth than do most *Leptodeira*. These teeth are very large anteriorly and decrease in size posteriorly. (See fig. 20.) The posterior part of the maxillary is curved medially; the posterior knob is relatively thin and plate-like. The dentary bears few teeth, but the anterior ones are very large.

The skull of *Hypsiglena ochrorhyncha* (U.M.M.Z. No. S-1777) differs from that of *Leptodeira* in that the lateral processes of the premaxillary are heavy at the base; the posterior edge slopes anteriorly; the anterior edge slopes posteriorly; distally the process is slender. The dorsal spine of the premaxillary is low and broad; it slopes posteriorly to fuse with the nasals. The nasal septum is continuous from the dorsal spine of the premaxillary. The postero-inferior process of the vomer curves posterodorsally and then curves sharply anterodorsally, enclosing a nearly round fenestra. (See fig. 17.) The postfrontal is long and pointed; it curves downward. The squamosals are flattened; their median edges are curved in a shallow S shape. On the quadrate are a large, elliptical, columellar process, a thick supracolumellar crest, and a

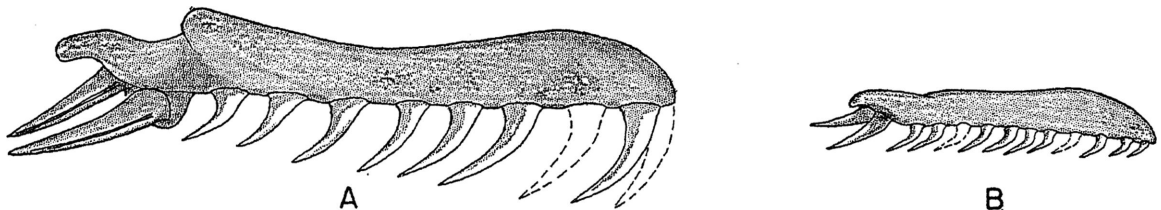


FIG. 20. Lateral view of right maxillaries. A. *Trimorphodon b. biscutatus*. B. *Hypsiglena o. ochrorhyncha*.

depression on the median and lateral surfaces of the bone. The pterygoid is somewhat more narrow than in *Leptodeira*, and there are fewer teeth. The maxillary is compressed and has few teeth. The posterior knob is thin and expanded and serves as the base for the two enlarged teeth without grooves. (See fig. 20.)

In *Trimorphodon* hypapophyses are present on the first 54 vertebrae. The parapophyses are rounded, and the articulating sur-

faces lie nearly on a dorsal-ventral axis. On the ribs costal processes are present except for the last 10 pairs. In *Hypsiglena* hypapophyses are present on vertebrae through the fortieth. The dorsal articulating surface of the parapophysis is slightly anterior to the ventral articulating surface. The costal processes of the ribs are located near the base and are in contact with the lateral crest on the centrum.

### HEAD GLANDS

As pointed out by Malcolm Smith (1943), the importance of the head glands, especially the parotid, cannot be neglected in opisthoglyph snakes. Considerable variation obtains in the genus *Leptodeira* and its allies. The following description is based on an adult specimen of *Leptodeira septentrionalis polysticta*. (See fig. 21.) The terminology used for the head glands is that of Smith and Bellairs (1947); that for the head muscles is from Radovanović (1935).

The premaxillary gland is crescent-shaped and lies beneath the rostral plate. It is thin and easily removed with the skin. There is a small nasal gland along the posterodorsal border of the external naris. The inferior labial gland is thin and elongate and extends along the lateral edge of the anterior two-thirds of the mandible. The superior labial gland is thicker than the inferior and lies below the upper labials. It extends posteriorly for a short distance beneath the anterior part of the parotid gland. According to Smith and Bellairs (*supra cit.*) the parotid gland or venom gland is a highly modified part of the superior labial gland. The parotid gland is of a coarser and tougher texture than the superior labial gland; it is flattened and covers the entire temporal region of the head, overlying the temporalis posterior, temporalis medialis, and masseter muscles, as well as the anterior part of the ligamentum zygomaticum. There is a single median duct leading from the gland to a small pocket in the mass of tissue lateral to the base of the enlarged posterior maxillary teeth.

With the exception of the species that comprise the *nigrofasciata* group of *Leptodeira*, all species have well-developed parotid glands

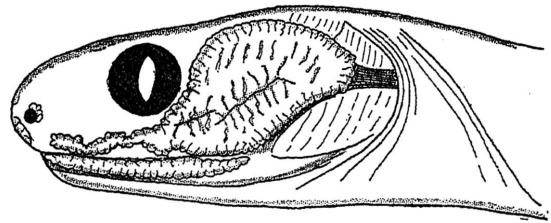


FIG. 21. Lateral view of the head of *Leptodeira septentrionalis polysticta* showing size and position of head glands.

similar to the gland described and figured for *L. s. polysticta*. In *L. nigrofasciata* the gland is small, and in *L. latifasciata* it is even smaller. (See fig. 22.) In *Trimorphodon* the gland is proportionately larger than in *Leptodeira*, extending posteriorly almost to the digastric muscle (depressor mandibulae of Haas, 1930); in *Hypsiglena* it is smaller.

As mentioned above under Dentition, the groove in the posterior maxillary teeth is deep in all forms of *Leptodeira*, except *L. latifasciata*, in which the groove is barely visible. The small size of the glands in this species is correlated with the condition of the teeth. *Hypsiglena* has a small gland, and the enlarged posterior maxillary teeth are without a groove. *Trimorphodon* has very large posterior maxillary teeth, with deep grooves. Cowles (1941) and Cowles and Bogart (1935) discussed the venom and its effects in *Hypsiglena* and *Trimorphodon*. Species in both genera have venom that will kill small lizards. Observations on captive specimens of three species of *Leptodeira* indicate that these snakes have venom of sufficient strength to kill small frogs. (See section on Food and Feeding.)

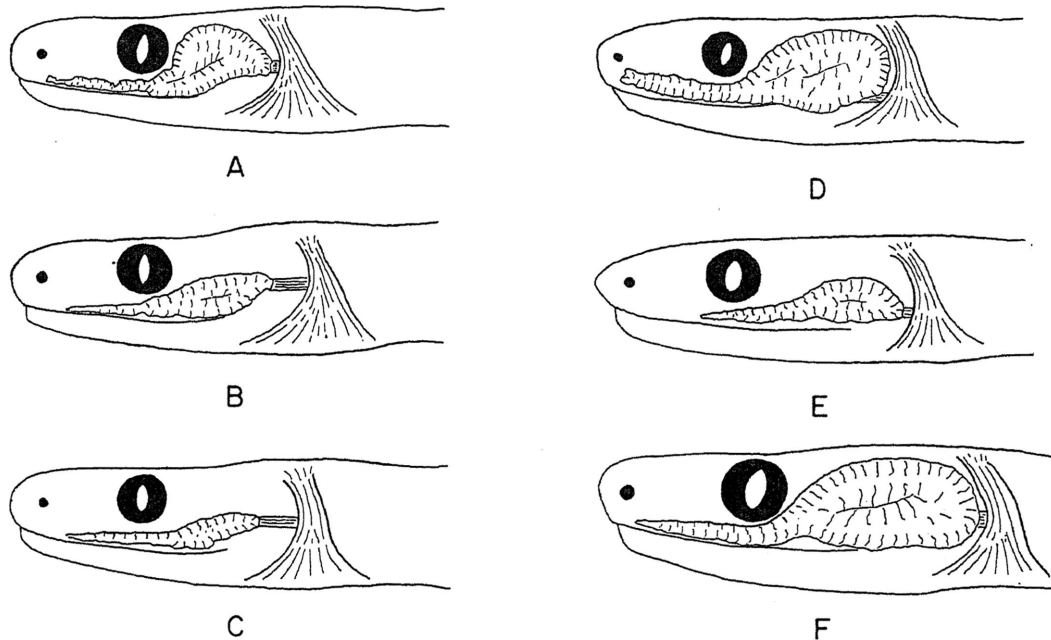


FIG. 22. Lateral view of the heads of *Leptodeira* and related genera showing relative size of the parotid (venom) gland. A. *Leptodeira septentrionalis polysticta*. B. *L. nigrofasciata*. C. *L. latifasciata*. D. *L. punctata*. E. *Hypsiglena torquata*. F. *Trimorphodon b. biscutatus*.

Smith and Bellairs (1947) stated that the differentiation of the parotid gland from the superior labial gland generally precedes the grooving of the teeth, but not always their enlargement. In the *Leptodeira-Hypsiglena-Trimorphodon* series, all species have en-

larged posterior maxillary teeth. The teeth of the species with the smallest parotid glands usually have no grooves, or only minute ones. The only exception, *L. nigrofasciata*, has grooved posterior maxillary teeth, but the parotid gland is small.

#### THE EYE

Walls (1942) studied the eyes of many colubrid snakes, including *Leptodeira annulata* (= *septentrionalis*) *polysticta*, *Trimorphodon lambda*, and *Hypsiglena ochrorhyncha*. The following discussion is a summation of the information presented by him.

In *Leptodeira* the rods are very numerous, long, and slender; the bodies, the ellipsoids of the cones, are perched on the tips of the rods. The outer segments of the cone themselves are very much larger than in pure cone diurnal forms such as *Natrix natrix* and *Coluber*. Rhodopsin is abundant, and the retina is so sensitive that the pupil closes completely as does that of a gecko. The type C element (small single cones present in few numbers)

has become a perfect rod and contains rhodopsin; the other two elements have outer segments that are intermediate between diurnal colubrid cones and full-fledged rods. Types A and B (A elements are large single cones; B elements are double cones) are much elongated, as if to be put into the background not only topographically but physiologically.

In *Trimorphodon* the outer segments of elements A and B are more or less enlarged and tend towards a cylindrical form. The type C element is even more rod-like. In *Hypsiglena* all three cone types have been converted into massive cylindrical elements. These are secondary rods and lack rhodopsin.

Walls (*op. cit.*) has shown that cones are primitive and rods are advanced. On the basis of this knowledge, it may be seen that the eye of *Trimorphodon* is somewhat advanced in having A and B elements rod-like and C element a well-developed rod, but without

rhodopsin. All the elements are well-developed rods in *Hypsiglena*, but none has rhodopsin. In *Leptodeira* elements A and B are intermediate between rods and cones, whereas element C is a well-developed rod with rhodopsin.

### HEMIPENES

The hemipenes of the various species of *Leptodeira* are capitate, spinous, and have a single sulcus spermaticus. As these have been described for each species in the section on the systematics of the genus, descriptions are omitted here, and the hemipenes of the species groups in *Leptodeira* and related genera are compared.

In the *annulata* group there is a large cup in the capitulum in *maculata* and in the northern subspecies of *annulata*. (See pl. 26, fig. 1.) It is somewhat smaller in *annulata annulata* and *bakeri* and absent in *frenata*. The capitulum is set off by a deep fold, and the distal spines are larger than the proximal ones, especially in *frenata*.

The cup is relatively small in the *septentrionalis* group. The capitulum is spinous, and the distal spines are smaller than the proximal ones. (See pl. 26, fig. 2.) In the hemipenes of the species of the *nigrofasciata*

group there is no cup in the capitulum, and the capitulum is spinous. The distal spines are longer than the proximal ones. (See pl. 27, fig. 1.) The hemipenes of *punctata* have a finely crenulated capitulum with a large cup. There are fewer spines than in the other species, and only those of the median row are enlarged, the distal one being the largest. (See pl. 27, fig. 2.)

In comparison with the general type of hemipenis found in *Leptodeira*, the hemipenes in the species of *Trimorphodon* are relatively longer, with a slender basal portion that is devoid of spines. There are no large spines on the distal part; the capitulum is flounced and has minute spines. The hemipenes of *Hypsiglena* also are without spines on the slender basal part; distally there are numerous small spines, and there are minute spines on the capitulum.



## ECOLOGY

THE SPECIES OF *Leptodeira* live in a variety of tropical habitats ranging from areas with a great amount of rainfall throughout the year that results in high tropical evergreen forests to those with prolonged dry seasons that support only a low deciduous scrub forest. Throughout the range of the genus temperatures are high, sometimes exceeding 40° C. in certain localities, and freezing temperatures are unknown. The following account of the ecological distribution of the forms of *Leptodeira* is based on personal field studies in México and on information supplied to me by various workers. The data are far from complete and need to be augmented by intensive field studies in different parts of the range.

In way of simplification I have defined seven major habitat types in which *Leptodeira* occur. These are based primarily on the structure of the vegetation, and no attempt has been made to analyze the floral components. The seven habitat types or vegetational formations may be divided into four that are essentially arid habitats (Open Scrub Forest, Dense Scrub Forest, Mixed Woodland and Savanna, and Deciduous Broad-Leaf Forest) and three that are humid habitats (Rain Forest, Wet Savanna, and Cloud Forest). The habitats are described briefly below:

**OPEN SCRUB FOREST:** In this type of forest, which usually consists of thorny leguminous trees and shrubs, the heights of the tallest trees may not exceed 3 or 4 meters. The trees have spreading crowns and are widely spaced. The understory consists of short grasses; often cacti are abundant. Usually the soils are sandy or rocky. There is little cover in the way of logs or other detritus. This habitat is present in the Pacific coastal lowlands in southern Sinaloa southward into the Balsas Basin in Michoacán and Guerrero. (See pl. 28, figs. 1 and 2.)

**DENSE SCRUB FOREST:** This type of habitat is similar to the preceding one but consists of higher and more closely spaced trees, resulting in more shade on the forest floor. There may be an herbaceous understory. Vegetation of this type is common in the low-

lands of northeastern México, on the Plains of Tehuantepec, along the Pacific coast of Central America, and the Caribbean coast of South America. The *cerrado* of southern Mato Grosso, Brazil, may be placed here. (See pl. 29, figs. 1 and 2.)

**MIXED WOODLAND AND SAVANNA:** Occurring in the eastern extremes of the Amazon Basin, as well as in parts of northern South America and in Central America, this habitat consists of open woodlands of leguminous or broad-leafed trees scattered in scrubby or grassy areas.

**DECIDUOUS BROAD-LEAF FOREST:** This is a habitat characteristic of the moderate slopes of the western edge of the Mexican Plateau; in *barrancas* this kind of vegetation often extends above the lower limits of the coniferous forest. Usually the forest consists of a mixture of tropical hardwoods and a discontinuous herbaceous layer. Small bromeliads are not uncommon, and often there is considerable ground cover in the way of logs and leaves. (See pl. 30, fig. 1.)

**RAIN FOREST:** A great variety of tropical hardwoods make up rain forest, the climax vegetation in tropical regions receiving a considerable amount of rainfall throughout the year. Often the crown of the forest is above 30 meters in height. In the extensive rain forests of the Amazon Basin there is little in the way of an understory and an herbaceous layer. In less well-developed rain forests there may be a rather continuous understory. Lianas and bromeliads are abundant; the large quantity of forest detritus and deep mulch provide good ground cover. (See pl. 31, figs. 1 and 2.)

**WET SAVANNA:** This grassland or low scrub habitat with scattered trees is found in southern México and at the base of the Yucatán Peninsula in northern Guatemala and British Honduras, as well as in northern South America. It is doubtful if it is a natural habitat for *Leptodeira*, for specimens encountered there probably came from the surrounding forests to feed on frogs that congregate in rain pools in the savanna.

**CLOUD FOREST:** The high forest composed of certain temperate species of trees and

found on humid slopes between elevations of 900 and 1500 meters is often termed cloud forest. The trees usually reach heights of 30 meters, are closely spaced, and support large numbers of bromeliads. The deep mulch and forest detritus provide good ground cover. (See pl. 30, fig. 2.)

Some species of *Leptodeira* are more or less restricted to one kind of habitat; others are found in strikingly different habitats in different parts of the range. (See table 28.) The species *latifasciata*, *maculata*, *nigrofasciata*, and *punctata* are found only in the scrub forests, whereas *splendida* occurs only in the Deciduous Broad-Leaf Forest. The other species have a wider ecological range. Often when the range of the species traverses the boundaries of radically different habitats,

the populations in the two habitats have differentiated on the subspecific level, e.g., *annulata annulata* in the Amazon rain forest and *annulata ashmeadi* in the scrub forests and open woodlands.

Morphological adaptations to certain environmental conditions are apparent in two populations of *Leptodeira*—*annulata annulata* and *septentrionalis ornata*. Both inhabit rain forests and independently have differentiated from round-bodied terrestrial stocks to forms having laterally compressed bodies, a reduced number of dorsal scale rows, and enlarged vertebral and paravertebral scale rows. These adaptations are for an arboreal life, as opposed to the terrestrial life of the other forms.

TABLE 28  
DISTRIBUTION OF THE FORMS OF *Leptodeira* IN MAJOR KINDS OF HABITATS

Form	Open Scrub Forest	Dense Scrub Forest	Mixed Woodland and Savanna	Deciduous Broad-Leaf Forest	Rain Forest	Wet Savanna	Cloud Forest
<i>a. annulata</i>	—	—	—	—	+	—	—
<i>a. ashmeadi</i>	+	+	+	+	—	+	—
<i>a. cussiliris</i>	+	+	+	+	—	—	—
<i>a. pulchriceps</i>	+	+	+	+	—	—	—
<i>a. rhombifera</i>	+	+	+	—	—	—	—
<i>bakeri</i>	+	—	—	—	—	—	—
<i>f. frenata</i>	—	—	—	—	+	—	—
<i>f. malleisi</i>	—	—	—	+	+	+	—
<i>f. yucatanensis</i>	—	+	—	+	—	—	—
<i>latifasciata</i>	+	—	—	—	—	—	—
<i>maculata</i>	+	+	—	—	—	—	—
<i>nigrofasciata</i>	+	+	—	—	—	—	—
<i>punctata</i>	+	—	—	—	—	—	—
<i>s. septentrionalis</i>	—	+	—	+	—	—	+
<i>s. larcorum</i>	+	+	—	—	—	—	—
<i>s. ornata</i>	—	—	—	—	+	—	—
<i>s. polysticta</i>	—	—	—	+	+	—	+
<i>s. splendida</i>	—	—	—	+	—	—	—
<i>s. bressoni</i>	—	—	—	+	—	—	—
<i>s. ephippiata</i>	—	—	—	+	—	—	—

## LIFE HISTORY

AS USUAL IN REGARD to most Neotropical snakes, little is known about the life histories of the various species of *Leptodeira*. The data presented here represent an accumulation of all known literature reports, personal ob-

servations, and unpublished information passed on to me by other workers. Data on growth rates and seasonal incidence are from the collection of *Leptodeira annulata* made in eastern Peru.

## REPRODUCTION

Snakes of the genus *Leptodeira* are oviparous and deposit from four to 13 eggs that are separate, thin shelled, leathery in texture, and light creamy white in color. Egg clutches are known from only six of the 20 forms. (See table 29.) The data presented by Haines (1940) are based on the egg laying of a female that was in captivity for six years; although the snake did not mate while in captivity, over a period of five years it deposited four clutches of eggs, some of which were fertile. This indicates that at least in *Leptodeira s. polysticta* the female is capable of retaining viable sperm for a number of years.

There is no available information on the incubation periods of *Leptodeira* eggs in nature, nor are there data pertaining to sites of egg deposition. Two of four eggs deposited by a captive *Leptodeira s. ornata* on February 11 hatched on May 1. The young weighed 1.8 and 2.3 grams and had total lengths of 230 and 235 mm. In this instance the incubation period was 79 days. Two of five eggs deposited by a captive *Leptodeira maculata* on June 18 hatched on August 13. The young weighed 2.3 and 2.2 grams and had total lengths of 205

and 195 mm. In this instance the incubation period was 57 days.

Further information concerning numbers of eggs was secured by an examination of females and a count of the number of eggs or large ova. Four specimens of *L. a. annulata* contained from four to seven eggs; three *L. a. cussiliris* contained three to six eggs; two *L. maculata* contained five and seven eggs; two *L. s. polysticta* contained 10 and 11 eggs. Specimens of *L. maculata* collected in early August contained eggs that were ready for deposition. Mating probably took place with the onset of the rainy season in early June, which indicates that the females retain the eggs for about two months. In regions where there are no marked rainy and dry seasons, such as in the Amazon Basin, mating may take place throughout the year. In the vicinity of Iquitos, Peru, females with well-developed eggs were found in January, March, and June. Furthermore, recent hatchlings were collected throughout the year. Of 10 hatchlings from the vicinity of Iquitos, one was collected in each of the following months: January, February, May, September, October,

TABLE 29  
DATA ON EGG CLUTCHES OF *Leptodeira*

Species	Number of Eggs	Average Measurements (in Mm.)	Average Weights (in Grams)	Date of Deposition	Size of Female (in Mm.)	Authority
<i>maculata</i>	5	28.0×13.0	2.7	June 18	640	Conant ( <i>in litt.</i> )
<i>punctata</i>	6	22.3×10.5	1.8	Aug. 17-18	565	Conant ( <i>in litt.</i> )
<i>s. septentrionalis</i>	12	—	—	—	—	Ditmars (1945)
<i>s. polysticta</i>	7	28.9×12.0	—	Mar. 20	960	Haines (1940)
<i>s. polysticta</i>	6	25.7×10.8	—	May 6	960	Haines (1940)
<i>s. polysticta</i>	9	23.7×11.8	—	Mar. 22-28	960	Haines (1940)
<i>s. polysticta</i>	12	21.1×11.8	—	May 7-14	960	Haines (1940)
<i>s. ornata</i>	4	34.5×11.7	3.1	Feb. 11	730	Conant ( <i>in litt.</i> )
<i>s. bressoni</i>	9	21.7×12.3	2.1	Feb. 20	860	Conant ( <i>in litt.</i> )

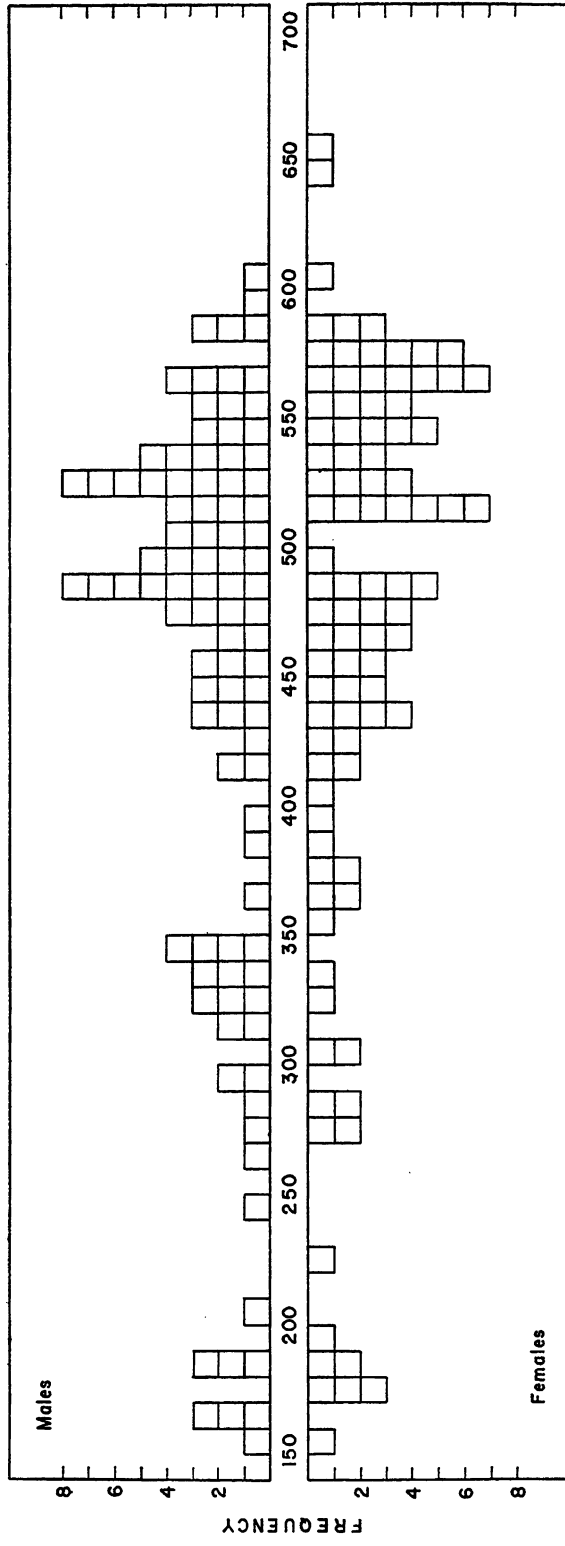


FIG. 23. Observed frequency of body lengths in *Leptodeira annulata annulata* from the vicinity of Iquitos, Ecuador. (96 males, 94 females.)

and December; two were collected in March and in August.

Oliver (1947) reported on *Leptophis richardi nigromarginatus* from Iquitos, Peru, and found by examination of mature eggs in adult females that there was no indication of a restricted breeding season in that species. Most studies of reproductive habits and cycles in snakes have dealt with species from temperate climates. The works of Blanchard on *Ophiodrys vernalis* (1933), *Storeria occipitomaculata* (1937a), *Diadophis punctatus edwardsi* (1937b), Blanchard and Blanchard on *Thamnophis sirtalis sirtalis* (1941), Carpenter (1952a) on three species of *Thamnophis*, and Edgren (1955) on *Heterodon platyrhinos* show that these snakes, living in temperate

latitudes with marked seasons, have a rather limited breeding season. This is usually shortly after emergence from hibernation in April or May. The young are born or hatch before the onset of cold weather in the autumn. The data presented here, together with those given by Oliver (*supra cit.*), indicate that, possibly owing to the absence of marked seasons in the upper Amazon Basin, snakes there may breed throughout the year. It is doubtful if this is true for all species of *Leptodeira*. Those species that live in arid regions marked by a short rainy season, such as in the Balsas Basin of México, show definite seasonal activity. In these regions the reproductive cycles probably more closely coincide with those of species that inhabit temperate regions.

### GROWTH AND LONGEVITY

To ascertain growth rates in a given species of snake under natural conditions, it is necessary to gather data by the marking, releasing, and recapturing of individuals over a period of years, or, less desirably, to measure a large series of specimens collected at one time from a limited area. Such data are not available for species of *Leptodeira*. Data given by Haines (1940) for a captive *L. s. polysticta* show that this individual increased in total length from 750 to 960 mm. during a period of six years.

An attempt to determine growth rate in a series of 190 specimens of *L. a. annulata* from Iquitos, Peru, shows little evidence of age groups. (See fig. 23.) Peters (1956a), working with *Dipsas catesbyi* from Iquitos, divided a series of 205 specimens into five age groups. Because his specimens, as well as those of *L. a. annulata*, were collected over a period of years, such groups are entirely artificial and are not used here. Females attain a slightly greater body length than do the males. The hatchlings having prominent umbilical scars vary from 150 to 200 mm. in body length. The smallest sexually mature individuals vary from 300 to 350 mm. in body length.

Studies on growth and maturity of snakes in temperate regions by Carpenter (1952b) and Siebert and Hagen (1947) indicate that, at least in *Thamnophis sirtalis sirtalis* and in *T. radix*, sexual maturity is reached by the second breeding season after birth. In the region where these studies were carried out the

growing season is about five months in duration, and between the time of birth and the second breeding season the snakes are slightly more than double their size at birth. Data presented by Dowling (1950) show that *Seminatrix pygaea pygaea* in central Florida, where the species is active most of the year, may reach maturity at the end of its first year. As *Leptodeira a. annulata* lives in a region where it is active throughout the year, the specimens in the class of 300- to 350-mm. size may be yearlings; thus it may be inferred that these snakes reach sexual maturity in about one year.

Relative growth of the tail and body in samples of three subspecies of *Leptodeira annulata* were analyzed. (See fig. 24.) From the graphs it is evident that there is a slightly more rapid rate of growth in tail length in *rhombifera* and *annulata* than in *cussiliris*, and that there is a greater divergence in growth rate between the sexes.

The literature reveals only four longevity records for snakes of the genus *Leptodeira*. Haines (1940) kept an adult female *L. s. polysticta* for a period of six years. Flower (1925) reported two records for *L. annulata* in the London Zoological Gardens—four years, 11 months, and 21 days; and four years, two months, and eight days. For the same species Conant and Hudson (1949) reported an individual living three years and six months.

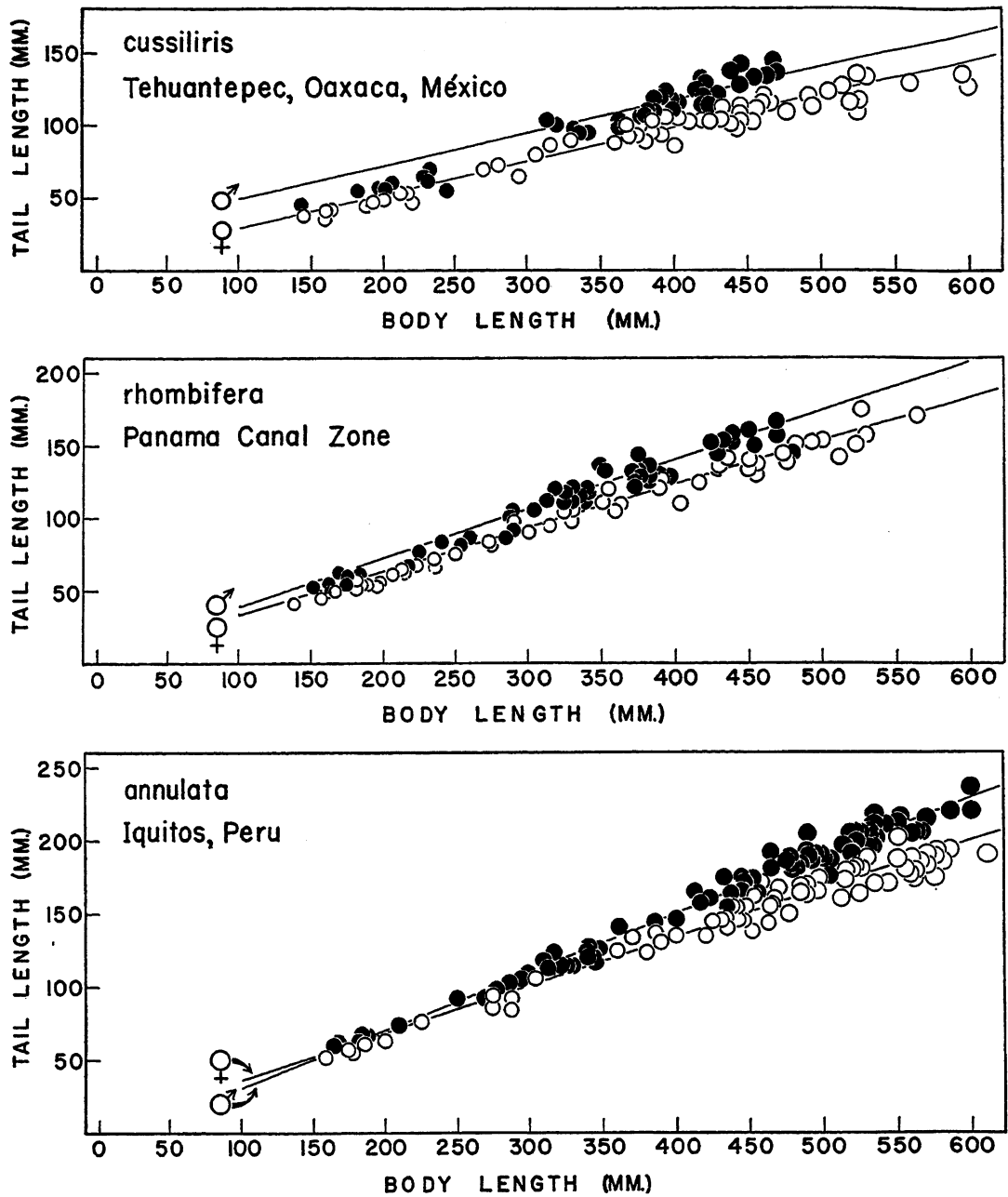


FIG. 24. Relative growth of body and tail in samples of three subspecies of *Leptodeira annulata*. Solid dots are males; open circles are females. The lines were calculated by the method of least squares.

## SEASONAL INCIDENCE

The only report of seasonal incidence in a Neotropical snake is that of Oliver (1947) for *Leptophis richardi nigromarginatus* from Iquitos, Peru. On the basis of 104 specimens of *Leptodeira a. annulata* with dates of collection from Iquitos, Peru, in the collection made by Dr. Harvey Bassler for the American Museum of Natural History, an analysis of seasonal incidence is possible. Analyses of observations on certain Mexican species also are included.

An analysis of the monthly variation in collections of *Leptodeira a. annulata* from the vicinity of Iquitos, Peru, shows two peaks of abundance, one in March and another in August. (See fig. 25.) There is a discrepancy in the percentage of total males and females collected in March as compared with the

close approximation in August. Only 11 per cent of the females were taken in March as against 33 per cent of the males. From the data given by Oliver (*supra cit.*) it may be seen that March is one of the wettest months and August one of the driest in the vicinity of Iquitos. Therefore, there appears to be no direct correlation between the number of snakes collected and the amount of rainfall.

That the peak of abundance in August is not the result of the hatching of the young is attested to by the fact that only two hatchlings were collected in that month. Such bimodal distributions of snake abundance in northeastern United States are due to the addition of young individuals to the population in late summer or early autumn and also to the more favorable temperature

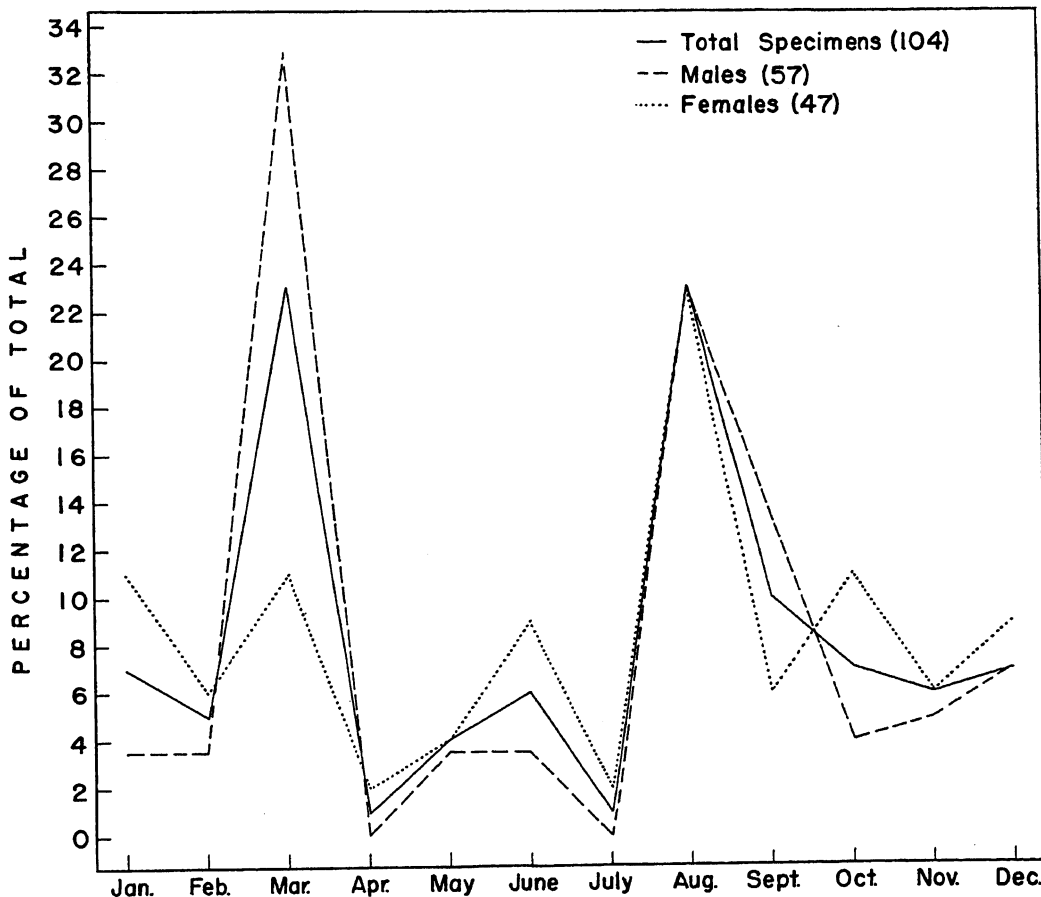


FIG. 25. Seasonal incidence of *Leptodeira annulata annulata* in the vicinity of Iquitos, Peru.

conditions of that season as compared with the usually hot and dry months of July and August. (See Conant, 1938, and Loveridge, 1927.) The spring peak in the temperate latitudes is due to the emergence of the snakes from hibernation and subsequent breeding activity, a time when the snakes are most active and more frequently encountered. The discrepancy between the numbers of males and females of *L. a. annulata* collected in March would seem to preclude the probability that this peak of abundance is due to breeding activity. As stated above these snakes probably breed throughout the year; if so, this fact eliminates breeding activity as the cause for the peaks of abundance in either March or August.

*Leptodeira a. annulata* feeds on frogs and toads, and the peaks of abundance may be correlated with amphibian activity. With the onset of the rainy season in March probably begins the breeding season of most of the amphibians, especially the hylids. Such activities in México attract many *Leptodeira*, and the same phenomenon probably is true for Iquitos. The second peak of abundance in the snakes, that in August, possibly may be correlated with a time of breeding of other frogs (leptodactylids?) when the ponds and streams have much less water, or perhaps at this time of the year recently metamorphosed frogs are especially abundant.

The human factor cannot be neglected when one tries to explain this seasonal incidence. During the drier months man is more active in the tropics, and possibly the greater activity of the workers in the Iquitos area in August resulted in the collecting of a relatively greater number of individuals. If so,

the graph of seasonal incidence of *Leptodeira* also shows, at least in part, seasonal activity of man in the vicinity of Iquitos.

When the graph showing seasonal incidence of *Leptodeira* is compared with that of *Leptophis richardi* (Oliver, 1947), it is apparent that the peaks of abundance for both species occur in March and in August, although the August peak is less pronounced in *Leptophis*. Both of these snakes are semi-arboreal and feed on frogs. *Leptophis* is diurnal, whereas *Leptodeira* is nocturnal.

In more arid regions *Leptodeira* shows a more marked seasonal incidence. Although collections are not available for every month of the year, on the basis of existing specimens and field observations certain conclusions are suggested. In the Tepalcatepec Valley near Apatzingán, Michoacán, México, field observations were carried on from April through August. In this region the annual rainfall is low and concentrated in the months from June through September. In April and May only two specimens of *Leptodeira maculata* were found, and these were under cover. In late June and early July, shortly after the rains commenced and amphibian congregations were at their height, 70 *Leptodeira maculata* were collected in a two-week period. Most of these were actively foraging at night. By early August when the breeding congregations of frogs had reached a meager number, fewer *Leptodeira* were encountered, nine being found in one week. In this region the seasonal incidence of *Leptodeira maculata* appears to be correlated directly with amphibian activity, which, in turn, is dependent upon the time of the rains.

## BEHAVIOR

Although possessing venom and enlarged posterior maxillary teeth, snakes of the genus *Leptodeira* are docile creatures, seldom, if ever, attempting to bite when captured or handled. The species *septentrionalis* and *splendida* have been observed to flatten the head by spreading the quadrates; the skin of the neck, however, is not distended. When encountered in the field these snakes either attempt to escape or coil and hide the head. This timid behavior has been observed in

*annulata cussiliris* and *maculata*. On the ground *Leptodeira* is capable of rather rapid movement, but not so fast as the more slender racers, e.g., *Coluber*, *Masticophis*, or *Salvadora*. The arboreal forms *septentrionalis ornata* and *annulata annulata* are morphologically adapted for living in trees and bushes; by compressing the body, they utilize the principle of the I-beam in moving from branch to branch. On repeated occasions a specimen of *ornata* was observed to extend its



body horizontally from a branch for approximately half of the total length of the snake. *Leptodeira frenata frenata*, *frenata malleisi*, and *septentrionalis polysticta* are semi-arboreal in their habits as indicated by their presence in epiphytic plants. Observations on *polysticta* and *frenata* show that these snakes

are capable of more rapid movement in bushes and trees than are the heavier-bodied terrestrial forms.

All species of *Leptodeira* are nocturnal. Although, according to Walls (1942), the eye is well adapted for diurnal sight, I know of no specimens found abroad during the day.

#### FOOD AND FEEDING

Snakes of the genus *Leptodeira* feed on small lizards and anurans, the latter apparently making up the bulk of the diet. Lizards were most commonly found in the stomachs of specimens collected during the dry season, a time when many frogs and toads are not active. Observations made on *L. annulata cussiliris*, *maculata*, *punctata*, and *septentrionalis polysticta* in México show that these snakes are frequently encountered at breeding congregations of frogs during the breeding season. Three *L. a. cussiliris* were found at a small pond near Zanatepec, Oaxaca, where there was a large breeding congregation of *Hyla robertmeriensi*. *Leptodeira maculata* was found in abundance in flooded fields near Apatzingán, Michoacán, where *Hyla smithi* was breeding. A juvenile *L. a. polysticta* was found grasping a metamorphosing *Hyla staufferi*. Smith (1943) reported *L. s. polysticta* feeding on the eggs of *Agalychnis moreleti* at Finca Juarez, Chiapas. The eggs of *Agalychnis* are suspended from leaves or branches of bushes that overhang ponds or streams. Richard Etheridge and I observed *polysticta* feeding on the eggs of *Agalychnis callidryas* near Catemaco, Veracruz. The snake was found in a bush at the edge of a pond; the distended mouth with the gelatin dripping from its jaws presented a weird sight. Eggs, presumably those of *Agalychnis dacnicolor*, were found in the stomach of a *Leptodeira s. bressoni* collected at Coalcomán, Michoacán. I know of no other snakes that feed on frog eggs.

The food items found in the stomachs of preserved specimens are listed in table 30.

Further items reported in the literature include *Ctenosaura similis similis* in *L. f. yucatanensis* (Barbour and Cole, 1906) and *Pteronohyla fodiens* in *L. s. polysticta* (Firschein, 1951). Captive specimens feed on small frogs and lizards. Ditmars (1945) reported that captive *L. s. septentrionalis* ate mice. This is, so far as I know, the only report of *Leptodeira* feeding on warm-blooded prey.

Observations were made on feeding habits of captive *L. f. frenata*, *maculata*, *punctata*, *s. ornata*, and *s. polysticta*. All these were fed frogs. When small frogs were placed in the cage the snakes would grab hold of one, usually quickly work to the head, and swallow the frog in much the same manner utilized by *Thamnophis* or *Natrix*. Sometimes the frog was still alive during the swallowing process, which indicates that with small prey the snake may not engage the enlarged, grooved fangs and inject venom. With larger frogs the snake strikes, grabs hold, and rapidly chews, opening its mouth widely until the enlarged, grooved fangs are engaged. Then it holds the prey until movement stops. The length of time necessary for the venom to take effect varies with the size of the snake and that of the frog; however, on the basis of my limited observations two to five minutes seem to suffice for most frogs. Data on the effect of the venom on large frogs and lizards are lacking. In view of the fact that the venom of several species of opisthoglyph colubrids is of sufficient potency to result in the death of human beings, investigations of the properties of these venoms is of considerable importance.



## PHYLOGENETIC RELATIONSHIPS

THE FOLLOWING INTERPRETATION of the interrelationships of the species of *Leptodeira* and of the relationship of that genus to other colubrine genera is based on the data given in

the sections on Systematics, Morphology, and Ecology and of corresponding situations that have been studied in other groups of animals.

## INTERSPECIFIC RELATIONSHIPS

With the use of general characters of scutellation, proportions, and coloration, as well as the nature of the dentition, osteology, head glands, and hemipenes, the nine species of *Leptodeira* may be placed in four species groups. The species *latifasciata*, *nigrofasciata*, and *punctata* are divergent from the main stock of *Leptodeira*. *Punctata* is a small snake that differs from all others in having fewer ventrals, caudals, and labials; it has a spotted color pattern unlike that of any other member of the genus. In general appearance it resembles *Hypsiglena* and probably represents an early stem from the main evolutionary line. In the species *latifasciata* and *nigrofasciata*, placed together in the *nigrofasciata* group, the long bands reach the ventrals, lateral intercalary spots are absent, the body is rounded, and the number of teeth is reduced. Furthermore, the nature of the quadrate and vomer is diagnostic. (See section on Morphology.) The parotid gland is small in both species. The posterior enlarged maxillary teeth have deep grooves in *nigrofasciata* and minute ones in *latifasciata*. The relationships of this group to the rest of the genus is not clear; probably it represents a second early divergence from the main evolutionary stem of *Leptodeira*.

In any attempt to ascertain the relationships and phylogeny of the other species in the genus, careful attention must be given to the apparently adaptive characters such as the numbers of ventrals, caudals, dorsal scale rows, and the body shape. The number of dorsal scale rows is fewer in those forms that are attenuate and have a laterally compressed body. Correlated with the reduced number of scale rows is the enlargement of the vertebral and paravertebral rows. Furthermore, these snakes have a high number of ventrals and caudals. This mode of adaptation to an arboreal means of life developed independently

in two species of *Leptodeira*. Characters that are not considered to be of an adaptive nature, especially as regards terrestriality versus arboreality, are color pattern, numbers of labials and oculars, dentition, and hemipenes.

On the basis of the characters given in the section on Morphology, the remaining six species of *Leptodeira* may be divided into two groups. The *annulata* group includes the species *annulata* with five subspecies, *bakeri*, *frenata* with three subspecies, and *maculata*. The *septentrionalis* group includes *septentrionalis* with four subspecies and *splendida* with three.

Of these two groups I consider *annulata* to have given rise to the *septentrionalis* group early in the evolutionary history of the former, but later than the differentiation of *punctata* and the *nigrofasciata* groups. Of the subspecies of *annulata*, *rhombifera* in northern Central America normally has the greatest number of dorsal scale rows (23 to 25), often has three preoculars, attains a relatively large size, and is terrestrial. It most closely approaches the terrestrial *septentrionalis*, and I consider it to be closest to the ancestral form of the two groups. *Maculata* represents a population that differentiated in México from the *annulata* prototype. The northern subspecies of *annulata*, *cussiliris*, represents a population that differentiated in southern México from a *rhombifera*-like stock; *cussiliris* has fewer body blotches, smaller lateral intercalary spots, and fewer ventrals and caudals than *rhombifera*. The South American *kugleri* differs from *rhombifera* mostly in having two longitudinal nape bars. The transition from the *rhombifera* color pattern without bars to that of *ashmeadi* takes place through Darien, Panamá, and northern Colombia. The presence of two nape bars in *pulchriceps* suggests close relationship with *ashmeadi*. Because of

its laterally compressed body and enlarged vertebral and paravertebral scale rows, adaptations for an arboreal existence, *annulata* is strikingly different from the other subspecies and is the most specialized form in the group. Intergrading populations between *annulata* and the terrestrial forms *ashmeadi* and *pulchriceps* are found in British Guiana and in southeastern Bolivia, respectively.

Isolated on Aruba Island off the coast of Venezuela, *bakeri* is obviously closely related to the terrestrial subspecies of *annulata*, from which it differs in having fewer caudals and ventrals and a different color pattern.

*Leptodeira frenata* differs from *annulata* in having fewer teeth, a slightly different hemipenis, and in certain osteological characters. Of the two species, *annulata rhombifera* and *frenata malleisi* are closest in color pattern and scutellation. Consequently, I believe that *malleisi* is most like the ancestral stock of the species *frenata* and gave rise to *frenata* and *yucatanensis*, subspecies that differ from each other and from *malleisi* primarily in color pattern.

In the *septentrionalis* group, *septentrionalis* is the most generalized form, and although differing in color pattern and in

the number of ventrals, it resembles *annulata rhombifera* in having 23 scale rows, three preoculars, and a relatively heavy body. On dispersing southward through Central America and western South America the *septentrionalis* stock differentiated into *polysticta*, *ornata*, and *larcorum*. The subspecies *polysticta*, and more so *ornata*, became adapted for an arboreal existence. In both, the body is elongate and slender, but in *ornata* there has been also a reduction in the number of scale rows, accompanied by a corresponding enlargement of the vertebral and paravertebral rows, and a lateral compression of the body. This adaptation parallels that in *annulata annulata*.

A *Leptodeira splendida* stock probably differentiated from a rather early *septentrionalis* stock in western México, a population that may well have resembled a more terrestrial phase of the present *septentrionalis polysticta*. *Leptodeira splendida bressoni* most closely resembles *polysticta* in color pattern, but differs in having fewer ventrals and caudals. I believe that a *bressoni*-like form was ancestral to *ephippiata* and *splendida*, both of which differ from *bressoni* chiefly in color pattern.

#### INTERGENERIC RELATIONSHIPS

In defining genera, Inger (1954) has shown the desirability of correlating morphological characters with the ecological implications of morphological adaptation in natural groups of species. A generic concept based entirely on morphological similarity can bring about groupings of unrelated species, e.g., the lumping of the African snakes of the genus *Crotaphopeltis* with *Leptodeira*. Morphological characters useful in showing relationships in one group of snakes may be of no significance in another. The presence or absence of a loreal is used as a character to separate certain genera. Oliver (1948) found the presence or absence of a loreal in *Leptophis* (= *Thalerophis*) to be significant only at the specific level. A single or divided anal plate is a constant characteristic of many genera of snakes, but in *Trimorphodon* the species *vandenburghi* has a single anal plate, and the other species have a divided one. Such examples also serve to illustrate the possible dangers in one's

separating genera on the basis of only one or two morphological characters, for in doing so the actual generic relationships may be obscured. The presence or absence of grooves in the posterior maxillary teeth has been used as a single criterion for the separation of many genera of colubrid snakes and also has been the basis for subfamilial groupings. Most systematists are now aware of the limited value of this character in showing generic relationships. Primarily on the nature of the posterior maxillary teeth, *Hypsiglena* has been lumped with and split from *Leptodeira*. Dunn (1936) considered the nature of the teeth as of little importance and lumped the genera that were previously separated by this character. Taylor (1938), on the other hand, considered the nature of the teeth as diagnostic characters and separated the genera.

The American snakes of the family Colubridae are a diverse lot that seem to defy classification into subfamilial and sometimes

generic categories. The first definite step towards a classification of American colubrids was that of Cope (1893b); this was corrected, modified, and supplemented by Dunn (1928) in his arrangement of the American genera. Dunn used the characters of the hemipenis and vertebrae to divide the American colubrids into four subfamilies. The subfamily Colubrinae, which contains *Leptodeira* and its relatives, is characterized by hemipenes with a single sulcus spermaticus and hypapophyses absent from the posterior vertebrae. On the basis of the hemipenes Dunn broke the colubrids into several subgroups. One of these, characterized by a capitate hemipenis, contains the genera *Hypsiglena*, *Leptodeira*, and *Trimorphodon*. The following discussion of intergeneric relationships includes these three genera and *Pseudoleptodeira* proposed by Taylor in 1938.

All these genera are nocturnal, have elliptical pupils, enlarged posterior maxillary teeth, and venom glands. So far as is known, all species in these genera are oviparous. The following generic characters are other than those discussed in the section on Morphology.

*Trimorphodon* has maxillary teeth that decrease in size posteriorly, with the last two enlarged and grooved, two apical pits, and a long hemipenis with flounces and with or without spines; there are 23 to 27 dorsal scale rows that are slightly oblique, two or three loreals, usually three preoculars and three postoculars, 213 to 275 ventrals, 76 to 102 caudals, and a single or a divided anal plate. The dorsal body pattern consists of large blotches or long bands. Most of the species reach a relatively large size, and individuals often exceed 1000 mm. in total length. The genus ranges from southwestern United States southward to western Nicaragua in dry environments; several species are found on the Mexican Plateau, others being restricted to the lowlands. Snakes of this genus appear to be partial to rocky areas and feed chiefly on lizards and small mammals.

*Leptodeira* has maxillary teeth that increase in size posteriorly, with the last two enlarged and grooved, two apical pits, and a short hemipenis with large spines but no flounces; there are 17 to 25 scale rows, one loreal, one to three preoculars, usually two postoculars, 150 to 211 ventrals, 54 to 107

caudals, and a divided anal plate. The dorsal body pattern consists of large or small blotches, or long bands. The size is medium to large, individuals seldom exceeding 1000 mm. in total length. The genus ranges through the lowlands to elevations of about 2000 meters from northern México to northern Argentina. Some species are found in dry environments; others, in wet. Although lizards are eaten, frogs and toads form the greatest part of the diet.

*Hypsiglena* has maxillary teeth that increase in size posteriorly, with the last two enlarged and without a groove, one apical pit, and a short hemipenis without flounces or large spines; there are 19 to 23 scale rows, one loreal, two or three preoculars, two postoculars, 154 to 204 ventrals, 36 to 68 caudals, and a divided anal plate. The dorsal body pattern consists of dark spots on a light ground color. The size is medium to small, seldom reaching 700 mm. in total length. This genus ranges throughout the arid and semi-arid parts of the United States from Washington and Kansas southward over the Mexican Plateau, the Pacific coast of México, and Baja California. Snakes of the genus *Hypsiglena* are found in arid environments to elevations of about 2500 meters. The food consists mainly of small lizards.

*Pseudoleptodeira* has maxillary teeth that increase in size posteriorly, with the last two enlarged and with faint grooves (grooves absent, according to Taylor, 1938), two apical pits, and a short hemipenis with small spines and no flounces. There are 19 to 23 dorsal scale rows, two preoculars, two postoculars, one loreal, 175 to 192 ventrals, 66 to 89 caudals, and a divided anal plate. The color pattern consists of long dark bands separated by narrow light interspaces or small dark blotches on a light ground color. The size is medium, not known to exceed 700 mm. in total length. This genus is known only from arid habitats in the lowlands of southern México. Nothing is known of the food habits.

Of the groups under consideration *Trimorphodon* appears to be more distantly related to the others than they are to one another. The characters of the oblique scale rows, two or three loreals, flounced hemipenis, decreasing size of the maxillary teeth, and general nature of the skull set *Trimor-*

*phodon* off from the other genera. No species of any of the genera shows characteristics intermediate with *Trimorphodon*. If this genus is related to the others, it must have diverged early from the evolutionary stock.

As pointed out by Dunn (1936) and Tanner (1944) *Hypsiglena* and *Leptodeira* are closely related. The chief diagnostic characters are the nature of the hemipenis, the number of apical pits, and the nature of the posterior maxillary teeth. Aside from these differences and those of morphology and coloration, there are geographical and ecological differences between these genera. They are essentially allopatric groups; their ranges overlap only on the Pacific coast of México and in northeastern México. Normally, *Hypsiglena* lives at higher elevations and in more arid habitats than *Leptodeira* does. Among the species of the two genera *Leptodeira punctata* is intermediate in many characteristics. In characters of scutellation and color pattern it is more like species of *Hypsiglena* than other *Leptodeira*. However, the hemipenes, dentition, and apical pits are typically those of *Leptodeira*. The geographical range of *Leptodeira punctata* is intermediate between the general ranges of the two genera; *punctata* is found in the lowlands of northwestern México and onto the lower parts of the western portion of the Mexican Plateau. I can find no evidence to contradict the belief that *Hypsiglena* and *Leptodeira* are monophyletic natural groups, with diagnostic morphological, geographical, and ecological attributes.

The snakes grouped in the genus *Pseudoleptodeira* by Taylor (1938) differ from *Leptodeira* solely in the reduced size of the parotid gland and the size of the grooves in the posterior maxillary teeth. Accordingly, I have included these species in the genus *Leptodeira*, thereby relegating *Pseudoleptodeira* to the synonymy of *Leptodeira*.

The determination of the phylogeny of the genera is a task made difficult by the lack of knowledge of the evolutionary significance of such diagnostic characters as apical pits and the various penial decorations. Smith and Bellairs (1947) believed that in the development of the poison apparatus in opisthoglyph snakes the glands differentiated

and increased in size and may even have become functional before the teeth become grooved. A general practice among students of ophidian evolution has been to consider forms with the higher numbers of scale rows, head shields, and ventral scutes more primitive than those with lower numbers. Certain of these characters are highly adaptive, and as illustrated by two species of *Leptodeira* such adaptation may be intraspecific. As stated above, *Trimorphodon* is farther removed from *Leptodeira* and *Hypsiglena* than they are from each other. If *Trimorphodon* did arise from the same ancestral stock that gave rise to *Leptodeira* and *Hypsiglena*, the generic differentiation of *Trimorphodon* must have been much earlier than the differentiation of *Leptodeira* and *Hypsiglena*. In my way of thinking the prototype of *Leptodeira* and *Hypsiglena* must have been a snake without grooved posterior maxillary teeth (venom glands may have been present), with the regular complement of colubrid head shields, smooth scales in no more than 25 rows, and a color pattern consisting of blotches, spots, or bands. The nature of the apical pits and hemipenis cannot be determined. From this prototype *Leptodeira* differentiated by developing grooves in the posterior maxillary teeth, two apical pits in the dorsal scales (if the prototype did not already have two), and a spinous hemipenis. *Hypsiglena*, on the other hand, did not develop grooves in the teeth, possessed only one apical pit, and became endowed with hemipenes with small spines.

At one time the African genus *Crotaphopeltis* was thought to be congeneric with *Leptodeira*. Barbour and Amaral (1927) separated the two groups as follows: *Leptodeira* with a wide maxillary diastema, long tail, more than 55 caudals, two pairs of chin shields, one to three rows of gulars, capitate hemipenis, and divided anal; *Crotaphopeltis* with a short diastema, short tail, fewer than 55 caudals, three to four pairs of chin shields, no gulars, non-capitate hemipenis, and single anal. The two groups represent entirely different lines of evolution and should not be considered closely related, and certainly not congeneric.

## EVOLUTIONARY HISTORY OF THE GENUS

The genus *Leptodeira* is a member of the New World group of colubrids that evolved in the Americas. Because of the lack of fossils of these snakes, a reconstruction of the evolutionary history of any of the genera must be based primarily on the morphology and distribution of the living species and correlated with what is known of the fossil history of other groups of animals. The mammalian fossils offer the most complete information concerning paleogeography and evolution of any group of vertebrates in the Americas. (See Simpson, 1940, 1950, and 1953.) Consequently, I have relied heavily on the data furnished by the paleo-mammalogists. A discussion of the evolutionary history of *Leptodeira* follows the brief outline given below of Cenozoic geology and paleogeography in Middle and South America.

## CENOZOIC HISTORY OF LATIN AMERICA

The following account of geological history and paleogeography has been compiled from many sources. The primary ones for Middle America are Eardley (1951), Sapper (1937), and Schuchert (1935), and, for South America, Darrah (1945), Jenks (1956a), and Weeks (1947 and 1948). Many individual papers that deal with local areas or specific situations are listed with the discussion of that particular subject.

The distinction between the Mesozoic and Cenozoic eras is evidenced in the great unconformity of deposits resulting from the widespread Laramide orogeny at the end of the Cretaceous (Eardley, *op. cit.*). Throughout the Mesozoic and Cenozoic eras ancient land masses persisted in central México, northern Central America, the Guianas in northeastern South America, and in eastern Brazil. (See Darrah, 1944; Schuchert, 1935.)

The Cenozoic history of Latin America has been one of submergence and emergence that resulted in the continental isolation of South America and the formation of isolated land masses in Middle America. Simpson (1943, 1950, and 1953) and Mayr (1946) have discussed this aspect of the geological history in reference to the distribution of mammals and birds. The region between southern México and continental South America has

been divided by four primary portals, which may be summarized as follows:

1. Colombian Portal: A seaway extending on the north from at least the Golfo de Urabá in extreme northwestern Colombia southward through the Chocó, separating South America from Middle America, and existing from the end of the Paleocene to the middle Pliocene. (See Simpson, 1953, for a discussion of the duration of this portal.)

2. Panamanian Portal: A narrow seaway through the region of the Isthmus of Panamá, existing from the upper Eocene through the middle of the Miocene. This portal together with the one in northwestern Colombia resulted in the formation of an archipelago in the region that is now eastern Panamá.

3. Nicaraguan Portal: A seaway of variable width across southern Nicaragua and northern Costa Rica and existing from the upper Eocene through the upper Miocene. This portal separated upper Central America from lower Central America.

4. Tehuantepec Portal: A rather narrow seaway across the Isthmus of Tehuantepec in southern México, existing for a short period in either the late Miocene or the early Pliocene, and serving to separate North America from Central America.

The presence of a sea barrier at the Isthmus of Tehuantepec in the Miocene or Pliocene has been used many times in the explanations of the present geographical distribution and evolutionary history of various groups of animals. Among the most notable herpetological works in this respect are those by Burt (1931), Gloyd (1940), Oliver (1948), and Stuart (1941, 1950, and 1951). For the most part these workers have followed the conclusions of Spencer (1897), Vaughan (1919), and Schuchert (1935) that the portal was open in late Miocene to early Pliocene. Dickerson (1917) and Woodring (1931) concluded that the portal was in existence before the late Miocene. Olson and McGrew (1941) presented data implying that the portal was closed at the end of the Miocene. Their conclusions were based on the presence of early Pliocene horses in Honduras. Recent findings of non-marine Miocene deposits in the isthmian region as reported by Durham, Arel-

Iano, and Peck (1952) and Stirton (1954) suggest that there was no Miocene seaway at the Isthmus of Tehuantepec. These findings limit the duration of the Tehuantepec Portal to the lower Pliocene. The limited duration of a seaway in that area does not invalidate the fact that the Isthmus of Tehuantepec has been, and still is, a barrier to the dispersal of some animals, as well as a highway for others. Climatic fluctuations during the Cenozoic may have caused vast ecological changes in the region; the ecological conditions may have acted alternately as barriers and highways, thus producing the same effect as an opening and closing sea portal.

The Yucatán Peninsula was submerged during most of the Cenozoic; parts of it emerged during the Pliocene, with the peninsula finally emerging at the end of the Pliocene. (See Sapper, 1937; and Hatt *et al.*, 1953.)

Mountain building and general uplift took place throughout much of the region at the end of the Cretaceous. Although the Mexican Plateau was uplifted at that time, it was not raised to its present elevation. The first uplift of the Andean chain occurred at the end of the Cretaceous. Following this uplift, which was more pronounced in the western Andes, i.e., more in southern Colombia to Chile than in northeastern Colombia and Venezuela, the mountain masses were reduced to maturity or old age at not a great elevation above sea level. (See Jenks, 1956b; Lewis, 1956; and Olsson, 1956.) Towards the end of the Miocene, uplift began throughout Middle America. This uplift included widespread volcanic activity. The diastrophism carried through the Pliocene and continues to the present time. Through this uplift the present Mexican Plateau, Sierra Madre Oriental, Sierra Madre Occidental, and Sierra del Sur of México were formed. Likewise the highland masses of Central America in Chiapas and Guatemala and in Costa Rica and Panamá were formed. Renewed uplift of the Andes occurred at the end of the Pliocene and continued through the Pleistocene, also accompanied by widespread volcanic activity.

Several minor points are of paleogeographic interest. Apparently Aruba Island has been without a land connection with the South American mainland since the late Cre-

taceous (Hummelinck, 1940). According to Schuchert (1935) and Tamayo (1949) a structural trough in the Balsas Valley in southwestern México was present throughout the Cenozoic. Pleistocene glaciation with corresponding climatic shifts was widespread in the high Andes and localized in the highest mountains of Middle America. (See Flint, 1947.)

On the basis of the aforementioned geological history and from the available paleobotanical data (Berry, 1918; and Olson and McGrew, 1941) it is possible to postulate certain conditions and changes in the climate and flora of Latin America throughout the Cenozoic era. The Paleocene and Eocene, at least in the Northern Hemisphere, were times of generally warm and humid climates which permitted the development of luxuriant vegetation even in the high latitudes (Flint, *op. cit.*). Beginning with the late Oligocene there was gradual desiccation and cooling, resulting in the restriction of tropical conditions and an expansion of xeric ones. This trend, of course, was repeatedly interrupted by climatic shifts during the Pleistocene. Consequently, it may be assumed that until the Pliocene there were present in México and northern Central America warm, moist, and moderately elevated uplands; this stage was followed by uplift and temperature reduction. This elevation of the mountain masses interrupted the climatic patterns and initiated the development of semi-arid conditions along the Pacific coastal regions from the Azuero Peninsula of Panamá northward. There are small areas of mesic conditions present along the coast, probably resulting from local wind systems. The development of the widespread semi-arid scrub forest has left isolated patches of relict mesic forest. According to the data presented by Olson and McGrew (1941) the climatic conditions of the Caribbean lowlands of Honduras in the early Pliocene were such that there were humid and subhumid floras, elements of which now exist in the present Central American and Amazonian rain forests. The extensive tropical rain forest in the Amazon Basin probably did not reach its present distribution until late Pleistocene. Earlier in the Cenozoic much of the basin was an epeiric sea in which there was a deposition of sediments resulting from



the erosion of the Andes. (See Haseman, 1912; and Oliveira, 1956.) The savanna and open woodlands that now exist in south-central Brazil and in northern South America were probably continuous or nearly so sometime during the late Pliocene and probably into the Pleistocene. Evidence for this is the presence of isolated patches of this habitat throughout the eastern part of the Amazon Basin. (See Ducke and Black, 1953; Smith, 1945; and Veloso, 1947.) Also, such a habitat was necessary for the dispersal of horses into southern South America in the late Pliocene (Savage, 1955). The arid region in north-eastern Brazil, which resulted in a scrub forest known as the *caatinga*, may be a result of Pleistocene climatic changes. This arid region separates the rain forests of the Atlantic coast of Brazil and those in the Amazon Basin. Because of the little differentiation shown by the animals that inhabit both areas of rain forest, but not the *caatinga*, it may be assumed that these forests were continuous in the late Cenozoic.

The development of the present-day climatic conditions and resulting habitats on the Pacific coast of South America is not entirely clear. At present the Pacific slopes and lowlands of Colombia and northern Ecuador receive an abundance of rainfall throughout the year. This is due to two factors—the presence of the high Andes, which cause the precipitation of moisture on the western slopes, and the warm counter equatorial current, El Niño, moving southward from the Gulf of Panamá. (See Murphy, 1936.) The ocean currents in this region may not have followed the same courses when the Colombian and Panamanian portals were open. Possibly such changes in ocean currents combined with the much lower Andean range resulted in less humid conditions on the Pacific slopes. Consequently, the heavy rain forests of western Colombia and northwestern Ecuador may not have developed until after the closure of these portals in the Pliocene, or until after the uplift of the Andes in late Pliocene and Pleistocene time. The coastal region of northern Chile and all but the northern part of Peru are exceedingly arid at the present time. The coast here is bordered by the cold Humboldt Current, and local on-shore winds bear little moisture. Prior to the great uplift of the

Andes in the late Pliocene and Pleistocene, moisture may have been carried to the coastal region by the trade winds from the southeast. Geological evidence based on tuff deposits in Peru indicate that the xeric conditions developed during the Pleistocene (Fenner, 1948).

Schuchert (1935) indicated a land connection from Central America to the Greater Antilles during parts of the Cenozoic. Again, specialists are not in agreement on this situation, although most geological and zoological evidence does not support such a land connection. As this problem does not enter into the evolutionary history of *Leptodeira*, it is not discussed here.

The accompanying paleogeographic maps (maps 12–25) are based on Schuchert (*op. cit.*) and Weeks (*op. cit.*). Evidence presented by more recent workers and from various other sources was used to modify the basic plan. The maps should be considered as a loose interpretation of the paleogeography of Latin America.

#### EVOLUTION IN THE GENUS *Leptodeira*

A reconstruction of the evolutionary history of any group of animals for which there is not a complete fossil record of necessity must be based on an interpretation of the processes responsible for the development of the extant species. Lack of knowledge concerning the rates of evolution in various groups precludes the possibility of “dating” the different events. Being completely aware of the absence of such essential information, I am presenting my interpretation of the evolution of the species and subspecies of *Leptodeira*. Admittedly, I am entering the realm of speculation; however, I feel that after the presentation of the foregoing factual information concerning these snakes some speculation is in order.

Previous generic revisions have included general discussions of possible evolutionary history with such statements as “After the ancestor of the *alternatus* group had entered South America, it spread . . .” (Stuart, 1941), and “. . . the ancestral population that was to give rise to *riveti* may have been isolated in northwestern South America by the Panamanian-Colombian water gap” (Oliver, 1948). Such descriptions of probable means of origin and dispersal of various

groups are of considerable aid to future workers working with genera or species that may have undergone similar evolutionary histories. With this in mind, I wish to carry the process one step farther—a step, I hope, that will help to clarify the historical events and their relationships to the evolution and dispersal of the herpetofauna of tropical America. Maps 12 through 25 are based on the Cenozoic history of the American tropics given above; superimposed upon them are the dispersal patterns of *Leptodeira* during the given periods throughout the Cenozoic. It should be emphasized that the evolutionary history, *although probably following the sequence that I have outlined, may not be correctly placed temporally*. I have started the evolutionary history of the genus in the Miocene, for it is unnecessary to go back farther in geological time to explain the events. I shall tell the story of evolution in the genus *Leptodeira* as though it were true, and let it speak for itself.

According to the basic principles of American herpetogeography proposed by Dunn (1931) and Schmidt (1943), there were successive faunal waves spreading southward from the Holarctic region during the late Mesozoic and Cenozoic. The earlier of these faunal waves (Dunn's "South American Faunal Element") entered South America before the isolation of that continent from North and Middle America prior to the Eocene. During the isolation of South America that element of the herpetofauna underwent differentiation into the host of genera and species that either remained in South America or dispersed northward after the connection of the continents in the Pliocene. However, some of the South American element stayed behind in Middle America, and subsequent differentiation of related stocks resulted on both sides of the Panamanian Portal. For this group which underwent differentiation in Middle America while related stocks were differentiating in South America, Stuart (1950) proposed the designation "Autochthonous Middle American Element." Successive faunal waves (Dunn's "Old Northern Faunal Element") came into Middle America where the older Old Northerners and members of the Autochthonous Middle American Fauna underwent generic differ-

entiation and dispersal. The younger Old Northerners differentiated and dispersed from a more northern center, such as the Mexican Plateau. At a later date the more recent waves (Dunn's "Holarctic Faunal Element") spread southward; these, however, are of little importance in the tropical regions. (For a complete discussion of relationships of these elements, see Dunn, 1931; Stuart, 1950, 1957.)

Dunn's faunal arrangement was at the family level, and Stuart's work followed that of Dunn. The colubrid snakes differentiated on both sides of the Panamanian Portal, into the xenodontines in South America and the colubrines in Middle and North America. With respect to Dunn's arrangement, *Leptodeira* must be considered a member of the Old Northern Faunal Element.

After the genus is placed in the over-all historical zoogeographical scheme, it is necessary to ascertain the general region in which generic differentiation occurred. It is stated above that the genera *Leptodeira* and *Hypsiglena* are closely related and probably differentiated from a common ancestral stock. Inspection of the present geographical ranges of these genera shows that *Hypsiglena* ranges northward from the southern part of the Mexican Plateau throughout the arid and semi-arid regions of western United States,<sup>1</sup> and that *Leptodeira* is found throughout the lowlands and slopes to moderate elevations of the American tropics. The present geographical ranges of the two genera are sympatric in the lowlands of western México. As there is no evidence that there were widespread xeric conditions throughout Central America in the Cenozoic, there is reason to believe that the range of *Hypsiglena* never extended much farther to the south than it does at present. Furthermore, the greatest differentiation of *Leptodeira* is found in southern México and northern Central America. Of

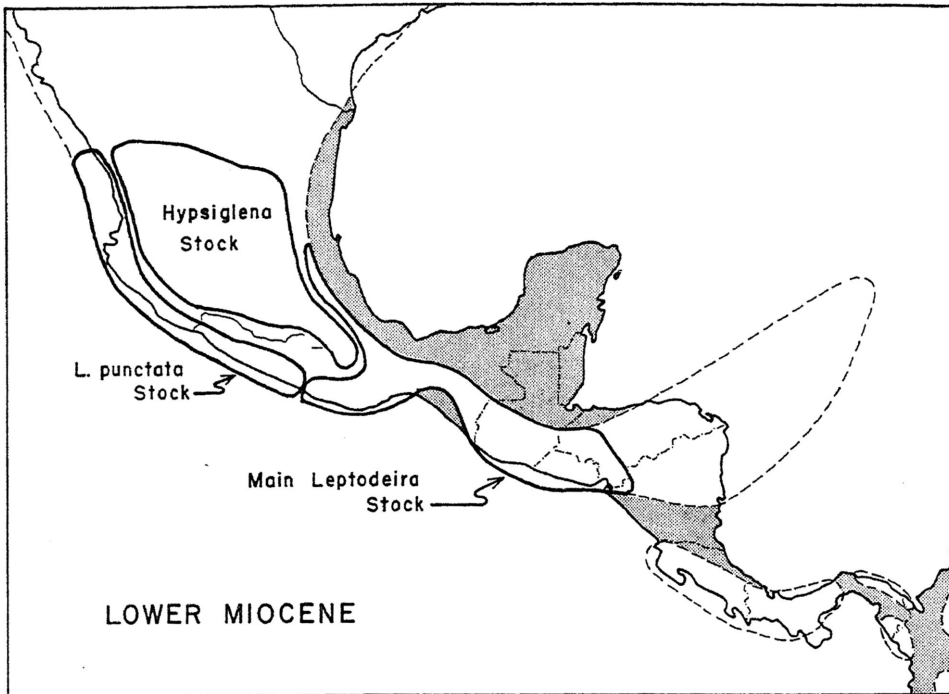
<sup>1</sup> Records for *Hypsiglena torquata* from Central America and South America are not accepted as valid. Peters (1956b) has discussed the status of the South American records. The specimen reported by Taylor (1954) is a juvenile *Leptodeira septentrionalis ornata*; Jan's (1871) records also probably are referable to this form. Günther (1860b) described *Hypsiglena torquata* from a specimen purportedly from Laguna Island, Nicaragua, a locality which I believe is in error.

the nine species, seven are found in that region, one is to the northwest in México, and one is isolated on Aruba Island off the coast of Venezuela. Only two species enter South America. Because *Leptodeira* did not have a secondary center of differentiation and dispersal in South America, it is assumed that the ancestral stock did not reach South America until after the closure of the Panamanian and Colombian portals in the Pliocene. Likewise, there is no evidence for isolation and subsequent differentiation of a *Leptodeira* stock in lower Central America, so it may be assumed that the ancestral stock did not reach that region until after the closure of the Nicaraguan Portal in the upper Miocene. As the climate of Middle America in the early Cenozoic was one of warm and moist conditions, *Hypsiglena*, as it now exists, probably was not present. With the gradual desiccation that began in the Oligocene, environments suitable for *Hypsiglena* began to develop. Consequently, the choice of a time and place of generic differentiation is dependent upon the differentiation of environmental types in a region more or less in the middle of the over-all distribution of the two genera. A logical choice of place seems to be the southeastern slopes of the region that is now the Mexican Plateau. By early Miocene time the development of semi-arid conditions along the Pacific slopes and in the uplands may have progressed to the point at which this type of environment contrasted with the more mesic forest environments to the east and south in Central America. From the ancestral prototype *Hypsiglena* developed towards a small terrestrial type and dispersed northward in the semi-arid environment. Snakes of this genus do not inhabit diverse habitats, and throughout their evolutionary history they have undergone little differentiation. On the other hand, *Leptodeira* dispersed throughout the lowland regions, coming in contact with varied environments. Through the presence of such physical barriers as the Tehuantepec Portal and diverse environmental conditions the *Leptodeira* stock underwent group and specific differentiation. (See map 12.)

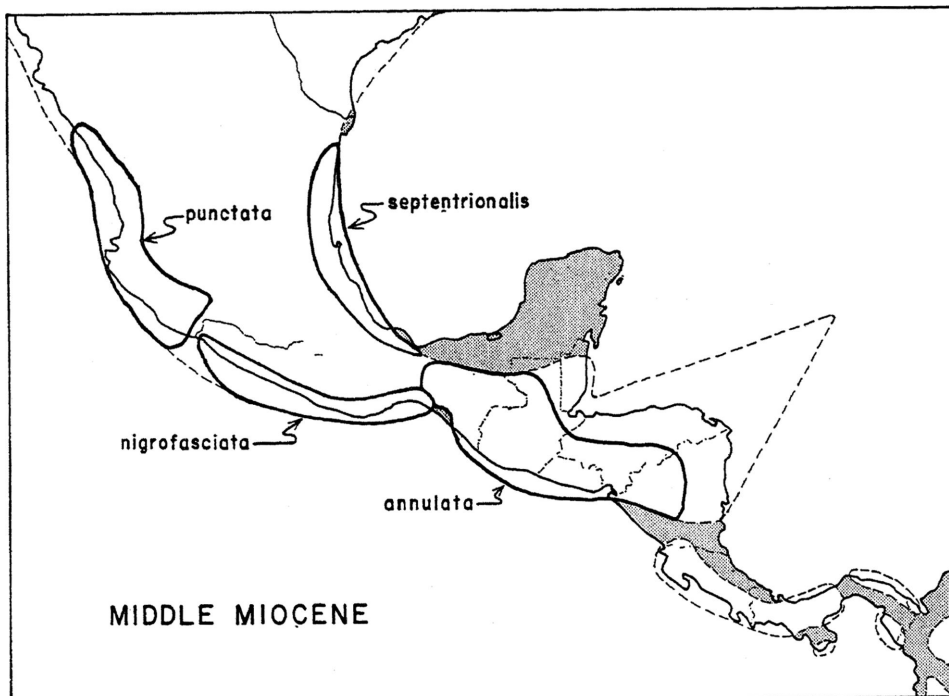
*Leptodeira punctata*, which in certain characters is intermediate between other *Leptodeira* and *Hypsiglena*, is considered to be a

direct descendant of the *Leptodeira-Hypsiglena* prototype. It retained the cup in the capitulum of the hemipenis and developed grooved posterior maxillary teeth. At the time when the generic stocks were separating, *punctata* dispersed through the lowlands of western México. Of the other three groups of *Leptodeira* the species *annulata rhombifera*, *septentrionalis septentrionalis*, and *latifasciata* are considered to be the primitive members. The *nigrofasciata* group represented by a *latifasciata*-like prototype probably differentiated from the main *Leptodeira* stock in early-middle Miocene and dispersed through the Pacific lowlands of southern México, perhaps eliminating the more primitive *punctata* in that area. By middle Miocene time the prototype of the *septentrionalis* group existed in the lowlands of eastern México, and the *annulata* group stock had spread southeastward from southern México to northern Nicaragua. (See map 13.)

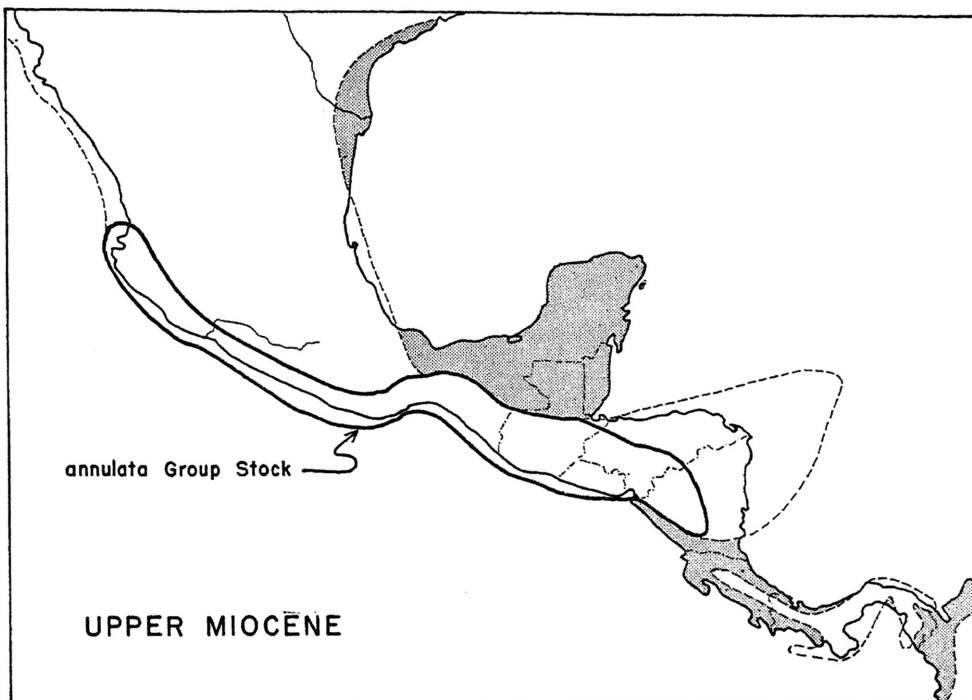
From this stage in the evolution of the genus, each group is discussed independently. Of the *annulata* group, the prototype of which was distributed throughout northern Central America in the middle Miocene, by upper Miocene time the stock had spread northward along the Pacific coastal lowlands of México to a point north of the Balsas Valley. (See map 14.) With the uplift of the mountain masses in northern Central America and México that began at the end of the Miocene, climatic changes resulted in the development of arid conditions along the Pacific coast of most of México and Central America. This uplift separated the *annulata* stock in northern Central America into a Caribbean population, destined to become *frenata*, and one on the Pacific slopes that, because of the closing of the Nicaraguan Portal, now spread southward into Panamá. The latter population was the ancestral stock of the species *annulata* and was inhabiting the dry environments along the Pacific coast. In the early Pliocene the Tehuantepec Portal opened and separated the Central American and Mexican populations of the *annulata* stock. This separation resulted in a differentiation of that population along the Pacific slopes of México that resulted in the development of *Leptodeira maculata*. Thus, in the early Pliocene the original *annulata* group



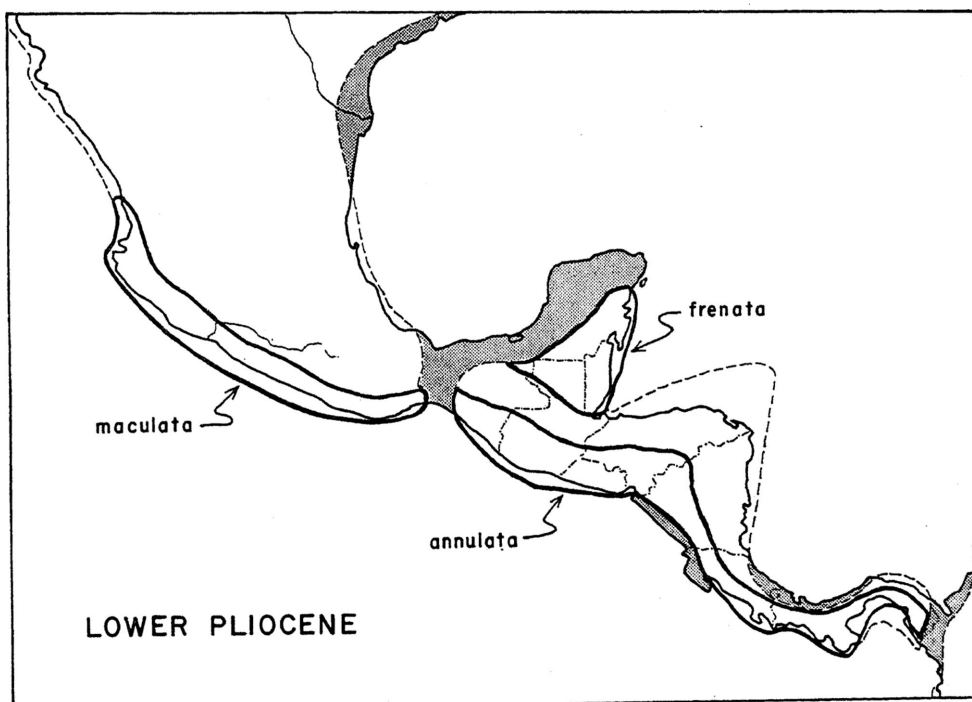
MAP 12. Distribution of *Hypsiglena* and *Leptodeira* ancestral stocks in the lower Miocene. In maps 12-25 the area enclosed by the heavy solid line is the presumed distribution of the form indicated; the dashed line represents the shore line at that particular time; the shaded area indicates present land areas that were under water in that particular geological time.



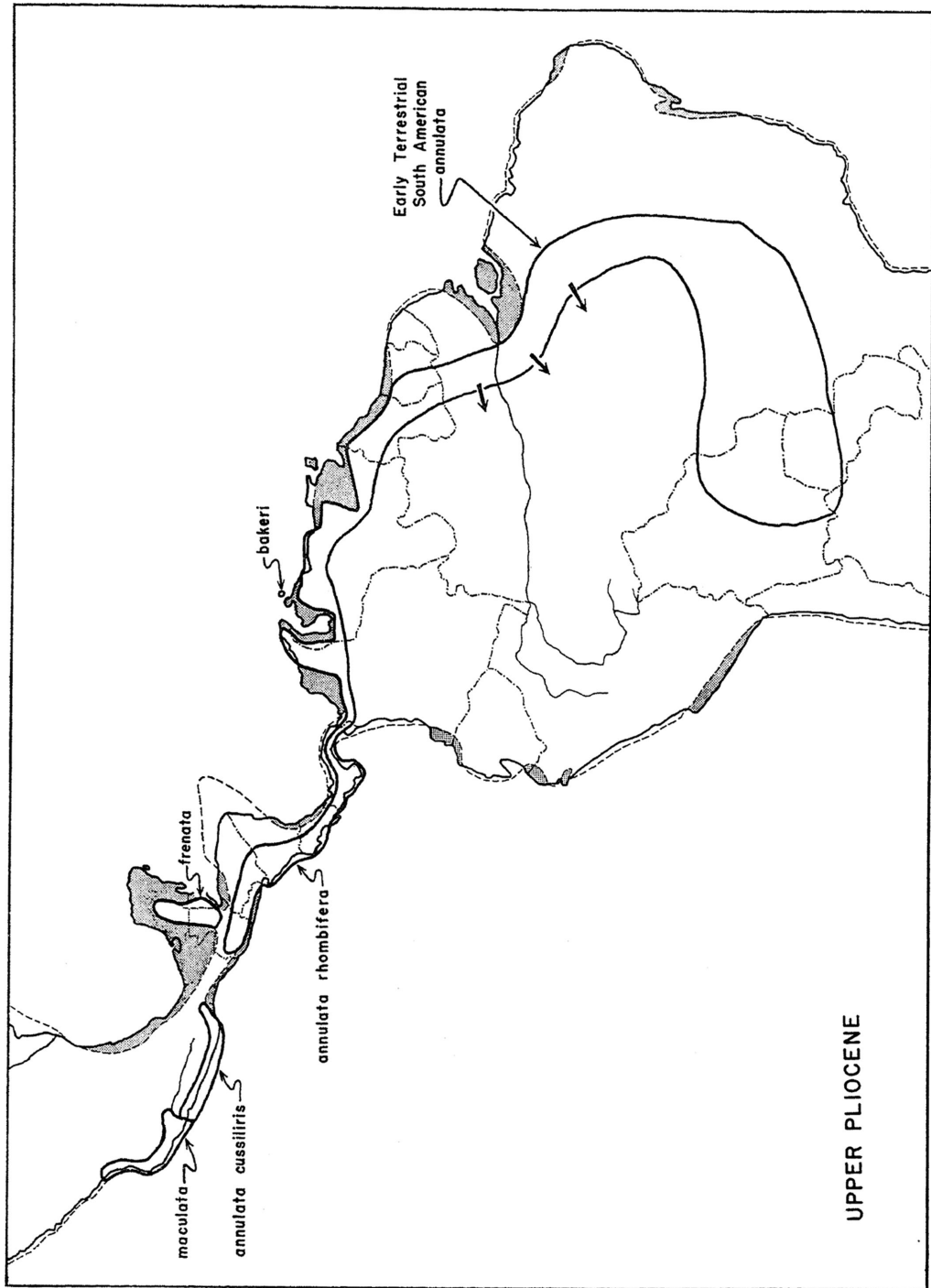
MAP 13. Distribution of the groups of *Leptodeira* in the middle Miocene. (See map 12 for explanation.)



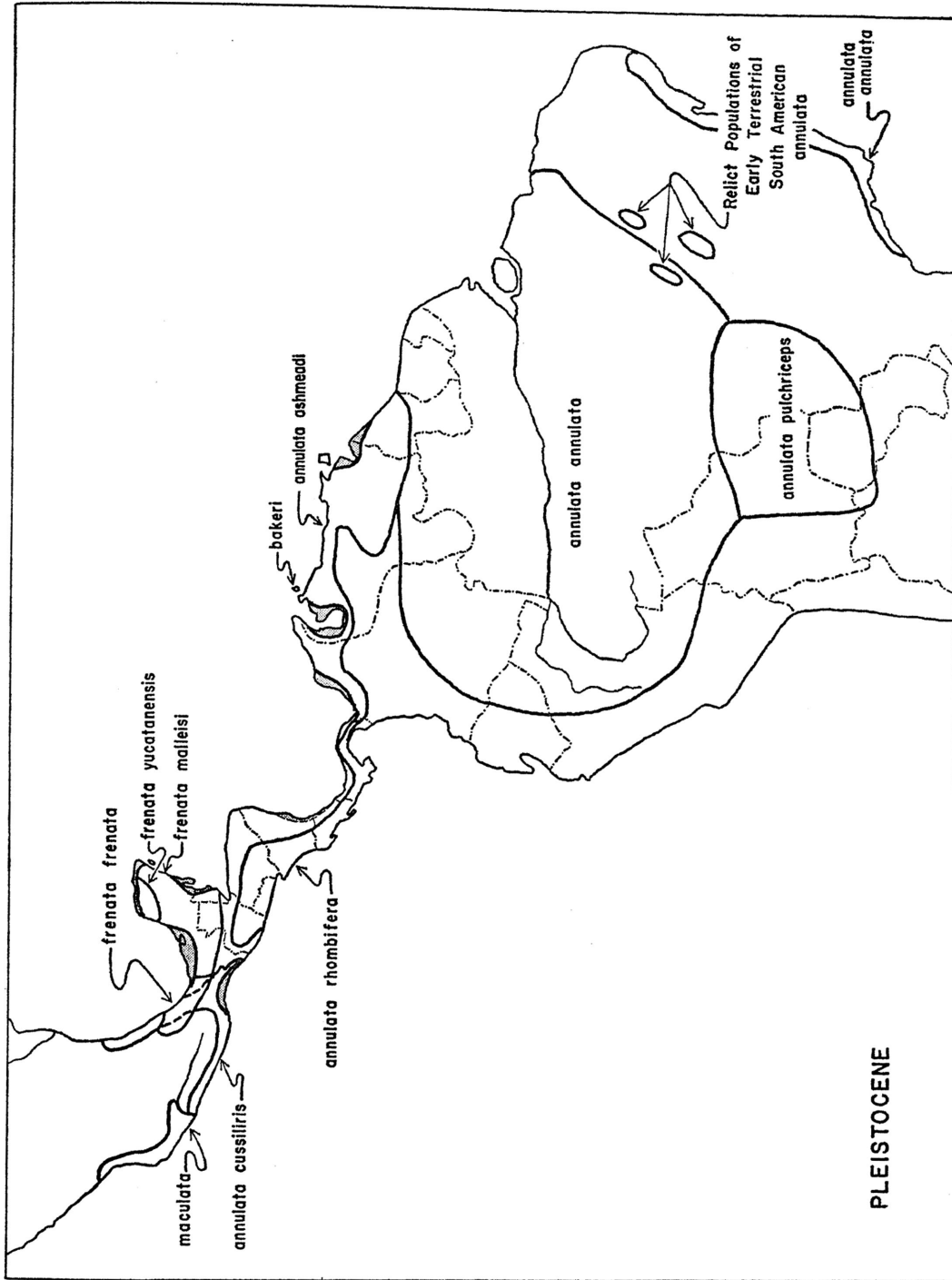
MAP 14. Distribution of the *annulata* group of *Leptodeira* in the upper Miocene. (See map 12 for explanation.)



MAP 15. Distribution of the *annulata* group of *Leptodeira* in the lower Pliocene. (See map 12 for explanation.)



MAP 16. Distribution of the *annulata* group of *Leptodeira* in the upper Pliocene. Arrows in eastern Brazil represent the modification of the terrestrial stock in this area for an arboreal mode of life in the Amazon Basin. (See map 12 for explanation.)



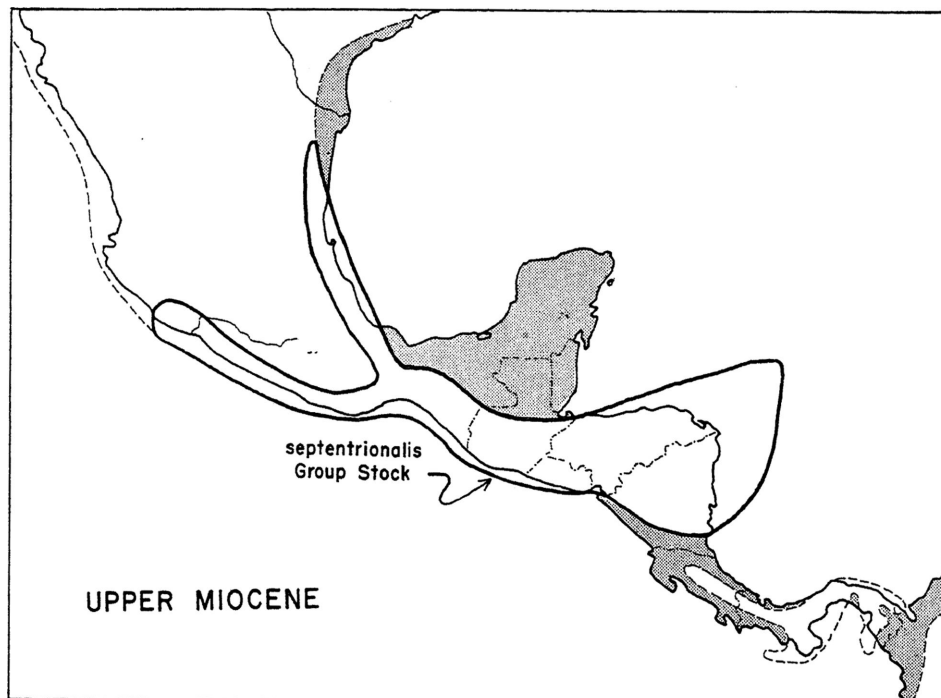
MAP 17. Distribution of the *annulata* group of *Leptodeira* in the Pleistocene. (See map 12 for explanation.)

stock was divided into three populations—*frenata* in the southeastern part of the Yucatán Peninsula, *maculata* in the Pacific lowlands of México, and *annulata* in the Pacific lowlands of Central America. (See map 15.) With the closure of the Tehuantepec Portal *annulata* spread from northern Central America into southern México, as far north as the Río Balsas, and differentiated into the subspecies *cussiliris*, which successfully competed with *maculata* and eliminated that species from the southern part of its former range. Meanwhile in Central America *annulata rhombifera* was developing. With the closure of the Panamanian and Colombian portals in the upper Pliocene the *annulata* stock moved into South America following the dry habitats that cross from the Pacific lowlands of Panamá to the Caribbean lowlands of northern South America. (See Dunn, 1940.) This terrestrial *annulata* stock spread through the scrub forest, savanna, and open woodland habitats eastward across northern South America and then southward to southern Mato Grosso, eastern Bolivia, and

northern Paraguay. In the open woodland-rain forest ecotone along the eastern edge of the Amazon Basin this terrestrial *annulata* stock began to develop into an arboreal forest form, destined to become *annulata annulata*. (See map 16.)

Also, during the upper Pliocene a population of the early terrestrial South American *annulata* stock reached Aruba Island; through its isolation there it subsequently differentiated into *bakeri*. In the late Pliocene the *frenata* stock in the southern part of the Yucatán Peninsula dispersed northward as the peninsula emerged.

During the Pleistocene *annulata cussiliris* spread into the lowlands of eastern México and southeastward along the coast of Chiapas. The *frenata* stock dispersed through mesic habitats in the Yucatán Peninsula and westward into southern Veracruz, differentiating into *frenata frenata* in Veracruz and *frenata yucatanensis* in northern Yucatán. The original stock is most closely resembled by *frenata malleisi* which inhabits the southern part of the Yucatán Peninsula, Tabasco,



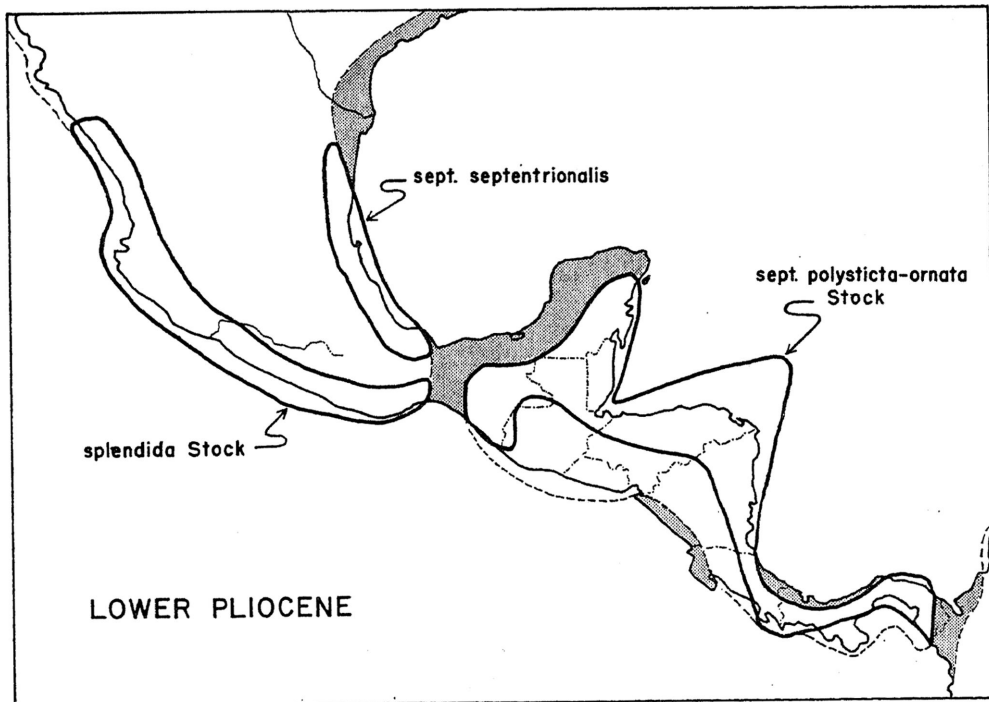
MAP 18. Distribution of the *septentrionalis* group of *Leptodeira* in the upper Miocene. (See map 12 for explanation.)



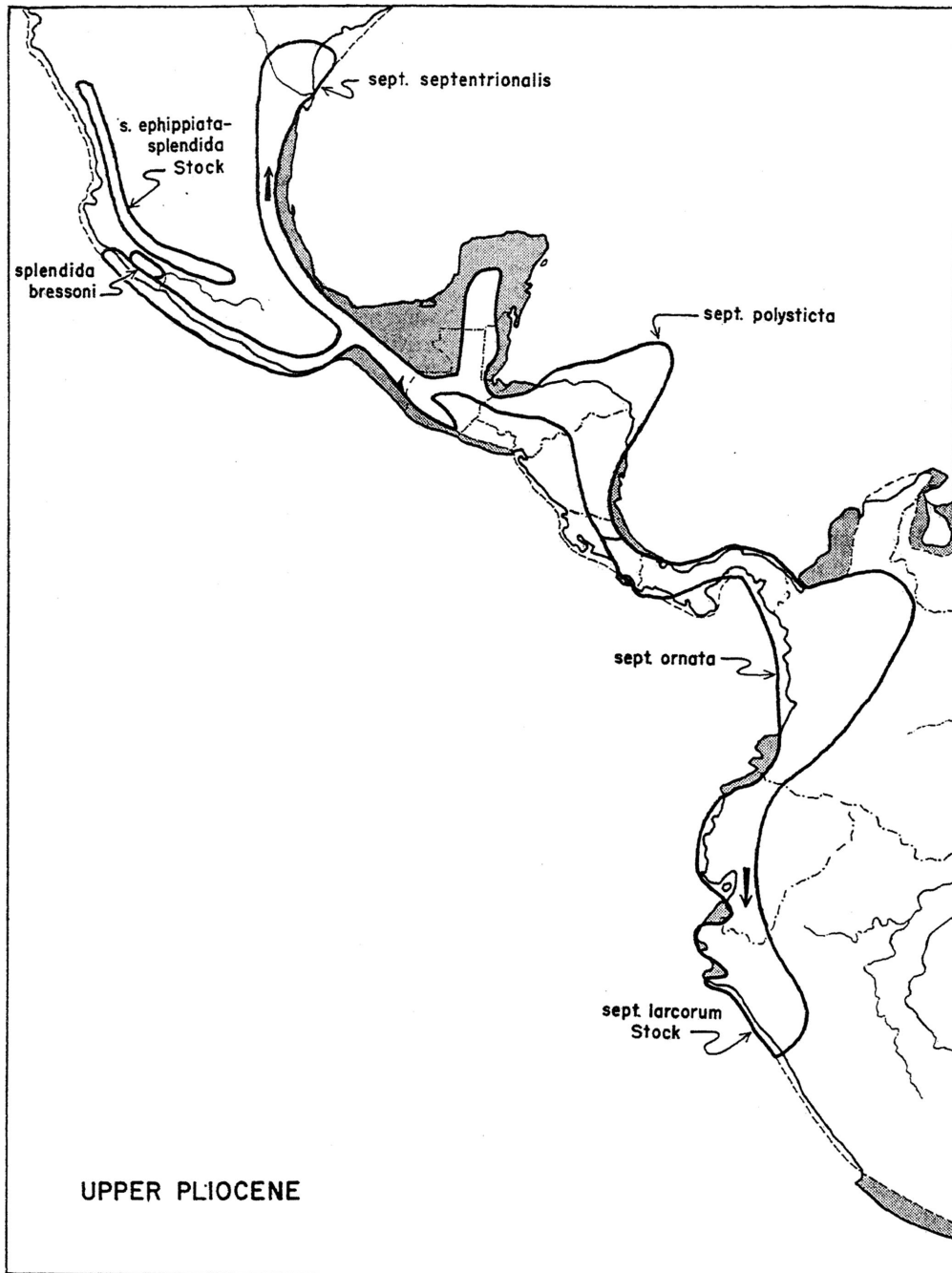
and northern Chiapas. In South America the continuity of the open forest-savanna habitat along the eastern edge of the Amazon Basin was interrupted by the spread of the rain forest. This resulted in the isolation of a population of terrestrial *annulata* in eastern Bolivia, northern Paraguay, and the southern part of the state of Mato Grosso, Brazil; this population differentiated into *annulata pulchriceps*. The terrestrial *annulata* in northern South America was diverging from the Central American *annulata rhombifera* and developed into the present *annulata ashmeadi*. Remnants of the previously widespread early terrestrial South American *annulata* stock still exist in isolated patches of open woodland and savanna in the rain forests of eastern Brazil. With the completion of the differentiation of an arboreal form from the early terrestrial stock in the savanna-rain forest ecotone, this form, *annulata annulata*, spread throughout the forests of the Amazon Basin. It followed the forest habitat eastward and then southward along the Atlantic coast of Brazil. This coastal population at present is

isolated from the Amazonian population through the development of arid conditions in extreme northeastern Brazil. (See map 17.) Thus, during the Pleistocene the present taxa and distribution patterns were established.

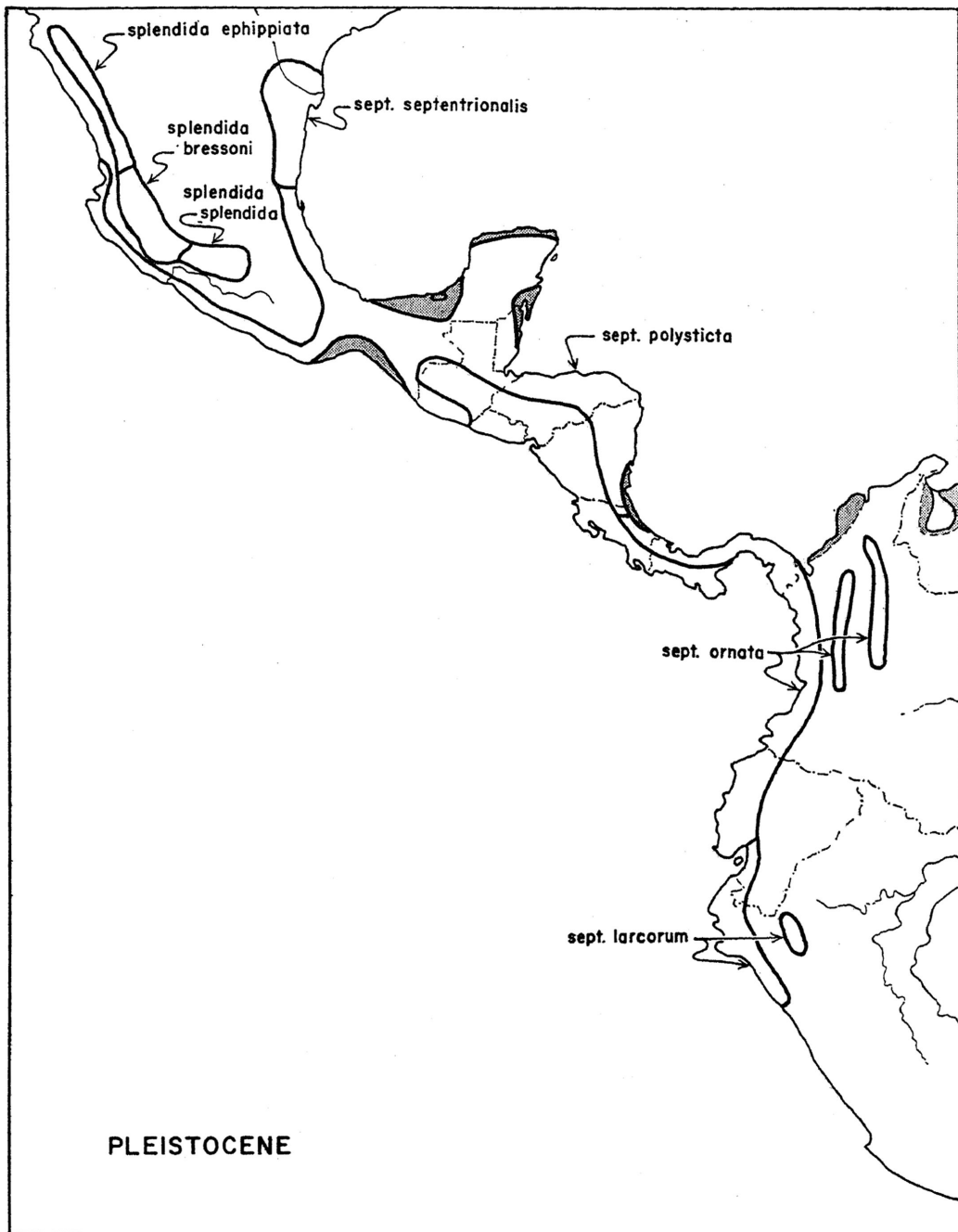
Returning now to the *septentrionalis* group, which in middle Miocene times was developing in the lowlands of eastern México, we find that by late Miocene the *septentrionalis* stock had spread through northern Central America and along the Pacific coast of México. (See map 18.) This stock inhabited the more mesic habitats and thus avoided competition with members of the *annulata* group. By early Pliocene time when the Tehuantepec Portal was open, the *septentrionalis* stock was separated into three populations—one in eastern México destined to become *septentrionalis septentrionalis*, one in Central America representing the stock that would give rise to *septentrionalis polysticta* and *s. ornata*, and one in western México destined to become *splendida*. (See map 19.) The uplift at the end of the Miocene had restricted the *septentrionalis* stock in Central



MAP 19. Distribution of the *septentrionalis* group of *Leptodeira* in the lower Pliocene. (See map 12 for explanation.)



MAP. 20. Distribution of the *septentrionalis* group of *Leptodeira* in the upper Pliocene. Arrows in northeastern México and in western Ecuador indicate areas in which the trend is from semi-arboreal snakes to terrestrial snakes. (See map 12 for explanation.)



MAP 21. Distribution of the *septentrionalis* group of *Leptodeira* in the Pleistocene.

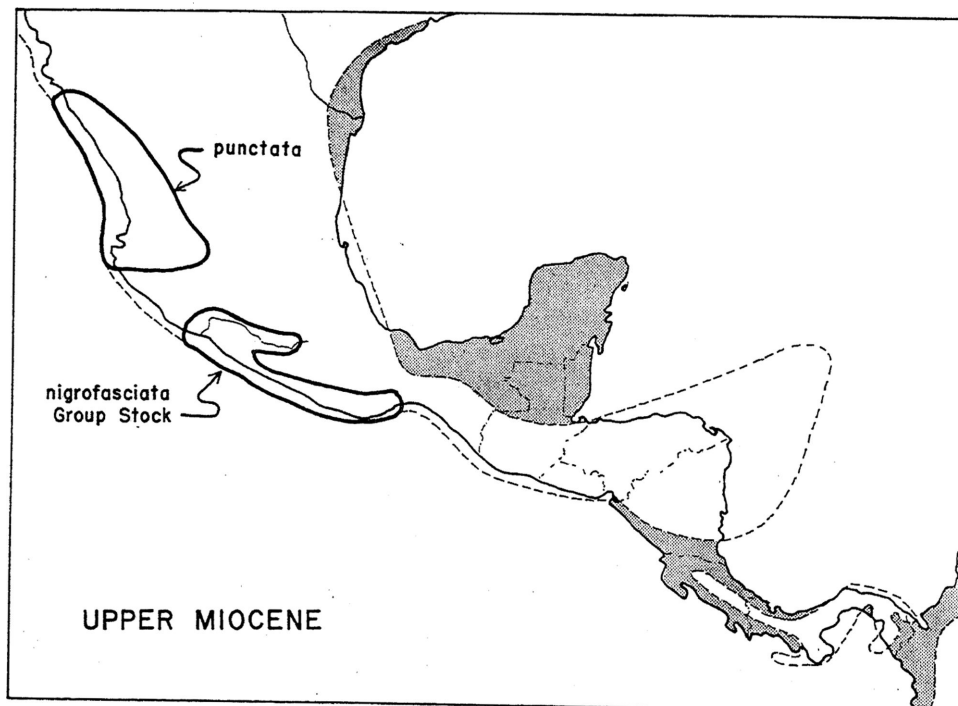
America to the Caribbean lowlands; closure of the Nicaraguan Portal in the late Miocene permitted the dispersal of this stock into lower Central America. By late Pliocene time when the Tehuantepec Portal had closed,

and South America was connected with Central America, the *septentrionalis* stock spread southward in mesic habitats into South America, crossing from the Caribbean slopes in lower Central America to the Pacific slopes

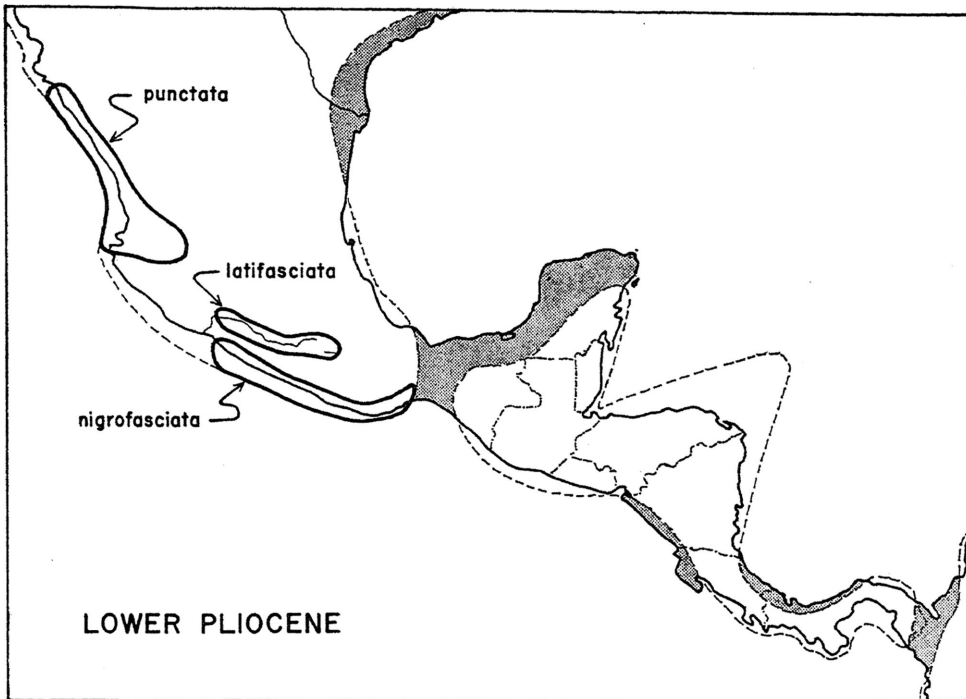
in South America. The population of northern Central America (*s. polysticta*) was differentiating from that in southern Central America and dispersed northward into México, interbreeding with the *septentrionalis* stock from eastern México, but remaining reproductively isolated from the *splendida* stock in western México. The southern Central American population (*s. ornata*) spread through the lowlands and moderately elevated parts of the northern Andes and entered the Cauca and Magdalena valleys in Colombia. As the snakes moved southward they encountered drier conditions in the Cajamarca Valley and along the coast of Peru. This paralleled the more arid conditions developing in the northern part of the range of the species in northeastern México and southern Texas, whereas in the middle of the range (southern México and to northern Ecuador) the species inhabited humid forests. This difference in habitat resulted in a differentiation of the populations in the humid-forest habitats for an arboreal existence, while the terminal populations continued as

terrestrial forms. The development of less favorable conditions on the Pacific coast of México forced the *splendida* stock into the higher elevations on the slopes of the Mexican Plateau and in the Sierra de Coalcomán and in the Sierra de Coalcomán in southern Michoacán. The population in the Sierra de Coalcomán differentiated into *bressoni*, while the *splendida-ephippiata* stock was developing on the slopes of the plateau. (See map 20.)

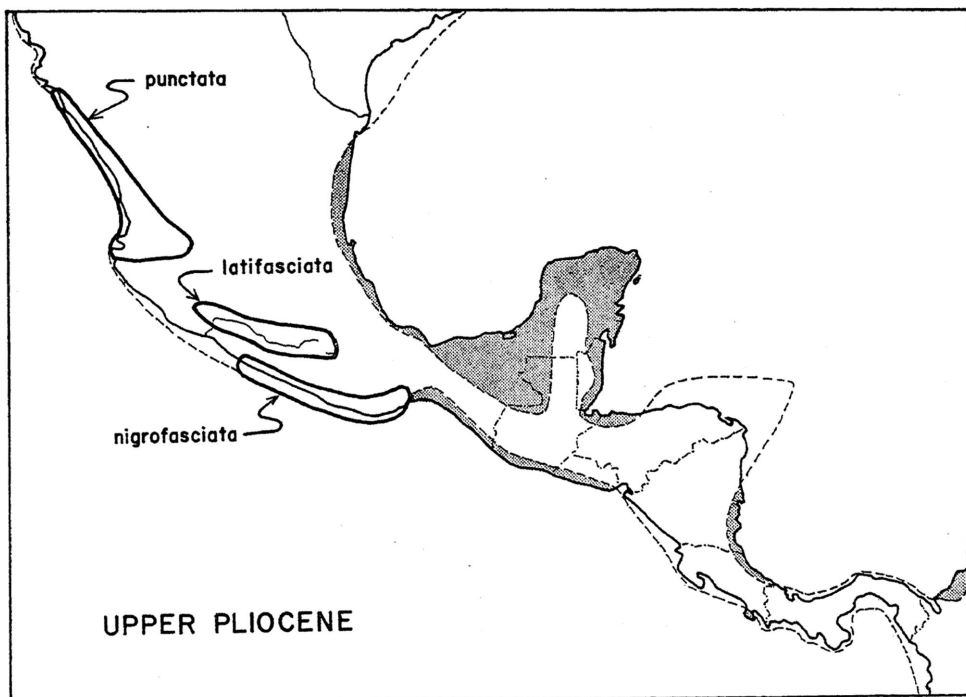
By Pleistocene time the elevation of the Andes had separated the populations of *septentrionalis* in the Cauca and Magdalena valleys of Colombia and the Cajamarca Valley of Peru from the continuous coastal populations. Because there has been little differentiation in the isolated populations, it may be assumed that this separation has not been of long duration. The arboreal populations of *septentrionalis*, the subspecies *polysticta* and *ornata*, reached their present status, while differentiation of the terminal populations, *septentrionalis* and *larcorum*, resulted in their being terrestrial snakes living in semi-arid and arid habitats. The *splendida* population in



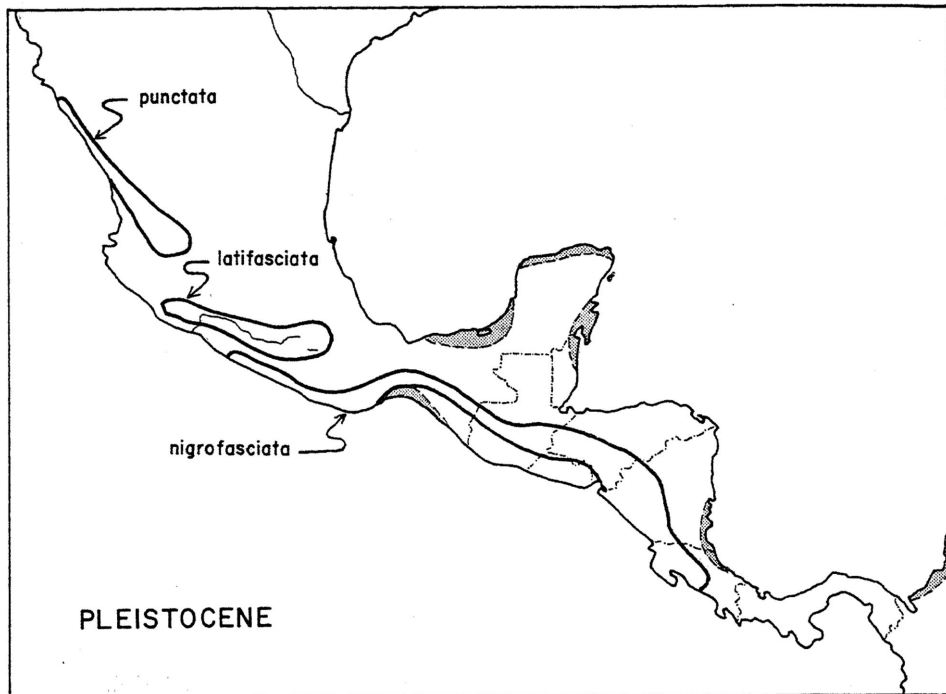
MAP 22. Distribution of the *nigrofasciata* group of *Leptodeira* and of *L. punctata* in the upper Miocene. (See map 12 for explanation.)



MAP 23. Distribution of the *nigrofasciata* group of *Leptodeira* and of *L. punctata* in the lower Pliocene. (See map 12 for explanation.)



MAP 24. Distribution of the *nigrofasciata* group of *Leptodeira* and of *L. punctata* in the upper Pliocene. (See map 12 for explanation.)



MAP 25. Distribution of the *nigrofasciata* group of *Leptodeira* and of *L. punctata* in the Pleistocene. (See map 12 for explanation.)

the Sierra de Coalcomán, *bressoni*, invaded the *splendida* population on the slopes of the Mexican Plateau, separated the populations that give rise to *splendida splendida* and *splendida ephippiata*, and brought the differentiation and distribution of the forms that comprise the *septentrionalis* group to their present status. (See map 21.)

Because their evolutionary history is not so complex as that of the *annulata* group or the *septentrionalis* group, the differentiation of the *nigrofasciata* group and that of *punctata* are discussed concurrently. In the middle Miocene *punctata* ranged along the Pacific lowlands of western México north of the Río Balsas. Later in the Miocene, prior to the uplift of the Mexican Plateau, it dispersed through the western part of the region that is now the Sierra Madre Occidental and the Mexican Plateau. At the same time the *nigrofasciata* group stock spread into the Balsas Basin and probably was continuous throughout the area that is at present the Sierra del

Sur in Guerrero and Oaxaca. (See map 22.) With the uplift of the sierras and the plateau at the end of the Miocene, *punctata* was restricted to the coastal lowlands and to the region that is at the present time southern Nayarit and central Jalisco where the Mexican Plateau gradually declines to the coastal lowlands. The rise of the Sierra del Sur separated the stock of the *nigrofasciata* group into a coastal population (*nigrofasciata*) and an inland population (*latifasciata*) in the Balsas Basin. (See map 23.) By this time the differentiation of the species had taken place. In either the late Pliocene after the closure of the Tehuantepec Portal or sometime during the Pleistocene *nigrofasciata* moved southward, probably utilizing the subhumid corridor (Stuart, 1954a) through northern Central America, and spread through the dry habitats of Central America as far south as Costa Rica. *Latifasciata* spread throughout the Balsas-Tepalcatepec Basin and moved into Colima. (See maps 24 and 25.)

## SUMMARY AND CONCLUSIONS

THE GENUS *Leptodeira* Fitzinger, 1843, includes as absolute synonyms the generic names *Megalops* Hallowell, 1861, *Anoplophallus* Cope, 1893, and *Pseudoleptodeira* Taylor, 1938. Nine species comprise the genus; five of these are monotypic; one embraces five subspecies, one includes four subspecies, and two others each contain three subspecies, making a total of 20 forms. Two subspecies are described as new in this paper.

The genus is characterized by maxillary teeth that increase in size posteriorly followed by a diastema and two enlarged, grooved fangs. There are two apical pits, elliptical pupil, divided anal, smooth dorsal scales, normal complement of colubrid head shields, and a capitate hemipenis with many large spines.

Four species groups are separated on the nature of the hemipenes, the dentition and certain skull elements, particularly the quadrates, vomers, and maxillaries. Analysis of the characters shows that the most useful in a systematic study of the snakes are the numbers of ventrals, caudals, and dorsal scale rows, the numbers of upper labials and preocular scales, the number, shape, and size of the body blotches, and the nature of the dorsal head pattern.

Analysis of numerous character clines shows that parallel clines may exist in two or more species in certain characters, but that in others the clines may diverge. Discontinuous clines are common. In some cases these are correlated with striking morphological changes between populations and become incorporated in the characteristics of subspecies.

Studies of the skull of *Leptodeira* indicate that the skull is a normal colubrid type without striking specializations. Certain skeletal elements readily identify it from related genera. The poison glands (modified posterior portions of parotid glands) are large and produce a venom of sufficient strength to kill small frogs and lizards.

The distribution of the genus is essentially throughout the American tropics to elevations of about 2000 meters. Some forms are restricted to semi-arid habitats; others live in tropical rain forest. Two species range from semi-arid to wet forest environments; each has a subspecies adapted to arboreal life in the forest by having a reduced number of dorsal scale rows, enlarged vertebral and paravertebral scale rows, and a laterally compressed body.

Snakes of this genus feed primarily on frogs and toads; some lizards are included in the diet. The snakes are nocturnal and appear to reach their greatest abundance at times of congregations of breeding frogs. So far as is known, all species are oviparous and may lay as many as 13 eggs.

On penial characters *Leptodeira* may be placed with *Hypsiglena* and *Trimorphodon* as a subgroup of colubrine snakes. If *Leptodeira* is related to *Trimorphodon*, they must have diverged early in their evolutionary history. *Hypsiglena* and *Leptodeira* are closely related and evolved from a common ancestral stock. The African snakes of the genus *Crotaphopeltis* that have been placed in the genus *Leptodeira* represent a separate evolutionary line of colubrine snakes.

Based on the Cenozoic history of tropical America, studies of the morphology and distribution of the snakes, and the fossil record of other animals, the evolutionary history of *Leptoderia* has been reconstructed. This shows that *Leptodeira* and *Hypsiglena* underwent generic differentiation from a common ancestral stock in southern México during the early Miocene. By middle Miocene time the groups of *Leptodeira* had diverged. The present distribution and differentiation are a result of the effects of sea portals across Middle America that isolated populations often for long periods of time, and the Cenozoic orogenies that changed the uniform climatic conditions of Middle America and produced arid as well as humid habitats.

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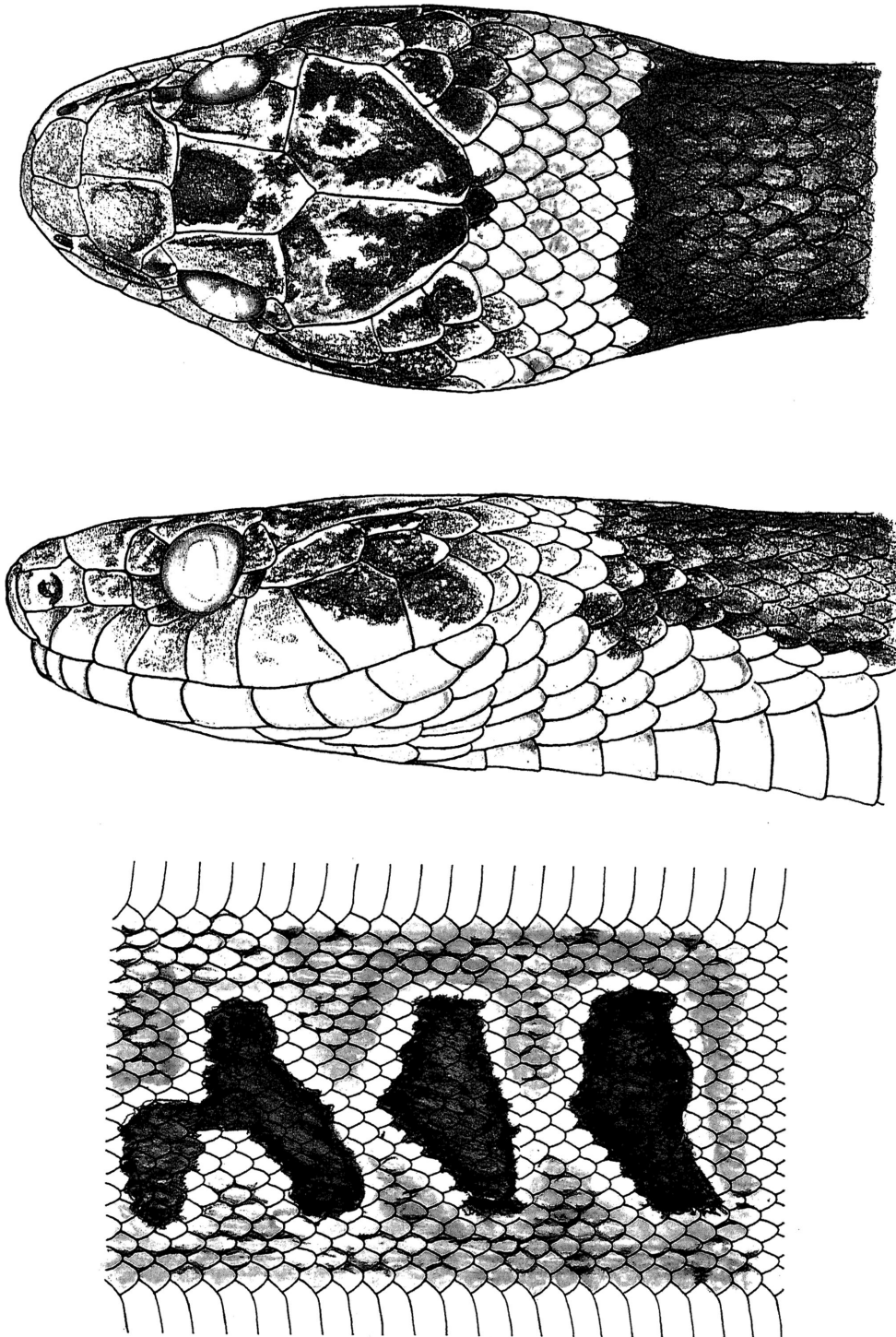
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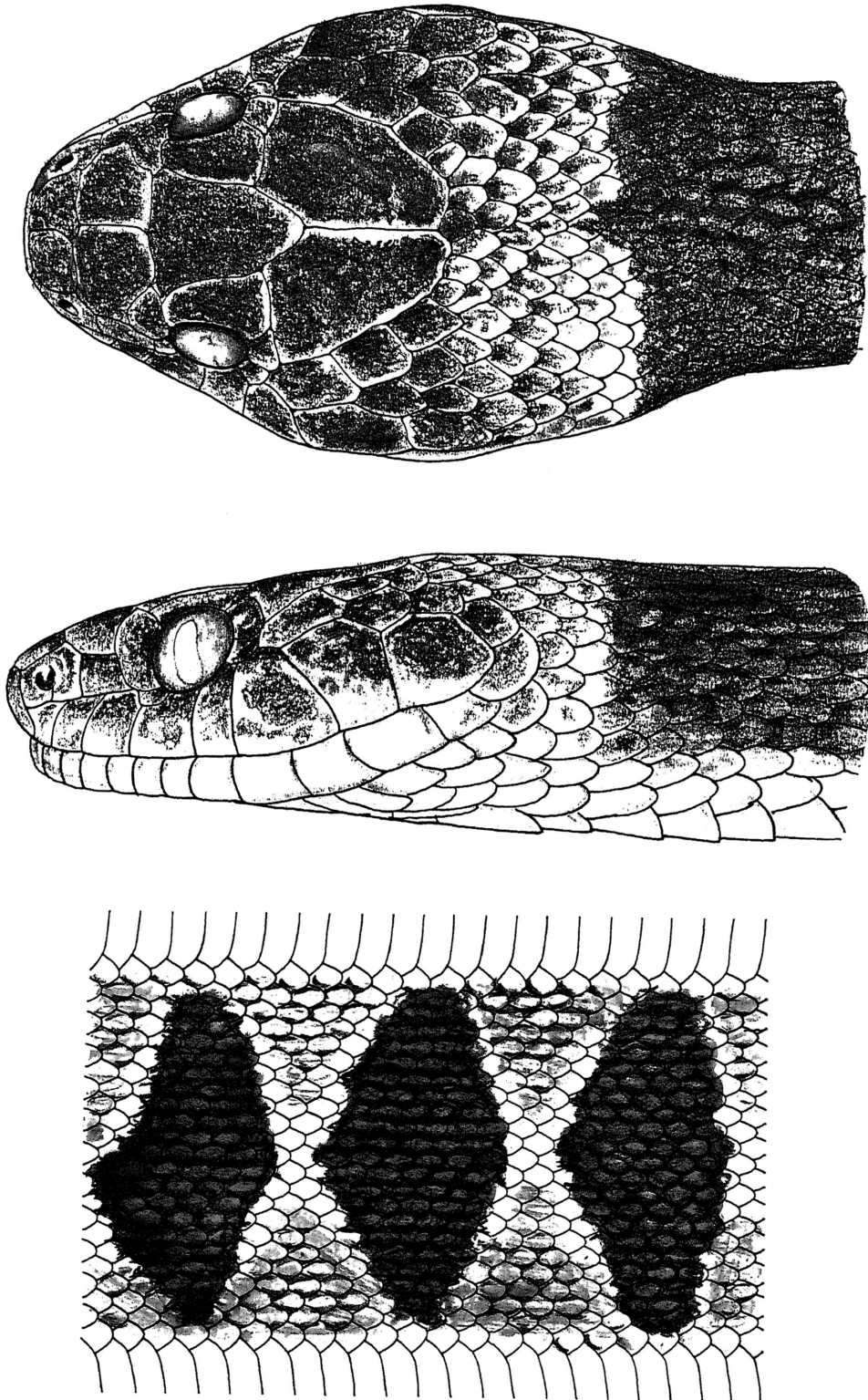
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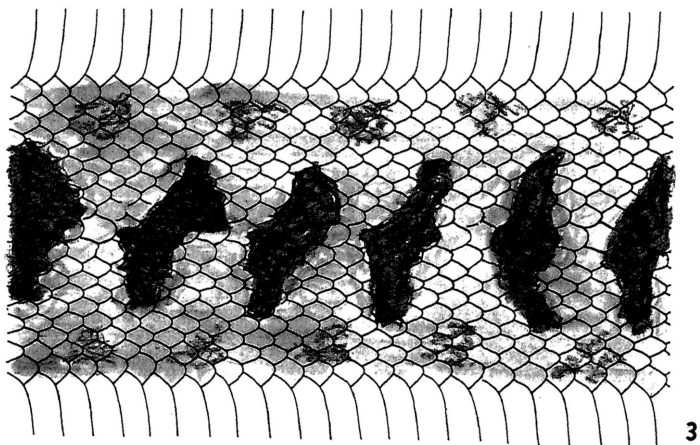
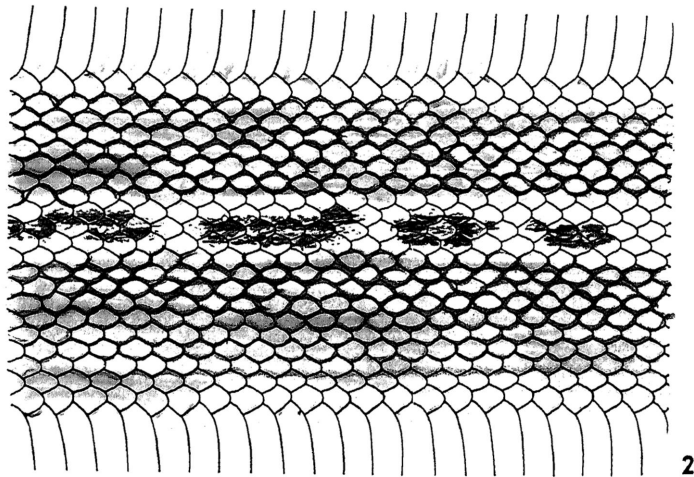
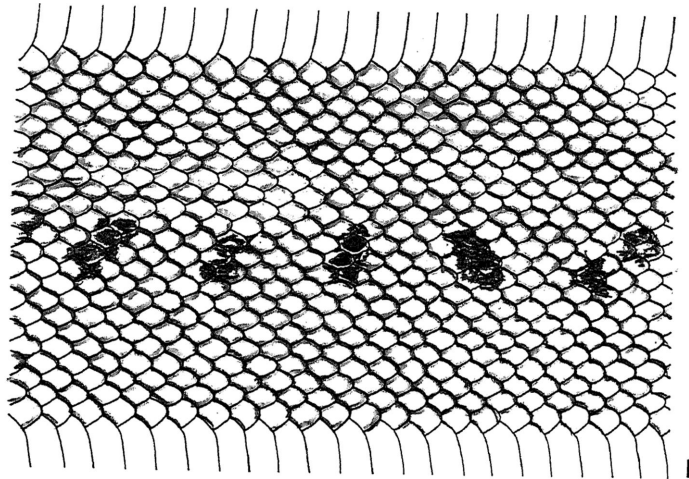




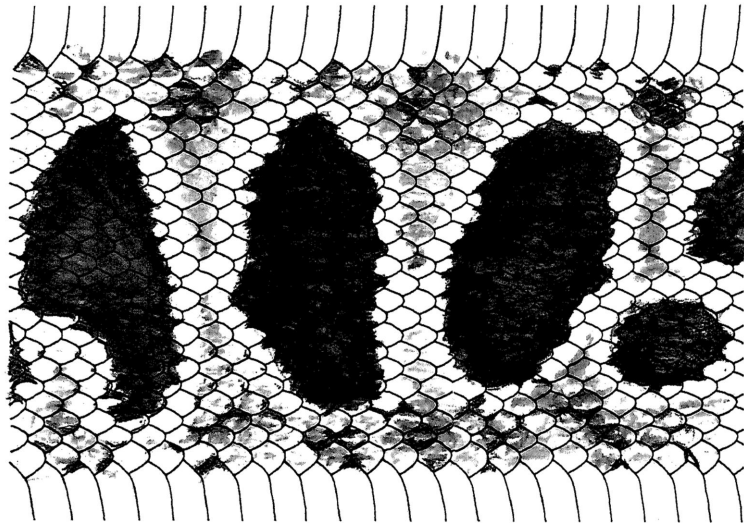
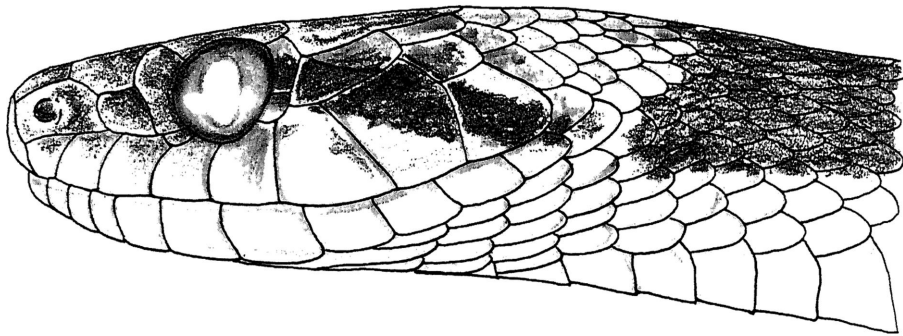
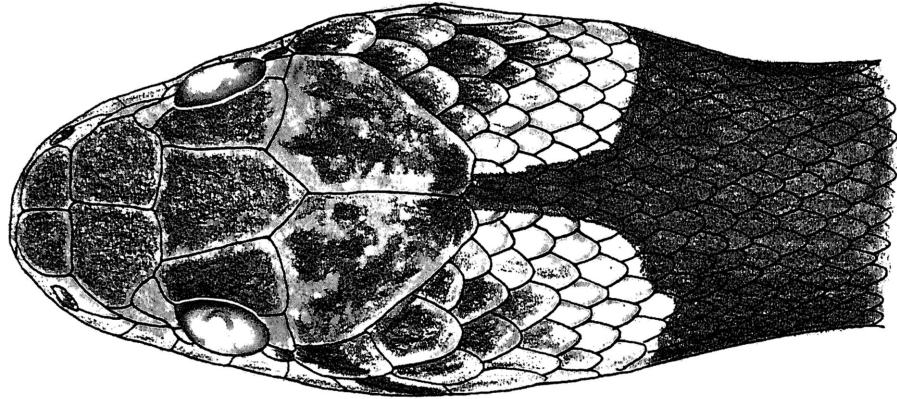
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata cussiliris*, holotype, U.M.M.Z. No. 82617, from 6 kilometers south of Tehuantepec, Oaxaca, México



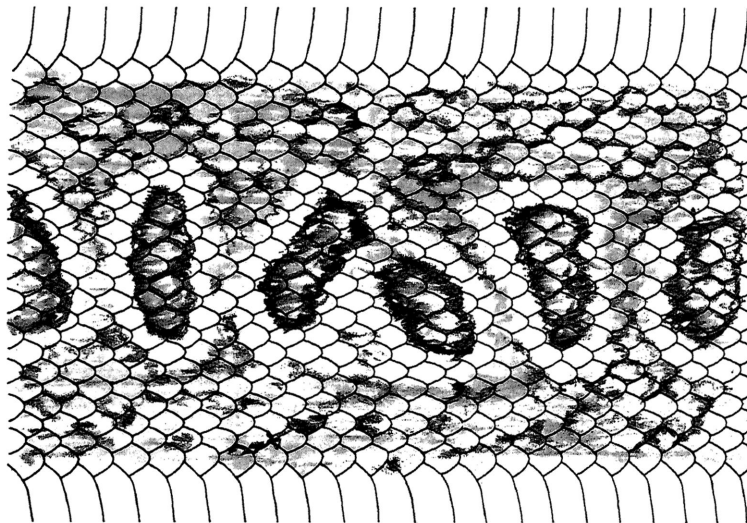
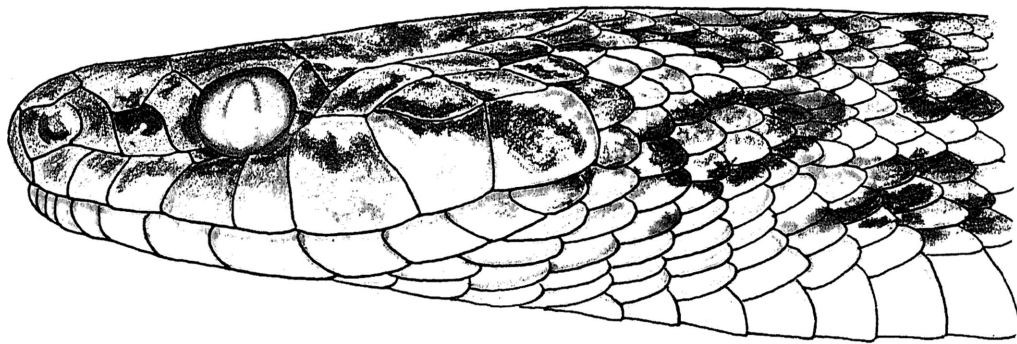
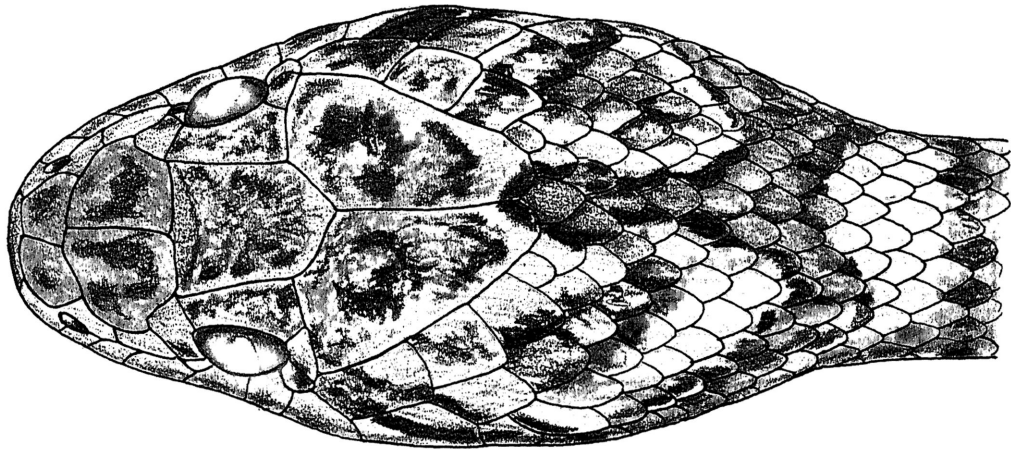
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata cus-*  
*siliris*, U.M.M.Z. No. 104071, from 5 miles northeast of Gómez Farías, Tamaulipas, México



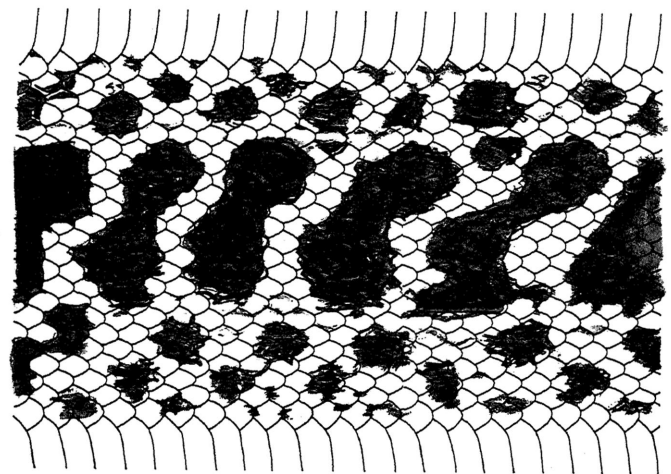
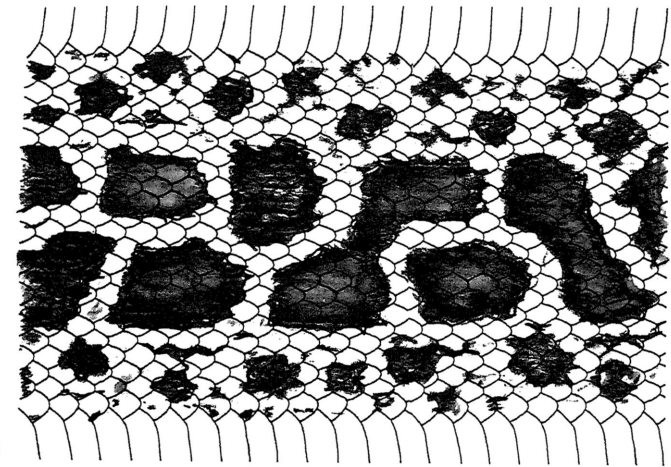
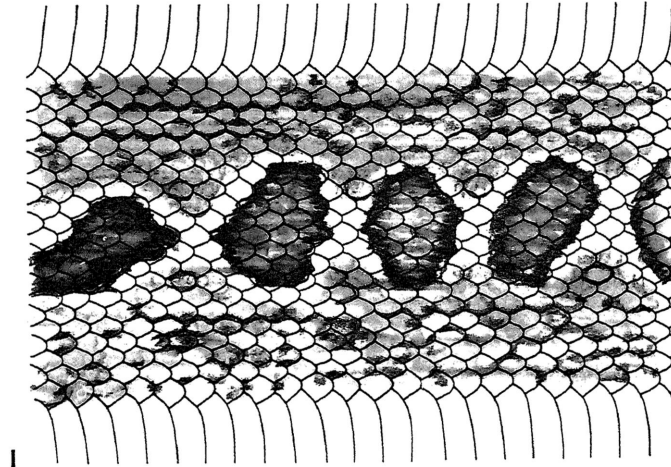
Dorsal body patterns of *Leptodeira*. 1. *L. annulata cussiliris*, U.I. No. 17820, from El Limoncito, Guerrero, México. 2. *L. splendida bressoni*, U.M.M.Z. No. 104490, from Coalcomán, Michoacán, México; holotype of *L. duellmani*. 3. *L. septentrionalis ornata*, A.M.N.H. No. 18296, from Boca de la Raspadura, Chocó, Colombia



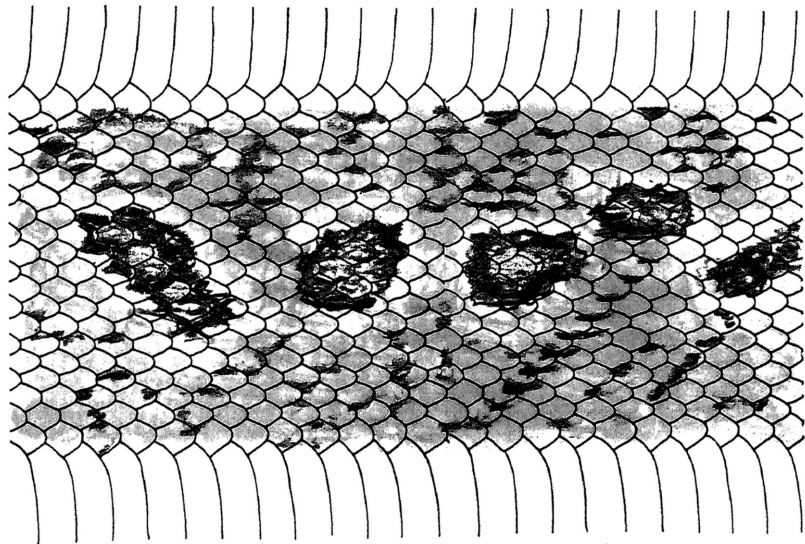
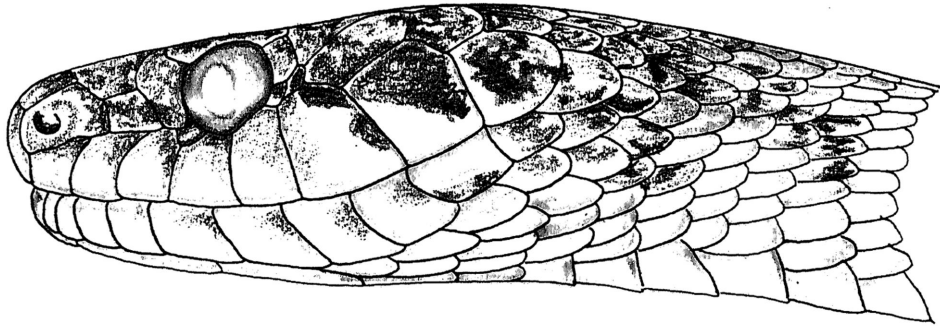
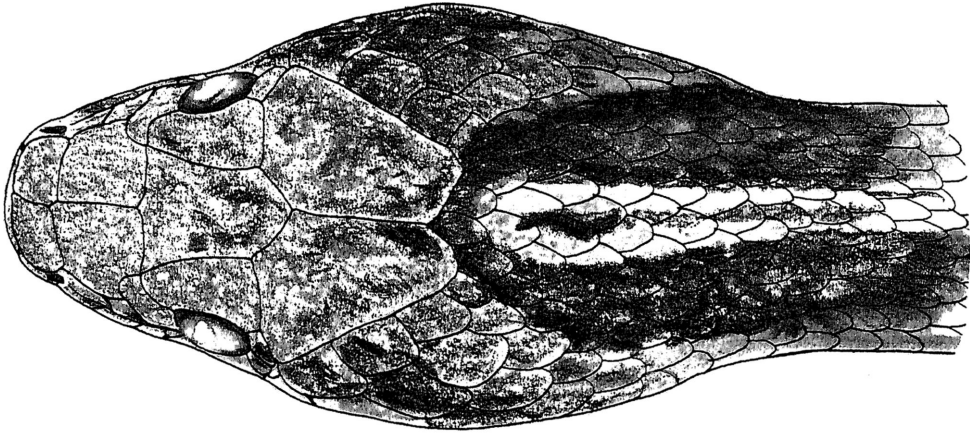
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata rhombifera*, U.M.M.Z. No. 107259, from Finca La Trinidad, Jutiapa, Guatemala



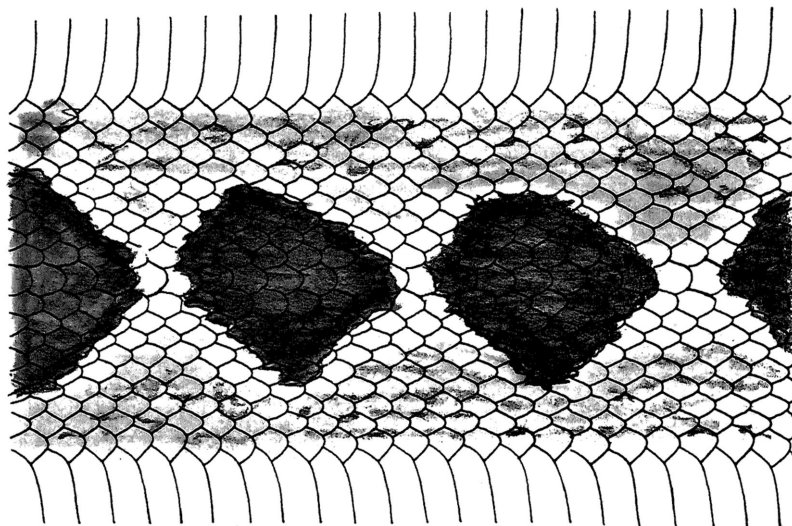
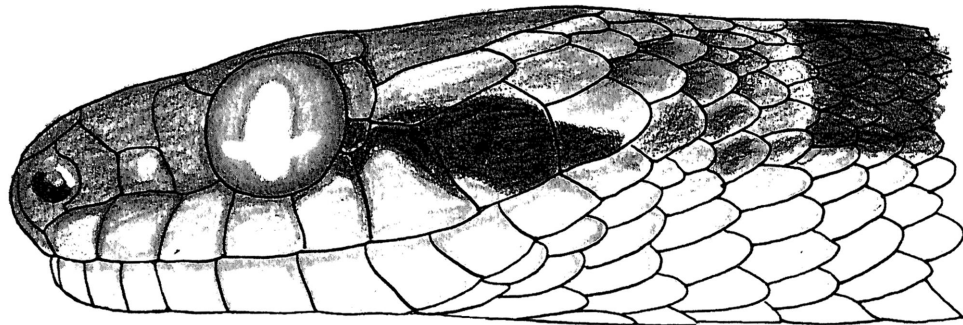
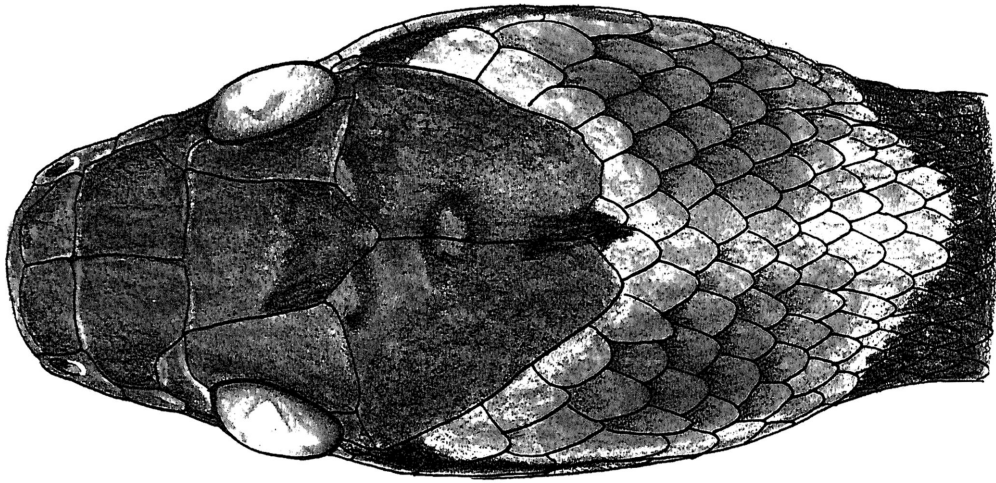
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata rhombifera*, C.N.H.M. No. 68084, from Chitre, Coclé, Panamá



Variation in dorsal body pattern in *Leptodeira annulata rhombifera*. 1. A.M.N.H. No. 71676, from Panamá Vieja, Panamá, Panamá. 2. U.M.M.Z. No. 98104, from Jutiapa, Jutiapa, Guatemala. 3. U.M.M.Z. No. 107256, from Finca La Trinidad, Jutiapa, Guatemala

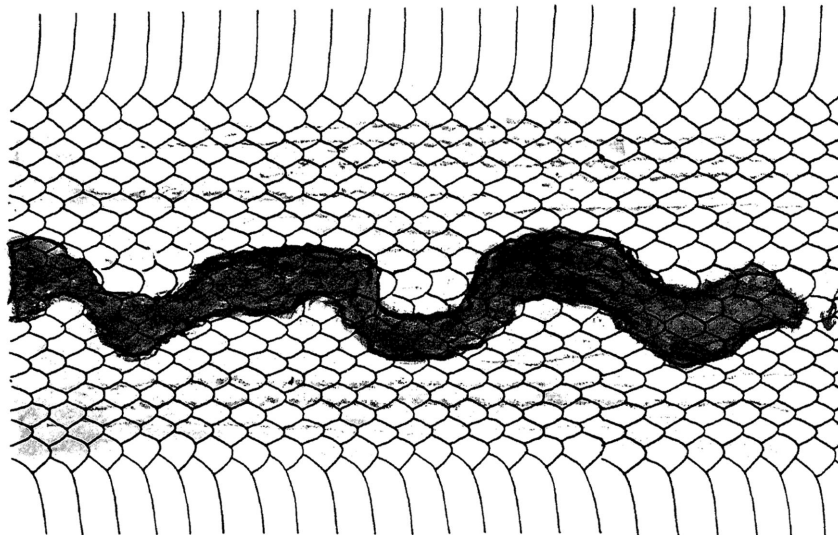
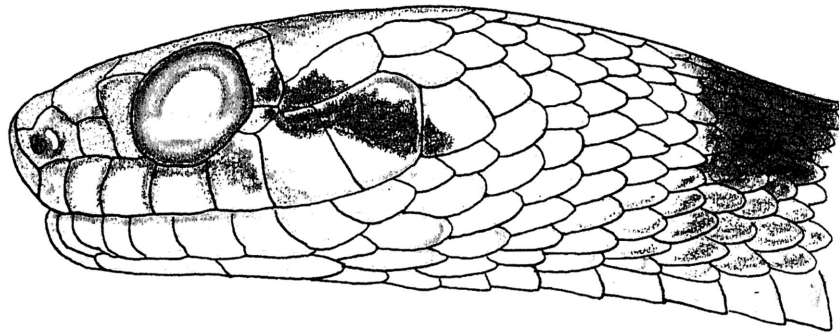
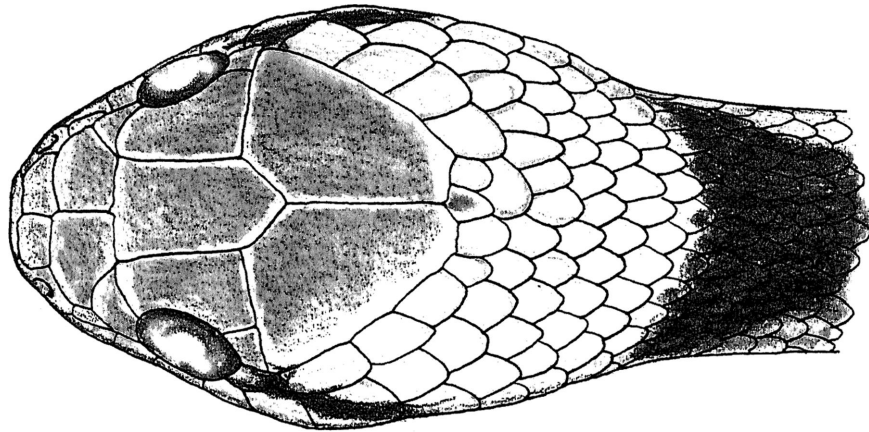


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata ashmeadi*, U.M.M.Z. No. 111307, from Riecito, Falcón, Venezuela

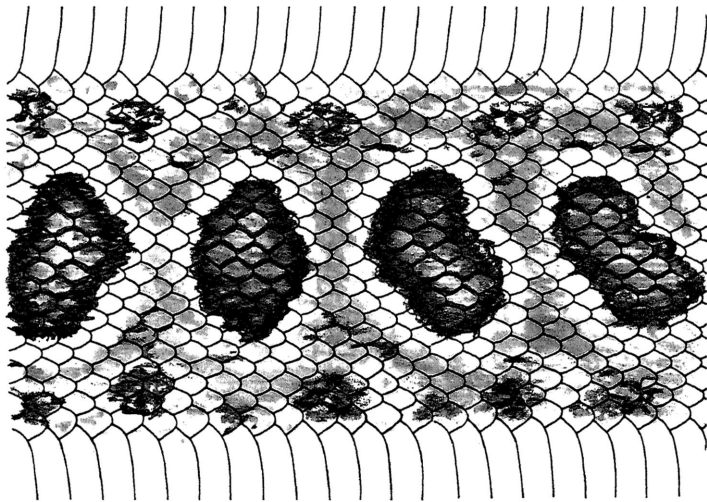
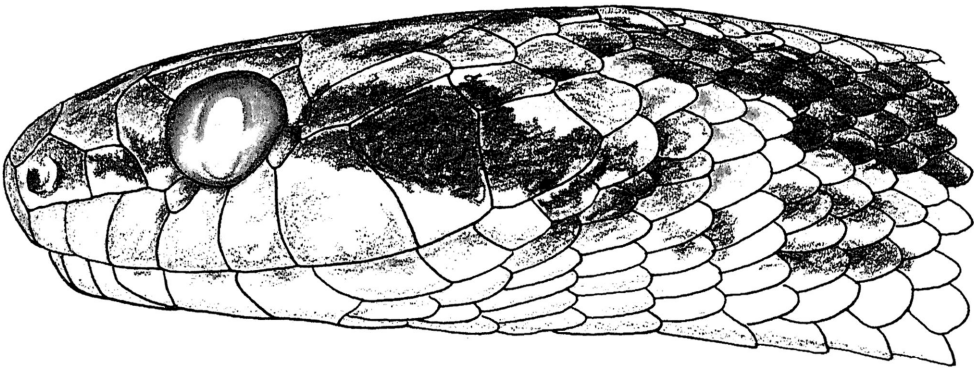
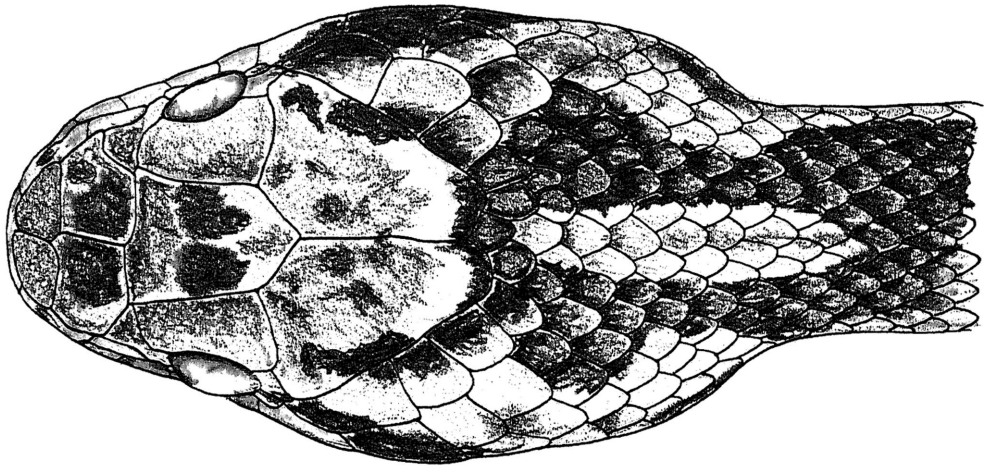


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata annulata*, A.M.N.H. No. 71118, from Río Ucayali, Peru

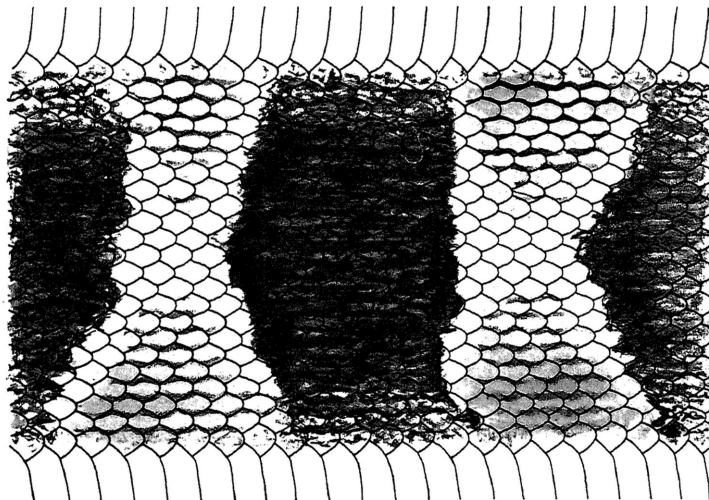
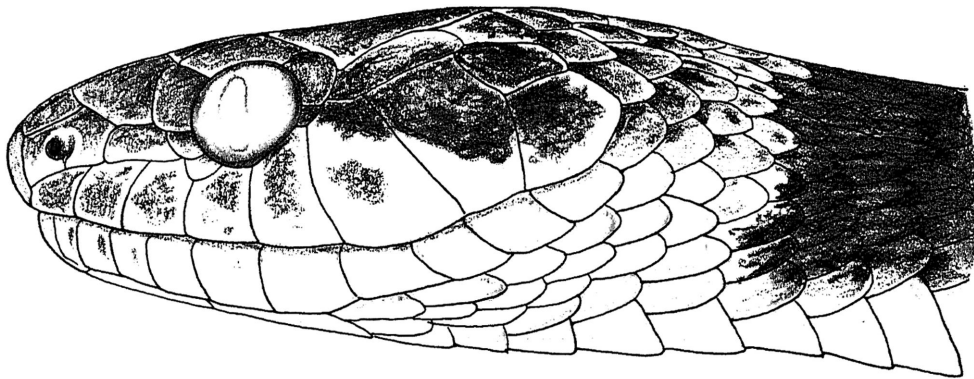
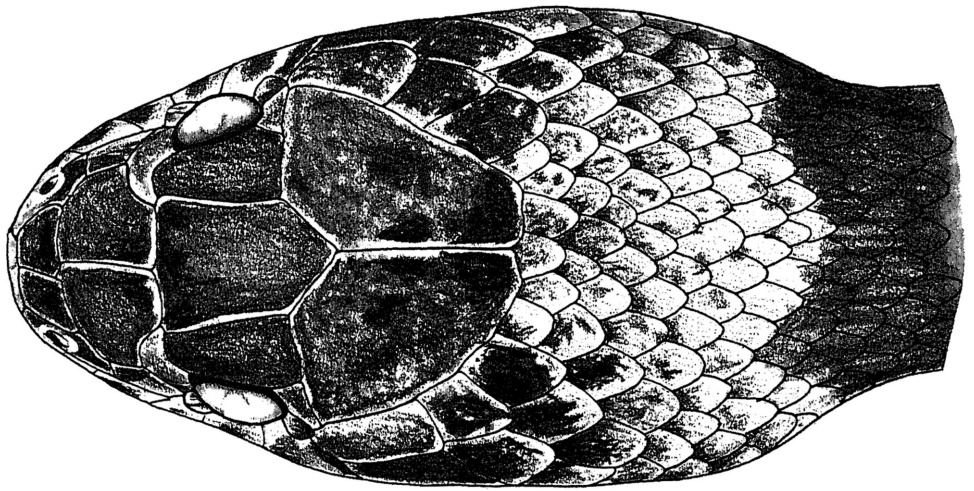




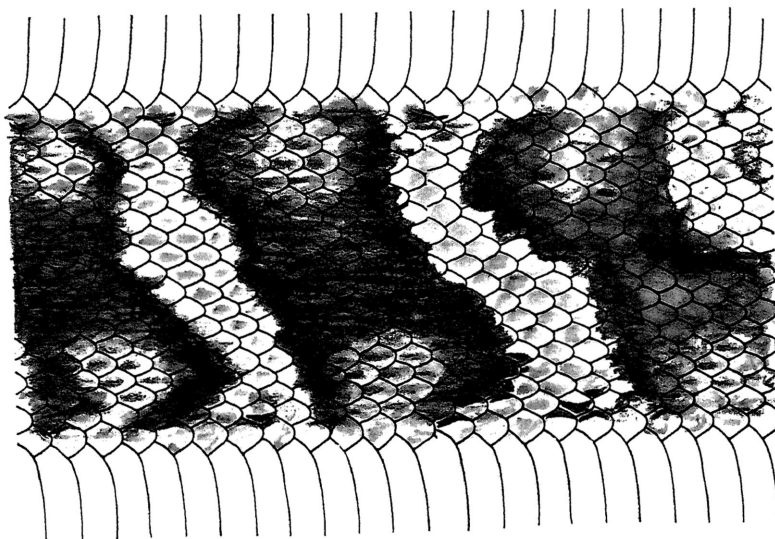
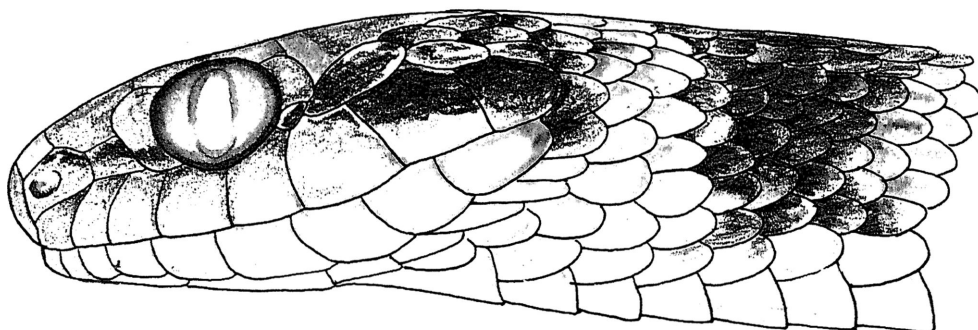
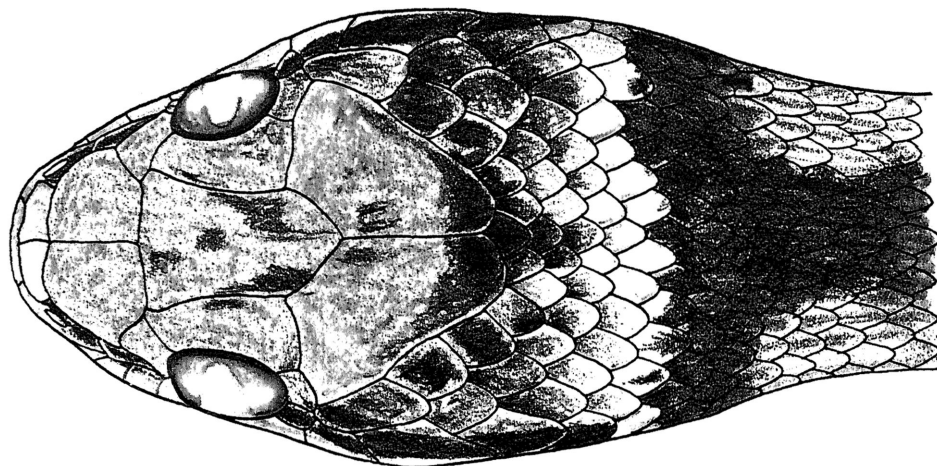
Dorsal and lateral views of the head and dorsal body pattern of a juvenile of *Leptodeira annulata annulata*, A.M.N.H. No. 57270, from Parinari, Río Samiria, Peru. Note white occipital region characteristic of juveniles, and zig-zag dorsal body pattern



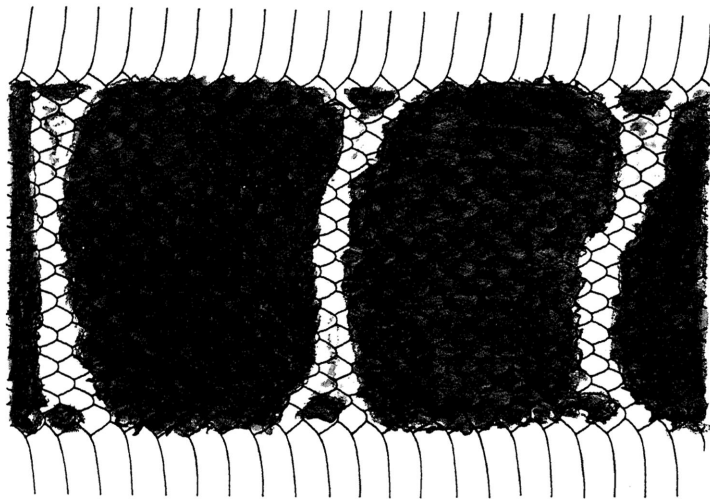
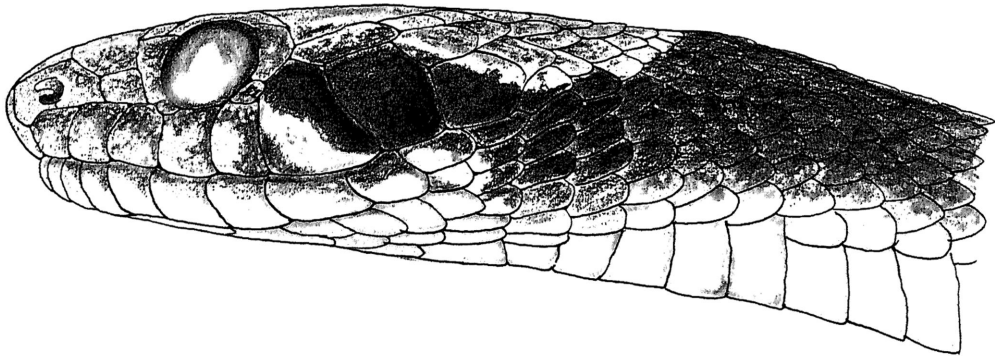
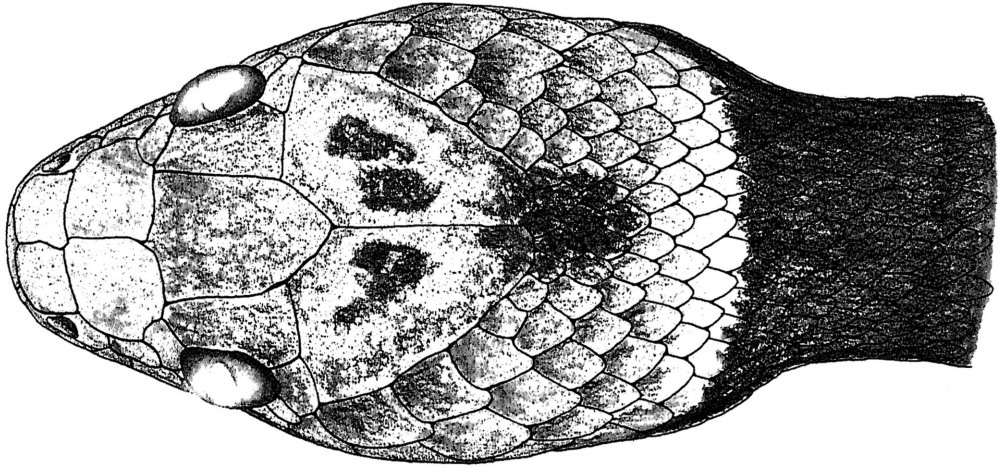
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira annulata pulchriceps* holotype, D.Z. No. 2578, from Bodoquena, Mato Grosso, Brazil



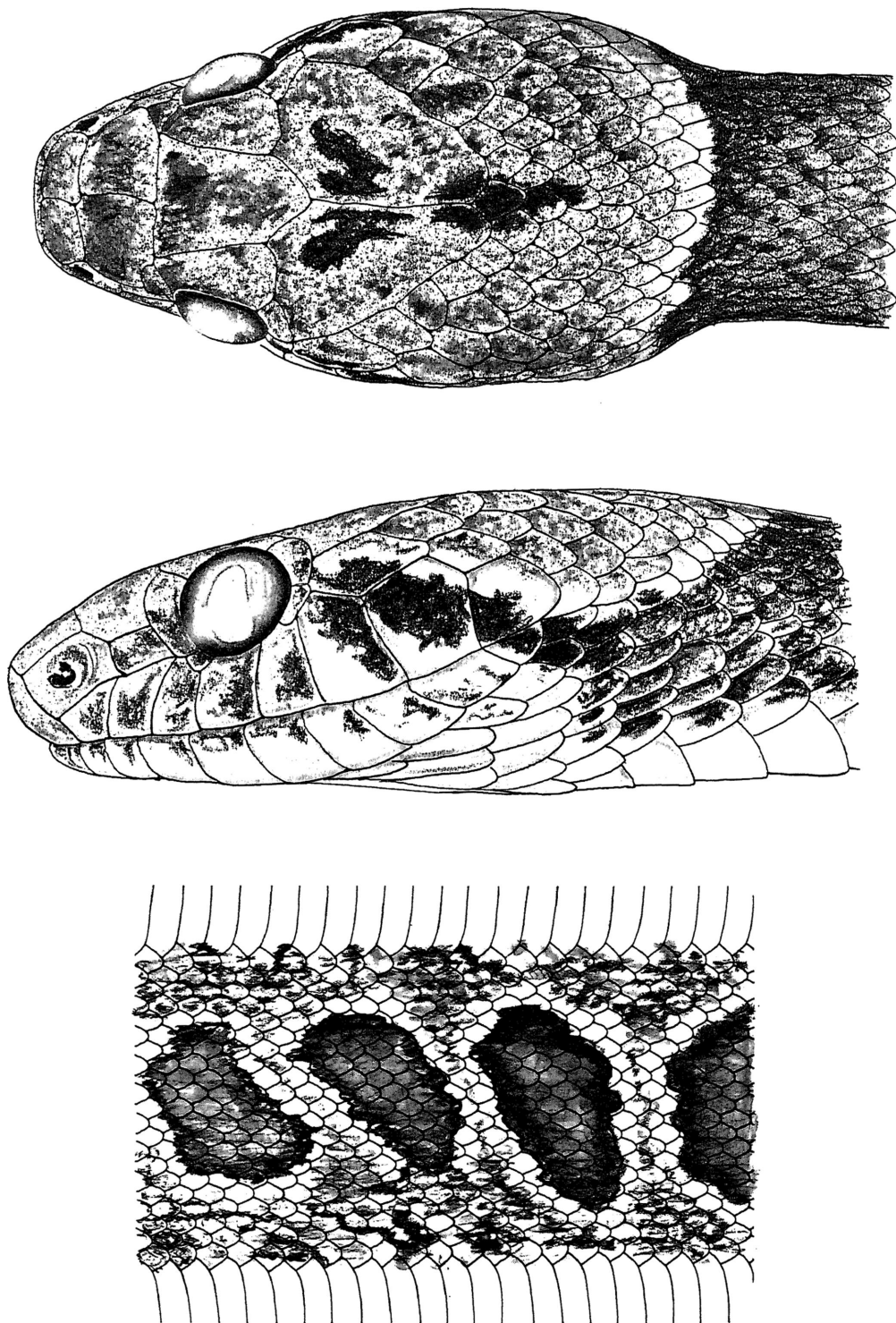
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira maculata*, C.N.H.M. No. 39089, from Apatzingán, Michoacán, México



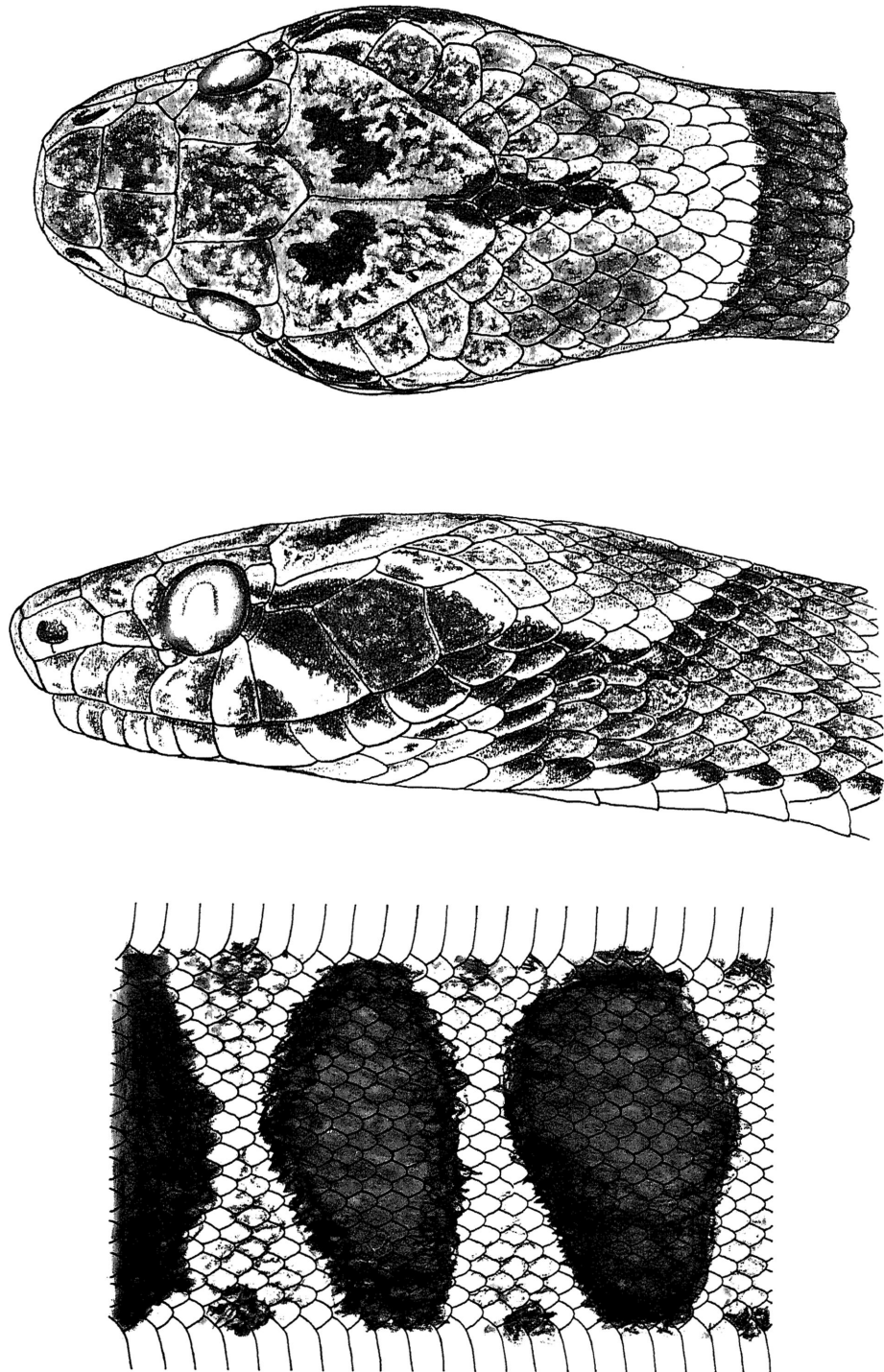
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira bakeri*, A.M.N.H. No. 69124, from Aruba Island, Dutch West Indies



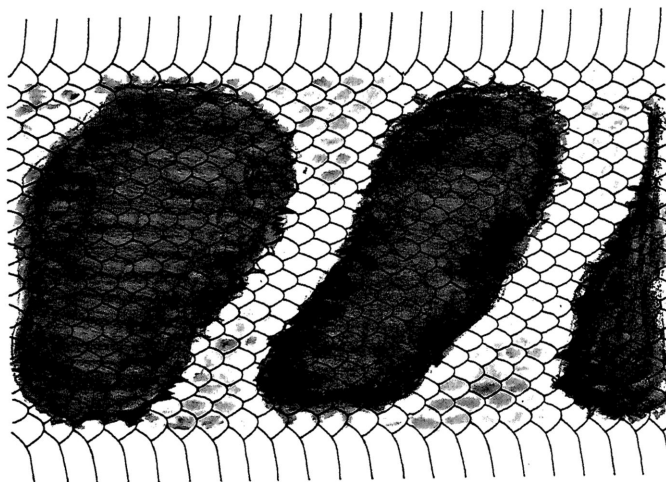
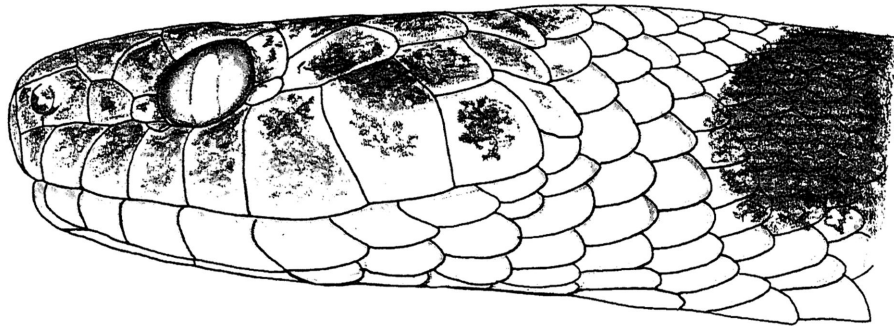
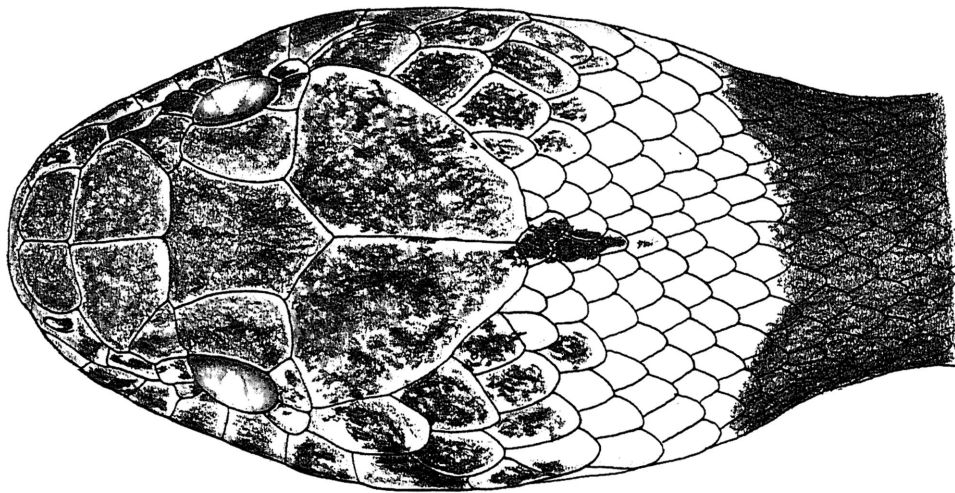
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira frenata frenata*, E.H.T.-H.M.S. No. 27619, from San Juan de la Punta, Veracruz, México



Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira frenata malleisi*, U.S.N.M. No. 111258, from Palenque, Chiapas, México

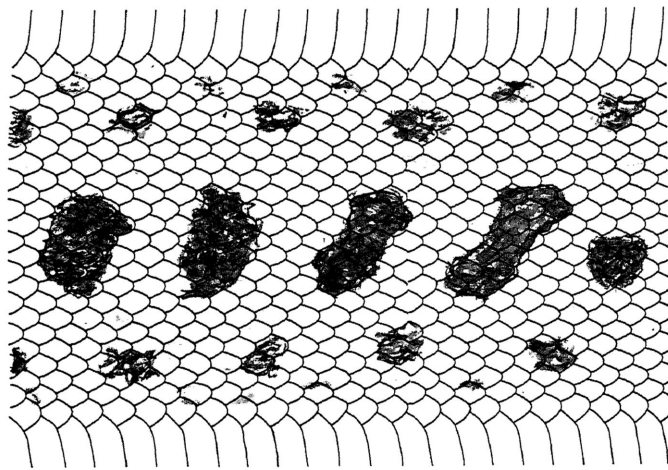
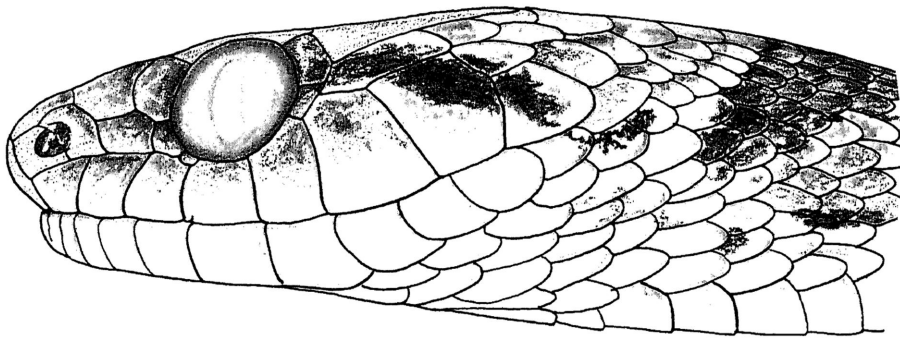
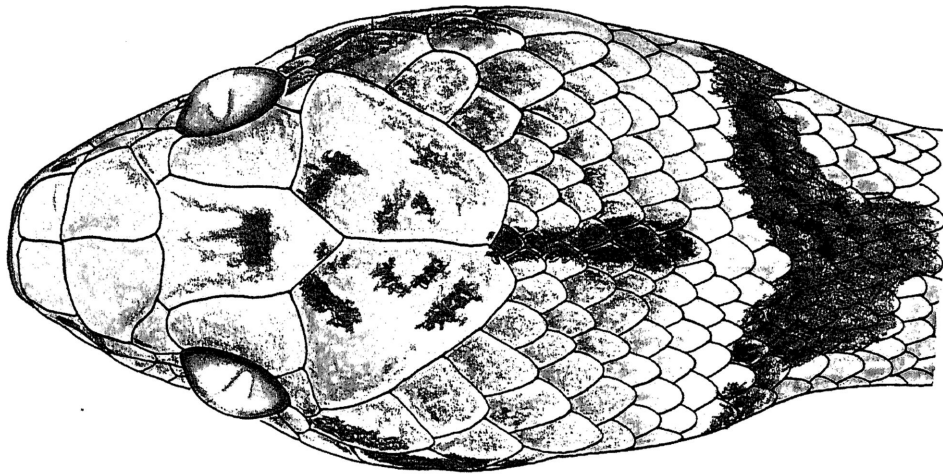


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira frenata yucatanensis*, M.C.Z. No. 7242, from Chichén Itzá, Yucatán, México

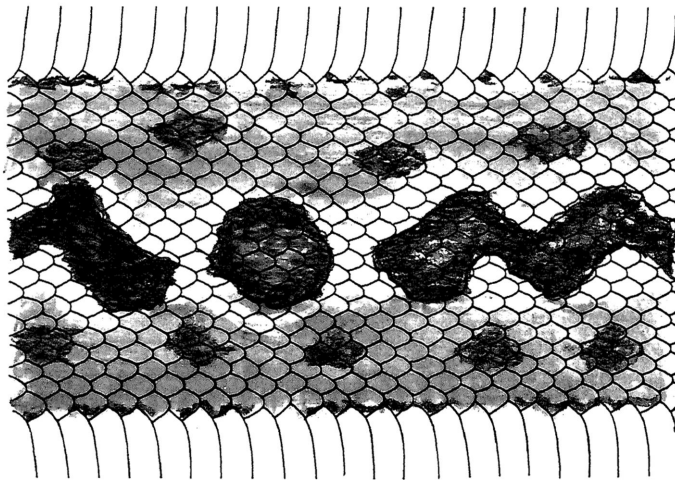
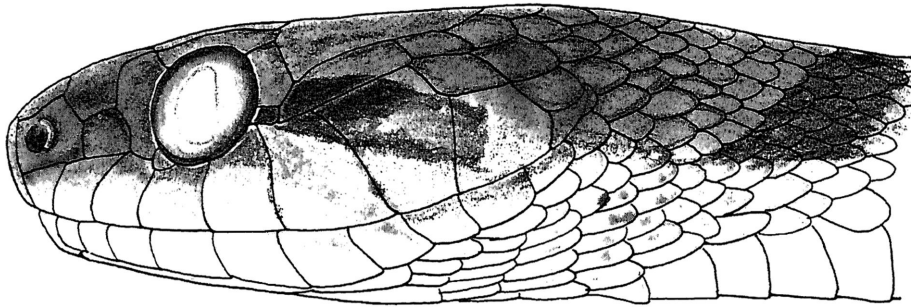
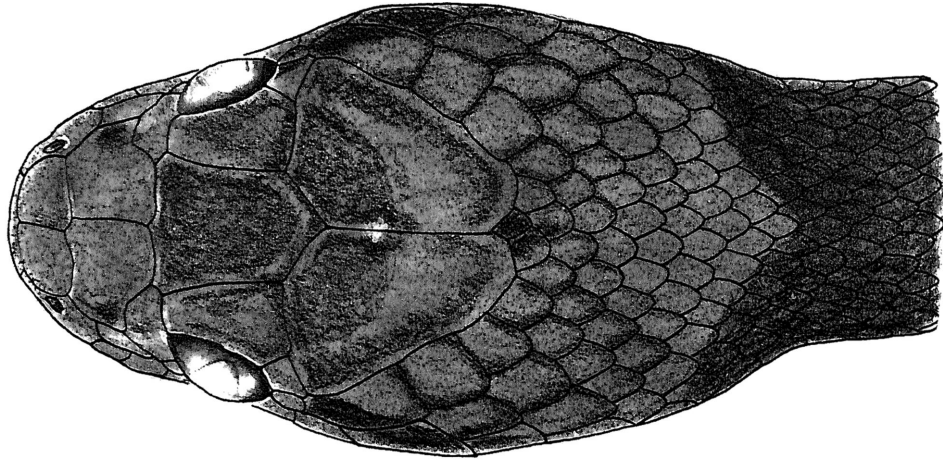


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira septentrionalis septentrionalis*, Ch.A.S. No. 6349, from 20 miles northwest of Edinburg, Hidalgo County, Texas

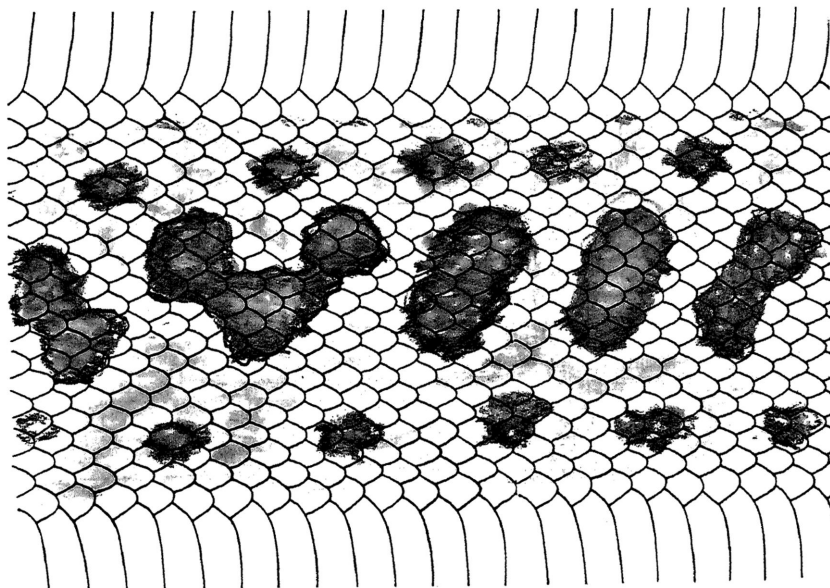
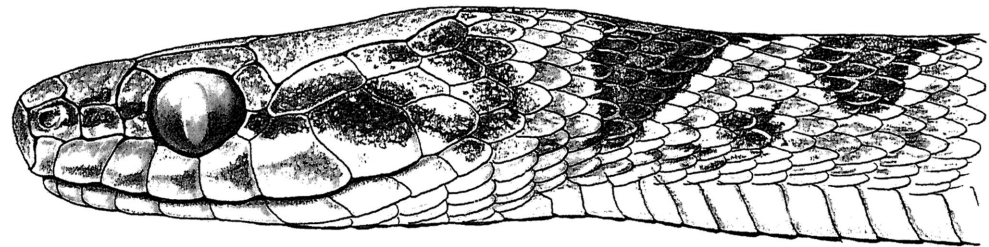
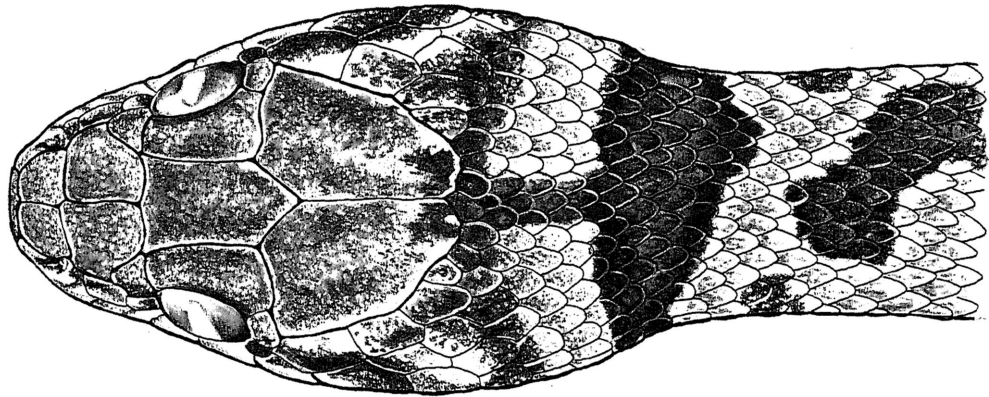




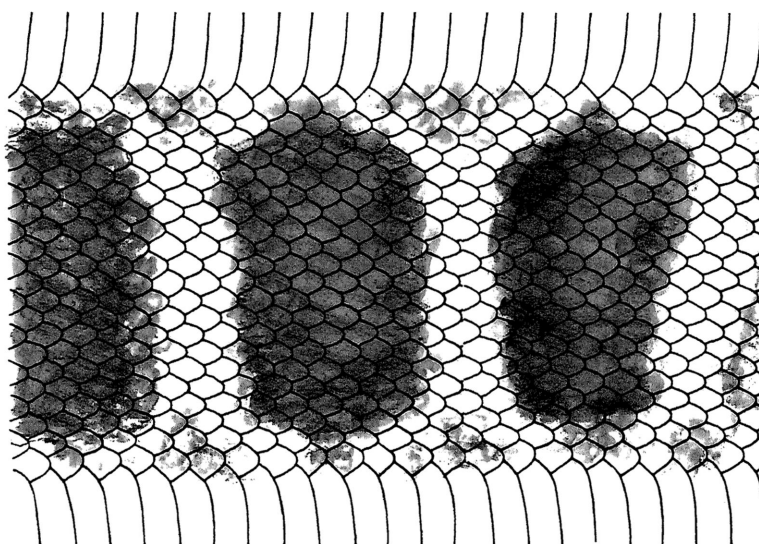
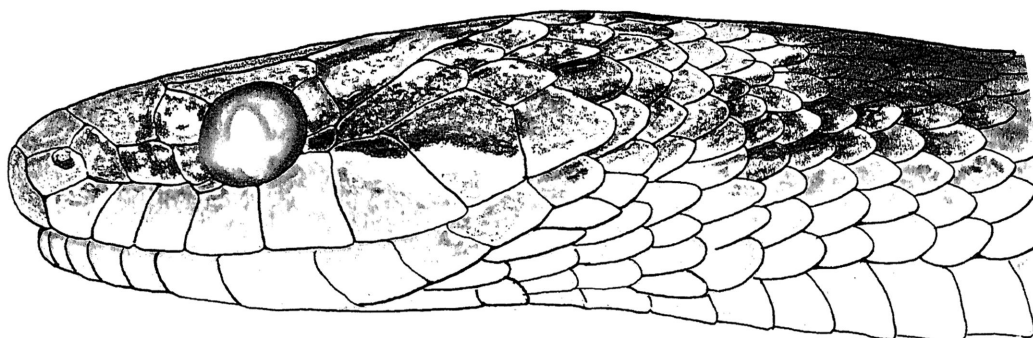
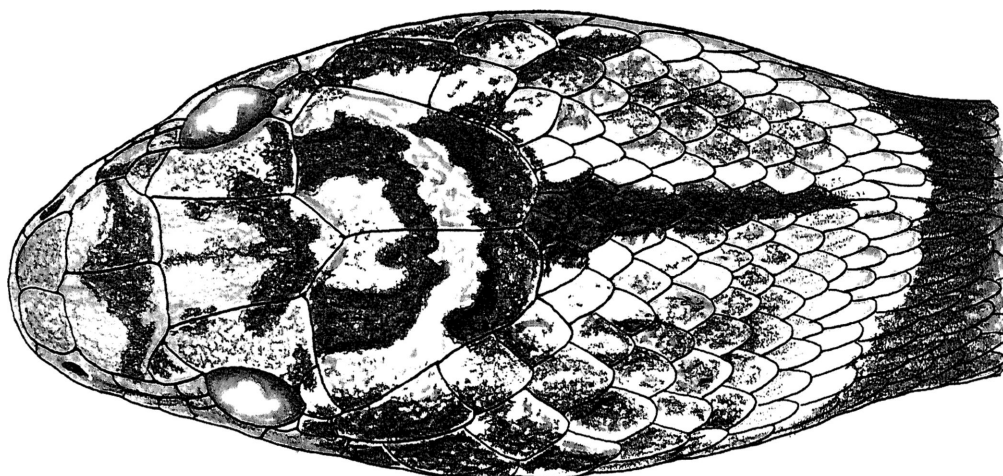
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira septentrionalis polysticta*, U.M.M.Z. No. 91058, from Panzos, Alta Verapaz, Guatemala



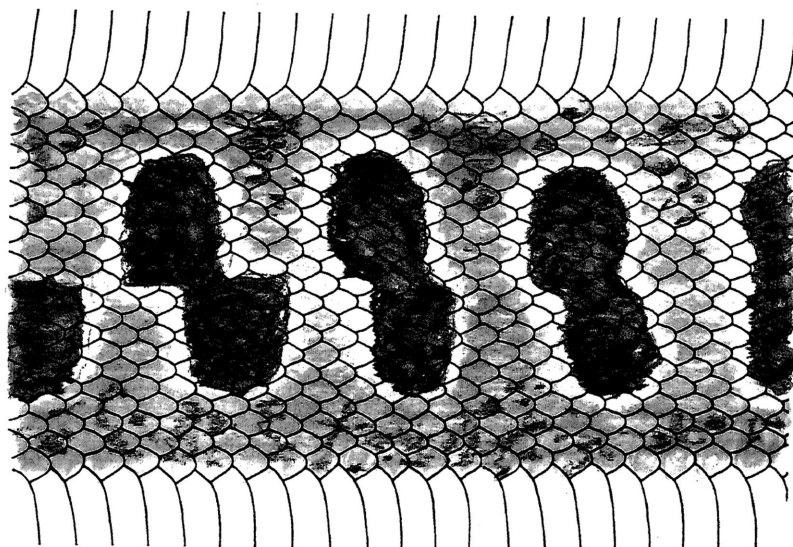
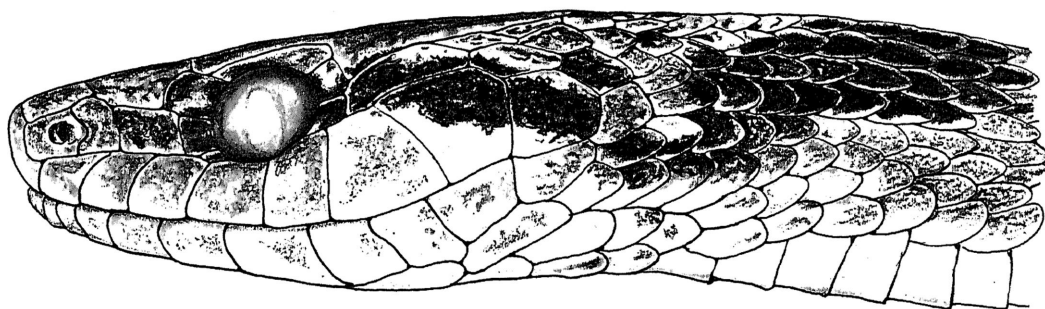
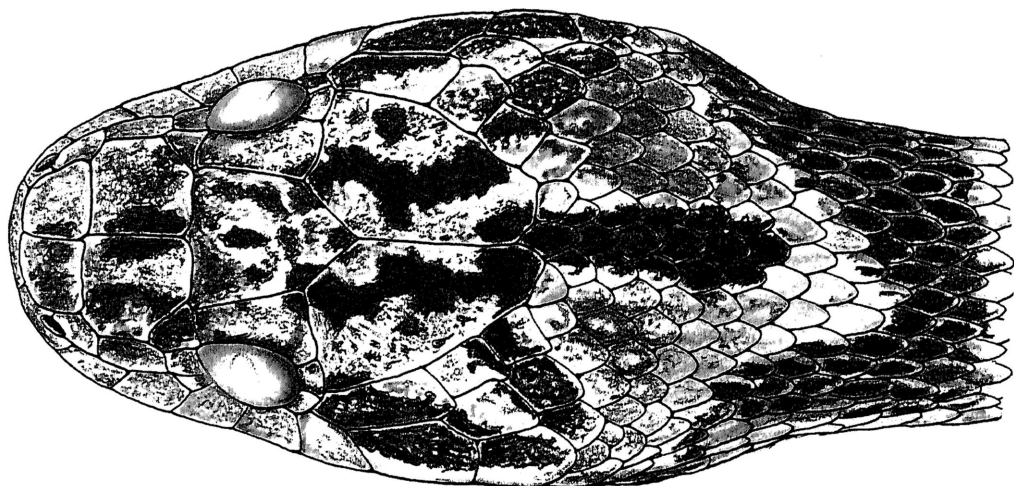
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira septentrionalis ornata*, C.N.H.M. No. 68076, from Finca Arce, Panamá, Panamá



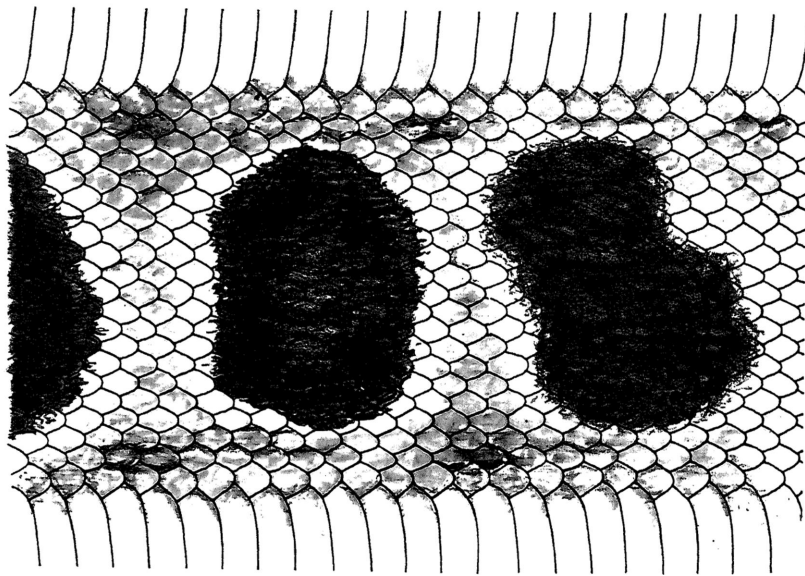
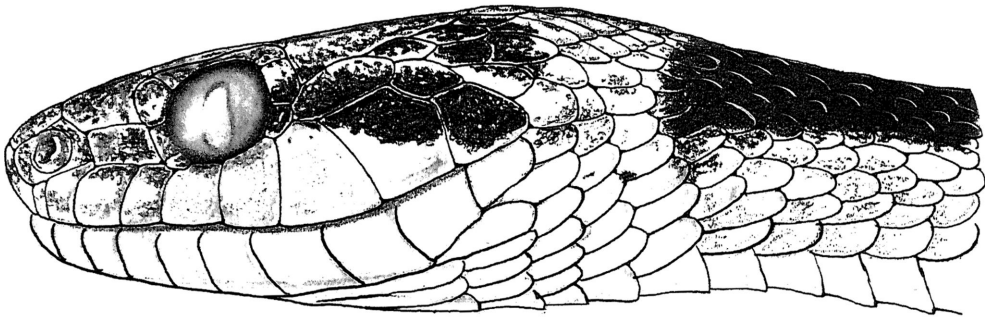
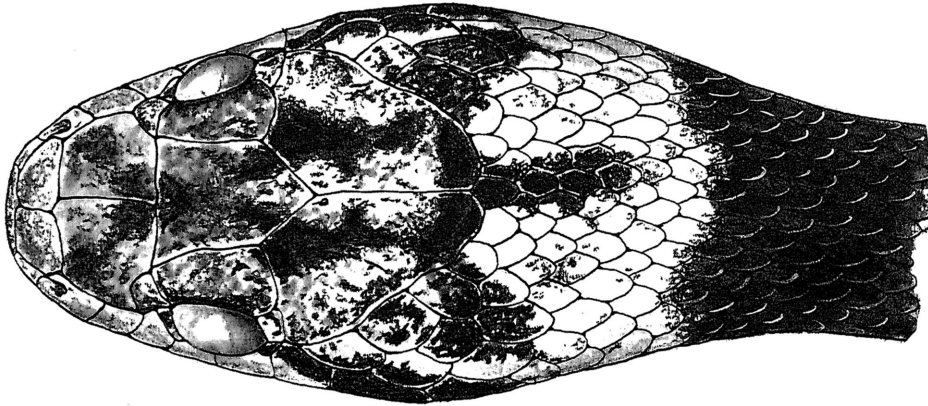
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira septentrionalis* *larcorum*, U.M.M.Z. No. 111308, from Perico, Cajamarca, Peru



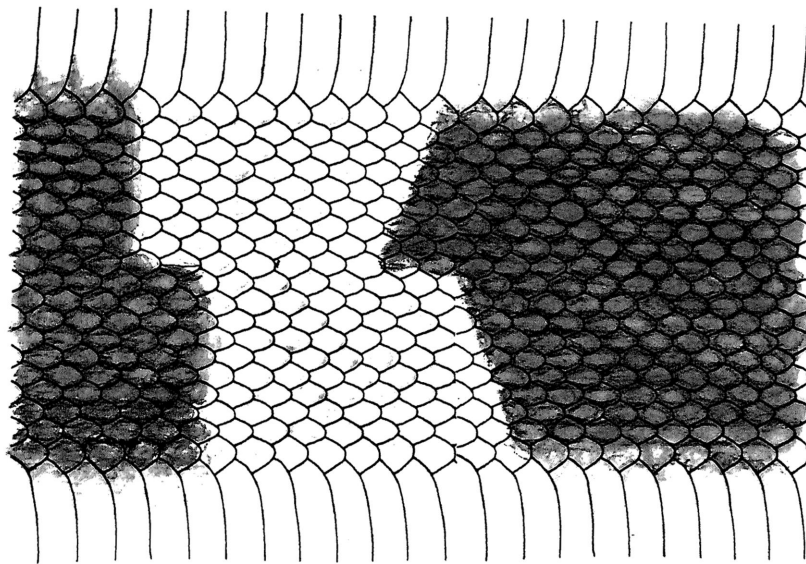
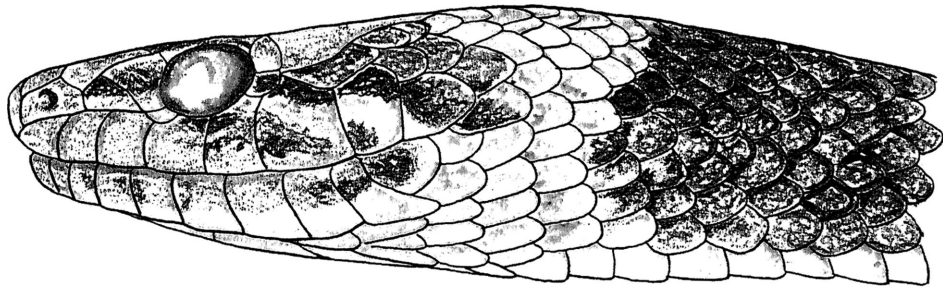
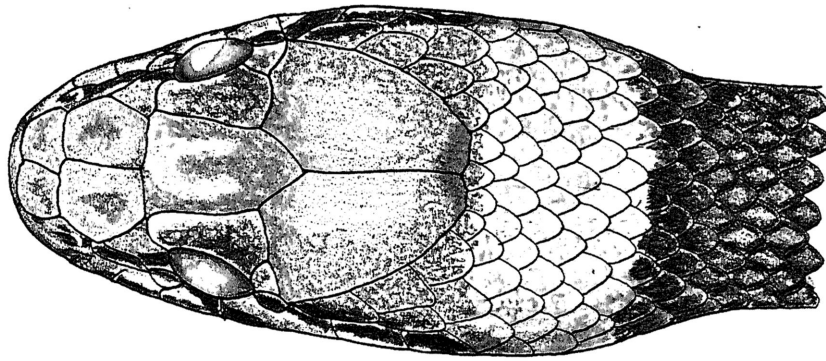
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira splendida ephippiata*, M.V.Z. No. 50835, from Guirocoba, Sonora, México



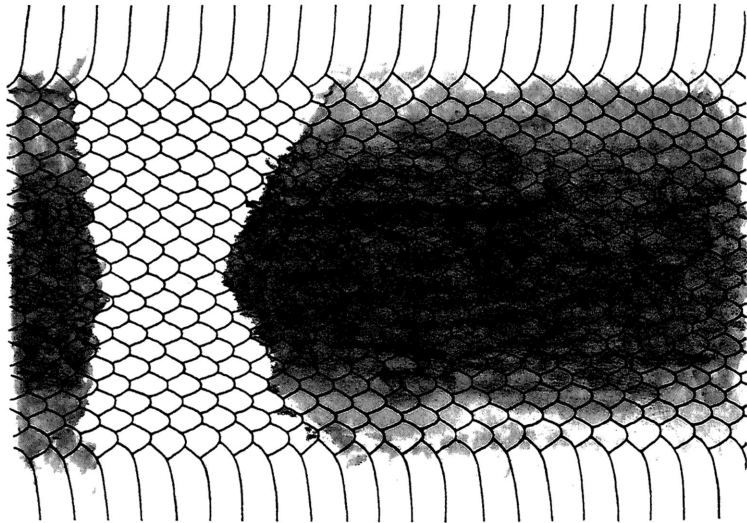
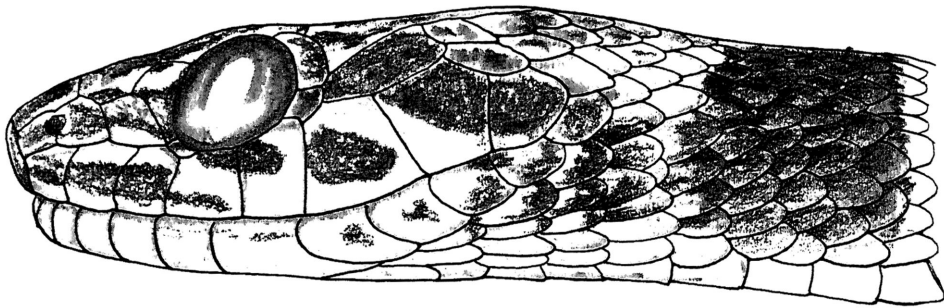
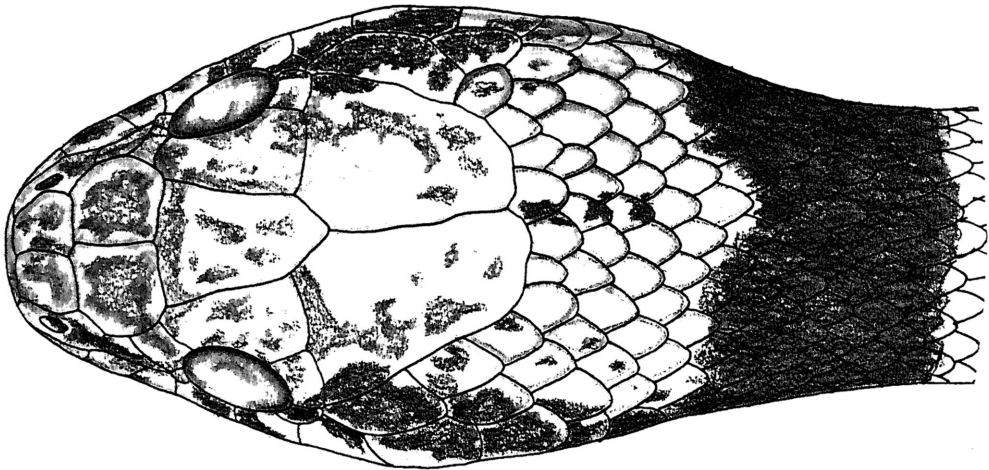
Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira splendida bressoni*, U.M.M.Z. No. 112436, from Uruapan, Michoacán, México



Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira splendida splendida*, T.C.W.C. No. 4115, from 12 kilometers northwest of Axochiapan, Morelos, México

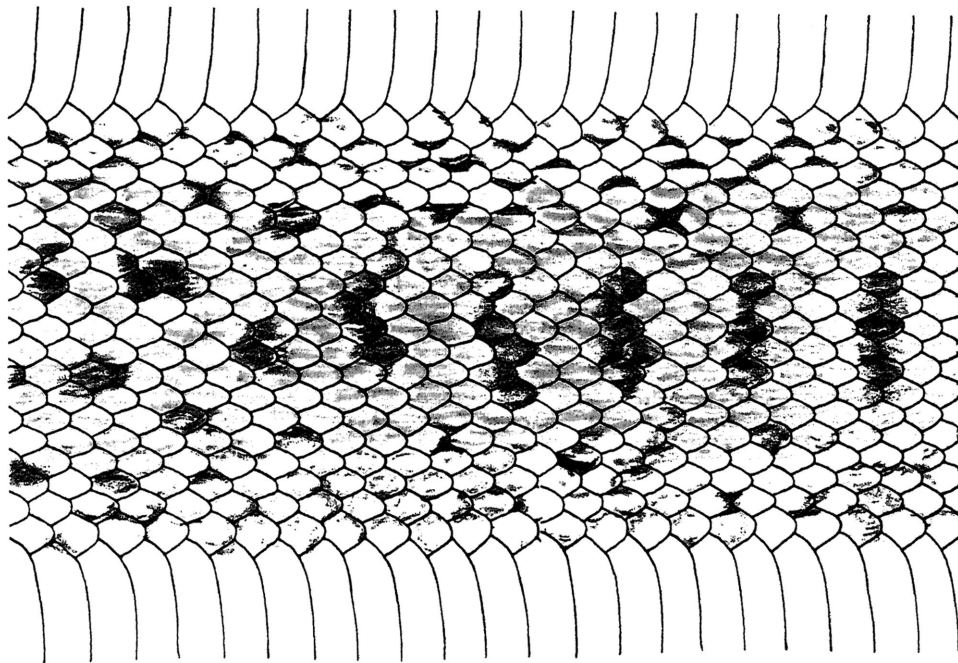
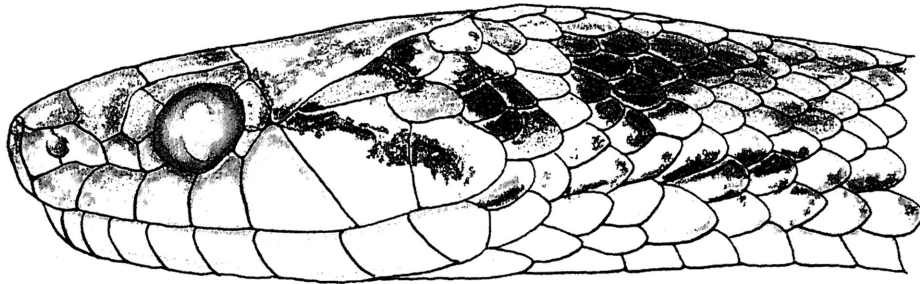
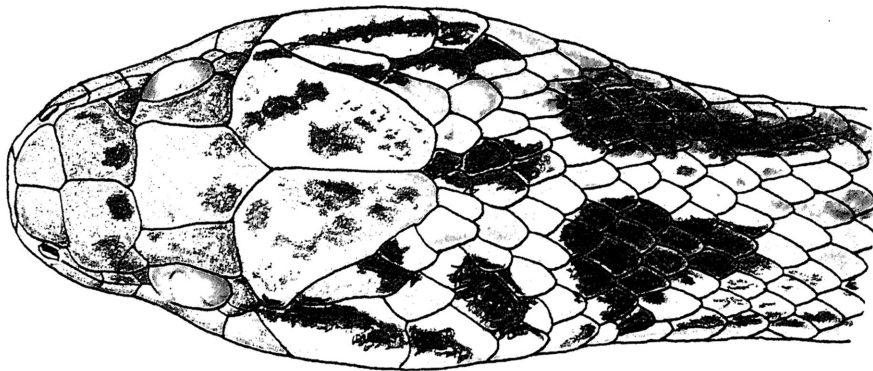


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira nigrofasciata*, U.I. No. 3788, from La Concepción, Oaxaca, México

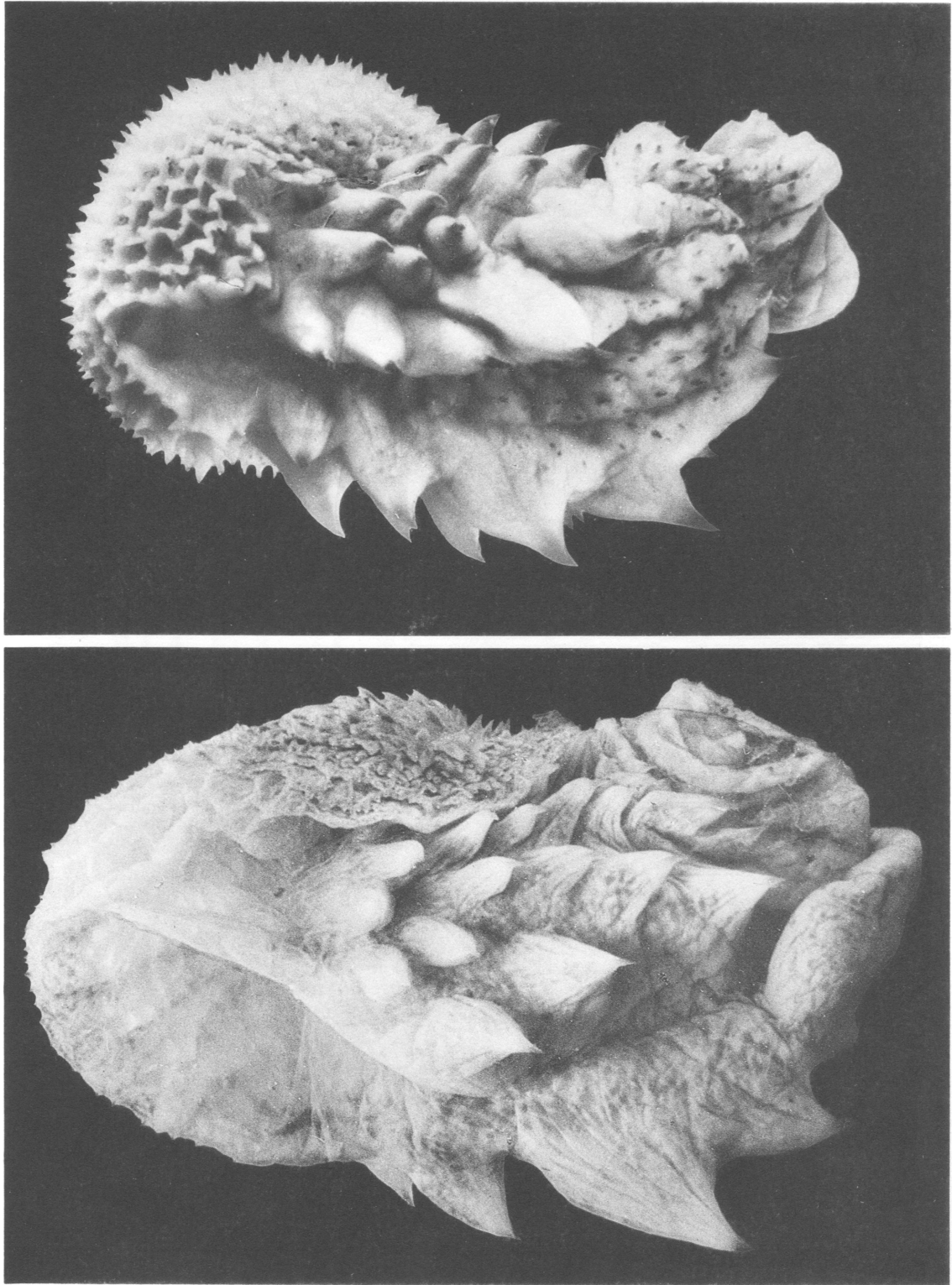


Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira latifasciata*, U.I. No. 18721, from Hacienda El Sabino, 20 miles south of Uruapan, Michoacán, México





Dorsal and lateral views of the head and dorsal body pattern of *Leptodeira punctata*, A.M.N.H. No. 62265, from Acajoneta, Nayarit, México



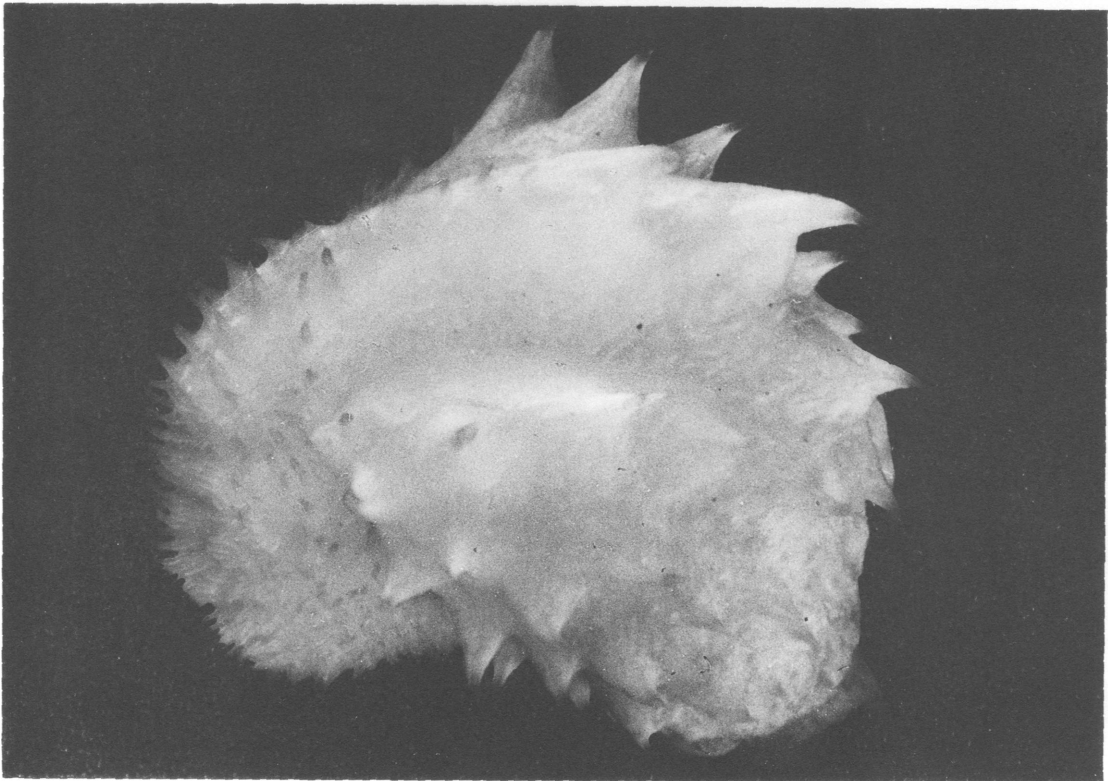
2

Everted right hemipenes of *Leptodetira*. 1. *L. maculata*, U.M.M.Z. No. 112464. 2. *L. septentrionalis polysiata*, U.M.M.Z. No. 88306

1

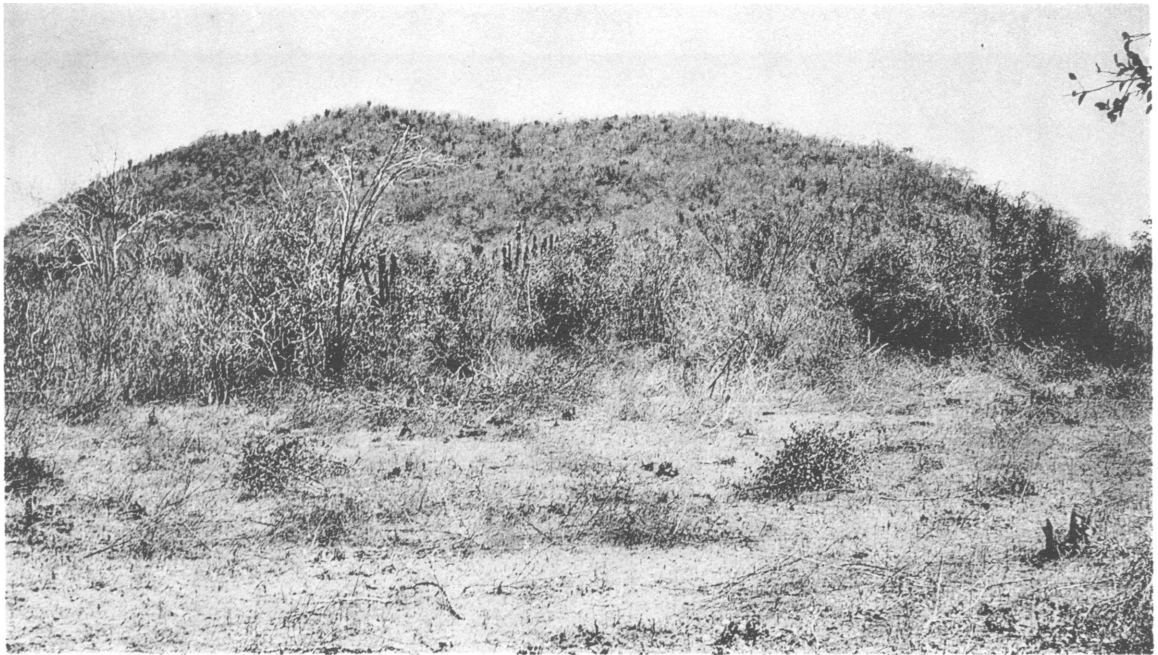


2

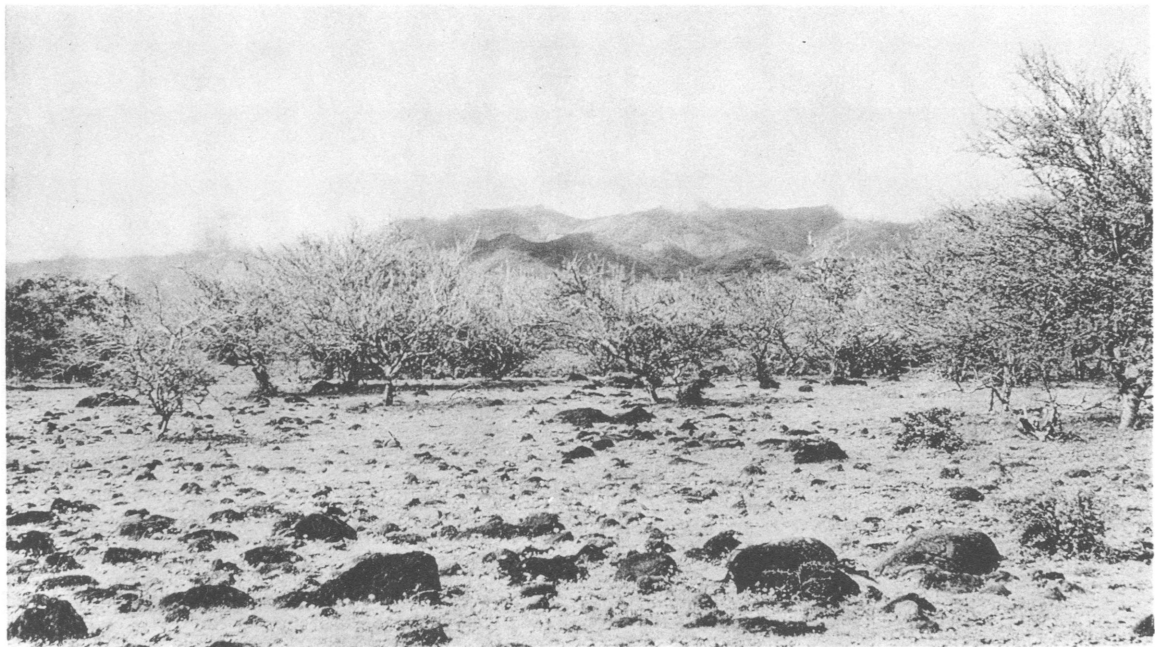


1

Everted right hemipenes of *Leptodeira*. 1. *L. nigrofasciata*, U.I. No. 27563. 2. *L. punctata*, U.M.M.Z. No. 114475



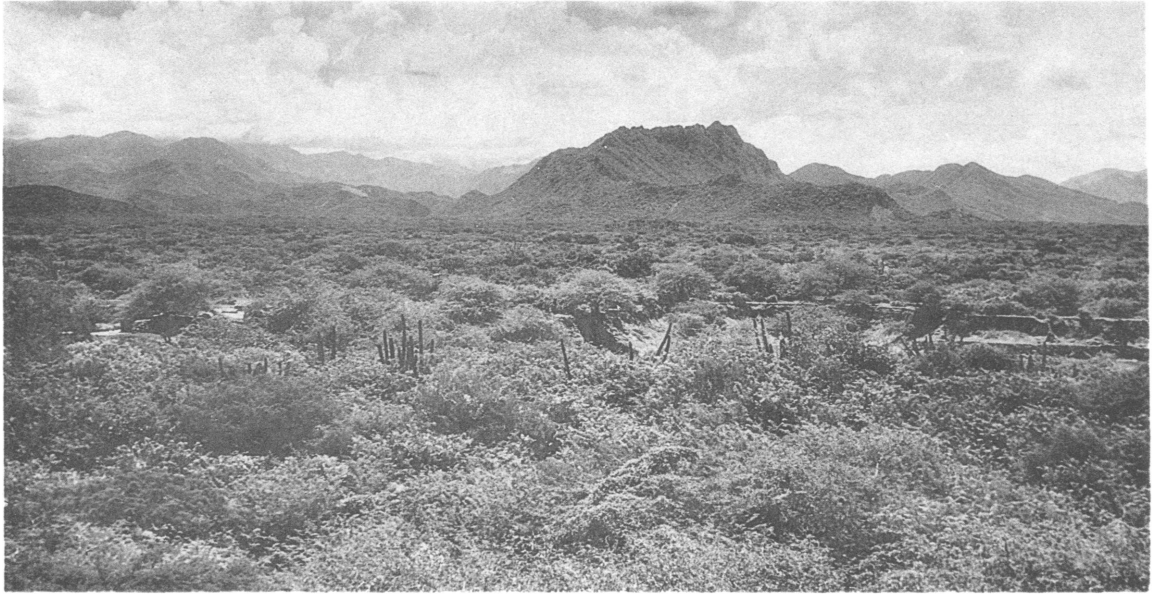
1



2

1. Open scrub forest on the Pacific coastal plain just north of Mazatlán, Sinaloa, México. *Leptodeira maculata* and *punctata* inhabit this area

2. Open scrub forest 2.7 miles north of Capirio (elevation 200 meters), Michoacán, México. *Leptodeira latifasciata* and *maculata* inhabit this area



1



2

1. Dense scrub forest near Tehuantepec, Oaxaca, México. *Leptodeira annulata cussiliris* and *nigrofasciata* are found here. Photograph by Emmet T. Hooper

2. Scrub forest "cerrado" near Carmen, Departamento Santa Cruz, Bolivia. *Leptodeira annulata pulchriceps* inhabits this area. Photograph by Carl Gans



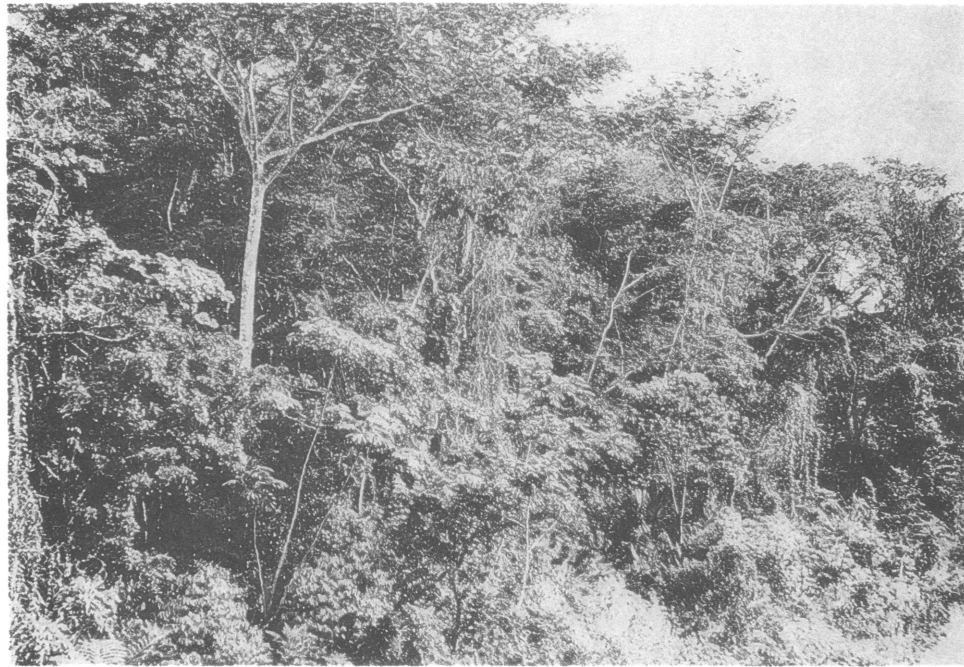
1. Broad-leaf deciduous forest 14 miles southwest of El Batel, Sinaloa, México. *Leptodeira splendida ephippiata* occurs here. Photograph by Richard G. Zweifel



2. Cloud forest near "Rancho del Cielo," 5 miles northwest of Gómez Farías, Tamaulipas, México (elevation about 1100 meters.) *Leptodeira septentrionalis septentrionalis* has been collected in clearings in this forest. Photograph by Charles F. Walker



1



2

1. Tropical rain forest near Mucambo, Pará, Brazil. *Leptodeira annulata annulata* inhabits this area. Photograph by Stanley A. Cain

2. Tropical rain forest near Palomares, Oaxaca, México. *Leptodeira septentrionalis polysticta* inhabits this area