GENERA OF PITVIPERS

W. L. Burger, 1971

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GENERA OF PITVIPERS (SERPENTES: CROTALIDAE)

by

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Submitted to the Department of Zoology
and the Faculty of the Graduate School
of the University of Kansas in partial
fulfillment of the requirements for the
degree of Doctor of Philosophy.

October ~~April~~, 1971

Committee in Charge

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INTRODUCTION

Several years ago I became interested in the rattleless, scale-snouted pitvipers that are abundant in the neotropics and the orient. Whereas rattlesnakes (Sistrurus and Crotalus) and moccasins (Agkistrodon) are relatively well known, the tropical groups are not. Duellman (1958:7) aptly described the paucity of knowledge concerning systematics of the neotropical herpetofauna. His comments apply equally well to the oriental herpetofauna: many ill-defined species of questionable or unknown relationships, few specimens from widely scattered localities, and unwarranted lumping and splitting of species and genera by investigators who have worked with only a part of the entire problem. To these chaotic conditions I might add that of the man-made jungle of literature; some 673 scattered fragments published in 9 languages are listed in a bibliography, reduced to 218 items of literature that are cited below.

My treatment is systematic in nature and mostly concerns morphological features. Zoogeography and phylogeny are discussed, but other non-systematic subjects, such as habits, habitat, and life history, are not treated.

This report concerns all genera of pitvipers as genera but not in greater detail. The material was gathered to accompany definitive treatments of the genera that are centered in Middle America and northern South America. Most new information relates to snakes of the genera Bothriechis, Bothriopsis, Ophryacus, and Porthidium.

I plan to follow this general account with monographs of the four above genera.

Crotalus and *Sistrurus* have been treated in detail by Gloyd (1940) and Klauber (1956). *Agkistrodon* and related genera are under study by Gloyd; here they comprise the *Agkistrodontinae* and genera *Agkistrodon*, *Calloselasma*, and *Hypnale*.

Studies of *Bothrops* (*sensu stricto*), *Lachesis*, *Ovophis*, *Trimeresurus*, and *Tropidolaemus* are not planned. Adequate samples of these genera are not contained in collections in the United States.

The arrangement of genera that I propose includes *Lachesis*, *Crotalus*, and *Sistrurus* without change and divides other genera as follows:

Auctorum	Proposed
Bothrops	*Bothriechis*
	Bothriopsis
	Bothrops
	Ophryacus
	Porthidium
Agkistrodon	*Calloselasma*
	Hypnale
	Agkistrodon
Trimeresurus	*Ovophis*
	Trimeresurus
	Tropidolaemus

ACKNOWLEDGEMENTS

For their generous assistance and for the benefit of their contagious enthusiasm I am deeply indebted to Hobart M. Smith, Edward H. Taylor, and William E. Duellman, under whose directions at different times this study was made. The subject was suggested for a doctoral dissertation by Smith. In 1947, as a graduate student at the University of Illinois, I began an investigation of the species of Bothrops (auct.) of Mexico and Central America. With the sponsorship of Donald W. Hoffmeister, Director of the Museum of Natural History, trips were made to Venezuela and Mexico. My brother, Jack T. Burger, who accompanied me to Oaxaca and Chiapas, and the late Lowell S. Miller, my partner in Venezuela, were enthusiastic associates. In Venezuela, Jose M. Cruzient, then Director of the Museo Nacional de Ciencias Naturales gave me much needed support and assistance. Fuller acknowledgement of help in Venezuela and Guyana by many friends there has been made previously (Burger, 1956).

When I transferred to the University of Kansas and continued my studies under the direction of Edward H. Taylor, resources of the Museum of Natural History were made available by former Director E. R. Hall. There full-time attention to research during parts of 1955-1956 was supported by the National Science Foundation. During December, 1955, a profitable trip to museums in the eastern United States was financed by the University of Kansas Endowment Association.

For their hospitality, assistance, and many stimulating conversations I am also grateful to Walter Auffenberg, Bayard H.

Brattstrom, Pete S. Chrapliwy, the late Doris M. Cochran, Roger Conant, Carl Gans, Howard K. Gloyd, Max K. Hecht, Arthur Loveridge, Samuel B. McDowell Jr., Sherman A. Minton Jr., James A. Oliver, James A. Peters, Clifford H. Pope, Philip W. Smith, Robert G. Webb, and Ernest E. Williams.

Through the generous assistance of Herschel H. Flowers and Edward Seligmann I have had the great advantage of observing live individuals of various Costa Rican pitvipers.

Through the courtesy of the authorities and curators of the large North American collections, I borrowed or studied on visits all of their accessions through 1955. Only selected specimens among later accessions have been seen. Foreign collections were not visited. Information on these collections, obtained by correspondence, concerns small numbers of specimens, in most instances only type specimens. I am grateful to the following curatorial personnel for their assistance: J. G. Battersby, Donald W. Davis, Josef Eisett, Jean Guibe, Alphonse Hoge, Alan E. Leviton, Edmond V. Malnate, Hymen Marx, Robert Mertens, Neil D. Richmond, Charles F. Walker, Ernest E. Williams, Richard G. Zweifel.

Librarians of various institutions have helped in the seemingly endless task of obtaining elusive publications. Vicco von Stralendorff, Associate Librarian of Franklin College, has been especially helpful in obtaining urgently needed publications by interlibrary loan.

Finally I am grateful to Frank B. Cross, William E. Duellman, and Henry S. Fitch for critically reviewing the manuscript.

MATERIAL AND METHODS

In this study I gathered detailed information from 708 specimens in liquid preservative. These represent the genera for which definitive studies were made, namely Ophryacus, Bothriechis, Bothriopsis, and Porthidium. In addition, 87 skeletons were studied and hundreds of preserved specimens of the other 10 genera of pitvipers were examined for comparative purposes. Although the skeletons number less than one-fourth those studied by Brattstrom (1964:188), the ones I studied were selected to include all genera and species groups and certain key species that Brattstrom did not include.

For each specimen belonging to target genera information was gathered on a standard data sheet that covered 33 details of proportion, scutellation, and coloration. A data sheet that covered 14 items was used in recording information for each skull. This information was also obtained for specimens of Lachesis and Bothrops (sensu stricto).

Specimens of other genera of pitvipers were examined late in my investigation to obtain information directly related to diagnoses and definitions of genera. I had the satisfaction of confirming information of previous authors. Little new information was obtained for members of the genera Agkistrodon, Calloselasma, Crotalus, Hypnale, Sistrurus, Trimeresurus, and Tropidolaemus.

The synonymies that accompany my systematic accounts include all synonyms, all name-combinations, and citations to the names used in all important literature on the genus, species, or subspecies. The synonymies are as complete as I can make them for publications that resent new data or new ideas. The author of a name directly follows he name in the synonymy without an intervening comma, and the type ocality and holotype are given in parentheses. Originators of new ombinations that utilize previously described specific or subspecific ames are set off by an intervening comma. Different names and ombinations are arranged in chronological order, as are citations of a iven name. Generic synonymies are included. Synonymies for species nd subspecies will follow in appropriate monographs.

Gross measurements (of body and tail lengths) were taken to the earest millimeter with a meter stick. Smaller measurements (widths nd circumferences) were made with calipers to the nearest 0.1 mm.

Unless otherwise indicated, colors were described from preserved ecimens. In such specimens patterns are significant, whereas specific lor shades are not. Because live colors are different, notes on them e emphasized.

Few, if any, of the attributes described are invariant. The normal usual condition, that which occurs in 75 percent or more of specimens, the one described. Conditions that occur less often are indicated in rentheses.

In the lists of specimens examined localities and specimens appear the following order: states in alphabetical order in each country, calities in alphabetical order in each state; museum abbreviation in phabetical order as given below; museum number in numerical order ter the abbreviations. Localities that have not been located to state e listed first in that political unit under the heading "No specific cality."

Abbreviations for museum collections are:

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CHAS	Chicago Academy of Sciences
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History and/or Chicago Natural History Museum
IBH	Institute Butantan, Herpetology Section, São Paulo
KU	University of Kansas Museum of Natural History, Lawrence
MCZ	Museum of Comparative Zoology, Harvard University
MNHN	Museum National d'Histoire Naturelle, Paris
NMW	Naturhistorisches Museum, Wien
NRS	Naturhistoriska Riksmuseet, Stockholm
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
SNG	Senckenbergischen Naturforschenden Gesellschaft, Frankfort am Main
TCWC	Texas Cooperative Wildlife Collection, Texas Agricultural and Mechanical College.
UIMNH	University of Illinois Museum of Natural History, Urbana
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum, Washington, D.C.

TERMINOLOGY

Most of the terms used here for structures are in standard use. Definitions are available in either J. A. Peters' (1964) special dictionary or Klauber's (1956) account of rattlesnakes. Only when additional information is presented, or when alternate meanings or methods need to be eliminated, are terms included in the alphabetical list that follows:

Apicals. The plates or small scales between the internasal plates on the top of the snout of many crotalids. There may be only two symmetrical apicals, but more often they are more numerous and quite varied in size and arrangement.

Apical scale pits. Paired depressions, symmetrically placed on each side of the keel of dorsal scales and usually nearest the posterior end of the scale. Also called apical fossae. Apical scale pits are present in various primitive pitvipers in many genera.

Chinshields. The single pair of large plates bounding the mental groove just behind the mental plate of pitvipers. Also called genials. Many other snakes have two pairs of chinshields.

Dorsal capping scales. Scales, usually a symmetrical pair, overlapping the dorsal proximal portion of the terminal caudal scute.

Frontorostrals. The assemblage of all median dorsal head scales from rostral plate to frontal region. The median frontorostrals are counted along the median line traversing the prefrontal and internasal regions. Included in the count, therefore, are intercanthals, and either apicals or internasals. In the absence of a frontal, the midpoint of the line connecting the anterior tips of the supraoculars is used for the posterior boundary of the series.

Gulars. The small chin scales between the two rows of infralabials and not otherwise specifically designated (Peters, 1964:143, definition 1). The gulars are usually smooth but are strongly keeled in Tropidolaemus. Median gulars are counted in a line from chinshield to first ventral. Anteriormost median gulars bound the mental groove like miniature posterior chinshields.

Intercanthals. Plates or scales filling the median prefrontal area between the canthals. These may consist of a pair of large plates but more often there are numerous small scales (Peters, 1964:167, definition 1). The least number of longitudinal rows between the canthals are counted.

Interictals. The supracephalic scales occupying the posterior part of the head from oral rictus to oral rictus (Figure 1). These are arranged in longitudinal rows, the lowest several of which correspond to temporals and the mediad several of which are rather irregularly disposed. For consistency, the interictals are counted between the last supralabials. The term occipital is often applied to large plates covering the same general part of the head.

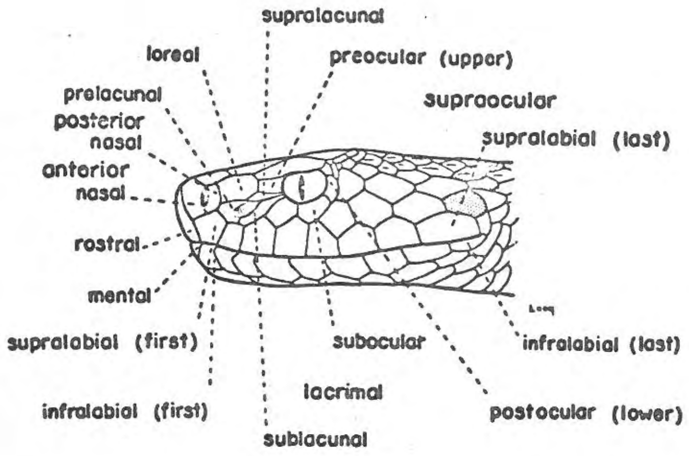

FIG. 1. Lateral view of head of Porthidium barbouri (MCZ 42679) showing important plates. The path followed in counting interictals is shaded. X 3.

Internasals. The more or less enlarged plates along the margin of the crown above the nasals and anterior to the canthals (Peters, 1964: 170, definition 2). In Agkistrodon, Sistrurus, and several species of Porthidium, two large internasals occupy the entire space from rostral to prefrontal. In other crotalids, in which there is greater subdivision of head shields, the term is reserved for the plates along the margin of the snout, contacting the nasals. In contrast to authors who restrict the term internasal to the marginal plates bordering both the rostral and nasals, I prefer to use it for all marginal (but none other than marginal) plates in the internasal region. Most plates that contact both the loreal and nasals have their greatest area above the nasals and hence are considered internasals.

Interoculars. The irregularly disposed scales or plates in the frontal region of many advanced pitvipers. In referring to the interoculars, the minimum longitudinal rows are implied, if not always specified. They are counted along the path between the supraoculars that traverses the fewest scales, which is usually across the anterior part of the frontal area. The term intersupraocular, available for precisely the same scales, is thought to be unnecessarily cumbersome. In the primitive species that have variable remnants of a frontal, one interocular may be present (a full-sized frontal) or there may be two or more interoculars according to the extent of fragmentation of the frontal. Among advanced pitvipers the number of interoculars is

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Lacrimal. The enlarged subocular at the lower anterior border of the eye (Peters, 1964:182, definition 2). Also called the anterior subocular.

Lacunalabial. A large plate extending from the labial margin along the anterior margin of the loreal pit to the loreal plate. The lacunalabial is regarded as the product of a secondary fusion of the prelacunal and one supralabial (usually the second).

Lacunals. The plates commonly called pit-border scales forming the inner border of the pit are called lacunals by Klauber (1952:9), Lowe and Norris (1954:51), and Peters (1964:182). In rattleless genera there are generally three lacunals arranged roughly like the sides of a right triangle with the base (sublacunal) parallel to the upper lip, the perpendicular side (prelacunal) behind the posterior nasal, and the hypotenuse (supralacunal) sloping posteriorly to contact the sublacunal immediately in front of the preoculars (or eye). In addition to lacunalabial (above) important taxonomic variations are the fusion of either or both the supra- and sublacunal to the middle and lower preocular, respectively, or fragmentation of the sublacunal.

Loreal. The enlarged plate or plates in front of the preoculars and above the supralacunal (Peters, 1964:193).

Loreal pit. A deep depression on the side of the head of pitvipers partially occupying the posterolateral vacuity of the maxillary. It is located below and back of the nostril. The pit opens into the posterior chamber of a sense organ discussed elsewhere. The plates composing the rim of the pit (lacunals or pit-border scales) and the smaller associated scales (foveals) below and in front of the lacunals are discussed individually. The pit is also called the facial pit or the lacrimal pit.

Marginals. The lateral dorsal head scales anterior to the supraocular. The term marginal may be used collectively for well-differentiated internasals, canthals, and postcanthals, but more often it is used for small undifferentiated scales occupying the lateral edge of the dorsal surface of the head between the rostral and the supraocular, or occupying a designated portion of this area. Peters (1964:198) used the term for body scutes of turtles and crocodilians.

Nasal pad. The flexible posterior wall of the nostril, which by moving forward acts as a valve. The nasal pore usually pierces the nasal pad.

Nasal pore. A minute opening situated on the nasal pad of many snakes (Peters, 1964:220). In crotalids it varies considerably in size, position, and shape and is absent in the genera Tropidolaemus, Sistrurus, and Crotalus.

Nasals. The plate or plates surrounding the nostril (Peters, 1964: 219). In crotalids, the nasal is often divided in two. Whether completely divided or not, the anterior moiety is called the anterior nasal or prenasal, the posterior moiety, the posterior nasal or postnasal. Smith (1946:82) suggested that the two parts of the nasal be called preseminasal and postseminasal, respectively.

Nasorostrals. The scales between prenasal and rostral (Peters, 1964: 221). In *Porthidium nummifer mexicanum* a vertical column of three moderate-sized nasorostrals completely separates the rostral from the prenasal. A more common condition, seen in *Porthidium nummifer nummifer* and often in *Bothriechis schlegeli* is occurrence of disjunct dorsal and ventral nasorostrals at the upper and lower anterior corners of the prenasal. The lower nasorostral is what Klauber (1952:9) named the postrostral.

Oculabials. The rows of scales between suboculars and supralabials, but including neither. This terminology differs from that of Klauber (1952:9), who suggested the term interoculabials for the scales between the eye and upper lip including both suboculars and supralabials. The oculabials are anterior extensions of the lowest several rows of occipitals. The number of rows usually decreases anteriorly so that it is often convenient to indicate the subtending supralabial.

Oral rictus. The corner of the mouth.

Paranals. Enlarged scales forming lateral margin of anus. Paranals are counted from the anteriormost scale that projects posterior beyond the last ventral to (but not including) the first subcaudal. The posteriormost paranal is almost as large as the first subcaudal but does not meet the corresponding scale on the other side.

Paraventrals. The ventral row of dorsal scales, usually larger and less well keeled than those above (and colorational elements occupying the same approximate position).

Postcanthal. The undifferentiated marginal head scale(s) contacting the upper preocular between the canthal and supraocular.

Prelacunal. Anterior pit-border plate. *See* lacunal.

Preoculars. The plates along the anterior margin of the eye. Most rattleless pitvipers have three preoculars, of which the upper is the largest and the middle and lower bound the lacrimal groove. Either or both of the lower two preoculars may be fused to lacunals, or be excluded from the orbit.

Subcaudals. Longitudinal series of entire, paired, or (posteriorly in *Lachesis muta*) further subdivided plates or scales beneath the tail. The subcaudals (often simply called caudals, less often urosteges) are counted from the first entire plate or the first half plate that meets another from the other side to (and including) the terminal caudal plate. Each transverse series of scales is counted as one subcaudal.

Subfoveals. The scales between the sublacunal and supralabials. Usually, they are anterior continuations of the lowermost row or rows of oculabials.

Sublacunal. Lower pit-border plate. See lacunal.

Subloreals. Scales situated beneath the loreal and in front of the prelacunal. Often the subloreals form a vertical row separating the prelacunal from the postnasal. Small scales, often contiguous with the subloreals, above and below the nasals are distinguished as supranasals (between nasals and internasals) and subnasals (between nasals and supralabials). The term subloreal was proposed by Smith (1946:79); Klauber (1952:9) proposed a second term, prefoveal, for precisely the same scales.

Subnasals. The scales that sometimes extend between the nasals and supralablals. They are usually contiguous with subloreals and reach the nasorostral only in extreme cases.

Subtending scales. The scales that circle the tail in contact with the terminal caudal scute. Included in the "count" are the dorsal capping scales and the subcaudal(s).

Superciliaries. Scales or granules between the upper margin of the eye and the supraocular plate in Bothriechis schlegeli. The "eye-lashes" of this species are enlarged superciliaries. Median and lateral rows may be distinguished.

Supralacunal. Upper pit-border plate. See lacunal.

Supranasals. The small scales between nasals and internasals, present in only a few crotalids, as, for example, in *Bothriechis schlegeli*.

Ventrals. Large transverse plates on the lower surface of the body. The conventional method of counting ventrals (or gastrosteges) is the method followed in this study. Start with the anteriormost plate that is wider than long and finish with the plate preceding the anal. Peters' (1964:380) second definition of ventral count corresponds. Dowling (1951) suggested that the count start instead with the first plate that contacts the lowest row of dorsals on both sides. In actual practice this method usually excludes the first two to four enlarged transverse plates of most crotalids and in these (as in many other broad-headed snakes) offers no increase in objectivity over the conventional method. The first ventral by either technique bears no constant relationship to the first vertebrae. The first ventral by the Dowling criterion usually lies beneath the third or fourth vertebrae, whereas first ventral by the conventional definition usually lies beneath the first vertebrae or the posterior part of the skull.

NOMENCLATURE

Pitvipers are numerous and varied. Their nomenclature is not overtly important nor particularly interesting. For these reasons nomenclatural homework and footwork generally tend to fall behind other work. In compensation the effort here may seem extravagant, but is as accurate and complete as possible in the prescribed limits.

Family names are in one section of classification; an alphabetical guide is not deemed necessary. Because generic (including subgeneric) and specific (including subspecific) names are scattered on the following pages, alphabetical lists are provided; generic and subgeneric names of pitvipers (the entire family Crotalidae) lead nomenclatural lists, followed by a list of all nominal species and subspecies of rattleless pitvipers.

With a two-century accumulation of nomenclatural complexities, names that have come into use (including five that are in present use) have not always been the first valid name or the name that is most appropriate by the earliest type designation. If guided by personal preference alone, I would follow the Law of Priority, letting the axes of synonymy, homonymy, and prior generotype designation fall where they may. However, the changes that would result would be a burden to nontaxonomists investigating medically important species. The principle of conservation provides that plenary action be requested to prevent changes in long familiar names of important species. I plan to request appropriate action in another paper to provide for the stability of *Bothrops*, *Bothrops jararaca*, and *Trimeresurus trigonocephalus*. When special considerations are lacking, names are changed as demanded by the International Code of Zoological Nomenclature (Stoll _et al._, 1964).

Genera

Two genera were not validly published: _Atropos_ Oken, 1815; _Cenchris_ Grenovius, 1763. All other genera and subgenera of pitvipers are listed in Table 1.

Discounted Names

In addition to the nomenclaturally acceptable names in the main list below, many published names are not available or do not seem important enough to include in the main list. These names are briefly discussed below and are listed alphabetically at the end of this section.

Names that appeared in publications that are not consistently binomial are not validly published according to the International Code (Stoll _et al._, 1964:11). Thereby eliminated is the specific name _Trigonocephalus lancifer_ Oken (1816) and the names proposed by Higgins (1873). The nomenclatural productions of Higgins (1873) are unique but not consistently binomial. Klauber (1956:85) commented upon Higgins' allocation of several Asiatic pitvipers to _Crotalus_, as _C. trimeresurus_, _C. peltopelor_, _C. halys_, and _C. hypnale_. Other ineptly titled pitvipers (or possible pitvipers) listed by Higgins include _Vipera Lachesis bufocephalus_ (_sic_), _V. L. variegata_, _V. L. os flavus_, and _Vipera Calamaris venenosus_.

TABLE 1. Alphabetical Synonymy of Pitviper Genera

Name, author, and date	Allocation
Acontias Troost, 1836 (preocc.)	*Agkistrodon*
Aechmophrys Coues, 1875	*Crotalus*
Agkistrodon Palisot de Beauvois, 1799	*Agkistrodon*
Ancistrodon Wagler, 1830 (invalid emendation)	*Agkistrodon*
Aploaspis Cope, 1866	*Crotalus*
Atropophis Peters, 1872	*Trimeresurus*
Atropos Wagler, 1830 (preocc.)	*Trimeresurus*
Bothriechis Peters, 1860	*Bothriechis*
Bothriopsis Peters, 1861	*Bothriopsis*
Bothrophis Fitzinger, 1843	*Trimeresurus*
Bothrops Wagler, 1824	*Bothrops*
Calloselasma Cope, 1859	*Calloselasma*
Caudisona Fitzinger, 1826 (preocc.)	*Sistrurus*
Caudisona Laurenti, 1768	*Crotalus*
Cenchris Daudin, 1803	*Cenchris*
Cophias Merrem, 1820	*Lachesis*
Craspedocephalus Kuhl, 1822	*Trimeresurus*
Crotalinus Rafinesque, 1818 (invalid emendation)	*Crotalus*
Crotalophorus Houttuyn, 1764	*Crotalus*
Crotalus Linnaeus, 1758	*Crotalus*
Cryptelytrops Cope, 1860	*Trimeresurus*
Halys Gray, 1849 (preocc.)	*Hypnale*

Hypnale Fitzinger, 1843	*Hypnale*
Lachesis Daudin, 1803	*Lachesis*
Leiolephis Duméril, 1853 (preocc.)	*Calloselasma*
Megaera Wagler, 1830	*Trimeresurus*
Ophryacus Cope, 1887	*Ophryacus*
Parias Gray, 1849	*Trimeresurus*
Peltopelor Günther, 1864	*Trimeresurus*
Porthidium Cope, 1871	*Porthidium*
Rhinocerophis Garman, 1881	*Bothrops*
Scytale Sonnini and Latreille, 1802	*Agkistrodon*
Scytalus Rafinesque, 1819	*Agkistrodon*
Sistrurus Garman, 1883	*Sistrurus*
Teleurasphis Cope, 1859	*Bothriechis*
Thamnocenchris Salvin, 1860	*Bothriechis*
Thanatophis Posado Arango, 1889	*Bothriechis*
Thanatos Posado Arango, 1889	*Bothriechis*
Tisiphone Fitzinger, 1826 (preocc.)	*Agkistrodon*
Toxicophis Troost, 1836	*Agkistrodon*
Trigalus Rafinesque, 1815	*Bothrops*
Trigonocephalus Oppel, 1811	*Lachesis*
Trimeresurus Lacépède, 1804	*Trimeresurus*
Trimesurus Swainson, 1839 (invalid emendation)	*Trimeresurus*
Tropidolaemus Wagler, 1830	*Tropidolaemus*
Urocrotalon Fitzinger, 1843	*Crotalus*

Urocrotalum Agassiz, 1846 (invalid emendation)	*Crotalus*
Uropsophus Wagler, 1830	*Crotalus*

A difference of one letter is sufficient to prevent homonymy in generic names or (with certain specified exceptions) species names (Stoll *et al*., 1964:53). Nevertheless the majority of small variations in spelling are either unintentional misspellings (*lapsi calami*) or *nomina nuda*, without clear indication of their application. Such have no nomenclatural status. The following six names are inconsequential variations of this sort: *Bothrops castelnaue* Cope (1958), and *B. castelnavii* Cope (1871) for *B. castelnaudi*; *Lachesis alternans* Beddard (1913) probably *lapsus calami* for *Lachesis alternatus*; *Bothrops nigricauda* Maslin (1942) probably *lapsus calami* for *B. nigroviridis*; *Bothrops hypoprora* and *B. nommifera piccadoi* listed by Bucherl (1963: 79), obviously *lapsi calami* for *Bothrops hyoprora* and *B. nummifer picadoi*, respectively.

Bothrops boussingaulti was listed by Posada Arango (1889:47; 1890: 343) without indication of the application of the name. The catalog of the Museum Nacional d'Histoire Naturelle, Paris, lists a holotype and two other specimens under the name. In these usages it is a *nomen nudum* and an unpublished manuscript name, respectively, without nomenclatural status, and has not been used subsequently.

Snakes other than pitvipers.—Either by original designation or because of erroneous localities, other kinds of snakes have been mistakingly allocated to genera of rattleless pitvipers.

Vipera (*Echidna*) *semifasciatus* Merrem, 1820 (America Meridionali) and *V.* (*E.*) *acontia* Merrem, 1820 (America) are probably viperids, with erroneous localities. I plan to suggest in a later paper that they be legally suppressed. *Lachesis libanotica* Hemprich, 1827 is a *nomen udum* referring to an undiagnosed snake, possibly venomous, from Lebanon. ertens (1967:153) allocated the name tentatively to the synonymy of *ipera bornmuelleri* Werner, 1898.

Echidna ocellata Tschudi, 1845 (Peru), cited as *Bothrops ocellatus* y Jan (1957:51) is a junior synonym of the African viperid, *Bitis tropos* (Linnaeus, 1766).

Cenchris ocellata Gray, 1831 is a junior synonym of the boid, *nygrus carinatus* (Schneider, 1801).

Coluber trinoculus Beckstein, 1802 was listed by Lichenstein (1818) s *Trigonocephalus trinoculus*. It is a junior synonym of *Vipera sselli* (Shaw, 1802).

Neurodromicus dorsalis Cope, 1873, described from the Oligocene eodon beds of northeastern Colorado and originally assigned with alifications to the Crotalidae, was transferred to the Boidae by nzolini (1952). Auffenberg (1963:157) suggested that the type ecimen is not a fossil but a Recent vertebra, which he tentatively entified as *Sistrurus catenatus*, that became mixed with material from e fossiliferous bed.

Trigonocephalus alternatus binocularis, *T. flavescens*, and *T. olecomorphus*, all described by Bacque, 1916, have been assigned as nonyms to the colubrid species *Drymobius bifossatus*, (Raddi, 1820)

Xenodon merremi (Wagler, 1824), and *Leimadophis almadensis*, (Wagler, 1824) respectively (Amaral, 1930a:58).

An alphabetical list of all the variously discounted, rejected, and misapplied names that are discussed just above follows:

acontia, *Vipera* (*Echidna*), Merrem, 1820
alternans, *Lachesis*, Beddard, 1913
binocularis, *Trigonocephalus alternatus*, Bacque, 1916
boussingaulti, *Bothrops*, Posada Arango, 1889
bufocephalus, *Vipera Lachesis* (*sic*), Higgins, 1873
castelnaue (*sic*), *Bothrops*, Cope, 1858
castelnavii, *Bothrops*, Cope, 1871
dorsalis, *Neurodromicus*, Cope, 1873
flavescens, *Trigonocephalus*, Bacque, 1916
ypoprora, *Bothrops*, Bucherl, 1963
lancifer, *Trigonocephalus*, Oken, 1816
libanotica, *Lachesis*, Hemorich, 1827
igricauda, *Bothrops*, Maslin, 1942
ocellata, *Cenchris*, Gray, 1831
ocellata, *Echidna*, Tschudi, 1845
ocellatus, *Bothrops*, Jan, 1857
s flavus, *Vipera Lachesis* (*sic*), Higgins, 1873
eltopelor, *Crotalus*, Higgins, 1873
iccadoi, *Bothrops nummifera*, Bucherl, 1963
colecomorphus, *Trigonocephalus*, Bacque, 1916
emifasciatus, *Vipera* (*Echidna*), Merrem, 1820

trimeresurus, *Crotalus*, Higgins, 1873

trinoculus, *Coluber*, Beckstein, 1802

trinoculus, *Trigonocephalus*, Lichtenstein, 1818

variegata, *Vipera* *Lachesis* (*sic*), Higgins, 1873

venenosus, *Vipera* *Calamaris* (*sic*), Higgins, 1873

Available Names of Species and Subspecies

Nomenclaturally acceptable names are in another list below (Table 2). Valid emendations are substituted for the original name. All names in the genitive singular case are terminated with one "i". With these exceptions each name is cited in its original form. Further bibliographic information about the descriptions appears in the appropriate synonymy and in the bibliography.

Nomina Dubia

Three nominal species are provisionally relegated to synonymy, indicated by a question mark in the preceding list. They are *Bothrops* *amarali* Briceno Rossi (1934), *Coluber* *ambiguus* Gmelin (1789), and *Vipera* *caerulescens* Laurenti (1768). They probably all best qualify as *nomina* *dubia*. Other *nomina* *dubia* that are not assigned in the list include *Trigonocephalus* *sagittiformis* Schinz (1833), *Trigononcephalus* *savianus* Filippe (1848), *Bothrops* *neuvoiedee* *vezuelenzi* (*sic*) Briceno Rossi (1934), and *Lachesis* *wettsteini* Werner (1923). The Official List of Rejected Names is an appropriate place for all of them, as I plan to formally propose in a later paper.

Trivial name, original generic name, author, and date	Present name
acrochordus (Bothrops) (sic) García, 1896	Lachesis muta muta
acutimentalis (Trimeresurus) Werner, 1926	Trimeresurus purpureomaculatus purpureomaculatus
acutus (Halys) Günther, 1888	Calloselasma acutus
affinis (Bothrops) Gray, 1849	Bothrops atrox atrox
affinis (Bothrops) Bocourt, 1868 (nec Gray)	Porthidium nummifer occiduus
affinis (Trigonocephalus) Gray, 1849	Hypnale halys
affinis (Trigonocephalus) Günther, 1860 (nec Gray)	Hypnale himalayanus
albocarinatus (Bothrops) Shreve, 1934	Bothriopsis albocarinata
albolabris (Trimesurus) (sic) Gray, 1842	Trimeresurus albolabris
alboviridis (Trimeresurus) Taylor, 1917	Tropidolaemus wagleri
alecto (Coluber) Shaw, 1802	Lachesis muta muta
alternatus (Bothrops) Duméril, Bibron, and Duméril, 1854	Bothrops alternatus
alticola (Bothrops) Parker, 1934	Bothriopsis albocarinatus
amarali (Bothrops) Briceno Rossi, 1934	? Bothrops atrox atrox

ambiguus (Coluber) Gmelin, 1789	? Bothrops atrox atrox
ammodytes (Scytale) Latreille, 1802	Lachesis muta muta
ammodytoides (Bothrops) Leybold, 1873	Bothrops ammodytoides
anamallensis (Trimeresurus) Günther, 1864	Trimeresurus malabaricus
andersoni (Trimeresurus) Theobald, 1868	Trimeresurus purpureomaculatus purpureomaculatus
andiana (Bothrops) Amaral, 1923	Bothrops andianus
annamensis (Ancistrodon) Angel, 1933	Calloselasma rhodostoma
annectans (Trimeresurus) Schmidt, 1936	Porthidium ophryomegas
aquaticus (Coluber) Shaw, 1802	Agkistrodon piscivorus piscivorus
arboreus (Trigonocephalus) Cope, 1869	Bothriopsis bilineatus bilineatus
asper (Trigonocephalus) Garman, 1883	Bothrops atrox atrox
ater (Lachesis) Daudin, 1803	Lachesis muta muta
atrofuscus (Acontias) Troost, 1836	Agkistrodon contortrix mokeson
atrox (Coluber) Linnaeus, 1758	Bothrops atrox atrox
aurifer (Thamnocenchris) Salvin, 1860	Bothriechis aurifer aurifer
austrinus (Agkistrodon) Gloyd and Conant, 1943	Agkistrodon contortrix contortrix

[illegible]	Bothrops neuwiedi lutzi
barbouri (Lachesis) Dunn, 1919	Porthidium barbouri
barnetti (Bothrops) Parker, 1938	Bothrops barnetti
bernoullii (Bothrops) F. Müller, 1878	Bothriechis bicolor
bicolor (Bothrops) Bocourt, 1868	Bothriechis bicolor
bicolor (Trimesurus) (sic) Gray, 1853	Trimeresurus erythrurus
bilineatus (Ancistrodon) Günther, 1863	Agkistrodon bilineatus bilineatus
bilineatus (Cophias) Wied-Neuwied, 1825	Bothriopsis bilineatus bilineatus
blomhoffi (Trigonocephalus) Boie, 1826	Hyphale halys blomhoffi
boliviana (Bothrops) Amaral, 1927	Bothrops neuwiedi bolivianus
borneensis (Atropophis) Peters, 1872	Trimeresurus puniceus
brachystoma (Teleuraspis) Cope, 1860	Porthidium lansbergi lansbergi
brammianus (Bothrops) Bocourt, 1868	Porthidium godmani godmani
brasiliensis (Coluber) Lacépède, 1789	Bothrops jararaca
brazili (Bothrops) Hoge, 1953	Bothrops brazili
brevicaudus (Agkistrodon) Stejneger, 1907	Hypnale halys brevicaudus
browni (Agkistrodon) Sheve, 1938	Porthidium barbouri

[illegible]	Bothrops ammodytoides
caerulescens (Vipera) Laurenti, 1768	? Bothrops atrox atrox
cantori (Trigonocephalus) Blyth, 1846	Trimeresurus cantori
capitetriangulatus (Coluber) Lacépède, 1789	Trimeresurus trigonocephalus
caraganus (Trigonocephalus) Eichwald, 1931	Hypnale halys caraganus
caribbaeus (Trigonocephalus) Garman, 1887	Bothrops caribbaeus
carinatus (Trimesurus) (sic) Gray, 1842	Trimeresurus purpureomaculatus purpureomaculatus
castelnaudi (Bothrops) Duméril, Bibron, and Duméril, 1854	Bothriopsis castelnaudi castelnaudi
catenata (Scytale) Latreille, 1802	Lachesis muta muta
caucasicus (Ancistrodon) Nikolsky, 1917	Hypnale halys caucasicus
celebensis (Tropidolaemus) Peters, 1872	Tropidolaemus wagleri
cenchris (Trigonocephalus) Schlegel, 1837	Agkistrodon contortrix and Agkistrodon piscivorus
ceylonensis (Trimesurus) (sic) Gray, 1842	Agkistrodon hypnale
chaseni (Trimeresurus) Smith, 1931	Ovophis chaseni
chloromelas (Lachesis) Boulenger, 1912	Bothriopsis oligolepis
cinereus (Bothrops) Gray, 1842	Bothrops atrox atrox

colgadora (Thanatophis) Garcia, 1896	Bothriechis schlegeli schlegeli
colombianus (Bothrops) Rendahl and Vestergren, 1941	Bothrops microphthalmus colombianus
colombiensis (Trigonocephalus) Hallowell, 1845	Bothrops colombiensis
contortrix (Boa) Linnaeus, 1766	Agkistrodon contortrix contortrix
convictus (Trimeresurus) Stoliczka, 1870	Ovophis convictus
coorgenis (Lachesis) Rao, 1917	Trimeresurus malabaricus
cornutus (Trimeresurus) Smith, 1930	Trimeresurus cornutus
cotiara (Lachesis) Gomes, 1913	Bothrops cotiara
crotalinus (Coluber) Gmelin, 1789	Lachesis muta muta
cupreus (Scytalus) Rafinesque, 1819	Agkistrodon contortrix mokeson
darwini (Atropos) Duméril, Bibron, and Duméril, 1854	Trimeresurus strigatus
diporus (Bothrops) Cope, 1862	Bothrops neuwiedii diporus
dirus (Bothrops) Jan, 1875	Bothrops atrox atrox
dunni (Trimeresurus) Hartweg and Oliver, 1938	Porthidium lansbergi dunni
elegans (Craspedocephalus) Gray, 1849	Trimeresurus mucrosquamatus
elegans (Trimesurus) (nec Gray, 1849) Gray, 1853	Trimeresurus popeorum
erythromelas (Bothrops) Amaral, 1923	Bothrops erythromelas

fasciatus (Lachesis) Boulenger, 1896	Trimeresurus fasciatus
flavomaculatus (Megaera) Gray, 1842	Trimeresurus flavomaculatus
flavoviridis (Bothrops) Hallowell, 1860	Trimeresurus flavoviridis flavoviridis
fluminensis (Bothrops) Amaral, 1932	Bothrops neuwiedii fluminensis
fonsecai (Bothrops) Hoge and Belluomini, 1959	Bothrops fonsecai
formosensis (Trimeresurus) (nec Maki), Mell, 1931	Ovophis monticola makazayazaya
formosensis (Trimeresurus) Maki, 1931 (March 20)	Trimeresurus stejnegeri formosensis
formosus (Trigonocephalus) Schlegel, 1844	Trimeresurus sumatranus
furia (Bothrops) Wagler, 1924	Bothrops atrox atrox
garciai (Trimeresurus) H. M. Smith, 1940	Porthidium melanurum
glaucus (Coluber) Gmelin, 1789	Bothrops lanceolatus
godmani (Bothriechis) Günther, 1863	Porthidium godmani godmani
goyazensis (Bothrops) Amaral, 1925	Bothrops neuwiedi goyazensis
gracilis (Trimeresurus) Oshima, 1920	Trimeresurus gracilis
gramineus (Coluber) Shaw, 1902	Trimeresurus gramineus
hageni (Bothrops) Lidth de Jeude, 1886	Trimeresurus sumatranus

halys (Coluber) Pallas, 1776	Hypnale halys halys
himalayanus (Halys) Günther, 1864	Hypnale himalayanus
histrionicus (Trigonocephalus) Duméril, 1853	? Agkistrodon contortrix
holosericeus (Cophias) Wied-Neuwied, 1821	Bothrops atrox atrox
hombroni (Tropidolaemus) Guichenot, 1853	Tropidolaemus wagleri
huttoni (Trimeresurus) M. A. Smith, 1949	Trimeresurus huttoni
hyoprora (Bothrops) Amaral, 1935	Porthidium hyoprorum
hypnal (Cophias) Merrem, 1820	Agkistrodon hypnale
iglesiasi (Bothrops) Amaral, 1923	Bothrops iglesiasi
immaculatus (Trimeresurus) Peters, 1872	Tropidolaemus wagleri
inaequalis (Lachesis) Magalhaes, 1920	Bothrops alternata
insularis (Lachesis) Amaral, 1921	Bothrops insularis
intermedia (Trigonocephalus) Strauch, 1868	Agkistrodon halys intermedius
itapetiningae (Lachesis) Boulenger, 1907	Bothrops itapetiningae
jararaca (Cophias) Wied-Neuwied, 1824	Bothrops jararaca
jararacussu (Bothrops) Lacerda, 1884	Bothrops jararacussu
jerdoni (Trimeresurus) Günther, 1875	Trimeresurus jerdoni

kaulbacki (*Trimeresurus*) Smith, 1940	*Trimeresurus kaulbacki*
kodairai (*Trimeresurus*) Maki, 1931	*Trimeresurus gramineus*
labialis (*Trimeresurus*) Steindacher, 1867	*Trimeresurus labialis*
lanceolatus (*Coluber*) Lacépède, 1789	*Bothrops lanceolatus*
lansbergi (*Trigonocephalus*) Schlegel, 1841	*Porthidium lansbergi lansbergi*
lateralis (*Bothriechis*) Peters, 1852	*Bothriechis lateralis*
laticinctus (*Agkistrodon*) Gloyd and Conant, 1934	*Agkistrodon contortrix laticinctus*
leptura (*Bothrops*) Amaral, 1923	*Bothriopsis punctata*
leucostigma (*Bothrops*) Wagler, 1824	*Bothrops atrox atrox*
leucostoma (*Toxicophis*) Troost, 1836	*Agkistrodon piscivorus leucostomus*
leucurus (*Bothrops*) Wagler, 1824	*Bothrops atrox atrox*
lichenosa (*Bothrops*) Roze, 1958	*Bothriopsis castelnaudi lichenosa*
lojana (*Bothrops*) Parker, 1930	*Bothrops lojana*
luteus (*Trimeresurus*) Boettger, 1895	*Trimeresurus luteus*
lutzi (*Lachesis*) Miranda Ribeiro, 1915	*Bothrops neuwiedi lutzi*
mcgregori (*Trimeresurus*) Taylor, 1919	*Trimeresurus mcgregori*

macrolepis (Trimeresurus) Beddome, 1862	Trimeresurus macrolepis
maculatus (Trimesurus) (sic) Gray, 1842	Tropidolaemus wagleri
makazayazaya (Trimeresurus) Takahashi, 1922	Ovophis monticola makazayazaya
makii (Trimeresurus) Klemmer, 1963	Trimeresurus stejnegeri formosensis
malabaricus (Trigonocephalus) Jerdon, 1854	Trimeresurus malabaricus
malcolmi (Trimeresurus) Loveridge, 1938	Trimeresurus sumatranus malcolomi
marajoensis (Bothrops) Hoge, 1966	Bothrops marajoensis
marchi (Bothrops) Barbour and Loveridge, 1929	Bothriechis aurifer marchi
marmorata (Cenchris) Boie, 1827	? Agkistrodon contortrix
mattogrossensis (Bothrops) Amaral, 1925	Bothrops neuwiedi mattogrossensis
medusa (Lachesis) Sternfield, 1920	Bothriopsis medusa
megaera (Coluber) Shaw, 1802	Bothrops atrox lanceolata
megaspilus (Trigonocephalus) Cope, 1859	Hypnale halys subspecies
melanurus (Trimeresurus) L. Müller, 1924	Porthidium melanurum
melli (Lachesis) Vogt, 1922	Trimeresurus jerdoni melli
meridionalis (Bothrops) Müller, 1885	Bothrops jararaca

meridionalis (*Trimeresurus*) Bourret, 1935	*Trimeresurus jerdoni meridionalis*
meridionalis (*Trimeresurus*) Bourret, 1935	*Ovophis monticola tonkinensis*
mexicanus (*Atropos*) Duméril, Bibron, and Duméril, 1854	*Porthidium mexicanum*
microphthalmus (*Bothrops*) Cope, 1872	*Bothrops microphthalma*
millardi (*Ancistrodon*) Wall, 1908	*Agkistrodon hypnale*
minasensis (*Bothrops*) Amaral, 1925	*Bothrops neuwiedi uruta*
mokasen (*Agkistrodon*) Beauvois, 1799	*Agkistrodon contortrix mokasen*
mokesin (*Cenchris*) Daudin, 1803	*Agkistrodon contortrix mokasen*
montanus (*Thanatos*) Posada Arango, 1889	? *Bothriopsis castelnaudi quadriscutata*
monticelli (*Lachesis*) Peracca, 1910	*Bothriopsis punctata*
monticola (*Ancistrodon*) Werner, 1922	*Agkistrodon monticola*
monticola (*Trimeresurus*) Günther, 1864	*Ovophis monticola monticola*
moojeni (*Bothrops*) Hoge, 1966	*Bothrops moojeni*
mucrosquamatus (*Trigonocephalus*) Cantor, 1839	*Trimeresurus mucrosquamatus*
mutabilis (*Trimeresurus*) Stoliczka, 1870	*Trimeresurus labialis*
mutus (*Crotalus*) Linnaeus, 1766	*Lachesis muta muta*

nasus (*Rhinocerophis*) Garman, 1881	*Bothrops ammodytoides*
nasutus (*Bothrops*) Bocourt, 1868	*Porthidium nasutum nasutum*
neelgherriensis (*Trigonocephalus*) Jerdon, 1854	*Trimeresurus strigatus*
neglecta (*Bothrops*) Amaral, 1923	*Bothrops pirajai*
neuwiedi (*Bothrops*) Wagler, 1824	*Bothrops Neuwiedi neuwiedi*
nigroadspersus (*Bothrops*) Steindachner, 1870	*Bothriechis schlegeli nigroadspersus*
nigromarginatus (*Trigonocephalus*) Kuhl, 1820	*Trimeresurus trigonocephalus*
nigroviridis (*Bothriechis*) Peters, 1860	*Bothriechis nigroviridis*
nitidus (*Lachesis*) Günther, 1859	*Bothriechis schlegeli schlegeli*
noctivaga (*Lachesis muta*) Hoge, 1966	*Lachesis muta rhombeata*
notata (*Bothriechis nummifera*) Fischer, 1880	*Porthidium mexicanum*
nummifer (*Atropos*) Rüppell, 1845	*Porthidium nummifer nummifer*
obscurus (*Trimeresurus*) Theobald, 1896	? *Trimeresurus purpureomaculatus purpureomaculatus*
occidentalis (*Trimeresurus*) Pope and Pope, 1933	*Trimeresurus occidentalis*
occiduus (*Bothrops nummifer*) Hoge, 1966	*Porthidium nummifer occiduum*
okinavenis (*Trimeresurus*) Boulenger, 1892	*Trimeresurus okinavensis*
oligolepis (*Lachesis bilineatus*) Werner, 1901	*Bothriopsis oligolepis*

olivacea (Megaera) Gray, 1842	Trimeresurus trigonocephalus
ophryomegas (Bothrops) Bocourt, 1868	Porthidium ophryomegas
orientalis (Trimeresurus) Schmidt, 1925	Ovophis monticola makazayazaya
ornata (Megaera) Gray, 1842	Trimeresurus flavomaculatus
pallasi (Echidna aspis) Merrem, 1820	? Hypnale halys
paramonovi (Ancistrodon halys) Nikolsky, 1931	Hypnale halys (subspecies)
paranaensis (Bothrops neuwiedi) Amaral, 1925	Bothrops neuwiedi paranaensis
patagonicus (Bothrops) F. Müller, 1885	Bothrops ammodytoides
patoquilla (Thanatos) Posada Arango, 1889	? Bothriechis nigroviridis
pauloensis (Bothrops neuwiedi) Amaral, 1925	Bothrops neuwiedi pauloensis
persicas (Ancistrodon halys) Rendahl, 1933	Hypnale halys persicas
peruvianus (Lachesis) Boulenger, 1903	Bothriopsis peruviana
pessoai (Bothrops) Prado, 1939	Porthidium hyoprorum
philippensis (Trimesurus) (sic) Gray, 1842	Tropidolaemus wagleri
piauhyensis (Bothrops neuwiedi) Amaral, 1925	Bothrops neuwiedi piauhyensis
picadoi (Trimeresurus nummifer) Dunn, 1939	Porthidium nummifer picadoi
picta (Lachesis) Tschudi, 1845	Bothrops picta
pictigaster (Agkistrodon mokeson) Gloyd and Conant, 1943	Agkistrodon contortrix pictigaster

olivacea (*Megaera*) Gray, 1842	*Trimeresurus trigonocephalus*
ophryomegas (*Bothrops*) Bocourt, 1868	*Porthidium ophryomegas*
orientalis (*Trimeresurus*) Schmidt, 1925	*Ovophis monticola makazayazaya*
ornata (*Megaera*) Gray, 1842	*Trimeresurus flavomaculatus*
pallasi (*Echidna aspis*) Merrem, 1820	? *Hypnale halys*
paramonovi (*Ancistrodon halys*) Nikolsky, 1931	*Hypnale halys* (subspecies)
paranaensis (*Bothrops neuwiedi*) Amaral, 1925	*Bothrops neuwiedi paranaensis*
patagonicus (*Bothrops*) F. Müller, 1885	*Bothrops ammodytoides*
patoquilla (*Thanatos*) Posada Arango, 1889	? *Bothriechis nigroviridis*
pauloensis (*Bothrops neuwiedi*) Amaral, 1925	*Bothrops neuwiedi pauloensis*
persicas (*Ancistrodon halys*) Rendahl, 1933	*Hypnale halys persicas*
peruvianus (*Lachesis*) Boulenger, 1903	*Bothriopsis peruviana*
pessoai (*Bothrops*) Prado, 1939	*Porthidium hyoprorum*
philippensis (*Trimesurus*) (*sic*) Gray, 1842	*Tropidolaemus wagleri*
piauhyensis (*Bothrops neuwiedi*) Amaral, 1925	*Bothrops neuwiedi piauhyensis*
picadoi (*Trimeresurus nummifer*) Dunn, 1939	*Porthidium nummifer picadoi*
picta (*Lachesis*) Tschudi, 1845	*Bothrops picta*
pictigaster (*Agkistrodon mokeson*) Gloyd and Conant, 1943	*Agkistrodon contortrix pictigaster*

pifanoi (*Bothrops*) Sandner Montilla, 1961	*Bothrops pifanoi*
pirajai (*Bothrops*) Amaral, 1923	*Bothrops pirajai*
piscivorus (*Crotalus*) Lacépède, 1789	*Agkistrodon piscivorus piscivorus*
pleuroxanthus (*Lachesis*) Boulenger, 1912	*Bothrops microphthalma microphthalma*
popei (*Agkistrodon strauchi*) Mell, 1931	*Hypnale monticola*
popeorum (*Trimeresurus*) Smith, 1937	*Trimeresurus popeorum*
porphyraceus (*Trimeresurus*) Blyth, 1860	*Trimeresurus purpureomaculatus purpureomaculatus*
pradoi (*Trimeresurus*) Hoge, 1947	*Trimeresurus pradoi*
praetextata (*Vipera*) Gravenhorst, 1832	? *Calloselasma rhodostoma*
proboscideus (*Bothriopsis*) Cope, 1876	*Porthidium nasutum nasutum*
pubescens (*Trigonocephalus*) Cope, 1869	*Bothrops neuwiedi pubescens*
pugnax (*Toxicophis*) Baird and Girard, 1853	*Agkistrodon piscivorus leucostomus*
pulcher (*Trigonocephalus*) Peters, 1862	*Bothrops pulchra*
punctatus (*Lachesis*) García, 1896	*Bothriopsis punctata*
punicea (*Cophias*) Boie, 1827	*Trimeresurus puniceus*
purpureomaculatus (*Trigonocephalus*) Gray, 1832	*Trimeresurus purpureomaculatus purpureomaculatus*

purpureus (*Trimesurus*) (*sic*) Gray, 1842	*Trimeresurus purpureomaculatus purpureomaculatus*
quadriscutatus (*Bothriopsis*) Peters, 1861	*Bothriopsis castelnaudi quadriscutata*
quadriscutatus (*Bothrops*) (*nec* Peters) Posada Arango, 1889	? *Bothrops xanthogrammus*
rhodostoma (*Trigonocephalus*) Boie, 1827	*Calloselasma rhodostoma*
rhombeata (*Lachesis*) Wied, 1825	*Lachesis muta rhombeata*
rhombifer (*Trigonocephalus*) Cuvier, 1817	*Lachesis muta muta*
rhomboatus (*Bothrops*) (*sic*) García, 1896	*Bothrops atrox atrox*
riograndensis (*Bothrops neuwiedi*) Amaral, 1925	*Bothrops neuwiedi pubescens*
riukiuanus (*Trimeresurus*) Hilgendorf, 1880	*Trimeresurus flavoviridis flavoviridis*
roedingeri (*Bothrops*) Mertens, 1942	*Bothrops roedingeri*
rowleyi (*Bothrops*) Bogert, 1968	*Bothrops aurifer aurifer*
rozei (*Bothrops*) Peters, 1968	*Porthidium lansbergi lansbergi*
sabini (*Bothrops*) Gray, 1842	*Bothrops atrox atrox*
sagittiformis (*Trigonocephalus*) Schinz, 1822	*Nomen dubium*
sanctaecrucis (*Bothrops*) Hoge, 1965	*Bothrops sanctaecrucis*
sandakanensis (*Bothrops*) Lidth de Jeude, 1893	*Trimeresurus puniceus*
savianus (*Trigonocephalus*) Filippi, 1848	*Nomen dubium*

schadenbergi (Trimeresurus) Fischer, 1885	*Trimeresurus flavomaculatus*
schlegeli (*Trigonocephalus*) Berthold, 1846	*Bothriechis schlegeli schlegeli*
schultzei (*Trimeresurus*) Griffin, 1909	*Trimeresurus schultzei*
scutigera (*Bothriechis*) Fischer, 1880	*Bothriopsis godmani godmani*
septentrionalis (*Bothrops atrox*) Müller, 1885	*Bothrops atrox atrox*
smaragdinus (*Bothrops bilineatus*) Hoge, 1966	*Bothriopsis bilineatus smaragdinus*
sphenophrys (*Bothrops*) Smith, 1959	*Ophryacus undulatus*
steinegeri (*Ancistrodon halys*) Rendahl, 1933	*Hypnale halys* (subspecies)
steinegeri (*Trimeresurus*) Schmidt, 1925	*Trimeresurus steinegeri steinegeri*
stenophrys (*Lachesis*) Cope, 1876	*Lachesis muta stenophrys*
strauchi (*Ancistrodon*) Bedriaga, 1912	*Hypnale strauchi*
strigatus (*Trimesurus*) Gray, 1842	*Trimeresurus strigatus*
subannulatus (*Trimesurus*) (sic) Gray, 1842	*Tropidolaemus wagleri*
subscutatus (*Bothrops*) Gray, 1842	*Bothrops atrox atrox*
sumatranus (*Coluber*) Raffles, 1822	*Trimeresurus sumatranus*
sumatrenis (*Trigonocephalus wagleri*) Gray, 1849	*Tropidolaemus wagleri*

supraciliaris (*Bothrops* *schlegeli*) Taylor, 1954	*Bothriechis* *schlegeli* *nigroadspersus*
surucucu (*Bothrops*) Wagler, 1824	*Lachesis* *muta* *muta*
sutus (*Thanatos*) Posada Arango, 1889	*Porthidium* *nasutum* *sutum*
taeniatus (*Bothrops*) Wagler, 1824	*Bothrops* *atrox* *atrox*
takarensis (*Trimeresurus*) Nagai, 1928	*Trimeresurus* *flavoviridis* *takarensis*
taylori (*Agkistrodon* *bilineatus*) Burger and Robertson, 1951	*Agkistrodon* *bilineatus* *taylori*
tessellatus (*Bothrops*) Wagler, 1824	*Bothrops* *atrox* *atrox*
tibetanus (*Agkistrodon*) Barbour, 1912	*Hypnale* *strauchi*
tigrina (*Vipera*) (*nec* Lacépède) Lichtenstein	? *Bothrops* *neuwiedi*
tigrinus (*Coluber*) Lacépède, 1789	*Bothrops* *atrox* *atrox*
tinkhami (*Trimeresurus* *flavoviridis*) Gloyd, 1955	*Trimeresurus* *flavoviridis* *tinkhami*
tisiphone (*Coluber*) Shaw, 1802	? *Agkistrodon* *piscivorus* *piscivorus*
tonkinensis (*Trimeresurus*) Bourret, 1934	*Trimeresurus* *monticola* *tonkinensis*
torvus (*Thanatos*) Posada Arango, 1889	*Bothriechis* *schlegeli* *schlegeli*
trianguligera (*Bothriechis*) Fischer, 1883	*Porthidium* *godmani* *godmani*

triangulum (Cophias) Boie, 1827	Bothrops jararaca
trigonocephala (Vipera) Latreille, 1801	Trimeresurus trigonocephala
undulatus (Trigonocephalus) Jan, 1859	Ophryacus undulatus
unicolor (Trigonocephalus bilineatus) Jan, 1859	Bothriopsis bilineata bilineata
urutu (Bothrops) Lacerda, 1884	Bothrops neuwiedii urutu
ussuriensis (Ancistrodon Blomhoffi) Amelianov, 1929	Hypnale halys brevicaudus
variegata (Megaera) Gray, 1842	Trimeresurus flavomaculatus
varietas (Trigonocephalus atrox) Rüppell, 1845	Bothrops atrox atrox
venezuelae (Bothrops) Sandner Montilla, 1961	Bothrops pifanoi
venezuelensis (Bothrops lansbergi) Roze, 1959	Bothrops lansbergi lansbergi
veraecrucis (Bothrops nummifer) Burger, 1949	Porthidium nummifer nummifer
verrucosus (Bothrops) Posada Arango, 1909	Lachesis muta muta
vezuelenzi (Bothrops neuvoiedi) (sic) Briceno Rossi, 1934	Nomen dubium
viridis (Coluber) Beckstein, 1802	Trimeresurus gramineus
wagleri (Cophias) Boie, 1827	Tropidolaemus wagleri
wardi (Trigonocephalus) Jerdon, 1854	Trimeresurus malabaricus
weigeli (Vipera) Daudin, 1803	? Bothrops atrox atrox
wettsteini (Lachesis) Werner, 1923	Nomen dubium

xanthogrammus (Trigonocephalus) Cope, 1868	Bothrops xanthogramma
xanthomelas (Trimeresurus) Günther, 1889	Trimeresurus jerdoni xanthomelas
yucatanicus (Trimeresurus) Smith, 1941	Porthidium lansbergi yucatanicum
yunannensis (Trimeresurus) Schmidt, 1927	Trimeresurus stejnegeri yunannensis
zara (Trigonocephalus) Gray, 1849	Hypnale hypnale

TAXONOMIC CHARACTERS

The Egg Laying Habit

In a number of reptilian lines, the egg laying habit (ovipary) is modified. Fertilized eggs are retained in the oviduct so that hatching is simultaneous with laying. Initially the habit of retaining eggs through most or all of incubation may be a device for protecting the eggs or better regulating their temperature. Circulatory exchange between mother and embryo is developed to varying extents, approaching in some reptiles the efficiency of fetal nourishment of placental mammals. In transitional stages, the distinction between ovovipary (passive retention of eggs) and vivipary (maternal nourishment of developing embryos) is not easy to make nor is such a distinction necessary for the present discussion. I will distinguish all kinds of live-bearers (whether ovoviparous or viviparous) from egg layers. Although most viperoid snakes bear live young, an interesting assortment of vipers and pitvipers lay eggs. The superfamily comprises approximately 6 genera that are entirely oviparous, 5 genera that include some oviparous species, 10 genera with all live bearing species, and 3 genera for which information is lacking. Fitch (1970:185) treated both habits in a balanced account of reproductive cycles. For present taxonomic application, attention is directed principally to the occurrence of ovipary.

Viperidae.—In the Atractaspinae, Causus, and Atractaspis are oviparous, and information on Azemiops is lacking. In the Viperinae, certain species of Vipera, Pseudocerastes and Echis are oviparous. Pseudocerastes persicus fieldi is oviparous, whereas information is lacking on two other forms of Pseudocerastes. Echis colorata is oviparous, whereas E. carinatus has live young. Vipera xanthina palaestinae is oviparous, whereas V. xanthina raddei has live young, and V. russeli, which usually produces live young, occasionally lays fertile eggs. Most other species of Vipera (Fitch, 1970:188, cited information for 4 such species) and all species of Bitis and Atheris have live young.

Crotalidae.—The distribution of ovipary in pitvipers is less orderly. In Asia probably all species of Ovophis and Calloselasma, but only a small portion of the species of Hypnale and Trimeresurus, lay eggs. Hypnale is the most primitive genus of the family, whereas the two species of Calloselasma (C. acutus and C. rhodostoma) that lay eggs are relatively advanced. Ovophis is primitive among Asiatic scalesnouts, but the species of Trimeresurus that lay eggs (T. mucrosquamatus and T. flavoviridis) are no more primitive than close relatives that bear live young. The one oviparous American pitviper, the Bushmaster, Lachesis muta, is a giant with many specializations of scutellation. Eight other American genera of pitvipers are composed of snakes that bear live young.

Size

Difference in length and girth are apparent to the most casual observers of pitvipers. These are matters of great interest and importance because the gravity of the bite depends on the size of the offending snake (both the length of the fangs and the quantity of venom injected increase with size). Although also potentially of taxonomic value, size and proportions are difficult to use because of the complexity of influencing factors. Genetic potentialities, ontogeny, sexual dimorphism, and general and local environmental factors (food supply, length of growing season, _etc_.) are obvious variables.

In considering length in rattlesnakes, Klauber (1956:141, table 4:1) used six different measures for interspecific comparison: (1) smallest measured specimen, (2) average size at birth, (3) smallest gravid female, (4) large adult male, (5) largest measured specimen, and (6) maximum report believed reliable. Effective consideration of these features is possible with the extensive information available for rattlesnakes, whereas paucity (often absolute lack) of critical information limits present possibilities with other pitvipers. The importance of field studies of growth for intelligent appraisal of size is demonstrated by extreme errors made in past attempts to appraise age-size groups of reptiles solely on the basis of measurements of preserved specimens.

With these limitations, comparison of maximum lengths of the different species of rattleless pitvipers seems to be the only effective approach. The figures for maximum length are sufficient to suggest that many differences exist but not to verify or specify the amount of difference. The measurements are given in millimeters, which may be converted to inches with all justified accuracy by multiplication by 0.04. As examples and as a basis for consideration of the largest representatives, maximum lengths of snakes of the genera *Bothrops*, *Lachesis*, and *Porthidium* are given in tables 3 and 4. They are measurements of females except those for *Bothrops insularis*, *B. neuwiedi*, *Porthidium godmani*, and *P. godmani*, which are males. Figures for *Porthidium* are from my measurements of preserved specimens. Those for *Bothrops* and *Lachesis* are published records based variously on fresh or preserved specimens. These snakes show the full range for maximum lengths of American rattleless pitvipers, incompassing ranges of maximum lengths for snakes of the genera *Agkistrodon*, *Bothriechis*, *Bothriopsis*, and *Ophryacus* (not itemized here).

General impressions of size furnished by tables 3 and 4 are supported by the trends in size of specimens that I have seen. The adult lengths of American rattleless pitvipers (except the Bushmaster) vary from under two feet (600 mm) in some species to well over seven feet (about 2 m) in others. The entire range is found in species of *Bothrops* (*sensu stricto*) and is practically the same as that noted in rattlesnakes (Klauber, 1956:140), the largest kinds of which will be cited here for comparison. The maximum recorded size of two species of *Bothrops* and two species of *Crotalus* exceed two meters (about seven feet). These, with their maximum lengths, are *Crotalus adamanteus*, 2440 mm; *Bothrops jararacussu*, 2200 mm; *Crotalus atrox*, 2130 mm; *Bothrops atrox*, 2100 mm. Exceeding these formidable snakes is the bushmaster, *Lachesis muta*, which is the longest viperoid snake, reaching 2.6 meters (nine feet) and possibly 4.2 meters (14 feet).

TABLE 3. Maximum Total Lengths (mm.) of Lachesis (last two forms) and Porthidium. Names are trivial. (Obtain complete names in Table 2.)

barbouri	510	occiduum	753
dunni	537	ophryomegas	665
godmani	641	picadoi	1202
hyoprorum	785	sutum	441
lansbergi	601	vulcanicum	696
melanurum	516	yucatanicum	553
mexicanum	934		
nasutum	506	muta	2600
nummifer	680	stenophrys	2100

TABLE 4. Maximum Total Lengths (mm.) of Bothrops. Names are trivial. (Obtain complete names in Table 2.)

alternata	1690	itapetiningae	400
ammodytoides	637	jararaca	1600
andiana	605	jararacussu	2200
asper	2020	lanceolata	2100
atrox	1900	lojana	610
barnetti	713	microphthalma	941
brazili	1158	neuwiedi	948
caribbaea	972	picta	786
colombiana	1360	pirajai	1130
cotiara	980	pradoi	1190
erythromelas	540	pulchra	763
fonsecai	872	roentingeri	328
iglesiasi	660	xanthogramma	1550
insularis	1000		

Four other species of *Bothrops* reach maximum sizes far exceeding a meter. Ranging in size from 1.7 to 1.4 meters from largest to smallest, they are *B. alternata*, *B. jararaca*, *B. xanthogramma*, and *B. microphthalma*. Most of the other *Bothrops* and all species of *Bothriopsis*, *Bothriechis*, *Porthidium*, and *Ophryacus* have maximum lengths between 1.2 meters (4 feet) and 0.5 meters (20 inches). The smallest include *Bothrops erythromelas*, *Porthidium melanurum*, and *P. barbouri*, all of which reach lengths of about 0.5 meters; *B. itapetiningae*, 0.4 meters; and *B. roentingeri*, 0.3 meters. The last five species are relatively rare and may be found to exceed presently recorded sizes. Consider, for example, the smallest of the above species, *B. roentingeri*, known from only two specimens. Its closest relative, *B. ammodytoides*, reaches 0.6 instead of 0.3 meters.

Separate tabulation of maximum lengths of males and females (not presented here) suggests sexual dimorphism with females usually exceeding males. With the possible exception of several species, noted parenthetically after the genus, females are longer than males in *Bothrops* (possible exceptions, *B. insularis* and *B. neuwiedi*), *Lachesis*, *Bothriechis*, *Bothriopsis*, *Porthidium* (possible exceptions, *P. nummifer* and *P. godmani*), and *Ophryacus*. Data are meager and sampling so varied that detailed statistical consideration is unwarranted.

Tail

Lacking paired muscular appendages, snakes use both head and tail for many actions performed by legs in other terrestrial vertebrates. The diverse modifications of the tail of pitvipers are evidence of considerable selection pressure and suggest that the extent of use of the tail is probably not appreciated.

Terrestrial pitvipers.—The tail of most terrestrial pitvipers is a short tapering structure slightly longer and larger anteriorly in the male than in the female. Its shape, relative length, color, and scutellation are important variables. Data obtained in the present study add nothing to the detailed study of relative tail length by Klauber (1943). The color of the tail may be different from that of the body. Brightly colored tails are often (but apparently not in every instance) used by juvenile pitvipers to lure prey within reach (Burger and Smith, 1950; Neill, 1960). Much of the interesting variation in terrestrial pitvipers involves the subcaudals and the terminal caudal scute, which are described in special sections below.

Tree vipers.—Bothriechis, Bothriopsis, Ophryacus, and Tropidolaemus are arboreal, as are most species of Trimeresurus, one peculiar species of Bothrops (B. insularis), and young of some other species of Bothrops. In arboreal pitvipers the body is compressed and the tail is prehensile. Compression of the body (and the base of the tail) is an adaptation for vertical rigidity in accord with the principle of the I-Beam. The distal third or half of the tail is a slender section of nearly uniform girth, which even in preserved specimens is usually curved sharply to form a hook or a tight coil. In Bothriechis this portion of the tail has the lower two rows of dorsal scales strongly keeled. These, like the heavily keeled lateral gular scales of Tropidolaemus, may be slip-proof grasping devices.

The terminal caudal scale may be moderately developed and the subcaudals divided (Trimeresurus, Ophryacus and Bothriopsis), or the terminal caudal scute much reduced and the subcaudals entire (Bothriechis). As mentioned above, the last group also has strongly keeled lateral scales on the tail. Other arboreal pitvipers have the lower lateral scale rows progressively more weakly keeled, like those of terrestrial pitvipers.

In the genus Trimeresurus, T. jerdoni, T. mucrosquamatus, T. kaulbacki, and perhaps some other related species do not have prehensile tails. Distinctly prehensile tails characterize most other species of Trimeresurus, including all known species of the T. stejnegeri, T. puniceus, T. purpureomaculatus, T. sumatranus, and T. albolabris groups (as defined by Maslin, 1942).

Among vipers, species of Atheris are arboreal, with compressed body and prehensile tail. These snakes are generally similar to pitvipers of the genus Bothriechis and of the Trimeresurus albolabris and T. stejnegeri groups. The lack of facial pit and detailed differences in the cephalic scutellation are significant; otherwise Atheris differs no more from these pitvipers than do the different genera of pitvipers from one another. It is significant to note this great similarity of snakes of different families when evaluating the results of parallel evolution toward arboreal existence in different lines of pitvipers.

Tail spine.—The last bone of the pitviper tail is a short rod of several fused vertebrae, encased in a sheath of fused scales. The tail spine of rattleless pitvipers was studied in some detail 80 years ago (Garman, 1889) as the precursor of the rattle of rattlesnakes. Although large tail spines are suggestive and the bushmaster, with the largest tail spine, invites comparison with the rattle, these tail spines are all much smaller than rattles and occur in snakes with divided caudals, whereas rattlesnakes have entire caudals.

Asiatic Hypnale (H. hypnale and H. nepa) have the simplest and probably the most primitive tail spine. It is a short cone ending in a small, rounded tip that is turned slightly downward. Subtending scales number 4 to 6. Sutures and shielding scales are lacking.

Asiatic Calloselasma (C. acuta and C. rhodostoma) have the end of the tail laterally compressed, nearly twice as high as wide. Scales in the row adjacent to the subcaudals are columnar structures, over twice as high as long. I cannot guess the significance of the laterally compressed tail tip.

Agkistrodon, comprising three American species, have large tail tips. The caudal spine is long, large in circumference, equivalent in length to 4 to 6 subcaudals, and has 6 to 8 subtending scales. A pair of well-developed capping scales extend over the dorsal base of the tail spine. The tip of the spine is directed posterior or slightly upturned in A. piscivorus, is directed slightly down in A. bilineatus and is turned sharply downward in A. contortrix.

In Porthidium the tail spine has a rounded or sharp tip and lateral sutures. In species of the godmani and lansbergi groups the spine is equivalent in length to 3 or 4 subcaudals whereas in the nummifer group it is equivalent to 5 or 6 subcaudals.

The tail spine of Bothriopsis is moderately long, equivalent to 3 to 6 subcaudals, and swollen near the end. The tip may be blunt (B. punctatus) or sharp and upturned (B. bilineatus). Subtending scales number 4 or 5.

The tail spine of tree vipers of the genus Bothriechis is very small, scarcely larger than adjacent scales, almost hidden in dorsal view, and shorter ventrally than two adjacent subcaudals.

The tail spine of species of Bothrops (sensu stricto) is relatively long, equivalent in length to 4 to 7 subcaudals. Those of B. alternatus and B. ammodytoides are swollen near the end and blunt tipped. Those of B. neuwiedi and B. cotiara have slender, tapering tips. That of B. barnetti has a blunt, downturned tip. That of B. itapetiningae has a pointed upturned tip.

Sistrurus and Crotalus.—The rattle is the most elaborate specialization of the pitviper tail. Concerning its origin Klauber (1956:135) wrote "...We visualize, first, a modification in the conical scale terminating the tail of some early crotalid, whereby successive sheddings were retained. Regardless of the mechanical details of how the earlier cones slipped backward in relation to the later ones, yet remained attached, it is evident that the first rattles were formed as small cones on a sharp tailed snake. Hence small rattles, and a relatively long tail are to be considered primitive. With the long tail, the primitive rattler also had more subcaudal than most of its descendants of today. Thus there are strong indications that the ancestral rattler had some of the characters of the existing Sistrurus miliarius, although it need not have been, and probably was not, so small a snake. For the theory of the evolution of the rattle that involves the protection of the snake from being trampled by primitive hoofed animals requires a more dangerous snake than miliarius."

Subcaudals occur in three different arrangements. All except the tail spine are divided in a majority of genera and species. Characteristically an occasional individual has a few entire subcaudals, usually on the anterior half of the tail. The divided condition is characteristic of Hypnale, Trimeresurus, Ophryacus, Tropidolaemus, Bothrops, the bilineatus and punctatus groups of Bothriopsis and Calloselasma rhodostoma. The second subcaudal arrangement is entire subcaudals, with subcaudals in a single row like ventral scutes. Occasional individuals have scattered subcaudals divided or a row of several divided subcaudals (as ventrals are similarly infrequently divided). The entire condition occurs in Porthidium, Bothriechis, Sistrurus, and Crotalus, all of the Western Hemisphere. A third arrangement mixes divided and entire subcaudals with entire subcaudals predominate anterior to midtail and divided subcaudals predominate posterior to midtail. However, the pattern of assortment is just as characteristic as former arrangements. The assortment of anterior entire subcaudals and divided posterior subcaudals occurs in Agkistrodon, Ovophis, the castelnaudi group of Bothriopsis, and Calloselasma acuta.

Apical Scale Pits

The dorsal scales of many snakes have minute depressions, apical scale pits, situated near the posterior tips of the scales. The depressions are the orifices of skin glands which have no known function. Klauber (1956:322) commented: "Some have thought they might have a connection with skin shedding; others have associated them with scent in sex recognition or some tactile function."

Reinhardt (1961:127) presented data on the variation of the apical scale pits in 191 species of snakes. Elapids and hydrophids have no pits, whereas colubrids are quite varied in this respect: some lack them, others have one pit, and others a pair of pits in each dorsal scale. The occurrence of the first two conditions in relatively advanced colubrids, coupled with the absence of pits in elapids and hydrophids (obvious derivatives of colubrids) suggests that in these snakes the paired condition is primitive and the pitless and single-pitted conditions are derived from the first condition. Duellman (1958:126) discussed the number of apical pits as one of the important distinctions between <u>Leptodeira</u> and <u>Hypsiglena</u>. Malnate (1960) made extensive use of this feature in dividing the old genus <u>Natrix</u> (<u>sensu lata</u>) into its constituent genera.

The distribution of the pitless and paired-pit condition among solenoglyphous snakes is instructive. Of six viperids examined by Reinhardt (<u>loc</u>. <u>cit</u>.) all have paired apical scale pits except the highly specialized Saw-Scaled Viper, <u>Echis carinatus</u>. Of 34 pitvipers examined in the present study over half lack apical scale pits.

Agkistrodontinae.—Most species have paired apical pits. In *Hypnale halys* and *H. hypnale* the pits are much less in diameter than the distance between a pit and the keel. In *Agkistrodon piscivorus*, *A. bilineatus*, *A. contortrix*, and *Calloselasma acutus*, the pits are greater in diameter than the distance to the keel. Pits are lacking in *Calloselasma rhodostoma*.

Porthidium.—Small paired pits, like those of *Hypnale halys* and *H. hypnale*, are present in *Porthidium barbouri*, *P. godmani*, and *P. melanurum*. Apical pits are lacking in *P. nasuta* and *P. nummifer*.

Sistrurus and *Crotalus*.—*S. ravus* and *S. catenatus* have small paired pits. Klauber (1956:322) implied that they are present in all rattlers for he wrote "...in the rattlers they are only faintly evident as a pair of minute indentations at the posterior tips of some of the dorsal scales. They are more apparent toward the tail or on the tail. A few rattlesnakes, including the neotropical rattler (*C. durissus*), the speckled rattler (*C. mitchelli*), the massasauga (*C. catenatus*), and their subspecies, have more prominent pits than others. In some forms the scale pits are accentuated by dots of color; this is particularly true of the Aruba Island rattler (*C. unicolor*)."

Lachesis and *Bothrops*.—Prominent paired apical pits occur in *L. muta* and in certain species of *Bothrops* — *B. picta*, *B. neuwiedi*, and *B. alternatus*. None is evident in some species of *Bothrops*, including *B. atrox* and *B. jararaca*.

Tropidolaemus, *Trimeresurus*, *Bothriechis*, *Bothriopsis*, and *Ophryacus*.—Snakes of these genera seem to lack apical pits. Certainly that is true of the following species that have been examined: *Tropidolaemus wagleri*, *Trimeresurus gramineus*, *T. puniceus*, *T. flavomaculatus*, *T. annamallensis*, *Bothriechis nigroviridis*, *B. lateralis*, *B. schlegeli*, *Bothriopsis bilineatas*, *B. medusa*, *B. punctatus*, *B. oligolepis*, and *Ophryacus undulatus*. The lack of apical pits in all of the arboreal pitvipers that have been examined lends indirect support to the hypothesis that the glands are associated with scent in sex recognition. Trailing by scent as practiced by many terrestrial snakes is difficult or impossible in bushes or trees.

Microsculpturing

The early description by Leydig (1873:753) of the distinctive microsculpturing of the dorsal scales of snakes includes observations of several vipers. The only more recent investigations are those of Picado (1931a and 1935) concerning Costa Rican pitvipers. He found microscopic features that were constant within the species and quite different between the species that he studied, namely *Lachesis muta*, *Bothrops atrox*, *Bothriechis schlegeli*, *B. lateralis*, *B. nigroviridis*, *Porthidium nummifer*, *P. lansbergi*, *P. nasutum*, and *Crotalus durissus*. Colubrids and elapids that Picado examined lacked distinctive epidermal ornamentation, whereas the single hydrophid that was examined, *Pelamis platurus*, had microsculptured scales like the above pitvipers. This feature deserves thorough study among the solenoglyphs.

Loreal Pit

Pitvipers are characterized by and named for presence of a loreal or facial pit on each side of the head. The loreal pit is situated between the eye and nostril. Actually each pit is a pair of cavities separated by a membrane. The anterolateral cavity opens conspicuously to the exterior; the posteromedial cavity is adjacent internally and posteriorly to the anterolateral cavity. The thin pit membrane that separates the two cavities is evident through the orifice of the anterolateral cavity. The inner wall of the posteromedial cavity fills the entire hollowed-out portion of the maxillary bone; this same cavity has a small opening to the outside at the anterior border of the eye. The loreal pit was described in detail by Lynn (1931) and Noble and Schmidt (1937). Klauber (1956:369) gave an excellent summary of knowledge about it.

The pits are thermoreceptors of great sensitivity. By providing a mechanism for sensing very slight differences in temperature, the pits greatly improve the ability to strike endothermal prey. This function was first elucidated by Noble and Schmidt (1937). Neurophysiological investigations of the pit by Bullock and Cowles (1952) have given a more precise idea of its function. Evidence from the latter authors seems to discount the suggestion of Block (1950: 284) that this organ works like a pneumatic radiant-energy detector. Instead Bullock and Cowles favor the hypothesis that detection is by specialized molecules activated by energy absorbed as in the eye. An air-to-air rocket used by the U.S. Air Force is called the Sidewinder, because it is aimed by a detection device similar to the pitviper facial pit.

The labial pits of some boids and the supranasal sacs of some viperids have been compared to loreal pits. The first are thermoreceptors of a simpler, less sensitive sort than loreal pits. The function of the supranasal sacs is unknown, although probably sensory. Principally on the basis of their different structure and enervation, Lynn (1935) concluded that none of the three organs are homologous.

The exact position and shape of the external opening to the loreal pit varies somewhat in different pitvipers. Some differences in these respects noted late in the present study have not been as thoroughly studied as they deserve. For one thing the groove that runs from the loreal pit to the orbit is usually more or less covered by the edges of adjoining scales but it is widely open in some species, for example in Hypnale strauchi and Trimeresurus flavomaculatus. The opening of the inner chamber, near the front of the eye, may differ in some details. Smith (1943:478) commented "In the Asiatic species of Trimeresurus the opening is within the orbital margin, and can be seen in preserved specimens as a comparatively large aperture by pressing back the anterior surface of the eyeball. In Ancistrodon the opening is slightly more external and may be on the rim of orbit or even just external to it. According to Lynn this opening is surrounded by a sphincter muscle and is capable of considerable dilatation, but is usually found to be tightly closed. Such is not my experience with the Asiatic species of Trimeresurus but it is correct for the American species of that genus [Bothrops, etc.] which I have examined."

There is considerable variation in the position of the pit relative to an imaginary line projected from the ventral edge of the eye to the ventral rim of the nostril, henceforth termed the naso-ocular line.

The data suggest the following tentative conclusions:

(1) A pit very nearly centered on the naso-ocular line is primitive among pitvipers, occurring in primitive (and some advanced) species of Hypnale, Porthidium, Bothriopsis, Trimeresurus, and Bothrops.

(2) The pit tends to be more ventral in most advanced terrestrial groups. Accordingly most of the pit is below the line in Lachesis muta, in Calloselasma rhodostoma, in Porthidium nummifer, and in most species of Bothrops and Crotalus.

(3) The pit tends to be more dorsal in many advanced arboreal groups. Tropidolaemus wagleri has the pit entirely above the naso-ocular line. In Bothriechis schlegeli, Ophryacus undulatus, and several Trimeresurus, most of the pit is above the line.

(4) Exceptions to the above generalization are evident even with the present limited data and cannot be accounted for by any explanation apparent to me. For example, the rattlesnake, Crotalus intermedius, has a pit entirely above the naso-ocular line, whereas the arboreal Trimeresurus cornutus has the pit entirely below the line.

These comments are based on examination of about 40 species, the results of which may be summarized as follows:

Agkistrodon, *Calloselasma*, and *Hypnale*.—In most species of *Hypnale* (*H. halys*, *H. himalayanus*, and *H. strauchi*), the pit is centered, or very nearly centered, on the line connecting the lower borders of the eye and the nostril. In *Agkistrodon* (*A. contortrix*, *A. piscivorus* and *A. bilineatus*) and in *Calloselasma acutus* the pit is lower on the side, although the upper part of the pit intercepts the naso-ocular line. In *C. rhodostoma*, the pit is entirely below the naso-ocular line.

Porthidium and *Bothriechis*.—In members of the *godmani* and *lansbergi* groups of *Porthidium* the loreal pit is centered on the naso-ocular line. In members of the *nummifer* group it is shifted ventral to a position below the line. In most species of *Bothriechis* the pit is centered on the line or displaced slightly ventral, but in the advanced species *B. schlegeli* most of the pit is above the line.

Ophryacus and *Bothriopsis*.—In *Ophryacus undulatus* the ventral portion of the pit is crossed by the naso-ocular line. In *Bothriopsis bilineatus* the pit is centered on the line.

Ovophis, *Tropidolaemus*, and *Trimeresurus*.—In *Ovophis monticola* the pit is entirely below the naso-ocular line. In *Tropidolaemus wagleri* the pit is entirely above the naso-ocular line. This condition is approached by some arboreal species of *Trimeresurus* (*T. gramineus*, *T. erythrurus*) that have more of the pit above than below the naso-ocular line but most species of *Trimeresurus* have the pit centered on the line (*T. stejnegeri*, *T. trigonocephalus*, *T. gracilis*) or contacting but more or less below the line (*T. flavoviridis*, *T. elegans*, *T. mucrosquamatus*, *T. jerdoni*, and *T. puniceus*). Only *T. cornutus* has the pit entirely above the naso-ocular line.

Bothrops.—In certain species of *Bothrops* (*B. pictus* and *B. alternatus*) the loreal pit is centered on, or a short distance below and in contact with, the naso-ocular line. In other (probably the majority of) species the pit is entirely or nearly all below the naso-ocular line. Such is the case in *B. atrox*, *B. jararaca*, *B. jararacussu*, and *B. cotiara*.

Nasal Pore

Maslin (1942:18) called attention to the value of the nasal pore as a taxonomic character in pitvipers. This structure is a minute pit in the nasal pad, on the posterior margin of the nostril. The pit opens into a duct leading to the lateral nasal gland, the function of which is unknown. The pore, duct, and gland vary in size and shape in different snakes. Kathariner (1900:415) and Radovanovic (1935:321) in their anatomical investigations of the nasal passage of snakes described these structures.

Maslin (*loc. cit.*) found nasal pores in 24 species of *Trimeresurus* and illustrated some of the variations in their shape and position. He did not find nasal pores in *Tropidolaemus wagleri* and *T. philippenensis* nor in a number of species of *Bothrops* and related American pitvipers.

He concluded that the presence of nasal pores is a significant taxonomic character. Although his observations regarding Trimeresurus have proved valid, those on Tropidolaemus and Bothrops have been supplemented by later investigations.

Soon after publication of Maslin's observation, Malcolm Smith (1942) suggested that this feature is of doubtful taxonomic importance as it is universally present in snakes.

The truth lies somewhere between the opposed conclusions of Maslin and Smith. Nasal pits are more widespread among pitvipers than Maslin at first recognized but they are not universally present among snakes as Smith thought. Kathariner (loc. cit.) could find no trace of nasal pores in a sea snake, Pelamis bicolor. In his unpublished thesis Maslin observed that the nasal pore is present in Tropidolaemus wagleri although situated differently than in Trimeresurus and that nasal pores are absent in Crotalus.

On the basis of a hurried survey of representative pitvipers, the value of the position of the pit as a generic character seems to be assured, although full evaluation of its evolutionary changes must await more detailed investigation. Brief description of the differences follows.

Trimeresurus and Ovophis.—A conspicuous nasal pore is situated close to the external margin of the nasal pad which slopes gradually inward.

Lachesis.—A conspicuous nasal pore is situated at the internal margin of the nasal pad.

Agkistrodon, Bothrops, Bothriechis, Bothriopsis, Calloselasma, Hypnale, Ophryacus, and Porthidium.—The nasal pore is situated close to the inner edge of the nasal pad, which slopes abruptly inward. The pore is as large as in Trimeresurus but is less conspicuous because of its position deep in the nostril. Under some conditions of preservation the pore is difficult to find. Hoge's (1953:15) report that no nasal pore occurs in Bothrops brazili is regarded with skepticism.

Sistrurus and Crotalus.—No nasal pore is evident.

Hemipenis

Since the pioneer work of Cope (1894b) the paired male intromittent organs of lizards and snakes have been used in taxonomy. The guide by Dowling and Savage (1960) gives an excellent general description of the squamate hemipenis and an indication of the features that are useful in classification.

The viperoid hemipenis is a divided organ with a bifurcate sulcus spermaticus and with diversely differentiated ornamentation of spines, calyces, and less often, flounces or papillae. It varies in length, in the extent of division, and in shape.

Although Cope (1894b), Dunn (1928a), and Bogert (1940) have used hemipenial characters to distinguish subfamilies and genera of colubrid snakes, not much effective use has been made of them to distinguish genera of vipers or pitvipers. As a matter of fact, most pitviper genera cannot be distinguished by this structure. The hemipenis furnishes evidence for distinguishing species and small phylogenetic lines (Pope and Pope, 1933). Differences between the different phylogenetic lines and even between some closely related species in large genera like Trimeresurus or Crotalus are greater than the differences between genera.

Because I have not had many ideal preparations of hemipenes and because in American pitvipers the hemipenis is less valuable than many external features, I have not been exhaustive in gathering data on this feature. Information is summarized in definitions of genera.

Even with fragmentary data several phylogenetic trends may be hypothesized: (1) deeper division of the organ in advanced representatives, (2) modification of the spines into papillae in several phylogenetic lines, (3) occasional modification of simple calyces into spinulate calyces or into flounces, and (4) frequent increase in proportionate size of the differentiated distal (calyculate or flounded) part of the hemipenis. I feel certain that other trends could be revealed if good preparations of most species were available.

Many primitive hinge-fanged snakes have hemipenes that are bifurcate for about half their length and that are armed with spines proximally and calyces distally. Such is the case for the following: the viper Azemiops feae, a number of Asiatic species of Hypnale and Calloselasma (C. acutus, H. halys, H. himalayanus, H. monticola, and H. strauchi), several species of Trimeresurus (mucrosquamatus and stejnegeri), all species of Bothriechis and Porthidium that have been examined, Bothriopsis castelnaudi, and Lachesis muta. In the above forms the calyculate end of each lobe of the hemipenis comprises 0.15 to 0.25 of the total length of the hemipenis.

The hemipenes of Ovophis monticola and Ophryacus undulatus are much like those described in the preceding paragraph but are bifurcate for about 0.6 or 0.7 of their length. That of Tropidolaemus wagleri is of an advanced type, spinous to its extreme tip and lacks calyces.

Most vipers have deeply cleft hemipenes that are spinulate proximally and calyculate distally. The hemipenis of Vipera berus has only spines.

Certain species of Hypnale and Calloselasma are mentioned above. Three species of Hypnale and all of the species of Agkistrodon (sensu stricto) have deeply divided hemipenes with diverse specializations in ornamentation: spinulate calyces, flounces, or papillae. For example, although the American species comprise a relatively compact group (Fitch, 1960:114), the distal part of the hemipenis is calyculate in A. bilineatus, calyculate with densely spinulate ridges in A. contortrix, and predominantly flounced in A. piscivorus.

Among predominantly South American pitvipers a phylogenetic sequence can be hypothesized:

1. The half divided hemipenis of Bothriopsis.

2. The deeply divided hemipenis with small calyculate apex of Bothrops of the neuwiedi group.

3. The deeply divided hemipenis with large calyculate apex of Bothrops of the atrox group.

Data are too meager to substantiate this arrangement, much less to elaborate more detailed analyses of changes in the hemipenes of the other pitvipers.

Cranium

Keys to pitviper skulls were presented by W. Peters (1862:670) and Ruiz (1951:109) and many details of cranial osteology were treated by Brattstrom (1964:189). Only points of particular value can be considered here. Peters and Ruiz (supra cit.) found that the pterygo-palato-maxillary arch varied significantly. Shape of the palatine, shape of the maxillary cavity, posterior extent of teeth on the pterygoid, proportionate length of ectopterygoid and posterior part of pterygoid are significant variables.

It is interesting to note that on the basis of craniological features Brattstrom (1964:229) distinguished Trimeresurus (here Tropidolaemus) wagleri from other species of Trimeresurus and Bothrops (here Porthidium) nummifer and Bothrops (here Bothriechis) schlegeli from South American species of Bothrops. He suggested subgenera. In contrast I recognize distinct genera since otherwise certain genera are distinctly polyphyletic groupings. The discussion of generic status explains my decision.

Hyobranchium

Phylogenetic significance has been seen in the variation of the hyobranchium of lizards (Camp, 1923:339; McDowell and Bogert, 1954:42, 50, 85; Underwood, 1957:222) and of snakes (Smith and Warner, 1948: 189). Most of the significant differences that have been described have been between taxonomic categories of the range from superfamily to subfamily and only a few such differences between closely related genera or between lesser categories. Hence the paucity of significant differences among solenoglyphous snakes, to be described presently, is not surprising. Hyobranchia of 21 species representing ten crotalid genera and one viperid genus have been examined in the present study.

The hyobranchium of vipers and pitvipers is a single cartilaginous structure shaped like a tuning fork or, lacking the body of the fork, U-shaped. This is the colubroid type described by Smith and Warner (1948:191). The posteriorly directed cornua, considered as hypohyals by the same authors, are regarded currently as the first branchial arch (McDowell and Bogert, 1954:85; Romer, 1956:423). The paired branchials converge a short distance behind the fork (within the distance covered by two or three ventral scutes) and run along parallel to one another. The posterior parts of the branchials extend along each side (and are bound to) the hyoglossal muscle. The branchials and the hyoglossal muscle end at the same point, which can be indicated by the ordinal number of the underlying ventral scute. The branchials extend farther posterior in the more primitive species of Agkistrodon, Porthidium, and Bothriopsis than in other pitvipers.

In the former species the ends lie beneath the nineteenth to twenty-second ventral scute, whereas in others that have been examined, beneath the fourteenth to seventeenth ventrals.

The body of the hyoid (basihyal) connects the anterior ends of the branchials and may extend some distance forward. Although this anterior extension often resembles the lingual process of lizards (which penetrates the tongue), it is located just beneath the skin, nowhere near the tongue. The length of the basohyal from the anterior tip to the posterior notch between cornua can be measured in lengths of ventral scutes. It varies from approximately 1/2 the length of a ventral scute to two ventral-scute-lengths. The extreme reduction indicated by the first value, with the basohyal a crosspiece little wider than adjacent parts of the branchials, has apparently been reached independently in several different lines of pitvipers.

In different species of Agkistrodon and Hypnale there are considerable differences in the length of the basihyals and of the branchials. The length of the basihyal in lengths of ventral scutes is as follows: 1½ in H. hypnale, less than 1 in A. bilineatus and A. piscivorus, ½ in A. contortrix. In the last species the basihyal makes a crosspiece no wider than adjacent parts of the branchials. The posterior ends of the branchials reach ventrals 19 to 22 in H. hypnale and A. contortrix, whereas in A. piscivorus and A. bilineatus they are shorter, terminating beneath ventrals 12 to 16.

It is interesting to note that the long branchials of H. hypnale and A. contortrix are equaled only by those of Porthidium barbouri, P. godmani, and Bothriopsis medusa, which are regarded as the most primitive representatives of these genera. The last three species have short basohyals, extending one or two ventral scutes. Porthidium mexicanum, Bothriechis lateralis, and Lachesis muta have basohyals like those of Agkistrodon contortrix but the branchials are shorter, ending beneath the fourteenth to seventeenth ventral.

The other pitvipers that have been examined have basohyals between one and two ventral scutes in length and branchials that end beneath the fourteenth to seventeenth ventral. Such was found to be the case in Bothrops atrox, Bothriopsis punctata, Ophryacus undulatus, Trimeresurus gramineus, T. flavoviridis, T. sumatranus, Tropidalaemus wagleri, Sistrurus ravus, S. catenatus, Crotalus triseriatus, and C. horridus. Among true vipers, Vipera berus and V. russeli (the only viperids examined) also have hyobranchia of this description.

Lungs and Pulmonary Arteries

In advanced snakes only the right lung of the normal pair is well developed. The left lung is either absent or — as is the case in most colubrids and in some elapids, viperids, and crotalids — a small rudiment of the left lung (functionless or nearly so) communicates to the trachea near the posterior end of the heart. In snakes of the last three families, an accessory tracheal lung is present, extending forward from the heart to the head as an extension of the left lung, which it tends to replace. Species with a well developed tracheal lung tend to reduce the alveolar structure in the right lung, which remains as a smooth-walled sack. The extent of development of the tracheal lung and the relative size of the smooth-walled and alveolar portion of the right lung varies greatly in different snakes. Among solenoglyphous snakes that have been studied, Lachesis muta retains the alveolar structure of the right lung, and the dorsal wall of the trachea, although it is greatly expanded, does not show an alveolar structure. Aspis cerastes, Atractaspis irregularis, and Atractaspis bibroni have narrow tracheal lungs and the alveolar part of the right lungs is well developed. In most solenoglyphous snakes the tracheal lung is strongly developed and comprises the bulk of the respiratory tissues, whereas the alveolar structure of the right lung is reduced, reaching slightly posterior to the heart at most. The presence of the left lung as a small rudiment or the complete absence of the left lung seems to vary among different species without regard to phylogeny or taxonomic boundaries (Table 5). These variations were described long ago by Cope (1894a) and more recently noted by Wolf (1933) and Brongersma (1949, 1951).

The main branches of the pulmonary artery in higher snakes were also described by Brongersma (1949, 1951), who found considerable variation. In Bitis, Lachesis, Bothrops (atrox, jararucussu, and alternata examined), Bothriopsis (B. bilineatus), Hypnale (H. hypnale), and Crotalus (durissus and scutulatus), the main division is into dorsal and ventral branches which correspond to the left and right pulmonary arteries of snakes with both lungs well developed.

TABLE 5. Occurrence of Rudimentary Left Lungs among Solenoglyphs

Family Group	Present	Absent
Viperidae	*Bitis arietans*	*Causus rhombeatus*
Crotalidae:		
Agkistrodontinae	*Agkistrodon contortrix*	*Agkistrodon piscivorus*
Lachesinae	*Bothrops pictus*	*Bothrops atrox*
	Bothriechis schlegeli	
	Tropidolaemus wagleri	
	Trimeresurus erythurus	
Crotalinae	*Crotalus durissus*	*Crotalus horridus*
	Crotalus adamanteus	
	Crotalus viridis	
	Sisturus catenatus	

This arrangement occurs in Hypnale hypnale. Vipera, Aspis, Atractaspis, Trimeresurus, Porthidium, Bothriechis, and Sistrurus have only the dorsal branch, with a small diverticulum directed ventral and to the left and connected in some to the left aortic arch by a ligament that is probably a remnant of the ductus arteriosus. Probably this diverticulum represents the base of the left pulmonary artery. In Atractaspis and Cerastes the right pulmonary has a secondary division into a ventral and dorsal branch. In Causus, the right pulmonary has lost all connection with the right lung; it consists only of an anterior branch which ranges along the right side of the trachea, while the left pulmonary artery parallels it on the left side of the trachea and both serve the well developed tracheal lung. Brongersma (1949:63) concluded that "As far as the limited number of species and specimens examined by me allow of definite conclusions, the main branches of the pulmonary artery appear to be constant in each species and in the majority of the genera."

No phylogenetic sequence of types was suggested by Bongersma, nor is any discernible to me. However, the generic consistency is interesting. On the basis of these features, Brongersma (loc. cit.) wrote, "The only exception is the genus Bothrops, in which B. nummifer, B. schlegelii and B. lansbergi differ from the other species. It may be mentioned that these three belong to the group of species that have single subcaudals, while the other Bothrops species examined by me belong to the group of species having paired subcaudals. Further studies will have to show, whether the three species mentioned above should be referred to a separate genus." As indicated elsewhere, Brongersma's suggestion is supported by other lines of evidence and the indicated genera are separated in the present paper. As a matter of fact, in the above descriptions of pulmonary arteries, the revised generic nomenclature is used.

Musculature of Trunk

The myology of the trunk region of snakes was studied extensively by Mosauer (1935), but no later investigations of this subject have appeared and no new data are presented here. Mosauer recognized three main myological types represented in the Boidae, the Colubridae (in which he included the Elapidae and Hydrophidae), and the Viperidae (including the Crotalidae). He (1935:118) described the viperid type of epaxial muscles as follows: "The semispinal is part of the medial column arises as a distinct tendon from the postzygapophysis. The medial tendon of the M. longissimus is attached to the spinous process. Both facts seem to be more indicative of boid than of colubrid conditions. There is no well-developed M. interarticularis superior and the M. interarticularis inferior is short and inconspicuous. The intercostal muscle, the M. transversohypapophyseus, extends over the whole ventral surface of the vertebral column. The musculature of vipers and pitvipers is so much alike that their separation into two families appears to be myologically unjustified." The solenoglyphous snakes on which this description was based were _Causus lichtensteini_, _Vipera ammodytes_, _Bitis arietans_, _Agkistrodon_ mokasen, Agkistrodon piscivorus, Lachesis muta, Sistrurus catenatus, and Crotalus horridus. Among these, Causus showed the peculiarity that the semispinalis arises by fleshy fibers from the postzygapophysis, instead of by a tendon, as in other snakes. With minor variations, the viperid type of epaxial musculature is also found in a colubrid, the Hognosed Snake, Heterodon nasicus, and in an elapid, the Death Adder, Acanthophis antarcticus.

On the basis of the usual type of trunk musculature that occurs in the snakes of advanced families (and apparently disregarding the situation in Heterodon and Acanthophis), Mosauer (loc. cit.) further concluded that the Viperidae are more primitive in some respects than are present-day Colubridae and that these facts militate against the idea that the Viperidae developed from the Colubridae.

Another interpretation of the same data is readily apparent — that the ancestral colubrid that produced Heterodon and the typical advanced colubrid also produced the line of solenoglyphous snakes. A line of rear-fanged snakes derived from this ancestral colubrid is precisely the ancestor of viperid snakes that other lines of evidence indicate.

Serology

Great progress has been made in the study of detailed differences in blood proteins. Antigens in the serum can be analyzed according to their reaction to antisera produced in experimental animals or by chromatographic techniques. The possible contributions of experimental serology to the knowledge of phylogenetic relationships and classification of animals were enthusiastically described by Boyden (1942), who presented evidence to show that the chemical nature of antigens and antibodies may be relatively conservative characteristics.

One is led to the conclusion that, at least in some instances, the taxonomic value of serological characters may be equal to (but no greater than) that of conservative morphological characteristics. The relative difficulty of adequate serological techniques suggests the present advisability of focusing serological investigations on critical phylogenetic and taxonomic problems rather than attempting broad general application of the technique. The critical problems of crotalid phylogeny, described elsewhere in this paper, would seem to be good topics for such projects.

In a serological study of North American reptiles, Cohen (1955) included information on two species of each of the genera Crotalus, Sistrurus, and Agkistrodon. He concluded tentatively that the massasauga (Sistrurus catenatus) is more closely related to the other rattlesnakes (Crotalus) than to the moccasins (Agkistrodon) but cautioned that "A more intensive serological study of other species of Crotalus, Agkistrodon, and Sistrurus would be necessary to completely verify the above results." I might add the comment that the key to these and most other reptilian relationships lies in tropical representatives, and that information on species of the neotropical genera, Bothrops, Lachesis, and Porthidium, would be necessary to satisfactorily assay the question of the relationships of terrestrial pitvipers of the Western Hemisphere.

CLASSIFICATION

The general classification of advanced snakes proposed here is in some respects that of Underwood (1967). The ranks of taxa, for example Family Crotalidae for pitvipers instead of subfamily, are matters of bookkeeping and filing — human whims rather than biology. Paleontologists, working with restricted data, prefer larger groupings than those proposed below.

Families

Suborder Caenophidia
  Superfamily Colubroidea
    Family Colubridae, and others that are not of present concern.
  Superfamily Elapoidea (Proteroglypha)
    Family Elapidae. Perhaps 4 or 5 subfamilies.
    Family Hydrophidae. Two subfamilies.
  Superfamily Viperoidea (Solenoglypha)
    Family Viperidae
      Subfamily Atractaspinae
      Subfamily Viperinae
    Family Crotalidae
      Subfamily Agkistrodontinae

Subfamily Lachesinae

Subfamily Crotalinae

Crotalidae Oppel

Crotalini Oppel, 1811:50.

Aplipuria Rafinesque, 1815:77 (part).

Diplipuria Rafinesque, 1815:77 (part).

Crotalidae, Gray, 1825:204; Gray, 1842:47; Gray, 1849:3; Cope, 1864: 231; Günther, 1864:383; Garman, 1883:110 (Bothrophera also used for a category above family); Cope, 1896:212, Cope, 1900:1130; Taylor, 1922:283; Santos, 1943:11; Cochran, 1943:4; Smith and Taylor, 1945:177; Klauber, 1956:12; Grocott and Sadler, 1958:15; Abalos, Baez, and Nader, 1964:269; Villa, 1962:40; Minton, Dowling, and Russell, 1968:38.

Crotaloidea, Fitzinger, 1826:34.

Cophiadae Boie, 1827:511.

Bothrophes Fitzinger, 1843:28; Schreiber, 1875:181.

Teleuraspides Cope, 1871:205.

Trigonocephalidae Hoffmann, 1890:1798 (appears as alternate for Crotalidae).

Cophiinae, Cope, 1896:212 (part).

Viperidae, Stuart, 1963:127 (part).

Agkistrodontinae - New Subfamily

Diagnosis.—See key below.

Composition.—Agkistrodon, Calloselasma, and Hypnale.

Lachesinae Cope

Lachesinae Cope, 1900:1130 (part); Santos, 1943:11; Machado, 1945:47; Abalos, Baez, and Nader, 1964:269.

Diagnosis. —See key below.

Composition.—Asia: Ovophis, Trimeresurus, and Tropidolaemus. America: Ophryacus, Bothriechis, Bothriopsis, Bothrops, Lachesis, and Porthidium.

Crotalinae Oppel

Crotalini Oppel, 1811:50.

Crotalinae, Cope, 1859:334 (part); Boulenger, 1896:518; Griffin, 1916:222; Smith, 1943:477; Dunn, 1944a:213; Machado, 1945:47; Marx and Rabb, 1965:194; Hoge, 1966:109; Roze, 1966:271.

Diagnosis.—See key below.

Composition.—Sistrurus and Crotalus.

Key to Subfamilies and Genera

1. Rattle present; posterior 9 to 10 caudal vertebrae fused into shaker (Crotalinae). 2

   Rattle lacking; posterior caudal vertebrae separate and not enlarged. 3

2. Top of head with large plates anteriorly, usually 9 in number, including a single frontal and a pair of large symmetrical parietals in contact with each other; distance between ends of caudal lymphopophyses less than one-third distance between lymphopophysis and pleuropophysis; American. . . . . <u>Sistrurus</u>

   Top of head with scales and plates of varying size anteriorly; frontal and parietals, if present, separated by small scales; distance between ends of lymphopophyses greater than distance between lymphopophysis and pleuropophysis; American . . . . . <u>Crotalus</u>

3. Top of head with large plates anteriorly, usually 9 in number, including a single frontal and a pair of large symmetrical parietals in contact with each other; basal portion of pterygoid longer than ectopterygoid; pterygoid teeth extending to point posterior to articulation with ectopterygoid (Agkistrodontinae). 4

Top of head with scales and plates of varying size anteriorly[1]; frontal and parietals, if present, separated by small scales; basal portion of pterygoid shorter than ectopterygoid; pterygoid teeth usually not extending to point posterior to margin of articulation with ectopterygoid (Lachesinae)[2] 5

4\. Dorsal scale rows 17 to 21, strongly or weakly keeled[3]; subcaudals divided; lateral caudal scutes longer than high; palatine lacking dorsal appendage; palatal teeth 3 or more; Asiatic . . . . . *Hypnale*

Dorsal scale rows 23 or 25, smooth or keeled; subcaudals divided or entire anteriorly and divided posteriorly; lateral caudal scutes higher than long; palatine having elongate dorsal appendage; palatal teeth 1 or 2; Asiatic . . . . *Calloselasma*

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[1] *Bothriopsis medusa* and *Porthidium godmani* have pterygoid teeth that extend to a point posterior to the junction of ectopterygoid and pterygoid.

[2] *Porthidium barbouri* has a large portion of specimens with a colubrid pattern of supracephalic plates like *Agkistrodon* and *Sistrurus*. Supracephalic scutes of *Trimeresurus macrolepis* are large but not in the colubrid pattern.

[3] Some races of *Hypnale halys* have 23 rows of dorsal scales.

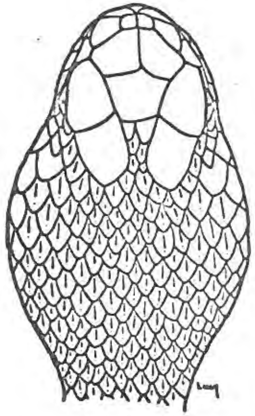

FIG. 2. Dorsal view of head of plated variant of *Porthidium barbouri* (MCZ 42679). X 3.

FIG. 3. Ventral view of posterior portion of tail of *Porthidium godmani vulcanicum* (ANSP 22572). X 1.3.

Dorsal scale rows 23 or 25, strongly keeled; subcaudals entire anteriorly and divided posteriorly; lateral caudal scutes longer than high; palatine lacking dorsal appendage; palatal teeth 3 or more; American . . . . *Agkistrodon*

5. Gular scales keeled; nasal pore rudimentary; lower lumen of fang medial; frontal with center depressed; Asiatic. . . . .*Tropidolaemus*

Gular scales smooth; nasal pore well developed; lower lumen of fang anterior; frontal without depressed center. 6

6. Distal subcaudals in 4 or 5 rows; concave aponeurosis on anterior margin of maxillary cavity; American. . . . . *Lachesis*

Distal subcaudals in 1 or 2 rows; anterior margin of maxillary cavity having convex aponeurosis or lacking aponeurosis 7

7. Nasal pore on external margin of nasal pad; Asiatic 8

8. Subcaudals anteriorly entire, posteriorly divided; pterygoid teeth extending past midpoint of junction of ectopterygoid to pterygoid . . . . . *Ovophis*

Subcaudals divided; pterygoid teeth extending to midpoint of junction of ectopterygoid to pterygoid . . . . *Trimeresurus*

9. Terrestrial; tail not prehensile 10

Arboreal; tail prehensile. 11

10. Subcaudals entire; palatine rounded, not forked anteriorly. . . . . *Porthidium*

Subcaudals divided; palatine forked anteriorly. *Bothrops*

11. Subcaudals entire; lateral caudal scales strongly keeled distally . . . . *Bothriechis*

Subcaudals divided or anteriorly entire and posteriorly divided; lateral caudal scales having keels reduced from anterior to posterior 12

12. Eyelash scales; interoculars 11 or more; anterior border of maxillary cavity divided into two distinct curvatures by rounded projection . . . *Ophryacus*

No eyelash scales; interoculars 10 or less; anterior border of maxillary cavity a simple uninterrupted curve . . . . *Bothriopsis*

Identification By Above Key.—Since the above key is not infallible, identifications may need to be confirmed according to diagnoses and distributions in accounts below. Parts of the cranium may have to be exposed to confirm critical identifications.

Generic Status

Since the generic arrangement of pitvipers proposed here is novel, I feel obliged to state my notion of the functional design of genera. The following principles have been used here to establish convenient-sized, well-distinguished, natural groups.

1. Phylogeny. The genus should have the evolutionary unity of a phylogenetic line or of a cluster of lines with a common origin, known or hypothesized, within the perimeter of the genus. Thus, all genera should be monophyletic. *Bothrops* (*sensu lato*) is not.

2. Convenient size. Since any grouping above the species is subjectively determined — its upper and lower limits factors of evolutionary accident and human whim — taxonomists should select convenient-sized groups (provided the groups are distinct and monophyletic) for their first name category. Why not design a filing system for convenience? When convenient gaps, cleared by extinction, are present, I am of the opinion that groups of up to about 25 species make convenient genera. Larger genera are cumbersome, although in the case of certain successful evolutionary lines large genera may be required by the evolutionary circumstances and by practical problems of convenient diagnosis. *Trimeresurus* (*sensu stricto*) with 35 species may be a case in point; although two distinct lines have been traced, distinguished by hemipenes, arboreal representatives have converged to the extent that females of different species representing the two separate evolutionary lines can not be distinguished conveniently (Pope and Pope, 1933:12). In contrast *Bothrops* (*sensu lato*) is

readily divisible into convenient-sized genera. Having established the size gap that separates the large genera in a family or subfamily, the taxonomist can apply this measure to phylogenetic side lines. When small groups within a family are bounded by the kind of gap that distinguishes maximum-size genera, they should be accorded generic rank. Among major neotropical groups of pitvipers, four have 6 to 23 species each and two groups that are as distinct as the four have one species each. All six are treated here as genera. McDowell (1961) expressed similar sentiments more eloquently in his favorable review of Malnate's (1960) realignment of the species formerly contained in *Natrix*.

3. *Generic characters*. In exploring and questioning sterotyped genera in classifications that they inherit, taxonomists should not discount generic characters that are morphological simply because of past misuse. Shorn of authoritarian stigma and properly elucidated, morphological characters still supply the backbone of generic classification. Sophistocates of recent times have given heavy bias to ecological, cytogenetic, physiological, and biochemical features. The important point is that any difference is a good taxonomic character within the bounds of its consistency but the degree of consistency is erratic from group to group. Recent phylogenetic and taxonomic conclusions based on one feature — whether vertebrae, venom, muscles, or other — are valid to the extent of intelligent coordination of information on other significant features. Often such conclusions have been invalid because they lacked such coordination

and often they have been largely valid despite claims of reliance upon some supposedly infallible feature — say serology — because in reality they have drawn upon evidence from other characters.

Proposed Generic Arrangement of Pitvipers

Although the unsatisfactory status of Trimeresurus and Bothrops has been evident for decades, efforts to resolve the situation in a simple way have failed because of (1) the degree of diversity in the American representatives and in the Asiatic representatives that prevents them from being separated readily according to continent; and (2) the existence of alleged annectant species like Bothriopsis castelnaudi, connecting otherwise distinct groups like the Central American arboreal pitvipers with entire subcaudals to the South American arboreal pitvipers with divided subcaudals. A "birds-eye view" of the entire complex, taken without close regard to the regional assemblages, seems to reveal a confusing tangle of diversity and apparent morphological overlapping.

A regional approach has helped unravel patterns of phylogeny. From México, the investigation has been extended to Central America; to adjacent northern South America; and then, in so far as limited collections permitted, to the rest of South America. Comparison of the American stocks to those in Asia (hampered by poor representation of the latter) has also been attempted. Provisional conclusions are reported.

México.—In the first analysis of the Mexican scale-snouted pitvipers, six groups seem to be represented there: (1) mountain vipers -- *barbouri* and *godmani*; (2) jumping vipers -- *nummifer*, *ociduus*, *mexicanum*, and *melanurum*; (3) hognosed vipers -- *nasutum*, *dunni* and *yucatanicum*; (4) treevipers -- *schlegeli*, *aurifer*, *bicolor*; (5) mountain treeviper -- *undulatus*; and (6) barba amarilla -- *asper*. All of them have been included in the genus *Bothrops*. As a matter of fact, the first three kinds are similar in scutellation, skeleton, hemipenis, and general habitus. As close relatives they are best grouped together in *Porthidium*. The last three groups listed above seem distinct from each other and from *Porthidium*. Genera for the principal Mexican groups are:

Porthidium: mountain vipers, jumping vipers, and hognosed vipers

Bothriechis: treevipers

Ophryacus: mountain treeviper

Bothrops: barba amarilla

Central America.—Except for *Ophryacus* these groups can be followed south into Central America, where *Porthidium* and *Bothriechis* are well represented; *Bothrops* includes only the wide-ranging barba amarilla (*B. asper*); another distinct kind of pitviper ranges through lower Central America, the bushmaster (*L. muta*), for which a generic name is already in vogue; and a treeviper with divided subcaudals, that is very different from *Bothriechis*, ranges from Ecuador and Colombia into Darién, Panamá. The last two groups, not represented in the Mexican list, are:

Lachesis: bushmaster

Bothriopsis: South American treevipers

South America. —Bothriechis schlegeli ranges from Central America into northern South America. Porthidium has only two species in northern South America and one in the Amazon Valley. Lachesis muta ranges widely. The fer-de-lance, Bothrops atrox, and B. asper occur along with a large number of more or less close relatives. Encountered for the first time is a superficially distinctive group of ground vipers (neuwiedi, ammodytoides, and others) which aggrees with the fer-de-lance line in fundamental features of tail scutellation and skeleton. The two seem best associated in the genus Bothrops as the neuwiedi group and the atrox group, respectively. A distinctive group of treevipers (castelnaudi, punctatus, bilineatus, and others) completes the South American assemblage. They comprise the sixth genus of American scale-snouted pitvipers. Although represented by one species each in Central America, Bothrops and Bothriopsis are centered in South America, where they are represented, respectively, by 39 and 11 species and subspecies.

Asia. —Trimeresurus is widely distributed over southeastern Asia and fringing archipelagos. Two small groups are quite distinct: the mountain vipers (monticola and relatives) and the keel-chinned vipers (wagleri and relatives). The distinctiveness of the latter group has been described (Maslin, 1942; Brattstrom, 1964). Skeletal and other considerations suggest that both groups are early offshoots from the line which led to the advanced groups. Maslin (1942) distinguished two main phylogenetic lines of Trimeresurus based on the structure of the hemipenes. With their meager representation in U.S. collections, I have not attempted a definitive investigation of the species and species-groups of Trimeresurus. Genera recognized are:

Trimeresurus: Asiatic scale-snouted pitvipers

Ovophis: Mountain pitvipers

Tropidolaemus: Keel-chinned pitvipers

Although the above approach is unlikely to draw unrestrained applause from philosophers or statisticians, the groups that emerge are, I think, natural phylogenetic lines that are morphologically distinct. The differences between these genera and their hypothesized phylogenetic interrelationships are subjects of later discussion.

My arrangement is not a resurrection of the scheme devised by Peters (1862) and Cope (1896), but the resemblance in the arrangements is closer than a simple comparison of names would suggest. Of the seven genera of scale-snouted pitvipers in Cope's (1896) outline, four correspond to genera in the present scheme.

Perhaps the most significant argument in favor of the generic fragmentation suggested above is a practical matter relating to the distinction of Agkistrodon and Hypnale from Bothrops (auct.) and Trimeresurus (auct.). The morphological gap (in scutellation and skeleton) between the American species of Agkistrodon and the godmani group of Porthidium (part of Bothrops auct.) is quite small. Similarly the gap between Hynale and Ovophis (part of Trimeresurus auct.) is quite small. If my conclusions are correct, both of these gaps are smaller than gaps within the old Trimeresurus (auct.) and Bothrops (auct.). It follows that taxonomists who prefer genera larger than the twelve genera recognized here are left with one logical alternative. They must outdo the master lumper, Boulenger (1896), and return all rattleless pitvipers, except perhaps Lachesis, to a single genus, Agkistrodon. Schlegel (1837) used essentially this arrangement, with the name Trigonocephalus assigned to the expansive genus so circumscribed. With 137 species and subspecies, distributed over most of the tropical and warm temperate regions of America and Asia, such a genus would lack the mnemonic effectiveness in phylogeny and zoogeography that is the keystone of modern binomial nomenclature.

Historical Summary of Genera

The first named pitvipers were three rattlesnakes comprising the genus Crotalus and one rattleless pitviper, Coluber atrox, described by Linnaeus in the Tenth Edition of the Systema (1758). In the Twelfth Edition (1766) Linnaeus added descriptions of Crotalus mutus and Boa contortrix. Laurenti (1768) described Coluber nepa and Vipera caerulescens. Gmelin in his revision of the Thirteenth Edition of the Systema (1789) questioned the generic allocation of Crotalus mutus but did not clarify the situation by describing the species anew as Coluber crotalinus and by adding descriptions of Coluber glaucus and Coluber ambiguus, which are very similar to Linnaeus' Coluber atrox. Lacépède (1789) contributed type descriptions of

Coluber lanceolata, Coluber brasiliensis, and Crotalus piscivorus.

The seven biological species and subspecies that are treated in these early publications are Bothrops atrox atrox, B. lanceolatus, Lachesis muta muta, Agkistrodon contortrix contortrix, A. piscivorus piscivorus, and Hypnale nepus. In the type descriptions they were distributed among all the known genera of snakes. Finally, in 1799 Palisot de Beauvois described a genus, Agkistrodon, for rattleless pitvipers.

The five extra trivial names from these early decades that are not assigned above to species are of more than passing interest. Coluber brasiliensis Lacépède is probably the earliest name for the snake now known as Bothrops jararaca. Coluber glaucus Gmelin is a synonym of Bothrops lanceolata and Coluber crotalinus Gmelin is a synonym of Lachesis muta muta. Vipera caerulescens Laurenti and Coluber ambiguus Gmelin are synonyms of Bothrops atrox. Because no good can come from the availability of these long unused names with their inadequate descriptions and inexact localities, I plan to formally request that the slate be cleaned by placing them on the Official List of Rejected Names.

During the Nineteenth Century numerous new species were described — dates are cited in the alphabetical list above (Table 2) — and a total of 33 nominal genera was produced for the 12 genera of rattleless pitvipers now recognized. The nuances of nomenclatural byplay swell the list of nominal genera further with seven homonyms, five invalid emendations, and two unnecessary new names.

Although the majority of these nominal genera were never accepted, the number of genera that were recognized gradually grew. First the concept that vipers and pitvipers were distinct groups developed during the early decades of the Nineteenth Century, with publications by Oppel (1811), Gray (1825), Fitzinger (1826), and Boie (1827). Next rattlesnakes were separated from rattleless pitvipers; Schlegel (1837) indicated them as *Crotalus* and *Trigonocephalus*. Among rattleless pitvipers Wagler (1830) and Fitzinger (1843) had already distinguished six genera and Gray (1849) distinguished eight, of which *Cenchris* (part of *Agkistrodon*), *Lachesis*, and *Craspedocephalus* (*Bothrops*) were American. The last three are distinct from one another but many of the other groups distinguished as genera by Gray are fragments of *Agkistrodon* or *Trimeresurus*.

In a series of independent contributions published between 1858 and 1896, Edward D. Cope and Wilhelm K. H. Peters devised a classification of rattleless pitvipers that was based on scutellation and skull. Until very recently Peters' five-page paper on the cranial differentiation of pitvipers (1862) was the only comprehensive report on the subject. Wilhelm Peters died in 1883 and Cope, in his last published account (1896), used the following arrangement of genera:

I. Subcaudals in two rows
  Top of head scaled; subcaudals four-rowed at end;
    a caudal spine . . . . *Lachesis*
  Top of head with small scales; tail normal. . . . *Cophias*

Top of head with large imbricate shield-like scales . . . . *Peltopelor*

Top of muzzle scaled; rest of head shielded . . *Hypnale*

Top of head with nine shields; scales carinate . . . . *Trigonocephalus*

Top of head with nine shields; scales smooth . . . . *Calloselasma*

II. Subcaudals in one row

Body and tail cylindrical, not prehensile; head scaly . . . . *Bothriopsis*

Body and tail compressed, prehensile; head scaly, scales normal . . . . *Bothriechis*

As *Bothriechis*, but horn-like scale over eye. . . . . *Ophryacus*

As *Bothriechis*, but a row of scales outside the superciliary shield. . . . . *Teleuraspis*

Body and tail not prehensile; nine normal head shields . . . . *Agkistrodon*

In Boulenger's catalog of snakes (1896) all rattleless pitvipers with small plates or scales on top of the head were lumped in *Lachesis*, distinguished only from *Agkistrodon* with large supracephalic scales. For over a quarter of a century an atmosphere of authority stifled further efforts to assay the evolution and classification of rattleless pitvipers. *Lachesis* (*sensu lato*) persisted in the literature as late as the 1920's, when Amaral (1921b) and Werner (1923) used it for the fer-de-lance and relatives.

During the four subsequent decades little new evidence was presented on generic distinctions among rattleless pitvipers, but the tide of opinion slowly shifted. The change began before 1920.

Mocquard (1905) presented reasons for segregating the Bushmaster in _Lachesis_, leaving the rest of the American and the Asiatic scale-snouted pitvipers in _Trimeresurus_. For zoogeographic reasons Stejneger (1907) preferred not to have Asiatic and American pitvipers in the same genus. His restriction of _Trimeresurus_ to the Asiatic species was followed by Barbour (1912), Oshima (1912), and Wall (1921), whereas many of their contemporaries continued to follow Boulenger. In 1926 Amaral, impressed with the new discovery of oviparity in the Bushmaster, restricted the genus _Lachesis_ to it and separated the American _Bothrops_ from the Asiatic _Trimeresurus_ for geographic reasons. The recognition of three genera has prevailed generally, on this shaky foundation. The inconclusiveness of the evidence has been regularly underlined by a persistent minority who lump American and Asiatic species in _Trimeresurus_; Schmidt (1950), M. A. Smith (1943), McDowell and Bogert (1954), and Neill (1963) are examples.

Perhaps Stejneger and Barbour's (1940) exchange of views on the subject shows the state of affairs as well as anything that has been written, although their data were incomplete.

Barbour:

"Several colleagues are trying to make me believe that the Old World pitvipers, which we have called _Trimeresurus_, and the New World species, Bothrops, are all congeneric. I have always had a feeling that they were better kept apart, most of the Old World species having prehensile tails which is not the case with most of the New World forms. Bothrops schlegelii, of course, has a completely prehensile tail and I suspect B. nigroviridis has also.

"To elaborate the pitviper remarks it may be noted that Trimeresurus flavoviridis of Riu Kiu has a long, straight tail and looks suspiciously Bothrops-like in other respects. So there may be two genera each with representations in the Old World and the New but this we do not really know yet. Not improbably studies of the properties of the venoms may throw light on the subject.

"I have been cudgelling my mind to think of some other character which would set off the groups of species, one from the other, but I can't do it and yet the distribution does not suggest a common origin for the whole lot. On the chance that you may have been thinking along the same lines I am dropping you this line of inquiry."

Stejneger:

"With regard to Bothrops my own standpoint is about the same as with Natrix: I don't want to change the present current nomenclature until someone makes a thorough study of all the groups of species (not only tails and scales and intromittent organs) demonstrating the amount and quality of their relationships. What is the use of shifting about from one uncertainty to another? The Trimeresurus-Bothrops complex is certainly not as homogeneous as the Agkistrodon.

I don't believe that the nomenclature should be made the football of a game of venting individual theories of origin and distribution in paleogean times. The object of Nomenclature is primarily to be a convenience to help one talking of these creatures and the present one is certainly helpful and convenient in that it tells you whether the snake I am talking about is an old world or a new world form."

Hints that a more equitable arrangement is possible have appeared in the last several decades.

In 1942 Maslin called attention to differences in nasal pores and presented a key to the species of Trimeresurus. M. A. Smith (1942) pointed out that Maslin's observations were incomplete but he missed the significance of the position of the nasal pore, which remains a useful character. Ruiz (1951) indicated differences in the skulls of Trimeresurus and Bothrops but, lacking information on many phylogenetically important species, he obtained results that are less significant than those of W. Peters (1862), which Ruiz overlooked.

Amaral (1946) reviewed the generic arrangement a second time, repeating his earlier (1926) conclusions. In the later paper Amaral divided the species of Bothrops into six provisional subgenera, which he left unnamed. These subgenera correspond roughly to the genera here proposed except that the species barbouri, castelnaudi, medusa, melanura, and undulata were assigned to groups that are different from mine.

Smith and Taylor (1945:179) made the footnote comment on Bothrops: "...American species themselves rather clearly belong to more than one genus: certain ones of these are easily defined, while others are not."

Brattstrom's (1964) review of the osteology and the evolution of pitvipers contributed useful information on 12 of the 74 species and subspecies of Bothrops (auct.) and 8 of the 49 species and subspecies of Trimeresurus (auct.). The lack of data on important phylogenetic lines and key species was a severe handicap, invalidating many of the conclusions concerning the evolution of these pitvipers. Individual points are discussed in appropriate sections of the present report. Hoge (1966:109) commented in part that "...the Bothrops group should be divided into several genera or subgenera...".

The arrangement of genera that I propose is surprisingly like that devised by Cope and Peters before 1896 (Table 6).

HYPNALE FITZINGER

Agkistrodon (nec Palisot de Beauvois), Stejneger, 1907:449; Ruiz, 1951:110; Klemmer, 1963:397; Werler and Keegan, in Keegan and MacFarlane, 1963:273; Brattstrom, 1964:229.

Hypnale Fitzinger, 1843:28 (Cophias hypnale Merrem, 1820; original designation); Gunther, 1864:394; Cope, 1896:212.

Halys Gray, 1849:14 (preoccupied); Peters, 1862:671; Gunther, 1864:392.

Diagnosis.—Asiatic pitvipers having large supracephalic shields in the colubrid pattern; palatine triangular, lacking dorsal appendage, bearing 3 to 5 teeth (Figure 4); pterygoid teeth 7 to 16 extending posterior past articulation with ectopterygoid; dorsal

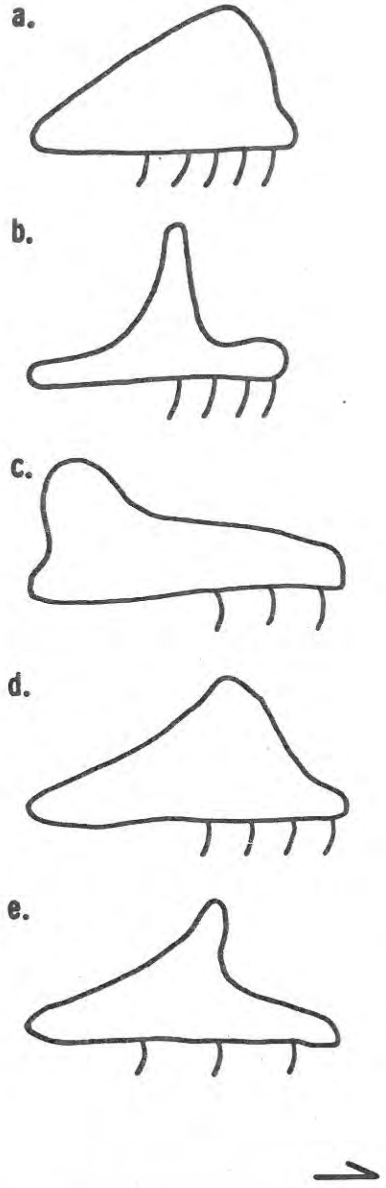

FIG. 4. Comparison of palatines (diagramatic and not scaled): a, *Hypnale*; b, *Calloselasma*; c, *Agkistrodon*; d, *Porthidium*; e, *Bothrops*.

TABLE 6. Correspondence of Generic Arrangement of Late Nineteenth Century and Present Generic Arrangement

Unique to arrangement of Peters (1862) and Cope (1896)	Similar in two arrangements	Unique to present arrangement
Cophias	Agkistrodon	Bothrops
Peltopelor	Bothriechis	Ovophis
Teleuraspis	Bothriopsis	Porthidium
Trigonocephalus	Calloselasma	Trimeresurus
	Hypnale	Tropidolaemus
	Lachesis	
	Ophryacus	

scales in 17 to 21 rows, scales strongly or weakly keeled; subcaudals divided; lateral caudal scales longer than high; ecopterygoid slender, straight, bifurcate; basal portion of pterygoid longer than ectopterygoid; margin of maxillary curve a simple curve; nasal pore situated near internal rim of nasal pad.

Definition.—Size small to moderate, maximum total lengths 0.4 to 0.7 m.; dorsal markings consisting of dark brown spots or crossbands; cranium long and narrow, its width much less than its length; border of maxillary cavity a simple curve; prootic sloping gradually ventrolateral with no dorsolateral ridge; anterior foramen of prootic divided by heavy bony partition into small lower and large upper foramen; palatine teeth 3 to 5; dorsal extension of palatine a broad triangular or rounded projection; pterygoid teeth 8 to 13, extending beyond articulation with ectopterygoid; basal part of pterygoid longer than ectopterygoid; ectopterygoid straight, slender, cylindrical; squamosal long and slender, its greatest width one-fourth to one-third its length, its length over one-half length of quadrate; quadrate much shorter than length of cranium; mandibular teeth 12 to 14; splenial separate from angular (fused in H. hypnale).

Composition.—H. halys (Pallas) with about seven subspecies, H. himalayana (Gunther), H. hypnale (Merrem), H. nepa (Laurenti), H. strauchi (Bedriaga), and H. monticola (Werner).

Distribution.—Much of Asia from southern Siberia, Korea, and Japan to the mouth of the Volga River, northern Iran, Mongolia, and much of northern and western China; Western Himalayas from Chitral to Sikkim; Ceylon and southern India.

CALLOSELASMA COPE

Leiolepis Duméril, 1853:531 (Trigonocephalus rhodostoma Boie; monotypy; preoccupied by Leiolepis Cuvier, 1829, Sauria); Duméril, Bibron, and Duméril, 1854:1488.

Calloselasma Cope, 1859:336 (new name for Leiolepis Dumeril, 1853, preocc.); Günther, 1864:391; Cope, 1896:212; Chernov, 1957: 790; Campden-Main, 1970:96.

Agkistrodon (nec Palisot de Beauvois), Stejneger, 1907:449.

Ancistrodon, Smith, 1943:495 (part).

Diagnosis.—Asiatic pitvipers having large supracephalic shields; palatine having elongate dorsal appendage and 1 to 4 teeth; dorsal scales in 23 or 25 rows, strongly keeled or smooth; ectopterygoid slender, straight, and bifurcate; basal portion of pterygoid longer than ectopterygoid; pterygoid teeth 8 to 13, extending posterior past articulation with ectopterygoid; margin of maxillary cavity a simple curve; lateral caudal scales higher than long; subcaudals all divided or some basal subcaudals entire; nasal pore situated near internal rim of nasal pad.

Calloselasma agrees with Agkistrodon and Hypnale in supracephalic scutellation and proportions and dentition of the pterygoid. Calloselasma differs from Agkistrodon and Hypnale in shape and dentition of the palatine and the shape of the lateral caudal scales.

Definition.—Size large, reaching a total length of 0.9 m in C. rhodostoma and 1.5 m in C. acutus; dorsal pattern consisting of dark brown spots or crossbands; cranium long and narrow, its width much less than its length; border of maxillary cavity a simple curve; prootic sloping gradually ventrolateral with no dorsolateral ridge; anterior foramen of prootic divided by heavy partition of bone into small lower and large upper foramen; palatine having elongate dorsal appendage; pterygoid teeth 8 to 13, extending beyond articulation with ectopterygoid; basal part of pterygoid longer than ectopterygoid; ectopterygoid slender, straight, cylindrical; squamosal long and slender, its greatest width one-fourth to one-third its length, its length over one-half length of quadrate; quadrate much shorter than length of cranium; mandibular teeth 12 to 14; splenial separate from angular; distal one-third of tail nearly twice as high as wide; scales adjacent to distal subcaudals columnar structures over twice as high as long.

Composition.—C. rhodostoma (Boie) and C. acutus (Günther).

Distribution.—Formosa, Hainan, and southern China through Laos, Vietnam, Cambodia, Thailand, and Malaya, to Java and Sumatra.

AGKISTRODON PALISOT de BEAUVOIS

Agkistrodon Palisot de Beauvois, 1799:381 (A. mokasen); Stejneger, 1907:449; Gloyd and Conant, 1943:147 (synopsis of American species); Dunn, 1944a:213; Ruiz, 1951:110, pl. 1-2; Klauber, 1956:259 (correct spelling); Klemmer, 1963:397; Werler and Keegan, in Keegan and MacFarlane, 1963:273; Brattstrom, 1964: 229.

Scytale Sonnini and Latreille, 1801:158 (name preoccupied by Menachen, 1778); Harlan, 1827:50.

Cenchris Daudin, 1803:188 (*Crotalus piscivorus* Lacépède); Harlan, 1827:49; Wagler, 1830:175.[4]

Trigonocephalus (*nec* Oppel), Kuhl, 1822:483; Wagler, 1830:173; Schlegel, 1837:527 (part); Duméril, 1853:132; Duméril, Bibron, and Duméril, 1854:1488; Cope, 1859:335; Cope, 1896:212.

Tisiphone Fitzinger, 1826:34 (*Scytale cupreus* Rafinesque; preoccupied by *Tisiphone* Huebner, 1819, Lepidoptera); Peters, 1862:671.

Ancistrodon (invalid emendation of *Agkistrodon*, Wagler, 1830:176; Baird, 1854:13; Peters, 1862:671; Cope, 1859:335; Garman, 1883: 120; Smith, 1943:495.

Acontias Troost, 1836:176 (*A. leucostoma* Troost; *nec* Cuvier, 1817, Viperidae).

Toxicophis Troost, 1936:190.

Diagnosis.—American pitvipers having large supracephalic shields in the colubrid pattern; palatine lacking dorsal appendage, having 3 or more teeth; dorsal scales in 23 or 25 rows, strongly keeled; subcaudals of basal third or more of tail entire; ectopterygoid broad and strongly curved; basal portion of pterygoid longer than ectopterygoid; pterygoid teeth 12 to 21, extending posterior past

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[4] *Cenchris* Gronovius, 1763, is nomenclaturally unavailable according to opinions 20 and 89 of the International Commission on Zoological Nomenclature.

articulation with ectopterygoid; margin of maxillary cavity with definite projection; lateral caudal scales longer than high; nasal pore situated near internal rim of nasal pad.

Agkistrodon agrees with Calloselasma and Hypnale in supracephalic scutellation and proportions and dentition of the pterygoid. Agkistrodon differs from Calloselasma in shape and dentition of the palatine and the shape of the lateral caudal scales. Agkistrodon differs from Hypnale in the number of dorsal scale rows, in the arrangement of subcaudals, and in many aspects of the skull.

Definition.—Size moderate to large, reaching a total length of 1.5 m; dorsal pattern consisting of brown or black crossbands; cranium moderately short and broad, its width equal to or slightly greater than its length; border of maxillary cavity divided by projection; prootic sloping gradually ventrolateral with no dorsolateral ridge; anterior foramen of prootic divided by heavy partition of bone into small lower foramen and large upper foramen; palatine with 3 to 5 teeth; dorsal extension of palatine a broad triangular or rounded projection; pterygoid teeth 14 to 17, extending beyond articulation with ectopterygoid; basal part of pterygoid longer than ectopterygoid; ectopterygoid broad and strongly curved with dorsal surface forming smooth convex curve; squamosal long and slender, its greatest width one-fourth to one-third its length, its length over one-half length of quadrate; quadrate as long as or slightly shorter than cranium; mandibular teeth 12 to 21; splenial separate from angular; hemipenis divided for three-quarters length; apical portion calyculate in A. bilineatus, finely flounced and calyculate in A. piscivorus.

Composition.—Three American species — *A. bilineatus* Günther, *A. contortrix* Linnaeus, and *A. piscivorus* — with a total of ten subspecies.

Distribution.—Eastern North America from Massachusetts and Connecticut to Florida and west to Kansas, Oklahoma, and south and west Texas; much of México through Central America to Nicaragua.

OVOPHIS NEW GENUS

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part); Rooij, 1917:281 (part).

Trimeresurus (*nec* Lacépède), Stejneger, 1907:465 (part); Taylor, 1922:283 (part); Pope, 1935:403 (part); Bourret, 1936:456 (part); Maslin, 1942:18 (part); Smith, 1943:502 (part); Tweedie, 1954:116 (part); Klemmer, 1963:429 (part); Werler and Keegan, *in* Keegan and MacFarlane, 1963:277 (part); Brattstrom, 1964:250 (part).

Type species.—*Ovophis monticola* is hereby designated type species of the genus *Ovophis*.

Diagnosis.—Asiatic rattleless, scale-snouted pitvipers; nasal pore situated prominently near external rim of nasal pad; supraocular scales small; gular scales smooth; subcaudals single and paired; border of maxillary cavity having rounded projection forming two distinct curvatures; ectopterygoid having truncate anterior dorsolateral projection; pterygoid teeth extending nearly to posterior margin of articulation with ectopterygoid; basal portion of pterygoid shorter than ectopterygoid (Figure 5); splenial fused to angular; nasal pore near external rim of nasal pad.

In contrast *Tropidolaemus* has rudimentary nasal pore, strongly keeled gulars, and splenial separate from angular. *Trimeresurus* has a shorter series of pterygoid teeth than *Ovophis*.

Definition.—Size moderate, total length to 1.1 m; dorsal pattern consisting of dark brown spots; cranium moderately wide, its greatest width greater than its length; border of maxillary cavity forming a simple curve; prootic sloping evenly ventrolaterally without distinct dorsolateral ridge; anterior foramen of prootic not divided by bony partition; palatine having 4 teeth; dorsal projection of palatine a broad, very much rounded triangle with highest point slightly posterior to three-fourths length of palatine; pterygoid teeth 11, extending to or nearly to posterior edge of articulation with ectopterygoid; basal portion of pterygoid longer than ectopterygoid; ectopterygoid curved and extremely broad with truncate dorsolateral projection; squamosal long and narrow, its greatest width about one-third its length; quadrate shorter than cranium; mandible with splenial separate from angular, having 17 teeth; hemipenis divided for about two-thirds length, basal two-thirds spinous, distal one-third calyculate.

Composition.—Four species, one with three subspecies: *Ovophis chaseni* (Smith), *O*. *convictus* (Stoliczka), *O*. *monticola monticola* (Günther), *O*. *monticola mkazayazya* (Takahashi), *O*. *monticola tonkinensis* (Bourret), *O*. *okinavenis* (Boulenger).

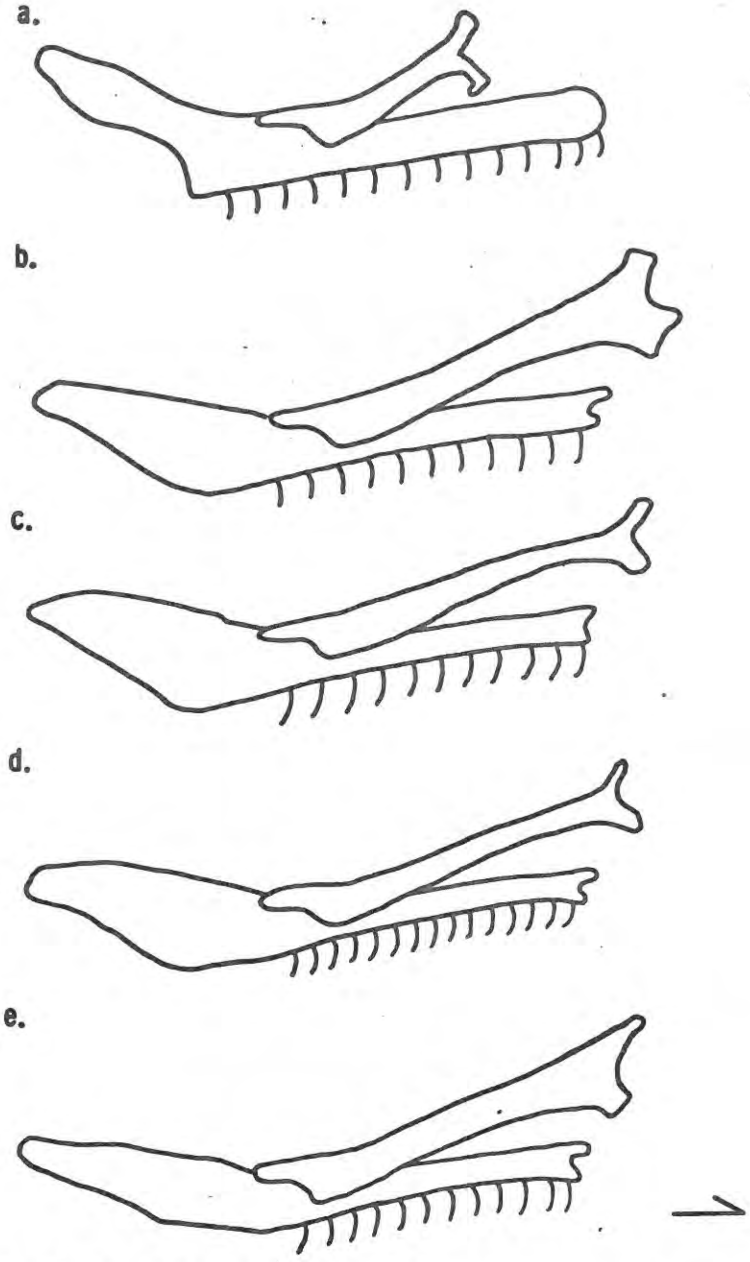

FIG. 5. Comparison of pterygoid (toothed) and ectopterygoid (diagramatic and not scaled): a, *Hypnale*; b, *Ovophis*; c, *Porthidium*; d, *Bothrops*; e, *Trimeresurus*.

Distribution.—Mountains of the Indo-Chinese region from southern China to Nepal, Assam, Burma, Malaya, Formosa, Okinawa, and Borneo.

TRIMERESURUS LACEPEDE

Trimeresurus *Lacépède*, 1804:195 (*T. viridis* Beckstein; subseq. desig., Stejneger, 1907:465); Peters, 1862:671; Günther, 1864:384; Stejneger, 1907:465 (part); Rooij, 1917:281 (part); Taylor, 1922:283 (part); Amaral, 1926b:34; Pope, 1935:403; Bourret, 1936:456 (part); Smith, 1942:256 (systematic status; part); Smith, 1943:502 (part); Dunn, 1944:213; Ruiz, 1951:110 (part; skull); Tweedie, 1954:116 (part); Klemmer, 1963:429 (part); Werler and Keegan, *in* Keegan and MacFarlane, 1963:277 (part); Brattstrom, 1964:250 (part).

Craspedocephalus Kuhl, 1822:417.

Atropos Wagler, 1830:175 (*Cophias punicea* Reinwardt *in* Boie, 1827; subseq. desig. Fitzinger, 1843: *nec* Leach, 1915, Psocoptera); Dumeril, 1953:139 (part); Duméril, Bibron, and Duméril, 1854: 1517; Peters, 1862:671; Gray, 1849:13.[5]

Megaera *Wagler*, 1830:174 (*Vipera trigonocephala* Sonnini and Latreille; monotypy); Peters, 1862:671.

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[5] Neither *Atropos* Rafinesque, 1815, nor *Atropos* Oken, 1815, need be considered. The former is a *nomen nudum*. The latter was not validly published inasmuch as Oken's "Lehrbuch" is not consistently binomial.

Bothrops (*nec* Wagler), Wagler, 1830:271 (part); Duméril, Bibron, and Duméril, 1854:1517.

Trigonocephalus (*nec* Oppel), Schlegel, 1837:527 (part).

Trimesurus Swainson, 1839:363 (invalid emendation of *Trimeresurus* Lacépède); Gray, 1842:48 (part); Gray, 1849:7 (part).

Bothrophis Fitzinger, 1843:48 (*T. viridis* Cuvier; orig. desig.).

Parias Gray, 1849:11 (*Megaera flavomaculatus* Gray; subseq. desig., M. Smith, 1943:502).

Cryptelytrops Cope, 1859:334 (*Trimeresurus carinatus* Gray; monotypy).

Peltopelor Günther, 1864:390 (type *Trimeresurus macrolepis* Beddome; monotypy); Cope, 1896:212.

Atropophis Peters, 1872:41 (*nomen novum* for *Atropos* Wagler, preoccupied).

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part).

Diagnosis.—Asiatic rattleless, scale-snouted pitvipers; nasal pore situated prominently near external rim of nasal pad; supracephalic scales small or regrouped into plates not arranged as in *Agkistrodon* and *Sistrurus*; gular scales smooth; subcaudals entirely divided; border of maxillary cavity having a distinct projection that forms two separate curvatures; ectopterygoid extremely broad, having pterygoid teeth extending to posterior one-half of articulation with ectopterygoid; truncate anterior dorsolateral projection splenial fused to angular; nasal pore situated near external rim of nasal pad.

Trimeresurus and *Ovophis* have the nasal pore located near the external rim of the nasal pad, whereas the nasal pore is rudimentary in Tropidolaemus. The splenial is separate in Tropidolaemus and fused to the angular in the first two genera. Ovophis has the subcaudals partly entire and partly divided and interoculars smooth, whereas Trimeresurus has subcaudals divided and interoculars keeled (in most species). Tropidolaemus has keeled gular scales, whereas they are smooth in Ovophis and Trimeresurus.

Definition.—Moderate to large size snakes reaching total lengths from 0.4 to 1.2 m in all but one species, 1.4 m in T. kaulbacki; dorsum gray or brown having darker gray or brown spots or crossbands or green, either plain or having ventrolateral stripes; nasal pore on external rim of nasal pad; cranium with varied proportions, its greatest width slightly more, equal to, or slightly less than length; border of maxillary cavity having a distinct projection forming two separate curvatures; prootic sloping evenly ventrolaterally without distinct dorsolateral ridge; anterior foramen of prootic not divided by bony partition; palatine having 0 to 4 teeth; dorsal projection of palatine broad and rounded, having highest point anterior to mid-length of palatine; pterygoid teeth 10 to 12, teeth extending to posterior one-half or three-fourths of articulation with ectopterygoid; basal portion of pterygoid shorter than ectopterygoid; ectopterygoid extremely broad, with truncate anterior dorsolateral projection; squamosal long and narrow, its greatest width about one-third its length; quadrate shorter than cranium; mandible with splenical fused to angular, having 11 or 12 teeth; hemipenis either (1) short and thick, having numerous, well developed spines or (2) long and slender, entirely devoid of spines.

Composition.—Seven species groups including 26 species. *Trimeresurus albolabris* group: *T. albolabris* Gray, *T. fasciatus* Boulenger, *T. labialis* Steindachner, *T. macrolepis* Beddome, *T. mutabilis* Stoliczka, *T. popeorum* Smith. *Trimeresurus gramineus* group: *T. gramineus* (Shaw), *T. stejnegeri* Schmidt. *Trimeresurus jerdoni* group: *T. flavoridis* (Hallowell), *T. jerdoni* (Günther), *T. strigatus* Gray. *Trimeresurus mucrosquamatus* group: *T. elegans* (Gray), *T. mucrosquamatus* (Cantor). *Trimeresurus puniceus* group: *T. borneenis* (Peters), *T. cornutus* Smith, *T. gracilis* Oshima, *T. kanburiensis* Smith, *T. malabaricus* (Jerdon), *T. puniceus* (Boie), *T. trigonocephalus* Sonnini and Latreille. *Trimeresurus purpureomaculatus* group: *T. cantori* Blyth, *T. erythrurus* Cantor, *T. purpureomaculatus* (Gray). *Trimeresurus sumatranus* group: *T. flavomaculatus* (Gray), *T. schultzi* Griffin, *T. sumatranus* (Raffles).

Distribution.—Most of southeastern Asia.

TROPIDOLAEMUS WAGLER

Tropidolaemus Wagler, 1830:175 (*Cophias wagleri*; monotypy); Duméril, 1853:535; Duméril, Bibron, and Duméril, 1854:1523; Peters, 1862: 671.

Trigonocephalus (*nec* Oppel), Schlegel, 1837:527 (part).

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part); Rooij, 1917: 281 (part).

Trimeresurus (nec Lacépède, 1804), Bourret, 1936:456 (part); Ruiz, 1951:110 (part; skull); Tweedie, 1954:116 (part); Klemmer, 1963:429 (part); Werler and Keegan, in Keegan and MacFarlane, 1963:277 (part); Brattstrom, 1964:250 (part).

Bothrops (nec Wagler), Maslin, 1942:18 (included T. wagleri and T. philippensis).

Diagnosis.—Asiatic rattleless, scale-snouted pitvipers; nasal pore rudimentary; opening in suture beside nasal pad; supracephalic scales small; gular scales strongly keeled; subcaudals entirely divided; border of maxillary cavity having rounded projection forming two distinct curvatures; ectopterygoid having truncate anterior dorsolateral projection; pterygoid teeth extending to posterior one-third of articulation with ectopterygoid; basal portion of pterygoid shorter than ectopterygoid; splenial separate from angular.

Tropidolaemus is relatively stout and broad headed, has strongly keeled gulars, and splenial separate from angular as contrasted to the other Asiatic genera.

Definition.—Moderately large snakes, reaching maximum total lengths of 0.7 m; dorsum yellow and green variously marked with white, brick red, dark green, or black spots or crossbands, or almost entirely black; cranium extremely short and broad; lower lumen of maxillary fang medial; border of maxillary cavity having projection that forms two distinct curvatures; prootic with an irregularly sinuous ridge that extends from near anterior end of squamosal to external auditory meatus; anterior foramen of prootic not divided by bony partition; palatine having 5 or 6 teeth; dorsal extension of palatine broad and low, with highest point anterior to mid-length of palatine; pterygoid teeth 12 to 15, extending onto posterior one-third of articulation with ectopterygoid; ectopterygoid broad and curved, having truncate anterior dorsolateral projection; squamosal slender, its greatest width less than one-third its length, and short, its length less than one-half that of quadrate; quadrate longer than cranium; mandible having 11 to 16 teeth; splenial separate from angular; hemipenis spinous to extreme tip, entirely lacking calyces.

Composition.—Monotypic, containing only Tropidolaemus wagleri (Boie).

Distribution.—Malay Peninsula, Indonesia, and the Philippine Islands.

OPHRYACUS COPE

Trigonocephalus (nec Oppel), Jan, 1859:157 (part).

Teleuraspis (nec Cope), Garman, 1883:126 (part).

Ophryacus Cope, 1887b:88 (Trigonocephalus undulatus Jan; monotypy).

Bothrops (nec Wagler), Günther, 1895:188 (part); Amaral, 1926b:34 (systematic status; part); Smith and Taylor, 1945:179; Amaral, 1946:13 (systematic status; part); Ruiz, 1951:110 (part); Klauber, 1956:117 (part); Klemmer, 1963:402 (part); Brattstrom, 1964:246 (part).

Lachesis (nec Daudin), Boulenger, 1896:529 (part).

Trimeresurus (nec Lacépède), Duméril, Bocourt, and Mocquard, 1909: 937 (part); Smith, 1941:61 (part); Pope, 1955:224 (part);

Neill, 1964:39 (part).

Diagnosis.—Mexican arboreal pitvipers having distinctive tail, cephalic scutellation, coloration, and skull; subcaudals divided; terminal caudal scute elongate; lateral caudal scutes unmodified; interoculars 13 to 18; frontorostrals 8 to 10; dorsal blotches rounded and situated high on back; border of maxillary cavity divided into two distinct curvatures by rounded projection; ectopterygoid having truncate anterior dorsolateral projection; quadrate shorter than cranium; prootic having distinct dorsolateral ridge; anterior foramen of prootic bipartite; width of posterior end of squamosal more than one-half its length; nasal pore situated near internal rim of nasal pad.

Like Bothriopsis, Ophryacus has the nasal pore situated deep in the nostril, a prehensile tail, divided subcaudals, elongate terminal caudal scute, and unmodified lateral caudal scales. In critical features of the skull Ophryacus is intermediate between Bothriopsis and Trimeresurus. The projecting supraocular scale, the coloration of rounded blotches high on the back, and the numerous interoculars and frontorostrals of Ophryacus (Figure 2) are superficial distinctions from Bothriopsis. Bothriechis is also arboreal but has entire subcaudals, terminal caudal scute very small, and scales of lateral caudal rows strongly keeled on the posterior third of the tail. The Asiatic Tropidolaemus, Ovophis, and Trimeresurus have distinctive nasal pores. The prehensile tail and green color sets Ophryacus aside from terrestrial genera.

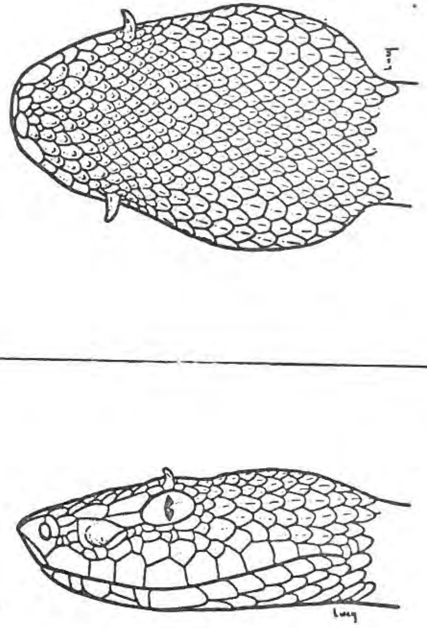

FIG. 6. *Ophryacus undulatus*. Topotype. USNM 6319a (X 2), Orizaba, Veracruz, Mexico. *Top*—Dorsal view of head. *Bottom*—Lateral view of head.

Definition.—Size moderate, reaching maximum total length of 0.7 m; approximately as high as wide at mid-body; head slightly wider than body; coloration green stippled with black and having two series of rounded brown spots on each side; supracephalic scales small and numerous; marginals 5; frontorostrals 8 to 10; interoculars 13 to 18; interictals 26 to 31; supralabials 9 to 12; infralabials 11 to 12; dorsals strongly keeled, in 21 rows; ventrals 162 to 172; subcaudals 39 to 45 (Tables 8 and 9); cranium moderately wide, its greatest width greater than its length; border of maxillary cavity having slight rounded projection dividing border into two distinct curvatures (similar to Ruiz, 1951, fig. 2); prootic with distinct dorsolateral ridge forming angle between side and top of skull in ear region; bony partition dividing anterior foramen of prootic into small lower and large upper foramen; palatine with 4 teeth; dorsal extension of palatine a broad, rounded triangle with its apex near anterior end of palatine and with sides nearly straight; pterygoid teeth 10, extending to posterior one-third of articulation between ectopterygoid and pterygoid; basal portion of pterygoid shorter than ectopterygoid; ectopterygoid broad and flat with truncate anterior dorsolateral projection; squamosal short and broad, its greatest width about two-thirds its length; quadrate shorter than cranium; mandible having 9 teeth and splenial fused to angular; hemipenis deeply bifurcate; length of lobe three-fifths length of penis; undivided base bare except for two enormous spines at point of bifurcation; proximal two-fifths of lobe equipped with large spines reducing in size distally; distal three-fifths of lobe with spinous calyces; transition from

2/5

spines to calyces abrupt; penis in situa extends to subcaudal 11.

Composition.—Ophryacus is monotypic, comprising O. undulatus.

Distribution.—Ophryacus undulatus occurs in high mountains bordering the Mexican Plateau in Guerrero, Oaxaca, and Veracruz.

BOTHRIECHIS PETERS

Bothrops (nec Wagler), Duméril, Bibron, and Duméril, 1854:1517 (part); Dunn, 1919:214; Amaral, 1926:34 (systematic status; part); Amaral, 1930c:233 (part); Smith and Taylor, 1945:179; Amaral, 1946b:13 (systematic status; part); Ruiz, 1951:110 (part); Maldonado-Koerdell, 1953:132 (part); Klauber, 1956:117 (part); Peters, 1960:494 (part) Klemmer, 1963:402 (part); Brattstrom, 1964:246 (part).

Bothriechis Peters, 1859:278 (Bothriechis nigroviridis Peters; monotypy); Cope, 1860:345; Peters, 1862:671 (part); Cope, 1876a: 149; Cope, 1887b:88; Günther, 1895:188 (part).

Teleuraspis Cope, 1859:338 (Trigonocephalus schlegeli Berthold; subseq. desig., Dunn and Dunn, 1940:69); Cope, 1860b:345; Cope, 1876a:149; Garman, 1883:126 (part); Cope, 1887b:88.

Thamnocenchris Salvin, 1860:459 (Thamnocenchris aurifer Salvin; monotypy); Cope, 1862:337.

Bothriopsis (nec Peters), Bocourt, 1876:409.

Lachesis (nec Daudin), Boulenger, 1896:521 (part); Griffin, 1916:222 (part).

Trimeresurus (*nec* Lacépède), Duméril, Bocourt, and Mocquard, 1909: 927 (part); Smith, 1941:61 (part); Pope, 1955:224; Neill, 1964:39.

Diagnosis.—Central American arboreal pitvipers having nasal pore situated deep in nostril and distinctive prehensile tail, ectopterygoid, and palatine; length of terminal caudal scute less than that of 2 preceding subcaudals; subcaudals entire; first and second rows of dorsal scales on terminal one-third of tail heavily keeled; either middle of supracephalic surface devoid of enlarged plates or frontal and parietals, when present, separated from each other by small plates or by scales; ectopterygoid broad and slightly curved, without truncate dorsolateral projections; palatine triangular with apex near or posterior to mid-palatine (Figure 5).

Other arboreal pitvipers (*Bothriopsis*, *Ophryacus*, *Trimeresurus*, and *Tropidolaemus*) have dorsolateral projections of the ectopterygoid, differently shaped palatine, and differently modified tail. None have heavily keeled lower scalerows on the terminal one-third of the tail. In *Trimeresurus* the nasal pore is situated on the external margin of the nasal pad and in *Tropidolaemus* it is rudimentary.

Definition.—Moderate to large-sized snakes, reaching maximum lengths of 0.7 to 0.9 m; mid-body much higher than wide. Adult coloration in all species but one green, either plain, with ventrolateral yellow stripes, or with yellow and black stippling and spots; *schlegeli* variously brown-banded, yellow with black dots, or greenish brown with red markings. Supracephalic scutes enlarged, approaching in *B. aurifer* the condition in *Porthidium barbouri*, or

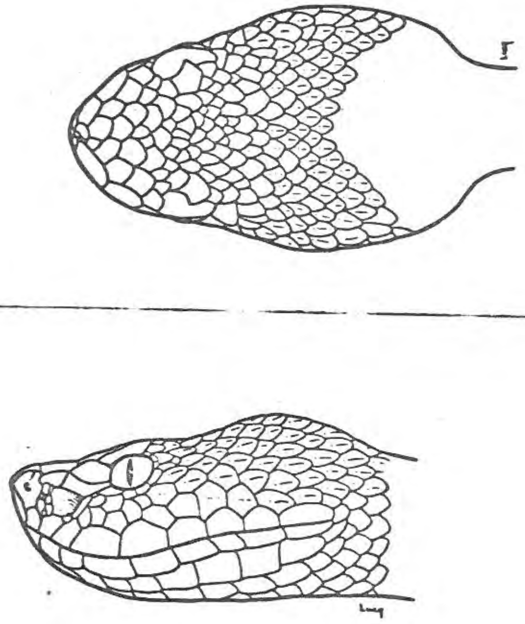

FIG. 7. *Bothriechis nigroviridis*. KU 31954 (X 2), San Isidro del General, Costa Rica. *Top*—Dorsal view. *Bottom*—Lateral view.

subdivided into scales; frontorostrals 2 to 12; interoculars 3 to 12; interictals 18 to 35; supralabials 8 to 11; infralabials 9 to 13; dorsal scales above rows 1 to 3 distinctly keeled; dorsal scales in 19 to 25 rows; ventrals 138 to 175; subcaudals 36 to 73 (tables 7 and 8). Cranium moderately wide, its greatest width slightly greater than its length; border of masillary cavity with slight projection, forming 2 distinct curvatures; dorsal portion of prootic sloping ventrolaterally without dorsolateral ridge; anterior foramen of prootic divided in two by thin bony partition that approaches external orifice; palatine with 3 to 5 teeth; dorsal extension of palatine a broad triangle with apex near or posterior to mid-palatine; pterygoid teeth 11 to 18, extending to (or nearly to) posterior margin of articulation between ectopterygoid and pterygoid; basal portion of pterygoid shorter than ectopterygoid; ectopterygoid broad and slightly curved with anterior convexity of lateral margin but no anterior bifurcation; squamosal long (about three-fifths as long as quadrate) and moderately wide, its greatest width one-third or slightly more of its length; quadrate as long as or slightly shorter than cranium; mandible with 12 to 18 teeth and with splenial and angular separate. Hemipenis divided for over one-half its length; large spines interspersed with some smaller spines covering base of each lobe and adjacent part of undivided base, giving way abruptly to spinulate calyces terminally; calyculate terminal portion over one-third length of hemipenis.

Composition.—*Bothriechis* is composed of a compact group of five upland tree vipers and the specialized, widespread species, *B. schlegeli*. Of the upland forms *marchi* is regarded as a subspecies of *B. aurifer* and specifically distinct from *B. nigroviridis*, with which it previously has been linked. Although *B. schegeli* is unique in several respects its origin lies close to other existing *Bothriechis*.

Bothriechis nigroviridis group
- *B. aurifer aurifer*
- *B. aurifer marchi*
- *B. bicolor*
- *B. lateralis*
- *B. nigroviridis*

Bothriechis schlegeli group
- *B. schlegeli schlegeli*
- *B. schlegeli nigroadspersus*

Distribution.—Species of *Bothriechis* range from eastern Oaxaca and Chiapas, México to Colombia, western Ecuador, and western Venezuela. The genus is restricted to the Central American highlands, except for *B. schlegeli*, which inhabits lowland rain forest and ranges into South America.

BOTHRIOPSIS PETERS

Bothrops (*nec* Wagler, 1824), Wagler, 1830:271 (part); Duméril, Bibron, and Duméril, 1854:1517; Amaral, 1926b:34 (systematic status; part); Dunn, 1944:213 (part); Amaral, 1946b:13 (systematic status;

part); Ruiz, 1951:110 (part); Klauber, 1956:117; Peters, 1960: 494; Klemmer, 1963:402; Brattstrom, 1964:246.

Atropos (*nec* Wagler), Duméril, 1953:139.

Bothriopsis Peters, 1861a:359 (*Bothriopsis quadriscutatus* Peters = *B. castelnaudi quadriscutatus*; monotypy); Bocourt, 1876:409; Cope, 1887b:88.

Trigonocephalus (*nec* Oppel), Schlegel, 1837:527 (part); Peters, 1862: 672.

Bothriechis (*nec* Peters), Günther, 1895:188 (part).

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part).

Trimeresurus (*nec* Lacépède), Pope, 1955:224; Neill, 1964:39.

Diagnosis.—South American arboreal pitvipers with distinctive caudal scutellation and skull; subcaudals partly or entirely divided; lateral caudal scutes unmodified; terminal caudal scute longer than two preceding subcaudals; supraoculars not projecting; interoculars 3 to 9; frontorostrals 3 to 7; nasal pore near inner margin of nasal pad; border of maxillary cavity an uninterrupted curve; ectopterygoid lacking anterior dorsolateral projections; quadrate relatively short.

Bothriopsis and *Ophryacus* are the only American arboreal pitvipers having unmodified lateral caudal scutes and having subcaudals partly or entirely divided. In the cranial features cited above *Bothriopsis* differs from *Ophryacus*, *Tropidolaemus*, and *Trimeresurus*. Only relatively minor external differences distinguish *Bothriopsis* from *Ophryacus*. The latter has a projecting "eyelash" scale over each eye and more numerous interoculars and frontorostrals than the latter. *Tropidolaemus* has a rudimentary nasal pore and

Trimeresurus has the nasal pore near the external margin of the nasal pad. Other genera of pitvipers are terrestrial and differ drastically from *Bothriopsis*.

Definition.—Medium to large sized snakes; four species reaching maximum lengths of 0.7 to 0.8 m; *B. bilineata*, *B. punctata*, and *B. castelnaudi* reaching maximum lengths of 0.9, 1.1, and 1.2 m respectively; mid-body higher than wide. Coloration varied, green or brownish with ventrolateral yellow stripes, dark spots, or dark crossbands; *B. castelnaudi plorator* marbled black and white. Supracephalic surface covered with scales; enlarged supracephalic scutes usually present only in *B. medusa*, separated from one another by rows of small scales; frontorostrals 3 to 7; interoculars 3 to 9; interictals 19 to 35; supralabials 7 to 9; infralabials 8 to 12; dorsal scales in 19 to 35 rows; ventrals 155 to 250; subcaudals 41 to 93 (see Tables 12 and 13). Cranium not especially broad, its greatest width equal to or slightly less than its length; border of maxillary cavity a simple uninterrupted curve; prootic with dorsolateral ridge which is well developed in *B. bilineata* and *B. punctata* but low and rounded in *B. medusa*; anterior foramen of prootic divided by bony partition into small lower and large upper foramen; palatine with 3 to 8 teeth; dorsal extension of palatine with highest point at or posterior to mid-palatine, narrow, and digitiform in *B. medusa*, broad and low in *B. bilineata*, or acute triangle with apex directly forward in *B. punctata*; pterygoid teeth 14 to 21, extending posterior beyond articulation of ectopterygoid and pterygoid; basal portion of pterygoid shorter than ectopterygoid; ectopterygoid moderately slender, curved to present an upper convex surface and a lower concave surface and forked anteriorly; squamosal two-thirds as long as quadrate, narrow, its greatest width less than one-third its length; quadrate shorter than cranium; mandible having separate splenial and angular and having 16 to 20 teeth; hemipenis divided for one-half its length; proximal three-fourths having scattering of large recurved spines; calyculate distal half of each lobe cylindrical, slightly tapering, having blunt rounded end (Vellard, 1946:282).

Composition.—The genus is composed of three groups, the *B. castelnaudi* group with three species, the *B. punctatus* group with two species, and the *B. bilineata* group with two species. The nominate species of the first and last groups are polytypic: *B. bilineata* has two subspecies, *B. castelnaudi* has four.

- *Bothriopsis castelnaudi* group
  - *B. albocarinatus*
  - *B. castelnaudi castelnaudi*
  - *B. castelnaudi lichenosus*
  - *B. castelnaudi plorator*
  - *B. castelnaudi quadriscutatus*
  - *B. medusa*
- *Bothriopsis punctatus* group
  - *B. oligolepis*
  - *B. punctatus*
- *Bothriopsis bilineatus* group
  - *B. bilineatus bilineatus*

B. bilineatus smaragdinus

B. peruvianus

Distribution.—Central and northern South America from Brazil and Bolivia to Panamá. Most species occur in, or adjacent to, the Andes of northern South America. *Bothriopsis bilineata* and *B. castelnaudi* range widely through the Amazon Valley and beyond. *Bothriopsis punctata* ranges a short distance into Panamá.

BOTHROPS WAGLER

Coluber (*nec* Linnaeus, 1758), Linnaeus, 1766:383 (part); Lacépède, 1789:80 (part).

Vipera (*nec* Laurenti, 1768), Laurenti, 1768:103 (part); Latreille, 1802:325 (part).

Bothrops Wagler, 1824:50 (part; *B. lanceolatus*; subseq. desig., Fitzinger, 1843); Wagler, 1830:271 (part); Duméril, Bibron, and Duméril, 1854:1517 (part); Garman, 1883:12 (part); Cope, 1887b: 88; Günther, 1895:188 (part); Amaral, 1926b:34 (systematic status; part); Dunn, 1944:213 (part); Smith and Taylor, 1945: 179 (part); Amaral, 1946b:13 (systematic status; part); Ruiz, 1951:110 (part); Maldonado-Koerdell, 1953:132; Klauber, 1956: 117; Peters, 1960:494; Klemmer, 1963:402; Brattstrom, 1964:246.

Craspedocephalus (*nec* Kuhl), Fitzinger, 1826:62 (part); Gray, 1849:6.

Trigonocephalus (*nec* Oppel), Schlegel, 1837:527 (part); Peters, 1862:672.

Rhinocerophis Garman, 1881:85 (*R. nasus* Garman).

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part); Griffin, 1916:222 (part).

Trimeresurus (*nec* Lacépède), Duméril, Bocourt, and Mocquard, 1909: 927 (part); Smith, 1941:61 (part); Pope, 1955:225 (part); Neill, 1964:39 (part).

Diagnosis.—South American terrestrial pitvipers having small supracephalic scales, subcaudals divided, nasal pore situated deep in nostril, and distinctive skull; palatine uniquely bifurcate; border of maxillary cavity an uninterrupted curve.

In contrast, *Porthidium* has entire subcaudals and a two-part curve in the border of the maxillary cavity, *Agkistrodon* has enlarged supracephalic scutes and the ectopterygoid shorter than the basal portion of the pterygoid, and *Lachesis* has subdivided distal subcaudals and a hollow aponeurosis. Other American genera are distinctly arboreal. Among Asiatic genera *Trimeresurus* and *Ovophis* have the nasal pore situated close to the external margin of the nasal pad and *Tropidolaemus* has the nasal pore reduced to a rudiment.

Definition.—Medium to very large snakes, with maximum lengths ranging from 0.3 or 0.4 m to 3.0 m; varying in proportions from moderately slender as in *B. atrox* to heavy bodied as in *B. alternata*. Coloration variously spotted or banded. Supracephalic surface covered with scales or small scutes; frontorostals 2 to 8; interoculars 3 to 14; interictals 31 to 34; supralabials 7 to 12; infralabials 8 to 14; dorsal scales in 19 to 33 rows; ventrals 137 to 230; subcaudals 26 to 74. Cranium not especially broad, its greatest width equal to or slightly less than its length; border of maxillary cavity simple uninterrupted curve; prootic having well-developed dorsolateral ridge extending anterior from external auditory meatus; anterior foramen of prootic divided by bony partition into small lower and large upper foramen; palatine having 2 to 5 teeth; dorsal extension of palatine either narrow and digitiform or broad and angular, having anterior border perpendicular to ventral border or sloping anterodorsal; pterygoid teeth 14 to 21 in *B. atrox* and *B. jararacussu*, 9 to 11 in *B. alternata*, *B. cotiara*, and *B. neuwiedi*, extending to point just short of posterior margin of articulation between ectopterygoid and pterygoid; ectopterygoid slender and curved, having concave margins, convex upper surface, concave lower surface, and bifurcate anterior end; squamosal moderately long and slender, its greatest width about two-fifths its length and its length about three-fifths length of quadrate; quadrate shorter than cranium; mandibular teeth 10 to 12 in *B. alternata* and *B. neuwiedi*, 14 to 17 in *B. atrox* and *B. jararacussu*; splenial and angular separate, except in *B. alternata* which has the two fused together. Hemipenis deeply divided having calyculate ends abruptly differentiated from spiny base.

Vellard (1946:282) distinguished a southern group of species (*B. neuwiedi*, *B. alternata*, and *B. cotiara*) from a northern group (*B. atrox*, *B. jararaca*, and *B. jararacussu*) by the structure of the hemipenis. The hemipenis of the former group is short and has a short conical calyculate apex with a small rounded tip. Species of the northern group have longer hemipenes, in which the calyculate apex is a slightly tapered cylinder comprising at least one-third the total length of the organ and with a blunt tip, like a finger. Hemipenes of the small southern species *B. itapetiningae*, *B. erythromelas*, and *B. ammodytoides* are like those of the so-called northern group.

Composition.—Forty taxa are contained in four species groups. The *Bothrops atrox* group has lacunalabials and includes the following 20 species and subspecies: *B. andiana*, *B. asper*, *B. atrox*, *B. barnetti*, *B. brazili*, *B. caribbaea*, *B. insularis*, *B. jararaca*, *B. jararacussu*, *B. lanceolata*, *B. lojana*, *B. marajoensis*, *B. moojeni*, *B. picta*, *B. pifanoi*, *B. pirajai*, *B. pradoi*, *B. pulchra*, *B. santaecrucis*, and *B. xanthogramma*. The *Bothrops neuwiedi* group has the prelacunal separate from the supralabials and includes the following 15 species and subspecies: *B. iglesiasi*, *B. itapetiningae*, *B. neuwiedi neuwiedi*, *B. neuwiedi boliviana*, *B. neuwiedi dipora*, *B. neuwiedi fluminensis*, *B. neuwiedi goyazensis*, *B. neuwiedi lutzi*, *B. neuwiedi mattogrossensis*, *B. neuwiedi paranaensis*, *B. neuwiedi pauloensis*, *B. neuwiedi piauhyensis*, *B. neuwiedi pubescens*, and *B. neuwiedi urutu*. The *Bothrops alternatus* group includes the following three species: *B. alternata*, *B. cotiara*, and *B. fonsecai*. These are large snakes, reaching maximum lengths of 0.8 to 1.4 m, and have the prelacunal separate from the supralabials, one internasal on each side, and 9 to 14 interoculars. The *Bothrops ammodytoides* group includes the following 4 species and subspecies: *B. ammodytoides*, *B. microphthalma microphthalma*, *B. microphthalma colombiana*, and *B. roentingeri*. These are small snakes reaching maximum lengths of 0.5 to 0.7 m except that the only two specimens of the last species are 0.25 to 0.35 m long. They have the prelacunal separate from the supralabials, two internasal on each side, and 4 to 9 interoculars.

Distribution.—With the exception of *B. asper*, which ranges north from South America to southern Tamaulipas, México, and *B. lanceolata* and *B. caribbaea*, which occur on Martinique and Saint Lucia, respectively, in the Lesser Antilles, this genus is restricted to South America. The species are especially numerous in upland areas, such as the central and northern parts of the Andes and the Brazilian Plateau. The Argentine *Bothrops ammodytoides* ranges as far south as any snake in the hemisphere. Chile is the only South American country in which *Bothrops* is absent.

LACHESIS DAUDIN

Crotalus (*nec* Linnaeus, 1754), Linnaeus, 1766:372 (part); Schlegel, 1837:555 (part).

Lachesis Daudin, 1803b:349 (genotype *Crotalus mutus* Linnaeus; monotypy); Wagler, 1830:175; Gray, 1849:4 (part); Duméril, Bibron, and Duméril, 1854:1483; Peters, 1862:673; Garman, 1883:122; Cope, 1887:62; Boulenger, 1896:529 (part); Duméril, Bocourt, and Mocquard, 1909:951; Griffin, 1916:222 (part); Werner, 1923:227 (part); Amaral, 1925b:93; Amaral, 1926b:43 (systematic status); Dunn, 1944:213; Amaral, 1946b:13 (systematic status); Ruiz, 1951:110; Klemmer, 1963:427; Brattstrom, 1964:222.

Trigonocephalus Oppel, 1811:154 (*Scytale ammodytes* Sordelli and Latreille; subseq. desig.; Schlegel, 1837:527 (part).

Trigalus Rafinesque, 1815:77 (*nomen novum* for *Trigonocephalus*).

Cophias Merrem, 1820:154 (*Coluber crotalinus* Gmelin; subseq. desig.)

Bothrops Wagler, 1824:50 (part; B. lanceolatus; subseq. desig., Fitzinger, 1843:29).

Diagnosis.—Large, terrestrial pitvipers with distinctive habitus, skull, and scutellation; terminal caudal scute long; subcaudals paired proximally, in four or five rows distally; dorsal spine sharply ridged; dorsal scales heavily tuberculate; nasal pore situated in internal edge of nasal pad; concave aponeurosis on anterior margin of maxillary cavity; quadrate relatively short; pterygoid teeth not extending beyond middle of articulation with ectopterygoid (Figure 8).

The above described arrangement of subcaudals is unique among pitvipers. The egg-laying habit is unique among American pitvipers. The rattlesnakes, Sistrurus and Crotalus, have the anterior maxillary aponeurosis smoothly convex; otherwise they agree with Lachesis in the cranial features indicated above. In contrast to Lachesis, Porthidium has entire subcaudals, pterygoid teeth extending beyond the middle of the articulation with the ectopterygoid, and a smoothly convex maxillary aponeurosis; Bothrops has normally divided distal subcaudals, a relatively long quadrate, and an evenly curved maxillary cavity; Agkistrodon has the ectopterygoid shorter than the basal portion of the pterygoid, pterygoid teeth extending posteriorly beyond articulation of pterygoid with ectopterygoid, distal subcaudals not subdivided, and a full complement of large supracephalic scutes. Other American pitvipers are tree snakes (Bothriechis, Bothriopsis, and Ophryacus) with distinctive arboreal adaptations. Of Asiatic pitvipers, Ovophis and Trimeresurus have the nasal pore situated near

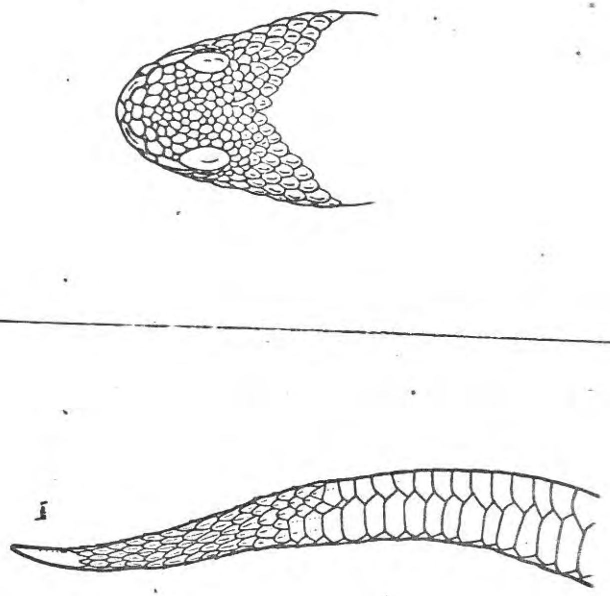

FIG. 8. Lachesis muta muta. USNM 76325, Bahia, Brazil. Top—Dorsal view of head (X 1). Bottom—Ventral view of tail (X 1.3).

the external rim of the nasal pad, a relatively long quadrate, pterygoid teeth extending to posterior one-half or three-quarters of articulation of pterygoid and ectopterygoid; and Tropidolaemus has the above cranial distinctions, has strongly keeled gular scales, and lacks nasal pores.

Definition.—Distinctive habitus with head ovate and covered above with small, convex, tuberculate scales; length commonly exceeding 2.5 m; maximum length exceeding 3.5 m. Color pattern consisting of dark diamonds straddling spine, with lateral apices nearly reaching ventrals. Frontorostrals 5 to 9; interoculars 9 to 15; intercictals 23 to 36; supralabials 8 to 10; infralabials 13 to 16; dorsal scales in 31 to 37 rows; ventrals 200 to 231; subcaudals 47 to 56. Cranium broad, its greatest width considerably greater than its length; border of maxillary cavity interrupted by a large aponeurosis with central concavity; prootic having well-developed dorsolateral ridge extending anterior from external auditory meatus; anterior foramen of prootic divided by bony partition into small lower and large upper foramen; palatal teeth 2 to 4; dorsal projection of palatine a broad triangle with apex very slightly rounded and with distinctly concave anterior margin; pterygoid teeth 9 to 11, extending to anterior one-fourth of articulation of ectopterygoid to pterygoid; basal portion of pterygoid shorter than ectopterygoid; ectopterygoid moderately broad, having anterior end bifurcate, medial margin concave, and lateral margin nearly straight; squamosal moderately long and slender, its greatest width about one-fourth its length; quadrate considerably shorter than cranium, the former when projected on cranium from supraoccipital ridge forward not reaching point of narrowest interorbital width; mandibular teeth 9 to 12; splenial separate from angular. Hemipenis divided for half its length; undivided base covered with small spines on medial surface and nearly bare on lateral surface; distal lobes covered with large recurved spines proximally; conical calyculate end about one-fifth total length of hemipenis.

Composition.—The genus is monotypic, consisting of *L. muta*, with three subspecies.

Distribution.—*Lachesis muta* ranges from Nicaragua to Brazil.

PORTHIDIUM COPE

Atropos (*nec* Wagler), Duméril, 1853:536 (part); Duméril, Bibron, and Duméril, 1854:1517 (part).

Bothriechis (*nec* Peters, 1859), Peters, 1862:671 (part); Günther, 1895:188 (part).

Porthidium Cope, 1871:207 (*Triogonocephalus lansbergi* Schlegel; subseq. desig., Dunn and Dunn, 1940:69); Cope, 1876a:140; Cope, 1887b:88.

Bothriopsis (*nec* Peters), Cope, 1876a:149; Bocourt, 1876:409.

Trigonocephalus (*nec* Oppel), Garman, 1883:125 (part).

Teleuraspis (*nec* Cope), Garman, 1883:126 (part).

Thanatos Posada Arango, 1889:46 (*Thanatos sutus* Posada Arango; present designation).

Thanatophis Posada Arango, 1890:343 (*nomen novum* for *Thanatos*)[6].

Lachesis (*nec* Daudin), Boulenger, 1896:529 (part).

Trimeresurus (*nec* Lacépède), Duméril, Bocourt, and Mocquard, 1909: 937 (part); Smith 1941:61 (part); Pope, 1955:224; Neill, 1964:39.

Bothrops (*nec* Wagler), Amaral, 1926b:34 (systematic status; part); Prado, 1939a:1 (part); Dunn, 1944a:213 (part); Smith and Taylor, 1945:179 (part); Amaral, 1946b:13 (systematic status; part); Ruiz, 1951:110 (part); Maldonado-Koerdell, 1953:132; Klauber, 1956:117; Peters, 1960:494; Klemmer, 1963:402; Brattstrom, 1964:246.

Agkistrodon (*nec* Palisot de Beavois), Shreve, 1938:9 (part).

Diagnosis.—Central American terrestrial pitvipers having the nasal pore situated deep in the nostril, entire subcaudals, and a distinctive skull; dorsal surface of head devoid of enlarged plates or when prefrontals, frontal, and parietals present these plates separated by rows of small scales.

Porthidium differs from *Bothrops* by having entire instead of divided subcaudals (Figure 3) and by having a two-part curve in the border of the maxillary cavity and a triangular palatine. In contrast to *Porthidium*, *Agkistrodon* has subcaudals partly or entirely divided and a full complement of large supracephalic scutes, and *Lachesis* has the subcaudals divided proximally and subdivided and spinous distally. Additional American pitvipers include rattlesnakes (*Crotalus* and

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[6] *Thanatophis* was unnecessary because *Thanatos* Posado Arango is not a homonym of *Thanatos* Koch.

Sistrurus) and arboreal pitvipers (Bothriechis, Bothriopsis, and Ophryacus). Asiatic Trimeresurus, Tropidolaemus, and Ovophis span most of these differences but have craniological distinctions and the nasal pore is either rudimentary or located on the external rim of the nasal pad.

Definition.—Size moderate to large snakes, reaching maximum lengths from 0.5 to 1.2 m; in proportions ranging from moderately slender (P. ophryomegas) to relatively stout (P. nummifer); body as wide as head and at mid-body as wide as high in repose, capable of extreme lateral compression in lansbergi and nummifer groups. Coloration tan, gray, or brown, having darker brown markings; either spotted with separate medial and lateral blotches or transversely banded. Supracephalic scutes enlarged (Figure 2), approaching in godmani group the condition of Agkistrodon or Sistrurus, or subdivided into scales as exhibited by the lansbergi and nummifer groups; frontorostrals 2 to 7; interoculars 1 to 12; interictals 16 to 30; supralabials 7 to 12; infralabials 9 to 13; dorsal scales above rows 1 to 3 strongly keeled and in P. lansbergi slightly and in P. nummifer strongly tuberculate; dorsal scales in 17 to 27 rows; ventrals 116 to 177; subcaudals 22 to 57; terminal caudal scute conical, equal in length to 3 or 4 subcaudals (see tables 1 and 2). Cranium variable in proportions; border of maxillary cavity having slight projection dividing border into two distinct curvatures; anterior foramen of prootic divided by bony partition; dorsal process of palatine a broad triangle with rounded apex situated slightly anterior to mid-palatine;

3 or 4 palatal teeth; pterygoid teeth 9 to 14 and extending nearly to posterior margin of articulation of pterygoid to ectopterygoid (15 or 16 pterygoid teeth in *P. godmani*, extending posterior past articulation of pterygoid and ectopterygoid); basal portion of pterygoid shorter than ectopterygoid, except in *P. godmani* and *P. barbouri*; ectopterygoid usually slender with concave margins and anterior bifurcation (broadened with convex lateral margin in *P. nummifer*); squamosal two-thirds to three-fourths as long as quadrate; quadrate shorter than cranium; dentary bearing 11 to 16 teeth; splenial and angular separated in all but *P. nasutum*. Hemipenis divided for about one-half its length; large spines interspersed among spinules covering base of each lobe and adjacent parts of undivided base, giving way abruptly to spinulate or papillate calyces terminally.

Composition.—*Porthidium* is composed of three species groups — the *godmani* group made up of two species, the *lansbergi* group made up of four species, and the *nummifer* group composed of two species. Differences between the groups are discussed elsewhere in the account of phylogeny. The arrangement used here closely resembles that suggested by Dunn (1919:214), Smith (1940:62), and Burger (1950:59). Species included are as follows:

Porthidium godmani group
- *P. barbouri*
- *P. godmani godmani*
- *P. godmani vulcanicum*

Porthidium lansbergi group

- *P. hyprorum*
- *P. lansbergi lansbergi*
- *P. lansbergi dunni*
- *P. lansbergi yucatanicum*
- *P. nasutum nasutum*
- *P. nasutum sutum*
- *P. ophryomegas*

Porthidium nummifer group

- *P. melanurum*
- *P. nummifer nummifer*
- *P. nummifer mexicanum*
- *P. nummifer occiduus*
- *P. nummifer picadoi*

Distribution.--The genus *Porthidium* ranges from Guerrero and San Luis Potosí, México, southward to Venezuela, Ecuador, and the Amazon Basin in Brazil. Most species occur only in Central America and southern México; two species range from Central America south into South America; one species is confined to South America.

SISTRURUS GARMAN

Crotalus (*nec* Linnaeus, 1758), Linnaeus, 1766:372 (part); Fleming, 1822:294.

Crotalophorus (*nec* Houttuyn), Gray, 1825:205.

Caudisona (*nec* Laurenti), Fitzinger, 1826:34.

Sistrurus Garman, 1883:110, 118, 176 (*Crotalus miliarius* Linnaeus); Garman, 1892:290 (generic nomenclature); Gloyd, 1940:31, Klauber, 1956:49.

Diagnosis.—Rattle; top of head with large plates anteriorly, usually 9 in number, including a single frontal and a pair of large, symmetrical parietals in contact with each other; distance between ends of lymphopophyses less than one-third distance between lymphopophysis and pleuropophysis; lateral process of squamosal if well developed forming fork with main bone at angle of 80° or less; nasal pore absent.

Definition.—Size small and medium; top of head covered by 9 plates in symmetrical arrangement as follows: pair of internasals, pair of prefrontals, single median frontal, pair of supraoculars, pair of parietals; rostral six-sided, higher than wide and truncate above except wider than high and pointed at apex in *S. ravus*; dorsal scale rows at midbody 25, 23, or 21; subcaudals mostly entire; pattern of dark blotches: middorsal series of large blotches and 1 to 3 series of smaller lateral blotches; hemipenes bilobed, deeply forked; basal spines numerous, robust, gradually diminishing in size distally; gradual distal transition from spines to calyces fringed with spinules; palatine triangular, bearing 1 to 3 teeth; pterygoid teeth 5 to 9; mandibular teeth 8 to 11.

Composition.—*Sistrurus catenatus* (three subspecies), *S. miliarius* (three subspecies), and *S. ravus*.

Distribution.—Southeastern Arizona and the Rio Grande Valley to western New York and southern Ontario; Florida Gulf Coast, lower Mississippi Valley, Atlantic Coastal Plain northward into North Carolina; southern tip of the Mexican Plateau in Puebla, México, Hildalgo, Oaxaca, and Veracruz.

CROTALUS LINNAEUS

Crotalus Linnaeus, 1758:214 (*Crotalus horridus*); Gloyd, 1940:79; Klauber, 1956:29.

Crotalophorus Houttuyn, 1764:290 (invalid emendation of *Crotalus*)[7].

Caudisona Laurenti, 1768:92 (*Crotalus horridus* Linnaeus).

Crotalinus Rafinesque, 1818:446 (invalid emendation of *Crotalus*).

Uropsophus Wagler, 1830:176 (*U. triseriatus* Wagler).

Urocrotalon Fitzinger, 1843:29 (*Crotalus durissus* Linnaeus).

Aploaspis Cope, 1866:310 (*Caudisona lepida* Kennicott).

Aechmophrys Coues, 1875:609 (*Crotalus cerastes* Hallowell).

Haploaspis Cope, 1883:13 (invalid emendation of *Aploaspis*).

Diagnosis.—Rattle; top of head with scales of varying size anteriorly; more than one scale in the frontal region; parietals, if enlarged, not in contact or symmetrical; distance between ends of

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[7] *Crotalophorus* Gronovius, 1763, is nomenclaturally unavailable, according to opinions 20 and 89 of the International Commission on Zoological Nomenclature.

caudal lymphopophyses greater than distance between lymphopophysis and pleuropophysis; lateral process of squamosal forked at an angle of 80° or less with main bone; nasal pore absent.

Definition.--Size small, medium or large; supracephalic plates more or less subdivided into smaller scales; internasals and prefrontals in symmetrical pairs, sometimes subdivided; rostral variable in relative height and shape; dorsal scales in 21 to 31 rows; pattern of dark spots, blotches, or crossbands; hemipenes bilobed, deeply forked; lobes slender or short and robust; basal spines numerous, robust or slender, stopping near common base of two rami or extending slightly beyond on mesial surfaces; spines changing abruptly to fringes or calyces; palatine triangular or anteriorly knobbed, bearing 0 to 4 teeth; pterygoid teeth 4 to 11; mandibular teeth 6 to 13.

Composition.—Twenty-seven species, including those listed by Klauber (1956:29) and Crotalus lannomi Tanner (1966:298).

Distribution.—North and South America and adjacent islands from southern Canada to northern Argentina and southern Brazil, except rain forest of Amazon Valley.

ZOOGEOGRAPHY AND PHYLOGENY

Thanatophidian Distribution

Generalities.—The over-all distribution of pitvipers and of other major kinds of terrestrial venomous snakes has not been evaluated since Darlington (1957) included several pages on the subject in his book on zoogeography. Summaries are given here to support discussions of zoogeography and phylogeny that follow. These summaries are confined to introductory considerations, accounts of each family and summations and comparisons of regional assemblages in terms of total numbers of genera, species, and species and subspecies. Darlington's (1957) account and Klemmer's (1963:255) annotated list are prime sources of information. Other sources are cited where used.

As a general rule the most cold-tolerant snakes have inherent heat requirements that are greater than those of anurans and urodelans and less than those of cold-tolerant representatives of reptile orders other than snakes. This generalization applies particularly in limital northern latitudes, where it is an accurate summation in three of the four areas reported by Darlington (1957: 557). In the South Temperate Zone, lizards and the rhynchocephalian, Sphenodon punctata Gray, exist in cooler regions than snakes. The difference in cold tolerance of snakes in the north and in the south conforms to the hypothesis that certain kinds of snakes arose in the complex tropical-subtropical interphase of Eastern Asia and lost their cold tolerance during the process of spreading through the tropics to the South Temperate Zone.

Because of the heat requirements of venomous snakes, polar and subpolar regions lack them, except in northwestern Europe where *Vipera berus* (Linnaeus) reaches the Arctic Circle. The ranges of distribution of other viperids and of crotalids are within the 50° latitudes. Those of elapids are within the 40° latitudes. Among crotalids *Hypnale*, *Agkistrodon*, *Sistrurus*, and *Crotalus* set or approached northern boundaries of venomous snakes, whereas other genera are restricted to the middle latitudes.

Only the tropics and adjacent borders of the temperate zone are rich in species of venomous snakes. Highland areas of the tropics and the subtropical, warm temperate interphase have been important centers of evolution of viperoid snakes. The most obvious of such centers are southeastern Asia, the fringes of the Mexican Plateau, the Central American highlands, the northern parts of the South American Andes, and the Brazilian Plateau.

Oceanic islands separated from continents by wide expanses of ocean have reduced ophiofaunas and few or no terrestrial venomous snakes. Terrestrial venomous snakes are lacking from the Greater Antilles, Bermuda, Madagascar, New Zealand, and Pacific islands east of the Fiji Islands. Venomous snakes are lacking from the Lesser Antilles except for one species of *Bothrops* endemic to Martinique and a second species endemic to Saint Lucia. They occur in similarly reduced numbers in a number of archipelagos: the Riu Kiu Islands,

B. insularis

Indonesian islands between Borneo and New Guinea, and Pacific islands from New Guinea to the Fiji Islands.

Continental islands have assemblages of venomous snakes equal to or somewhat smaller than those of similar areas of adjacent continents. Certainly that is the case for England, many Mediterranean islands, Ceylon, Sumatra, Java, Borneo, Formosa, and Trinidad.

Faunal regions.—For describing distributions and comparing regional thanatophidian assemblages on subsequent pages, the major fauna regions (often called zoogeographic realms) are most useful. These are the six faunal regions that Darlington (1957:426) described in detail. For present purposes transition areas are arbitrarily assigned to one of the contiguous regions, as follows:

Ethiopian Region: Africa south of the Sahara.

Palaearctic Region: Eurasia above the tropics, Mediterranean Africa, and arbitrarily the transition areas of desert north Africa and of Arabia.

Oriental Region: Tropical Asia and associated islands, including Ceylon, Sumatra, Java, Borneo, the Phillippines, Formosa, and arbitrarily the transition zone of the Indo-Australian Archipelago to, but not including, New Guinea.

Australian Region: Australia, New Guinea, and small adjacent islands.

Nearctic Region: North America above the tropics and arbitrarily the transition zone fringing the Mexican Plateau.

Neotropical Region: South America, including Trinidad, Central America, México to the Isthmus of Tehuantepec in the highlands and to Tropic of Cancer in the coastal lowlands, and arbitrarily the Lesser Antilles.

Families.—Elapidae. Erect-fanged land snakes occupy tropical and warm temperate regions between the 40° latitudes. They are abundant in the Ethiopian Region (with 9 genera, 19 species, 35 species and subspecies) and in the Oriental Region (with 5 genera, 26 species, 45 species and subspecies). Ogmodon vitianus Peters, a Fiji Island endemic, sets the eastern record of definitely indigenous snakes in the southwest Pacific. Temperate regions have fewer elapids, as evidenced by the Palaearctic Region (with 3 genera, 6 species, 7 species and subspecies). One stock of elapids, comprising the three genera of coral snakes, inhabits the Western Hemisphere. Two small genera, Micruroides Schmdt and Leptomicrurus Schmidt are nearctic and neotropical, respectively. Because of the great proliferation of Micrurus Wagler, the Neotropical Region has a total (including the two species of Leptomicrurus) of 97 species and 184 species and subspecies. The Nearctic Region has Micrurus and Micruroides with a total of 3 species and 5 species and subspecies.

Viperidae. True vipers are lacking in the Western Hemisphere and in the Australian Region. They are most abundant in the Ethiopian Region (5 genera, 34 species, 61 species and subspecies) and in the Palaearctic Region (5 genera, 19 species, 41 species and subspecies). The palaearctic species are concentrated in southern Europe and western Asia. Only Vipera berus ranges east of Lake Baikal, occupying a broad zone of Siberia and China north of 40° N latitude. Much of temperate China and adjacent Russia is devoid of viperids. In their important account of the zoogeography of the family, Marx and Rabb (1965) failed to record this gap and failed to distinguish between the post-Pleistocene range of V. berus, in the north, and the older, relictual distribution of V. russeli, far to the south in the Oriental Region. Their (1965: fig. 45) map does not accurately depict the eastern portion of the distribution of Vipera. Besides the latter species the Orient has the rare and localized Azemiops feae Boulenger, which is another relict, and Echis carinatus (Schneider), which ranges from North Africa through India to northern Ceylon. Oriental viperids total 3 genera, 3 species, and 6 species and subspecies.

Crotalidae. Pitvipers are lacking in the Australian Region, the Ethiopian Region, and in most of the western half of the Palaearctic Region. The range of crotalids thus complements the range of viperids. Together viperids and crotalids occupy all faunal regions except the Australian Region. Their ranges are mutually exclusive except for the viperid relicts, Azemiops feae and Vipera russeli which are deep in pitviper territory and the extensive ranges of Hypnale halys, Vipera berus, and Echis carinatus, which are post-Pleistocene expansions. Of pitvipers the Palaearctic Region has 4 genera, 4 species, and 13 species and subspecies, most of them confined to eastern China and the Riu Kiu Archipelago. The only widespread, polytypic species is Hypnale halys, which ranges from Japan and Pacific Siberia to the mouth of the Volga in European Russia. Crotalids reach their zenith in the Neotropical Region (with 7 genera, 49 species, 90 species and subspecies). They are less abundant in the Oriental Region (with 5 genera, 48 species, 56 species and subspecies) and in the Nearctic Region (3 genera, 26 species, 56 species and subspecies).

Regional assemblages.—When total numbers of genera, species, and species and subspecies are obtained for all terrestrial venomous snakes in each faunal region (Table 7), significant similarities and differences emerge. Although present attention is focused on numerical comparisons, some zoogeographic and ecologic implications are unavoidable.

The regions with large land masses in the tropics have the most species and subspecies: Neotropical, 184; Oriental, 107; Australian, 103; Ethiopian, 96. The last three numbers vary no more than six above or below their mean, 102. The total for the Neotropical Region is 80 per cent greater than the mean of the other totals. For most of its Cenozoic history the Neotropical Region was divided by marine portals into two or more parts, whereas the other regions have been separated from one another by barriers but probably have not been divided internally for sustained periods of time. The similar totals for the regions of the Old World tropics beg explanation. A simple, perhaps too simple, hypothesis is that each of these regions has approximately the same number of ecological niches at these tropic

TABLE 7. REGIONAL THANATOPHIDIAN FAUNAS

Numbers of Genera, Species (parentheses), and Species and Subspecies

Family	Ethiopian	Nearctic	Neotropical	Oriental	Palaearctic	Australian
Elapidae	9 (19) 35	2 (3) 5	2 (48) 94	5 (26) 45	3 (6) 7	24 (79) 103
Viperidae	5 (34) 61	0 (0) 0	0 (0) 0	3 (3) 6	5 (19) 41	0 (0) 0
Crotalidae	0 (0) 0	3 (26) 56	7 (49) 90	5 (48) 56	4 (4) 13	0 (0) 0
Total	14 (53) 96	5 (29) 61	9 (97) 184	13 (77) 107	12 (29) 61	24 (79) 103

levels, filled by approximately the same number of species and subspecies of venomous snakes. In contrast, regional totals of families and genera in these regions are quite diverse. The regions are occupied by one family (Australian), two families (Neotropical and Ethiopian) or three families (Oriental). Regional totals of genera number 9 to 24.

The two temperate faunal regions (the Nearctic and the Palaearctic) each have 29 species and 61 species and subspecies. The Palaearctic Region has 12 genera, whereas the Nearctic Region has 5 genera. The same numbers of species and of species and subspecies in the two regions is probably the result of balanced coincidences, the greater ecological diversity of the Palaearctic countered by greater destruction during the Pleistocene when glaciers trapped organisms against the great highlands that extend across Eurasia.

The vast proliferation of elapids in the Australian Region, where they are virtually the only Caenophidia, demonstrates competitive and hence complementary relationship of different thanatophidian families and similar but less intense relationship with the colubrids. Although figures are far from final, present figures indicate that Australian elapids comprise almost as many genera as the combined total of all venomous snakes in both the Oriental and Ethiopian regions and approximately the same number of species and subspecies as each other region. In Australia elapids fill niches elsewhere occupied by colubrids and thanatophidian families. Only five genera of the

Colubridae have reached Australia. They are Natrix, Achrochordus, and 3 genera of the Homalopsinae, all five aquatic and potentially tolerant of salt water.

The comparatively few thanatophidian genera in the Nearctic and Neotropical regions suggest that these groups traveled from Asia to the Western Hemisphere (a conclusion that Darlington, 1957, reached for many vertebrate groups) and that Bering Land Bridge has served as a rigidly selective filter, perhaps admitting only one stock of elapids and two or three stock of crotalids.

Origin of Superfamily and Family

Present evidence favors the theory that viperoid (solenoglyphous) snakes were derived from one line of colubrids and the elapoid (proteroglyphous) snakes were derived from another colubrid line. In the line that led to the viperoids the anterior end of the maxillary was lost along with all teeth in front of rear fangs. In the line leading to the elapoids, the posterior end of the maxillary was reduced. Existing hydrophids and elapids show progressive reduction of solid teeth behind the fangs until only fangs are left.

Pitvipers were probably derived from vipers at the level between existing atractaspines and existing viperines. This event occurred in highlands of southeastern Asia during late Cretaceous or earlier, at a time when viperine snakes had already spread across southern Asia to Europe.

Marx and Rabb (1965:197) commented on the close resemblance of Vipera to pitvipers. The small species of Vipera with large supracephalic scutes, V. ursini and V. berus, are similar to the small species of Hypnale. The arrangement of large scutes in these pitvipers is more complete and hence more primitive than that of the above mentioned species of Vipera. Evidently separation of pitvipers occurred from a stock close to Vipera but more primitive than any existing species of Vipera.

Pitvipers parallel vipers closely and exceed them in distribution and in number of species (160 pitvipers as compared to 60 vipers) but not in ecological diversity. Moreover, atractaspine vipers (Azemiops Boulenger, Atractaspis Smith, and Causus Wagler) are more primitive than any pitvipers. The pit-organ thermoreceptor of pitvipers and the rattle of Sistrurus and Crotalus are marks of specialization that exceed viperid structures. Both structures are fully developed as they now exist. Annectant stages showing relationships with predecessors are unknown.

Dullemeijer (1959b:74) described the architectonic influence of the presence of the pit-organ on the bones and muscles adjacent to the pit. Beyond the pit and the imposing number of adjacent parts of the head influenced by presence of a pit, no consistent differences between vipers and pitvipers have been discovered.

Phylogeny in Eastern Hemisphere

Viperidae.—Marx and Rabb's (1965:197) discussion of the distributional history of viperids offered significant new insight. The main part of their hypothesis convincingly outlined a history as follows:

1. Viperids arose in the Oriental or southeastern Palaearctic Region. Azemiops of southeastern Asia is a relict, remaining from an early chapter of viperid evolution.
2. Primitive viperids and advanced viperids reached the Ethiopian Region before the Tethys Sea separated Africa and Asia in late Cretaceous time. In Africa the primitive stock is represented by Atractaspis and Causus. Advanced viperids with small supracephalic scales and elliptical pupils, also isolated in Africa at the same time produced Bitis, Atheris, and Adenorhinos.
3. During the time of separation from the late Cretaceous until the Miocene the Bitis-Atheris-Adenorhinos stocks evolved in Africa isolated from the Vipera-Echis-Cerastes-Eristocophis stocks in the Palaearctic and Oriental regions.
4. Echis extended its range to the southern Sahara and Atractaspis reached Israel and Sinai in the time interval since Miocene.

Marx and Rabb (1965:199) attributed the present-day range of Vipera in the Oriental Region to late Tertiary extensions. This generalization applies to some species and not to others. The eastern Asiatic portion of the range of V. berus, north of the Oriental Region, is such an extension. In contrast, the range of V. russelli has features of a relict with a long history in the Oriental Region.

Elapidae.—Although elapids are not directly related to pitvipers, they probably arose in southeastern Asia about the same time as viperids. It is clear that primitive and advanced stocks of elapids reached Africa along with the viperid stocks prior to the appearance of the Tethys Sea in late Cretaceous.

The adaptive radiation of elapids in Australia is a classic example that parallels the radiation of marsupial mammals there. How did elapids reach Australia whereas viperoid and most colubrid snakes did not? The answer does not involve the early appearance of elapids, which could not be true as related to colubrids. Instead the answer lies in a primitive stock of burrowing elapids that had sufficient tolerance for salt water for rafting to Australia and to islands from New Guinea to the Fijis, a stock probably close to the ancestry of the Hydrophidae.

The unbalanced nature of the Australian fauna indicates that the continent was separated from the Asiatic continent by salt water through both Tertiary and Quarternary periods. If there was ever a land connection for passage of terrestrial vertebrates from Asia to

Australia it was a very selective filter during the late Paleozoic or early Mesozoic that admitted only 2 families of fresh water fish, three families of frogs, the tuatara and scattered groups of invertebrates. That later vertebrate groups reached Australia by island hopping is indicated by the small number of groups and by tolerance for salt water that the groups exhibit. For example, Australian colubrids are a small selection of amphibious groups.

Successive replacements.—The theory that successive replacements of early radiations by later radiations were important in southeastern Asia was developed by Darlington (1957:548) and mentioned by Marx and Rabb (1965:195). Attention has been directed at the topographically diverse area enclosed in a circle within a radius of 750 miles and a center in northwestern Yunnan (Pope, 1936:386). Such an area encloses part or all of the range of an imposing array of viperoid snakes which for phylogenetic reasons are thought to represent four major radiations (Table 8).

Crotalidae.—After origin of pitvipers from vipers in southeastern Asia, pitvipers replaced vipers in most of the Oriental Region and in the eastern part of the Palaearctic Region. Spread of pitvipers to the west was prevented by a well established fauna of advanced viperines, especially in areas west of India. Hypnale spread through southeastern Asia and gave rise to Calloselasma, Ovophis, and directly or indirectly Tropidolaemus. Trimeresurus arose from Ovophis. Tropidolaemus is something of a puzzle, more primitive in some respects than Ovophis and yet advanced in others.

TABLE 8. Selected Viperoid Snakes of Southeastern Asia

Radiation	Snakes	Significance
1	*Azemiops feae*	Represents most primitive subfamily of viperids.
2	*Vipera russeli*	Advanced viperid with discontinuous range.
3	*Hypnale halys*, *H. himalayanus*, *H. strauchi*, *H. monticola*	Most primitive genus of crotalids.
4	*Ovophis monticola*, species of *Trimeresurus*, *Calloselasma acuta* and *C. rhodostoma*	*Ovophis* is intermediate between *Hypnale* and *Trimeresurus*. *Calloselasma* was derived from *Hypnale*.

Detailed phylogeny of species of Trimeresurus must await their definitive treatment. In his key to species of Trimeresurus, Maslin (1942:21) distinguished species groups. Beyond that, Brattstrom's phylogenetic tree (1964:244) had little evidence to support it; his arrangement of T. monticola and close relatives high in the tree is contrary to present indications.

Bering Land Bridge

The Bering Land Bridge was the portal by which terrestrial animals gained entry to America from Asia. Darlington (1957:561) concluded that "Emydine turtles, Testudo, Crocodylus, skinks, several genera of colubrid snakes, elapids, and pitvipers all seem to have moved from the Old World to North America and South America." Brattstrom (1964: fig. 40) showed a strip of Trimeresurus extending across Bering Straits during the Cretaceous-Eocene. Tropical and subtropical vegetation that occupied Alaska at that time was probably in the form of forests less dense than present tropical forests and supporting only some tolerant tropical and subtropical animals. Evidently Hypnale and Trimeresurus reached the Western Hemisphere during the Paleocene or earlier.

Mountains Fringing Mexican Plateau

The mountains that fringe the Mexican Plateau have relicts of the two lines of pitvipers that crossed the Bering Bridge and a large assortment of primitive derivatives, including Ophryacus undulatus, Agkistrodon bilineatus taylori, Sistrurus ravus, three species of Porthidium, and numerous species of Crotalus. Evidently Hypnale reached the area and gave rise to Agkistrodon and Porthidium. Porthidium gave rise to Sistrurus and Sistrurus to Crotalus.

The species groups of Porthidium represent one primitive group and two divergent evolutionary lines: 1) snakes of the godmani group are of moderate size and proportions and have large head scutes, few dorsal scalerows, and separate lateral and dorsal blotches; 2) snakes of the lansbergi group are small or moderate in size and proportions and have enlarged supraoculars and snout pointed and turned up in all except P. ophryomegas (the snout of this snake is normal or moderately turned up); and 3) snakes of the nummifer group are large, heavy-bodied, broad-headed, normal-snouted, and have narrow supraoculars and knobbed scales. The godmani group is in the line of divergence of Porthidium from Hypnale. The lansbergi and nummifer groups diverged independently from the godmani group. Porthidium nasutum, which is similar to P. godmani in some respects and specialized in others, is close to the ancestry of the lansbergi group. Advanced members of this group are slenderer, with more numerous ventrals and subcaudals, and with less distinctly turned-up snouts; hyoprorum is a close derivative of nasutum, whereas lansbergi and ophryomegas are more distant derivatives in two different directions. In the nummifer group the two species represent two different specialized lines: P. melanurum is primitive in most aspects of its scutellation and specialized in coloration, supraoculars, and large number of interictals; P. nummifer (especially P. nummifer mexicanum) is advanced in size, proportions, scutellation, and coloration. Furthermore, in several advanced features, it bears a striking resemblance to Lachesis muta. This resemblance and the conclusion that it is the result of convergence instead of close relationship is discussed in the account of Lachesis muta.

Ophryacus is a relic of Trimeresurus and of the phylogenetic line that reached South America before the late Paleocene Portal isolated it. This line produced Bothriopsis in South America and Bothrops arose from Bothriopsis.

South America

With Bothriopsis so poorly represented in collections, comments on phylogeny of species must be highly speculative. Four species, comprising the B. castelnaudi group, are tan or brown with well developed dark brown or black crossbands and some subcaudals entire. The small B. medusa is the most primitive; it has relatively few dorsal scalerows, ventrals, and subcaudals, an enlarged frontal, and a pattern of brown blotches. Bothriopsis albocarinata is similar to B. medusa in some respects and is also relatively primitive. Both of these species occur in the Andes, whereas the one of adjacent lower elevations — B. castelnaudi — is more advanced.

Two species, comprising the B. bilineata group are green and have subcaudals all divided. The group is an offshoot of the B.

castelnaudi group. *B. peruviana* is primitive; *B. bilineata* is relatively advanced.

Two species comprising the *Bothriopsis punctatus* group are intermediate between the previous groups. They have divided subcaudals and are marked with dark blotches. The Andean species, *B. oligolepis* is primitive; that of the Pacific slopes, *B. punctatus* is advanced.

In *B. castelnaudi* and *B. bilineata*, the two polytypic species in this genus, the subspecies situated farthest from the Andes in eastern South America — *B. c. castelnaudi* and *B. b. bilineata* — are more advanced in scutellation and coloration. Their most primitive conspecifers — *B. c. cuadriscutata* and *B. b. smaragdinus* — occur in the upper Amazon Valley.

Although the species of *Bothrops* have not been studied thoroughly enough for formulation of a detailed phylogeny, some general ideas have been formed. Apparently, the early generic stock split into two lines: (1) one with a lacunalabial, the *Bothrops atrox* group, and (2) one with separate prelacunal and second supralabial, the *Bothrops neuwiedi* group. Most of the relatively generalized members of the former group (*B. picta*, *B. loiana*, and *B. andiana*) occur on the Andean and Pacific slopes, whereas the primitive members of the latter group occur on the Brazilian Plateau. The groups probably differentiated in these two upland areas when they were separated by water. If *Bothriopsis*, having lacunalabials, is ancestral to *Bothrops*, as I have hypothesized, then the *Bothrops atrox* group may be more primitive than the *B. neuwiedi* group. The *Bothrops alternata* group and the *Bothrops ammodytoides* group are derived from the *Bothrops neuwiedi* group.

The origins of *Bothriechis* and *Lachesis* are uncertain. I am inclined to associate *Bothriechis* with *Porthidium* but there is no strong evidence. *Bothriechis* evolved through most of the Tertiary isolated in Central America. Most of the species have restricted, disjunct ranges and seem to be relicts of a retreating group. Only *B. schlegeli* has the characteristics of a successful expanding species. It may be postulated that *B. nigroviridis* and *B. aurifer* are the most primitive of existing species — the former with its dark markings, large supraoculars, and few ventrals and subcaudals; the latter with its large frontal, occasional spotting, and relatively few ventrals. *Bothriechis bicolor* and *B. lateralis* are advanced; in these the adult coloration is plain or striped and the ventrals, dorsals, and interictals are numerous. *Bothriechis schlegeli* presents a rather distinctive line combining primitively few ventrals and caudals with many advancements: "eyelashes"; very small, heavily keeled head scales; numerous dorsals and interictals; and color polymorphism. However, its kinship to the others is clear; its ancestral line must have included snakes similar to *B. nigroviridis*.

Lachesis is strikingly different from any other pitviper; I hypothesize that it can only be a relic of a primitive stock that is otherwise extinct. In the past, close relationships of *Lachesis* to other existing pitvipers have been suggested. Traditionally *Lachesis* has been associated with *Bothrops* (*sensu lato*). Boulenger (1896:529) lumped *Bothrops*, *Trimeresurus*, and *Lachesis* together under the last name. The inference that the three are closely related has persisted. Because of similarities in skulls, Brattstrom (1964:222) concluded that *Lachesis* is much closer to the rattlesnakes than to *Bothrops* (*sensu lato*). To consider these conflicting points of view, I have compared *Lachesis* with several possible relatives in Table 9. No close relationship is evident with any of these American genera. In the oviparous habit, *Lachesis* is uniquely primitive. Its hemipenis is primitive like that of *Porthidium* and a number of other pitvipers. Its relatively short quadrate is like that of rattlesnakes and *Agkistrodon*. The aponeurosis on the rim of the maxillary cavity and the short series of ectopterygoid teeth are advancements shared with rattlesnakes. The spinous distal subcaudals, long terminal spine, and the concavity of the maxillary aponeurosis are unique advancements. The large size, extreme tuberculation of the body scales, and sharp spine are specializations shared with a number of advanced species of *Crotalus*, *Bothrops*, and *Porthidium*.

The characteristics of *Porthidium* used in Table 9 relate specifically to *P. nummifer mexicanum* which is superficially similar to *Lachesis muta*. In the extreme tuberculation of body and head scales and in coloration, the resemblance is striking. Gray (1849:14) identified a number of Central American specimens of *P. n. mexicanum* as *L. muta*. However, *Lachesis* and *Porthidium* are distinct in many important characters. Differences cited in Table 9 include the extent of the pterygoid teeth, the shape of the anterior margin of the

TABLE 9. Comparison of *Lachesis* to Presumed Relatives

Characteristic	*Sistrurus* and *Crotalus*	*Lachesis*	*Bothrops* (*sensu stricto*)	*Porthidium*
Reproduction	viviparous	oviparous	viviparous	viviparous
Hemipenis				
Portion that is bifurcate	three-fourths or more	one-half	three-fourths or more	one-half
Portion involved in distal differentiation	one-half or more	one-fifth	one-third	one-fifth
Head scales	large or small	small	small	small
Pterygoid teeth in relation to articulation between pterygoid and ectopterygoid	not beyond middle	not beyond middle	beyond middle	beyond middle
Border of maxillary cavity	aponeurosis	concave aponeurosis	none	aponeurosis
Quadrate	short	short	long	long or short
Subcaudals	entire	divided and subdivided	divided	entire

maxillary cavity, the arrangement of subcaudals, and the kind of reproduction.

Presumed relationships between genera are shown in a phylogenetic tree (Figure 9).

EXCHANGES BETWEEN SOUTH AMERICA AND MIDDLE AMERICA

After the Middle Pliocene when the Colombian Portal was closed and connections completed from South America to México, exchanges occurred in both directions. *Bothriechis schlegeli*, *Porthidium lansbergi*, and *P. nasutum* reached South America. There *P. nasutum* gave rise to the Amazonian species, *P. hyoprorum*. From the opposite direction *Bothriopsis punctatus* extended its range a short distance into Panamá. *Lachesis muta* reached Nicaragua and *Bothrops asper* reached México.

Many other minor changes in distribution occurred during the closing chapter of geological history. The many instances of scattered relic populations are cases in point. Beyond the element of environmental change the similarity breaks down in different ways. For example, cases of populations of *Porthidium ophryomegas* and *P. lansbergi* that are isolated in arid areas differ markedly from scattered populations of *Lachesis muta* and *Bothriopsis bilineata* in South America. All four however are instances of species that had relatively extensive ranges and that persist in scattered areas whereas environmental changes in intervening areas have caused extinction.

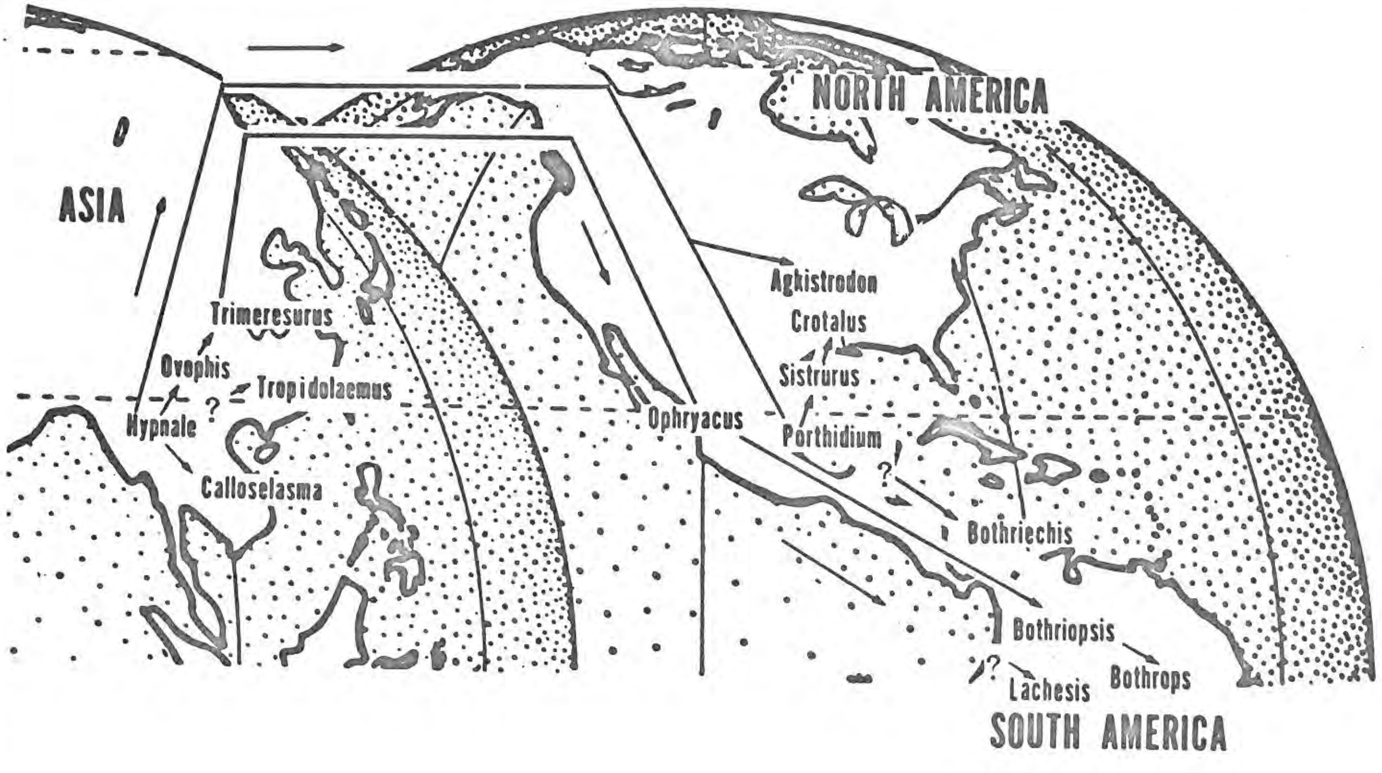

FIG. 9. Phylogenetic relationship of pitviper genera.

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