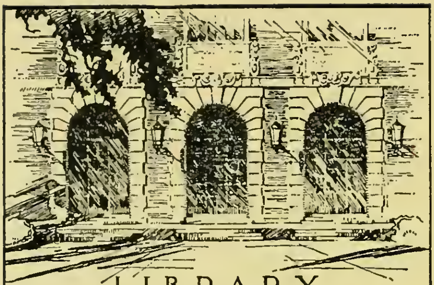

COMPARATIVE OSTEOLOGY OF THE SNAKE FAMILIES TYPHLOPIDAE AND LEPTOTYPHLOPIDAE

JAMES CARL LIST

ILLINOIS BIOLOGICAL MONOGRAPHS
36

THE UNIVERSITY OF ILLINOIS PRESS, URBANA

ILLINOIS BIOLOGICAL MONOGRAPHS

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THE UNIVERSITY OF ILLINOIS PRESS · URBANA AND LONDON · 1966

THIS MONOGRAPH IS A CONTRIBUTION FROM THE DEPARTMENT OF ZOOLOGY,
UNIVERSITY OF ILLINOIS. ISSUED OCTOBER, 1966

Library of Congress Catalog Card No. 66–63773.

ACKNOWLEDGMENTS

The writer is particularly grateful to Dr. Hobart M. Smith of the Department of Zoology of the University of Illinois for suggestions and direction throughout the course of this work. Both the Department of Zoology and the Museum of Natural History of the University of Illinois aided in various ways, as did the Department of Biology of Loyola University, Chicago, where much of the work was done.

Thanks are due to the following museums and institutions for loans of specimens: the Australian Museum, Sydney, N.S.W.; the California Academy of Sciences at San Francisco; the Chicago Natural History Museum; the Museum of Comparative Zoology of Harvard University; the National Museums, Colombo, Ceylon; the University of Illinois Museum of Natural History; the U.S. National Museum; and the Zoological Society of San Diego.

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INTRODUCTION

The Typhlopidae and Leptotyphlopidae (*auctorum*) are families of peculiar, small, burrowing snakes, most of them being less than a foot long when mature. They are found throughout the warmer parts of the world in both tropical forest and semi-desert conditions. They are quite secretive and, aside from food habits, very little has been reported of their natural history.

Interest in them has lain chiefly in their numerous and often extreme burrowing modifications and in their primitive, lizard-like features. Their scales, for example, are so polished and close-fitting that scale counts are made with difficulty. Some of the enlarged head scales in particular have such fine and closely applied edges that the outline of a scale can be determined only by critical angles of lighting. The tail is very short; the snout is sometimes flattened and spadelike; the eyes are quite reduced and lie beneath the skin, hence the name "typhlops" (clouded eyes) and the common name of "blind snakes." Skeletal modifications associated with burrowing are discussed in the various sections to follow. Primitive features include the presence of pelvic vestiges, a coronoid, a tabular, paired parietals, a distinct proatlas, etc.

The two families differ from each other in several basic respects and have long been distinguished on the basis of skeletal characters. Within the Typhlopidae, however, so little is known of the anatomy of the rarer forms that scalation has been the only generic criterion. The skeletons of *Helminthophis* and *Typhlopis* are still not figured or adequately described. The usual arrangement of the genera is as follows:

A. Usually with well-developed pelvic vestiges; maxilla toothless—Leptotyphlopidae. A single genus, *Leptotyphlops*.

AA. Pelvis usually reduced to a pair of ischia; maxilla bearing teeth—Typhlopidae.
  B. Head with small scales like those on body; rostral scale reduced, invisible from above—*Typhlophis.*
  BB. Head with enlarged scales; rostral large, visible from above.
    C. Two enlarged preanal scales; a loreal scale present—*Anomalepis.*
    CC. No enlarged preanals; loreal absent or fused with upper nasal.
      D. Prefrontal scale fused with upper nasals; rostral and frontal scale in contact—*Typhlops.*
      DD. Separate prefrontals.
        E. Prefrontal scales in contact between rostral and frontal—*Helminthophis.*
        EE. Prefrontals separated by rostro-frontal contact—*Liotyphlops.*

The genus *Leptotyphlops* includes approximately fifty species, which occur in Africa and from southwestern U.S. south through Mexico to Argentina. There are very few Asian and no Australian species. *Typhlops,* the largest of the genera, includes about 180 species, some twenty of which are found in Mexico, the West Indies, and south to Argentina. The others are Old World forms found in Africa and the Mediterranean region, eastward through Madagascar and southern Asia to Australia, the Philippines, and other South Pacific islands. The most widely distributed and best known species, *T. braminus,* is native to Ceylon, India, and the Philippines. It seems to have become established recently in Guam, Hawaii, Mexico, and, in the opposite direction, the Mascarenes. There are five species of *Anomalepis* (found from Panama to Peru), three of *Helminthophis* (from Costa Rica to Venezuela), one of *Typhlophis* (in Brazil and the Guianas), and ten of *Liotyphlops* (from Costa Rica to Paraguay). There is thus a total of almost 250 species of these blind snakes, and, although a number of names have been reduced to synonymy, the list continues to grow by the description of one or two new species nearly every year.

Of this number, not more than 10 per cent have been examined for internal features. Relatively few studies have considered the soft anatomy. Haas's work (1930) on the head musculature and Robb's work (1960) on the general internal anatomy are outstanding exceptions. Nakamura (1941) reported on the circulatory system of *T. braminus.* Aota (1940) reported a histological study of the skin and its sense organs in one species. Brongersma (1958) reported on the respiratory and circulatory systems. Mosauer (1935) included *Typhlops* in his work on the trunk musculature of snakes. For the most part it is the skeleton which has received attention, and even these descriptions are often incomplete or involve only a part of the skeleton such as the pelvic girdle. Only Evans (1955) has adequately described the entire skeleton of a species, utilizing a series of specimens to determine possible variations. A number of papers dealing with parts of the skeleton will be mentioned later in their respective sections. Some of the more extensive works, however, may be summarized briefly at this point. Duerden and Essex (1923) and Essex (1927) described the pelvic vestiges of a number of species. Haas (1930) thoroughly described the skulls of two species of *Typhlops* and one of *Leptotyphlops*. Brock (1932) described the skull of *Leptotyphlops nigricans*. Mahendra (1936) reported several unique features of the skeleton of *T. braminus*. Dunn (1941), Dunn and Tihen (1944), and Tihen (1945) have authored the only papers on the skeletons of *Anomalepis* and *Liotyphlops*. McDowell and Bogert (1954) in their work on *Lanthanotus* included considerable discussion of the blind snakes and proposed removal of all the blind snakes except *Leptotyphlops* from the Ophidia. Underwood (1957) has criticized this proposal as well as other parts of the *Lanthanotus* paper.

However, even these studies were sometimes based on a single specimen or on one or two species. Also, much of the early work was done on dried skeletal materials in which small sutures are often obscured and where superficial bones like the orbitals might have been lost with removal of the skin. In view of the significant position these snakes must occupy near the base of any classification of the Ophidia, it seems worthwhile to review past work and to add to our still meager knowledge of the anatomy of the groups with the aim of clarifying the phylogenetic relationships of the blind snakes with each other and with the lizards.

The approach has been: (1) to review previous descriptions and reexamine the described species; (2) to examine species whose skeleton had been unknown to date; and (3) to determine the degree of intra- and interspecific variation of the skeleton, especially of those characters on which previous taxonomic conclusions have been based.

This study developed a number of unexpected contradictions with previous descriptions. In some cases these are no doubt due to different methods of preparation of the specimens. In other cases simply better lighting or more completely cleared specimens might account for the differences. Other factors include variability of the structures and differences of interpretation.

Besides adding to our picture of the interrelationships of the blind snakes, this examination of a series of specimens has (1) revealed further correlations between their skeletal structure and their burrowing mode of life, and (2) suggested a reinterpretation of the homologies of certain of their skeletal elements.

A word of explanation may be said here about certain terms which are used in the following pages. "Blind snakes" will serve as a collective term for all six genera. "Typhlopid" here refers to the genus *Typhlops* only. "Leptotyphlopid" likewise refers to the single genus. "Anomalepid" includes the four remaining genera: *Anomalepis, Liotyphlops, Helminthophis,* and *Typhlophis.*

The work is based on examination of seventy-five specimens, representing thirty-two species of *Typhlops, Leptotyphlops,* and *Liotyphlops.* Identification of each specimen was checked by means of an appropriate key wherever possible. Most of the others were certified personally by the lending curator. At first, the sexes were determined. In these snakes this requires dissection, and the practice was discontinued because of the tendency of dissected areas to disintegrate too rapidly during subsequent treatment in potassium hydroxide.

The skeletons were prepared for examination by a modification of the technique described by Davis and Gore (1936) and others. The specimens are macerated in 1 to 4% potassium hydroxide, heavily pigmented ones bleached in 1½% hydrogen peroxide, the skeleton stained with Alizarine Red S (alizarine sulfonate of sodium), and the specimen further cleared by storage in glycerine. This method is one of the best for the study of small skeletons *in situ.* Every bone and tooth was quite distinct in one specimen in which the skull was less than two millimeters long.

In some cases clear observation required some dissection and removal of skin and other tissues. In order to avoid inadvertant removal of any superficial bones like the orbitals this dissection was done only after clearing and staining.

Observations were made with a binocular dissecting microscope. Figures are by the author and were drawn on cross-ruled paper with the aid of a Whipple micrometer disc in an ocular of the microscope.

THE SKULL

The snakes are a group of highly specialized reptiles whose affinities with the rest of the class have been the subject of much speculation. They are commonly accepted as highly modified lizards. If they are an offshoot of the Lacertilia, one might expect to find lizard-like features in the more primitive snakes like the boids, aniliids, xenopeltids, uropeltids, and the blind snakes. Interest in the relationships between snakes and lizards has led to frequent examinations of the skulls of these various groups, especially the blind snakes. The earliest description of the skulls of the latter seems to be that of Muller (1831) of *Typhlops lumbricalis*. Duméril and Bibron (1834–54) illustrated the skulls of *T. reticulatus* and *Stenostome* (= *Leptotyphlops*) *deux-raies*. Jan and Sordelli (1860–66) figured the skulls of *T. braminus* and *richardi* and *Leptotyphlops dimidiata* and *albifrons*. Peters (1882) figured the skull of *T. dinga* (= *schlegeli*) and *L. macrolepis*. Boulenger (1890, 1893) figured the skulls of *T. diardi* and *T. lumbricalis*.

Many of the early illustrations are quite generalized, with the result that small sutures and relationships of some bones are often obscure. Later studies, of which Haas's is perhaps the best example, have utilized serial sections, minute dissections, or alizarin preparations, and most of our detailed knowledge of the anatomy of these snakes dates from these studies. Haas's work (1930) on the skull and jaw musculature of the blind snakes is quite detailed, with numerous very well-executed figures of the skulls of *T. punctatus*, *braminus*, and *Leptotyphlops albifrons*, including serial sections. Brock (1932) reconstructed the skull of *Leptotyphlops nigricans* from serial sections, reporting the presence of a tiny tabular bone between the quadrate and the otic capsule. Mookerjee and Das (1932) noted the paired parietals of *T. braminus*. Mahendra (1936) dissected and figured four alizarin-stained specimens of *T. braminus*, recording for the first time in the blind snakes the presence of small postfrontals. Dunn (1941) described the skeleton of an alizarin-stained *Anomalepis aspinosus*, figuring the jaw mechanism and parts of the skull, including free orbital bones. Dunn and Tihen (1944) described and figured the skull of *Liotyphlops albirostris* from three similarly prepared specimens, noting the close resemblance between this genus and *Anomalepis*. Tihen (1945) added to Dunn's description of *Anomalepis* and made comparisons of skeletal features in *Typhlops*, *Leptotyphlops*, *Liotyphlops*, and *Anomalepis*. Smit (1949) figured sections and reconstructions of the skull of *T. delalandii*. McDowell and Bogert (1954) discussed at length the cranial features of the blind snakes (including figures of *T. punctatus* and *Leptotyphlops dimidiata*) and concluded that the Typhlopidae have had a saurian ancestry separate from the leptotyphlopids and higher snakes and are sufficiently distinct to be removed from the Ophidia.

The detailed descriptions and figures in these later papers make extensive repetitions unnecessary here. However, each of the studies is largely based on an examination of a single species, or at the most, three or four species out of the two hundred or more known kinds of blind snakes. It is worthwhile to summarize the preceding work and to point out a number of variations, discrepancies, and contradictions that have come to light in the course of the present study of thirty-two species.

This in itself is a small sample, of course, but a good one nevertheless in view of the scarcity of most species in collections (many are known only from type specimens or type series) and the reluctance of museums to loan scarce materials for a procedure which destroys all parts of the specimen except the skeleton.

The occipital region of the skull of these snakes shows a great deal of interspecific variation. A basioccipital and paired exoccipitals are always present, but the supraoccipital may be single, paired, or fused with the exoccipitals (or absent). The basioccipital in *Typhlops* is flat and roughly triangular, with its apex directed posteriad. The anterior edge (the base of the triangle) is straight or slightly concave and meets the rear edge of the basisphenoid. Laterally the bone is bordered by the lower edges of the exoccipitals and prootics. A single median foramen is present in some species. The posterior end enters into the formation of the foramen magnum to varying degrees, tending to be crowded out by approximation of the postero-ventral tips of the exoccipitals dorsal to it. This posterior end of the basioccipital normally articulates with the hypocentrum of the atlas, fitting against a calcified cartilage facet of the latter. Of the species of *Typhlops* examined here, the basioccipital is completely excluded from the foramen only in *braminus*, the exoccipitals in this case meeting each other behind the former.

The basioccipital of *Liotyphlops* is very much the same as in *Typhlops:* roughly triangular, the posterior tip articulating with the hypocentrum and entering into the formation of the foramen magnum.

In *Leptotyphlops* this bone has the same general form and relationships as in the typhlopids. It is more likely, however, to be completely excluded from the foramen magnum by posterior extensions of the exoccipitals. It is thus excluded in *L. nigricans, emini, bakewelli,* and *magnamaculata.* There is an interesting correlation between this exclusion from the foramen and the great reduction or absence of the hypocentrum of the atlas. In the four species just mentioned the hypocentrum is absent or quite vestigial. In other species, where the basioccipital participates in the foramen, the hypocentrum is relatively well developed.

The exoccipitals are irregular bones, the major part of each forming the lateral wall of the foramen magnum and of the occipital region of the skull. This central portion of the bone may be thought of as having three extensions. (1) Curving toward the midline is a dorsal piece which, with its opposite, forms the roof of the foramen magnum. This dorsal piece is usually separated from the opposite one by a considerable gap. (2) The second extension is a postero-ventral piece which also curves toward the midline, lying above the basioccipital and tending to exclude it from the foramen. The end of this extension articulates with an anterior facet on the corresponding side of the atlas. (3) The third is a slender anteroventral piece of variable length which lies along the lateral edge of the basioccipital, separating the latter in part from the prootic above. Near the base of this extension of the exoccipital is a foramen of variable size, through which exit the seventh, ninth, and tenth cranial nerves.

In *Typhlops* the relationship between the exoccipital and adjacent bones is varied. In most species the exoccipital is separate, meeting the prootic firmly but separated from the supraoccipitals by a gap. In other species it is fused with the supraoccipital (*T. braminus* and *boettgeri*), and in *T. lineatus* it is fused with both the supraoccipital and prootic. In *Liotyphlops* it is fused with the prootic. In all the species of *Leptotyphlops* examined here it is a separate bone with approximately the same shape and relationships as in most *Typhlops.*

The supraoccipitals in nearly all the blind snakes are paired, ovoid or rectangular, and rather widely separated from the surrounding bones. The only exceptions are the single median supraoccipital of *Liotyphlops, Anomalepis,* and *Leptotyphlops dimidiata,* and the previously noted instances of fusion with the exoccipitals. Of course, in those instances where the supra- and exoccipitals seem to be fused the former may actually be absent, for there are no visible lines or other evidences of fusion. As can be seen in the accompanying plates, however, in these specimens the single bone covers about as much area dorsally as do the separate bones in other species. If the supraoccipital is in fact absent, the exoccipital has expanded anteriad to replace it. The pairing of the supraoccipitals is in itself a rare condition in vertebrates, and it has been suggested (McDowell and Bogert, 1954) that such a supraoccipital is merely an unfused part of the exoccipital (if paired) or a sort of fontanel bone (if median), the true supraoccipitals being absent. As in other doubtful situations in these snakes, embryological observations would be quite helpful.

The prootics are rather large convex bones covering the otic region, meeting all three occipital bones to the rear and the parietal and basisphenoid in front. They are closely applied to the exoccipitals but often widely separated from the others. The maxillary and mandibular branches of the trigeminal nerve exit by an especially large gap between the prootic and parietal where they approach the basisphenoid. In another smaller gap between the prootic and exoccipital (largely a notch in the edge of the latter) a very minute columella may be visible. Its presence in or absence from some species could not be definitely determined. The prootics are separate bones in *Leptotyphlops, Anomalepis,* and most *Typhlops,* but are fused with the exoccipitals in a few *Typhlops* and in *Liotyphlops.* Such fusion of the prootics and exoccipitals is common in lizards but among snakes seems to be limited to these few cases. It has been reported in *T. richardi, braminus,* and *bituberculatus.* In the specimens of *richardi* and *braminus* available to me, however, the prootics are quite separate. Mahendra (1936) noted the same discrepancy with respect to *braminus.* As mentioned previously, in *T. lineatus* the prootics are fused with both the ex- and supraoccipitals.

The parietals of *Typhlops* are the largest bones of the skull. They are bordered by the frontals, basisphenoid, prootics, and supraoccipitals and are rather widely separated from all of them. The chief characteristic of the parietals here is the downgrowth of their lateral edges to meet the basisphenoid. They thus form the side walls as well as the roof of this region of the skull. Such extreme downgrowth is typical and quite characteristic of all snakes, although the same arrangement occurs in amphisbaenid and dibamid lizards. Ordinarily, the parietals of snakes are fused into a single large unit, and early comparative anatomists, including even Williston (1925), spoke of the parietals of the Ophidia as "always fused." The paired condition of the parietals of many of the blind snakes is thus an unusual feature. Mookerjee and Das (1932) called attention to the paired parietals of *T. braminus,* but Haas and others even as early as Jan and Sordelli had previously figured this condition. Most species have them fused, but even in the most common, fused conditions they usually show various degrees of mid-dorsal notches, grooves, fissures, etc. (Plates 1, 4, 7, 10). In the early developmental stages it is likely that the parietals are separate in all *Typhlops.* One discrepancy between the present studies and a statement in the literature may be mentioned: *T. richardi* was figured by Jan and Sordelli with paired parietals, but in the one specimen of *richardi* available to me they are well fused. In view of the numerous evidences of embryological fusion mentioned above, one might expect to find some intraspecific variations in this respect, although none were encountered in the specimens at hand.

In *Liotyphlops* and *Anomalepis* the parietals are paired. In *Leptotyphlops* they are nearly always well fused; only in *L. emini* are they separate. A peculiar feature of the parietals of *L. humilis* (noted also by McDowell and Bogert) is a large unossified central area which often contains scattered calcareous granules (Plate 10). Upon dissection, the area seems as firm as the surrounding bone although it does not stain with alizarin.

Separate, paired parietals, as paired skull bones in general, are usually considered to be primitive in comparison with their single fused homologue. Fossil evidence supports this, although Mehely (1907) in a review of the Lacertidae believes that paired conditions may appear in descendants of ancestors having the fused condition. The value of this opinion may be somewhat reduced, however, by the fact that several other tenets of his review contradict generally held ideas of lizard evolution. In this connection, a very novel situation has been noted by Grobman (1943) in the salamander *Gyrinophilus porphyriticus,* where the anterior ramus of the premaxillary is continuous with its opposite member in the larva but becomes separated by a suture or fissure in the adult.

With respect to the parietals of the blind snakes, at least, it seems safe to consider the paired condition as the primitive one. The greater tendency for fusion of those bones in *Leptotyphlops,* both in per cent of species and degree of fusion, goes along with the other features that they share with more advanced snakes.

The basisphenoid is the chief bone of the floor of the cranium. It is broad posteriad where it meets the basioccipital, prootics, and parietals, tapering to a point anteriad between the ventral parts of the frontals. In its relationship to the surrounding bones it shows the same wide fissures which characterize the bones of the dorsal occipital region. McDowell and Bogert (1954) attached some significance to this fissure between the parietal and basisphenoid as a peculiarity of *Typhlops,* stating that in typical snakes and *Leptotyphlops* "the ventral extremity of the parietal forms a firm suture with the lateral edge of the basisphenoid." However, in all but one of the species (*maximus*) of *Leptotyphlops* examined by me the fissure between these two bones is quite as pronounced as in the average *Typhlops.* A second difference in the basisphenoids of these two genera noted by the above authors is the shape of the anterior tip and the relative length of the bone: "In snakes and leptotpyhlopids the basisphenoid is pointed anteriorly, extends as far forward as does the frontal, and meets the vomer. In the typhlopids the basisphenoid is truncated or emarginated anteriorly, does not extend nearly so far forward as does the frontal and is separated from the vomer by a median vacuity." This distinction is generally true, but examination of other species again shows a number of exceptions and intermediate conditions. In seven species of *Typhlops,* for example, the anterior end is quite pointed and in at least three it reaches the vomers. On the other hand, in some *Leptotyphlops* the basisphenoid is bluntly rounded and does not reach the vomers, leaving a small fontanel in the cranial floor. This part of the basisphenoid in *Liotyphlops* has an unusually long contact with the parietal and a very broad anterior tip which narrows abruptly as it approaches the vomers. In all three of these genera the tip of the bone is often cleft by a median fissure.

The frontals of the blind snakes are always paired, as in other snakes, and, like the parietals, extend ventrally to the basisphenoid, separating the orbits and forming the side walls of this part of the skull. They vary somewhat in detail, however, among the genera. One difference is in the manner of formation of the interorbital partition. In *Leptotyphlops* there is an extensive descending portion which is more or less vertical in plane, and which turns down sharply from the dorsal horizontal plate. This angle between the dorsal and vertical processes extends forward to a posterior "finger" of the prefrontal. In *Typhlops* and *Liotyphlops* the descending process curves ventrally more gradually, thus is not so sharply defined from the dorsal part, and the posterior tip (orbital process) of the prefrontal is very low in the orbit (Plates 2, 5, 8). McDowell and Bogert feel that the low position of this orbital process indicates a very small descending plate of the frontal, saying, "we must rely on this (the orbital process) to distinguish between the descending lamina and dorsal plate of the frontal, for the frontal bone itself shows no sharp angulation or supraorbital shelf"; and that the interorbital cavity here is formed not by the descending processes but "by the outward inflation and billowing of the dorsal plate of the frontal." In most *Typhlops,* however, there is a fairly well-defined crest along the frontal above the orbit. Lateral to this ridge the bone does not turn directly ventral as in *Leptotyphlops*, but curves ventro-laterally. It seems best to consider this low crest as the line between the dorsal and descending plates and the latter portion of the bone as differing from that of *Leptotyphlops* only in being convex rather than plane. The presence of a very small descending plate is indeed suggested by the lower direction of the orbital process of the prefrontal in *Typhlops,* but there is no crest or angle on the frontal in this low position and it seems unlikely that this orbital process would follow so exactly the movement of the line of division between these two regions of the bone. It is more likely that the slight difference in orientation of the prefrontal is associated with the unusually expanded nasal region of *Typhlops.* The flaring, swollen outline of the nasal region of the skull is quite distinctive in this genus.

A second variation of the frontals is the extent to which they approach each other in the mid-ventral line. The previously mentioned descending processes turn medially just dorsal to the basisphenoid and approach each other. In most of the blind snakes the opposite processes do not meet, although they come close in *Liotyphlops*, but in a few species of *Leptotyphlops* these parts of the frontals are in contact with each other for some distance immediately dorsal to the basisphenoid, completely encircling the brain at this level (Plate 12). The dorsal part of the frontal varies considerably in relative length among these three genera. It is longest in *Typhlops* and also rather constricted in the center, flaring laterally where it meets the parietal behind it and the nasal region ahead. The frontal is notably shorter in *Leptotyphlops* and not at all widened anteriad. It is unusually short in *Liotyphlops.*

The presence or absence of postfrontals in *Typhlops* has been an unsettled matter for some time. None of the early writers made any mention of them. Haas remarked that both the Typhlopidae and Leptotyphlopidae lack "das Supratemporale (Squamosum), das Transversum, und das Postfrontale." Mahendra (1936) reported tiny bones in *T. braminus,* "Perhaps . . . representing both the postfrontals and postorbitals," and expressed some surprise that previous workers had missed them. These bones in his preparations occurred "in the form of three or fewer small pieces at the anterior outer borders of the parietals." Mahendra was apparently the first to use the clearing and alizarin procedure in preparing his specimens of *Typhlops* and he attributed the demonstration of these tiny pieces to this technique. My experience in the present study leads me to conclude that these bones are of very infrequent and irregular occurrence, even within a species. For example, using the same alizarin technique and excellent lighting I could not find any such structures in several specimens of the same species (*braminus*) from various parts of the world. Mahendra's photograph (1936, fig. 1, D) is not at all clear in this respect, and I had about concluded that he was mistaken when similar small pieces were noted in a specimen of *T. reticulatus.* In this latter specimen (Plate 4) the structures are not true bone but calcified cartilage. They appear to be functionless. One is separate, lying just at the antero-lateral corner of the parietal; the opposite one is attached to that point of the parietal. This single specimen, out of some fifty Typhlops examined, was the only one to show these bones. The location of these rudimentary pieces makes it most likely that they represent postfrontals rather than postorbitals, since the latter in lizards are normally more posterior. *Leptotyphlops* is apparently completely lacking in postfrontals or other free bones in the orbital region.

Both *Liotyphlops* and *Anomalepis,* on the other hand, have a well-developed pair of orbital bones on either side, noted first in *A. aspinosus* by Dunn (1941). One of these two bones lies horizontally above the eye parallel to the edge of the frontal, its posterior end resting on a conspicuous postorbital process of the frontal and its anterior end curving down slightly in front of the eye. The second orbital bone in *aspinosus* is somewhat larger. One curved part lies below and behind the eye and from this a slender process extends directly posteriad to a point lateral to the parietal. It lies free, with no contact with any other bone. These bones of the orbital region were tentatively homologized by Dunn with, respectively, the supraorbital and the posterior orbital (= fused postorbital and postfrontal) of varanid lizards. Dunn's reference specimen had been damaged and the articular relationships of these bones were not clear. Tihen later (1945) found in a well-preserved specimen of *A. dentatus* a supraorbital and a postorbital "nearly identical" with those described by Dunn. He noted in addition that the anterior end of the supraorbital is forked, contacts the dorsal part of the maxilla, and serves as a pivot for the latter, which is moved forward and backward by the pterygoid-ectopterygoid combination. The posterior end of the supraorbital is well braced against the lateral projection from the frontal. Dunn and Tihen had previously (1944) noted an identical kinetic arrangement of the maxilla and supraorbital of *Liotyphlops albirostris.* The supraorbital of this genus is quite like that of *Anomalepis,* but its posterior orbital is much smaller and less complex, a simple curved rod lying lateral to the supraorbital. The specimens of *L. albirostris* examined by me confirm Tihen's descriptions.

A different and well-supported interpretation of the homologies of these orbital bones has been suggested by McDowell and Bogert. Pythons and a few other snakes have a supraorbital, but it bears no close resemblance in shape or position to that bone of the anomalepids. On the other hand, examination of the bones of the orbital region of lizards shows a pair of bones there with relationships that strongly suggest the anomalepid supraorbital. The first is the palpebral (anteriormost supraocular osteoderm) which extends across the lateral surface of the prefrontal to approach or make contact with the ascending facial process of the maxilla. The second is the postfrontal, a bone lying above and behind the eye and attached to a lateral postorbital extension of the frontal (and the parietal). The possibility is suggested, therefore, that the dorsal orbital bone of *Anomalepis* and *Liotyphlops* "represents a fusion of the palpebral with the postfrontal," the anterior end (which articulates with the maxilla) being the palpebral, the posterior end (which meets the frontal) being the postfrontal.

With respect to the second of these orbital bones of the anomalepids it seems quite likely that it also represents a fusion of two bones present in lizards: the jugal and the postorbital. The jugal in anguinid lizards lies in exactly the same position as the anterior part of the *Anomalepis* "postorbital." That is, it lies in part below the eye, curving up behind it to meet the postfrontal. In its form and position the long posterior extension of the "postorbital" is highly suggestive of the true postorbital of lizards. In *Liotyphlops* this slender posterior piece is missing and the smaller and simpler "postorbital" here has very much the same form and relationships as the jugal in anguinid lizards.

The maxilla of the anomalepids is a rather flat, triangular, freely movable bone. The base of the triangle is transversely oriented and bears four or five teeth. The apex of the triangle extends forward and dorsad alongside the prefrontal, ending in a shallow fork which articulates with the palpebral portion of the "supraorbital." It does not contact the prefrontal and, in *Liotyphlops,* at least, upon manipulation seems to be only loosely attached, if at all, to the latter. A small projection on the posterior side of the tooth-bearing portion fits into the forked end of the ectopterygoid.

The maxillary teeth of *Liotyphlops* have an unusual form that seems to have escaped notice to date. Rather than the slender, finely pointed, recurved teeth of higher snakes (typical also of the other blind snakes), *Liotyphlops* has a spade-shaped tooth: its broad, somewhat flattened, obtusely pointed tip is notably wider than the base of the tooth (Plate 3). Teeth with a similar outline are seen in *Iguana,* at least, and probably other lizards, although it is by no means the typical lizard tooth.

The maxilla of *Typhlops* is basically the same as in anomalepids in form and position. Although freely movable it is connected by way of a ligament from its dorsal part to the side of the prefrontal and the septomaxilla. In the absence of the support afforded by the palpebral in the anomalepids this ligamentous attachment serves as a pivot for the maxilla. The tooth-bearing base of the maxilla here is also oriented transversely, with from three to seven curved teeth. The teeth are apparently replaced often, for in several specimens a tooth (red with alizarin) was noted in the intestine. The type of replacement is the same as that of leptotyphlopids, higher snakes, and anguinomorphan lizards. The young tooth develops beside the older one, rather than below it, and forces it out from the side.

The maxilla of *Leptotyphlops* is of an entirely different type. It is lizard-like, immovable, and closely attached to the bones of the lateral nasal region, chiefly the septomaxilla, although it may also contact the premaxilla, the prefrontal, or the vomer. Compared to the maxilla of *Typhlops* the facial plate here is reduced. This maxilla, therefore, is more like that of typical snakes which is reduced to a slender rod (tooth-bearing, however). It does not bear teeth, and its shape is irregular and variable from species to species. In most, however, it bears two characteristic processes. One is a prominent posterior extension which may be slender and rodlike or rather broad and flattened in a horizontal plane. The second is a vertical crest along the ventral edge of the bone, irregularly notched and perforated by two to four holes. McDowell and Bogert noticed an encircling suture separating the posterior process from the main part of the maxilla in *L. dimidiata* and suggested that the posterior portion represents the ectopterygoid. More will be said of this shortly. Undoubtedly the ventral edge of the maxilla formerly bore teeth, and its present ragged and perforated margin suggests degenerate tooth sockets.

The bones of the palatal region of the blind snakes vary interestingly among the genera. The most primitive, yet somewhat unusual, arrangement is that of *Liotyphlops*. Here the pterygoid is a simple slender rod extending forward from the region of the exoccipital to contact a process of the palatine. Its anterior part angles slightly mediad. Its posterior end makes no articulation with the skull, lying free in the muscles below the occipital region. The ectopterygoid is also a slender rodlike bone but much shorter, lying along the anterior end of the pterygoid. Its posterior end lies against the medial surface of the pterygoid, and for a short distance it extends forward parallel to the latter. It then angles laterad and crosses above the pterygoid, terminating in a blunt fork which receives a short process from the base (tooth-bearing portion) of the maxilla. Except for its free posterior end the pterygoid has basically the same relationships with other bones as in lizards: meeting both the ectopterygoid and the palatine anteriad. The position of the ectopterygoid between the maxilla and pterygoid is also normal. The rather loose connections between all these bones is unusual, of course, in view of their normally rigid articulations in other reptiles, and is associated with the mobility of the maxilla. The palatine in lizards is a Y-shaped bone, its two anterior processes meeting the vomer (and the opposite palatine) and the maxilla, and the posterior process meeting the pterygoid. The palatine of *Liotyphlops* seems easily derivable from this lizard type. The medial process meets the posterior tip of the vomer and the opposite palatine. The maxillary (antero-lateral) process, however, is quite short and is unusual in its failure actually to contact the maxilla. The pterygoid (posterior) process of the palatine is slender and, in order to meet the pterygoid, extends more ventrad than posteriad. A nearly identical set of bones occurs in the maxillary kinetics of *Anomalepis,* with the possible exception of the palatine, whose presence or absence was not certainly determined in the specimens available to Dunn and Tihen.

In *Typhlops* the arrangement of these bones has been modified through the loss of the ectopterygoid as a separate element. The palatine here is more robust, its major portion extending in a slight curve from the midline of the palate, where it abuts against the posterior tip of the vomer, laterad and ventrad to the maxilla. Its rounded lateral end fits into a pocket of the maxilla or, more often, into a foramen which penetrates the bone. From about the center of the palatine a slender process extends ventrad to meet the pterygoid. Dunn and Tihen noted that the bone usually called "palatine" in this genus corresponds in its relation to both the palatine and ectopterygoid of *Liotyphlops* and suggested that the latter two bones have fused in *Typhlops.* McDowell and Bogert supported this view: "For this there is some additional evidence not cited by these authors. In *Typhlops* the pterygoid is bilobate anteriorly, strongly suggesting the furcation seen in lizards and many snakes into two processes, an external process for the ectopterygoid and an internal process for the palatine. But the so-called 'palatine' of *Typhlops* is attached not to the internal process but to the external (ectopterygoid) lobe. Yet the element cannot be a simple ectopterygoid, for it extends inward to articulate with the vomer, as does the palatine in other squamatans (except the majority of snakes)."

I suggest an alternative explanation which seems to fit the observations equally well. That is the possibility that the ectopterygoid has fused not with the palatine, but with the pterygoid. In the first place, as will be seen later in a consideration of the hyobranchium and the pelvic girdle, although conditions in the anomalepids are generally more primitive they are often too specialized to represent stages through which the corresponding typhlopid structures have passed. Hence, the short maxillary process of the palatine of *Liotyphlops* and its failure to meet the maxilla need not have preceded the state of the palatine of *Typhlops.* Although there are some unusual orientations and differences in sizes of processes in this group of bones in the anomalepids, so far as their contacts with each other are concerned the only point of departure from the normal lizard relationships is the "most remarkable" lack of contact between palatine and maxilla. It is possible that this short maxillary process is a condition which has appeared since the separation of the anomalepid and typhlopid lines and that in the latter the palatine has always bridged the space between the vomer and maxilla, at the same time sending a process posteriad to the pterygoid, as it does now in lizards. Further support is given to this suggestion by the manner of articulation in *Typhlops* of the end of the palatine fitting into a foramen of the maxilla. In *Liotyphlops* the anterior end of the ectopterygoid is forked, receiving here a projection of the maxilla. Were it still the ectopterygoid meeting the maxilla in *Typhlops,* then a similar type of articulation would be expected. The anterior end of the *Typhlops* pterygoid is always forked, but between species it varies considerably in the length of the rami and in its exact relationships to the palatine. The rami may be well developed (as in *T. lumbricalis*) with the pterygoid process of the palatine received rather loosely between them. In this condition, with slender rami, the anterior end of the pterygoid suggests the combined pterygoid and ectopterygoid of *Liotyphlops.* A fusion and slight shortening of these two bones in the latter genus would result in a structure quite like the pterygoid of *T. platycephalus, braminus,* and especially *lumbricalis.* In most species of *Typhlops* the rami of the pterygoid are shorter and stouter and their articulation with the palatine becomes more complex. McDowell and Bogert, as quoted above, describe the palatine of *Typhlops* as attached not to the internal ramus but to the external. To me, the opposite seems true: the pterygoid process (postero-ventral) from the palatine contacts chiefly and most intimately the internal (medial) ramus of the pterygoid, while the external ramus (= the ectopterygoid?) extends somewhat laterad to brace against the base of the pterygoid process or against the body of the palatine itself. In some species a small secondary process is developed on the pterygoid process of the palatine which fits between the two rami of the pterygoid.

The pterygoid-palatine-maxilla series in *Leptotyphlops* has yet a third arrangement. The pterygoid is a slender, slightly curved bone, shorter than in the other blind snakes, reaching posteriad no farther than the rear of the basisphenoid. Posteriad it is unattached. Anteriad it is closely applied to the pterygoid process of the palatine. The palatines in this genus differ from the preceding in their form and in their larger size. They are still basically triradiate, however, contacting the vomer, the pterygoid, and (usually) the maxilla. The body of the palatine is a broad flat plate, usually perforated by a foramen. Its vomerine process is broad and not well distinguished from the body of the palatine. It is expanded and often curled ventrad as it abuts against the posterior tip of the vomer. The pterygoid process is slender and lies against the ventrolateral surface of the anterior end of the pterygoid. The maxillary process is slender and may not contact the maxilla. For those palatines which do touch the maxilla (on its medial surface) there is no differentiated articular facet for their reception (except in *L. emini*), although the distal end of the maxillary process itself in one species (*maximus*) is expanded where it meets the maxilla. With the rigid attachment of the maxilla there is apparently no fore and aft movement possible in this series of bones.

In the past, the ectopterygoid had been considered absent in *Leptotyphlops*. However, McDowell and Bogert noticed a definite suture delimiting the peculiar posterior extension of the maxilla in *L. dimidiata*. They suggested that this piece represents the ectopterygoid partially fused to the maxilla. Certainly it is a logical position and there is otherwise no counterpart in either snakes or lizards of this extension of the maxilla. In most species this remnant of the ectopterygoid (if it is such) is completely fused to the maxilla. A suture between the two was visible in only one of the species examined by me (Plate 12: *maximus*).

Mention may be made here of a pair of weakly calcified cartilages (?) that are present in most of the species of *Leptotyphlops* in this study and are noted here for the first time. They are rodlike, horizontal, variable in size, quite flexible upon manipulation, and lie just below and more or less parallel to the maxillary processes of the palatine bones (Plate 12). The figures of Haas on the musculature of this region show no ligaments or tendons here that might have sesamoid-like calcification. The only bones from this area of the palate that might be represented by such rudiments are the ectopterygoids, parts of which may be represented here by these rather degenerate calcifications. More likely they are a sort of heterotopic "bone" developed in the connective tissue of the palate and serving to strengthen it against the teeth of the dentary which lie below it in this area.

The paired vomers of the blind snakes are all basically the same. In ventral view each has a flat anterior expansion which curves posteriad and ends in a hook. The middle section of the bone usually consists of a smaller, hookless expansion. The posterior part of each vomer in *Liotyphlops* is a slender, finger-like process, its tip barely in contact with the respective palatines (which are braced chiefly against each other). In *Typhlops* and *Leptotyphlops* this posterior part is extended a short distance ventrad as a vertical plate against which is braced the expanded end of the palatine. The vomers in all these genera lie just ventral to the medial edges of the septomaxillae. In cross section the horizontal portion of each vomer is seen to have a short dorsal vertical plate, separated in the midplane by a thin cartilaginous septum. Those of *Leptotyphlops* are considerably larger and more closely applied to one another, even partially fused in one specimen of *nigricans*.

These paired bones of the palate of lower tetrapods (here called vomers) have been subject to changes of terminology which are reflected in some of the works pertaining to the blind snakes. "Vomer" was the original name for these bones, which were believed to be homologous to the single vomer of mammals. A later view held that the mammalian vomer is the homologue of the parasphenoid of other vertebrates, and the vomers of reptiles then became known as "prevomers." Some of the papers cited here use this latter term. Parrington and Westoll (1940) have been followed by most comparative anatomists in a return to the original view, holding that the parasphenoid of lower vertebrates has been lost in mammals.

The septomaxillae are prominent bones in a ventral view of the skull, although in *Leptotyphlops* they may be largely covered by expansions of the vomers and maxillae. Each septomaxilla encloses one of the Jacobson's organs. Ventrally it is overlapped by the edges of the vomer, premaxilla, and prefrontal (it is fused with the latter in *Liotyphlops*) and, in *Leptotyphlops,* the maxilla. Dorsad it is concealed by the overlying frontal and nasal. To the rear it reaches the descending portion of the frontal except in *Leptotyphlops.* Laterad it is largely concealed by the prefrontal. Low on the lateral wall of the septomaxilla there is a horizontal shelf which usually forms a small part of the bony anterior naris. In *Typhlops* there is a tendency for the edge of this shelf to curve upward, and in *Leptotyphlops* it is a highly developed ascending process which is characteristically perforate where it enters the bony naris (Plate 11). A second characteristic of the bone in *Leptotyphlops* is its much reduced contact with the premaxilla, a result of the expansion of the vomer.

Finally, mention must be made of a pair of squarish bones apparently unique to *Liotyphlops* and (possibly) *Anomalepis.* First noted by Dunn and Tihen in the former genus, they were tentatively identified by them as extensions of the frontals, or as epipterygoids, or laterosphenoids (= the very large orbitosphenoids of amphisbaenids?). Although the relationships of these bones to the adjacent ones are somewhat obscured by the dense connective tissue of the palate, their arrangement in the two specimens of *Liotyphlops albirostris* at hand does not agree with that described by Dunn and Tihen. As figured by these authors (1944, fig. 4) the bones correspond very well to what I see as antero-ventral extensions of the frontals: i.e., they are directly above the palatines, posterior to the vomers, and overlapped slightly by the anterior edge of the basisphenoid. Yet in my two specimens I note a pair of apparently separate bones which do not seem to be shown in Dunn and Tihen's figure. These are in a more anterior position, immediately ahead of the ventral extensions of the frontals, and dorsal to the tips of the vomers. Each is definitely separated from the frontal by a fissure, but their borders match closely (Plate 3). They seem to meet the posterior extremities of the septomaxillae, and it is not certain that they are separate from them. Whether they are distinct bones, processes of the frontals, or septomaxillae, they have no counterpart in the other blind snakes.

The prefrontals of the blind snakes are all rather similar. They are separate bones except for their fusion with the septomaxillae in *Liotyphlops.* They cover the sides of the rostrum and, especially in *Typhlops,* contribute as well to the floor of this region. Posteriad there is an orbital process lying against the frontal. Anteriad in *Typhlops* and *Liotyphlops* the prefrontal forms a part of the border of the naris, but in most *Leptotyphlops* it has shortened to such an extent that the exposed septomaxilla replaces it in the border (Plate 11).

Correlated with the burrowing mode of life, the nasal bones and general nasal region are quite expanded, especially in *Typhlops,* less so in *Leptotyphlops.* The nasals are separate in all the *Typhlops* examined and in *Anomalepis aspinosus.* They are fused in *Liotyphlops,* several species of *Leptotyphlops,* and *A. dentatus.* In cross section, a descending plate of each bone is seen to form an internasal septum. The nasal always contributes to the border of the bony naris. A slitlike extension of the naris separating the nasal and the prefrontal was considered by McDowell and Bogert to be characteristic of *Leptotyphlops* (and nearly all higher snakes) but to be absent in *Typhlops.* Such a fissure between the two bones is present, however, in several species of *Typhlops.* The rather striking foramina in the nasals of the blind snakes are passages for the exit of nerves to the numerous sense receptors in the skin of the rostrum.

An unusual feature of the nasals noted in *Liotyphlops* and in two species of *Leptotyphlops* is the presence of a short and incomplete transverse fissure near the rear of each bone. The appearance is that of a partially fused fontanel bone. The condition may be correlated with the greater length of the nasals in these two genera, for no such fissures were noted in *Typhlops*, where these bones are much shorter. More likely, the fissures are merely elongate foramina for the passage of sensory nerves.

The premaxillae, like the nasals, reflect the burrowing life of these snakes in their great enlargement, which often suggests a shield across the ventral edge of the rostrum. They are consistently fused in all the blind snakes. The resulting bone forms the anterior face of the rostrum (except in *Liotyphlops*) and curves ventrad where it meets the septomaxillae and vomers. In *Typhlops* it is in broad contact with the septomaxillae and has a pointed posterior process, the tip of which usually lies between the vomers but may or may not actually contact them. On the other hand, in *Leptotyphlops* this posterior palatal process is shorter and broader and firmly meets the much wider vomers. The premaxilla-septomaxilla contact is considerably reduced, although there is some interspecific variation here.

THE LOWER JAW

In a comparison of the genera of blind snakes the structure of the lower jaw and its suspension seem particularly significant. Two fundamentally different types of mandibles occur, emphasizing, as much as any other part of the skeleton, the distinctness of the leptotyphlopids and the typhlopid-anomalepid group.

In *Typhlops* the rather flattened quadrate is connected to the exoccipital and extends forward and downward to its articulation with the mandible. The relative shortness of the mandible here, and in other blind snakes, necessitates this forward direction of the quadrate, which in typical snakes is vertical or directed posteriad. The attachment of the quadrate directly to the cranium is similar to that of lizards, the other blind snakes, and a fossil snake *Dinilysia*, but differs from typical snakes where a well-developed tabular bone is interposed. The anterior part of the quadrate has a dorsal expansion in the form of a winglike plate. This is a process absent in some of the other blind snakes and all higher forms but suggestive of the outer conch of the quadrate in some diploglossan lizards. The anterior articular end of the quadrate is rounded, usually capped with calcified cartilage, and fits into a similarly capped, concave facet of the mandible.

The major part of the mandible of *Typhlops* is a curved, bladelike bone formerly called the articular. However, it has a number of variable and indistinct lines, fissures, and foramina, and it is likely, as indicated by McDowell and Bogert, that its composition includes the surangular and prearticular as well as the articular, although the boundaries of these elements are obscure. There is a retroarticular process of the mandible of variable length (usually about half that of the quadrate) extending below the quadrate.

At the anterior end of this compound "articular" is a group of three or four bones, firmly attached to it and to each other. No movement among themselves is possible for the bones in this group. The most prominent of them is the coronoid, a flat, triangular bone lying against the medial surface of the compound bone, its apex (the coronoid process) tall and usually sharply pointed and lying just lateral to the maxilla when the jaws are closed. McDowell and Bogert figure the horizontal base of the coronoid in *T. punctatus* as emarginate near the center, a part of the compound bone (surangular?) being thus exposed in medial view. They attach some significance to this form of the coronoid since it resembles the similarly notched coronoids of the anguinomorphan lizards. The coronoid is indeed so notched in *punctatus* and *schlegelii* but in a few other species it is so slightly notched that the compound bone is not exposed and in most species the base is perfectly straight with not even a slight emargination. In the general form of coronoid, *Typhlops* resembles one of the two groups of anguinomorphan lizards (the diploglossa) but differs from the other (the platynota) and the typical snakes. In the snakes and platynotans the coronoid process arises from the posterior portion of the bone, the anterior half of the bone having a more or less horizontal upper border. In *Typhlops* and the diploglossans, on the other hand, the coronoid process is more in the center of the bone and the entire dorsal border is involved in the development of the process. There is some interspecific variation in the form of the process (Plates 2, 5, 8). It is pointed in some, rounded in others, the front may be concave or convex, etc.

The dentary is small and toothless, although, like the maxilla of *Leptotyphlops,* its edge is sometimes ragged and irregular, suggesting former tooth fossae. The dentaries are rigidly joined to each other in the midline by ligaments or cartilage and little or no movement between them is possible.

At least among reptiles, the splenial is unusual in its extensive lateral exposure. It partially conceals the dentary in lateral view. It lies close against the ventral surface of the latter, curving up around it both laterally and medially. In lateral view it meets the compound bone (surangular portion) in a long, oblique suture. In medial view it extends somewhat farther posteriad to about the middle of the base of the coronoid, lying below and forming a horizontal suture with the latter. The length of the splenial and its extensive contact with the coronoid and the dentary makes the mandible a rigid unit. Here again *Typhlops* resembles the diploglossans and differs from the platynotans and snakes (including *Leptotyphlops*) where the splenial is short and may even fail to reach the coronoid, permitting the formation of a vertical hinge joint here and of a more or less movable "foremandible" composed of the dentary and splenial. There are some variations in the size of the splenial of *Typhlops*, in the degree of its lateral exposure, and in its junction with the compound bone (the latter may overlap it). It is extremely reduced in *T. braminus*, having here almost none of the normal relationships.

The angular in *Typhlops* is even more variable. It lies below the compound bone, its anterior end meeting or overlapping the posterior end of the splenial, and is visible in both medial and lateral views. It is as long as the splenial in some species, quite vestigial in others, and absent (or fused with the compound bone) in still others (Plates 2, 5, 8). It is longest in *T. braminus* where the splenial is so much reduced.

A small columella is present in all the species of *Typhlops* examined. It barely extends through a small fenestra ovalis (a notch in the fissure between the exoccipital and prootic), and in well-cleared specimens its greatly expanded foot plate can be seen within the otic capsule. The columella and fenestra are usually concealed in lateral view by the posterior end of the quadrate. In a few species the columella is freely movable upon touch, but in most the foot plate seems firmly attached within the capsule.

No evidence of a tabular has been reported in any *Typhlops*, nor was any noted in the present series.

In *Liotyphlops* the lower jaw is basically the same as in *Typhlops*, but some notable differences can be mentioned. In the first place, there is a small, inverted, comma-shaped bone near the posterior end of the quadrate. Two interpretations of this bone have been made. Dunn and Tihen called it the tabular, a bone that connects the parietal and quadrate in the Squamata. McDowell and Bogert suggest that it is more likely a reduced squamosal, insofar as it is "lateral to the quadrato-cranial articulation, considerably anterior to the paroccipital process, and isolated from the parietal. . . ." The squamosal is absent in snakes, but in most lizards it occupies a position alongside and dorso-lateral to the tabular. The posterior end of the squamosal extends down to meet the quadrate while the other end goes forward and laterad to meet the postorbital and form with it a strong temporal arch. The fact that *Anomalepis* has a postorbital "makes it the more likely that the closely related *Liotyphlops* might possess the other constituent of a temporal arch, the squamosal."

McDowell and Bogert do not include *Liotyphlops* in their list of material examined and presumably have relied on the figures and descriptions of Dunn and Tihen. It is necessary, therefore, to note that on the basis of the specimens in the present study the quadrate, tabular, and compound bone of the lower jaw in Dunn and Tihen's figure all seem considerably displaced dorsad and anteriad and the tabular is more horizontal than vertical. The tabular in the specimens at hand is not "considerably anterior to the paroccipital process" but is only slightly, if at all, anteriad. Also, it lies directly above the end of the quadrate and is hardly more lateral than is the posterior end of the tabular of most lizards. It is, indeed, "isolated from the parietal," but were it a squamosal it would be even farther removed from the presumed position of the missing postorbital. The best evidence supporting the "tabular" interpretation of this bone is the close resemblance in both its form and orientation in *Liotyphlops* to the ventrally curving posterior end of the tabular in lizards, especially in those where the tabular is somewhat reduced in size. The tabular of the gecko *Coleonyx,* for example, except for its remaining contact with the parietal, is very similar to that of *Liotyphlops.* In this gecko, however, the contact of the tabular is only with a long posterior projection from the rear corner of the parietal which overlies the otooccipital region. In the absence of this extension of the parietal, the tabular of *Coleonyx* would have exactly the spatial relationships of the bone in *Liotyphlops.*

The quadrate of *Liotyphlops* is like that of *Typhlops* in its suspension and its orientation, but it differs somewhat in form. Except for a very small anterior elevation, the prominent dorsal plate of the quadrate in *Typhlops* is absent here, but a similar dorsal projection, smaller and not so flattened, is present at the other (posterior) end of the quadrate. The form of this rear end of the quadrate suggests a loose articulation with the tabular (Plate 2), but such a connection could not be determined certainly.

The compound bone of the mandible here is more slender than that of *Typhlops,* the articular facet for the reception of the quadrate is poorly developed, and the retroarticular process is extremely long, much longer than the quadrate itself. The front of the coronoid is much more convex and the coronoid process is directed more posteriad than in *Typhlops.* The base of the coronoid is straight, with no emargination.

The bone here termed splenial in *Liotyphlops* has been figured as the angular by Dunn and Tihen. From the relationship of the bone to the dentary in this genus, and in view of the stages of reduction of the angular to be seen in *Typhlops,* it seems more likely that the bone in *Liotyphlops* is the splenial and that the angular is absent.

The dentary is similar to that of *Typhlops* except that it bears teeth.

Earlier workers, from Peters and Boulenger to Dunn, had overlooked these teeth (Taylor, 1939, detected the teeth in *Anomalepis*). Dunn and Tihen, however, reported the presence of a single tooth on the dentary. There is apparently some variation in the number of teeth here, for in one of the two specimens at hand there are two teeth on each dentary, and in the other specimen there are three on each dentary. The specimen with the two teeth per dentary is quite small (68 mm). Its teeth stand in a line almost at right angles to the main axis of the skull (the medial tooth is very slightly ahead of the lateral one) and both seem to be functional. In the larger specimen (158 mm) two of the teeth are likewise in an almost transverse line, are of approximately the same size, and seem to be functional. The third tooth here is much smaller, apparently a replacement tooth, and stands behind the lateral functional tooth. These teeth of the dentary are rather bluntly pointed, only slightly curved, and do not show the spadelike outline of the maxillary teeth.

A slightly movable columella is present, covered in lateral view by the posterior end of the quadrate. It is relatively larger and better developed than those of *Typhlops.*

The following description of the lower jaw of *Anomalepis* is based on the papers by Dunn (1941) and Tihen (1945). As figured by Dunn the quadrate of *Anomalepis* is intermediate in outline between that of *Typhlops* and *Liotyphlops,* with a flat dorsal plate present in the middle of the bone, giving it a low triangular shape. The slender compound bone of the mandible here is similar to that of *Liotyphlops* also in the possession of a very long retroarticular process. Tihen reported the possible presence of a separate surangular in one imperfectly cleared and stained specimen but "confirmation of this point is needed." The coronoid is concave in front, and has a low and broadly rounded dorsal process and a slender anterior extension of the base, being thus rather distinct from both *Typhlops* and *Liotyphlops.* The base is not emarginate. A bone obviously comparable to the splenial of *Liotyphlops* is figured by Dunn as the angular, but, as pointed out above, it is more likely a splenial, the angular being absent. The dentary bears a single tooth in the two cleared and stained specimens which have been examined by the above two authors, but Dunn was unable to find teeth here in three out of four untreated specimens. Their occurrence may thus be irregular.

With respect to *Typhlophis* and *Helminthophis,* the only published descriptions of the skeletal anatomy are a few comments by McDowell and Bogert, including reference to the lower jaw: *Typhlophis* lacks a tabular, has a more pointed coronoid, and the dentary bears a single tooth; *Helminthophis* likewise has a single tooth on the dentary.

The lower jaw and quadrate of *Leptotyphlops* differ considerably from those just described. The quadrate is a longer, more slender, slightly flattened bone, with no evidence of the dorsal wing so characteristic of *Typhlops,* although its posterior end is often expanded in a manner suggestive of the rear end of the quadrate of *Liotyphlops* (Plates 2, 11). This expansion in *Leptotyphlops* is flat and, if well developed, is usually perforated by a foramen. Other variations occur in this part of the quadrate. A small piece of calcified cartilage may be present as a separate element at the end of the quadrate, it may be fused with the latter, or it may be attached but delimited by a suture. Brock (1932) reported the presence of a tiny tabular in this area from a study of serial sections of *L. nigricans.* As described by her, it is "wedged between the quadrate and otic capsule," but in the accompanying lateral view of the skull (1932, fig. 1) it is visible on top of the posterior end of the quadrate. No bone or calcification was noted *between* the quadrate and prootic in any of the species on hand, including *L. nigricans,* even upon careful dissection of well-cleared specimens. McDowell and Bogert likewise found no sign of a tabular in their *Leptotyphlops* material, which also included *nigricans.*

In the specimens examined in the present work, a number of things suggest that in *Leptotyphlops* the tabular is in various stages of degeneration and fusion with the quadrate: the fused or separate calcified cartilage at the end of the quadrate, the frequent expansion of this end of the bone, and especially its resemblance in some species to the quadrate *plus* the tabular of *Liotyphlops.* The anterior end of the quadrate is more highly modified for articulation with the mandible than is that of *Typhlops.* The articular portion is saddle-shaped, rather like a heterocoelous centrum, and fits into a similar but more concave "saddle" of the compound bone of the mandible.

The latter is quite short and has a strangely distorted appearance, with irregular protuberances and foramina of various sizes (Plates 2, 11). It probably consists of the fused articular, prearticular, and surangular, but no sutures are present and the limits of each of these components are obscured. A very short retroarticular process is present.

The coronoid has a shortened and distorted appearance like the compound bone. It lies largely on the medial surface of the latter, with only the highly variable coronoid process visible in lateral view. The base of the coronoid also is irregular without definite anterior and posterior parts.

A separate angular is present, lying chiefly along the ventro-lateral surface of the compound bone, its posterior end fused to the latter in *L. dulcis.* This lateral exposure is unlike the angular of typical snakes, in which the bone is limited to the medial surface of the mandible. Its anterior end is bluntly rounded or flattened and meets the similarly shaped posterior end of the splenial. The junction of these two bones is usually visible in lateral view just posterior to the rear edge of the dentary. However, the small splenial lies almost entirely against the medial surface of the dentary and may be so short that it does not appear at all in a lateral view. All or most of the dorsal edge of the splenial is separated from the dentary by the open Meckelian groove, a characteristic also of the typical snakes and platynotan lizards. The wide separation of the splenial and coronoid in the development of the hinge joint here is the most extreme of any snake or lizard.

The dentary is large and well developed compared to that of the other blind snakes. It appears to be compressed antero-posteriorly. The teeth, usually four or five in number, are limited to the anterior part of a conspicuously enlarged flange. The teeth are usually sharply pointed and slightly recurved, except in one puzzling case (a specimen of *L. magnamaculata*) where they are short and perfectly square-cut (Plate 11). A postero-dorsal projection of the dentary extends back over the compound bone.

The "foremandible" here, consisting of the dentary and splenial, is freely movable. This vertical hinge is a major point of distinction between *Leptotyphlops* and the other blind snakes, and is a point of resemblance to the typical snakes and some groups of the platynota. The articulation is chiefly between the ends of the splenial and the angular, the postero-dorsal piece of the dentary serving to limit the dorsal movement of the tooth-bearing dentary-splenial unit.

THE VERTEBRAL COLUMN AND RIBS

Locomotion in snakes is peculiar. The vertebral column, the ribs, the costal and cutaneous musculature, and the ventral scutes have taken over this function and the vertebrae show a number of correlated modifications. First, they are more numerous than in any other group of vertebrates. Some living species have over 400 and in one extinct species, *Archaeophis proavus,* 565 have been counted (there is some evidence that *Archaeophis* may have been a fish (McDowell and Bogert, 1954)). Further, the division of the column into the usual regions (cervical, thoracic, etc.) is not at all clear. Additional articulations, the zygosphenes and zygantra, although not unique to snakes, are quite characteristic of them (zygantral articulations are known in several families of lizards, both living and fossil, but not in the amphisbaenids nor, apparently, in any other snakelike lizard). Usually, all the precaudal vertebrae except the atlas and axis bear ribs.

These modifications of the vertebrae have attracted the interest of various investigators, and the general anatomy of the snake vertebral column has been known for some time. Owen (1853) presented a detailed account of the vertebrae of several snakes, and a number of textbook writers have added to the subject: Huxley (1871), Williston (1925), Kingsley (1925), Goodrich (1930), and others. A recent review of these and other more specific papers is that of Sood (1948), which also includes studies of serial sections.

With respect to the Typhlopidae and Leptotyphlopidae, Mookerjee and Das (1933) reported the presence of ventral foramina in the vertebral centra of *Typhlops braminus.* Mahendra (1936) noted the separate hypocentrum of the atlas and the simpler zygosphene-zygantrum relationship in the same species. Dunn's (1941) study of a cleared and alizarin-stained specimen of *Anomalepis* found the vertebrae to "closely resemble those of *Typhlops braminus* as figured by Mahendra." He also found that "the odontoid is a part of the axis and not a separate bone," but did not mention a free hypocentrum. Dunn and Tihen (1944) noted the presence of hypapophyses on the atlas, axis, and other anterior vertebrae of *Liotyphlops albirostris.* Tihen (1945) noted the number of vertebrae and ribs of a second cleared and stained specimen of *Anomalepis* but did not clarify the atlas-axis arrangement. Hoffstetter (1946) described the only known extinct species of *Typhlops* on the basis of two collections of vertebrae: *Typhlops grivensis* from the Vindobonian (Miocene) of France, and *T. cariei* from subfossil deposits on Mauritius Island of the Mascarenes.

A. Regions of the Vertebral Column

The vertebral column of serpents has been variously interpreted with respect to its natural divisions. Most early writers referred to only two regions, a precaudal (or presacral) and a caudal (or postsacral), although Rochebrune (1881) distinguished five parts on the basis of slight and highly variable features: cervical, thoracic, pelvic, sacral, and coccygeal. The most recent and most acceptable scheme is that of Sood (1941, 1948), in which the major division into precaudal and caudal is retained (in the absence of a definite sacrum the terms pre- and postsacral seem inappropriate). In each of these Sood recognizes three subdivisions: cervical, thoracic, and lumbar, and antero-, mid-, and postero-caudal.

However, applications of the names and criteria of Sood to the vertebral column of the blind snakes would result in considerable distortion of some of the terms. For example, in Sood's scheme the thoracic vertebrae are those with well-developed hypapophyses. In the snakes considered here, this would include only five or six anterior vertebrae, leaving 90 per cent of the column as "lumbar." In view of this difficulty I use here a terminology similar to that applied to the Amphisbaenidae by Zangerl (1945). That is: (a) cervical, to include the atlas and axis, (b) thoracolumbar, or those vertebrae following the axis and bearing normal unforked ribs, (c) cloacal, those bearing forked ribs or forked transverse processes, and (d) caudal, those with unforked transverse processes. Although this system is satisfactory for these two families of snakes, its use is limited by the fact that the regions are not completely comparable to those of other vertebrates. Further, the position of the hyoid in *Typhlops,* for example, suggests that several additional vertebrae are true cervicals.

B. The Atlas and Axis

The atlas in the blind snakes is unusual in that its elements remain separate even in the adult. It is basically the same in all three genera considered here (*Typhlops*, *Liotyphlops*, and *Leptotyphlops*). There are some differences in the atlas of *Anomalepis,* but the two published descriptions of the anatomy of this genus have been incomplete in this respect.

The separation of the three units comprising the atlas of these snakes was first noted by Mahendra (1936). The two lateral elements (Plate 14) apparently represent the neural arches. Ventrally, each arch is rather expanded, with an articular surface anteriad for meeting the exoccipital and one posteriad for meeting the broad face of the odontoid process. Both anterior and posterior facets are turned slightly mesiad; they do not face directly forward nor directly to the rear. These articular surfaces, like most others in the skeletons of these snakes, are composed of calcified cartilage. The upper part of each arch is flattened, curving over the nerve cord toward the midline but not quite contacting the arch of the opposite side and with no indication of a neural spine. These dorsal units slightly overlap the anterior edge of the neural arch of the axis, without any real articulation.

The ventral element of this ring of three bones has been called "odontoid" (Mahendra, 1936, and Sood, 1948) or simply "ventral bone" (Dunn and Tihen, 1944). On the basis of its position and relationship to the neural arches it almost certainly represents the hypocentrum of the atlas, the pleurocentrum having fused with the axis to form the odontoid process. Such separate hypocentra are known in the atlases of *Seymouria, Sphenodon,* and Crocodilia, occasionally in amphisbaenids, other living and extinct reptiles, and even in the developmental stages of the human atlas. The hypocentrum of the blind snakes is slightly movable, bears a blunt hypapophysis, and has two calcified cartilage articular surfaces, one anteriad for meeting the basioccipital and one posteriad for meeting the face of the odontoid. Both of these surfaces also face slightly dorsad.

The axis is a more typical vertebra, somewhat wider than it is high, with a centrum, a complete neural arch, neural spine absent or very poorly developed, a pair of postzygapophyses, a pair of zygantra, etc. (Plate 14).

The nature of the odontoid process is not completely clear. There are at least two possible explanations. First, the odontoid may be represented by a small blunt knob of calcified cartilage immovably fixed to the anterior face of the centrum of the axis. Its separate origin, however, is clearly indicated by a groove which sets it off from the rest of the axis (Plates 1, 14). These small knobs have been found in both species of *Typhlops* which have been dissected for them (*lineatus, richardi*). Because of the surrounding arches of the atlas and other obscuring tissues, their presence in other species has not been determined.

The second possibility is that the odontoid is more like a separate centrum, a broad piece as wide as the pleurocentrum of the axis and bearing its own hypapophysis. It has an extensive, slightly convex articular surface which meets both neural arches and the hypocentrum of the atlas. It is completely fused with the true centrum of the axis. The knob of calcified cartilage would then represent a proatlas, a piece which often contributes to the formation of the axis of amniotes and which appears to be the remains of a now extinct vertebra originally intercalated between the present atlas and the skull. Like the separate hypocentrum of the atlas, a separate proatlas (single or paired) is found in *Sphenodon*, Crocodilia, and other living and extinct reptiles. Embryological studies by Hayek (1923, 1924) indicate that in the Squamata and in mammals the proatlas is attached to the anterior end of the odontoid process.

I am inclined to this second explanation, for several reasons: (1) The body of the axis of these snakes projects beyond the anterior edge of the neural arch, as if a piece had been added. (2) The axis is the only vertebra which bears *two* hypapophyses, adding further to the impression of a duplication. (3) The ventral foramina of a thoracolumbar vertebra occur in the anterior half of the centrum, at the base of the hypapophysis, if it is present. When such foramina are present on the axis they occur nearer the center, at the base of the *second* (posterior) hypapophysis (Plates 3, 9). (4) When rudiments of axis ribs are present they lie opposite the center of the vertebra, not at the anterior end as is normal. (5) The odontoid of *Amphisbaena* is described and figured by Zangerl (1945, pp. 765–766) as "very well developed, in fact as big as the centrum of the axis proper and often wider than the latter." Two hypapophyses are shown in an accompanying figure, one on the odontoid, one on the axis proper. No proatlas is figured or reported for the amphisbaenids.

The separate neural arches and hypocentrum of the atlas, and perhaps the nature of the odontoid, is a primitive arrangement. Yet, its persistence in other groups of reptiles reduces its significance as an indicator of primitiveness *within the class.* Immature specimens of *Thamnophis radix,* for example, among the most modern of the serpents, show basically the same condition of the atlas and axis: a dorsally divided neural arch, a distinct hypocentrum of the atlas, and two hypapophyses on the axis.

In most snakes the axis bears a pair of ribs, but these are usually absent in the blind snakes. The following were the only instances noted in the specimens considered here. One specimen of *Leptotyphlops humilis cahuilae* had a pair of rudimentary ribs associated with the axis. These did not articulate and were embedded in the tissues a short distance lateral to the axis. Of two specimens of *Typhlops lumbricalis,* one had a similar pair of small axis ribs (one-tenth normal length), the other had none. One *T. s. schlegelii* had a pair of axis ribs of almost normal size. One *T. lineatus* (Plate 1) had a tiny ossification to the left of the axis, probably representing a rib vestige. One *T. jamaicensis* had here a small pair of ribs about one-fourth normal length.

The cervical vertebrae as just described are typical of *Typhlops.* Within the genus there is little variation. The paired ventral foramina are present on the axis in some species, absent in most. A pronounced neural ridge is present in *T. braminus.* Otherwise, with the possible exception of the proatlas, which was not sought in most specimens, all the above features are present and about equally developed in all the *Typhlops* examined.

In the two specimens of *Liotyphlops* available the atlas and axis are essentially as in *Typhlops* (Plates 1–3). Neither bears ribs. The neural arches are separate pieces. The hypapophysis on the hypocentrum of the atlas is perhaps less well developed. Dunn and Tihen reported ribs on the axes of three specimens of *Liotyphlops albirostris.* In two specimens of the same species examined by me there is no evidence of axis ribs. However, the ribs of the first thoracolumbar vertebra are quite small, and the presence of ribs on the axis may well be a variable feature, as it seems to be in *Typhlops.*

In *Leptotyphlops* there is the same general form and arrangement of the cervical vertebrae (Plates 1–3, 10–12). There is considerable variation, however, in the degree of development of the hypocentrum of the atlas and the hypapophyses of the axis. Both tend to be reduced in comparison to those of *Typhlops.* The hypocentrum is of moderate size in *L. maximus, dulcis,* and *humilis,* quite small in *emini,* and absent in *nigricans* and *magnamaculata.* In no case does it have a well-developed hypapophysis. The hypapophyses of the axis are usually present, but small, and sometimes fused to form a single process (Plate 2).

In the two published descriptions of the skeleton of *Anomalepis,* (Dunn, 1941 and Tihen, 1945), the atlas is described as divided ventrad but not dorsad. Dunn remarks that "the odontoid is part of the axis and not [as in *T. braminus* (Mahendra, 1936)] a separate bone" and makes no mention of any other separate bone. Presumably, then, the hypocentrum of the atlas is absent. In the specimen examined by Tihen the ventral division of the atlas and other ventral features of the anterior vertebrae could not be determined. In Dunn's specimen hypapophyses were "present on the odontoid, on the centrum of the axis, and on the centra of the next three vertebrae." The axis does not bear ribs.

The vertebral anatomy of the other genera, *Helminthophis* and *Typhlophis,* has not been described.

C. The Thoracolumbar Region

These vertebrae make up most of the length of the column. They show some trends and gradual changes from one end of the column to the other but are basically the same throughout (Plate 13).

They differ from typical snake vertebrae chiefly in their depressed form and in the absence of neural spines and hypapophyses (the latter present only on the anterior few vertebrae). The centra are procoelous and depressed, about twice as wide as they are high. The anterior cotyloid cavity does not face directly forward but slightly ventrad. Also, the posterior condyle faces slightly dorsad as well as to the rear.

The most notable feature of the centrum, one which has aroused some interest, is the presence of obvious foramina on the ventral surface. These openings are usually in the anterior half of the centrum, they may be laterally paired or single and median, and they extend completely through the centrum into the neural canal. They were noted in other ophidian vertebrae by Owen (1866) but apparently escaped the attention of later authors. Mookerjee and Das, unaware of Owen's statements, could find no other reference to the apertures when they reported them (single and median) in *Typhlops braminus.* Sections made by these authors showed that in the anterior region of the body branches of the vertebral artery pass through these openings rather than through the intervertebral spaces with the spinal nerves. In the posterior regions vessels from the dorsal aorta enter the foramina.

Similar, but paired, foramina are known in boids, colubrids, and elapids among the snakes, and in several rather unrelated groups of lizards (geckos, pygopodids, amphisbaenids, and some scincomorphs).

Mahendra (1935) confirmed the presence of the median apertures in *T. braminus,* but doubted that they were homologous to the paired ones of lizards because of (1) their more anterior location on the centrum and (2) their position at the apex of two slight converging ridges, rather than on opposite sides of a median ridge as in lizards.

In the examination of the several species of *Typhlops* considered here, almost all possible intermediate conditions were noted. In some species (*T. lumbricalis, reticulatus, rostellatus,* and *schlegelii*) the foramina are regulary paired throughout the thoracolumbar region. In *T. flaviventer, polygrammicus, platycephalus,* and *richardi* (and others) their size varies widely in successive vertebrae and even between the two sides of the same vertebra. Often only one of the pair is present, and, although it is not medial, it is usually larger in size, suggesting that arteries from both sides pass through it. Occasional vertebrae lack any evidence of foramina.

The position of the foramina also shows some variation relative to the ends of the centra. In general, the apertures in middle and posterior vertebrae are quite near the anterior end of the centrum; in the anterior vertebrae the apertures are more nearly in the center.

Finally, in eight specimens of *Typhlops braminus* examined here, and in *T. vermicularis,* the foramina are large and medial throughout most of the column but smaller and paired in the anterior few vertebrae of the same snake.

They are undoubtedly homologous to the paired foramina in the centra of other snakes and lizards.

In *Leptotyphlops* there is a reduction in size of the foramina and a less regular occurrence. They are well developed in *L. emini,* paired anteriad and single (not medial) elsewhere. They are few in number (sometimes a total of only five or six), small, and of irregular occurrence in most species, and are completely absent in *magnamaculata* and some specimens of *humilis cahuilae.*

One specimen of *Liotyphlops albirostris* has regular paired foramina throughout the thoracolumbar region; a second has scattered foramina of variable size.

For *Anomalepis,* Dunn reports "The more anterior vertebrae have a 'subcentral foramen'—as reported for *T. braminus.* The posterior vertebrae lack the foramen. The vertebrae in general closely resemble those of *T. braminus* as figured by Mahendra."

The vertebrae of *Helminthophis* and *Typhlophis* are undescribed.

It seems likely that these foramina mark the line of junction of the two sclerotome halves which formed the vertebra. In a typical vertebrate embryo the intersegmental arteries (paired dorsal branches of the dorsal aorta) lie originally between the somites but come to be included between the sclerotome halves of the developing vertebra.

These ventral vertebral foramina, if really intersegmental in position, represent an unusual and primitive arrangement. Yet, like the primitive features of the atlas, their persistence in the vertebrae of more modern snakes like the elapids and colubrids (even *Thamnophis*) reduces their special significance in *Typhlops.*

The body of the centrum varies somewhat in different parts of the thoracolumbar region. The anterior centra are short and the more posterior centra become progressively longer and more slender.

Hypapophyses are present on, at the most, the anterior four or five thoracolumbar vertebrae. The more posterior of these hypapophyses are quite reduced.

The neural arches are broad bands nearly as long as the centrum. The rear edge of each overlaps the anterior edge of the succeeding arch both dorsad and laterad down to the level of the zygapophyses. In lateral view, therefore, the intervertebral opening is quite small, appearing only below the zygapophyses. In most snakes a second portion of the opening is visible above the zygapophyses. Disregarding their well-developed processes, the neural arches are about as high as they are wide. The neural canal is generally circular except for a somewhat flattened floor. In an occasional axis or succeeding vertebra or two, a low mid-dorsal ridge may be present. Otherwise, there is no evidence of a neural spine.

The processes borne on the neural arch are of three types: for the articulation of ribs, for the articulation of one vertebra with another, and for the attachment of muscles.

The pre- and postzygapophyses are large and prominent. They have the usual articular relationships to each other: the former facing up, toward the midline, and forward, the latter facing down, to the side, and to the rear.

Very well developed in the blind snakes are the metapophyses or mammillary processes, lateral extensions from the prezygapophyses serving for muscle attachment. Each is a bluntly pointed projection from the base of the prezygapophysis, lying below the level of the latter's articular surface, and directed forward and laterad. They are present throughout the thoracolumbar region, being largest in the middle and posterior sections. Such processes in snakes were noted by Sood (1948), who reported them in a number of families. Mosauer (1935) had previously figured them under the name of "accessory processes."

A pair of unusual intravertebral foramina were noticed in the neural arches of *T. lineatus* and *Leptotyphlops humilis*. In lateral view each foramen occurs at about the center of the arch (Plate 13). Although small they seem to extend through to the neural canal, and they are of regular occurrence throughout the thoracolumbar region. Their position corresponds approximately to that of the ventral apertures of the centrum and, while blood vessels are not visible in these cleared specimens, it seems likely that small dorsal branches of the intersegmental arteries (vertebral or intercostal) enter the neural canal through these foramina.

These could not be found in the vertebrae of other species of blind snakes. It is possible that they are present but obscure because of their small size and the abundant muscles of this region. They are present in the vertebrae of other snakes (*Python* and *Thamnophis*, for example).

The zygantra and zygosphenes have a rather simple arrangement in the blind snakes. The first to comment upon and figure these articulations in *Typhlops* was Mahendra (1936, fig. 7), using alizarin preparations of *T. braminus*. However, his description and figure, showing the zygosphenes overlapping the edge of the preceding neural arch, appear erroneous. I have noted in several similarly prepared specimens that the posterior edge of the neural arch is often thin, quite transparent, and nearly invisible except under certain angles of lighting. In such cases the underlying zygosphenes and the anterior edge of their neural arch are plainly visible and do appear to lie at the surface.

The zygantra of most snakes are paired pockets in the mesial and posterior surface of the neural arch. Each one receives a wedge-shaped process, the zygosphene, from the anterior edge of the following arch, but the articulation involves more than the pocket and wedge. Only the tip of the zygosphene is accommodated by the pocket; the rest of its articular surface (ventro-lateral) meets an oppositely directed facet on the mesial surface of the preceding arch. This latter facet, although not depressed, is continuous with the pocket and is here considered a part of the zygantrum.

Sood (1948) in a study of serial sections of the vertebrae of *T. braminus* remarked. "The zygosphene, consequently, does not appear to fit into a cavity as in other snakes, but forms a pair of lateral articular processes which lie under flap-like projections on the postzygapophysial region of the preceding vertebra."

In the species of *Typhlops* in which isolated vertebrae were examined for these features, the articulations show little variation and are basically the same as those of other groups of snakes (Plate 13). Both zygosphenes and zygantra are relatively smaller, especially the actual pocket of the zygantrum, but they are by no means rudimentary. They are more nearly on a level with the zygapophyses, rather than dorsal to them.

The vertebrae of *Liotyphlops* (Plate 13) are almost identical with those just described, the only apparent differences being a slightly more depressed neural arch and less well-developed metapophyses.

The vertebrae of *Leptotyphlops* (Plate 13) are also basically like those of *Typhlops*, but there are some quantitative differences. The neural arch is not quite so depressed, and the neural canal is somewhat higher than it is wide. The level of the zygantral articulations is slightly above that of the zygapophyses. There is a broad and very slightly elevated neural ridge. The reduction and irregularity of the ventral foramina has been mentioned.

The significance of the ratio of number of vertebrae to number of scale rows has been the subject of some debate. Stehli (1910) concluded from a study of various lizards that the primitive arrangement is a single row of scales for each body segment. Camp (1923, p. 400) presents considerable evidence to the contrary and notes that Stehli's view "would involve the derivation of the normal zonurids from the degenerate *Chamaesaura,* the normal teiids from the worm-like *Bachia,* and many other equally startling cases." He concludes: "The best evidence seems to show that the most primitive features of the squamation of lizards are: (1) uniform granular scales on all parts of the body . . . ; (3) transverse rows of ventral scales not in correspondence with each pair of ribs. . . . The frequency of the lesser number of ventral skin segments aligns itself with the frequency of attachments of the specially developed layers of the rectus muscle concerned with serpentiform or worm-like terrestrial locomotion."

Camp's theory seems applicable also to the snakes. Certainly the 1:1 ratio is typical of the more advanced families of snakes.

In the blind snakes a number of different dorsal scales/vertebrae ratios occur (Table 1). "Two scales per segment" has been reported by three authors for *Typhlops, Liotyphlops,* and *Anomalepis.* In most species of *Typhlops,* however, the ratio is nearer 1.7:1, varying from 1.5:1 to 2.2:1. Although not statistically significant, the figures suggest a correlation between a high number of dorsal scales and a higher ratio. Only in those species with about 400 scale rows (e.g., *schlegelii* and *polygrammicus*) does the ratio reach 2:1.

Mahendra (1936) reported for *T. braminus* that "The ribs alternate with two scale rows. . . ." In the specimens of *braminus* examined here the ratio is considerably lower (1.6 to 1.7:1), and even Mahendra's photograph (1936, fig. 9) seems to show pairs of ribs covering slightly less than two scale rows each. This lack of a definite 1:1 or 2:1 correlation between the scales and ribs of *Typhlops* may be a primitive condition or just another special peculiarity. The reduction of the mid-ventral scales of *Typhlops,* which are barely, if at all, distinguishable from the adjacent dorsals, is no doubt an associated feature. Although the mechanics of their burrowing seems not to have been studied, it is doubtful that the "caterpillar" type of locomotion, accomplished in most snakes by definite rib and ventral scute connections, would occur in these blind snakes.

With respect to the vertebrae of *Typhlops* it is interesting to note an apparent geographic variation in the number of thoracolumbar vertebrae in the widely distributed *T. braminus:* Ceylon—172, 174; Madagascar—176; Java—176, 177, 178; Thailand—175; Philippine Islands—168, 169; Mexico—166. The close agreement between Mexican and Philippine specimens is especially interesting in view of Taylor's (1940) suggestion that the Mexican population of *braminus* is of Philippine origin.

Dunn and Tihen (1944) report "two scales to each segment" in three specimens of *Liotyphlops albirostris*, but scale counts are not given. In the two specimens of *albirostris* examined here a ratio of 1.7:1 occurs, agreeing well with most *Typhlops.*

Dunn's cleared specimen of *Anomalepis aspinosus* had a ratio "close to 2:1," although the vertebral count was not certain.

These ratios in *Helminthophis* and *Typhlopis* are as yet unknown, but are probably close to those of the preceding genera.

Leptotyphlops is also reported to have two scales to each segment, but the scales/vertebrae relationship noted in this investigation is almost exactly 1:1. Minor departures from this ratio are most likely due to errors in counting scales. In this feature the genus resembles the higher snakes.

Vertebrae of the thoracolumbar region always bear ribs. These are slender, curved, directed somewhat posteriad, and frequently cartilage-tipped. They are basically single-headed (syncephalic), articulating with a rounded prominence, the synapophysis, situated low on the neural arch (Plate 13). This terminology follows that of Remane (1936), the synapophysis representing the fused diapophysis and parapophysis. The articular facet of the typhlopid rib head is a simple shallow cup. This facet is probably, for reasons given below, not so much a fusion of the tuberculum and capitulum as it is a new formation between the much reduced latter structures.

A small projection extends dorso-posteriad from the proximal end of the rib (Plate 13), apparently representing a reduced tuberculum. It does not articulate with the vertebra. An identical process occurs on the ribs of garter snakes (*Thamnophis radix*). On the opposite side of the articular cup of the rib in *Typhlops* is a smaller, poorly developed, blunt process which, like the dorsal one, plays no part in the articulation of the rib. In *Thamnophis* a similar, but well-developed, ventral process is present and makes contact with a ventral extension of the synapophysis, serving to brace the rib and restrict its movement toward the mid-ventral line. The major part of the synapophysis here is a hemispherical protuberance quite like that in *Typhlops.* These ventral projections from the rib heads of both genera seem best interpreted as capitula. The great reduction of the capitular process in *Typhlops* and the very simple rib-vertebra articulation is further indication of the reduced role of the ribs in the locomotion of the blind snakes.

The ribs of *Liotyphlops* and *Leptotyphlops* (Plate 13) are quite like those just described for *Typhlops.* The only notable difference is a greater reduction of the capitular process in *Leptotyphlops.*

D. The Cloacal Region

The vertebrae of this region differ only slightly from the thoracolumbar group. They are more compressed in appearance longitudinally, being relatively higher and rather short. The ventral foramina are often present but of irregular occurrence and size. Pre- and postzygapophyses are present and well developed. Metapophyses are present but reduced in size. Zygantra and zygosphenes are quite reduced or absent, especially in the last vertebra or two. Hypapophyses are absent. The most notable feature of this region of the column is the ribs. They are forked, the two pieces first diverging and then curving toward each other, lying in a vertical plane (Plates 19–22). Such forked ribs enclose lymph hearts and are typical of snakes and some lizards. These forked ribs, or lymphapophyses, are usually fused with the vertebrae in the blind snakes, but the anterior ones may be slightly movable. They vary in number from two to five pairs in the species examined, but within a species are relatively constant (Table 1). The thoracolumbar ribs just anterior to these forked ones occasionally show tendencies toward the forked condition by bearing a short dorsal process and by curving upward briefly before continuing their normal ventro-lateral direction (Plates 19–22). The posterior lymphapophyses decrease in size, especially the dorsal piece. This latter finally becomes incorporated into the base of the lower one, and the simple transverse process of the caudal vertebra appears. In this antero-posterior transition the thoracolumbar rib seems to be homologous to the ventral piece of the cloacal rib and to the transverse process of the caudal vertebra.

In both *Liotyphlops* and *Leptotyphlops* the vertebrae and forked ribs of this region are similar to those of *Typhlops* just described. Dunn reported for *Anomalepis* three pairs of "immovable forked lateral processes" similar to those of *Typhlops.*

E. The Caudal Region

These vertebrae appear still more compressed from front to rear, often being nearly twice as high as they are long in the mid-caudal region. They are simplified, without zygantra and zygosphenes and with reduced zygapophyses and metapophyses. There are occasional ventral foramina. The open haemal arches, characteristic of the caudal vertebrae of most snakes, are completely absent. Transverse processes are present on all these vertebrae, but are quite reduced posteriad. The terminal two to four vertebrae commonly fuse to form a blunt tip of the column, although their processes and intervertebral foramina persist, indicating the number of vertebrae involved.

The most unusual feature of the caudal region of the column is the presence in some species of *Typhlops* of a mid-ventral rodlike ossification associated with the fused terminal vertebrae (Plate 14). In *T. polygrammicus* and *vermicularis* these structures are well developed; in *T. lineatus, rostellatus,* and *jamaicensis* they are rudimentary. Their form and location are reminiscent of the urostyle of frogs. They are directed forward but the appearance of the fused terminal vertebrae in some of the above species suggests that the tip of the vertebral column itself has been bent down and forward. The major part of the frog urostyle develops from an ossified hypochordal rod, and these structures in *Typhlops* may have a similar embryonic origin. In spite of their well-ossified nature in the first two species they appear to be functionless, embedded in the tissue of the tail. No mention of any such structure in snakes was encountered in the literature.

The preceding description applies quite well to the caudal vertebrae of *Liotyphlops* and *Leptotyphlops,* except that no evidence of the "urostyle" was seen here.

Table 1, which follows, shows the scales/vertebrae ratios of representative species of blind snakes. The usual system of counting dorsal scales in the blind snakes is to begin with the rostral scale and include the mid-dorsal head scales (prefrontal, frontal, interparietal, and interoccipital). However, in order to obtain a more valid ratio, the dorsal scale counts in Table 1 begin immediately *behind* these head scales and continue to the level of the anus. Figures in parentheses under precaudal vertebrae refer to cervicals, thoracolumbars, and cloacals respectively; under caudal vertebrae they refer to the separate ones and the fused terminal ones respectively. The figures for *Anomalepis* are from data presented by Dunn (1941); those for the last three specimens of *Liotyphlops* are from Dunn and Tihen (1944). Dashes indicate that scale counts were not recorded before the specimens were cleared.

TABLE 1

DORSAL SCALES/VERTEBRAE RATIOS

	Dorsal Scales	Precaudal Vertebrae	Ratio	Sub-caudal Scales	Caudal Vertebrae
Liotyphlops albirostris	344	207(2–202–3)	1.7:1	16	16(13–3)
“ “	353	208(2–203–3)	1.7:1	15	16(14–2)
“ “	–	252(2–245–5)	"2:1"	–	8
“ “	–	238(2–231–5)	"2:1"	–	9
“ “	–	234(2–227–5)	"2:1"	–	10
Anomalepis aspinosus	328	173(2–168–3)	1.9:1	–	–
Typhlops braminus	–	171(2–166–3)	–	–	10(7–3)
“ “	–	172(2–168–2)	–	–	10(7–3)
“ “	282	174(2–169–3)	1.6:1	12	10(7–3)

TABLE 1—Continued

	DORSAL SCALES	PRECAUDAL VERTEBRAE	RATIO	SUB-CAUDAL SCALES	CAUDAL VERTE-BRAE
Typhlops braminus	300	177(2–172–3)	1.7:1	12	10(8–2)
“ “	292	179(2–174–3)	1.6:1	11	10(8–2)
“ “	309	181(2–176–3)	1.7:1	12	10(7–3)
“ “	–	181(2–176–3)	–	–	11(8–3)
“ “	312	180(2–175–3)	1.7:1	12	11(8–3)
“ “	300	182(2–177–3)	1.6:1	11	11(8–3)
“ “	–	183(2–178–3)	–	–	11(8–3)
“ *blanfordi lestradei*	435	237(2–231–4)	1.8:1	10	11(8–3)
“ *boettgeri*	377	200(2–194–4)	1.9:1	8	7(4–3)
“ *flaviventer*	–	207(2–201–4)	–	–	13(10–3)
“ *lineatus*	–	254(2–249–3)	–	–	8(5–3)
“ *lumbricalis*	279	169(2–164–3)	1.7:1	10	10(8–2)
“ *platycephalus*	371	222(2–215–5)	1.7:1	11	11(7–4)
“ *polygrammicus*	–	221(2–214–5)	–	–	18(15–3)
“ “	392	194(2–189–3)	2.0:1	19	16(13–3)
“ “	393	193(2–188–3)	2.0:1	19	16(13–3)
“ “	409	206(2–201–3)	2.0:1	16	14(10–4)
“ *pusillus*	290	158(2–153–3)	1.8:1	12	12(8–4)
“ *reticulatus*	213	143(2–138–3)	1.5:1	10	9(6–3)
“ *richardi*	331	204(2–199–3)	1.6:1	13	13(9–4)
“ *rostellatus*	320	183(2–177–4)	1.7:1	14	10(8–2)
“ *schlegelii schlegelii*	407	189(2–182–5)	2.2:1	8	9(5–4)
“ “ *mucruso*	456	202(2–195–5)	2.3:1	7	8(5–3)
“ *vermicularis*	346	193(2–187–4)	1.8:1	13	12(8–4)
Leptotyphlops dulcis dissectus	–	216(2–210–4)	–	–	16(13–3)
“ “ “	–	218(2–212–4)	–	–	16(13–3)
“ *emini*	242	224(2–218–4)	1.1:1	21	25(22–3)
“ *humilis cahuilae*	–	259(2–252–5)	–	–	21(19–2)
“ “ “	–	269(2–263–4)	–	–	20(18–2)
“ *magnamaculata*	222	231(2–225–4)	.96:1	19	19(16–3)
“ *maximus*	199	202(2–196–4)	.99:1	14	17(15–2)
“ *nigricans*	207	198(2–193–3)	1.0:1	28	29(26–3)

THE HYOID

The hyoid of the blind snakes is quite varied in form and position and has received the attention of several investigators. There are two distinct types. One is a Y-shaped form somewhat like the hyoid of higher snakes, but with the anterior median process highly developed and with the posterior cornua more divergent (Plates 15–18). This type is found more or less embedded in the base of the tongue in *Typhlops* and in a more superficial position in *Leptotyphlops.* The second type, known in

Anomalepis and *Liotyphlops,* is so unique that it was at first taken to be a reduced scapulocoracoid. It is a slender, threadlike structure, superficial in position, immediately behind the head, and has the form of an M with its legs bent back upon themselves (Plates 2, 3, 17, 18).

A generally accepted scheme of homologies of the parts of these hyoids has not yet been reached. Dunn and Tihen (1944), the discoverers of the peculiar M-shaped hyoid of *Liotyphlops,* considered it a vestigial pectoral girdle because of (1) its unusual, most unhyoid form, (2) its resemblance to the girdle of the burrowing lizard *Dibamus,* and (3) the presence at the anterior end of the trachea of a small inverted U-shaped element which much more closely resembles the usual ophidian hyoid. They did mention but discounted at that time an alternative explanation which seems to be the correct one. That is, the small anterior element is the cricoid cartilage, and the larger M-shaped thread is the hyoid.

Warner (1946) found the same M-shaped structure in *Anomalepis* and established it as a hyoid by demonstrating that the muscles attached to it are those normally originating or inserting on the hyoids of other snakes. She considered the legs of the M as thyrohyals and the middle section as the basihyal, following the usual terminology of ophidian hyoids.

In a later paper Smith and Warner (1948) discarded as inappropriate the term thyrohyal for the legs of the M, instead calling them hypohyals and homologizing them with the posterior cornua in all other snakes. In this interpretation the middle "V" portion is the basihyal and the recurved extensions of the legs (directed toward the angles of the jaws) are ceratohyals, the entire structure thus being derived from the hyoid (second visceral) arch.

McDowell and Bogert (1954) argue against this latter view, suggesting that the M-shaped arch of *Anomalepis* and *Liotyphlops* represents a sort of "floating" hypohyal (that is, free from the basihyal) as seen in the anguinid lizard *Celestus,* for example, but differing from the latter in the retention of ceratohyals and in the midline junction of the left and right hypohyals. The more anterior U- or Y-shaped element in these genera, between the rami of the lower jaw, then represents the basihyal.

This latter interpretation is in part unacceptable, insofar as the Y-shaped element between the lower jaws cannot be the basihyal. An identical structure is present in the same location in both *Typhlops* and *Leptotyphlops,* genera which have also the larger and more typical basihyal farther to the rear (Plate 17). This far anterior structure is almost certainly the cricoid cartilage. It is partially calcified and is clearly evident in most of the species of *Typhlops* and *Leptotyphlops* examined by me. Its cricoid nature is indicated by its position below the glottis, its shape, its occasional fusion with the adjacent tracheal rings (both are derived from the sixth visceral arch), and its relationship to a pair of dorsal arytenoid cartilages, which are also partially calcified (Plate 17).

Where then is the basihyal of *Anomalepis* and *Liotyphlops?* It may indeed be missing. It seems to be absent in some burrowing snakes of other families (*Rhinophis, Cylindrophis,* and *Eryx*) and in at least two species of *Typhlops* examined in the present study (*pusillus* and *lumbricalis*). In these forms, however, there is no tendency toward a fusion of the remaining lateral pieces of the hyoid. If *Liotyphlops* and *Anomalepis* are without a basihyal, then such an unusual fusion of lateral hyoid elements has occurred.

An examination of Cope's numerous figures of saurian hyoids (1900, Plates 1–4) suggests still another interpretation of this M-shaped hyoid. The hypohyals of lizards are, as McDowell and Bogert have pointed out, directed forward from their point of junction with the basihyal. The ceratohyals of lizards, on the other hand, whether fused with the hypohyals or forming sharp-angled articulations with them, are always directed posteriad. In several species of lizards the distal (posterior) portions of the ceratohyals are recurved, terminating in an anteriorly directed hook (Plate 18).

The following modification of Smith and Warner's terminology, therefore, seems to provide the most likely explanation. The middle "V" portion of the M represents not the basihyal alone but the basihyal (only the broad, shallow apex of the V) *plus* the hypohyals (the anteriorly directed portions of the V). Each entire leg of the M, including its recurved portion, then represents a ceratohyal. The chief difficulty in this view is the unusual form of the section to be called basihyal—a simple transverse rod, slightly convex posteriad. In lizards and in both *Typhlops* and *Leptotyphlops* this part of the hyoid nearly always has a highly developed anterior glossohyal process. The presence of such a process is not an absolute criterion of the basihyal, however. The process is quite reduced or completely absent in the typical snakes, and even in *Typhlops* there is variation in its development (e.g., it is extremely short in *T. polygrammicus*). In view of the above, and pending determinative embryological work, it seems reasonable to call the small midsection of this peculiar hyoid a basihyal rather than considering the latter structure absent.

The hyoids of *Typhlops* have in the past been described as simple Y-shaped structures, buried in the tongue musculature, with the apex of the Y directed forward and with rather divergent posterior horns. They are small, usually 2 mm or less in length, and are located some distance behind the head. This Y-shaped form is the only type observed in this genus to date. It has been considered to be the fused basihyal and hypohyals (Smith and Warner, 1948) and the basihyal alone (McDowell and Bogert, 1954). In the examination of the several species of *Typhlops* included here, however, considerable interspecific variation of the hyoid was found, with three distinct types present (Plates 15, 18).

The first is the Y-shaped type noted by previous authors. Such hyoids in the blind snakes are usually composed of calcified cartilage, although in two species (*boettgeri* and *schlegelii*) they appear to be true bone. There is also variation in the relative size of the entire hyoid, in its antero-posterior location, and in the degree of development of the glossohyal process. In one species this latter process may be almost absent, while in another it may comprise over half the total length of the hyoid. The hyoid may barely cover one body segment or may extend across five or six. Within a species, however, all of these features seem to be quite constant. In every one of ten specimens of *T. braminus*, for example, the hyoids were of indentical size and shape and lay between ribs 8 and 14. The second type of hyoid in *Typhlops* is composed of this Y-shaped calcified cartilage *plus* two slender bones, more or less parallel and immediately behind the former structure. The third type consists of the pair of parallel bones only, the Y-shaped cartilage being absent.

As in *Anomalepis* and *Liotyphlops,* a comparison of these hyoids of *Typhlops* with those of lizards sheds considerable light on their homologies. In most lizards the hyoid consists of a basihyal plus anteriorly directed hypohyals (cartilage), posteriorly directed and sometimes recurved ceratohyals (cartilage), and the first pair of ceratobranchials (almost always bone) (Plate 18). An additional pair of cartilaginous rods is often present. They represent the second pair of ceratobranchials and are attached to the basihyal, lying between the first ceratobranchials. However, in the limbless lizards there is a decided tendency toward the reduction of the hyoid—first a loss of ceratohyals, then of the hypohyals. This leaves finally (as in *Anniella pulchra*) only a forked basihyal and the first pair of ceratobranchials, *exactly the situation* found in some *Typhlops.*

In view of these intermediate stages of hyoid reduction in lizards, the basic hyoid elements in *Typhlops* clearly represent the basihyal and the first pair of ceratobranchials. The three types of *Typhlops* hyoids seem to represent further stages of simplification of the usual saurian hyoid. The most primitive of the three types is that one composed of both the calcified basihyal and the osseous first ceratobranchials, as in *T. reticulatus* and *blanfordi.* Further reduction of this stage has apparently occurred through the loss of the basihyal, leaving the parallel ceratobranchials, as in *lumbricalis* and *pusillus.*

In the case of the simple Y-shaped hyoids (*T. braminus, polygrammicus,* and others) the homologies are not so clear. There are at least three possibilities, none of which is likely to be established without embryological evidence. (1) The ceratobranchials may be absent, the remaining Y representing an elongate basihyal alone. (2) The ceratobranchials may have lost their usual osseous nature and fused with the posterior extensions of the basihyal. (3) The Y may represent the basihyal plus the *second* pair of ceratobranchials. I doubt these latter two possibilities, inasmuch as there is no evidence of a fusion of parts in any Y-shaped hyoid, nor is there any sign of the second ceratobranchials in any *Typhlops* nor in any limbless lizard. The first suggestion has two points in its favor: (1) the Y's can be arranged in a series showing a gradual increase in the development of their posterior extensions, from the very short one of *T. blanfordi* (and *Anniella*) to the longer, more typical ones; (2) where both basihyal and ceratobranchials are present, the length of the posterior extensions of the basihyal is inversely proportional to the length of the ceratobranchials, suggesting that the basihyal extensions may become elongate in "compensation" for a reduction of the ceratobranchials.

In *Leptotyphlops* the hyoid is much less variable (Plate 16). It is Y-shaped and always composed of calcified cartilage. It differs from that of *Typhlops* in the greater development of the posterior cornua and in their more parallel positions. The parallel or slightly convergent relationship of these parts is considered typical of the hyoids of higher snakes. However, the posterior horns of some species of *Leptotyphlops* are quite divergent. In this genus, at least, the degree of divergence seems generally correlated with the relative length of the hyoid, the shorter ones being the more divergent. This character of the ophidian hyoid may, therefore, be primarily a reflection of its length.

Although the typical hyoid of *Leptotyphlops* is longer and the horns usually more parallel than those of *Typhlops*, there are examples in both genera of intermediate conditions. I believe, therefore, that the Y-shaped hyoids of these two genera are perfectly homologous and that even the long slender hyoid of *L. dulcis* represents only a basihyal with highly developed processes. In the absence of contradictory embryological evidence, this line of thought can be extended to include even the slender, hairpin-like, calcified cartilage hyoids of the highest snakes, which differ from those of *Leptotyphlops* chiefly in the reduction or absence of the glossohyal process.

The relationship between the Y-shaped and M-shaped hyoids of the blind snakes is not entirely clear. Both types are obviously derived from the basic lizard hyoid, but it seems highly unlikely that either could have given rise to the other. The anomalepid type is certainly the more primitive in its retention of hypohyal and ceratohyal elements, but the extreme reduction of its basihyal and the absence of ceratobranchials precludes the derivation from it of the *Typhlops* or *Leptotyphlops* types.

Hyoid structure, then, indicates the wide phylogenetic separation of the *Typhlops* and the anomalepid lines. *Leptotyphlops,* of course, on the basis of other features is rather far removed from both of these lines.

THE PELVIC GIRDLE

No known snake shows any trace of the pectoral limbs or girdle, but the presence of vestigial elements of the pelvic girdle characterizes four of the more primitive families (the Boidae, Aniliidae, Typhlopidae, and Leptotyphlopidae). The source of much of the early interest in the blind snakes was the occurrence of these rudimentary girdles. They are figured in some of the early herpetological works (e.g., Peters, 1882). Duerden and Essex (1923) described and figured the girdles of *Leptotyphlops nigricans* and four species of *Typhlops,* noting for the first time the cartilaginous elements in the girdle of *Typhlops* and interpreting the ossified rods here as ischia. Essex (1927) in connection with other studies of degenerative evolution in reptiles, figured the girdles of eight additional species of *Typhlops* and five of *Leptotyphlops.* His study involved more than a hundred specimens and pointed out a number of inter- and intraspecific variations. Later writers have commented on the girdles of various species.

Leptotyphlops has by far the most elaborate pelvic girdle among blind snakes. In most species separate pairs of bones representing ilia, ischia, pubes, and even femora lie immediately anterior to the anus (Plates 19, 20). The three rod-shaped bones of each half of the girdle radiate from an acetabular region, normally without fusion (the ilium and pubis are fused in *L. bakewelli*). The ilia and the pubes are more consistently ossified. The ilia are directed upward, to the rear, and slightly laterad. They usually lie medial to the adjacent thoracolumbar ribs and have no direct connection with the axial skeleton. The pubes may either converge or diverge anteriad. The ischia vary considerably in their development and may be true bone or calcified cartilage. They converge posteriorly and are loosely connected in some species to form what has been called a symphysis. Even in those cases where the ischia are quite close to one another, however, each is separately movable so that symphysis, in the proper sense of the word, does not exist. Nevertheless, their connection with each other may be considered a primitive feature not present in the girdles of other snakes. The distal end of any or all of these bones may bear a slender calcified cartilage tip (Plates 19, 20). Whether these bits of cartilage deserve recognition as hypoischia, for example, is doubtful, in view of their occasional presence even on the femur. They more likely represent an unossified portion of the cartilage precursor of these replacement bones. Such cartilages are not figured by Essex, although similar cartilages are shown on the ischia of his *Typhlops*.

The wholly cartilaginous girdle of *Leptotyphlops albifrons* is reduced unusually. Each half is triradiate apparently representing the fused ilium, ischium, and pubis. A femur is absent. Tihen (1945) quotes an oral communication from Mr. Leonard Laufe to the effect that some species of *Leptotyphlops* completely lack a girdle, but no examples are given.

The femur is a bone or calcified cartilage of variable shape and development. At best it is unequally tripartite. One piece is directed toward the acetabulum, another longer one ventrad and to the rear, and the third upward, laterad, and to the rear. The latter projection bears a cornified clawlike cap which may even extend to the surface by way of a pore in the skin. Essex noted this condition in only one of nearly 100 dissected specimens of *L. nigricans*—a male with well-developed testes. Essex suggested that the claw might be protruded only at the breeding season, functioning in courtship as does the similar spur of some male boids. However, the only specimen of the present series with such exposed claws was an immature female *L. dulcis dissectus*. The claws were undoubtedly better developed in the ancestors of this group, and their present infrequent exposure seems best explained as merely an extreme development of a now variable and nonfunctional structure (List, 1955). The femur of some species is very small, may occur as two pieces, and lacks a claw.

The girdle of *Typhlops* is much simpler, although a number of interspecific and intraspecific variations may occur (Plates 19, 21, 22). Normally a pair of bony rods, the ischia, lie more or less parallel to each other just anterior to the anus. Additional cartilaginous elements represent ilia and pubes in some species. They are only rarely calcified or osseous, and are never as prominent as the ischia. Evans (1955) reported the first instance of an ossified (calcified?) pubis in *Typhlops*, finding it in only one of seventeen specimens (*T. jamaicensis*). Three of his specimens had ilia which were also osseous or calcified. A single specimen (*T. schlegelii*) of the present series had a pair of tiny ossifications representing ilia. The most unusual girdle was that of *T. pusillus:* a robust, well-ossified bone with three processes, apparently the fused ilium, ischium, and pubis. In a specimen of *T. lineatus* the girdle was almost entirely cartilaginous. Only the left side was visible, consisting of a slightly calcified ilium and ischium. Essex consistently figured a slender or bluntly rounded cartilage, the hypoischium, at the posterior tip of each ischium. These may have been present in the specimens examined by me, but uncalcified cartilage is not easily visible in these cleared tissues, and they were definitely observed in only two species.

Pelvic girdles have to date not yet been observed in the other genera of blind snakes (*Anomalepis, Helminthophis, Liotyphlops,* and *Typhlophis*). However, the larger of the two specimens of *Liotyphlops albirostris* in this series has a girdle in the form of a pair of broad cartilages just anterior to the anus (Plate 19). Each lies chiefly in a transverse plane, with a dorsal iliac process and a continuous ventral part of doubtful homology which extends mediad and slightly forward (suggesting a pubis, rather than an ischium). A single small granule of calcification occurs in one of the cartilages. Like the cartilaginous ilia and pubes of *Typhlops,* these pelvic bars of *Liotyphlops* are probably of irregular occurrence.

DISCUSSION

The anatomy of the blind snakes shows an unusual mixture of primitive and very specialized features. Most of the latter are obvious reflections of the burrowing mode of life, are found in other fossorial squamatans, and may thus be disregarded in consideration of evolutionary relationships. Their very short tail, for example, is a feature also of most of the amphisbaenid lizards and such burrowing snakes as the uropeltids. The shortened tail is extreme in some species of *Typhlops,* where it may comprise only 1 per cent of the total length. The great reduction or absence of neural spines and hypapophyses of the vertebrae may also be considered as extremes of a trend in burrowers. Johnson (1955) found some reduction of these processes to be characteristic of other burrowing snakes, and the vertebrae of amphisbaenids are quite like those of *Typhlops* in their lack of neural spines and hypapophyses, except for the latter on a few anterior vertebrae. The broad premaxillae, fused into a single unit, and the generally enlarged nasal region, again most extreme in *Typhlops,* are further indications of a burrowing existence. The unusual perforations in the nasal bones of *Typhlops* facilitate the innervation of the abundant sense receptors in the skin of the rostrum. Simplification of the hyoid apparatus of fossorial lizards is also apparently correlated with burrowing, to judge from the reduction. However, the functional significance of this latter trend is not clear, since the tongue is not correspondingly reduced. The loss or reduction of postfrontals is probably also a correlation since it is known in such semiburrowers as the coral snakes and the burrowing vipers.

Some of the specialized skeletal features of the blind sakes which are not obviously correlated with fossorial life include: (1) the rotation of the maxilla to a transverse position in the typhlopids and anomalepids and the highly unique suspension of the bone in the latter group; (2) the reduction or loss of teeth and tooth-bearing bones in all the groups—from the maxilla in *Leptotyphlops,* from the dentary in the others; (3) the highly developed hinge in the mandible of *Leptotyphlops;* and (4) the posterior migration of the hyoid in all but the anomalepids.

Basic primitive features, presumably retained from squamatan ancestors, include: (1) the pelvic vestiges, with even an ischiac "symphysis" in an occasional *Leptotyphlops;* (2) lack of a definite scales/vertebrae ratio in the typhlopids and anomalepids; (3) a distinct proatlas and three separate elements comprising the atlas; (4) paired parietal bones, especially frequent in *Typhlops;* and (5) the attachment of the quadrate directly to the skull.

The first suggestion of a change in the classification of the blind snakes since the original establishment of the Typhlopidae and Leptotyphlopidae was Taylor's (1939) proposed erection of the family Anomalepidae, with *Anomalepis* as the monotypic genus: "This small group of snakes associated in the genus *Anomalepis* differs from both the families Typhlopidae and Leptotyphlopidae in such a way as to preclude their inclusion in either family." The basis for his proposal was the presence of teeth on both the maxilla and dentary and the distinctive arrangement of head shields.

Dunn (1941) disputed Taylor's proposal, pointing out that it "disregards entirely the obvious characters of scalation and dentition, disregards the obvious relationship of *Anomalepis* to *Helminthophis,* and is directly contradicted by the osteology," which basically resembles that of *Typhlops.*

Tihen (1945) agreed with Dunn that Taylor's action was premature and that "recognition of a family Anomalepidae containing the single genus *Anomalepis* is unwarranted." He also felt, however, that there had been a tendency "to minimize the importance of certain features in which the *Anomalepis-Liotyphlops* compex differs from both *Typhlops* and *Leptotyphlops*" and that the former genera plus *Helminthophis* are worthy of consideration as a valid family or "more likely" a subfamily group, the Anomalepinae.

Among the characters which are unique (with rare exceptions) to one or more of the anomalepid genera are: (1) the presence of bones in the orbital region and their role in the kinetics of the maxilla; (2) the presence of one, two, or three teeth on a reduced dentary; (3) the presence of "laterosphenoids"; (4) independent ectopterygoids; (5) a distinct tabular; (6) a separate surangular in *A. aspinosus;* (7) the unusual W-shaped hyoid apparatus and its more anterior position; (8) absence of an angular; (9) a very reduced and cartilaginous pelvic girdle or none at all; (10) a single median supraoccipital; (11) nasals fused as a single large plate; and (12) the odd maxillary teeth of *Liotyphlops.* The first seven of these represent a more primitive state than the corresponding conditions in *Typhlops,* where loss or fusion of various bones has occurred. In spite of the greater reduction of the pelvic girdle and the loss of the angular (the only features in which they are more advanced than *Typhlops*), the anomalepids as a group are much more primitive than their obvious relative *Typhlops.* That they are more nearly related to *Typhlops* than to *Leptotyphlops* is indicated by their scalation, their scales/vertebrae ratio, and especially such skeletal features as the transversely oriented, toothed, movable maxilla, and the fundamental correspondence of their lower jaws. In view of this closer relationship between *Typhlops* and the anomalepids, Tihen felt that recognition of three equivalent families of blind snakes was not warranted.

I believe, however, that the twelve features listed above, considered as a whole, are sufficient justification for the establishment of the Anomalepidae, to include the genera: *Anomalepis, Liotyphlops, Helminthophis* and *Typhlophis.* The latter two are placed here on the basis of statements by McDowell and Bogert (1954) that "*Typhlophis* has a skull very similar to that of *Liotyphlops,* differing in only a few minor details," and that *Helminthophis* has the anomalepid type of hyoid. This peculiar anomalepid hyoid and the impossibility of deriving any of the typhlopid types from it, or vice versa, is the character most suggestive of a rather distant phylogenetic separation of the two lines.

These three families of blind snakes are certainly not equally related to each other. However, this argument against the third family loses force in view of the current differences of opinion as to whether the typhlopids and anomalepids even belong in the same suborder with the leptotyphlopids and other snakes. Further, the "equivalence" of vertebrate families or other taxonomic categories above the species can never be more than approximate, even within a taxon, because the groups of any one taxonomic level will vary in number of species, unique features, etc., and because of the subjective value or weight placed on a taxonomic criterion, such as the emphasis laid upon the hyoid in this present discussion.

The second major conclusion from this study concerns the relationships of the blind snakes to lizards, and their proper relation to the serpents. Snakes are normally classified as the suborder Ophidia (Serpentes) of the order Squamata, the other suborder including the lizards, the Sauria (Lacertilia). Recently, Schmidt (1950) proposed the elevation of both groups to ordinal rank, feeling that evolution in the snakes "both in progressive lines and in adaptive radiation" justifies their equal rank with their ancestral order. Similarly the birds and mammals are now accorded equal rank with their ancestral class Reptilia. The fundamental relation of the two groups to each other has long been recognized and is based on a number of anatomical features which distinguish them from other reptiles.

For the most part the snakes comprise a distinctive group, to be distinguished from nearly all lizards by: (1) a greatly elongated body; (2) complete absence of pectoral limbs and girdle, and absence or great reduction of the pelvic limbs and girdle; (3) great flexibility of the jaws, permitting the swallowing of large prey; (4) an immovable transparent "spectacle" covering the eye; (5) a platytrabic skull; (6) zygosphenes and zygantra; (7) an elongate and retractile tongue; (8) the downgrowth of the parietals to form a closed brain case; (9) enlarged transverse ventral scales; (10) absence of an external ear; and other more minor features.

The blind snakes, of course, unique in some respects, fit this general picture. Until recently their taxonomic position in the Ophidia had not been seriously questioned, although Mosauer (1935) referred to the muscle arrangement of *Typhlops punctatus* as "so unlike that of any other ophidian that its position within this group is certainly not confirmed by myology." The blind snakes have always been placed at or near the base of the suborder Ophidia, but opinions have differed as to their proper relationships to the other families. In Boulenger's classification (the first to be based on any comprehensive study) the two families of blind snakes as well as some other burrowers like the uropeltids and aniliids were excluded from any direct ancestral position leading to later forms because of their extreme fossorial adaptations. Other workers, from Cope (1900) and Gadow (1901) to Schmidt (1950) have taken the same view. The "classical" theory held by the early herpetologists placed the boids as the most primitive of living snakes and suggested that the original derivation of the ophidian stock was from a group of supraterranean lizards having both limbs and eyelids. Camp (1923) and later workers felt that this ancestral group had given rise to both the snakes and the modern varanid lizards.

Mahendra (1938), however, considered the blind snakes to be the most primitive groups, as apparently did Walls (1940, 1942). The latter has become a leading exponent of an opposing theory of the evolutionary origin of snakes, to the effect that the ancestral stock was a burrowing, elongate, limbless lizard with vestigial eyes. Some of the unusual features of the ophidian eye have suggested to him an evolutionary "recovery" of the eye from some such degenerate condition as that of *Typhlops*. Further support for at least the general aspects of this second theory of the origin of snakes has come from a number of workers, particularly Angus Bellairs and others in England.

A major change in thought on the taxonomic position of the blind snakes is found in the recent extensive work of McDowell and Bogert (1954) on *Lanthanotus* and the anguinomorphan lizards. In the first place, several anatomical resemblances between *Leptotyphlops* and the higher, typical snakes suggest that they represent a monophyletic group that quite early branched into two lines, and "it would appear that the Leptotyphlopidae are, if anything, even closer to the platynotan lizards, particularly the group represented today by *Lanthanotus*, than are the other snakes." In the second place, McDowell and Bogert concluded that "there is little to show that the typhlopids are related to the snakes and Leptotyphlopids," rather, they show evidence of relationship to the diploglossan lizards. "It seems clear that the typhlopids should be removed from the Ophidia or Serpentes. It is equally clear that the many peculiar specializations of the typhlopids (particularly the unique upper jaw mechanism) warrant their separation from the Diploglossa and, indeed, from the Anguinomorpha. Whether these odd burrowers deserve special subordinal rank or should be regarded as merely an infraorder of the Sauria remains a matter for the judgment of the majority of taxonomists."

Before we comment on these conclusions, a brief characterization of the pertinent groups of lizards may be helpful. The Anguinomorpha are an infraorder of the Sauria, distinguished, among other things, by a tongue which has a forked inelastic front portion. This portion may be retracted into a sheath formed by an elastic rear portion. The infraorder has two distinct superfamilies; the Platynota and the Diploglossa. In the former the anterior bony naris extends backwards as a slit between the nasal bone and the prefrontal, the jaws have a more or less distinct intramandibular hinge and are primarily developed for the seizure of prey, the splenial is shorter, and an open Meckelian groove lies above the splenial. Most recent workers feel the Ophidia are most nearly related to this superfamily. The Diploglossa lack the posterior slit of the naris, have jaws primarily developed for crushing, a longer splenial, no open Meckelian groove, and no indication of an intramandibular hinge. Three families are included in this latter group: (1) the Anguinidae, (2) the Anniellidae, and (3) the Xenosauridae.

It seems fairly certain that *Leptotyphlops* is properly a genus of the Ophidia. Some of the more important resemblances between the leptotyphlopids and most other snakes are as follows:

1. The vertebral centra taper (very slightly) posteriad, and the prezygapophyses extend considerably farther laterad than do the synapophyses.
2. Extensive lateral plates of the parietals meet the basisphenoid, forming the side walls anterior to the prootic.

3. Lateral plates of the frontals separate the orbits and form an anterior extension of the brain case.
4. The exoccipitals meet dorsally to exclude the supraoccipital from the foramen magnum.
5. Both lacrimal and jugal bones are absent.
6. A median plate of each nasal bone separates the nasal cavities by a double-layered septum.
7. The nasal is separated from the prefrontal by a slitlike posterior extension of the anterior bony naris.
8. An extensive facial wing of the maxilla covers a large area of the side of the snout in many platynotans and other lizards, but it is quite reduced in *Leptotyphlops* and completely absent in other snakes.
9. Temporal arch elements are lacking.
10. The Meckelian groove is open above the splenial.
11. The surangular, prearticular, and articular are fused to form a single unit.
12. The mandible is separated by more or less vertical sutures into a fore part (dentary and splenial) and a hind part.

These rather basic resemblances indicate a definite phylogenetic relationship between the two groups. Of the above features, numbers 1, 3, 6, 7, 9, 10, and 12 are also common to platynotans (or at least *Lanthanotus*), emphasizing the probably ancestral position of those lizards.

That the leptotyphlopids are much too specialized to have given rise to other snakes, however, is suggested by a number of their unusual features:

1. Presence of the most highly developed intramandibular hinge joint of any squamatan, resulting in a freely movable foremandible.
2. The loss of all maxillary teeth.
3. The slender rodlike form of the pterygoid and its dissociation from the quadrate-mandible articulation.
4. Disappearance or great reduction of the tabular.
5. The extremely shortened mandible and the correspondingly long, narrow, forward-directed quadrate.
6. Loss of the postfrontals.
7. Reduction or loss of the ectopterygoid.
8. In some species the exclusion of the basioccipital from the foramen magnum.

A number of distinctly primitive, lizard-like features combine with these specializations. In addition to those previously mentioned, which are held in common with the other blind snakes, these include the rigid attachment of the maxilla to the skull, the only slightly recurved teeth, and the nearly vertical position (rather than horizontal) of replacement teeth.

The most valid representation of the family Leptotyphlopidae on an ophidian phylogenetic tree, therefore, would seem to be a small, unbranched twig springing from the "proto-boid" stock at the very base of the tree. Its inclusion is justified by its numerous ophidian features; a position near the base is called for by its primitive features; and its specializations preclude the descent of any other known snake from such an ancestor.

The relationships of the typhlopids and anomalepids to the snakes are much less clear. These groups superficially resemble the leptotyphlopids and might be thought to be rather closely related to them and to occupy a similar position on the ophidian tree, but basic skeletal differences distantly separate the two lines. A few features remove the typhlopids even further from *Leptotyphlops* than from the higher snakes. For example, the snakes and typhlopids have a fenestra ovalis and exposed columella while *Leptotyphlops* lacks them; there is an extensive contact between the splenial and coronoid in *Typhlops,* a short contact in typical snakes, and a wide gap between them in *Leptotyphlops;* the mandible of *Typhlops* has no hinge, snakes have a suggestion of one, and *Leptotyphlops* has a freely movable one.

McDowell and Bogert have pointed out a number of important anatomical features in which the typhlopids and anomalepids differ from the typical snakes and *Leptotyphlops.* They state, however, that retention of the former groups in the Ophidia might be justified if any one of three hypotheses could be proven:

1. The typhlopids, though now very distinct from snakes, are derived from snakes and represent only a much modified ophidian line.
2. The typhlopids are close to the ancestry of the ophidians, and their numerous differences from the snakes and leptotyphlopids are but the result of the retention in the typhlopids of ancestral characteristics lost by other ophidians.
3. The typhlopids on one hand, the snakes and leptotyphlopids on the other, have diverged from each other at an early date but are derived from a common ancestor.

My work leads me to agree that the first hypothesis can be ruled out in view of a number of primitive, lizard-like features of *Typhlops* and its relatives which are unknown in the snakes and *Leptotyphlops* (e.g., retention of an immobile symphysis of the mandibles and, in the anomalepids, retention of a jugal and of hypohyal and ceratohyal elements of the hyobranchium). The second possibility is contradicted by the presence in *Typhlops* of numerous specialized features (e.g., the loss of much of the maxilla and its unique suspension, and loss of all palatal, premaxillary, and most dentary teeth). If the third hypothesis were true, the typhlopids would share with the other snakes a series of characters indicative of this relationship and absent in other squamatans. McDowell and Bogert feel, however, that this is not the case, "for the characters common to typhlopids and to the other 'Ophidia' appear to be either common to all Anguinomorpha and anguinomorph descendants or of such general or capricious occurrence in the Squamata as to appear valueless." It is with this last opinion that I take issue.

Several of the distinctions between *Typhlops* and the other snakes, leptotyphlopids, and platynotans pointed out by McDowell and Bogert do not hold up when a number of species are examined:

1. The posterior prolongation of the external bony naris as a slit between the nasal and the prefrontal is given as "the most distinctive and diagnostic feature of the platynotan skull," characteristic of typical snakes and *Leptotyphlops* but absent in *Typhlops* and the diploglossans. On the contrary, the slit is present in five species of *Typhlops* studied here, and it is not present in all the species of *Leptotyphlops* (Plates 2, 8, 10).

2. In the typhlopids the manner of enclosure of the brain by the parietals, frontals, and basisphenoid is held to have "no particular resemblance" to that of snakes and leptotyphlopids. It is pointed out specifically that (a) in *Typhlops* the parietal is separated from the basisphenoid by a fissure but forms a suture with it in other snakes; (b) the frontals of *Typhlops* have quite small descending processes and large inflated dorsal plates, while in other snakes the brain enclosure in this region and the separation of the orbits is accomplished chiefly by the large descending processes of the frontals; and (c) in *Typhlops* the basisphenoid is truncate or emarginate anteriorly and does not extend forward to the vomers, leaving a median vacuity here (partially filled by the laterosphenoids in *Liotyphlops*), while in other snakes it is directed anteriad and does meet the vomers, eliminating the median vacuity. In the description of the skull in the present work a number of contradictions to (e.g., parietal-basisphenoid sutures in some *Typhlops* and parietal-basisphenoid fissures in some *Leptotyphlops*), variations from (e.g., in form and anterior extent of the basisphenoid), and alternatives to the points of view stated by McDowell and Bogert have been pointed out. Collectively, they reduce considerably any distinctions between the brain cases of the two groups. It is true that at least two other quite unrelated groups of squamatans (*Dibamus* and the amphisbaenids) may have the brain case formed in about the same way and that this general feature by itself is therefore no guarantee of snake affinities. However, the specific manner of enclosure is not appreciably different in the typhlopids and other snakes.

3. The septomaxilla of *Typhlops* is said to "show no resemblance to that of the leptotyphlopids, snakes or platynotan lizards. There is no ascending lateral process, but rather the lateral extremity of the bone is horizontal and without upward flexure." It is true that this bone in *Typhlops* is greatly enlarged and has relationships not seen in these other groups, but in some species the lateral edge is turned up, to varying degrees, although not to the extent seen in *Leptotyphlops* (Plates 5, 8).

4. The coronoid of *Typhlops* is said to resemble that of both the platynotans and diploglossans in that it possesses both anterior and posterior descending processes, the notch between them exposing a portion of the surangular. However, in about half of the species examined here the base of the coronoid is more snakelike in being straight, with no notch and thus no definite descending processes. The dorsal projection of the bone, the coronoid process, arises in the middle of the bone in *Typhlops* and diploglossans and from the posterior part in typical snakes and platynotans. Of that of *Typhlops* it is said that "there is no suggestion of the highly peculiar coronoid of the leptotyphlopids." The process in *Leptotyphlops,* although rather knobby and distorted like the rest of the coronoid, definitely arises from the center of the bone and to that extent it resembles that of *Typhlops.*

5. One of the more basic resemblances of the snakes and platynotans is the posteriorly tapering centrum of the vertebra, with the condyle set off by a constriction. Among snakes such vertebrae are known at least in the Boidae and more primitive colubrids. The vertebrae of *Leptotyphlops* are described as having centra which are tapered posteriorly, but in the specimens at hand, this is only faintly indicated. Certainly the form of their centra (and the rest of the vertebra as well) is much closer to that in *Typhlops* than to that of a boid. The vertebrae of *Typhlops* are said to show none of the platynotan-like features seen in the snakes (including *Leptotyphlops*). There is no indication of the tapered centrum, but the condyle is distinctly set off by a constriction (Plate 13).

6. Doubt arises concerning the homology of the zygantra and zygosphenes of *Typhlops* to those of other snakes and *Leptotyphlops* because in the latter two these articulations are well dorsal to the level of the zygopophyseal joint, while in the former both joints are at the same level. The difference in the levels of these articulations in the two groups is extremely slight and insignificant. At the most, it is probably only a reflection of the slightly higher neural arch of the leptotyphlopids (the vertebrae in general are somewhat more depressed in *Typhlops*) (Plate 13).

7. The typhlopids are said to differ from the snakes and leptotyphlopids in the absence of ceratobranchial elements. However, as pointed out in the preceding discussion of the hyoid, a hyobranchium consisting

solely of the first ceratobranchials occurs in some species of *Typhlops.* This is beside the point, of course, if the hyoid of typical snakes consists of only the basihyal, as was suggested earlier.

8. The pairing of the supraoccipitals in some species of *Typhlops* is considered an anomalous condition since the bone is seldom if ever anything but a median azygous bone in vertebrates. By an unusual coincidence, *every species of Leptotyphlops that has ever been figured,* from Jan and Sordelli's work to that of McDowell and Bogert, has been a species with a single, unpaired supraoccipital. Yet in all seven of the species illustrated in the present book the supraoccipitals are paired, and except for their slightly larger size, they are quite like those of *Typhlops.* The two genera are therefore alike in sharing this highly unusual characteristic (Plate 10).

The above considerations reduce the distinctions between the typhlopid-anomalepid group and the other snakes considerably. Also, two basically ophidian features of the blind snakes support the impression that they are all truly snakes. One of these is mentioned by McDowell and Bogert, but the significance of the other has apparently escaped the attention of previous writers. The first is the fact that the exoccipitals meet each other in the mid-dorsal line to exclude the supraoccipital(s) from the foramen magnum. It has been suggested that the variability of the bones of the occipital region reduces the significance of this feature. But this variability is always with respect to the bones *anterior to* the exoccipital—fusion with the prootics or with the supraoccipitals, or with both, or the pairing of the latter—never with respect to the basic form of the exoccipitals. Those parts of the exoccipitals which actually enclose the foramen magnum are quite constant in their basic form (except in *Leptotyphlops humilis,* where they are widely separated dorsad). The second resemblance seems fundamental and has to do with the development of the metapophyses of the vertebrae. McDowell and Bogert refer to them in *Leptotyphlops* but not in *Typhlops.* They are even more highly developed, however, in the latter genus and give the vertebrae in dorsal view their very characteristic hourglass appearance. These processes are one of the more prominent features of the vertebrae of all the blind snakes (Plate 13). Although they are somewhat reduced in size in the vertebrae of boids, they are quite prominent in the higher snakes, being especially long and slender in the racers (*Masticophis*). Metapophyses are *not* present in amphisbaenids, *Ophisaurus,* platynotans, nor in any other lizard, to judge from the numerous figures of Camp (1923). This would seem to be one of the more significant features linking all the blind snakes with the higher forms.

There still remains, of course, a number of unsnakelike characters, the more important of which are the rigid dentary symphysis, the closed

Meckelian groove, the long splenio-coronoid suture, and the unique form and suspension of the maxilla. In spite of these peculiarities, the evidence as a whole favors the inclusion of all the blind snakes in the Ophidia and the third hypothesis mentioned above as the correct one—the typhlopids and anomalepids on the one hand, the snakes and leptotyphlopids on the other, have diverged from each other at an early date but are derived from a common ancestor.

Underwood (1957) criticized various points of McDowell and Bogert's 1954 work, including their suggestion that the Typhlopidae be removed from the Serpentes. He has pointed out a number of ophidian features of *Typhlops,* particularly in their soft anatomy: circulatory system, eye structure, thymus bodies, liver and gall bladder relationships, even the snakelike odor of cloacal gland secretions. "*Typhlops* combines a number of distinctly ophidian features with a few which are clearly primitive from an ophidian standpoint. To these it adds a number of divergent features (a few of them shared with *Leptotyphlops*). In my opinion this argues that the Typhlopidae are divergent descendants of ancestral snake stock. . . . I strongly urge that the Typhlopidae should be retained in the Serpentes."

Robb (1960), on the other hand, has concluded that "the numerous peculiarities of the internal organs of *Typhlops* support the hypothesis that the group should indeed be removed from the Ophidia." She suggests that the typhlopids "should either be given subordinal rank, equivalent to the Sauria and the Serpentes, or be made an infra-order of the Sauria." Her paper describes in detail for the first time the digestive, circulatory, respiratory, and reproductive systems of *Typhlops.* She notes "points of dissimilarity of structure between this genus and the snakes, in every system examined," with the respiratory and reproductive systems having the most striking peculiarities. Specifically, there are two elongate lungs, both apparently functional, lying one ahead of the other. On the basis of blood supply, the anterior one appears to represent the left lung and the posterior one the right. Although this is a unique arrangement, it may well be viewed as just one more solution to the ophidian problem of what to do with two lungs in a very slender body.

Robb reports a truly startling situation in the nature of the hemipenes, which are slender, solid, protrusible structures. Each consists in large part of apparently erectile tissue, bears a longitudinal external groove but no spines, and when retracted is coiled within a sheath that lies in the tail and opens into the cloaca. Robb notes: "Hence, in that it is solid, and externally grooved, and is retracted into the resting position, each hemipenis of *Typhlops* bears a greater superficial resemblance to the single penis of the crocodiles and chelonians, than to the hemipenis of other snakes."

It seems to me that this statement holds only if the hemipenis is considered in isolation. In that they are paired, and are contained in definite sheaths, and lie in the tail (posterior to the anus, not in the cloaca proper), these typhlopid copulatory structures still basically represent the squamatan pattern. Further, I should like to suggest that the hemipenes of *Typhlops* may merely represent a very primitive condition, from which the hemipenes of modern snakes (and lizards) could have been derived by the simple reduction and loss of the solid, grooved, protrusible portions of the system, the sheaths themselves then serving as copulatory organs when evaginated. In this view, the hemipenes of a modern snake are homologous to the typhlopid *sheaths* and not at all homologous to the solid copulatory structure that each of the latter contains. Robb mentions, incidentally, that "at its posterior end, the sheath becomes fairly loosely attached to the hemipenis, and *somewhat inverted* within its own cavity. This is, of course, especially the case *when the hemipenis is protruded* into and beyond the cloaca" (italics mine).

In any case, in spite of the above (and other) unusual features of the typhlopid soft anatomy, the basic nature of the animals seems to me to be ophidian.

One final point may be noted. When this present work was begun it was anticipated that there might appear enough skeletal variations to suggest the establishment of subfamilies or new genera. This was particularly expected in the large genera *Typhlops* and *Leptotyphlops.* Although a number of interspecific variations were noted they showed no correlation with each other, and none by itself seems important or constant enough to serve as a sole generic criterion. Such a feature as the paired or fused parietals would appear to be important, for example, were it not for known intermediate conditions and even changes from the paired to the fused state during postembryonic development. Possibly some of the more bizarre species of *Typhlops,* those with quite flattened snouts, for example, might be worthy of generic differentiation, but none such was included in this study. On the present evidence, therefore, there seems to be no basis for subdividing either *Typhlops* or *Leptotyphlops.*

SUMMARY

The skeletons of thirty-two species of blind snakes were studied in an effort to clarify the taxonomy and phylogeny of the groups. As a whole, these snakes show a peculiar combination of primitive, lizard-like characters and highly specialized features. Some of the latter are

obviously correlated with the burrowing mode of life and others are not.

A. Reinterpretations of a number of skeletal homologies or other features have been suggested by this study, largely due to the utilization of a greater variety of species compared to previous works. These reinterpretations include the following:

1. The hyoid of the anomalepids consists of a reduced basihyal, a pair of anteriorly directed hypohyals, and a pair of posteriorly directed and recurved ceratohyals. All these elements are fused to form a threadlike structure in the general form of an M with the legs bent back upon themselves.
2. The hyoid apparatus of *Typhlops* may consist of either the basihyal or the second ceratobranchials or both. The hyoid of *Leptotyphlops* consists of the basihyal alone, with elongate posterior extensions. The hyoid of most higher snakes is most likely the basihyal alone, minus the anterior glossohyal process.
3. The odontoid process of all the blind snakes is quite broad, about as large as the pleurocentrum of the axis, and the small knob of calcified cartilage on the anterior face of the axis represents the proatlas.
4. The ectopterygoid in *Typhlops* seems to have fused to the pterygoid rather than to the palatine, as has been previously suggested.
5. The ventral vertebral foramina, whether paired or single, are homologous to each other and to the similar foramina of other snakes and lizards. They are passages for adult derivatives of the intersegmental arteries of the embryo.
6. In the blind snakes the articular cup of the rib seems to represent not a fusion of capitulum and tuberculum but a new formation between them, since rudimentary capitula and tubercula are still present.
7. The small bone near the rear end of the quadrate in *Liotyphlops* is the tabular, not the squamosal.
8. The bone below and behind the dentary in *Liotyphlops* is the splenial, not the angular.
9. The zygantra and zygosphenes of the blind snakes, although somewhat reduced, are basically the same as those of higher snakes.
10. The dorsal scales/vertebrae ratio is not 2:1 in the typhlopids (Mahendra, 1936, and others) and leptotyphlopids (Schmidt, 1950). Rather, in the typhlopids and anomalepids there is no definite ratio; it ranges from 1.5:1 to 2.3:1. In *Leptotyphlops* the ratio is 1:1, as in higher snakes.

B. Skeletal features noted for the first time in the blind snakes and described above include:

1. The presence of a pelvic girdle in *Liotyphlops*.
2. The unusual "urostyle" at the tip of the tail in some species of *Typhlops*.

3. Variations in the hyobranchium of *Typhlops*, including the presence of ceratobranchials.

4. The presence of three teeth (rather than one), including a replacement tooth, on the dentary of *Liotyphlops*.

5. The unusually compressed maxillary teeth of *Liotyphlops*.

6. Evidence of a tabular in various species of *Leptotyphlops*.

7. Ossified or calcified ilia and pubes in some species of *Typhlops*.

8. Vestiges of postfrontals in a second species of *Typhlops* (*reticulatus*).

9. Calcified palatal cartilages in *Leptotyphlops*.

10. The paired condition of the parietals and supraoccipitals in some species of *Leptotyphlops*.

C. On the basis of the skeletal features outlined in the previous sections of this work, two major conclusions are reached:

1. There is justification for the erection of a third family of blind snakes, the Anomalepidae, composed of four genera: *Anomalepis, Liotyphlops, Helminthophis,* and *Typhlophis*.

2. The typhlopids and anomalepids are properly placed in the Ophidia. Examination of a variety of species shows insufficient justification for their removal from the snakes. Arguments for removing them, as set forth in recent works, are considered inadequate in the light of the present study of a series of species.

ABBREVIATIONS USED IN PLATES

Ad — arytenoid
An — angular
Ar — articular
At — atlas
Ax — axis
Bh — basihyal
Bo — basioccipital
Bs — basisphenoid
C — coronoid
CbI — ceratobranchial I
CbII — ceratobranchial II
Ch — ceratohyal
Cl — claw
Con — condyle
Cot — cotyle
Cp — composite bone
Cr — cricoid
Ct — capitulum
D — dentary
Ec — ectopterygoid
Eo — exoccipital
F — frontal
Fe — femur
Gh — glossohyal process
Hc — hypocentrum
Hh — hypohyal
Hp — hypapophysis
Hy — hyobranchium
IF — intervertebral foramen
Il — ilium
Is — ischium
J — jugal
LF — lateral foramen
M — maxilla
Met — metapophysis
N — nasal
NA — neural arch
NC — neural canal
Od — odontoid process
P — parietal
P — pubis
Pa — proatlas
Pc — pleurocentrum
Pf — prefrontal
Pal — palatine
Pl — palpebral
Pm — premaxilla
Po — prootic
Pof — postfrontal
Poz — postzygapophysis
Prz — prezygapophysis
Pt — pterygoid
Pu — pubis
Q — quadrate
Rb — rib
S — splenial
Sm — septomaxilla
So — supraoccipital
Sp — laterosphenoid (?)
Syn — synapophysis
T — tendon (?)
Tb — tabular
Tb — tuberculum
TC — tracheal cartilage
V — vomer
VF — ventral foramen
Zn — zygantrum
Zs — zygosphene

In all figures the scale line equals one millimeter.

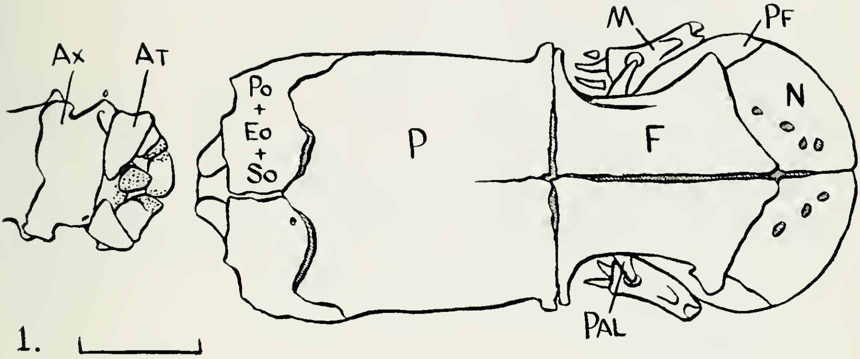
PLATE 1

Skulls, minus lower jaw, dorsal view.

Fig. 1. *Typhlops lineatus* JCL 1013.

Fig. 2. *Liotyphlops albirostris* USNM 61989.

Fig. 3. *Leptotyphlops bakewelli* USNM 25242.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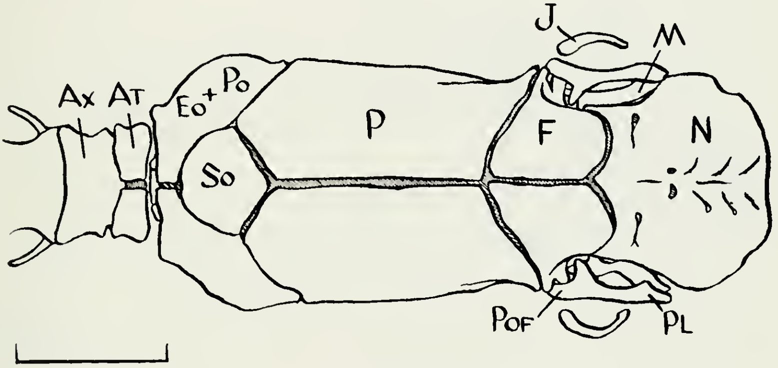
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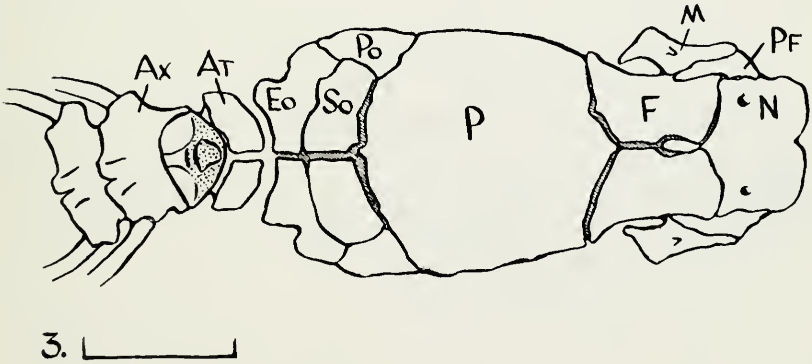
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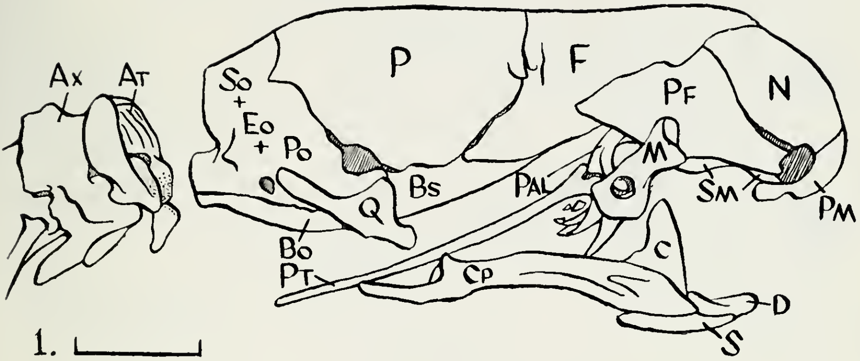
PLATE 2

Skulls, lateral view.

Fig. 1. *Typhlops lineatus* JCL 1013.
Fig. 2. *Liotyphlops albirostris* USNM 61989.
Fig. 3. *Leptotyphlops bakewelli* USNM 25242.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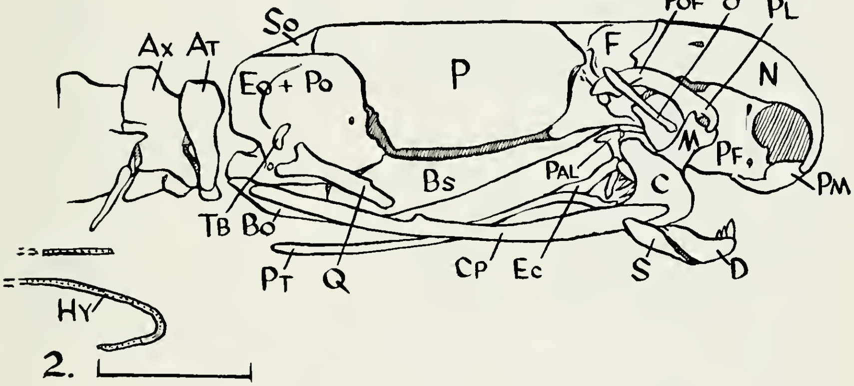
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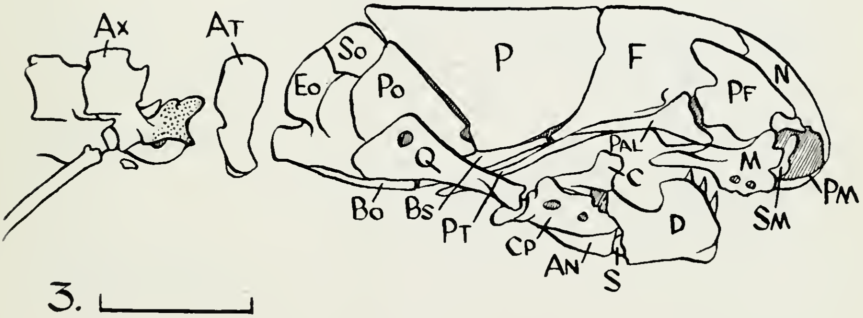
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3.

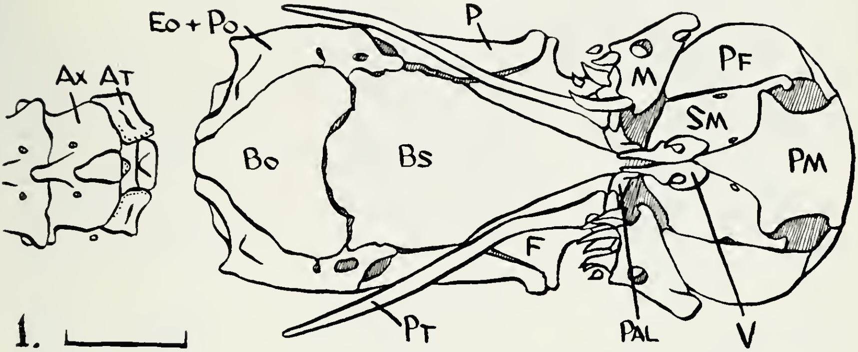
Plate 3

Skulls, minus lower jaw, ventral view.

Fig. 1. *Typhlops lineatus* JCL 1013.

Fig. 2. *Liotyphlops albirostris* USNM 61989.

Fig. 3. *Leptotyphlops bakewelli* USNM 25242.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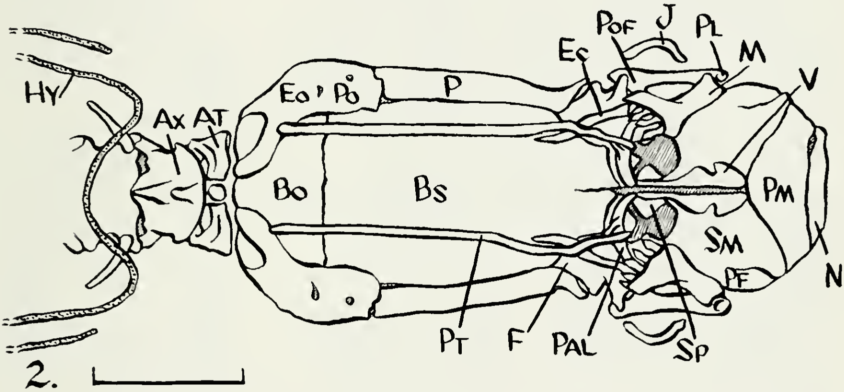
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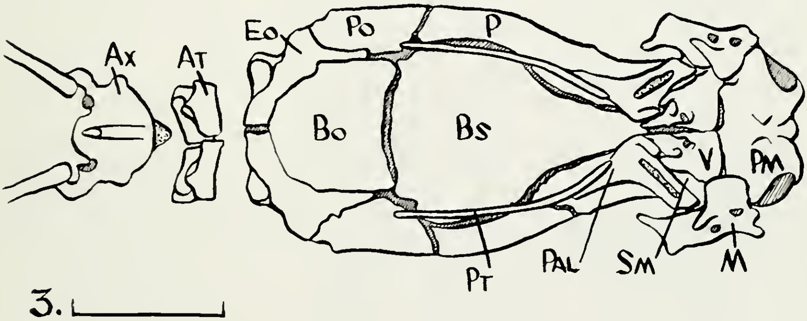
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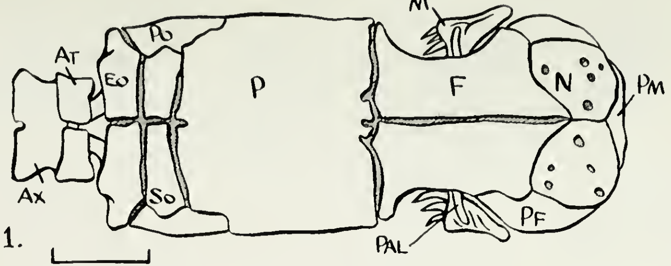
Plate 4

Skulls, minus lower jaw, dorsal view.

Fig. 1.	*Typhlops vermicularis*	CNHM	28572.
Fig. 2.	*Typhlops reticulatus*	CNHM	35592.
Fig. 3.	*Typhlops platycephalus*	MCZ	38337.
Fig. 4.	*Typhlops rostellatus*	MCZ	38370.
Fig. 5.	*Typhlops polygrammicus*	JCL	1018.
Fig. 6.	*Typhlops lumbricalis*	MCZ	22279.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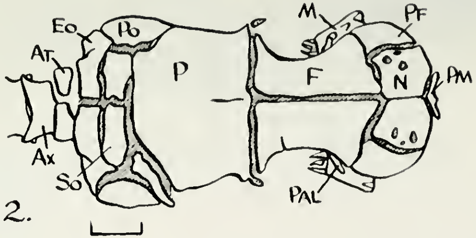
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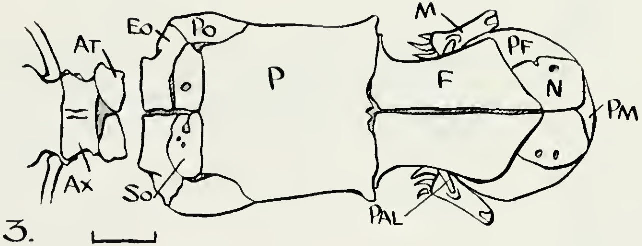
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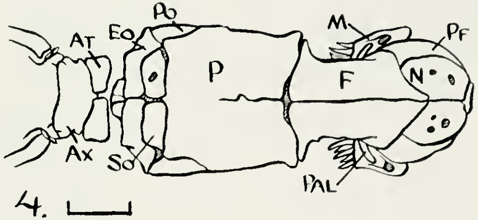
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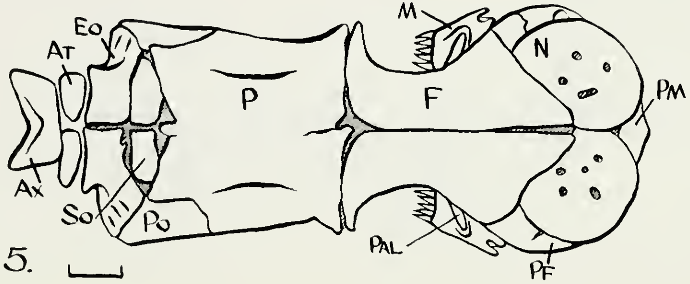
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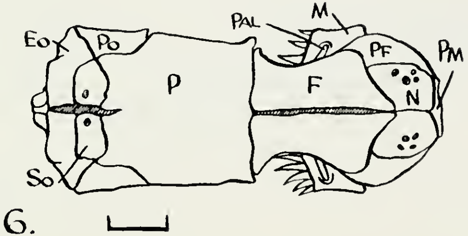
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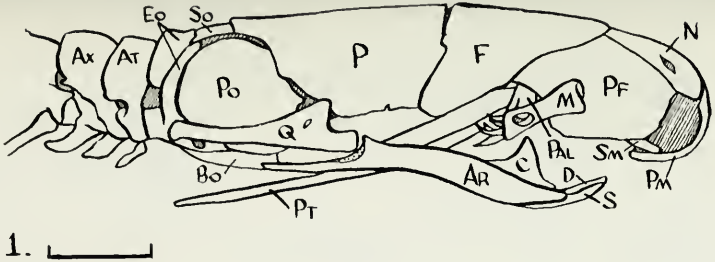
PLATE 5

Skulls, lateral view.

Fig. 1. *Typhlops vermicularis* CNHM 28572.
Fig. 2. *Typhlops reticulatus* CNHM 35592.
Fig. 3. *Typhlops platycephalus* MCZ 38337.
Fig. 4. *Typhlops rostellatus* MCZ 38370.
Fig. 5. *Typhlops polygrammicus* JCL 1018.
Fig. 6. *Typhlops lumbricalis* MCZ 22279.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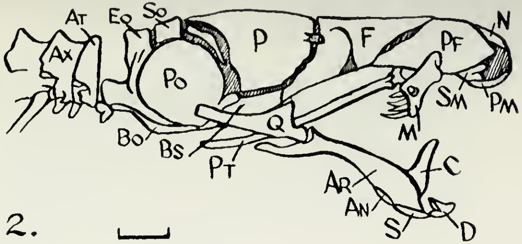
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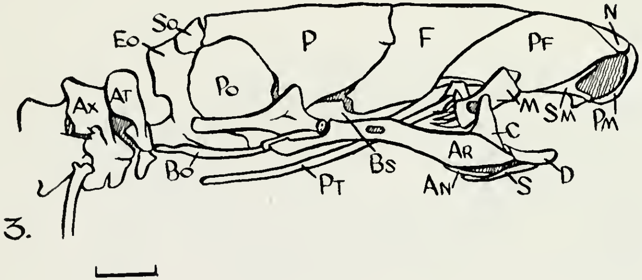
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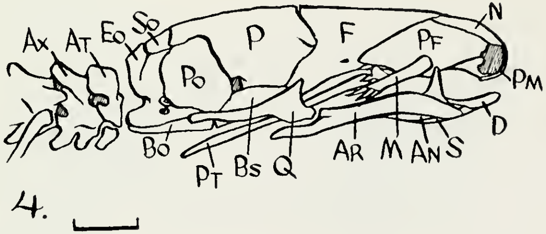
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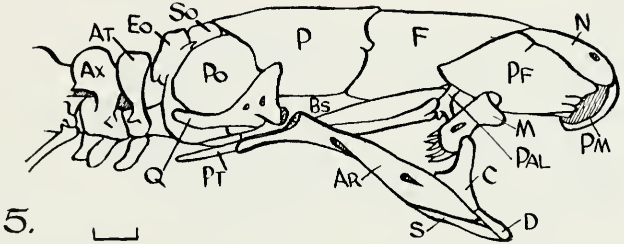
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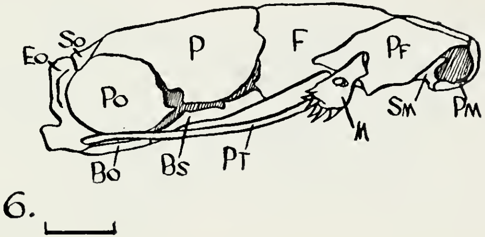
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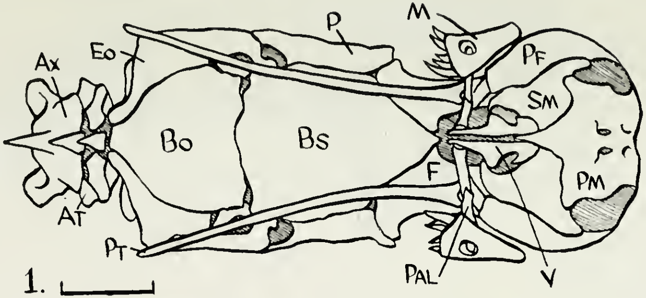
PLATE 6

Skulls, minus lower jaw, ventral view.

Fig. 1. *Typhlops vermicularis* CNHM 28572.
Fig. 2. *Typhlops reticulatus* CNHM 35592.
Fig. 3. *Typhlops platycephalus* MCZ 38337.
Fig. 4. *Typhlops rostellatus* MCZ 38370.
Fig. 5. *Typhlops polygrammicus* JCL 1018.
Fig. 6. *Typhlops lumbricalis* MCZ 22279.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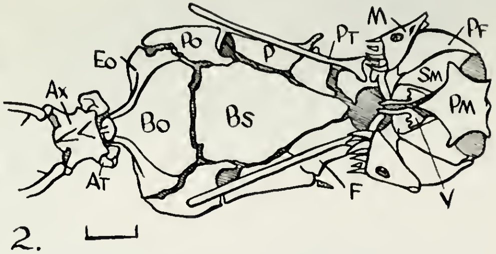
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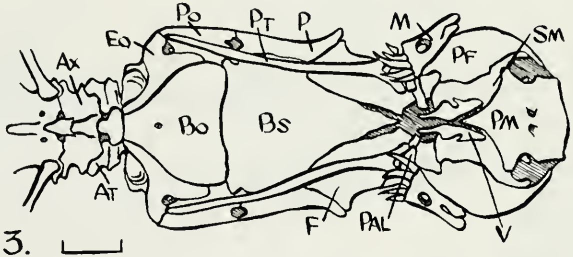
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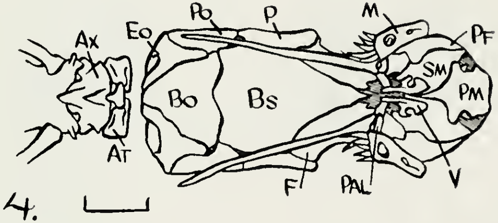
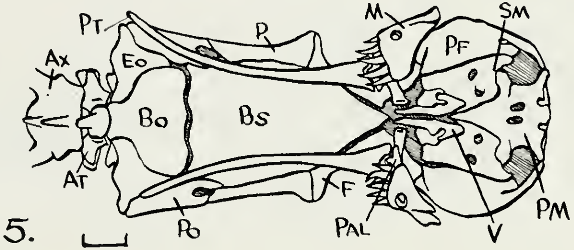
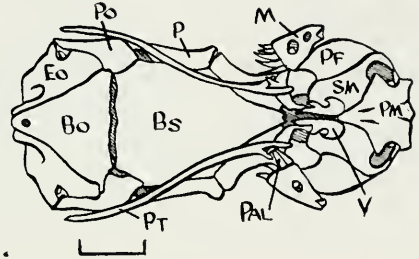
3.


Po
P
M
Eo
Pf
Ax
Sm
Bo
Bs
Pm
At
F
Pal
V

4.


Pt
M
Sm
P
Ax
Pf
Eo
Bo
Bs
At
F
Po
Pal
V
Pm

5.

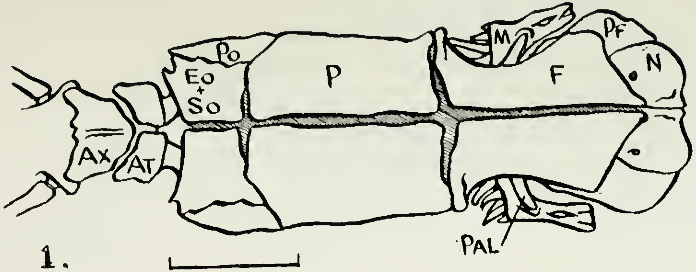

Po
M
P
Pf
Eo
Sm
Pm
Bo
Bs
Pt
Pal
V

6.

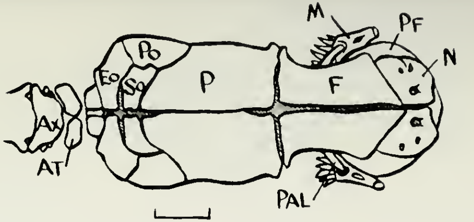
Plate 7

Skulls, minus lower jaw, dorsal view.

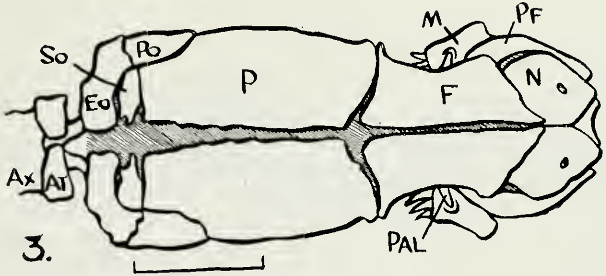
Fig. 1. *Typhlops braminus* JCL 1022.
Fig. 2. *Typhlops flaviventer* JCL 1012.
Fig. 3. *Typhlops pusillus* MCZ 8758.
Fig. 4. *Typhlops blanfordi lestradei* MCZ 48077.
Fig. 5. *Typhlops boettgeri* JCL 1014.
Fig. 6. *Typhlops schlegelii mucruso* MCZ 30058.


Po
Eo + So
P
M
PF
N
F
Ax
AT
PAL

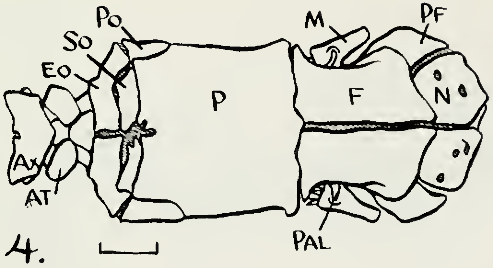
1.


M
PF
N
Po
Eo
So
P
F
Ax
AT
PAL

2.


M
PF
So
Po
P
N
F
Eo
Ax
AT
PAL

3.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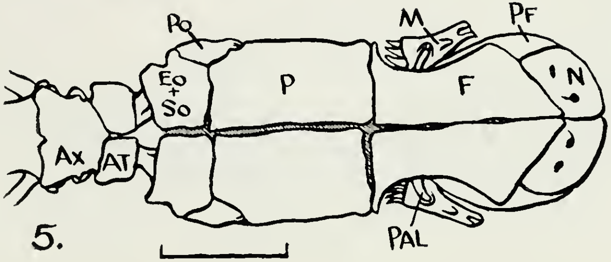
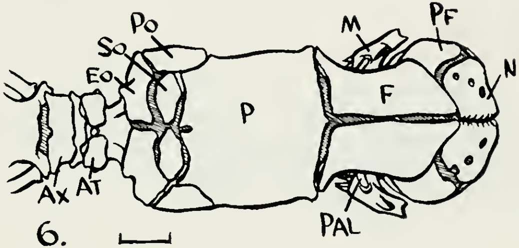
So
Eo
P
M
PF
F
N
Ax
AT
PAL

4.


Po
M
PF
Eo + So
P
F
N
Ax
AT
PAL

5.


Po
So
Eo
M
PF
N
F
P
Ax
AT
PAL

6.

PLATE 8

Skulls, lateral view.

Fig. 1. *Typhlops braminus* JCL 1022.

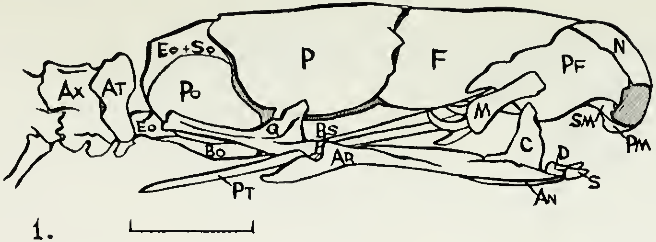
Fig. 2. *Typhlops flaviventer* JCL 1012.

Fig. 3. *Typhlops pusillus* MCZ 8758.

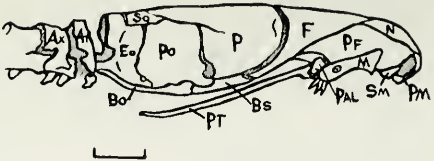
Fig. 4. *Typhlops blanfordi lestradei* MCZ 48077.

Fig. 5. *Typhlops boettgeri* JCL 1014.

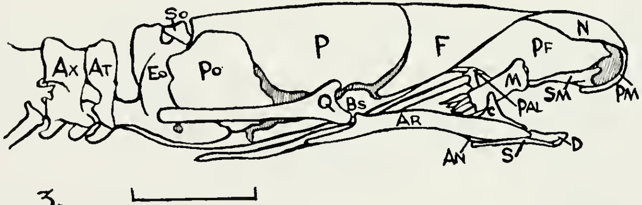
Fig. 6. *Typhlops schlegelii mucruso* MCZ 30058.


Eo+So
P
F
PF
N
Ax
AT
Po
Eo
Q
BS
M
C
SM
PM
Bo
AR
D
S
PT
AN

1.


So
F
N
PF
Ax
At
Eo
Po
P
M
Bo
Bs
PAL
SM
PM
PT

2.


So
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F
N
PF
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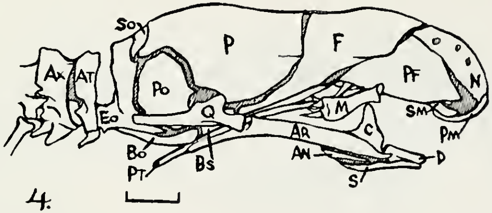
AT
Eo
Po
M
PAL
SM
PM
Q
Bs
C
AR
AN
S
D

3.


So
P
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PF
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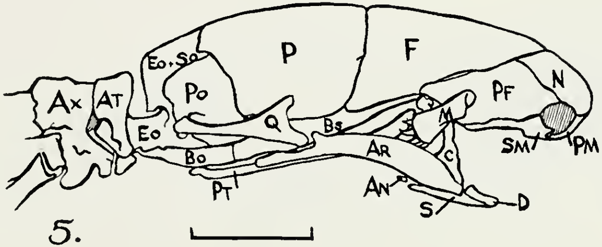
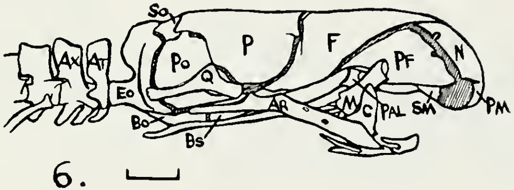
AT
Po
Eo
Q
M
SM
PM
AR
C
Bo
AN
PT
Bs
S
D

4.


P
F
Eo+So
Po
PF
N
Ax
AT
Eo
Q
Bs
M
AR
SM
PM
C
Bo
PT
AN
S
D

5.

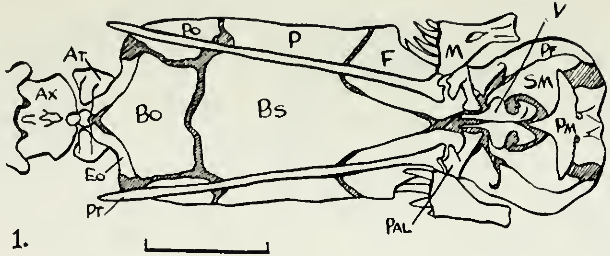

So
P
F
N
PF
Po
Ax
At
Q
Eo
AR
M
C
PAL
SM
PM
Bo
Bs

6.

PLATE 9

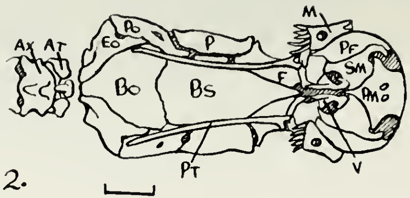
Skulls, minus lower jaw, ventral view.

Fig. 1. *Typhlops braminus* JCL 1022.
Fig. 2. *Typhlops flaviventer* JCL 1012.
Fig. 3. *Typhlops pusillus* MCZ 8758.
Fig. 4. *Typhlops blanfordi lestradei* MCZ 48077.
Fig. 5. *Typhlops boettgeri* JCL 1014.
Fig. 6. *Typhlops schlegelii mucruso* MCZ 30058.



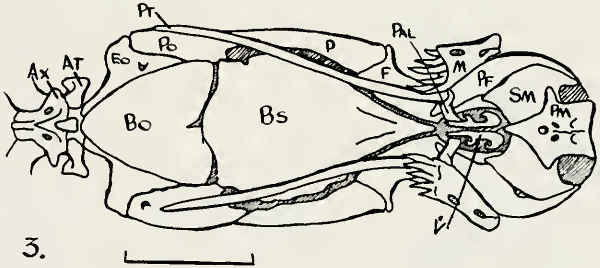
Ax
At
Bo
Bs
Po
P
F
M
V
PF
SM
PM
Eo
PT
PAL

1.



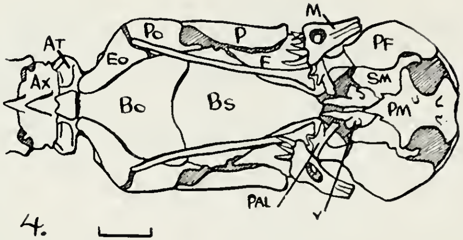
Ax
At
Eo
Po
P
Bo
Bs
F
M
PF
SM
PM
PT
V

2.



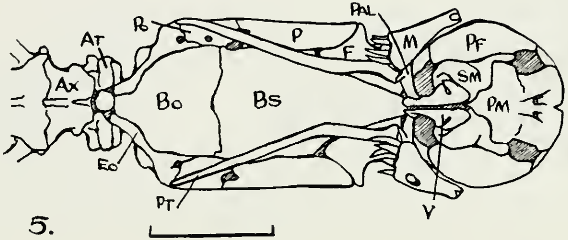
PT
Ax
At
Eo
Po
P
PAL
F
M
PF
SM
PM
Bo
Bs
V

3.



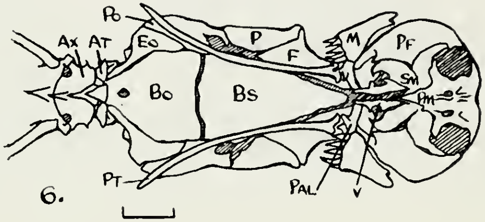
At
Ax
Po
P
M
PF
Eo
F
SM
Bo
Bs
PM
PAL
V

4.



Po
At
P
PAL
F
M
PF
SM
Ax
Bo
Bs
PM
Eo
PT
V

5.



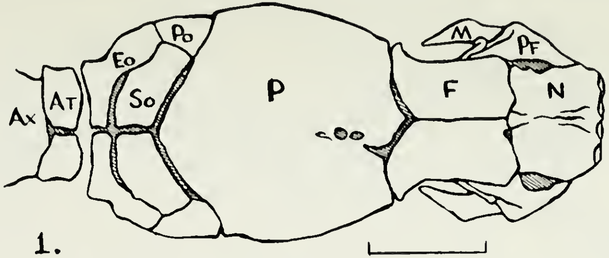
Po
Ax
At
Eo
P
F
M
PF
SM
Bo
Bs
PM
PT
PAL
V

6.

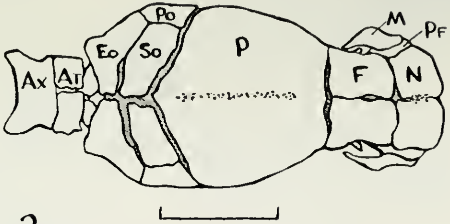
PLATE 10

Skulls, minus lower jaw, dorsal view.

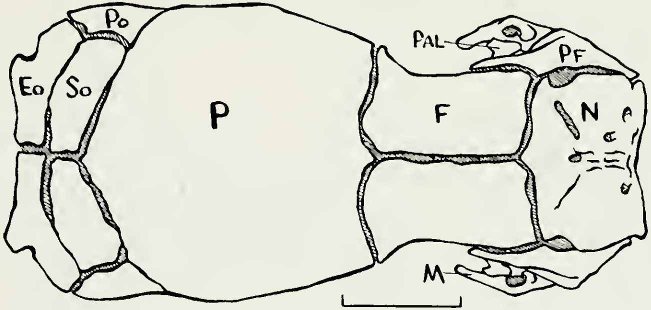
Fig. 1. *Leptotyphlops dulcis dissectus* USNM 99821.
Fig. 2. *Leptotyphlops nigricans* MCZ 21473.
Fig. 3. *Leptotyphlops maximus* UIMNH 34999.
Fig. 4. *Leptotyphlops emini* CNHM 56374.
Fig. 5. *Leptotyphlops magnamaculata* CNHM 87.
Fig. 6. *Leptotyphlops humilis cahuilae* JCL 1000.


Ax
AT
Eo
So
Po
P
F
N
M
PF

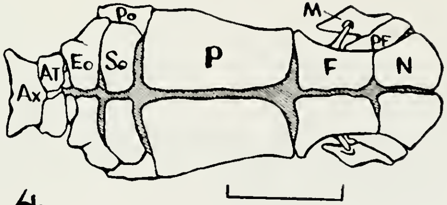
1.


Ax
AT
Eo
So
Po
P
F
N
M
PF

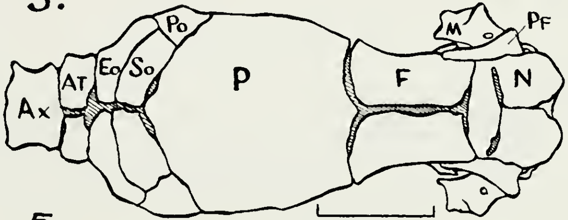
2.


Eo
So
Po
P
F
N
PAL
PF
M

3.


Ax
AT
Eo
So
Po
P
F
N
M
PF

4.


Ax
AT
Eo
So
Po
P
F
N
M
PF

5.

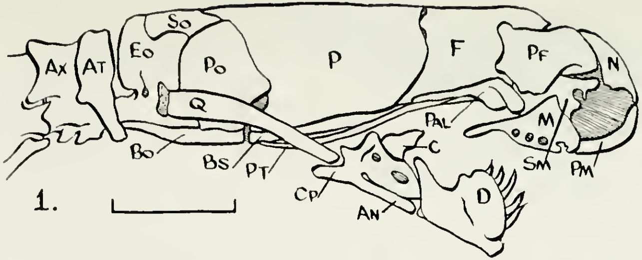

AT
Eo
So
Po
P
F
N
M
PF

6.

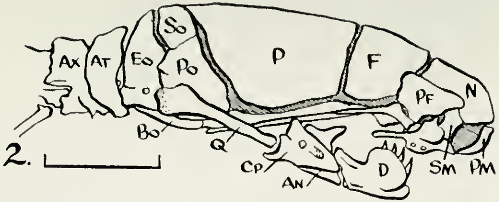
PLATE 11

Skulls, lateral view.

Fig. 1. *Leptotyphlops dulcis dissectus* USNM 99821.
Fig. 2. *Leptotyphlops nigricans* MCZ 21473.
Fig. 3. *Leptotyphlops maximus* UIMNH 34999.
Fig. 4. *Leptotyphlops emini* CNHM 56374.
Fig. 5. *Leptotyphlops magnamaculata* CNHM 87.
Fig. 6. *Leptotyphlops humilis cahuilae* JCL 1000.


Ax
At
Eo
So
Po
P
F
Pf
N
Q
Pal
M
Bo
Bs
Pt
C
Sm
Pm
Cp
An
D

1.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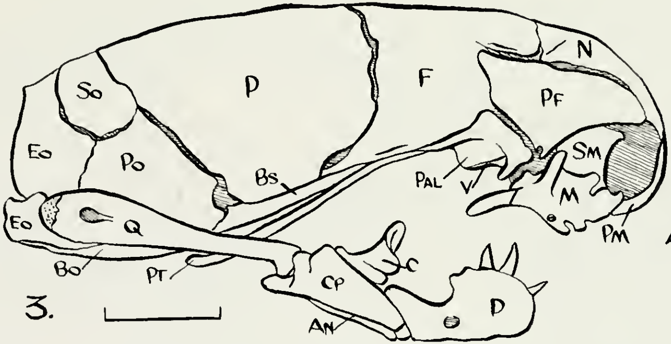
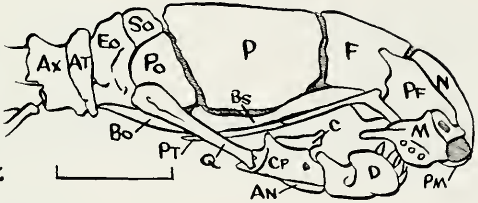
Eo
So
Po
P
F
Pf
N
Bo
Q
Cp
An
D
Sm
Pm

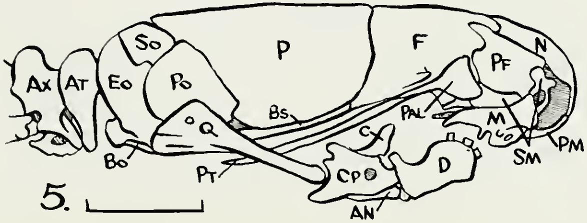
2.


So
P
F
N
Pf
Eo
Po
Bs
Pal
V
Sm
M
Pm
Eo
Q
Bo
Pt
Cp
C
An
D

3.


Ax
At
Eo
So
Po
P
F
Pf
N
Bs
Bo
Pt
Q
C
Cp
M
D
Pm
An

4.


Ax
At
Eo
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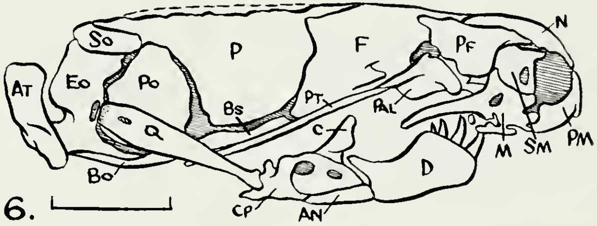
Pf
N
Bs
Pal
Q
M
Bo
C
Sm
Pm
Pt
Cp
D
An

5.

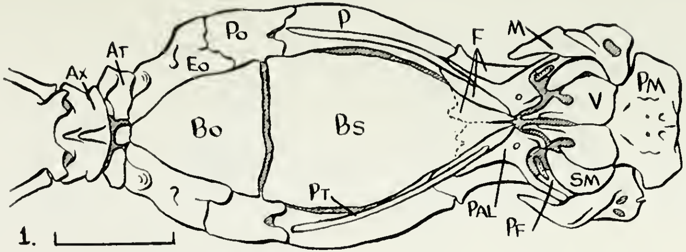

So
P
F
Pf
N
At
Eo
Po
Bs
Pt
Pal
Q
C
Bo
M
Sm
Pm
D
Cp
An

6.

Plate 12

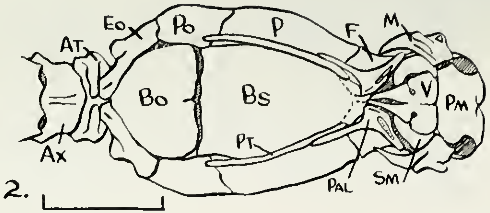
Skulls, minus lower jaw, ventral view.

Fig. 1. *Leptotyphlops dulcis dissectus* USNM 99821.
Fig. 2. *Leptotyphlops nigricans* MCZ 21473.
Fig. 3. *Leptotyphlops maximus* UIMNH 34999.
Fig. 4. *Leptotyphlops emini* CNHM 56374.
Fig. 5. *Leptotyphlops magnamaculata* CNHM 87.
Fig. 6. *Leptotyphlops humilis cahuilae* JCL 1000.



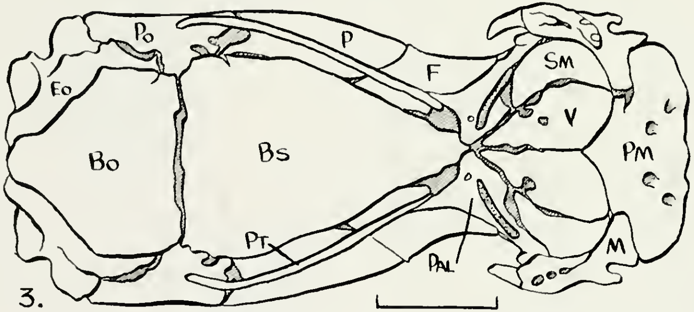
Ax
At
Eo
Po
P
F
M
Bo
Bs
V
Pm
Pt
Pal
Pf
Sm

1.



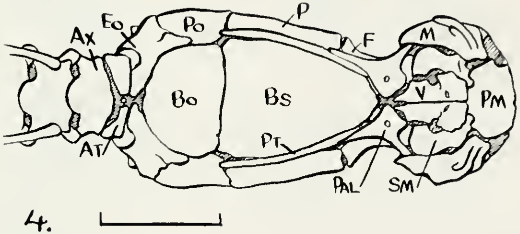
Eo
Po
P
F
M
At
V
Bo
Bs
Pm
Ax
Pt
Pal
Sm

2.



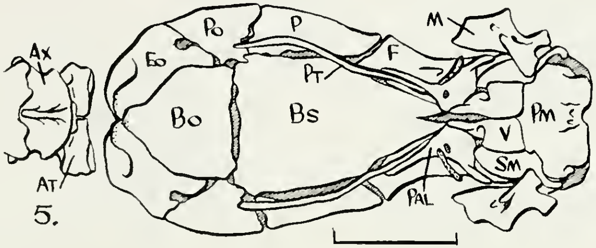
Po
P
Sm
F
Eo
V
Bo
Bs
Pm
Pt
M
Pal

3.



P
Eo
Po
F
M
Ax
V
Bo
Bs
Pm
At
Pt
Pal
Sm

4.



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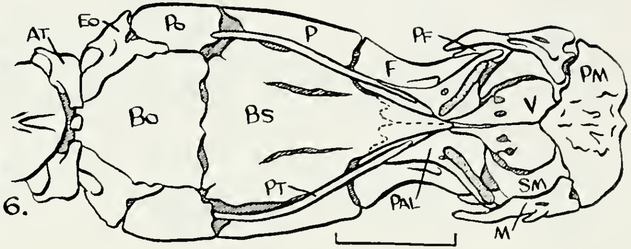
Po
P
M
Eo
F
Pt
Bo
Bs
Pm
V
At
Sm
Pal

5.



At
Eo
Po
P
Pf
Pm
F
V
Bo
Bs
Pt
Sm
Pal
M

6.

PLATE 13

Thoracolumbar vertebrae, at mid-body.

Fig. 1. *Liotyphlops albirostris* USNM 61989.

Fig. 2. *Typhlops lineatus* JCL 1013.

Fig. 3. *Leptotyphlops humilis humilis* JCL 1020.

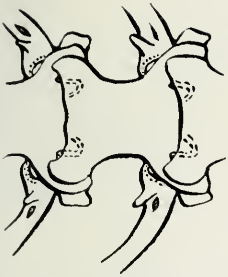
A. Dorsal.

B. Lateral.

C. Ventral.

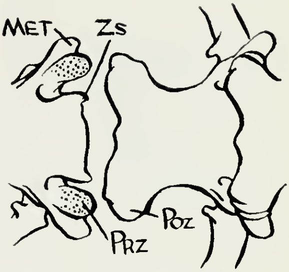
D. Anterior.

E. Posterior.

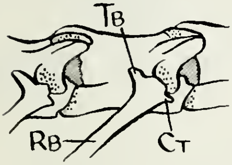


1.A

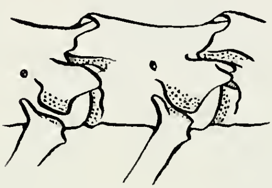
2.A



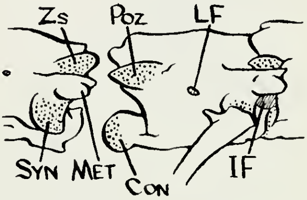
3.A



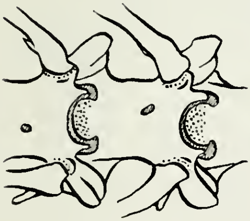
1.B



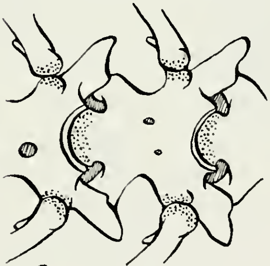
2.B



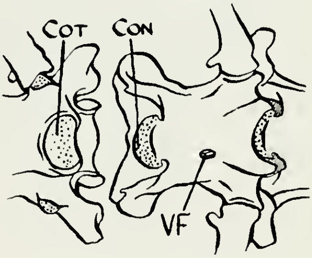
3.B



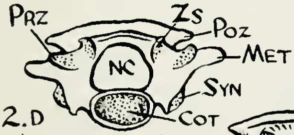
1.C



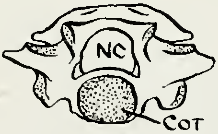
2.C



3.C



2.D



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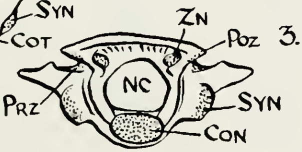

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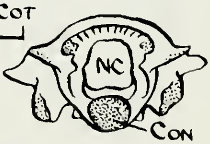
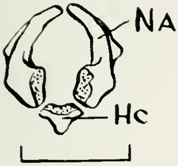


3.E

Plate 14

Atlas (Fig. 1), axis (Fig. 2), and terminal caudal vertebrae with "urostyle" (Figs. 3–7).

Fig. 1. *Typhlops richardi* MCZ 38350.
Fig. 2. *Typhlops richardi* MCZ 38350.
Fig. 3. *Typhlops polygrammicus* JCL 1018.
Fig. 4. *Typhlops vermicularis* CNHM 28572.
Fig. 5. *Typhlops rostellatus* MCZ 38370.
Fig. 6. *Typhlops jamaicensis* MCZ 7370.
Fig. 7. *Typhlops lineatus* JCL 1013.
A. Anterior.
B. Posterior.
C. Right side.



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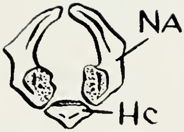

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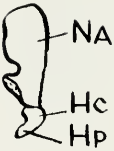

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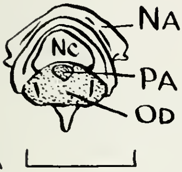

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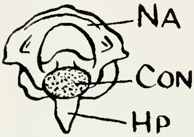

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2. C

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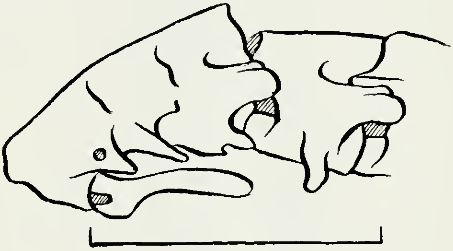

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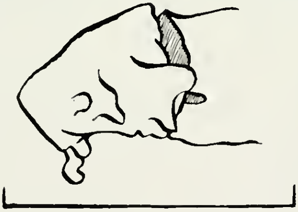

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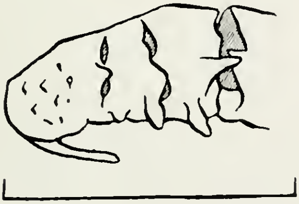


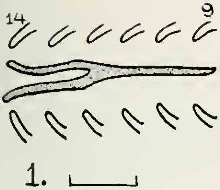
6.

7.

Plate 15

Hyobranchia and adjacent rib tips, ventral view.

Fig. 1. *Typhlops braminus* JCL 1022.
Fig. 2. *Typhlops polygrammicus* JCL 1018.
Fig. 3. *Typhlops pusillus* MCZ 8758.
Fig. 4. *Typhlops vermicularis* CNHM 28572.
Fig. 5. *Typhlops boettgeri* JCL 1014.
Fig. 6. *Typhlops reticulatus* CNHM 35592.
Fig. 7. *Typhlops lumbricalis* JCL 1007.
Fig. 8. *Typhlops schlegelii schlegelii* MCZ 29174.
Fig. 9. *Typhlops blanfordi lestradei* MCZ 48077.



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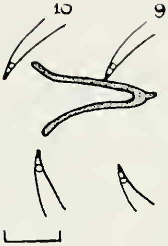

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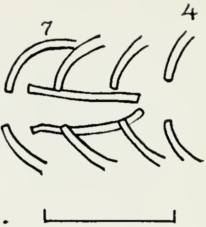

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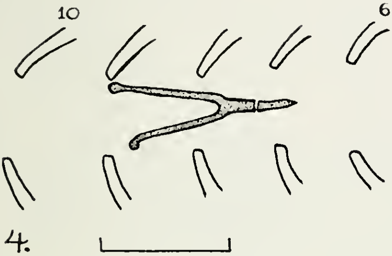

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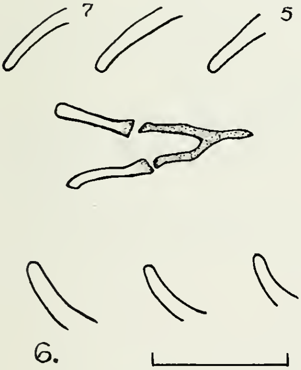

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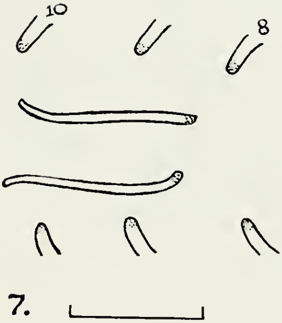

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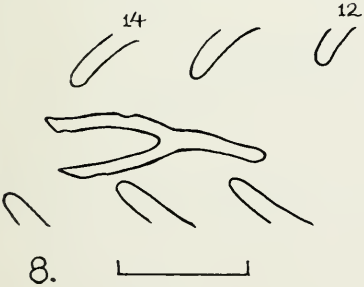

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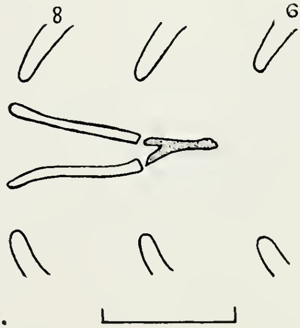
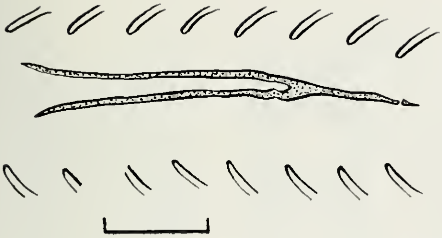


9.

PLATE 16

Hyobranchia and adjacent rib tips, ventral view.

Fig. 1. *Leptotyphlops humilis humilis* JCL 1025.
Fig. 2. *Leptotyphlops nigricans* MCZ 21473.
Fig. 3. *Leptotyphlops dulcis dissectus* USNM 99821.
Fig. 4. *Leptotyphlops emini* CNHM 56374.
Fig. 5. *Leptotyphlops humilis cahuilae* JCL 1000.
Fig. 6. *Leptotyphlops magnamaculata* CNHM 87.
Fig. 7. *Leptotyphlops phenops* CNHM 36345.
Fig. 8. *Leptotyphlops maximus* UIMNH 34999.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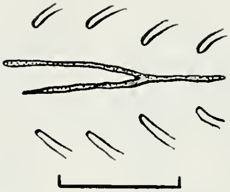
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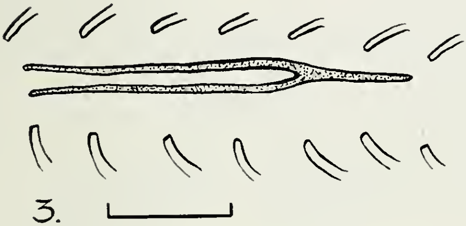
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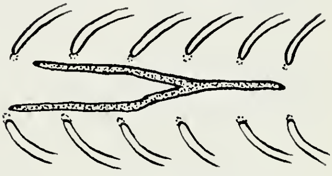
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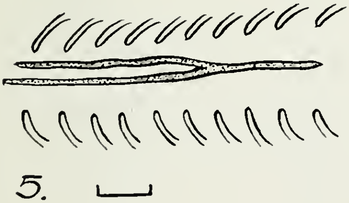
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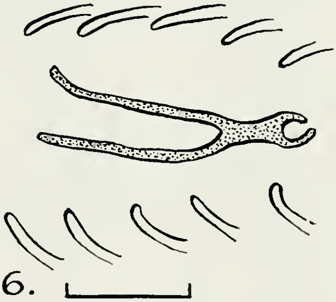
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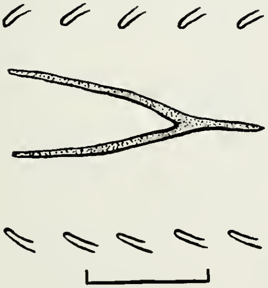
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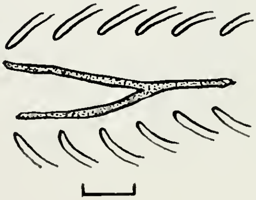
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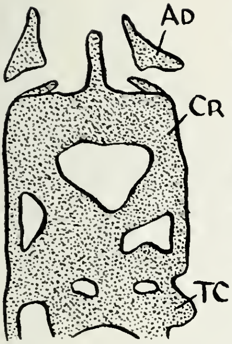
Plate 17

Laryngeal cartilages (Figs. 1–4); laryngeal and tracheal cartilages and hyobranchium (Figs. 5–8); ventral views.

Figs. 1 and 5. *Typhlops reticulatus* CNHM 35592.
Figs. 2 and 6. *Typhlops polygrammicus* JCL 1017.
Figs. 3 and 7. *Liotyphlops albirostris* USNM 61989.
Figs. 4 and 8. *Leptotyphlops humilis humilis* JCL 1020.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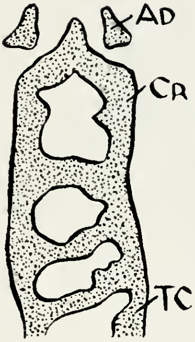
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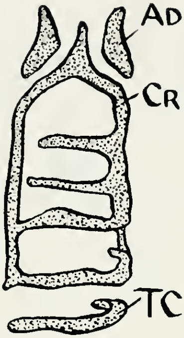
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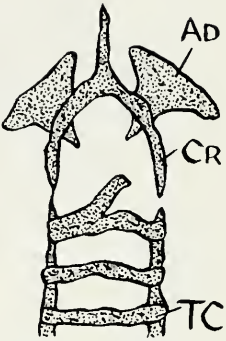
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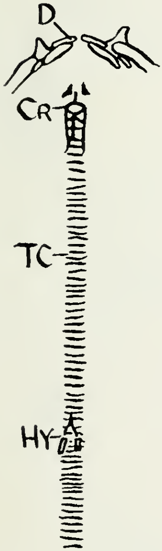
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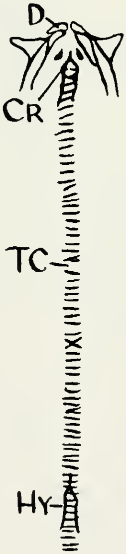
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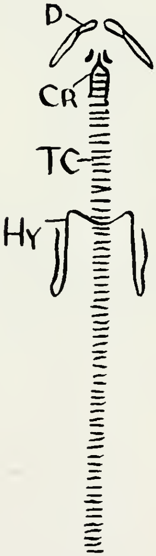
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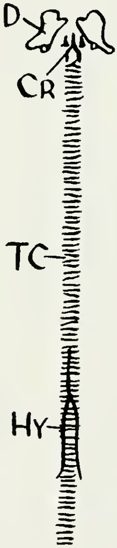
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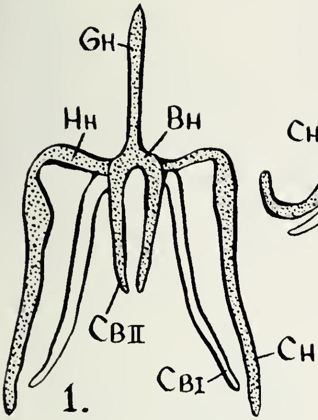
8.

PLATE 18

Saurian and ophidian hyobranchia. Figs. 1–3 and 5–7 after Cope, 1900.

Fig. 1. *Sauromalus ater.*
Fig. 2. *Ctenosaura teres.*
Fig. 3. *Xenosaurus grandis.*
Fig. 4. *Liotyphlops albirostris* USNM 61989.
Fig. 5. *Anguis fragilis.*
Fig. 6. *Rhineura floridana.*
Fig. 7. *Anniella pulchra.*
Fig. 8. *Typhlops platycephalus* MCZ 38337.
Fig. 9. *Typhlops lehneri* MCZ 48929.
Fig. 10. *Typhlops lumbricalis* USNM 66887.
Fig. 11. *Leptotyphlops bakewelli* USNM 25242.
Fig. 12. *Thamnophis radix.*



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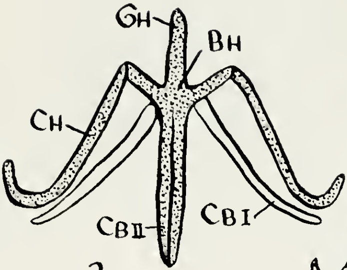

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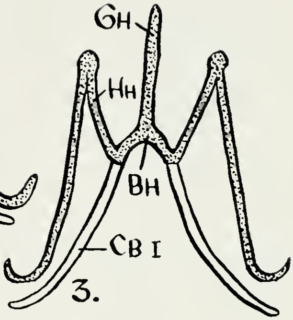

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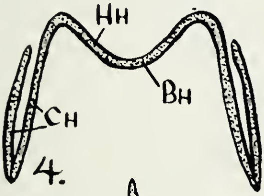

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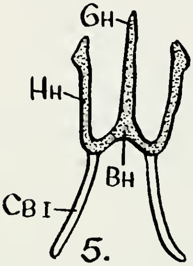

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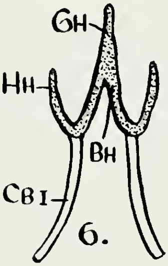

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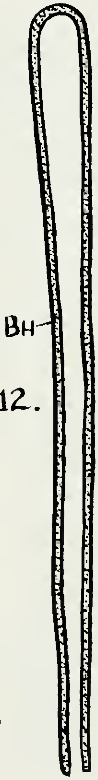

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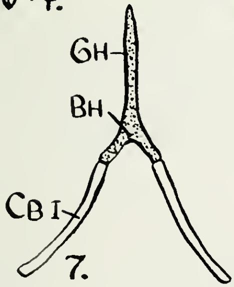

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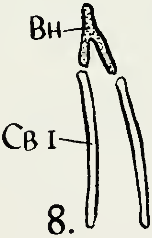

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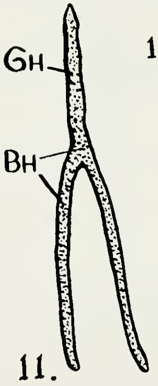

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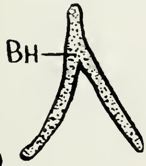

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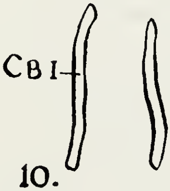
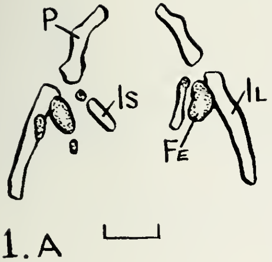


10.

PLATE 19

Pelvic girdles and adjacent ribs.

Fig. 1. *Leptotyphlops dulcis dissectus* MCZ 39681.
Fig. 2. *Leptotyphlops bakewelli* USNM 25242.
Fig. 3. *Typhlops platycephalus* MCZ 38337.
Fig. 4. *Liotyphlops albirostris* USNM 61989.
Fig. 5. *Typhlops rostellatus* MCZ 38370.
Fig. 6. *Typhlops richardi* MCZ 38350.
Fig. 7. *Typhlops lumbricalis* USNM 66887.
Fig. 8. *Typhlops lineatus* JCL 1013.
Fig. 9. *Typhlops lehneri* MCZ 48929.
A. Ventral.
B. Right side.



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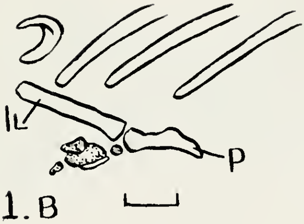

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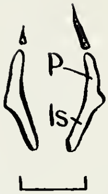

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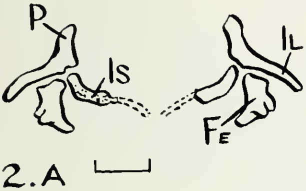

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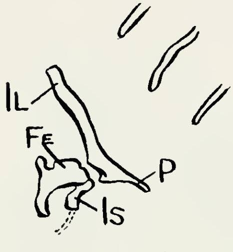

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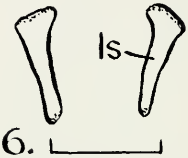

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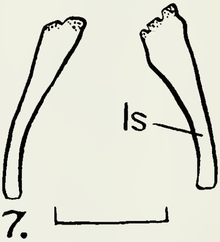

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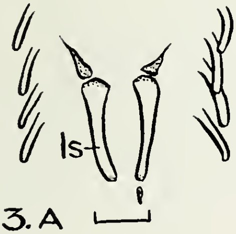

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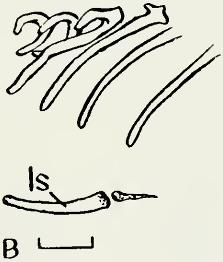

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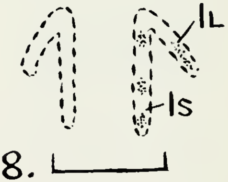

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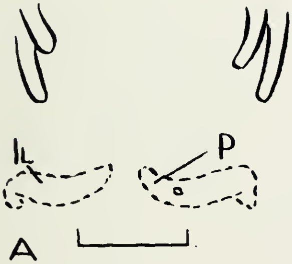

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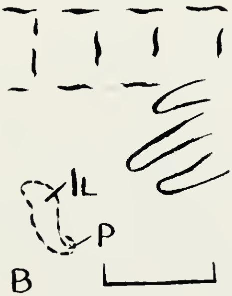

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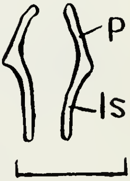


9.

Plate 20

Pelvic girdles and adjacent ribs.

Fig. 1. *Leptotyphlops humilis cahuilae* JCL 1000.

Fig. 2. *Leptotyphlops magnamaculata* CNHM 87.

Fig. 3. *Leptotyphlops dulcis dissectus* USNM 99821.

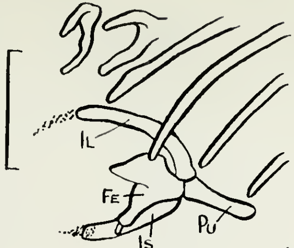
Fig. 4. *Leptotyphlops emini* CNHM 56374.

Fig. 5. *Leptotyphlops nigricans* MCZ 21473.

Fig. 6. *Leptotyphlops maximus* UIMNH 34999.

A. Right side.

B. Ventral.



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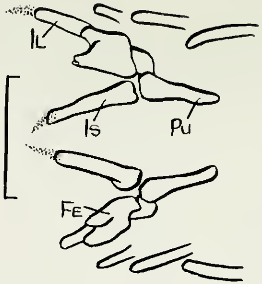

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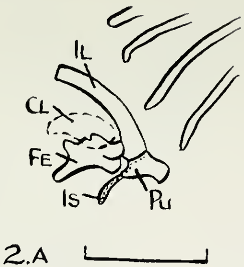

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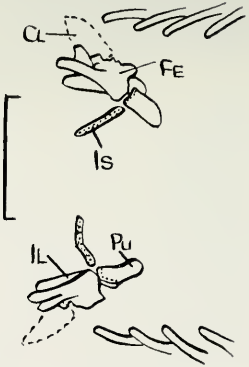

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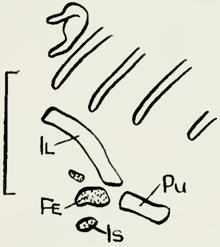

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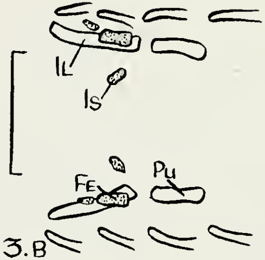

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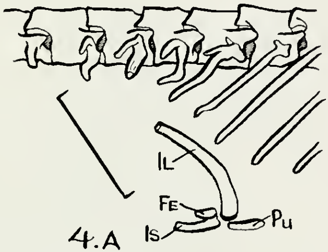

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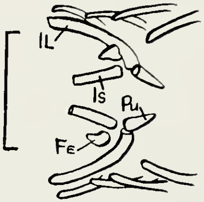

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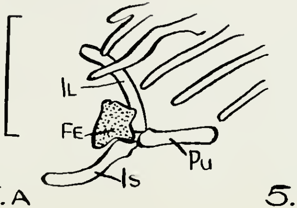

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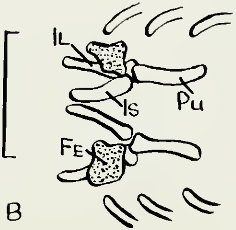

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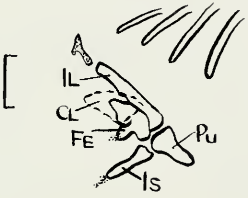

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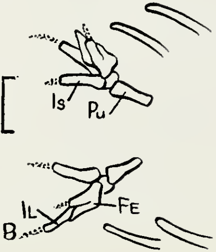


6.B

PLATE 21

Pelvic girdles and adjacent ribs.

Fig. 1. *Typhlops boettgeri* JCL 1014.

Fig. 2. *Typhlops pusillus* MCZ 8758.

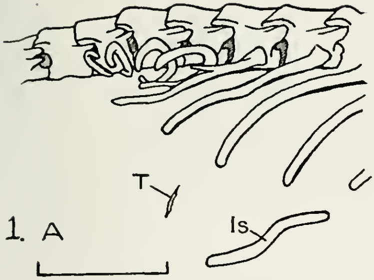
Fig. 3. *Typhlops braminus* JCL 1022.

Fig. 4. *Typhlops polygrammicus* JCL 1018.

Fig. 5. *Typhlops vermicularis* CNHM 28572.

A. Right side.

B. Ventral.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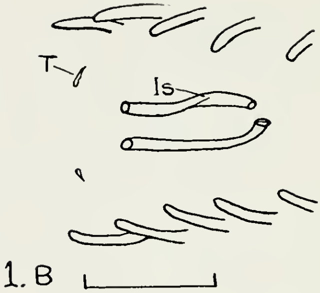
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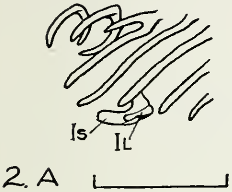
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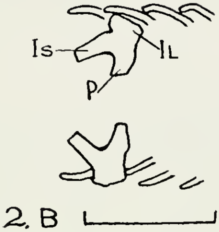
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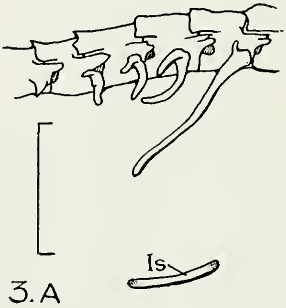
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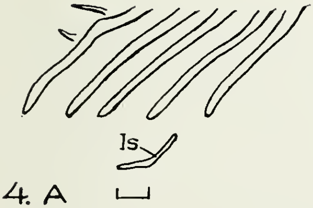
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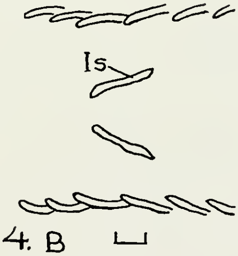
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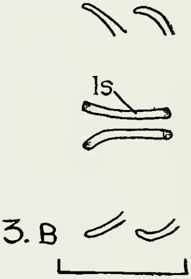
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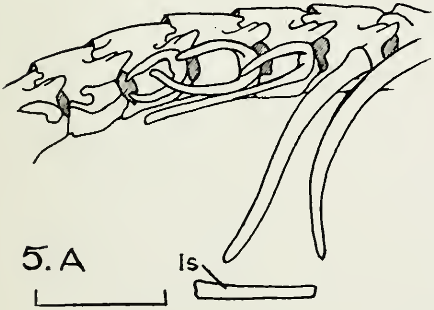

5. A

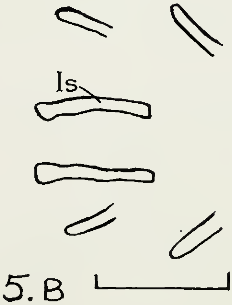
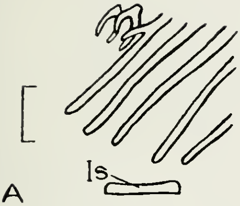

5. B

Plate 22

Pelvic girdles and adjacent ribs.

Fig. 1. *Typhlops blanfordi lestradei* MCZ 48077.
Fig. 2. *Typhlops schlegelii mucruso* MCZ 30058.
Fig. 3. *Typhlops schlegelii schlegelii* MCZ 29174.
Fig. 4. *Typhlops reticulatus* CNHM 35592.
A. Right side.
B. Ventral.



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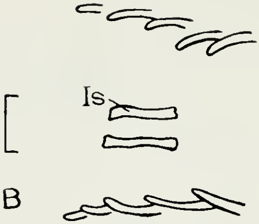

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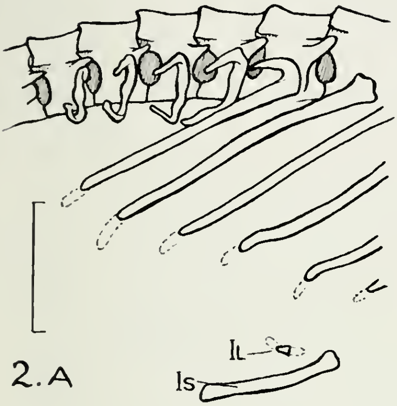

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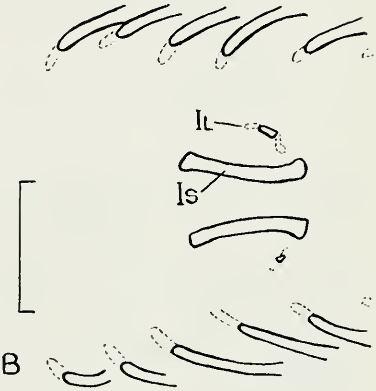

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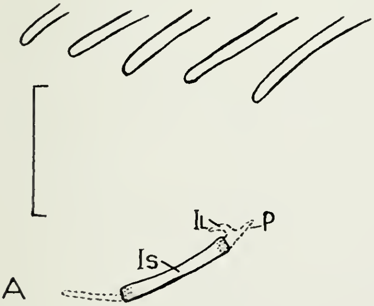

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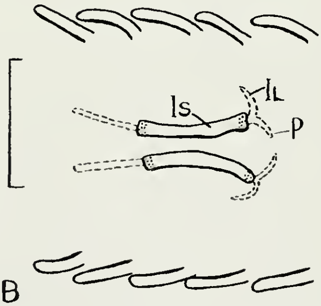
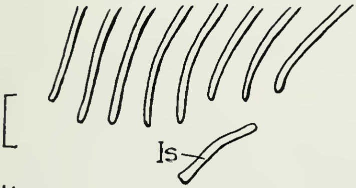
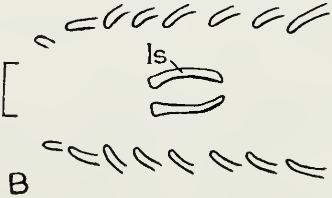


3. B



4. A



4. B

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MATERIALS EXAMINED

Museums or collections are indicated by the following abbreviations: CNHM, Chicago Natural History Museum; JCL, James C. List, private collection; MCZ, Museum of Comparative Zoology, Harvard; UIMNH, University of Illinois Museum of Natural History, Urbana; USNM, United States National Museum, Washington, D.C.

Leptotyphlops albifrons USNM 25243, Nicaragua.
" *bakewelli* USNM 25242, Nicaragua.
" *conjuncta* JCL 1015, Smithfield, Transvaal.
" *dulcis dissectus* MCZ 39681, Tulsa, Oklahoma.
" " " USNM 99821, Lake City, Kansas.
" " " USNM 99822, " " "
" " " USNM 99823, " " "
" *emini* CNHM 56374, Belgian Congo.
" *humilis cahuilae* JCL 1000, Imperial Co., Calif.
" " " JCL 1026, " " "
" " *humilis* JCL 1020, San Diego Co., "
" " " JCL 1023, " " " "
" " " JCL 1024, " " " "
" " " JCL 1025, " " " "
" " *segregus* USNM 17017, Tucson, Arizona.
" " " USNM 17015, " "
" " " USNM 17016, " "
" *longicauda* MCZ 40116, Ngatana, Kenya.
" *magnamaculata* CNHM 87, Old Providence Island, West Indies.
" *maximus* UIMNH 34999, Guerrero, Mexico.
" *nigricans* MCZ 21473, Grahamstown, South Africa.
" *phenops* CNHM 36345, Yucatan, Mexico.
" " CNHM 20606, " "
Liotyphlops albirostris USNM 61989, Panama.
" " MCZ 31541, Chiriqui, Panama.
Typhlops ater JCL 1006, Soa Konorra, Halmahera.
" *blanfordi lestradei* MCZ 48077, Mushungero, S.W. Uganda.
" *boettgeri* JCL 1014, Majunga, W. Madagascar.
" *braminus* USNM 72319, Bangkok, Thailand.
" " USNM 78164, Silay, Philippine Islands.
" " USNM 80575, Victorias, " "
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" " CNHM 53270, Mindanao, " "
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" " JCL 1003, Majunga, Madagascar.
" " JCL 1021, Miyanapalava, Ceylon.
" " JCL 1022, Dadanduwa, "
" *flaviventer* JCL 1012, Soa Konorra, Halmahera.
" *jamaicensis* MCZ 7370, Kingston, Jamaica.
" *lehneri* MCZ 48929, Acosta District, Venezuela.
" *lineatus* JCL 1002, no data.
" " JCL 1013, Buitenzorg, Java.
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" *lumbricalis* JCL 1007, Havana, Cuba.
" " MCZ 22279, Soledad, "
" " USNM 66887, Santo Domingo.
" *microstomus* CNHM 36347, Yucatan, Mexico.

Typhlops platycephalus CNHM 38581, Rio Piedras, Puerto Rico.
" " MCZ 38337, Canovenas, " "
" " USNM 27324, Bayamon, " "
" " USNM 29364, Mayaguez, " "
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" " JCL 1018, no data.
" " JCL 1019, no data.
" *punctatus* CNHM 58351, Katire, Anglo-Egyptian Sudan.
" " CNHM 21082, Sangmelina, Cameroons.
" " MCZ 7843, Kribi, "
" " JCL 1009, Duala, "
" " JCL 1010, " "
" *pusillus* MCZ 8758, Ennery, Haiti.
" *reticulatus* CNHM 35592, Santo Cruz, Bolivia.
" *richardi* MCZ 38350, Tortola Island.
" *rostellatus* MCZ 38370, Canovanas, Puerto Rico.
" *schlegelii mucruso* CNHM 52900, Anglo-Egyptian Sudan.
" " " MCZ 30058, Mwaya, Tanganyika.
" " " JCL 1008, Cubal, Angola.
" " *schlegelii* MCZ 29174, S. Rhodesia.
" *simoni* JCL 1011, Haiffa, Israel.
" *vermicularis* CNHM 28572, Benyamina, Israel.

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