

THE SYSTEMATIC POSITION  
OF  
*LANTHANOTUS*  
AND THE  
AFFINITIES OF THE  
ANGUINOMORPHAN LIZARDS

SAMUEL BOOKER MCDOWELL, JR., AND  
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## INTRODUCTION

THE PRESENT COLLABORATIVE WORK on *Lanthanotus* grew out of researches by the junior author. The junior author, while engaged in a study of geographic variation in the American beaded lizards (*Heloderma*), obtained permission from Mr. Arthur Loveridge to extract and examine the skull of a specimen of *Lanthanotus* in the Museum of Comparative Zoölogy of Harvard College. At that time it was expected that the Bornean lizard, usually referred to the Helodermatidae, would be similar in essential features to the American *Heloderma*, and the only question then in mind was exactly how close the presumed special affinity might be.

But even cursory examination of the external features of *Lanthanotus* showed the Bornean lizard to be very distinct from *Heloderma*, although curiously similar to *Varanus* in many features, such as absence of large transverse scutes beneath the digits and presence of small, pustule-like "scale pits" on the dorsal surface. Examination of the skull and tongue revealed numerous important features in which *Lanthanotus* differs not only from *Heloderma* but from all other living lizards. So different, in fact, is *Lanthanotus* from other lizards that the exact affinities of the Bornean lizard present a considerable question. In the effort to answer this question the authors have made extensive comparisons between possible relatives, and it is the result of these comparisons that is here presented.

In our studies we have relied principally on comparison of skulls, tongues, and external features. This restriction has been imposed both by the nature of our data on *Lanthanotus* and by the fact that many of the related families are known only from fossilized skeletons. In our study we have worked on the assumption that an intensive study of such a complex and plastic structure as the skull gives a sampling of the phenotypic effects of a sufficiently large number of genes to allow conclusions on at least the broader aspects of phylogeny.

Restricted as have been our comparisons, the present authors have perhaps examined as many variable structures as have any

previous workers on the phylogeny of lizards. The earlier classifications of Gray, Duméril and Bibron, and Wagler were based almost entirely on the tongue and dentition. Cope introduced into the field the variations of the skeleton, and his system was adopted with relatively minor modification by Boulenger. But even Cope and Boulenger, although vastly increasing the scope of research beyond that of their predecessors, utilized but a small number of skeletal parts in their comparisons, laying particular importance on such features as the form of the clavicles, interclavicles, and frontals, the nature of the temporal fossae, and the median sutures of the skull.

Camp introduced numerous variables from the "soft anatomy," such as throat musculature, abdominal musculature, and correspondence of scales with metamerism, as well as emphasizing the tongue and hemipenis, previously used by Cope. Perhaps the major innovation in Camp's classification was his method of interpretation. While previous workers had attempted to find characters constant for a given group, and limited themselves to working only with these "conservative" or "phylogenetic" characters, Camp in many cases made skillful use of "adaptive" characters, characters that are of variable occurrence within a group but none the less may give valuable hints on the relationships of that group.

Since the publication of Camp's classification there have been no major innovations in the classification of lizards. The classification used by Romer (1945) is essentially a revamping of Camp's classification to fit the conventional taxonomic hierarchy with but slight change in allocation of groups.

At the present time, there is much need for a revised classification of the entire Squamata, a project that would require a careful study of the anatomy of more different species than have been examined by workers up to this time. Moreover, in recent years much intensive work has been done on special organ systems of squamates, which already is throwing new light on old problems of squamate phylogeny. The work of Walls,

Underwood, and Rochon-Duvigneaud on the eye, of Bellairs and Boyd on the nasal region, of Haas on the head musculature, and of the South African school on the structure of the head as revealed by the microtome all offer

new morphological variables for the use of the worker on squamatan phylogeny. It is hoped that in the near future these new data will be incorporated into the taxonomy of the lizards and snakes.

## THE EARLESS MONITOR, *LANTHANOTUS BORNEENSIS* STEINDACHNER

*Lanthanotus* WAS DESCRIBED in 1878 from a specimen from Sarawak. Few specimens have since been reported, and in the present year, 76 years after the publication of Steindachner's description, *Lanthanotus* remains one of the rarest of reptiles in collections. This has been particularly unfortunate, for it has become a zoogeographic puzzle and the basis of considerable speculation, while its rarity in collections has prevented confronting speculation with solid fact. The zoogeographical puzzle of *Lanthanotus* is created by

the considerable superficial resemblance of the Bornean lizard to the beaded lizards (*Heloderma*) of the southwestern United States and northern Middle America.

Through the most generous courtesy of Mr. Arthur Loveridge of the Museum of Comparative Zoölogy, the present authors have had opportunity to study the external features of this remarkable lizard, and to remove the skull and tongue for anatomical study and comparisons with other lizards. The results of these comparisons are presented here.

### GENERAL DESCRIPTION

#### EXTERNAL APPEARANCE

The original description of *Lanthanotus* by Steindachner (1878) now appears quite oldfashioned for the reason that it is accompanied by an illustration of excellent quality, not only from the standpoint of scientific accuracy, but from an esthetic standpoint as well. This illustration is reproduced here as plate 1 and gives a much better presentation of the external features of the earless monitor than could any verbal description.

As will be seen from Steindachner's illustration, the body is elongated and slightly depressed in form, the neck of about average length for a lizard, but rather stout. The head is rather small and only moderately distinct from the neck and about equal to the neck in length. The head is depressed in form, with rounded contours, and without a flat dorsal table. The tail is nearly circular in cross section and only slightly longer than the head and body. An interesting point to be noted in Steindachner's illustration is that the tip of the tail appears to be capped by a blunt scar. This suggests (but does not prove) that *Lanthanotus*, like *Heloderma*, *Varanus*, the amphisbaenids, and the snakes, is incapable of regenerating the damaged tail.<sup>1</sup>

<sup>1</sup> Dr. John Hendrickson, of Singapore, has since informed us that a specimen of *Lanthanotus* in the Raffles Museum has the tip of the tail blunted and healed over with scar tissue, showing more or less definitely that *Lanthanotus* does not regenerate the tail.

The limbs are short and nearly equal, and both the manus and pes are pentadactyl. The appressed manus and pes are separated from each other by a considerable interval, an indication of the shortness of the limbs and the lengthening of the body. The digits are short and thick, without thickening at the phalangeal articulations, and bear short and rather feeble claws. The second, third, and fourth digits are subequal.

The nostrils are small, widely separated from each other and from the tip of the snout, rather dorsal in position. The lips are thick and probably glandular. The muzzle is blunt and rounded. There is a mental groove. The eye is rather small and provided with both upper and lower lid. The lower lid is unusual in being provided with a transparent window, as in *Cabrita*, *Macroscincus*, and some other genera. There is no trace of an external ear. The gular fold is absent.

The muzzle is covered with small granular scales without differentiation into labials, nasals, loreals, or other plates, and there is no rostral. The other scales of the head are slightly larger, while across the temples there extend about three longitudinal rows of enlarged tubercles. In spite of de Rooij's (1915, p. 137) statement to the contrary, these tubercles contain osteoderms. On the body we find three pairs of longitudinal rows of similar enlarged tubercles. These tubercles are opaque to X-rays and probably contain osteoderms. On the sides of the body, just

dorsal to the enlarged belly scales, there are two or three irregular rows of tubercles that extend from the axilla to the groin. The tubercle rows of the body, except for the row lateral to the dorsal row, are continued on the tail to the tip. The anterior limb is without tubercles, but there are a double row on the posterior face of the thigh and a single fibular row. The under surface of the body and tail is covered with regular transverse rows of enlarged, flat, feebly imbricate, rectangular scales. There is no anal scale differentiation.

When examined under magnification (see pl. 2) each tubercle may be seen to be surmounted by a large scale that does not cover the tubercle. The remainder of the tubercle is covered by tiny granules. The large scale is bluntly keeled and bears numerous tiny, pustule-like "scale pits." The granules are

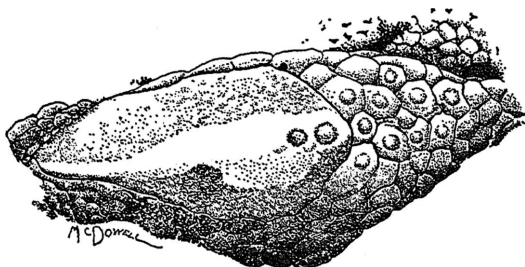


FIG. 1. *Lathanotus borneensis*. One enlarged crestal and surrounding granules, showing the pustule-like organs on the scales. Drawing by McDowell.

hemispherical in form, and many bear each a single "scale pit." The skin between the rows of large tubercles is corrugated into a mass of numerous small tubercles, each tubercle covered with many small granular scales. The under surface of the toes is covered with small granules.

The color (in the alcoholic specimen) is a warm reddish earth-brown above, fading to ocher on the ventral surface. The ventral surface is obscurely mottled and striped with burnt sienna.

#### TONGUE

The tongue is deeply incised terminally, forming two very acute anterior tines (see fig. 29). The organ is divided into two portions, the elongated, narrow, and inelastic fore tongue, and the wide and sheath-like hind

tongue. The fore tongue is smooth, but the hind tongue is covered with long and closely packed papillae. The division into fore tongue and hind tongue is made by a sharp transverse fold. The fore tongue is not connected to the floor of the mouth by a frenum, but the hind tongue is broadly joined to the floor of the buccal cavity.

#### SKULL

The details of skull structure are discussed below in the comparative section of this paper. Therefore, we give but a brief and general account of the skull here.

The skull is blunt anteriorly, with a relatively short muzzle and an elongated brain case, and is depressed. The following measurements may give a better description of the general proportions:

Condylbasal length (from anteriormost point of premaxilla to tip of occipital condyle)	23.5 mm.
Facial length (from anteriormost point of premaxilla to frontoparietal suture)	12.8
Median cranial length (from middle of frontoparietal suture to upper margin of foramen magnum)	11.2
Lateral cranial length (from right extremity of frontoparietal suture to tip of right paroccipital process)	12.8
Width across malar eminences	10.4
Preorbital width	8.0
Prenarial width	6.4
Interorbital width (width of roof of skull between orbits at narrowest point)	4.9
Minimum cranial width (width of brain case at narrowest point)	5.0
Paroccipital width (width of skull at tips of paroccipital processes)	11.2
Quadratic width (width of skull across most prominent parts of quadrate bones)	14.0
Depth (measured at epipterygoid in the skull without lower jaw)	5.7
Mandibular length (length, as taken by calipers, of lower jaw from symphysis to tip of right postarticular process)	22.6
Coronoid depth (depth of lower jaw at apex of coronoid process)	4.5

The external naris is very large and prolonged backward by a slit separating the nasal from the prefrontal and maxilla, having

a comma-like shape. The naris is bordered by the premaxilla, nasal, a small portion of the frontal, the prefrontal, and maxilla. It contains a large septomaxillary bone. The orbit is elliptical and directed somewhat dorsally.

the vomers and palatines. There is a lozenge-shaped suborbital fenestra that is bordered by the palatine, pterygoid, and ectopterygoid, but not by the maxilla. The internal naris is long and narrow and is bor-

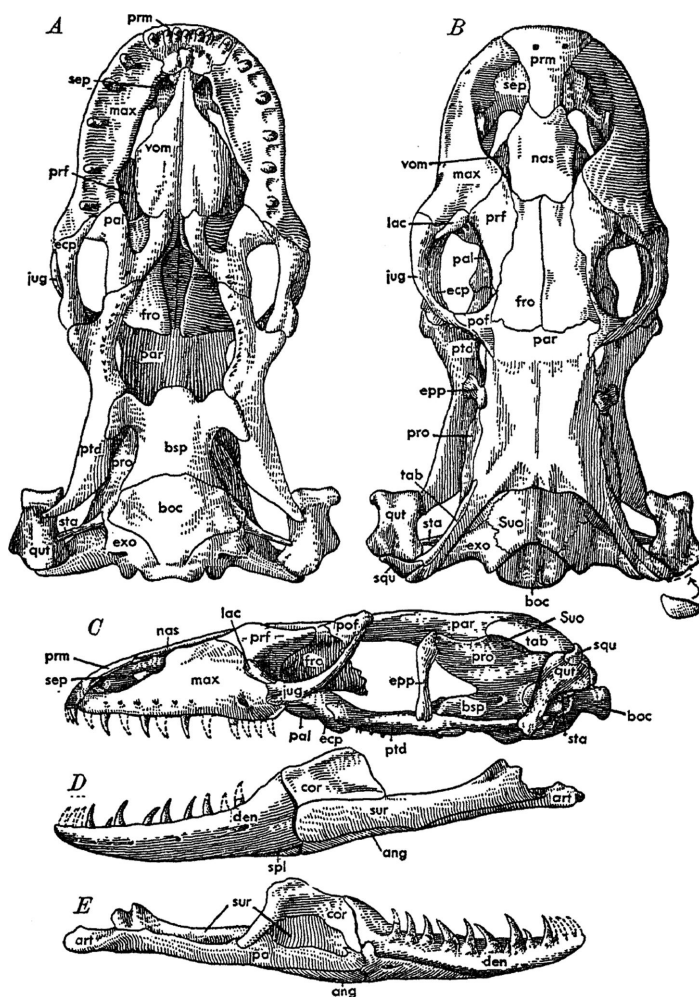


FIG. 2. *Lanthanotus borneensis*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell.

It is bordered externally by the postfrontal, jugal, lacrimal, prefrontal, and a tiny portion of the frontal. Internally it is walled off from the nasal chamber by the prefrontal and palatine. The orbits are separated from each other by the very large descending processes of the frontals, which meet ventrally with

dered by the maxilla, palatine, vomer, and septomaxilla. The interpterygoid vacuity is very large, wide, and miter-shaped and is bordered by the palatines, pterygoids, and sphenoid, but not by the vomers. Like the suborbital fenestra, the interpterygoid vacuity is continuous with the orbital chamber.

The temporal fossa is continuous anteriorly with the orbital chamber, ventrally with the interpterygoid vacuity and the posterior pterygocranial vacuity, and posteriorly with the lateral occipital fenestra. *Lanthanotus* lacks the upper temporal arch, and in consequence the squamosal bone is reduced to a small ossicle attached to the dorsal surface of the quadrate and not bordering the temporal fossa. The temporal fossa, which actually represents the combined superior temporal fossa and inferior temporal emargination of most other lizards, is bordered by the ectopterygoid (narrowly), the jugal, parietal, tabular (supratemporal of some authors), and quadrate. As in other Squamata, the fossa is undefined ventrally, the jugal-quadratojugal bar being absent. *Lanthanotus* is unusual in that neither the postfrontal nor the postorbital borders the temporal fossa, being excluded by the enlarged jugal. Quite possibly the jugal of *Lanthanotus* is a compound bone, representing the fusion of the normal jugal with the postorbital, a bone otherwise absent in *Lanthanotus*.

The postorbital arch is complete and formed by the postfrontal and (possibly compound) jugal.

The posterior craniopterygoid vacuity is bordered anteriorly by the basiptyergoid process of the sphenoid, laterally by the pterygoid, posteriorly by the quadrate and paroccipital process of the exoccipital, medially by the exoccipital, basioccipital, and sphenoid. It is traversed posteriorly by the stapes, which runs from the fenestra ovalis to the quadrate. The lateral occipital fenestra is small and narrowly elliptical. It is bordered by the parietal, pro-otic, and paroccipital process of the exoccipital.

The lower jaw is relatively straight, without the marked sigmoid flexure usual in lizards. The postarticular process for the depressor mandibularis is relatively short, being no longer than the articular cotyle for the quadrate. The coronoid process is high but longitudinally produced and blunt. On the inner side of the jaw, posterior to the coronoid, there is a deep fossa, as in most lizards, between the prearticular and surangular. This fossa lodges the foramen for the mandibular nerves and blood vessels. The splenial is separated from the dentary

almost completely by the open Meckelian groove.

The most notable feature of the lower jaw is the presence of a vertical hinge in the central portion of the ramus. This hinge is indicated laterally by a deep vertical suture between the dentary anteriorly and the coronoid and surangular posteriorly; medially it is indicated by a suture of corresponding position between the dentary and splenial anteriorly and the coronoid, prearticular, and angular posteriorly.

Teeth are present on the premaxillary, maxillary, palatine, and pterygoid, as well as on the dentary. The marginal teeth (premaxillary, maxillary, and dentary) are recurved and fang-like without grooves, except for a fine vertical fluting at the base, and with very small medullary foramen. The tooth emplacement is of the pleurodont type. Tooth replacement is alternate.

The premaxillary bones are fused and have long ascending internarial laminae which meet the nasals. The nasals are fused. The frontals are separate and almost excluded from the orbits by the prefrontal and postfrontal. These latter two bones meet, but a small isolated extension of the frontal forms part of the orbital margin. The parietals are fused, and there is no pineal foramen. The parietals have long posterolateral processes that run back, median to the tabulars, towards the dorsal heads of the quadrates. The supraoccipital is median and nearly horizontal, lying on the dorsal surface of the skull.

The prefrontals are large and overlapped anteriorly by the maxillae. They bear an angulated crest around their orbital rim. The jugal is simply arc-shaped, and runs up to meet or nearly meet the parietal dorsally behind the postfrontal. The postfrontal is triangular in form. The lacrimal is simple and without an orbital flange. The lacrimal foramen is double.

The vomers are dilated laterally and triangular in form. The palatines are triradiate, with an antero-internal vomerine process, an antero-external maxillary process, and a posterior pterygoid process. The ectopterygoid is simple and enters the lateral border of the skull anteriorly. The pterygoid is triradiate, with an antero-internal palatine process, an antero-external ectopterygoid process, and a

dilated posterior quadrate process.

The brain case is long and well closed posteriorly, since the pro-otic is a large element, with its entire dorsal border pressed against the lateroventral border of the parietal. There is a rather short epipterygoid bone, which articulates dorsally with the elongate anterior process of the pro-otic. The tabular is large. The quadrate is inclined forward ventrally and provided with but a slight ridge-like external conch.

The bones of the lower jaw are all quite distinct from one another. The dentary is short and bow-shaped and is joined to its fellow at the symphysis by strong ligaments. The splenial is confined to the inner surface of the jaw. The angular is but narrowly exposed laterally. The prearticular and coronoid are sutured together anteriorly to exclude the splenial from the surangular. The ventral margin of the medial surface of the coronoid is deeply excavated to expose the surangular.

#### POST-CRANIAL SKELETON

The axis bears a strong odontoid peg and has a large and hatchet-shaped neural spine. Ventrally it bears two hypapophyses, arranged in tandem. For the remainder of the post-cranial skeleton we must depend on the roentgenograms (pl. 4, figs. 2 and 3). These roentgenograms were prepared after the re-

moval of the skull, hyoid, and first two vertebrae; vertebral counts must therefore be altered from those apparent in the roentgenograms to take into account the atlas and axis. The vertebral count appears to be:

Cervical (without a rib connected to the sternum)	9
Anterior thoracic (with sternal ribs)	3
Posterior thoracic (with ribs not reaching sternum)	23
Lumbar (without movable ribs)	1
Sacral (with parapophyses attached to ilium)	2
Caudal	68

There are six pairs of cervical ribs. Abdominal ribs appear to be present, but their exact number cannot be counted.

In the shoulder girdle, the clavicle is thin, sigmoidally curved, and undilated. The interclavicle appears to lack transverse processes. The scapula bears a single anterior emargination, the coracoid two, as well as the preglenoid foramen. The phalangeal formula of the manus is 2-3-4-4-3.

The pelvis is typically lacertilian, with dorsal backwardly inclined ilia, ventro-anterior pubes, and ventroposterior ischia. The pubic symphysis is broadly separated from the ischiadic symphysis. The pectineal process of the pubis is very slight. There is a pubic foramen. The phalangeal formula of the pes is 2-3-4-4-3.

### *LANTHANOTUS* COMPARED WITH *SHINISAURUS*

#### HISTORICAL RÉSUMÉ

That *Lanthanotus* might be closely allied to *Shinisaurus* was first suggested by Nopcsa (1932). The monotypic genus *Shinisaurus*, as well as the species, *crocodilurus*, had been described two years previously by Ahl (1930) on the basis of specimens from Kwangsi, southern China. Although Ahl was ignorant of the morphology of the lizard, aside from external features, tongue, and dentition, the odd appearance of *Shinisaurus* led him to erect for it a monotypic family, the Shinisauridae. Since then, Fan (1931) has redescribed *Shinisaurus* and presented photographs, as well as other important information. Nopcsa's short paper dealt with the putative affinities of *Shinisaurus* and *Lan-*

*thanotus* and was based on a comparison of roentgenograms of the two forms and on external appearance. Darlington (1948) appears to be the most recent authority to touch on the relationships of this peculiar reptile, and notes (p. 120) that "Another lizard, *Shinisaurus*, rather recently discovered, and known only from the mountainous Yaoshan region of eastern Kwangsi in southern China, is now placed in a family by itself, but, as Loveridge has shown me, it resembles *Lanthanotus* and may be related to it."

The American Museum of Natural History possesses a specimen of *Shinisaurus* (A.M.N.H. No. 44928) from Yaoshan. Dr. Georg Haas has dissected the head musculature on the specimen, and an unfortunately

rather poorly preserved eye has been sent to Mr. Garth Underwood for examination. The skull, prepared from the remainder of the head, is discussed in this paper. Dr. Haas and Mr. Underwood will present their findings separately.

#### COMPARISONS

**EXTERNAL FEATURES:** *Shinisaurus* shows some resemblance to *Lanthanotus* in general form and lepidosis. Both animals are of medium size, as far as lizards are concerned,

structures involved. In *Lanthanotus* the external ear is, in truth, lacking, and the scales of the side of the head are continued back on the side of the neck without interruption or unconformity. In *Shinisaurus*, as in the Mexican *Xenosaurus*, the tympanum is present but covered by finely granular skin, its anterior margin being demarcated by enlarged tubercular scales, while the posterior border is less definitely marked off by enlarged granules. The presence of the mesotic cavity beneath the tympanum imparts a

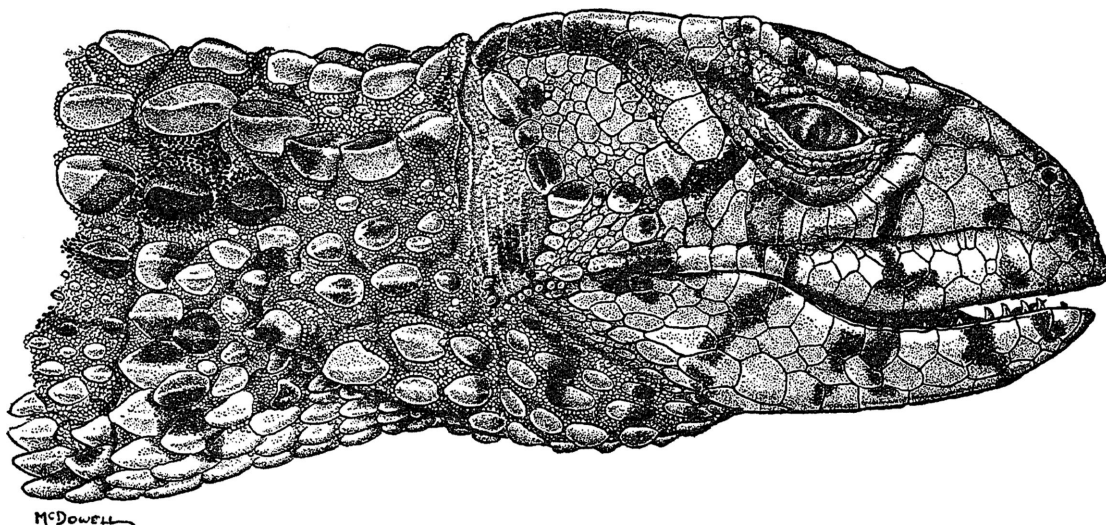


FIG. 3. *Shinisaurus crocodilurus*. Much enlarged. Yaoshan, Kwangsi, China.

with the tail longer than the body, without a noticeable gular fold, without exposed tympanum, with a neck somewhat longer than average for a lizard, and with large keeled scales mixed with the smaller scales of the dorsal surface to form a double crest down the middle of the back that continues along the dorsal surface of the tail. In both there is a double lateral row of enlarged scales extending from groin to axilla, with some suggestion of its presence on the side of the neck. Moreover, both lizards have pustule-like organs (possibly of tactile function) on the large lateral scales, and in each these organs are arranged in longitudinal series on the scale.

But on closer inspection the external similarities appear to be outweighed by the differences. Whereas the ear is obscured in both, there are noteworthy differences in the

translucence to the skin in that region, a translucence that appears as a bluish discoloration in the preserved specimen. All this is as in *Xenosaurus*, save that in that genus the tympanic region is comma-shaped, while in *Shinisaurus* the region is in the form of a narrow vertical rectangle.

The lower eyelid of *Lanthanotus* is provided with a transparent window, but this is not even remotely suggested in the lower lid of *Shinisaurus*. While the head of *Lanthanotus* is long, flattened, bulging at the temples, with smoothly rounded contours throughout, that of *Shinisaurus* is short, deep, and compressed, with flat temples, a strongly arched dorsal profile to the muzzle, and with an obtusely angulate canthus rostralis and a right angle between the flat and vertical temple and the flat and horizontal dorsal cranial table. Whereas the nostrils of

*Lanthanotus* are widely separated from each other and from the tip of the muzzle, the nostrils of *Shinisaurus* are placed near the tip of the muzzle and not widely separated.

In the lepidosis of the head *Shinisaurus* shows marked departure from the condition in *Lanthanotus*, but bears considerable resemblance to that of *Xenosaurus*. Although the Chinese lizard (like the Mexican *Xenosaurus*) does not show the large regular head scutes of the Anguinidae, there are enlarged labial scutes, a rostral, canthals, enlarged supraoculars, a distinct row of small median supraoculars that completely bound the semicircular medial border of the enlarged supraocular series, and there is a parietal plate. In all these details *Shinisaurus* agrees with *Xenosaurus* and is quite different from *Lanthanotus*. For in the latter form the lips are bordered by minute granular scales, scales that are actually smaller than the surrounding head scales. In *Lanthanotus* there is no trace of a rostral, nor are there any specialized canthals, while the scales over the eye are small, in numerous longitudinal series, and arranged in nearly straight longitudinal rows, without trace of differentiation into supraoculars. As might be expected in a form lacking a pineal foramen in the skull, *Lanthanotus* is devoid of a parietal scale.

In *Shinisaurus* the torso is shorter, and the limbs are longer, than in *Lanthanotus*, so that in the former genus the appressed fore limb and hind limb overlap, while in *Lanthanotus* the longest finger fails to meet the longest toe. The digits of *Lanthanotus* are much shorter and stouter than are those of *Shinisaurus*, and are covered ventrally by granular scales, while those of *Shinisaurus* are covered ventrally by a single row of transversely enlarged scutes.

Even in the arrangement of tactile organs there is an important difference between *Lanthanotus* and *Shinisaurus*. In the latter genus these are confined to the large body scales (here called crestals), but in the former genus they are present on the granular dorsal scales surrounding the crestals as well. The dorsal scales of *Shinisaurus* fall into three groups defined by both size and form:

**CRESTALS:** The large scales that form the dorsal scaly crests; these are convex, with rather sharp longitudinal keels.

**CALCULES:** Much smaller and more numerous scales; these are quite convex, but not keeled.

**GRANULES:** Very small, flat scales, distinguishable only with the aid of a strong magnifying glass.

In *Lanthanotus* crestals are present, but there is no distinction between calcules and granules, there being a complete transition from very small granules between the crestal rows to larger calcules surrounding the crestals.

In the arrangement of the crestals *Shinisaurus* closely resembles *Xenosaurus* (in which genus, however, the crestals are blunt and resemble ornamental tack heads) and bears only a superficial resemblance to *Lanthanotus*. In *Xenosaurus* and *Shinisaurus* the crestals of the body are arranged in transverse chevrons, the apex directed caudally, so that clearly defined longitudinal crests are formed only along the side of the midline of the back. In *Shinisaurus* this double median dorsal crest is continued onto the dorsal surface of the tail, which is otherwise devoid of crestals, whereas in *Xenosaurus* there is no caudal crest and the crestals are irregularly disposed on the tail. In *Lanthanotus* the crestals are arranged in three pairs of longitudinal crests: a dorsolateral crest running along the upper sides from the level of the axilla to the level of the groin; a dorsal pair running along the back, just lateral to the middorsal line, from behind the head to the tip of the tail; and a lateral pair running along the lower sides, beginning at the axilla and extending back over the thigh to continue to the tip of the tail; in addition there is a double row of smaller crestals running along the side of the tail ventral to the caudal continuation of the lateral row. There is no suggestion of a chevron-like arrangement of the crestals in *Lanthanotus*, and the crestals of the six longitudinal rows are in more or less straight transverse series. It is tempting to consider the chevron-like arrangement of crestals in *Shinisaurus* and *Xenosaurus* as related to the quincuncial arrangement of dorsal scales seen in the Anguinidae, and the straight transverse arrangement of crestals seen in *Lanthanotus* as related to the annular scale arrangement seen in *Varanus*.

In the form of the crestals themselves

there is also a difference between *Lanthanotus* and *Shinisaurus*. In *Lanthanotus* each crestal is placed on a raised wart that is otherwise covered with very small scales. In *Shinisaurus* the crestals are on skin that is not raised above the level of the surrounding skin, being thus similar to the condition in *Xenosaurus*.

The presence of a double dorsal crest of crestal scales in both *Shinisaurus* and *Lanthanotus* is a point of resemblance that Nopcsa (1932) stresses in his discussion of the relationship between the two genera. This characteristic loses some significance when one remembers that *Crocodylurus* of the unrelated Teiidae shows a similar development. Moreover, the resemblance between the tails of *Shinisaurus* and *Lanthanotus* cannot be called close. The tail of *Shinisaurus* is relatively much longer than that of *Lanthanotus* and is strongly compressed, while that of the Bornean lizard is cylindrical. In *Shinisaurus* there is but one pair of crests, while in *Lanthanotus* there are three pairs. Even the structure of the crests is different in the two genera. The difference in form of crestal scales observed on the back (crestal on flat skin as opposed to crestal on a raised tubercle) is to be observed on the tail as well. Moreover, in *Shinisaurus* each crestal is in contact with the crestal immediately behind it, but in *Lanthanotus* the crestals of a row are separated from one another by granular skin.

*Shinisaurus* agrees in coloration with *Xenosaurus* in considerable detail. On the other hand, there is no particular resemblance between *Shinisaurus* and *Lanthanotus* in coloration, aside from the general drabness of tone. In *Lanthanotus* (preserved) the body is reddish brown above, fading to an ocher on the belly. There is no sign of pattern except for vague and irregular brownish spotting on the belly. In preserved *Shinisaurus*, as in *Xenosaurus grandis*, the body is olivaceous above, cream-colored beneath, and shows a sharp pattern of black markings. As in *Xenosaurus grandis*, there are two dark postocular streaks in *Shinisaurus*, one running backward at about the level of the inferior border of the postorbitosquamosal arch, the other running back across the middle of the temporal region. *Shinisaurus* also has vertical

black striping on the lips, a feature not seen in *Xenosaurus grandis*, but present, though not strongly developed, in *X. rackhami*. There is a black spot on the side of the neck of *Shinisaurus*, easily homologized with the dark neck ring of *Xenosaurus*. The tail of *Shinisaurus* is ringed with light-centered dark bands, very much as in *Xenosaurus*.

**TONGUE:** The tongue is of the diploglossine type in both *Shinisaurus* and *Lanthanotus*; that is, the posterior part is thick and elastic and serves both as an extensor and sheath for the more slender and inelastic fore portion. But in *Lanthanotus* this fore portion is parallel-sided and deeply incised, approaching the condition in *Varanus*, while in *Shinisaurus* the tongue is like that of *Xenosaurus* and *Gerrhonotus*, with but slight terminal division, a more or less triangular form, and imperfect division of the fore tongue from the hind tongue.

**OSTEOLOGY:** In general form the skull of *Shinisaurus* is very different from that of *Lanthanotus*. While the skull of *Lanthanotus* is depressed and flattened dorsally, that of *Shinisaurus* is compressed and elevated, with strongly arched dorsal profile. In *Shinisaurus* the postorbital part of the skull is much shorter than the combined orbital and preorbital portions, but in *Lanthanotus* the postorbital cranium is equal to approximately half of the length of the skull. In *Lanthanotus* the pineal foramen (parietal foramen) is absent; it is present and rather large in *Shinisaurus*. In *Shinisaurus* the temporal arch is stronger than in the majority of lizards; in *Lanthanotus* the arch is absent.

The premaxillae are fused in both genera and in both genera there is a median tubercle on the palatal surface; in both, the premaxilla is pierced by a small foramen; in neither is the maxillo-premaxillary suture interrupted by a fenestra. But in form the premaxilla of *Shinisaurus* is quite different from that of *Lanthanotus*. In *Shinisaurus* the bone is rather narrow at the dental border, but it expands laterally at the anterior border of the anterior naris, then narrows abruptly to form a straight and longitudinal median border to the naris. As a result, the conjoined premaxillae of *Shinisaurus* have a cruciform appearance when seen from above. In *Lanthanotus* the bone is widest at the dental bor-

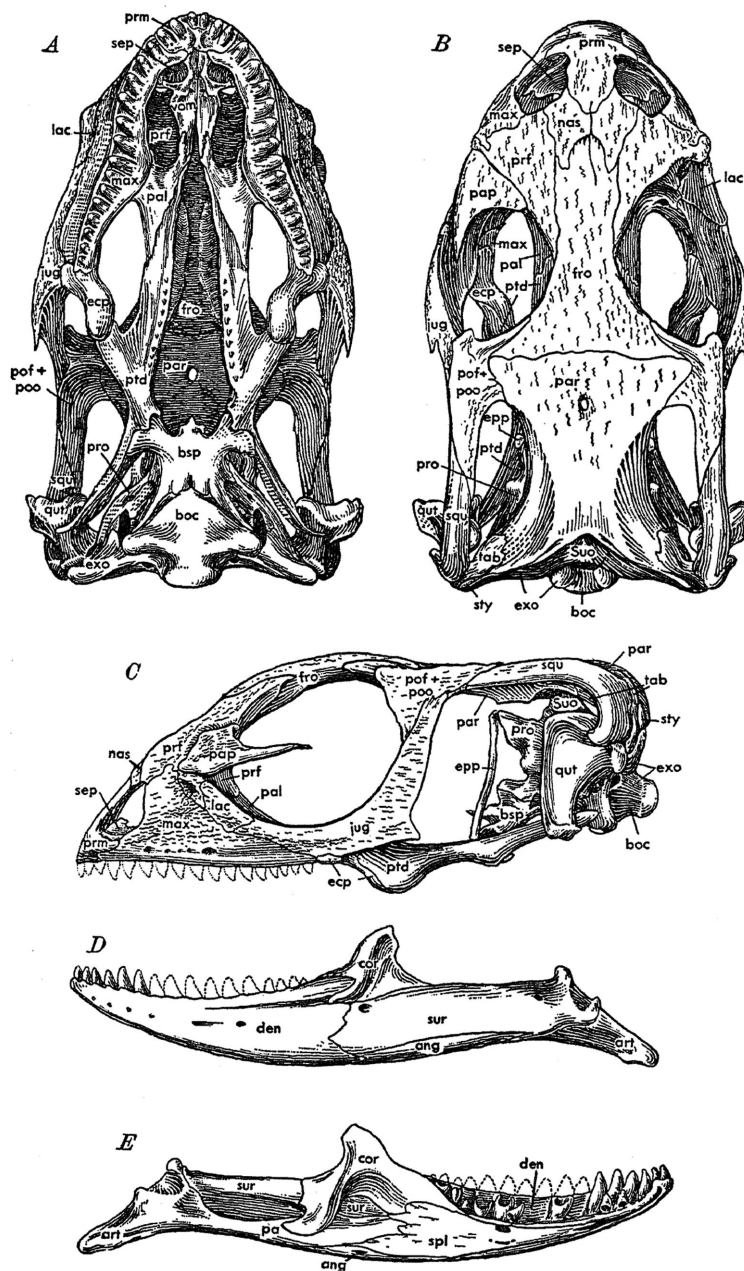


FIG. 4. *Shinisaurus crocodilurus*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Right palpebral and stapedes are omitted. For abbreviations, see page 141. Drawing by McDowell.

der and gradually narrows posteriorly, so that the conjoined premaxillae form a triangular figure.

The maxilla of *Shinisaurus* is most unlike

that of *Lanthanotus*. In *Shinisaurus* only the most anterior tip of the maxilla contributes to the ventral border of the anterior naris, the premaxilla instead forming the

major portion of the ventral narial border; but in *Lanthanotus* over half of the length of the maxilla lies on the ventral border of the naris. Indeed, it might be said that the entire dorsal border of the maxilla of *Lanthanotus* borders the naris, for the naris is prolonged backward as a slit extending to the frontal, excluding the maxilla from the prefrontal and nasal. In *Shinisaurus* the ascending facial wing of the maxilla (immediately behind the anterior naris) is located in the anterior third of the bone and forms a nearly vertical posterior border to the naris; in *Lanthanotus* the facial wing is placed in the posterior half of the maxilla and forms a sloping, diagonal posterior border to the naris. In *Shinisaurus* the maxilla is produced back beneath the orbit so that half the tooth row is suborbital in position; in *Lanthanotus* the maxilla is not produced beneath the orbit and the tooth row is preorbital. In *Shinisaurus* the palatine and ectopterygoid facets of the maxilla are rather widely separated, and the maxilla in consequence enters into the lateral border of the suborbital fenestra; in *Lanthanotus* the palatine and ectopterygoid meet to exclude the maxilla from the suborbital fenestra. On the palatal surface, the maxilla of *Shinisaurus* possesses an inwardly directed process at its anteromedial corner, this process separating in part the vomer from the premaxilla; in *Lanthanotus* this process is absent and the premaxillovomerine suture uninterrupted and long. The maxilla of *Shinisaurus* is coarsely sculptured, except along the labial border and on the palatal and medial surfaces, and furrowed, this sculpture resulting from the fusion of osteoderms to the bone; there is no such sculpture or osteodermal coating in *Lanthanotus*.

The septomaxilla of *Shinisaurus* is a thin lamina of bone, somewhat convex dorsally and concave ventrally, and devoid of any scroll-like processes; it slopes inward and upward to be at its most elevated point along the midline of the skull, but even here makes no internarial septum and is relatively low (ventral to the midline of the naris). In *Lanthanotus* the septomaxilla is of a very different construction: the bone is relatively heavy, with a complexly sinuate surface; at its lateral margin the bone gives forth an ascending tab-like scroll of bone (forming

about one-third of a circle in curvature) that rises vertically to a point dorsal to the level of the subnarial border of the maxilla; along the midline the septomaxilla rises high and forms a complete internarial septum.

In *Shinisaurus* the nasals are separate, but in *Lanthanotus* they are fused. The nasals of *Shinisaurus* have an osteodermal coating that is absent in *Lanthanotus*. Laterally, the nasal forms a suture with the prefrontal in *Shinisaurus*, but in *Lanthanotus* a posterior slit-like extension of the anterior naris separates the nasal and prefrontal completely. In *Lanthanotus* the two (fused) nasals are in contact with each other for their entire length and form a nearly straight transverse suture with the frontal; in *Shinisaurus* the two (suturally distinct) nasals are separated from each other posteriorly for nearly half their length by a broad and convexly rounded tongue of bone formed by the frontal bones.

The prefrontal of both *Shinisaurus* and *Lanthanotus* possesses a well-developed supraorbital process running back along the lateral (orbital) border of the frontal, but while this process meets the post-frontal in *Lanthanotus* it is widely separated from that bone in *Shinisaurus*. In *Shinisaurus* the prefrontal is dorsal to the maxilla and forms an interdigitated horizontal suture with that bone; the maxilloprefrontal suture is quite short. On the other hand, in *Lanthanotus* the prefrontal is mainly posterior to the maxilla and forms a long, smoothly sinuate suture with that bone, the suture being nearly vertical. In *Shinisaurus* the prefrontal bears on its orbital margin an articular facet for a large comma-shaped palpebral bone; in *Lanthanotus* the palpebral is absent, and there is in consequence no facet on the prefrontal.

Both genera have a well-developed lacrimal bone, and in both genera the sutural contacts of the bone are the same: prefrontal, maxillary, jugal, and palatine. But in *Shinisaurus* the prefrontal extends downward in front of the lacrimal, so that the suture of the anterior border of the lacrimal with the prefrontal is nearly as long as the lacrimal-maxillary suture; in *Lanthanotus* the prefrontal has no ventral extension anterior to the lacrimal. Most important, the lacrimal foramen of *Shinisaurus* is single, as in the vast majority of lizards, but in *Lanthanotus* the foramen is

double, as in *Varanus*. The lacrimal of *Shinisaurus* is sculptured, while that of *Lanthanotus* is smooth and rather bead-like.

The jugal of *Shinisaurus* is very different from that of *Lanthanotus*. In *Shinisaurus* the bone is roughly L-shaped, with a horizontal suborbital ramus and a nearly vertical postorbital ramus. Along the orbital border of the bone there is no angulation to demark these rami from each other, but on the temporal border the demarcation is sharp, for it is indicated by a triangular backwardly directed process. In *Lanthanotus* there is no distinction between suborbital and postorbital rami, but instead the bone has a simple bow-like shape, approximately equal to one-sixth of a circle in arc. In *Shinisaurus* the jugal is dilated and plate-like in form, with a sculptured surface, but the jugal of *Lanthanotus* is round in cross section. Anteriorly, the jugal of *Shinisaurus* is L-shaped in cross section, for in addition to the vertically oriented lateral surface of the bone there is a horizontal suborbital lamina that is closely applied to the dorsal surface of the maxilla; in *Lanthanotus* the bone is round in cross section anteriorly. In *Lanthanotus* the jugal runs upward and inward posterior to the post-frontal to meet (on one side) or almost meet the parietal, suggesting the possibility that the jugal has fused with the postorbital; in *Shinisaurus* the postorbital rami of two jugals are nearly parallel, without mesiad convergence, and widely separated from the parietal.

In *Shinisaurus* the post-frontal and postorbital are fused, while in *Lanthanotus* the postorbital is either absent or fused to the jugal. Owing to the presence of a temporal arch in *Shinisaurus* and the absence of the arch in *Lanthanotus*, there is considerable difference between the two genera in the form of the post-frontal. In *Shinisaurus* the bone has a horizontal dorsal surface extending outward to the lateral border of the skull; here the surface of the bone is sharply deflected downward as a vertical lateral surface meeting the jugal; at the point of angulation a longitudinal crease is formed, the crease elevated to a blunt crest beginning at the orbital border as an anteriorly directed tuberosity and extending back along the temporal arch for the full length of the combined post-frontal postorbital. In *Lanthanotus* the bone

is smaller than in *Shinisaurus* and has a smoothly curving surface without angulation or crest; the post-frontal curves evenly into the jugal arch and does not extend to the lateral border of the skull. *Shinisaurus* has a strong posterior spine of the post-frontal (actually representing the postorbital) that runs back to form a major part of the dorsal surface of the temporal arch; this process is, of course, absent in *Lanthanotus*. In *Shinisaurus* the post-frontal bears osteoderms and is sculptured, but in *Lanthanotus* the bone is smooth.

The frontal of *Shinisaurus* is very different from that of *Lanthanotus*. In *Shinisaurus* the frontals are fused, but in *Lanthanotus* they are separate. In dorsal view, the frontal of *Shinisaurus* is very narrow at its midorbital portion and the orbital margin is very concave; in *Lanthanotus* the frontals are moderately broad, with nearly straight orbital borders. The frontal of *Shinisaurus* is sculptured by an osteodermal incrustation, but the frontals of *Lanthanotus* are smooth. Most distinctive, however, is the relative development of the descending olfactory processes on the ventral surfaces of the frontals. In *Shinisaurus* these processes are but little developed and cannot be said to underarch the olfactory nerves except at the most anterior extremity; instead, they form curbs bounding a median path for the nerves. In lateral view the olfactory laminae hardly project into the orbit, and anteriorly the laminae terminate upon the prefrontals, not even meeting the palatines. In *Lanthanotus*, on the other hand, the olfactory laminae are enormous and underarch the olfactory tracts ventrally, but do not meet each other; the laminae project far into the orbit and, indeed, completely separate the two orbits from each other; anteriorly the olfactory laminae meet not only the palatine but the dorsal surface of the vomer as well.

In both genera the parietals are fused, but while *Shinisaurus* has a large parietal foramen for the pineal organ, the foramen is absent in *Lanthanotus*. In *Shinisaurus* the total length of the parietal is slightly less than that of the frontal, but in *Lanthanotus* is conspicuously greater. In *Shinisaurus* the parietal is separated by a gap from the epipterygoid and brain case, but in *Lanthanotus* the parietal

not only meets the epipterygoid but is applied along the entire dorsal border of the pro-otic and supraoccipital, forming a complete bony casing for the posterior part of the brain. The lateral borders of the parietals of *Shinisaurus* are concave, but in *Lanthanotus* the lateral borders of the portion of the parietals roofing the brain case are convex. In *Lanthanotus* the dorsal surface of the parietal posteriorly bears a scar marking the insertion of nuchal muscles, but in *Shinisaurus* no nuchal muscles reach the dorsal surface of the parietal. In both genera, as in most lizards, the postero-lateral corners of the parietals are produced backward and laterally as struts bearing against the paroccipital processes. In *Shinisaurus* these strut-like processes are broad and directed almost entirely laterally, with but little backward tilt, but in *Lanthanotus* they are slender and directed as much backward as laterad. The parietals of *Shinisaurus* have an osteodermal incrustation absent in *Lanthanotus*.

Both genera have a large tabular applied against the lateral surface of the postero-lateral strut of the parietal. The bone is not sufficiently distinctive in the two genera to require comment. The squamosal is very different in the two genera, as might be expected of two lizards so different in degree of development of the temporal arch. In *Lanthanotus* (without arch) the squamosal is reduced to a small triangle of bone capping the quadrate; in *Shinisaurus* (with exceptionally strong temporal arch) the bone is strong, horizontal in its anterior portion forming the temporal arch, but curled downward posteriorly to meet the quadrate. Anteriorly the bone makes a strong and very oblique suture with the post-frontal-postorbital and makes a very narrow contact with the jugal; posteriorly the squamosal makes contact laterally with the tabular and ventrally with the quadrate. The squamosal of *Shinisaurus* bears a dorsal blunt crest continuous with the crest upon the post-frontal-postorbital. A row of large osteoderms is implanted upon this crest.

In *Shinisaurus* there is a small ossicle lying in a groove upon the occipital surface of the parietal. In the single available skull there is no trace of the bone on the right side, but the groove for its reception is impressed upon the parietal and the bone may have been lost

in preparation; on the left side the bone is well developed and sutures with the tabular and abuts ventrally against the paroccipital process. There is no trace of this bone in *Lanthanotus*.

The vomer of *Shinisaurus* is relatively much smaller than that of *Lanthanotus* and quite differently shaped. In neither genus are the vomers fused, but in *Lanthanotus* they are appressed for almost their entire length, while in *Shinisaurus* they are posteriorly separated for about one-fourth of their length by a narrow anterior extension of the interpterygoid vacuity. In *Lanthanotus* the ventral surface of the vomer is without sculpturing or foramina, but in *Shinisaurus* there is a longitudinal crest opposite the opening for the organ of Jacobson. This crest is paired, and the two crests border a deep median furrow; at the posterior end of the furrow the vomers are pierced by a pair of small foramina. In *Lanthanotus* the vomer forms only the median boundary of the entrance to the organ of Jacobson, but in *Shinisaurus* there is a transverse spur (bearing a small foramen) that forms the posterior border of the opening as well. The vomer of *Lanthanotus* is much more expanded transversely than that of *Shinisaurus*. In *Lanthanotus* the suture between the vomer and the palatine is nearly transverse, but in *Shinisaurus* the mesial surface of the anterior tip of the palatine sutures with the lateral surface of the posterior tip of the vomer, and the suture in consequence is nearly longitudinal.

The palatine of *Lanthanotus* lies almost entirely posterior to the level of the posterior extremity of the maxilla, but in *Shinisaurus* the palatine lies median to the maxilla and does not extend posterior to the level of the posterior extremity of the maxilla. The palatine of *Lanthanotus* is much more deeply cleft anteriorly (between its vomerine and maxillary rami) than that of *Shinisaurus*. The palatine of *Shinisaurus* is edentulous but that of *Lanthanotus* bears a few small teeth. In *Lanthanotus* the palatine-pterygoid suture is nearly transverse, but in *Shinisaurus* the suture is longitudinal, and the pterygoid extends along nearly the whole of the medial border of the palatine, almost to meet the vomer. In *Shinisaurus* the palatine is well separated from the ectopterygoid, but

in *Lanthanotus* the two bones are in sutural contact anteriorly, excluding the maxilla from the suborbital fenestra.

As mentioned above, the pterygoid of *Shinisaurus* differs notably from that of *Lanthanotus* in its great forward extent, for while the pterygoid of *Lanthanotus* does not extend forward to the level of the posterior extremity of the maxilla, that of *Shinisaurus* extends forward to the level of the midpoint of the maxillary bone. The pterygoid of *Shinisaurus* nearly excludes the palatine from the border of the interpterygoid vacuity, but in *Lanthanotus* the contribution of the palatine to the border of the vacuity is nearly equal to that of the pterygoid. In addition, the median border of the pterygoid anterior to the basal articulation with the sphenoid is nearly straight in *Shinisaurus*, and consequently the interpterygoid vacuity is in the form of a long and acute isosceles triangle; in *Lanthanotus* the median border of the pterygoid is emarginated, so that the interpterygoid vacuity is rather short, broad, and miter-shaped. The posterior ramus of the pterygoid (extending from the articulation with the sphenoid backward and lateral to the quadrate) is more dilated in *Lanthanotus* than in *Shinisaurus*. In both genera, as in most lizards, the pterygoid has an anterolateral branch that forms a suture with the posterior end of the ectopterygoid, but in *Shinisaurus* this ectopterygoid branch is much longer than in *Lanthanotus* and extends forward over the dorsal surface of the ectopterygoid nearly to meet the jugal; there is no suggestion of this dorsal extension of the pterygoid upon the ectopterygoid in *Lanthanotus*. In *Shinisaurus* the pterygoid forms a greater portion of the border of the suborbital fenestra than does the palatine, but these proportions are reversed in *Lanthanotus*. In both genera the pterygoid is toothed.

The ectopterygoid of *Shinisaurus* is of more twisted form than that of *Lanthanotus*, and the tuberosity abutting against the coronoid bone of the lower jaw better developed. In both genera the ectopterygoid reaches the lateral border of the skull just behind the maxilla and beneath the jugal. In *Lanthanotus* the anterior portion of the ectopterygoid is elevated above the level of the maxillary dental border, and the ventral bor-

der of the anterior half of the ectopterygoid is dorsal to the level of the ventral border of the palatine; in *Shinisaurus*, however, the more normal condition prevails and the ventral border of the anterior portion of the ectopterygoid is continuous with the dental border of the maxilla and ventral to the level of the ventral border of the palatine.

In *Shinisaurus* the epipterygoid is long, slender, and sinuously curved, in accordance with the very deep skull; in *Lanthanotus*, with a markedly depressed skull, the epipterygoid is short, stout, and straight but for a slight backward hooking of the dorsal extremity. In *Shinisaurus* the dorsal end of the epipterygoid is unmodified and joined very loosely to the pro-otic, well separated from the parietal; in *Lanthanotus* the dorsal extremity of the epipterygoid is somewhat expanded and firmly joined to both the parietal and the pro-otic.

The form of the basisphenoid and its strong and pedunculate basiptyergoid processes is similar in the two genera except for the form of the basisphenoid-basioccipital suture. In *Lanthanotus* the suture is nearly transverse with a slight arc, convex anteriorly; in *Shinisaurus* the suture is obtusely angulate, the basisphenoid receiving a broadly wedge-shaped anterior border of the basioccipital between a pair of triangular arms that extend backward to the level of the fenestra ovale. In addition, in *Shinisaurus* there is a foramen in the basisphenoid on the midline at the point of juncture with the basioccipital; this foramen is absent in *Lanthanotus*.

The basioccipital is of quite different form in the two genera. In *Shinisaurus* the lateral muscular tuberosity is large and bulbously constructed; in side view the tuberosity is seen to be the ventral continuation of a strong, ventrally directed muscular tuberosity of the exoccipital; except for the occipital condyle, the muscular tuberosity is the most posterior portion of the basioccipital. In *Lanthanotus* the tuberosity is small and weak, continued to the tuberosity of the exoccipital only by a narrow lateral horizontal crest, and lies on the anterior part of the ventral surface of the basioccipital, immediately behind the suture with the basi-

sphenoid. In both genera the basioccipital forms the median part of the occipital condyle, but in *Shinisaurus* the basioccipital portion of the condyle is relatively greater than in *Lanthanotus*.

In both *Lanthanotus* and *Shinisaurus* the pro-otic extends anterior to the anterior semicircular canal both above and below the emargination for the trigeminal nerve ( $V_2$  and  $V_3$ ), and in both genera the pro-otic forms the dorsal border for the foramen for the ventral branch of the entocarotid artery and Vidian nerve (the basisphenoid forming the ventral border); in neither genus is the pro-otic produced laterally as a horizontal plate of bone dorsal to the entocarotid-Vidian foramen (in other words, there is no "entocarotid-fossa"). But in other respects the two genera are quite different in respect to the pro-otic bone. In *Shinisaurus* the bone has greater vertical height and less horizontal length than that of *Lanthanotus*, reflecting the deeper and shorter brain case proportions of the Chinese lizard. In *Lanthanotus* the dorsal border of the pro-otic is closely appressed to the parietal and is straight; in *Shinisaurus* the pro-otic fails to meet the parietal at any point and the dorsal border of the pro-otic is emarginated. In *Lanthanotus* the anterior wing of the pro-otic that runs forward dorsal to the trigeminal notch to meet the epipterygoid arises from the entire anterior border of the anterior semicircular canal, so that the semicircular canal is completely excluded from the trigeminal notch; in *Shinisaurus* the dorsal anterior wing of the pro-otic arises only from the dorsal two-thirds of the anterior border of the semicircular canal, so that the lower third of the bony sheath of the semicircular canal borders the trigeminal notch.

The exoccipital (to which, as in other Squamata, the opisthotic is fused to form the paroccipital process) is not greatly different in the two genera. In both genera its paroccipital process forms the suspensorium for the quadrate and abuts against the posterior extremities of the squamosal and tabular and parietal; in both genera it, together with the pro-otic, forms the border of the fenestra ovale; in both genera it contains the jugular foramen on its lateral surface and the hypoglossal foramen on its posterior

(occipital) surface; in both genera it forms the lateral portion of the occipital condyle and all of the lateral, as well as part of the dorsal, border of the foramen magnum. However, in *Lanthanotus* the hypoglossal foramen is enlarged and appears to have contained the vagus (X) as well as the hypoglossal (XII), as in *Varanus* and the mosasaurs, while in *Shinisaurus* the vagus makes its normal exit from the jugular foramen. There is also considerable difference in the development of the muscular tuberosity. In *Lanthanotus* the tuberosity is very weak and reduced to a narrow crest and lies posterior, rather than dorsal, to the tuberosity of the basioccipital, so that a considerable portion of the exoccipital is visible below on the floor of the brain case. In *Shinisaurus* the tuberosity is strong and inflated, but is dorsal to, and continuous with, the tuberosity of the basioccipital, so that the basioccipital conceals the exoccipital from ventral view, except for the paroccipital process and condylar portion.

In both genera the supraoccipital forms the median dorsal portion of the border of the foramen magnum; in both it is unpaired, without foramina, and with a low, blunt, median ridge. In *Lanthanotus* the anterior (dorsal) border of the supraoccipital is broadly and convexly rounded for its entire length and is smoothly continuous with the dorsal border of the pro-otic; the dorsal border of the supra-occipital is firmly articulated for its entire length with the extreme posterior edge of the parietal. In *Shinisaurus* the dorsal (anterior) border of the supraoccipital is set off from the dorsal border of the pro-otic by an emargination and is produced into an anteriorly directed median pointed process; it is only this median process that meets the parietal, and rather than abutting against the posterior edge of the parietal, abuts against the ventral surface of the parietal along the midline, slightly anterior to the posterior margin of the dorsal parietal plate.

The quadrate of *Shinisaurus* shows marked differences from the quadrate of *Lanthanotus* largely as a result of the presence of a middle ear cavity and tympanic membrane in the Chinese genus and their absence in the Bornean lizard. In *Shinisaurus* there is an outer conch of the quadrate, with sharp lateral

margin and conspicuously excavated posterior (otic) surface; this conch is absent in *Lanthanotus*. Moreover, in *Shinisaurus* there is a compressed vertical crest on the median surface of the quadrate, this crest bracing the quadrate against the branch of the protic that extends backward along the paroccipital process.

The lower jaw of *Lanthanotus* is subequal in length to the skull; in *Shinisaurus* the lower jaw is conspicuously longer than the skull. This difference is largely the result of the much greater length of the postarticular process in *Shinisaurus* than in *Lanthanotus*, in turn a result of the presence of a middle ear in *Shinisaurus*, its absence in *Lanthanotus*. In *Shinisaurus* the postarticular process is the ventral border of the middle ear; so it does not receive the depressor mandibulae except at the posterior tip of the process after an interspace for the ear; in the absence of a middle ear only that portion of the postarticular process for the depressor muscle is required in *Lanthanotus*. Thus the postarticular process of *Lanthanotus* is very short and directed straight back, along the main axis of the jaw, while in *Shinisaurus* the process is long and deflected. In neither genus is the postarticular process twisted upon its axis as it is in the Anguinidae.

In accordance with the longer maxillary tooth row, the dentary bone of *Shinisaurus* is proportionately longer than that of *Lanthanotus* (greater, rather than less, than half of the length of the jaw). Most important of the numerous differences in jaw structure is the method of attachment of the dentary bone, for while *Shinisaurus* has the dentary firmly sutured into a rigid position in the jaw, as in the vast majority of lizards and the Typhlopidae, that of *Lanthanotus* is movably articulated as in the Platynota and Leptotyphlopidae, and, to a greater or lesser extent, the more typical snakes. Indeed, *Lanthanotus* shows a perfection of the jaw hinge not seen in *Varanus*, and seen among living forms only in the Leptotyphlopidae.

In *Shinisaurus* the dentary is firmly joined to the splenial, the dorsal border of the splenial being firmly attached for its entire length (except for the small internal mental foramen) to the dentary, thus closing the Meckelian groove except anterior to the

splenial. In *Lanthanotus* the Meckelian groove is open between the dorsal border of the splenial and the dentary for almost the entire length of the dentary, for only at the extreme posterior extremity of the dentary and splenial does the splenial send up a small tab of bone to meet the dentary. In *Shinisaurus* the dentary sends back a strong process to overlap the coronoid laterally and firmly unite the two bones; in *Lanthanotus* the dentary meets the coronoid in nearly edge-to-edge contact, and a movable joint is produced. In *Shinisaurus* the dentary is firmly attached to the surangular by a V-shaped suture (convex anteriorly), but in *Lanthanotus* the juncture is loose and movable and nearly straight vertically. In *Shinisaurus* the posteroventral corner of the dentary is drawn out into a pointed process inserted into a corresponding emargination in the anterior extremity of the angular, establishing a rigid connection; in *Lanthanotus* the dentary scarcely articulates with the angular, and what juncture exists is straight and vertical.

The splenial of *Lanthanotus* is vertically truncate behind, its posterior margin parallel to that of the dentary. Thus the splenial lies entirely anterior to the coronoid and meets that bone in but a slight corner-to-corner contact; the splenial-prearticular suture and splenial-angular suture are each vertical and lie along the same straight vertical line. In *Shinisaurus* the splenial is produced backward on the inner side of the jaw, as is usual in lizards, and extends posterior to the dentary for a considerable distance. Consequently in *Shinisaurus* the splenial forms a long horizontal suture with the ventral border of the anterior portion of the coronoid; posteroventrally the splenial sends back a long triangular process that reaches posterior to the level of the apex of the coronoid process and forms a long horizontal suture by its dorsal border with the ventral border of the prearticular, while the ventral border of this process of the splenial forms an even longer horizontal suture with the dorsal median border of the angular. To sum up: in *Lanthanotus* the dentary and splenial are together joined to the more posterior elements of the mandible by a vertical hinge, present in the same position on both the median and lateral surfaces. *Shinisaurus*, however, has the more normal

mandible with dentary and splenial in rigid position and with a series of sutures oriented longitudinally behind the level of the tooth row. Such sutures, being transverse to the plane of movement seen in the hinge of *Lanthanotus*, would actually strengthen the jaw through utilization of the principle of polylamination and increase rigidity.

The coronoid of *Shinisaurus* is of quite different form from that of *Lanthanotus*. In the Chinese lizard the coronoid process is higher and more anteriorly placed than in the Bornean form, while the ventral emargination on the median surface that exposes the surangular medially is smaller, with much less anterior extent.

The dentition is also different in detail. Both genera show alternate, rather than successive, dental replacement of the anguinoid (interdental) type, and both have a pleurodont emplacement. But the pleurodonty of *Shinisaurus* is much greater than that of *Lanthanotus*, for while the Bornean species has the teeth ankylosed to the bones of the skull principally by the proximal bases of the teeth, with but little ankylosis of the buccal surface, the Chinese lizard has the teeth ankylosed mainly by their buccal surfaces, rather slightly by the proximal surfaces. The form of the individual tooth is also different, for while the tooth of *Lanthanotus* has an expanded and vertically striated base and a narrow, compressed, and rather sharply recurved and pointed crown, the tooth of *Shinisaurus* is slightly tapered proximally, smooth and unstriate, round in cross section, blunt terminally (but distally tapered), and only slightly recurved.

Very little weight can be given to dental counts based on a single specimen of each species, but nonetheless it may be worth while to record such counts here. (The first number entered in each count is for the right side, the second for the left.)

	<i>Shinisaurus</i>	<i>Lanthanotus</i>
Premaxilla	3-3	4-4
Maxilla	14-14	11-12
Palatine	0-0	1-2
Pterygoid	10-9	11-13
Dentary	15-16	12-12
Vomer	0-0	0-0

The hyoid of *Shinisaurus* is similar to that of *Lanthanotus* in regard to elements present; there is an anterior median glossohyal or hyoid copula or basihyal; at the posterior extremity of this element there are two pairs of elements, an anterolaterally directed pair of ceratohyals and a posterolaterally directed pair of ceratobranchials (branchial cornua); but one pair of ceratobranchials (the first) is present, and these are terminated by very short epibranchials; there are no hypohyals or second epibranchials. The two genera differ considerably in the form of the glossohyal; in *Shinisaurus* its median awl-shaped process is very long and extends anterior to the anteriormost extremity of the ceratohyal for a distance equal to the length of the ceratohyal; in *Lanthanotus* the median glossohyal process is short and exceeded in anterior extent by the ceratohyal. Posteriorly, the glossohyal of *Shinisaurus* is hardly dilated, and the ceratohyal and ceratobranchial, which are borne on a slight lateral pedicle of the glossohyal, arise near the midline; in *Lanthanotus* the lateral pedicle of the glossohyal for the ceratohyal and ceratobranchial is produced laterally, making the glossohyal Y-shaped (nearly T-shaped) and causing the ceratohyal and ceratobranchial to arise far from the midline.

We have examined the shoulder girdle of *Shinisaurus* by dissection, but have only roentgenograms of this region in *Lanthanotus*. The interclavicle of *Shinisaurus* is cruciform, with long transverse processes and a short and rather poorly defined anterior process; as far as can be determined from the roentgenograms, *Lanthanotus* lacks the transverse processes of the interclavicle. The clavicle of *Shinisaurus* is in the form of an elongated S, but with a narrow, moderately long, snag-like process on its posterior border running back to the lateral extremity of the transverse process of the interclavicle; *Lanthanotus* appears to lack this snag-like process.

The phalangeal count for both manus and pes is the normal 2-3-4-5-3 in *Shinisaurus*, but the unusual 2-3-4-4-3 in *Lanthanotus*.

For the vertebral count in *Shinisaurus* we are dependent on a roentgenogram, as we are for *Lanthanotus*.

	<i>Shinisaurus</i>	<i>Lanthanotus</i>
Cervical (without sternal rib)	7	9
Anterior thoracic (sternal ribs)	5	3
Posterior thoracic (no sternal ribs)	12	23
Lumbar (no movable ribs)	0	1
Sacral (parapophyses attached to ilium)	2	2
Caudal	43	68

*Shinisaurus* lacks abdominal ribs, but the roentgenogram of *Lanthanotus* shows structures that appear to be abdominal ribs unconnected with the vertebral ribs.

#### CONCLUSIONS

The numerous differences between *Lanthanotus* and *Shinisaurus* make it most unlikely that the two genera are at all closely related. Both genera show affinity to the Anguinomorpha (Platynota and Diploglossa) in such features as the tongue with papillae and divided into an anterior and a posterior portion by a transverse fold, alternate and interdental method of dental succession, presence of premaxillary foramina, fusion of the premaxillae, failure of the parietal to send down long descending processes anterior to the pro-otic to meet the epipterygoid, absence of all but the first of the ceratobranchials, exposure of Meckel's cartilage anterior to the splenial bone, extension of the pro-otic anterior to the anterior semicircular canal and its articulation with the epipterygoid, and the simple supraoccipital-parietal articulation. Aside from features common to all, or the vast majority of, the Anguinomorpha, *Shinisaurus* shows a remarkable lack of resemblance to *Lanthanotus*.

Many of the characters distinguishing *Lanthanotus* and *Shinisaurus* from each other are characters that also distinguish the *Varanus*-like group (Platynota) from the *Anguis*-like group (Diploglossa), and it seems likely that while *Lanthanotus* represents a relatively specialized platynotan lizard, *Shinisaurus* is but a moderately aberrant diploglossan. Features indicating this most evidently are:

1. Presence of a highly developed jaw hinge in *Lanthanotus* and the absence of any intramandibular joint in *Shinisaurus*, result-

ing in marked differences in the sutural pattern of the lower jaw.

2. Failure of the dental series to extend beneath the orbit in *Lanthanotus*, whereas in *Shinisaurus* half the tooth row is suborbital in position.

3. Exclusion of the maxilla from the suborbital fenestra in *Lanthanotus*, but not in *Shinisaurus*.

4. Backward prolongation of the external naris as a narrow longitudinal slit extending to the frontal in *Lanthanotus*, but absence of any backward prolongation of the naris in *Shinisaurus*.

5. Great development of the subolfactory process of the frontal in *Lanthanotus*, as compared with rather feeble development of the process in *Shinisaurus*.

6. Sharply pointed and recurved teeth in *Lanthanotus*, with basal expansion and the attachment chiefly by the proximal surface, as contrasted to obtusely pointed, barely recurved teeth in *Shinisaurus*, with the base narrow and attachment chiefly by the buccal surface.

7. Form of the tongue, which has the fore portion long, deeply incised, and parallel-sided in *Lanthanotus*, while it is provided with but a short, weakly incised, triangular fore portion in *Shinisaurus*. (The tongue of *Shinisaurus* is macroscopically virtually identical with that of *Gerrhonotus*, *Ophisaurus*, and *Xenosaurus*.)

*Shinisaurus* has been considered the sole representative of a family, the Shinisauridae, of unknown affinities. From what has been said above it seems apparent that the closest relationships of the Chinese lizard are with the Diploglossa (here restricted to the families Anguinidae, Xenosauridae, and Annielidae), but the more precise affinities of *Shinisaurus* require further consideration.

In two features of its skull *Shinisaurus* differs from all other Diploglossa: the extreme depth and compression, and the entrance of the prefrontal into the posterior border of the external naris. In the Platynota the prefrontal also might be said to enter the naris, but the arrangement of bones is actually altogether different from that in *Shinisaurus*. In *Shinisaurus* the naris is not at all drawn backward, but rather has a straight vertical pos-

terior border; the prefrontal truly borders the naris, for it is applied against the connective tissue forming the anterior sac-like nostril. In the Platynota the naris is drawn back as a narrow slit, the ventral border of which is in part formed by the prefrontal, but the prefrontal is far separated from the soft tissue of the nostril. The condition in *Shinisaurus* therefore is not to be compared with that in the Platynota but is closely analogous with the arrangement of bones seen in *Chamaeleo* and some Agamidae, such as *Uromastix*. Since the chameleons and *Uromastix* show no other special resemblances to *Shinisaurus* except for the very short and deep snout, it seems probable that it is the great compression of the skull in both *Shinisaurus* and the agamoids that is responsible for lifting the nasal above the facial process of the maxilla to allow the prefrontal to intercede between those bones, and the backward displacement of the naris to meet the anterior border of the prefrontal.

But while *Shinisaurus* is unique among diploglossans in the compression of the head and corresponding modification of the bony sutures of the snout, in a great number of its structural features the Chinese lizard most closely resembles the broad-headed Mexican *Xenosaurus*. The most impressive of these structural resemblances are:

1. Disintegration of the head scutes into small polygonal tesserae. In the Anguinidae and Anniellidae the head scutes are large and regular.

2. Presence of pustule-like organs on the larger scales. This is not the case in any anguinid or in *Anniella*.

3. Separation of the large scales of the dorsal surface (which are reduced in number) by broad areas of granular scutellation. The appearance of the dorsal scutellation is quite similar in *Shinisaurus* and *Xenosaurus*, save that in the former the crestal scales are relatively larger and more regularly arranged. None of the Anguinidae or *Anniella* has a similar dorsal scaly covering, but instead the scales are large, regular, imbricated, and flat, forming a continuous cuirass over the dorsal surface.

4. General color pattern. In general coloration *Shinisaurus* and *Xenosaurus* are very similar, being olive-brown above, with black-

ish cross bars and a black nuchal mark, and with a dark line beginning behind the eye and running along the temporal arch. No anguinid or anniellid has a similar color pattern.

5. Covering of the tympanum by scaly skin, together with superficial position and large size of the tympanic membrane. In the majority of diploglossans the tympanic membrane is small, unscaled, and sunken. In others (e.g., *Anniella*) the tympanic meatus may be quite completely closed over by a thick wall of tissue, but the combination of a large, superficial tympanum with a scaly tympanic covering is found only in *Shinisaurus* and *Xenosaurus* among Diploglossa.

6. Reduction of body osteoderms, which are not imbricated, and fusion of cephalic osteoderms to the cranial bones, forming a rough cranial sculpture. *Anniella*, which shows no particular resemblance to *Shinisaurus* and *Xenosaurus* in other respects, does have the osteoderms totally suppressed; in all the Anguinidae there are imbricate osteoderms on at least part of the body.

7. Nasals deeply separated posteriorly by a median anterior process of the frontal. In no other diploglossans is the separation of the nasals by the frontal so well developed.

8. Extremely strong temporal arch, with a longitudinal, raised crest. In *Anniella* the arch is completely absent; in the Anguinidae the arch is rather weak, without a longitudinal dorsal keel; in *Xenosaurus* the arch is even stronger than in *Shinisaurus*.

9. Dilated and sculptured postorbital branch of the jugal. This dilation is very characteristic of *Shinisaurus* and *Xenosaurus* and does not occur in other Diploglossa.

10. Frontal very narrow between the orbits. The frontal of *Xenosaurus* has about the same relative width as that of *Shinisaurus*, and in both it is much more constricted inter-orbitally than in other Diploglossa.

11. Fusion of postorbital and postfrontal. This is seen nowhere else among the living Diploglossa.

12. Entrance of the ectopterygoid into the lateral border of the skull beneath the jugal. We have found this in but two other diploglossans, the Chinese *Ophisaurus* (*Dopasia*) *harti*, and *Anniella*, forms that are otherwise quite different from *Shinisaurus*

and *Xenosaurus*. In the others, the jugal excludes the ectopterygoid from the lateral cranial border.

13. Development of an inner, as well as an outer, conch of the quadrate. This is not seen in any other diploglossan.

14. Failure of the parietal to meet either the epipterygoid or pro-otic. This is not seen among other diploglossans.

15. Presence of a small additional ossicle in the region of the quadrate suspension.

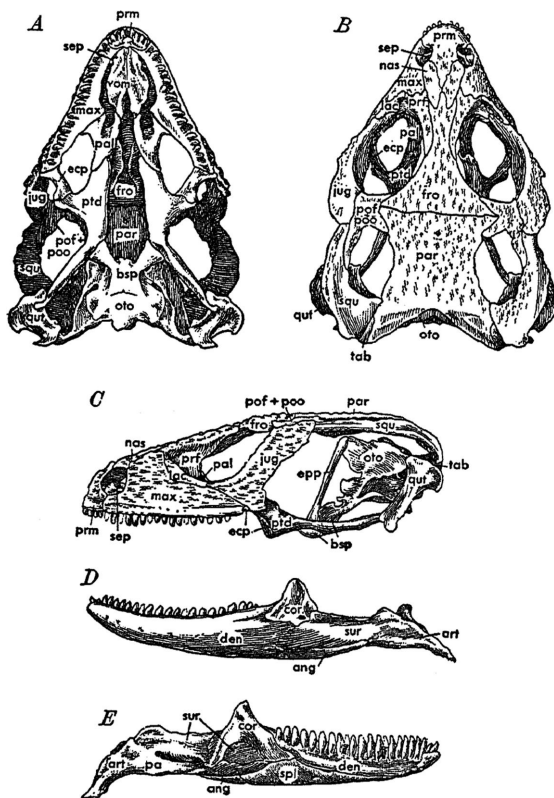


FIG. 5. *Xenosaurus grandis*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapes omitted. For abbreviations, see page 141. Drawing by McDowell after Barrows and Smith (1947).

This bone, identified by Barrows and Smith (1947, p. 243) as an epiphysis of the paroccipital process, may be a stylohyal. At any rate, it is not to be found in Anguinidae or *Anniella* but is characteristic of *Shinisaurus*, *Xenosaurus*, and at least one fossil genus here referred to the Xenosauridae (see below).

16. Failure of the pro-otic to develop a strong horizontal lamina dorsal to the extracranial course of the entocarotid artery (failure to form a carotid fossa). In *Xenosaurus* this lamina is rudimentary or, more probably, vestigial, since the great development of this lamina in such diverse lizards as iguanoids, gekkotans, scincoids, lacertoids, and teioids, all forms without the specialized tongue and dental replacement of the Anguinomorpha, suggests that a deep and broad "carotid fossa" is a primitive squamatan feature. In *Anniella* and *Ophiodes* the fossa is barely present also, but in the rest of the Diploglossa the fossa is deep and rather wide.

17. Nearly straight lateral border of the interpterygoid vacuity. This is not seen in other Diploglossa.

Thus there is a list of at least 17 characteristics seen in both *Shinisaurus* and *Xenosaurus* and absent in all or nearly all the other Anguinomorpha. This does not include more general resemblances between *Shinisaurus* and *Xenosaurus* seen in many anguins as well. Some of the latter that might be mentioned are: fusion of the frontals, lack of a foramen on the maxillo-premaxillary suture, obliqueness of the palatine-ptyergoid suture, lack of rotation of the post-articular process of the lower jaw, relatively blunt teeth, and articulation of the supraoccipital with the ventral surface (rather than the posterior edge) of the parietal. It is hard to assess the presence in both *Shinisaurus* and *Xenosaurus* of a palpebral. A palpebral bone is also found in *Anniella* (though not nearly so well developed), but is said to be absent in Anguinidae. However, it is possible that the anguins possess a palpebral, or at least a rudiment of that bone, in close association with the bony supraorbital osteoderms found in that group, but not in *Anniella*, *Xenosaurus*, or *Shinisaurus*. It might be well to point out here that the sclerotic ring is not characteristic of *Xenosaurus*, as stated by Barrows and Smith (1947, p. 267), but is found in nearly all lizards, including all anguins and *Anniella*.

The great structural similarity between *Shinisaurus* and *Xenosaurus* seems best expressed by including the Chinese lizard in the Xenosauridae, rather than in a monotypic family. In addition to the living *Shinisaurus*

and *Xenosaurus*, the Xenosauridae might well include the fossil genera *Melanosaurus*, *Exostinus*, and *Necrosaurus* (equivalent to *Palaeovaranus* and including *Melanosauroides* Kuhn). A comparison of *Shinisaurus* with these fossil genera may throw some light on the precise affinities of the living genera with one another.

*Melanosaurus* is known from a nearly complete skull [A.M.N.H. (G.P.) No. 5168] and parts of another [A.M.N.H. (G.P.) No. 5175] and associated dermal scutes, vertebrae, and fragmentary limbs. It is of lower Eocene age, from the Clark's Fork Basin Wasatch. It is important to note that almost all of Camp's statements (1923) on the "Glyptosauridae" were based on examination of this material, which he referred to *Xestops*, and that his figures of *Xestops* are actually of this genus. Accordingly, most of Camp's characterization of his Glyptosauridae is a statement of the osteological characters of the Xenosauridae as revealed in this early and primitive member. Gilmore (1928, p. 138) created a new genus *Melanosaurus* for Camp's supposed *Xestops* material, but referred it to the Anguinidae (Gilmore's spelling is Anguidae), as have subsequent workers. It appears that Gilmore had no skeletal material of *Xenosaurus* available for comparison, since elsewhere he removed *Exostinus* from the Xenosauridae, where it had been placed by Cope, after comparing it with anguinids.

*Melanosaurus* shows the alternate and interdental tooth replacement and premaxillary foramina characteristic of the Anguinomorpha and shows its diploglossan, as opposed to platynotan, affinities by its pattern of mandibular sutures, suborbital continuation of the tooth row, and blunt, erect teeth. In general, it shows a very unspecialized diploglossan morphology, with much resemblance to such primitive Anguinidae as *Gerrhonotus* or *Diploglossus*, but there are certain features that indicate that even at this early date the distinctive features of the Xenosauridae were already recognizable. Features that indicate the xenosaurid affinities of *Melanosaurus* are the following:

1. Presence of a peculiar separable ossicle in the region of the quadrate suspension (identified as a paroccipital by Camp in 1923, but called an epiphysis of the paroccipital

process by Barrows and Smith). As noted by Gilmore (1928, p. 141) this element is unknown as a separate entity in any anguinid; it is found in both *Shinisaurus* and *Xenosaurus*.

2. Presence of an inner wing-like conch on the quadrate. This is not found in any of the Anguinidae, but it is present in both *Shinisaurus* and *Xenosaurus*.

3. Much dilated and sculptured post-orbital ramus of the jugal. This again is characteristic of the living Xenosauridae and unknown in any living or fossil anguinid.

4. Co-ossification of the cranial osteoderms with one another, as well as with the underlying bones. This consolidation of the cranial osteoderms and skull gives the cranial bones their sculptured appearance and is characteristic of the Xenosauridae as compared with the Anguinidae.

5. Lack of anterior expansion of the frontal anterior to the orbital emargination. This is as in *Shinisaurus* and *Xenosaurus*, but cannot be matched by any anguinid, although there is some variation in the latter group in the precise form of the frontal bone. In the living *Diploglossus*, *Celestus*, *Sauresia*, *Wetmorena*, and *Ophiodes*, and their probable fossil ancestor *Xestops*, there is no orbital emargination and the lateral border of the frontal is straight, so that the two frontals together form a trapezoid approaching a rectangle in shape. Moreover, all these forms have the frontals distinct from each other, while those of *Melanosaurus* are fused, as in *Shinisaurus* and *Xenosaurus*. In the living *Gerrhonotus* and *Abronia*, as well as their fossil representative *Peltosaurus*, the frontals are fused and emarginated over the orbits, as in xenosaurids, but differ in being widened anteriorly, so that the frontals together form an hourglass-like figure, save that there is a simply concave, not doubly convex, lateral margin. In *Glyptosaurus* of the Eocene and Oligocene the frontals varied from completely fused through intermediate degrees of separation to complete separation, and the lateral margin was not like that of any of the other anguinids, for while it was only slightly emarginate along the orbital border, it was deeply concave along the prefrontal border. The genera *Ophisaurus* and *Anguis*, as well as the genus *Anniella*, have the fron-

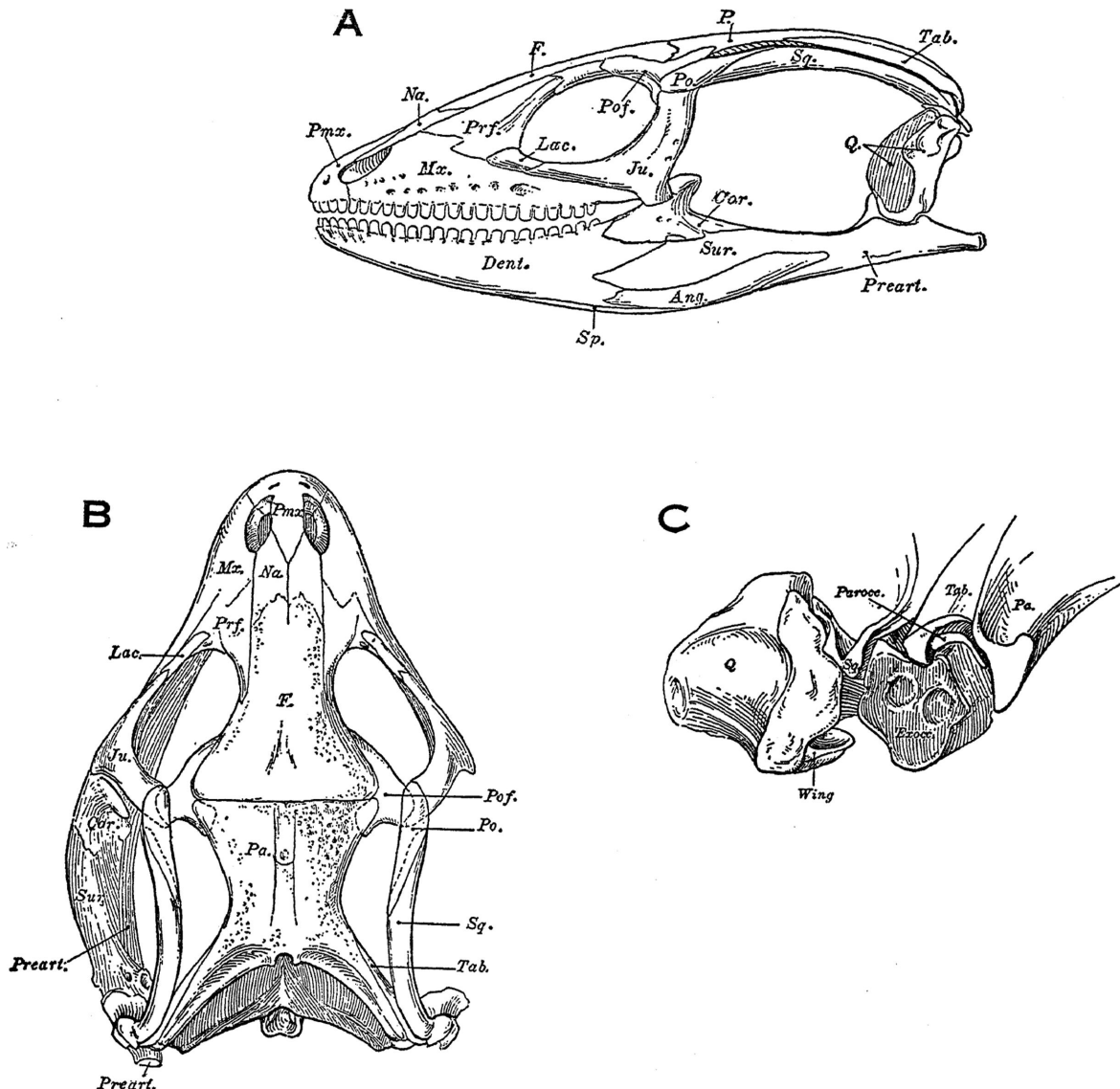


FIG. 6. *Melanosaurus maximus*. A. Lateral view of skull and mandible. B. Dorsal view of skull and left mandible. C. Transverse section through skull at tip of paroccipital process. *Abbreviations:* ang, angular; cor, coronoid; dent, dentary; exocc, paroccipital process, representing paroccipital fused to exoccipital; f, frontal; ju, jugal; lac, lacrimal; mx, maxilla; na, nasal; p and pa, parietal; parocc, small ossicle lying in ear region of xenosaurids, considered a paroccipital by Camp (1923) and by Gilmore (1928), here considered a stylohyal; pmx, premaxilla; po, postorbital; pof, postfrontal; preart, prearticular; prf, prefrontal; q, quadrate; sp, splenial; sq, squamosal of squamates; sur, surangular; tab, tabular; wing, internal wing of quadrate. Dorsal and lateral views of skull partially restored, particularly in premaxillary region. From Gilmore (1928).

tals distinct, but otherwise shaped much as in *Gerrhonotus*; however, in *Anguis* and *Ophisaurus* the osteoderm over the frontal has a straight lateral border simulating the condition in *Diploglossus* and *Celestus*.

6. Indications of a longitudinal crest along the temporal arch. This is distinctive of the xenosaurs.

In certain features *Melanosaurus* is more primitive than either *Xenosaurus* or *Shinisaurus*. Thus the frontal is less constricted between the orbits than in the modern genera; there are indications of large and regular head scutes upon the parietal and probably on the frontal as well; the postorbital and post-frontal are distinct; and teeth are present on the vomer and palatines, as well as on the pterygoids. The failure of the post-frontal to fuse with the postorbital is hard to explain, since the otherwise *Gerrhonotus*-like *Peltosaurus*, a contemporary of *Melanosaurus*, had these bones fused as in living xenosaurs, rather than separate as in living anguinids. *Melanosaurus* is also more primitive than the two living genera of xenosaurs in having large, partly imbricated osteoderms. It is quite possible that even in the Wasatch Eocene *Melanosaurus* was an antiquated and outmoded type of xenosaur, but what little evidence exists seems to indicate that the separation between *Shinisaurus* and *Xenosaurus* occurred at a post-Wasatchian time, since the two living genera share in common several specializations beyond the level attained by *Melanosaurus*.

In some features *Xenosaurus* is more like *Melanosaurus* than it is like *Shinisaurus*. Such features are: skull broad and depressed (usually so, in fact); dentary teeth numerous (21 in *Melanosaurus*, 22 in *Xenosaurus*); and teeth without even a trace of the slightly recurved shape seen in *Shinisaurus*. This would give additional evidence that the high, compressed skull of *Shinisaurus* is a specialization of that genus, as is the form of the individual teeth, and would further suggest that in the evolution of the Chinese genus there has been a reduction in dental number. On the whole, however, *Shinisaurus* appears to have retained more *Melanosaurus*-like features than has *Xenosaurus*. Thus *Shinisaurus* retains pterygoid teeth; large, albeit non-imbricate, osteoderms; a less expanded squamosal that

fails to suture with the parietal; and a less well-developed jugal-squamosal contact, there being no long jugal-squamosal suture as exists in *Xenosaurus*.

The next genus to be considered is *Necrosaurus* (long known by the invalid name *Palaeovaranus*) from the Quercy, and including *Melanosauroides* Kuhn (1940, p. 479), as pointed out by Hoffstetter (1943), from the middle Eocene of Europe. *Necrosaurus* has long been classified with *Varanus* in the Platynota, family Varanidae, but in 1943 Hoffstetter pointed out that the naris is not produced backward as a slit and that the vertebrae lack a strong precondylar constriction; for this reason he erected a family Necrosauridae, but left this family in the Platynota. The characteristics Hoffstetter put forth for separating the Necrosauridae from the Varanidae are equally strong in separating the Necrosauridae from the Platynota and ally the group with the Diploglossa. Examination of Kuhn's description and plate of *Necrosaurus* ("*Melanosauroides*") *maximus* and of Hoffstetter's description of *Necrosaurus cayluxi* indicates that *Necrosaurus* is closely related to the Xenosauridae, and particularly close to *Shinisaurus*. Both species have been found in association with osteoderms that are nearly identical with those of *Shinisaurus* in being oval in outline, without lips for imbrication with other osteoderms, provided with a median longitudinal keel but otherwise without sculpture, and in being relatively large (some nearly equal in length to the quadrate). No such osteoderms have been recorded for platynotans. The posterior half of the lower jaw of *N. maximus* shows all three of the posterior elements (articular, prearticular, and surangular) fused into a single compound bone, as in Diploglossa, but not as in Platynota. Unfortunately, knowledge of the mandible is as yet too incomplete to allow statements on the presence or absence of an intramandibular hinge, but nothing of the known jaw fragments suggests its presence.

In addition to the remarkably close resemblance to *Shinisaurus* in osteodermal structure there is a close similarity in dental form. The teeth are completely pleurodont, as in Diploglossa, rather than of the subpleurodont (with reduced buccal ankyloses)

type seen in *Platynota* and do not have the expanded proximal ends so characteristic of platynotan teeth. Instead of the sharp point and strong recurving seen in *Platynota*, the teeth are blunt and slightly recurved at the distal end, very much as in *Shinisaurus*. It would appear from Kuhn's plate of *N. maximus* that the number of dentary teeth did not exceed 18, and although the jaws he figures are broken and partly covered by other bones, it is also apparent that the dentary could not have borne fewer than 13 teeth.

The jugal of *N. maximus* is preserved but disarticulated. As in *Xenosauridae* it is much dilated. The frontals appear to have been fused, as in the xenosaurs, some anguinids, and some of the aigialosaurs and mosasaurs, but not the majority of *Platynota* and *Diploglossa*. The structure of the temporal arches, or even their presence or absence, cannot be determined.

The skull of *Necrosaurus maximus* is disarticulated and incomplete, but judging from the length of the quadrate relative to the width of the frontal and parietal, the general proportions of the head probably were of the deep and compressed form seen in *Shinisaurus*. Almost certainly they were not of the depressed and broadened form seen in *Melanosaurus* and *Xenosaurus*. On the other hand, the length of the frontal and parietal suggests that the skull was rather elongate, rather than shortened as in *Shinisaurus*.

While the dental form, osteoderm structure, and probable head form would seem to ally *Necrosaurus* with *Shinisaurus*, the middle Eocene genus is less specialized than the Recent *Shinisaurus*. According to Hoffstetter the maxilla and nasal form a suture in *Necrosaurus*, indicating that the fossil did not have the *Chamaeleo*-like snout, with prefrontal entering the narial border, seen in the Recent genus. The frontal, described by Hoffstetter, is certainly diploglossan in the failure of the subolfactory processes to join each other and in being (to judge from Kuhn) not especially large (as they are in *Lanthanotus*), but it appears to have been less emarginate between the orbits than in *Shinisaurus*, and more as in *Melanosaurus*. Hoffstetter says that the nasal process of the premaxillary is rather short, as it is in *Shinisaurus*, but not in *Xenosaurus* where it is rather long and

meets the frontal beneath the nasals. *Melanosaurus* is unknown in this respect.

According to Hoffstetter the caudal chevrons of *Necrosaurus* are of the varanid type of articulation. The caudal vertebrae of *Shinisaurus* have not been examined, but Barrows and Smith (1947, p. 255) describe the chevrons as intercentral and freely articulated in *Xenosaurus*, which is perhaps all that Hoffstetter means to imply by "les vertèbres caudales avec leurs os-chevrons articulés restent bien dans le style varanien."

It would appear, then, that in middle Eocene times a line of xenosaurids characterized by slight recurving of the teeth and at least some compression of the skull had already become distinct in the Old World. The fact that *Necrosaurus* had the frontal as broad between the orbits as in *Melanosaurus* also suggests that the resemblance between *Xenosaurus* and *Shinisaurus* in extreme frontal width is the result of parallelism. However, it must be remembered that both *Melanosaurus* and *Necrosaurus* were gigantic in size when compared to their Recent representatives, for the skull was probably in the neighborhood of 3 inches in length in the fossils, while the present-day forms have a cranial length scarcely exceeding an inch. Since it is a general rule that the orbit is relatively larger in small animals than in their larger relatives, and in ontogeny the eye grows less rapidly than the remainder of the head, it seems quite likely that the proportions of the frontal have here been influenced more by absolute size than by adaptive changes. When we compare the giant *Melanosaurus* and *Necrosaurus* with the equally gigantic *Glyptosaurus* and with the largest *Peltosaurus* skulls, as well as with large Recent *Diploglossus*, it appears that, size for size, the *Xenosauridae* have been characterized from their inception by a relatively narrow frontal, and that this has been accentuated in the living members by diminution in size.

The genus *Exostinus* was erected by Cope (1873, p. 16) for a frontal bone, jugal fragment, and a dentary with teeth, all from the *Oreodon* beds of the White River Oligocene (Cedar Creek, Colorado). In his original description Cope compared *Exostinus* with *Peltosaurus*, a true anguinid very closely related to the living *Gerrhonotus* and *Abronia*.

But later Cope (1900, p. 539) made the statement that *Exostinus* resembles *Xenosaurus* and may belong to the same family. Gilmore (1928), who nowhere shows evidence of having osteological material of *Xenosaurus*, tentatively assigned *Exostinus* to the Iguanidae, hinting at special affinities of the fossil with *Phrynosoma*.

In his decision Gilmore was influenced not only by a study of Cope's type but also by study of a second specimen referred to this species, this specimen apparently consisting in the main of both lower mandibles. Says Gilmore (1928, p. 23): "The coronoid is contracted anteroposteriorly and does not develop an anterior lateral process, as in many of the lizards, a feature that would at once separate it from all known extinct Anguinae." Reference to the figure accompanying Gilmore's description seems to show that what has actually happened is that a posteriorly directed process of the posterodorsal corner of the dentary overlaps the anterior corner of the coronoid bone laterally. Such a process is, indeed, absent from Anguinae, and also from *Xenosaurus* and *Melanosaurus*. But in *Shinisaurus* the process is present and very strong. The reference of *Exostinus* to the Xenosauridae appears to be established by the combination of the following characters: frontals narrow between the orbits, fused with each other, strongly sculptured dorsally, with rather weak and well-separated subolfactory processes ventrally, without anterior expansion; jugal dilated and sculptured on its external face; dentary with coronoid articulation as in *Shinisaurus*; tooth replacement alternate and interdental; teeth highly pleurodont, with unexpanded proximal ends, slightly recurved at their distal extremities (the teeth very much as in *Shinisaurus*).

In spite of its American distribution, *Exostinus* seems to be more like the Old World *Necrosaurus-Shinisaurus* group in dental form, dentary-coronoid articulation, and, to judge from the width of the frontal at its parietal border, narrowness of the skull. On the other hand, as Gilmore figures the jaw of the second specimen, *Exostinus serratus* Cope had the postarticular process of the mandible twisted and dilated as in the *Gerrhonotus*-like and *Diploglossus*-like Anguinae. Without more complete material *Exostinus* indicates

nothing more than that a xenosaurid occurred during Oligocene times in what is now one of the least tropical regions of North America.

In addition to ascribing an additional specimen to Cope's species *Exostinus serratus*, Gilmore (1928, p. 23) described a new species of *Exostinus* from the Lance, *Exostinus lancensis*. The time difference between Lance Cretaceous and *Oreodon* beds Oligocene is a great difference indeed, and one is therefore led to a certain degree of skepticism concerning the validity of referring the Lancean species to *Exostinus*. Nevertheless, *Exostinus lancensis* shows a maxillary sculpture, dental form, and dental succession exceedingly like those of *Shinisaurus*, and a referred parietal is described as sculptured anteriorly and smooth posteriorly, again as in *Shinisaurus*. However, *Exostinus lancensis* is too poorly known to give any definite information. There is a suggestive similarity in dental form between *Exostinus lancensis* and its contemporaries and compatriots *Parasaniwa obtusa* and *P. wyomingensis*.

Later, Gilmore (1941) described a facial region of a lizard from the North American Oligocene as *Exostinus*. Since this specimen was not accompanied by a frontal it is not positive that this specimen actually represents *Exostinus*, but the close similarity between dentitions of this specimen and of Cope's type makes it extremely probable that Gilmore's reference of the specimen to *Exostinus* is correct. The whole face is so encrusted with osteoderms (this in itself is evidence against iguanoid affinities) that cranial sutures cannot be made out, but the general shape is very much like that of *Shinisaurus*, but less abbreviated. The form of the individual teeth is as in *Shinisaurus*, and there is considerable resemblance in dental number, since Gilmore gives for the fossil: combined premaxillary count eight (six in *Shinisaurus*); maxillary 14 (as in *Shinisaurus*); dentary 14+ (15/16 in *Shinisaurus*). The vertically triangular form of the anterior naris seen in *Shinisaurus* is strongly suggested in the fossil. If the correctness of Gilmore's allocation of this fragment to *Exostinus* be assumed, it seems quite safe to say that *Exostinus* was an early xenosaurid quite closely related to the living *Shinisaurus*. Probably the two genera

can be distinguished by the presence of four premaxillary teeth in the fossil *Exostinus*, three in the living *Shinisaurus*.

This would appear to indicate that during Oligocene times, at least, *Shinisaurus*-like xenosaurids occurred in the Western Hemisphere and, should Gilmore's *Exostinus lancensis* prove to be a true *Exostinus*, in the uppermost Cretaceous. Gilmore has also ascribed some fragments from the Polecat Bench (upper Paleocene) to the genus *Exostinus* (Gilmore, 1942), but while these fragments appear to be xenosaurid they are not certainly referable to the genus *Exostinus*.

The possibility of such an early date for *Exostinus* as Lancean Cretaceous would suggest that the Wasatch *Melanosauroides* was a "persistent primitive" even in early Eocene times, and would therefore place the separation between the *Shinisaurus*-like and *Xenosaurus*-like forms in the late Cretaceous. However, until more complete remains of the Lancean xenosaurids are discovered any dis-

cussion of the date of separation of the two lines must be considered idle conjecture.

To summarize: *Shinisaurus* appears to be most closely related to *Xenosaurus* among living lizards, a relationship best expressed taxonomically by referring *Shinisaurus* to the Xenosauridae. The separation between *Shinisaurus* and *Xenosaurus*, however, appears to have been a relatively ancient one, for the middle Eocene *Necrosaurus* had already acquired the osteodermal structure so characteristic of *Shinisaurus*, and very probably the compressed skull as well. The Wasatchian *Melanosaurus* appears to be a very primitive xenosaurid that may have been ancestral to both the modern *Xenosaurus* and the *Shinisaurus*-*Necrosaurus* group. *Exostinus*, at least the Oligocene forms referred to that genus, is a North American genus very close to the Chinese *Shinisaurus*. In spite of a few superficial similarities, *Shinisaurus* has no affinities with *Lanthanotus* beyond being a member of the same infraorder (Anguimorpha).

## LANTHANOTUS COMPARED WITH HELODERMA

### HISTORICAL RÉSUMÉ

Boulenger (1885) provisionally placed *Lanthanotus* after the Helodermatidae, with the comment that it might constitute a distinct allied family, the Lanthanotidae, as proposed in the original description (Steindachner, 1878). Judging only by some of the external features, Shufeldt (1890) was inclined to doubt that *Lanthanotus* and *Heloderma* are closely related. Hoffmann (1890) the same year placed the two genera in separate families. Boulenger (1899), after examining roentgenograms of *Lanthanotus*, considered its affinities with *Heloderma* to be fully confirmed. De Rooij (1915) followed Boulenger and provided a description of the family Helodermatidae that included both genera.

Camp (1923) included *Lanthanotus* in the Helodermatidae, as implied by his listing of Borneo in the range of that family, but he said little concerning the supposed resemblances of *Heloderma*, except for a comment that both genera are included among the Anguimorpha possessing pterygoid teeth. In

his synopsis of the characters for the Helodermatidae (p. 501) he noted that the family possessed osteoderms, although these structures are all but absent in *Lanthanotus*. Indeed, Gadow (1901) had noted the difference between *Heloderma* and *Lanthanotus* in development of osteoderms and recognized the family Lanthanotidae, which he placed between the Helodermatidae and the Varanidae. Van Denburgh (1922) noted that the Helodermatidae contained a single genus, *Heloderma*, and thereby excluded *Lanthanotus*, which was not mentioned. More recently, Romer (1945) included Borneo within the range of the Helodermatidae, implying the inclusion of *Lanthanotus* in that family. But in the same year Loveridge (1945) listed the Lanthanotidae as a separate family.

### COMPARISONS

**EXTERNAL FEATURES:** There is some external resemblance of *Heloderma* to *Lanthanotus*, but the similarity largely is of a negative nature, that is, a resemblance resulting from the common absence of specializations seen in other lizards. Such resemblances would in-

clude the pentadactyl manus and pes, the cylindrical tail (modified by fat deposition in well-nourished *Heloderma suspectum*), the absence of sharp ridges or crests on the head, and the absence of the regular, large head plates of the Anguinidae. Lizards of the two genera are further alike in having a regular transverse arrangement of belly scales, a tail of moderate length (not much, if at all, longer than the body), and non-imbricate and transversely arranged body scales.

Resemblances that may be of a more positive nature are: the elongate torso and the shortened limbs with the appressed pes and manus failing to meet. The head of each is rather depressed, with rounded contours, bulging at the temples; the nostrils are separated from each other by a wide gap; the digits are rather short, the central three (ii, iii, and iv) subequal in length; the neck is rather long. Enlarged crestal scales are present, surrounded by granules.

But there are numerous important differences. *Heloderma* possesses a gular fold, while *Lanthanotus* does not. In *Heloderma* the tympanum is exposed and sunk in a deep and conspicuous external pit; in *Lanthanotus* there is no trace of an external ear. The lower eyelid of *Lanthanotus* possesses a transparent window, lacking in *Heloderma*. *Heloderma* has a well-differentiated head scutellation, in which it is possible to distinguish supralabials, infralabials, a rostral and post-rostrals, a mental and chin shields (genials), prenasals and postnasals, internasals, lorilabials, loreals, preoculars, suboculars, and canthals. In *Lanthanotus* there is no distinction of special head shields, and the regions covered by special shields in *Heloderma* are covered in *Lanthanotus* by granular skin. In *Heloderma* the digits bear on their plantar surfaces a single row of transversely dilated scales, whereas in *Lanthanotus* there are small granules on the plantar surfaces of the digits. In *Lanthanotus* the crestal scales are confined to a few special rows on the dorsal surface of the head and body, but in *Heloderma* they are evenly distributed over the entire dorsal surface and nearly conceal the granules, except when the skin is much stretched. *Heloderma* lacks scale organs (or "pits"), although these are present in rather specialized condition in *Lanthanotus*.

**TONGUE:** In both *Lanthanotus* and *Heloderma* the tongue is diploglossine, with a non-distensible anterior portion and an elastic posterior portion that serves both to extend and to ensheath the anterior moiety. But there are important differences. In *Heloderma* the distinction between anterior and posterior portion is more vague and gradual than in *Lanthanotus*, the elongated and pointed papillae of the hind portion grading into small nodular papillae on the fore portion of the tongue in *Heloderma*, while in *Lanthanotus* the elongated, club-shaped papillae of the hind portion are abruptly replaced by poorly defined flat, squamous papillae on the fore portion. In *Heloderma* there are a feeble fold and a groove separating the anterior and posterior portions of the tongue, the groove being poorly defined even when the tongue is retracted. But there is a very strong transverse fold, enclosing an anterior pocket, in *Lanthanotus*; this fold distinguishes fore tongue and hind tongue even when the tongue is moderately extended. In both *Heloderma* and *Lanthanotus* the tongue is deeply bifurcate anteriorly, but in *Heloderma* the tines are wide and triangular, while in *Lanthanotus*, the tines are slender and whip-like. The fore tongue of *Heloderma* is of a triangular form, widening out to merge with the wide hind tongue. In *Lanthanotus* the fore tongue is parallel-sided and narrow, and the transition in width from fore tongue to hind tongue is abrupt.

**OSTEODERMS:** In adult *Heloderma* the osteodermal covering of the dorsal surface of the body, head, and tail is complete. The osteodermal covering of the head is particularly well developed, and the osteoderms are closely bound to the skull, fusing with the parietals, frontal, nasals, prefrontals, and post-frontal. In addition, osteoderms roof the temporal region and are present on the pre-anal region as well as on the anterior surfaces of the limbs.

In *Lanthanotus* there are no osteoderms on the limbs. On the body and tail osteoderms are found only in the crestals of the modified scale rows. On the head, the osteoderms are few and confined to the following regions: a temporal row running from the orbit to the quadrate, apparently marking the position of a former temporal arch; a smaller row of

three minute nodules, running parallel to the anterior portion of the lateral border of the parietal; a small row on the lower temporal region; and a few on the occipital region that represent anterior continuations of the crestal rows of the neck.

In *Lanthanotus* the osteoderms are quite free of the skull. There are no osteoderms bordering the nostril or orbit in *Lanthanotus*, a further difference from *Heloderma*.

In *Heloderma* there are three transverse rows of osteoderms for each thoracic vertebra, two for each caudal; in *Lanthanotus* there is one row of osteoderms for each caudal vertebra.

**SKULL:** There is some resemblance between *Heloderma* and *Lanthanotus* in general form of the skull. In both, the skull is depressed, with a short and rounded muzzle, with the jugal strongly arched outward beneath the orbit to form a rather mammal-like malar eminence, with a complete postorbital arch, without a temporal arch, without a pineal foramen, with a flat dorsal surface of the parietal area, there being no sagittal crest, with strong, recurved teeth on the margins of the jaws, and with small teeth on the palatine and pterygoid.

On the other hand, there are also important differences in general cranial form: the brain case of *Heloderma* shows no indication of the elongation seen in *Lanthanotus*; the frontal is much broader in *Heloderma* than in *Lanthanotus*, so that the orbits are directed more dorsally in the latter genus than in the former; the skull is broadest across the jugals in *Heloderma*, but broadest across the quadrates in *Lanthanotus*.

In both *Heloderma* and *Lanthanotus* the premaxilla is small, solidly coössified to its partner, and bears approximately (variable in *Heloderma*) four small, simple, recurved teeth. In both, the bone makes extensive contact with the septomaxilla on its internal surface and unites with the maxilla to form a rather short suture beneath the anteroventral corner of the external naris. But there is a considerable difference in the form of the premaxilla between the two genera. In *Heloderma* the coössified premaxillae form a T-shaped structure, the longitudinally oriented ascending process meeting the transversely oriented dental process at a right angle. In

*Lanthanotus* the ascending process grades evenly into the dental process, forming a gently curved lateral margin and giving the conjoined premaxillae a roughly triangular form.

In both *Lanthanotus* and *Heloderma* the nasal is separated from the maxilla and prefrontal by a posterior extension of the external naris, the nasal forming a straight suture anteriorly with the ascending process of the premaxilla, a longer, V-shaped suture posteriorly with the frontal; otherwise, the bone is isolated. In both genera the lateral border of the nasal is notched anteriorly, the notch presumably indicating the position of the fleshy nasal capsule. But in *Heloderma* the nasals are separate from each other, as in the Anguinidae, while in *Lanthanotus* the nasals are coössified, as in the Varanidae.

In both *Heloderma* and *Lanthanotus* the maxilla has its articular surface for the palatine far posterior and adjacent to the articular surface for the ectopterygoid, the maxilla being excluded from the suborbital fenestra by a palatine-ectopterygoid juncture. In both genera the median margin of the palatal plate of the maxilla is curled downward anteriorly, so that a vague fossa, median to the tooth row, is formed on the anterior palatal surface of the bone. The sutural connections of the maxilla are the same in the two genera: antero-externally, with the premaxilla; antero-internally, with the septomaxilla; postero-externally, with the prefrontal, lacrimal, and jugal; posteroventrally, with the ectopterygoid and palatine; internally, bordering the choana; dorsally, bordering the external naris. In both genera the maxillary teeth are few in number (less than a dozen), are strongly recurved and pointed; they are solid, fused in pleurodont fashion to the internal surface of the external edge of the maxilla, and bear a fluting of fine longitudinal grooves at the base. But in *Lanthanotus* the palatine process of the maxilla, for the reception of the anterior end of the palatine bone, is distinct and marked off from the median border of the palatal plate of the maxilla by a distinct notch, while in *Heloderma* the mesial border of the palatal plate is a smooth curve, without distinction of a palatine process.

The maxillary teeth of *Lanthanotus* are sub-

equal, but in *Heloderma* there is a marked enlargement of the teeth in the middle of the series, the teeth becoming much shorter both

*derma* bear a deep groove on the antero-internal face and a shallower groove on the postero-internal face (see Odermatt, 1940);

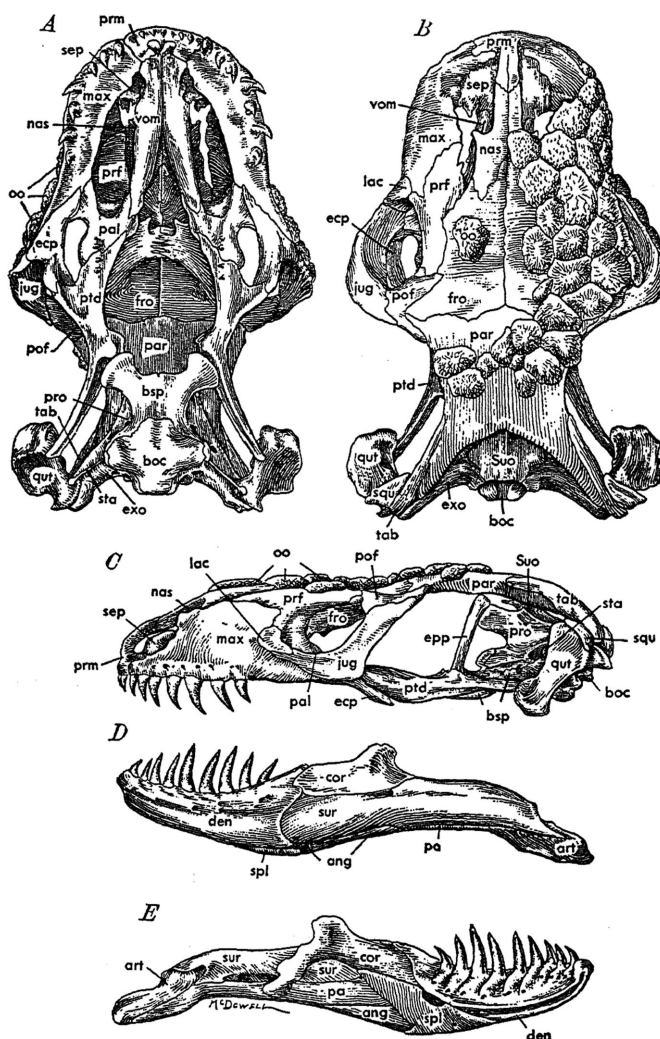


FIG. 7. *Heloderma horridum*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell, after a drawing by Alma Froderstrom.

forward and posteriorly. In *Lanthanotus* the crowns of the teeth are compressed into recurved hooks of longitudinally elliptical cross section; in *Heloderma* the crowns are approximately circular in cross section. Most striking of all, the maxillary teeth of *Helo-*

there is no trace of such grooving in *Lanthanotus*.

*Heloderma* and *Lanthanotus* resemble each other in possessing a lacrimal and in lacking a palpebral bone.

The prefrontal bone has almost the same

sutural relationships in the two genera: posterodorsally, as well as internally, with the frontal; externally, with the lacrimal and maxilla; internally, with the palatine. There is a difference between the two genera in the construction of the lacrimal foramen, a difference that causes the prefrontal of *Heloderma* to articulate with the jugal, in addition to the articulations named above. In *Heloderma* the orbital surface of the lacrimal bone is simple and the lacrimal foramen is single; in *Lanthanotus* the orbital border of the lacrimal bears a mesially directed pillar, which joins the prefrontal to divide the lacrimal foramen in two, a dorsal foramen and a ventral. This ventral foramen of *Lanthanotus* is bordered ventrally by the lacrimal and palatine, which form a suture. In *Heloderma*, on the other hand, the jugal extends forward to border the (single) lacrimal foramen ventrally, making contact with the prefrontal and separating the lacrimal from the palatine. There is close agreement between *Heloderma* and *Lanthanotus* in the relationships of the posterior or supraorbital process of the prefrontal; in both genera it extends back to make a short contact with the post-frontal. In *Lanthanotus* this prefrontal-post-frontal contact does not exclude the frontal from the orbital margin, however, for a small isolated portion of the frontal may be seen in dorsal view bordering the orbit at the region of the prefrontal-post-frontal contact. Some *Heloderma* skulls show this feature as well, but many have the frontal completely excluded from the orbital rim. (See fig. 7.)

The frontals of *Heloderma* are similar to those of *Lanthanotus* in being paired, in forming the extreme posterior border of the external naris, and in having strong descending processes. In both *Heloderma* and *Lanthanotus* the descending processes are much stronger than in lizards of such families as the Anguinidae and Xenosauridae, and may be seen in lateral view to run the entire length of the orbit, rather than to fade out posteriorly as they do in the anguinoids. In both *Heloderma* and *Lanthanotus* the descending process of the frontal is in contact with the dorsal surface of the palatine; in *Heloderma* the contact is very slight, while in the Bornean genus the contact is more ex-

tensive, and a distinct suture is formed. Even in *Lanthanotus*, however, the contact is reduced, for the vomer intervenes anteriorly to form a suture with the descending process of the frontal and excludes the latter from the palatine. In *Heloderma* the vomer is separated from the frontal by a gap. The descending frontal laminae of *Heloderma* meet one another beneath the olfactory tracts in an interdigitating suture; in *Lanthanotus* the laminae are separated from each other by a gap, presumably filled in life by the cartilage of the cultriform process of the sphenoid (trabeculae cranii). Even though *Lanthanotus* lacks the median contact of the descending laminae, that genus possesses much stronger descending laminae than does *Heloderma*. The posterior border of the lamina slopes downward and forward in *Heloderma*, but in *Lanthanotus* the border slopes downward and backward, so that the most posterior portion of the lamina is also the most ventral. Moreover the laminae of *Heloderma* descend for only half of the depth of the orbit, while those of *Lanthanotus* descend the full depth of the orbit. The result is that while the orbits of *Heloderma* are rather broadly continuous with each other both ventrally and posteriorly, those of *Lanthanotus* are separated from each other by a double interorbital septum formed of the descending processes of the frontals. As mentioned above, the frontals of *Heloderma* are proportionately much broader than those of *Lanthanotus*.

Both *Heloderma* and *Lanthanotus* possess a strong, triangular, post-frontal bone, which is devoid of a temporal process. In both genera the postorbital is apparently absent, but as noted above the postorbital of *Lanthanotus* is probably present but fused to the jugal, while the postorbital of *Heloderma* appears to be truly lacking. There is a strong jugal in both genera, but the shape of the bone in the Bornean form differs from that in the American genus. In *Heloderma* the postorbital portion of the jugal is compressed and flattened into a strap-like arch; in *Lanthanotus* the postorbital portion is of rounded, prismatic form. In *Heloderma* the dorsal extremity of the jugal is broadly excluded from the parietal by the post-frontal. Moreover, this dorsal extremity is expanded. In *Lanthanotus* the dorsal extremity of the jugal

(probably representing the fused postorbital) is bluntly pointed and extends along the postero-internal border of the post-frontal to meet the parietal. In *Heloderma* the jugal is L-shaped, there being a rather sharp angulation between the horizontal suborbital portion of the bone and the roughly vertical postorbital portion. The posterior border of the bone bears, at the point of angulation, a short and obtuse process that is directed downward and backward. In *Lanthanotus* the jugal arch forms a smooth and unbroken curve from the maxilla to the parietal, and there is no suggestion of a posteroventral process. As mentioned above, the jugal of *Heloderma* extends far forward to border the lacrimal foramen ventrally, even extending through the foramen for a short distance into the olfactory chamber. In *Lanthanotus* the jugal is of much shorter anterior extent and does not reach the lacrimal foramen. In *Heloderma* the jugal excludes the ectopterygoid from the lateral border of the skull; in *Lanthanotus* the ectopterygoid is permitted entrance to the lateral border of the skull posteroventrally to the jugal-maxillary articulation. In *Heloderma* the jugal is met by a process of the pterygoid that extends along the dorsal surface of the ectopterygoid; in *Lanthanotus* the jugal and pterygoid are well separated.

Both *Lanthanotus* and *Heloderma* have a pair of large septomaxillary bones, the usual condition in the Squamata, but the two genera differ considerably in the form of these elements. In *Heloderma* the median vertical lamina of the bone extends farther posteriorly than does the horizontal lateral plate, whereas the reverse is true in *Lanthanotus*. In *Lanthanotus* the lateral border of the bone is turned upward into a strong ascending lateral pillar, but in *Heloderma* this pillar is represented only by a minute spine.

The vomers are very different in the two genera. In both, the vomer articulates anteriorly with the premaxilla (and sometimes in *Heloderma* with the extreme antero-internal corner of the maxilla) and septomaxilla; posteriorly it articulates with the internal process of the palatine. But in *Lanthanotus* there is an additional articulation posteriorly with the descending lamina of the frontal, as noted above. In *Heloderma* the vomers are

separated from each other for at least their posterior halves by a triangular gap; in *Lanthanotus* the vomers are in contact with each other except at their extreme posterior ends. In *Lanthanotus* the mesial border of the vomer is curled up to form the ventral half of the internasal septum; in *Heloderma* the mesial border is not at all curled up, and the internasal septum is formed of membranous connective tissue. In *Lanthanotus* the lateral border of the vomer is produced outward as a large obtusely triangular plate, so that the combined vomers are rhomboidal in shape; in *Heloderma* the lateral border of the vomer is straight or even slightly concave, the combined vomers forming a chevron-like figure. The vomer is deeply constricted immediately posterior to its anterior termination in *Lanthanotus*, but in *Heloderma* the constriction is hardly noticeable.

The palatine of both *Heloderma* and *Lanthanotus*, as in lizards generally, is a triradiate structure, there being an internal process that runs forward to articulate with the vomer, an external process that bears the sphenopalatine canal and runs forward to articulate with the maxilla and ectopterygoid, and a posterior process that runs backward to articulate with the pterygoid. In both *Heloderma horridum* and *Lanthanotus* the posterior process bears two or three very small teeth, and in both genera the external process forms a strong suture with the antero-internal border of the ectopterygoid, thus excluding the maxilla from the suborbital fenestra, and the dorsal surface of the external process is articulated to the ventral border of the orbital plate of the prefrontal. But in *Lanthanotus* the external process of the palatine is extended laterally to meet the lacrimal and form part of the border of the lacrimal foramen; in *Heloderma* the palatine is excluded from the lacrimal bone and foramen by the jugal, as noted above. The cleft between the external and internal processes of the palatine is considerably deeper in *Lanthanotus* than in *Heloderma*.

The ectopterygoid of both genera articulates anteriorly with the palatine, maxilla, and jugal, posteriorly with the lateral process of the pterygoid. In *Heloderma* the articulation between jugal and ectopterygoid is much reduced by the intervention of the maxilla,

and the jugal excludes the ectopterygoid from the lateral border of the skull. In *Lanthanotus* the articulation between jugal and ectopterygoid is extensive, and the ectopterygoid enters the lateral surface of the skull.

The pterygoid in both genera, as in most lizards, is a triradiate structure, there being an internal process articulating with the palatine, a lateral process articulating with the ectopterygoid, and a posterior process, the median surface of which abuts the basiptyergoid process and extends backward to form a loose and ligamental articulation with the quadrate. In both genera the pterygoid is toothed anteriorly, this pterygoid tooth row being a continuation of the palatine row. But the tooth row of *Lanthanotus* is much longer than that of *Heloderma* and runs back nearly to the basiptyergoid articulation, whereas that of *Heloderma* is confined to the portion of the internal process anterior to the base of the lateral process. There are about 10 teeth in the pterygoid row of *Lanthanotus*, less than half that number of teeth in *Heloderma*. In *Heloderma* the lateral process extends over the dorsal surface of the ectopterygoid to meet the jugal, but this is not the case in *Lanthanotus*. In both genera the basiptyergoid facet is well formed as a longitudinal groove on the medial surface of the posterior process of the pterygoid, about at the midpoint of the bone, and in both genera there is a tab-like process that fits beneath the anterior corner of the basiptyergoid process in articulation. But there is a difference in the form of the pterygoid posterior to the basiptyergoid articulation. In *Heloderma* the posterior process is undilated and prismatic in form, but in *Lanthanotus* the bone is posteriorly dilated and compressed like the blade of a goose quill.

The parietals of *Heloderma* are similar to those of *Lanthanotus* in being fused and in lacking a pineal foramen. In both genera the posterolateral corner of the bone is drawn out into a long process that extends to the region of the cranioquadrate articulation and bears the tabular bone. In both genera the medial portion of the dorsal surface of the parietal is flat, there being no sagittal crest. But this latter resemblance is more apparent than real, for the condition in *Lanthanotus* is really much more like the sagittal crest of *Varanus*

than like the flat parietal of *Heloderma*. The temporal muscles of *Heloderma* never extend to the dorsal surface of the parietal, but instead originate from the ventral surface of the lateral border of the parietal bone, where they leave a deep muscular scar. In *Lanthanotus* there is no muscular scar on the ventral surface of the parietal, and presumably no muscle originates from the ventral parietal surface. Instead, the temporalis<sup>1</sup> originates from the lateral border of the dorsal surface of the bone, leaving a deep crescentic scar on the lateral dorsal surface of the parietal. The flat middle portion of the parietals of *Lanthanotus* would thus correspond to the sagittal crest of some varanids. The situation is analogous to that in many groups of mammals, in which the smaller forms of a group may have paired lyrriform crests for the temporalis, with a median amuscular portion (in the foxes, for example), while the larger forms may have the temporal muscles extended high on the head to originate from a median sagittal crest (as in the wolves). The posterior margin of the fused parietal mass of *Lanthanotus* is deeply but roundly emarginate as in *Heloderma*. Unlike *Heloderma*, however, *Lanthanotus* has deep V-shaped muscle scars near the midline of the posterior portion of the dorsal surface of the parietals, these scars indicating the insertion of the nuchal muscles. In *Heloderma* the insertion of the nuchal muscles is marked only by a vague gutter running parallel to the posterior border of the parietal for most of the width of the latter. The parietals of *Lanthanotus* are relatively much longer than those of *Heloderma*, in conjunction with the elongation of the posterior part of the skull in *Lanthanotus*. In *Heloderma* the parietals extend out some distance lateral to the juncture of the parietal with the epiptyergoid

<sup>1</sup> Adams (1919) terms the reptilian adductor of the mandible the *M. capiti-mandibularis* as distinct from the mammalian *M. temporalis*. His reason appears to be that the capiti-mandibularis of reptiles has given rise not only to the temporalis of mammals, but to the pterygoideus group and massetericus as well. But the portion of the reptilian capiti-mandibularis here in question, the part originating from the dorsal part of the brain case, appears both from its innervation and its origin and insertion to be homologous with the *M. temporalis* of man and the other mammals. For that reason we use the term common in human anatomy.

and pro-otic, and the pro-otic-parietal articulation is very short. This is not the case in *Lanihanotus*, for in that form the lateral border of the parietal runs parallel and adjacent to the dorsal border of the pro-otic, and the dorsal head of the epipterygoid is exposed to dorsal view, rather than concealed by the parietal as in *Heloderma*. The juncture between pro-otic and parietal is very extensive in *Lanihanotus*, and the entire dorsal border of the pro-otic is pressed against the parietal. In *Heloderma* there is no direct union between supraoccipital and parietal, cartilage intervening between the two bones. But in *Lanihanotus* the supraoccipital makes a long suture with the posterior edge of the parietal. Although *Heloderma* resembles *Lanihanotus* in lacking any external indication of a pineal, there is a deep pit on the ventral side of the parietal of *Heloderma*, indicating the position of the epiphysis, which is not even suggested in *Lanihanotus*. Were the epiphyseal pit of *Heloderma* to penetrate the parietals as a pineal foramen it would be much farther back than in the majority of lizards, as it would be in the posterior half of the parietal mass. This would be suggestive of the fossil varanid *Telmasaurus* (cf. Gilmore, 1943, pp. 379-381, fig. 17).

In both *Heloderma* and *Lanihanotus* the tabular is long and attached to the lateral surface of the posterolateral process of the parietal. In both it is produced backward and downward to meet the quadrate, squamosal, and quadratic process of the exoccipital ("paroccipital" of Cope) and to exclude the parietal from the quadrate. In both genera the squamosal is reduced to a small triangular bone attached to the dorsal extremity of the quadrate.

*Heloderma* resembles *Lanihanotus* in having no internal conch or flange on the shaft of the quadrate, but the two genera differ greatly in the development of the external conch of the quadrate. In *Heloderma* the external conch is large, with a rounded, convex outer margin that embraces an extensive posterior fossa. In *Lanihanotus* the conch is reduced to a rather low and straight lateral vertical crest on the shaft of the quadrate, with straight border and without posterior fossa. This is presumably a reflection of the differences between the two genera in ear de-

velopment, for the border of the external conch of the quadrate typically serves to suspend the anterior portion of the tympanic membrane, while the posterior fossa of the conch actually represents the anterior portion of the mesotic fossa, the quadrate forming the anterior wall of the middle ear.

In both genera the ventral foot of the epipterygoid is set upon the dorsal surface of the pterygoid, just slightly anterior to the basiptyergoid articulation, and the dorsal extremity of the epipterygoid ("columella cranii") articulates with the anterodorsal corner of the pro-otic and the pro-otic flange of the parietal. In both genera the epipterygoid is relatively short and stout (in accord with the depression of the skull) and nearly straight. In *Lanihanotus* the bone is nearly vertical, but in *Heloderma* as the bone ascends it also is inclined somewhat backward and inward.

The sphenoid of *Heloderma* is fused to the basioccipital, but that of *Lanihanotus* is separated from the basioccipital by a strongly arched suture. In both genera there is a pair of strong and pedunculate basiptyergoid processes near the anterior extremity of the sphenoid, but the processes are more widely separated from each other in *Lanihanotus* than in *Heloderma*. In both genera the pituitary fossa is deep, located between the basiptyergoid processes, and marked off posteriorly from the cranial chamber by a strong clinoid ridge, which bears the abducent foramina. In neither genus is the cultriform process ossified, its place being taken functionally by the trabecular cartilage. A marked difference between the two genera is the form of the canal for the entocarotid artery and Vidian nerve (petrosal nerves). (It may be noted here that dissection of *Heloderma suspectum* reveals that the vessel in question is homologous to the entocarotid of mammals, since it is enwrapped in the tympanic plexus, even though it does not enter the cranial chamber.) In *Heloderma* the entrance to the canal is located far back at the posterior extremity of the lateroventral surface of the sphenoid. The canal continues forward for almost the entire length of the sphenoid to its exit at the base of the anterior border of the basiptyergoid process. On the external surface of the sphenoid of *Heloderma*, lateral

to the underlying entocarotid-Vidian canal, there is a longitudinal groove overhung by a ledge of bone for the pterygoid musculature; this appears to be the remnant of a considerably larger fossa (the so-called "carotid fossa") seen in anguine and xenosaurs and particularly prominent in cordylids and gekkotans. In *Lanthanotus*, on the other hand, the entrance to the carotid-Vidian canal is in the anterior portion of the sphenoid, just behind the base of the basiptyergoid process, the point of exit being as in *Heloderma*. There is no "carotid fossa." In accordance with the more elongate posterior portion of the skull, the sphenoid of *Lanthanotus* is relatively much longer than that of *Heloderma*.

The basioccipital of *Lanthanotus* has much weaker muscular tubera than does that of *Heloderma*. The ventral muscular tuber of the exoccipital in *Lanthanotus* is completely exposed to ventral view and forms, together with the more anterior tuber of the basioccipital, a continuous horizontal lateral crest beneath the lateral aperture. In *Heloderma* the tuber of the exoccipital is largely dorsal to the tuber of the basioccipital, hence largely concealed from ventral view, and forms an angulated crest, together with the basioccipital tuber, which is both ventral and posterior to the lateral aperture. The lateral aperture (in *Heloderma* for the internal jugular vein, glossopharyngeal, vagal, and accessory nerves), lying just above the tuber of the basioccipital and bordered by the basioccipital, exoccipital, and opisthotic, is large (larger than the fenestra ovalis) and vertically elliptic in *Heloderma*. In *Lanthanotus* the aperture is much smaller (smaller than the fenestra ovalis) and horizontally laceriform. The occipital condyle of both genera is of the normal lacertilian type, being reniform and composed of the basioccipital medianly and of the exoccipitals laterally.

The foramen magnum is also quite normal, being bordered by the supraoccipital dorsally, exoccipital laterally, and (narrowly) by the basioccipital ventrally. The hypoglossal foramen of *Lanthanotus* is relatively larger than that of *Heloderma*. The paroccipital process (opisthotic and exoccipital coössified), which is the chief support of the quadrate in both genera, is shorter and stouter in *Lanthanotus* than in *Heloderma*. In both genera the pro-

otic sends back a process along the anterodorsal surface of the paroccipital process to meet the posterior extremity of the tabular. In both genera the tuber of the exoccipital is set off from the base of the paroccipital process by a notch, so that the base of the stapes is visible from a ventral view.

In both *Heloderma* and *Lanthanotus* the pro-otic is produced far anterior to the endotic capsule along the sphenoid border. In both genera the anterodorsal portion of the pro-otic is produced forward to meet the head of the epiptyergoid, and in both genera this dorsal anterior process is separated from the ventral anterior process by a deep emargination for the fifth nerve and stapedia artery. In *Lanthanotus* the dorsal process of the bone extends farther forward than the ventral, while the reverse is true in *Heloderma*. More important, however, is the form of the dorsal border of the pro-otic. In *Heloderma* there is a strong emargination in the dorsal border of the pro-otic behind the tip of the anterodorsal (epiptyergoid) process, the emargination extending back to the pro-otic-supraoccipital suture; thus the pro-otic articulates with the parietal only at its more anterior point. In *Lanthanotus* the dorsal border of the pro-otic is straight, from its articulation with the epiptyergoid to its articulation with the supraoccipital, and in continuous contact with the parietal. The pro-otics of *Heloderma* converge towards each other at their juncture with the supraoccipital and are separated from each other by that bone for a distance less than the width of the occipital condyle. In *Lanthanotus* the pro-otics are parallel and separated from each other by the supraoccipital for a distance greater than the width of the foramen magnum.

In both *Heloderma* and *Lanthanotus* the supraoccipital is large, with a low sagittal keel, and borders the foramen magnum. In *Heloderma* the bone extends under the parietals to attach, by means of intervening cartilage, to the ventral surface of the parietals some distance anterior to the posterior border of the latter bones. In *Lanthanotus* the supraoccipital is articulated to the posterior-most border of the parietal by direct contact. In *Heloderma* the supraoccipital is strongly inclined and is acuminate anteriorly; in *Lanthanotus* the supraoccipital is nearly horizon-

tal and is broadly truncate anteriorly.

The stapes extends from the fenestra ovalis to the quadrate in both genera. In *Heloderma* the bone is slender and clubbed at the end, but in *Lanthanotus* the bone is stout and tapers to a blunt point.

The lower jaw is about equal in length to the premaxillary-condylar length of the skull in both genera; in both it consists of the same elements: dentary, splenial, coronoid, angular, and surangular. In both genera the tooth row is much less than half as long as the jaw and consists of a relatively small number of teeth (about 13 in *Lanthanotus*, nine or 10 in *Heloderma*), and the teeth are sharply pointed and recurved. The lower jaw of *Heloderma* is much heavier than that of *Lanthanotus* and distinctly curved sigmoidally, while that of *Lanthanotus* is nearly straight.

The dentary of *Lanthanotus* is relatively longer than that of *Heloderma*, as might be expected from the larger number of mandibular teeth in the former genus. In both genera the teeth are solid, pleurodont, and recurved, with a fine fluting of grooves at the base, the grooves being very small. In *Heloderma* there are an additional anterior and a posterior venom groove, as in the maxillary dentition, these grooves being conspicuous and deep, at least the anterior groove; there are no such grooves in *Lanthanotus*.

The most striking feature of *Lanthanotus* setting it off from *Heloderma* is the presence in the Bornean genus of the "varanoid hinge" in the lower jaw. In *Lanthanotus*, as in monitors, mosasaurs, and their closer allies, the suture of the dentary with the surangular is replaced by a much looser articulation, and the surangular border of the dentary is nearly straight. This is the extent of hinge development of the monitors (*Varanus*), but *Lanthanotus* has gone even farther in hinge development: in *Varanus* the splenial on the inner side of the jaw is extended well behind the level of the lateral hinge, being produced along the ventral border of the mesial surface of the coronoid; in *Lanthanotus* the sutures of the bones of the mesial surface of the jaw are aligned to form a vertical joint corresponding in position to the lateral dentary-surangular hinge. The articulation of the splenial with the angular and prearticular is vertical and is in line with the vertical suture

between the mesial surfaces of the coronoid and dentary.<sup>1</sup> In *Heloderma suspectum* there is no suggestion of the hinge; the surangular edge of the dentary is emarginate; the splenial is produced back along the ventral border of the mesial surface of the coronoid; the suture between the splenial and the angular and prearticular is diagonal and not at all in line with the equally diagonal internal coronoid-dentary suture. In *Heloderma horridum*, however, there is a suggestion of the hinge on the outer surface of the lower jaw. But there is no suggestion of a joint on the inner surface (see fig. 7). In both the living species of *Heloderma* (figs. 7, 32), the splenial is in contact with the surangular on the mesial surface of the jaw, separating the coronoid from the prearticular.

There seem to be no other important differences between the two genera in the form of the lower jaw except in the splenial-dentary articulation. In *Lanthanotus* the Meckelian groove is open, separating splenial from dentary except at the extreme posterior portion of the splenial, where that bone sends up a small tab-like process to meet the dentary. In *Heloderma* the Meckelian groove is always open at the extreme posterior end, but may or may not be closed for a short distance slightly anterior to this. In both genera the dentary rises high behind the tooth row, but in *Heloderma* the splenial is also high at this point, rising above the midpoint of the depth of the jaw at the posterior end of the dentary. In *Lanthanotus* the splenial does not reach the midpoint of the depth of the jaw. In both genera the muscular process (for the temporalis) of the coronoid bone is in hind half of that bone and does not rise immediately behind the dentary as it does in anguroids. In both genera the postarticular process for the depressor mandibulae is of moderate size, and there is no inward or outward process at the mandibuloquadratic articulation.

**HYOID APPARATUS:** In both *Heloderma* and *Lanthanotus* the hyoid is of a rather simplified, and presumably advanced, type, and the two genera are in fairly close agreement. In both, the glossohyal is long, slender, and

<sup>1</sup> The mosasaurs have this joint much modified as a specialized hinge, as described by J. T. Gregory (1951).

pointed. In the form of the posterior extremity of the glossohyal, however, there are differences: in *Heloderma* the glossohyal is but moderately expanded posteriorly, the expansion forming a spoon-like dilation; in *Lanthanotus* the glossohyal is abruptly expanded posteriorly into a T-shaped figure, the left hypohyal and ceratobranchial being widely separated from the right hypohyal and ceratobranchial. In both *Heloderma* and *Lanthanotus* the hypohyal is simple and cylindrical, but the element appears to be considerably more elongate in *Lanthanotus* than in *Heloderma*, for in the former genus it extends forward beyond the glossohyal, while in the latter it is only half as long as the glossohyal. An important difference between *Heloderma* and *Lanthanotus* is that the former retains slender and hook-shaped ceratohyals, while these elements are entirely lacking in the latter genus. In both genera there is but one pair of ceratobranchials, the first. The ceratobranchials in both *Lanthanotus* and *Heloderma* are long, gently sigmoidal, cylindrical bones terminated by a very short epibranchial.

**VERTEBRAL COLUMN AND RIBS:** Of *Lanthanotus* we have but the axis prepared; however, a very good series of roentgenograms of this lizard permits some knowledge of the postcranial skeleton. *Heloderma* is represented in our collections by skeletons of both of the two species.

The vertebral form of *Lanthanotus* is rather different from that of *Heloderma*. Though both have the central condyle slightly oblique (to judge from the axis and lateral roentgenogram of *Lanthanotus*) and wider than deep, and have the centrum tapered posteriorly, the condyle of *Heloderma* is no wider than the centrum anterior to it, so that no constriction of the centrum is apparent. In *Lanthanotus* the centrum is very much as in *Varanus*, as may be seen both from the form of the axis and from the roentgenogram of the vertebrae of the shoulder region; the centrum is constricted just anterior to the condyle, and the condyle is much wider than the centrum immediately before it. The intercentrum of cervical iii, which forms the hypapophysis of the axis, is nodular in form in *Heloderma* and conspicuously discontinuous with the haemal carina

of the axis; in *Lanthanotus* the intercentrum is compressed and would appear to be but a continuation of the haemal carina were it not for the suture, which may be made out by careful observation. It appears from the roentgenogram that at least the more posterior thoracic vertebrae of *Lanthanotus* bear neural spines, which are compressed and rectangular in form, and run the length of the midline of the neural arch. In *Heloderma* the neural spines are all but slightly compressed and arise only from the more posterior half of the neural arch.

As to ribs, *Heloderma* has two lumbar vertebrae (presacrals without free ribs) and four sternal ribs. In *Lanthanotus* there appear to be but one lumbar vertebra and three sternal ribs.

**LIMBS AND LIMB GIRDLES:** The clavicle of both *Heloderma* and *Lanthanotus* appears to be simple, undilated, and imperforate. Both genera appear to agree in the possession of a simple interclavicle without transverse processes. No important departures in structure of the scapula from the condition in *Heloderma* are apparent in the roentgenogram of *Lanthanotus*, but *Lanthanotus* appears to have the coracoid doubly emarginate anteriorly rather than entire, as it is in *Heloderma*. In *Lanthanotus* the phalangeal formula of both manus and pes is 2-3-4-4-3, while *Heloderma* has the more normal 2-3-4-5-3.

#### DISCUSSION AND CONCLUSIONS

It would appear that *Lanthanotus* and *Heloderma* have a large number of anatomical features in common; the more important of these features appear to be:

1. Posterior prolongation of the external naris.
2. Shortening of the dental rows.
3. Subpleurodont, recurved teeth.
4. Formation of the suborbital fenestra.
5. Structure of the skull arches.
6. Toothed palate.
7. Distinctness of the frontals.
8. Large size of the subolfactory processes of the frontals.
9. Absence of the pineal foramen.
10. Lack of fusion of lower jaw elements.
11. Very slight lateral exposure of angular.
12. Absence of transverse processes on interclavicle.
12. Distinct malar eminence of skull.

More careful analysis of this list of characteristics shared by the two lizards does not, however, lead us to the opinion that *Heloderma* and *Lanthanotus* are very closely related. Thus, characteristics 1, 2, 3, 4, 7, 8, 10, and 11 are features common to most of the platynotan lizards, that is, the living monitors (*Varanus*) and the fossil saniwines, mosasaurs, dolichosaurs, and their closer relatives. The toothed palate is a feature not shown by the present-day monitors (*Varanus*), but the closely related fossil genus *Saniwa* had a well-developed palatal dentition, and it appears that this feature is of little significance, particularly when we remember that closely related species of lizards (*Crotaphytus collaris* and *C. wislizenii*) may differ from each other in this respect, or (e.g., in the tropical members of *Gerrhonotus*) the character may be of but subgeneric value. The malar eminence may be a feature of convergence, since in *Lanthanotus* the arrangement of bones in this region is very different from the arrangement seen in *Heloderma*. As to the skull arches, the disappearance of the postorbital from the orbital border is a feature seen in all the anguinomorph (platynotan and diploglossine) lizards save some *Diploglossus*. The total disappearance of the postorbital bone in both *Lanthanotus* and *Heloderma* is merely a reflection of the loss in both lizards of the temporal arch; it is questionable whether the loss indicates any close affinity between the two genera or not. The absence of this arch is a feature of but little importance, for the temporal arch has been independently eliminated in numerous groups of lizards, such as the geckos, amphisbaenids, pygopodids, anneliids, dibamids, anelytropids, and feylinids.

It is the differences between the beaded lizards (*Heloderma*) and *Lanthanotus* that are the most striking. In general, *Lanthanotus* appears to be a typical platynotan lizard, showing in full the complex of characters so diagnostic of that group, while *Heloderma* seems a much more primitive platynotan in which the platynotan character complex has not yet been fully assembled, and many diploglossine features yet remain. The most important platynotan features found in *Lanthanotus*, but not in *Heloderma*, are dentary-surangular "hinge"; fusion of nasals; reduc-

tion of osteoderms; reduction of the outer conch of the quadrate; constriction of the vertebral centra, with consequent flaring of the condyles; extension of the M. temporalis onto the dorsal surface of the parietal; presence, to judge from the cranial foramina, of a common foramen for the hypoglossal and vagus nerves; and elongation and narrowing of the fore tongue.

It would appear that *Lanthanotus* is a rather highly developed platynotan, convergent to a far more primitive platynotan, *Heloderma*, in the loss of the temporal arch and pineal foramen, as well as in the reduction of the interclavicle. It is, of course, conceivable that *Lanthanotus* is a specialized helodermatid convergent towards the Platynota, but such a hypothesis would require far more independent duplication of morphological detail than the hypothesis here accepted. It seems much easier for two lizards independently to drop a skull arch and a pineal foramen, particularly when there is ample precedent for such convergence, than for two groups of lizards independently to acquire the same form of vertebrae, quadrate, basicranium, tongue, and lower jaw.

Recent authors follow Camp (1923) in placing *Heloderma* in the Diploglossa, the section of anguinomorph group containing principally the Anguinidae, Anniellidae, Xenosauridae, and Pygopodidae, and contrasting with the Platynota, or *Varanus*-like forms. Camp states (1923, p. 326), "The Helodermatidae are included [in the Anguioidea, the group containing the anguinids, *Anniella*, and the Xenosauridae] because of the presence of a Geniomyoideus muscle, and because of their relationship to the Glyptosauridae,—true anguroids which are in some characters intermediate between the Anguidae and Helodermatidae." The "glyptosaurus," classified by Camp as a separate family but now generally placed in the Anguinidae, were an early Tertiary group showing resemblance to *Heloderma* in their pitted and tuberculated osteoderms and in the form of the jugal bone. The genus *Glyptosaurus* Marsh seems closest to *Heloderma* in the irregular arrangement of small polygonal osteoderms on the dorsal surface of the head.

But it also appears that the various "glyptosaurus," as might be expected from

their early advent, are the most primitive of the Anguinomorpha, showing none of the specializations of the later groups but retaining a heavy armor of osteoderms as in the scincormorphs and usually retaining a distinct suture between the frontals. While we fully admit the large number of resemblances between *Heloderma* and the glyptosauroids, it appears to us that these resemblances are merely primitive anguinomorph characters and demonstrate nothing more than that *Heloderma* very early split off from an as yet unspecialized anguinomorph stock.

What seems more important is that in most of its specializations *Heloderma* has traveled the same path as the Platynota, although the genus has not progressed so far. It seems probable that *Heloderma* represents an early off-shoot of the platynotan stem, and hence the genus might better be classed with that group than with the diploglossines. Platynotan features of *Heloderma* are:

1. External naris extended back to separate the nasal from the maxillary and prefrontal.
2. Teeth recurved and with a fluting of tiny grooves at their bases.
3. Tooth rows shortened, resulting in a forward migration of the posterior end of the maxillary, in turn resulting in the approximation of the maxillary extremities of the palatine and ectopterygoid, thus excluding the maxillary from the suborbital fenestra.

4. Subolfactory laminae of frontals very strong, their bases strongly and sharply defined posteriorly, the processes meeting beneath the olfactory tracts.

5. Frontals distinct.

6. Lateral exposure of angular slight.

7. Meckelian groove between splenial and dentary completely or almost completely open.

8. Surangular bone distinct.

9. Muscular process of coronoid bone arising from the posterior half of that bone after a long plateau in the profile of the dorsal border of the lower mandible.

10. Body osteoderms not overlapping.

11. Tongue deeply forked at tip.

12. Tail not autotomous, incapable of regeneration.

13. Dentary of reduced posterior extent, not extending back to the level of the coronoid process.

14. Tooth row not extending beneath the eye.

15. Caudal chevrons set on pedicles and movable, at least posteriorly.

To summarize, *Lanthanotus* appears to be but distantly related to *Heloderma*, its resemblances to that genus being either convergent or generalized platynotan characteristics. *Heloderma* appears to be a primitive platynotan retaining many diploglossine features.

## LANTHANOTUS COMPARED WITH VARANUS

### HISTORICAL RÉSUMÉ

Off hand, it seems strange that *Lanthanotus* has never been compared with *Varanus*. For the most part this can be attributed to the fact that specimens of *Lanthanotus* have been available to relatively few investigators. Indeed Shufeldt (1890) was forced to the bitter, but unfortunately apt, remark, "The ultimate fate of an important form of reptile should not be to place it in a jar of alcohol, stand it on a shelf, and then ascertain how many years it will take to have nearly all its characters rot within a spirit-preserved skin."

Up to now our arguments have been of a negative nature; that is, we have stressed the dissimilarities between *Lanthanotus* and the various lizards that have been suggested as

close relatives of the Bornean form. Such arguments must necessarily seem weak, for the reason that even closely related forms may show a large number of anatomical differences when carefully compared. In comparing *Lanthanotus* and *Varanus* we are on firmer footing, however, for here a large number of positive resemblances are to be found. Indeed, the number of detailed resemblances between *Lanthanotus* and *Varanus* seems so great that it is difficult to doubt that the two genera are closely related.

### COMPARISONS

**EXTERNAL FEATURES:** The numerous differences in external form between *Lanthanotus* and *Varanus* are summarized in table 1.

TABLE 1

COMPARISON OF EXTERNAL CHARACTERS OF *Lanthanotus* AND *Varanus*

<i>Lanthanotus</i>	<i>Varanus</i>
No gular fold	A gular fold
No external ear	Tympanum exposed and conspicuous
Lower eyelid with a transparent window	Lower eyelid opaque
No pineal stigma	A prominent pineal stigma
Head blunt, with rounded temples	Head pointed, with flat temples
Torso long, the limbs short; appressed manus and pes not meeting	Torso moderate, the limbs moderate to long; appressed manus and pes overlapping
Tail not compressed	Tail compressed, sometimes very much so

But there are very important similarities, as well. In both genera the under sides of the toes are covered with minute granules, rather than the usual transverse scutes. In both the nostrils are widely separated from each other and from the tip of the snout. In both there is little or no specialization of head scales, and the lips are covered by small scales rather than by specialized labials.

A particular resemblance is seen in the scale organs or scale "pits." These structures (which are actually small raised pustules and form pits only when collapsed by drying) are found in both genera and are arranged in the same fashion; that is, on the enlarged crestal scales and also on the small granules surrounding the crestals. In both genera the femoral pores are absent, although in *Varanus* there are usually two pairs of pores just anterior to the cloaca, the pores being absent in *Lanthanotus* and some specimens of *Varanus*.

There is a close agreement between *Lanthanotus* and *Varanus* in the scutellation of the body, particularly when such a monitor as *Varanus* (*Tectovaranus*) *dumerili* is used for comparison. In the two genera the arrangement of scales is much the same: a large crestal, which is bluntly keeled, lies upon a raised wart, the sides of the wart being covered by small granules; the entire dorsal surface is covered by a mosaic of these warts. In *Lanthanotus* the crestals are confined to certain definite longitudinal tracts on the body and tail, forming longitudinal crests; in *Varanus* there is no such regularity and the crests are poorly defined. But in *V. dumerili* it is possible to make out on the tail the same longitudinal crests seen in *Lanthanotus*; moreover, in *V. dumerili* the double dorsal

crest of the tail may be traced forward along the midline of the back to the nuchal region, as in *Lanthanotus*.

**TONGUE:** The tongue of *Varanus* is very similar in form to that of *Lanthanotus* and differs principally in the greater elongation of the fore portion and the absence of papillae.

**OSTEODERMS:** The osteoderms of *Varanus*, when present, are similar to those of *Lanthanotus* is being confined to the skin and not fused with the underlying bones. In *Varanus* as in *Lanthanotus* the osteoderms are much reduced and do not meet one another to form a shield.

**SKULL:** The general form of the skull in *Varanus* is subject to variation, as may be noted in the paper by Mertens (1942), who recognizes eight subgenera. However, as might be guessed from the external appearance of the head, the skull of all species of *Varanus* differs from that of *Lanthanotus* in having a much longer and more pointed muzzle, a shorter postorbital portion, and a temporal arch. None the less, the skull of *Varanus* is more like that of *Lanthanotus* than is that of any other living lizard.

The premaxilla of *Varanus* differs from that of *Lanthanotus* in having much longer ascending processes, as might be expected from the more elongate snout. But there is close agreement between the two genera in that the base of the ascending process is broadened to merge gradually with the transverse dental ramus of the bone. In both genera the premaxillae are fused. The two genera further agree in possessing premaxillary foramina.

The nasals are coössified in both genera (ex-

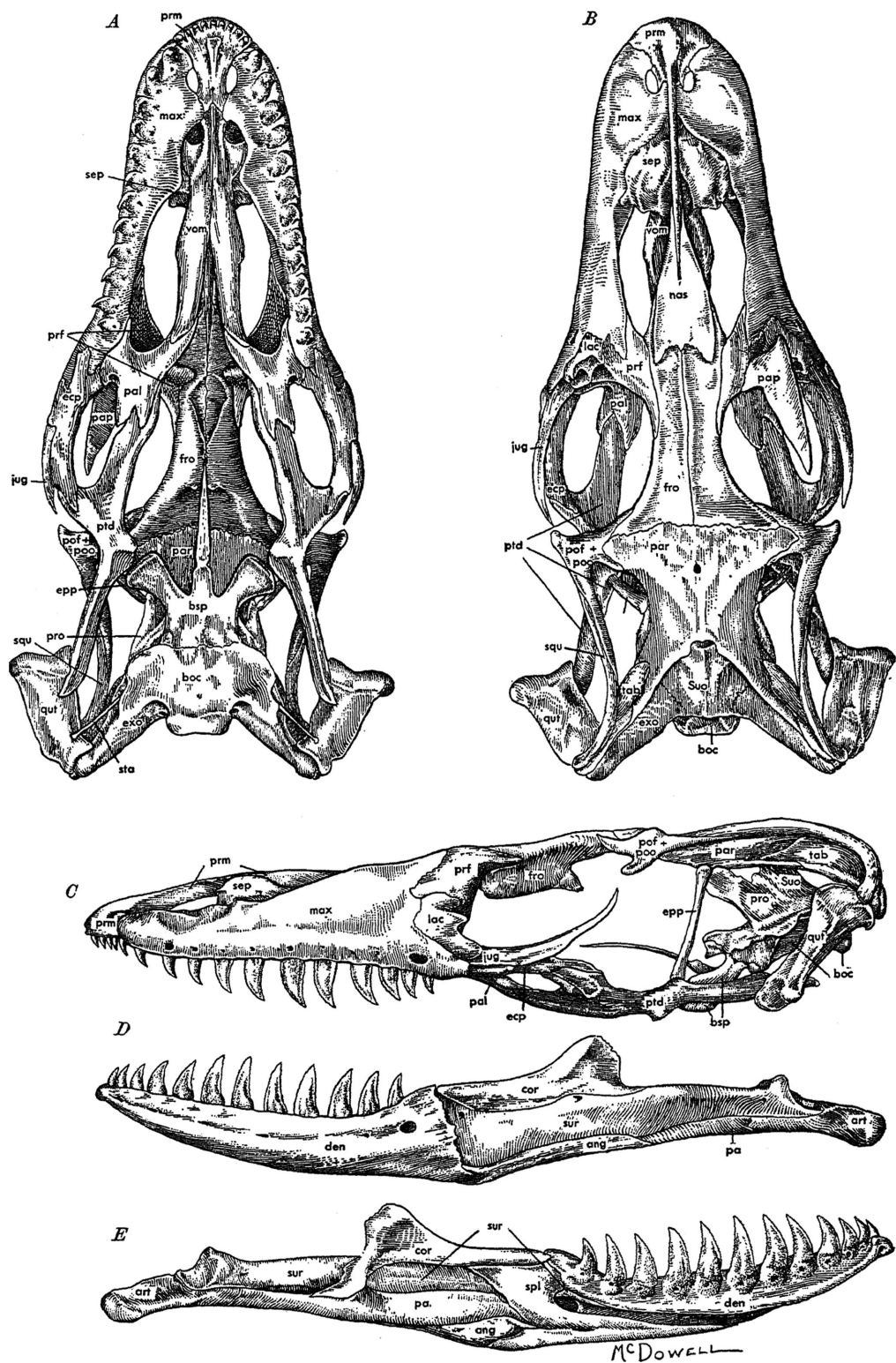


FIG. 8. *Varanus varius*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell.

cept in the subgenus *Odatria* of *Varanus*), and in both genera (Mertens, 1942) they are isolated from the maxilla and the prefrontal by a backward prolongation of the anterior naris. The only notable difference between the nasal of *Lanthanotus* and that of *Varanus* is that the lateral margin of the bone in *Varanus* is simply and smoothly concave, without trace of the anterior emargination for the nasal capsule seen in *Lanthanotus*.

The maxillary bone of *Varanus* is so similar to that of *Lanthanotus* that extensive comparison seems pointless. However, the process at the postero-internal corner of the bone for the anterior process of the palatine is usually not so well developed in *Varanus* as in *Lanthanotus*. Moreover, in *Varanus* there is a distinct, usually large, foramen on the premaxillo-maxillary suture, while this foramen is absent in *Lanthanotus*. The primitive monitor dentition, as seen in such forms as *V. salvator*, is identical with that of *Lanthanotus*, the teeth being solid, pointed and recurved, compressed, and without grooves (except for a fine basal fluting; in some *Varanus*, such as *V. niloticus* and *V. exanthematicus*, the maxillary teeth of adults may be blunted, however, to form crushing molars).

The septomaxillary bone of *Varanus* is very like that of *Lanthanotus*; in both genera the lateral portion of the bone extends farther posteriorly than does the median portion. But in *Varanus* the ascending lateral pillar is not so well developed as in *Lanthanotus*.

As in *Lanthanotus*, the prefrontal bone of *Varanus* is separated from the jugal by a palatine-lacrimal contact. The prefrontal of *Varanus* is in all respects very similar to that of *Lanthanotus* and differs principally in bearing a falciform palpebral bone that may be a modified osteoderm. The arrangement of bones in the region of the lacrimal foramen is of the same peculiar type in both *Lanthanotus* and *Varanus*. In both, the lacrimal foramen is double, a median column of the lacrimal dividing the foramen into a dorsal and a ventral portion. In *Varanus* the ventral foramen is completely surrounded by the lacrimal, without the intervention of the prefrontal, but otherwise the two genera are identical in the arrangement of the elements of the lacrimal region. In neither genus does the

jugal border the lacrimal foramen.

The lacrimal of *Varanus* differs from that of *Lanthanotus* in having a greater spread on the lateral surface of the muzzle and in having its orbital margin extending posteriorly as a spine lateral to the lacrimal foramen.

The jugal of *Varanus* is like that of *Lanthanotus* in being a simply curved, crescentic element articulating anteriorly with the lacrimal, palatine, and maxilla, more posteriorly with the ectopterygoid. Although the jugal of *Lanthanotus* runs up along the side of the postfrontal to meet the parietal, the jugal of *Varanus* almost never meets the postfrontal, thus leaving a hiatus in the post-orbital arch. In *Varanus*, as in *Lanthanotus*, the postorbital limb of the jugal is not compressed but rather triangular or round in cross section; in both genera the jugal tapers to a point dorsally.

Most of the species of *Varanus* differ from those of *Lanthanotus* in having the cheek flat, with the jugal and maxillary forming no malar eminence. But in some of the Australian forms, such as *V. (Varanus) varius*, *V. (Odatria) acanthurus*, and *V. (Odatria) semiremex*, there is a malar eminence very similar in form and construction to that of *Lanthanotus*, and the sides of the muzzle have the same parallel form seen in *Lanthanotus*.

The frontal of *Varanus* is similar to that of *Lanthanotus* in being separate from its fellow and in possessing a strong descending subolfactory lamina. The subolfactory lamina of *Varanus* is more like that of *Lanthanotus* than like that of *Heloderma* in being abruptly truncated posteriorly, so that its ventro-posterior corner extends as far back as the posterior extremity of its dorsal base. On the other hand, the subolfactory processes of *Varanus* meet in an interdigitating suture beneath the olfactory tracts as they do in *Heloderma*, but not as in *Lanthanotus* where the processes are larger than they are in the lizards of the two other genera. Moreover, the frontals in *Varanus* do not meet the palatine or the vomer.

The post-frontal of most species of *Varanus* appears to be different from that of *Lanthanotus* in that there is a posterior process arising from its ventral extremity to run back along the temporal arch to meet the squamosal. However, in a specimen of *V.*

(*Odatria*) *semiremex boulengeri* figured by Mertens (1942, p. 132, fig. 7) there is a suture between the post-frontal and the backward process, and it may be seen that the backward process of the post-frontal of *Varanus* is in reality the fused postorbital, as might also be inferred from fossil examples of *Telmasaurus* and *Saniwa*. The true post-frontal is thus very similar in *Lanthanotus* and *Varanus*, of a triangular form, notched dorsally for the frontal and parietal. *Varanus* differs from *Lanthanotus* in having a postorbital.

The vomer of *Varanus* is very different from that of *Lanthanotus* and somewhat resembles that of *Heloderma*. In *Varanus* the lateral and median edges of the vomers are curled up so that the bones are quite concave dorsally, but there is no suggestion of the median internasal septum seen in *Lanthanotus*. Anteriorly there is a lateral flange, absent in *Lanthanotus*, that runs outward to meet the maxilla; in addition, the anterior extremity of the vomer makes a short suture with the maxilla; thus a triangular foramen is formed, bounded laterally by the maxillae, medially by the vomer, posteriorly by the lateral flange of the vomer. The vomers of *Lanthanotus* are laterally dilated and triangular in form, but those of *Varanus* are narrow, parallel-sided, and strap-like in shape. Although smooth in *Lanthanotus*, in *Varanus* the ventral surface of the vomers bears a pair of deep grooves anteriorly where the tines of the deeply forked tongue lie when this organ is retracted. The vomers of *Varanus* are separate for nearly or quite half of their length posteriorly, a further difference from *Lanthanotus*.

The palatine, pterygoid, and ectopterygoid of *Varanus* are as in *Lanthanotus*, except that there are no palatine or pterygoid teeth in *Varanus* (although these were present in the fossil varanid *Saniwa*), and the pterygoid of *Varanus* is not so dilated posteriorly as in *Lanthanotus*. In some *Varanus* the pterygoid may meet the jugal, as in *Heloderma*. In *Varanus*, as in *Lanthanotus*, the ectopterygoid reaches the lateral border of the skull.

The parietals of *Varanus* are fused, as in *Lanthanotus*, but differ from those of the latter genus in being relatively much shorter and in being penetrated by the pineal foramen. Also, the nuchal muscles do not extend

onto the dorsal surface of the parietal in *Varanus*, while in *Lanthanotus* the muscles leave deep scars on the posterior portion of the dorsal surface of the parietal bones. But in other respects the bones are remarkably similar in the two genera. In neither genus does the parietal extend lateral to the epipterygoid articulation; in both genera the temporal musculature originates from the dorsal surface of the parietal, rather than from the ventral surface. In some species of *Varanus*, as *V. (Varanus) gouldi* and particularly *V. grayi*, the two muscle masses may be closely approximated at the midline, with a narrowly compressed sagittal crest between them. However, in such forms as *V. (Odatria) caudolineatus* as figured by Mertens (1942, pl. 22, fig. 158) there is a wide amuscular parietal table, and the form of the parietal is almost exactly as in *Lanthanotus*, except for its shorter proportions and pineal foramen. The fact that the skull of *V. caudolineatus* figured by Mertens is of approximately the same size as the skull of *Lanthanotus* examined by us suggests that relative growth may be a determining factor in sagittal crest development.

*Varanus* differs from *Lanthanotus* in the length of the pro-otic-parietal juncture, for in *Varanus* only the more anterior portion of the dorsal border of the pro-otic is in contact with the parietal, and a large foramen is formed beneath the quadratic limb of the parietal, the foramen being bordered dorsally by the parietal, anteriorly by the pro-otic, and posteriorly by the supraoccipital.

The tabular of *Varanus* is similar to that of *Lanthanotus*, from which it differs in having a strong and complete temporal arch. Accordingly, the postorbital, absent in *Lanthanotus*, is large in *Varanus* (but fused to the post-frontal), and the squamosal, reduced to a tiny splinter attached to the dorsal end of the quadrate in *Lanthanotus*, is, in *Varanus*, a strong bone of longitudinally strap-like form. In the subgenus *Tectovaranus* of *Varanus* the temporal arch is strongly dilated and nearly roofs over the dorsal temporal fenestra.

The epipterygoid of *Varanus* has the same articulations and connections as that of *Lanthanotus*, but in accordance with the deeper skull the epipterygoid of *Varanus* is more elongate and slender than that of *Lanthanotus*; in addition, the bone is more back-

wardly inclined in *Varanus* than in *Lanthanotus*.

The resemblance between *Lanthanotus* and *Varanus* in form of the quadrate is extremely close; indeed, the quadrate of *V. bengalensis* appears to be identical in shape to that of *Lanthanotus*, with the reduced outer (tympanic) conch. This resemblance is particularly notable when one remembers that *Varanus* has a well-developed tympanum, a feature usually associated with a strong tympanic conch of the quadrate.

The difference between *Varanus* and *Lanthanotus* in the articulation between the pro-otic and the parietal is noted above. Aside from this difference and the greater elongation of the brain case seen in *Lanthanotus*, the pro-otic bones of the two genera are very similar. In both the pro-otics are parallel and well separated by the supraoccipital. The supraoccipital is very similar in the two genera, being rounded off anteriorly and articulated to the posterior edge of the parietal. In the larger forms of *Varanus* the supraoccipital is strongly tilted, but in *V. (Odatia) caudolineatus* the supraoccipital is nearly identical with that of *Lanthanotus*, being broad and nearly horizontal. The paroccipital process of *Varanus* is as in *Lanthanotus*, except that its ventral margin is broadly joined by a lamina of bone to the muscular tuber of the basioccipital, this lamina concealing the base of the stapes from ventral view. The occipital condyle is as in *Lanthanotus*.

The basioccipital also is like that of *Lanthanotus*, and its muscular tuber is a continuation of the plane of the tuber of the basisphenoid without angulation. The basisphenoid with its basipterygoid processes is very similar in the two genera, but in *Varanus* the cultriiform process of the parasphenoid is usually ossified, while in *Lanthanotus* only its extreme posterior portion is bony.

A notable resemblance between *Lanthanotus* and *Varanus* lies in the arrangement of the cranial foramina. As in *Lanthanotus*, the entocarotid-Vidian canal of *Varanus* is very short and hardly more than a tunnel through the base of the basipterygoid process. In *Varanus* the "carotid fossa" is absent except

at the anterior end of the sphenoid, an approach to the total absence of the fossa seen in *Lanthanotus*. *Varanus* again resembles *Lanthanotus* in the shape of the lateral aperture (in *Varanus* for the jugular vein and nerve IX), which is horizontal and laceriform. The hypoglossal foramen of *Varanus* is relatively very large, a further resemblance to *Lanthanotus*. In *Varanus*, and presumably *Lanthanotus* as well, this foramen also conveys nerves X and XI.

The stapes of *Varanus* is more slender than that of *Lanthanotus*, but otherwise similar. As in Anguimorpha generally, the base of the stapes is simple and imperforate.

In the lower jaw there is great similarity between *Lanthanotus* and *Varanus*, the most important resemblance being the common possession of a dentary-surangular hinge on the outer surface of the jaw. As noted above in the account of *Heloderma* (p. 42) the jaw of *Lanthanotus* is of a more extreme platynotan type than is that of *Varanus* itself in that the bones of the median surface of the jaw are arranged to form a vertical suture on the inner side of the jaw corresponding in position with the external dentary-surangular hinge. In this respect *Lanthanotus* is like the Cretaceous relatives of the Varanidae, the Aigialosauridae, and the Dolichosauridae and makes a decided approach to the hinge seen in the members of the Mosasauridae. In both *Varanus* and *Lanthanotus* the Meckelian groove between the splenial and dentary is open except at the extreme posterior end, where a small tab of the splenial extends dorsally to meet the dentary. However, in *Varanus* the splenial is more than half as deep as the jaw at the posterior end of the dentary, while in *Lanthanotus* it is not. The form of the coronoid in *Varanus salvadorii* is very like that in *Lanthanotus*. In both *Varanus* and *Lanthanotus* the angular has only slight lateral exposure, and in both genera the articular, prearticular, and surangular are distinct. In *Varanus* the jaw is more sharply curved sigmoidally than in *Lanthanotus*.

**HYOID APPARATUS:** The glossohyal of *Varanus* is nearly identical with that of *Lanthanotus* and has the posterior portion widened in similar fashion. However, while

in *Lanthanotus* the lateral processes of the glossohyal are perpendicular to the median process and the element is thus T-shaped, in *Varanus* the processes are more backwardly inclined and the element is thus Y-shaped. The ceratohyal elements are also very similar in the two genera, and in both *Lanthanotus* and *Varanus* they extend as far forward as does the glossohyal. *Varanus* differs from *Lanthanotus* in possessing a pair of hypohyals, but in *Varanus* the hypohyals are not articulated to the ceratohyals but float in the tissue lateral to those elements. *Varanus* and *Lanthanotus* agree in having but one pair of ceratobranchials, and in both genera these elements are elongate, simple, and cylindrical. In both genera the ceratobranchials are tipped with epibranchials, but in *Lanthanotus* the epibranchials are quite short, whereas in *Varanus*, in correlation with the longer and more extensible tongue, the epibranchials are elongate.

**VERTEBRAL COLUMN AND RIBS:** As noted above in the account of *Heloderma* (p. 43) the vertebrae of *Lanthanotus* are very similar to those of *Varanus* in having the centra constricted posteriorly and the condyle wide and flaring. There is further agreement in that the intercentrum of the third vertebra is very closely molded to fit the ventral surface of the axis and appears as but a continuation of the axial hypapophysis. *Varanus* differs from *Lanthanotus* in having two hypapophyses on the axis, arranged in tandem fashion. *Varanus* has three pairs of sternal ribs, as in *Lanthanotus*, and though most *Varanus* have two lumbar vertebrae, a skeleton of *V. exanthematicus albigularis* (A.M.N.H. No. 69963) has but one, as in *Lanthanotus*.

**LIMBS AND LIMB GIRDLES:** *Varanus* has the normal phalangeal formula in both manus and pes of 2-3-4-5-3, but in *Lanthanotus* the fourth digit of both manus and pes has but four phalanges. In *Varanus* the interclavicle is anchor-shaped, but in *Lanthanotus* the interclavicle lacks transverse processes. Otherwise the two genera are very similar and appear to have the same number of scapulo-coracoid fenestrae (scapula with one anterior emargination, coracoid with two anterior emarginations and a small preglenoid foramen).

## DISCUSSION AND CONCLUSIONS

The number of resemblances between *Lanthanotus* and *Varanus* forces us to the conclusion that the two genera are closely related. The most important of the numerous resemblances between the two genera appear to be in:

The structure of the teeth.

The arrangement of the bones in the lacrimal region.

The large size of the descending processes of the frontals.

The combination of fused nasals with separate frontals.

The enlarged hypoglossal foramen.

The short entocarotid-Vidian canal and reduced "carotid fossa."

The origin of the temporal musculature from the dorsal surface of the parietal.

The presence of the platynotan hinge in the lower jaw.

The reduction of the outer conch of the quadrate.

The form of the vertebral centra.

The extent of the ceratohyal as far forward as that of the glossohyal.

The form of the distal part of the tongue.

The presence of small granules on the under surfaces of the digits.

The presence of scale organs or "pits" on the granular as well as the crestal scales.

The failure of the osteoderms of the head to fuse with the skull.

On the other hand, there are sufficient differences between *Lanthanotus* and *Varanus* to justify keeping the two genera in separate families. The most important differences are given in table 2.

It will be noted that in all these features *Varanus* appears to be the more primitive form. We conclude that *Lanthanotus* is not a primitive pre-platynotan intermediate between the Helodermatidae and the Varanidae but rather is an advanced and specialized platynotan lizard that has evolved along somewhat the same but by no means identical lines as the beaded lizards (Helodermatidae). *Lanthanotus* is not so closely related to the beaded lizards as it is to the monitors.

It does not seem possible that *Lanthanotus* is a recent off-shoot of the varanids, for certain of its structural features are distinctly more primitive than those of the monitors.

TABLE 2

DIFFERENCES BETWEEN *Lanthanotus* AND *Varanus*

<i>Lanthanotus</i>	<i>Varanus</i>
Postorbital portion of the skull elongated	Postorbital skull short
Temporal arch and postorbital bone absent	Temporal arch and postorbital bone present
Pineal foramen absent	Pineal foramen present
Entire dorsal border of pro-otic in contact with the parietal	Only anterior dorsal border of pro-otic in contact with the parietal
Subolfactory laminae of frontals (separate) larger	Subolfactory laminae of frontals (united) smaller
A splenial-angular hinge as well as a dentary-surangular hinge	Only the dentary-surangular hinge
Hypohyal absent	Hypohyal present
Fourth digit with 4 phalanges	Fourth digit with 5 phalanges
Interclavicle without transverse processes	Interclavicle with transverse processes
No external ear	Tympanum exposed
Lower eyelid with a "spectacle"	Lower eyelid opaque

These features are:

1. The short, blunt muzzle. It may be inferred that the long rostrum of the varanids is a secondary elongation superimposed upon a blunted muzzle, rather than a heritage from ancestral anguinids, with a pointed muzzle. Evidence for this is the primitiveness among Platynota of the lizards of the family Helodermatidae, which have a blunt muzzle, and the construction of the muzzle in varanids themselves. It will be seen when the skull of a varanid is examined that the elongation of the snout in this group is entirely prenasal and that the nostrils lie relatively near the eyes. In anguinids the nostrils are placed near the tip of the snout. If we truncate the snout of a *Varanus* a short distance anterior to the nostrils to conform with the anguinid proportions we find that the shape of the muzzle thus produced is in close agreement with the form of muzzle seen in *Lanthanotus*.

2. The presence of papillae on the basal portion of the tongue. In *Varanus* the lingual papillae are absent as such. *Lanthanotus*, in possessing the papillae, thus comes much closer to the Anguinidae than does *Varanus*.

3. The form of the vomer. The absence of lingual grooves on the ventral surface of the vomer sets apart *Lanthanotus* not only from the living Varanidae but from the Cretaceous relatives of the varanids, the Mosasauridae. The absence of the grooves suggests a very early separation of the Lanthanotidae from

the platynotan stem. Moreover, *Lanthanotus* shows a more primitive choanal structure than *Varanus* in that the maxilla fails to send inward a process to suture with the vomer behind the orifice of the organ of Jacobson, so that the bony separation between choana and opening of the organ of Jacobson is formed by the septomaxilla alone.

4. Presence of palatal teeth. The palatal teeth of the Varanidae appear to have been lost before the Miocene with the extinction of the primitive subfamily Saniwinae (Cretaceous to Oligocene), and their presence in *Lanthanotus* would put the origin of that genus at least in pre-Miocene times.

5. Completion of the postorbital arch. In its complete arch *Lanthanotus* shows a more usual and primitive condition than do the varanids, where the continuity of the arch is broken by failure of the jugal to meet either the postfrontal or postorbital.

The monitor-like group (Platynota) has been important since the early Cretaceous, and there are several extinct groups. In view of the obvious connection of *Lanthanotus* with this series, a comparison of the Bornean lizard with the fossil forms may prove rewarding.

The living family Varanidae is represented in the Cretaceous and Eocene by the subfamily Saniwinae. To this subfamily the following genera may be assigned with near certainty: *Saniwa*, upper Palaeocene of Belgium,

Wasatch Eocene to *Oreodon* beds Oligocene of North America; *Telemasaurus* (Gilmore, 1943), Djadochta (upper Cretaceous) of Inner Mongolia. Doubtful genera are: *Palaeosaniwa* (Gilmore, 1928), based on vertebrae from the Belly River (upper Cretaceous) of Canada and the Lance (upper Cretaceous)<sup>1</sup> of Montana and, although definitely platynotan, not positively varanid; *Parasaniwa* (Gilmore, 1928), from the Lance formation, quite atypical for Platynota in dental form and probably diploglossan, although the scantiness of material prevents any statement on taxonomic position; *Provaranosaurus* (Gilmore, 1942), from the Polecat Bench (upper Paleocene), known from a fragmentary maxilla and dentary and so different from known platynotans (the teeth are round in cross section, without basal striations, and without recurving distally, and, to judge from maxillary foramina, very numerous, over 20, for a varanid) that it is most uncertain that the genus is properly referred to the Varanidae.

In addition to these three questionable genera, Romer (1945) lists under Varanidae three genera that are definitely not varanid in relationships: *Progonosaurus*, referred to the Testudinata by Fejérváry in 1935; *Palaeo-varanus*, a synonym of *Necrosaurus*, and as discussed above (p. 30) a probable relative of *Xenosaurus* and *Shinisaurus*; and *Polyodontosaurus* (Gilmore, 1932), based on the anterior half of a lower jaw without teeth from the Belly River. Gilmore himself in his original description pointed out that *Polyodontosaurus* shows not the least sign of varanid affinities, and we see much room to question even Gilmore's reference of the jaw to the Squamata. *Polyodontosaurus* shows a deeply thecodont dentition, seen in Squamata only among the mosasaurs, forms without any resemblance to *Polyodontosaurus*; the Belly River fossil has a strong sutural mandibular symphysis that is prolonged downward and backward in a slight prominence, again most unlike Squamata; most unsquamatan of all, on the inner side of the

mandible the angular is produced forward as a narrow and elongate process along the dorsal border of the splenial. All these features make it seem far more likely that *Polyodontosaurus* is a dinosaurian than that it has any affinities to the Squamata.<sup>2</sup>

*Saniwa* is known from nearly every bone of the skeleton, and its osteology has been described in detail by Gilmore (1928). *Telmasaurus*, known from the posterior cranial roof and parts of the post-cranial skeleton, does not appear to differ from *Saniwa* except in its much more posteriorly placed parietal foramen. *Saniwa* is remarkably similar to the modern *Varanus*, considering the difference in time, and is everywhere as in the modern genus except for the following details: the premaxilla is relatively smaller; the maxilla is relatively higher anteriorly, lower posteriorly, and with its dorsal border more strongly inflected (very suggestive of *Heloderma*); the upper lacrimal foramen is surrounded by the lacrimal alone, rather than by the lacrimal and prefrontal; the vomer is slightly wider; the palatine and pterygoid bear teeth; the lamina of bone arising from the exoccipital and connecting the muscular tuber of the basioccipital with the paroccipital process is notched (thus approaching *Heloderma*); the postorbital and post-frontal are distinct; possibly, the jugal meets the post-frontal; the teeth are more numerous (about 24 on maxilla, 22 on dentary); and there is only one coracoid emargination (an approach to the unemarginated coracoid of *Heloderma*).

It will be seen that while *Saniwa* may bring the Varanidae somewhat closer to *Heloderma* than might be suspected from a study of the living genera alone, except in the presence of palatal teeth *Saniwa* makes no more definite approach to *Lanthanotus* than does the living *Varanus*, and in some features such as dental number and the form of the exoccipital and coracoid is somewhat less like *Lanthanotus* than are the living monitors.

We may conclude that while the Varanidae are closer to *Lanthanotus* than is *Heloderma*, neither the living nor the fossil members of the Varanidae can be considered as on the direct phyletic line leading to *Lanthanotus*.

<sup>1</sup> A.M.N.H. (G.P.) No. 1309, a vertebra with zygosphenes and ventrally grooved centrum (see Gilmore, 1928, p. 164, pl. 11) may be an anteriormost thoracic vertebra of this genus. It is without data but was mixed with material from New Jersey in the Cope collection.

<sup>2</sup> In a paper overlooked at the time this paragraph was written, C. M. Sternberg (1951) suggests that *Polyodontosaurus* is a troodont ornithischian.

There remain three families, the Aigialosauridae, Dolichosauridae, and Mosasauridae, all of Cretaceous age, among the Platynota. These three families appear to be very closely related to one another, and, as will be seen

from the next section, appear to be much nearer to the ancestry of *Lanthanotus* than either of the two families (Varanidae and Helodermatidae) of Platynota considered thus far.

### LANTHANOTUS AS A LIVING AIGIALOSAURIAN

The close resemblance between *Lanthanotus* and the living *Varanus* in both external appearance and in osteology suggests comparison with the families represented principally in the Cretaceous, namely, the series including the Aigialosauridae, Dolichosauridae, and Mosasauridae, which have their

affinities with the Varanidae. All three of these families appear to be closely related to one another, with the aigialosaurids perhaps the forms least modified from the common ancestral condition. Nopcsa (1903) and also Williston (1904) have shown that the mosasaurs of the upper Cretaceous were derived

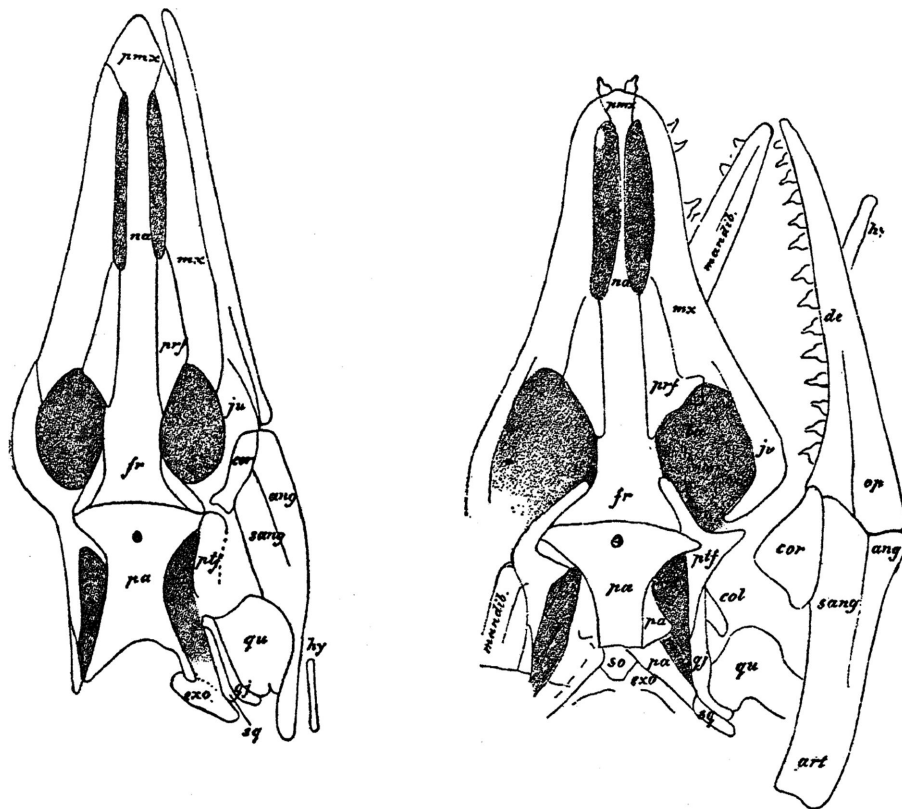


FIG. 9. Skulls and jaws of Aigialosauridae. Left, *Aigialosaurus*; right, *Opetiosaurus*. Abbreviations: ang, angular; art, articular; col, epipterygoid or "columella cranii"; cor, coronoid; de, dentary; exo, exoccipital; fr, frontal; hy, hyoid arch fragments; ju, jugal; la, lacrimal; mandib, lower mandible; mx, maxilla; na, nasal; op, splenial or "opercular"; pa, parietal; pmx, premaxilla; prf, prefrontal; proot, pro-otic; pt, pterygoid; ptf, fused postfrontal and postorbital; qu, quadrate; sang, surangular; so, supraoccipital; sq, tabular, wrongly homologized with squamosal. From Nopcsa.

from the lower Cretaceous Aigialosauridae, and Nopcsa has argued that the Dolichosauridae of the upper and lower Cretaceous were in all probability derived from aigialosaurids through a *Mesoleptos*-like ancestor.

For convenience we may term these three families the aigialosaurians, and it is principally with the most generalized family, the Aigialosauridae, that we deal. The Dolichosauridae, in most of the specializations in which they have progressed beyond the aigialosaurids, have also departed from *Lanthanotus*. Such specializations are lengthening of the neck, which has more than 13 cervical vertebrae; compression of the tail; loss of abdominal ribs; reduction of the preacetabular pubis; and loss of teeth from the palate.

The marine Mosasauridae of the late Cretaceous is a highly peculiar group. The limbs are transformed into swimming (or, more probably, braking and stabilizing) paddles by extreme reduction of the propodials and mesopodials and marked hyperphalangy, the sacrum is lost, and the skull is peculiar both for its muzzle and for its ear region. The premaxillary beak is extremely produced and the premaxilla fused to the nasals (free nasals have been reported, but these more likely represent fragments of the septomaxilla). The quadrate is peculiar in being pierced for the stapes, as in the trionychoid and pleurodiran turtles, while the squamosal may fuse with the tabular. The vagus appears to have passed through the hypoglossal foramen, as in *Varanus* and *Lanthanotus*. The teeth appear thecodont, owing to the development of a labial wall of the dentary and maxilla. (For descriptions of mosasaurid anatomy, see particularly Camp, 1942; for jaw structure, see Gregory, 1951.) It is obvious that the specializations of the mosasaurs remove that group from any possible ancestry to *Lanthanotus*.

Aside from a tendency to fuse the frontals and to develop a very massive quadrate bone (both of which are approaches to the mosasaurid structure), the Aigialosauridae are more typical in structure, and quite similar to the Varanidae, except in jaw and limb structure. Interestingly, in their departures from the varanids the aigialosaurids approach *Lanthanotus*. (For descriptions of the Aigialosau-

ridae and Dolichosauridae, see Kramberger, 1892; Nopcsa, 1903, 1908, 1923; and Kornhuber, 1873, 1901). As in the mosasaurs, the Aigialosauridae have the intramandibular hinge of the lower jaw perfected beyond the level seen in the Varanidae, and almost exactly as in *Lanthanotus*. Not only is there an external joint between the dentary and surangular bones, but on the internal surface of the jaw the splenial is vertically truncated posteriorly to form a hinge with the angular corresponding in position with the hinge on the external surface between the dentary and surangular. Thus in the aigialosaurs, as in *Lanthanotus* but not as in *Varanus*, *Saniwa*, or *Heloderma*, the splenial does not extend along the ventral border of the coronoid. Striking as is this resemblance between the aigialosaurians (for it is also to be seen in the mosasaurs and apparently in the dolichosaurs as well), it is not the only hint of aigialosaurid-*Lanthanotus* affinities given by the lower mandible. In the aigialosaurs, as in *Lanthanotus*, the coronoid bone is very deep anteriorly (anterior to the coronoid process), rather than shallow as in the varanids and *Heloderma*. Again as in *Lanthanotus* the splenial in the Aigialosauridae is more shallow posteriorly than it is in the varanids, being less than half as deep as the jaw posteriorly.

The skull of the Aigialosauridae (see Zittel, 1932, pp. 331-332; Kramberger, 1892) is essentially as in *Varanus*, with pineal foramen, complete temporal arch, short brain case, and long muzzle. But in the one important feature in which the aigialosaurian skull differs from that of the varanids it resembles that of the living *Lanthanotus*, namely, in the completion of the postorbital arch by a contact between the jugal and the post-frontal.

Like *Lanthanotus*, the aigialosaurs possessed abdominal ribs. In this feature these lizards appear to differ from other Platynota.

In limb structure there is again a striking similarity between the aigialosaurs and *Lanthanotus*. In both the limbs are shortened, and the tibia is even shorter than the shortened femur. In both (except the questionable aigialosaur *Mesoleptos*, which approached in this respect the Dolichosauridae), the fore limbs are as long as the hind limbs. A particu-

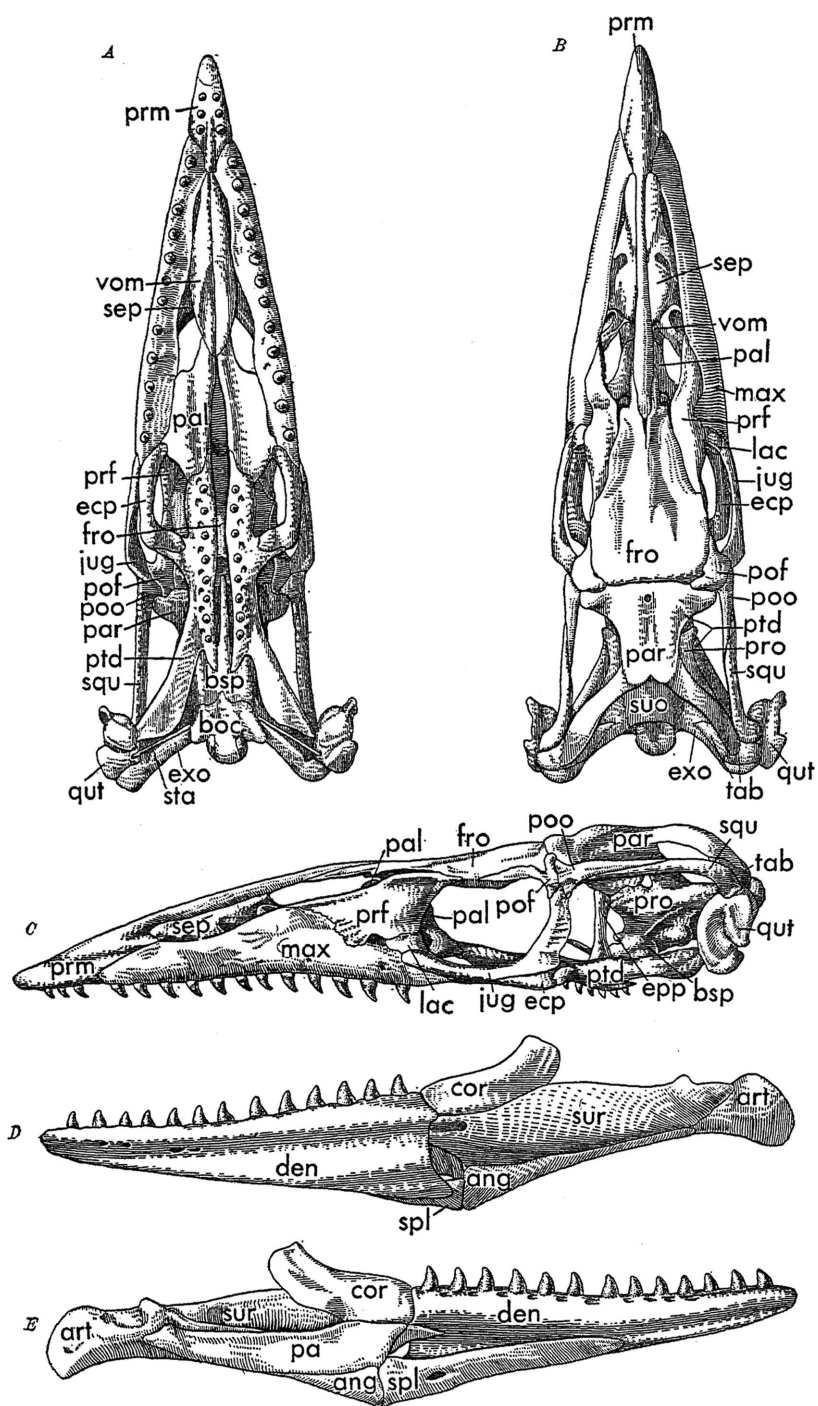


FIG. 10. *Tylosaurus dispelor* (Mosasauridae). A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Articulations and internal view of mandible and ventral view of frontal restored from *Tylosaurus proriger*; vomer restored from *Platecarpus*. Drawing by McDowell.

lar resemblance is seen in the pes of *Aigialosaurus* to that of *Lanthanotus*; in both, the fourth digit has but four<sup>1</sup> (rather than the normal five) phalanges (see Kramberger, 1892). Unfortunately, the fourth digit of the manus is not known in the aigialosaurs. Kornhuber (1901) figures five phalanges on the fourth toe of *Opetiosaurus*, but this seems far from certain, to judge by his photograph.

The resemblance in jaw and limb structure between *Lanthanotus* and the Aigialosauridae appears too detailed to dismiss as the result of parallelism. The two groups are alike in important specializations: the development of a complete intramandibular hinge involving both external and internal surfaces of the lower jaw; the narrowing of the splenial; shortening of the limbs and reversal of the proportions of femur to tibia; and reduction of the phalangeal number of the fourth digit.

The two groups are also alike in the retention of generalized features lost by some or all of the other Platynota: abdominal ribs present; palatal teeth present; postorbital arch complete; neck not lengthened; pubis complete; sacrum present; tail not oar-like; quadrate normal; premaxillae not fused to nasals; and no hyperphalangy.

As might be expected in the comparison of a Neocomian reptile with a living one, *Lanthanotus* appears more specialized than any aigialosaur in certain features: lengthening of the brain case; loss of the temporal arch; contact of jugal with parietal (possibly through fusion of jugal and postorbital); better development of malar eminence than in *Aigialosaurus* (but *Opetiosaurus* makes a close approach to *Lanthanotus*); increased number of cervical vertebrae (nine against

seven); and absence of transverse processes of the interclavicle.

*Lanthanotus* may be more primitive than the known aigialosaurs in having teeth on the palatine as well as on the pterygoid (only the latter bone has palatal teeth in the aigialosaurs) and in its rather short and blunt muzzle.

On the other hand, *Lanthanotus* does show some resemblances to the Dolichosauridae, a group generally conceded to be closely allied to the Aigialosauridae. Principal among these resemblances are the relatively short and blunt facial part of the skull, relatively "normal" quadrate (without the massiveness and flattening seen in the Aigialosauridae and Mosasauridae), and imperfect interclavicle. It is possible that the absence of the temporal arch in *Lanthanotus* is a further resemblance to the dolichosaurs, since the skull of *Adriosaurus* suggests that the arch was absent. But unfortunately no dolichosaurian skull has yet been found in a sufficiently good state of preservation to allow any certainty on this point.

However, *Lanthanotus* lacks the principal specializations of the Dolichosauridae, lengthening of the neck and compression of the tail, and is too primitive to have been derived from any known dolichosaur. Since the dolichosaurs are almost certainly derivatives of the aigialosaurs, any argument as to whether *Lanthanotus* is a descendant of a primitive dolichosaur or an aigialosaur becomes largely a quibble over the point at which to draw the line between the two fossil groups.

At any rate, the complete postorbital arch, highly developed jaw hinge, reduced phalangeal number, and shortened limbs of *Lanthanotus* all suggest that its precise affinities are with the aigialosaur-dolichosaur-mosasaur complex, rather than with the varanids or *Heloderma*.

<sup>1</sup> This reduction of phalanges is seen also in at least one dolichosaur, *Pontosaurus* (see Kornhuber, 1873).

## LANTHANOTUS AS A "STRUCTURAL ANCESTOR" OF THE SNAKES

### SNAKES AS MODIFIED PLATYNOTANS

FOR SOME TIME it has been generally conceded that the snakes represent a limbless stock derived from the platynotan (*Varanus*-like) lizards. Bellairs and Underwood (1951, p. 232) came to the conclusion that "While the Platynota in general, and the Dolichosauridae in particular, show many snake-like features, they appear to differ markedly from all snakes in the structure of the skull and in certain other characters. It is suggested that the evidence is inadequate to establish close relationship between the snakes and any of the known platynotid types; the origin of snakes from unknown platynotids during the early Mesozoic remains a possibility." In view of the doubt concerning snake-platynotan relationship implied in this statement, we propose to examine the evidence bearing on the origin of snakes from a monitor-like lizard. The chief points appear to be the following:

1. Inability to regenerate the tail. The snakes, like the present-day Platynota (*Heloderma*, *Varanus*, and *Lanthanotus*) are unable to regenerate a new tip to the tail when that member is injured, but instead form a simple scar at the point of injury, rather than a regenerating blastema. In this feature the platynotans and snakes are unusual among Squamata, and this feature is known elsewhere within the group only among the amphisbaenids and Chamaeleonidae.

2. Form of the tongue. The snakes have the tongue much specialized along diploglossal lines. The fore tongue is long, narrow, and deeply bifurcate, while the hind tongue is much modified to act as a sheath for the fore tongue and is covered with an epithelium similar to that of the lining of the mouth. In some snakes (all Boidae, *Cylindrophis* and its relatives, and many colubrids, such as *Zaocys* and *Masticophis*) there is a row of papillae along the lateral margin of the protrusible portion of the tongue, suggesting the tongue structure of *Lanthanotus*, but in others the protrusible tongue is smooth and very like that of *Varanus*.

3. The form of the vertebral centra. In

the Boidae and such primitive Colubridae as *Pareas* and *Heterodon*, or even in some of the more specialized viperids, such as *Bitis*, the centrum is constricted posteriorly and the condyle is widened, flaring, and flanged dorsally, as in the more advanced Platynota. (Indeed, all snakes of the boid-colubrid series have the vertebral condyles and centra of the platynotan type, but in some it is modified by a pair of longitudinal muscular scars that obscure the posteriorly tapered form of the centrum.) Moreover, the condyle of snakes is obliquely pointed dorsally, a particular resemblance to all the platynotans save the mosasaurs.

4. Caudal chevron (haemapophysis) attachment. In snakes, as in most of the platynotans, the chevrons are attached to the centra anterior to the condyles. This feature is almost unique among Squamata but is seen in such anguinids as *Ophisaurus*. Non-platynotans (and part of the caudal column of *Heloderma*) otherwise have the chevrons intercentrally articulated to the caudal vertebrae.

5. Form of the teeth. Except for a few peculiar genera, such as *Iguanognathus*, with flag-like terminal flanges on the teeth, the snakes all show a tooth structure remarkably similar to that characteristic of the Platynota. The teeth are solid (except for the narrow medullary canal, and in some, except for the venom canal) and without basal fossae for the replacement teeth, the replacement being alternate rather than successional (Bogert, 1943), with the possible exception of the Sibynophinae, which are peculiar in other respects. Particular similarity is seen in the recurved and acute form of the crown and the finely fluted base with a very small medullary foramen. The detailed resemblance in tooth structure between snakes and platynotan lizards is so close that it is difficult to avoid believing that the two groups are closely related.

6. Posterior prolongation of the external bony naris. The most distinctive and diag-

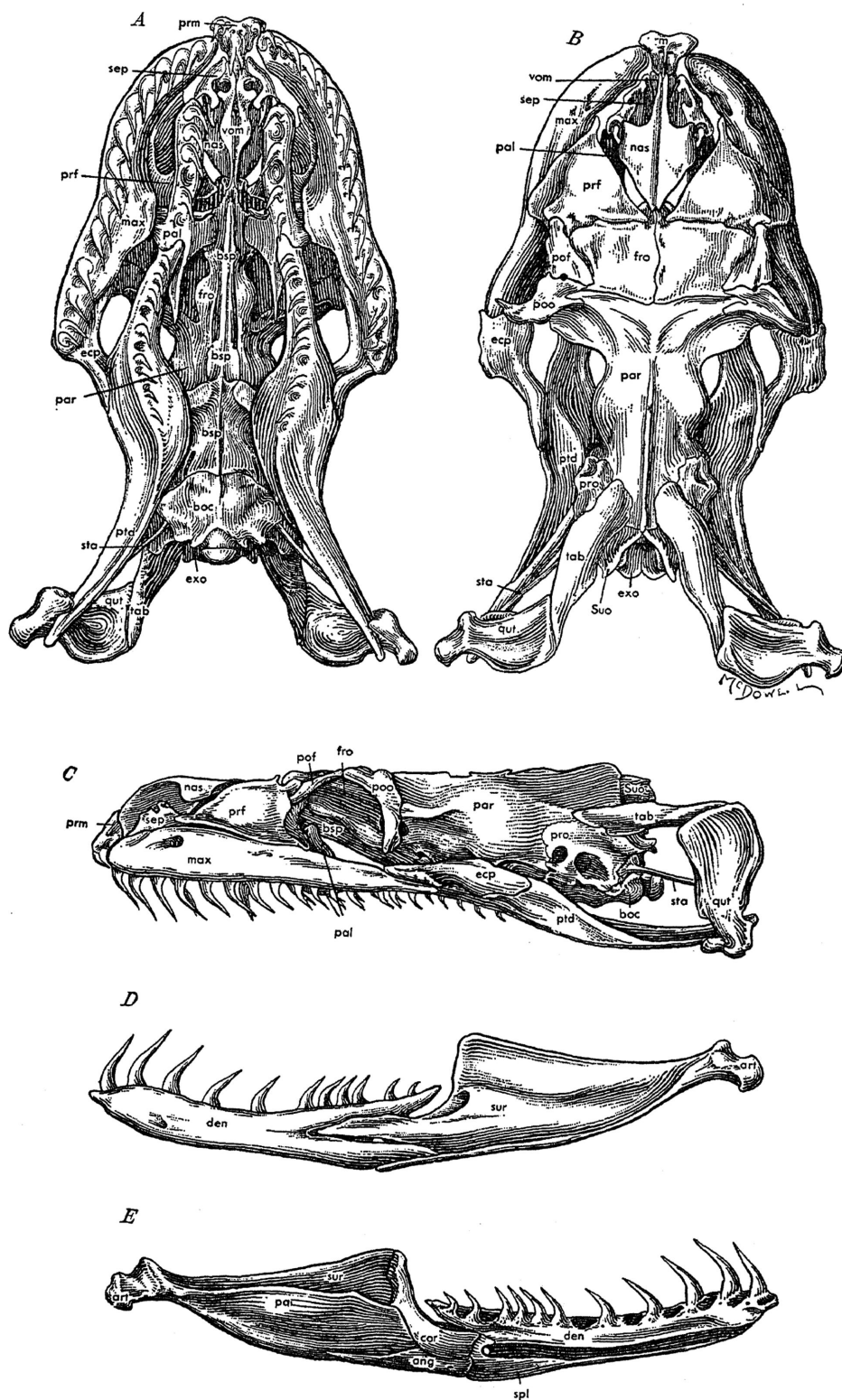


FIG. 11. *Python* ("Morelia") *argus*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell from a specimen lent by Mr. Carl Kauffeld.

nostic feature of the platynotan skull is the posterior extension of the external naris as a slit separating the nasal from the maxilla and prefrontal, and it is at least suggestive that the snakes show just this condition. In the typical colubroids the primitive separation

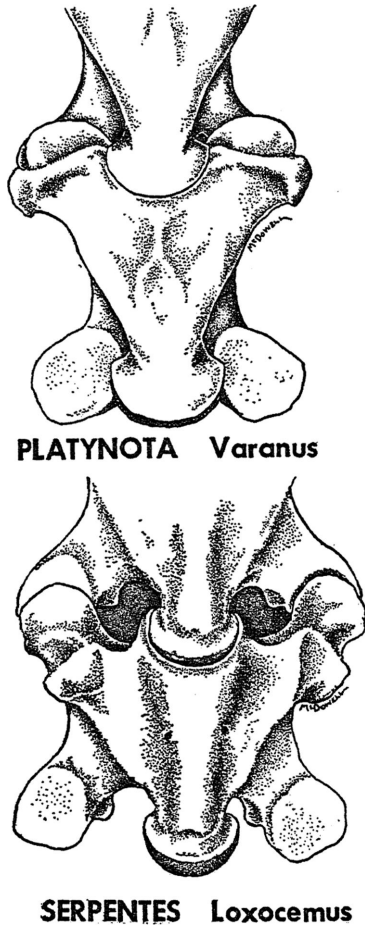


FIG. 12. Posterior thoracic vertebrae of a platynotan lizard and a snake in ventral view, showing the similar obliquity of the condyle and the precondylar constriction. Drawing by McDowell.

of nasal from maxilla and prefrontal by an obvious slit is seen, and the same may be said of the very primitive boids *Python* ("Morelia") *argus* and *Python* ("Chondropython") *viridis*, and occasionally in *P. molurus* and *P. sebae*, although in these latter two snakes the slit, if present at all, is very narrow. In more advanced boids the prefrontal bone becomes hypertrophied and

comes to overlap the nasal, but never is any nasoprefrontal suture developed, and the union is a very loose one of connective tissue only. In at least one colubrid (*Aspidura trachyprocta*) and in Hydrophiinae the median edge of the prefrontal comes in contact with the lateral edge of the nasal, but here also no suture is formed.

7. The pattern of dorsal median cranial sutures. The snakes show the pattern: premaxillae fused, nasals fused, frontals separate, parietals fused. No group of lizards except the platynotans and the burrowing scincoid *Feylinia* show such a pattern of median fusions. The nasals of snakes are generally said to be separate; so they appear when viewed from above. But in the Serpentes the inner margins of the nasals are turned down within the nasal chamber to form an internasal septum. These inner laminae are solidly fused to each other, at least in boids and some colubrids.

8. The great development of the descending laminae of the frontals. In snakes these laminae are very highly developed and wall off the brain case anteriorly. Aside from the aberrant amphisbaenids, only the Platynota among lizards approach this condition, the other groups (*Gekkota*, *Anniella*) with frontals underarching the olfactory tracts having much less well-developed descending processes.

9. Double lacrimal foramen. Although the vast majority of snakes have the lacrimal foramen single, snakes of the primitive genus *Sibynophis* retain a double foramen very similar to that of the Platynota.

10. Shortened entocarotid canal. In snakes such as *Python* with skulls large enough to permit probing of the foramina this canal may be found median to the basipterygoid process; its anterior and posterior openings are placed as in *Varanus* and *Lanthanotus*. We have found similarly placed foramina in the smaller skulls of colubrids, and the shortened entocarotid canal is probably a general feature of snakes.

11. Unmistakable signs of the aigialosaurian hinge on the mesial surface of the lower jaw. Although but few snakes (for example, the Sibynophinae, *Xenopeltis*, *Fimbrios*) have a highly developed movable articulation between the dentary and the surangu-

lar, most of the colubrids and many boids (*Python reticulatus*, for example) have a pattern of sutures on the inner surface of the jaw that suggests the former presence of a hinge like that of *Lanthanotus*, the aigialosaurs, and the mosasaurs. The posterior margin of the splenial is straight, rather than festooned, and vertical rather than diagonally slanted. The superior ramus of the dentary is bilobate, the lower lobe being truncated on a level with the vertical posterior border of the splenial, though the more dorsal lobe (bearing the tooth row) extends farther back. Thus a vertical seam is seen in the more advanced platynotans, such as *Lanthanotus* and the aigialosaurs, but is not to be found elsewhere among lizards. Examination of fresh specimens shows that limited motion is possible at this seam.

12. Lack of lateral exposure of the angular. In snakes the angular is confined to the inner surface of the jaw, whereas in most lizards most or all of the angular lies on the external surface of the jaw. But the platynotans, particularly the aigialosaurian group, are exceptional among lizards (even differing in this respect from the anguinoids) in having the angular bone median and snake-like.

Although any one of these features might be explained in terms of convergent resemblance, it is difficult to believe that all these features taken together do not indicate a special relationship between snakes and monitor-like lizards. That such gifted workers as Cope, Boulenger, Nopcsa, and Camp have agreed on a platynotan origin of the snakes makes such an origin seem the more likely.

The chief difficulty in deriving the snakes from the platynotans is that, whereas various platynotan lizards show ophidian features, no known platynotan (with one possible exception) appears to show a sufficient number of ophidian features in combination to give tangible evidence of being even closely related to the ophidian ancestor.

The Varanidae resemble the snakes in such features as tongue structure, texture of the hemipenis, dentition, and the form of the bony naris. On the other hand, in having a pineal foramen, a poor juncture of pro-otic with parietal, a long snout and a short brain case, a strong temporal arch, well-developed ear, and an opaque eyelid, as well as in the narrow form of the vomer (which does not

articulate with the frontal), and the absence of a hinge suture on the internal face of the mandible, the Varanidae appear too distant from the snakes to suggest ancestry of any but the most remote collateral form.

Some workers, notably Nopcsa (1908), have suggested the Dolichosauridae as an ancestral stock for the snakes. The Dolichosauridae do resemble snakes in their elongated and slender form, zygantral articulations of the vertebrae, relatively small skull, and reduced limbs. Further resemblance is seen in that the anterior limbs are more reduced than the posterior limbs (in snakes the pectoral girdle and limbs are completely absent, but the pelvic girdle is persistent in some of the more primitive forms). But as Camp (1923, p. 322) and Bellairs and Underwood (1951) point out, there is no particularly great resemblance apart from general platynotan features. The long neck of the dolichosaurs has been put forth as a resemblance to snakes, but since we have no knowledge of how long the neck is in snakes, in the absence of any differentiation between cervical and thoracic column, this seems too indefinite a character to be of use. The skull of the dolichosaurs was similar to that of the varanids, with long, although blunt, snout and short brain case, a pineal opening, and possibly a temporal arch, and offers the same difficulties in deriving the skull of snakes as does that of the monitors. In the dolichosaurs the preacetabular pubis is said to be absent (Camp, 1923). This would seem to rule out the dolichosaurs as direct ancestors of the snakes, for *Cylindrophis* and *Anomalochilus* possess a strong preacetabular pubis, though there is no pubic symphysis present. The only pelvic girdle element (exclusive of the femur) present in typical pythons and boas and in *Ilysia* is anterior to the acetabulum and horizontal, and we may suspect that this bone also represents a pubis.

The mosasaurs were favored by Cope (1869) as ancestors of the ophidians. But this can scarcely be correct. The peculiarly specialized ear region alone is sufficient to rule them off the line of direct ancestry. In the Mososauria the quadrate completely surrounds the ear opening (seen elsewhere in vertebrates only among Testudinata), and the tabular extends inward along the paroccipi-

tal. The squamosal is well developed in the mosasaurs, and the temporal arch is strong; in snakes the squamosal is absent, as is the arch. In the mosasaurs the varanid skull proportions are exaggerated, and the muzzle is extremely elongated and pointed, the brain case much shortened. The structure of the brain case appears to have been identical with that seen in the Varanidae. Thus the brain case is quite open owing to the failure of the pro-otic and supraoccipital to fit snugly against the parietal, and the olfactory processes of the frontals, though meeting with each other beneath the olfactory tracts, nevertheless fail to extend very deeply between the two orbits. Moreover, the mosasaurs depart farther than do even the varanids from the ophidian pattern in the fusion of the frontals and the failure of the vertebral condyles to face upward as well as backward.

On the other hand, the mosasaurs have paralleled the snakes in one feature of the lower jaw not observed in any other Platynta; the posterior descending branch of the coronoid bone that lies on the median face of the jaw is absent. This appears to be correlated with the absence of a tuberosity on the ectopterygoid to abut against the coronoid and prevent mediad displacement of the jaw. Furthermore, in the mosasaurs the descending laminae of the parietals are larger than in *Varanus*, but not nearly so well developed as in *Lanthanotus*, and, of course, far short of the development seen in snakes.

The secondary development of thecodonty and the loss of palatine teeth, as well as the close approximation of the pterygoids to each other posteriorly, are all specializations of the mosasaurs that would seem to preclude direct ancestry to the Ophidia. In fairness to Cope, however, it should be pointed out that he never suggested direct descent of snakes from known mosasaurs and was not personally familiar with the European fossils then

classified as Dolichosauridae (but including the forms now separated as Aigialosauridae).

But even the probable ancestors of the mosasaurs, the Aigialosauridae, combine with typical mosasaurian specializations a very *Varanus*-like skull. So, while lizard-like (rather than snake-like) in such features as strong temporal arch, pineal foramen, long snout and short brain case, and well-developed limbs, the aigialosaurs all show modification towards the mosasaurs that eliminates possibility of ancestry to the snakes. Such modification is seen in fusion of the frontals, massive quadrate, and loss of palatine teeth.

In spite of all the objections to each of the fossil aigialosaurian families as an ancestral group to the snakes, it does appear that the aigialosaurian group more nearly approaches the snakes than do either the varanids or helodermatids in several important features: development of an inner mandibular joint corresponding to the external joint and producing a very snake-like pattern of splenial, angular, and coronoid; conspicuous shortening of the limbs and reduction of the phalangeal count (this is obscured by hyperphalangy in the mosasaurs, but even here it is important to note that the fourth digit has no more phalanges than the third); and probable reduction, at least to a limited extent, of the middle ear cavity, as indicated by the form of the quadrate, and, in the case of the mosasaurs at least, by approximation of the pterygoid to the basisphenoid, restricting the Eustachian opening (the mosasaurian pterygoid has a small notch on its median border, just behind the sphenoid articulation, presumably for a very small Eustachian passage). In view of the close approximation in morphology between the fossil aigialosaurians and the snakes considerable interest must attach to a comparison between the snakes and *Lanthanotus*, a probable surviving aigialosaurian form.

## OPHIDIAN FEATURES OF *LANTHANOTUS*

In certain morphological features, such as the form of the septomaxilla, the remarkable Bornean lizards shows similarities to the snakes seen nowhere else among lizards, while it furthermore shows in combination all the important snake-like characters seen elsewhere among the Platynta.

### EXTERNAL RESEMBLANCES

Most striking of resemblances in external appearance is the total absence of an external ear in both *Lanthanotus* and the snakes, the scales being continuous and without unconformity over the otic region.

Almost as striking is the presence in the

lower eyelid of *Lanthanotus* of a transparent window. Walls (1942a) has shown from the ontogeny of the uropeltids that it is probable that the spectacle of the ophidian eye is derived from just such a structure. Although this structure occurs elsewhere in lizards, it occurs in no other anguinomorph.

The absence of the pineal foramen of the skull is reflected in the absence of a pineal stigma externally, another resemblance in external appearance. Similarly, the absence in both snakes and *Lanthanotus* of the temporal arch is reflected by the bulging and rounded temporal region seen in both.

Although *Lanthanotus* has functional limbs, they are relatively short, the appressed manus and pes being separated by a considerable interval, and the digits being relatively short, with but four phalanges on the fourth finger and toe. In its elongated dorsal region, nearly as long as the tail, *Lanthanotus* approaches the proportions of most (but by no means all) snakes.

#### RESEMBLANCES IN TONGUE STRUCTURE

In having a highly retractile tongue that is deeply incised terminally and has the posterior portion modified to act as a sheath for the narrow fore tongue, *Lanthanotus* resembles the snakes. Moreover, *Lanthanotus* has not gone beyond the snakes in tongue specializations as has *Varanus*, for *Lanthanotus* still retains some of the lingual papillae, as do the boa-like and python-like snakes, as well as many colubrids. However, no known snake has the dense brush of papillae on the hind tongue seen in *Lanthanotus*; rather the papillae are reduced to a single or double row on each lateral margin of the more posterior portion of the protrusible fore tongue.

#### SIMILARITIES IN DENTITION

The shape of the teeth is similar in *Lanthanotus* and in the Ophidia. In both, the teeth are pointed and recurved, with a very small medullary foramen and with fine vertical striations at the base. In both, tooth replacement is alternate. However, this is a resemblance shared with other Platynota. It is in the location of the teeth that *Lanthanotus* shows special resemblance to snakes.

In a primitive snake such as *Python*, *Xenopeltis*, or *Loxocemus* there are teeth on

the premaxilla, maxilla, palatine, and pterygoid, the palatine and pterygoid teeth being well developed. Only in *Lanthanotus* among known Platynota is the full complement present. In *Heloderma* the premaxillary and maxillary teeth are well developed, but there are few teeth on the pterygoid and palatine, and in the skull of one species, *H. suspectum*, no palatal teeth are to be found. In *Saniwa ensidens* Gilmore (1928, p. 61) found a fully toothed palatine, but the pterygoid row appears to have been more reduced than that of *Lanthanotus*, with somewhere in the neighborhood of five teeth. In the mosasaurs and aigialosaurs the pterygoid was well provided with teeth, but the palatine was edentulous. The dolichosaurs were without palatal teeth of any kind, a point that argues strongly against their close relationship to the ophidians.

#### SIMILARITIES IN SKULL STRUCTURE

*Lanthanotus* shows a considerable resemblance to the snakes in the general form of the skull. The skull of snakes is blunt anteriorly, with a rounded muzzle (except in specialized burrowers such as *Rhinophis*), very much as in *Lanthanotus* (however, *Lanthanotus* shares this snake-like feature with the Dolichosauridae and Helodermatidae). As in *Lanthanotus* and no other platynotan, the brain case of snakes is long and the muzzle short. As in *Lanthanotus* (and also *Heloderma*) the temporal arch and pineal foramen are absent in snakes.

The premaxilla of *Lanthanotus*, while not showing any great differences from that seen in such a snake as *Python*, nevertheless does not show any greater resemblance than does that of some of the mosasaurs such as *Clidastes* or the dolichosaurs, but the septomaxilla of *Lanthanotus* has a resemblance in general form to that of snakes that cannot be matched in any other lizard. In *Lanthanotus* the lateral border of the septomaxilla is curled up to rise as a tab-like lamina above the level of the dorsal border of the maxilla; this has never been described for any other lizard but is universal among snakes. Indeed, the entire form of the septomaxilla of *Lanthanotus* is like that of the more primitive colubrid snakes; the boids and their relatives are similar, but the lateral ascending tab bears a backwardly directed spine at its distal end.

In *Lanthanotus* (and also *Heloderma*) the maxilla fails to meet the vomer behind the palatal opening for the organ of Jacobson, but in *Varanus* the contact is present. In the snakes there is no contact between maxilla and vomer, the motility of the maxilla having required the breaking of all "entangling alliances" with other cranial bones. It appears easier to derive the motile ophidian maxilla from one like that of *Lanthanotus* than from a maxilla bound to the vomer.

The vomer of *Lanthanotus* shows much similarity to that of the boid snakes. Points of particular similarity are the widely dilated form with obtusely triangular lateral margin; close approximation of the two vomers to each other for their entire length, but failure to coössify except anteriorly; and absence of ventral sculpturing or any median ventral anterior spine. Most noteworthy, however, is the sutural contact of the vomer with the descending subolfactory lamina of the frontal in both *Lanthanotus* and snakes. In this feature *Lanthanotus* differs from most if not all other lizards and foreshadows one of the characteristic cranial modifications of the snakes. In snakes the vomer, rather than being associated with the palatines as a palatal element, has either reduced or lost its palatine connections and become an important element in a closely bound rostral complex of bones, the complex consisting of nasals, vomers, septomaxillae, and premaxilla. In most snakes this rostral complex is movable in the vertical plane, and the vomer is its chief or only means of attachment to the remainder of the skull, the vomerofrontal contact being modified to form a ginglymous joint. *Lanthanotus* shows the condition expected of an intermediate between snakes and lizards—the vomer strongly attached to the palatine, but attached to the frontal as well.

The nasal of *Lanthanotus* more closely approaches that of snakes than does that of any other platynotan. Platynota other than *Lanthanotus* have the nasals narrowed and triangular, with straight lateral borders; in snakes and *Lanthanotus* the nasals are widened transversely, with a strong anterior notch in the lateral border to accommodate the narial sac. [Some burrowing snakes deviate from this pattern in that the nasals are

broad for their entire length, apparently to brace the premaxilla. Examples are *Oligodon*, *Heterodon*, *Loxocemus*, *Xenopeltis*, *Eryx*, *Cylindrophis*, and, to a much lesser extent, *Hemachatus*. In *Phyllorhynchus* the nasals are broad right triangles with the shorter leg applied to the frontal, the hypotenuse forming the lateral margin, and the longer leg applied to its corresponding member of the opposite side along the midline. On the other hand, the burrower *Ilysia* (= *Anilius* Oken, non-binomial) retains the anterior notch for the nasal sac, for here the premaxilla is braced not against the anterior border of the nasal, but against the median surface of the nasal and the septomaxilla by means of a long, posteriorly directed median spine of the premaxillary bone.]

One of the most striking snake-like features of *Lanthanotus* is the form of the frontal bone. In most lizards, except amphisbaenans, the right and left orbits of the dried skull are continuous, being separated in life only by a membrane of connective tissue. This is true even in forms such as *Varanus*, *Anniella*, *Heloderma*, or the Gekkota that have well-developed subolfactory processes of the frontals. In snakes, on the other hand, the orbits of the dried skull are separated by bone, for the subolfactory laminae of the frontals extend downward for the entire depth of the orbit, enclosing a continuation of the cranial chamber between the eyes. (In some snakes, such as *Masticophis*, *Hoplopeltura*, *Psammophis*, and *Miodon*, fenestration of the skull in the region of the optic foramen may secondarily obscure this feature.) *Lanthanotus* agrees with snakes, rather than with lizards, in the great degree of development of the descending subolfactory laminae of the frontals, for these structures completely separate the orbits. It may also be said that the shape of the frontals as seen from above is in close agreement with the frontals of the Cretaceous snake *Dinilysia*, as figured by Smith Woodward (1901), but in that genus the prefrontal does not meet the post-frontal.

*Lanthanotus* departs from other platynotans and approaches the snakes in the great length of the parietal bones, forming a rather long and tubular, and to this extent snake-like, brain case, in contrast to the short and broad brain case of most other

lizards. Moreover, there is no foramen for a pineal organ (true also of *Heloderma*), and the parietal is sutured to the dorsal borders of the pro-otic and supraoccipital, so that posteriorly the brain is completely enclosed, as in snakes. However, the brain case of *Lanthanotus* is lizard-like anteriorly in the presence of a strong epipterygoid and the failure of the parietals to descend to meet the sphenoid, thus leaving the brain unprotected laterally anterior to the pro-otic. None the less it does appear significant that *Lanthanotus* shows a more consolidated and complete covering of bone for the brain than is seen in any other platynotan, and in addition shows a closer approach to the snakes than does any other platynotan in general proportions of the brain case.

In lacking both a temporal arch and any sign of roofing for the temporal fossa, *Lanthanotus* more closely approaches snakes than does any other platynotan (with the possible exception of the dolichosaurs, in which it is by no means certain that there was a temporal arch). *Heloderma* also lacks a temporal arch, but in that genus the parietal partially roofs the temporal fossa in that it receives all muscular attachment on its ventral rather than its dorsal surface. But *Lanthanotus*, unlike snakes, still retains a vestigial squamosal capping the quadrate.

*Lanthanotus* differs from all living snakes and is typically lacertilian in the suspension of the quadrate. In *Lanthanotus* the quadrate is almost entirely suspended from the paroccipital process of the exoccipital (more correctly from the opisthotic, which fuses with the exoccipital to form the paroccipital process), and its attachment to the large tabular is minor and cannot provide much support. In all living snakes the quadrate is quite separate from the paroccipital process and is entirely supported by the tabular. This is true even of such snakes as *Ilysia* and *Cylindrophis* which have the tabular completely adnate to the skull and the paroccipital process approximated to the quadrate bone. In both *Cylindrophis* and *Ilysia* the joint apparatus and ligaments that suspend the quadrate involve only the quadrate and tabular and do not extend to the paroccipital process. But in the fossil (upper Cretaceous) South American snake *Dimilysia* (see Smith Woodward, 1901)

we find a quadrate suspension very like that of *Lanthanotus*, with the paroccipital abutting against the quadrate and the quadrate-tabular juncture slight. The fact that *Lanthanotus* agrees better with a fossil snake of known primitiveness than with modern forms suggests that the numerous resemblances between the living Bornean lizard and snakes may indicate a true phyletic affinity rather than mere parallelism.

The brain case of *Lanthanotus* shows some resemblance to that of snakes in the absence of the "entocarotid fossa," that is, there is no projecting ledge of bone just dorsal to the course of the entocarotid artery over the lateral surface of the pro-otic. The quadrate shows ophidian features in the absence of any well-marked conch for a tympanic cavity and in the bluntness of all its contours.

As noted above, the lower jaw in both snakes and *Lanthanotus* conforms closely to the aigialosaurian pattern, characterized by the modification of the sutures on the inner side of the mandible to form a hinge joint between the splenial and angular corresponding to a similar joint on the external face between the dentary and surangular. In all snakes, however, this joint has been specialized beyond the stage seen in *Lanthanotus*; in the snakes a mechanism is developed whereby the dentary is allowed to swing inward but cannot be flexed outward to any great extent. This mechanism involves the extension forward of an arrowhead-shaped tongue of bone from the surangular, this tongue of bone fitting into a fossa on the lateral surface of the dentary, limiting the laterad motion of the latter bone but not impeding mesiad motion because of the absence of any sutural contact. (Although the above is true of the vast majority of snakes, various genera show modifications of the general ophidian pattern. Thus in *Acrochordus* the anterior tongue-like process of the surangular is somewhat deflected laterally, allowing the dentary considerable laterad as well as mesiad motion. In *Sibynophis* great freedom is allowed the dentary because the bone is deeply emarginated opposite the anterior surangular tongue, and there is no portion of the dentary abutting against this process of the surangular. A similar condition exists in *Xenopeltis* but is aided by the rubbery elasticity of the bone itself. On the

other hand, in *Crotalus* and some of the Old World *Trimeresurus* the angular and the splenial are fused, so presumably there is no hinge action. A similar fusion of angular and splenial occurs in *Grayia*, where, in addition, the surangular tongue lies on the ventral rather than the lateral surface of the jaw. In the specialized burrower *Ilysia* both the splenial and the angular bones have been lost, and the dentary has developed a great, posteriorly directed pocket that fits over the lateral surface of the surangular tongue, reversing

the usual relationship. This modification gives the jaw of *Ilysia* great rigidity, thus allowing the lower jaw to assist the upper in forming a rigid rostrum for burrowing.)

While the presence of an aigialosaurian hinge in the lower jaw does not in itself indicate any more affinity of the snakes to *Lanthanotus* than to mosasaurs, dolichosaurs, and aigialosaurs, it is important because it shows *Lanthanotus* to be much more snake-like than *Varanus*, the lizard most frequently compared to snakes by anatomists.

### THE FOSSIL FAMILIES OF SNAKES

What is said above applies to snakes in the strictest sense of the word, that is, the snakes of the families Ilysiidae, Uropeltidae, Xenopeltidae, Boidae, Colubridae, Amblycephalidae, and Viperidae of Boulenger (1893, 1894, 1896). (The contents of these groups have been shifted about by subsequent workers, as in the case of the Neotropical forms placed in the Amblycephalidae by Boulenger, and some groups, such as the Elapidae and Crotalidae, have been raised from subfamily to family rank. None the less, if all these families are considered as a unit, there has been no generic assemblage recognized by Boulenger that has been removed to some other group of Squamata, nor has any genus known to science at the time Boulenger completed his "Catalogue of the snakes" been added to the group. There is no evidence that this series of families does not together constitute a natural group.)

There remains some doubt as to the proper taxonomic position of *Dinilysia* of the Cretaceous on account of its very primitive quadrate suspension, but its phyletic affinities appear to be definitely with this series of families. Of the Eocene Palaeophididae, a marine group of snake-like forms (for a general account and descriptions of the North American species, see Gilmore, 1938b) little can be said at present, since the family is known only from vertebrae and ribs. Supposedly, the family differs from living snakes in the absence of tubera costarum (present in the Cretaceous *Dinilysia*) and in having the parapophyses of the vertebrae extended laterally as far as the prezygapophyses. But

both these features are to be found in the living *Acrochordus*, a snake that further agrees with the palaeophidids in the thickening and slight carination of the centrum just beneath the anterior articular cotyle. It is by no means necessary to assume from this that *Acrochordus* is closely related to the palaeophidids (the neural spines of *Acrochordus* are very different from those of the palaeophidids), and the similarity may be but a reflection of the adaptation of both to completely aquatic habits. None the less, the various peculiarities of the Palaeophididae can be matched by various typical ophidians, although nowhere, so far as known, in combination. It seems almost certain that the Palaeophididae are to be ranked with the typical snakes, but in the absence of cranial material very little can be said of their precise affinities and they give no very useful information on the question of ophidian ancestry.

Janensch (1906) redescribed as a snake a marine fossil from the European Eocene Monte Bolca deposits, famed for their fine representation of Eocene teleosts. This fossil, *Archaeophis*, is known from the complete skeleton but, to judge from the illustrations, is not well preserved, and the skull is particularly fragmentary. The ribs are without tubera costarum. The snout is pointed, with the tooth rows relatively straight and converging near the tip of the pointed snout; the point of the snout does not appear to have extended much beyond the tip of the lower jaw. The ribs appear to be very slender, almost filiform. The maxilla

extended back to a point near the quadrato-mandibular articulation. The bone considered to be the quadrate by Janensch is slender, rather slightly expanded and abruptly truncate at either end, and without any noticeable sculpture. The teeth are particularly remarkable in that they are so ornamented by cutting keels as to be polygonal in cross section. In the vertebral column there are several remarkable features: the vertebrae appear relatively smooth and unsculptured, and the zygapophysial joints, as figured by Janensch, are most unusual, for the prezygapophysis is reduced to a small spine, and the plane of the articular surface of the post-zygapophysis is vertical, not horizontal. In spite of the narrowness of the vertebra there does not appear to have been a compressed neural spine.

All these features are at variance with any known snake, and there is no more resemblance to the Palaeophididae or *Dinilysia* than to living ophidians. Indeed, looking at Janensch's figures, we are led to suspect that *Archaeophis* might not even be reptilian, for there is much to suggest (though not enough to prove) affinities with the teleost fishes, particularly some eel of the *Ophichthus*-like group. The teeth of *Muraena* come far closer to those of *Archaeophis* than do those of any snake; the very slender ribs of *Archaeophis* are most un-ophidian in appearance, but compare well with those of the epipleural series in fishes; the zygapophysial articulation is decidedly *Ophichthus*-like, as is the vertebral form; the pointed snout can be matched among the snake-eels, but not among snakes, while the extreme backward extent of the maxilla is far more moray-like than snake-like. A partial conformation of this is the form of the "maxilla" as depicted by Janensch. At about the midpoint of its length the maxilla has a transverse break that slopes downward and slightly backward, and is broadened into an elliptical foramen at the center of its course. Possibly this is but a break in the specimen, which is not in good condition, but it is suspiciously like the articulation between the maxilla and ethmopremaxillovomerine bone of an eel. The "quadrate" of *Archaeophis* agrees well with the branchial bones of eels in its general form, while the "pterygoid" does not compare un-

favorably with an upper pharyngeal bone.

Against affinity with the eels may be mentioned the apparent procoely of the vertebrae and the presence of medioventral processes on the vertebrae, while the presence of scale-like structures is a departure from the ophichthids and would suggest such eels as *Anguilla* and *Simenchelys*, forms that do not present the dental and cranial resemblances seen in the ophichthids. For the present it would appear best to consider *Archaeophis* a vertebrate of uncertain position. It would certainly be premature to base any conclusions about ophidian ancestry on such a doubtful form.

The genera *Pachyophis*, *Mesophis*, and *Symoliophis* form a group of genera that appears to be quite natural, but the affinities of this group are by no means certain. Much the best known is *Pachyophis* (see Nopcsa, 1923), and even this genus is known only from the vertebrae, ribs, and fragments of the upper and lower jaws. The vertebrae of *Pachyophis* are of the type common to both platynotan lizards and snakes but have certain peculiarities found in neither group. Thus the anterior vertebrae are elongated, but the middle and posterior thoracics are stout and pachyostotic, with the ribs apparently dilated in a most peculiar manner. Such differentiation of the vertebral column suggests derivation from a long-necked, dolichosaur-like platynotan, the elongated anterior vertebrae corresponding to cervicals, but this would be a suggestion only, for since the vertebrae are in increased number it is possible that there has been a disproportionate increase in the length of the anterior column. The ribs are without tubera costarum. The jaw fragments suggest, as far as they go (which, unfortunately, is not very far), that the jaws were of the kinetic type. Nopcsa compares them to dolichosaur jaws, but in the absence of any good information on the jaw structure of dolichosaurs, it might be better simply to say that they are of the aigialosaurian type. The maxilla does not show the backward prolongation beneath the orbit so characteristic of snakes as compared with platynotan lizards. Since this backward prolongation of the maxilla in snakes is certainly secondary and exceeds that seen in any lizard, and since the typical snakes of the present day show unmistakable

evidence of an aigialosaurian lower jaw complicated by additional specializations, these few details of jaw structure are what might be expected of a very primitive snake. But the specializations of the vertebral column, certainly not snake-like, and the absence of any very definite evidence of ophidian features save limb reduction make it less than certain that the *Pachyophis* group represents more than a snake-like convergence of the dolichosaurs, and *Symoliophis* seems distinctly dolichosaurian rather than ophidian.

Inasmuch as *Pachyophis* of the Neocomian was contemporaneous with the earliest known dolichosaurs, it is even open to doubt that the Pachyophididae are descended from true dolichosaurs. It is most unlikely that the fossil record as known today has given us a complete picture of the platynotan adaptive radiation in Cretaceous times, and while dolichosaurs approach the pachyophidids more closely than any other known lizards, it is quite possible that some unknown, rather

dolichosaur-like family represents the true ancestor. Whether or not this "unknown dolichosaur-like family" might be a Cretaceous lanthanotid it is impossible to say, particularly since the vertebrae of *Lanthanotus* are hardly known. But again we must say that the Pachyophididae, though inviting speculation, are too poorly known and too incompletely linked to the true snakes to warrant any place in present theorizing as to the origin of the snakes.

Besides the typical snakes and certain poorly known fossils discussed above, there remain two families usually placed in the Ophidia, the Typhlopidae and Leptotyphlopidae. Neither of these families has been considered in the above account because both are so different, not only from the typical snakes but from each other, that it is not at all certain that these families lie on the same phylogenetic line that leads from the lizards to the ophidians. Therefore, each is considered separately.

### THE LEPTOTYPHLOPIDAE

The Leptotyphlopidae show a peculiar combination of specializations and degenerations accompanying a burrowing mode of life with primitive, lizard-like features not seen in the typical snakes. The anatomy of these diminutive, snake-like reptiles is far from completely known. Our account of the osteology of the Leptotyphlopidae is based partly on the papers of Brock (1932) and Haas (1930) and partly on personal examination of skulls of *Leptotyphlops humilis*, *L. nigricans*, and particularly *L. dimidiata*.

The lower jaw of the Leptotyphlopidae shows the typical aigialosaurian arrangement of bones and hinge without the specializations seen in snakes. Thus there is no tongue-like process of the surangular extending laterally along the dentary (see figs. 13, 32), a resemblance to the aigialosaurian lizards (including *Lanthanotus*) and a departure from the snakes. The joint is freely movable over a wide arc. The Meckelian groove is broadly open and completely separates the dorsal border of the splenial from the dentary in *Leptotyphlops dimidiata*, but Brock figures a

very small, tab-like process of the splenial in *L. nigricans*, this process meeting the dentary at the extreme posterior extremity, as in *Varanus* and *Lanthanotus*. The open splenial portion of the Meckelian groove is characteristic both of snakes (exceptionally absent, as in the colubrid *Aspidura*) and platynotan lizards. The angular bone has more lateral exposure than in snakes, where the angular is confined to the median surface of the jaw, and is thus more like that of the platynotan lizards. The surangular, prearticular, and articular are fused, as in snakes and not as in the platynotan lizards. In snakes and the aigialosaurian lizards, particularly *Lanthanotus*, the postarticular process of the lower mandible is much shortened; in the leptotyphlopids, it is absent altogether. In the Leptotyphlopidae there is a high and recurved process arising from the conjoined surangular and prearticular (but probably formed from the surangular alone) anterior and dorsal to the articular cotyle. Such a process is present in *Lanthanotus* (but not nearly so well developed) but is not known

among the typical snakes. The surangular is peculiar in being fenestrated on the lateral wall of the masseteric fossa.

In the typical snakes the dentary tooth row is drawn back on a special process of the dentary posterior to the splenial angular

hinge, a specialization beyond the platynotant lizards. In the Leptotyphlopidae exactly the reverse is true; the dentary tooth row is shortened and confined to the anterior half of the dorsal border of the dentary. The dentary is further peculiar in the development of

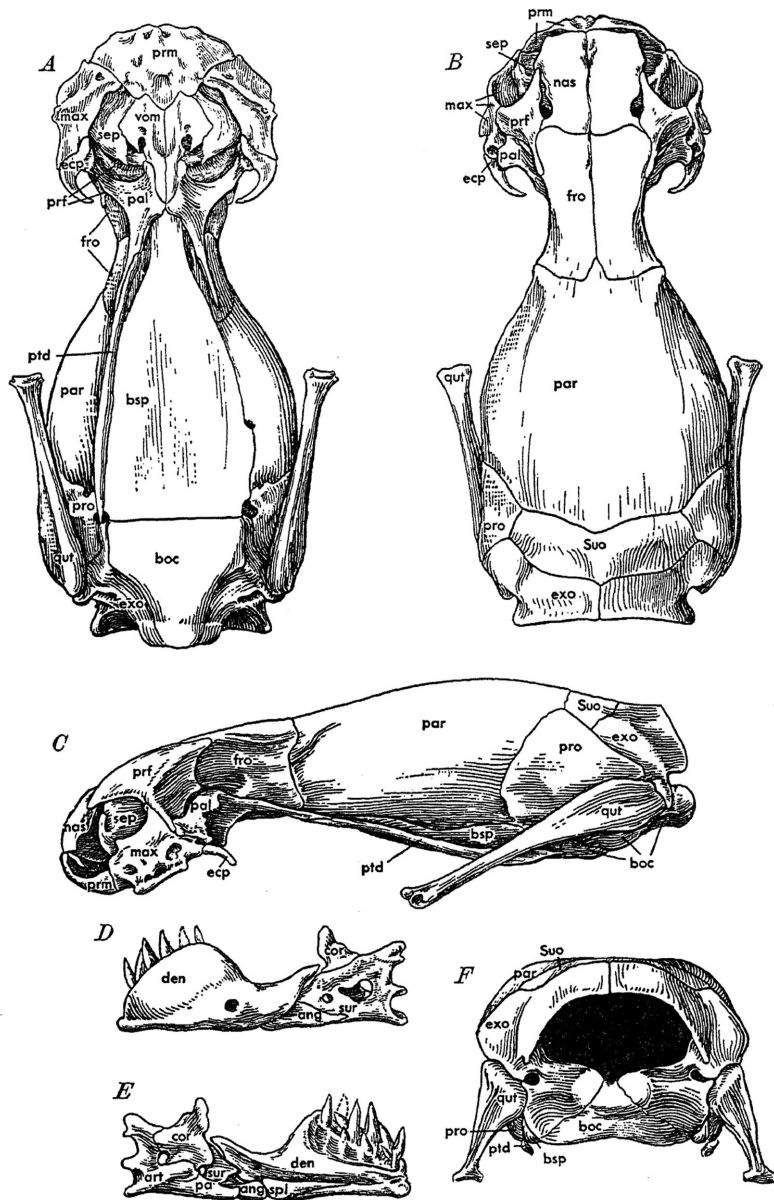


FIG. 13. *Leptotyphlops dimidiata*. A. Ventral view of skull. B. dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. F. Occipital view of skull. For abbreviations, see page 141. Drawing by McDowell.

a large, conch-like flange to bear the teeth.

The coronoid is of a peculiar nobby form, so distorted by the extreme shortening of the lower jaw that it is impossible to homologize its various processes and fossae to corresponding structures in other members of the Squamata with any degree of precision. The coronoid is far separated from the splenial, the most extreme development of the aigialosaurian hinge among Squamata.

The premaxillae are fused and, in accordance with the burrowing habits of the leptotyphlopids, much expanded. In being sutured to the maxilla the premaxilla of *Leptotyphlops* is lizard-like and unlike that of the vast majority of snakes. However, not much importance can be attached to this, for several advanced colubroids, such as the proteroglyph *Elaps* and the peculiar *Dasyplexis*, have redeveloped a premaxillomaxillary contact. In lacking a median ventral tubercle the premaxillaries of *Leptotyphlops* resemble those of most snakes and differ from those of Platyntonia. The premaxilla bears no teeth, in which respect it is less primitive than that of such snakes as *Python*, *Xenopeltis*, *Loxocemus*, and *Ilysia*.

The vomer is of a very peculiar form in that the palatine articulations extend forward nearly to the openings for the palatal orifices of the organs of Jacobson. As in snakes and *Lanthanotus* there is no connection between vomer and maxilla. The connections of the vomer are much as in *Lanthanotus* in that the bone is joined dorsally to the frontal but retains a very broad and rigid connection with the palatine (determined by dissection of *Leptotyphlops humilis*).

The septomaxilla is of the type seen in snakes and *Lanthanotus*; that is, the lateral extremity is curled upward to form a lateral, ascending, tab-like process. The septomaxilla of *Leptotyphlops* is peculiar in the great development of the dome roofing over the organ of Jacobson.

The maxilla of the leptotyphlopids is lizard-like, rather than ophidian, in being rigidly connected to the skull; it is like that of the platynotans in lacking any suborbital extent, and thus different from that of the vast majority of snakes. From the posterior extremity of the maxilla there extends downward and backward a flattened and pointed

hook-like process (see fig. 13). On the dorsal surface of the maxilla of *Leptotyphlops dimidiata* a distinct transverse suture separates this process from the body of the maxilla, may be traced around the edges of the maxilla to the inner and outer margins of the palatal surface, but becomes very vague on the center of the palatal surface of the maxilla. This strongly suggests that the hook-like posterior process of the maxilla represents an ectopterygoid bone partially fused to the maxilla. Otherwise, the ectopterygoid is absent in the Leptotyphlopidae, and the maxilla possesses an anomalous process not represented in other squamates. If this element is a true ectopterygoid, the arrangement of bones in this region of the leptotyphlopoid skull is as in platynotan lizards and quite different from that obtaining in most snakes, for the maxillary process of the palatine articulates with both the maxilla proper and the presumptive ectopterygoid, excluding the maxilla from the suborbital fenestra (in the case of the leptotyphlopids, "suborbital emargination" might be a more accurate term, since the failure of the presumed ectopterygoid to meet the pterygoid or palatine leaves the fenestra undefined posteriorly).

In snakes, probably in consequence of the posterior elongation of the maxilla and its loss of sutural contacts, the ectopterygoid-maxillary articulation is shoved far posterior to the palatine-maxillary articulation, and the maxilla enters more or less broadly into the suborbital fenestra. [This is not the case in all snakes. In the peculiar and quite possibly very primitive Asiatic snake *Achalinus* the ectopterygoid extends along the dorsal surface of the maxilla nearly or quite to meet the maxillary process of the palatine. Since *Achalinus* combines a boid-like form of septomaxilla with the general features of the colubrids it is possible that it represents a very primitive radiation of the snakes, but there is no very positive evidence of this.

On the other hand, in the African genus *Miodon* there is no reason to doubt that we are here dealing with a very progressive and specialized genus, very possibly derived from *Lycophidion* (with the maxilla entering the fenestra), which it resembles in the form of the maxilla and prefrontal, exclusion of the frontal from the orbit by the prefrontal, very

short tabular, general scutellation, and the hemipenis. In *Miodon* the inner prong of the anteriorly bifurcate ectopterygoid is produced forward to meet the maxillary process of the palatine and the inner, hook-like process of the maxilla so characteristic of the *Lycophidion*-like forms. Thus two fenestrae are formed, an outer bordered by the maxilla and ectopterygoid, and an inner bordered by the ectopterygoid, palatine, and (narrowly) pterygoid. If we consider the inner of these fenestrae to constitute the true suborbital fenestra, then the maxilla is excluded, but comparison with *Lycophidion* shows that what actually has occurred is a subdivision of the suborbital fenestra by the ectopterygoid. In the more specialized vipers the maxilla is so much shortened (secondarily) that the palatine and ectopterygoid (and sometimes prefrontal as well) meet or nearly meet to exclude the maxilla from the suborbital fenestra.]

While the maxilla of *Leptotyphlops* resembles that of the platynotan lizards in its rigidity, shortness, and exclusion from the suborbital fenestra, it is snake-like in the reduction of its extent over the face. In *Varanus*, *Heloderma*, *Lanthanotus*, and many other lizards the lateral surface of the prefrontal is produced forward as a large triangular process (apex directed rostrally), but this triangular anterior extension of the prefrontal is concealed from lateral view by the high, ascending, facial lamina of the maxilla, the maxilla covering most of the side of the snout. In snakes the ascending facial lamina of the maxilla is absent, the maxilla being reduced to a tooth-bearing rod of bone that does not contribute to the lateral wall of the snout. In such snakes as the boas and pythons that retain the anterior process of the prefrontal, this process is completely exposed laterally (but most colubrids, vipers, proteroglyphs, and such forms as *Loxocemus*, *Xenopeltis*, and *Cylindrophis* have reduced or lost this anterior projection of the prefrontal). In this respect *Leptotyphlops* is like snakes, for the triangular anterior lamina of the prefrontal is completely exposed. In the loss of all maxillary dentition the leptotyphlopids are specialized beyond both snakes and platynotans.

The nasals of *Leptotyphlops* are like those

of *Lanthanotus* and snakes in being expanded transversely to form a partial roof for the olfactory chamber, but there is no anterior emargination for the narial sac, for the entire lateral border of the nasal anterior to a contact with the anterior extremity of the prefrontal is applied against the soft tissue of the anterior naris. The nasals have strong, median, descending laminae that form a bony septum between the nostrils, as in many or most snakes and *Lanthanotus*.

Although obscured by tough connective tissue there is, in the leptotyphlopids, a remnant of the slit-like extension of the naris to separate the nasal and prefrontal, a feature characteristic of the platynotans and the snakes (with the possible exception of the specialized African python, *Calabaria*). We find in *Leptotyphlops dimidiata* an elliptical fenestra between the nasal and the prefrontal, and although Brock does not figure this for *L. nigricans*, we find it in that species as well. Anteriorly, this elliptical vacuity is separated from the vacuity for the naris by a contact between the lateral border of the nasal and the anterior extremity of the triangular anterior lamina of the prefrontal, but no true suture appears to be formed. Posteriorly, the nasal and prefrontal meet in a very short suture and thus barely separate the frontal from the vacuity (seen also in most Hydrophiinae and possibly in *Aigialosaurus*).

Like snakes, but unlike platynotan lizards, the Leptotyphlopidae have no lacrimal bone. Again like snakes and unlike the Platynota, the leptotyphlopids lack a jugal. In the absence of a post-frontal or postorbital, the leptotyphlopids differ both from the platynotans and most (but not all) snakes; among the snakes, absence of a post-frontal appears to be correlated with burrowing habits (examples are *Elaps*, *Micrurus*, and *Atractaspis*).

The frontal bones of the Leptotyphlopidae are of the type seen in both snakes and *Lanthanotus*. They are distinct from each other and send down very long descending (subolfactory) laminae so that the orbits are completely separated by an anterior extension of the cranial chamber. Along the upper rim of the orbit the prefrontal sends back a finger-like supraorbital process along the frontal bone, as in snakes (except *Acrochordus* and some vipers) and platynotans,

as well as most other saurians. Again as is normal for Squamata generally, the frontal is nearly flat and horizontal dorsal to the supraorbital process of the prefrontal; that part of the frontal ventral to the supraorbital process of the prefrontal represents the vertical subolfactory process. The leptotyphlopids differ from both snakes and platynotans (as well as lizards generally) in that the descending process of the frontal surrounds the optic foramen, rather than lying anterior and dorsal to it.

The palatine is very lizard-like in being triradiate. One branch extends forward and inward to form a very strong articulation with the vomer; a second branch extends forward and outward to articulate with the maxilla and the presumed ectopterygoid; the third branch is very slender and extends backward to suture by squamous overlap with the pterygoid. All this is as in platynotan lizards and quite unlike the condition seen in the vast majority of snakes. Typically, in the snakes the palatine is quadriradiate, and there is a longitudinal, anterior, tooth-bearing branch extending forward from the anterior border of the bone, lateral to the vomerinae branch and median to the maxillary branch. Moreover, in snakes the palatine-vomerine juncture is weak or absent; in some snakes (for example, *Dendroaspis*) the palatine may lack the maxillary branch. In all true snakes the maxillary branch of the palatine (when present) has shifted its main attachment from the maxilla to the prefrontal, a modification necessitated by the freedom of the maxillary bone. However, *Leptotyphlops* is lizard-like in having only a slight contact between the prefrontal and maxillary branch of the palatine, the palatine being firmly attached to both the maxilla and the presumed ectopterygoid.

But it is not certain that these lizard-like features of the palatine of *Leptotyphlops* are not secondary adaptations. In *Leptotyphlops* the palatine is completely edentulous, and this may well account for the absence of the tooth-bearing branch so characteristic of snakes, for several true snakes without palatal teeth (such as *Rhinophis*) also lack this branch of the palatine bone. The rigidity of the maxilla, which may be a secondary feature of the leptotyphlopids, may account for

the lizard-like relations of the maxillary process of the palatine.

The pterygoid of the leptotyphlopids is very degenerate and not similar to that of either the snakes or lizards, for it is reduced to a slender, edentulous rod, slightly dilated posteriorly, which lies close against the brain case along the lateral border of the basisphenoid without approaching the quadratomandibular juncture. In several snakes, such as *Pareas* and most vipers and cobras, the pterygoid does not reach the quadratomandibular joint, but the pterygoid is nevertheless directed towards that joint and connected to it by a ligament. In *Leptotyphlops* the pterygoid extends some distance posterior to the level of the quadratomandibular joint and bypasses the articulation completely.

The parietals of *Leptotyphlops* are decidedly snake-like in that they form a complete lateral wall for the brain case anterior to the pro-otic and enter into a long suture with the basisphenoid. The parietals of *L. dimidiata* at least are completely fused, and there is no pineal foramen, but in some of the smaller species it is possible that there is relatively little calcification dorsally. Thus, while dissection reveals the parietals of *L. humilis* to be fused and complete dorsally, the parietals fail to stain with alizarin red sulfonate on the dorsal surface.

There is no trace of an epipterygoid, a further resemblance to the true snakes, and the foramen for the trigeminal nerve (branches V2 and V3) is snake-like in lying entirely or almost entirely in the pro-otic and in being divided into two parts by a bony partition. The cranial foramina are anomalous in lacking a fenestra ovale, external fenestra rotundum, or jugular foramen.

As in snakes and *Lanthanotus*, there is no temporal arch, nor can we detect in our material any sign of a squamosal or tabular. However, Brock (1932) figures and describes (in *L. nigricans*) a small ossicle capping the quadrate that she identifies as a tabular. This may well be the correct homology for the ossicle, but it should be remembered that in lying above the quadrate, rather than between the quadrate and the parietal, the ossicle shows some resemblance to the vestigial squamosal of *Lanthanotus* and *Heloderma*. The quadrate suspension of the Leptotyphlopidae is lizard-

like and more primitive than that of any true snake, save the upper Cretaceous *Dinilysia*, in that the quadrate is slung from the paroccipital process.

The quadrate of the leptotyphlopids differs from that of the typical ophidians, for it is directed downward and sharply forward, rather than being vertical or inclined backward. In form the quadrate is long and narrow, without trace of wings or conchs.

The exoccipitals are snake-like in that they meet each other behind the supraoccipital to exclude the supraoccipital from the foramen magnum. [This is not true of all snakes, however, for in *Phyllorhynchus* and at least some skulls of *Dasyplexis*, the supra-occipital very narrowly wedges its way between the exoccipitals to enter (barely) the dorsal border of the foramen magnum. In the Tropical American Boinae the supraoccipital overlaps the conjoined exoccipitals nearly or quite to enter the foramen magnum.]

The teeth of the Leptotyphlopidae are confined to the dentary bone and show alternate replacement. However, the replacement teeth are not horizontal, as in snakes, but lie next to their presumptive sockets in a nearly vertical position; it is probably this saurian feature that necessitates the peculiar dental conch of the dentary bone. Not as in snakes, the teeth are hardly recurved in the leptotyphlopids, and this slight curvature together with the compressed form of the crown gives the leptotyphlopoid tooth a strong resemblance to the tooth of such a platynotan as *Lanthanotus* or *Varanus salvator*. In most snakes the bone forms a slight rim all around the base of the ankylosed tooth, but in *Leptotyphlops*, as in Platynota, there is no bony rim on the lingual side of the dental base.

Essex (1927, pp. 908-914, text figs. 39-49) has described and figured the pelvic girdle for several species of "*Glauconia*" (= *Leptotyphlops*). (There is no trace of a pectoral girdle in the Leptotyphlopidae.) Essex confirms the presence of an ischiadic symphysis in some species (*L. nigricans* and *macrolepis*), but finds in such species as *L. albifrons* that the girdle is much more degenerate. In all, to judge from his figures, the ischia converge, but the pubes diverge. A strong claw supported by the vestige of the hind limb in more or less undifferentiated form ("femur") is

present and may perforate the skin. In the presence, at least in some species, of an ischiadic symphysis, the Leptotyphlopidae are more primitive and hence more lizard-like than any ordinary snake.

The vertebrae of leptotyphlopids are of the common platynotan-ophidian type; that is, the centra are tapered posteriorly, the condyle is directed obliquely upward and is very slightly broader than the precondylar centrum; zygosphenes and zygantra are present. The vertebrae are decidedly more snake-like than lizard-like in that the prezygapophyses extend considerably farther laterad than do the parapophyses. Moreover, the prezygapophyses bear short cylindrical processes extending laterally from just beneath the articular surfaces. In addition, the centra have a rather vague and rounded longitudinal median ventral ridge, as in most snakes but not platynotan lizards. There are distinct tubera costarum on the ribs, but the rib articulation is very simple, the parapophysis presenting a simple oval condyle, the rib a corresponding cotyle; the parapophyses are not produced ventrally. Neural spines are absent, an apparent burrowing modification, since it is also found in burrowing genera of typical Ophidia (such as *Rhinophis* and *Miodon*). Hypapophyses are present on only the first three or four vertebrae and are completely fused to the centra. There are no haemal arches.

The tongue is much the same as that found in boids and many colubrids, for there is a fringe of papillae on the lateral margin posterior to the level of terminal bifurcation. The terminal bifurcation is not quite so extensive as is usual in snakes and is of about the proportions seen in *Varanus* (the length of the bifurcation not more than about five times the width of the tongue just behind the bifurcation).

From all this 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. The aigialosaurian jaw, lizard-like palatine, erect position of replacement teeth, short and stationary maxilla, ischiadic symphysis, probable exclusion of the maxilla from the suborbital fenestra, and the form of the individual teeth are all lizard-like or, more specifically, platynotan-like features, not seen

in the snakes, or to be seen only in those where the condition is obviously secondary and never in combination. At the same time it is quite impossible to derive the snakes from the leptotyphlopids, for their burrowing modifications, including the loss of all but the dentary teeth, the loss of the postfrontal, the reduction of the posterior portion of the ectopterygoid, the loss of the connection between the pterygoid and the quadratomandibular joint, all would eliminate any known leptotyphlopoid as a snake ancestor.

However, the leptotyphlopids possess features that appear to indicate genuine affinity with the other ophidians. First, both the leptotyphlopids and the snakes retain several features indicative of aigialosaurian ancestry in their jaw structure, the backward prolongation of the anterior naris between nasal and prefrontal, the vertebral form, and the *Lanthanotus*-like frontals and vomerine-frontal contact. Thus, even if the snakes and leptotyphlopids have arisen independently from two distinct lacertilian ancestors, the ancestral lizards were almost certainly members of a very closely knit group, the aigialosaurian Platynota. Thus, if the phylogenetic lines leading back from the snakes and from the leptotyphlopids do not actually join, at least they very closely approximate each other and cannot be separated on present evidence. Moreover, both snakes and leptotyphlopids resemble one family of aigialosaurians, the Lanthanotidae, more closely than they do other aigialosaurian groups. While this resemblance may be parallelism to a greater or less degree, it is so close that it suggests an underlying affinity that is real.

Secondly, there are several structural resemblances between snakes and leptotyphlopids suggesting that, if the two groups represent nothing more than parallel but separate off-shoots of the aigialosaurians, the parallelism has been very close indeed. Such resemblances are:

1. Great development of the descending wings of the parietals, forming a complete lateral wall for the brain case anterior to the pro-otic.
2. Loss of the epipterygoid, at least as an adult structure.
3. Great forward extent of the ossified basisphenoid.

4. Union of the two exoccipitals behind the supraoccipital, at least in most forms.

5. Reduction of the facial wing of the maxilla.

6. Loss of the lacrimal bone.

7. Loss of the jugal.

8. Total loss of the pectoral limbs and girdle, and marked reduction in the pelvic girdle.

9. Backward migration of the root of the tongue to a point well behind the head.

The most impressive fact brought out by this list is not any particular feature of resemblance but rather the number of the features present in combination. Thus the lacrimal and jugal have been lost quite independently in the snakes and in the Gekkota. Among numerous groups of lizards, particularly the scincids, parallel trends in limb reduction can be seen. The epipterygoid has been lost in chamaeleonids and dibamids, forms with little or no resemblance to the snakes. In the amphisbaenids we find the cranial closure by enlargement of the basisphenoid and hypertrophy of the descending wings of the parietals. The backward migration of the root of the tongue seems to involve merely the breakdown of distinction between the muscular trunks of the free tongue and the hyoidean musculature, a more extreme case of a modification seen to greater or less extent in all anguimorphs, and somewhat approached by the *Ameiva-Tupinambus* series of teiids, a group of very remote relationship to the snakes.

It would seem that the number of resemblances between snakes and leptotyphlopids is greater than that expected if we were dealing with quite independent but parallel phyletic lines. Although it might be expected that two parallel lines derived from very similar but separate ancestral forms would have more in common than parallelistic groups derived from ancestors unlike each other, so great is the similarity between snakes and leptotyphlopids that any morphological differences between the hypothetical saurian ancestor of the snakes and the hypothetical saurian ancestor of the leptotyphlopids must have been very minor indeed.

To sum up: There is no definite evidence that the snakes and leptotyphlopids are diphyletic, whereas there is much to suggest that they represent a monophyletic group

that at an early stage branched into two lines. Furthermore if the snakes and leptotyphlopids do represent a diphyletic group, the two respective ancestral (saurian) forms must have been very closely related to each other.

Such a conclusion strengthens a belief that the snakes originated from an aigialosaurian stock morphologically similar to the living *Lanthanotus*, for the resemblances of the leptotyphlopids to the aigialosaurians (particularly to *Lanthanotus*) are even greater than those of other snakes. This is particularly marked in the form of the intramandibular hinge (which lacks a special process of the surangular overlapping the dentary), the lizard-like vertical position of the replacement teeth, the short and immovable maxilla, and the strong articulation of the palatine to the vomer.

From the standpoint of time, of course, it is quite impossible to derive the snakes and leptotyphlopids from *Lanthanotus*, for an unquestionable snake (*Dinilysia*) occurs in the upper Cretaceous, and *Pachyophis*, which is possibly ophidian, in the Neocomian. All we wish to point out is that at least one aigialosaurian lizard, the Recent *Lanthanotus*, shows remarkable similarity to the snakes and leptotyphlopids in many anatomical features that appear to be of considerable importance. Possibly *Lanthanotus* is a little-modified relict of a very early Cretaceous family that gave rise to the snakes and the leptotyphlopids. The imperfectly known Neocomian genera *Mesoleptos* and *Eidolosaurus* might be fossil representatives of such a group, for, while they are usually placed in the Dolichosauridae or Aigialosauridae, they have the neck of a length intermediate between that of each of

the two families (see Nopcsa, 1923) and thus in this respect approach *Lanthanotus*. Unfortunately the skull is virtually unknown in both genera, while we have but scanty knowledge of the vertebrae of *Lanthanotus*.

Again it is also possible that better knowledge of the skull of the fossil family Dolichosauridae will reveal that those lizards possessed a skull with the snake-like features now known definitely only in *Lanthanotus*. It must be remembered that certain snake-like features of *Lanthanotus*, such as the transparent palpebral disc, tongue structure, and absence of the ear, may well have been present in the fossil aigialosaurians as well.

A third possibility is that the platynotans underwent a far greater adaptive radiation during early Cretaceous times than has been indicated by discoveries up to the present. That this is true is suggested by the fact that the Varanidae and Helodermatidae, though apparently more primitive than the aigialosaurians, are not known from so early an age. Very possibly *Lanthanotus* gives us but a small sample of the snake-like modifications developed in earliest Cretaceous times by as yet unknown platynotan families.

Although there is no proof that the Lanthanotidae were the direct ancestors of the snakes, including the Leptotyphlopidae but not the Typhlopidae, the combination in *Lanthanotus* of numerous snake-like features, some (such as the septomaxillary structure and the vomerine-frontal contact) not known elsewhere among lizards, materially strengthens the theory that the aigialosaurian platynotans represent the saurian group most probably ancestral to snakes.

## THE TYPHLOPIDAE

If we accept the aigialosaurian ancestry of the snakes, again including the leptotyphlopids but not, however, the typhlopids, it would appear highly improbable that the Typhlopidae (including Anomalepidae) are properly placed in the Ophidia, for the Typhlopidae show indications of derivation not from aigialosaurian forms but rather from some group of diploglossan anguimorphs.

This is particularly marked in the details of jaw structure. In the typhlopids there is no

trace of an intramandibular hinge; rather, the sutures of the jaw behind the dentary are oriented in a longitudinal direction, giving the jaw added rigidity by means of polylaminate structure. The dentary bears no teeth in *Typhlops*, a single tooth in *Anomalepis* and *Liotyphlops* (for the osteology of these last two genera, see Dunn, 1941; Dunn and Tihen, 1944). In accordance with its much reduced function the dentary is very short. Most unlike conditions in snakes and platy-

notans, the two dentary bones of the typhlopids are rigidly connected to each other by a nodule of cartilage; such a cartilage is found in some diploglossans (e.g., *Shinisaurus*), and a rigid symphysis is characteristic of the group. The snakes (including leptotyphlopids) and platynotan lizards agree with each other in the failure of the dorsal margin of the splenial to meet the dentary (except for

nected to the surrounding mandibular bones. The dentary-surangular suture is oblique and nearer to the horizontal than to the vertical; there is a strong dentary coronoid suture on the inner side of the jaw, this suture also being strongly oblique.

The splenial of the typhlopids is remarkable for its very large size and its very extensive lateral exposure. The very un-snake-like feature of concealment of the Meckelian cartilage by the splenial is noted above, but the splenial shows an additional feature that contrasts strongly with the aigialosaurian, leptotyphlopoid, and ophidian jaw structure and suggests the two primitive platynotan families Helodermatidae and Varanidae, as well as the diploglossan families Anguinidae, Xenosauridae, and Anniellidae. This feature relates to the form of the splenial-coronoid juncture. In the aigialosaurians and snakes the presence of an intramandibular hinge on the median as well as the lateral surface of the jaw much reduces the splenial-coronoid contact, for the splenial lies entirely anterior to the vertical hinge, the coronoid posterior. As a result, the only contact between the splenial and coronoid is a very short corner-to-corner, one-point articulation, and in the leptotyphlopids even this is lost and the splenial and coronoid are widely separated. But in the Typhlopidae the arrangement of sutures is as in Squamata that have never developed a median jaw hinge. The splenial extends far back along the ventral border of the coronoid and forms with that bone a long horizontal suture. This suture ends posteriorly only when the ventral border of the coronoid is deeply emarginated to expose a semi-circular area of the surangular. The splenial is extended back even beyond this point, but free of the coronoid, and reaches the level of the apex of the coronoid process. In extending back to the level of the apex of the coronoid process the splenial of the typhlopids resembles that of diploglossans and differs from that of all platynotans, including the Helodermatidae and Varanidae.

The coronoid bone itself is very different in the snakes and typhlopids. In most lizards the coronoid is a more or less triangular bone with the apex pointed upward (the coronoid process) and a horizontal base situated on the median side of the jaw along the dorsal bor-

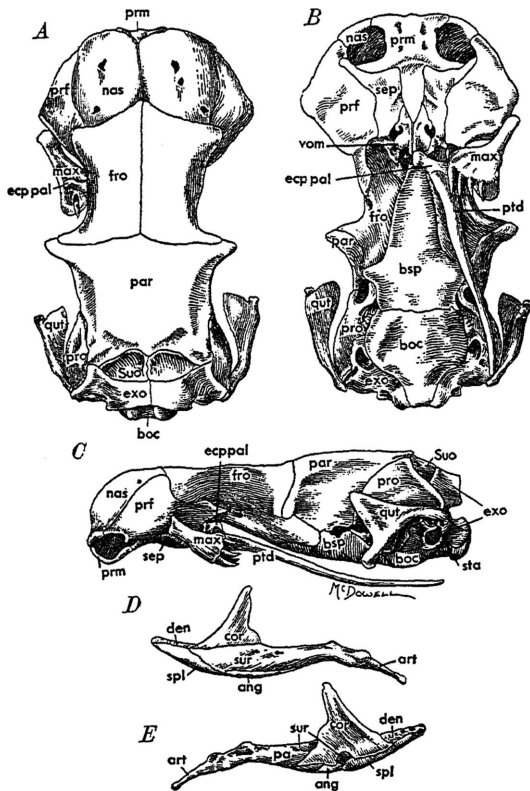


FIG. 14. *Typhlops punctatus*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell.

a very short and tab-like contact), thus exposing the Meckelian cartilage on the inner surface of the jaw for a considerable distance between the splenial and the dentary; the typhlopids are like the diploglossans (and most other lizards) in having the Meckelian cartilage covered over between the splenial and dentary by a long suture between the dentary and the dorsal border of splenial. The dentary of the typhlopids is rigidly con-

der of the prearticular. At about the middle, this horizontal base is emarginated to expose a semicircular portion of the surangular on the inner surface of the jaw, and thus by this emargination two descending processes of the coronoid are defined, an anterior (that is, anterior to the surangular exposure) and a posterior (posterior to the exposure). In the snakes and the Mosasauridae the posterior descending process has been lost; in the Leptotyphlopidae the entire coronoid is so peculiar in form (doubtless as a result of the extreme shortening of the lower jaw) that it appears impossible at present to homologize its various parts. The typhlopids are like the more normal lizards in the possession of both the anterior and the posterior descending processes of the coronoid. In this respect they resemble both the diploglossan and the platynotan (except the mosasaurs) Anguinomorpha, but in the form of the coronoid process the typhlopids are very different from both the platynotans and the snakes and resemble the diploglossans. In snakes and platynotans the dorsal border of the coronoid is horizontal anteriorly, and the coronoid process arises from the posterior part of the bone behind this horizontal plateau. In the diploglossans the entire anterior portion of the dorsal margin of the coronoid bone slopes upward and backward in a smooth curve to terminate in the apex of the coronoid process. The typhlopids are like the diploglossans in this respect, and there is a close resemblance between the typhlopids and the galliwasp (*Diploglossus* and *Celestus*) in the form of the coronoid bone. There is no suggestion of the highly peculiar coronoid of the leptotyphlopids.

In the typhlopids the postarticular process of the mandible is very long, a resemblance to the diploglossans and the primitive platynotans; in the snakes, as in *Lanthanotus*, the postarticular process is very short (relative to the length of the jaw) and in the leptotyphlopids is absent altogether.

The premaxilla is expanded transversely in the typhlopids and to this extent resembles that of the leptotyphlopids; moreover, it is without teeth. But otherwise the premaxilla of the typhlopids is very unlike that of the leptotyphlopids, and the resemblances are probably but the result in the two families

of modification of the snout for burrowing.

In the leptotyphlopids, as in snakes and platynotans, the premaxillae send back broad palatal processes that suture with nearly the entire anterior border of the vomers; although there is a slight premaxillary-septomaxillary contact lateral to the premaxillary-vomerine contact, this is slight and not a firm articulation. In the typhlopids, as in the diploglossans, the premaxilla sends back but a narrow process (along the midline) to form a very short articulation with the anterior margin of the vomer; instead, the septomaxilla takes over the greatest part in the bracing of the premaxilla and forms a strong suture with the premaxillary bone. In the leptotyphlopids the premaxilla does not form a strong suture with the anterior margin of the nasal, and this is true of snakes as well; in typhlopids the posterior dorsal margin of the premaxilla forms a long transverse or V-shaped suture with the anterior margin of the nasals.

The vomer in the typhlopids is very different from that seen in snakes, leptotyphlopids, and *Lanthanotus* in that it does not reach the frontal; instead, the lateral margin of the vomer is firmly sutured to the septomaxilla, and it is by that bone only that the vomer is suspended in the skull. Unlike conditions in the leptotyphlopids but like those in the snakes, the vomer of the typhlopids is very loosely articulated to the palatine.

The septomaxilla of the Typhlopidae is an enormous bone and forms a major part of the floor of the rostrum; it shows 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. In the typhlopids the septomaxilla fulfills the function of the vomer in the snakes and leptotyphlopids, for the septomaxilla is joined to the frontals by a strong suture, thus bracing the rostrum against the orbital region of the brain case.

The nasal bones of the typhlopids show no trace of platynotan heritage, for the lateral border of the nasal is firmly sutured to the dorsal border of the prefrontal. The bony anterior naris is circular, without trace of the backward slit-like extension of the cavity between nasal and prefrontal, a feature so characteristic of snakes, leptotyphlopids (see

above), and platynotans. The nasals are expanded.

The maxilla and its suspension from the skull are altogether peculiar in the typhlopids, and there is no parallel among other reptiles. What is perhaps the more primitive type of suspension is found in the anomalepine group of typhlopids (see Dunn, 1941, for *Anomalepis*; Dunn and Tihen, 1944, for *Liotyphlops*). The maxilla is a very short bone bearing but four or five teeth, all located beneath the eye (this in marked distinction to the leptotyphlopids and platynotans, but similar to diploglossans and most snakes). There is no extension of the maxillary bone beneath the naris, and the maxilla is far separated from the premaxilla. From the dorsal surface of the maxilla there extends upward a long preorbital process, which is concave on its posterior border and slanted somewhat anteriorly as well as dorsally. Since this preorbital process of the maxilla extends some distance dorsally and lies lateral to a considerable portion of the prefrontal, it is hard to escape the belief that this process represents the facial wing of the maxilla, a wing found in the majority of lizards, including both platynotans and diploglossans, but absent in both snakes and leptotyphlopids, where the maxilla lies ventral to the prefrontal.

The dorsal extremity of the preorbital process of the maxilla articulates with the "supraorbital" bone. The supraorbital of the anomalepines is a bone of questionable homology. It shows no resemblance to the "supraorbital" of pythons in either shape or position, for while the supraorbital of the pythons lies behind the prefrontal in a notch on the lateral border of the supraorbital shelf of the frontal, the supraorbital of the anomalepines is far more lateral—lateral indeed to all the other bones of the face and to the prefrontal. The relationships of the anomalepine supraorbital are, however, rather similar to those of the anteriormost supraocular osteoderm or the palpebral of lizards.

The lacertilian palpebral extends forward to a greater or less extent across the lateral surface of the prefrontal to meet or but narrowly miss the posterodorsal corner of the facial process of the maxilla. Posteriorly, the supraorbital terminates in a flattened and expanded area that rests upon a lateral pro-

jection formed by the frontal and parietal. This lateral triangular postorbital extension of the frontal and parietal (found in the typhlopines as well as in the anomalepines) is not to be seen in the snakes or leptotyphlopids but is very suggestive of the attachment surface for the postfrontal seen in most lizards. There is therefore a distinct possibility that the supraorbital bone of the anomalepines represents a fusion of the palpebral with the postfrontal.

Behind and beneath the eye of the anomalepines an obliquely placed bone extends downward and forward from the posterior extremity of the supraorbital (?=postfrontal) to articulate with the dorsal surface of the maxilla just behind the base of the preorbital process of the maxilla. In *Anomalepis* (Dunn, 1941), but not in *Liotyphlops* (Dunn and Tihen, 1944), the posterodorsal extremity of this bone is drawn out for some distance behind the palpebral articulation as a pointed, backwardly directed process that runs parallel and lateral to the parietal. This would appear to be a remnant of the anterior portion of the temporal arch, a structure completely absent in the snakes, leptotyphlopids, and *Lanthanotus*. Dunn states that this bone is not connected with the skull but is attached to the skin, and he further states that his cleared specimen had been mutilated in such a manner that dislocations of bones were obvious. From his picture (Dunn, 1941, p. 523) it appears that this bone, which he called the posterior orbital, may be anteriorly displaced in his specimen, for there is a notch in the anterior extremity of the dorsal border that would appear to fit the convexity in the ventral border of the posterior extremity of the supraorbital bone. Yet Dunn figures this notch as far anterior to the supraorbital convexity. More likely, Dunn has figured the supraorbital in a backwardly displaced position, for he shows the anterior extremity of the supraorbital as directly over the eye, whereas in a well-preserved and un mutilated *Liotyphlops* (Dunn and Tihen, 1944) the supraorbital extends far anterior to the eye to articulate with the preorbital process of the maxilla.

The portion of the "posterior orbital bone" of *Anomalepis* that extends behind the supraorbital as a partial temporal arch appears to

be homologous with the postorbital bone of lizards, for in all lizards with a well-developed temporal arch the postorbital forms the anterior portion of the arcade. In *Liotyphlops* this arch element is absent, and the "posterior orbital bone" has very much the relations of the jugal bone of anguimorph lizards.

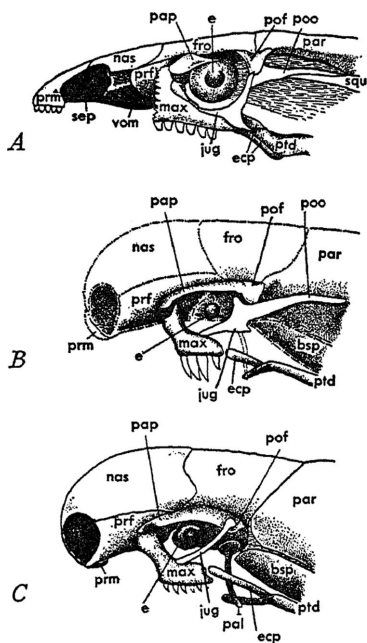


FIG. 15. Suggested derivation of the typhlopoid maxillary suspension. A. An anguine lizard (*Celestus costatus*), with the anterior portion of the maxilla removed artificially. B. Maxilla and its associated bones of *Anomalepis*, from Dunn (1944), with brain case (outlined in broken line) and articulations based on *Typhlops*. C. *Liotyphlops*, after Dunn and Tihen (1948). For abbreviations, see page 141. The bone labeled pap in A is the first supraocular osteoderm, probably homologous, wholly or in part, with the palpebral of some lizards. Drawing by McDowell.

The "posterior orbital" in this genus has its anterior ventral extremity beneath the eye and approximated to the maxilla upon the dorsal surface of that bone, immediately behind the preorbital process (facial wing) of the maxilla. This is exactly the position of the anterior extremity of the jugal in the lizards, and the suborbital position has generally been considered the principal criterion of homology in distinguishing the jugal from the other cir-

cumorbital bones in the study of the vertebrate skull.

It is therefore of considerable significance that the "posterior orbital bone" of *Liotyphlops* forms the entire suboptic border. The posterior end of the bone arches upward and backward to lie opposite the triangular expansion of the hind extremity of the "supra-orbital." As discussed above, there is some reason to suspect that this hind expansion of the supraorbital represents the post-frontal. If this be the case, the relationships of the posterior extremity of the "posterior orbital bone" of *Liotyphlops* are exactly those of the posterior extremity of the jugal of the anguimorph lizards, for in the Anguimorpha the jugal extends up behind the eye to meet the post-frontal, thus excluding the postorbital from the orbit.

The shape of the element in *Liotyphlops* is also similar to that of the jugal of the anguimorph lizards except for one minor feature: the jugal of lizards usually possesses a triangular spine directed backward upon the posterior border of the bone where the jugal turns upward from a suboptic to a post-optic position; in *Liotyphlops* there is no such spine. But if we examine the figure given by Dunn (1941, p. 523) of the postorbital element of *Anomalepis* we discover another small detail of resemblance, for ventral to the temporal arch remnant on the posterior surface of the bone the horizontal ventral border is carried back as a short triangular spine. Thus the postorbital of *Anomalepis* agrees well in both form and position with the combined jugal and postorbital of the anguimorph lizards, particularly the Diploglossa, and probably represents a fusion of these two elements.

In *Liotyphlops*, a form considered more specialized than *Anomalepis* because of its loss of loreal shield and rostrifrontal contact, the postorbital appears to have been lost as a unit, leaving the jugal alone, and the jugal has lost its posteroventral spine. This separates the anomalepines most sharply from the snakes and leptotyphlopids, where no indication of a jugal bone is to be seen and none of the circumorbital series (if present) extends beneath the eye. In the leptotyphlopids the circumorbital series has been suppressed entirely.

In the genus *Typhlops* (for skull, see Haas, 1930; Mahendra, 1936; Smit, 1949) the maxilla is of the same peculiar form seen in the anomalepines and has the same position relative to the other bones of the skull. But there has been a simplification of the suspensorial apparatus through the loss, at least as functional elements, of the bones here considered to represent the palpebral, post-frontal, post-orbital, and jugal. However, vestiges of these bones may remain, for Mahendra (1936, p. 133) finds two or three small ossicles in *Typhlops braminus* that may correspond to the post-frontal and postorbital.

Like the snakes, leptotyphlopids, and *Lanthanotus*, the typhlopids have the orbits completely separated by a chamber formed by the frontal bones, but a study of the relationship of the frontal to the prefrontal suggests that this chamber has been formed in two entirely different ways, the typhlopids showing one method of formation, the snakes, leptotyphlopids, and *Lanthanotus* exhibiting another. In the *Lanthanotus*-ophidian group the frontal is divided by a sharp angulation into two laminae: a dorsal plate, horizontal in plane, forming the roof of the skull in the orbital region; and a descending lamina, homologous with the subolfactory process of the frontal of such lizards as *Varanus* and *Heloderma*, which forms the internal wall of the orbit and is vertical in plane. These two laminae are further separated from each other by the position of the supraorbital process of the prefrontal bone, a finger-like process that extends back over the eye from the prefrontal and lies along the angulation separating the dorsal plate of the frontal from the descending lamina.

In the typhlopids the prefrontal has a posterior orbital process similar in form to the supraorbital process of the prefrontal seen in most lizards and in the snakes and leptotyphlopids, and we must rely on this to distinguish between the descending lamina and dorsal plate of the frontal, for the frontal bone itself shows no sharp angulation or supraorbital shelf. If the supraorbital process of the prefrontal be accepted as our criterion, it appears that in the typhlopids the descending lamina of the frontal is really quite small, about the proportionate size met with in the anguine, for the posterior process of the

prefrontal is very low in the orbit, near the ventral margin of the frontal, just above the optic foramen. Instead of a chamber between the orbits formed by the descending laminae of the frontal, the typhlopids have, it appears, an anomalous interocular cavity formed by the outward inflation and billowing of the dorsal plate of the frontal.

In the slight development of the descending laminae (subolfactory laminae) of the frontals the typhlopids differ not only from snakes and leptotyphlopids but from all the platynotan lizards, and agree far better with the Diploglossa. The eye appears to have been shifted to a more dorsal position (above the level of the optic foramen) by the enormous development of the Harderian gland.

The Typhlopidae resemble the snakes and Leptotyphlopidae in the absence of a distinct lacrimal bone. In this they also resemble the Gekkonidae, Pygopodidae, Ophiosepidae (see below for reasons for recognizing this family), Xantusiidae, and Dibamidae, as well as the Amphisbaenidae. It would appear from this list of families lacking a lacrimal that the presence of this bone as a distinct entity is largely dependent on the presence of movable eyelids, structures absent in all families lacking the lacrimal (with the exception of a few genera of geckos).

As in snakes and leptotyphlopids (also amphisbaenids and dibamids) the parietal of the typhlopids extends downward anterior to the pro-otic to form a lateral wall for the brain case and an increased area for muscular insertion. But while in snakes and leptotyphlopids the ventral extremity of the parietal forms a firm suture with the lateral edge of the basisphenoid, the parietal of the typhlopids is cut off from the basisphenoid by a horizontal slit filled by connective tissue. In some typhlopids (*Liotyphlops*, *Typhlops braminus*, for example) the parietals are separate; in others (such as *Anomalepis*, *Typhlops punctatus*) the parietals are fused.

In the typhlopids the basisphenoid is extended forward as a floor to the cranial cavity, a resemblance to the snakes and leptotyphlopids, but the resemblance is in no way detailed. In snakes and leptotyphlopids 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. In *Liotyphlops* this vacuity is partially filled by a pair of plate-like bones that Dunn and Tihen consider homologous to the laterosphenoids (postoptics) of lizards.

It would appear from all this that, though the brain case of the typhlopids is like that of snakes and leptotyphlopids in being closed, there is no particular resemblance in the method of closure. Indeed, there is considerably more resemblance in brain enclosure between the typhlopids and the amphisbaenids (to which the typhlopids do not show any indication of relationship) than between typhlopids and the snakes and leptotyphlopids, as may be seen from table 3.

type seen not in snakes but rather in a group of reptiles very distant from the snakes phylogenetically. In addition to the amphisbaenids, some other saurian groups show a brain case structure similar to that of the typhlopids. *Dibamus* shows the features in table 3 for the typhlopids and amphisbaenians but lacks the laterosphenoid elements, in this resembling the genus *Typhlops*. Yet it is no more likely that *Dibamus* is a relative of the typhlopids than that the amphisbaenians are so related, and it is very unlikely, for that matter, that the Dibamidae are related to the amphisbaenians.

There is one feature in the form of the brain case in which the typhlopids do show a special resemblance to the snakes: the exoccipitals meet each other above the medulla

TABLE 3  
CRANIAL FEATURES OF THE TYPHLOPIDAE AND AMPHISBAENIDAE COMPARED WITH  
THOSE OF THE SNAKES

Amphisbaenids, Typhlopidae	Snakes, including Leptotyphlopidae
Small descending processes of frontals, but inflated dorsal plates of frontals	Large descending processes of frontals, flat dorsal plates of frontals
Parietal separated from basisphenoid by a fissure	Parietal forming a suture with the lateral border of the basisphenoid
Basisphenoid (or fused basisphenoid and parasphenoid) not extending so far forward as does frontal, and not in contact with vomer, so that a large median fontanel is left on the floor of the cranium behind the vomer	Basisphenoid extends as far forward as does frontal, meets the vomer, so that there is no median fontanel in the post-vomerine region of the cranial floor
Laterosphenoids (orbitosphenoids of Zangerl, 1944; postoptics of Cope, 1900) form part of the anterior cranial floor (absent, or fused to septomaxillae?, in the genus <i>Typhlops</i> )	No laterosphenoids, at least as constituents of the ossified skull
Trigeminal foramen simple	Trigeminal foramen divided into two by a vertical strut of the pro-otic

The great differences in skull structure, as well as soft anatomy, between the typhlopids and the amphisbaenids (see Zangerl, 1944, for the morphology of the amphisbaenid skull) make it unthinkable that the typhlopids are closely related to the Amphisbaenidae. The important issue is that enclosure of the brain by the skull, long considered a cardinal argument for placing the typhlopids in the Ophidia (or Serpentes), fails utterly as a convincing point when the details of brain case form are examined, for the typhlopoid enclosure is of a

to form the entire dorsal border of the foramen magnum. But even here we might question the significance of this feature. Exclusion of the supraoccipital from the foramen magnum in snakes, leptotyphlopids, and typhlopids represents but the culmination of a trend already started in the anguinomorph lizards, where the supraoccipital contribution to the foraminal border is much reduced as compared to such lizards as teiids, lacertids, scincids, and iguanids. Moreover, degeneration of the ascending semicircular canals may

be responsible in part for the more anterior position of the supraoccipital, for the supraoccipital bone forms the bony roof for the anterior and posterior semicircular canal and appears to be very intimately connected with the dorsal portion of the posterior canal in Squamata.

There is also the matter of variability in this region that robs the character of some significance. Thus, as mentioned above, in not all snakes do the exoccipitals meet, the American colubrid *Phyllorhynchus decurtatus* being a notable exception. Among the typhlopids almost every conceivable modification of the occipital region occurs. Some that might be mentioned are:

1. Pairing of the supraoccipital by a persistent median suture. This is an anomalous condition, since the supraoccipital seldom if ever is anything but a median azygous bone in vertebrates, even at very early stages in their ontogeny. This has been recorded for *Typhlops lumbricalis*, *T. punctatus*, *T. delalandi*, *T. dinga* (= *T. schlegelii*).

2. Supraoccipital absent entirely, or possibly paired and fused with the exoccipitals. This has been recorded in *Typhlops braminus*, *T. richardi*, and *T. bituberculatus* and is true also of *Typhlophis squamosus* (which is otherwise like *Liotyphlops*).

3. Fusion of the exoccipital with the prototic, a feature of rather frequent occurrence in lizards (*Xenosaurus* and *Abronia*, for examples) but most unusual for snakes [*Typhlops richardi*, *T. braminus* (questioned by Mahendra, 1936), *T. bituberculatus*, *Liotyphlops albirostris*].

From the number of peculiar arrangements of occipital elements seen in the typhlopids it becomes apparent that this region is to be scrutinized for taxonomic characteristics only with the greatest caution, and moreover is not entirely unequivocal on the general relationships of the group. The peculiarity of pairing or of total absence of the supraoccipital, frequent among typhlopids, suggests a possibility (by no means proved, however) that the typhlopids may lack a true supraoccipital and that the paired "supraoccipital" may represent but an anterior unfused segment of the exoccipital. In at least some of the forms having an unpaired supraoccipital element, it does not have the close relationship to the

semicircular canals usually present in the squamates, and the element here may be a neomorphic fontanel bone, as is occasionally present in human infants. This is merely a possibility to be considered by future workers. One important point, the method of ossification (whether endochondral or intramembranous), has not yet been ascertained.

The palatal suspensorium of the maxilla is most complete in *Liotyphlops* (see Dunn and Tihen, 1944). Both a palatine and an ectopterygoid are present, but their relationships are somewhat anomalous. The palatine has no connection with the maxilla, a most remarkable feature. Instead, the palatine is a crescent of bone lying against the floor of the brain case, very loosely attached to the vomer (a snake-like feature not seen in lizards or leptotyphlopids) at its inner extremity, and attached to the pterygoid by a long and rod-like descending process on its outer extremity, this connection also being very loose. Such a palatine can be derived from the primitive squamatan Y-shaped palatine by reduction of the anterolateral (maxillary) process, and by extreme elevation of the anterior corpus of the palatine above the level of the pterygoid articulation of the posterior process. In some snakes the maxillary process of the palatine is absent, for presumably the same functional reason, the freeing of the kinetic maxilla from restrictive mesial articulations. The figure given by Dunn and Tihen (*supra cit.*) shows a minute spine of bone projecting lateral to the anterior base of the posterior (pterygoid) process. Such a spine might well represent the vestigial maxillary process of the palatine.

The palatine of *Liotyphlops* differs from that of other squamates (including the leptotyphlopids) in being widely separated from the prefrontal. In the other Squamata the anterior (choanal) border of the palatine (excluding the special dentigerous process found in most snakes) is approximated to the ventral border of the internal wing of the prefrontal (the wing of the prefrontal forming the anterior wall of the orbital cavity). This difference, however, reflects the modification not so much of the palatine as of the prefrontal, a modification induced by the peculiar suspension of the maxillary bone. In the typhlopids the prefrontal has retreated in-

ward away from the maxilla, allowing the latter bone great motility. This retreat has involved considerable reduction of the internal wing of the prefrontal, as well as the re-orientation of the wing in a nearly longitudinal rather than transverse plane; in turn, such reduction of the prefrontal has separated that bone widely from the palatine.

An additional difference between the palatine of *Liotyphlops* and that of snakes is the great length of the posterior (pterygoid) process in *Liotyphlops*, as contrasted to its near or total absence in snakes, where the internal (vomarine) and external (maxillary) processes of the palatine originate but a short distance anterior to the palatine-pterygoid suture. The Leptotyphlopidae agree with *Liotyphlops* (and most lizards) in the possession of a moderately long posterior process of the palatine, but differ strikingly in the position of the process. In the leptotyphlopids the vomarine (as well as the maxillary) process of the palatine descends to a level considerably below that of the pterygoid process; in *Liotyphlops* precisely the reverse is true and the pterygoid process extends far below the level of the rest of the palatine bone. In most lizards the pterygoid process of the palatine is produced downward, but not to the exaggerated extent seen in *Liotyphlops*.

The ectopterygoid of *Liotyphlops* is a simple rod of bone extending from the pterygoid forward and outward to meet the posterior extremity of the maxilla. The pterygoid is a simple rod of bone, with an obtuse angulation anteriorly. This anterior portion of the pterygoid is directed inward and slightly downward, corresponding to the anteromedian (palatine) process of the typically Y-shaped pterygoid seen in lizards; at its anterior extremity it receives the pterygoid process of the palatine. The posterior extremity of the ectopterygoid lies upon the angulation of the pterygoid bone; there is no anterolateral (ectopterygoid) process of the pterygoid. Posterior to the angulation, the pterygoid is a simple rod of bone extending straight back, without connection to the quadratomandibular joint or to basitrabecular processes. In snakes there may or may not be a short ectopterygoid process of the pterygoid, but there is no inflected palatine process, and the palatine articulation of the pterygoid lies

along the axis of the shaft of the pterygoid bone. In the leptotyphlopids the pterygoid is a simple rod, without flexure, and forms a long diagonal suture with the palatine, which appears to be immovable.

In *Anomalepis* Dunn found the pterygoid and ectopterygoid, but first (1941) reported the latter as a palatine. He corrected this later (Dunn and Tihen, 1944) on the basis of *Liotyphlops*, but failed to find a palatine. However, Dunn notes (Dunn and Tihen, 1944) that he made no special search for a palatine bone and that this element may well be present in *Anomalepis*. The palate of *Typhlops squamosus* (personal observation) is very similar to that of *Liotyphlops albirostris* as figured by Dunn and Tihen, but we find the ectopterygoid slightly furcated anteriorly and articulated to the maxilla by a double articulation (an articulation similar to that present in *Liotyphlops* together with a more internal juncture), and the ectopterygoid, rather than being straight, is somewhat curved (convex outwardly).

Thus the ectopterygoid of *Typhlops* is more like that of the majority of lizards and snakes than is the ectopterygoid of *Liotyphlops*. [It might be remarked here that *Typhlops* has a skull very similar to that of *Liotyphlops*, differing in only a few minor details: the absence of a supraoccipital, absence of the bone termed "tabular" by Dunn and Tihen, narrower premaxilla, somewhat greater anterior extent of the "supraorbital," the form of the ectopterygoid, and the proportions of the maxillary teeth (the second from the front longest, the posterior teeth decreasing in size), and the more pointed coronoid process.]

The palate of *Typhlops* is somewhat modified through a fusion of elements. Dunn and Tihen note that the "palatine" of *Typhlops* corresponds in its relations to the combined palatine and ectopterygoid of *Liotyphlops* and suggest that the "palatine" of *Typhlops* is a fused palatine and ectopterygoid. 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 squamates (except the majority of snakes).

In all the typhlopids the palate is edentulous, and the dentigerous process of the palatine found in snakes is totally absent.

The quadrate bone of the typhlopids is slung from the paroccipital process, as in lizards, leptotyphlopids, the fossil snake *Dinilysia*, but in no living snake, and it is strongly inclined forward and downward. On the anterior surface of the quadrate there is an angular lamina that terminates in a pointed apex directed upward and forward. In no snake, leptotyphloid, or platynotan lizard is there such a lamina, but the outer (tympanic) conch of the quadrate of diploglossan lizards is frequently of similar shape, with a sharp anterodorsal angle. In *Typhlophis*, at least, this lamina of the quadrate is nearly in a transverse plane, increasing the resemblance to the outer conch of the quadrate of the diploglossans.

Dunn and Tihen describe an element they term the tabular in *Liotyphlops*. This element has not been found in any other typhloid, and even in *Liotyphlops* it is not at all certain that this element is a tabular. The "tabular" of *Liotyphlops* is a slender splinter of bone lying lateral to the pro-otic above the apex of the anterior lamina of the quadrate; it is the most laterally placed bone of the skull except for the "postorbital" (jugal). In being lateral to the quadrato-cranial articulation, considerably anterior to the paroccipital process, and isolated from the parietal the "tabular" of *Liotyphlops* agrees better with a much reduced squamosal than with a tabular bone. The presence of the postorbital constituent of the temporal arch in *Anomalepis* makes it the more likely that the closely related *Liotyphlops* might possess the other constituent of a temporal arch, the squamosal.

The dentition of the typhlopids resembles that of lizards and leptotyphlopids in the vertical position of the replacement teeth. Tooth replacement is of the type characteristic of Anguimorpha, leptotyphlopids, and

snakes: the replacement teeth develop between the functional teeth to be replaced and force out the older teeth from the side, rather than developing at the base of the older tooth in a basal fossa of the tooth to be replaced and forcing out the old tooth from below. The teeth are therefore without basal fossae. In form, the teeth of the typhlopids are peculiar, being rather slightly recurved, sharply pointed, and nearly triangular in cross section. In all, the premaxilla and palate are without teeth, and the maxilla carries approximately five strong teeth. In *Typhlops* there are no other teeth, but in *Anomalepis*, *Liotyphlops*, *Helminthophis*, and *Typhlophis* there is a single tooth on the anterior end of the dentary.

Essex (1927, pp. 914-927, text figs. 50-84) has described and figured the pelvic girdle of several species of *Typhlops* (the pelvic girdle is absent in the Anomalepinae); it resembles that of the snakes and of the Leptotyphlopidae only in being degenerate. There is no trace of the pelvic limb, whereas in the snakes and leptotyphlopids there is usually a pelvic limb modified as a spur-like structure (in the snakes, at least, used in courtship) in those forms that possess a pelvic girdle at all. In snakes the right and left pelves are widely separated; in those leptotyphlopids with a strong pelvic girdle, the ischia are approximated or form a symphysis, and the pubes are widely separated and nearly parallel. In the Typhlopidae the ischia are parallel and the pubes vary from absence to median contact and the formation of a pubic symphysis (*Typhlops delalandi*). The only pelvic element ossified in the typhlopids is the ischium, but in snakes and leptotyphlopids the pubis and ilium (if present) are usually ossified, more frequently, indeed, than is the ischium. Most of the members of the genus *Typhlops* have a cartilaginous hypo-ischium, an element entirely absent in leptotyphlopids and snakes.

The vertebrae of the typhlopids show none of the platynotan-like features seen in the snakes (including Leptotyphlopidae). The centra are not tapered posteriorly, and the condyle is not set off by a precondylar constriction. Zygosphenozygantral articulations are present, but it is not certain that these articulations are homologous with the similarly named joints of snakes and leptotyphlopids, for in the latter two groups the zygospheno-

zygantral articulation is well dorsal to the level of the zygapophysial articulation, whereas in the typhlopids the zygosphenozygantral articulation is level with (but median to) the zygapophysial joint. There are no caudal chevrons or haemapophyses. Hypapophyses are confined to the anterior-most three or four vertebrae.

The tongue is long and extensile, without trace of papillae. It is rather similar to that of *Varanus*, but less deeply cleft terminally.

The form of the hyoid arch in the typhlopids is by no means uniform. In *Typhlops reticulatus* we have been unable to find a trace of a hyoid; in *Typhlops punctatus* the arch is represented by a single Y-shaped cartilage buried in the tissue at the base of the tongue well behind the head and in no way connected with the skin or the muscles immediately beneath the skin. In being confined to the tongue itself, the hyoid of *Typhlops* differs from that of ordinary snakes, leptotyphlopids, and the vast majority of lizards, where the posterior cornua of the hyoid lie close to the skin. But the entire hyoid of *Typhlops* is in agreement, both in form and position, with the basihyal (hyoid copula or glossohyal) alone of the normal squamatan hyobranchium. Smith and Warner (1948) regard the posterior cornua of the ophidian (including leptotyphlopids) hyoid as homologous with the hypohyal or with the hypohyal together with posterolateral extensions of the basihyal. However, in lizards the hypohyal is directed forward and laterally, whereas the cornua of the hyoid of snakes and leptotyphlopids run backward and laterally, paralleling the course of the saurian first ceratobranchial. It would appear that in leptotyphlopids and other snakes the first ceratobranchial and basihyal are fused to form the hyoid, the posterior cornua of which are superficial, as is the first ceratobranchial generally, and other elements are lacking. In some specialized burrowing snakes, *Cylindrophis* and *Rhinophis*, as well as in *Eryx*, the basihyal is absent, leaving but two isolated ceratobranchials (see Smith and Warner). On the other hand, in *Typhlops* all elements except the basihyal appear to have been lost.

But it appears that not all the typhlopids have the hyoid so much reduced as in *Typhlops*. In the Anomalepinae there is an ante-

rior element closely similar in shape to the basihyal of *Typhlops punctatus*, but placed far more anteriorly, between the rami of the lower jaw rather than behind the head. Posterior to the head there is a second transverse cartilaginous arch. This second arch was first described by Dunn and Tihen (1944) in *Lio-typhlops* and was considered by them, on account of its distinctness from the basihyal-like element, to represent a reduced scapulocoracoid. Warner (1946) showed the hyobranchial nature of the arch by dissection of the attached muscles, which are all visceral arch muscles, rather than appendicular muscles. This second arch is completely superficial in position. Smith and Warner (1948) regard the median portion of this arch as the basihyal, but certain difficulties are presented by such homology:

1. The central portion of the arch is superficial rather than buried in the intrinsic musculature of the tongue.

2. The median portion of the arch bears no anteriorly directed median lingual process, a process characteristic of the basihyal, but instead is actually arched backward on the median line.

3. Such homology completely ignores the anterior Y-shaped element on the Anomalepinae, an element similar in form and relationships to the basihyal of *Typhlops*.

On the other hand, there is much resemblance between the more posterior hyoidean arch of the anomalepines and the isolated "floating" hypohyal of such an anguinid as *Celestus*. The resemblances include curving forward of the lateral (posterior) extremity of the arch to form a hook-like structure approximating the jaw articulation, freedom from the basihyal, and anteroposterior orientation of the main shaft. The chief difference lies in the formation of a median symphysis of the right and left hypohyals in the anomalepines; this might indicate that the more median ceratohyals have been retained by the anomalepines, as well as the hypohyals, and the backwardly directed convexity of the median portion of the posterior arch would support such a view.

On such a view, the typhlopids differ from the snakes and leptotyphlopids in one specialized character, the absence in all forms of ceratobranchial elements, and one primitive

character, the presence in some genera of hypohyal and perhaps ceratohyal elements, in regard to the hyobranchial skeleton.

The relationship of *Lanthanotus* and the other aigialosaurian Platynota to the Ophidia (as used by most authors) hinges primarily on the relationship of the Typhlopidae to the other reptiles generally grouped in the Ophidia. In the above discussion we point out numerous resemblances between the snakes and leptotyphlopids on the one hand, and the aigialosaurian platynotans, particularly *Lanthanotus*, on the other. The Typhlopidae show none of these aigialosaurian features, but agree better, insofar as they agree with lizards at all, with the anguinid-like (diploglossan) lizards. If the typhlopids are in truth closely allied to the snakes, including leptotyphlopids, then it would appear that the numerous aigialosaurian features of the snakes and leptotyphlopids are but examples of convergence, and the ancestry of the ophidians is to be looked for among the diploglossan Anguinomorpha rather than among the platynotan anguinomorphs. Or, alternatively, we must believe that while the typhlopids, leptotyphlopids, and snakes are derived from a common aigialosaurian ancestor, the snakes and leptotyphlopids have retained the morphological heritage features of the aigialosaurians, while the typhlopids have undergone a retrogressive evolution in which they have duplicated in precise detail the arrangement of skull elements characteristic of the diploglossan division of the anguinomorphs. The third, and to us the most plausible explanation, is that the typhlopids represent a much-modified offshoot of the Diploglossa, convergent to the snakes and leptotyphlopids, while these last two groups represent either one or two offshoots from the aigialosaurian Platynota.

As shown above, the Typhlopidae differ in numerous important anatomical features from the snakes and leptotyphlopids; nevertheless, we might be justified in leaving the typhlopids in the Ophidia were it possible to prove any of the following hypotheses:

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 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.

The first hypothesis can be ruled out, for the typhlopids show a series of lizard-like, and therefore to be considered primitive, features unknown among snakes and leptotyphlopids. The most impressive of these are:

1. Retention of the dorsal or facial wing of the maxilla lying lateral to the prefrontal bone.

2. Retention of a posterior extension of the splenial running back to the level of the apex of the coronoid.

3. Simple and undivided trigeminal foramen.

4. Separation of the vomer from the frontal and basisphenoid by a large median vacuity in the floor of the brain case.

5. Retention in at least one genus (*Anomalepis*) of the anterior (postorbital) half of the temporal arch, and the possible retention in another (*Liotyphlops*) of a remnant of the posterior (squamosal) portion of the arch.

6. Retention in four genera (*Anomalepis*, *Liotyphlops*, *Helminthophis*, *Typhlophis*) of a jugal bone.

7. Retention in these genera of hyoid elements (probably the hypohyal and ceratohyal) lacking in all snakes.

8. Retention of an immobile and non-extensible mandibular (dentary) symphysis, bound by cartilage.

9. Presence of a tympanic wing of the quadrate.

10. Presence, at least in *Liotyphlops*, of bony laterosphenoids.

The second hypothesis fares no better, for the typhlopids are too specialized in many ways to have given rise to the snakes and leptotyphlopids. Among the most important of these specialized features may be listed:

1. Loss of the anterior half (or more) of the maxilla and the development of a unique kinetic maxillary suspension.

2. Loss of all palatal and premaxillary

teeth, as well as all or all but one of the dentary teeth (the single dentary tooth appears to be without a replacement tooth in *Typhlops* and probably in the other anomalepines).

4. Loss of ceratobranchials.

5. Loss of pelvic limb and some of the girdle, as well.

6. Tremendous expansion of the septomaxilla and the establishment of a septomaxillary-frontal suture.

7. Loss of a maxillary process of the palatine.

8. Tremendous inflation of the dorsal plate (supraorbital portion) of the frontal.

9. Great separation of palatine and prefrontal.

10. Absence or anomalous nature of "supraoccipital" (homology not certain) which, when present, is either paired or without its epiotic connections.

It may be said further against both the first and second hypotheses that no annectant forms are known between the typhlopids and the snakes or the leptotyphlopids. A superficial similarity exists between the typhlopids and the leptotyphlopids, but a study of the anatomy of the two groups shows that the typhlopids are even more distinct from leptotyphlopids than from the typical snakes. Thus the typhlopids have a very long postarticular process of the mandible, the snakes a short process, the leptotyphlopids none at all. The typhlopids have a very long splenio-coronoid suture, the snakes a very short one (when a coronoid is present), the leptotyphlopids a wide gap between the coronoid and splenial. The snakes and typhlopids have a very loose connection between palatine and vomer, the leptotyphlopids a very sturdy connection. Snakes and typhlopids have a fenestra ovale and an exposed stapes; the leptotyphlopids lack the fenestra, and the stapes is enclosed within the skull.

Those features in which the typhlopids and the leptotyphlopids resemble each other more than they do the snakes appear to be but primitive features that both have retained or burrowing modifications common to many fossorial Squamata. In the first category may be classed vertical position of replacement teeth; paraoccipital suspension of quadrate (seen in the Cretaceous snake *Dinilysia*); ab-

sence of a special dentigerous process on the anterior surface of the palatine; and lack of compressed laminae bordering the masseteric fossa of the lower jaw. To the second category may be ascribed such resemblances as reduced eye and associated structures; shortened lower jaw; expanded rostrum and premaxilla; reduced dentition; enlarged anterior head scutes (as in such fossorial forms as *Dibamus*, *Feylinia*, and *Anelytropsis*); thick and smooth cuticle; small gape; short and blunt tail (as in amphisbaenids); and loss of hypapophyses and caudal chevrons.

The third hypothesis, that the typhlopids on the one hand and the snakes and leptotyphlopids on the other have descended from a common ancestor but subsequently specialized in different directions, receives no more support than do the first two. If the hypothesis were true we might expect the typhlopids to share with the snakes and leptotyphlopids a series of morphological characters indicative of this common heritage and absent from other squamates. But this does not appear to be the case, for the characters common to typhlopids and to the other "Ophidia" appear to be either common to all Anguinomorpha and anguimorph descendants or of such general or capricious occurrence in the Squamata as to appear valueless. It is instructive to examine the characteristics considered diagnostic of the Ophidia (including Typhlopidae) and assay their value:

1. Closed bony brain case. The details of brain enclosure by the skull are much the same in snakes and leptotyphlopids and are not met with elsewhere. Therefore for this restricted group the character appears to be of some value when stated more precisely, as: parietals descending anterior to pro-otics to suture with the basisphenoid, forming a complete lateral cranial wall, and anteriorly meeting the hypertrophied subolfactory processes of the frontals, these latter meeting a long anterior extension of the basisphenoid (possibly a parasphenoid) to extend the cranial chamber between the orbits. Such precision is required if we are to distinguish the closed brain case of the "Ophidia" from that of such diverse groups as the Amphisbaenidae and Dibamidae. But, as discussed above, the "closed brain case" of the Typhlopidae re-

sembles that of snakes and leptotyphlopids no more than does that of the amphisbaenids, and, in the feeble development of the subolfactory processes of the frontals, less than does that of the Dibamidae. We must therefore dismiss brain case closure as a character indicating common origin of all the "Ophidia."

2. Platytrabic skull. The snakes differ from the lizards in the failure of the right and left trabeculae to fuse in midorbital region and form a trabecula communis. But Bellairs (1949, p. 502) states that in *Typhlops*, as in lizards, the trabecula communis does extend back between the centers of the eyes. Therefore this character must also be rejected.

3. No epipterygoid. This character by itself is worthless in this connection, since the epipterygoid has been lost in the Dibamidae, Amphisbaenidae, Chamaeleonidae, and some species of the Agamidae.

4. Movable connection of the two lower mandibles at the dentary symphysis. But in the Typhlopidae the symphysis is rigid and cartilaginous.

5. Zygosphenozygantral joints. This again appears a useless character for uniting typhlopids with snakes, for there is considerable difference between the zygosphenozygantral articulation of the Typhlopidae and that of the snakes and leptotyphlopids (see above). Zygosphenes and zygantra occur in some platynotans and in many or most of the Iguanidae. In addition, *Diploglossus* has the anterior border of the roof of the neural canal produced forward to articulate with the ventral surface of the posterior border of the roof of the neural canal of the preceding vertebra, but no articular facets are formed. In being on the same horizontal level as the zygapophyses, the articulation in *Diploglossus* is more like the zygosphenozygantral articulation of the typhlopids than is the zygosphenozygantral articulation of snakes.

6. No pectoral girdle. This is true also of most amphisbaenids, of *Anelytropsis*, and is almost true of *Anniella* (where there is a single very small cartilage).

7. Elongated and retractile tongue. But this is a general anguimorph feature and has been approached also, but in a different manner, by some of the Teiidae.

Resemblances that can be considered as

but features indicating derivation of both snakes and typhlopids from anguimorph ancestors are:

1. Alternate and interdental replacement of the teeth. The replacement teeth develop between the older teeth rather than in fossae at the base of the teeth and replace the older teeth from the side, rather than from below.

2. Presence of foramina piercing the premaxilla.

3. Retractility of the inelastic fore tongue.

4. Complete bony investment of the organ of Jacobson.

5. Reduced extracolumellar apparatus of the stapes.

6. Lack of second ceratobranchials.

7. Gall bladder exposed ventrally by the liver.

Finally, it appears significant that the same osteological features that distinguish the Diploglossa from the Platynota within the Anguimorpha also distinguish the Typhlopidae from the Leptotyphlopidae and snakes within the "Ophidia." Characteristics common to the Diploglossa and Typhlopidae, but absent in the Platynota and snakes (including *Leptotyphlops*), are:

1. Meckelian cartilage completely covered opposite the splenial bone by a suture between the dorsal border of the splenial and the dentary.

2. Lower jaw without trace of hinge joint.

3. Mandibular symphysis rigid.

4. Coronoid with its anterodorsal border sloping evenly upward from the anteriormost point to the apex of the coronoid process.

5. Splenial extending back to the level of the coronoid process.

6. External (bony) naris not extended back upon the face as a narrow slit lateral to the nasal.

We may conclude that there is little to show that the typhlopids are related to the snakes and leptotyphlopids. However, a number of morphological features show that the "normal" snakes and leptotyphlopids are closely related to the aigialosaurian Platynota, showing particular resemblance to *Lanthanotus*, while the Typhlopidae show clear evidence of relationship to the Diploglossa.

The problem of the precise taxonomic placement of the Typhlopidae is beyond the scope of this paper. 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, for it is a question not of phylogenetic relationships but of the weight (a subjective matter) of the peculiarities of these odd reptiles.

## INTERRELATIONSHIPS OF THE ANGUINOMORPHA

### FAMILIES REMOVED FROM THE ANGUINOMORPHA

THE PYGOPODIDAE, although referred by Camp to the Diploglossa, appear to share features with members of this group that are largely the result of adaptive convergence. The structure of the skull, tongue, and vertebrae, as well as the post-cloacal sacs of the pygopods, would seem to ally them with the gekkonids, as suggested by Boulenger (1885, p. 239).

Externally, the pygopods show strong evidence of gekkonid relationship in having

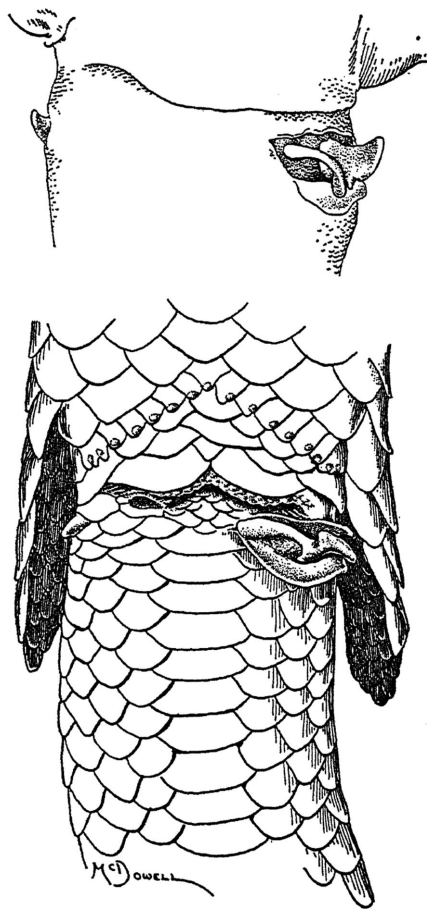


FIG. 16. (Upper) Postcloacal bones of a primitive gecko, *Coleonyx variegatus*. (Lower) Post-cloacal apparatus of *Pygopus lepidopus*, with the left post-cloacal sac opened to expose the entire post-cloacal bone. Drawing by McDowell.

post-cloacal sacs opening to the exterior by small slit-like pores about one scale row posterior to the cloaca. In *Pygopus* these openings are easily visible under magnification without disarranging the scales, but in *Lialis* the openings are covered by enlarged post-cloacal scales. When these scales are lifted, however, the post-cloacal pores can be seen, surrounded by very small but otherwise typical scales. In *Pygopus* we have found a large post-cloacal bone anterior to the pore, exactly as in geckos but not as in any other lizards except the probably gekkotan family Xantusiidae. Boulenger (1885, p. 239) states that the ischium projects externally as a small spur behind the cloaca, a most remarkable position for an ischium, since the ischium in other tetrapods lies anterior to the cloaca or excretory and genital outlets. Obviously the bone Boulenger refers to is the post-cloacal rather than the ischial bone.

Although Camp places the Pygopodidae in the Autarchoglossa, which he defines as having fewer than four transverse rows of ventral scales to each body segment, the scales having a narrow free margin when imbricate, the pygopods scarcely fit this definition. For although in *Pygopus* there are but three transverse rows of scales for each caudal chevron, in *Lialis* there are four. In all species of pygopods the body is covered by scales that overlap by a wide margin ("deciduous" arrangement).

The eye of the pygopods is also quite gecko-like. It is without movable lids but provided with a brille or spectacle and has a vertically elliptical pupil. According to Belairs and Boyd (1949) the lacrimal apparatus of *Lialis* is very similar to that of the geckos.

The tongue of the pygopodids agrees with that of the geckos with a remarkable precision in detail. In both groups it is thick and fleshy and not divided into two parts as it is in Diploglossa and Platynota. Moreover it is covered above with scale-like, flattened papillae. In both groups it is nicked at the tip, the two tines thus formed being very short, broad, and terminally obtuse or rounded. In both there is a smooth callus on the under

surface of each of the terminal tines, the remainder of the under surface presenting two pairs of longitudinal crests crossed by numerous transverse folds. It would be difficult or impossible to say whether an excised tongue had come from a gekkonid or a pygopodid.

In the skull there is such close agreement between the pygopods and the geckos that it is difficult to doubt that the two families are very closely related. As in the geckos but not the anguimorphs, the premaxilla bears no

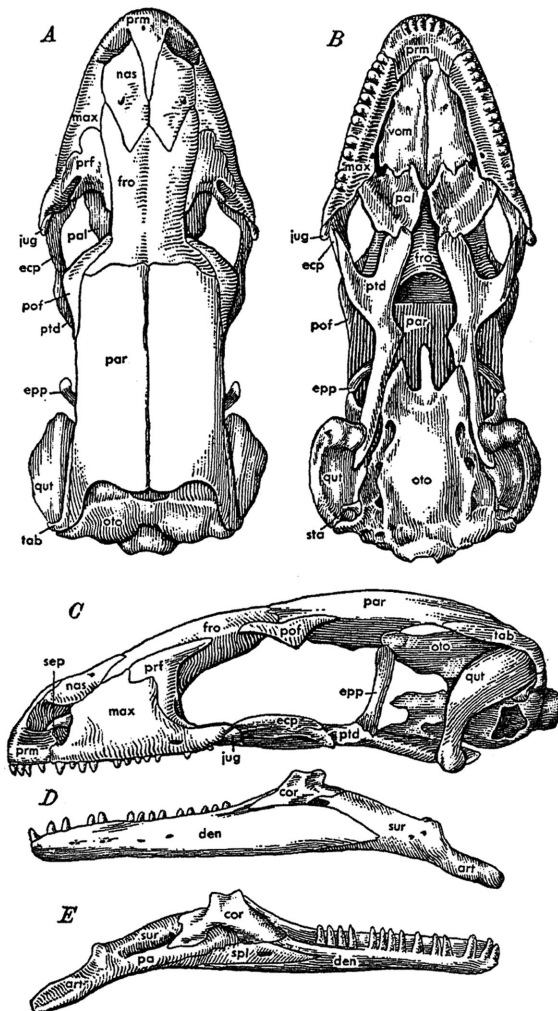


FIG. 17. *Pygopus lepidopus*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

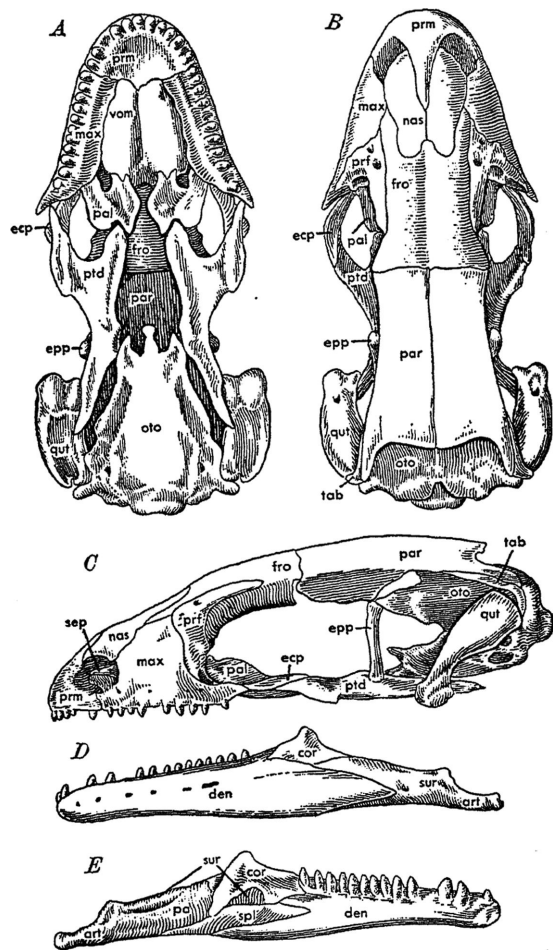


FIG. 18. *Pygopus nigriceps*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Jugals, post-frontals, and stapes omitted. Drawing by McDowell.

foramen or median-ventral process. The frontals of the pygopods are particularly gekko-like, being fused and with the descending processes meeting and fusing ventrally beneath the olfactory tract to form an olfactory tube that does not descend to the level of the middle of the orbit. The facial sutures are also as in geckos; the fused premaxillae send back a long and acute dorsal median process that separates the nasals for a considerable distance anteriorly. The nasals are quite separate and posteriorly are bounded laterally for some distance by anterolateral processes of the frontals. The nasal forms a long suture

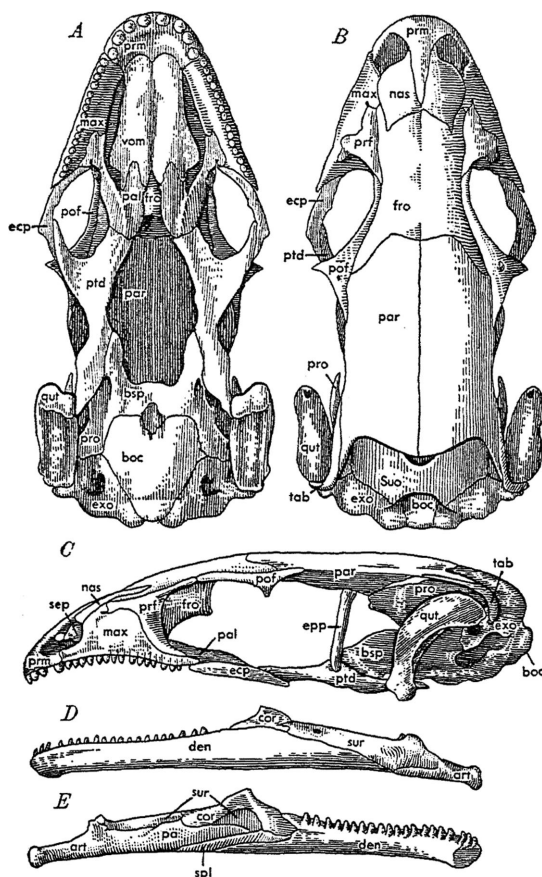


FIG. 19. *Delma fraseri*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapes omitted. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

with the maxilla but is quite excluded from the prefrontal by the anterolateral process of the frontal. All this is as in the great majority of geckos but not often seen in any anguinomorph, although somewhat approached by *Xenosaurus* (see fig. 34).

The postorbital and temporal arches are lacking in pygopods and geckos, the postorbital, squamosal, and jugal bones being absent. As in geckos, the pygopods lack a pineal foramen, while all except *Lialis* have the parietals separated by a median suture, a feature seen in most geckos but rare in the anguinomorphs. As in the geckos but not the anguinomorphs, the pygopods are without a distinct lacrimal bone. Boulenger (*supra cit.*)

pointed out the juncture of the prefrontal and post-frontal above the orbit as a feature distinguishing the pygopod skull from that of the geckos. But this distinction will not hold, for in *Aristelliger* (and probably other geckos as well) there is no prefrontal-post-frontal juncture, as in some pygopods.

In the palate there is also close agreement between pygopods and geckos. In both, the pterygoid makes or nearly makes contact through its anterolateral process with the maxilla, and the ectopterygoid is very small. In both, the palate is without teeth. In both, the vomer is wide, more or less oval in form, convex ventrally, and fused with its fellow for most of their length.

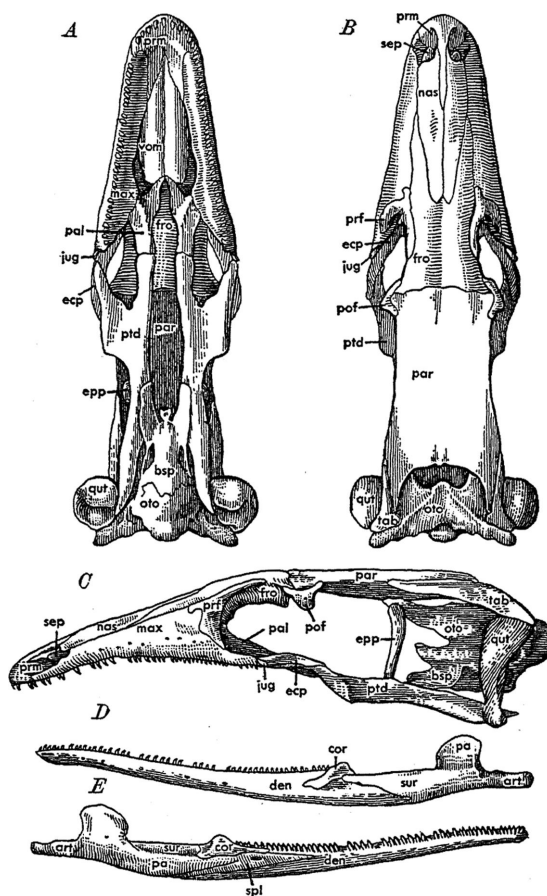


FIG. 20. *Lialis burtonis*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapes omitted. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

The most definite indications of pygopod-gecko affinity are to be seen in the structure of the brain case. In the pygopods the basiptyergoid process is of remarkable form, for instead of being defined posteriorly by a deep notch setting the process off from the brain case proper, it is continued back by a horizontal plate of bone penetrated by two foramina (for the entocarotid artery and palatine nerves?) to the basioccipital. Thus, the base of the brain case, instead of presenting the cross-shaped figure usual in lizards, has the form of a butterfly with extended wings. This remarkable form of basiptyergoid process occurs in only two other groups of lizards, namely, the Xantusiidae and the Gekkonidae.

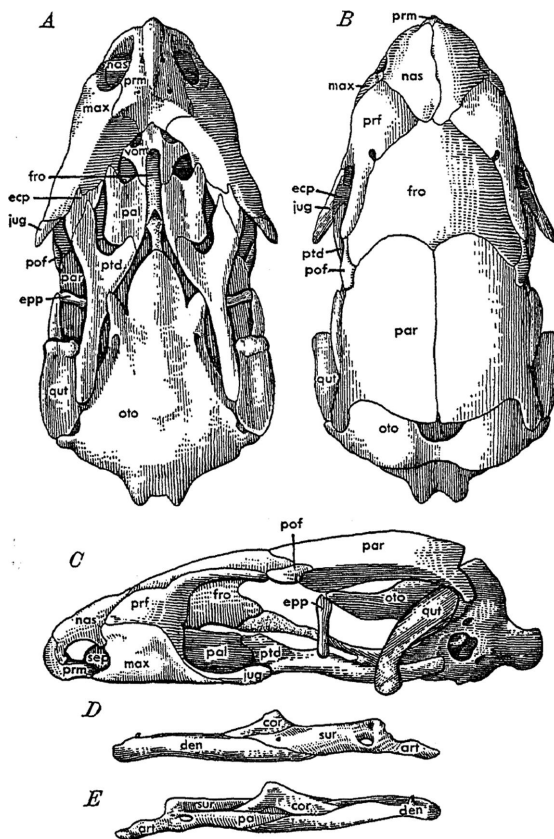


FIG. 21. *Aprasia repens*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapedes omitted; cartilaginous connection between frontal and sphenoidal rostrum is stippled. For abbreviations, see p. 141. Drawing by McDowell after a drawing by Alma Froderstrom.

A further resemblance to the geckos was noted during the preparation of the skulls of *Pygopus* and *Lialis*; the temporal region is invaded by a considerable quantity of calcareous material, probably homologous with the extensive endolymphatic system of the geckos.

The quadrate of the pygopods is gecko-like in having the outer conch highly developed, but directed backward rather than outward, so that the posterior fossa is both unusually deep and unusually narrow.

In the lower jaw there are resemblances to the geckos no less impressive than the post-cloacal apparatus and basiptyergoid apparatus. The bones have undergone extensive fusion and are like those of the gekkonids in arrangement but very different from the anguimorph pattern in that the angular has fused to the surangular. As in geckos the splenial has but slight anterior extent, not extending much farther forward than the coronoid and not extending past the posterior third of the dentary. This is in marked contrast to the anguimorphs, in which the splenial lies almost or entirely anterior to the coronoid and extends anteriorly past the midpoint of the dentary. The Meckelian groove of the pygopodids is thus closed almost entirely by the dentary alone, as in geckos, whereas in those anguimorphs in which the Meckelian groove is closed, the closure results from contact of dentary with splenial, and anterior to the splenial bone is open for a short distance. As in geckos but not anguimorphs, the pygopodids have a deep gutter, defined along its median edge by a strong shelf of the dentary, running along the median surface of the dentary at the base of the dental row. This is not to be seen in any true anguimorph, though it is present also in the Cordylidae.

The procoelous vertebrae of the pygopods are most unlike those of the Anguimorpha but similar to those of procoelous geckos. The centra are as broad posteriorly as anteriorly, while the condyle is abruptly narrower than the centrum but broader than it is in geckos (see Camp, 1923). Again as in geckos but not the anguimorphs, the centrum is constricted in the middle and retains distinct central foramina.

In view of all these resemblances of pygo-

pods to the geckos and the numerous differences from the anguinomorphs, we remove the Pygopodidae from the Anguinomorpha and transfer them to the Gekkota. The above account is based on the more typical pygopods, the Pygopodinae and Lialinae. Just what the affinities of the peculiar Australian genus *Ophioseps* may be we leave an open

(*vide* Jensen) has the parietals fused and the frontals separate,<sup>1</sup> precisely the reverse of conditions in *Aprasia*. The tongue structure and rather close resemblance to *Aprasia*, as well as the Australian distribution of *Ophioseps*, suggest strongly that it is indeed related to the pygopodids, although detailed comparisons with leptotyphlopids and typh-

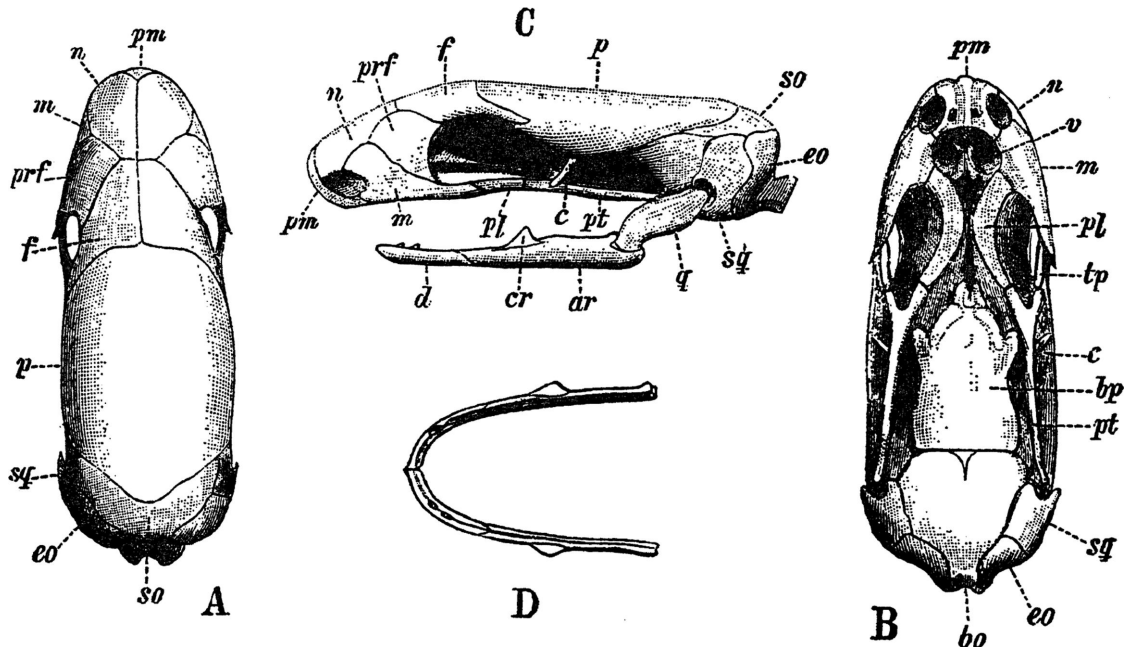


FIG. 22. *Ophioseps nasutus*. A. Dorsal view of skull. B. Ventral view. C. Lateral view of skull and lower jaw. D. Dorsal view of lower jaw. Abbreviations: ar, compound bone; bo, basioccipital; bp, basisphenoid; c, epipterygoid; cr, coronoid; d, dentary; eo, exoccipital (in part?); f, frontal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, probably the anterior part of the exoccipital (including the opisthotic), set off from the portion labeled eo by line, thought by Jensen to be a suture, but more probably the transparency produced by the posterior ascending semicircular canal; tp, ectopterygoid; v, vomer. From Jensen.

question, in the absence of material for examination. Jensen (1901) has figured the external appearance, tongue, and skull of this peculiar lizard. The tongue appears to be quite similar to that of the pygopods, and the external appearance is not too greatly different from that of the pygopod *Aprasia*. But the skull is somewhat like that of a leptotyphlopoid in lacking upper dentition (seen also in *Aprasia*) and in form is quite typhlopoid-like. It is not clear from Jensen's figure what the form of the basipterygoid region is in *Ophioseps*, but in *Aprasia* the basipterygoid processes have the characteristic gekkotan form. *Ophioseps*

lizards are much to be desired. At any rate, we see no reason to question Jensen's placing of *Ophioseps* in a distinct family, as Boulenger (1887) suggested. It is probable, however, that *Aprasia* should be transferred to the Ophiosepidae.

We may note in passing that it is probable that another family, the Xantusiidae, will be referred by future workers to the Gekkota. Camp (1923) has shown that the vertebrae of the Xantusiidae are similar in form to those

<sup>1</sup> These characters have been used taxonomically by Kinghorn (1923, 1926) in his revisions of the Pygopodidae.

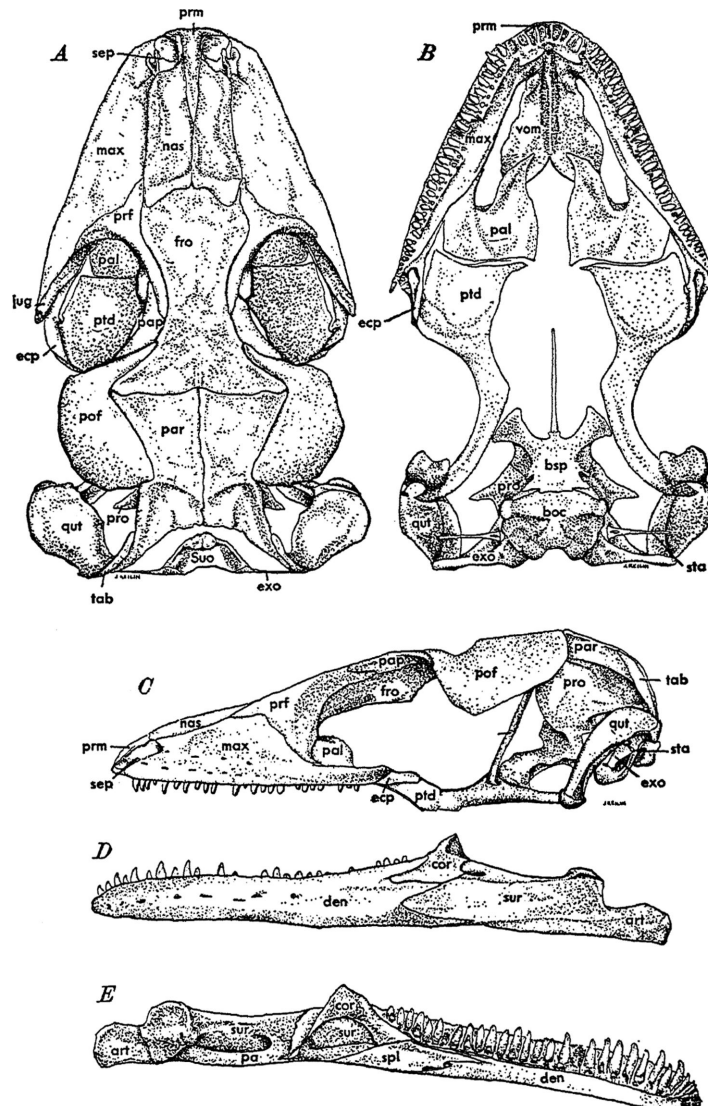


FIG. 23. *Aristelliger lar* (a gecko without movable eyelids). A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by Joan Keilen, from Hecht.

of the procoelous geckos and pygopods and quite different from those of other lizards, having the condyle narrower than the centrum and the centrum as wide posteriorly as anteriorly. In the skull, the xantusiids show gecko affinities in the failure of the parietal bone to fuse with its fellow, the absence of a pineal foramen, the absence of premaxillary foramina, fusion of lacrimal with prefrontal, depressed and broadened form, small ecto-

pterygoid, and particularly in the form of the base of the brain case. As noted above for the geckos and pygopods, the basipterygoid process in the Xantusiidae is continuous with the lamina forming the dorsolateral wall of the entocarotid fossa, so that the brain case has the gekkotan, extended-butterfly appearance rather than the usual cruciform shape, as seen from below. In the lower jaw, the Xantusiidae show gekkotan affinities in the

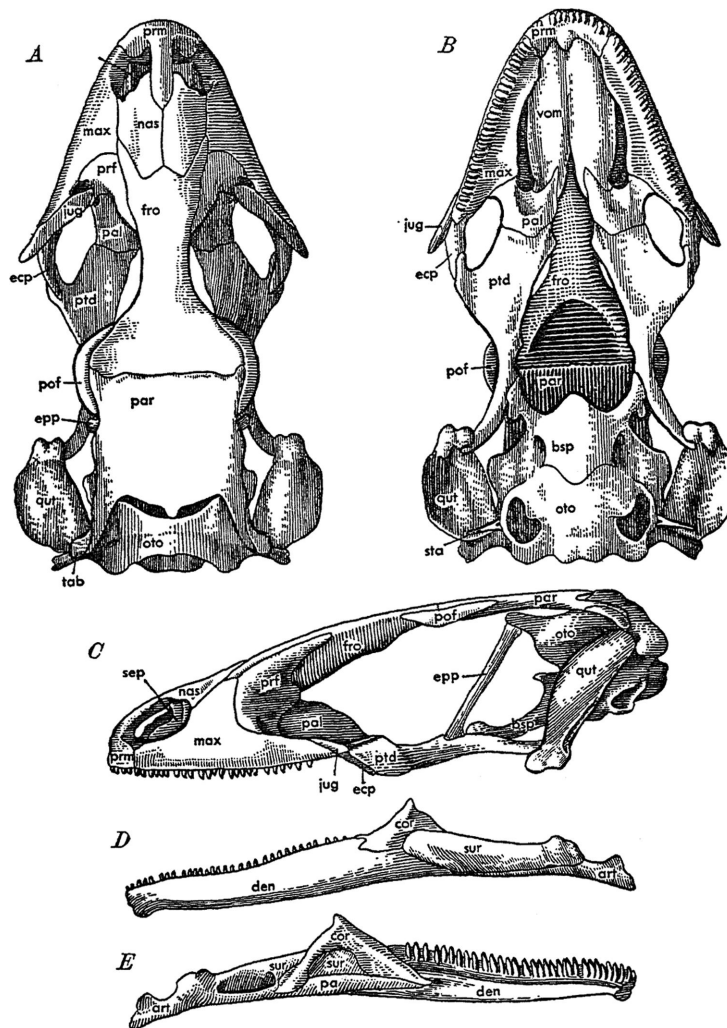


FIG. 24. *Coleonyx variegatus* (a gecko with movable eyelids). A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

fusion of the angular, surangular, prearticular, and articular. The splenial is fused to the dentary, and there is no trace of an open Meckelian groove. Though not so well developed as in the geckos and pygopods, the gutter of the dentary internal to the bases of the teeth is present in the Xantusiidae.

The tongue of the Xantusiidae is like that of the geckos, except that the four ventral crests are not so prominent. The xantusiids have a gekkotan eye, with elliptical pupil and brille. Walls (1942b, pl. 1) indicates affinities

of gekkonids, pygopodids, and xantusiids on the basis of his study of the visual cells. In the xantusiid *Lepidophyma* the general body squamation is gecko-like, with large tubercles interspersed among tiny granular scales, although the phyletic importance of this is uncertain. Lizards of the genus *Xantusia* are viviparous, as are few geckos, but both groups are alike in that ovulation involves but two eggs at a time (with rare exceptions), quite in contrast to all other families of lizards.

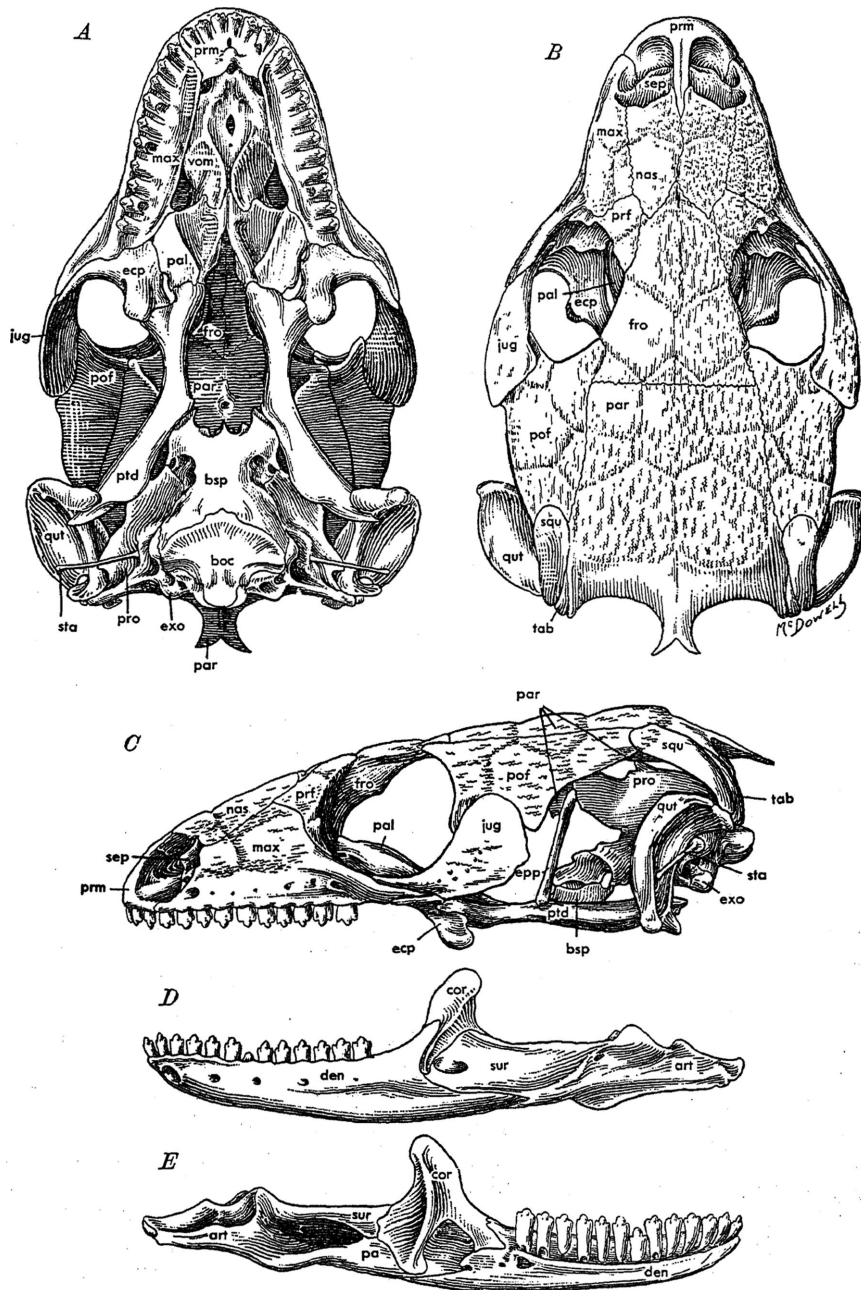


FIG. 25. *Xantusia riversiana*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell.

On the other hand, the Xantusiidae differ from the Gekkota and resemble the Scincomorpha in the presence of the temporal and postorbital arches, roofing of the supratemporal fossa by the parietal, failure of the

frontals to meet beneath the olfactory tracts, and absence of any post-cloacal apparatus.<sup>1</sup> It must also be remembered that the un-

<sup>1</sup> We have since been informed by Mr. Jay Savage that *Xantusia vigilis* has post-cloacal sacs and bones.

doubtedly gekkotan Eublepharinae are in some respects less gecko-like than the Xantusiidae in that the parietals are fused (as also in *Lialis*) and the eye is provided with movable lids. Because of these difficulties we leave the final allocation of the Xantusiidae to those who undertake a thorough study of the anatomy of both this family and the Gekkonidae.

Although the Cordylidae are referred by Camp (1923) and by Cope (1900) to the anguimorph lizards, the two groups have little morphological resemblance. Relationship with the Iguania has been suggested (Camp, 1923), but there is no definite evidence as yet of such affinity, even though further work may establish such a connection. On the other hand, the Cordylidae show considerable resemblance to the scincomorph family Gerrhosauridae, in both internal and external structure. The fact that both families are exclusively African and Malagasian in distribution lends further weight to these resemblances.

In general squamation there is much similarity between the zonures (Cordylidae) and the gerrhosaurids. Both groups have the scales arranged in transverse rows, strongly keeled dorsally, each containing an osteoderm. A particular and otherwise unique feature common to the two groups is the presence of a specialized spine-like scale on the ventral surface of the base of the tail, behind each of the lateral corners of the cloacal slit. Both the Gerrhosauridae (except the serpentiform *Paratetradactylus*) and Cordylidae have a complete set of femoral pores. Femoral pores are absent in the Anguimorpha, although pre-anal pores may be present in *Varanus*. Interestingly, neither the cordylids nor the gerrhosaurids possess pre-anal pores, in spite of their unusually complete femoral series. In both, the head is covered by large and regular scutes, differing from the arrangement seen in the Anguinidae in the absence of internasals, the supranasals meeting behind the rostral, and in having the interparietal separated from the frontal. There is indeed a striking similarity in arrangement of head scutes between *Cordylus* and *Gerrhosaurus*, and the only differences we can find are the imbrication of the temporals in *Cordylus*, juxtaposition in *Gerrhosaurus*; presence of several

scales on the anterior aural border in *Cordylus*, a single large scale in *Gerrhosaurus*; and numerous rows of scales on the throat in *Cordylus*, few in *Gerrhosaurus*.

Although the Gerrhosauridae are classified by Camp quite correctly as Scincomorpha, the Cordylidae as Diploglossa, *Gerrhosaurus* is far more like the anguinoids in external appearance than *Cordylus*, for its lateral fold of granular scales beginning immediately behind the ear, as well as its general proportions, gives the African lizard a close superficial similarity to *Gerrhonotus*. *Cordylus* lacks the lateral fold, as does its relative *Chamaesaura*. The genera *Pseudocordylus* and *Platysaurus* are even more unlike the diploglossal Anguimorpha in having the dorsal scales granular, with (*Pseudocordylus*) or without (*Platysaurus*) intermixed large scales.

The tongue is very similar in *Gerrhosaurus* and *Cordylus*. In both it is simple, without the division into fore and hind tongue seen in the Anguimorpha, nicked anteriorly, notched behind, and uniformly covered above with scale-like papillae. Beneath, it bears a callus under each of the two very obtuse distal tines and has a single median pair of rather diffuse longitudinal crests, crossed by numerous transverse mucous folds. In the gerrhosaurid *Tetradactylus* the dorsal papillae form transverse plicae.

The dentition of the zonures is of the normal pleurodont type seen in most lizards (including the gerrhosaurids), with vertical replacement, the teeth being extensively hollowed basally. This is in marked contrast to the dentition of the Anguimorpha, in which the replacement is alternate and the teeth not hollowed out basally.

In the structure of the skull the zonures and gerrhosaurids show close agreement. In both groups the supratemporal fossa is roofed over by the parietal, as in most scincomorphs but not the anguimorphs, although this condition is approached by *Varanus dumerili*. As in most scincomorphs, the parietal in both the zonures and gerrhosaurids sends down a tab-like process to articulate with the epipterygoid and epipterygoid wing of the prootic. In the Anguimorpha this process is vestigial or absent. In the gerrhosaurids and zonures, as in lizards generally, the post-orbital bone enters into the posterior border

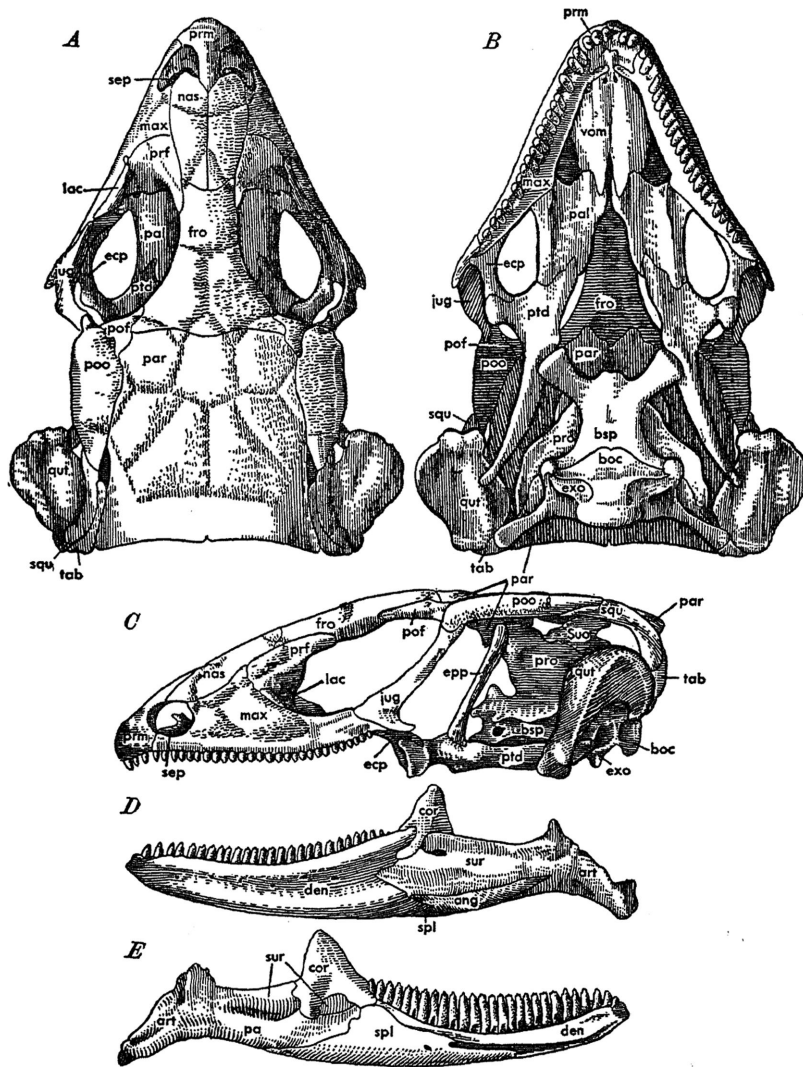


FIG. 26. *Cordylus giganteus*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapedes omitted. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

of the orbit. In the Anguinomorpha the post-orbital is constantly excluded from the orbit by the juncture of the jugal and post-frontal. In the Anguinomorpha the frontal has descending processes that curve medially to underarch the olfactory tracts to a greater or lesser extent. Although both the gerrhosaurs and zonures possess descending processes of the frontals, these are quite vertical and do not underarch the olfactory tracts.

A particular resemblance between the gerrhosaurs and the zonures is the construction

of the occiput, for these two groups show the sort of parietal-supraoccipital juncture seen elsewhere only in the Lacertidae (to which family the gerrhosaurs are generally conceded to be related) and an extreme development of this sort that is unique. The dorsal extremity of the supraoccipital, rather than being unexpanded or expanded in the plane transverse to the long axis of the skull, is dilated along the sagittal plane into a lamina that extends forward nearly to the level of the dorsal extremity of the epipterygoid

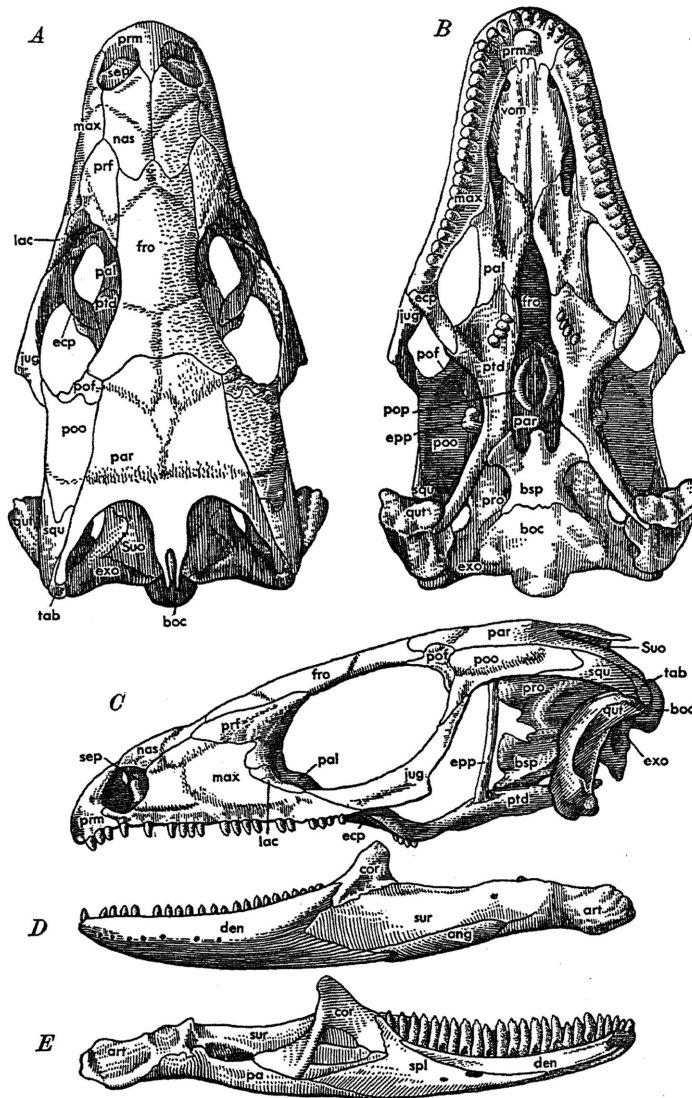


FIG. 27. *Gerrhosaurus albigularis*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapedes omitted; laterosphenoid or post-optic included, but omitted from all other drawings accompanying this paper. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

and posteriorly to the level of the quadrate-pro-otic articulation. Along this longitudinal supraoccipital crest the parietals are produced backward, at least along the midline, to the level of the quadrate-pro-otic articulation. In *Gerrhosaurus* there is a large semicircular posterior emargination in each parietal between the median (supraoccipital)

and lateral (quadratic) processes of the parietal; in *Cordylus* on the other hand, conditions are as in *Lacerta* and there is no emargination.

The pro-otic of the zonures is as in *Gerrhosaurus* and the vast majority of lizards and possesses a strong epipterygoid wing running anterior to the semicircular canal to

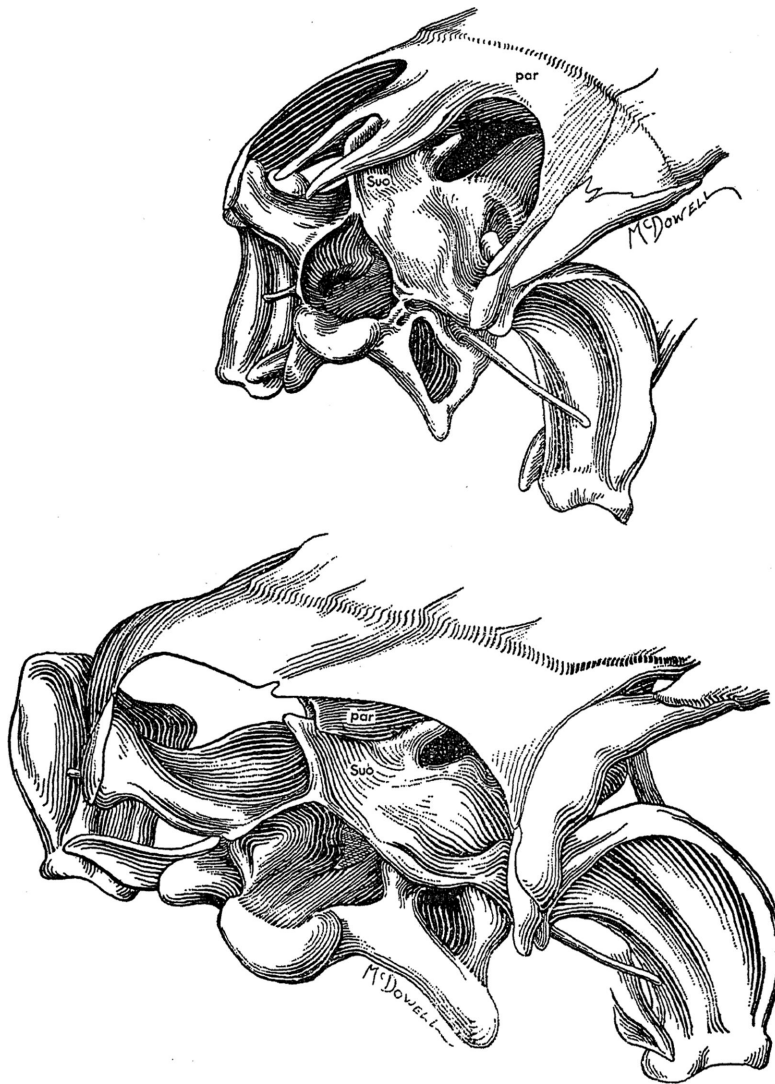


FIG. 28. Occipital views of the skulls of *Gerrhosaurus* (upper) and *Cordylus* (lower), showing the median longitudinal crest of the supra-occipital (suo) articulating with the parietal (par). Drawing by McDowell.

meet the dorsal portion of the epipterygoid. In the iguanoids, with which the cordylids have been compared, there is no production of the pro-otic anterior to the anterior semi-circular canal, and the bone is isolated by a considerable gap from the epipterygoid.

The entocarotid fossa for both the carotid artery and a muscle running from the brain case to the quadrate is nearly identical in the gerrhosaurus and zonures and quite different from that of the anguinomorphs. In the

zonures and gerrhosaurus the fossa is very wide and shallow, with its lateral wall flared out to form an angular projection completely concealing the more dorsal part of the brain case from ventral view. In the Anguinomorphs the entocarotid fossa may be deep or shallow but is always narrow so that the bulging sides of the more dorsal portion of the brain case may be seen from below.

In the zonures the hyoid apparatus differs from that of the anguinomorphs in possessing

the second ceratobranchial. The admittedly scincomorph gerrhosaurs are more anguinid-like in this respect than the zonures, for the gerrhosaurs lack the second ceratobranchial and retain the second epibranchial, as in *Gerrhonotus*.

In the shoulder girdle, the zonures differ from the gerrhosaurs in having the clavicle simple rather than dilated and perforated. In this one respect the zonures are more "anguinoid" than the gerrhosaurs. The two groups agree in having the formula of the coracoid and scapula O-X-X-O (no scapular fontanel or emargination, a scapulocoracoid fontanel, a lateral coracoid fontanel, no medial coracoid fontanel). This, however, is of general occurrence among lizards and is frequent among anguinomorphs as well as scincomorphs.

In the pelvic girdle the gerrhosaurs and zonures show close agreement, particularly in the form of the ischium, which differs from that of the anguinomorphs in having a strong process on its posterior border set off from the shaft of the bone by a marked thinning of the bone.

In only one feature of osteology do lizards of the family Cordylidae approach the Anguinomorpha, namely, the simple clavicle. Even here the clavicle is more sinuate in form than that of the anguinoids, and it is quite similar to that of such scincoids as *Eumeces schneideri*. On the other hand, in numerous features, such as tongue structure, tooth re-

placement and dental form, construction of the occiput, form of the base of the skull, form of the postorbital arch, and roofed temporal fossa, they show affinity to the scincomorphs, and the resemblance to the gerrhosaurs is particularly close, even to such details as head squamation and the presence of postcloacal spines. Indeed, there appear to be but two characters that distinguish the Cordylidae from the Gerrhosauridae, namely, absence of a lateral fold and simplicity of the clavicle in the Cordylidae. These characters alone do not seem to be of family significance, since the Anguinidae contain forms both with (as *Gerrhonotus* or *Ophisaurus*) and without (as *Celestus* and *Anguis*) a lateral fold, and the Madagascan gerrhosaurid *Tracheloptychus* has the fold restricted to the neck. Various skinks have the clavicle simplified; *Basiliscus* and *Laemantus* are included in the Iguanidae, even though they possess loop-shaped clavicles while the other genera do not; *Uroplates*, with simplified clavicles, is frequently referred to the Gekkonidae. It may therefore be wisest to follow the course taken by Cope (1871) and include the gerrhosaurs with the zonures in a single family, Cordylidae.

In any case, whether the two families are merged or kept separate, it seems necessary that the zonures be taken from the Anguinomorpha and placed near their relatives in the Lacertoidea.

#### CHARACTERS OF THE INFRAORDER ANGUINOMORPHA

With the removal of the anomalous Pygopodidae and Cordylidae, the Anguinomorpha become a more natural group set apart by several unique features from all other lizards and agreeing with one another in most aspects of their structure.

Especially characteristic of the group is the division of the tongue into a fore and hind portion by a transverse fold. This is a unique feature among lizards seen elsewhere only in the snakes, a group probably derived from the anguinomorphs. The fore portion of the anguinomorphan tongue is itself relatively inelastic and is conspicuously narrower than the hind portion. The broad and elastic hind

portion serves as a sheath for the fore tongue when the tongue is retracted, while the longitudinal expansion of this hind tongue sends forth the fore tongue when the whole tongue is extended.

No less characteristic is the dentition, which, although similar to that of the snakes, is unique among lizards but is approached, probably as an example of convergence, by some of the Teiidae. The teeth of the Anguinomorpha are nearly solid, without basal excavation, and are replaced alternately rather than successively. Tooth replacement is interdental, the replacement tooth lying behind, not beneath, the older tooth. (The

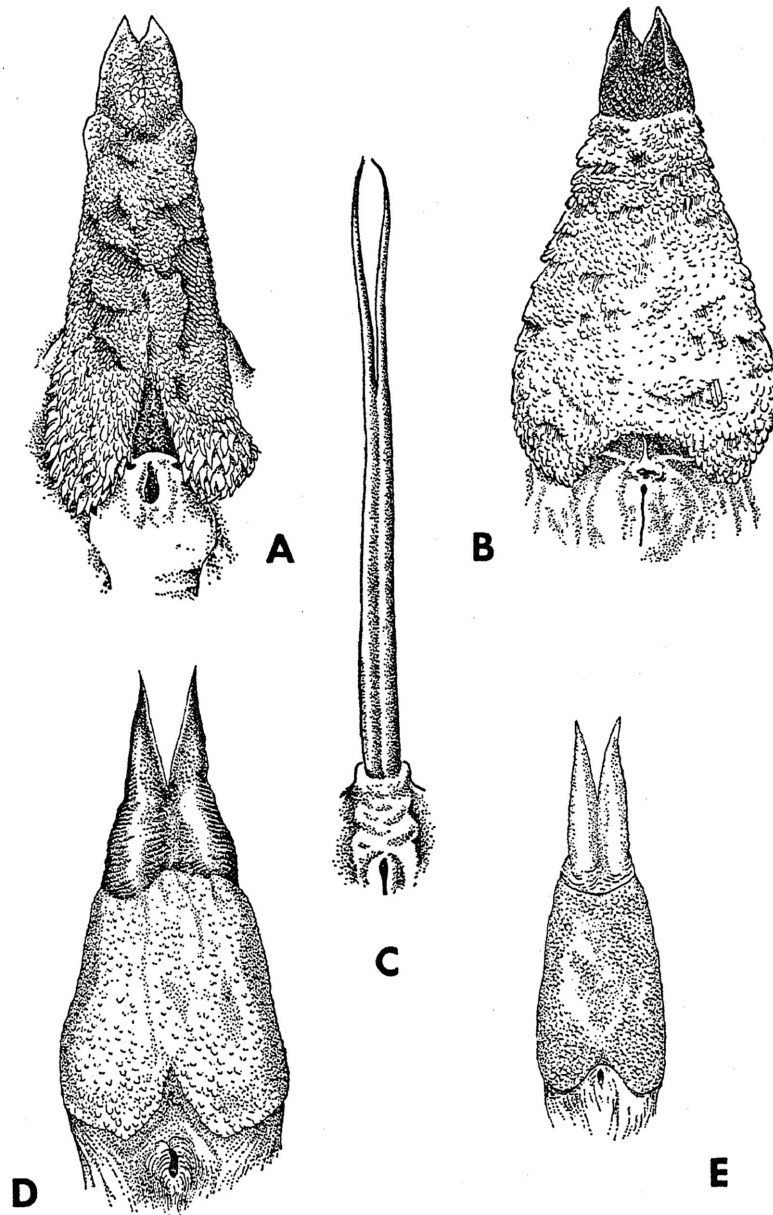


FIG. 29. Tongues, dorsal view, of Anguinomorpha. A. *Gerrhonotus multicarinatus* (Anguinidae), drawing by McDowell. B. *Shinisaurus crocodilurus* (Xenosauridae), drawing by McDowell. C. *Varanus monitor* (Varanidae), after Malcolm Smith. D. *Heloderma suspectum* (Helodermatidae), drawing by Alma Froderstrom. E. *Lanthanotus borneensis* (Lanthanotidae), drawing by Alma Froderstrom.

teiids resemble the anguinomorphs in lacking basal excavations in the teeth, but their replacement is successive.)

The structure of the postorbital arch is distinctive, although the total absence of this

arch in several groups of lizards prevents this from being as useful a diagnostic character as the tongue structure and dentition. In the Anguinomorpha (except some *Celestus* and *Diploglossus*) but not as in other lizards

(*Gerrhosaurus* not excepted, in spite of the statement of Siebenrock, 1892, to the contrary), the postorbital bone is completely excluded from the orbital margin, both internally and externally. In the monitors

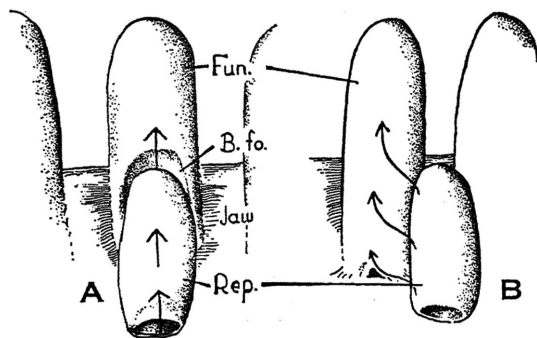


FIG. 30. Tooth replacement. A. Non-anguinomorph lizard. B. Anguimorph. *Abbreviations:* fun, functioning tooth; b. fo, basal fossa for replacement tooth seen in non-anguinomorph lizards; jaw, parapet of the jaw, against which the teeth are ankylosed; rep, replacement tooth. The arrows indicate the course of migration of the replacement tooth. Drawing by McDowell.

(*Varanus*) this character is obscured by fusion of the postorbital and postfrontal, but as pointed out above (p. 48) the condition is basically the same as in other anguimorphs.

Other characteristic features of the Anguimorpha are:

1. Premaxillae fused, but no median premaxillary tooth.
2. A single (the first) pair of ceratobranchials present.
3. Pro-otic bone produced anterior to the

anterior semicircular canal to meet the dorsal extremity of the epipterygoid.

4. Premaxillae pierced by foramina.

5. Septomaxilla completely roofing the organ of Jacobson.

6. Lacrimal present, extending onto the lateral surface of the muzzle.

7. Supraoccipital without dorsal longitudinal keel or crest, articulating with parietals anterior to the level of the quadratocranial articulation.

8. Laterosphenoid (postoptic) bones present but small and simple, isolated from other cranial bones and lying in the membrane separating the orbit from the cranial cavity.

9. Parietals fused.

10. Basipterygoid process not connected with the roof of the entocarotid fossa.

11. No post-cloacal apparatus of sacs and bones.

12. Meckelian groove open anterior to splenial.

13. A distinct angular bone that is not fused to any of the surrounding jaw elements.

14. Maxilla firmly united with surrounding bones.

15. No femoral pores, although pre-anal pores may be present.

16. Frontal bones with subolfactory (descending) processes, which may or may not meet each other.

17. Mylohyoideus making few interdigitations with the geniohyoideus.

18. Clavicles never forming complete loops.

The combination of all these features distinguishes the Anguimorpha from other Squamata, including the ophidians.

## MAJOR LINES OF ANGUIMORPHAN PHYLOGENY

The Anguimorpha are so sharply circumscribed a group that, although it is possible to say with fair assurance that the snakes are their derivatives, no statement can as yet be made as to what group of lizards is ancestral to the anguimorphs. This is unfortunate and adds difficulty to the classification of the group, for the reason that we cannot say with certainty which characters are primitive (held over from the ancestral group) and which are advanced (specializa-

tions superimposed on the ancestral morphology). A further complication is presented by the fact that many of the forms are represented today only by their fragmentary fossil remains, leaving us in doubt about important osteological features, as well as soft parts and physiological features.

None the less, it seems possible to divide the Anguimorpha into two main lines of descent, distinguished from each other principally by divergent modifications of the bones

in the region of the mouth, a structural divergence suggesting an early ecological divergence in the method of feeding.

#### THE DIPLOGLOSSAN LINE

One line, here termed the Diploglossa, and equivalent to the Diploglossa of Camp after the removal of his Pygopodidae, Zonuridae (=Cordylidae), and Helodermatidae, appears to retain the more usual, and presumably more primitive, type of jaw apparatus and insectivorous feeding habits. Further evidence of their primitive nature is given by their ability to regenerate the tail, as in the majority of lizards, Amphisbaenidae and Chamaeleonidae excepted, and the occurrence among some of the included forms of such generalized "scincoid" and "iguanoid" features as closely packed, straight, blunt teeth, cruciform interclavicle, slightly nicked tongue, presence of a second epibranchial, intercentral position of the caudal chevrons, and large intermedium of the carpus.

In the Diploglossa there is no possibility of motion in the lower jaw, the jaw elements all being quite rigidly sutured to one another. The dentary externally is sutured to the surangular and to the angular as well, for the latter bone lies in its more usual saurian position, entirely or almost entirely on the outer surface of the lower jaw, and with a long suture with the dentary. On the inner surface of the jaw the dentary is equally limited by being bound tightly to the dorsal border of the splenial, thus closing the Meckelian groove except at the internal mental foramen. The splenial is held motionless by its posterior extension along the ventral border of the coronoid, with which it forms a suture, and tight connection to the dorsal border of the prearticular bone. The splenial and angular make but a short, longitudinal "touch-and-go" contact along the ventral border of the jaw, and form no vertical contact. Posteriorly, rigidity of the jaw is achieved by actual fusion of articular, surangular, and prearticular.

The whole dental apparatus, with its supporting jaw apparatus, is well modified as a crushing and chewing device, excellent for the breaking of the indigestible chitinous exoskeleton of arthropods, allowing subsequent penetration of the prey by the digestive

juices of the alimentary canal. Since the dentition serves largely a crushing function, it is continued back beneath the orbit for some distance, the dental row of the lower jaw closely approaching the coronoid process. The functional importance of this becomes apparent if we recall that the lower jaw represents a lever of the second class, with, proceeding from the rear forward, fulcrum (quadrate-articular joint), applied torque (temporal musculature, inserting principally on the coronoid process), and resistance (prey clenched between the maxillary and dentary teeth). In order that the animal can chew, the moment of resistance (force of resistance normal to the level multiplied by the distance of the point of application from the fulcrum) must be less than the moment of applied torque (force of applied torque normal to the lever multiplied by the distance of the point of application from the fulcrum). Therefore a slight inefficiency is introduced by the fact that the distance of the tooth row (resistance) from the quadrate-articular joint (fulcrum) must always exceed the distance of the coronoid process (applied torque) from the quadrate articulation. The result is that a greater force must always be applied by the temporal muscles in chewing than is presented by the resistance of the morsel being chewed. (It is well to bear in mind, however, that the inefficiency of the second-class lever in this aspect of chewing is made up for by the greater gape of the mouth allowed by the use of a second-class lever than can be allowed by a lever system in which the masseteric muscles extend anterior to the crushing teeth and limit the gape of the jaws. The greater gape of diploglossid lizards allows a more accelerated and powerful snap of the jaws in the capture of prey than is allowed the mammals, which make up for this lack by the extreme development of the canines in the predaceous forms.) By having the dental series so far posterior and so near the temporal musculature, the Diploglossa have reduced this inefficiency to a minimum. Or perhaps it might be better to say that the pre-Anguimorpha reduced this inefficiency, for this is the usual masticatory system in lizards and probably represents a heritage of the diploglossans from the ancestral stock.

This approximation of dental series and

coronoid process has affected the form of the bones involved. The coronoid bone bears the coronoid process on its anterior portion, so that the anterior profile of the bone is a simple descending half of a parabola. In the upper jaw, the backward extension of the tooth row brings the maxilla some distance beneath the orbit. This results in the separation of the palatine and ectopterygoid articulations of the maxilla, allowing the maxilla to enter the rim of the suborbital fenestra; in addition, the maxillary process of the palatine is allowed to project transversely rather than forward and transversely to meet the maxilla, and the palatine is of a simple triangular, rather than furcate, form.

Since the Diploglossa have capitalized on the crushing action of the bite at the rear of the mouth rather than on the grasping snap at the front of the mouth, the bones of the muzzle are arranged to form a transverse buttress immediately before the orbits. This strengthens the skull opposite the posterior portion of the dentition, but there is little provision for bracing the tip of the upper jaw against resistance offered by struggling prey caught in the jaws other than the arching of the profile to act as a parabolic strut to brace the premaxillae. The nasal forms a strong suture with the maxilla and prefrontal,<sup>1</sup> so that a continuous bony arch is formed across the muzzle anterior to the orbit, while just within the orbit the jugal aids the preoptic wall of the prefrontal in forming a buttress for the posterior portion of the maxilla, transmitting forces from the maxilla to the roof of the muzzle.

#### THE PLATYNOTAN LINE

The other line of Anguinomorpha consists primarily of rather large to very large (for example, the mosasaur *Tylosaurus* and the living monitor *Varanus komodoensis*) predatory lizards, feeding on large prey and typically employing the dentition in the capture rather than in the mastication of food. The lower jaw is rather loosely constructed, and there is a progressive series within the group

in the development of an intramandibular hinge, possibly to allow expansion of the jaws in swallowing large prey and possibly to allow a free and slashing motion to the sharp teeth. In all the members of this predaceous group, the Platynota (equivalent to the Platynota of Camp plus the two genera of his Helodermatidae), there is less fusion of the surangular, prearticular, and articular than in the Diploglossa, for distinct sutures may be made out between the three bones. In all the splenial is of less posterior extent than in the Diploglossa, not extending back to the level of the midpoint of the coronoid, while in the diploglossans the splenial extends nearly or quite to the level of the posterior extremity of the coronoid.

Except for some varanids, such as *Varanus niloticus*, and some mosasaurs, such as *Globidens*, which are secondarily modified for crushing mollusks and Crustacea in their jaws, the platynotans represent a line in which the dentition is largely adapted for grasping, and the jaws meet little of the vertical resistance encountered in chewing. Rather, they meet with the nearly parallel resistance of squirming prey, a resistance met by the hook-shaped teeth rather than by special modification of the jaw.

Because the jaws are used primarily in the grasping snap, rather than in a crushing bite, there has been a forward displacement of the tooth row, which in the platynotans lies entirely anterior to the orbit, bringing the point of resistance farther from the fulcrum (quadrate-articular joint) and point of applied torque (insertion of temporal muscles) than in the Diploglossa. This severely reduces crushing power, which is of slight value, and to some extent holding power, which is compensated for by backward hooking of the teeth, but materially increases the speed and piercing power of the snap of the front of the jaws.

The forward displacement of the tooth row has brought about certain changes in the form of the lower jaw and palate. In the lower jaw it is chiefly the form of the coronoid bone that has been affected. The coronoid process is fixed in position, since the temporal musculature does not, of course, extend anterior to the eye. When the jaws are occluded the coronoid process must fit behind the eye and

<sup>1</sup> The exception is *Shinisaurus*, in which the great vertical depth of the snout behind the naris allows the prefrontal to enter the naris, separating nasal and maxilla, but the naris is in no way produced caudad.

its surrounding bones. With the forward migration of the posterior end of the tooth row and the posterior portion of the dentary to a point opposite the anterior extremity of the orbit, the coronoid becomes drawn out in advance of the coronoid process, so that the process lies in the posterior half of the bone, and the anterior profile of the bone extends into a horizontal plateau.

Similarly, the forward migration of the posterior end of the maxilla, correlated with the displacement of the dental series, has caused modification of the palate by bringing the anterior extremity of the ectopterygoid into contact with the palatine-maxilla juncture, excluding the maxilla from the sub-orbital fenestra. The forward migration of the hind portion of the maxilla has also brought the lateral (maxillary) process of the palatine somewhat forward and diagonal in position, giving the palatine a furcate form.

With the elongation of the snout concomitant with the anterior displacement of the dental series, the increase in importance of the bite of the most anterior teeth, and the decrease in importance of resistance to vertical thrust against the posterior part of the jaws, a new system of supporting and bracing struts for the muzzle has been developed. The diploglossan bracing of the tip of the muzzle against upward flexure formed a very much arched dorsal profile of the snout to act as a parabolic strut transmitting all horizontal components of thrust against the premaxilla to the posterior part of the skull, where forces were dissipated. This is not sufficient in the Platynota, where such a method would require an excessive deepening of the skull out of proportion to the other functional requirements of the skull. It would require, indeed, either added dead weight of tissue to fill up space, or increase in the size of cavities, such as the nasal or buccal chambers, that would necessitate considerable rearrangement of other organ systems, particularly the respiratory system. Since contraction and expansion of the buccal chamber is important to respiration in lizards, forming a partial vacuum drawing air through the choanae, the pumping required if the buccal chamber were increased in size would exact an exorbitant price in energy.

Another method of bracing the premaxillae

is seen in some of the beaked agamids, in which bony canthal crests act as bracing struts. But this method seems to be efficient only in forms such as agamids with short, deep, and highly arched muzzles. The degree of development of canthal crests required by a platynotan would probably be excessive, and in any case would require the addition of the dead weight of the bone.

The evolution of the jaws of the Platynota instead has involved the principle of polylamination. The external naris is extended back as a narrow slit to the frontal bone, separating the nasal from the maxilla and prefrontal. By this means three independent struts in trihedral arrangement are formed: a left and a right maxilla-prefrontal strut and a median strut formed of the nasals and dorsal processes of the prefrontals are oriented as vertical laminae, as usual in lizards, so that upward torque is translated into compressive force, which the bones are well able to withstand. But the Platynota are unusual among lizards in that the nasal-premaxillary strut is also transformed into a vertically oriented lamina by the development of a ventral bony crest on the nasal (the partial internasal septum), although this is foreshadowed in the Diploglossa. In all except the primitive *Heloderma* and some *Varanus*, the median strut is further strengthened by fusion of the nasals, and in the mosasaurs the nasals are fused to the premaxillae. The hypertrophied septomaxilla further serves to brace the nasal arch.

The development of the posterior narial slit, the most distinctive feature of the Platynota, while strengthening the tip of the muzzle against upward torque, has weakened the posterior portion of the jaw against upward thrust. In the vast majority of platynotans this is unimportant, but in some *Varanus* and some mosasaurs, such as *Globidens*, the dentition has become secondarily modified for crushing the exoskeleton of shellfish, and this has required a secondary bolstering against thrust on the posterior portion of the jaw. This has been accomplished by vertical dilation of the prefrontal-maxillary arch. Such means would be quite inadequate in a lizard the size of a diploglossan, but the large absolute size of the cancrivorous and molluscivorous monitors and mosasaurs makes this adjustment satisfactory for the purpose.

(Young cancrivorous monitors have, not the crushing teeth of the adult, but typical recurved prehensile teeth, which suggests that it is not until a large absolute size is reached

In *Heloderma suspectum* there is no hinge at all, but the presence of a rudimentary hinge between dentary and surangular in *Heloderma horridum*, pointed out to us by

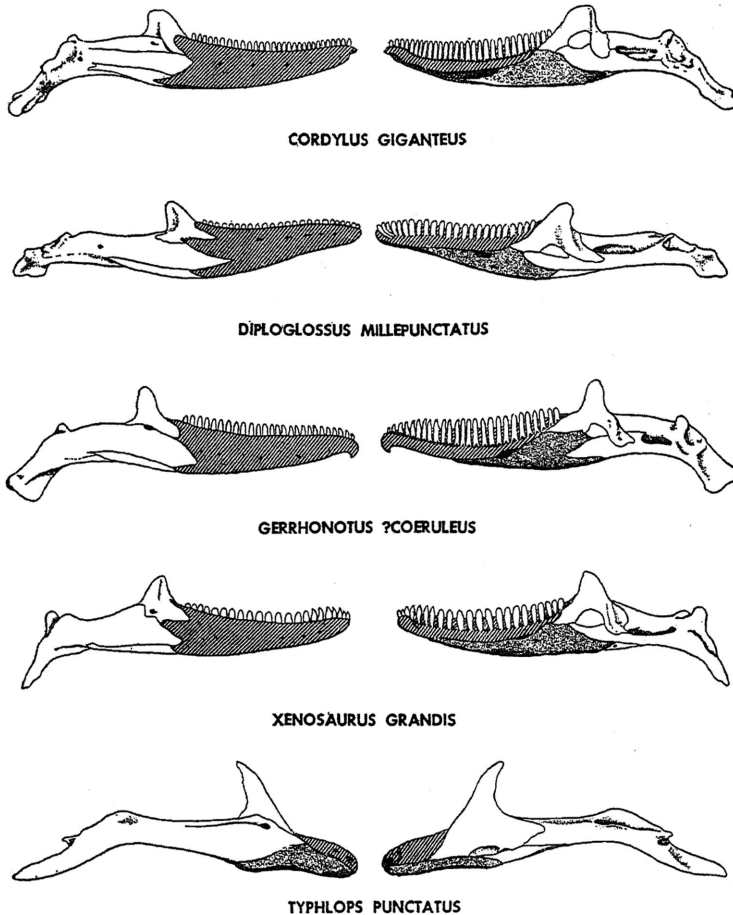


FIG. 31. Diagrams of rigid jaws of Squamata. Shown are a generalized non-anguinomorphan lizard (*Cordylus*), three diploglossan lizards (*Diploglossus*, *Gerrhonotus*, and *Xenosaurus*), and a typhlopod (*Typhlops*). The dentary is hatched, and the splenial is stippled. Drawing by McDowell.

that cancrivorous feeding habits are acquired.)

#### PROGRESSIVE MODIFICATION OF THE MANDIBLE IN THE PLATYNOTA

As noted above, there is a gradual series in the Platynota leading from a form such as *Heloderma*, with the lower jaw nearly as in *Diploglossa*, to the aigialosaurs, mosasaurs, and *Lanthanotus*, with a highly specialized hinge in the lower jaw.

Prof. A. S. Romer, suggests that this is possibly secondary in *suspectum*. But even though the hinge is rudimentary or absent in *Heloderma*, certain displacements in the arrangement of mandibular bones are present, displacements that more advanced platynotans capitalized on in the evolution of a more perfected joint. Chief among these has been an inward rotation of the angular around the ventral border of the jaw. This has slightly reduced the lateral contact of dentary and

angular, thus partially freeing that bone posteriorly. More important, medially the splenial and angular have acquired a strong articulation that lies at about the level of

much reduced in posterior extent, although still forming a long suture with the ventral border of the anterior portion of the coronoid bone. Unlike the state of affairs in the Diplo-

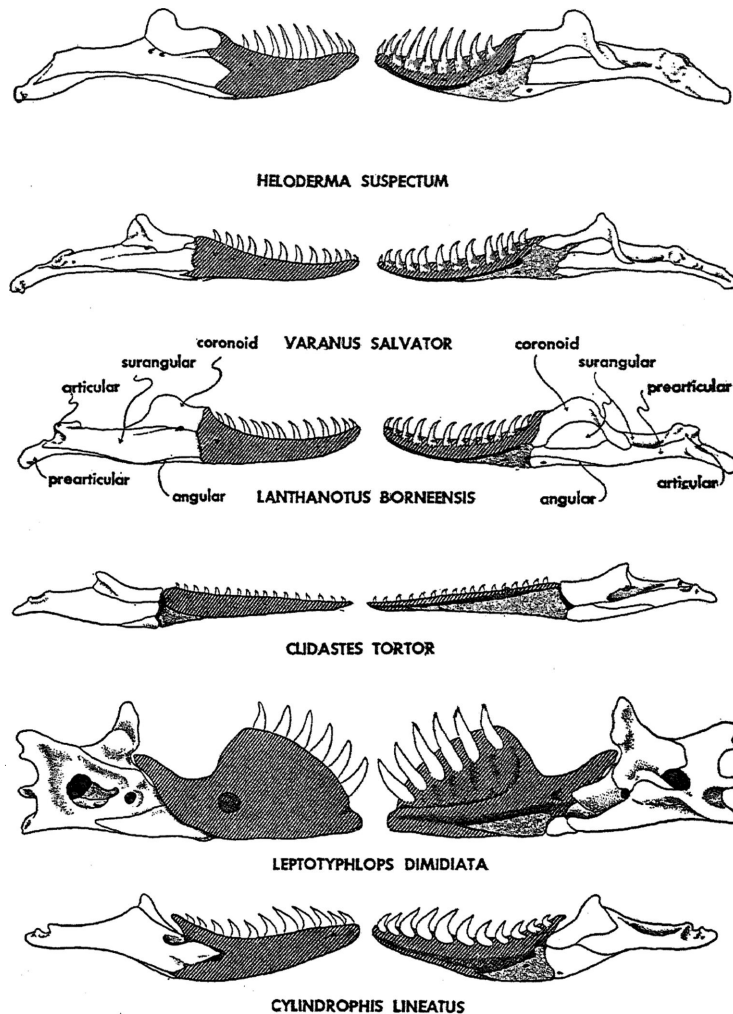


FIG. 32. Diagrams of hinged jaws of Squamata. Shown are four platynotan lizards (*Heloderma*, *Varanus*, *Lanthanotus*, and the mosasaur *Clidastes*), a leptotyphlopoid (*Leptotyphlops*), and a generalized snake (*Cyllindrophis*). The dentary is hatched, and the splenial is stippled. Drawing by McDowell.

the lateral dentary-surangular juncture. In diploglossans there is but slight, if any, contact of splenial and angular, and this takes place far behind the level of the dentary-surangular suture, indeed behind the coronoid process. The splenial is itself modified from the condition seen in Diploglossa, being

glossa, the splenial of *Heloderma* does not extend back to the level of the coronoid process. Moreover, in *Heloderma* the Meckelian groove is open except for a short distance immediately anterior to the internal mental foramen, so that the dentary is largely free of the splenial and, in *Heloderma horridum*, pos-

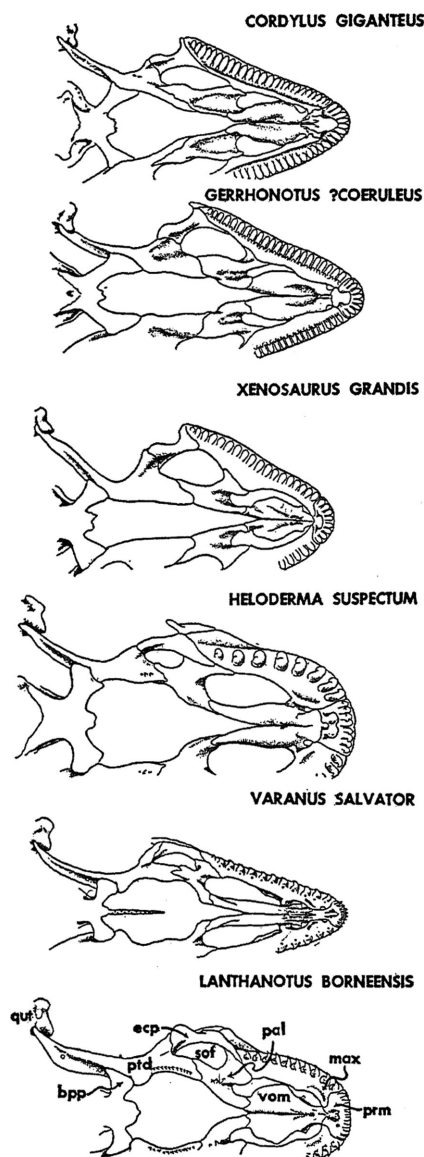


FIG. 33. Palatal bones of generalized non-anguinomorphans (*Cordylus*), two diploglossan anguimorphans (*Gerrhonotus* and *Xenosaurus*), and three platynotan anguimorphans (*Heloderma*, *Varanus*, and *Lanthanotus*). Specializations of platynotans seen are: reduced backward extent of maxillary tooth row, which is almost entirely anterior to palatine bone; exclusion of maxilla from suborbital fenestra and reduced size of latter; and great width of interpterygoid vacuity. Abbreviations: bpp, basipterygoid process; sof, sub-orbital fenestra; see also page 141. Drawing by McDowell.

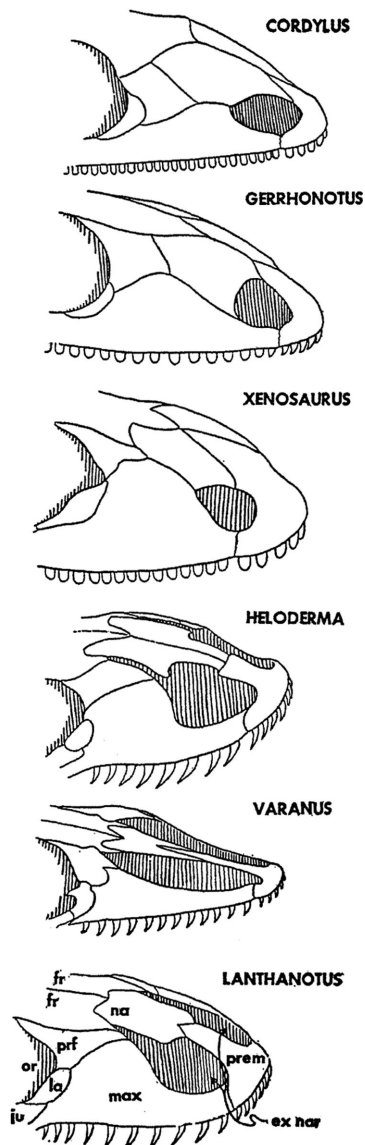


FIG. 34. Diagrams of sutures in facial region of skull of generalized non-anguinomorphans (*Cordylus*), two diploglossan anguimorphans (*Gerrhonotus* and *Xenosaurus*), and three platynotan anguimorphans (*Heloderma*, *Varanus*, and *Lanthanotus*). Specializations in platynotans are failure of maxillary tooth row to extend beneath orbit, and posterior prolongation of external naris as a slit running lateral to nasal. Abbreviations: ex nar, external naris; fr, frontal; ju, jugal; la, lacrimal; max, maxilla; na, nasal; or, orbit; prem, premaxilla; prf, prefrontal. Drawing by McDowell.

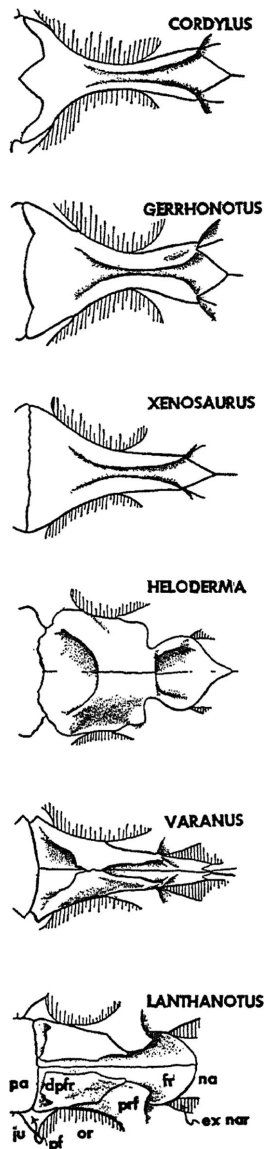


FIG. 35. Frontal bones, ventral view, of generalized non-anguinomorphans (*Cordylus*), two diploglossan anguinomorphans (*Gerrhonotus* and *Xenosaurus*), and three platynotans (*Heloderma*, *Varanus*, and *Lanthanotus*). Chief specialization of platynotans is great development of descending process of frontal, as compared to mere ridge seen in diploglossans (*Anniella* excepted). Abbreviations: dpfr, descending process of frontal; ex nar, external naris; fr, frontal; ju, jugal; na, nasal; or, orbit; pa, parietal; pf, postfrontal; prf, prefrontal. Drawing by McDowell.

sibly capable of some movement independent of the splenial. This does not seem to be of much importance in *Heloderma*, however, for it is at the slightly elastic dentary symphysis that most of the motion of the jaws takes place in broadening the gape.

In *Varanus* the arrangement of bones on the internal surface of the jaws is nearly as in *Heloderma*, save that even greater freedom from the splenial has been given the dentary by the opening of the Meckelian groove for its entire extent anterior to the internal mental foramen. On the lateral surface of the jaw a movable articulation is developed between the dentary and surangular. In some *Varanus*, such as *V. salvator* and *V. komodoensis*, the lateral contact between dentary and coronoid is reduced, but this appears to be a specialization within the group, for others, such as *V. niloticus*, *V. exanthematicus*, *V. rudicollis*, and *V. prasinus*, retain a broad lateral contact between coronoid and dentary, as in other Platynota and lizards generally.

There appears to be no very good information on the lower jaw of the Dolichosauridae, but since that family appears to be related to the Aigialosauridae through *Mesoleptos*, it is probable that the jaw structure was similar to that of the Aigialosauridae and Lanthanotidae. The remains of the mandible of *Pontosaurus* (Kornhuber, 1873) do not show any significant departure from the conditions seen in aigialosaurs.

In *Lanthanotus* and the Aigialosauridae the lateral surface of the lower jaw is as in such primitive varanids as the fossil *Saniwa ensidens* or the living *Varanus prasinus*, with a prominent hinge, but considerable specialization has taken place in the splenial-angular contact. The splenial is truncated vertically at its posterior extremity and no longer extends beneath the coronoid to meet the ventral edge of that bone. The angular-splenial juncture, which in the species so far discussed is in the form of a horizontal V and quite rigid, is, in the aigialosaurs and *Lanthanotus*, a vertical seam corresponding in position to the dentary-surangular hinge on the lateral surface of the jaw, and apparently bending with it. In the forms discussed above, any intramandibular motion that is possible involves the separation of the dentary and

splénial. In the Platynota, however, the joint is nearly perfected and the splénial capable of movement with the dentary. The Meckelian groove is completely open, however, except for a very short splénial-dentary contact behind the internal mental foramen; possibly a separation of the dentary from the splénial, in varanid fashion, is also involved in the intramandibular kinesis.

Different as the jaw of the aigialosaurs and *Lanthanotus* may seem as compared to that of more generalized platynotans, such as *Heloderma* or *Varanus*, it is only from such precursors that the aigialosaurian jaw can be derived. For it really represents the extreme modification of two features that distinguish even the most primitive platynotan from the *Diploglossa*, namely, the decrease in posterior extent of the splénial, and the development on the internal surface of the jaw of a vertical contact of the angular with the splénial at the level of the (lateral) surangular-dentary juncture. It is the jaw structure of *Lanthanotus* that most clearly demonstrates its affinity with the relatively advanced aigialosaurian group of platynotans. Even if we did not have such strong additional evidence as the precondylar constriction of the vertebral centra, posterior prolongation of the anterior naris between maxilla and nasal, and the shortened canal for the entocarotid artery, the jaw structure of *Lanthanotus* would be sufficient to warrant assumptions concerning platynotan affinities.

It is probable that the jaw structure of

snakes is derived from the aigialosaurian type, for snakes show the suture pattern of splénial, coronoid, and angular on the median surface of the jaw associated with the complete jaw hinge of the aigialosaurians, as well as the open Meckelian groove of the Platynota, and the platynotan loose mandibular symphysis (we do not consider the Typhlopidae ophidian). In the leptotyphlopids the hinge is excessively loose, and the fore jaw (dentary and splénial) is connected to the hind jaw (coronoid, surangular, angular, articular, and prearticular) only by ligaments. In the typical snakes the jaw is essentially as in the aigialosaurian lizards, except for two additional modifications: the surangular sends forward a tongue-like process that lies in a fossa on the lateral surface of the dentary, allowing more or less mediad motion of the dentary, but limiting laterad motion; and the tooth row of the dentary is extended back on a special process of the dentary, posterior to the level of the splenio-angular hinge, dorsal to the anterior portion of the surangular. This last modification appears to be correlated with the great posterior attenuation of the maxillary tooth row.

The mosasaurs, as described by Gregory (1951), have developed the most perfect intramandibular joint known among Squamata, excepting only the leptotyphlopids. Conditions are essentially as in the aigialosaurs, but definite articular surfaces are formed between the fore jaw and hind jaw.

## COMPARISON OF THE DIPLOGLOSSA AND THE PLATYNOTA

Just as the ancestor of the anguinemorphs is unknown, the diploglossan ancestor of the platynotans is as yet hypothetical. None the less, a comparison of the known groups of *Diploglossa* with the Platynota may prove useful.

### THE EUPOSAURS

The upper Jurassic Euposauridae may be related to the Anguinidae, but this is far from certain, and the apparently thecodont teeth cast doubt on their reference to the Squamata, though the structure of the cranium and ankle make such reference probable. Unfortunately, critical regions of the

skull are not shown in the best material (see Lortet, 1892). Furthermore we have no knowledge of the structure of the postorbital arch in the absence of distinguishing sutures, while the entire roof of the muzzle is broken away, and the details of the mandibular structure are obscured.

In the *Diploglossa* the supratemporal fossa may be roofed over by osteoderms, while the dorsal surface of the skull is unadorned by crests. However, grooves representing the positions of large epidermal scutes may be present. In *Euposaurus* the temporal fossa is roofed over, but there is no indication that this roofing is by osteoderms, and it may well

be by the parietal or postorbital, as in most scincomorphs, the teiids excepted. Moreover, the roof of the brain case is adorned with a sharp, transversely crescentic crest of bone, which does not occur in any anguinomorph. There are no indications of regular head shields, nor does *Euposaurus* show the warty sculpturing seen in the Xenosauridae. The absence of body osteoderms is a difference from conditions in the Anguinidae and decreases the probability that the roofing of the temporal fossa is osteodermal.

The form of the orbit is also quite peculiar, the frontal having a straight orbital border (seen in the Diploglossinae of the Anguinidae), while the orbit is notched posteriorly, a feature of the procolophonid Diadectia, but a peculiarity unknown in any reptile definitely known to be a squamatan.

The chief evidence for anguinomorph affinities of the Euposauridae is the simple, undilated, and imperforate clavicle, although Camp (1923, p. 319) notes that there is even some uncertainty of the clavicular morphology, as a result of the crushing of the known euposaurid material. Even if descriptions of the euposaurid clavicle are assumed to be correct, several scincids, such as *Eumeces*, have a simple clavicle, and clavicular form seems insufficient evidence for classification of the euposaurs as anguinomorphans.

The Euposauridae must be listed as a family of uncertain position, even as to ordinal assignment, and further discussion of them here seems profitless.

#### THE GLYPTOSAURS

In his classification Camp (1923) recognized, as had earlier authors, a family Glyptosauridae for the fossil Anguinidae (of the present authors' classification) with tuberculate sculpturing of the osteoderms. Since Camp transferred the Helodermatidae, regarded by previous authors as most closely related to the Varanidae, to the Diploglossa on the strength of the resemblance between the beaded lizards and the glyptosaurs, and since *Heloderma* appears to be the most primitive of the Platynta, the hypothesis immediately presents itself that the glyptosaurs represent the transition stage from diploglossan to platynotan.

From the standpoint of time, however, they could only be unmodified descendants of

an earlier intermediate stock, for advanced platynotans are found in the lower Cretaceous of Europe, while the earliest glyptosaurian finds are from the Paleocene. Gilmore (1943, p. 382) has described the genus *Isodontosaurus* from the Djadochta and referred it to the Anguinidae, principally on the basis of a resemblance in shape of the teeth to *Peltosaurus*. However, the arrangement of sutures on the associated jaw fragment clearly demonstrates that *Isodontosaurus* is not closely related to any of the anguinids, and in certain features is decidedly scincoid in appearance. These features are short anterior extent of splenial, which does not extend anterior to the sixth tooth, counting from the rear of the jaw; closure of the Meckelian groove anterior to the splenial; reduction in size of the internal mental foramen to a small pore; considerable anterior extent of the angular on the internal surface of the jaw, the bone extending forward to the level of the fourth tooth from the rear; and prearticular and coronoid making a long suture on the internal face of the jaw, to separate the surangular and splenial for a considerable distance. In all these features *Isodontosaurus* resembles the scincoids, and even more the iguanoids, while it differs from the anguinomorphs. Even the teeth, which were cited by Gilmore as indicating affinity between the glyptosaur *Peltosaurus* and *Isodontosaurus*, seem to speak against anguinomorph affinities of the Mongolian fossil, for in overlapping one another and in showing traces of polycuspy, they differ from the teeth of any known anguinomorph but closely resemble the dentition of the iguanoids. It seems best, for the present at least, to exclude *Isodontosaurus* from the Anguinomorpha. The remaining Cretaceous record for the anguinoids is Gilmore's (1928) *Peltosaurus piger* from the Lance. This species is based on two fragments of dentaries bearing a few teeth and appears to be nearly unidentifiable. In having large basal excavations in the teeth (to judge from Gilmore's illustrations) it is quite unlike other anguinomorphs, and its allocation to the glyptosaurs is questionable.

The chief point of resemblance between *Heloderma* and the glyptosaurs (aside from features common to all anguinomorphs) is in the head osteoderms of *Heloderma* and *Glyptosaurus* itself. In both genera the head

is incrustated with juxtaposed hexagonal or nearly hexagonal osteoderms, all of about equal size and somewhat irregularly disposed and without special differentiation of the supraocular series. In both genera these osteoderms are convex and studded with tubercles. The osteoderms of the body of *Glyptosaurus*, however, differ from those of *Heloderma* in being imbricate, with the consequent development of a smooth overlapping lip. None the less, the overlap of osteoderm upon osteoderm is less in *Glyptosaurus* than in other glyptosauroids.

There are also some resemblances in skull structure between *Heloderma* and *Glyptosaurus*, but none of these can be taken as approximation by *Glyptosaurus* to the platynotan conditions but appear to represent retention by *Heloderma* of certain characters general to the Diploglossa. Thus, in the lacrimal region, *Heloderma* differs from more advanced Platynota, such as *Varanus* and *Lanthanotus*, in having the jugal sutured with the prefrontal and the lacrimal foramen single. In this *Heloderma* agrees with *Glyptosaurus*, but it also agrees with the other diploglossans, and the lacrimal structure of *Heloderma* appears to be but a retained primitive feature.

The skull of *Glyptosaurus* (see Gilmore, 1928, and particularly Gilmore, 1938b) is quite typically diploglossan, with a strong suture between the nasal and the maxilla and prefrontal, a crushing dentition of blunt teeth extending some distance beneath the orbit, a rather deep and strongly arched muzzle, feebly developed and well-separated descending processes of the frontal extending but a short distance into the orbit, maxilla extending into the suborbital fenestra, a rigid lower jaw, without trace of symphyseal or intramandibular joint, Meckelian groove closed over (except anterior to the splenial), splenial and angular forming a horizontal and longitudinal suture along the ventral border of the jaw (but posteriorly, at the level of the coronoid process, this suture extends up into a more nearly vertical position on the inner face of the mandible, somewhat as in *Shinisaurus*), and splenial extended far back on the inner face of the mandible, reaching beyond the level of the apex of the coronoid process.

In addition, the osteodermal investment of the body (see Gilmore, 1938b) is of the type seen in *Gerrhonotus*, except that the individual osteoderms are heavier and more coarsely sculptured. The osteoderms are imbricate anteriorly and posteriorly, but are sutured to one another laterally; the osteodermal cuirass of the dorsal surface ends on the side of the body in a straight and even lateral horizontal border, indicating the presence of a lateral fold, as in *Ophisaurus* and *Gerrhonotus*. This is most unlike even *Heloderma* among the Platynota, in which the osteoderms are non-imbricate and there is no lateral fold.

The lower jaw of *Glyptosaurus* shows the same torsion of the posterior extremity seen in other Anguinidae, the morphologically dorsal surface of the postarticular process being directed inward and the tip of the postarticular process strongly flexed mesiad. This is not seen in Platynota. Moreover, as in anguinids but not platynotans, the articular, prearticular, and surangular are indistinguishably fused. The form of the coronoid bone is as in Anguinidae, not as in Platynota.

The form of the vertebrae is that seen in Diploglossa generally, without precondylar constriction or flaring of the condyle. That *Heloderma* has rather similar vertebrae seems more an indication of the primitiveness of that genus than an indication of special affinity to *Glyptosaurus*.

*Glyptosaurus* is known from the Eocene and Oligocene of North America, and from the Eocene of Europe and Mongolia. The European *Placosaurus* Gervais is probably synonymous (also the older name), and Kuhn's (1940) notes on *Placotherium* Weigelt make it clear that this European Eocene genus is very close to, if not synonymous with, *Glyptosaurus*. No member of the *Glyptosaurus-Placosaurus* group is known to have occurred at an earlier date than the earliest *Peltosaurus*, and the resemblance between *Glyptosaurus* and *Peltosaurus* in dentition, as well as possession by both of a very *Gerrhonotus*-like morphology, suggests that the *Glyptosaurus* series may have arisen from an early member of the *Peltosaurus* series.

But *Glyptosaurus* and its immediate allies are considerably more specialized than their peltosaurian ancestors. Chief among speciali-

zations is the disintegration of the typical large and regular head osteoderms (and presumably the overlying epidermal scutes) of the anguinids. In *Glyptosaurus* the head osteoderms are small and polygonal tesserae, seemingly without any special order in their arrangement. It is this feature that has led to comparison with *Heloderma*, but it might as easily be compared with the xenosaurid arrangement. A second specialization has been the widening of the frontals (which may or may not be fused) between the orbits to form a moderately large orbital roof, the frontal being conspicuously wider between the orbits than anteriorly. A third specialization, possibly responsible for the two specializations just mentioned, is great increase in size. *Glyptosaurus hillsi* had an estimated head length of 5 inches, considerably greater than that of any *Peltosaurus*, and even greater than any known *Heloderma*.

Quite probably *Glyptosaurus* (along with *Placosaurus* and *Placotherium*) represents an early gigantic line of Anguinidae, probably worthy of subfamily distinction on account of the breaking up of head osteoderms and very large size, as well as in the structural peculiarity of the broadened interorbital portion of the frontal. The group shows no definite approach to *Heloderma* or the other Platynota but rather shows affinities to the *Gerrhonotus*-like group of the Anguinidae in the lateral sutures and anteroposterior imbrications of the osteoderms and the presence of a lateral fold. Moreover, all the glyptosaurus, in this restricted sense, are too late in time to give any trustworthy evidence even of what a pre-platynotan anguinoid might have been like.

*Peltosaurus* was a smaller contemporary of *Glyptosaurus* and like the lizards of that genus had coarsely tuberculate osteoderms, but in general structure it appears to be much closer to the present-day anguinids with large and regular head osteoderms (and corresponding overlying epidermal scutes). Indeed there is very close agreement in both scutellation and skull structure between *Peltosaurus* and the living *Gerrhonotus liocephalus*. In the scutellation of the head the two lizards resemble each other, not only in possessing the same scutes (as far as can be made out in *Peltosaurus*), but in the details of their ar-

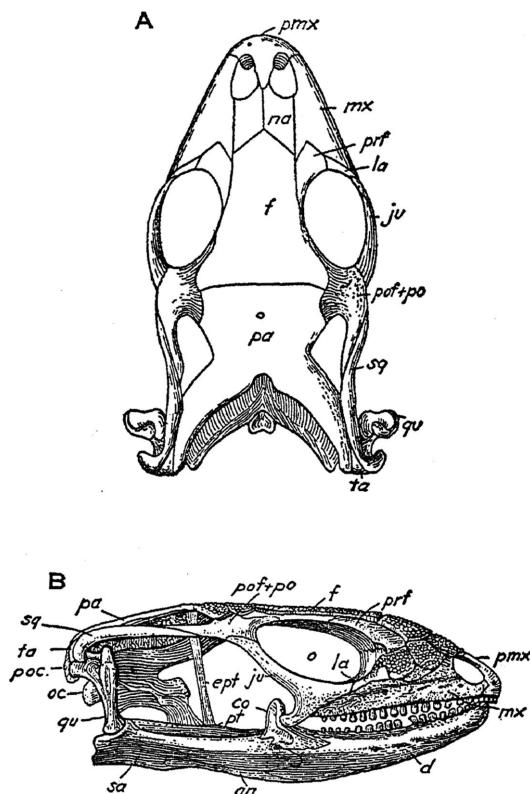


FIG. 36. *Peltosaurus granulatus*. A. Dorsal view of skull. B. Lateral view. Abbreviations: an, angular; co, coronoid; d, dentary; ept, epipterygoid; f, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; o, orbit; oc, occipital condyle; pa, parietal; pmx, premaxilla; poc, paroccipital process; pof+po, postfrontal and conjoined postorbital; prf, prefrontal; pt, pterygoid; qu, quadrate; sa, surangular; sq, squamosal; ta, tabular. From Gilmore.

range and contacts. Thus in both lizards the frontonasal is large and posteriorly wedged between the prefrontals nearly or quite to meet the frontal scute, while posteriorly the interparietal is separated from the frontal scute by a meeting of the frontoparietals on the midline (variable in *G. liocephalus*, but not seen elsewhere among living anguinids). In the skull *Peltosaurus* shows special resemblance to *Gerrhonotus liocephalus* in the probable separation of the nasal from the prefrontal by a maxillofrontal contact. In *Peltosaurus* the frontal osteoderms, and frontal bones as well, are fused to one another across the midline, as in the

living *Gerrhonotus* and *Abronia*, but in the very closely related Eocene European *Placosauriops* Kuhn (1940) and *Placosauroides* Kuhn (1940), the osteoderms, and probably the bones as well, are distinct, as in *Ophi-saurus*. Since *Glyptosaurus* appears to have been variable in this respect, it is quite possible that *Peltosaurus* was also variable and that *Placosauriops* and *Placosauroides* are but synonyms of *Peltosaurus*.

The grounds for separating *Peltosaurus* from the living *Gerrhonotus* are indeed tenuous, and the only significant characters separating the Oligocene members of *Peltosaurus* from the living genus appear to be the form of the crowns of the teeth, which are transversely compressed in *Peltosaurus*; and the form of the interclavicle, which is peculiar in the fossil in having the posterior process much shortened. The granular tuberculation of the osteoderms, used as a family character of the "Placosauridae" by Kuhn (1940), can be matched in the living *Gerrhonotus imbricatus* and probably in other living species as well. In having the occipital elements indistinguishably fused (see Gilmore, 1928, p. 128) *Peltosaurus* is like the living genus *Abronia*, but in the narrowness of the interpterygoid vacuity is more like *Gerrhonotus*, a resemblance further borne out by the presence of pterygoid teeth (frequently present in *Gerrhonotus*, but absent in *Abronia*).

Since *Peltosaurus* and the related, or possibly synonymous, genera *Placosauriops* and *Placosauroides* are typical anguiniids and show even less resemblance to the platynotans than does *Glyptosaurus*, the *Peltosaurus* series need not be considered further. *Peltosaurus* is definitely known from the Paleocene, Eocene, and Oligocene. Gilmore (1928, p. 136) has assigned some jaw fragments from the Lance to *Peltosaurus* as *P. piger*. This material is probably not anguinid, and is too fragmentary to make certain the generic assignment.

The genus *Xestops* is very incompletely known, being represented by a few fragmentary frontal bones, body osteoderms, and jaw fragments (the material described and figured by Camp, 1923, as *Xestops* is in actuality *Melanosaurus*). The dentition and granular relief of the osteoderms are similar to those of *Peltosaurus*, but there is even

greater resemblance in the ascertainable features to the living genera *Diploglossus*, *Celestus*, *Sauresia*, *Weimorena*, and *Ophiodes* (the Diploglossinae). Most indicative of affinity to the Diploglossinae is the form of the osteoderms (see Gilmore, 1928, p. 145), which are beveled and imbricate laterally, as in the Diploglossinae, rather than sutured to one another laterally, as in the Gerrhonotinae (including *Peltosaurus* and *Glyptosaurinae*). The asymmetrical carina of the individual osteoderm is also as in the Diploglossinae. No less characteristic is the form of the frontal, which has a nearly straight orbital border, as

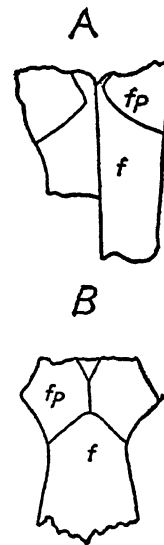


FIG. 37. Frontal bones, dorsal view (parietal border at top). A. *Xestops vagans*. B. *Peltosaurus granulatus*. Abbreviations: f, frontal osteoderm; fp, fronto-parietal osteoderm. From Gilmore.

in the Diploglossinae, rather than the concave orbital border of the other anguiniids. As in Diploglossinae, the frontals are narrow, separate, and covered by large and regular osteoderms. The teeth are as in *Peltosaurus* and *Glyptosaurus*, and show a form retained in the living Diploglossinae. Indeed, the known material of *Xestops* does not permit generic separation from the living lizards of the genera *Celestus* and *Diploglossus*; however, we retain the genus because the difference in time makes it likely that differences will be found when better material of *Xestops* is discovered. Perhaps the presence of a small oval patch of teeth on the pterygoid of *Xestops*

will distinguish the fossil genus from the recent forms, which have an edentulous palate, but the variability of palatal teeth in the living representatives of *Gerrhonotus* makes even this doubtful.

In view of the fragmentary nature of the remains of *Xestops* and the high probability of their reference to the Diploglossinae, we do not attempt to compare *Xestops* with the Platynota, but rather compare its living representatives with the platynotan lizards.

As indicated above (pp. 28-33) *Melanosaurus*, *Exostinus*, and *Necrosaurus* (including *Melanosauroides*) appear to be related to *Xenosaurus* and *Shinisaurus*, and they are compared with the platynotans in the section below on the xenosaurs.

#### THE GALLIWASPS

Although undoubtedly Anguinomorpha, the galliwaspes (*Celestus*, *Diploglossus*, *Sauresia*, *Wetmorena*, and *Ophiodes*, as well as the fossil *Xestops*) appear to be the most primitive members of the group in structural features. The living genera still retain a dental form otherwise characteristic of the lower Tertiary Anguinidae: the tooth is blunt, with the crown compressed into an anteroposteriorly oriented keel, and ornamented with a fine vertical fluting. The teeth are strongly pleurodont, unexpanded proximally, and without basal fossae for replacement teeth (this last is a distinctive characteristic of all the Anguinomorpha). The galliwaspes are the only group of anguinomorphs in which the postorbital enters the orbit, and even here the feature is not constant. The osteoderms of the body are imbricate laterally, as well as anteriorly and posteriorly, not as in the gerrhonotines and glyptosaurines in which the osteoderms are sutured to one another laterally, and the xenosaurs in which the osteoderms are isolated from one another. To judge from the scincids, gerrhosaurines, and related groups the lateral imbrication of osteoderms is a primitive feature. The lack of a lateral fold in the Diploglossinae appears to be a primitive feature correlated with the lateral imbrication of the osteoderms; the freedom of the individual osteoderm requires no specially modified area of the skin for expansion and contraction of the girth of the body. All have a regular series of head osteo-

derms conforming to the typical anguinid pattern and not greatly different from the pattern seen in scincids, lacertids, teiids, and xantusiids.

Externally, the Diploglossinae show considerable resemblance to the Scincidae and long were classified in that family, but internally there is no very definite suggestion of scincid affinities, but there is abundant evidence of anguinid relationships, as shown by the following features:

1. Stout blunt teeth without basal fossae for replacement teeth, the replacement teeth developing between the older teeth and entering the emplacement fossae of the jaw bones from behind rather than from beneath.

2. Jugal frequently meeting the postfrontal to exclude the postorbital from the orbital border.

3. Frontal with distinct descending (subolfactory) processes that are well-separated from each other and do not extend far into the orbit.

4. Tongue divided into a relatively inelastic and narrow fore tongue and a broad, expansible, papillate hind tongue, the fore tongue rather short but distinctly cleft.

5. Caudal chevrons fused to the middles of the caudal centra.

6. Large imbricated osteoderms with an anguinoid rather than scincoid canalicular system.

7. Maxillary dentition extending beneath orbit.

8. Maxillary bone bordering the suborbital fenestra.

9. Bony anterior naris not produced back as a slit lateral to the nasal bone.

10. Meckelian groove closed by suture of splenial with dental shelf of dentary, but open anterior to the splenial.

11. Splenial and angular forming no vertical suture.

12. Splenial extending far back, beyond the level of the apex of the coronoid process.

13. Completely fused articular, prearticular, and surangular.

14. Ability to regenerate the tail.

15. Shape of coronoid essentially as in *Anguis*, *Gerrhonotus*, *Ophisaurus*, and other Anguinidae.

There seems little doubt that the Diploglossinae are true anguinids, but their proba-

ble primitiveness suggests comparison with the Platynota, a group probably derived from very primitive *Diploglossa*. In certain features the diploglossines resemble the Platy-

noid process behind the midpoint of the bone.

3. The arrangement of sutures on the face is perhaps "preadaptive" to the development of the characteristic platynotan facial slit.

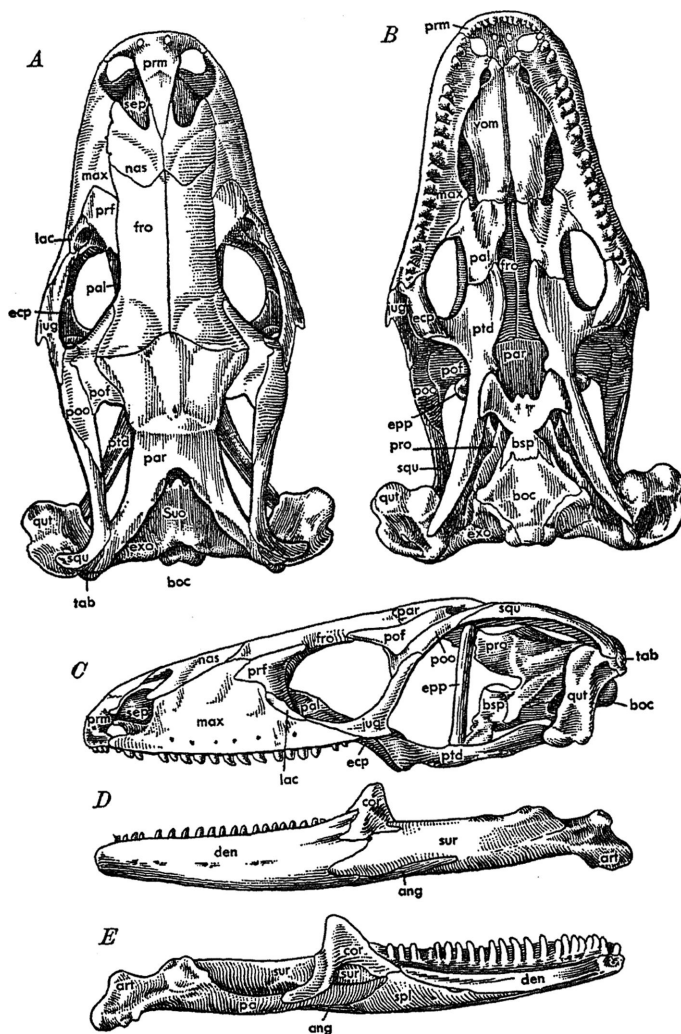


FIG. 38. *Diploglossus millepunctatus*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. Stapedes omitted. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

nota more than do the remaining Anguinidae:

1. The tongue is more deeply cleft than in many other *Diploglossa* (such as *Gerrhonotus* or *Xenosaurus*).

2. Although the form of the coronoid bone is as in other *Diploglossa*, there is platynotan resemblance in having the apex of the coro-

In the *Diploglossinae* the frontal is produced forward to separate broadly the prefrontal from the nasal. This brings the anterolateral tip of the frontal near the posterodorsal corner of the bony naris, seen also in some *Gerrhonotus* (as *liocephalus*), most *Peltosaurus*, and most *Glyptosaurus*, as well as the

majority of lacertids and scincids and many Gekkota, and hence quite possibly a primitive squamatan feature. It is easier to derive the platynotan slit from this type, in which only a short suture (the maxillonasal) need be eliminated, than from the usual gerrhonotine type, in which the posterior extension of the naris must be considerably longer and usually two sutures (maxillonasal and maxillopre-frontal) must be opened up. On the other hand, a derivation of the platynotan muzzle type from the galliwasp pattern would require a secondary backward migration of the anterior process of the frontal.

4. The vertebrae of *Celestus* and *Diploglossus* are more like those of *Varanus* than are those of any other diploglossan, for there is a slight but distinct precondylar constriction, and the condyle is so oblique that most of its articular surface is concealed from ventral view. On the other hand, this may be but parallelism, for *Heloderma*, which appears definitely to be platynotan in its skull structure, has vertebrae of the gerrhonotine type.

5. The details of the base of the brain case of the Diploglossinae make a greater approximation to the platynotan condition than in other Diploglossa. This is seen in the slightly more anterior position of the muscular tuberosities of the basioccipital and the greater contribution of the exoccipital to the floor of the brain case.

On the other hand, the Diploglossinae are far too specialized to be directly ancestral to the Platynota. The straight and nearly parallel orbital borders of the frontals appear to be an early specialization, as well marked in the Eocene *Xestops* as in any living form. All Diploglossinae share with the other anguinids the specialization of inward torsion of the articular portion of the lower mandible and marked twisting of the postarticular process. The genus *Ophiodes* is nearly limbless and is further specialized in the heaviness of the columella auris of the stapes (much as in *Anniella*). In the other genera the phalangeal count is reduced to 2-3-4-4-3; such a count is seen in the aigialosaurians, but the persistence in both *Varanus* and *Heloderma* of the primitive 2-3-4-5-3 would seem to indicate that the phalangeal reduction has been independently reached in the galliwasp and

the aigialosaurians. A further peculiarity seen in all the Diploglossinae except *Ophiodes* is the presence of an enlarged, tubercle-like osteoderm on the lateral surface of the base of the tail a short distance behind the cloacal slit. This is not to be confused with the trihedral spine at the lateral corner of the cloacal slit seen in the Cordylidae, for it is both differently placed and differently shaped.

We may mention that the hyoid arch of *Celestus* and *Diploglossus* approaches that of the primitive platynotans more than does that of any other diploglossan, for it has the hypohyal isolated and not articulated with the ceratohyal, and lacks floating second epibranchials. In the character of the hyoid arch, the Diploglossinae appear to be too specialized to give rise to the other Diploglossa, but the hyoid of the Platynota in which the structure is known could be derived without serious difficulty from that of *Celestus*.

It seems definite that the Diploglossinae as we know them today could not give rise to the Platynota or, for that matter, to the remaining Diploglossa. But to the extent that the galliwasp retain primitive features not shown by other diploglossans, they do show a closer approximation to the platynotans than do the other Diploglossa, with the possible exception of the Xenosauridae (see below).

#### THE GERRHONOTINES

The genera *Gerrhonotus*, *Abronia*, *Ophisaurus* (including *Pseudopus*, *Dopasia*, and probably the fossil *Ophisauriscus*, *Propseudopus*, and *Parapseudopus*) as well as the fossil *Peltosaurus*, *Placosauriops*, and *Placosauroides*, form a natural group, characterized by the possession of a lateral fold of soft skin covered with small non-osseous scales between the dorsal and ventral armor of laterally sutured but anteroposteriorly imbricate osteoderms, a feature seen elsewhere in the Glyptosaurinae, and the presence of large and regular head osteoderms. The orbital border of the frontal is concave; the frontals are distinct from each other (*Ophisaurus*, *Placosauriops*, *Placosauroides*) or fused (*Gerrhonotus*, *Abronia*, *Peltosaurus*). As in the galliwasp, glyptosaurines, *Anguis*, and *Anniella*, the posterior portion of the lower mandible

shows the characteristic anguinid twisting. Some of the genera, such as *Gerrhonotus*, retain as isolated vestiges the second epibranchials, a primitive feature not seen in other Anguinomorpha, and the limbed forms

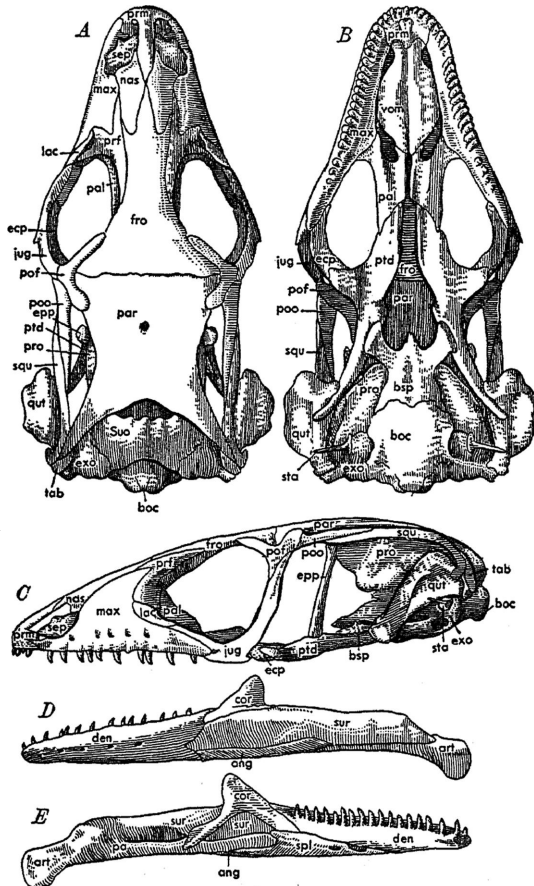


FIG. 39. *Gerrhonotus (Elgaria) kingi*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

have the primitive phalangeal count of 2-3-4-5-3. But in its characteristic osteoderm arrangement, shared only with the Glyptosaurinae, the subfamily Gerrhonotinae appears to be a more advanced group than the Diploglossinae and almost undoubtedly derived from the fossil *Peltosaurus*.

Representing as they do a specialized line of anguinids, the gerrhonotines show less re-

semblance to the platynotans than does *Celestus*, for here the frontals are often completely fused, the angular has a large external exposure, the coronoid process lies in the anterior half of the coronoid bone, and vertebral condyles are no wider than the precondylar centra. The lateral fold characteristic of the group is, moreover, a further departure from platynotan or pre-platynotan conditions. In addition to the very non-platynotan features noted above, the gerrhonotines share with other diploglossans the following additional features distinguishing them from the platynotans:

1. Osteoderms anteroposteriorly imbricate.
2. Large, regularly arranged head scutes.
3. Descending processes of frontal small, separated from each other by a gap.
4. Maxilla entering suborbital fenestra.
5. Tooth row extending beneath the orbit.
6. A firm maxillonasal suture present.
7. Splenial extending far back, behind the level of the coronoid process.
8. Splenial and angular forming no vertical suture at the level of the dentary-surangular suture.
9. Meckelian groove covered over by suture of splenial with dentary.
10. Surangular, prearticular, and articular indistinguishably fused.
11. Tail capable of regeneration.
12. Interclavicle cruciform.
13. Tongue with but feeble furcation anteriorly, and with rather poor differentiation of fore tongue from hind tongue.

According to Tihen (1949), in *Abronia deppei* the osteoderms have disappeared over most of the body, a purely fortuitous resemblance to the Platynota, since other members of the genus have very heavy osteoderms of a form very similar to the armor of *Peltosaurus*.

#### THE SLOW-WORM

The European and North African *Anguis* is perhaps the most modified of the Anguinidae, being limbless, although with internal girdles, without interclavicle, and with rather platynotan teeth. The teeth are compressed, recurved, and fang-like, with a faint anterior groove, and rather similar to the teeth of *Varanus*, although more nearly round in cross section. In addition to this resemblance

in shape of the teeth, *Anguis* resembles the platynotans in such features as the retention of a frontal suture and in the persistence of traces of the sutures between the articular, surangular, and prearticular.

However, these resemblances to the platynotans appear to be the result of parallelism, for *Anguis* shows the following features common among the Diploglossa, but not found among platynotans:

1. Nasal and maxilla forming a strong suture.
2. Frontals with the descending (subolfactory) processes separated from each other by a membranous interval.
3. Dental series extending back some distance beneath the orbit.
4. Splenial extending far back, posterior to the level of the apex of the coronoid process.
5. Meckelian groove closed by juncture of the splenial and dentary.
6. Angular with very slight internal exposure, forming no vertical suture with splenial.
7. Coronoid process in middle of coronoid bone, the anterior profile of that bone a simple concave curve.

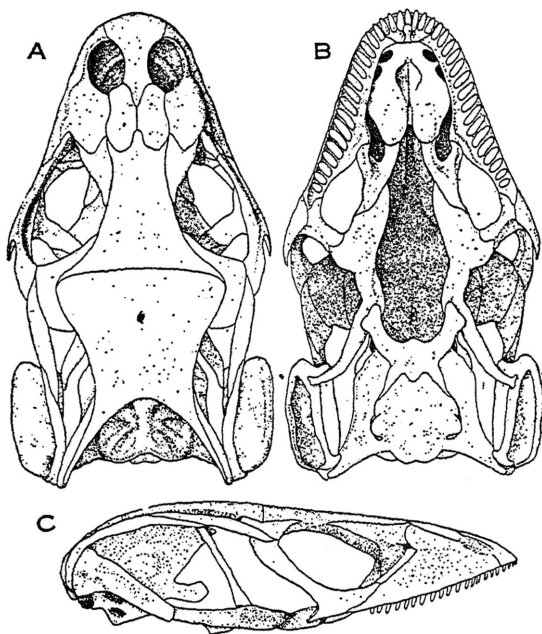


FIG. 40. *Abronia graminea*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. Drawing by Hugh Chrisp, from Tihen.

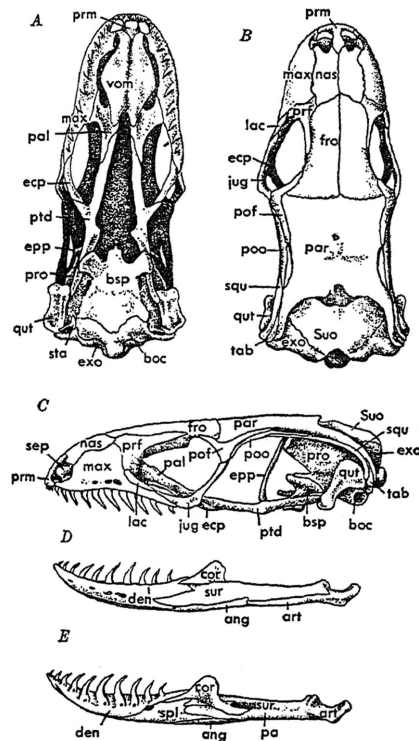


FIG. 41. *Anguis fragilis*. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. After Malcolm Smith.

8. Maxilla bordering suborbital fenestra.
9. Head covered by large and regular osteoderms with corresponding ceratinous scutes.
10. Vertebral centra not constricted anterior to the condyles, the condyles only moderately oblique.
11. Caudal chevrons not placed on pedicles of the centra of the caudal vertebrae.
12. Tail capable of regeneration.

It would appear that the resemblances between *Anguis* and the Platynota are the result of the dietary modifications of the slow-worm. The slow-worm feeds largely on worms, and hence the chief duty of the teeth is holding wriggling prey, rather than crushing it. Indeed the dentition of *Anguis* is better described as convergent to the amphisbaenians than as parallel in modification to the platynotans. With weakening of the jaws, fusion of the posterior mandibular elements

of *Anguis* has perhaps gone into a secondary degeneration. The persistent frontal suture is probably a primitive feature, since it is seen in *Celestus* and in *Ophisaurus*.

*Anguis* is perhaps derived from the Old World lizards of the genus *Ophisaurus*, particularly of the subgenus *Dopasia*, to which the slow-worm shows particular resemblance in its style of limb girdle reduction (loss of interclavicle, retention of other pectoral girdle elements, reduction of sacrum to one vertebra, elimination of median pelvic symphyses). Some of the Old World *Ophisaurus* approach *Anguis* in the extreme reduction of the external ear ("*Hyalosaurus*").

We have examined the skull of the Chinese *Ophisaurus* (*Dopasia*) *harti*. This lizard resembles *Ophisaurus* in the presence of a lateral fold, but in its skull and dentition is more like *Anguis* and *Anniella*. Thus the teeth are recurved and fang-like, the palatine extends rather far forward to form a considerable portion of the roof of the choanal furrow, the Meckelian groove extends onto the lateral surface of the dentary, and the teeth are rather widely spaced. In general, the skull resembles that of *Anguis*, but has the narrowed and elongated general proportions of *Ophisaurus* and a very well-developed palatal dentition. In two features it shows special resemblance to *Anniella*: the prefrontal extends along the dorsal border of the orbit to meet the postfrontal, and the septomaxilla is very closely joined to the vomer to surround the opening of the organ of Jacobson.

It is interesting in this connection that Cope (1900, pp. 490-494) finds certain features in *Ophisaurus gracilis* (probably very close to *O. harti*) in the structure of the limb girdles that recall conditions in *Anguis*. Thus the interclavicle is absent, as in *Anguis* but not *Ophisaurus ventralis*, and the femur is absent, again a resemblance to *Anguis* and a departure from *O. ventralis*.

The chief difficulty in deriving *Anguis* from *Ophisaurus* is the presence of a lateral fold in the latter genus, its absence in the former. But in *Ophisaurus* the lateral fold is in a somewhat rudimentary state as compared to that of *Gerrhonotus* or even *Abronia*, begins some distance behind the ear, and contains rather large scales rather than granules.

Secondary loss of the lateral fold in *Anguis* could be accomplished by backward extension over the body of the "morphogenetic field" of the neck, where the fold is absent in *Ophisaurus*. *Celestus* appears to show a primary absence of the fold, so that the possibility always exists that *Anguis* is an Old World representative of the Celestinae. However, this seems improbable, for in its unconstricted vertebral centra, concave orbital margin of the frontal, anteriorly placed coronoid process, and wide lateral exposure of the angular, *Anguis* differs from *Celestus* and resembles the gerrhonotines.

In addition to its fang-like dentition, *Anguis* shows other peculiarities distinguishing it from the other Anguinidae, of which the most striking is the displacement of the Meckelian groove, which anterior to the splenial runs onto the extreme ventral border of the lateral surface of the dentary, rather than being confined to the internal surface. Another peculiarity is the anterior development of the anterior border of the palatine, so that the vomer extends conspicuously behind the anterior palatine margin.

#### THE CALIFORNIA LIMBLESS LIZARD

The small burrowing lizard *Anniella* appears to be closely related to *Anguis*, as shown by the lateral displacement of the pre-splenial Meckelian groove, anterior displacement of the anterior palatine margin, and a dentition nearly identical with that of the European genus. *Anniella* appears to represent the extreme development of features seen in *Anguis* but has specializations of its own, such as loss of the temporal arch.

*Anniella* shows some convergence towards the platynotans in several features of skull structure:

1. Reduction of suborbital extent of the tooth row. In *Anniella* the maxillary dentition does not extend posterior to the level of the lacrimal foramen, and in this feature the little burrowing lizard is like the predaceous platynotans. However, *Anniella* shows signs that this is a rather recent adaptation in that the maxilla still extends far back beneath the orbit to the level of the posterior border of the eye. (A skull, A.M.N.H. No. 31753, shows considerably greater posterior extent of the maxilla than is figured by Bellairs, 1950; pos-

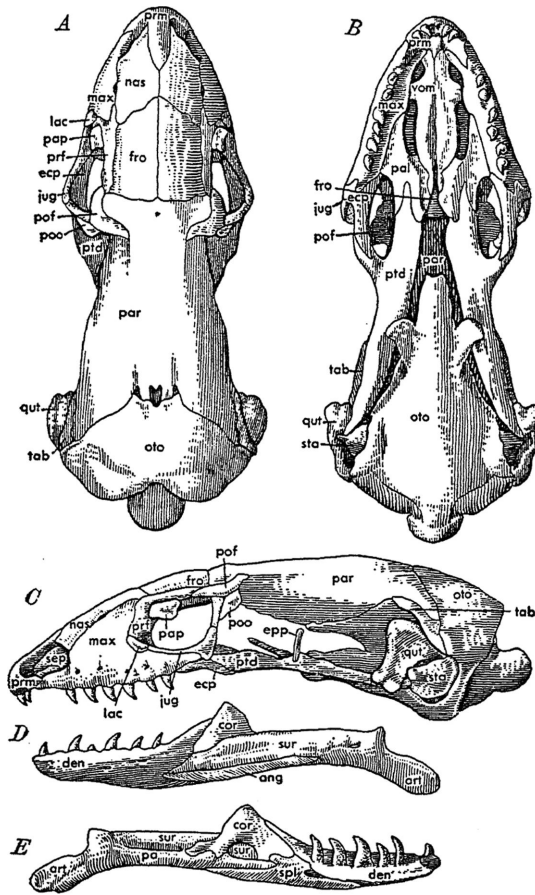


FIG. 42. *Anniella pulchra*. A. Dorsal view of skull. B. Ventral view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. For abbreviations, see page 141. Drawing by McDowell after a drawing by Alma Froderstrom.

sibly *Anniella* is in a period of transition towards a shorter maxilla, as indicated by considerable variability in this character.)

2. The recurved, fang-like teeth, as noted above in the discussion of *Anguis*, which has nearly identical teeth.

3. Meeting of the descending processes of the frontals beneath the olfactory tracts.

4. Exclusion of the maxilla from the infra-orbital fenestra by meeting of palatine and ectopterygoid.<sup>1</sup>

<sup>1</sup> Toerien (1950) figures the maxilla entering broadly into the fenestra and notes this in his text. Apparently *Anniella* is variable in this feature.

5. Retention of traces of sutures between surangular, prearticular, and articular, as in *Anguis* as well.

6. Presence of a bony palpebral, as in *Varanus* and the mosasaurs. This is not shown in Bellairs' (1950) figures, but was discovered in the preparation of our skull and drawn *in situ* before final maceration of the skull. The fact that this bone dropped off during preparation may explain why Bellairs failed to find it. It might also be added that this same specimen showed a pair of post-orbitals, situated behind the post-frontals and excluded from the orbital rim by the ligamentous vestige of the upper portion of the jugal. These also are loosely attached to the skull and fell off during maceration, a circumstance that may explain why they were not noted by Bellairs. In being excluded from the orbit they are in agreement with the post-orbitals of the other anguimorphs and differ from those of the scincomorphs and ascalabotans. Coe and Kunkel (1906) note both the palpebral ("supraorbital") and post-orbital.

The palpebral is also found in xenosaurs.<sup>2</sup>

In spite of the number of resemblances to the platynotan characteristics, it does not appear that these indicate any particular relationship, since it will be noted that the most important features in which *Anniella* shows resemblance to the platynotans (that is, reduction in posterior extent of tooth row, recurved and pointed teeth, exclusion of the maxilla from the suborbital fossa, completion of the subolfactory arch of the frontals) could as well be considered as amphisbaenian-like features. Indeed *Anguis* and *Anniella* appear to be anguimorph analogues of the (?scincomorph) amphisbaenians, and like them are what might be termed "micropredators" in contrast to the platynotans, which are macropredators. Both the micropredators and macropredators use the jaws in the same way, that is, as organs for the capturing and holding rather than the mastication of food. Perhaps the primary difference between the two types is that micropredators feed on weak and soft-bodied prey that may be

<sup>2</sup> The presence of a distinct palpebral is probably correlated with the absence of other supraorbital osteoderms.

swallowed whole, while the macropredators feed on more resistant food that frequently must be torn from the carcass in pieces. Hence we do not find the special muzzle-bracing specializations of the platynotans in *Anguis* or *Anniella*, nor the modifications of the jaws for engulfing large prey.

The jaw structure of *Anniella* in no way approaches the platynotan jaw. In spite of Cope's statement (1900, p. 673) that the Meckelian groove is open, we find it closed on the two pairs of jaws available to us. Probably Cope refers to the portion of the Meckelian groove anterior to the splenial bone, since this is open in *Anniella*, as in other Anguinomorpha. On page 669 of the same work Cope states that the spleniomeckelian groove is closed, a statement in accord with the specimens at our disposal. It might be added that in *Anniella* the presplenial (open) portion of the Meckelian groove is like that of *Anguis*, but not of any other anguinomorph jaw, in running on the ventral edge of the lateral surface of the lower mandible. In fact, the lower jaw of *Anniella* is nearly identical with that of *Anguis* and has the angular bone almost entirely confined to the lateral surface of the jaw and forming no vertical suture with the splenial, the coronoid bone as in *Anguis* and with its process at the middle of the bone, the splenial with great backward extent, reaching behind the level of the coronoid process, and the general proportions and sculpturing also as in *Anguis*.

The palate of *Anniella* is as in *Anguis* and very different from that of the platynotans in that the anterior border of the palatine is far forward, conspicuously anterior to the posterior extremity of the vomer, and anterior to the anterior tip of the interpterygoid vacuity. Since the Platynota have the anterior border of the palatine farther posterior than in any of the Diploglossa save the Xenosauridae, well posterior to the vomer and tip of the interpterygoid vacuity, it seems most unlikely that the platynotans and *Anniella* have any close affinity. The base of the skull is also very similar to that of *Anguis* and quite different from that of the platynotans, or any of the other Anguinomorpha for that matter, in the development of a very broad (rather than narrow and cultriform) parasphenoid

extending well forward of the basipterygoid processes to the level of the posterior extremities of the suborbital fenestrae.

On the muzzle, *Anniella* has a strong suture between the nasal and the maxilla, broken only by a small and isolated foramen, and a short but distinct suture between the nasal and the prefrontal, as in *Anguis* and some of the gerrhonotine lizards but unlike conditions in either *Celestus* or the more primitive gerrhonotines and, of course, very unlike conditions in the Platynota, in which the anterior naris is extended back as a slit to the frontal, excluding the nasal from the maxilla and prefrontal. The nasals are broad and separated from each other by a sharp suture.

In the vertebral column, the centra are unconstricted, and the caudal chevrons are fused to the caudal centra and not placed on pedicles. Even the most primitive platynotan (*Heloderma*) has distinct pedicles for the caudal chevrons, and as far as known, all Platynota have the chevrons freely articulated to the caudal centra. On the other hand, *Anguis* has a vertebral column very similar to that of *Anniella*.

In external appearance, the large and regular head shields and large quincuncially arranged body scales of *Anniella* make it most unlike any platynotan.

So similar is *Anniella* in both osteology and general appearance to *Anguis* that we are tempted to include the California genus in the Anguinidae. However, *Anniella* shows peculiar modifications of its own that seem quite sufficient to justify recognition of the family Anniellidae. These are loss of the temporal arch; great development of the descending wings of the parietals; formation of a long and continuous parieto-pro-otic suture; completion of the subolfactory arch of the frontals; and loss of pineal foramen.

It will be noted that in these features *Anniella* appears to differ from its closest relatives in much the same ways that *Lanthanotus* differs from its closest relatives, the aigialosaurs. Since nothing is known about the habits of *Lanthanotus* the reasons for such convergence cannot yet be guessed, but a comparison of *Anniella* with *Lanthanotus* may be instructive.

*Lanthanotus* COMPARED WITH *Anniella*

*Lanthanotus* and *Anniella* agree in having the brain case relatively more elongated than in their closest relatives so that the brain case as measured from the quadrate-cranial articulation to the frontoparietal suture is equal in length to the facial portion of the skull (measured from the frontoparietal suture to the tip of the premaxilla). However, in other general proportions there is much difference between the two genera. In *Anniella* there is a further posterior extension of the brain case behind the level of the quadratocranial articulation as a result of the inflation and backward projection of the occiput; consequently the brain case of *Anniella* is relatively much more elongate than that of *Lanthanotus*. The skull of *Anniella* is narrow anteriorly, broad posteriorly, giving it a somewhat conical form, whereas that of *Lanthanotus* is as broad across the postorbital arches as across the widest posterior point, and the muzzle is broad and blunt so that a lozenge-like general form results. The narrower jaw of *Lanthanotus* is longer than the skull, as in lizards generally, whereas the lower jaw of *Anniella* is conspicuously shorter than the skull, an indication of the degree of postquadrate hypertrophy of the skull in the California lizard.

The closest resemblance to be seen between *Lanthanotus* and *Anniella* is in the closure of the brain case by close contact of parietal with pro-otic. Even here, however, there is considerable difference in detail. In *Anniella* the parietal sends down strong lateral descending processes that form a large portion of the lateral wall of the brain. In *Lanthanotus* the parietal has no descending processes, and it is the pro-otic that forms the lateral wall of the brain case. In *Anniella* the great development of the lateral descending processes of the parietal results in the extreme reduction of the epipterygoid, and the epipterygoid does not quite meet the pro-otic. In *Lanthanotus* the epipterygoid is much better developed and rises as high as does the pro-otic, with which it is in contact dorsally. The occipitoparietal articulation is also quite different in the two genera. In *Lanthanotus* the juncture is essentially as in *Varanus* save that the plane of the supraoccipital is nearly hor-

izontal and the anterior border of the supraoccipital is broad and round and makes an extensive edge-to-edge contact with the parietal. In *Anniella* the occipitoparietal contact is much specialized in that the parietal is brought back nearly to the level of the jaw articulation to meet with the convex and nearly horizontal supraoccipital. On the midline the supraoccipital sends forward a cartilaginous peg which runs for a short distance beneath the median suture of the two parietal bones (for a detailed account of the occipitoparietal articulation in *Anniella*, see Bellairs, 1950).

Another resemblance between *Anniella* and *Lanthanotus* is the absence in both of the temporal arch. However, the general pattern of cranial arches is otherwise quite different in the two lizards. In *Lanthanotus* the quadrate is borne by a well-developed arch formed by parietal, pro-otic, and tabular and held away from the brain case. In *Anniella* the tabular is very short, and the articulation of the quadrate with the skull is nearly flush with the lateral wall of the brain case. The postorbital of *Lanthanotus* is probably fused to the jugal, and the postorbital arch is quite complete. In *Anniella* the postorbital is quite free and connects only with the post-frontal while the failure of the jugal to meet the post-frontal causes the postorbital arch of *Anniella* to be broadly discontinuous behind the eye.

The absence of a pineal foramen in both *Anniella* and *Lanthanotus* is a further resemblance between the two lizards. However, although there is no open foramen in *Anniella*, there is a median point-like thinning of the bone a short distance behind the frontoparietal suture, which is not seen in *Lanthanotus*.

Although there are a few points of such similarity between *Anniella* and *Lanthanotus* the resemblances cannot be considered as detailed and indeed are also to be seen in amphisbaenids or, except for closure of the brain case, in pygopodids. It seems that the resemblances between *Lanthanotus* and *Anniella* are not sufficiently close to justify suspicion of burrowing habits in *Lanthanotus*, and there is certainly no evidence of any close phyletic affinity between the two genera.

## THE XENOSAURS

The Xenosauridae are represented today by two genera, *Shinisaurus* and *Xenosaurus*, and were represented in the Tertiary and perhaps the Lancean Cretaceous by *Melanosaurus*, *Exostinus*, and *Necrosaurus*. The interrelationships and diagnostic features of the xenosaurids are discussed above (p. 25) and need not be dwelt upon here. The family appears to have been represented in the Lance. Such antiquity has not been established by definite finds for any group of Diploglossa but is inferred by presence in the Anguinidae of primitive features absent in the earliest xenosaurids. In some features the xenosaurs make a closer approach to the Platynota than do the other Diploglossa:

1. Caudal chevrons not fused to vertebral centra (see Barrows and Smith, 1947).
2. Septomaxilla with a dorsal keel, faintly suggestive of the much stronger keel seen in Platynota.
3. Presence of an ossicle (?stylohyal) at the tip of the paroccipital process, seen also as a variation in *Varanus*.
4. Isolation of the body osteoderms and disintegration of the head osteoderms.
5. Presence of pustule-like (tactile?) organs on the larger scales, as in *Varanus* and *Lanthanotus*.
6. Similarity in form of the interclavicle between *Xenosaurus* and *Varanus* (the interclavicle anchor-shaped).

However, in other respects the xenosaurids are less like the platynotans than are some of the anguinids. The tongue of the xenosaurs is but slightly bifid anteriorly; the frontals are fused; the face is shortened rather than

lengthened; the quadrate has the conchs hypertrophied rather than reduced; the mandibular symphysis is exceptionally firmly bound, and the jaws have great rigidity; the tympanum is superficial and scaly rather than deep and bare as it is in *Heloderma* and *Varanus*.

Certain features point to a derivation of the xenosaurs from the Gerrhonotinae, although the xenosaurs do not show the mandibular torsion characteristic of the anguinids. The frontals of the xenosaurs are fused and narrowed between the orbits, a combination seen elsewhere only among the gerrhonotines among possible relatives; the nasal and prefrontal form a long suture, not seen among the diploglossines but frequent among the gerrhonotines. The arrangement of dermal folds in the axillary and inguinal region of both *Shinisaurus* and *Xenosaurus* suggests the former presence of a lateral fold.

It would thus appear that there is no very definite evidence of affinity between xenosaurs and platynotans, aside from common anguimorph features. None the less, xenosaurs may retain some primitive features (as the organs on the scales) elsewhere retained in the Platynota but lost in most of the diploglossans. The primitive Diploglossinae also retain some platynotan-like features but not the same features seen in the Xenosauridae. It would thus appear that, while it is almost certain that the Platynota are derived from early Diploglossa, none of the known diploglossans shows sufficient resemblance to the platynotans to give any positive clue as to the more precise ancestry of the Platynota.

## PHYLOGENY OF THE ANGUINOMORPHA

Inferences concerning relationships discussed in previous sections of this paper are summarized in the phylogenetic chart (fig. 43).

The most primitive known Anguinomorpha appear to be the *Celestus*-like and *Diploglossus*-like group of the Diploglossa, represented in the Eocene by *Xestops*, although almost certainly dating back to an earlier time, and still surviving in Tropical America. With their descendants, the *Celestus*-like group

(the subfamily Diploglossinae of the family Anguinidae) differs from more primitive, that is, non-anguimorph, lizards in dentition (the replacement teeth developing between the older teeth, and the older teeth without basal fossae for replacement teeth), jaw structure (the combination of Meckelian groove open anterior to splenial, the splenial rather narrowly or not at all excluded from the internal, or subcoronoid, exposure of the surangular by the prearticular, and distinct

angular), the form of the premaxilla (the right and left premaxillae fused, but without a median tooth, and the premaxillae pierced by a foramen). Particularly characteristic is the form of the tongue, which is divided by a fold into two portions: an inelastic bifid fore portion, and an extensile and primitively papillate hind portion that serves as a sheath to the fore portion when the tongue is retracted.

In the viscera, the ventral exposure of the gall bladder and the usually retroperitoneal position of the corpus adiposum are characteristic of the Diploglossinae. That this group represents a relatively advanced saurian stock is shown not only by the unique tongue structure and dentition, but also by the presence in all members of features indicative of high specialization, such as complete dorsal roofing of the organ of Jacobson by the septomaxilla, absence of all but the first ceratobranchial, reduced occipital (post-parietal) exposure of the tabular, failure of the clavicles to form complete loops, and absence of a caecum coli.

While primitive in many respects, particularly in osteoderm structure and occasional entry of the postorbital into the orbital border, the surviving Diploglossinae are specialized in certain features along lines of their own, as seen in the nearly straight and parallel orbital borders of the frontals and the reduction of the phalangeal count to 2-3-4-4-3, as well as the enlarged postcloacal osteoderm and frequently spinous hemipenis.

Probably from a primitive diploglossine ancestry may be derived the Gerrhonotinae, specialized primarily in the structure of the osteoderms, which are sutured to one another along their lateral borders, though imbricate anteriorly and posteriorly, and without the beveled lateral imbrication surfaces seen in the Diploglossinae; in conjunction with the specialization of the osteoderms, a lateral fold of small, unossified scales is developed to allow body expansion. (The osteodermal structure of the peculiar living genus *Coloptychon* has not been described; see Tihen, 1949.) In many of the members of this group the frontals are fused, while in others the limbs are much reduced. The group goes back at least to the Paleocene, in which it is represented by *Peltosaurus*. The earlier fossils have the same dental form seen in *Diploglossus* and

*Celestus*, but the living forms have lost the fine vertical fluting of the dental crowns.

The Glyptosaurinae represent an Eocene and Oligocene line of Anguinidae, similar to *Peltosaurus* in most features, including the lateral fold and the form of the osteoderms, but specialized in the breaking up of the head osteoderms and the greater roofing of the orbits by the frontal, as well as by increased size. The frontals are sometimes fused, and it seems likely that the glyptosaurs are derived from the Gerrhonotinae. The dental form is like that of the Diploglossinae and the fossil Gerrhonotinae.

The Anguininae, represented by the European *Anguis*, lack a lateral fold and have the osteoderms imbricate laterally, but the osteoderms do not have the beveled lateral borders, the asymmetrical carina, or the rectangular form of the osteoderms of the Diploglossinae, and the absence of the lateral fold appears to be secondary, associated with the great reduction of the osteoderms by vacuolization and thinning of the bony lamella. In most features of the skull and dentition *Anguis* appears to be close to the gerrhonotine genus *Ophisaurus*, particularly the east Asiatic subgenus *Dopasia*, and in that genus the lateral fold is reduced in anterior extent. *Anguis* is specialized in the fang-like recurved teeth, a feature already strongly foreshadowed in *Ophisaurus harti*, and in the rostral displacement of the anterior border of the palatine, as well as in the lateral displacement of the presplenial Meckelian groove. Like *Dopasia*, *Anguis* has the limb girdles strongly reduced.

The California *Anniella*, the only genus of the Anniellidae, possesses all the peculiar features of *Anguis*, to which it is perhaps most closely related, and has added important specializations of its own. Of these perhaps the most important are closure of the brain case by great development of the lateral descending wings of the parietal, reduction of the suborbital portion of the tooth row, loss of the temporal arch, and juncture of the subolfactory processes of the frontal. But in one feature, at least, *Anniella* is closer to *Ophisaurus* (*Dopasia*) *harti* than to *Anguis*: the prefrontal excludes the frontal from the margin of the orbit.

The Xenosauridae appear to represent a late Cretaceous offshoot of an early *Pelto-*

*saurus*-like gerrhonotine stem. The chief peculiarities of the group appear to be the broadening of the jugal, great development of the conchs of the quadrate, presence of a small ossicle near the tip of the paroccipital process, reduction of the osteoderms, disintegration of the head osteoderms, and narrowing of the frontal. The fusion of the frontals and suggestion of a lateral fold indicate gerrhonotine ancestry, and the most primitive known member of the family, *Melanosaurus*, still shows a *Peltosaurus*-like arrangement of head osteoderms and contiguous, laterally sutured dorsal osteoderms. One group of xenosaurids, represented in the New World by the fossil *Exostinus* and in the Old World by the fossil *Necrosaurus* and the living *Shinisaurus*, developed leaf-shaped osteoderms and a deep and compressed skull. Another line, represented by the living Middle American genus *Xenosaurus*, reduced the osteoderms to tiny nodules and developed a broad and flattened skull.

Returning to the very base of the Anguinomorpha we may trace the second major line, the platynotans, distinguished from the first line (*Diploglossa*) discussed above by the modification of the jaws primarily as prehensile rather than crushing structures. The most characteristic features of the group are the development of a longitudinal facial slit in the bony roof of the snout, the completely preorbital position of the maxillary tooth row, and the greater or less development of an intramandibular hinge, involving a shortening of the posterior portion of the splenial.

The Helodermatidae, represented by the genus *Heloderma*, now living in Mexico and parts of the southwestern United States and known as fossil in the Oligocene, appear to be the most primitive family of the group in retaining an anguinid-like brain case and lacrimal region and in having the intramandibular hinge but little developed, while the body is covered with large (but separated) osteoderms. *Heloderma* has become specialized, however, in the development of an extensive venom apparatus, with grooved premaxillary, maxillary, and mandibular teeth, the loss of the temporal arch, closure of the parietal foramen, and rod-shaped interclavicle.

The Varanidae have the hinge in the lower jaw scarcely better developed than in *Heloderma*, but have reduced the muscular tuberosities of the brain case and developed a characteristic lacrimal, with two canalicular foramina. The earliest fossil group, the Saniwinae, showed some resemblance to *Heloderma* in the form of the maxilla and the presence of palatal teeth, but the living Varaninae are specialized in the loss of palatal teeth and the incomplete postorbital arch.

The remaining families, all of which are extinct with one exception, form a closely knit series characterized by the reduction in the phalangeal count so that the fourth digit has no more phalanges than the third, the high development of the intramandibular hinge, and the failure of the splenial to extend along the ventral border of the coronoid.

One family of this series, the Aigialosauridae, known from the Neocomian (lower Cretaceous), secondarily shortened the neck to seven vertebrae and fused the frontals, while the quadrate became massive and palatine teeth disappeared and the pterygoid dentition remained strong. The upper Cretaceous family Mosasauridae can be derived directly from the Aigialosauridae, with the additional peculiarities of modification of the limbs as paddles (this involving some degree of hyperphalangy), loss of the sacrum, and fusion of the nasal with the premaxilla.

Another family, the Dolichosauridae, known from both lower and upper Cretaceous, specialized in the lengthening of the neck (with over a dozen vertebrae), the loss of palatal dentition, and shortening of the rostral portion of the skull.

A fourth family, the Lanthanotidae, now surviving in Borneo and without fossil representatives unless two very poorly known Neocomian genera (*Mesoleptos* and *Eidolosaurus*) belong to the group, has a neck of moderate length (nine vertebrae) and is specialized mainly in the shortening of the face, lengthening of the brain case, closure of the posterior portion of the brain case, loss of temporal arch and parietal foramen, and hypertrophy of the descending lamina of the frontal.

It may be remarked that the Typhlopidae appear to be a line derived from some an-

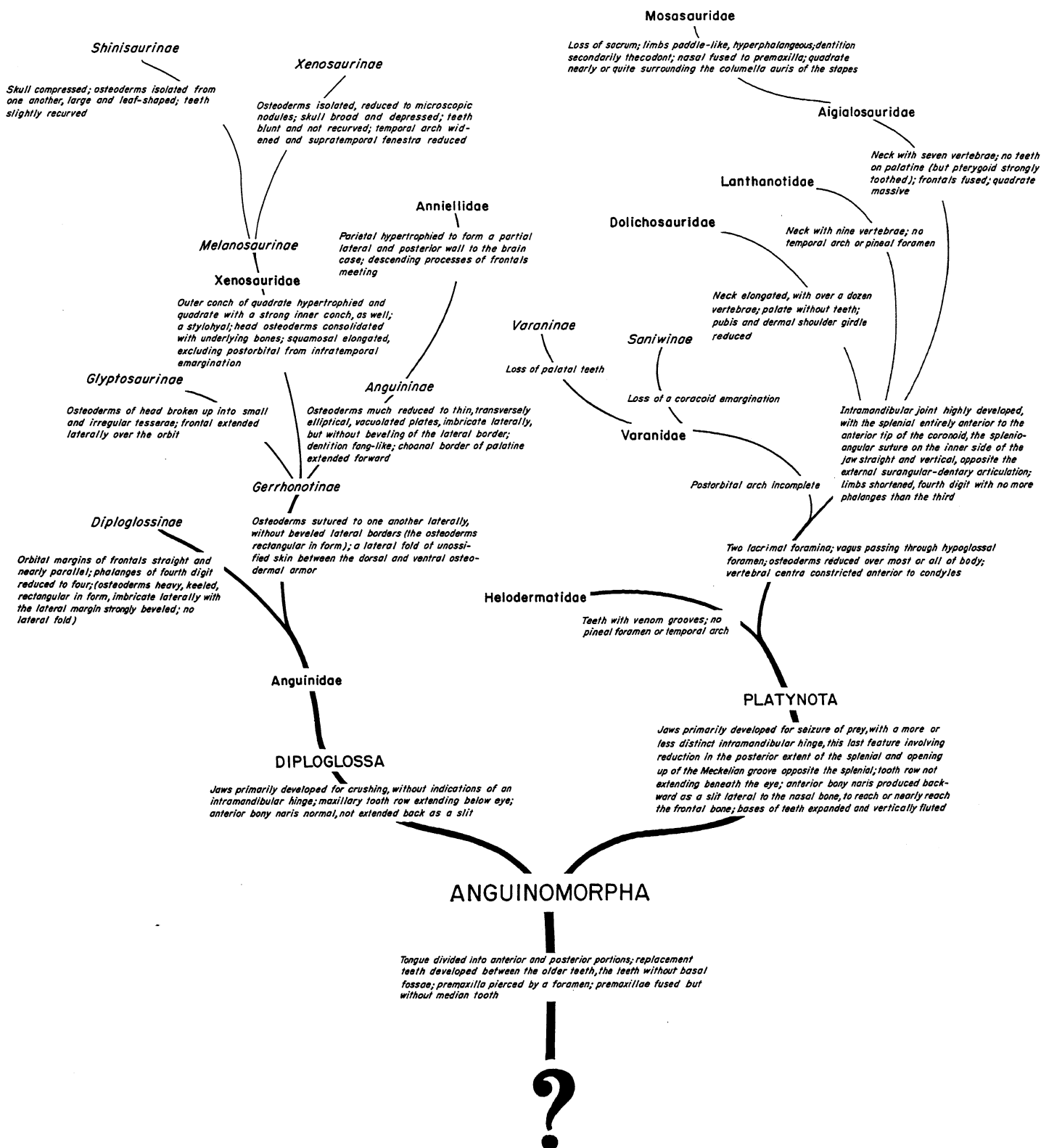


FIG. 43. Phylogeny of the families and subfamilies of Anguinomorpha, with brief statements of the major specializations of each phyletic line.

guinid-like *Diploglossa*, chiefly specialized in the development of a highly kinetic maxilla and the reduction of the limbs.

The remaining "Ophidia" appear to be a derivative of the advanced platynotan group

(aigialosaurid-dolichosaurid-lanthanotid series), distinguished principally by the great reduction of the pelvic girdle and the loss of the pectoral girdle.

## CLASSIFICATION OF THE ANGUINOMORPHA

We append a classification of the Anguinomorpha including the changes proposed in the preceding pages. Throughout the text we have used the terms for groups used by Camp (1923) and Romer (1945), such as "Diploglossa," "Platynota," for the reason that these terms are those most familiar to herpetologists and paleontologists. Since present practice is to use names based on a type genus, followed by an appropriate suffix, in forming the names of higher categories, we give below alternate names for the higher categories formed in the manner now current.

In forming the names for such categories as families and superfamilies, we have added the proper suffix to the stem rather than the root of the generic name (the form of the genitive case after dropping the genitive ending). Thus, the names Anguinidae, from the Latin *anguis* (genitive *anguin-is*), rather than Anguidae, and Helodermatidae, rather than Helodermidae, are used here.

The listing of the generic names is to indicate the scope of each group as we understand it and does not represent any serious attempt to revise the genera of Anguinomorpha, a Herculean task for which we are not prepared. The need for generic revision is particularly obvious in the case of the mosasaurs, where numerous generic names have been given to what is not always comparable material. It might be noted also that some of the morphological features considered of generic value in mosasaurs (for example, the shell-crushing dentition of *Globidens*) are considered as only subgeneric in value by Mertens in the parallel cases among the varanids. In the case of the lizards related to *Gerrhonotus* we accept Tihen's (1949) beliefs as to mutual relationships, but we feel that his contention that *Abronia* "is the best defined and most easily recognized of any of the gerrhonotine genera proposed by Gray" is most conveni-

ently expressed by regarding *Abronia* as a distinct genus from *Gerrhonotus*, and reducing the other genera recognized by him (*Elgaria* and *Barisia*) to subgenera of *Gerrhonotus*. A revision of the genera of Diploglossinae has not been attempted but is much needed.

### INFRAORDER ANGUINOMORPHA

**DEFINITION:** Tongue characteristic, with a bifid, inelastic fore portion, set off by a transverse fold from the elastic hind portion, the hind portion serving as a sheath to the fore tongue when the tongue is retracted; tooth replacement alternate and interdental (the replacement teeth developing between the older, functional teeth and replacing them by anterior rather than upward migration); teeth without basal fossae for replacement teeth; premaxillae fused, but without a median tooth; premaxilla pierced by a foramen; lacrimal present; maxilla firmly united to the surrounding bones; angular distinct, not fused to surrounding jaw elements; Meckelian groove open anterior to the splenial; septomaxilla roofing the organ of Jacobson.

#### SUPERFAMILY DIPLOGLOSSA

##### ALTERNATE NAME: ANGUINOIDEA

**DEFINITION:** Splenial extending far back, at least to the level of the coronoid process not forming a vertical suture with the angular at the level of the surangular-dentary suture; Meckelian groove closed (except anterior to the splenial) by a suture between the dorsal border of the splenial and the dental shelf of the dentary; external bony naris not prolonged backward as a slit lateral to the nasal bone but cleanly bored as a round or oval foramen; maxilla extending far back beneath orbit to behind the level of the middle of the eye; proximal bases of the teeth not expanded or fluted.

## FAMILY ANGUINIDAE

DEFINITION: Temporal arch present; post-orbital broadly entering the dorsal border of the infratemporal emargination; conchs of quadrate not excessively produced, the inner conch absent or but vaguely defined; no stylohyal ossicle; dorsal surface of skull smooth but covered by an incrustation of sculptured osteoderms; jugal not expanded; temporal arch without longitudinal dorsolateral keel; pro-otic forming but a short and very imperfect juncture with the parietal.

## SUBFAMILY DIPLOGLOSSINAE

DEFINITION: Head with large and regular osteoderms and associated epidermal scutes; orbital borders of frontals nearly straight and parallel; osteoderms heavy, imbricate laterally, as well as anteriorly and posteriorly, with beveled lateral borders, rectangular in form; no lateral fold; teeth blunt or conical; anterior (choanal) border of palatine posterior to vomer and to anterior extremity of interpterygoid vacuity; phalangeal formula reduced to 2-3-4-4-3.

GENERA: *Xestops*, Eocene (? to Oligocene) of North America; *Diploglossus*, continental Tropical America; *Celestus* (distinct from *Diploglossus*?), Central America and the West Indies; *Sauresia*, *Wetmorena*, Hispaniola; *Ophiodes*, South America.

## SUBFAMILY GERRHONOTINAE

DEFINITION: Head with large and regular osteoderms and associated epidermal scutes; orbital border of frontal strongly concave, but overlying osteoderm may have straight lateral border; osteoderms heavy to thin, or even absent over parts of body, but always of rectangular form, the lateral edge not beveled, sutured to one another laterally, but imbricate anteriorly and posteriorly; a lateral fold of unossified granules between the dorsal and ventral osteodermal armor; teeth varying from blunt to fang-like (both extremes being seen within the genus *Ophisaurus*, where *O. apodus* has molar-like teeth, but *O. harti* has *Anguis*-like teeth); anterior (choanal) border of palatine posterior to vomer and to anterior extremity of interpterygoid vacuity; phalangeal formula of forms with ambulatory limbs the normal 2-3-4-5-3.

GENERA: *Peltosaurus*, Paleocene (?) to

Oligocene of North America; *Placosauriops*, *Placosauroides*, Eocene of Europe; *Ophisaurus* (including *Pseudopus*, *Dopasia*, *Hyalosaurus*, *Propseudopus*, *Parapseudopus*, and *Ophisauriscus*), Eocene to Recent of Europe, Recent of North Africa, Asia, and North America; *Gerrhonotus* (including *Elgaria*, *Barisia*), western North America, Central America; *Abronia*, Mexico, Central America; ?*Coloptychon*, Panama.

## SUBFAMILY GLYPTOSAURINAE

DEFINITION: Head with numerous irregular polygonal osteoderms; frontal forming a fairly extensive orbital roof; osteoderms and lateral fold as in the *Gerrhontinae*.

GENERA: *Glyptosaurus* (including *Helodermoides*, Oligocene of North America, and probably *Placotherium*, *Placosaurus*, Eocene of Europe, in which case the name of the genus and subfamily should become, respectively, *Placosaurus* and *Placosaurinae*), Eocene of Europe, Mongolia, and North America; Oligocene of North America.

## SUBFAMILY ANGUININAE

DEFINITION: Head with large and regularly arranged osteoderms and scutes; frontal with concave lateral border; osteoderms transversely elliptical, imbricate, but without special articular surfaces, very thin and more or less vacuolate; teeth recurved, minutely grooved, and fang-like; anterior border of palatine in advance of the posterior extremity of the vomer and the anterior extremity of the interpterygoid vacuity; no lateral fold.

GENUS: *Anguis*, Miocene to Recent of Europe, Recent of North Africa and western Asia.

## FAMILY ANNIELLIDAE

DEFINITION: Temporal arch absent; post-orbital vestige bordering temporal fossa; conchs of quadrate narrow; dorsal cranial bones smooth, without osteodermal incrustation; pro-otic and parietal forming a long firm suture to close the brain case posteriorly; head with large and regular epidermal scutes; frontals meeting beneath olfactory tracts; palatine as in *Anguis*; teeth similar to those of *Anguis*; stapes with very short and stout columella auris, as in *Ophiodes*.

GENUS: *Anniella*, California and Baja California.

## FAMILY XENOSAURIDAE

DEFINITION: Temporal arch very strong, with a longitudinal dorsolateral keel; squamosal elongated, excluding the postorbital from the infratemporal emargination; conchs of quadrate hypertrophied, the outer conch broad and flaring, the inner conch strongly developed and well defined; a small ossicle (probably the stylohyal) near the lateral extremity of the paroccipital process; dorsal cranial bones, except posterior part of parietal, roughened by the complete fusion with the skull of the osteodermal incrustation; jugal expanded and sculptured; pro-otic hardly meeting parietal; frontal as in Anguinidae (the descending processes not meeting).

## SUBFAMILY MELANOSAURINAE

DEFINITION: Osteoderms sutured to one another laterally, as in the Gerrhonotinae; skull depressed; teeth blunt; supratemporal fenestra large, the squamosal separated from the parietal.

GENUS: *Melanosaurus*, Eocene of North America.

## SUBFAMILY SHINISAURINAE

DEFINITION: Osteoderms isolated from one another, large, longitudinally elliptical, with a median carina; skull compressed; teeth bluntly pointed, slightly recurved and moderately long; supratemporal fenestra large, the squamosal separated from the parietal.

GENERA: *Exostinus*, upper Cretaceous? to Oligocene of North America; *Necrosaurus* (including *Melanosauroides* and equivalent to *Palaeovaranus*), Eocene of Europe; *Shinisaurus*, southern China.

## SUBFAMILY XENOSAURINAE

DEFINITION: Osteoderms isolated, nodular in form, microscopic in size; skull depressed; teeth blunt; supratemporal fenestra reduced in size, the squamosal in contact with the parietal posteriorly.

GENUS: *Xenosaurus*, southern Mexico and adjacent Central America.

## SUPERFAMILY PLATYNOTA

## ALTERNATE NAME: VARANOIDEA

DEFINITION: Splenial with reduced posterior extent, not extending back to the level of

the apex of the coronoid process, forming a vertical suture with the angular at the level of the dentary-surangular suture; Meckelian groove open for a considerable distance between the dentary and the splenial; external bony naris extended back as a slit in the bony roof of the muzzle lateral to the nasal, this slit reaching or almost reaching the frontal; maxilla extending but a short distance beneath the eye or not at all, the maxillary tooth row entirely preorbital; proximal bases of the teeth expanded and sculptured with a fine vertical fluting.

## FAMILY HELODERMATIDAE

DEFINITION: Jugal extending forward to meet prefrontal; lacrimal foramen single; vagus passing through the jugular foramen; splenial sutured along ventral margin of coronoid; descending processes of frontals meeting to underarch the olfactory tracts, but not separating the orbits; teeth with venom channels; no temporal arch; no pineal foramen; pro-otic and parietal forming a very short and imperfect contact; vertebral centra not constricted anterior to condyles; vertebral central articulations oblique; phalangeal formula 2-3-4-5-3; sacrum of two vertebrae; pelvis complete; cervical vertebrae eight; no coracoid emarginations; interclavicle longitudinally rod-shaped; postorbital arch complete; osteoderms large, covering dorsal surface and outer surfaces of limbs.

GENUS: *Heloderma*, Oligocene of North America, Recent of Mexico and southwestern United States.

## FAMILY VARANIDAE

DEFINITION: Jugal not meeting prefrontal; lacrimal foramen double; vagus passing through hypoglossal foramen; splenial sutured along ventral border of coronoid; descending processes of frontal meeting to underarch olfactory tracts but not separating orbits; teeth without venom canals; temporal arch present; pineal foramen present; pro-otic and parietal forming a very short and imperfect contact; vertebral centra constricted anterior to condyles; vertebral central articulations oblique; phalangeal formula 2-3-4-5-3; sacrum of two vertebrae; pelvis complete; cervical vertebrae nine; at

least one coracoid emargination; interclavicle anchor-shaped; postorbital arch broken.

#### SUBFAMILY SANTIWINAE

DEFINITION: Palate toothed; a single coracoid emargination; postorbital not fused to post-frontal.

GENERA: *Telmasaurus*, upper Cretaceous of Mongolia; *Palaeosaniwa*, ?*Parasaniwa*, upper Cretaceous of North America; *Saniwa*, Paleocene to Oligocene of North America and Europe.

#### SUBFAMILY VARANINAE

DEFINITION: Palate without teeth; usually two coracoid emarginations; postorbital and post-frontal usually fused.

GENERA: *Varanus* (including *Megalia*, *Odatria*, *Polydaedalus*, *Indoivanus*, *Psammosaurus*, *Empagusia*, *Dendrovaranus*, and *Tecovaranus* as subgenera, *vide* Mertens, 1942), Eocene (?) to Pliocene of Europe, Pliocene to Recent of Asia, Pleistocene to Recent of Australia, Recent of Africa.

#### THE "AIGIALOSAURIAN" GROUP

The next four families appear to be more closely related to one another than to the preceding families and form the so-called "aigialosaurian" group. They share these features: jugal not reaching prefrontal; two lacrimal foramina; vagus probably passing through the hypoglossal foramen; osteoderms vestigial or absent; teeth without venom canals; limbs much shortened and phalangeal count reduced (secondarily increased in Mosasauridae), the fourth digit having no more phalanges than the third; intramandibular joint of lower jaw highly developed, the splenial and angular forming a hinge suture on the inner side corresponding in position to the outer surangular-dentary hinge suture; splenial barely touching the coronoid, lying entirely anterior to that bone; splenial vertically truncated posteriorly.

#### FAMILY AIGIALOSAURIDAE

DEFINITION: Temporal arch present; frontals fused; descending processes of frontals meeting to underarch olfactory tracts but not separating orbits; pineal foramen present; vertebral central articulations oblique; no hyperphalangy; sacrum of two vertebrae; pelvis complete; cervical vertebrae seven; in-

terclavicle anchor-shaped; palatine toothless, pterygoid strongly toothed; quadrate massive; muzzle elongated and pointed.

GENERA: *Aigialosaurus*, *Carsosaurus*, *Opetiosaurus*, lower Cretaceous of Europe. ?*Mesoleptos* and ?*Eidolosaurus* (very poorly known, may be lanthanotids), lower Cretaceous of Europe.

#### FAMILY MOSASAURIDAE

DEFINITION: Temporal arch present; frontals fused; descending processes of frontals meeting to underarch olfactory tracts but not separating orbits; pineal foramen present; vertebral central articulations not oblique; hyperphalangy present; no sacrum; interclavicle absent or reduced; pelvis much reduced; cervical vertebrae seven; palatine toothless, pterygoid strongly toothed; quadrate massive, surrounding the columella auris of the stapes; muzzle long and pointed, the nasal fused to the premaxilla; teeth secondarily thecodont, lodged in an uncompartimented groove.

GENERA: All upper Cretaceous. *Amphikepubis*, *Ancylocentrum*, *Baptosaurus*, *Cliadistes*, *Diplotomodon*, *Elliptonodon*, *Holcodus*, *Holosaurus*, *Plotosaurus*, *Macrosaurus*, *Nectoporphus*, *Plesiotylosaurus*, *Polygonodon*, *Sironectes*, North America; *Globidens*, North America, Europe, North Africa, and Indonesia; *Platecarpus*, North America, Europe, North Africa; *Tylosaurus*, North America and Africa; *Mosasaurus*, North America, Africa, Europe; *Leptosaurus*, North Africa; *Comiasaurus*, *Dollosaurus*, *Hainosaurus*, *Phioplatecarpus*, *Pregnathosaurus*, Europe; *Taniwhasaurus*, New Zealand.

#### FAMILY DOLICHOSAURIDAE

DEFINITION: Temporal arch?; frontals separate; palate without teeth; pineal foramen present; vertebral central articulations oblique; no hyperphalangy; sacrum of two vertebrae; pelvis with pubis reduced; interclavicle reduced; cervical vertebrae 13 or more; quadrate not massive; muzzle short and blunt.

GENERA: *Acteosaurus*, *Adriosaurus*, *Pontosaurus*, ?*Pachyophis*, ?*Symoliophis* (these last two genera may be ophidian), lower Cretaceous of Europe; *Dolichosaurus*, upper Cretaceous of Europe.

## FAMILY LANTHANOTIDAE

DEFINITION: No temporal arch; frontals separate, their descending processes not quite meeting to underarch the olfactory tracts but completely separating the orbits; no pineal foramen; brain case closed posteriorly by the formation of a long and firm sutural contact between the parietal and the pro-otic; no hyperphalangy; sacrum of two vertebrae; pelvis complete; interclavicle apparently reduced to a longitudinal rod; cervical vertebrae nine; both palatine and pterygoid with a few teeth; quadrate not massive; muzzle short and blunt.

GENUS: *Lanthanotus*, Sarawak, Borneo.

COMPARISON WITH THE CLASSIFICATION  
OF ROMER (1945)

Forms and groups removed from the Anguimorpha:

Pygopodidae, to Gekkota  
Cordylidae, to Lacertoidea  
Euposauridae, *incertae sedis*  
*Isodontosaurus*, ? to Iguania  
*Polyodontosaurus*, ? to Ornithischia  
*Progonosaurus*, to Testudinata, *fide* Fejérváry, 1935  
*Provaranosaurus*, *incertae sedis*

Forms added to the Anguimorpha:

Platynota, reduced from coordinate rank  
*Exostinus*, removed from Iguanidae

Families here suppressed:

Shinisauridae, placed as subfamily of Xenosauridae

Families here recognized, but not recognized by Romer:

Lanthanotidae, removed from Helodermatidae

Forms transferred within the Anguimorpha:

*Melanosaurus*, to Xenosauridae from Anguinidae  
"*Palaeovaranus*" (properly, *Necrosaurus*), to Xenosauridae from Varanidae

*Lanthanotus*, to Lanthanotidae from Helodermatidae

Helodermatidae, to Platynota or Varanoidea from Diploglossa or Anguinoidea

Changes in preferred name and alternate names here proposed:

Anguimorpha, for Anguimorpha

Anguinoidea, for Diploglossa of Camp (1923), as here emended; Anguimorpha of Romer, as here emended

Anguinidae, for Anguidae

Varanoidea, for Platynota

*Necrosaurus*, for *Palaeovaranus*, following Hoffstetter, 1943

## SUMMARY

THE EXTERNAL FEATURES of the Bornean lizard, *Lanthanotus borneensis* Steindachner, are described, together with the skull, the hyoid, the tongue, and the roentgenogram of the postcranial osteology. The various theories concerning the relationships of *Lanthanotus* are evaluated.

The belief that *Lanthanotus* is related to the Chinese lizard *Shinisaurus crocodilurus* Ahl is shown to be unsupported by either the internal or external morphology. Nor is there evidence of close relationship between *Lanthanotus* and *Heloderma*, although these two genera are most frequently placed together in the family Helodermatidae.

On the other hand, structural resemblances between *Lanthanotus* and *Varanus* are found to be both numerous and important. However, it is here shown that there is still greater affinity between *Lanthanotus* and three Cretaceous families believed to be closely related to *Varanus*, the Aigialosauridae, Mosasauridae, and Dolichosauridae. *Lanthanotus* represents a monotypic family closely related to aigialosaurs and dolichosaurs.

*Lanthanotus* shows many of the features to be expected in an ancestor of the snakes, and the close similarities between *Lanthanotus* and the boid-like, colubrid-like, and particularly the leptotyphlopoid snakes, materially strengthen the argument that the snakes are derived from platynotan (*Varanus*-like) lizards.

In contrast to other limbless reptiles commonly referred to the Serpentes, the Typhlopidae show no particular resemblance in cranial structure to either the platynotan lizards or the snakes (including *Leptotyphlops*). Reasons are advanced for believing that the Typhlopidae are wrongly placed in the Serpentes (or Ophidia) and represent a line of anguinid-like lizards that has become convergent to the Serpentes.

Incidental to the work upon which we base the conclusions summarized above, several additional observations have been made on the anatomy and relationships of the saurian infraorder Anguinomorpha. The most important conclusions reached are as follows:

1. The family Pygopodidae is not related

to the Anguinomorpha but represents an aberrant line of geckos, modified by a reduction of the limbs but retaining many features of the gekkonids.

2. The family Cordylidae (long known as Zonuridae) is not related to the Anguinomorpha but instead is closely related to the Gerrhosauridae, a family that differs in relatively minor ways from the Lacertidae.

3. The fossil family Euposauridae, frequently placed in or near the Anguinomorpha, shows no clear evidence of affinity to the Anguinomorpha and is not even definitely referable to the Squamata.

4. After the removal of these three families, the Anguinomorpha become a natural group, the members of which are characterized by their peculiar tongue structure, their method of tooth replacement, and a unique combination of osteological characters. The group, here considered an infraorder, contains the families Anguinidae (*Anguinae auct.*), Xenosauridae, Anniellidae, Helodermatidae, Varanidae, Aigialosauridae, Mosasauridae, Dolichosauridae, and Lanthanotidae.

5. This group, the Anguinomorpha, appears to have undergone an early separation into two main lines of evolution, here considered taxonomically as two superfamilies: Diploglossa (or Anguinoidea) and Platynota (or Varanoidea).

6. The line here called Diploglossa (Anguinidae, Xenosauridae, and Anniellidae) includes the more primitive families, primarily adapted to a crushing action of the jaws, with rigid mandibles. None of the known forms can be considered directly ancestral to the platynotan line.

7. The remainder of the Anguinomorpha represent a line (Platynota or Varanoidea) the jaws of which are primarily adapted for a grasping action, with a progressive development through the families of a hinge in the middle of the ramus of the lower jaw. This line includes forms distinctly more predatory in habits than is usual in the members of the first line.

8. The beaded lizards (*Heloderma*) have most recently been classified among the members of the first (diploglossan) line. But

careful study of the morphology of *Heloderma* shows it to be close to *Varanus*, and a member of the second (platynotan) series, as was believed by most of the earlier workers. Although specialized in many respects, in other features of its structure *Heloderma* appears to be near the ancestral form that gave rise to the Platynta.

9. Upon examination of the skull, the Chi-

nese genus *Shinisaurus* of previously unknown affinities proves to be a close relative of the Mexican genus *Xenosaurus*. The fossil genera *Exostinus*, *Melanosaurus*, and *Necrosaurus* (also known as *Palaeovaranus*) also appear to be members of the Xenosauridae.

A revised classification of the Anguino-morpha is presented.

### CRANIAL MATERIAL EXAMINED

#### Anguino-morpha

##### Anguinidae

- Diploglossus millepunctatus* (1)
- Celestus costatus* (2)
- Celestus cresculus* (1)
- Celestus* species (1, cleared)
- Wetmorena haetiana* (1, cleared)
- Sauresia sepsoides* (1, cleared)
- Ophiodes striatus* (1)
- Gerrhonotus tcoeruleus* (1)
- Gerrhonotus imbricatus* (1)
- Gerrhonotus kingi* (1)
- Gerrhonotus liocephalus* (observations made during dissection of the head of 1 specimen)
- Ophisaurus apodus* (2)
- Ophisaurus ventralis* (3)
- Ophisaurus harti* (1)
- Anguis fragilis* (1 dry and 1 cleared)

##### Anniellidae

- Anniella pulchra* (1, plus an additional lower mandible)

##### Xenosauridae

- Shinisaurus crocodilurus* (1)
- Xenosaurus grandis* (1, plus another examined during dissection by Georg Haas)

##### Helodermatidae

- Heloderma horridum* (5)
- Heloderma suspectum* (9, plus 1 cleared, and observations made during dissection of the head of 1 other specimen)

##### Varanidae

- Varanus komodoensis* (9)
- Varanus salvator* (4)
- Varanus varius* (2)
- Varanus niloticus* (20)
- Varanus salvadorii* (1)
- Varanus exanthematicus* (7)
- Varanus bengalensis* (2, plus an additional lower mandible and observations made during dissection of the head)

##### Lanthanotidae

- Lanthanotus borneensis* (1)

#### Gekkota

##### Pygopodidae

- Pygopus* (*Pygopus*) *lepidotus* (2)

- Pygopus* (*Cryptodelma*) *nigriceps* (1)

- Delma fraseri* (2)

- Lialis bertonis* (2)

##### Ophiosepidae

- Aprasia repens* (1)

##### Xantusiidae

- Xantusia vigilis* (1)
- Xantusia henshavi* (1)
- Xantusia riversiana* (1)
- Lepidophyma flavimaculata* (1)

##### Gekkonidae

- Aristelliger lar* (1)
- Aristelliger praesignis* (1)
- Coleonyx variegatus* (3)
- Gehyra oceanica* (1)
- Gonatodes fuscus* (1)
- Hemidactylus* species (2)
- Hoplodactylus pacificus* (1)
- Phyllodactylus tuberculosus* (1)
- Sphaerodactylus torrei* (1)
- Tarentola mauretania* (1)
- Tarentola americana* (1)
- Thecadactylus rapicaudus* (1)
- Uroplatus fimbriatus* (1)

##### Scincomorpha

##### Lacertidae

- Lacerta ocellata* (2)
- Lacerta viridis* (2)
- Ophisops elegans* (1)

##### Dibamidae

- Dibamus novaeguineae* (1)

##### Cordylidae

- Cordylus giganteus* (3)
- Platysaurus capensis* (1, cleared)
- Gerrhosaurus flavolineatus* (2)

##### Scincidae

- Eumeces copei* (1)
- Eumeces schneideri* (1)
- Eumeces obsoletus* (3)
- Tiliqua scincoides* (2)
- Tribolonotus novaeguineae* (1)

##### Teiidae

- Alopoglossus festae* (1)
- Proctoporus ocellifer* (1)
- Neusticurus eupleopus* (1)

- Cercosaura ocellata* (1)  
*Ophiognomon trisanale* (1)  
*Prionodactylus vertebralis* (1)  
*Euspondylus spinalis* (1)  
*Euspondylus* species (1)  
*Arthrosaura tyleri* (1)  
*Anadia bogotensis* (1)  
*Gymnophthalmus laevicaudatus* (1)  
*Bachia* species (1)  
*Ameiva bifrontata* (1)  
*Ameiva thoracica* (1)  
*Ameiva ameiva* (1)  
*Teius teyou* (1)  
*Crocodilurus lacertinus* (1)  
*Cnemidophorus* species (1)  
*Dicrodon lentiginosus* (1)  
*Dracaena* species (3)  
*Kentropyx striatus* (1)  
*Kentropyx calcaratus* (1)  
*Tupinambus nigropunctatus* (2)  
*Tupinambus teguixin* (5)  
*Tupinambus* species (2)
- Amphisbaenia
- Amphisbaenidae
- Amphisbaena alba* (1)  
*Rhineura floridana* (observations made during the dissection of the head of 1 specimen)
- Iguania
- Agamidae
- Physignathus lesueuri* (1)  
*Amphibolurus barbatus* (1)  
*Uromastix hardwicki* (1)  
*Uromastix* species (1)  
*Calotes versicolor* (1, plus an additional lower mandible)  
*Liolepis belliana* (1)
- Chamaeleonidae
- Chamaeleo chamaeleo* (3)  
*Chamaeleo dilepis* (1)  
*Chamaeleo gracilis* (1)  
*Chamaeleo verrucosus* (13)
- Iguanidae
- Amblyrhynchus cristatus* (2)  
*Brachylophus fasciatus* (1)  
*Conolophus subcristatus* (7)  
*Cyclura cornuta* (3)  
*Cyclura stejnegeri* (1)  
*Cyclura* species (7)  
*Ctenosaura similis* (3)  
*Ctenosaura* species (6)  
*Sauromalus varius* (1)  
*Iguana iguana* (12)  
*Dipsosaurus dorsalis* (3)  
*Crotaphytus collaris* (3)  
*Crotaphytus wislizeni* (1)  
*Hoplurus quadrimaculatus* (1)  
*Hoplurus cyclurus* (1)
- Chalarodon madagascariensis* (1)  
*Leiocephalus carinatus* (2)  
*Holbrookia texana* (2)  
*Uma inornata* (1)  
*Sceloporus magister* (1)  
*Sceloporus occidentalis* (6)  
*Sceloporus orcutti* (3)  
*Sceloporus poinsetti* (1)  
*Sceloporus undulatus* (2)  
*Uta ornata* (2)  
*Polychrus marmoratus* (2)  
*Chamaeleolis chamaeleontides* (1)  
*Deiroptyx vermiculatus* (1)  
*Anolis lineatopus* (1)  
*Anolis sagrei* (2)  
*Anolis carolinensis* (5)  
*Anolis dominicensis* (1)  
*Anolis equestris* (2)  
*Basiliscus basiliscus* (1)  
*Basiliscus vittatus* (2)  
*Phrynosoma m'calli* (1)  
*Phrynosoma blainvilli* (1)  
*Phrynosoma asio* (1)  
*Phrynosoma cornutum* (2)  
*Phrynosoma douglassi* (2)  
*Phrynosoma modestum* (2)  
*Phrynosoma platyrhinos* (2)  
*Phrynosoma solare* (3)  
*Phrynosoma orbiculare* (1)
- Typhlopoidea
- Typhlopidae
- Typhlophis squamosus* (1, cleared)  
*Helminthophis flavoterminalis* (1)  
*Typhlops punctata* (1)  
*Typhlops reticulata* (1)  
*Typhlops lumbricalis* (1)
- Serpentes
- Leptotyphlopidae
- Leptotyphlops dimidiata* (1)  
*Leptotyphlops humilis* (1)  
*Leptotyphlops nigricans* (1)
- Boidae
- Python reticulatus* (5)  
*Python amethistinus* (2)  
*Python molurus* (7, plus observations on the dissection of the heads of 2 others)  
*Python sebae* (5)  
*Python anchietae* (1)  
*Python regius* (1)  
*Python curtus* (4)  
*Liasis childreni* (1)  
*Liasis mackloti* (1)  
*Liasis olivaceus* (1)  
*Liasis fuscus* (2)  
*Liasis albertisi* (1)  
*Bothrochilus boa* (1)  
*Morelia argus* (3)

- Chondropython viridis* (3)  
*Calabaria reinhardti* (2)  
*Aspidites melanocephalus* (1)  
*Boa constrictor* (8)  
*Eunectes* species (5)  
*Epicrates cenchris* (3)  
*Epicrates striatus* (2)  
*Epicrates inornatus* (1)  
*Corallus enhydris* (2)  
*Corallus caninus* (5)  
*Candoia carinata* (1)  
*Lichanura roseofusca* (1)  
*Charina bottae* (1)  
*Ungaliophis continentalis* (1, plus 1 cleared)  
*Loxocemus bicolor* (1, plus observations on the  
dissection of the head of another)  
*Trachyboa gularis* (1)  
*Tropidophis melanurus* (2)  
*Tropidophis maculatus* (1)  
*Tropidophis pardalis* (1)  
*Acrantophis madagascariensis* (1)  
*Sanzinia madagascariensis* (1)  
Xenopeltidae  
*Xenopeltis unicolor* (2)  
Ilysiidae  
*Ilysia scytale* (3)  
*Cylindrophis lineatus* (1)  
Colubridae  
*Pareas moellendorffi* (1)  
*Sibynophis collaris* (1)  
*Achalinus spinalis* (1)  
*Aspidura trachyprocta* (1)  
*Acrochordus javanicus* (2)  
*Nothopsis rugosus* (1, cleared)  
*Xenopholis scalaris* (1, cleared)  
*Mehelya capensis* (1)  
*Lycophidion capense* (1)  
*Polemon barthi* (1)  
*Miodon gabonensis* (1)  
*Helicops angulatus* (1)  
*Helicops leopardinus* (1)  
*Limnophis bicolor* (1)  
*Hydraethiops melanogaster* (1)  
*Grayia smythi* (1)  
*Grayia ornata* (1)  
*Pseudaspis cana* (2)  
*Boaodon lineatus* (1)  
*Lycodon aulicus* (1)  
*Liopholidophis lateralis* (1)  
*Dryocalamus davidsoni* (1)  
*Oligodon quadrilineatus* (1)  
*Leiosophis gigas* (4)  
*Leiosophis bicincta* (1)  
*Uromacer* species (1)  
*Carphophis amoena* (3, cleared)  
*Diadophis punctatus* (4)  
*Xenodon severus* (1)  
*Xenodon merremi* (1)  
*Heterodon platyrhinos* (3)  
*Rhadinaea cobella* (1)  
*Phyllorhynchus decurtatus* (2)  
*Cerberus rhynchops* (1)  
*Elaphe porphyracea* (1)  
*Elaphe mandarinus* (1)  
*Elaphe taeniurus* (1)  
*Elaphe carinata* (1)  
*Elaphe situla* (1)  
*Elaphe schrencki* (1)  
*Elaphe dione* (2)  
*Elaphe climacophora* (2)  
*Elaphe obsoleta* (7)  
*Elaphe vulpina* (1)  
*Elaphe guttata* (2)  
*Dasyptelis scaber* (5)  
*Arizona elegans* (2)  
*Dryomarchon corais* (2)  
*Spilotes pullatus* (2)  
*Chironius carinatus* (1)  
*Chironius fuscus* (1)  
*Leimadophis melanotus* (1)  
*Drymobius boddaerti* (1)  
*Drymobius margaritiferus* (1)  
*Salvadora hexalepis* (2)  
*Salvadora mexicana* (1)  
*Salvadora bairdi* (1)  
*Salvadora intermedia* (1)  
*Coluber constrictor* (3)  
*Masticophis flagellum* (2)  
*Pseustes poecilonotus* (1)  
*Leptophis mexicanus* (2)  
*Leptophis occidentalis* (1)  
*Philothamnus carinatus* (1)  
*Dendrophis boiga* (1)  
*Zamenis viridiflavus* (1)  
*Boiga dendrophila* (2)  
*Oxybelis fulgidus* (1)  
*Oxybelis aeneus* (5)  
*Pituophis melanoleucus* (2)  
*Rhinocheilus lecontei* (1)  
*Cloelia cloelia* (1)  
*Scaphiophis albopunctatus* (1)  
*Lampropeltis getulus* (3)  
*Lampropeltis dolia* (1)  
*Lampropeltis micropholis* (1)  
*Lygophis lineatus* (1)  
*Thamnophis sirtalis* (4)  
*Natrix sipedon* (2)  
Elapidae  
*Ophiophagus hannah* (1)  
*Pseudohaje goldii* (2)  
*Pseudohaje nigra* (1)  
*Boulengerina annulata* (1)  
*Hemachatus haemachatus* (2)  
*Naja naja* (9)  
*Naja nigricollis* (1)  
*Naja haje* (1)

*Naja nivea* (2)  
*Naja melanoleuca* (5)  
*Dendroaspis viridis* (3)  
*Acanthophis antarcticus* (1)  
 Hydrophididae  
*Pelamydrus platurus* (1)  
 Viperidae  
*Causus rhombeatus* (1)  
*Bitis arietans* (1)  
*Bitis gabonica* (2)  
*Bitis nasicornis* (1)  
*Atheris squamigera* (partial dissection of 1 specimen)  
*Agkistrodon contortrix* (5)  
*Agkistrodon bilineatus* (2)  
*Agkistrodon piscivorus* (8)  
*Agkistrodon acutus* (1)  
*Agkistrodon halys* (1)  
*Trimeresurus wagleri* (1)  
*Trimeresurus stejnegeri* (1)

*Trimeresurus alternatus* (1)  
*Trimeresurus atrox* (2)  
*Trimeresurus dunni* (1)  
*Trimeresurus schlegeli* (1)  
*Trimeresurus nummifer* (1)  
*Lachesis muta* (3)  
*Sistrurus catenatus* (1)  
*Sistrurus miliaris* (1)  
*Crotalus durissus* (2)  
*Crotalus atrox* (4)  
*Crotalus adamanteus* (4)  
*Crotalus horridus* (2)  
*Crotalus cerastes* (1)

In addition we have seen cranial material of the following fossil genera: *Peltosaurus*, *Glyptosaurus*, *Melanosaurus*, *Heloderma* (*matthewi*), *Mosasaurus*, *Clidastes*, *Tylosaurus*, and *Platecarpus*.

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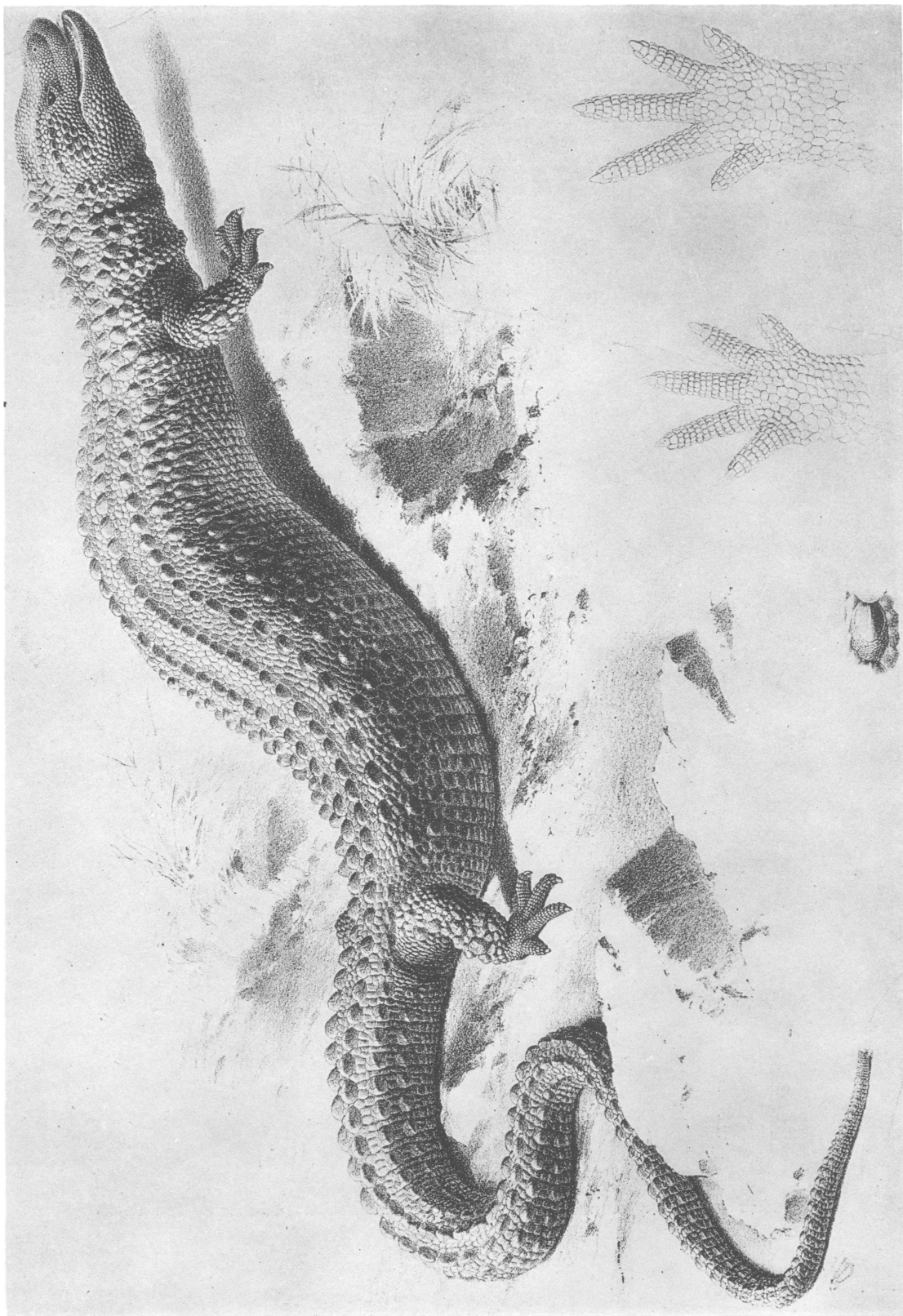
#### ABBREVIATIONS USED IN TEXT FIGURES

Unless otherwise noted in the legends, the abbreviations used in each text figure are as follows:

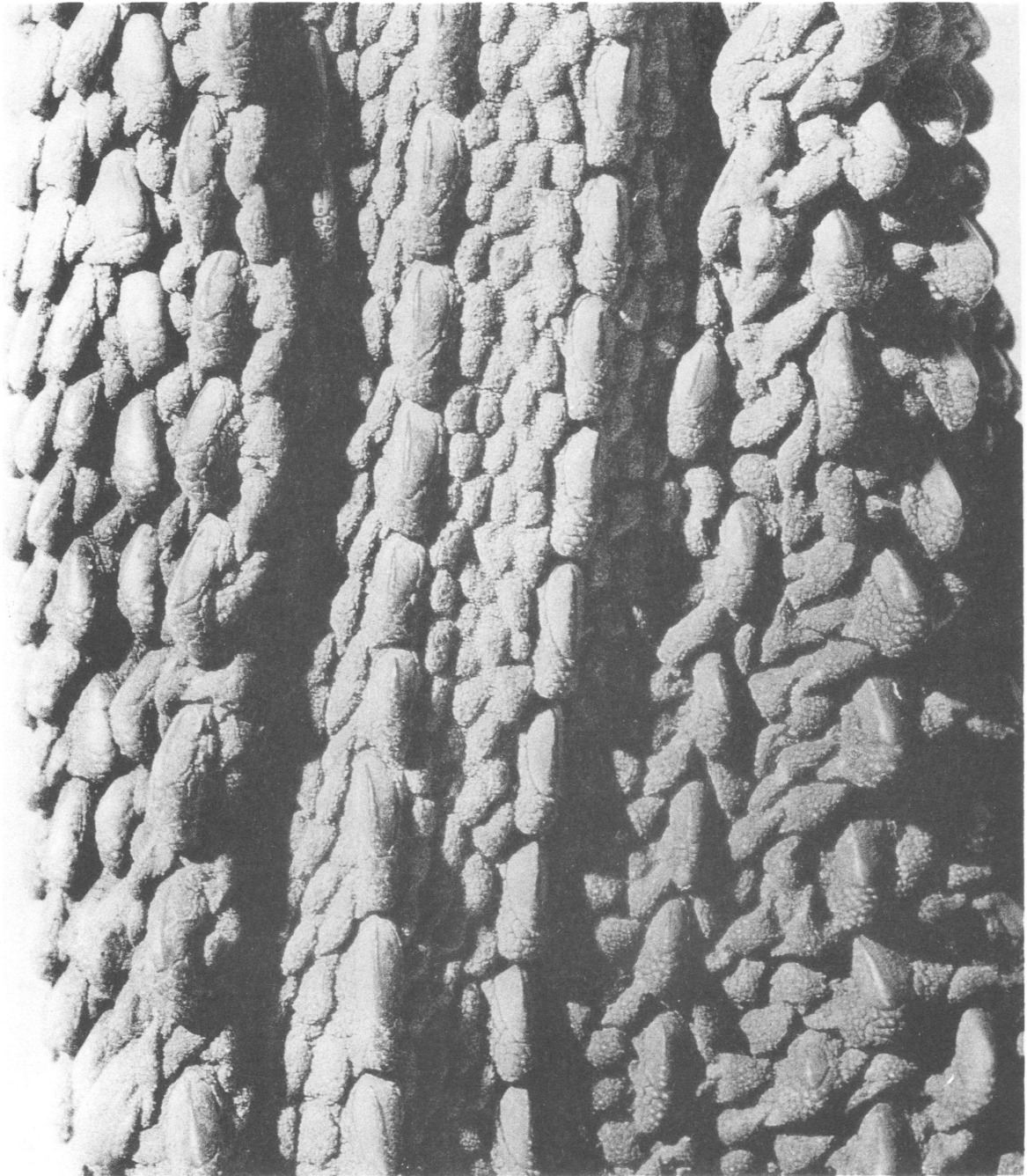
- |  |  |
|--|--|
| ang, angular bone                        | exo, exoccipital bone                            |
| art, articular bone                      | fro, frontal bone                                |
| boc, basioccipital bone                  | jug, jugal bone                                  |
| bsp, basisphenoid bone                   | lac, lacrimal bone                               |
| cor, coronoid bone                       | max, maxilla                                     |
| den, dentary bone                        | nas, nasal bone                                  |
| e, eye                                   | oo, osteodermal ornamentation of skull           |
| ecp, ectopterygoid bone                  | oto, oto-occipital complex                       |
| ecppal, fused ectopterygoid and palatine | pa, prearticular bone                            |
| epp, epipterygoid bone                   | pal, palatine bone                               |
|  | pap, palpebral bone                              |
|  | par, parietal bone                               |
|  | pof, postfrontal bone                            |
|  | pof+poo, fused postfrontal and postorbital bones |

poo, postorbital bone  
pop, postoptic or laterosphenoid bone  
prf, prefrontal bone  
prm, premaxilla  
pro, pro-otic bone  
ptd, pterygoid bone  
qut, quadrate bone  
sep, septomaxilla

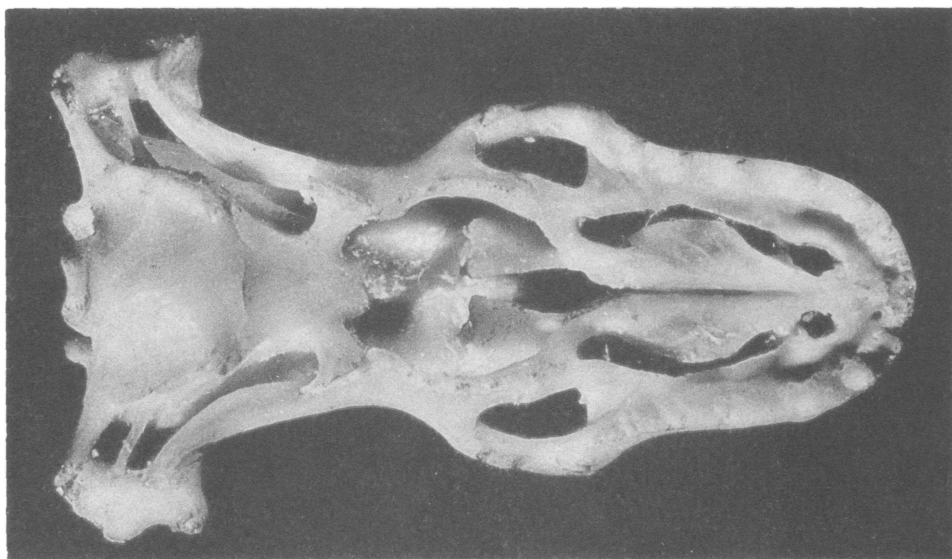
spl, splenial bone  
squ, squamosal bone of squamates  
sta, stapes  
sty, probable stylohyal bone  
suo, supraoccipital bone  
sur, surangular bone  
tab, tabular bone  
vom, vomer



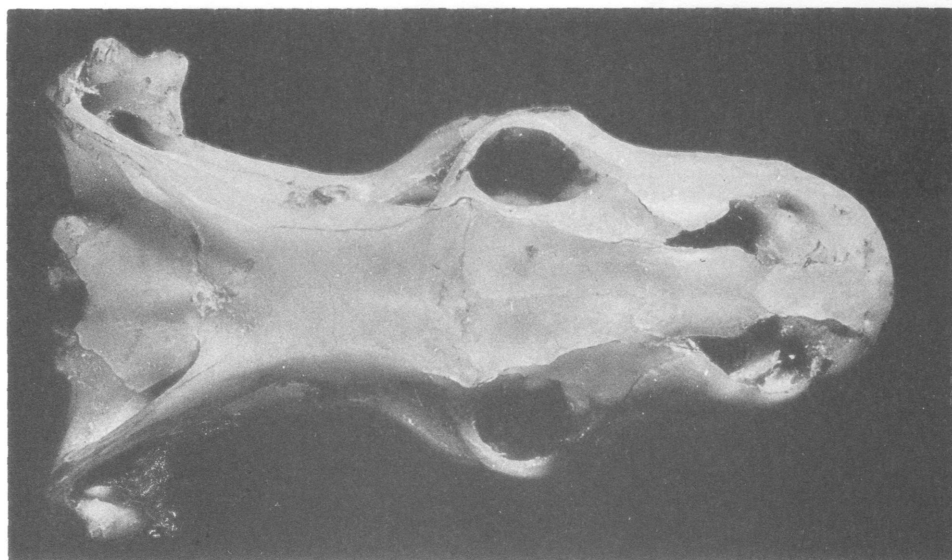
*Lanthanotus borneensis*. From Steindachner



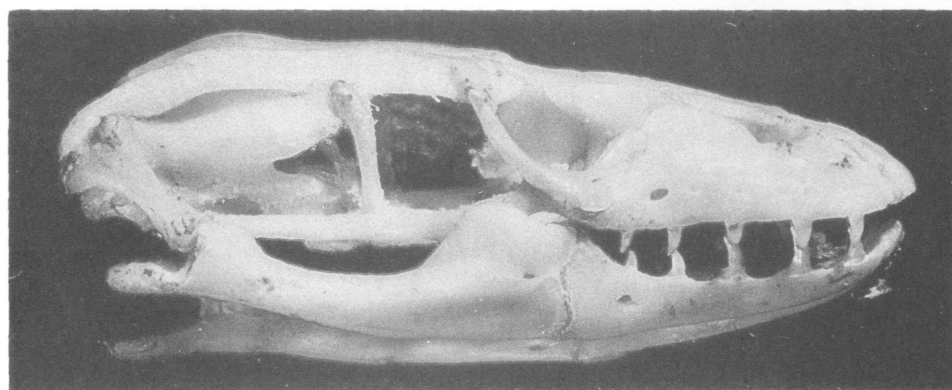
*Lanthanotus borneensis*. A much enlarged view of the dorsal scales, anterior end at top



1

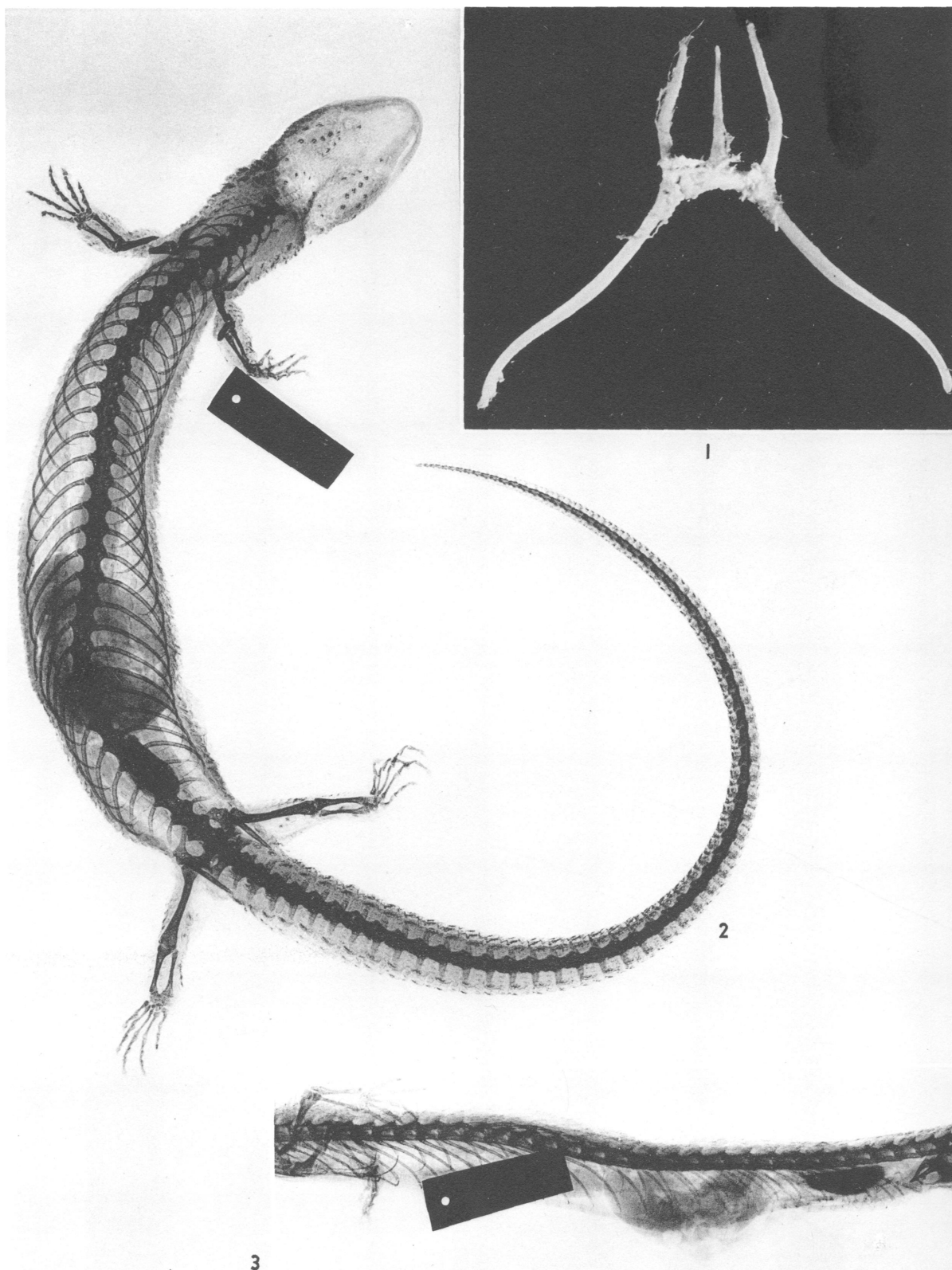


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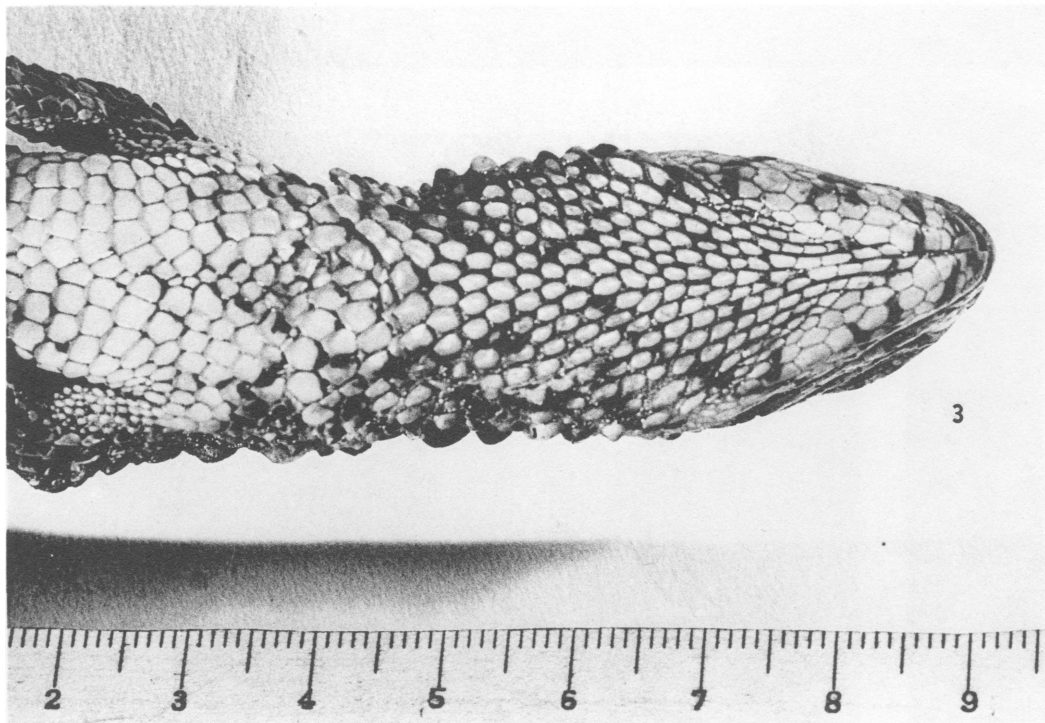
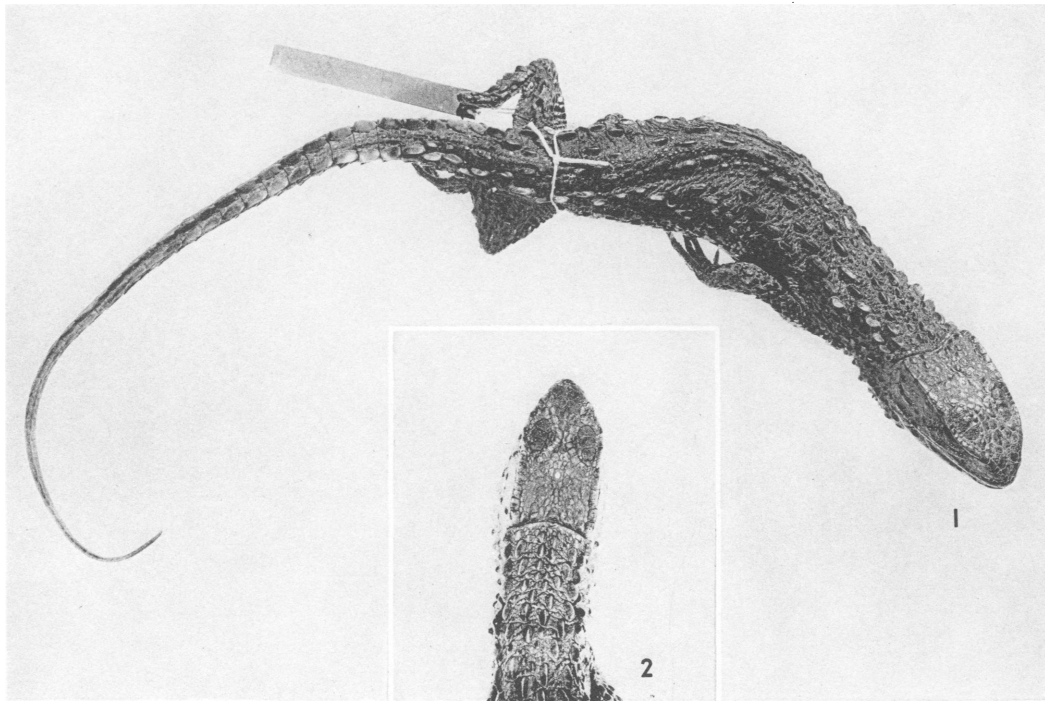


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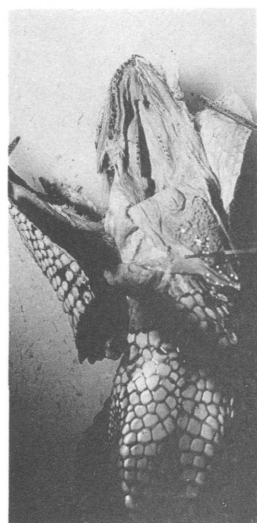
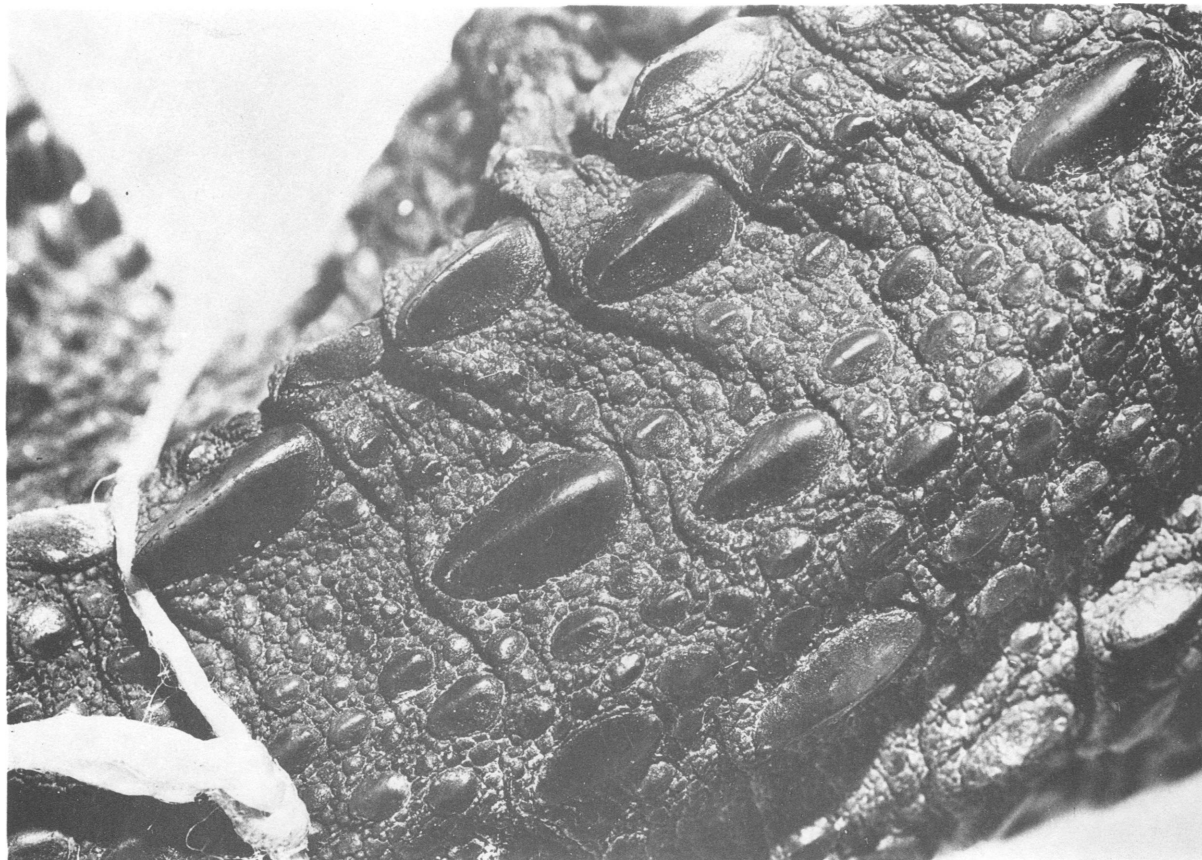
Skull of *Lanthanotus borneensis*. 1. Ventral view. 2. Dorsal view. 3. Lateral view



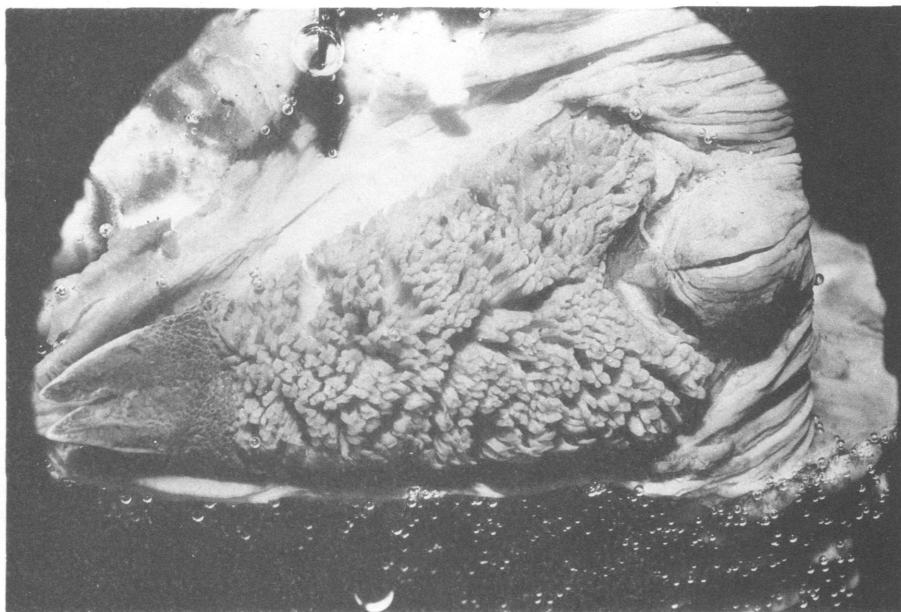
*Lanthanotus borneensis*. 1. Dorsal view of hyoid arch. 2. Roentgenogram of entire animal after removal of skull, hyoid, and first two vertebrae, dorsal exposure. 3. Roentgenogram of trunk, anterior end at left, lateral exposure



*Shinisaurus crocodilurus*. 1. Entire animal, dorsolateral view. 2. Head and neck, dorsal view.  
3. View of throat



2

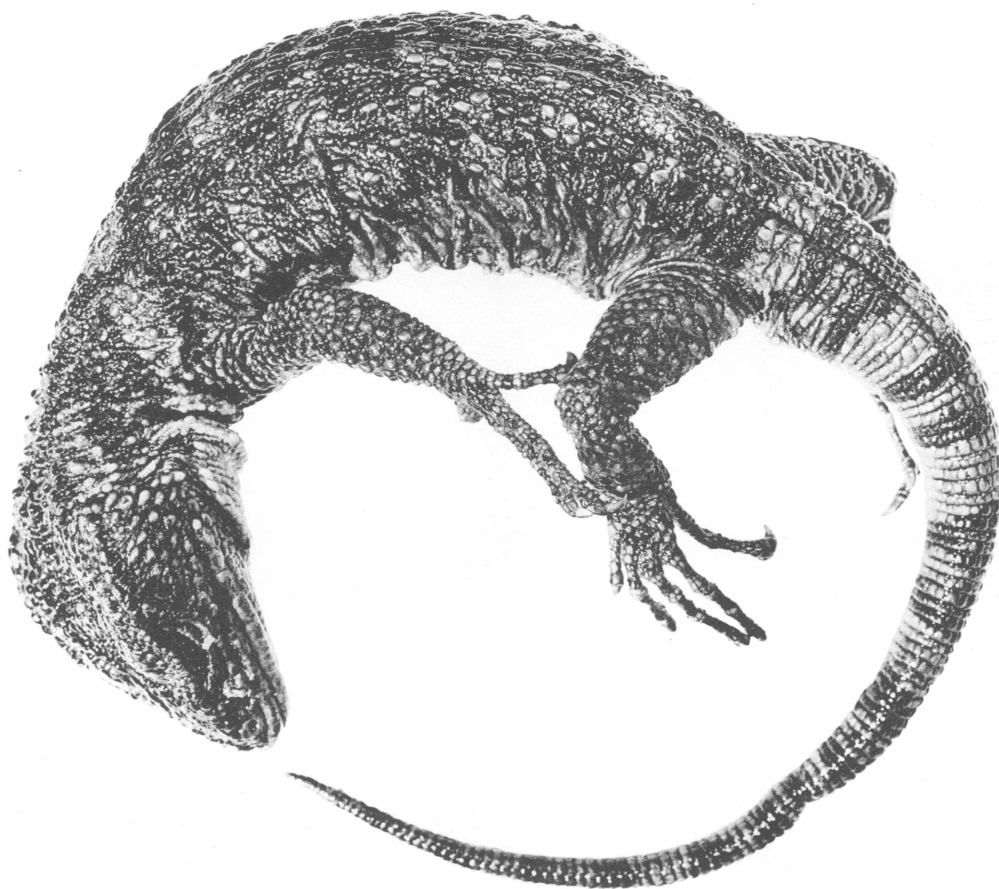


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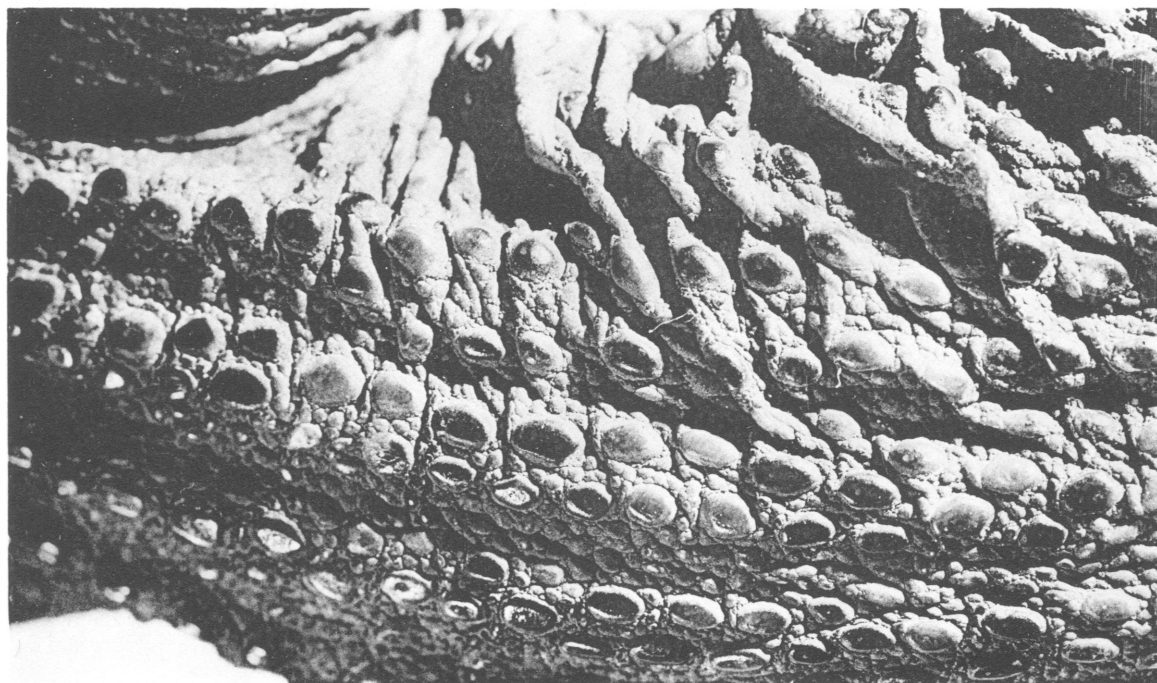
*Shinisaurus crocodilurus*. 1. Much enlarged view of scales of flank, anterior end at right. 2. Dissection to show the soft tissue of palate, particularly the "paleochoanate" form of the entrance to the organ of Jacobson and the internal nares. 3. Dorsal surface of tongue



Roentgenogram of *Shinisaurus crocodilurus*

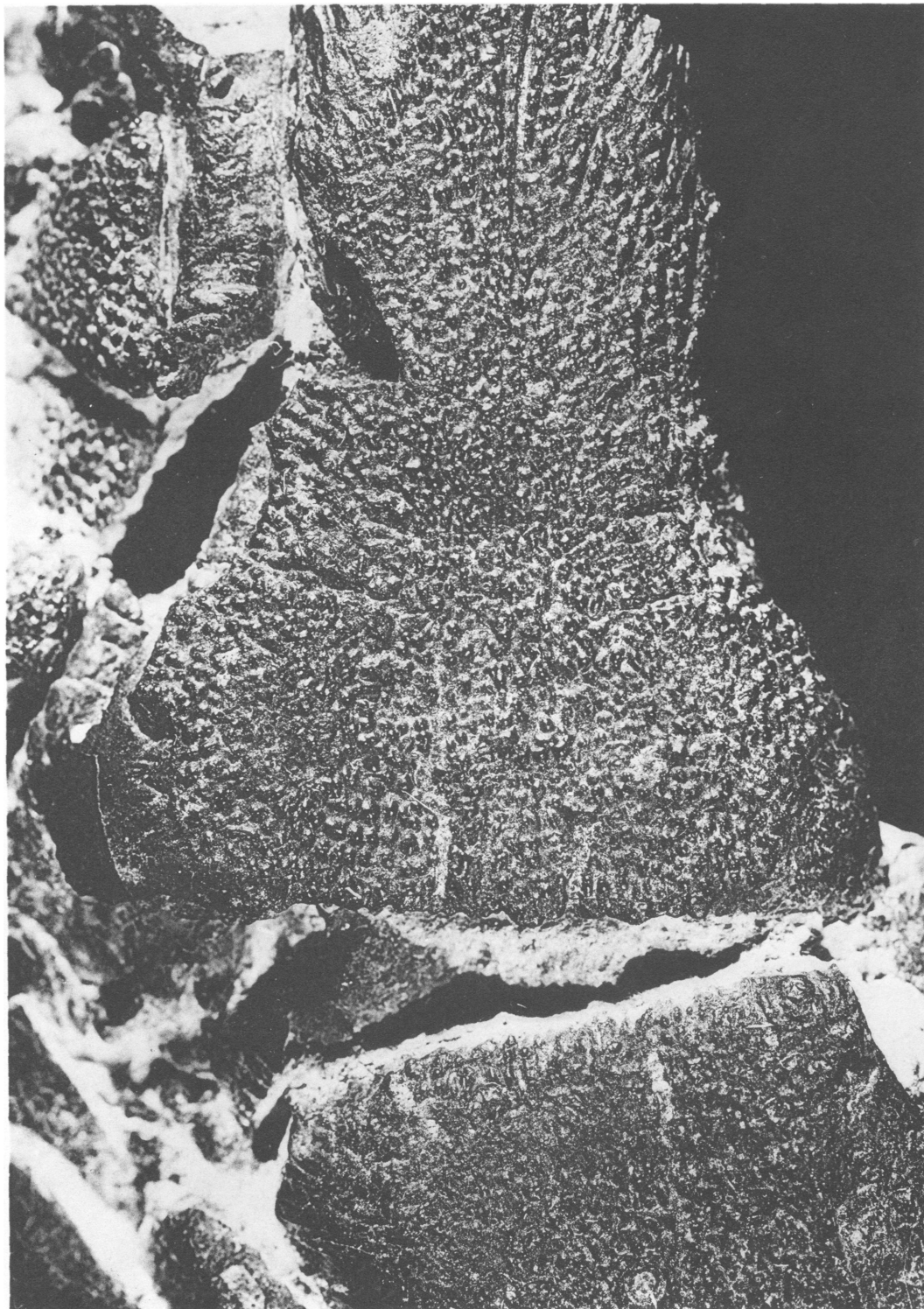


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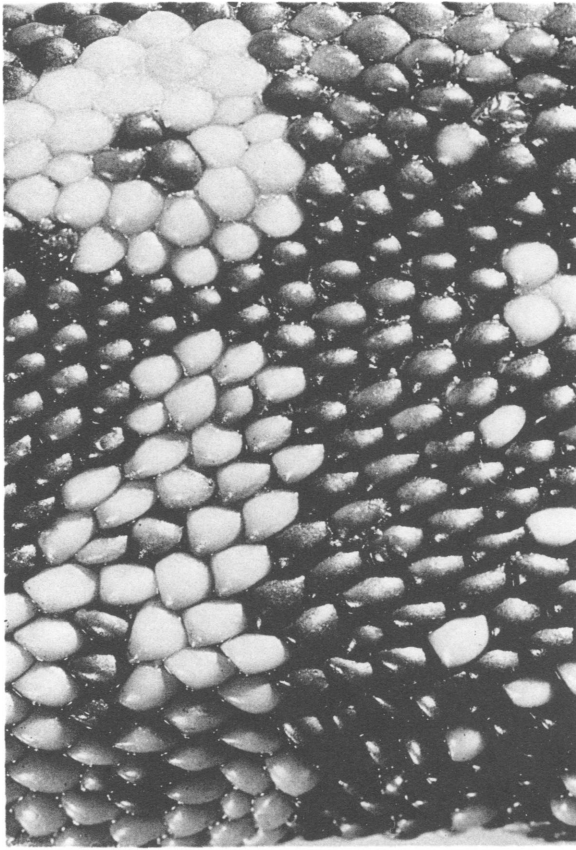


2

*Xenosaurus rackhami*. 1. Entire animal. 2. Enlarged view of scales of flank, anterior end at right



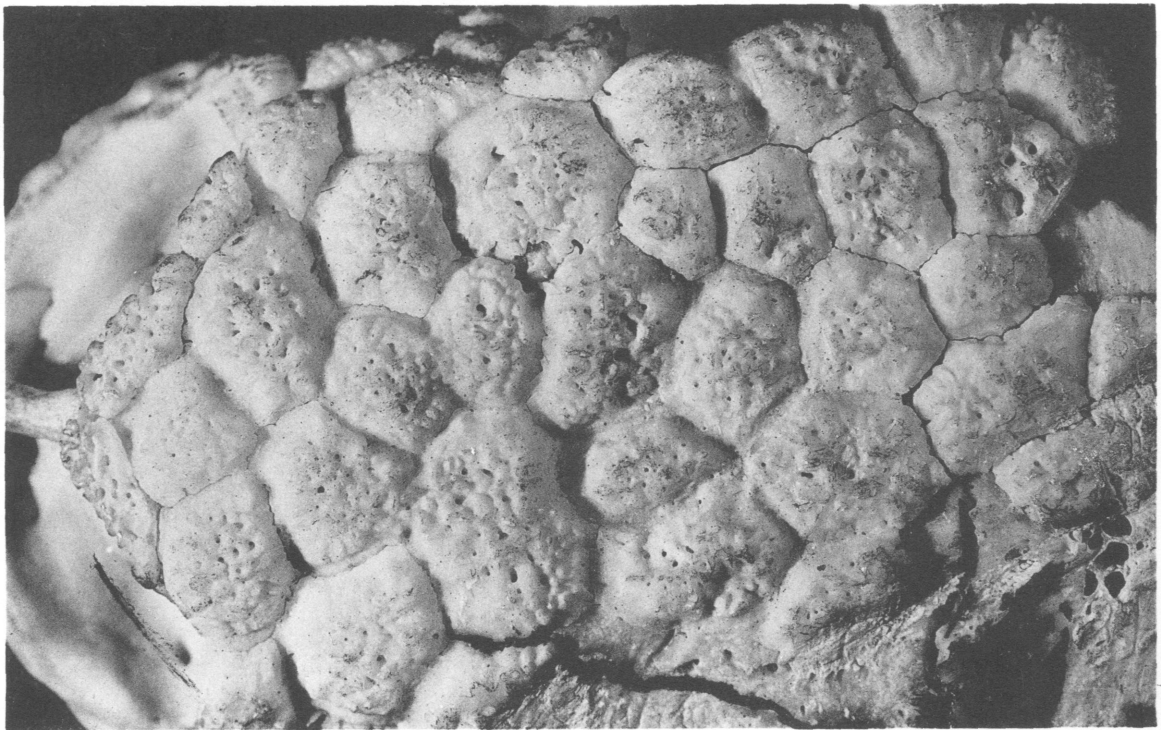
Enlarged view of the frontal of *Melanosaurus maximus*, type specimen. Notice sculpture of numerous hemispherical tubercles and poor definition of scute sutures, a characteristic feature of xenosaurids



1

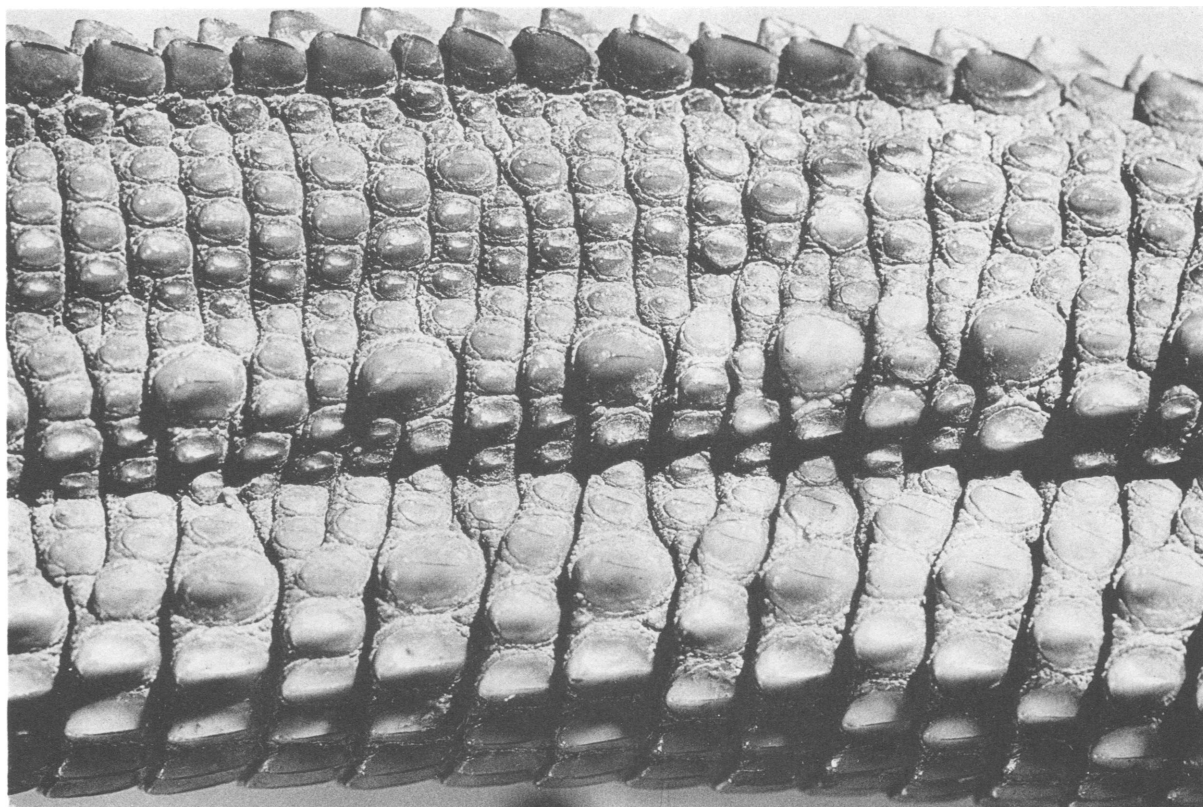


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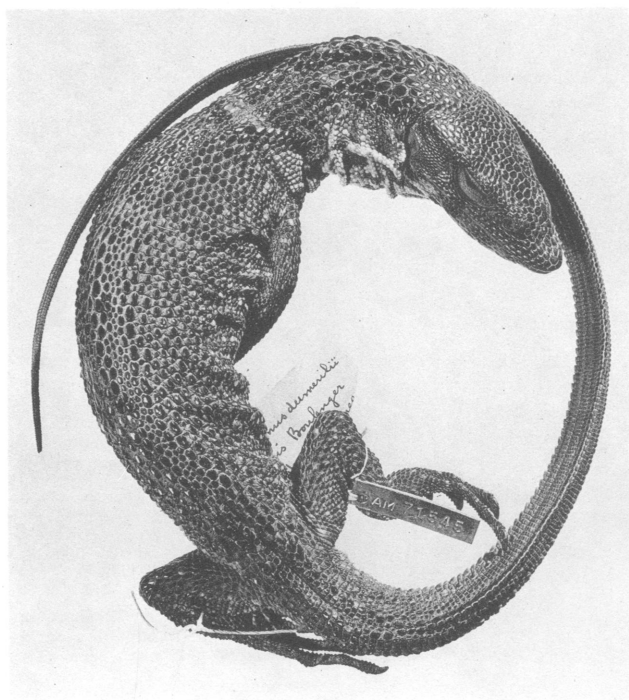


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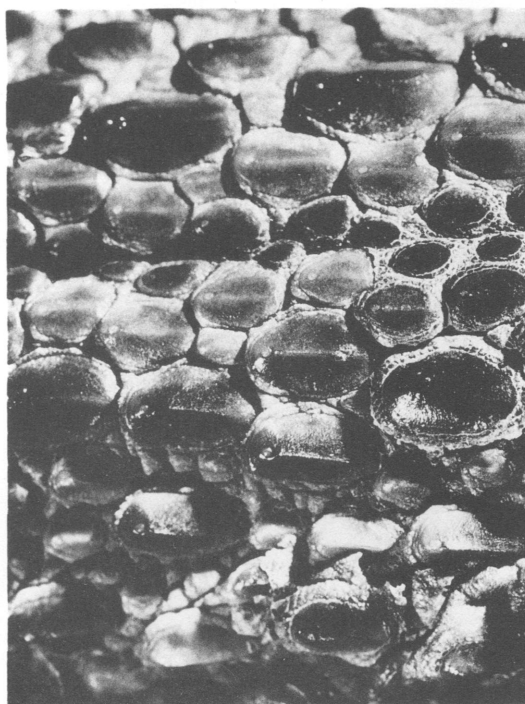
*Heloderma horridum*. 1. Enlarged view of the scales of the flank. 2. Entire animal. 3. Enlarged view of the frontal osteoderms, showing platynotan type of osteodermal sculpture (the tubercles poorly defined and tending to fuse and the surface conspicuously pitted)



1

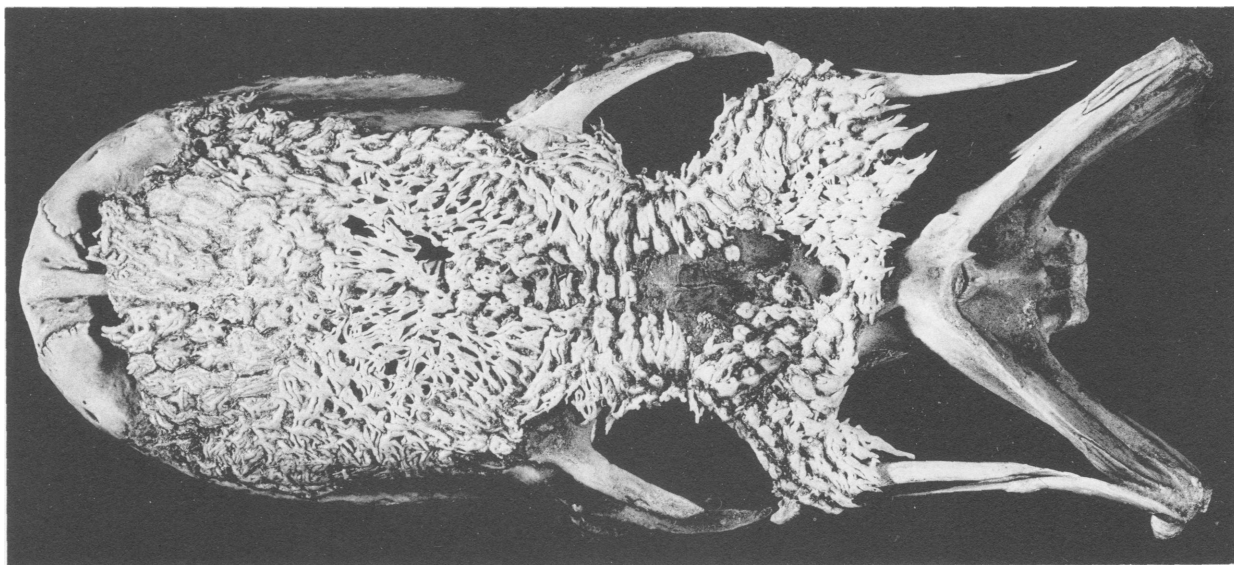


2



3

*Varanus (Tectovaranus) dumerili heteropholis*. 1. Enlarged view of side of tail, anterior end at right. 2. Entire animal. 3. Enlarged view of dorsal scales, anterior end at right

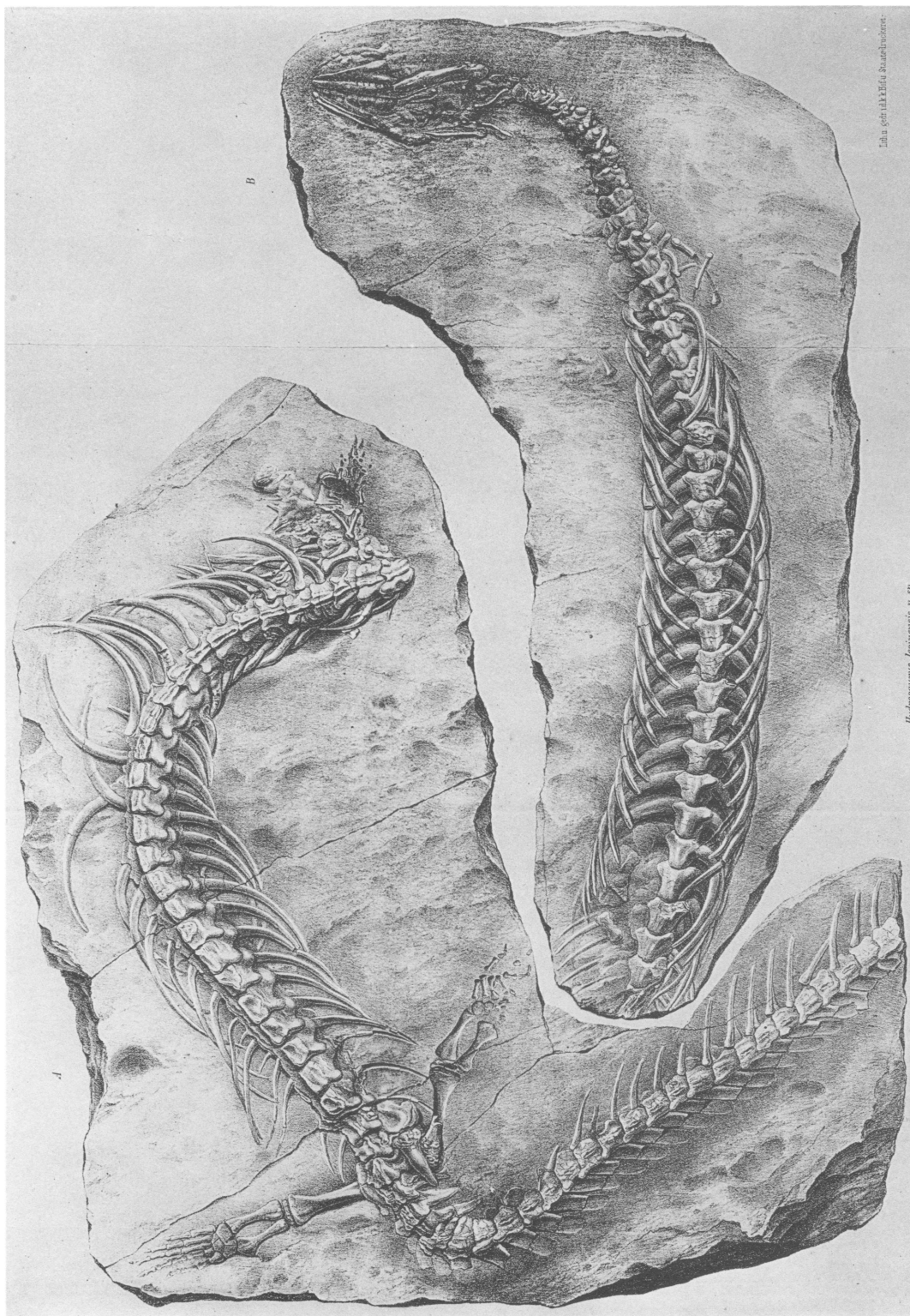


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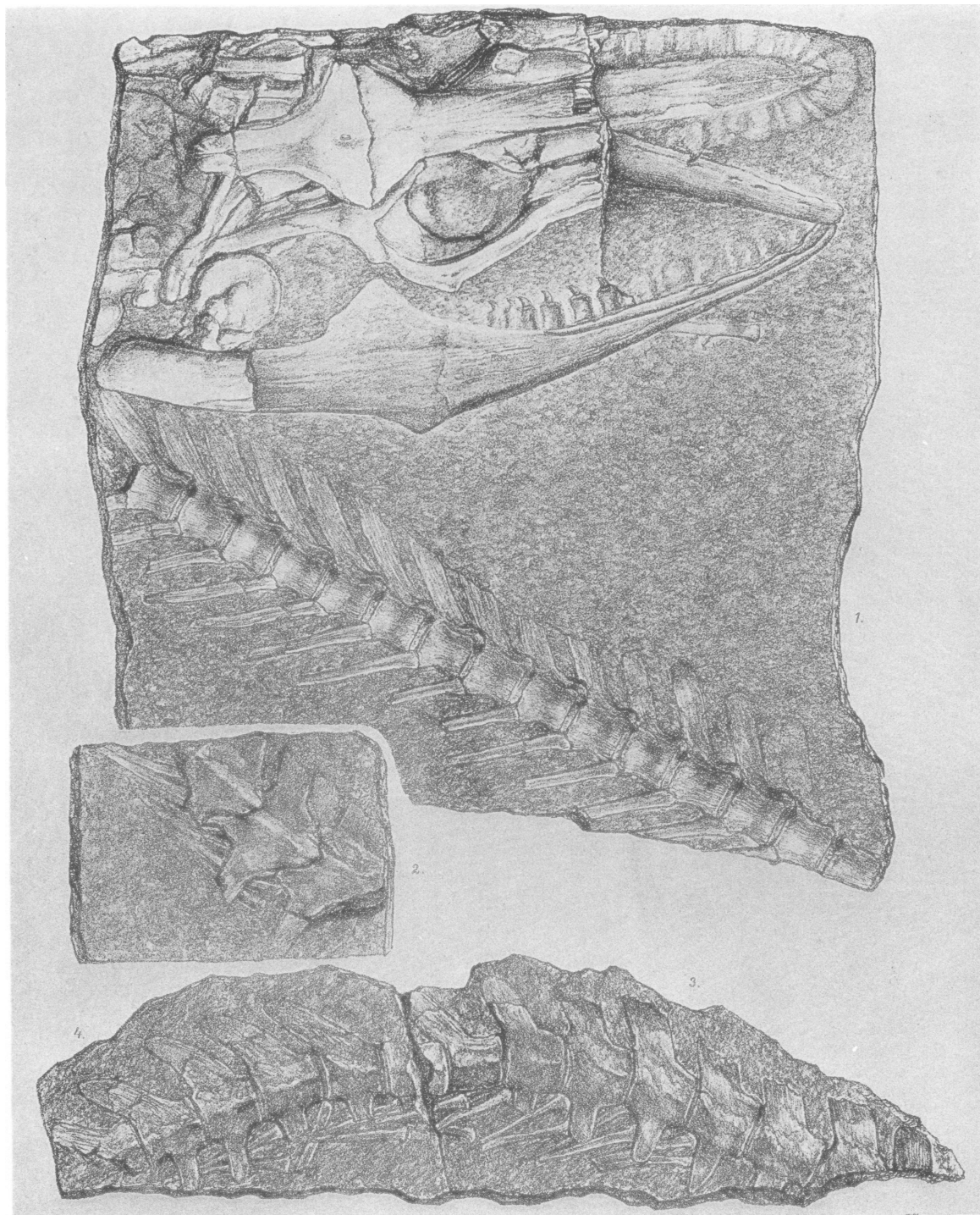


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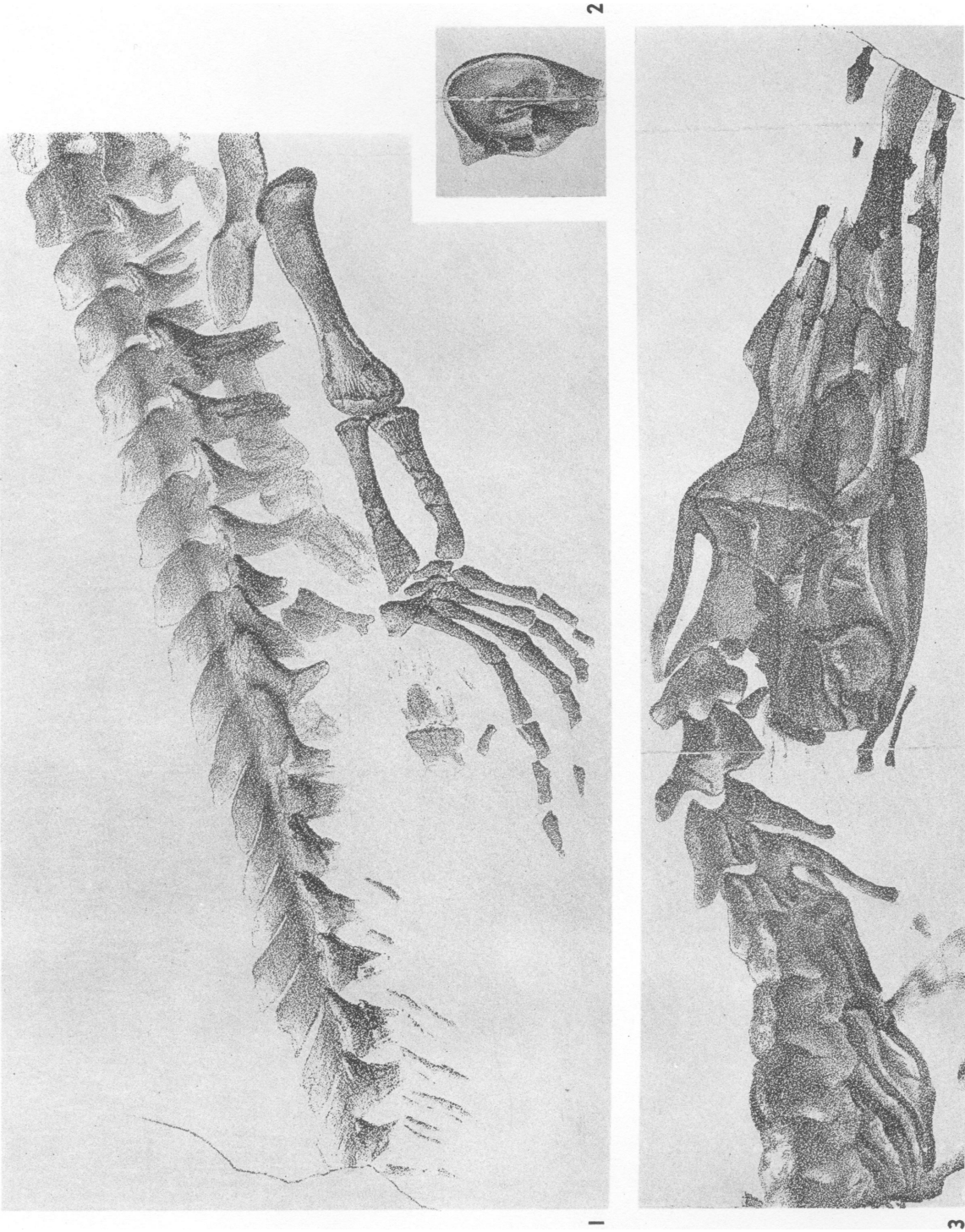
*Varanus (Varanus) komodoensis*. 1. Dorsal view of skull with osteoderms in place. 2. Enlarged view of osteoderms over anterior extremity of frontal, showing the tubercles completely fused and highly developed pitting



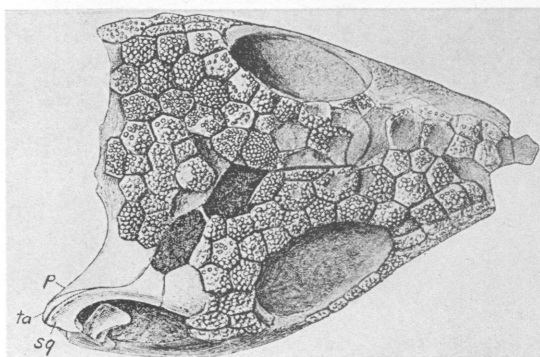
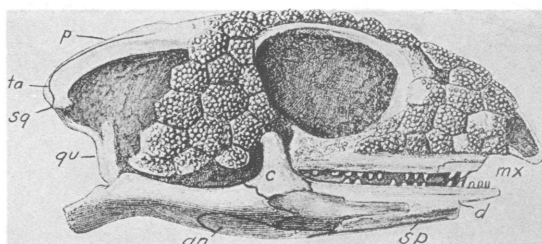
*Pontosaurus lesinensis*, a lower Cretaceous dolichosaur. From Kornhuber



*Opetiosaurus buccichi*, a primitive aigialosaurid. Skull and caudal vertebrae. From Kornhuber



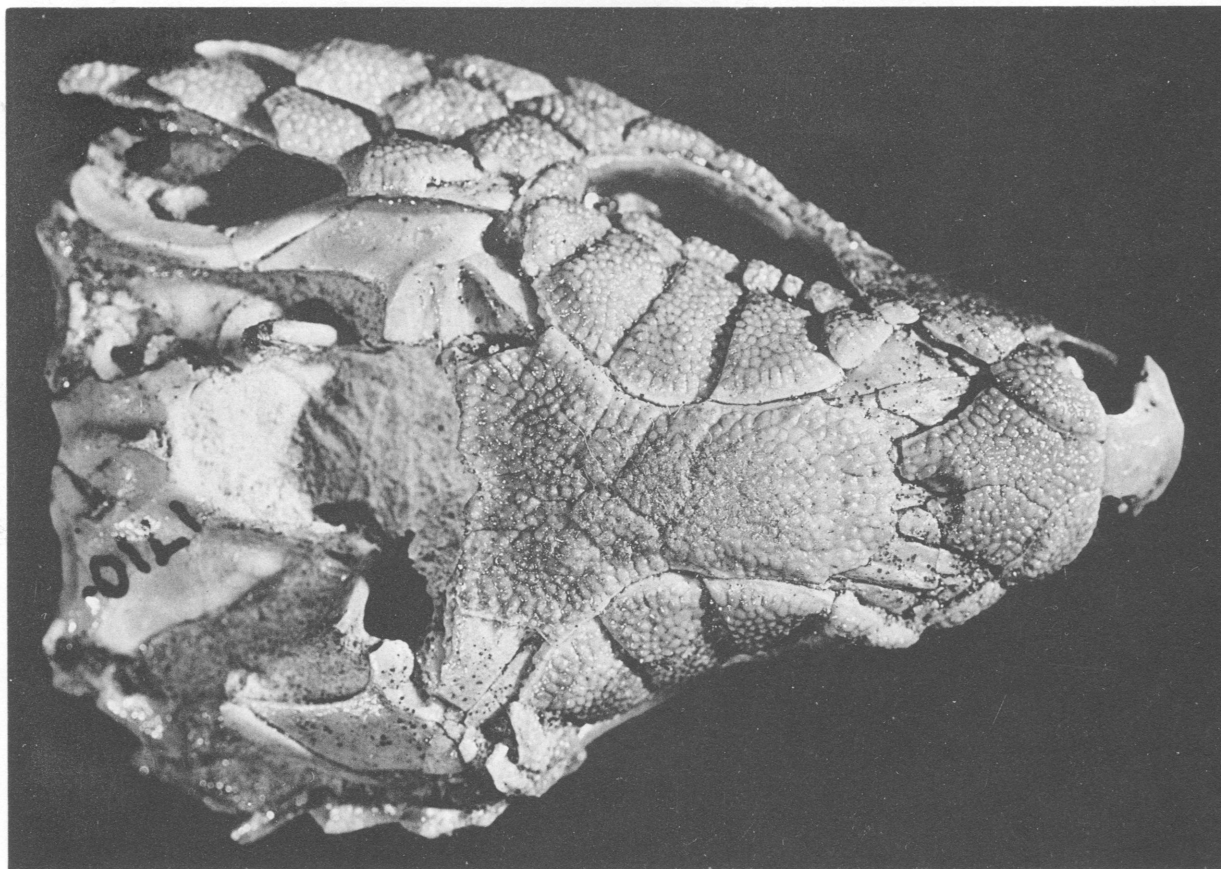
*Aigialosaurus dalmaticus*. 1. Hind limb and pes. 2. Right quadrate bone. 3. Skull and cervical vertebrae. From Kramberger



1



2



3

1. *Glyptosaurus montanus*. Lateral and dorsal views of skull, with osteoderms. Abbreviations: an, angular; c, coronoid; d, dentary; mx, maxilla; p, parietal; qu, quadrate; sp, splenial; sq, squamosal; ta, tabular. From Gilmore

2. Frontal osteoderms of an Oligocene species of *Glyptosaurus*. Note well-defined and hemispheric tubercles and absence of pitting. (Compare pls. 9 and 10, fig. 3)

3. *Peltosaurus granulatus*. Dorsal view, showing osteodermal sculpture