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Curator of Fossil Reptiles, Amphibians, and Fishes

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INTRODUCTION

GENERAL REMARKS

IN 1939, during quarrying operations that were being carried on by the Work Projects Administration near Paulison Avenue, on the boundary between Clifton and Passaic, New Jersey, the skeleton of a small reptile enclosed in a block of sandstone was blasted out of its original position in the beds which were being worked. The block with its contained skeleton was recognized by one of the workmen as something unusual and was put to one side on the bank, where it remained for some months. During the early part of 1940 it was called to the attention of Mr. Fred A. Betz of Passaic, Mr. Nicholas Martini, Director of the Department of Public Works of the City of Passaic, and Mr. O. A. Kennedy, Principal of the Senior High School of Passaic.

On February 8, 1940, a request for the identification of the specimen came to the American Museum of Natural History from Mr. Raymond G. Parks, the Assistant Chief Engineer, Department of Public Works of the City of Passaic. This request was submitted to Dr. Barnum Brown, at that time Curator of Fossil Reptiles, who immediately made a visit to the site where the specimen had been discovered and concluded arrangements to have the fossil presented to the American Museum of Natural History. This was done through Mr. Martini.

Various members of the American Museum staff visited the site, namely, Dr. Brown, Dr. George Gaylord Simpson, Mr. Charles Lang, Dr. Erich M. Schlaikjer, and the writer. Attempts were made to recover more material, and to further this end a cash reward was offered to the workman who might find additional bones. By making the workmen aware of the desirability of recovering any material that might show up and by fairly frequent trips to the quarry, we made some additional discoveries, notably a palate with a very fine dentition and the arch on either side back to the quadrates, and a portion of another skull. Other bones were found, but these were for the most part fragmentary and of little value.

It might be well, to have the record as straight as possible, to quote a memorandum written by Dr. Brown on July 17, 1940, giving details regarding the discovery of the original skeleton and the subsequent search for additional material:

"The skeleton, A.M.N.H. No. 1676, of the new procolophonid was found in the WPA quarry on Paulison Avenue, Passaic, N. J. It was blasted out more than a year ago and was recognized by a Negro workman at the time. It, with other blocks, was put on the bank and was not called to the attention of Mr. Betts, the City Engineer, and the Superintendent of Schools until the early part of 1940.

"Some time during the early summer of 1940 three or four bones, apparently dinosaur bones, were found by the same Negro and a friend of his and taken to the home of the latter. These were purchased on July 16. About the same time, in the early summer, the Superintendent of the work found the leg of an animal having three toes, but as no more of the animal was seen by the quarrymen this block was thrown into the material being used for waterways. From the description apparently this was a dinosaur leg approximately the size of *Anchisaurus*.

"On July 16 Dr. Erich Schlaikjer and I visited the quarry and I found a part of a skull, A.M.N.H. No. 1677, in the strata at the very top of the quarry back of the face where the men are now working—stratigraphically about 25 feet higher than the procolophonid stratum. A blast had shattered this specimen, and two parts of the skull were exposed showing a bluish white. We dug below this point in the shattered material and found two other fragments, all of which unite."

The third skull, A.M.N.H. No. 1678, was obtained in October of 1940. Since that time a few fragments of a problematical nature have been discovered.

It was intended that Dr. Schlaikjer should study this material. However, with Dr.

Schlaikjer's entrance into the Army, it was felt that perhaps the work might be delegated to some other person, in order that publication of this important and interesting specimen should not be unduly delayed. Dr. Schlaikjer therefore very kindly and wholeheartedly released the material for study by the present writer.

At this place I wish to express my great appreciation to Dr. Schlaikjer for releasing the material. The science of vertebrate paleontology in general and the American Museum of Natural History in particular owe Dr. Brown a lasting debt for the foresight and energy with which he carried through the negotiations that made possible the presentation of the material to this Museum. In this connection our appreciation and gratitude are extended to Mr. Martini, to Mr. John Schneider, Chief Engineer of the Passaic Department of Public Works, to Mr. Parks, to Mr. Betts, and to Mr. Kennedy. It was through the fine cooperation of all of these gentlemen that we were able to procure the specimens to be described below.

Valuable advice during the course of my work on this specimen was given by Profs. William King Gregory of the American Museum and Alfred S. Romer of Harvard University. The material was all most skillfully prepared by Mr. Otto Falkenbach of the American Museum paleontological laboratory, to whom particular credit is due. This was a most difficult, long, and tedious task of paleontological preparation, and it was carried through to completion by Mr. Falkenbach with consummate skill. The illustrations, requiring a great amount of careful study and observation, were made by Mr. John C. Germann.

Photographs of the quarry where the American Museum materials were found were made by Mr. Louis A. Monaco.

At this place I wish to express my special appreciation for the kindness of the late Mr. Charles W. Gilmore, until the time of his death Curator of Fossil Reptiles at the United States National Museum, in making the type specimen of *Hypsognathus fenneri* available for comparative studies in New York.

As the skeleton was first prepared its affinities with the Cotylosauria soon became apparent. These relationships were shown by the form of the vertebrae and the articulation of the ribs. Moreover, the general shape of the skull showed that this new specimen was a procolophonid not unlike the genus from the Elgin sandstones of Scotland, named by Owen *Leptopleuron* and commonly known in the literature by Mantell's name, *Telerpeton*.

In 1928 Gilmore described a small reptile of cotylosaurian relationships from the Brunswick formation of New Jersey. This specimen, which was named by Gilmore *Hypsognathus*[1] *fenneri*, came from an underpass that was being constructed at the intersection of Broad Street, Clifton, with the tracks of the Delaware, Lackawanna, and Western Railroad, a locality which is about 3 miles from the quarry where our new material was found.

The question immediately arose as to the possible identity between the two finds. It seemed logical to suppose that since the new material came from a locality not far distant from, and within the same formation as, the type of *Hypsognathus fenneri*, there might be at least a generic identity between the two sets of materials. Unfortunately the specimen described by Gilmore, now in the United States National Museum, consists of a natural mold of the skeleton in a block of sandstone, with a portion of the specimen missing. What is more unfortunate is that the missing portion includes the entire skull and dentition, only the lower surface of the mandible being represented. It is an interesting fact, however, that a cast of the lower surface of

[1] *Hypsognathus* Gilmore, 1928, is not to be confused with *Hypsignathus* Allen, 1861, the latter being a bat. Nor are these names to be considered as homonyms, even though there is a difference of but one letter between them. The recommendations under Article 36 of the International Rules of Zoological Nomenclature state quite definitely that once a new generic name is introduced which differs from an established name merely by one letter, it is not for this reason to be rejected.

It is not stated in the original description of *Hypsognathus* what constitutes the basis for the derivation of this name. Of course, if the attributive ὑψι was intended, then it might be argued that there had been an error in transliteration, so that *Hypsognathus* might very well become a homonym of *Hypsignathus*. On the other hand, the attributive ὑψος might have been intended, in which case there would be no apparent error of transliteration. Since no proof to the contrary is evident, this latter interpretation seems to be the proper one to assume.

the mandible, made from the type specimen, fits almost exactly over the palate and the quadrates of the American Museum specimen, A.M.N.H. No. 1677.

Because of this, because the materials in the National Museum and the American Museum came from localities near each other, because these materials came from the same geological formation, because they belong to the Cotylosauria, and because they are of approximately the same size throughout, it is felt that they represent in all probability a single genus and species. The very nature of the type specimen of *Hypsognathus fenneri*

makes it almost impossible to establish conclusive proof of an identity between it and the new materials. Conversely, conclusive proof of a specific or a generic difference between them is likewise impossible. Therefore, the identity of the materials is accepted here on the basis of probabilities involved, and the new materials to be described are considered as supplementary to the type, establishing definitely the anatomical characters and the taxonomic position of *Hypsognathus fenneri*. This will be the basic assumption upon which rest the description and discussion presented in the following pages.

STRATIGRAPHIC RELATIONSHIPS

Before attempting a description of the new materials, it may be advisable to consider as fully as possible the question of stratigraphic relationships between these fossils and the type of *Hypsognathus fenneri*, described by Gilmore.

As already stated, the type of *Hypsognathus fenneri* came from an excavation for an underpass at the interesection of Broad Street and the Delaware and Lackawanna Railroad in Clifton, New Jersey, while the new materials came from a quarry on the western boundary between Clifton and Passaic. Incidentally, it might be pointed out that while many statements have been made to the effect that these fossils were found in Passaic, actually they came from a spot just across the boundary line so that they really were found in Clifton. By an airline, the two localities are just 2.6 miles apart, the quarry being southeast of the underpass.

Both localities come within the upper portion of the Brunswick formation of the Newark series, the sediments of which have been described in the following words.

"West of the rocks just described [sandstones separating the Hackensack meadows from the Passaic River valley] appears another similar series of sandstones, but much harder and thicker bedded and of lighter color. It extends through Newark, Avondale, and the western part of Passaic, where the rock has been extensively quarried for building stone. Its upper beds merge into a thick

mass of shale of red color, with interbedded sandstone, which extends westward nearly to the base of first Watchung Mountain. . . . " (U. S. Geol. Surv. Folio 157, p. 8).

Since the sediments of the Newark series dip to the westward, it would seem evident that the type of *Hypsognathus* comes from a horizon higher in the Brunswick formation than do the new materials. Whether or not the difference in level is great or significant is a debatable question.

Applying the methods of structural geology to the problem, the following results are obtained.

The underpass where the type of *Hypsognathus* was found, which may be designated as locality 1, is 2.6 miles northwest of the quarry here designated as locality 2, where the new fossils were found. On a line at right angles to the strike of the sediments, the distance between the two, hereby designated as a–b, may be reduced to 2.2 miles. (See fig. 2.)

According to Folio 157 the dip of the sediments in this region varies from 10 to 15 degrees. Assuming the distance a–b of 2.2 miles or 11,600 feet to be the hypotenuse of a right-angled triangle, of which one angle, θ, is either 10 degrees or 15 degrees, a maximum and a minimum vertical separation within the sediments for the two localities may be calculated according to the formula, $BC = AB (\sin \theta)$.

When calculated by plane trigonometry these theoretical vertical separations work
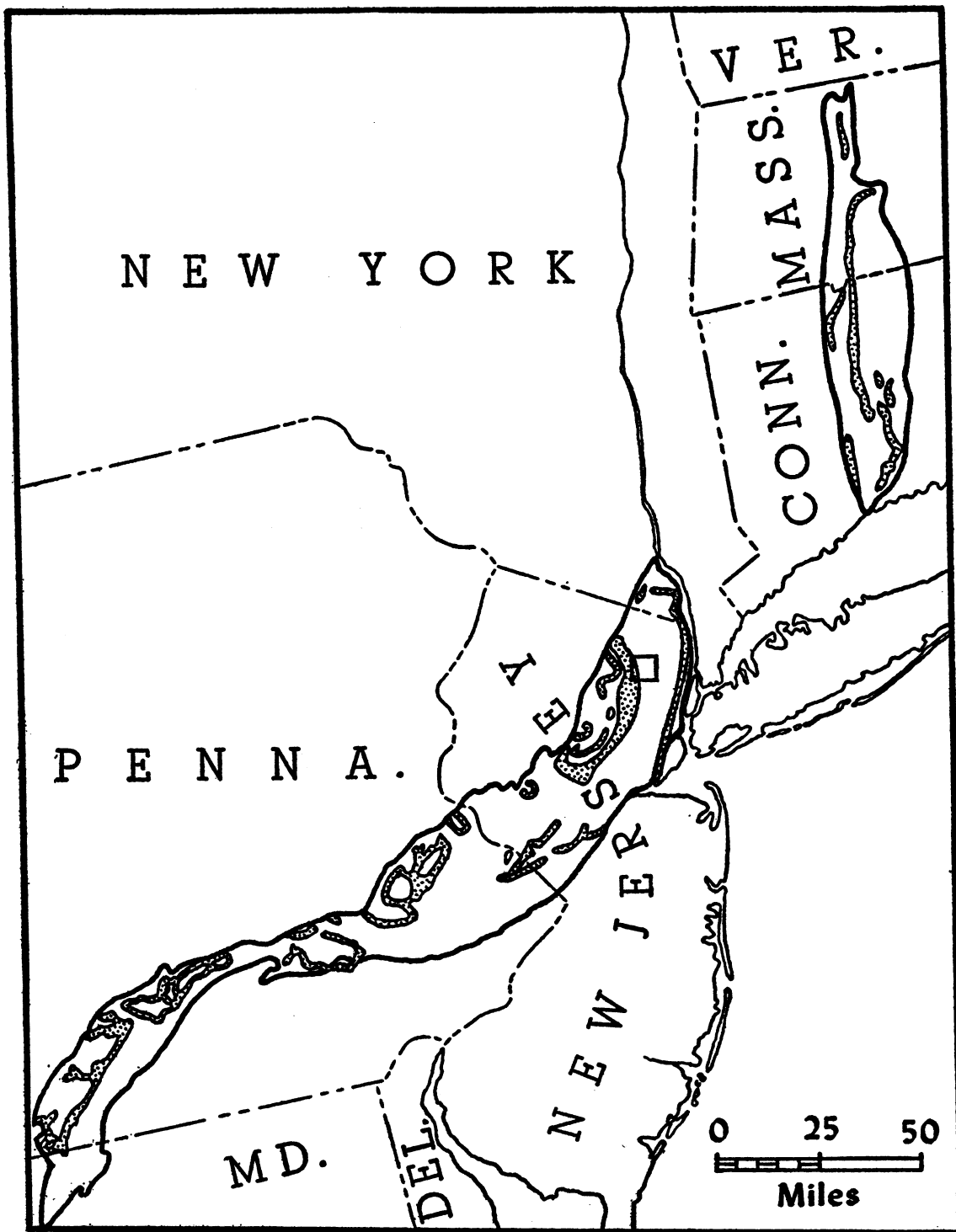
FIG. 1. Map to show the extent of Triassic exposures in northeastern United States. The heavy lines enclose exposures of the Newark series in the Connecticut Valley and in New Jersey and Pennsylvania. Dotted areas represent intrusive flows of diabase and basalt. The small square in northern New Jersey represents the area included in the map shown in figure 2. This map is based upon the Geologic Map of the United States published by the United States Geological Survey in 1932.
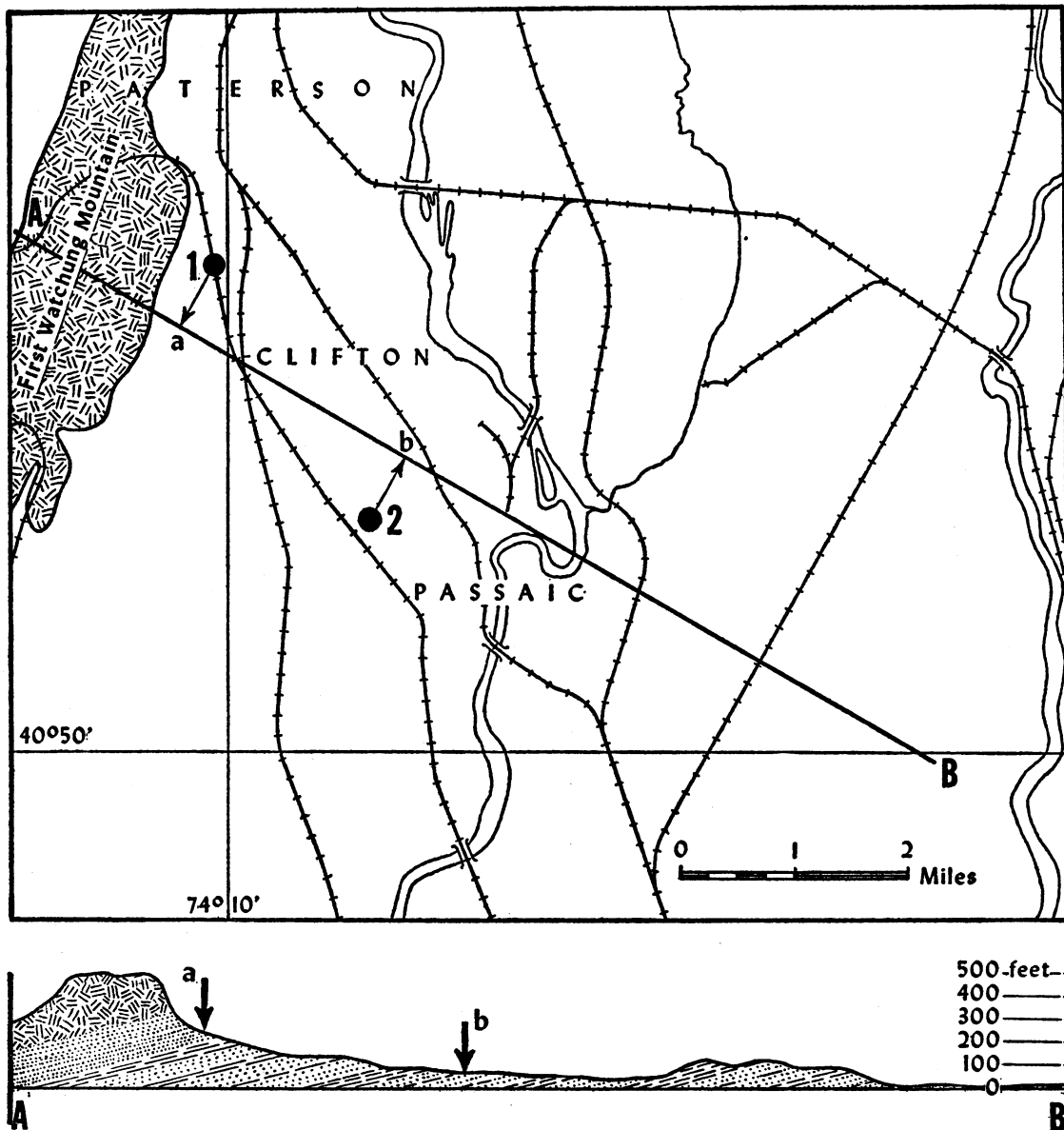
FIG. 2. Map and structure section to show the localities and the stratigraphic relationships of the sites where *Hypsognathus* has been found. 1. Locality at underpass of highway beneath the Delaware, Lackawanna, and Western Railroad in Clifton, New Jersey, where the type of *Hypsognathus fenneri* was discovered. a. Projection of this locality to the line of the structure section, A-B. 2. Locality in the quarry at the boundary between Clifton and Passaic, New Jersey, where the American Museum materials of *Hypsognathus fenneri* were found. b. Projection of this locality to the line of the structure section, A-B. The entire area of this map is included within the Brunswick formation of the Newark series. Map based upon the geologic and topographic maps of the Passaic Quadrangle, published in Folio No. 157 of the United States Geological Survey, 1908. In the structure section, A–B, the arrows marked a and b show the approximate stratigraphic relationships of the type and the referred materials, respectively, of *Hypsognathus fenneri*.

out as 2014 feet on the basis of a 10-degree dip and 3003 feet upon the basis of a 15-degree dip.

Such vertical distances between two localities would in a simple case indicate a considerable sedimentary time lapse between the two horizons. In the present instance, however, the problem is complicated by the fact that we know of the existence of many faults within the upper Brunswick sediments. How great these faults are in their throws and how frequently they occur are matters that cannot be determined. It is certain, however, that there must be a considerable degree of repetition of beds within the Brunswick formation, so that the actual stratigraphic separation of the two localities is nowhere near so great as it might appear to be. Indeed, it is conceivable that the two localities are located within essentially the same stratigraphic horizon. Actually the probabilities are against this, and it is very probable that the vertical distance between the two localities within the Brunswick formation may be on the order of some hundreds of feet.

In this connection it might be pointed out that Kümmel, an authority on the Newark series, has estimated that actual thicknesses range from 36 to 67 per cent of the measured extent of exposures. On this basis, then, the difference in stratigraphic levels between the two localities in question would vary from a minimum of 640 feet to a maximum of 2020 feet. The total thickness of the Brunswick formation has been estimated by Kümmel as between 6000 feet and 8000 feet.

The question that confronts us is this, Does such a vertical separation have a real significance in so far as taxonomic relationships are concerned? Here we are pretty much in the realm of subjectivity, and any pronouncement is largely a reflection of the personal bias of whoever makes it. It is the opinion of the present writer that this difference, even though it may seem rather large, is of little import in the problem at hand. There is so little variation in the general expression of the Brunswick formation, from bottom to top, that one is led to the conclusion that this unit represents a single cycle of sedimentation. While a distance of some hundreds of feet in vertical thickness may represent a considerable time lapse, it is of little significance in the matter of specific relationships because this amount of sedimentation went on during a period of climatic, and correlatively of zoologic, uniformity. In other words, it is felt that while there may have been an appreciable lapse of time between the deposition of the two horizons at which the materials under consideration were found, this time lapse is insignificant when compared to the time lapse of the Upper Triassic, during which the 15,000 feet of the Newark series were accumulating. Oppositely, it should be remembered that these beds of the Brunswick formation are relatively coarse clastics, and therefore they may represent a rate of sedimentation so rapid that a difference of several hundred feet is of little temporal significance.

Perhaps a few remarks might be made as to the stratigraphic conditions at the quarry where our new materials were found. Here the Brunswick formation is exposed as a series of heavy, block-like sandstones, with intercalated lenses of shale. The beds dip gently to the west, and a number of faults are apparent, even within the small area of the quarry.

It is not known exactly where the skeleton, A.M.N.H. No. 1676, was found. Seemingly it came from about the middle of the quarry. The skull found by Dr. Brown, A.M.N.H. No. 1677, was found on the surface on the top of the quarry, but it was obviously out of place.

The third skull, A.M.N.H. No. 1678, found by Dr. Simpson, came from the floor near the middle of the quarry. Dr. Glenn L. Jepsen of Princeton University, on a trip to the quarry with the writer, found a part of a vertebra in the west face of the quarry.

The photographs reproduced in plates 25 and 26 will give some idea of the size of the quarry and the manner in which the sediments are exposed.

DESCRIPTION

TAXONOMY AND DIAGNOSIS

COTYLOSAURIA
DIADECTOMORPHA
PROCOLOPHONIDAE

HYPSOGNATHUS GILMORE

GILMORE, 1928, Proc. U. S. Natl. Mus., vol. 73, art. 7, p. 2. TYPE: *Hypsognathus fenneri* Gilmore.

Hypsognathus fenneri Gilmore

Hypsognathus fenneri GILMORE, 1928, *ibid.*, vol. 73, art. 7, pp. 1–8, pl. 1.

TYPE: U.S.N.M. No. 11643, bone impressions of the lower jaw and much of the axial skeleton anterior to the pelvic region, preserved in a very hard piece of sandstone.

TYPE LOCALITY: Clifton, Passaic County, New Jersey.

HORIZON: Brunswick formation, Triassic.

SPECIMENS UNDER CONSIDERATION: A.M.N.H. No. 1676, a partial skeleton, containing the following elements: skull and mandible; 21 presacral vertebrae, 20 of these in series; 12 left ribs; 15 right ribs; right scapula, humerus, radius and ulna, manus; part of a left manus; some isolated carpals (?). A.M.N.H. No. 1677, a partial skull with the palatal and quadrate regions exposed.

A.M.N.H. No. 1678, premaxillary-maxillary region with teeth. Various isolated bone fragments, no numbers.

All these specimens came from a sandstone quarry in the Brunswick formation and were found within a short distance of one another. The quarry is located near the public incinerator at 555 Paulison Avenue, Passaic, New Jersey. The relationship of this locality to the type locality for *Hypsognathus fenneri* has been pointed out above.

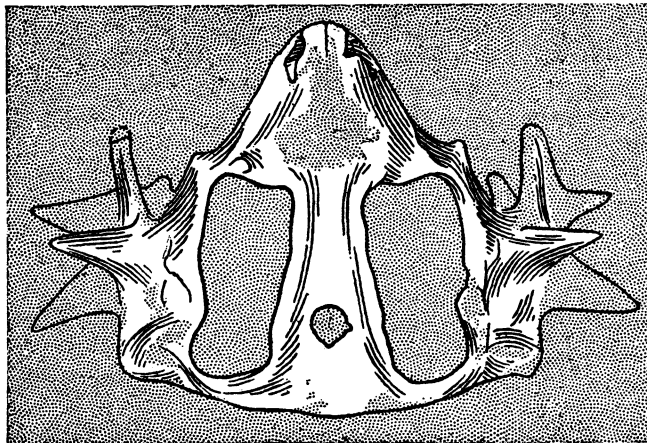REVISED DIAGNOSIS: A small procolophonid of Upper Triassic age. Characterized by

FIG. 3. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1676, dorsal view of skull as exposed in matrix, after preparation. Natural size.

the very broad skull, in which the orbits are extraordinarily elongated—more so than in any of the other Procolophonidae. The orbits are transversely broad both anteriorly and posteriorly. The pineal foramen is large. There are an anterior point on the jugal and four large points or spikes on the side of the skull, probably on the quadratojugal. There are seven upper teeth on each side, two in the premaxillary and five in the maxillary. Of the two premaxillary teeth, the first is much enlarged, so that it overhangs the anterior dentary tooth; both are peg-like. Of the maxillary teeth, the first is small and round in

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cross section, while the remainder are very broad and chisel-like, increasing in breadth from the front to the back end of the row. Of the five dentary teeth, the posterior three are transversely broad and alternate with the four broadened maxillary teeth. The teeth are essentially acrodont. The mandible is heavy, transversely swollen and deep, with a rounded symphyseal region.

The vertebrae are characteristically cotylosaurian, with broad, heavy, neural arches. The ribs are holocephalous and articulate with transverse processes from the centra. The scapula is elongated and the limbs are slender.

Since the genus *Hypsognathus* is at the present time monotypic, the same diagnosis serves for both genus and species.

THE SKULL AND MANDIBLE

Before the discovery of this new material near Passaic the skull of *Hypsognathus* was quite unknown, while the mandible was known only from the impression of its lower surface preserved in the sandstone slab of the type specimen. In this new specimen the skull is well preserved and for the most part uncrushed, while the mandible is locked in place so firmly that we have not been able to remove it for study. Unfortunately the lower surface of the mandible is somewhat crushed and broken, and part of it is missing, so that a direct comparison between this region and the same portion in the type is very difficult. Nevertheless, after a careful comparative study it was felt that there was enough similarity so that the two mandibles might be considered as belonging to a single genus and probably a single species of the Cotylosauria. It was this fact, together with the striking similarity in size between the two specimens, that led, as much as anything, to the conclusion that the new material might be identified as specifically identical with the material originally found at Clifton, a relatively short distance away.

The skull in *Hypsognathus* is at once distinguished by its unusual breadth and by the prominent horns or spikes on either side of the head. In addition, it is notable because of the great length and breadth of the orbits as well as by the unusual size of the pineal foramen. Altogether it bears a striking resemblance to *Leptopleuron*, generally known by the name of *Telerpeton*, the small procolophonid from the Lossiemouth Beds, near Elgin, Scotland.[1]

Perhaps the characters enumerated above might be discussed in a little more detail. As for the skull in *Hypsognathus*, in proportions it is somewhat broader than it is long, in which respect it shows the culmination of a trend of development that can be traced from Permian to Upper Triassic times. This trend has its beginnings in the genus *Nyctiphruretus* from the Permian of Russia, from whence it can be traced to the South African Triassic genus, *Procolophon;* it can then be followed through the Lower Triassic form, *Sclerosaurus*, of central Europe, and it terminates in the Middle and Upper Triassic genera, *Leptopleuron* [*Telerpeton*] of Scotland and *Hypsognathus* of North America. This same trend appears in the development of other anatomical characters, as will be shown below.

In *Nyctiphruretus* the orbits are large and slightly elongated, and their posterior bor-

[1] The name *Telerpeton elginense* Mantell has been almost universally applied to the procolophonid from the Lossiemouth Beds, ever since Mantell's description of 1852. Many authors seem to have overlooked the fact that there was a prior description of this animal by Owen in 1851, evidently based upon the same material that subsequently came into Mantell's hands. Owen's description was published in the "Literary gazette" and it is probably because of this appearance in a nonscientific journal that it has been generally overlooked. In 1912 von Huene called attention to Owen's prior description of this form, but he did not use the prior name because no figures accompanied Owen's description.

"Wie aus dem Literaturverzeichnis nervorgeht, ist der Name *Leptopleuron lacertinum* R. Owen der älteste und sollte eigentlich angewendet werden. Ich habe vorlaufig noch gezögert, dies zu tun, weil der ersten Beschreibung, oder eigentlich nur Erwähung, keine Figuren beigegeben sind" (von Huene, 1912, p. 82).

Owen actually gave an adequate description, and the fact that no figure accompanied it does not invalidate his name. It is indeed unfortunate that this name has priority over the name *Telerpeton*, which has become well established and well known through long years of usage, but such is the case. Williston recognized *Leptopleuron* as the valid name and indicated *Telerpeton* as a synonym in his "Osteology of the reptiles," published in 1925.
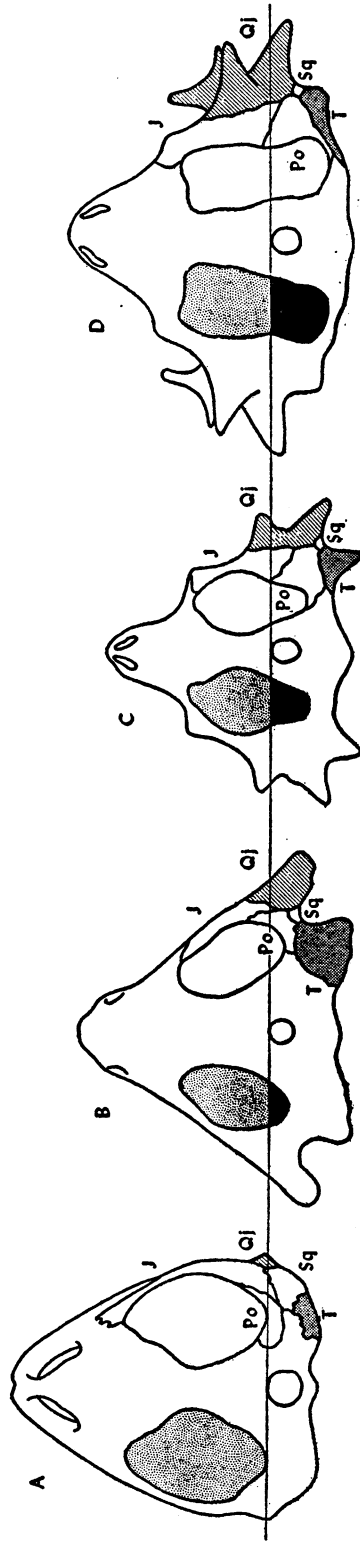
FIG. 4. Comparative diagrams to show the trends of development in the skull of the Procolophonidae. A. *Nyctiphruretus*, Upper Permian, Russia. (From Efremov, 1940b.) B. *Procolophon*, Lower Triassic, South Africa. (From Broili and Schröder, 1936). C. *Leptopleuron* [= *Telerpeton*], Middle Triassic, Scotland. (From von Huene, 1920.) D. *Hypsognathus*, Upper Triassic, New Jersey. In this figure are shown particularly: elongation of the orbitotemporal opening behind the front border of the pineal foramen; development of spikes on the quadratojugal and tabular bones; changes in proportion of the jugal, postorbital, and squamosal bones. Abbreviations: J, jugal; Po, postorbital; Qj, quadratojugal; Sq, squamosal; T, tabular. All skulls three-fourths natural size.

ders are opposite the anterior edge of the pineal foramen. In *Procolophon* the orbit is elliptical or moderately elongated, its posterior border being opposite the posterior border of the pineal foramen. The same seems to be true in *Sclerosaurus*. In *Leptopleuron*, however, the elongated orbits extend back to a point slightly behind the pineal foramen, while in *Hypsognathus* the posterior borders of the orbital openings are considerably behind the posterior edge of the pineal foramen. The orbit in this New Jersey reptile is broad at the front, and its front border is rather straight and transversely directed. The orbital opening is also broad at the back, while in its posterior third there is a slight constriction due to a sweeping in of its outer edge, opposite the pineal foramen.

How did this elongation, whereby the orbital opening extends back into the temporal region, come about? It might be assumed on the one hand that the elongation was brought about by a simple backward migration of the posterior portion of the orbital opening. On the other hand, it might be assumed that there was thinning of the skull roof immediately behind the orbit, caused by the development and action of the capiti-mandibularis muscles. Such a progressive thinning of the skull roof would result finally in an emargination contiguous with the orbit, and thus there would be formed what might be called a "pseudo-supratemporal opening," or what von Huene has called the "orbitotemporal opening." Whatever the method of development, this opening had an origin seemingly quite independent of the true supratemporal fenestra as found in other orders of reptiles, but it served a similar purpose, namely, as an accommodation for the bulging of the heavy muscles that close the jaws.

The formation of this elongated orbitotemporal opening can be correlated particularly with the shortening of the jaw and the specialization of the dentition in the higher procolophonids. For instance, in such a basic and ancestral type of procolophonid as *Nyctiphruretus*, the dentition is unreduced and unspecialized, and the articulation of the lower jaw upon the quadrate bone is at the back of the skull. Consequently there was ample room for the accommodation of the capiti-mandibularis muscles, which close the jaws and which run from the parietal region to the coronoid, behind the orbit. In the more highly specialized procolophonids, however, and especially in *Leptopleuron* and *Hypsognathus*, the teeth are much reduced as to number and greatly transformed as to shape and function. With this development there was a shortening of the lower jaw and a concomitant forward migration of the quadrate upon the skull. Naturally this development brought the capiti-mandibularis muscle mass in close proximity to the posterior border of the true orbit, so that any fenestration of the skull roof behind the orbit was almost certain to become immediately confluent with the orbit. Add to this the fact that the shortening of the lower jaw and the specialization of the dentition were in the direction of an increasingly stronger bite, with a correlative increase in the power and therefore the bulk of the capiti-mandibularis complex. This too must have hastened and facilitated the fenestration of the skull roof, with the consequent formation of the long orbitotemporal opening.

This development of a pseudo-temporal fenestra contiguous with the orbit in the more advanced procolophonids is here regarded as an interesting parallelism to the development of the true and separate supratemporal opening in the more advanced reptiles. For instance, the back portion of the orbitotemporal elongation in *Hypsognathus*, that portion which accommodated the strong jaw muscles, was very likely bounded by the postfrontal, parietal, and postorbital bones, a condition that may be contrasted with the typical supratemporal fenestra, bounded posteriorly by the parietal and squamosal bones. In those reptiles characterized by the supratemporal fenestra, this opening is separated from the orbit by a postorbital bar, or a combined postorbital-postfrontal bar. Yet in spite of these differences, the parallelism is there, and probably for the same reason.

A restoration of the musculature of the head in *Hypsognathus* is shown by figure 6. In this restoration the capiti-mandibularis is shown as a tripartite muscle, the three heads of which originate on the back part of the skull and insert in the coronoid region of the mandible. The superficial head is shown as

originating on the outer portion of the skull, probably on the squamosal, quadrotojugal, quadrate region, so that it has a very low angle in relation to the horizontal ramus of the mandible. The medial portion is shown as occupying the middle part of the skull, probably including the postfrontal, proötic, and quadrate bones. The deep portion of the muscle mass probably arose on the parietal. It was the action of these last two heads, the capiti-mandibularis medius and profundus, that probably resulted in the development of the posterior portion of the elongated skull opening.

From the under portion of the parietal a long depressor mandibulae probably extended to the angular region of the mandible. The various portions of the pterygoid com-
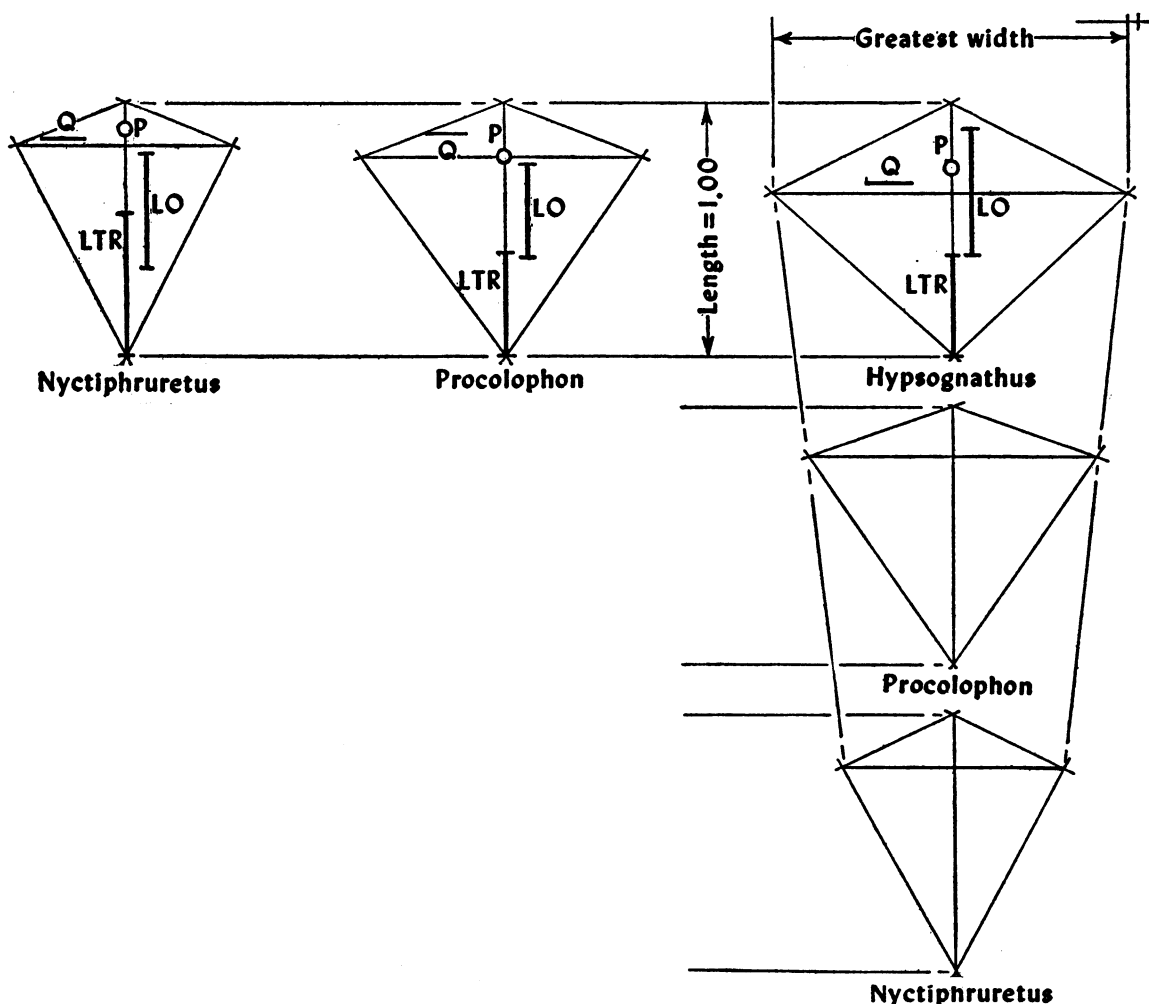
FIG. 5. Comparative diagrams to show the trends of development in the skull of the Procolophonidae, as illustrated by *Nyctiphruretus* (Upper Permian), *Procolophon* (Lower Triassic), and *Hypsognathus* (Upper Triassic). This figure shows: broadening of the skull (Permian through Triassic); elongation of the orbitotemporal opening (Triassic); shortening of the upper tooth row, correlated with reduction in number of teeth (Permian through Triassic); forward migration of quadrate-articular joint, correlated with shortening of the lower jaw (Triassic). Abbreviations: LO, length of orbit; LTR, length of upper tooth row; P, position of pineal foramen; Q, position of quadrate-articular joint. Not to scale; reduced to a uniform skull length.

plex extended from the pterygoids to the posterior and inner parts of the mandible.

Another interesting development in the orbital region of *Hypsognathus* is the upwardly directed orbits. This is a development the beginnings of which may be seen in *Procolophon*. In the South African form the orbits are essentially normal as to shape, but as to direction a certain divergence away from the more laterally directed orbits of the prim-
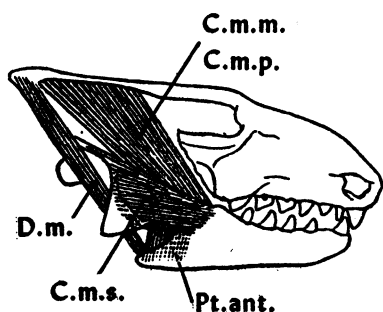

FIG. 6. *Hypsognathus fenneri* Gilmore. Diagram to show the probable arrangement of muscles controlling the movements of the lower jaw. This shows how the bulging of the heavy temporal muscles was accommodated by the development of the elongated orbitotemporal opening. Abbreviations: C.m.s., capiti-mandibularis superficialis; C.m.m., capiti-mandibularis medius; C.m.p., capiti-mandibularis profundus; D.m., depressor mandibulae; Pt.ant., pterygoideus anterior. Natural size.

itive cotylosaurians is to be seen. This is more pronounced in certain Triassic procolophonids of central Europe, still more so in *Leptopleuron*, and it reaches an extreme in *Hypsognathus*. Indeed, it might be said that the orbits in the New Jersey form look almost straight up.

This change in the direction of the orbits was the result primarily of transverse growth in the skull, from the primitive Permian and Lower Triassic procolophonids to the most specialized Upper Triassic genera. As the skull broadened, it flattened out, and with this flattening there was an accompanying change in the pointing of the orbits from a lateral to an almost vertical direction. There is good reason to think that virtually none of this effect may be attributed to crushing, but rather is a natural effect of evolutionary growth. This trend is shown by figure 7,

which consists of a series of cross sections showing the skull roof between the orbits, the angles at which the orbits are placed, and the angles at which the orbits are directed.

It might be supposed from the upwardly directed orbits that *Hypsognathus* had eyes that looked up, but such was not necessarily the case. Together with the flattening and widening of the skull, which was essentially the cause of the orbital depression, there was probably a compensation in the eyeball and its muscles so that it was directed essentially horizontally, even though the orbit was placed at a low angle. For instance, it will be seen by figure 8 that the direction in which the orbits are directed in *Hypsognathus* is not much different from what is the case in *Alligator*. Yet the eyes of the alligator look horizontally, and by inference the same probably was true in this little Triassic reptile.

Hypsognathus shows a most interesting development of the spikes or points on the sides of the skull, and in this regard it is clearly more specialized than any of the other procolophonids. Opposite the anterior border of the orbits, just below the juncture of the maxilla and the jugal, there is a prominent point, which evidently is developed upon the anterior edge of the jugal bone. There is a similar point on the skull of *Leptopleuron*, and in both genera it is the termination of a sudden downward sweep of the maxillary-jugal arch. This point is opposite the last maxillary tooth and is placed at some distance laterally from this tooth, so that there is an arcade between the point and the tooth.

Behind this anterior point there are four prominent spikes, probably of quadrotojugal, and possibly in part of quadrate, origin. Of these, the lowest spike arises just externally to the quadrate articulating surface, and it projects forward. There might be mentioned in addition a small projection or point, also directed forward, which is placed just internally to this spike. Above this are two spikes, one in front of the other, and both directed laterally. Finally, above the anteriormost of these two spikes there is another large spike, also directed laterally. Certainly it seems logical to suppose that these three large, laterally directed spikes are of quadratojugal origin. Altogether these spikes make a bristling array, and they are perhaps more adequately shown

by figures than they can be described in words. (See fig. 9, and pls. 27, 28.)

It is interesting to notice in this connection that the development of these spikes seem-

ingly has caused a great expansion of the quadratojugal bone, so that this element, instead of occupying its primitive position in front of the quadrate, has now extended both
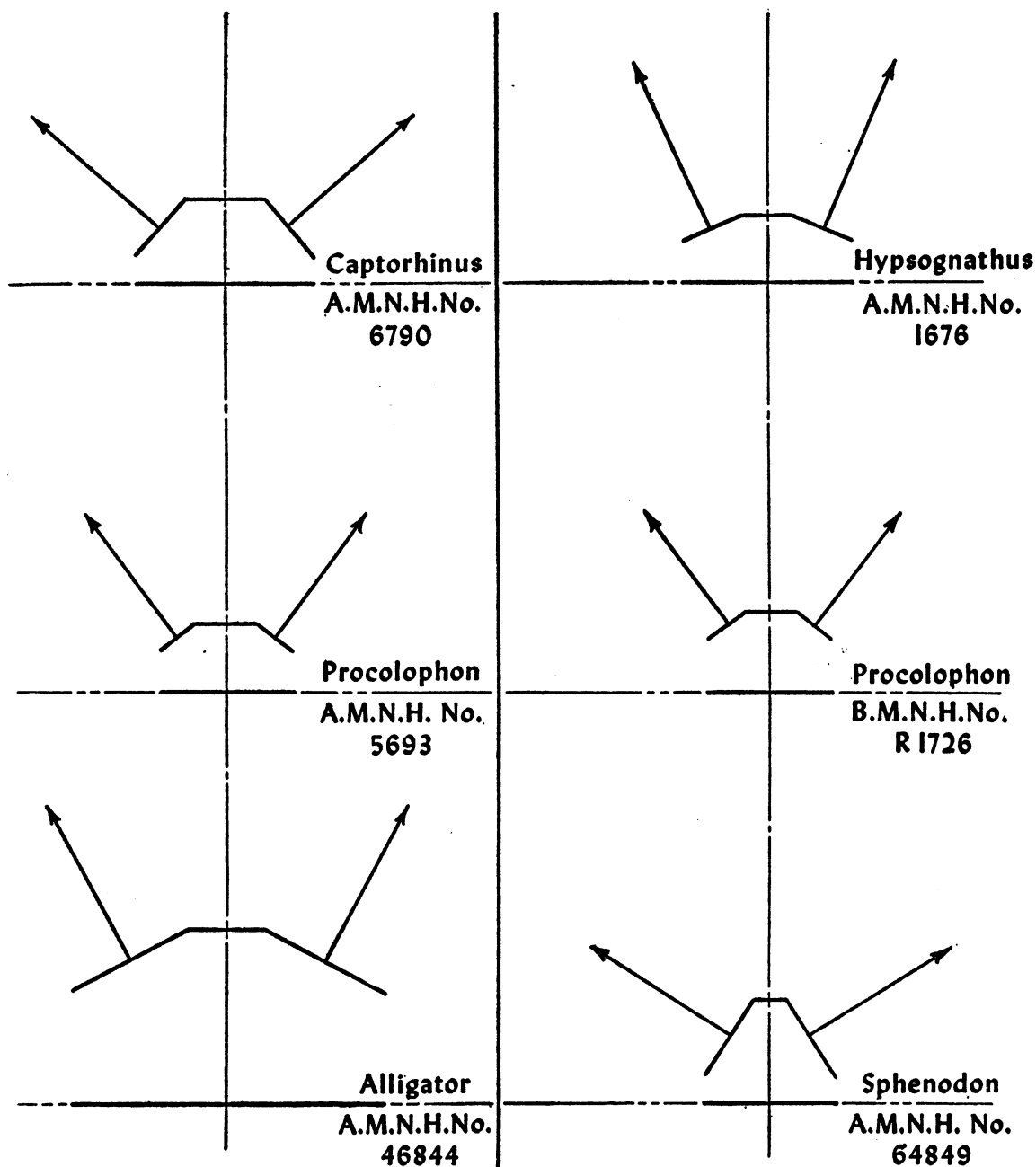

FIG. 7. Diagrammatic cross sections of skulls to show differences in the angle of the orbits in certain reptiles, as indicated. The skull roof between the orbits is shown by the upper horizontal line, placed at the proper distance above the palate, shown by the lower horizontal line. The arrows are drawn at right angles to the orbits.

in front of and behind the quadrate. In fact, its anteroposterior diameter represents a considerable fraction of the total skull length.

The postero-external corner of the skull forms a sharp angle, which is developed either on the quadratojugal or on the tabular bone,

H-Hypsognathus
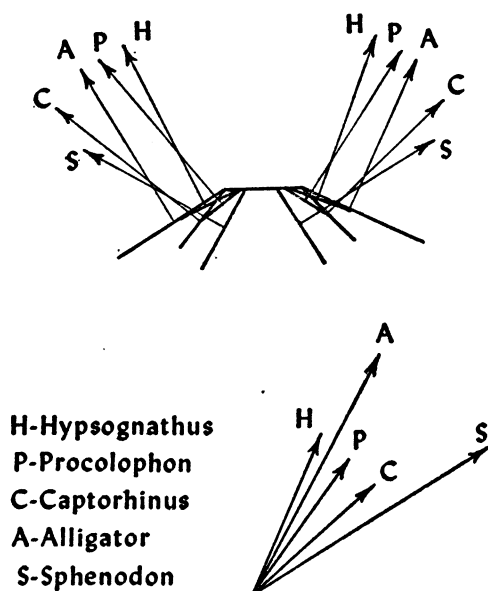P-Procolophon
C-Captorhinus
A-Alligator
S-Sphenodon

FIG. 8. Diagrammatic cross sections of skulls to show the differences in the angles of the orbits in certain reptiles, as indicated. In the upper figure the diagrams shown in figure 7 are superimposed. The lower figure shows a comparison of the directions toward which the orbits face. These diagrams indicate the narrow skull of *Sphenodon*, with the orbits facing laterally, as compared with the flatter skulls and more upwardly directed orbits of the procolophonids. Also shown are the progressive flattening of the skull and upward turning of the orbits in a series from *Captorhinus* to *Procolophon* to *Hypsognathus*.

a question that will be discussed at greater length below.

Thus there are seven points or spikes on each side of the skull, including the anterior point on the jugal and the postero-external angle of the skull. In *Leptopleuron* there are four such points, seemingly homologous with four of the points in *Hypsognathus*. According to von Huene's figures, there are three spikes in *Sclerosaurus*, all on the back portion of the skull and all pointing in a general backward

direction. Of these, he suggests that the largest spike originates upon the "supratemporal," while the two smaller spikes are of squamosal and quadratojugal relationships. In *Procolophon* certain large skulls, those of the so-called "males," show an enlargement of the quadratojugal to form a sort of backwardly directed process. In this genus, too, the tabular is pointed. Finally, in *Nyctiphruretus* the quadratojugal is expanded laterally as a very small point. Therefore there has been a progressive evolutionary development in the number and the size of the spikes on the skull of the Procolophonidae from Permian through Upper Triassic times.

What was the purpose of this progressive specialization in the procolophonids? Perhaps the spikes of the most advanced forms were of a defensive nature, at least in part; certainly they would seem to be analogous to the points or "horns" on the skull in certain modern lizards, such as *Phrynosoma* of North America or *Cordylus* of Africa. It is probable that *Hypsognathus*, a cotylosaur, played the same role in the reptilian ecology of Triassic North America that some lizards do at the present time, and therefore it is not surprising if we find adaptations in this little cotylosaur that foreshadow in a fashion the specialization that took place in some of the Squamata of later days.

Up to this point nothing has been said about the interrelationships of the skull bones. Unfortunately, in the best of the three American Museum skulls, A.M.N.H. No. 1676, the sutures are not satisfactorily shown. This is owing to the mode of preservation, whereby the surface of the skull is fragmented and flaky and therefore crisscrossed by multitudinous cracks, so that any sutures are so obscured by this pattern of fine lines as to be well-nigh invisible. Consequently the skull is rather deceptive, because, since it is beautifully and completely preserved as to form, it at first glance gives the impression of affording complete osteological information, The impression is illusory; the skull does show us very well the manner in which *Hypsognathus* became specialized over other procolophonids as regards size, proportions, the development of spikes, and the like, but as to the changes in the individual skull bones that must of necessity have been correlative with the

changes in the skull, we must for the most part rely upon speculation.

Luckily, some sutures do show up on the two other skulls, namely, A.M.N.H. Nos. 1677 and 1678, but these skulls are so incompletely preserved that the evidence afforded by them is not extensive. For instance, No. 1677, a very fine palate, shows the relationships between premaxillaries, jugals, quadrates, and palatines, evidence which is supplemented to some extent by No. 1678.

formed coordinates as do the sutures in the skull of *Procolophon* with the original grid.

It is felt that this restoration gives a reasonably accurate interpretation of the interrelationships of the superior skull bones in *Hypsognathus*, since from the deformed Cartesian diagram it would appear that the skull of *Hypsognathus* became specialized over the primitive procolophonid condition mainly by a broadening of its lateral and posterior regions, so it is logical to think that there
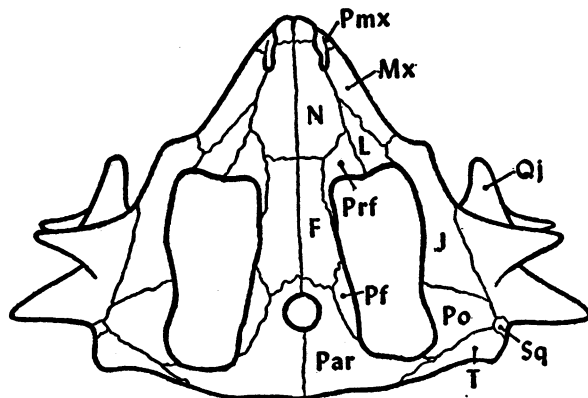

FIG. 9. *Hypsognathus fenneri* Gilmore. Dorsal view of the skull showing the suggested arrangement of the bones. Abbreviations: F, frontal; L, lacrimal; J, jugal; Mx, maxilla; N, nasal; Par, parietal; Pf, postfrontal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Qj, quadratojugal; Sq, squamosal; T, tabular. Natural size.

As for the skull roof, there is nothing much to be done except to attempt a reconstruction, which is shown in figure 9. In making this restoration, the method of deformed Cartesian coordinates was employed. The skull of *Procolophon* was used as a basis for the interpretation, and in this case Broili and Schroeder's figure, published in 1936, was utilized. A system of rectangular coordinates was superimposed upon this figure. Then upon a dorsal view of the skull of *Hypsognathus* the intersections of the lines forming the grid covering the *Procolophon* skull were plotted so that they occupied as nearly as possible similar topographic positions in the two skulls. When the points were connected deformed coordinates were obtained. Then sutures were drawn in, having as nearly as possible the same relationships with the de-

has been a correlative broadening of the skull bones lateral and posterior to the orbits. This has involved in particular the jugal, quadratojugal, postorbital, and tabular. As can be seen, the quadratojugal is assumed to be modified by the development of the spikes. The squamosal, already small in the more primitive procolophonids, seemingly has been further reduced by the lateral growth of the tabular and the posterior development of the quadratojugal.

The ventral aspect of the skull in *Hypsognathus* is at the same time very interesting and very baffling. Its interpretation must be based mainly upon A.M.N.H. Nos. 1676 and 1677, with some minor supplementary information furnished by No. 1678. As aids in the study of this region, other genera of Cotylosauria are helpful, particularly *Nyctiphruretus*

(as figured by Efremov), *Procolophon* (especially as it is figured by Broili and Schröder in their paper of 1936), *Diadectes*, and, to a lesser degree, *Captorhinus* and *Seymouria* (the latter as described and figured by White).

region. It is difficult to believe that the palate would be so completely open as this, although the internal nares may have been relatively large; therefore we are forced to the conclusion that a part, at least, of this fenestration is artificial, perhaps the result of poor preser-
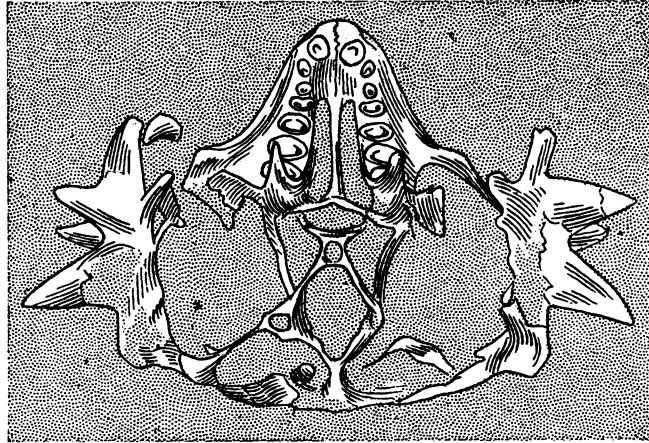

Fig. 10. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1676, palatal view of skull as exposed in matrix after preparation. Natural size.

The evidence shown by the American Museum specimens of *Hypsognathus* as to the structure of the palate is not very satisfactory. In No. 1676 the palate appears to be fenestrated by two very large choanae, one on either side, which run from the general vomer region far back into the pterygoid

vation caused by a breaking down of the thin bones of the palatines and pterygoids either before or during the process of fossilization. To increase the difficulties of study and interpretation, this palate is partly hidden by the mandible, which is solidly fastened to the skull by the interlocking upper and lower teeth.
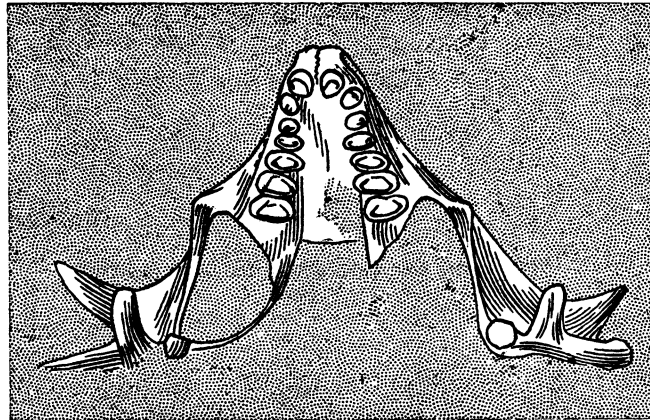

Fig. 11. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1677, palate as exposed in matrix, after preparation. Natural size.

The palate in No. 1677 appears to be solid, and for a time this was indeed very puzzling to the author. However, after conversations with Mr. Falkenback, the preparator, the matter was made clear. When this specimen was first found, the anterior part of the skull was exposed from above. The fossil consisted in part of the original bone, in part of a natural mold in the rock matrix. Mr. Falkenbach worked the specimen out first from the dorsal side. Then he flowed tinted plaster into that part of the specimen preserved as a natural mold. Finally he turned it over and removed the rock still adhering to the fossil. Thus the palatal and quadrate regions were beautifully exposed, partly as the original bone, partly as plaster which had filled the natural mold. One could say that the preparation of the specimen paralleled in part the "waste mold" method of casting.

It so happens that the palate in this specimen was originally present only as a natural mold, so that it is now preserved only by the plaster which was run into that mold. Therefore, unless one is acquainted with these facts as to the preparation of the specimen, one is apt to be misled by its appearance. Since this palate is of plaster, the interior nares are no longer preserved; indeed it is unlikely that they were preserved in the natural mold as it originally existed. Consequently the palate has a completely solid appearance which is deceptive as far as its true nature is concerned.

One can only speculate upon the basis of the material now at hand, but it is probable that *Hypsognathus* had a pair of rather large internal nares as is the case in *Procolophon*. Such would seem to be the case from the evidence afforded by No. 1676. Moreover, it would appear from this specimen that the anterior borders of the choanae were opposite the first broad maxillary tooth—that the palate was solid back to this point.

In front of these nares are the palatal plates of the premaxillae; between them are the vomers and probably an anterior extension of the pterygoids. Where the palatines fitted in it is difficult to say.

The back of the palate in this animal is perhaps more of an enigma than its anterior region, because the evidence afforded by the two specimens, Nos. 1676 and 1677, cannot be completely correlated. In the skull, No. 1676, there are well-developed flanges, arising on either side just medially to the last cheek tooth and curving down in a semicircular sweep. These processes, which terminate acutely, extend down to a point below the bases of the posterior dentary teeth (when the jaws are closed), and they fit closely against the inside of each mandibular ramus. They are certainly pterygoid in origin, and they may include the ectopterygoids as well. It is as if the pterygoids-ectopterygoids of *Procolophon* had drawn together and folded down so that their free borders were directed ventrally rather than laterally. As shown by No. 1676, these flanges served not only for the attachment of strong pterygoideus anterior muscles, but also as limiting buttresses to restrict the jaws to an orthal plane of motion, thereby eliminating any large amount of lateral swing. The wear on the upper cheek teeth of No. 1677 indicates that there was very little lateral movement during occlusion. An analogous condition is seen in *Sphenodon*, in which there is a lateral and downwardly directed process of the pterygoid combined with a similar process of the ectopterygoid, the two together forming a guide against which the inner surface of the ramus works during closure of the jaws.

The baffling thing about this is that the palate, No. 1677, in which the dentition and portions of the skull as far back as the quadrates are well preserved, shows no trace of this pterygoid-ectopterygoid flange. The place where it should arise on either side, namely, the inner surface just inside of the posterior cheek teeth, is quite smooth, and there is no evidence whatsoever that the flange has been broken away. It just is not there. In this specimen there is a long quadrate ramus of the pterygoid, curving back to meet the quadrate.

How the difference between the two specimens is to be explained is at present an insoluble problem to the writer. From the resemblance of the two specimens in all other particulars, and from the fact that they were found close together in the same quarry, one cannot escape the conclusion that they are conspecific. Yet there is this anatomical dif-

ference which can hardly be explained upon grounds of sexual dimorphism or even of individual variation, since it concerns a deep-seated basic character, not an external feature. At the present time there is little to be said but that the two specimens are quite different in this respect.

Midway between the pterygoid flanges in No. 1676 the median portions of the pterygoids turn down abruptly, at what is virtually a right angle to the palatal plane. Two wings are sent out to right and to left, and

ably is in part misleading. Even supposing there is a solid connection between the median and lateral portions of each pterygoid, the bone is still made complex because of the quadrate ramus and, in addition, the backwardly produced process (here identified as pterygoid) running back to the neurocranium. At the present time this seems to be the most logical interpretation of the material.

The articulating portion of the quadrate consists of a rounded ball. Lateral to it is the ventral, forwardly produced point or process
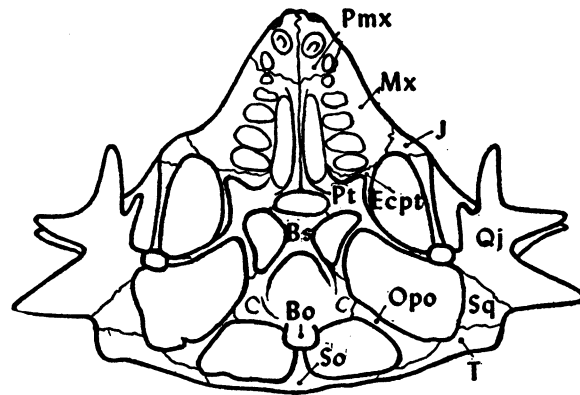

FIG. 12. *Hypsognathus fenneri* Gilmore. Palatal view of the skull showing the suggested arrangement of the bones. Abbreviations: Bo, basioccipital; Bs, basisphenoid; Ecpt, ectopterygoid; J, jugal; Mx, maxilla; Opo, opisthotic; Pmx, premaxilla; Pt, pterygoid; Qj, quadratojugal; So, supraoccipital; Sq, squamosal; T, tabular. Natural size.

these form the anterior border of a forwardly directed interpterygoid fossa. On either side, where these median wings join the pterygoid flanges, there are two backwardly produced processes, also presumably of pterygoid relationships, which go back on either side to meet the neurocranium.

From the above description it will be seen that the pterygoids in *Hypsognathus* are interpreted as rather complex bones. This complexity may not be quite so great as indicated, if the posterior portions of the palatal vacuities are artificial rather than real. For instance, as shown in the palate of No. 1676, it would appear that these vacuities or choanae are produced so far back as to separate the pterygoid flanges from the median portions of these bones, an appearance that prob-

which is associated with the group of spikes on the quadratojugal. The quadrate articulation in *Hypsognathus* is about two-thirds of the way back on the skull, as measured from front to back. Above it are the jugal and the quadratojugal, the latter exposed in the ventral view as the three lower of the four large lateral spikes. Presumably the lower surface of the squamosal would be posterior to the jugal, but nothing can be said as to its exact limits. It is supposed that the lower surface of the tabular formed the postero-external corner of the skull.

From the squamosal-tabular region to the middle region, the back border of the skull on its ventral surface was probably formed by the supraoccipital, while a bar running from a point about midway between the midline

and the postero-external corner to the neuro-cranium possibly represents the opisthotic or paroccipital.

The bottom of the braincase, as represented by the basioccipital, basisphenoid, and parasphenoid, is missing in skull No. 1676. The braincase is revealed as a comparatively large cavity, as is typical in the procolophonids, pierced dorsally by the large pineal foramen.
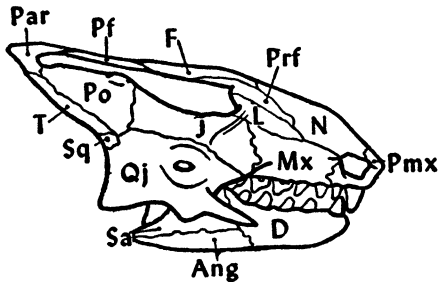

FIG. 13. *Hypsognathus fenneri* Gilmore. Lateral view of skull and mandible, showing the suggested arrangement of the bones. Abbreviations: Ang, angular; D, dentary; F, frontal; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; Par, parietal; Pf, postfrontal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Qj, quadratojugal; Sa, surangular; Sq, squamosal; T, tabular. Natural size.

A reconstructed side view of the skull is shown in figure 3 of plate 27 and also in text figure 13. It should be pointed out that in this latter figure, as in figures 9 and 12, the location of the sutures are for the most part hypothetical. It is felt, however, that a careful study of the material at hand and its comparison with similar materials of other procolophonids make the placing of these sutures approximately correct. In working out this diagram particular attention was given to the problem of changes of proportion within the skull during evolutionary development, a procedure that was followed in drawing the diagrams of the skull as seen in dorsal and ventral views, and already explained in a preceding paragraph.

Especially noticeable in the side view of the skull is the comparative shortness of the lower jaw, and of course the forward placing of the quadrate on the skull. As already mentioned, the quadrate articulation in *Hypso-*

gnathus is about two-thirds of the way back on the skull, which may be contrasted with the very posterior position of the articulation in the more primitive procolophonids, and in most of the other cotylosaurs, for that matter. In this respect *Hypsognathus* may be compared with *Diadectes* in a very general way, for in this latter genus the quadrate articulation also has moved forward to a certain extent. In *Diadectes*, the articulation has also pushed ventrally.
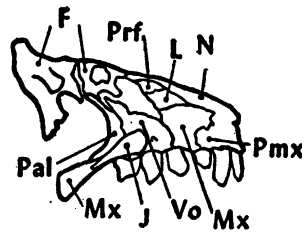
A comparison of the position of the quad-

FIG. 14. *Hypsognathus fenneri* Gilmore. Diagram to show an interpretation of the elements of A.M.N.H. No. 1678. Abbreviations: F, frontal; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; Pal, palatine; Pmx, premaxilla; Prf, prefrontal; Vo, vomer. Natural size.

rate in three genera of procolophonids, *Nyctiphruretus*, *Procolophon*, and *Hypsognathus*, is shown in figure 5, in which various other skull proportions are also compared.

At this place some attention should be given to specimen A.M.N.H. No. 1678, which is shown in figure 2 of plate 27. The probable relationships of the bony elements in this partial skull are shown by text figure 14.

In this specimen only the front portion of the skull is preserved, and it is exposed as a sort of combined lateral and median view. As in the other specimens, interpretations of individual bones are difficult, due in part to crushing and in part to the obliteration of suture lines, but with these considerations in mind, the following explanation of the material is offered.

It would seem that the anterior third of the specimen consists of the external surface pushed in against the median region of the skull. Thus we see here the right premaxilla and a part of the maxilla, above the anterior four teeth. Also, in this region there are seem-

frontal bones showing, the probable interrelaingly surfaces of the nasal, lacrimal, and pretionships of which are indicated in figure 14.

It is even difficult to be certain as to the identity of the six teeth seen in this specimen. Are these the first two premaxillary teeth and the following four maxillary teeth, or are the first two teeth the right and left first premaxillary teeth crushed against each other, in which case the following teeth are the second right premaxillary tooth and the succeeding three maxillary teeth? Of the two interpretations, the latter one appears to be more nearly correct to the writer.

External to the last two teeth showing in this specimen is a bony protuberance which is taken to be a part of the jugal. There appears to be a suture between this bone and the maxilla internal to it.

An interesting feature of this skull is a vertical bony plate extending up into the interior region of the skull above the posterior three teeth, the plate being very definitely divided into anterior and posterior portions by a vertical suture. This is interpreted as the right-hand member of paired septae forming the external walls for the nasal passage. The anterior bone of this septum would seem to be the vertical plate of the vomer, while the posterior bone, joining it, is here regarded as of palatine origin.

At the back of the specimen, dorsally, is what is taken to be the frontal bone, with a median interorbital septum extending down to meet the posterior tip of the vomer-palatine septum. It shows some complexities which in the present state of the specimen are difficult to interpret with any degree of satisfaction.

There are seven upper teeth on each side, all of which appear to be fully acrodont. There has been some divergence of opinion as to this character in the teeth of the Procolophonidae, certain authors maintaining that the teeth are acrodont, others that they are thecodont. Boulenger, in his description of *Leptopleuron* [*Telerpeton*], stated that "the teeth were implanted in sockets, not acrodont as believed by Huxley" (Boulenger, 1904, p. 473). However, the bulk of the evidence indicates that the condition of the teeth in the Procolophonidae tends more towards acro-

donty than towards thecodonty. Thus, Broom had the following to say on this subject:

"The condition of the teeth I do not look upon as a character of much importance in the matter of broad classification, but the teeth in *Procolophon* are by no means thecodont in the ordinary sense. Owen, in 1876, rightly stated that 'the base of the tooth seems to be confluent with the osseous substance of the jaw'; and Lydekker, in 1890, stated that the marginal teeth are 'completely anchylosed to the bone.' Most likely in the young condition the teeth developed in sockets, but in the adult they must be regarded much more acrodont than thecodont" (Broom, 1905c, p. 216).

In a later paragraph of this same paper Broom states that "the teeth cannot be regarded as thecodont, being nearly as typically acrodont as in *Sphenodon*" (Broom, *loc. cit.*).

Broili and Schröder discussed this problem at some length in 1936 and came to the conclusion that in *Procolophon* the teeth are more or less intermediate between the acrodont and thecodont condition, in other words, that the teeth in this genus are *protothecodont*. This conclusion was based upon their observation that while the teeth seem to show attachment to the bone they nevertheless are implanted to a certain extent and in addition have pulp cavities.

Incidentally, it might be pointed out that the teeth of the primitive Permian procolophonid, *Nyctiphruretus*, are acrodont, according to Efremov. Therefore any departure from this condition in the Procolophonidae must be regarded as a specialization.

Of the seven upper teeth, the anterior two are attached to the premaxillary bone, the remainder to the maxillary. Among the Procolophonidae, *Hypsognathus* has the most specialized dentition, as regards not only the reduction in the number of teeth, but also in the transformation of the posterior maxillary teeth to form broad cutting blades. In these respects it is approached closely by *Leptopleuron* [*Telerpeton*].

The reduction in the upper dentition in that branch of the Procolophonidae terminating in *Hypsognathus* may be indicated as follows:

PLATES 25-33

1. General view of the quarry in which the American Museum materials of *Hypsognathus* were found. A.M.N.H. No. 1676 seemingly came from the quarry floor, at the foot of the talus and near the left side of this picture. A.M.N.H. No. 1677 was found on the top of the quarry in a loose block. A.M.N.H. No. 1678 was found on the quarry floor near the middle of the picture. Other specimens, all very fragmentary, were scattered at various points through the quarry

2. Quarry face, showing the massive, blocky sandstone layers

1

2

3
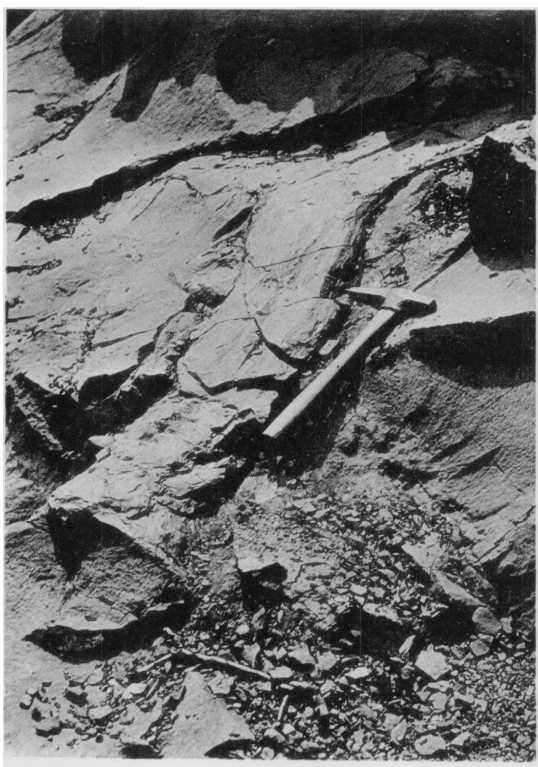
1. Detail of the quarry face, showing a lens of friable shale between the massive sandstone layers
2. A secondary "mud dike" formed in a joint within the blocky sandstone
3. Detail of the quarry face showing the alternation of heavy sandstones and friable shales
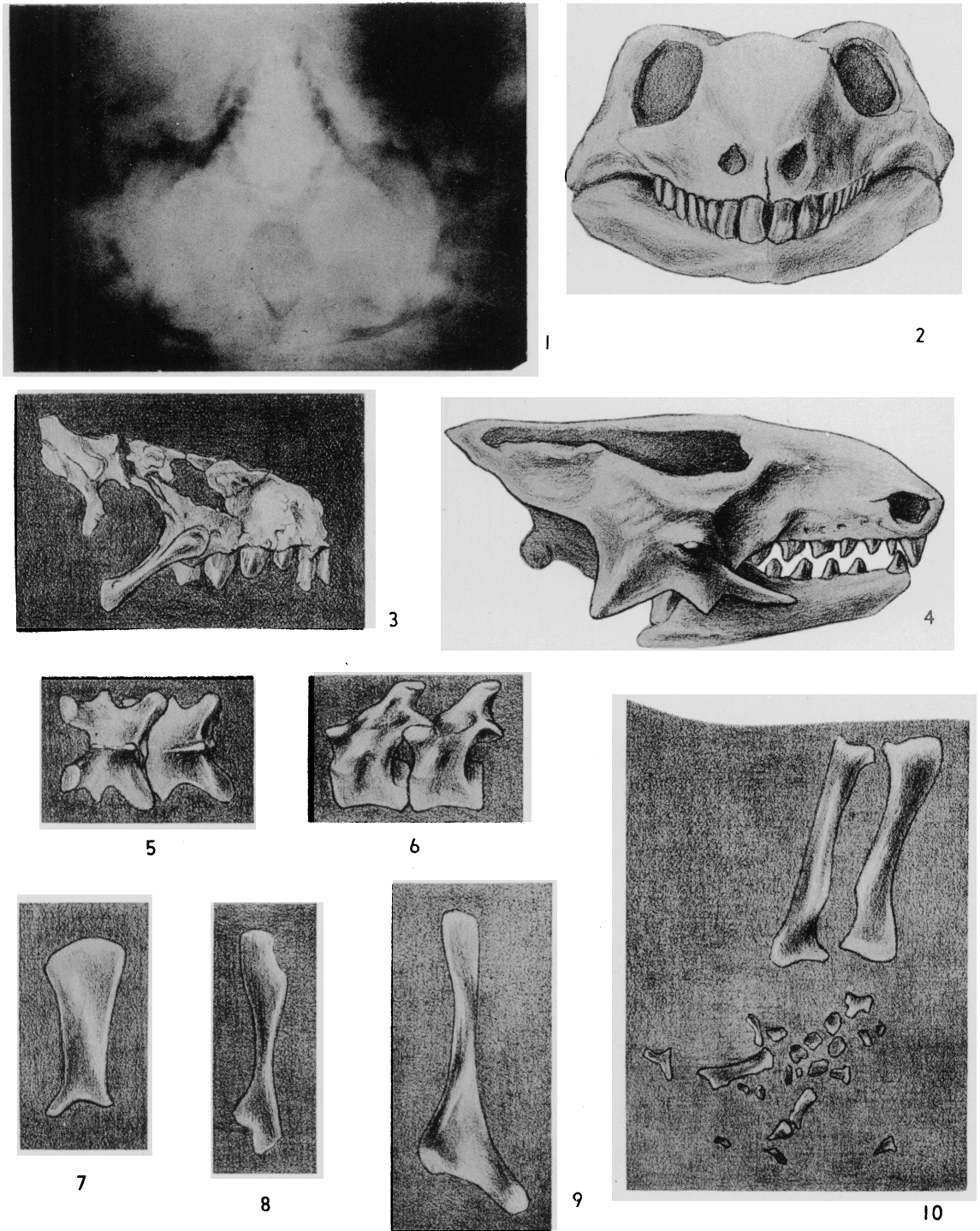
1. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1676. X-ray photograph of skull in matrix, before preparation. ×1
2. *Procolophon trigoniceps* Owen. A.M.N.H. No. 5693. Skull, front view, for comparison with the similar view of *Hypsognathus fenneri* shown in plate 28. × 1½
3. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1678. Partial skull, lateral view, as exposed in matrix, after preparation. For an interpretation of this specimen, see text figure 14. × 1½
4. *Hypsognathus fenneri* Gilmore. Restoration of the skull and mandible as seen in lateral view. ×1½
5–10. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1676. Various portions of the postcranial skeleton as exposed in the matrix, after preparation. × 1½. 5, Eleventh and twelfth presacral vertebrae, dorsal view 6, The same, lateral view. 7, Right scapula, internal surface. 8, Right humerus, ventral surface. 9, The same, dorsal surface. 10, Right radius, ulna, and manus, ventral surface
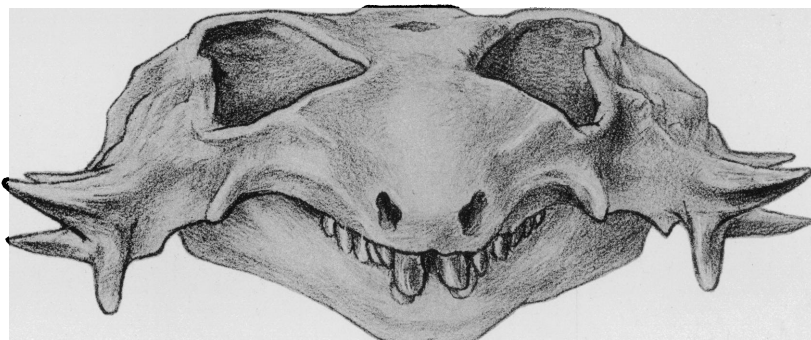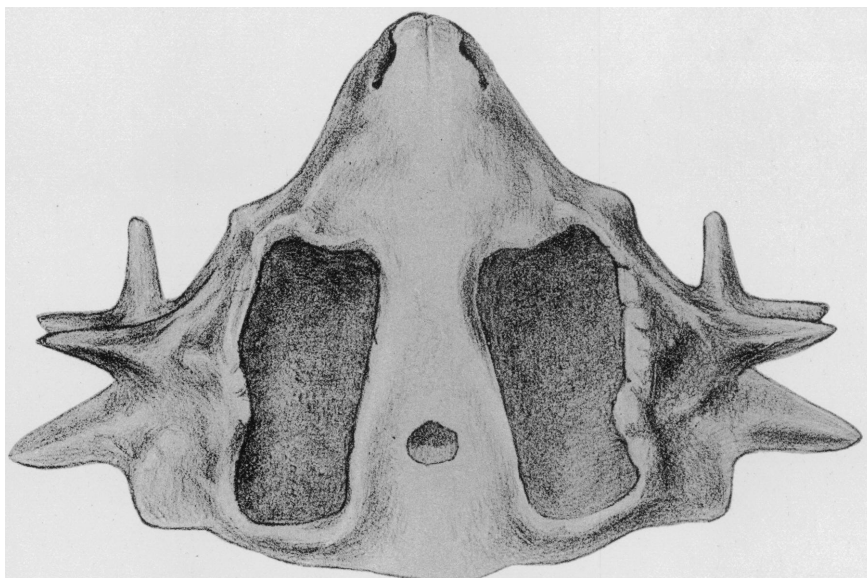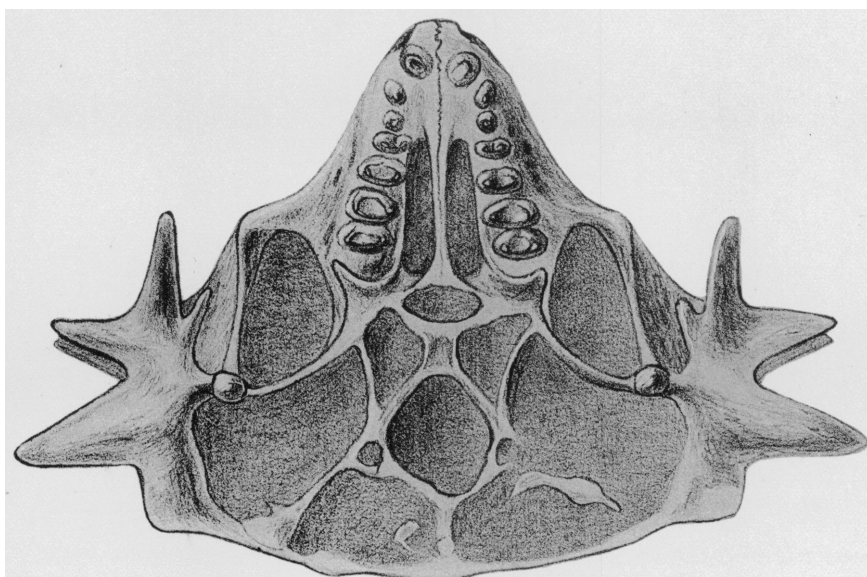
Hypsognathus fenneri Gilmore. A.M.N.H. No. 1676. Skull.
1. Front view (compare with pl. 27, fig. 2, to see the degree of specialization of *Hypsognathus* over *Procolophon*)
2. Dorsal view
3. Palatal view
All figures ×1½
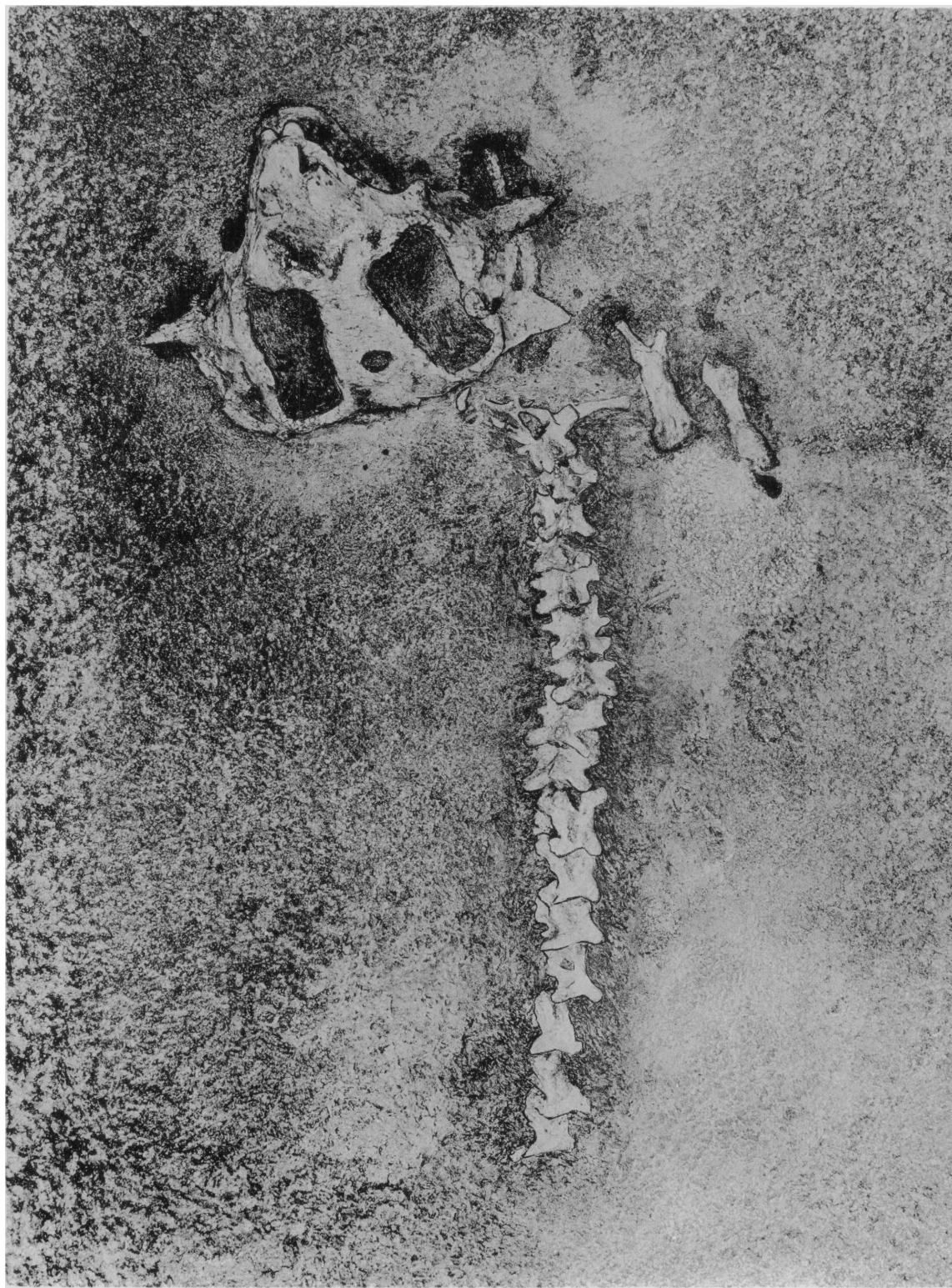
Hypsognathus fenneri Gilmore. A.M.N.H. No. 1676. Skeleton as exposed in matrix, after preparation. Dorsal view, ×1
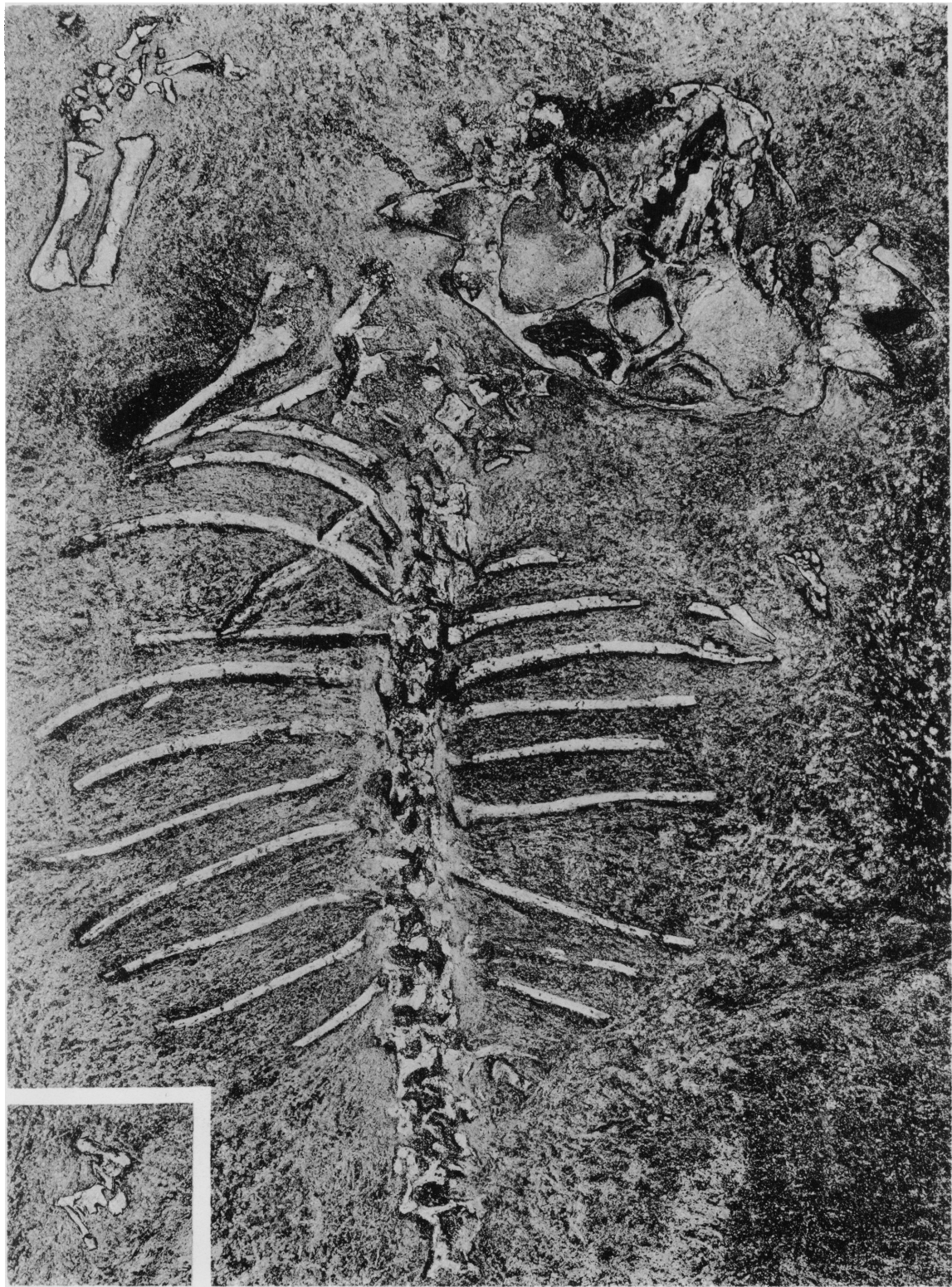
Hypsognathus fenneri Gilmore. A.M.N.H. No. 1676. Skeleton as exposed in matrix, after preparation. The last preserved presacral vertebrae, separated from the remainder of the series, are shown in inset. Ventral view, ×1
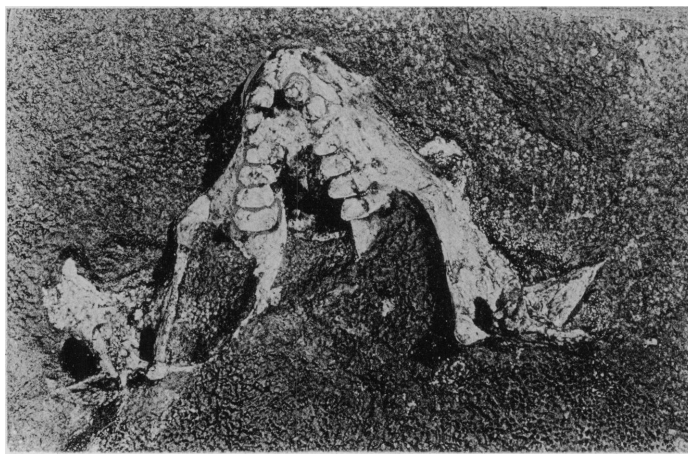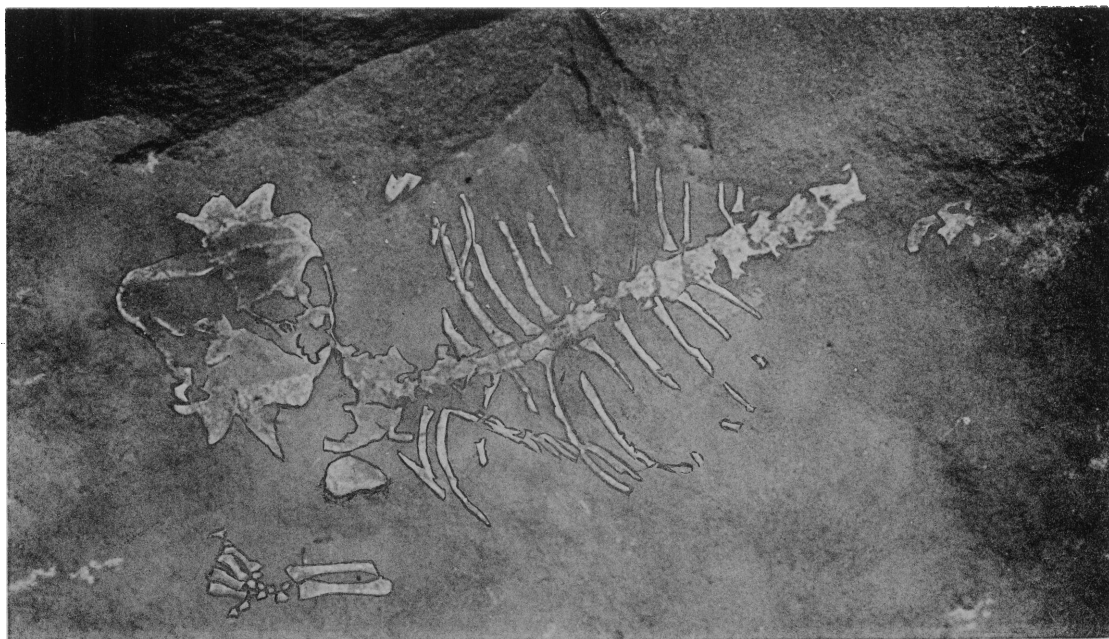
Hypsognathus fenneri Gilmore

1. A.M.N.H. No. 1676. Ventral view of the skeleton as it was first discovered. ×½
2. A.M.N.H. No. 1677. Anterior portion of skull as exposed in matrix, after preparation. Palatal view, ×1
3. A.M.N.H. No. 1678. Anterior portion of skull as exposed in matrix, after preparation. Lateral view, ×1

Hypsognathus fenneri Gilmore. U.S.N.M. No. 11643. Type specimen. This is an impression in the rock of the lower surface of the mandible and the axial skeleton, anterior to the pelvic region. There is no fossil bone present. ×1
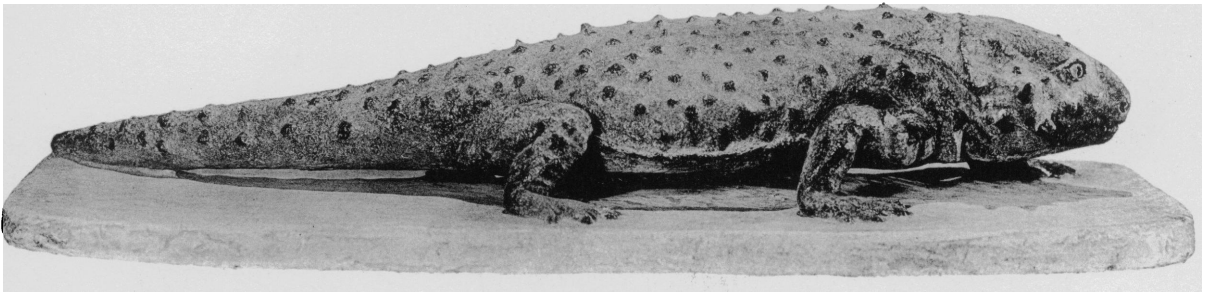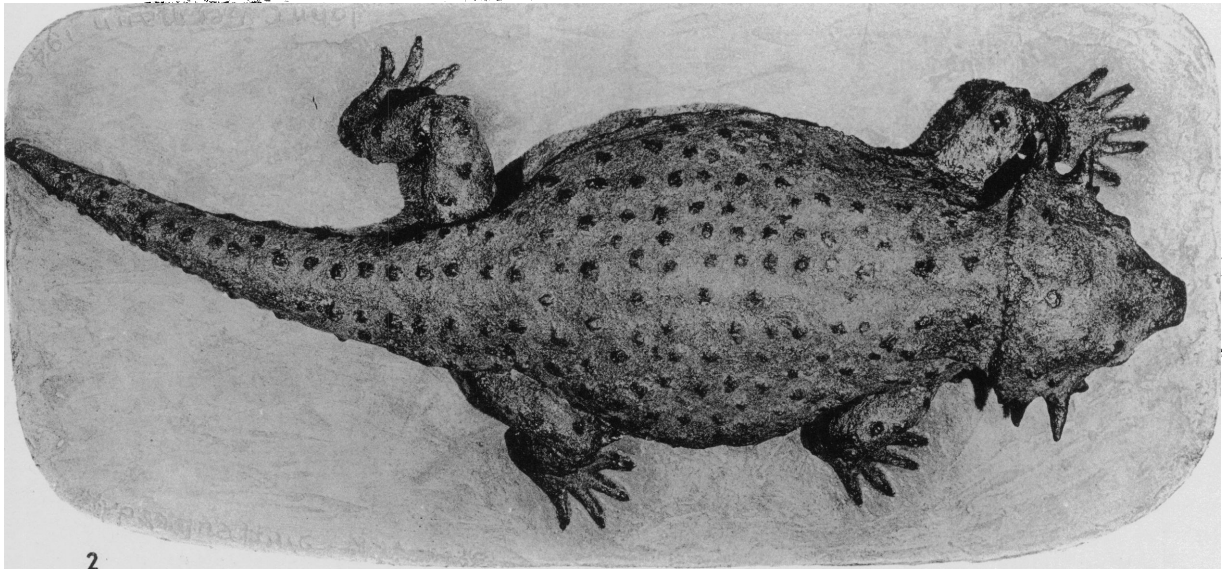
Hypsognathus fenneri Gilmore.   Restoration by John C. Germann.   1, Lateral view; 2, dorsal view.   About ×½

Nyctiphruretus	*Procolophon*	*Sclerosaurus*	*Leptopleuron*	*Hypsognathus*
Total 30	11	9	7	7
Pmx. 9	4		2	2
Mx. 21	7		5	5

The anterior premaxillary tooth is enlarged and approximately round in cross section. During occlusion the anteriormost of the dentary teeth closed along the posterior surface of this upper tooth, so that this surface is worn flat or, rather, it is slightly grooved, in a manner analogous to the wear of the incisor teeth in the rodents, among the mammals.

The second and third teeth, that is, the second premaxillary tooth and the first maxillary tooth, are almost round, the former being
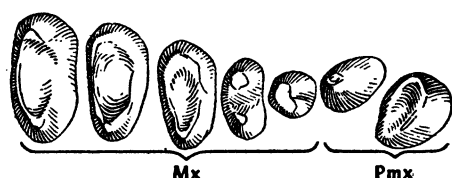
FIG. 15. *Hypsognathus fenneri* Gilmore. A.M.N.H. No. 1677, crown view of right upper teeth. Three times natural size.

much larger than the latter. Both of these teeth are worn along their inner surfaces by the dentary teeth's biting inside them. Thus it is evident that the first three teeth in the upper jaw bit over the anterior teeth of the dentary, and because of their arrangement in an arc around the front of the skull they must have limited the final phase of occlusion to an almost strictly orthal motion.

The four posterior teeth are broadened progressively from front to back, so that the last of these teeth, the fifth maxillary tooth, is approximately twice as wide as the first of the broad teeth, the second maxillary tooth.

The transverse cutting edge of the chisel-like teeth is slightly convex posteriorly, and it forms the back border of the tooth. On the anterior face of the tooth, in front of this posterior cutting edge, is a semicircular pocket facing upward and bounded on either side by a sloping front surface.

In the one specimen containing lower teeth,

namely, No. 1676, these teeth are very difficult to see because the lower and upper dentitions are tightly occluded. From what can be seen in lateral view, externally and internally, certain facts as to the lower dentition can be ascertained.

In the first place, it is evident that there are five dentary teeth, just as is the case in *Leptopleuron* [*Telerpeton*]. Moreover, it is evident that *Hypsognathus* is similar to the Scottish genus in that the anterior dentary tooth is an enlarged, rounded tooth, biting behind the enlarged premaxillary tooth, while the four remaining teeth are broadened as are the four posterior maxillary teeth. It seems evident that these broad lower teeth bite between the upper teeth, the first of the broadened dentary teeth occluding between the first and second maxillary teeth, the last of the dentary teeth between the fourth and fifth maxillary teeth.

It would appear that the form in the lower teeth is just the opposite to that in the uppers, that there is a high cutting edge forming the anterior border of the tooth and behind this a sloping posterior surface indented by a median pocket.
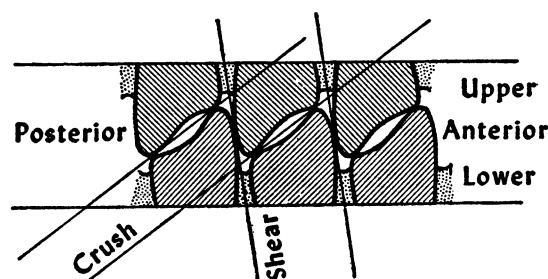

FIG. 16. Mechanics of occlusion between the upper and lower teeth in *Hypsognathus fenneri*.

Thus, when the upper and lower teeth came together, the cutting edges would slice past each other, the posterior edge of the upper teeth opposing the anterior edge of the following lower tooth. At the same time there would be a sliding motion between the slop-

ing surfaces of the teeth, between the anterior sloping surface of the upper tooth and the posterior sloping surface of the lower tooth immediately preceding it. Concomitantly the "pockets" would come opposite each other, as these sloping surfaces slid past each other. Therefore the food would be cut and sliced by the high cutting edges of the teeth, ground by the sliding surfaces, and pressed together by the pockets.

The mandible is of the characteristic procolophonid form and is distinguished by its relative heaviness. The horizontal rami are deep and thick, and the symphyseal region is blunt and rounded. The coronoid is high, and it thrusts up inside the jugal when the jaw is closed. Indeed, the upgrowth of the dentary and surangular to this high coronoid region indicates a considerable insertion for the capiti-mandibularis profundus, the temporal

portion of the capiti-mandibularis muscles. It is evident that there was considerable power in the jaws of this little reptile.

Gilmore demonstrated from the type specimen, in which the mold of the lower surface of the jaw is well preserved, that the postarticular process is short and wide. Moreover, his specimen shows that the large splenial fails to reach the symphysis; it also does not cover the anterior portion of the Meckelian groove.

As has already been shown, a cast made from the natural mold of the lower surface of the mandible in the type specimen fits very well with the American Museum material, so with the evidence as supplied by the type and by No. 1676 we are able to obtain rather complete information as to the structure of the lower jaw. This is pictured by text figure 13 and figure 4 of plate 27.

THE VERTEBRAE AND RIBS

There are 20 vertebrae in series behind the skull in specimen A.M.N.H. No. 1676 of *Hypsognathus*, while in addition there is another vertebra separated from the series, and located posteriorly and to one side of the twentieth vertebra. No other vertebrae are preserved in this specimen.

In *Nyctiphruretus*, the most primitive of the procolophonids, there are 25 presacral vertebrae, three sacrals, and 28 to 30 caudals. Watson, in his description of *Procolophon*, shows 26 presacral vertebrae and three sacrals. Huxley, in describing *Leptopleuron* [*Telerpeton*], stated that "it may be safely assumed that the cervicodorsal series contains not fewer than twenty, and not more than twenty-two vertebrae. There are certainly not more than two sacral vertebrae" (Huxley, 1867, p. 80). As against this it should be pointed out that Owen, in his original description of *Leptopleuron*, indicated 26 presacral vertebrae for this genus. (Owen, 1851.) Boulenger, in 1904, stated that "The number of praesacral vertebrae in specimen B was twenty" (Boulenger, 1904, p. 474). Still another interpretation was given by Gilmore, who said that "Telerpeton from the Triassic of Eligin [sic], Scotland, has 24 presacral vertebrae in the complete series, and from the

fragmentary evidence at hand it would seem that the specimen now before me [*Hypsognathus*] may have had an equal number of vertebrae in the complete presacral series" (Gilmore, 1928, p. 5).

Since *Leptopleuron* is specialized to a degree comparable with *Hypsognathus*, it seems probable that the vertebral formula may have been similar in the two genera. Whether this formula contained the 26 presacral vertebrae characteristic of *Procolophon* or showed a certain degree of reduction is a question that cannot be answered upon the basis of present available evidence. It is possible, however, that the 21 vertebrae preserved in the specimen at hand represent almost a complete presacral series.

These vertebrae are characteristically cotylosaurian, being amphicoelous and having very broad, heavy, neural arches. The neural arches of the anterior vertebrae in this series are beautifully exposed in the dorsal view of the skeleton. They show very well the broad character of the arches and the widely separated, horizontal zygapophyses, of which the anterior ones look up, the posterior ones look down. They show also short neural spines, somewhat expanded at their tops.

Behind the twelfth vertebra the vertebral

column has been twisted, so that oblique views of the left sides of the neural arches, rather than dorsal views, are shown by the specimen in dorsal aspect. These posterior presacral vertebrae, seen in partial side view, emphasize the fact that the vertebrae in *Hypsognathus* are relatively long as compared with the vertebrae in other cotylosaurians. A beginning of this lengthening in the vertebrae is to be seen in *Nyctiphruretus* and in *Procolophon*, so it is evident that the evolution of the Procolophonidae has been characterized by a limited but nonetheless definite drawing out of the vertebral column.

For instance, in a primitive cotylosaurian such as *Seymouria* the breadth of the neural arch at the posterior zygapophyses in the middorsal region is approximately the same as the length of three articulated neural arches. In *Nyctiphruretus* and *Procolophon*, owing to the elongation of the vertebrae, the neural arch breadth, measured in the manner defined above, is equal to the length of two articulated neural arches. In *Hypsognathus* the elongation has been carried further so that the breadth is equal to a length of about one and one-half arches. This lengthening can be seen in the ventral view of the specimen, in which the centra are exposed.

As seen ventrally, the centra appear to be broadened (as well as lengthened) and on each there is a low, median keel. On either side of this keel there is a depression, an inheritance of the "pinched in" region on the centra of primitive cotylosaurians such as *Seymouria*.

I have not been able to determine for certain the presence of intercentra between any of the centra in *Hypsognathus*. This accords with Gilmore's observation on the type, in which he was unable to find any evidence for intercentra. It also accords with the evidence afforded by *Leptopleuron*, the genus most closely related to *Hypsognathus*, for according to Boulenger, "Having had gutta-percha and wax impressions made of the specimen described by Huxley, and also from examination of the type specimen, I can state that intercentra were absent between the dorsal vertebrae . . ." (Boulenger, 1904, p. 474).

It might be said, however, that in the more primitive procolophonids intercentra were definitely present. Thus, Efremov shows well-developed intercentra between the centra in the presacral series of *Nyctiphruretus*, and in *Procolophon* "there are intercentra between all the presacrals" (Watson, 1914, p. 740). It is evident, therefore, that in the interval between Lower and Upper Triassic times the intercentra in the Procolophonidae were lost.

Because of the manner in which our skeleton of *Hypsognathus* is preserved, it is not possible to present a detailed description of the atlas and axis in this reptile.

Since the sacral and caudal vertebrae are not preserved in *Hypsognathus*, any remarks concerning them must be purely speculative. It is felt, however, that a brief discussion of the possibilities is in order at this place.

The evidence as to the number of sacral vertebrae in the procolophonids is conflicting. Huxley, in his description of *Leptopleuron*, made the statement that "There are certainly not more than two sacral vertebrae." No evidence was presented to support this rather categorical remark. Whether or not Boulenger was influenced by Huxley's opinion it is difficult to say; at any rate he figured *Leptopleuron* as having but two sacral vertebrae.

As opposed to this, the work of other authorities would seem to indicate three sacral vertebrae in even the most primitive procolophonids. Efremov shows three sacrals in the Permian form, *Nyctiphruretus*, while Watson shows a similar number in the Lower Triassic *Procolophon*. Because of the undoubtedly good evidence available to both Efremov and Watson, it is felt that their opinions should be given precedence over the earlier, and perhaps not well-substantiated, views of Huxley and of Boulenger. Certainly, since there were three sacral vertebrae in the most primitive of the procolophonids, there probably were at least three in such highly advanced types as *Leptopleuron* and *Hypsognathus*. As might be expected of a primitive form, *Nyctiphruretus* shows a fairly long tail, somewhat longer than the presacral series of vertebrae. As mentioned above, this tail consists of some 28 to 30 vertebrae.

In Watson's restoration of *Procolophon*, he indicates a short tail, some two-thirds the length of the presacral series of vertebrae and

consisting of about 20 caudal vertebrae. Von Huene has placed a very short tail on *Sclerosaurus*, but in his restorations of *Koiloskiosaurus* and *Leptopleuron* long tails are shown—just why, it is difficult to say.

In his description of *Leptopleuron*, Boulenger makes a statement to the effect that "The length of the tail is still unknown; but it was probably not much longer than in the type specimen figured by Mantell" (Boulenger, 1904). Boulenger, in his restoration of this animal, shows a short tail of about 17 vertebrae, having a length equal to about two-thirds of the presacral length. It might be said that Mantell considered the tail in this genus to be very short.

It is evident, therefore, that the Procolophonidae as a group were characterized by short tails, and there is every reason to believe that this was true in the case of *Hypsognathus*. Indeed, it is probable that *Hypsognathus* closely resembled *Leptopleuron* in this respect.

The American Museum specimen of *Hypsognathus* shows 12 ribs preserved on the left side and 15 on the right side. It is quite evident that there were more than 15 ribs on each side in this animal, but the exact number can only be guessed at.

The primitive procolophonid, *Nyctiphruretus*, as described and figured by Efremov, shows an interesting and rather unusual reduction in the number of ribs. According to this author there were no cervical ribs on the first three vertebrae, while the last five vertebrae preceding the sacrum also lacked ribs. Thus, in this animal having 25 presacral vertebrae, there were only 17 pairs of ribs. This is an unexpected specialization in so early a reptile, although considering the many other specializations shown by the procolophonids it may not be quite so unusual as it appears to be at first sight.

In *Procolophon*, as figured by Watson, only the last three vertebrae in the presacral series lacked ribs. If Efremov has interpreted his material correctly it would appear that *Nyctiphruretus* is somewhat off the main line of evolution leading to the later procolophonids, at least as regards this particular character. It should be pointed out, however, that in other respects this Permian form constitutes a most satisfactory structural ancestor for the Triassic procolophonids.

From the evidence of these early procolophonids, it seems likely that there was a certain amount of reduction in the number of ribs in *Hypsognathus*.

As in other procolophonids, the ribs of *Hypsognathus* are simply shaped and single headed. These ribs articulate with short transverse processes, which latter project on either side from the centra.

As preserved, the ribs are rather straight, giving to the body the appearance of being very broad and flat. Although this effect is to some degree deceptive and due in part to crushing, nevertheless the presence of certain anterior ribs on the right side, which show their natural curves, indicates that the body in *Hypsognathus* was very broad. In fact, with a broad, heavy body, a short tail, and a skull decorated with spikes on either side, *Hypsognathus* must have had in life the proportions and perhaps something of the appearance of a large "horned toad" (*Phrynosoma*).

THE FORE LIMB

Of the appendicular skeleton, only the right fore limb is adequately preserved.

The scapula is high and narrow, in which respect it resembles the scapula in other procolophonids, especially *Procolophon* as figured by Watson, and *Leptopleuron, Koiloskiosaurus* and *Sclerosaurus* as figured by von Huene. The bone, of which only one side is exposed, is not easy to interpret, especially since its lower portion is partially missing, while other bones have been crushed into this region. The surface exposed is here regarded as the medial side of the scapular blade. The anterior and posterior edges of the blade are comparatively straight, and they diverge away from each other in rising from the lower to the upper limits of the bone; thus at its superior edge the scapular blade is somewhat greater in its anteroposterior dimension than it is at the lower end of the bone. The superior edge forms a gentle, convex curve between the anterior and posterior edges.

At the lower end of the bone are two apparent projections, the forward one of which is directed anteroventrally, while the posterior one is directed downward. Of these the forward one is interpreted as possibly the scapular process of the clavicle. The other "process" is actually the portion of a rib which has been crushed down upon the scapula in such a way that it appears to be an integral part of this latter bone. This conclusion is substantiated by a careful examination and measurements of both sides of the slab.

It is quite apparent from what may be seen of the scapula in *Hypsognathus* that the bone has become rather highly specialized as compared with the same element in the Permian cotylosaurs. This specialization has taken place by a vertical elongation of the bone, with a resultant straightening of its edges, and it probably represents an adaptation for quick and rapid movements on land. None of the other elements in the pectoral girdle are present.

The humerus is a long and slender bone, in which respect it is greatly advanced over the thick, heavy humerus of the early Permian cotylosaurs. The development of rather delicately formed limb bones was a process begun early in the history of the procolophonids, as is shown by Watson's figure of *Procolophon*. But even though the humerus may have been slenderly proportioned in *Hypsognathus* and in other procolophonids, it nevertheless has retained the primitive "twisted" character so typical of the cotylosaurs, so that in this present specimen the expanded proximal end is at right angles to the expanded distal end.

The articulation occupies the proximal end of the bone, and because of the simplification of this bone as compared with the same element in the earlier cotylosaurs, there is a corresponding simplification of the proximal articular surface. Instead of being a screw-shaped surface, it appears to be more in the form of a simple elongation, expanded at its lateral and medial ends and rather constricted in the middle.

Proximally the humerus is flattened on both the anterior and posterior surfaces. On the anterior surface, however, a laterally placed crest runs down onto the shaft of the bone from the corner of the articulation; this is the deltoid crest, along which are located the insertions for the deltoid and pectoralis muscles. There is no supinator process on the shaft of this bone, as is characteristic of the Permian cotylosaurs.

In its middle portion the humerus is constricted, and below that it expands into the radial and ulnar condyles, of which the former is particularly prominent. One cannot be cer-
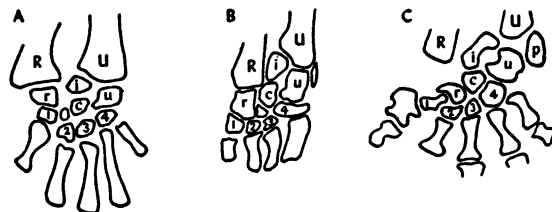
FIG. 17. Diagram to show a comparison of the restored left manus in *Hypsognathus* and *Procolophon*. A. *Hypsognathus*. B. *Procolophon* (from Watson, 1914). C. *Procolophon* (from Broom, 1903). Abbreviations: R, radius; U, ulna; r, radiale; i, intermedium; u, ulnare; p, pisiform; c, centrale; 1,2,3,4, carpals. Not to scale.

tain from this specimen as to the presence of an entepicondylar foramen, but from the relative lack of ectepicondylar expansion it would seem fairly certain that a foramen was lacking on the outer side of the bone.

The radius and ulna are strong bones, slightly shorter than the humerus. The radius is irregularly subcylindrical and somewhat expanded at its distal end. The ulna, which is slightly longer and heavier than the radius, is expanded at either end. This bone is not so straight as the radius but is somewhat bowed, as may be seen by figure 10 of plate 27.

The carpal bones of the right manus are somewhat displaced, but it would appear that they are almost all present. Unfortunately these bones have suffered some erosion, particularly around their edges, so that they are all more or less nodular and difficult to differentiate from each other. Assuming that their arrangement was similar to the arrangement of the carpals in *Procolophon*, a reconstruction of the carpus may be attempted, as shown in figure 17.

In the present state of the specimen portions of four metacarpals are represented by bones of varying degrees of preservation. Also there are a few fragments that may represent phalanges. From a photograph that was made of the specimen soon after its discovery (see pl. 31) it would appear that originally all five metacarpals were visible. During the preparation of the fossil, however, in spite of the meticulous care exercised in the development of the specimen, there was a certain amount of loss in this region of the foot. This was due to the fact that the matrix was extremely hard, while certain of the metacarpals were preserved as the merest film of bone which, while showing the shape of the ele-

ments, failed to stand up during the process of the preparation work. In the restoration of the foot shown by the text figure 17 the photograph of the specimen as originally found was used as guidance for drawing the metacarpals.

There is nothing to be said concerning the pelvis and the hind limb in *Hypsognathus*. Some inference as to the structure of these elements may be had by reference to Watson's description and figure of *Procolophon*, in which the pelvis is shown as a somewhat modified but nonetheless primitive cotylosaurian structure with plate-like pubes and ischiae, while the hind limb is seen to be comparable in length and weight to the fore limb.

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS)

	Hypso-gnathus Type U.S.N.M. No. 11643	*Hypso-gnathus* A.M.N.H. No. 1676	*Hypso-gnathus* A.M.N.H. No. 1677	*Hypso-gnathus* A.M.N.H. No. 1678	*Procolo-phon* From Watson (Figure)	*Nyctiphru-retus* From Efremov (Figure)
Skull						
Length	—	50.0	—	—	50.0	54.0
Greatest width	—	70.5	74.0	—	—	47.0
Breadth across quadrates	49.0	—	45.0	—	57.0	42.0
Preorbital length	—	22.0	21 app.	—	18.0	20.0
Orbital length	—	24.3	—	—	18.4	25.0
Depth, anterior border orbit	—	20 e	—	20 app.	17.3	13.0
Breadth of palate	—	10.5	9.0	—	—	37.0
Mandible						
Length	43.0	34 e	(34+)	—	44.0	47.0
Depth of ramus	—	12.5	—	—	8.0	7.5
Length of upper dentition	—	21.5	19.8	20 e	21.0[a]	30.0
1st premaxillary tooth (length ×width)	—	2.4×3.3	3.2×2.9	—	—	—
1st maxillary tooth (length ×width)	—	—	1.8×2.1	—	—	—
5th maxillary tooth (length ×width)	—	—	2.6×5.5	—	—	—
Length of presacral vertebrae	—	177 e	—	—	154.0	173.0
Length of 10 dorsal vertebrae	85.0	72.0	—	—	70.0	73.0
Dorsal vertebrae						
Length centrum	—	6.6	—	—	—	—
Breadth, neural arch	—	11.4	—	—	14.0	13.0
Humerus, length	—	30.0	—	—	32.0	—
Radius, length	—	22.3	—	—	21.0	—
Ulna, length	—	22.9	—	—	23.0	—

[a] From Broili and Schröder.

TABLE 2

COMPARATIVE RATIOS AND INDICES

	Hypsognathus	*Procolophon*	*Nyctiphruretus*
$\dfrac{\text{Skull length}}{\text{Skull width}} \times 100$	141	114	87
$\dfrac{\text{Orbital length}}{\text{Skull length}} \times 100$	49	37	46
$\dfrac{\text{Upper dentition}}{\text{Skull length}} \times 100$	43	42	56
$\dfrac{\text{Mandible (art.)}}{\text{Skull length}} \times 100$	70	88	87
$\dfrac{\text{Skull length}}{\text{Presacral vertebrae}} \times 100$	28	32	31

A BRIEF REVIEW OF THE PROCOLOPHONIDAE[1]

FROM THE FOREGOING DESCRIPTION it is apparent that *Hypsognathus* is a procolophonid cotylosaur, showing many resemblances to *Procolophon* itself, but related particularly to *Leptopleuron*. Since there are a number of genera of Procolophonidae described in the literature, it may be well at this place to review briefly the family, in order that a summary statement may be at hand showing the constitution of this group of Permo-Triassic cotylosaurs and the distinguishing characters of its included genera.

ORDER COTYLOSAURIA
SUBORDER DIADECTOMORPHA

Cotylosaurs of small to large size; skull broad in comparison to width; jaw articulation frequently moved forward, and quadrate vertical; large pineal opening. Skeleton generally primitive.

FAMILY PROCOLOPHONIDAE

Small reptiles. Skull triangular; orbits large and variously elongated; large pineal foramen; lacrimals small and excluded from nares; tabulars large; no supratemporals. Vertebrae with broad cotylosaurian arch but with short spines; vertebral centrae generally somewhat elongated; about 24 presacral and three sacral vertebrae; limb bones comparatively slender.

SUBFAMILY PROCOLOPHONINAE

Specialized procolophonids. Strongly triangular skull; quadratojugal and tabular frequently modified by spike-like processes; jaw articulation shifted forward and otic notch widely open; skull bones smooth. Teeth reduced in number, round or transversely broad and much reduced or absent on palate. Intercentra absent in advanced forms; tail relatively short. Tibiale and fibulare separate. Triassic.

GENUS PROCOLOPHON OWEN

Procolophon OWEN, 1876, p. 25.

Skull triangular and simple; quadratojugal often produced as a "spike," seemingly a male character; orbits moderately elongated. Ten to 11 large upper teeth, three or four of peg-like shape in premaxilla, seven transversely broadened teeth in maxilla; nine or 10 teeth in mandible. Lower Triassic.

Procolophon trigoniceps Owen

Procolophon trigoniceps OWEN, 1876, p. 25, pl. 20, figs. 4–7. Lower Triassic, Karroo Series, *Procolophon* zone. Donnybrook, South Africa.

Procolophon minor OWEN, 1876, p. 26, pl. 20, figs. 8–12.

Procolophon griersoni SEELEY, 1878, p. 797, pl. 32, figs. 1–3.

Procolophon cuneiceps SEELEY, 1878, p. 799, pl. 32, figs. 7, 8.

Procolophon laticeps SEELEY, 1878, p. 801, pl. 32, figs. 4–6.

The types for the four last-mentioned species came from Donnybrook.

Procolophon platyrhinus SEELEY, 1905, p. 226, fig. 35.

Procolophon sphenorhinus SEELEY, 1905, p. 226, fig. 36.

The types for the two last-mentioned species came from Fernrocks, Tafelberg, South Africa.

Procolophon baini Broom

Procolophon baini BROOM, 1905b, p. 332. Locality unknown.

GENUS LEPTOPLEURON OWEN

Leptopleuron OWEN, 1851, p. 900.
Telerpeton MANTELL, 1852, p. 100.

A small procolophonid. Skull specialized with quadratojugal produced into two spikes; tabular also pointed; orbitotemporal openings greatly elongated, extending behind pineal foramen. Seven upper teeth, of which two are in premaxilla and five in maxilla; maxillary teeth broad; five teeth in mandible. Middle Triassic.

Leptopleuron lacertinum Owen

Leptopleuron lacertinum OWEN, 1851, p. 900.
Telerpeton elginese MANTELL, 1852, p. 100, pl. 4. Middle Triassic, Lossiemouth beds, Elgin, Scotland.

Owen's names have clear priority over Mantell's, unfortunate though this may be.

GENUS **SCLEROSAURUS** VON MEYER

Sclerosaurus VON MEYER, *in* Fischer de Wald-
heim, 1857, p. 136; VON MEYER, 1859, p. 35.
Aristodesmus SEELEY, 1896, p. 167.

A large procolophonid. Skull specialized,
with two well-developed spikes on the squa-
mosal and the quadratojugal, and behind
them a very large posterior spike, directed
posterolaterally. Orbitotemporal openings
greatly elongated. Nine upper teeth, of which
two are in the premaxilla and seven in the
maxilla; maxillary teeth somewhat broadened
transversely; eight teeth in mandible. Tail
short. Dorsal bony plates. Lower Triassic.

Sclerosaurus armatus von Meyer

Sclerosaurus armatus VON MEYER, *in* Fischer de
Waldheim, 1857, p. 136, pl. 3; VON MEYER, 1859,
p. 35, pl. 4.
Labyrinthodon rütimeyeri WIEDERSHEIM, 1878,
p. 1, pls. 1–3.
Aristodesmus rütimeyeri (Wiedersheim) SEELEY,
1896, p. 167.
Lower Triassic (Upper Buntsandstein). Basle,
Switzerland.

GENUS **THELEGNATHUS** BROOM

Thelegnathus BROOM, 1905a, p. 274.

"Very closely allied to Procolophon"
(Broom, 1936, p. 390). Known material in-
sufficient for a diagnosis. Lower Triassic.

Thelegnathus browni Broom

Thelegnathus browni BROOM, 1905a, p. 274.
Lower Triassic, Karroo series, *Cynognathus* zone
(?). Aliwal North, South Africa.

At the present time this genus and species
are based upon very insufficient evidence, as
far as the literature is concerned. When more
is known of this form it may prove to be dis-
tinct, although it is possibly of the genus *Pro-
colophon*, and perhaps even referable to the
species *P. trigoniceps*.

GENUS **KOILOSKIOSAURUS** VON HUENE

Koiloskiosaurus VON HUENE, 1911, p. 81.

A large procolophonid. Skull smooth, with-
out extended spikes on the side; orbitotem-
poral openings elongated, extending as far
back as posterior border of pineal foramen.
Nine or 10 teeth in skull, of which those in the
maxilla are somewhat chisel-shaped; seven
or eight teeth in the lower jaw. Lower Triassic.

Koiloskiosaurus coburgensis von Huene

Koiloskiosaurus coburgensis VON HUENE, 1911,
p. 81, fig. 1. Lower Triassic (Middle Buntsand-
stein). Mittelberg, near Coburg, Germany.

GENUS **HYPSOGNATHUS** GILMORE

Hypsognathus GILMORE, 1928, p. 2.

The most highly specialized of the procolo-
phonids. Skull very broad and very flat;
quadratojugal modified to form four spikes,
three directed laterally and one forward;
orbitotemporal openings extremely long, ex-
tending almost to the posterior edge of the
skull and behind the pineal foramen. Seven
teeth in the skull, of which two are in the pre-
maxilla and five in the maxilla; five teeth in
mandible; posterior teeth very broad and
chisel-shaped. Body depressed and broad.
Upper Triassic.

Hypsognathus fenneri Gilmore

Hypsognathus fenneri GILMORE, 1928, p. 2, figs.
1–3, pls. 1–3. Upper Triassic, Newark series,
Brunswick formation. Clifton, New Jersey.

GENUS **MYOCEPHALUS** BROOM

Myocephalus BROOM, 1936, p. 391.

Like *Procolophon* but with mandible deep-
ened in anterior portion and teeth reduced in
number. Eight upper teeth, of which three are
in the premaxilla and five in the maxilla;
maxillary teeth increase in size from first to
fourth, the latter being much enlarged; fifth
maxillary tooth small. Quadratojugal not ex-
tended into spike-like process. Orbits small.
Lower Triassic.
Though clearly related to *Procolophon*, this
is certainly a distinct genus.

Myocephalus crassidens Broom

Myocephalus crassidens BROOM, 1936, p. 391,
fig. 2C, D. Lower Triassic, Karroo series, *Cyno-
gnathus* zone. Aliwal North (?).

GENUS **MICROTHELEDON** BROOM

Microtheledon BROOM, 1936, p. 391.

Characters indeterminate. Lower Triassic.

Microtheledon parvus (Broom)

Thelegnathus parvus BROOM, 1905a, p. 275.
Microtheledon parvus (Broom) BROOM, 1936,
p. 391, fig. 2F, G.

Lower Triassic, Karroo series. Aliwal North, South Africa.

This form is based upon such insufficient material that at the present time it has no real standing.

Genus SPONDYLOLESTES Broom

Spondylolestes Broom, 1937, p. 299.

A very small procolophonid. Skull triangular and snout pointed. Orbit round, its posterior border being in front of the pineal foramen. Pineal foramen small. Teeth rounded in cross section, but with flattened tips. Thirteen dentary teeth. Lower Triassic.

Spondylolestes rubidgei Broom

Spondylolestes rubidgei Broom, 1937, p. 299, fig. 1. Lower Triassic, Karroo series, *Lystrosaurus* zone (?), Bethesda Road, South Africa.

Seemingly a small, primitive member of the Procolophoninae.

Genus ANOMOIODON von Huene

Anomoiodon von Huene, 1939, p. 508.

A small procolophonid. Skull triangular and simple, without specializations of the quadratojugal; orbit considerably elongated, its posterior border on a line with the posterior border of the pineal foramen. Teeth conical, probably seven in the skull; five teeth in the lower jaw. Lower Triassic.

Anomoiodon liliensterni von Huene

Anomoiodon liliensterni von Huene, 1939, p. 508, pls. 20, 21. Lower Triassic (Middle Buntsandstein). Hildburghausen, Germany.

Subfamily NYCTIPHRURETINAE

Primitive procolophonids. Skull not strongly triangular; quadratojugal and tabular do not bear spikes; jaw articulation at back of skull and otic notch distinct; surface of skull bones sculptured. Teeth sharply pointed and very numerous; numerous teeth on bones of palate. Intercentra present; tail relatively long. Tibiale and fibulare coalesced. Upper Permian.

Genus NYCTIPHRURETUS Efremov

Nyctiphruretus Efremov, 1938, p. 775.

Skull generally triangular, with huge orbits; pineal foramen very large and located near posterior border of skull; quadratojugal very small, but showing a slight pointed lateral projection. Teeth numerous and undifferentiated; pterygoids broad and tooth-bearing; teeth also present on palatines and prevomers. Lower jaw slender. Vertebral centra slightly elongated; intercentra present; three sacral vertebrae. Tail rather long, equal to or longer than the combined length of presacral vertebrae and skull, whereas in Triassic procolophonids it is shorter than the combined length of presacral vertebrae and skull. Cleithrum present; limbs slender and feet elongated. Upper Permian.

Nyctiphruretus acudens Efremov

Nyctiphruretus acudens Efremov, 1938, p. 775, fig. 4. Upper Permian, "Zone III" Red marls horizon of the Kimja River and lower course of the Mezen River, Mezen District, U.S.S.R.

Genus NYCTEROLETER Efremov

Nycteroleter Efremov, 1938, p. 776.

Skull elongated, with large orbits, but not so large as in *Nyctiphruretus*. Skull flattened as compared with *Nyctiphruretus*. A deep otic notch, as in primitive cotylosaurs; tabular projected back over otic notch. Lower jaw long and thin. Numerous teeth, somewhat differentiated as to size; teeth on pterygoid, palatines, and prevomers, but not so numerous or strong as in *Nyctiphruretus*. Upper Permian.

Nycteroleter ineptus Efremov

Nycteroleter ineptus Efremov, 1938, p. 776, fig. 5. Upper Permian, "Zone III" Red marls horizon of the Kimja River, Mezen District, U.S.S.R.

Genus OWENETTA Broom

Owenetta Broom, 1939, p. 319.

Skull generally triangular, moderately flat, with large, rounded orbits; pineal foramen of moderate size, about on a line with posterior borders of orbits; small, lateral pointed projections, probably on the quadratojugal; tabulars large. Teeth numerous (about 40 in premaxilla and maxilla) and undifferentiated; pterygoids bearing teeth.

Owenetta rubidgei Broom

Owenetta rubidgei Broom, 1939, p. 319, figs. 1, 2. Upper Permian, Karroo series, *Cistecephalus* zone. Locality not given.

This form is in many respects the most primitive of the procolophonids.

EVOLUTION, DISTRIBUTION, AND RELATIONSHIPS
OF THE PROCOLOPHONIDAE

EVOLUTIONARY DEVELOPMENT

THE FOREGOING REVIEW of the family Procolophonidae, and the comparative descriptions and discussions that preceded it, will give some basis for a discussion of the evolutionary development of this group of cotylosaurs, although much of the background for the discussion that follows naturally must be obtained from the literature and from the material itself. Most of the literature pertinent to this question will be found listed in the bibliography at the end of this paper.

The Procolophonidae are the last of the Cotylosauria, and they are indeed the only cotylosaurs to survive into and through Triassic times. As shown by recent discoveries in Russia (Efremov, 1938, 1940a, 1940b), this family of reptiles had its beginnings in Upper Permian times in forms that foreshadowed in a general way the specializations that became so well established in, and are so typical of, the Triassic procolophonids.

In the first place, there can be no doubt that these reptiles are rather closely related to the diadectids, a fact that has been expressed by Romer (1945, p. 592) by his inclusion of the family Procolophonidae in the suborder Diadectomorpha. This procedure is certainly justified on all morphological grounds.

The primitive, Upper Permian procolophonids described by Efremov and by Broom are less diadectomorph-like than are the typical Triassic forms, as might be expected in annectant types such as these seem to be. In fact, *Nyctiphruretus* and *Owenetta* approach in many respects the primitive cotylosaurian condition as seen in the early seymouriamorphs, for in these genera the skulls are rather low and broad, the quadrate-articular joint is placed at the extreme posterior border of the skull, and there are numerous teeth, not only along the margins of the upper and lower jaws, but also on the various palate bones of the skull. On the other hand, there are definite foreshadowings of the procolophonid habitus in the skull and skeleton of

one of these early forms, *Nyctiphruretus*. In this genus the skull has already become rather triangular in shape, as seen from above, while the orbits are very large. This enlargement of the orbits is important, for it was a characteristic and a dominant trend in the development of the Triassic procolophonids. In *Nyctiphruretus* the quadratojugal bone is small, but nevertheless it extends laterally in the form of a small point. Here again is an important trend, established in the Upper Permian, which was to become increasingly dominant during the Triassic history of the family. It is the enlargement and lateral extension of the quadratojugal "spike" that give to the Lower Triassic genera their characteristic triangular-shaped skulls, while it is the reduplication of spikes on this bone that marks the extreme specialization of the Upper Triassic forms.

Also, in *Nyctiphruretus* the tabular is pointed, and this also establishes a trend of development that is quite characteristic of the Triassic procolophonids. The very large and well-developed pineal foramen might be mentioned as a diadectomorph character appearing in *Nyctiphruretus* and antecedent to the large pineal foramen seen in the Triassic procolophonids.

In the postcranial skeleton of *Nyctiphruretus* there are other procolophonid characters appearing that point to developmental trends that were to be characteristic of the family in Triassic times. For instance, there is a certain amount of elongation in the centra of the presacral vertebrae, an elongation that is increasingly pronounced in the later genera. This elongation is not great—indeed, it is not particularly visible at a casual glance—but measurements and ratios show that it is, nevertheless, present and typical of the procolophonids as compared with other diadectomorphs and cotylosaurs. On the other hand, the tail in *Nyctiphruretus* is comparatively long, whereas upon the basis of the best available evidence it would seem as though the tail

in the Triassic procolophonids was comparatively short. This is an evolutionary trend involving a reduction in the number of caudal vertebrae rather than any particular changes in the proportions of the individual vertebral elements.

In *Nyctiphruretus* the limb bones are slender, as is the case in the Triassic procolophonids, a condition to be contrasted with the rather robust limbs of other cotylosaurians, derived in turn from the very heavy limbs of the labyrinthodont ancestors to the reptiles. The slenderness of the limb bones in the procolophonids may be correlated with the fact that these animals from their very beginnings were comparatively small reptiles. Finally there might be mentioned the fact that the feet in the Triassic procolophonids are short, a character that is hardly noticeable in *Nyctiphruretus*.

Such is the picture of the ancestral procolophonid. *Nycteroleter*, known only from the skull, seemingly represents a side branch, perhaps somewhat off the line of evolutionary development that led to the more highly specialized procolophonids of Triassic time. From the Permian heritage as exemplified by *Nyctiphruretus*, the habitus of the Triassic Procolophonidae was established by the following evolutionary developments, all of which must be considered as of genetic origin and expression:

1. Retention of comparatively small size
2. Progressive elongation of orbit, or "orbitotemporal opening"
3. Enlargement and progressive complications of the quadratojugal bone, to form laterally placed "spikes"
4. Enlargement and modification of the tabular bone to form a point
5. General forward migration of quadrate articulation and concomitant shortening of the mandible

6. Opening of the otic notch
7. Backward prolongation of postarticular process of lower jaw
8. Progressive reduction of teeth
   a. Elimination of teeth on palate
   b. Reduction of teeth in premaxilla, maxilla, and dentary
9. Specialization of teeth
   a. Enlargement of anterior teeth to form peg-like "incisors"
   b. Broadening of posterior teeth to form broad chisels
10. Moderate elongation of presacral vertebrae
11. Shortening of tail to less than presacral-skull length
12. Simplification of pectoral girdle, disappearance of cleithrum
13. Establishment and retention of slender limbs
14. Shortening of feet

These evolutionary trends can be followed, for the most part, through all the Triassic procolophonids; indeed, they may all be correlated to form a comprehensive and convincing picture of phylogenetic progression. The phylogeny of the procolophonids, as seen in the skull and jaw, is illustrated in figure 18.

In this connection it might be pointed out that Efremov has shown that *Nyctiphruretus*, though approaching rather closely the structural ancestry for the Triassic procolophonids, must be regarded as slightly off the direct line of development. Such is very often the case, however, in the study of paleontology, and therefore it is not to be wondered at in the present instance. Thus, there is a certain degree of reduction in the ribs and there is a coalescence of the tibiale and fibulare in the hind foot that would preclude this genus from being the actual direct ancestor of such forms as, for instance, *Procolophon* and other lower Triassic types. Nevertheless the approach of *Nyctiphruretus* to the true ancestry of the later procolophonids must be rather close.

DISTRIBUTION IN TIME AND SPACE

From the foregoing discussion and review it will be seen that the Procolophonidae are found at the present time on three continents and at four geologic levels. They are found in Russia and South Africa in beds of Upper Permian age, in central Europe and South Africa in beds of Lower Triassic age, in Scotland in beds of Middle Triassic age, and in North America in sediments of Upper Triassic age. It is evident that this distribution of the family, both geographically and geologically, represents only a partial picture of the past distributional history of these reptiles. Moreover, the distribution of the
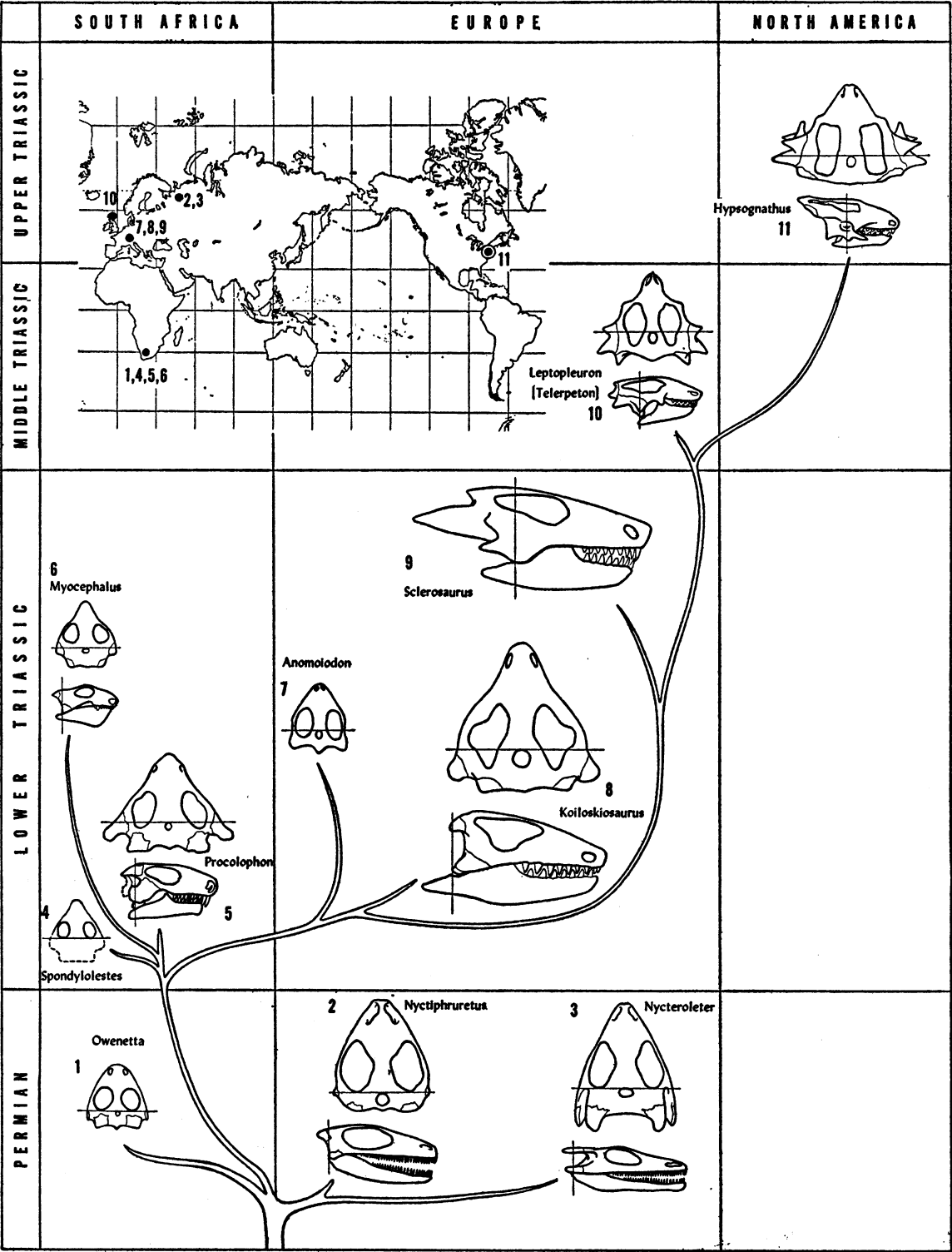
FIG. 18. Phylogeny and distribution of the genera of Procolophonidae.

procolophonids as known from extant material is rather spotty, that is, they are found in certain restricted areas, widely separated from one another over distances of continental magnitude. There are probably Triassic exposures other than those from which procolophonids are now known, where these reptiles will at some future date be discovered.[1] So our knowledge of the group is certainly incomplete at the present time.

Even so, it is possible from the material known to us to obtain a fairly distinct picture as to the distribution and the intercontinental migrations in this family of reptiles.

The presence of Nyctiphruretinae in the Upper Permian sediments of Russia and South Africa suggests that the Old World was the general region of origin for the family, a conclusion that is strengthened by the complete absence of primitive procolophonids from the Wichita-Clear Fork sequence of Texas and adjacent areas.

By Lower Triassic times these animals had spread through Europe, but whether they reached Asia or North America (this latter continent via a Bering connection) is at the present time not known, and may never be known, owing to the lack of Lower Triassic continental facies in these regions.

It is evident, however, that the development of the family continued in the European region, whatever may have been its fate elsewhere, for in the Middle Triassic of Scotland we find a highly specialized procolophonid, obviously derived from the stock that had produced certain of the Lower Triassic forms of central Europe. Soon after this the family appears in North America, to be represented by *Hypsognathus*, the most advanced of all the procolophonids. It is interesting to note the fairly close resemblances between the two latest genera, the one from Scotland, the other from New Jersey. Here we see the last expression of the Cotylosauria before the final extinction of the order.

Thus it is we get a glimpse of how the Procolophonidae, arising in Eurasia and Africa during Upper Permian times, spread widely over the face of the globe during the Triassic period, so that the family probably was, during a considerable portion of its evolutionary history, of cosmopolitan extent.

Some observations might be made at this place with regard to the bearing of the distribution of the Procolophonidae upon the question of a supposed continent of Gondwanaland. Support for the idea of a Gondwanaland mass, either in the form of adjacent and contiguous southern continents or in the form of broad land bridges connecting these continents, comes in no small degree from the evidence of fossil vertebrates of Permian and Triassic age. Thus, the presence in Brazil of reptiles closely related to the Karroo reptiles of South Africa has been cited as evidence favoring the former existence of a connecting land bridge between the continents of Africa and South America. Perhaps some of this evidence is illusory.

For example, the genus *Procolophon* is very typical of one horizon in the Karroo series, and therefore it is generally considered as a characteristic Karroo reptile. As mentioned above in a footnote, word has recently been received of the presence of procolophonids in Brazil. Now if these were the only extant records, the evidence in favor of a Brazilian-South African land connection would seem to be verified by the facts at hand. The presence, however, of procolophonids in northern, central, and western Europe and in eastern North America shows that these reptiles were once very widely spread over the surface of the earth, a condition that was probably true among various other Permo-Triassic reptilian groups. It happens that we have some locality records for the procolophonids which may be missing for certain of their contemporaries. This being the case, it can readily be seen that the spread of the procolophonids from an Old World center of origin to the New World might have been effected quite as readily by means of a northern route of intercontinental migration as by the frequently postulated southern one of Gondwanaland.

The continental Triassic of North America is very much limited in its temporal extent, and within it fossil vertebrates are not too abundant. Consequently, the paucity of the

[1] In a recent letter from Mr. Llewellyn I. Price of the Divisão de Geologia e Mineralogia, Brasil, I am informed that fossils of presumable procolophonid relationship have been discovered in the Triassic of Brazil.

Triassic fauna of North America, caused by the imperfection of the geologic record, may color the evidence with regard to the possibility of a former Gondwanaland connection across the South Atlantic. Certainly the discovery of procolophonids in the Triassic of western North America and in the newly discovered Triassic sediments of Yunnan, China, would make the intercontinental migrations of this group by way of a northern route appear even more probable than their spread across a southern land bridge, and there are strong reasons to believe that such discoveries in western United States and in western China may be made at some future date. There is a very great amount of knowledge still to be unearthed regarding the Triassic in both these regions.

ECOLOGICAL RELATIONSHIPS

In a preceding paragraph *Hypsognathus* was compared with the American horned lizard, *Phrynosoma*, of Recent times. This comparison sums up the probable ecological relationships not only of *Hypsognathus* but of the other Triassic procolophonids as well. These little reptiles were the "lizards" of their day, fulfilling a role in animal interrelationships that was filled during Permian times by the captorhinomorphs, and in later times by the lizards themselves.

Of course there were other small, lizardlike reptiles in addition to the procolophonids living during the Triassic; it would seem, however, that none of the other Triassic forms occupied quite the same ecologic niche that was held by the procolophonids. These were the small ground dwellers, living among such undergrowth as might be at hand, and probably burrowing in the soil. They were probably insect eaters in the beginning, but it would seem likely, because of the specializations in the jaws and dentition, that they turned to a fairly specialized diet at an early stage in their evolutionary history. Just what this diet was is of course conjectural, but it is not entirely out of order to suggest that it may have been a plant diet of some sort, or perhaps a mixed herbivorous-insectivorous diet. The reduced number of teeth in the more specialized procolophonids, with the anterior teeth rather in the form of nipping "incisors" and the posterior teeth modified to form sharp, cutting "molars" suggests an analogy with some of the rodents among the mammals. This analogy is strengthened by the evidence indicating very strong jaw muscles in the procolophonids.

As far as the postcranial skeleton is concerned, the evidence would indicate that *Hypsognathus*, for instance, was a broad, flat animal, not unlike the American horned lizard, *Phrynosoma*, or the Australian moloch, *Moloch*, in shape. It evidently scurried across the ground on comparatively slender and short limbs. The spiked skull may have given it some protection against its enemies, which were the larger reptiles. Perhaps it had spines in the skin of the back and sides, as is the case in the modern spiny lizards.

Upon suppositions such as these a three-dimensional restoration of *Hypsognathus* has been made by Mr. Germann, a picture of which is to be seen in plate 33. This represents the possible appearance of the last of the procolophonids. It is probable that the earlier Triassic genera were not unlike *Hypsognathus* in their general appearance, although of course they showed fewer specializations. The differences externally between these earlier forms and the Upper Triassic types would be the lack, in the older genera, of spikes on the skull, and probably of spines on the back.

IT HAS BEEN SHOWN in this paper that *Hypsognathus* is a highly specialized proco-lophonid—in fact, the most highly developed member of the family in many respects. Therefore, in any phylogenetic outline for this group of reptiles, *Hypsognathus* stands at the top of the tree. Moreover, in the pre-ceding discussions it has been considered as of Upper Triassic age, which if correct again puts it at the top of the series, not only morphologically but also temporally.

Perhaps it may be well at this place to go into the question of the relationship of *Hypsognathus* to the age of the sediments in which it was found.

There has been a good deal of discussion in the past concerning the age of the Newark series, and such correlations as have been made have been based upon the contained plants, invertebrates, and vertebrates. Of these the plants are in some localities fairly abundant, the invertebrates are scanty and not very conclusive, while the only numerous vertebrates are the fishes. The terrestrial vertebrates in the Newark series are all too few, but such as they are they have the virtue of being rather highly organized animals, and as such they might be expected not to extend over long periods of geologic time.

The earlier correlations of the Newark series, based for the most part upon the con-tained fossil plants, tended to place these sediments rather high in the Triassic system. Eastman (1911, pp. 23–24) cited a statement by Ward on this subject, as follows:

"Professor Lester F. Ward, writing in 1891, expressed the view that the flora of the New York-Virginia area fixes the horizon of the so-called 'Newark formation' 'with almost ab-solute certainty at the summit of the Triassic system, and narrows the discussion down chiefly to the verbal question whether it shall be called Rhaetic or Keuper. . . . The beds that seem to be most nearly identical, so far as the plants are concerned, are those of Lunz, in Austria, and of Neue Welt, in Switzerland. These have been placed by the best European geologists in the Upper

Keuper. Our American Trias can scarcely be lower than this, and it probably cannot be higher than the Rhaetic beds of Bavaria.' "

After making a careful comparison between the Newark fishes and fishes of several Euro-pean faunas, Eastman came to the conclusion that the Triassic sediments of the eastern portion of North America are older than would seem apparent from the evidence of the plants. Thus, "the Triassic fish fauna of eastern North America is of a more or less manifold nature, and corresponds in a general way to the interval between the Uppermost Muschelkalk and the basal division of the Keuper in the Mediterranean region" (East-man, 1911, p. 32).

With regard to the terrestrial vertebrates, Lull (1915) made the following remarks:

"So far as the terrestrial vertebrates are concerned the evidence is at present less con-clusive. *Rutiodon* spp. [*Clepsysaurus*] and *Stegomus arcuatus* from the lower series of coarse granitic sandstones below the anterior trap sheet are most nearly allied to *Mystrio-suchus* and *Aëtosaurus* respectively, from the Stubensandstein (Middle Keuper) of Würt-temberg; while the first recorded dinosaur footprint is from the anterior shales in the Connecticut valley in America, and, if I am not mistaken, from the Triassic conglomerate of South Wales, Upper Keuper in age, in Europe (Sollas 1879). . . . "

"In the Connecticut valley the upper series of sandstones and shales contain the foot-prints in great profusion, and in fewer in-stances the bones of dinosaurs and other forms of the newer Newark fauna, all of which are apparently not earlier than the Upper Keuper. The coming of the dinosaurs from the Old World, the time of which may pos-sibly be definitely fixed, is an event of such moment that it may well usher in the begin-ning of a new period of geologic time, and thus the Newark system as a whole may bridge the time between the Triassic and the Jurassic . . . " (Lull, 1915, p. 20).

In discussing the age of continental Trias-sic beds in North America, von Huene in
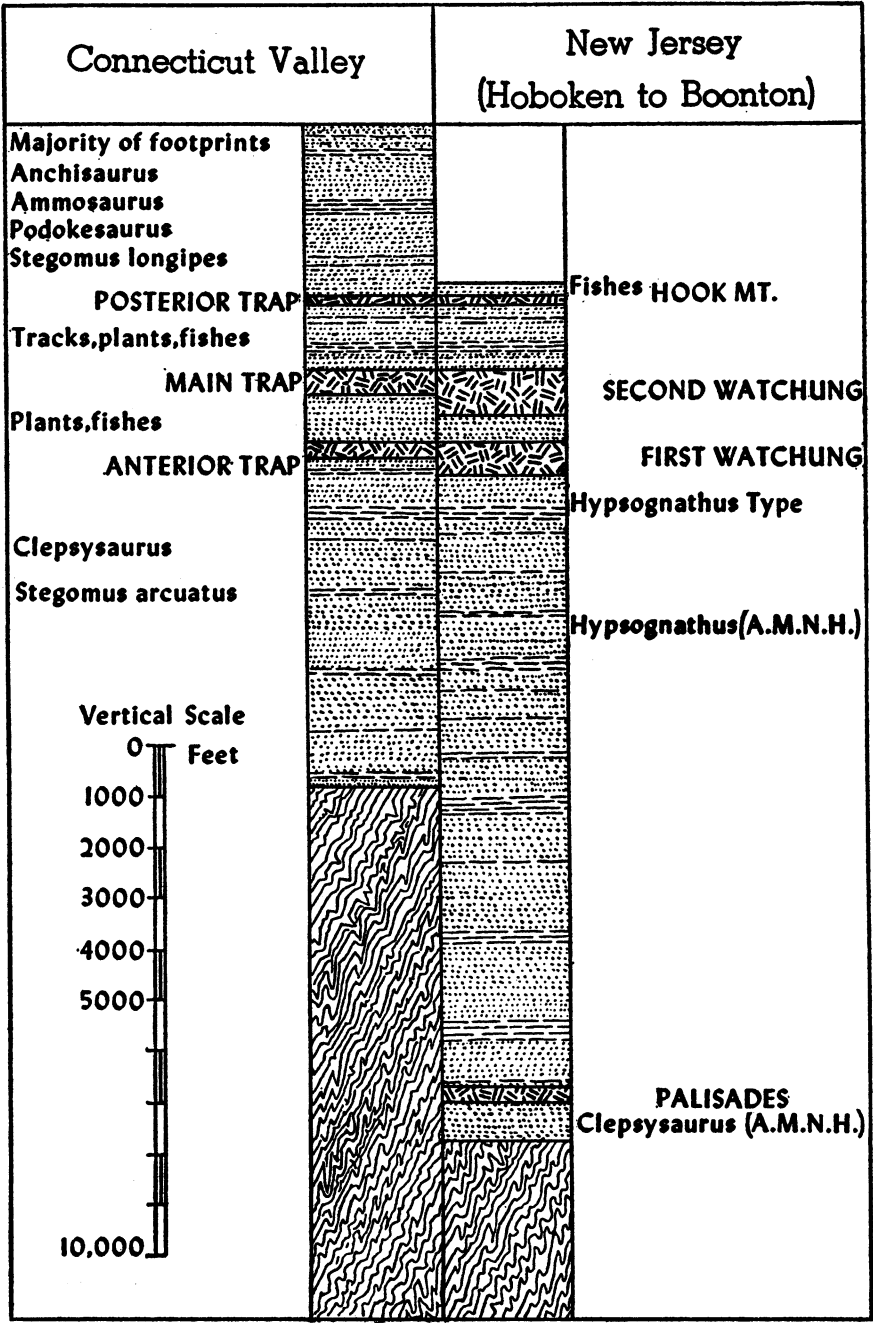
FIG. 19. Columnar sections to show the probable relations of the intrusive sheets, the sediments and their contained fossils in the Newark series of the Connecticut Valley and of northern New Jersey.

FIG. 20. Suggested correlation of Upper Permian and Triassic sediments in North America, Europe, and Africa. The shaded areas show the levels at which genera of the Procolophonidae occur.

1926 had the following to say about the age of the Newark series:

"The plants, especially abundant in the South, have been compared by Fontaine, and later by Stur and by Ward, with the flora of the 'Lettenkohle' from Lunz in the northern Alps, and from Neue Welt near Basel. Jones considers the Ostracods as similar to those of the German Keuper. The rich fish fauna was considered by Agassiz and Newberry as equivalent to that of the upper German Keuper, but Eastman, having treated the whole fish fauna, and also being familiar with the European fish faunas, considers them as more ancient. He says that several species of *Seminotus* (=*Ischypterus*) are nearly related to those from Perledo and Besano in the Italian Alps, and therefore correlates the fish fauna with the upper Muschelkalk or Lettenkohle.

"From all of this it must be concluded that the numerous but not yet sufficiently known Parasuchians and Labyrinthodonts from North Carolina, Virginia, Pennsylvania, New Jersey, Connecticut and Massachusetts do not belong to the youngest, but to the middle Trias, which would be about the time between upper Muschelkalk and lower Keuper, but that the Saurischians in Connecticut and Massachusetts belong to the upper Keuper or the Rhaetic. This also seems to be the view of Lull,[1] who, in 1915, assembled the American evidence on this question, but without comparing extensively with European evidence.

"It is evident that these continental Triassic deposits comprise a long period, the close of which about coincides with the close of Triassic time, and whose middle and older part is about a parallel of the German 'Lettenkohle.' The beginning of these deposits is probably at least in the time of the earlier or later Muschelkalk.

"From these considerations it seems that in the eastern Trias the equivalent of the lowest Trias is missing, and even in the central and western continental Trias such equivalents are at least not shown" (von Huene, 1926, pp. 6-8).

This statement by von Huene is a modification of his earlier views (1922) whereby he

[1] Von Huene seemingly has misinterpreted Lull here. See Lull's statement, quoted above.

regarded the Triassic sediments of eastern North America as contained entirely within the upper portion of the Middle Triassic, that is, within the American equivalents of the central European Upper Muschelkalk plus the Lettenkohle.

In contrast with von Huene's opinion as to the extent in time of the Triassic in eastern North America there may be quoted an opinion of Berry, as expressed a few years before von Huene's paper was published:

"That portion of the Newark which is fossiliferous, and this includes the Connecticut, New Jersey, Pennsylvania, Virginia, and North Carolina areas, is not 'probably of Jura-Trias age,' but is most clearly and conclusively shown by its fishes, reptiles, mammals, and plants to be not older than the Keuper of Europe, nor younger than the uppermost Triassic."

"Paleontologically, and by that I mean, both paleozoologically and paleobotanically there is absolutely no age distinction between the northern and southern areas of Newark rocks. All of the extant evidence is in harmony in pointing to a late Triassic age, and this evidence is overwhelmingly strong for the Virginia and North Carolina areas" (Berry, 1923, p. 83).

This view was essentially the same as that held by Schuchert, who indicated the Newark series, composed of the Stockton, Lockatong, and Brunswick formations, as equivalent to the European Keuper. (Schuchert, 1924, p. 456.)

From the several opinions, quoted above, it can be seen that there have been promulgated four general schemes regarding the correlation of the Newark series. In the first place, there is the view advanced a half century ago on the basis of paleobotanical evidence that the Newark series is essentially of Upper Triassic age, being equivalent to the Keuper and Rhaetic of Europe. This view has been favored by later American authorities, such as Berry and Schuchert.

Second, there is the correlation of Eastman, based upon the fish fauna, which places the Newark in a lower position, more or less as of upper Middle Triassic age, or perhaps transitional between the Middle and Upper Triassic.

Third, there is the opinion of Lull, founded

to a considerable extent upon the terrestrial vertebrates, which places the Newark series very high, perhaps as a transitional series between the Triassic and Jurassic.

Finally, there is von Huene's correlation, based also upon the terrestrial vertebrates and weighted by an intimate and long acquaintance with the Triassic of central Europe, whereby the Newark series is indicated as of considerable duration, extending from the upper portion of the Middle Triassic through the whole of the Upper Triassic.

Does the presence of *Hypsognathus* in the Newark series afford any resolution to these varying opinions as to the age of the Triassic in eastern North America? In the first place, it must be remembered that *Hypsognathus* was found near the top of the series, in rocks that are mapped as of Brunswick age on the Geologic Map of the United States published by the United States Geological Survey in 1932. Even so, the occurrence of this genus, as recorded by the two known discoveries, is seemingly lower than the fish fauna from Boonton, New Jersey. *Hypsognathus* comes from the sandstones and shales in front of the first Watchung trap sheet, while the Boonton fishes are from a locality behind Hook Mountain, the third successive trap sheet in this section of New Jersey. Of course the entire picture may be complicated or obscured by faulting within the Brunswick formation; on this point no satisfactory solution is apparent at the present time. But even though there may be a considerable amount of faulting, it appears that the Boonton fishes can hardly be any lower in the series than *Hypsognathus*, and the probabilities are all in favor of their being higher.

It was upon the basis of these fishes, and in addition the fishes found between the Main Trap sheet and the Posterior Trap sheet in Connecticut, that Eastman placed the Newark series down in the Middle Triassic.

It will be recalled that *Hypsognathus* in its various specializations shows a considerable degree of advancement over the genus *Leptopleuron* or *Telerpeton*, from the Lossiemouth Beds of Scotland. *Leptopleuron*, hitherto the most advanced procolophonid both in its anatomical features and in its stratigraphic position, has been regarded by von Huene as of uppermost Middle Triassic age, for this authority, on very good grounds, considered the Lossiemouth Beds as equivalent to the Lettenkohle of Germany. This being the case, there is every reason to regard the sediments in which *Hypsognathus* was discovered as of later age than the Lossiemouth of Scotland or the Lettenkohle of Germany—in other words, as of Upper Triassic age. Naturally it is quite possible that a highly specialized genus such as *Hypsognathus* might be contemporaneous with its less-specialized close relative, *Leptopleuron*. On the other hand, the arguments for considering it as of later age are certainly as valid, at least upon the basis of existing evidence, as are those for favoring the contemporaneity of the two genera. Therefore, the evidence of *Hypsognathus* favors the interpretation whereby the Newark series is placed rather high in the Triassic sequence. This interpretation certainly runs counter to Eastman's view of an earlier age for the fish-bearing and related sediments of the Newark series.

This suggestion of a high position in the Triassic for *Hypsognathus* properly affects only the Brunswick formation. Perhaps von Huene was right in regarding the lower reaches of the Newark series as extending down into the Middle Triassic. Altogether, the question still remains an open one, for there seems to be no completely satisfactory way at the present time for reaching a definite solution of this vexing problem in correlation.

SUMMARY AND CONCLUSIONS

FROM WHAT HAS GONE BEFORE, certain facts have been established, and from these facts certain conclusions can be drawn with what is felt to be a reasonable degree of accuracy.

The facts are these:

Hypsognathus, first described by Gilmore in 1928, and now more fully described upon the basis of new materials that supplement the type, is a procolophonid cotylosaur, the remains of which have to date been found only in the Brunswick formation of the Newark series of eastern North America. It is clearly the most highly specialized of the Procolophonidae, and it probably represents the last appearance of the Cotylosauria before the extinction of the order.

Hypsognathus is distinguished by the great breadth of the skull, and especially by the development of four large spikes on either side of the skull. Of these, three are directed laterally and one forward, and it would seem probable that they are all a part of the quadratojugal bone. At the back of the skull the tabular bone forms a sharp angle.

Another feature very characteristic of *Hypsognathus* is the elongation of the orbito-temporal openings, so that each opening is approximately half the length of the skull. These openings are thought to have accommodated the eyes in their forward portions, and the bulging of the capiti-mandibularis muscles in their posterior portions. Thus a "false" upper temporal opening was developed in this genus that paralleled the true upper temporal opening of other reptiles.

In *Hypsognathus* the lower jaw is short and the dentition much reduced as to the number of teeth present in upper and lower jaws. In the skull there are seven teeth on each side, two in the premaxilla and five in the maxilla. The first tooth is large and overhanging, and the last four teeth are transversely broad and crested. There are five dentary teeth, of which the four posterior ones are broad and crested, and these bite alternately between the broad upper teeth.

The skeleton, as far as known, is rather similar to the skeleton in other procolophonids. One notable feature is a certain degree of elongation of the presacral vertebrae. The vertebrae show the characteristic broad cotylosaurian neural arch, and the spines are short. The limbs in *Hypsognathus* are slender.

The conclusions are these:

A comparison of *Hypsognathus* with other procolophonids shows, as has already been said, that this is the most highly specialized member of the family. The family *Procolophonidae* had its beginnings in Upper Permian times, in the genera *Nyctiphruretus* and *Nycteroleter* of Russia, and *Owenetta* of South Africa. These genera, while showing certain procolophonid traits such as the triangular skull, the large orbit, the large pineal foramen, and the slender skeleton, retain, on the other hand, numerous primitive cotylosaurian characters.

From them, the evolution of the Procolophonidae can be traced through *Procolophon* from the Lower Triassic of South Africa, through the Lower Triassic genera of central Europe, such as *Koiloskiosaurus* and *Sclerosaurus*, to its culmination in the Middle Triassic genus *Leptopleuron* of Scotland and the Upper Triassic genus *Hypsognathus* of North America.

This record of the evolutionary history in one cotylosaurian family indicates that these, the last representatives of the order, were widely spread animals, of almost cosmopolitan distribution. The evidence indicates that the center of origin for the family probably was in Eurasia and Africa. From there the procolophonids spread during the extent of Triassic times to other parts of the Old World, and to the New World probably by way of a Bering land bridge. Of course the distribution of the family might be explained by the assumption of the former existence of a southern Gondwanaland, but the distribution can be explained equally well without making such an assumption. Morover, if procolophonids are ever found in the recently discovered Triassic sediments of eastern Asia, as may well be the case, the arguments favoring a northern route of migration between the Old World and the New World will be strengthened at the expense of the theory of a Gondwanaland route of faunal interchange.

Finally, the presence of *Hypsognathus* in

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the Newark series may have some bearing on the age of these rocks. Since *Hypsognathus* is definitely more highly specialized than *Leptopleuron* of Scotland, it is probably of an age later than that of the Scottish form. *Leptopleuron* comes from the Lossiemouth beds, which von Huene considers to be of uppermost Middle Triassic age, about equivalent to the Lettenkohle of Germany. Therefore it is reasonable to assume that the Newark series are, at least in part, of Upper Triassic age. This accords with the evidence for the age of these sediments as adduced from the record of fossil plants and other reptiles. It is somewhat at variance with the age for the Newark as postulated by Eastman upon the basis of his studies of the contained fossil fishes.

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