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THE FAMILY DIADECTIDAE

AND ITS BEARING ON
THE CLASSIFICATION OF REPTILES

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INTRODUCTION

Studies for this paper were undertaken several years ago as part of a program for review of the order Cotylosauria. The publication by White (1939) on *Seymouria* and that by Price (1935) on *Captorhinus*, as well as additional unpublished studies, formed a part of this program. The researches were interrupted by the war and there seems to be little prospect that a coordinated study can be undertaken in the near future. When, in recent months, work was resumed on the diadectids, it was my plan merely to present an analysis of the cranial morphology of the genus *Diadectes*. Comparative studies were, however, inevitable, and they have led to an expansion of this paper to include an analysis of the relationships of primitive reptiles and of the bearing of these relationships upon the classification of the reptiles.

There has been a strong tendency to rely upon horizontal classifications in taxonomic studies of the Lower Permian vertebrates of North America. This tendency has resulted in the inclusion of almost all reptiles of this age into two large groups, the order Cotylosauria and the order Pelycosauria. The extensive treatment of the latter by Romer and Price (1940) seems to show that the Pelycosauria represent a coherent assemblage. The order Cotylosauria, founded by Cope in 1880 on the family Diadectidae, has not received the same critical analysis. This group has come to include all primitive reptiles with roofed temporal openings. In the course of the present studies serious doubts have arisen concerning the validity of this association. The conclusions concerning relationships of the reptiles usually classified as cotylosaurs have an important bearing upon the classification of the reptiles as a whole. A somewhat different scheme of classification has been developed and is presented in the final pages of this paper.

The family Diadectidae offers an excellent point of reference for such studies, since the morphology of included genera, especially *Diadectes*, has been moderately well known for many years, and since new materials have added important details to this knowledge. Emphasis in the morphological section is upon cranial details of *Diadectes*, as little can be added to the general picture of the post-

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cranium. In the course of preparation of this paper, much of the known diadectid material has been examined. A considerable part of the data used in the reconstructions of the skulls of *Diadectes* has come from heretofore undescribed specimens collected by Dr. A. S. Romer and his parties and by me in recent years. I wish to acknowledge Dr. Romer's courtesy in permitting me to study his materials. My thanks also go to Dr. W. K. Gregory of the American Museum of Natural History of New York, to Dr. E. C. Case of the University of Michigan, and to the United States National Museum for the opportunities to study their collections. I wish also to express my thanks to Mr. Bryan Patterson and Dr. Rainer Zangerl of Chicago Natural History Museum and to Dr. T. Stanley Westoll of the University of Aberdeen for various helpful suggestions. The drawings are the work of Mr. John Conrad Hansen, Staff Artist.

SYSTEMATICS OF THE DIADECTIDAE

THE CONSTITUTION OF THE ORDER COTYLOSAURIA

Cope (1878, p. 505) gave the generic name of *Diadectes* to a fragment of lower jaw with two well-preserved teeth (A.M.N.H. 4360) and to fragments of vertebrae. This material came from the Lower Permian of Texas and may be assumed with confidence to have come from the Wichita beds. The same writer (1880a, p. 304) described a skull referred by him to the genus *Empedocles* (Cope, 1878, p. 516). An error in interpretation of the occipital condyle of this skull, from which the basioccipital was missing, led Cope (1880a) to found a new division of the Theromorpha that he called the Cotylosauria and that included the family Diadectidae. In later publications (1889, 1896a, b) Cope presented revised definitions of the Cotylosauria based on characters determined in large part from other specimens. These analyses established the Cotylosauria on a firmer basis and stressed the roofed character of the temporal region. Case (1911) redefined the group, as an order, as follows:

Primitive reptiles with the temporal region complete; over-roofed by two elements, squamosal and prosquamosal, or three, squamosal, prosquamosal, and quadratojugal. Quadrate covered or exposed. Ribs single-headed. Neural arches broad and low, the sides swollen and convex, spines short and stout.

The order is assumed to include all the early reptilia with complete skulls, indicating their primitive relationship to the *Stegocephalia*. It is meant to include the suborders *Diadectosauria*, *Pareiasauria*, *Procolophonia*, and *Pantylosauria*.

It should be noted that the order Cotylosauria was founded upon the family Diadectidae and that this family is basic to any conception of the order in spite of various changes that have occurred in such conceptions. Since *Empedocles*, the "genus" upon which the order was originally based, is synonymous with *Diadectes*, it is clear this genus is the "central" one within the order.

Case's conception of the Cotylosauria as an order including primitive reptiles with roofed skulls has been followed by most subsequent students of the primitive reptiles. As new material has been discovered, concepts of subordinal relationships have changed. It has been a common practice (Watson, 1917; Romer, 1933) to include three suborders in the Cotylosauria: Diadectomorpha, Captorhinomorpha, and Seymouriamorpha. The inclusion of the last has been questioned repeatedly during the last decades, as it is open to question whether the seymouriamorphs are reptiles. Romer, in his recent revision of *Vertebrate paleontology* (1945) and again in a more recent paper (1946), has referred the Seymouriamorpha to the class Amphibia, retaining only the Diadectomorpha and Captorhinomorpha as cotylosaurs. The Captorhinomorpha has come to occupy a central position in the order, while the Diadectomorpha, including the Pareiasauridae, is more commonly considered as a sterile side branch. Thus the group which formed the basis for the order now occupies a secondary position.

As a result of the present study, fundamental changes in the classification of the reptiles have been suggested in the closing pages of this paper. The Seymouriamorpha, Diadectomorpha, Pareiasauria, and Procolophonia are grouped under the order Diadecta. This order and the order Chelonia are placed in the subclass Parareptilia. The captorhinomorphs are placed in the infraclass Captorhina, which is grouped with the infraclasses Synapsida, Parapsida, Euryapsida and Diapsida in the subclass Eureptilia. The bases for these changes are presented in the body of this paper (see table, p. 45).

THE CONSTITUTION OF THE FAMILY DIADECTIDAE

Since the time that the genus *Diadectes* was named in 1878 some ten North American genera have been designated as belonging to the family Diadectidae. These are as follows:

Diadectes Cope, Proc. Amer. Phil. Soc., **17**, p. 505, 1878.
Empedocles Cope, Proc. Amer. Phil. Soc., **17**, p. 516, 1878.
Nothodon Marsh, Amer. Jour. Sci., (3), **15**, p. 410, 1878.
Helodectes Cope, Proc. Amer. Phil. Soc., **19**, p. 45, 1880.

Chilonyx Cope, Proc. Amer. Phil. Soc., **20**, p. 631, 1883.
Empedias Cope, Proc. Amer. Phil. Soc., **20**, p. 634, 1883.
Bolbodon Cope, Proc. Amer. Phil. Soc., **35**, p. 134, 1896.
Desmatodon Case, Ann. Carnegie Mus., **4**, p. 236, 1908.
Diasparactus Case, Bull. Amer. Mus. Nat. Hist., **28**, p. 174, 1910.
Diadectoides Case, Carnegie Inst. Wash., Publ. 145, p. 26, 1911.
Animasaurus Case and Williston, Amer. Jour. Sci., (4), **33**, p. 345, 1912.

Diadectes, Empedocles, Empedias, Bolbodon, Chilonyx, and *Helo-dectes* are names given to specimens from the Lower Permian red beds of northwest Texas. *Empedocles* was shown to be preoccupied (Cope, 1883) and the name *Empedias* was substituted for it. *Empedias* and *Diadectes* were thought by Cope to show important differences in dental structure. As Case (1911) pointed out, comparison is not possible because of the nature of the type material. *Empedias* is not a determinable genus. There are, however, no differences between any of the structures that can be observed in the type of *Empedias* and comparable structures in specimens referred to the genus *Diadectes.* Various specimens that were thought to be new species have been referred to *Empedias.* It is apparent that all these specimens are *Diadectes* and that the name *Empedias* should be dropped. Romer (1944) indicated that *Bolbodon* is synonymous with *Diadectes.* The genus *Bolbodon* was based primarily on dental and minor cranial characters. Case (1911) pointed out that the dentition was not an adequate basis for differentiation from *Diadectes* and that the cited differences in cranial proportions could be accounted for by distortion. The only differences that he noted between the genera were "the greater thickness of the bones of the skull and the less rugose surface." These two features are highly variable factors that change with age, and cannot be considered to be of generic, or even specific, significance. *Bolbodon* is clearly synonymous with *Diadectes,* as Romer has indicated.

The genus *Chilonyx* was based on an imperfect skull that had been originally identified as *Bolosaurus* by Cope. His description cited characters of dentition and details of skull proportion and sculpture. The type of *Chilonyx rapidens* Cope, the genotypic species (A.M.N.H. 4356), is a single tooth originally described as *Bolosaurus rapidens* by Cope (1878). The skull (A.M.N.H. 4357), upon which the generic description was based, is incorrectly cited by Case (1911) as a paratype of *Chilonyx rapidens* and as the "type" of the genus. Neither the single tooth nor the skull offers any basis for differentiation of *Chilonyx* from *Diadectes,* and the former must be regarded as synonymous with *Diadectes.*

Diadectoides is a small diadectid from the Clear Fork of Texas. Case (1911, p. 26) entertained the idea that it might be an immature specimen but rejected this in favor of the proposition that it was a new genus. He based his conclusion on limb proportions, the nature of the apices of the neural spines, and the presence of free neural arches. Additional materials, including various immature specimens that can be assigned to *Diadectes*, strongly suggest that the type of *Diadectoides* is merely an immature specimen of *Diadectes*. Essentially every feature of the skeleton points to immaturity. The ilium is free from the pubis and ischium, which have been lost; the ends of the femur, tibia, and fibula are incompletely ossified; and the neural arches and centra are not fused. Proportional differences probably are the result of differential growth rates. It seems almost certain that this specimen belongs to the Clear Fork species, *Diadectes tenuitectes*. *Diadectoides* may be considered a synonym of *Diadectes*.

Romer (1944) has pointed out that all known Clear Fork specimens of *Diadectes* may be referred to the species *D. tenuitectes* Cope until such time as valid specific differences are apparent. The present studies have failed to reveal any valid basis for differentiation. Much the same situation obtains for specimens from the Wichita. Several species have been named from specimens that appear to have come from these beds. The localities and horizons are not included in the data of many of the specimens collected by early expeditions into the red beds, but it is commonly possible to determine the general locality of specimens from the matrix and from the nature of preservation. On this basis it appears that the following "species" have come from the Wichita: *D. sideropelicus* Cope, *"Empedias" alatus* Cope, *D. latibucatus* Cope, and *D. phaseolinus* Cope. Case (1911) has stated that *"Empedias" alatus* and *D. sideropelicus* are indeterminate species. However, *D. sideropelicus* was the first-named species of the genus. The type is based on a fragment of lower jaw (A.M.N.H. 4360), which was misinterpreted as part of a maxillary. Two teeth are in a fair state of preservation and these are associated with fragments of vertebrae. The name *Diadectes* rests on this specimen. Its preservation is such that other specimens can be determined as members of the same genus but assignment of others to the same species raises difficult problems. All species except *"Empedias" alatus*, an indeterminate form, were defined on the basis of teeth. There is no adequate means of specific differentiation on the basis of dentitions. All mature specimens fall within

a rather narrow size range, and specimens in which there are well-preserved parts of the skulls and postcranial elements show no significant differences. The material now known offers no adequate basis for differentiating species of the genus *Diadectes* from the Wichita beds, so that all are best assigned to a single species until such time as evidence to the contrary comes to light. The first-named species, *D. sideropelicus*, is the one to which the Wichita specimens must be assigned, in spite of the rather poor condition of the holotype. Since no valid differentiation of better specimens seems possible, it is reasonable to assume that they and the type of *D. sideropelicus* are specifically identical. The fragments that form the type have no characters that are not repeated in other specimens of *Diadectes*. In view of the unsatisfactory condition of the holotype of *D. sideropelicus* Cope, an excellent specimen of this species (M.C.Z. 1105) is hereby designated as a neotype. This specimen consists of an excellently preserved skull and lower jaws, a complete series of presacral vertebrae, complete scapulo-coracoids, a clavicle, and well-preserved ribs.

Nothodon lentus Marsh (1878) was described from fragmentary material of doubtful association from the Abo formation of New Mexico. Case (1911) recognized this genus as the type of the family Nothodontidae. Later finds, however, particularly an excellently preserved skull, led to the conclusion that *Nothodon* was a synonym of *Diadectes* (Case and Williston, 1912). There can be no question that this is the correct disposition of Marsh's genus. The skull described by Case and Williston (1912) in all probability belongs to Marsh's species *lentus*. It differs distinctly in size and proportions from the skulls of *D. sideropelicus* and *D. tenuitectes*, from the Wichita and Clear Fork, respectively. So far as can be determined, all specimens of *Diadectes* from the Abo are to be referred to *D. lentus* (Marsh).

Helodectes Cope (1880b) was based on a fragment of jaw, probably maxillary, with a double row of teeth. Questionably associated were some apparently diadectid skeletal fragments. The material is so poor that the genus must be rejected as indeterminate. The materials can be referred only very doubtfully to the family Diadectidae. It is almost certain that the jaw fragments do not belong in this family but some of the postcranial fragments are diadectid. The specimen almost surely is composite.

Animasaurus carinatus Case and Williston (1912) was described on the basis of a fairly well-preserved skull (Yale Mus. 817) of dia-

dectid affinities, from Las Animas, Colorado. I have not had the opportunity to examine this skull. The published figure shows only one possibly significant difference from *Diadectes*. The pterygoids are short and the internal nares extensive. These points are not mentioned in the descriptions and since the palate was not completely cleared of matrix they may have less significance than the figure would indicate. In other respects the skull is typically diadectid. Other differences of the palate hardly can be considered of more than specific value in view of the relatively great variation that must be admitted for species of the genus *Diadectes*, unless we are to consider each specimen a separate species. *Animasaurus* may thus be referred to the genus *Diadectes*. The species is distinct from those of the Wichita and Clear Fork but is quite close to *Diadectes lentus of* the Abo. Characters of the palate, however, indicate that the two must be maintained as separate species. The Colorado specimen thus should be properly designated as *Diadectes carinatus* (Case and Williston).

Diasparactus zenos Case (1910) is a New Mexican diadectid that differs distinctly in characters of the skull and postcranial skeleton from *Diadectes* and is clearly a different genus.

Desmatodon hollandi Case (1908) was described from a fragment of maxillary with four teeth discovered at Pitcairn, Pennsylvania. The known characters are insufficient to permit a morphological differentiation from *Diadectes*. The principal interest in the specimen is that it indicates the presence of the diadectids in the eastern part of North America. Because of the geographic isolation of the type specimen the genus and species may be tentatively retained. A great deal of new material from the Dunkard has been collected in recent years and this, when worked up, may offer a basis for more precise assignment of the diadectids of the eastern part of the United States.

Summary.—There appear to be two well-defined genera of diadectids in the late Pennsylvanian and Lower Permian of North America, *Diadectes* and *Diasparactus*. There are three well-defined species of *Diadectes*, *D. lentus*, *D. sideropelicus*, and *D. tenuitectes*, from the Abo, Wichita, and Clear Fork, respectively, and a probable fourth species, *D. carinatus*, from Las Animas, Colorado. There is but one known species of *Diasparactus*, *D. zenos*, from the Abo. *Desmatodon hollandi* may represent a third genus, but clear-cut morphological bases for differentiation from *Diadectes* are not present in the one described specimen. The following list gives a

tabular view of the present status of the North American representatives of the family Diadectidae:

Family Diadectidae	Horizon	Age
Diadectes tenuitectes Cope	Clear Fork	Lower Permian
Diadectes sideropelicus Cope	Wichita	Lower Permian
Diadectes lentus (Marsh)	Abo	Upper Pennsylvanian
Diadectes carinatus (Case and Williston)	Abo equivalent	Upper Pennsylvanian
Diasparactus zenos Case	Abo	Upper Pennsylvanian
Desmatodon hollandi Case	Dunkard	Upper Pennsylvanian

EUROPEAN DIADECTIDS

Two European genera from the middle Rothliegende, *Phanerosaurus* H. v. Meyer and *Stephanospondylus* Stappenbeck, are closely allied to the Diadectidae. A third genus, *Sphenosaurus* H. v. Meyer, has been assigned tentatively to the family but the reference is uncertain. Stappenbeck (1905) assigned *Stephanospondylus* and *Phanerosaurus* to a new family, Stephanospondylidae. Cope had previously referred *Phanerosaurus,* which Stappenbeck divided into *Phanerosaurus* and *Stephanospondylus,* to the family Diadectidae. In this he was followed by Romer (1945).

The postcranial elements of both genera closely resemble those of *Diadectes.* The skull is known only in *Stephanospondylus* and in this genus only some of the skull bones have been preserved. These elements and the dentition are distinctly diadectid in cast although they show differences in size and in proportions from those of any North American genus of the family. The limits of the family Diadectidae as at present defined, however, are so broad that *Stephanospondylus* and *Phanerosaurus* may be referred to it without hesitation.

These specimens have not been available for study and it has been impossible to utilize them fully in the present paper. So far as can be told from the figures and descriptions, they do not add materially to the knowledge of diadectid structure available from North American genera nor do they contribute data that basically alter the concepts of the diadectid's position among the primitive reptiles.

MORPHOLOGY OF DIADECTES

INTRODUCTION

The morphology of *Diadectes* has been described in some detail by a number of writers, including Cope, Case, von Huene, Broom,

Watson, Williston, and Romer. As a result of these descriptions, postcranial structures are well understood and need little further consideration. The postcranial skeleton is decidedly stable throughout the genus and few differences of even specific value can be demonstrated. The neural spines of the vertebrae show the greatest variation. They are more strongly developed in *D. tenuitectes* than in *D. sideropelicus* and *D. lentus,* especially in the sacral and lumbar regions. This difference appears to be primarily associated with size. *Diasparactus* has long vertebral spines in the presacral, sacral, and anterior caudal regions. It differs from *Diadectes* in the proportions of most of its postcranial elements.

In spite of the fact that the skulls of a moderately large number of specimens of *Diadectes* have been described carefully, there are many points that need clarification. Most confusing, especially to one not thoroughly familiar with the genus, is the remarkable variation of characters that would seem at first glance to be of specific or even generic rank. On examination, however, it becomes apparent that there is no clear pattern of variation and that the variations at present offer little or no basis for taxonomic work.

The general morphology of the skull is illustrated in figures 1 to 4 inclusive. These are composites designed to show the external cranial morphology. The proportions and general configurations have been drawn primarily from an excellently preserved skull, M.C.Z. 1105. Details have been added from other specimens of *D. sideropelicus* as well as from specimens of *D. tenuitectes.* Neither *D. lentus* nor *D. carinatus* has been used extensively in making these reconstructions, so that the figures represent conditions as they exist in Clear Fork and Wichita specimens rather than in all species of *Diadectes.*

CRANIAL MORPHOLOGY

Lateral surface of the skull (fig. 1).—All the figured bones have been based on well-defined sutures except part of the junction between the intertemporal and supratemporal, which is not clearly defined in any skull examined. There is little variation between specimens in the proportions of the elements, so that the reconstruction may be taken as an accurate portrayal of conditions throughout the genus. In some skulls, however, the posterior angle of the quadratojugal is less abrupt than that shown in the figure.

It will be noted that the intertemporal is a large element that lies lateral to the parietal and supratemporal, and that the supratemporal

is shown to form a raised prominence lateral to the area in which the tabular presumably lies. In no specimen has a suture between what is presumed to be the tabular and the parietal been seen, although a
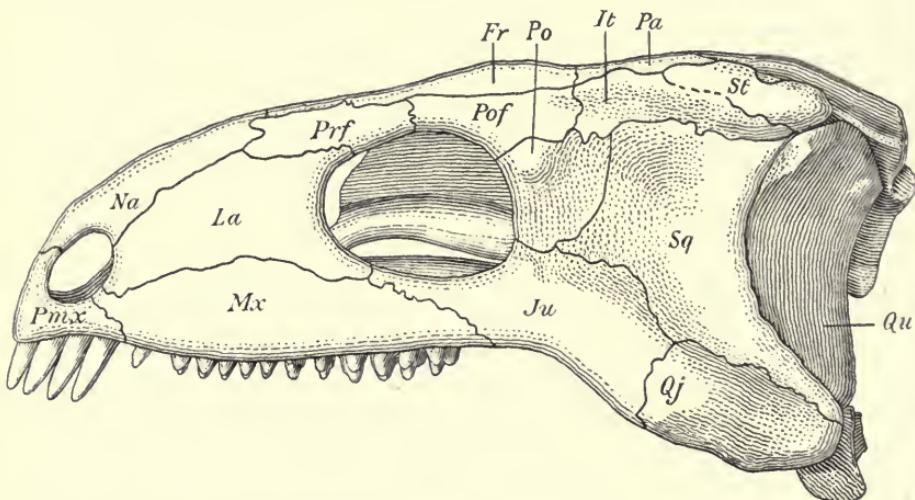
FIG. 1. Reconstruction of the lateral surface of the skull of *Diadectes*. $\times \frac{1}{2}$. *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *La*, lacrimal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxillary; *Po*, postorbital; *Pof*, postfrontal; *Prf*, prefrontal; *Qj*, quadratojugal; *Qu*, quadrate; *Sq*, squamosal; *St*, supratemporal.

radial pattern on some specimens suggests the approximate limits of the bone. The position inferred is correct for a tabular, lying between the occipital plate (interparietal plus supraoccipital) and the supratemporal. The structure has been interpreted in the past as a posterior spur of the parietal but, while such is a possibility, it may more reasonably be assumed to be actually a tabular indistinguishably fused to the parietal (see also fig. 2). The degree of development of the supratemporal prominence is highly variable and may be, in part at least, a function of the age of individuals. The articular surface of the quadrate is placed somewhat more posteriorly than it has been in various earlier reconstructions. This posterior position is the one that it occupies in the majority of the specimens.

Dorsal surface of the skull (fig. 2).—This reconstruction does not show surface patterns that occur in various skulls. These are variable and seem to be a function of age.

No depressions or vacuities are indicated in the temporal region. The figured condition is typical, but some skulls, such as A.M.N.H.

4559, 4370, 4839, and 4353, have temporal depressions or openings, as described by Case (1911) and von Huene (1913). These structures are not in the position of normal reptilian temporal openings and merely represent poorly ossified or unossified portions of the skulls. No other modifications of the skull accompany the development of these openings and, since they are variable within species and differ on the two sides of one individual, they cannot be considered important either functionally or taxonomically.

Palatal surface of the skull (fig. 3).—The reconstruction of the palate is based primarily on M.C.Z. 1105, with distortion eliminated
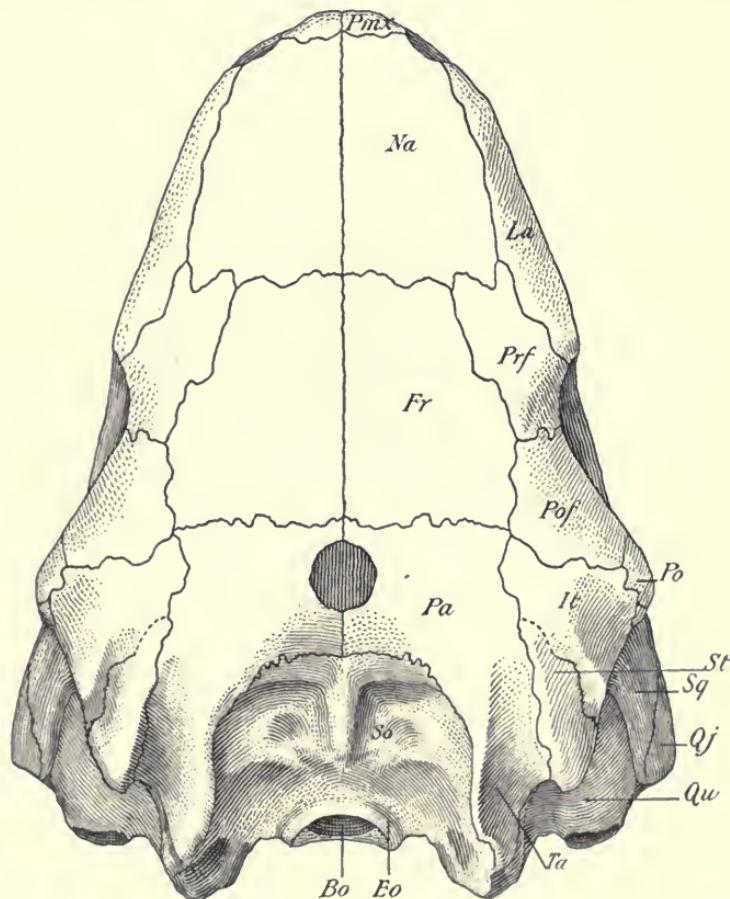
FIG. 2. Reconstruction of the dorsal surface of the skull of *Diadectes*. × ½. *Bo*, basioccipital; *Eo*, exoccipital; *Fr*, frontal; *It*, intertemporal; *La*, lacrimal; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxillary; *Po*, postorbital; *Pof*, postfrontal; *Prf*, prefrontal; *Qj*, quadratojugal; *Qu*, quadrate; *So*, supraoccipital; *Sq*, squamosal; *St*, supratemporal; *Ta*, tabular.

and details added from other skulls. There are several important points to be noted. The parasphenoid extends far back and flares broadly to form wings that underlie the basioccipital and the paroccipital process of the opisthotic. Two pairs of foramina are shown to penetrate the parasphenoid in the reconstruction. A small anterior pair appears between the basipterygoid processes, where openings for the internal carotids might be anticipated. Maximum development is shown in the reconstruction, but the degree of development actually is highly variable. In some skulls no such foramina exist, while in others only one foramen is present. The single foramen may represent one of the pair and lie to the side of the midline. In at least one instance studied, its companion is represented by a shallow, blind pit on the opposite side of the midline. The single foramen may, however, lie in the midline and represent a coalescence of the pair. These openings may be vestiges of carotid canals, but they certainly did not carry the carotids in any specimen of *Diadectes* examined during preparation of this paper. The variability suggests that there was no important function attached to the foramina, and this is supported by the fact that it has not been possible to trace the canals through the basisphenoid or to find a point of emergence in the brain case.

The second pair of foramina is much larger and lies posterolateral to the first pair. These foramina exhibit a similar degree of variability, being strongly developed in some skulls, poorly developed in others, and absent in several. There is, furthermore, no correspondence in variation of the first and second pair of foramina. Their maximum development is shown in the reconstruction. Their size suggests that they had some important function when present, but this is difficult to reconcile with the fact that they may be absent in skulls that are otherwise identical with those possessing them. Their state of development does not appear to be correlated with the age of the individual. The significance of these openings and of the variation that they underwent remains obscure.

The parasphenoidal rostrum has been described variously in previous papers. It has been shown as a distinct process extending to about the level of the posterior "molar" in A.M.N.H. 4352 by von Huene (1913); Watson (1916) described it as a long, powerful structure. Case and Williston (1912) noted that the bone was long in *D. lentus* with a thin upper edge and a broad, flat lower surface. In an earlier paper, Case (1905b) considered the rostrum to be absent in W.M. 1078. It is now clear from a large series of skulls that the rostrum is characteristically strong and that it passes forward to form

a keel that supports the sphenethmoid. Posteriorly it has a rectang-
ular cross section, and more anteriorly it is either somewhat diamond-
shaped, as in *D. sideropelicus,* or more or less triangular for much of
its length, as in *D. lentus.* The rostrum passes forward above the
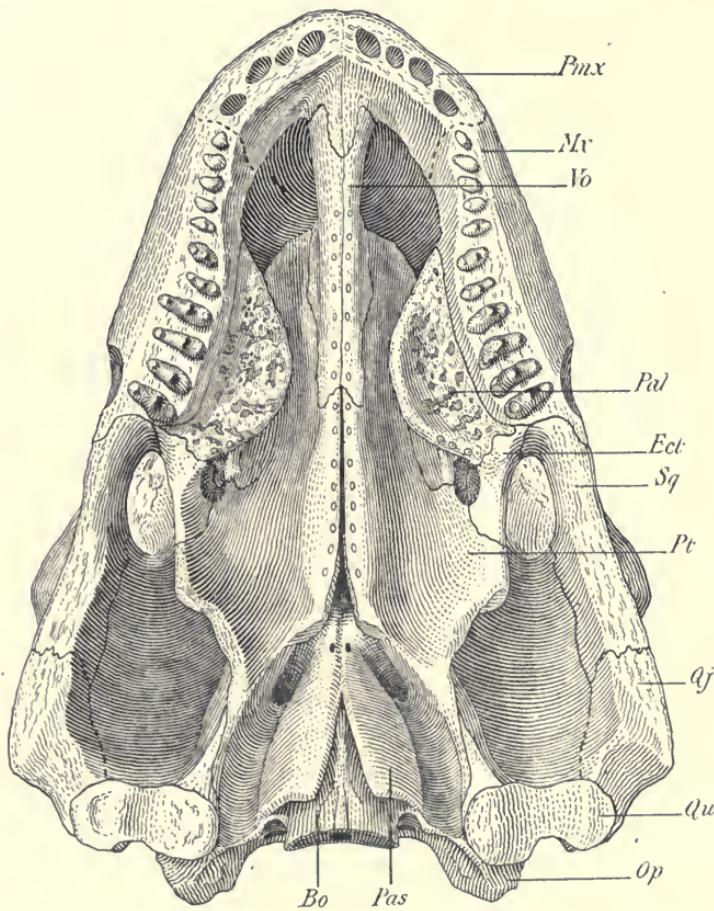
FIG. 3. Reconstruction of the palatal surface of the skull of *Diadectes.* $\times \frac{1}{2}$.
Bo, basioccipital; *Ect,* ectopterygoid; *Mx,* maxillary; *Op,* opisthotic; *Pal,* palatine;
Pas, parasphenoid; *Pmx,* premaxillary; *Pt,* pterygoid; *Qj,* quadratojugal; *Qu,* quad-
rate; *Sq,* squamosal; *Vo,* vomer.

closely spaced pterygoids and the vomer. Usually the vomer is a
paired bone, as shown in the reconstruction, but in a few specimens
it is single, and one fragmentary vomer has but a single row of teeth.

The short, stout basipterygoid processes project latero-ventrally
to make sutural junction with the pterygoids, as shown in figure
5,B. The epipterygoid does not enter into this union.

An outstanding feature of the palate is the process of the palatine, which shelves medially from the inner margin of the maxillary. This process, noted by several earlier writers, lies below the primary part of the palatine, creating an open space between the two parts of the bone. The ventral surface of the process is rough and there usually are a few small teeth along its posterior margin. This has been the basis for considering its primary function as masticatory. I am convinced, however, that it represents a partially developed secondary palate. The vomer and pterygoid form a strong, ventrally directed ridge that reaches just to the level of the palatine process. It seems highly probable that the space between these elements was covered by membrane to form a closed secondary palate and that air was conducted back at least to the posterior margin of the palatine. and probably farther, so that it entered into the throat.

The presence of an ectopterygoid in *Diadectes* has been questioned in several previous papers. Case (1905b) recorded a degenerate element (transverse) in W.M. 1078, but he and Williston (1912) stated positively that in *D. lentus* "there can be no doubt of its [the ectopterygoid's] absence." Von Huene (1913) recorded a large ectopterygoid (transverse) in *D. "molaris,"* A.M.N.H. 4352. During the present study this element has been identified in every specimen in which sutures were visible in the appropriate area of the palate. The apparent absence of the ectopterygoid in some specimens appears to result from fusion of this bone with the pterygoid and palatine. Medial to the ectopterygoid is a deep pit at the junction of the ectopterygoid, pterygoid, and palatine (fig. 3). In some specimens this depression appears to penetrate the bone as a fenestra, while in others it is merely a shallow pit. It lies in the position of an infraorbital fossa and may represent an incipient development of this opening.

Occipital surface (fig. 4).—There are several points in the occiput worthy of attention. Most are shown clearly in the figure and require only passing notice. The barrel-shaped basioccipital is shown to be pierced by a notochordal pit (see also fig. 6). This pit varies considerably in its development but commonly penetrates the basioccipital longitudinally for most of its length. The exoccipitals meet above the foramen magnum. The large foramen that lies on either side of the foramen magnum served as an exit for nerves and vessels carried by both the jugular and the hypoglossal foramina. Two hypoglossal foramina enter into the canal leading to this foramen, as shown in figure 6.

The lateral extension of the wings of the parasphenoid is shown in figures 3 and 4. The margins curve dorsally around the lateral margins of the paroccipital process. There is a deep cavity on each side of the basioccipital between the wings of the parasphenoid and the basioccipital. These pockets are partially merged in some specimens and discrete in others. The anterior termination of the pockets
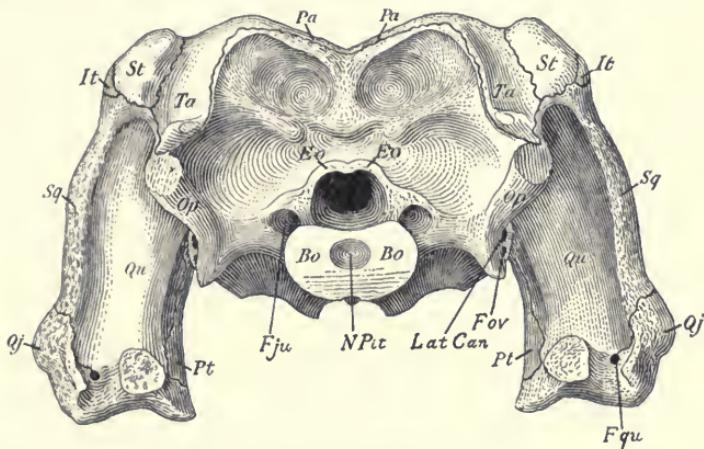

FIG. 4. Reconstruction of the occipital surface of the skull of *Diadectes*. $\times \frac{1}{2}$. *Bo*, basioccipital; *Eo*, exoccipital; *Fov*, fenestra ovalis; *Fju*, foramen jugularis; *Fqu*, quadrate foramen; *It*, intertemporal; *Lat Can*, canal lying dorso-lateral to tube leading to fenestra ovalis; *N Pit*, notochordal pit; *Op*, opisthotic; *Pa*, parietal; *Pt*, pterygoid; *Qj*, quadratojugal; *Qu*, quadrate; *Sq*, squamosal; *St*, supratemporal; *Ta*, tabular.

is blind in most specimens. Watson (1916) described a pair of small foramina at the anterior end of the pocket in A.M.N.H. 4378 but stated that he could not trace them into the bone; von Huene (1913) illustrated this same specimen and indicated that the foramina served for entrance of the internal carotid. In most specimens there are no such openings. A specimen sectioned in the course of this study shows that what appeared to be a foramen in the prepared specimen is merely a poorly ossified area. Whatever foramina are present in the few specimens that show an opening in this area must be considered to be unimportant and to have carried no nerves or vessels of major importance.

Near the dorso-lateral margin of each parasphenoidal wing, lying between the wing and the opisthotic, are two openings that have been figured by various writers. The ventral, or medio-ventral, opening is the fenestra ovalis, which lies at the end of a long tube leading from the vestibule of the inner ear. The dorsal, or dorso-

lateral, opening has been variously interpreted. Von Huene (1913) considered it to be an opening for cranial nerve VII, while Watson (1916) found no adequate explanation of its function. The interpretation of this feature is intimately associated with the interpretation of the inner ear and will be considered in more detail in the section concerned with that part of the skull. It is sufficient for the moment to state that the opening appears to have resulted from the nature of the association of the parasphenoid and opisthotic, combined with poor ossification of the latter, and that it was functionless.

The other features of the occiput and associated quadrate and otic regions are clearly portrayed in figure 4. The pattern of ridges and depressions on the occiput is associated with the cervical musculature as described by me in 1936. Various specimens differ markedly in the degree of development of this pattern. In no case are sutures clearly defined in the occipital region and differentiation of the elements is virtually impossible.

Inner and middle ear.—Otic structures are usually of cardinal importance in the determination of relationships among the vertebrates, and the primitive reptiles offer no exception to this general rule. Watson (1916) has described the inner ear of *Diadectes* in some detail. He figured the vestibule and semicircular canals. Most of this diagnosis has been confirmed by the present study. The vestibule is a large, open structure that is more or less triangular in horizontal section. The antero- and postero-lateral corners contain large and well-defined ampullar recesses. The crus communis entered the dorsal extremity of the utriculus through an opening located in the medial apex of the triangle at a level slightly higher than that of the ampullar recesses. The vestibule passes freely into the brain case and the medial part of the vestibular structures must have lain in part medial to the lateral osseous walls of the brain case. The vestibule is partially confluent with the jugular foramen and the recessus scalae tympani seems to have passed directly into the foramen. The tube leading to the fenestra ovalis passes postero-laterally from the vestibule. These features are illustrated in figures 5,A, 6, and 7. The semicircular canals are relatively unspecialized, with the posterior vertical canal only slightly shorter than the anterior vertical. These parts of the inner ear offer no particular problems.

The tube leading to the fenestra ovalis lies largely within the opisthotic. Near the posterior termination of the tube the parasphenoid makes up part of the lateral walls and for most of its length the parasphenoid forms the floor. Latero-dorsally to this tube is a
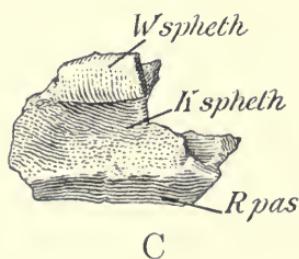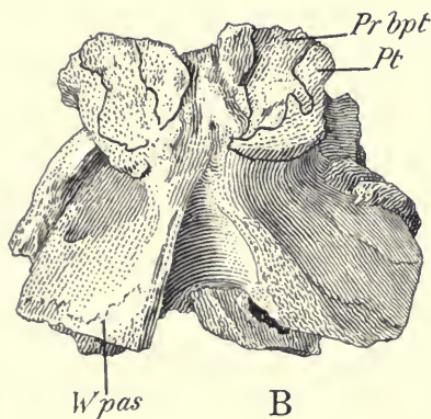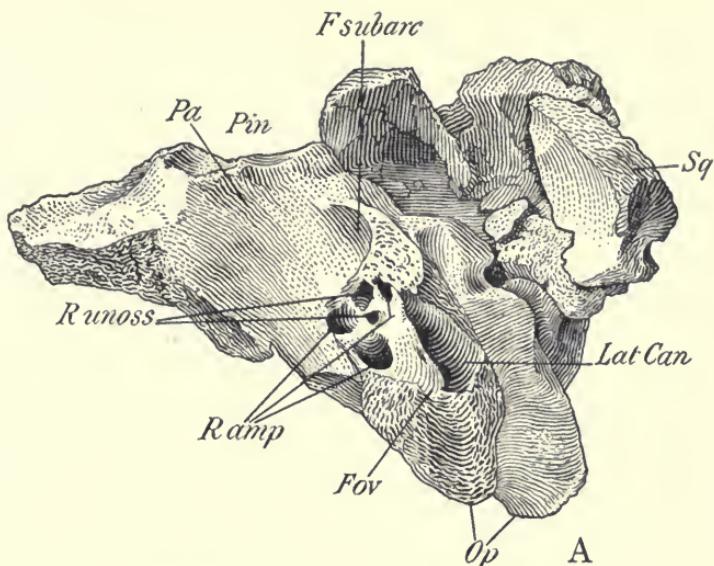
FIG. 5. Parts of skulls of *Diadectes*. ×½. (A) Walker Museum 44; ventral view of otic and parietal regions of skull with basicranium and part of proötic and opisthotic removed. (B) Walker Museum 44; ventral view of postero-ventral part of skull showing nature of basipterygoid processes. (C) Walker Museum 1695; lateral aspect of fragment of sphenethmoid and parasphenoid.

Fov, fenestra ovalis; *F subarc*, subarcuate fossa; *K spheth*, keel of sphenethmoid; *Lat Can*, canal dorso-lateral to tube leading to fenestra ovalis; *Op*, opisthotic; *Pa*, parietal; *Pin*, pineal opening; *Pr bpt*, basipterygoid process; *Pt*, pterygoid; *R amp*, ampullar recesses; *R pas*, rostrum of parasphenoid; *R unoss*, unossified recesses leading into unossified zone encompassed by semicircular canals; *Sq*, squamosal; *W pas*, wing of parasphenoid; *W spheth*, wing of sphenethmoid.

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second vacuity that issues dorsally, or dorso-laterally, to the fenestra ovalis (see p. 18 and figs. 5,A, and 7). In some specimens, as in W.M. 1695, this vacuity ends blindly at its anterior end; in others, such as A.M.N.H. 4843, figured by Watson, and W.M. 44, shown in figure 5,A, the opening is distinctly tubular and communicates anteriorly with a recess that lies within the zone encompassed by the semicircular canals but does not communicate with the canals. In some instances this unossified zone has one or more connections with the vestibule, as in W.M. 44, figure 5,A. In others, as in the sectioned specimen, there is no such communication with the vestibule or any connection with the tubular recess. This variation seems to furnish a partial answer to the nature of these structures, which Watson (1916) has called "quite unique." It must indicate that the structures were unimportant functionally, for, were they important, they would surely show equivalent development throughout the genus. So far as can be determined, they show little relationship to the age of individuals, although it might be anticipated that progressive ossification with increasing age would result in the conditions witnessed in specimens in which the tube and irregular recess of the canalicular zone were isolated.

The development of the tube appears to be fortuitous. The wing of the parasphenoid lies just below the opisthotic but, for most of its length, is free from this element. At its lateral margin the parasphenoid curves dorsally to meet a very thin, ridge-like descending process of the opisthotic. The vacuity so developed houses the tube that leads to the fenestra ovalis and is divided into a medial and a lateral portion by the walls of this tube, which are ventral projections of the opisthotic. The lateral portion of the vacuity constitutes the tube whose posterior termination appears to be a foramen, the opening that lies dorso-laterally to the fenestra ovalis. This space is variously developed in different specimens, being, for example, virtually absent in the sectioned specimen in which the parasphenoid is closely applied to the opisthotic. Its shape and extent tend to vary somewhat with the degree of ossification of the opisthotic.

Anteriorly the vacuity ends blindly in cases in which ossification is relatively extensive. With less ossification it communicates with the unossified zone in the vicinity of the semicircular canals. Neither the tube nor the recess has any important functional significance. Both are structures that result primarily from incomplete ossification, which is evident in many parts of the diadectid skull.

The structure of the middle ear is not well known. No well-defined stapes has been discovered. The otic notch is very large and is occupied in large part by the quadrate. The stapes must have been a short bone but probably had a long process, presumably cartilaginous, which passed from its main body to the large facet on the postero-ventral margin of the quadrate (see fig. 4). Little more can be said about this region, but it should be noted that the condition of the middle ear is distinctly amphibian and not reptilian.

Romer (1946) has suggested that the otic notch of *Diadectes* may have evolved by modification of the otic region in *Limnoscelis*, or a *Limnoscelis*-like ancestor in which the notch had been eliminated. He has diagrammed (1946, fig. 9) two interpretations of the development of this notch in *Diadectes*. One, following Watson, shows the changes required if the notch were derived from that of an embolomere without passing through a *Limnoscelis* stage. The other shows the changes that could produce the diadectid condition from *Limnoscelis*. It is Romer's opinion that only the latter offers a reasonable explanation of the features of the quadrate and associated elements. The principal point offered in support of the argument is that the dorsal margin of the diadectid quadrate is recurved to meet the paroccipital process of the opisthotic. This character is somewhat variable in *Diadectes* but is expressed to some degree in all specimens examined. In either line of development, however, the lower end of the quadrate must have migrated forward. In all cases in which the articular surface of this bone has come to lie anterior to the contact of the dorsal margin of the quadrate and the paroccipital process, recurvature of the upper end would appear inevitable. Apparently, either mode of development could produce the diadectid condition.

The stapes of *Diadectes* is unknown. It could be very instructive in determination of the course of development since, if it retained amphibian features, it probably has not passed through a *Limnoscelis* stage. There is only one point that applies in this matter. It is known that the quadrate of *Diadectes* has a strong extracolumellar facet which closely resembles that in a number of amphibians, particularly in certain of the embolomeres. This suggests that the stapes may have originated directly from the amphibian type and that it did not pass through a "reptilian" stage.

In the procolophonids, a group that appears to be rather closely related to the diadectids, there is moderately strong evidence that the somewhat *Diadectes*-like otic notch was developed from a stage

resembling that of *Seymouria* in a number of features (Efremov, 1940). The diadectids and procolophonids have many points of resemblance, as discussed on pages 33–36. This gives some reason to suppose that similar changes may have occurred in the two groups.

The diadectid structure was present very early in reptilian history, in the late Pennsylvanian. It is, of course, conceivable that this structure had passed through a true reptilian stage and undergone specialization leading to the development of a secondary otic
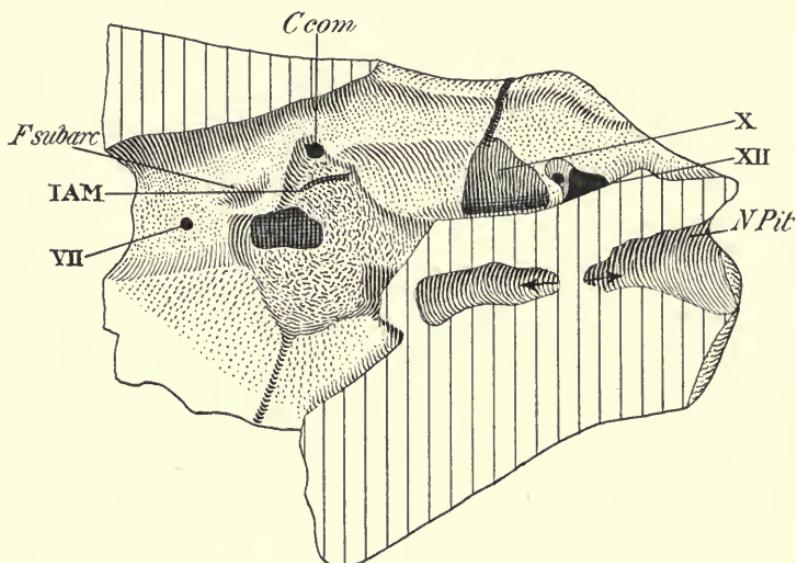
FIG. 6. Medial view of brain case of *Diadectes*. Drawn from wax model constructed from serial sections of skull taken at 1 mm. intervals. *C com*, opening of crus communis; *F subarc*, subarcuate fossa; *IAM*, internal auditory meatus; *N pit*, notochordal pit; VII, X, and XII, openings for respective cranial nerves.

notch by this time. There is, however, no direct evidence from the preceding deposits that contain adequately preserved remains of tetrapods to show that a *Limnoscelis* stage was developed at an appreciably earlier date. The time of occurrence of the diadectid otic structure, which would have to be considered as a marked specialization if it developed from a reptilian predecessor, suggests derivation directly from amphibian ancestors.

The conviction that the *Diadectes* otic notch could have come directly from an amphibian condition without an intervening *Limnoscelis* stage, the evidence of a change of this sort in the procolophonids, and the early appearance of the diadectid condition

seem to give strong support to the contention that *Diadectes* came
from the amphibians without an intervening stage in which the otic
notch had been lost.   This is a very important point in consideration
of the classification of the Reptilia (see p. 44).
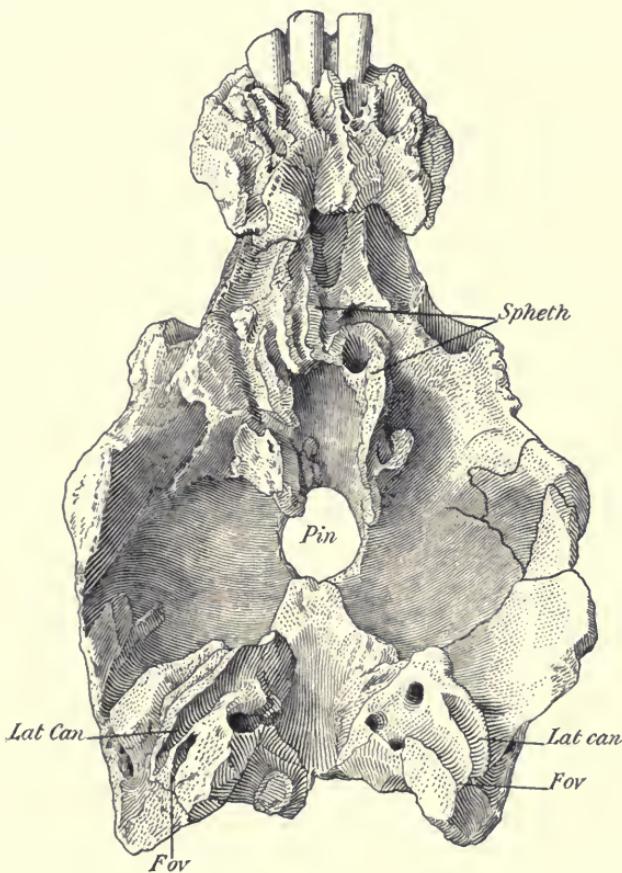
Fig. 7. Walker Museum 1695. Ventral view of skull of *Diadectes* ($\times \frac{1}{2}$) with
basicranium and palate removed. *Fov*, fenestra ovalis; *Lat can*, canal lateral to
tube leading to fenestra ovalis; *Pin*, pineal opening; *Spheth*, sphenethmoid.

Brain case.—Watson (1916) has given figures and a description
of the posterior part of the brain case of *Diadectes*. A new figure,
based on serial sections made at intervals of 1 mm., is given in
this paper (fig. 6). Relatively few details can be added to Watson's
figure, and the two figures agree in most particulars. Just anterior
to the large internal auditory meatus there is a shallow subarcuate
fossa comparable in development to that in the pelycosaurs.   The
proötic incisure is not as well defined as that figured by Watson.

Lateral to the incisure and slightly anterior to it is a short, stout epipterygoid (not shown in the figure), which rises to the parietal. The sella turcica is very large and is partially divided by a septum that arises in the midline on the posterior wall of the sella. No foramina have been found entering the sella. It would appear that the internal carotids entered this area without passing through bone. No exit for nerve VI has been identified.

The large internal opening of the jugular foramen is shown in the figure, as is the smaller double opening of the hypoglossal foramen. The jugular and hypoglossal foramina merge prior to their exit from the skull.

No specimen studied shows the complete sphenethmoid in place. Most instructive is W.M. 1695 (figs. 5,C, and 7). In this specimen the dorsal part of the element is well preserved and a fragment of the lower parts of the wings, the keel, and the attached parasphenoid is present. The sphenethmoid extended anteriorly from the level of the large pineal opening to about the anterior margin of the orbit. Posteriorly, it was composed of a pair of wings and a short, keeled base. More anteriorly, there was a median process, presumably developed by a dorsal extension of the keel, which isolated two tubular chambers through which the anterior parts of nerve I appear to have passed. The posterior part of the wings was strongly supported on each side by a process that passed latero-dorsally to articulate with the parietal. No additional details of this bone are available.

RELATIONSHIPS OF THE DIADECTIDS

INTRODUCTION

Diadectes has been assigned, almost without exception, to the order Cotylosauria.[1] The closest affinities within the order have been thought to be with the pareiasaurids. The primary bases for associating the suborder Diadectomorpha and the suborder Captorhinomorpha, the two suborders recognized if the Seymouriamorpha are removed from the Cotylosauria, are the roofed condition of the temporal region and the broad neural arches of the vertebrae. These characters appear to be an expression of primitiveness among reptiles, and, if we are to follow horizontal procedures in classifica-

[1] The order Cotylosauria is cited in several places in this section, although it has been dropped in the classification to be found on page 45. Retention in the present section is necessary for the sake of clarity in discussion of previous work in which the term has been used. It does not imply recognition of the validity of the order in contradiction to the conclusions reached in the final section of the paper.

tion, offer some basis for including in a single order all of the late Paleozoic and early Mesozoic reptiles that possess them. But the very fact that they seem to be expressions of primitiveness suggests that they might be found in divergent phyla and thus give a misleading appearance of relationship to members of divergent phyletic lines. This was recognized as early as 1914 by Watson and is emphasized by the removal of the Seymouriamorpha from the order Cotylosauria by certain workers, most recently by Romer (1945). The seymouriamorphs have both a roofed temporal region and broad neural arches. They have been removed by Romer because there is evidence, particularly in *Kotlassia* (Bystrow, 1944), that the seymouriamorphs are amphibians and not reptiles. Under this interpretation, characters that have been given as definitive of an order transcend ordinal boundaries and appear in two different classes. This is precisely what might be expected in transitional groups and it is primarily the nature of classifications that causes it to be an apparent anomaly.

There are two concepts that may be applied in interpretation of the appearance of similar features in members of two classes. One, and perhaps the most orthodox, is that the descendants in one class have derived their principal characters from close ancestors in the other class. Under this concept, the characters of the diadectomorphs and captorhinomorphs might be considered to have been derived from a common ancestry among the seymouriamorphs. The other, which is becoming more clearly recognized, is that characters that appear to be fundamental may arise independently in a series of lines that are following similar courses of evolution and that are at about the same level of development. If this were the case, it might be that the three major groups under consideration actually had separate origins among the amphibians or that at least two distinct phyletic lines were developed at that level. Since this is possible, it seems desirable to analyze the criteria that apply to relationships of the various forms, to determine, as far as possible, the phyletic relationships that may have existed. The present section is devoted to this end.

RELATIONSHIPS OF DIADECTIDS AND CAPTORHINOMORPHS

The classification on page 45 lists the infraclass Captorhina as a division of the subclass Eureptilia. This infraclass includes the primitive reptiles that have a roofed temporal region and either have lost the otic notch or have retained it in a vestigial state. The most

primitive forms are to be included in the Limnoscelidomorpha established by Romer (1946). More advanced animals such as *Captorhinus* and *Labidosaurus* form the Captorhinomorpha. *Captorhinus* is the best-known member of the Captorhina and most of the details of the internal structure of the skull have been drawn from this genus.

There are few basic similarities between the diadectids and the captorhinomorphs other than those common to primitive reptiles and reptile-like amphibians; that is, general resemblances in the temporal regions and in the vertebrae. There exist a number of clear cut differences of such significance that they appear to remove any known captorhinomorph, or any hypothetical reptilian ancestor, from the position of common ancestry to the captorhinomorphs and the diadectids. The structure of the temporal and otic regions is basically different in the two groups. *Diadectes* has a very strong otic notch. *Limnoscelis* shows a weakness in this area but at most only a vestige of an otic notch (Romer, 1946). *Captorhinus* has no notch whatsoever and the paroccipital process is confined to lateral extension, whereas in *Diadectes* it projects not only laterally but also dorsally, so that no post-temporal fossa exists. Price (1937) has shown that there is a vestigial otic notch in certain captorhinomorphs, but even this structure is very different from that in the diadectids. The quadrate in the diadectids is large, filling most of the notch, and has a strong ventro-posterior tuberosity that is not developed in any captorhinomorph. This is significant in indicating the amphibian-like nature of the middle ear.

The arrangement of the temporal bones is very different in *Captorhinus* and *Diadectes*. The temporal series of the latter includes an intertemporal, supratemporal and tabular, whereas in the former only a small element, which represents the supratemporal (or possibly the tabular), is present. The supratemporal and tabular are present in *Limnoscelis*. There is no intertemporal and the relationship of the postorbital, postfrontal, supratemporal and tabular is basically different from the arrangement of the same bones in *Diadectes*. The postorbital of *Limnoscelis* is in part posterior to the postfrontal, not dominantly lateral to it, and the supratemporal is disposed posteriorly to the postorbital and not in antero-posterior series with the postfrontal. The position of the tabular between the supratemporal and interparietal (postparietal or dermosupraoccipital) is comparable in *Limnoscelis* and *Diadectes*, but the extent of the tabulars differs materially. The tabular of *Diadectes* does not enter into the occipital surface as it does in *Limnoscelis*.

Basic differences occur in the basicranial region. The parasphenoid in the captorhinomorphs does not flare posteriorly, does not form large ventro-posterior pockets under the basioccipital and opisthotic, and does not enter into the formation of a tube leading from the middle ear to the fenestra ovalis, for no such structure is developed in the captorhinomorphs. The whole structure of the posterior basicranium and the middle ear is, in short, very different in the two groups; *Diadectes* is fundamentally amphibian-like and *Captorhinus* is distinctly reptilian.

Similar comparisons may be carried to the palate and to the brain case, and in the majority of instances the differences are of such a fundamental nature that it seems quite clear that no close relationship can exist between the captorhinomorphs and the diadectids and that any common ancestor must have been remote, well down among the amphibians. These two groups appear to be representatives of two distinct and widely separated phyletic lines.

RELATIONSHIPS OF THE DIADECTIDS AND SEYMOURIAMORPHS

These two groups show basic similarities that are as apparent as the distinctions between the diadectids and captorhinomorphs are clear cut. This is especially striking if comparisons are confined to *Seymouria* among the Seymouriamorpha, and somewhat less so if the more amphibian-like *Kotlassia* is used as a basis for comparison. It is difficult to determine whether *Kotlassia* represents a persistently primitive form in which initial characters of the Seymouriamorpha have been preserved or whether, as its stratigraphic position might suggest, it represents an expression of development of more amphibian-like characters through modification of the reptilian structures seen in *Seymouria*. Trends in the direction of *Kotlassia* are seen in various amphibian lines, and a rather close parallel to the possible degenerative development that might have taken place to produce structures of the *Kotlassia* type from those of the *Seymouria* type is shown by the embolomerous and rachitomous amphibians in their later stages. The interpretation of *Kotlassia* as a persistently primitive form and of *Seymouria* as a reptilian-like descendant would make tenable a hypothesis that *Diadectes* represents a further expression of this trend toward the reptiles. The alternate hypothesis would suggest that divergent evolution had taken place in the later phases of the two groups.

The most striking resemblances between *Seymouria* and *Diadectes* are in the otic, temporal, and basicranial regions. In both,

the parasphenoid is an important part of the passage from the inner to the middle ear. In both, the stapes was short and appears to have terminated in the otic notch while sending a strong cartilaginous process to the tuberosity on the postero-ventral margin of the quadrate. In both, the parasphenoid projects ventro-posteriorly in strong processes that form blind pockets under the basioccipital and opisthotic. In neither, did the internal carotids enter the skull through foramina in the parasphenoid-basisphenoid, although there is some indication that this may have been the condition in the ancestral diadectids. The paroccipital processes are similar in type, although they differ in detail, and are very different from those of typical reptiles.

More anteriorly, the parasphenoidal rostrum (parasphenoid-basisphenoid of White, 1939) passes above the pterygoids, which are fused in *Seymouria* and closely spaced in *Diadectes*. The rostrum is similar in the two, both in shape and in its relationship to the sphenethmoid (orbitosphenoid plus presphenoid), but, since the general plan is not basically different from that in some embolomerous and rachitomous amphibians and in most primitive reptiles, the evidence derived from this region is no more than suggestive of relationship.

The inner ear of *Seymouria* is poorly ossified, so that little comparison with that of *Diadectes* is possible. The opening to the middle ear lies more laterally in *Seymouria* than in *Diadectes*, but the nature of the passage is similar. Little evidence concerning relationships can be gained from the brain cases for, although the pattern in the two is basically similar, it does not differ radically from that found in such rachitomous amphibians as *Trematops* and in captorhinomorph and primitive pelycosaurian reptiles.

The palates in the two genera appear rather different at first glance. The differences are to be correlated primarily with the development of such specializations in *Diadectes* as the palatal process of the palatine and the strong ventral ridge formed by the vomer and the pterygoids. These structures do not suggest relationships, but the specializations of *Diadectes* do not preclude the possibility that a *Seymouria*-like form could have been ancestral. There is suggestion of a similar trend in the tendency for closure of the interpterygoidal vacuities. This vacuity is absent in *Seymouria;* the posterior part is closed by the parasphenoid and the anterior part is obliterated by junction of the pterygoids. Closure is nearly attained in *Diadectes sideropelicus* and *D. tenuitectes*. The vacuity

is, however, distinctly open in the more primitive species, *D. lentus*. In *Kotlassia* there is a well-developed interpterygoidal vacuity.

The patterns of the surficial bones of the skulls are strikingly similar. I am indebted to Dr. T. Stanley Westoll, whose keen insight into dermal patterns has enabled him to point out certain significant points of agreement. Most important resemblances occur in the temporal region. The arrangements of the postfrontal, postorbital, intertemporal, supratemporal, and tabular bones are nearly identical, and the minor differences that occur are correlated with modifications that produced the sloping occipital surface of *Diadectes* and reduction of the otic notch. In the course of these changes the parietal platform was shortened and the interparietal migrated to the occipital surface. The supratemporal became the terminal bone of the series that forms the dorsal margin of this otic notch and the tabular came to lie slightly more medially, primarily through a restriction of its postero-lateral extension over the otic notch. In spite of these modifications the patterns are so close that they provide a very strong argument for the close relationships of *Diadectes* and *Seymouria*.

The occiputs of *Diadectes* and *Seymouria* present a somewhat different appearance, but the structure is on the same general plan throughout. In *Seymouria* the supraoccipital is unossified. The exact limits of the interparietal bone have not been determined in *Diadectes*. The almost universal presence of this bone in primitive reptiles suggests that it was present and fused into the occipital complex. The occiput of *Diadectes* slopes decidedly forward while that of *Seymouria* is nearly vertical. The development of a sloping occiput appears to be correlated with greater mobility of the head and probably developed with increasing adaptation to terrestrial life. The absence of a post-temporal fenestra in *Diadectes* is a specialization probably correlated with the development of exceptionally heavy occipital musculature.

In spite of obvious differences in skull structure between *Diadectes* and *Seymouria*, the skulls of the two are so similar in fundamental structures and so different from skulls of forms not included in their respective suborders, that the conclusion that the forms are related seems inescapable. Each, while possessing reptilian characteristics, has basic amphibian structures. In each, these amphibianlike features are modified in similar ways, indicating that divergence from a more primitive stock was in the same direction and that the initial divergence from the primitive stock was probably confined

to a single ancestral phylum. The implication is not that *Seymouria* gave rise to *Diadectes* or that any diadectid gave rise to *Seymouria*, but that the two groups, Seymouriamorpha and Diadectomorpha, came from a common stock among the amphibians and that this common ancestral stock had diverged from all other lines of amphibians prior to the time that the diadectid and seymouriamorph stocks took origin. This relationship is portrayed in figure 8.

RELATIONSHIPS TO THE PAREIASAURIDAE

The pareiasaurs constitute a suite of large, primitive reptiles whose inclusion in the Cotylosauria has seldom been questioned, since the order was founded to include primitive reptiles with roofed temporal regions. Proximity to the diadectids and procolophonids has been accepted by most writers in recent years. This has led to the general tendency to include the three in the group Diadectomorpha, following the suggestions of Watson (1917).

Many of the resemblances of the diadectids and pareiasaurids are the result of modifications of a basically primitive general pattern correlated with size increase. There are a few specific similarities over and above resemblances resulting from possession of common primitive characters. The quadrate is swung forward to become essentially vertical in both groups and this has produced a widely open otic notch, secondarily covered in the pareiasaurs. The posterior part of the brain case in both is relatively long and low and similar in general structure. Both show a strong tendency toward closure of the interpterygoidal vacuities. The basisphenoid-parasphenoid of the pareiasaurs projects ventro-posteriorly in moderately strong processes but has little lateral extension. The sphenethmoid regions of the two groups show general similarities but differ markedly in detail.

In general pattern the palatal and surficial bones of the skull are similar, major differences being specialized features in one or the other group. Pareiasaurs show a much greater departure from the primitive dermal pattern in the temporal regions than does *Diadectes*, assuming the condition of *Seymouria* to be fairly primitive. Two elements are absent. It has been assumed that the missing bones are the intertemporal and supratemporal, and that the large bone which composes the postero-lateral portion of the skull roof is the tabular. This bone lies back of the postorbital between the interparietal and the squamosal. If it is the tabular, the elimination of the intertemporal and supratemporal occurred through an
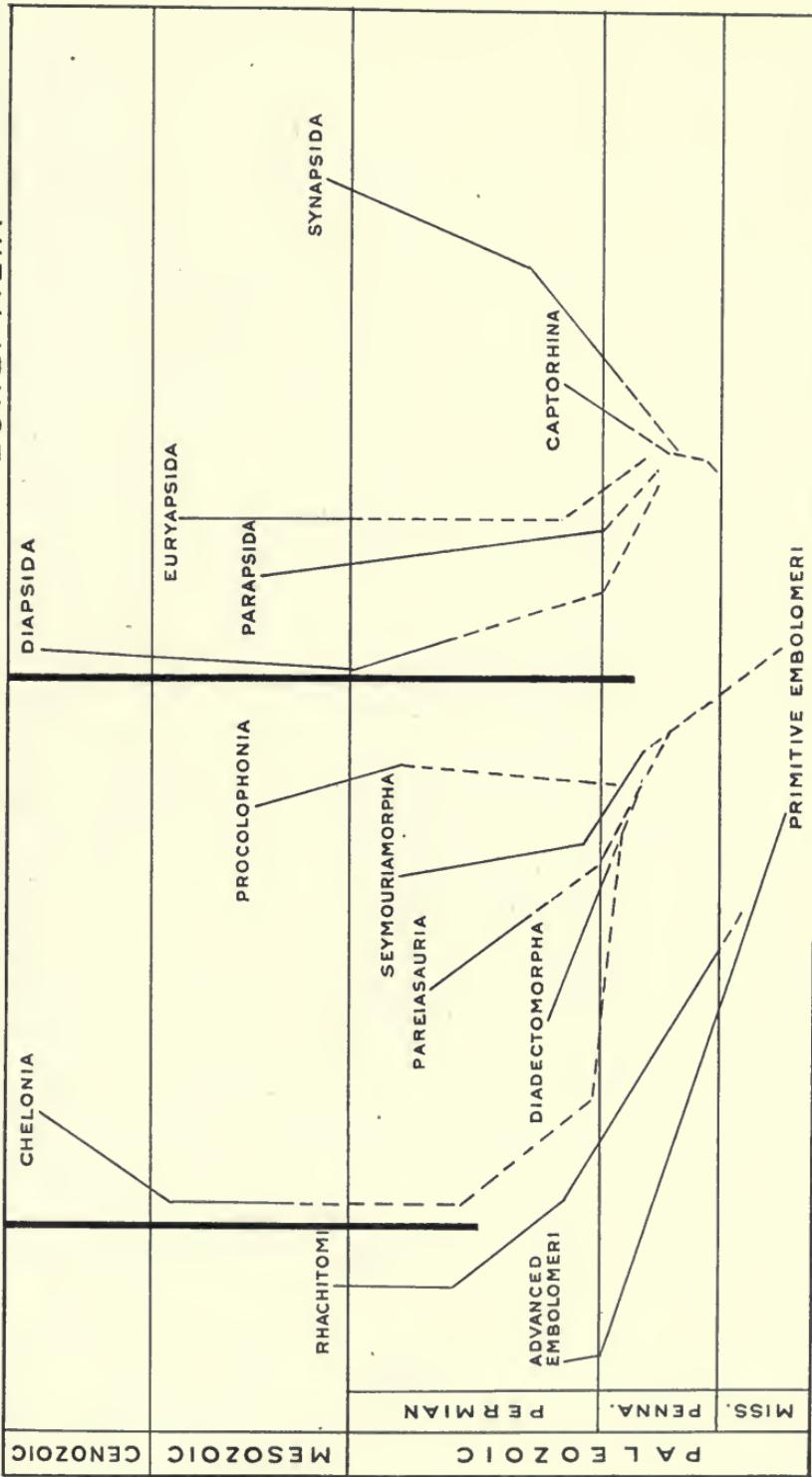
Fig. 8. Phylogenetic tree showing relationships of reptiles as suggested in text of paper.

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extension of the postorbital to occupy the posterior margin of the postfrontal and an extension of the tabular and squamosal into the area previously occupied by the supratemporal. In *Diadectes*, however, the tabular is showing a tendency toward reduction, as is the supratemporal. The intertemporal remains large. The tabular is medially disposed, as is part of this bone in *Seymouria*. If the tabular and supratemporal were lost and the postorbital were expanded dorsally the condition of the pareiasaurs would be produced, with the intertemporal as the persistent bone in precisely the position it occupies. It is suggested that the element heretofore identified in the pareiasaurs as tabular is in fact the intertemporal.

Between the forms there are certain particular differences that appear to be of considerable importance. The occiput shows a pronounced difference in that a post-temporal fossa is present in the pareiasaurs and not in the diadectids. There is no slope developed in the pareiasaurs comparable to that in *Diadectes*. The position of the fenestra ovalis and its relationship to the parasphenoid is very different in the two groups.

The weight of evidence, in spite of the differences both in specializations and in more fundamental features, appears to point toward a relationship of the Diadectidae and the Pareiasauridae. After an analysis of the resemblances and differences, Watson (1914a) stated that the Diadectidae and Pareiasauridae "are not in the least closely allied, but represent two lines differing fundamentally in the evolution of the brain case. . . ." Later studies have shown closer resemblances than were apparent in the materials available to Watson at that time. In 1917 he recognized closer affinity and regarded the Diadectidae, Pareiasauridae, and Procolophonidae as representing three superfamilies in the order Diadectomorpha under the superorder Cotylosauria. The Seymouriamorpha and Captorhinomorpha were recognized as orders equivalent to the Diadectomorpha under the Cotylosauria. Earlier (1914a), Watson had suggested that the seymouriamorphs be excluded from the Cotylosauria as being much more primitive than either of the other two groups. The principal basis for the inclusion of the three superfamilies in a single order, Diadectomorpha, was the position of the quadrate, its "vertical" orientation as expressed by Watson, and the consequent structure of the otic notch. A similar classification was used by Romer (1933), but the Cotylosauria was called an order and the lesser categories were reduced appropriately in rank. Later (1945), Romer dropped the Seymouriamorpha from the Cotylosauria.

That relationship at the ordinal level exists between the diadectids and pareiasaurids seems unquestionable, but the determination of the degree of relationship beyond this general association is less easy. It seems clear that *Diadectes* cannot possibly be ancestral to any pareiasaurid, nor is it possible that any form in the immediate ancestry of *Diadectes* could fill this position. Any common ancestor must have been below the level at which the specialized characters of the diadectid palate, dentition, occiput, and posterior part of the basicranium appeared. The otic structures of *Diadectes* could have given rise to those of the pareiasaurids, but it seems more probable, in view of the remoteness that must be assumed on the basis of other features, that these otic structures also may have developed in the diadectids after the separation from the common ancestry with the pareiasaurs. The affinities of *Diadectes* and the pareiasaurs would seem to be less close than those of *Diadectes* and *Seymouria*, except for the condition found in the quadrate regions. There is at least some evidence, as indicated in the next section dealing with the procolophonids, that this condition has arisen independently in different groups. *Diadectes* and the pareiasaurs show features suggesting that they are more closely associated than is either one with the captorhinomorphs. They are probably to be considered to fall within the large group in which similar evolutionary tendencies of the quadrate region, otic region, and palate occur. But it seems unwise to assume an association closer than would be implied by placing the two groups in the same order.

RELATIONSHIPS TO THE PROCOLOPHONIDAE

Knowledge of the procolophonids has been increased severalfold since the time that any survey of the general relationships of primitive reptiles has been undertaken. Watson's paper on *Procolophon trigoniceps* (1914b) explained most of the detail concerning this small reptile. The general structure had been well known prior to this date. In a paper on the Mesen fauna, Efremov (1940) summarized the constitution of the family, listing five previously described genera, *Leptopleuron* [= *Telerpeton*], from the Middle Triassic of Scotland, *Solerosaurus* and *Koiloskiosaurus* from the Lower Triassic of western Europe, and *Procolophon* and *Myocephalus* from the Lower Triassic of South Africa. A number of other genera have been named, largely from South Africa, but they need not be of concern in this work, since they offer little additional morphological data of use in determining broad relationships. To the five genera

cited, Efremov added two others, *Nyctiphruretus* and *Nycteroleter*, from the Upper Permian Kasan beds of Mesen. These two genera and *Procolophon* are the most useful for study of morphological detail and they show the maximum diversity occurring in the group as now known. They form the principal basis for our discussion.

Watson (1914b) pointed out that *Procolophon* was an advanced and specialized cotylosaur. He listed fourteen "advanced" characters and seven "specialized" characters. In considering the relationships of this form he pointed out that *Procolophon* belonged in that group of cotylosaurs in which the quadrate was vertical, i.e. that containing the Diadectidae and Pareiasauridae, and that it was very different from the Captorhinomorpha in this and other characters. This general placement has not been seriously questioned in subsequent papers. Resemblances between *Procolophon* and *Diadectes* are many, but some are masked by the more advanced position of *Procolophon* and by specializations of *Diadectes*. There is a close resemblance in the otic notch, and moderate similarity in the basicranial region, the brain case, and the otic region. The basisphenoid-parasphenoid of *Procolophon*, while short, shows a distinct posterior expansion somewhat like that in *Diadectes*, although less fully developed. There is an interpterygoidal vacuity in *Procolophon* but it is very short. The general structure resembles that found in *Diadectes lentus*. The relationships and shapes of the pterygoids, vomers, and palatines are similar except that no palatal process is developed from the palatine in *Procolophon*. The paroccipital process projects laterally in *Procolophon*, much as it does in *Diadectes*, and it does not make contact with the squamosal but with the bone usually identified as tabular. The post-temporal fossa is present in *Procolophon* and absent in *Diadectes*. The squamosal in *Procolophon* is an exceedingly small bone, reduced to cover only a small area between the large quadratojugal and the tabular. In view of the condition in *Diadectes* and the relationships of the so-called tabular of the procolophonids to other dermal bones and to the otic notch, it seems probable that the bone identified as the tabular is actually a persistent and expanded intertemporal.

The brain cases in the two genera are basically similar, but there are clear cut differences tending to mask the resemblances. Differences exist in the pattern of surface bones. The supratemporal is absent in *Procolophon*, the lacrimal is restricted so that it does not reach the external naris, and the pre- and postfrontals are reduced so that the dorsal rim of the orbit is formed by the frontal.

Work in recent years has shown that there is considerable variation in the shape and size of apparently mature skulls of *Procolophon*. Broili and Schröder (1936) have figured four skulls which indicate that rather marked differences exist in the shape and proportions of the otic notch. In a small skull, interpreted as a female, the notch is widely open, while in three other skulls, interpreted as males, the notch is moderately deep. In the skull with the most deeply incised notch the quadrate appears to slope somewhat posteriorly, while in the others it is more nearly vertical. This variation indicates that the notch itself cannot be relied upon too heavily as a basis for determination of relationships, and that the position of the quadrate, while more constant than the shape of the notch, must be considered subject to moderate variation even within a series of forms close enough in other respects to be placed in the same species.

The two genera *Nyctiphruretus* and *Nycteroleter*, described by Efremov (1940), are extremely important in a study of the relationships of the Procolophonidae. Efremov referred these genera to a new subfamily, Nyctiphruretinae, pointing out differences from *Procolophon* and closely related genera. Special interest is attached to these forms, as they come from older beds than do other well-known genera of procolophonids.

Nyctiphruretus is in most respects definitely a procolophonid. It has a moderately large squamosal, a small quadratojugal, and a moderately large lacrimal. Each of these elements has, however, been modified in the direction of *Procolophon* from the condition characteristic of the more primitive members of the order Diadecta. The palate has a long, V-shaped interpterygoidal vacuity occupied by a broad parasphenoid. Fusion of the parietals has not occurred. The vomers (prevomers of Efremov) are broad and not restricted as in *Diadectes* and *Procolophon*. The posterior part of the basicranium is of particular interest. The basioccipital is rounded as in *Procolophon*. The basisphenoid (probably basisphenoid-parasphenoid) is extended laterally into a wing and overlies the proximal end of the stapes. The stapes itself is relatively stout and has a strong distal articulation with the quadrate. This condition is unlike that in any other primitive reptiles, for even in *Captorhinus* and *Labidosaurus*, in which the stapes is connected to the quadrate, the articulation is much more ventral than that seen in *Nyctiphruretus*. There is no distal articulation in *Procolophon*. It is difficult to say, as Watson has indicated, whether this condition is primitive or specialized. *Nyctiphruretus* resembles *Diadectes* somewhat more

than does *Procolophon*, notably in the palate and basicranium.   It gives a better basis for interpretation of possible relationships.

Nycteroleter is similar in many respects to *Nyctiphruretus*, but it differs remarkably in the presence of a very deep otic notch rimmed dorsally by an extensive intertemporal and anteriorly and ventrally by a large squamosal.   The quadratojugal is small, like that in *Nyctiphruretus*, and in contrast to *Procolophon*.   The quadrate lies at the postero-ventral termination of the otic notch, and thus is far back in the skull.   The palate is primitive, except for the presence of a procolophonid-like array of palatal teeth.   The basisphenoid is long and narrow but broadens posteriorly.   It underlies part of the fenestra ovalis.   There is a long but very narrow parasphenoidal rostrum.   These characters represent important differences from *Nyctiphruretus*.   The resemblances of the pattern of the surficial bones, in which the tabular and supratemporal are absent, the lacrimal is restricted, and the jugal extended far anteriorly and posteriorly, as well as the resemblances of marginal and palatal dentition, strongly suggest the relationship to *Nyctiphruretus* that Efremov has proposed and Watson (1942) has confirmed.   On the other hand, the otic notch, the position of the quadrate, the size of the squamosal, the occiput, and several characters of the palate are distinctly like those of the seymouriamorphs.

Nycteroleter would appear to give some insight into the ancestry of the procolophonids, as Watson (1942) suggests.   Morphologically it lies very nearly intermediate between *Seymouria* and *Nyctiphruretus*.   Only certain specializations of the *Seymouria* palate appear to be contrary to such an interpretation.   In some respects the genus is more *Seymouria*-like than is *Diadectes*.   It is thus of particular interest as a second line of evidence suggesting that *Seymouria* is to be included in this general assemblage of primitive tetrapods that are near the reptilian-amphibian border line.

The diadectids and procolophonids are clearly related, but the relationship is moderately distant.   They must have had common ancestry above the level of separation from the stock leading to the captorhinomorphs, but this ancestry must have lain below the stage represented by *Seymouria*, so remote that few reptilian characters were strongly developed in the skull of the common ancestor.

RELATIONSHIPS TO THE CHELONIA

Most writers have conceded that the Chelonia have arisen from the primitive reptiles usually grouped together as cotylosaurs.   This

conclusion is based primarily on the skull structure, especially upon the absence of the temporal fenestrae in both groups. There seems to be little doubt, in view of the condition in *Triassochelys* (Jaekel, 1918; Abel, 1919) and other chelonians with primitive and relatively primitive skulls, that no true temporal fenestra has ever been developed, and that the broad opening in the temporal region of more advanced skulls has resulted from recession of the posterior margin of the squamosal. The closed opening, such as that present in *Hydromedusa*, probably resulted from secondary growth of the squamosal, although this has not been clearly demonstrated. Other skull features, including the pattern of the surface bones of the skull and the palate in more primitive chelonians, show definite resemblances to those of the cotylosaurs. There is less in the postcranium to indicate relationships, although the limb and girdle pattern in primitive chelonians is sufficiently generalized that derivation from any except the most primitive reptiles seems improbable. There is, however, little evidence of a trend toward the specializations of the chelonian postcranium in either the Diadecta or Captorhinomorpha. However, the similarities between primitive reptiles and turtles outweigh the differences to such an extent that various classifications have included the Cotylosauria and the Chelonia as equivalent orders under the subclass Anapsida.

Some writers have gone beyond the mere suggestion of general relationships to suggest a rather close affinity of the Chelonia and the diadectids (see especially Case, 1905b). The concept that *Diadectes* itself is close to the ancestry of the Chelonia has met with little acceptance. In many respects, however, the skulls of the diadectids and those of primitive turtles do show striking basic similarities. A number of the resemblances are repeated in other groups of Diadecta, especially in certain procolophonids, but the most striking resemblances are between *Diadectes* and primitive chelonians.

The most apparent and seemingly the most fundamental resemblances are in the quadrate region. Essentially all turtles have the articular surface of the quadrate well forward so that the quadrate is vertical. In primitive forms this results in the presence of an otic notch very similar to that in *Procolophon* and *Diadectes*. That this notch is primitive and retained from an ancestral type is indicated by its presence in the most primitive known turtle, *Triassochelys*. The structure in this form could have been derived from that of *Diadectes* with only minor modifications. Furthermore, the quadrate is expanded dorsally and has a strong pterygoid process that pro-

jects forward to articulate firmly with the pterygoid in a diadectid-like fashion. The quadrate forms an osseous support for the tympanic membrane, as it presumably did in *Diadectes*. There are, of course, differences, the most striking being the lack of a postero-ventral tuberosity of the quadrate in even the most primitive turtles. The chelonians have modified the quadrate condition radically in the course of their evolution, but even the most extreme changes, in which the stapes is completely surrounded by the quadrate and large chambers are developed by the quadrate and squamosal, could have been derived from the structure of *Triassochelys*. The basic position of the quadrate remains the same and the otic notch, modified even to the extent of being closed, can be identified. It seems almost certain that this otic condition was derived from one similar to that of the diadectids, not from that of the captorhinomorphs or any other reptilian group. There is convergent approach to this otic condition in some reptiles, especially various marine types, but their history leads back to a condition with closed otic notch and temporal fenestrae and does not approach the diadectid-triassochelyid condition.

There are important resemblances in the basicranial regions of the diadectids and the chelonians. The condition of the basicranium of *Triassochelys* is not known as adequately as could be desired, but certain features appear to be of interest. It is known that the parasphenoid extended well posteriorly and there is some suggestion that it was considerably expanded in its posterior portion. There is, throughout the Chelonia, a strong tendency toward lateral expansion of the parasphenoid-basisphenoid complex. In many types, such as *Chelone* and *Hydromedusa,* this complex passes laterally to contact the quadrate. The extent of the two bones varies, the quadrate expanding medially in some cases and the parasphenoid-basisphenoid extending well laterally in others. The relative extent of the two elements is less important than the fact that they cooperate in various types to form a partial, osseous floor to the middle ear. It will be recalled that the parasphenoid in *Diadectes* played a major part in the formation of the passageway from the inner to the middle ear. No direct contact of the quadrate and the parasphenoid was present in *Diadectes* but the two bones lay in proximity. Evidence in this region is by no means conclusive concerning relationships, but there is a suggestion of basic similarity.

More anteriorly, the basipterygoid process of the basisphenoid and the pterygoid bone are joined in a similar fashion in the Dia-

dectidae and Chelonia. The resemblance between *Diadectes* and the most primitive Chelonia is very close. Strong sutural connection and fusion do occur in other reptilian lines but only after a long history of freedom between the palate and the basicranial axis. This occurs, for example, in the therapsids but only in advanced types following upon a long series that includes the captorhinomorphs, pelycosaurs, and primitive therapsids. Similarly, in other lines, loss of kinetic characteristics is preceded by specializations not found in the diadectids and primitive chelonians. The trend in the diadectids is somewhat comparable to that in various lines of amphibians. The epipterygoid is excluded from the junction of the basicranial axis and the pterygoid, and the basisphenoid and pterygoid become very closely associated and then suturally joined. This last-mentioned stage is the one that obtains in the diadectids and the chelonians. It is a condition very different from that found among the captorhinomorphs and carnivorous pelycosaurs in which mobility is retained and the epipterygoid lies between the basisphenoid and the pterygoid. The trend towards this structure thus occurs in certain amphibian lines, in *Diadectes* and related forms, and in the chelonians. A similar trend is not observed in other reptilian lines except as a specialization late in their history, and conditions in these lines are sufficiently different from those of the diadectids and chelonians to suggest that the similarities result from convergence.

There is a strong parasphenoidal rostrum in diadectids and in chelonians. This is a structure common to most primitive reptiles and to many derived types and cannot be used as a basis for judgment concerning relationships. The position of the rostrum with respect to the pterygoids is similar in the diadectids and chelonians, for in both it rises above the close-set pterygoids except at the posterior end; but this similarity is a function of the structure of the pterygoids and not of the parasphenoid.

Few comparisons can be drawn in the sphenethmoid region. The chelonians have a strong supraseptale that is variously ossified in the adult. That this cartilage was strongly developed in the diadectids is evidenced by the large sphenethmoid complex seen in several skulls. This condition, however, is common to several reptilian groups, apparently to all primitive reptiles, and cannot be used as a basis for comparison until such time as more details of fossil types are known.

The occiputs of *Triassochelys* and *Diadectes* differ in one important respect: the post-temporal fossa is closed in the latter and open in

the former. Otherwise conditions are essentially similar. This closure is a specialization in *Diadectes* that is not found in other related lines and it would seem to exclude *Diadectes* from the direct ancestry of the Chelonia or of any other reptilian types.

There are strong resemblances between the palates of *Diadectes* and *Triassochelys*. The pterygoids in *Triassochelys* and other chelonians are joined in the midline to eliminate all of the interpterygoidal vacuity except a small posterior part that may be occupied by part of the parasphenoid. There is a strong tendency toward closure in *Diadectes*, especially in the most advanced species. Closure of the interpterygoidal vacuity occurs in other lines, for example, in the Nothosauria. Thus the character is not certainly indicative of relationship of diadectids and chelonians, but it is one more similarity that may be added to the series of similar characters and trends in the two groups. The suborbital fenestra is present in *Triassochelys* and is incipient to present in diadectids. The palatines are similar in general shape and in disposition, especially in their relationship to the internal nares, but there is no evidence of development of a secondary ventral process in *Triassochelys*. In various later turtles the vomers and palatines enter into the formation of a short secondary palate, but similar trends are also to be seen in the Lacertilia and in various Diapsida. The vomers of *Triassochelys* and *Diadectes* are very similar; in both they are compressed laterally and elongated to form a strong median keel between the internal nares. This condition is strongly modified in various lines of chelonians, but the resemblances between *Diadectes* and *Triassochelys* are striking enough to be strongly suggestive of rather close relationship. The palatal teeth in *Diadectes* and *Triassochelys* show certain resemblances, especially in the nature and position of vomerine teeth. There are, however, distinct differences. The posterior pterygoid teeth of *Triassochelys* are closely spaced in a subovoid area back of the vomer and the lateral pterygoidal teeth are arranged in distinct rows. The only pterygoidal teeth of *Diadectes* lie just posterior to the vomer in the midline of the palate and on the posterior margin of the flange of the pterygoid. The patterns of palatal teeth of the procolophonids, pareiasaurids, and *Triassochelys* are strikingly similar. Similarities and differences in dentition may be in large part due to short term adaptations and are not a particularly reliable basis for determinations of relationships among the Reptilia. The resemblances between the procolophonids, pareiasaurids, and *Triassochelys* are at best merely suggestive of similar trends that might possibly have some genetic significance.

The surface bones of the skulls of *Diadectes* and *Triassochelys* are for the most part similar in proportions and position. Only one bone has been identified in *Triassochelys* in the position of the inter-parietal and supratemporal of *Diadectes*. It has been called supra-temporal but its relationships are those of the intertemporal of *Diadectes* and it may represent this bone rather than the supratem-poral. The squamosal forms a large lateral plate in primitive chelonians and the quadratojugal is exceptionally strong. In both, the frontal is excluded from the orbital margin and the lacrimal extends from the orbit to the external nares. These features are in the main primitive among reptiles but the striking similarity of their development in the diadectids and *Triassochelys* is so strong that it suggests origin of the pattern in a not remote common ancestor among the primitive reptiles or very reptile-like amphibians. The most striking difference in the dorsal surface of the skull is the presence of the large parietal foramen in *Diadectes* and its complete absence in *Triassochelys*.

Comparisons of skulls of primitive chelonians and *Diadectes* strongly suggest that the order Chelonia came from the Diadecto-morpha. The skull of *Triassochelys* has in common with the mem-bers of this group a persistent otic notch modified by forward migration of the base of the quadrate. This condition, characteristic of many Diadecta, is found in no other reptilian groups, although a superficially similar pattern has developed independently among certain lizards. The relationship of the stapes to the quadrate and otic notch is typically amphibian in both and is less modified from what appears to be the primitive amphibian condition than it is in certain members of the Microsauria, Nectridia, and Urodela within the class Amphibia. This relationship is somewhat obscured in advanced turtles but the origin of the specialized conditions from a *Triassochelys*-like ancestor appears certain. It seems improbable that this condition in the primitive turtles could have come through any known channel except that represented by the Diadectomorpha. In addition to the similarities in the quadrate and otic regions, there is a similarity of trend and of actual structure in the basicranial region, especially in the parasphenoid-basisphenoid and their rela-tionships to the middle ear and in the basipterygoid processes and their relationships to the pterygoids. Confirmation of suggested relationships is found in the resemblances of the parasphenoidal rostra, the palates, and the patterns of the surficial bones.

The chelonian brain case is typically reptilian. It varies con-siderably in height but is commonly rather long and low, more like

that of *Diadectes* than *Procolophon*. The general structure is much like that of *Diadectes* but there are numerous differences in detail. Comparisons suffer from the fact that a truly primitive brain case among the turtles is not known. As in most primitive forms, the otic elements form a major part of the posterior lateral walls of the brain case in the chelonians and there is a broadly open internal auditory meatus. The structure of the inner ear in at least some chelonians is peculiar in that the lagena passes backward with appropriate reorientation of related hard structures. This is in distinct contrast to the condition in lizards and to the inferred condition in the captorhinomorphs. The evidence concerning this structure among the diadectids is inconclusive, since ossification is not complete. It is not possible to determine the position of the lagena; indeed, it is not possible to be certain that the structure was present. Evidence on relationships based on this region must remain inconclusive for the present. The type of brain case found in *Diadectes* is not greatly different from that of the Chelonia and could have occurred in the chelonian ancestry, but there is nothing definite to suggest that the chelonian brain case came from that of the diadectomorphs and not from some other primitive reptilian group. The principal characters in each are those characteristic of primitive reptiles in general. The height of the brain case in the procolophonids suggests that this group has departed somewhat from the type that might be ancestral to the Chelonia.

There is no sign of the ventral flanges of the parietals, so characteristic of the Chelonia, in any primitive reptilian group. Presumably this specialization occurred within the Chelonia. The condition in *Triassochelys* is unfortunately not known.

The postcranial structure of the chelonians is different from that in any other known reptilian line. No definite evidence can be derived from it. Certainly it indicates a rather lengthy period between any possible ancestral group and the first appearance of the turtles. The time between the last known Diadectidae and the first authentic Chelonia appears to be from Lower Permian to Upper Triassic. Intermediate forms have been reported, but evidence that they are chelonians seems inconclusive. The type of postcranium found in the diadectids could conceivably be ancestral to that of the turtles, and time is sufficiently long for chelonian specializations to develop. There is, however, no clear evidence of trend in the direction of the turtles in the diadectids. It is extremely odd that no remains of ancestral armored types have been found among the

abundant Middle and Upper Permian and Lower and Middle Triassic faunas of various parts of the world.

In summary, the position of the Chelonia in relationship to the Diadectidae seems to be as follows: The two groups show sufficient similarities of characters and trends in cranial structure that they may be considered as more closely related to each other than is either to any other group of reptiles. It seems highly probable that the Chelonia arose from the ranks of the Diadecta. Closest to them are the diadectids, but it is improbable that *Diadectes* itself is ancestral. Rather, it appears probable that a common line led to *Diadectes* and the Chelonia and that this line was separated from the lines leading to other Diadecta prior to the separation of the diadectids and the chelonians. If this concept is correct the Chelonia must have been established as a separate line in late Carboniferous times. There is as yet no fossil evidence of the group prior to the late Triassic unless it be in the Upper Permian *Eunotosaurus*.

THE BEARING OF THESE STUDIES ON THE CLASSIFICATION OF THE REPTILES

It appears possible on the basis of the present studies and of the earlier reports cited in preceding paragraphs to recognize two main branches of reptilian evolution. One includes the Seymouriamorpha, the Diadectomorpha, the Pareiasauria, the Procolophonia, and the Chelonia. The other includes the Captorhinomorpha, the Diapsida, and the Synapsida. Also probably to be included in this second line are the Protorosauria, the Sauropterygia, and the Ichthyopterygia, but the affinities of these are somewhat less certain. These two major divisions appear to have separated prior to the complete attainment of the reptilian threshold. This opinion will be evident from the inclusion of the Seymouriamorpha as a member of one of them. The two divisions seem to represent very distinct evolutionary sequences and logically should be separated in classification.

Present practice is to include both the Captorhinomorpha and Diadectomorpha in the order Cotylosauria. Westoll (1942) has suggested, however, that the separation of the captorhinomorphs, diadectomorphs, and seymouriamorphs was accomplished at a technically amphibian level. If the division of the reptiles proposed in the present paper be accepted, the position stated in the first sentence of this paragraph becomes untenable. The bracketing of the two groups is a natural outgrowth of horizontal classification

and was inevitable from study of the meager remains available to earlier workers; it should not be maintained in light of information concerning phyletic relationships that is now available.

If this be accepted it becomes necessary to modify the present classification of the reptiles as a whole. We may recognize two subclasses, rather than four or five. One, which we will term the **Eureptilia,** includes the captorhinomorphs as the infraclass Captorhina, and the infraclasses Synapsida, Parapsida, Euryapsida,[1] and Diapsida. These are typical reptiles characterized by lack of an otic notch or by a strong tendency toward its loss. They constituted the main radiation of the reptiles, which occurred in a series of phases in the Permian and the Mesozoic. The other subclass, which may be designated as **Parareptilia,** includes the Diadectomorpha, Procolophonia, Pareiasauria, and Seymouriamorpha in a group which may be designated as the order Diadecta and the order Chelonia. The included forms all have a strong otic notch, widely open in primitive members but modified in advanced Chelonia. This notch is characterized by a forward migration of the quadrate in all but the Seymouriamorpha and the primitive Procolophonia. The dermal pattern in the area of the otic notch gives striking evidence of relationships of certain members of the Parareptilia. The relationships of the intertemporal, supratemporal, and tabular are almost identical. In the course of evolution there is a tendency for reduction and eventual loss of these three bones. The first affected was the tabular, reduced in *Diadectes.* The supratemporal and tabular both appear to be absent in the Procolophonia, Pareiasauria and primitive turtles, leaving only the intertemporal, if the interpretations given in the comparative sections are correct. The final stage is seen in more advanced turtles in which all three are absent. Correlated with this loss is a tendency for increase in size of the postorbital or squamosal or of both elements. This pattern of changes of dermal bones is very different from that witnessed in the Eureptilia.

Patterns of modifications of the basicranium and middle ear are similar in the parareptilian groups. The parasphenoid tends to be broad posteriorly and to enter into the formation of a ventral partition under the stapes. This condition occurs in the Seymouriamorpha, Diadectomorpha, some Procolophonia and in various guises in the Chelonia. It is not apparent in the Pareiasauria.

[1] Used in the sense of E. H. Colbert (1945). The Parapsida include forms with the temporal fenestra above the supratemporal and postorbital, and the Euryapsida those forms with the fenestra above the squamosal and postorbital.

This classification eliminates the Cotylosauria from formal classification. In synoptic, tabular form the classification is as follows:

CLASS REPTILIA
    Subclass Parareptilia
        Order Diadecta
            Suborder Seymouriamorpha
            Suborder Diadectomorpha
            Suborder Procolophonia
            Suborder Pareiasauria
        Order Chelonia
            Suborder Amphichelydia
            Suborder Cryptodira
            Suborder Pleurodira
    Subclass Eureptilia
        Infraclass Captorhina
        Infraclass Synapsida
        Infraclass Parapsida
        Infraclass Euryapsida
        Infraclass Diapsida
            Superorder Lepidosauria
            Superorder Archosauria

The phylogenetic relationships as they appear on the basis of data now available are shown in figure 8. Inclusion of the Seymouriamorpha in the Reptilia, although rather usual practice, may be open to question. *Seymouria* itself has been variously classed as a reptile and as an amphibian. *Kotlassia*, on the other hand, seems at first sight to be definitely amphibian. It is not inconceivable, however, that *Kotlassia* may represent a regressive type that evolved away from the more reptile-like conditions represented by *Seymouria* through re-emphasis of amphibian characters developed *pari passu* with return to an aquatic environment; similar trends are known to have occurred in various lines of labyrinthodonts within the technical limits of the Amphibia. This has already been suggested by Romer (1945, pp. 149–150), but as occurring within the Amphibia; regression from a technically reptilian state to a technically amphibian one seems equally possible. Within the Seymouriamorpha the amphibian-reptilian boundary is nearly crossed, some features indeed being completely reptilian in *Seymouria* itself. Romer (1946) has indicated that the lateral line canals of the skull of *Seymouria* are strong evidence of the amphibian affinities of the suborder Seymouriamorpha, since they imply an amphibian type of ontogeny. His suggestion concerning the general nature of development seems well taken. In the transition from amphibians to reptiles, development through a larval stage must have been replaced, probably in a series

of slow, successive stages. Animals that possessed an intermediate type of reproduction and development must lie in a transition zone in which classification either as reptiles or as amphibians is impossible on the basis of criteria commonly used. In the case of *Seymouria* many adult osteological characters are those common to primitive reptiles. The ontogeny, on the other hand, appears to have been more like that of the amphibians than of the reptiles. This mixing of features of two classes makes classification difficult.

Similar conditions almost certainly occur in all major transitions; they are well recognized at the reptilian-mammalian boundary where various fossil forms, and even the living monotremes, can be assigned to the Reptilia or Mammalia only on the basis of arbitrarily established characters. This difficulty of assignment serves to emphasize the fact that transition zones do exist between classes. Forms falling within such zones show characters of both classes in various arrays and associations. The concept itself is perfectly clear; it is the method of expressing it in tabular classification that leads to difficulties. Reliance upon such classifications, valuable as they are in many respects, does sometimes tend to cast disrespect upon concepts that cannot accurately be expressed by them.

In this particular instance the principal problem is whether to include the Seymouriamorpha among the reptiles or the amphibians. To me this problem exists only when the necessity for tabular presentation arises. *Seymouria* can hardly be considered as either a reptile or an amphibian. It shows characters of the Parareptilia on the one hand and of the Amphibia on the other. Trends witnessed in the reptiles are clearly established in *Seymouria* but amphibian characters are preserved. The form lies in the transition zone. A possible solution would be to establish a separate class for such forms, but reflection will show that this could lead only to almost unlimited confusion in classification so long as the practical system now in vogue is followed. The assignment to the reptiles shown in the tabular classification thus has been adopted with full realization that the grouping cannot express the true situation and that assignment to the amphibians could be made with almost equal validity. The suborder has been placed in the reptiles since its closest affinities appear to be with known reptiles, members of the subclass Diadecta, rather than with any well-known amphibians, and because a number of features of *Seymouria* have passed the reptilian threshold and, as new characters, seem to be of greater importance than the other features retained from the amphibians.

ADDENDUM

Since the completion of this paper two important reports that have a bearing upon the subjects discussed have been published, one by E. H. Colbert and the other by W. K. Gregory. Colbert (1946) has presented a comprehensive review of the procolophonids, and Gregory (1946) has considered the relationships of the Chelonia at some length. Colbert's paper makes fundamental contributions to the knowledge of the structure and relationships of the procolophonids and gives a better basis for comparison with the diadectids. It does not, however, necessitate a revision of the concept of the general position of the group presented in the text of the present paper. Gregory's paper is more directly concerned with interrelationships of groups, particularly the diadectids, pareiasaurs, and chelonians, and must be given additional consideration.

The principal concern of Gregory's paper is the determination of the group of reptiles that gave rise to the turtles. He considers the cotylosaurs and placodonts as possible ancestral types, with the conclusion that the evidence is overwhelmingly in support of cotylosaurian ancestry. This is in general agreement with the conclusion reached in the course of the present study. It is only in the sections devoted to the precise relationships within this group that his conclusions differ from those presented in the present paper. He concludes that the Pareiasauria lie close to the ancestry of the Chelonia, considerably closer than do the Diadectidae. This is at variance with the conclusion reached in this paper, that the Diadectidae are close to the ancestry of the Chelonia.

The purpose of this addendum is to examine the weight of evidence bearing upon these two conclusions. It will be unnecessary to restate the morphological data, since these are given in detail in the two papers. There are, however, in the interpretation of the structure of the Diadectidae certain differences which will be mentioned and there is considerable difference concerning the weight that can be given to postcranial structures in determining broad relationships. Gregory considers the evidence of both the skull and the postcranium. Much of the comparisons of skulls seems to give strong indication that the Chelonia came from the Parareptilia, but only a few points seem to indicate a definite proximity to the pareiasaurs rather than the diadectids. The evidence of this relationship appears to be drawn primarily from comparisons of the postcrania.

In preparation of the present paper it seemed to me that appearances of relationships based on the postcranial structures were

likely to be deceptive. The similarities of the postcrania of the dia-
dectids, pareiasaurs, and chelonians appear to result primarily from
retention of basic, primitive features, attained in all lines as transi-
tion to terrestrial habits was initiated. The principal differences, as
well as a number of resemblances, seem to stem from modifications
of the basic reptilian structure in terms of adaptation to greater
perfection of terrestrial locomotion and as accommodations to
increase in size. These changes were carried farther in the pareia-
saurs than in the diadectids and were most fully expressed in certain
chelonians. There is something of a morphological series, but that
this is a phylogenetic series seems open to serious question when
cranial characters are brought into the picture.

The types that show the greatest similarities are all moderately
large. As Gregory has stated, the turtles probably arose from an
initially small group. It is very doubtful that some of these changes
which seem to imply relationships between the pareiasaurs and the
turtles would be found among small, ancestral parareptilian forms.
Convergence and parallelism in adaptations of a somewhat similar
nature, accompanied by increase in size, seem to offer a reasonable
alternative explanation. This would not, perhaps, be evident were
it not for various skull features which make it difficult to believe that
the turtles came from a stock very close to the known pareiasaurs.

The principal skull features that bear upon this point have been
discussed in comparison of the diadectids and pareiasaurs and the
primitive turtles. It will be necessary to repeat certain of these so
that they may be examined in the light of the points made by
Gregory. He gives evidence concerned with the surface bones of
the skull, the dentition, the occiput, the quadrate area and middle
ear, the palate, and the brain case.

Diadectes possesses a full complement of reptilian elements in
the surface bones. Pareiasaurs lack the tabular and supratemporal
according to the interpretation in the present paper. Gregory does
not show the "supratemporal" (intertemporal of this paper) in his
figures of *Diadectes* but implies its presence in a statement to the
effect that primitive reptilian elements were all present and that
this bone was lost during the evolution of the Chelonia. The posi-
tion of the squamosal and quadratojugal in *Diadectes* is much more
like that in *Triassochelys* than that in pareiasaurs, in which these
elements have grown backward to cover the otic notch.

Evidence of the dentition is, as Gregory implies, of doubtful
value in study of these relationships. It is true, as he points out,

that the palatal dentition of pareiasaurs is much more like that of *Triassochelys* than is the palatal dentition of *Diadectes.* It is true also that in some advanced procolophonids the palatal dentition is very similar to that of the pareiasaurs and to *Triassochelys.* Convergence has operated to produce this arrangement of rows of palatal teeth in a number of reptilian lines. Degeneration of marginal dentition to produce the edentulous character of the turtles could have occurred in either line, although, as Gregory states, less drastic modification is necessary from the pareiasaur stage.

It is clear that the occiput of pareiasaurs resembles that of *Triassochelys* more closely than does the occiput of *Diadectes.* The principal reason for this is that the post-temporal fossa is lacking in *Diadectes* and is present in the other two. In the evolution of the reptiles from the amphibians the paroccipital process underwent a ventro-lateral migration, so that in reptiles it passes laterally. But even before this rotation occurred the post-temporal fossa was present, as, for example, in *Seymouria.* Enlargement of this fossa occurred in most reptilian stocks as they became less amphibian-like, and the fossa is a common reptilian heritage and therefore an unreliable criterion for assessing relationships between various phyla. The closure of the fossa in *Diadectes* must be thought of as a specialization and not as a primitive character. It is a feature that has been noted above (p. 40) as sufficient to remove any known diadectid from the ancestry of the Chelonia, but it does not remove a close ancestral type from this position. On the other hand, the presence of the fossa in the pareiasaurs and chelonians does not seem to be an important basis for assuming close relationship. In other features of the occiput both *Diadectes* and the pareiasaurs are much like *Triassochelys.* Gregory has mentioned the fact that the exoccipital and opisthotic of *Diadectes* are not separate, but that they are separate in pareiasaurs and *Triassochelys.* The lack of separation in *Diadectes* is in keeping with the almost complete fusion of bones in the occipital region and it can hardly be thought that this represents a fundamental difference between this genus and others in which there is no fusion.

The quadrate and middle ear of all three show many similarities and it is partly on the basis of these that they may be included in one large group of reptiles. The quadrate area of *Diadectes* shows a striking similarity to that of *Triassochelys,* the quadrates differing principally in the presence of the facet in *Diadectes.* The quadrate of the pareiasaurs is similar in kind but less close in detail. It is

possible, as Gregory suggests, that the resemblances between *Diadectes* and *Triassochelys* might have resulted from convergence, but this might apply to essentially all of the structures which can be used as a basis for judging relationships. The association of a wide variety of similar characters suggests that actual phyletic relationship rather than convergence is involved, particularly as this pattern of associations is found in the wide variety of animals grouped in this paper as Parareptilia. Evidence from the quadrate area strongly suggests continuity of the whole group, and, with reference to the specific problem at hand, seems to point strongly to the diadectids rather than the pareiasaurs as close relatives of the Chelonia.

Gregory's reconstruction of the palate of *Diadectes* shows a number of differences from figure 3 of this paper. Most striking is the difference in the palatal flange. The figure in this paper is based on a suite of specimens from the Wichita and Clear Fork beds and represents clearly the conditions which they show. It is possible that this flange is variable in development, as are so many characters of *Diadectes*, and that the degree to which the bone invaded the supposed membranous palate differs markedly in individuals. Gregory shows part of the flange to be composed of the maxillary and does not label the posterior part. His text suggests that he considers it to be palatine; a number of Walker Museum specimens show the flange to be formed by the palatine alone. The interpterygoidal vacuity in Gregory's restoration is considerably more extensive than that in figure 3. A similar explanation of variability may account for this difference. These points do not enter into the question of relationships, although the restoration in the present paper shows a somewhat closer resemblance to *Triassochelys* than does that of Gregory. The whole cast of his restoration gives the impression of the primitive species *Diadectes lentus*. Gregory does not take up the posterior part of the basicranium in any detail. As explained in the text of this paper (p. 38), there are important items in this region, especially the posterior and lateral extensions of the parasphenoid and the entrance of this bone into the fenestra ovalis, which suggest that *Diadectes* is close to the turtles and that the pareiasaurs are well removed. This is especially evident when the structure of this region and that of the middle ear are considered together.

The differences in interpretation which have arisen appear to stem from two sources: analysis of the actual structures as shown in the fossils, and the weight that can be given to various items of

evidence. The interpretations are the same until the question of proximity of one or another group of Diadecta to the Chelonia is reached. There is no conclusive proof for either view. The interpretation must rest not only on the sum total of similar characters but also upon the estimate of the validity of the nature of similarities and differences. In keeping with this evaluation of the evidence, I feel that the Chelonia, while not coming from any known diadectid, arose from the stock that was leading to the family at a time prior to the appearance of many of the pareiasaurian specializations. This view is expressed in figure 8 of this paper.

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