Relationships of Diadectes[1]

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SCOPE OF THE STUDY

Diadectes, a genus of reptile from the lower Permian, has had a varied career with respect to its taxonomic position and has played a prominent role in controversies about origin and phylogeny of the reptiles. Confusion has arisen from two sources. First, the skull *Diadectes* is difficult to study because of the spongy texture of the bone as emphasized by Watson (1954), among others. Second, it is quite distinct morphologically from its contemporaries and predecessors, except for some rather poorly known genera that, together with the name genus, constitute the Family Diadectidae. The stock is ancient, going well back into the upper Carboniferous. It is only the rather late member, *Diadectes*, that can be studied in detail.

Watson (1954) surveyed the history of the genus. Prior to that time several roles had been suggested for *Diadectes*. It was the basis of the group of primitive reptiles termed cotylosaurs, and, of course, is the name bearer of the suborder Diadectomorpha, including the diadectids, procolophonids, and pareiasaurids.

Diadectes has been considered to be fairly close to the ancestry of the Chelonia (see, for example, Olson, 1947). Its morphology has been compared with that of seymouriamorphs, and relationships have been suggested. These supposed relationships to chelonians and to seymouriamorphs have led to speculations upon possible multiple origins of the reptiles (Olson, 1947, Watson, 1954).

Watson (1954) looked at *Diadectes* somewhat differently from anyone who had considered it previously, including himself. He placed the genus with the Sauropsida, using Goodrich's (1916) basic reptilian dichotomy of Sauropsida and Theropsida. So conceived, *Diadectes* is a very early representative of the sauropsids and, through its relatives, carries this stock very far back in reptilian history. In his study Watson gave a fairly detailed analysis of the skull, with interpretation at variance with earlier interpretations on some points.

Since 1954 *Diadectes* has been mentioned in a number of papers. Its phylogenetic position has been treated in particular by Vaughn (1955), Hotton (1959), Parrington (1962) and Olson (1962). Most of the recent studies have been concerned primarily with the auditory structures, following up Watson's (1954) interpretation of the middle ear as sauropsid. A most recent, published while this paper was in press, suggests that *Diadectes* should be considered an amphibian (Romer, 1964). The present paper has not been modified to conform to this assignment, although the suggestion has obvious merit.

For all that has been done, fully satisfactory knowledge of the skull of *Diadectes* is still wanting. This is especially true for the brain case and the ear region. The current investigation was undertaken in an effort to overcome this deficiency by a study of serial sections of the posterior part of an excellent skull. The right posterior quadrant of CNHM UR 27 was sectioned with an interval of .75 mm. between sections and records were made by nitrocellulose peels. Transverse sections were cut. They were numbered successively from posterior to anterior. Both graphic and model reconstructions were made, the latter in both wax and bioplastic.

A great deal of detail has emerged. Some of it clarifies old problems and some of it introduces new ones. A complete restudy of possibly related genera appears to be in order, using this new information as a starting point. This, however, will take a long time. In order not to hold up the information now at hand, this present article with more limited aims has been prepared.

The study of relationships is largely restricted to those between *Diadectes*, Chelonia and *Seymouria*. Data are presented in the form of reconstructions, descriptions, and figures of serial sections. Where possible, interpretations have been made, but there are structures revealed by the sections for which no explanations have as yet been found. A brief account of some of the data and some of the figures in the present paper was published while this paper was in press (Olson, 1965).
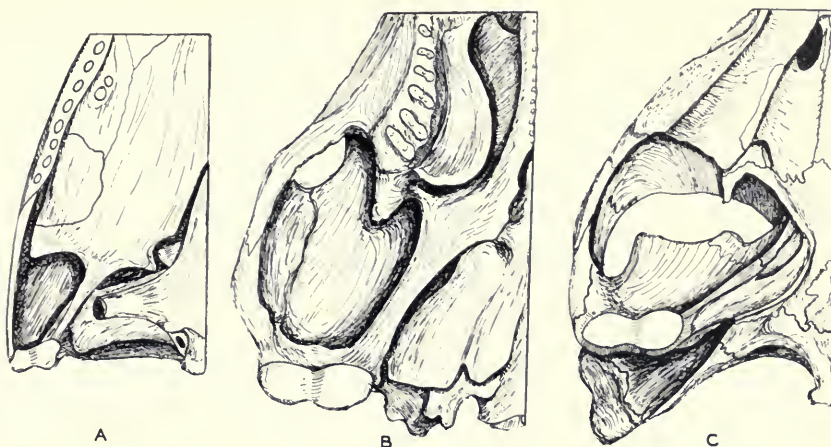
FIG. 99. Sketches of the left posterior portion of the skulls of A, *Seymouria*; B, *Diadectes*; and C, *Chelydra*, showing general features in ventral aspect. Not to scale.

For the comparisons between *Diadectes* and *Seymouria*, the posterior right quadrant of a specimen of *Seymouria* (USNM 17046) was sectioned in a comparable manner. An interval of .50 mm. between sections was used. This specimen was supplied by Nicholas Hotton III of the U. S. National Museum. I am grateful to the museum and to Dr. Hotton for permitting me to section part of it.

Modern Chelonia have been used for studies of the otic region and cranium. Rather thick sections of a skull of *Chelone* were cut and, for comparison, a head of this same genus was sectioned. Prepared materials of *Chelydra* provided additional information and various other turtles were used as they proved of help.

MORPHOLOGY AND COMPARISONS
GENERAL
Figures 99–101

The cited figures show comparable views of *Diadectes*, *Chelydra*, *Triassochelys* (fig. 100) and *Seymouria*. They speak for themselves with respect to the gross resemblances and differences of these genera. The palate and temporal regions of *Diadectes* and the illustrated turtles are clearly somewhat similar, although there are important differences. Other genera of Chelonia show varying degrees of similarity to *Diadectes*. Some are much less similar than the ones

FIG. 100. Sketches of the left posterior portion of skulls of A, *Diadectes*; B, *Triassochelys* [*Stegochelys*]; and C, *Seymouria*, showing general features of temporal regions. The ossified "stapedial" plate is removed in *Diadectes*. Numbers 1, 20, 40, etc., refer to approximate positions of serial sections in the sequences 1–87 in *Diadectes* and 1–77 in *Seymouria*. Not to scale.

figured. *Seymouria* is rather different from the other two in both palate and temporal regions.

The brain cases, seen in median, longitudinal section in figure 101, show resemblances which conform in general to the basic reptilian pattern. *Seymouria*, although quite distinct in the temporal and palatal areas, conforms rather closely to the others in this view. Comparisons such as those possible from these figures at a somewhat less detailed level, as far as the brain cases are concerned, have provided the primary bases for interpretations of relationships. They have been the best available, and thus useful, but it is now clear that they were less than sufficient for definitive interpretations. Details to be seen in the sections presented in the following pages of this paper by no means answer all of the questions. They give a basis for checking previous suggestions, offer some promising leads concerning the phylogenetic position of *Diadectes*, and they point to areas that should be studied among possible relatives of this genus.

THE MIDDLE EAR AND THE STAPES
Figures 102–107

The jaw mechanisms in *Diadectes* and many of the chelonians seem to have been basically alike. Very strong crushing action with little lateral movement is characteristic. There are many structural similarities. These are reflected in the quadrate bones and in their mode of participation in auditory structures. Somewhat similar arrangements are found elsewhere among the reptiles: in *Rothia*, among
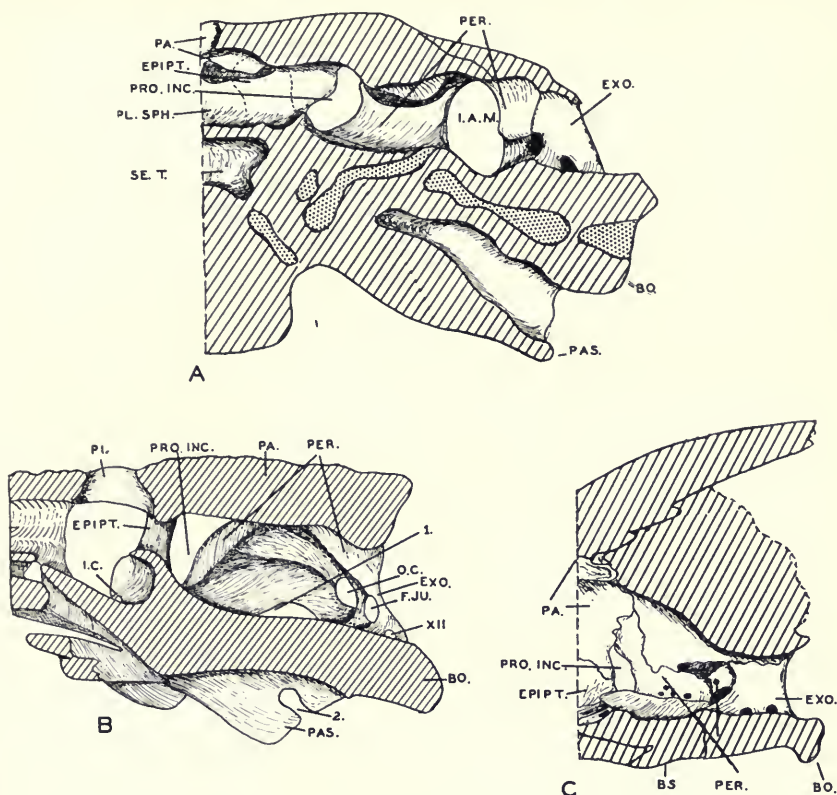
FIG. 101.   Posterior part of skulls of A, *Diadectes*; B, *Seymouria*; and C, *Chelydra*.   Skulls shown looking at midplane as exposed by longitudinal section. *Seymouria* and *Diadectes* reconstructed from bioplastic models and serial sections. Not to scale.

captorhinomorphs, in some of the placodonts, in *Trilophosaurus*, and in some of the mosasaurs.

There is a wide range of structural variation in the turtles.   The two used for detailed comparisons, *Cheyldra* and *Chelone*, are closer in structure to *Diadectes* than most.   They also have retained many of the general skull characteristics of Triassic turtles.   Along with the similarities, however, there are basic differences.   The quadrates in chelonians are strongly fixed to the squamosal and periotic, forming a massive structure which results in the enclosure of the middle ear and various associated blood vessels and nerves.   This does not occur in *Diadectes*.   Rather, the quadrate articulates with the skull roof in a fairly well developed ball and socket joint as shown in figure 102,

and also described by Watson (1954). There *is* an enclosure of parts of the ear and related structures, but it is accomplished differently, as will be described later.

The middle ear in the Chelonia is distinctive in the presence of a pericapsular sinus—a sinus that carries perilymph to the outside of the otic capsule in a space that normally would be considered the tympanic cavity (figure 103). The stapes,[1] or columella, penetrates
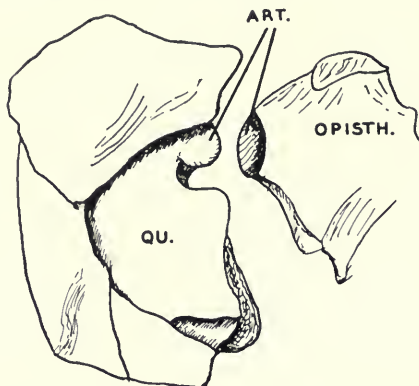

Fig. 102. The ball and socket arrangement of the articulation of the quadrate and periotic in *Diadectes*. The left side of the quadrate portion of the skull (CNHM UR 28) is shown with the periotic somewhat rotated to reveal the socket into which the ball of the quadrate fits.

this sinus in its passage to the fenestra ovalis. Lateral to the sinus, the stapes proper meets a short extrastapes which, in some cases, flares to produce a large, flat, ovoid tympanic plate. The stapes *in toto* is long, slender, and partially encased in a trough-like tympanic cavity formed by the quadrate and squamosal bones. The otic structure is definitive. Similar structure in *Diadectes*, if this could be demonstrated, would provide strong evidence of relationship to the Chelonia.

In an earlier study (Olson, 1947), I indicated that there appeared to be important resemblances between the otic region of *Diadectes* and turtles. Superficially, this is the case. Now that more details are available, however, the evidence argues, at least for the most part, to the contrary. The structures that are important for com-

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[1] The term stapes will be used throughout for consistency. Where differentiation of the inner and outer portions is used, these will be called the stapes and extrastapes respectively.
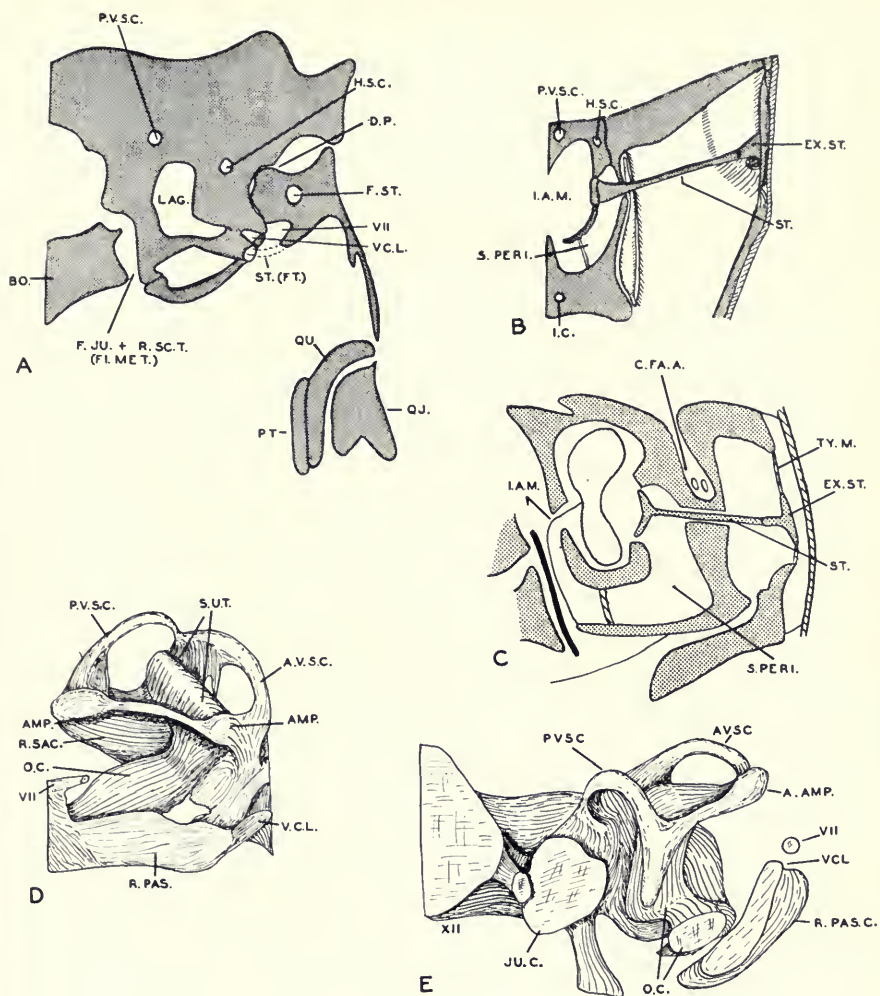
FIG. 103. Otic structures and related features in *Diadectes* and Chelonia. A, Diagrammatic reconstruction of the otic region of *Diadectes*, for comparison with B and C. Structures which have considerable anterioposterior spread have been brought into the same plane to show their general pattern. B, Diagrammatic reconstruction of otic region of the box turtle (*Terrepene*). C, More detailed reconstruction of otic region of the pond turtle (*Emys*). In A, B and C, various structures have been brought into the same plane. D, Reconstruction of the cast of the inner ear of *Diadectes*, drawn in lateral aspect from wax model based on serial sections. E, Posterior view of reconstruction of cast of brain cavity and otic region of *Diadectes*, based on wax model constructed from sections. B, after Wever and Vernon (1956); C, after deBurlet (1934). Not to scale.

FIG. 104. Transverse serial sections of the posterior part of the skull of *Diadectes* through the right tympanic cavity and associated areas. A through P go from posterior to anterior. The sections in A through P are 23–27, 29, 31, 32, 34, 37, 39, 42, 45, 50, 54, 56 respectively. For approximate locations see figure 100, A.

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parisons are intricate and complex. They are most clearly shown in the serial sections, many of which are presented in illustrations. Reconstructions, which are somewhat easier to follow, also portray much of the detail. The following descriptions and discussions lean heavily upon this illustrative material to avoid the long and tedious descriptions that would otherwise be needed.

1. *Pericapsular Sinus*

Diadectes does not seem to have a pericapsular sinus comparable to that present in living Chelonia. There are, however, two points of some significance. First, it is not clear whether or not there was such a sinus in primitive turtles. Even in extremely well preserved fossil materials it would be difficult to demonstrate positively that a pericapsular sinus was developed, although it could be shown that the arrangement of the hard structures was permissive. The fact is, of course, that no studies of this region in the earliest turtles have been made. The middle ear of chelonians could have arisen by a series of fairly straight-forward changes from the primitive reptilian ear. Whether this took place within Chelonia or before the group became established is not known.

The second point is that the tympanic cavity of *Diadectes*, while not like that of a turtle, also is not at all close to the type of structure found in generalized reptiles. It is highly specialized in a direction not commonly found among reptiles, although possibly recognizable in a few. There may have been an extra-capsular development of the perilymph sac, but, if so, this was different from that found in the turtles. These points can best be brought out by a detailed description of the pertinent parts of the tympanic cavity.

The essential details are shown in the reconstruction of the cavities in figure 103D, E and the sections in figure 104. There is a long tube, which we will call the otic canal (OC), leading posterolaterally from the saccular recess of the inner ear and opening into the tympanic cavity (fig. 103 and fig. 104, A–I). This opening, which has been considered to be the fenestra ovalis, is rimmed above by the periotic and below by the parasphenoid. Much of the tube, however, lies within the periotic, not floored by the parasphenoid as was thought previously. The periotic floor is thin, but distinct (see fig. 104, E–I).

Just where the fenestra ovalis lay is not completely clear. It was suggested (Olson, 1947, Watson, 1954) that it was at the posterolateral termination of the otic canal. This still seems to be the most likely location, but it is not out of the question that the stapes passed

part way up the tube to a membrane at some undeterminable position. Watson (1954) noted a shelf near the termination of the otic canal. He believed that this marked the site of contact of the stapedial foot and the periotic. In this event, the fenestra ovalis is represented by the termination of the otic canal. The "shelf" does not show up in any of the specimens studied in preparation of this article, but this may merely be the result of the excessive variation of structure characteristic of *Diadectes*. Until such time as a fully ossified stapes is found, and, of course, one may never have existed, the position of the fenestra ovalis probably cannot be fixed beyond question.

Lateral to the otic canal is a second tubular cavity (fig. 104, D–L). This cavity has been variously interpreted. Most probably it carried the lateral head vein. The evidence for this is best considered in connection with the interpretation of the stapes and will be deferred until that time (see p. 212).

Near the anterior end of the otic canal, the basal septum, which separates the otic canal from the recess between the periotic and parasphenoid, becomes reduced for a distance of about 1.5 mm. (fig. 104, I, J). A slot-like foramen provides an avenue of communication from the otic canal into the recess. At about this same level the periotic sends out a more ventral process (fig. 104, J) which forms a partially ossified septum between the recess floored by the parasphenoid and the floor of the otic canal. Thus a second recess is formed. There is less than full ossification of the cartilage in this region and some, but certainly not all, of this recess results from this circumstance.

It cannot be shown that the slit-like foramen and the recesses described above were related to the perilymph system. It is merely possible that they were. If this were the case and a partially extracapsular perilymphatic sinus were present in *Diadectes*, it would be necessary to conclude that its development was completely different from that known in turtles. It seems impossible that this hypothetical recess could have had any connection with the recessus scala tympani. Unless the perilymph duct followed a remarkably sinuous course within the otic capsule, it could not have had access to both the cranial cavity and the region where an extracapsular perilymphatic recess might have been present.

The recessus scala tympani probably was closely associated with the jugular canal (fig. 103, A–D). The canal leaves the brain case in partial confluence with the recess of the inner ear, as it does in many reptiles. The condition is quite similar, it would seem, to that found
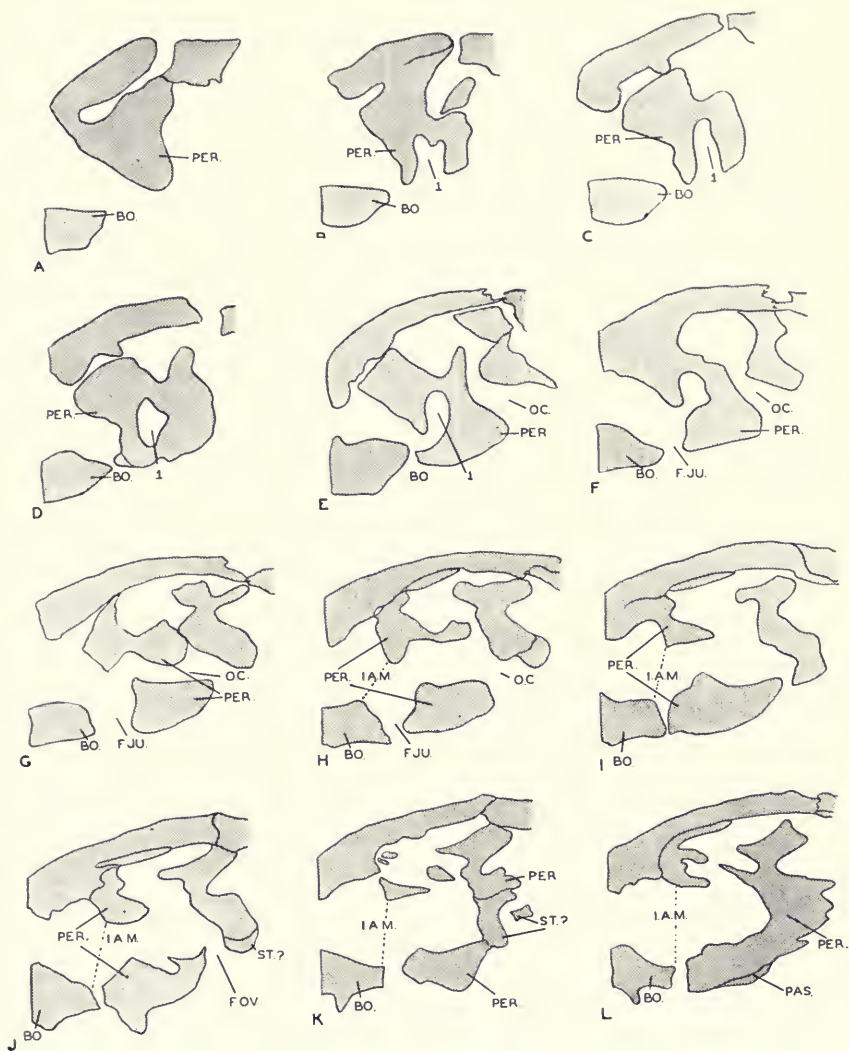
FIG. 105. Successive transverse serial sections of the posterior part of the skull of *Seymouria*. A through L, passing from posterior to anterior are sections 7 through 18, respectively. For approximate positions see figure 100, C. 1, A passage from the recess of the inner ear (D, E) leading to the external surface of the periotic as shown in B and C. This passage may have resulted from incomplete ossification, but also it may have had some unknown function.

in lizards. There is no indication in this area of development of a perilymph system like that found among the Chelonia.

The complexities of this part of the otic region in Chelonia and *Diadectes* have produced resemblances that are superficially similar. Basically, however, they are very different. The condition in turtles appears to be associated with the specialized development of the quadrate, periotic, and squamosal. In *Diadectes* the complexities are related, it would seem, to the remarkable development of the parasphenoid and its involvement in the otic structures.

Seymouria, as described in detail by White (1939), has some features of the otic region, as seen superficially, that resemble those found in *Diadectes* (figs. 105–107). This resemblance is largely confined to the expanded parasphenoid, the lateral position of the fenestra ovalis, and the involvement of the parasphenoid in the formation of the fenestra (figs. 105, G–K, 106, A–E and 107). Some details determined from the sectioned specimen used in the current study have a bearing on the possible relationships of these two genera.

The nature of the fenestra ovalis as revealed in sections is shown in figures 105, J and 107. It is not clear from the sectioned specimen whether or not the parasphenoid actually formed part of the rim of the fenestra ovalis, but it did, at least, lie just anterior to it. Whatever the exact relationships, it is clear that there is a rather long otic canal and that, as in *Diadectes*, this lies almost wholly within the periotic (fig. 105, G–J).

Posterior to the otic canal (fig. 105, F–H), as it enters the recess of the inner ear, the saccular recess is confluent with the exit of the jugular canal. There seems little doubt that the perilymphatic duct entered the recessus scala tympani in a manner very similar to that inferred for *Diadectes*. There is, however, no foramen in the floor of the otic canal, as there is in *Diadectes*. More anteriorly there is an opening in the base of the saccular recess and cranial cavity (fig. 106, B–E, symbol 2). This passes ventrally into the parasphenoidal recess between the periotic and basisphenoid above and the parasphenoid below. This part of the parasphenoidal recess is floored by what White termed the "basal tuber." Undoubtedly this complex was functional and something either entered or left the cranial cavity through the opening. Just what this may have been is uncertain and whether this structure has any relationship to the connection of the inner ear and the parasphenoidal recess in *Diadectes* is also unknown. The relationships of the parasphenoidal recess and its contents will
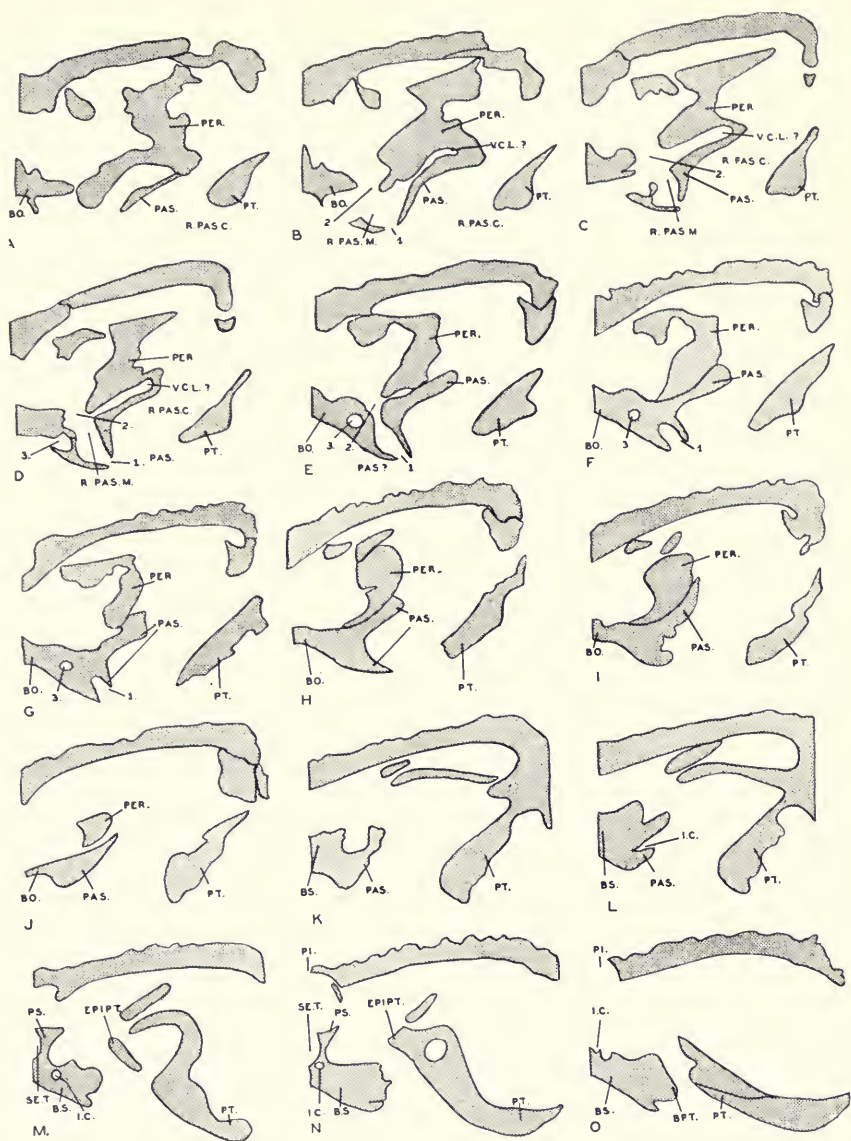
FIG. 106. Transverse serial sections through the posterior part of the skull of *Seymouria*. A through O passing from posterior to anterior, the sections are 20, 22, 23, 24, 27, 28, 29, 31, 33, 35, 38, 39, 44, 47, 51 respectively. For approximate positions see figure 100, C. 1, A notch or foramen in the postero-ventral margin of the parasphenoid. This leads into the mesial parasphenoidal recess. 2, An opening from the mesial parasphenoidal recess into the cranial and otic cavities. 3, A notch and canal in the inner margin of the parasphenoid and (?) basioccipital. See explanations in text and reconstruction in figure 107.
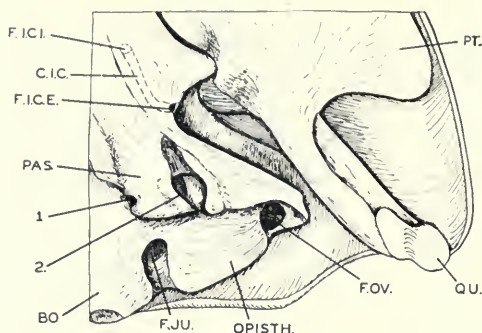
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Fig. 107. A portion of the left posterior part of the skull of *Seymouria* in ventral view. Based upon bioplastic models and serial sections. 1, A notch on the inner margin of the parasphenoid leading to canal in (?) basioccipital (see figure 106, D–G, symbol 3). 2, A notch or foramen in the postero-ventral part of the parasphenoid (see figure 106, B–E, symbol 1).

be considered more fully later, with the aid of the stapes as a guide to the position of some of the soft structures.

2. *The Stapes* (Figures 103, 104, 108 and 109)

A most important contribution of Watson's (1954) study of *Diadectes* was his analysis of the flat, bony plate that occupies the otic notch. Previously this had been ignored or called a part of the quadrate. Watson showed that it was part of the otic complex. He called it an ossified tympanic membrane, noting however, that it might be in part or wholly stapedial. While not always preserved, this ossified membrane does occur in a number of specimens. For convenience, in view of the question of its affinities, it will be termed here merely the "ossified plate."

This plate is well preserved in CNHM UR 27, sectioned in this study. Watson had examined this specimen (fig. 108, A and B) very briefly in the course of his study, but at that time preparation was incomplete. Later, it was possible to give a general description from the prepared specimen including remarks on some of the features of the stapedial shaft (Olson, 1962). The sections have revealed much additional detail and corrected some of the interpretations based on the prepared specimens. The stapes as now revealed proves to be quite unlike that of any other reptile in which this area is well known.

The ossified plate is roughly ovoid as seen in lateral aspect, but the posterior margin swings postero-medially and is somewhat thickened (fig. 108, A). The ventral portion of this inflected margin fits closely

over the quadrate tuberosity. It appears to have been attached to it, presumably by a ligament. On the inner surface of the flat portion of the ossified plate there is a deep groove which has the shape of an inverted V (fig. 108, E and F, also fig. 104, A–G). This runs horizontally for about one-third of the width of the plate. Anteriorly, the groove passes into a poorly defined trough, marked dorsally by a thickening of the ossified plate (fig. 108, G).

The stapedial shaft, as preserved, is short and thick. This, and what appears to be the stapedial part of the ossified plate (see fig. 108, B), constitute the extrastapedial portion of the stapes (fig. 108, A–G). The more medial portions, the stapes proper, are almost absent, presumably being largely cartilaginous. As shown in figures 104 and 108, part of the shaft makes broad contact with the periotic by means of a rounded process. This is the dorsal process of the stapes. There is a well developed stapedial foramen and canal. Presumably this carried the stapedial artery. Below it, on the ventral surface of the shaft, is a well defined groove, between the dorsal process and the process that passes toward the fenestra ovalis. Probably this carried the facial nerve (VII) and the lateral head vein. Traced forward, the presumed passage of the facial nerve lies between the periotic and a dorsal spur of the parasphenoid. This passageway leads to the "facial foramen" (fig. 104, P).

The stapedial process that leads to the fenestra ovalis is represented only by a short, slender spur. As noted earlier, there is no basis for precise location of the fenestra or for interpreting the nature of the stapedial foot.

In figure 108, D a second canal in the stapes is shown. This runs for a short distance through a lateral part of the shaft, opening postero-ventrally in a foramen that lies near the posterior end of the V-shaped groove in the ossified plate.

The various structures of the stapes just described—dorsal process, the V-shaped groove of the ossified plate, the second stapedial foramen, and the groove between the dorsal process and stapedial shaft—all may have been involved, among other things, in the course of the seventh cranial nerve. That this was so cannot, of course, be demonstrated and must remain conjectural. Figure 108, B illustrates the hypothetical course of the nerve as reconstructed under this interpretation. The chorda tympani, after its separation from the hyoidean branch of VII, is interpreted as swinging around the thick dorsal process, passing ventrally into the short "second" stapedial canal, issuing from this to pass forward in the V-shaped groove, continuing

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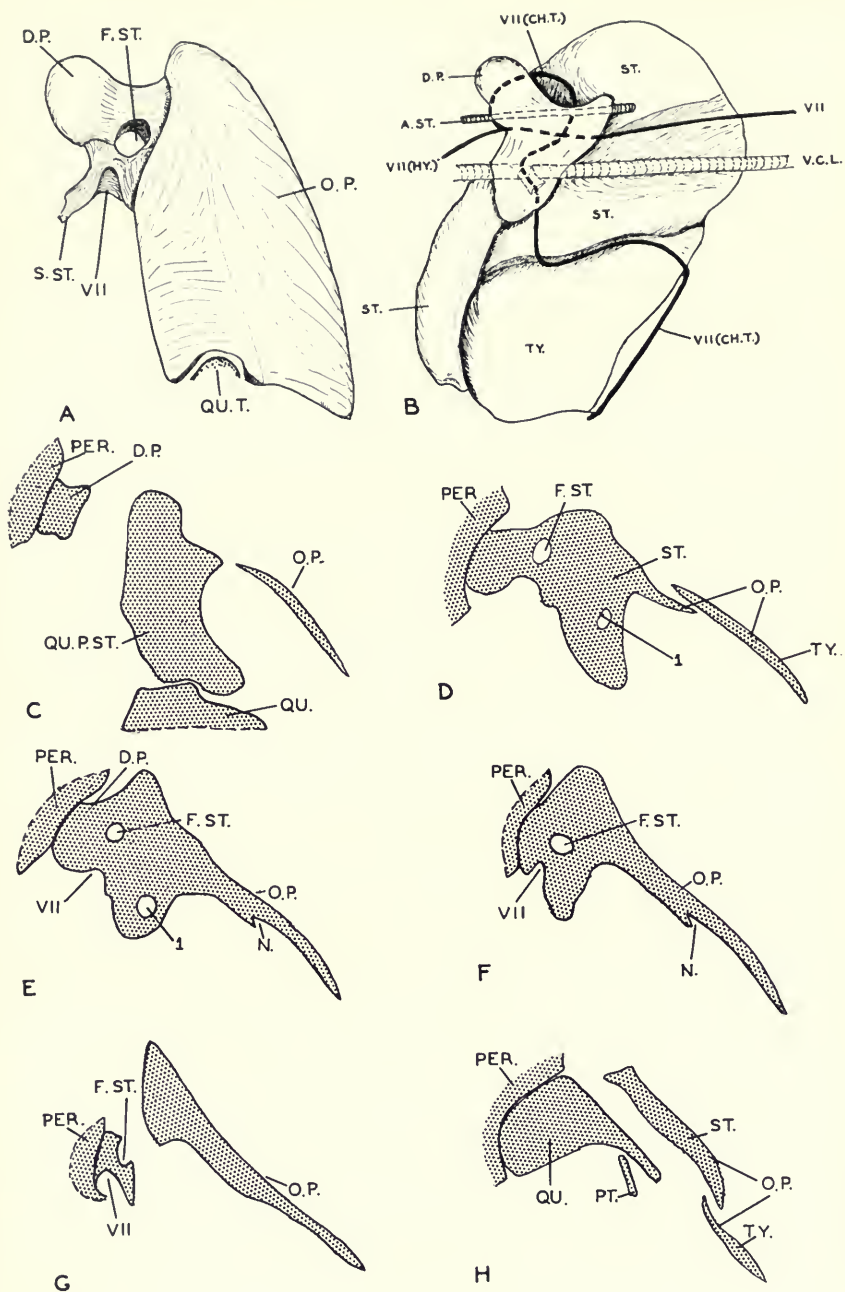
beneath the swelled dorsal portion of the plate to the quadrate, and then swinging down and backward to follow the quadrate to its articulation with the lower jaw. Here, presumably, the chorda tympani passed medially in a course over the posterior part of the quadrate to enter the lower jaw through a postcondylar foramen.

So interpreted, the chorda tympani, in spite of the complexities of its course, is pre-tympanic and basically similar to the chorda in modern lizards. The course across the plate, however, is subject to more than one interpretation. If the whole ossified plate is tympanic membrane, or if it is all stapes, then the chorda cuts across one or the other, as the case may be. The best evidence now available, however, suggests that the plate may be part stapedial and part tympanic membrane. The thickened and inflected posterior part (fig. 108, A–C) which reaches the quadrate tuberosity seems best interpreted as the quadrate process of the stapes (possibly including the ceratohyal part as well). Near the posterior and anterior ends of the V-shaped groove, the ossified plate appears to be double (fig. 108, D). A slender wing of the more ventral part passes upward outside of the more dorsal part of the plate. Near the anterior end another division is present (fig. 108, H). Here, however, the ventral part passes medially to the more dorsal portion. It seems at least reasonable to suppose that the lower portion is tympanic membrane and the upper portion stapes.

If this is correct, then the chorda tympani, as reconstructed, passed along the inner, upper margin of the tympanic membrane, and along the *ventral* margin of the stapedial plate. It was not, however, ventral to the shaft of the stapes, since it reached this position by passing through the short canal on the margin of the shaft after swinging over and around the dorsal process, but it might be considered in part post-tympanic. This position, then, while distinctive, is not fundamentally different from the general reptilian structure. It seems somewhat more sauropsid and theropsid, but shows notable departures from the conditions in either major group.

The stapedial artery presumably passed forward through the large stapedial foramen and canal (fig. 108, A and B). Beyond the stapes,

FIG. 108. The stapes of *Diadectes*. A, Posterior view drawn from wax models and from serial sections. B, Medial view with reconstruction of suggested positions of nerves and vessels. Drawn from wax models and serial sections. C–H, Selected transverse serial sections of the stapes passing from posterior to anterior; respectively, numbers 16, 20, 22, 26, 30, 42. For approximate positions see figure 100, A.

anteriorly, its course cannot be traced.   It must have entered into the recess between the periotic and the pterygoid-quadrate complex. If it supplied the adductor musculature, as is the case in many reptiles, it must have found some exit from this recess.   There is no evidence of such an exit.   In turtles, where a "trapping" of the artery occurs, there is a large foramen which provides for access to the adductor region (fig. 103, C).   It seems probable that there was a different circulatory arrangement in *Diadectes*.   The modification seen in crocodiles, with a major part of the circulation going through the cranial cavity, does not seem to have been followed, for no access of the stapedial artery to the cranial cavity is evident.   Thus, while there seems to have been modification of the arterial circulation, there is no evidence in material at hand as to the pattern of the modification.

THE PARASPHENOIDAL RECESS AND RELATED STRUCTURES

The parasphenoidal recess is defined here as the space between the expanded parasphenoid and the bones of the basicranial axis and otic region.   It occurs in *Seymouria* and *Diadectes*.   The analogous structure in Chelonia is formed by the exoccipitals, quadrate, squamosal, and periotic.   Although this cavity in turtles contains some of the same structures as those which presumably lay in the parasphenoidal recess, it is completely different in development.   The similarities must be considered the results of structural convergence.

The parasphenoidal recess in *Diadectes* and *Seymouria* is most clearly revealed in sections (fig. 104, *Diadectes*, and fig. 106, *Seymouria*).   Its extent and internal details tend to be obscure in prepared specimens.   Several specimens of *Diadectes*, however, have split through the recess and have shown the presence of the two major canals related to it—the otic canal and the more lateral one, here considered as the passageway for the lateral head vein.

Diadectes: The nature of the parasphenoidal recess in *Diadectes* is shown in sections in figure 104 and in reconstruction in figure 103. The lateral head vein is shown as lying near the lateral margin of the central portion of the recess.   More medially, separated from the recess by a thin septum, is the otic canal.   The lateral head vein appears to have entered the parasphenoidal recess at the antero-lateral margin of the main chamber.   In some specimens of *Diadectes* a clearly defined foramen occurs, but in others, such as the one sectioned, the opening is not distinct enough to appear as a foramen in prepared specimens. Anterior to the recess, the course of the lateral head vein

cannot be traced for more than the short distance through which it lay in a groove on the base of the periotic (fig. 104, K, L).

Just what occupied the rest of this central cavity of the recess in *Diadectes* is not clear. The possibility of an extracapsular perilymphatic sinus was noted earlier, but as pointed out, there is no good affirmative evidence. There may have been a venous sinus, related to the presumed passage of the lateral head vein, but again, positive evidence is lacking. It is possible, also, that the internal carotid artery traversed this space, for this is a reasonable place for it to have been. There is, however, no evident exit for the artery. It has, in fact, not been possible to find any trace of the course of this artery in *Diadectes*. It was noted earlier (Olson, 1947) that the course was not evident in prepared specimens, but it seems reasonable to suppose that it would be found in the basisphenoid in serial sections. This is usually the case, as in *Seymouria*, *Captorhinus*, Chelonia, Lacertilia and many pelycosaurs and therapsids. It is just possible that lack of ossification has obscured the course in *Diadectes*, but this seems unlikely in view of the pattern of unossified areas. Rather, it is more reasonable to assume that there was some specialization in the arterial circulation, a specialization that at present at least has defied detection except in the lack of evidence of a "normal" internal carotid artery.

The central portion of the parasphenoidal sinus is the most prominent. There is, however, a more mesial part, partially confluent with the central portion, and a small, but important dorso-lateral part (fig. 104, G and K). The mesial division is floored by a heavy flange of the parasphenoid. Presumably the posterior part of this bone formed an area of insertion of strong, ventral cervical muscles. Dorsal to the central portion of the recess, the parasphenoid swings past the ventro-lateral margin of the periotic, making contact with it, and then rises to create an extracranial space between itself and the lateral wall of the periotic (figs. 104, J–M and 109, A). At the posterior end of the recess the parasphenoid forms only a small spur. This lay just ventral to the most anterior part of the stapes and apparently served as a continuation of the conduit for the facial nerve which was carried to this point by the stapes (fig. 104, G–J).

More anteriorly (figs. 104, J–P and 109, B–D), the parasphenoid is enlarged, and develops a second dorsal arm that excludes the canal of the facial nerve from the margin of the periotic. Farther forward, the facial canal penetrates through this second dorsal arm. Just what function this enlarged part of the parasphenoid played is unclear.
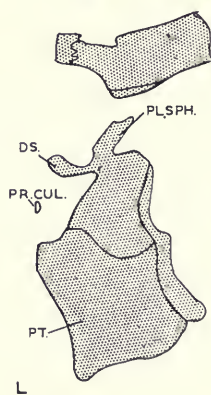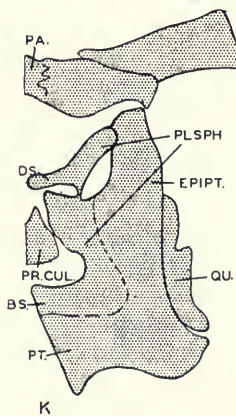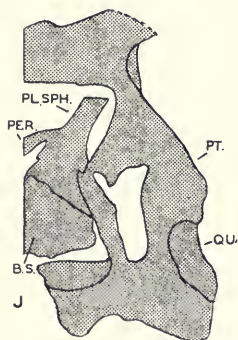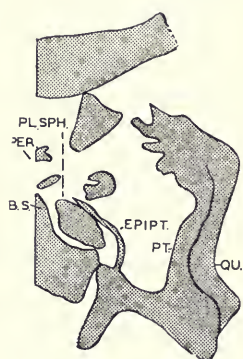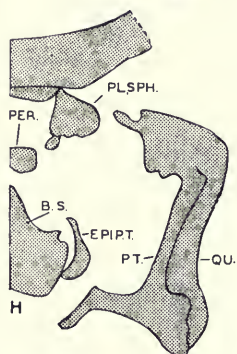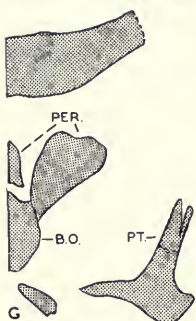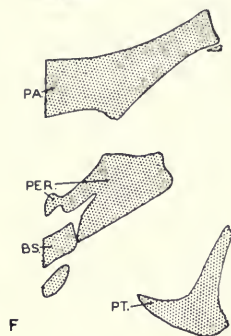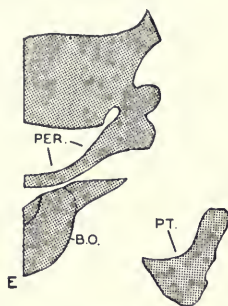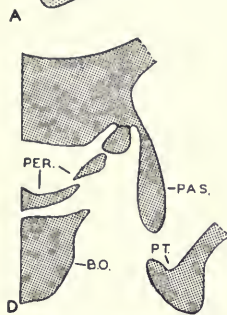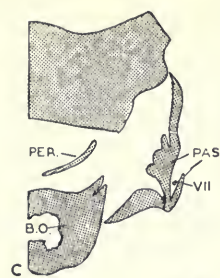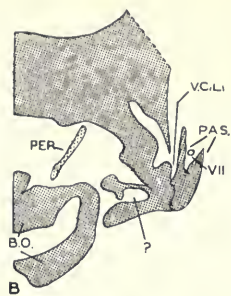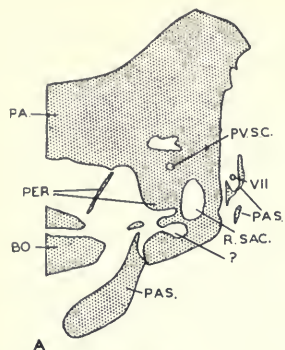
It flanks the area where the anterior semicircular canal makes lateral exit from the brain case. This does not help much in arriving at an explanation of its function, for the emergence of the canal represents an equally aberrant circumstance. In a following section more details concerning the anterior extension of the parasphenoid will be given, when its relationships to the formation of the wall of the brain case are taken up.

Seymouria: The parasphenoid and parasphenoidal recess are less well developed in *Seymouria* than in *Diadectes* but are extensive as compared to development in most other reptiles or amphibians. There are many similarities between the structures in the two genera. The relationship to the otic canal in *Seymouria* has already been discussed. The central portion of the recess in *Seymouria* (fig. 106, A–E) is laterally extensive but narrow dorso-ventrally. The dorso-lateral portion of the recess is present, but only very slightly developed. There is no massive anterior increase of the parasphenoid as in *Diadectes*. The mesial portion is most fully developed and forms the "basal tuber" of White (1939).

The central portion could have carried the lateral head vein, as has been suggested for *Diadectes*. There is an adequate area of entrance and a possible exit. There are no well formed foramina and there is no evident tube in the recess. The facial nerve probably lay medial to the short spur of the dorso-lateral portion of the parasphenoid but, in the absence of a stapes, it is difficult to define a precise position. In these respects, *Seymouria* probably was similar to *Diadectes*, although this is far from definite.

The mesial portion of the parasphenoidal recess has some distinct differences from its counterpart in *Diadectes*. Interpretations of the structures are difficult and problematical. The details of this portion are shown in sections in figure 106, B–G. The mesial parasphenoidal recess is deep, and the posterior margin of the parasphenoid bone undoubtedly served for muscle insertion as in *Diadectes*. A short distance anteriorly, however, there is a rather large foramen, or deep notch, which penetrates the parasphenoid and enters into the parasphenoidal space from a ventral and slightly lateral position. At the level of this foramen there is the large opening into the cranial cavity noted earlier (see fig. 106, B–E, symbol 2). This latter structure

FIG. 109. Transverse serial sections of the posterior part of the skull of *Diadectes* showing the anterior part of the sectioned region. A through L passing from posterior to anterior. Sections in sequence A to L are 48, 56, 57, 61, 63, 67, 70, 74, 76, 80, 82, 85 respectively. For approximate positions see figure 100a.

seems to pass mostly into the auditory recess, but ossification is rather poorly developed, and it may be that it passes into the cranial cavity as well. The opening through the parasphenoid seems to lead across the parasphenoidal recess in the direction of the second foramen.

Anteriorly to the opening into the brain case the floor of the cranial cavity is again closed, but a strong, inverted trough carries forward, eventually issuing from the parasphenoidal recess to the side of the otic part of the brain case (figs. 106, E–G and 107). The trough heads in the general direction of the more anteriorly placed foramen for the internal carotid artery.

At the level of the latero-ventral foramen in the parasphenoid, on the medial part of the parasphenoid, there is a hook-shaped structure that forms a partial recess, open dorso-medially but closed ventrally and laterally (fig. 106, D–G). Carried forward, this recess passes into a fully formed canal in the basisphenoid. After a distance of several millimeters, however, the canal simply disappears. There is no evidence of passage to the surface of the bone or of continuation in smaller canals. Almost certainly this structure was functional. Presumably it carried either arterial or venous circulation.

In one way or another all of the structures just described seem to have been related to the circulatory rather than to the nervous system, the two most reasonable associations. It is not impossible, of course, that the opening between the parasphenoidal recess and the brain case carried a perilymphatic structure, but it seems unlikely in view of the associated structures. The most suggestive feature is the course of the trough (fig. 106, E–G, symbol 1) leading forward after the closure of the foramen which passes into the cranial cavity. As indicated, this trough seems to go toward the foramen of the internal carotid artery. It is possible that the internal carotid, after separation from the stapedial artery, entered the parasphenoidal recess and then passed through it, anteriorly, to emerge prior to its entrance into the carotid foramen. This would be a fairly "normal" course for tetrapods at this general level of development.

It is further possible that within the recess it divided and sent a branch into the brain case through the opening between the otic and basisphenoid. This is not a "normal" situation, but certainly can't be ruled out. However, there is some evidence that the lateral head vein passed through the recess, although this is less clear than in *Diadectes*. It could be that venous drainage of the posterior part of the brain case issued from the foramen in question, rather than through

the jugular canal which is high and closely associated with the saccular recess of the inner ear.

These are little more than suggestions, highly speculative. Irrespective of the interpretations, it is evident that there are some notable similarities in this general area between *Diadectes* and *Seymouria*. Each has its own peculiarities, but resemblances are such that they do suggest a common ancestor with some of the properties common to the two.

Inner Ear and Brain Case

The osseous labyrinth and associated structures of the inner ear of *Diadectes* are well preserved. For the most part the patterns, as shown in figure 103, D and E, are those found in reptiles in which this region is not specialized. The backward swing of the saccular region, presumably marking the extension of a lagena into the otic canal, and the opening of the anterior vertical semicircular canal to the outside of the brain case, are the only marked departures from the generalized condition. The latter, as noted earlier, seems unexplainable at present. Possibly it is the result of an individual aberrancy, but this can't be determined without studies of more specimens.

The lagena in Chelonia (de Beer, 1937; Nick, 1912) projects backward, somewhat as it seems to have done in *Diadectes*. In Chelonia this has resulted in a modified structure of the recessus scala tympani. The detail involved in this determination is much greater than that available in *Diadectes*, so no comparison is possible. Almost nothing can be said about the inner ear of *Seymouria*. As White (1939) pointed out, ossification is such that little detail is preserved. There is an otic canal as in *Diadectes*. It passes somewhat more laterally and reflects a somewhat different position of the contained structures.

There are several points of special interest in the brain case. Some of these are shown in the medial views in figure 101. Although comparable structures, for the most part with the same general positions and relationships, can be identified in each genus, they do not indicate particularly close relationships. Each genus departs in its own way from the general reptilian conditions from which the resemblances stem.

Seymouria, if allowances are made for the lack of ossification, comes closest to a generalized reptilian pattern, such as that shown by *Captorhinus*, lizards, and such rhynchocephalians as *Sphenodon*. *Chelydra* is strongly ossified and is modified in particular by the in-

corporation of the parietal in the osseous lateral wall of the brain case. The epipterygoid is correspondingly reduced in height.

Diadectes is highly distinctive in many features. The brain case is long and low. As seen in the median section, the most striking feature is the very large pleurosphenoid. Otherwise in medial view it appears somewhat more "orthodox" than it does when studied in successive transverse sections. Representative sections, shown in figure 109, tell a fairly complete story. The complexities are clear. Some are the result of poor ossification, but for the most part they relate to peculiarities of the structure of *Diadectes*.

Figure 109, A shows a thin slip of bone (PER), closing the internal auditory meatus. This sharply reduces the cross-sectional area of the brain case over what it would appear to be in the absence of this ossification of the brain case wall. The slip of bone appears to be periotic, properly a portion of the proötic. In this section the dual character of the dorsal extension of the wing of the parasphenoid is just becoming evident. There is evidence of lack of ossification in the basicranial axis, possibly between the basisphenoid and basioccipital.

Figure 109, B shows the parasphenoid enlarged and double, and also records the opening of the anterior vertical semicircular canal to the exterior of the brain case. The opening passes into the space between the inner part of the parasphenoidal wing and the periotic. Figure 109, C shows strong reduction of the ossification of the periotic. This section lies just anterior to the opening of the facial canal through the parasphenoid (see fig. 104). Figure 109, B, C and D illustrate the great enlargement of the parasphenoid and then its disappearance. The slip of periotic, noted in the first section and continuing forward, is seen to enlarge rapidly to form a rather massive bone (fig. 109, C–G). Also, it appears, this ossification passes to the mid-line, ossifying trabecular cartilages near the dorsum sellae, much as occurs in pelycosaurs (Romer and Price, 1940) and some therapsids (Olson, 1944).

In figure 109, G–L, the pterygoid and quadrate (omitted from drawings of the earlier sections) are added. These sections show the massive development of the pleurosphenoid and the structure of the sutural cranio-palatal joint.

As far as I am aware, the cranial structure of no other reptile closely resembles that just described and figured for *Diadectes*. It is sufficiently different that even determination of the identities of some of the bones is not completely certain. Both the dual nature of the

periotic, and the interpretation of the large anterior element as pleurosphenoid may be questioned. The very great extent of the parasphenoid undoubtedly raises legitimate doubts about the identity of the bone so designated.

This cranial structure finds no counterparts in the Chelonia. *Seymouria* is certainly much more "orthodox," yet it does show some of the same pecularities in incipient stages, and this suggests development in the same general direction as *Diadectes*.

SUMMARY OF RELATIONSHIPS

The structures of the middle ear and brain case of *Diadectes* are in many respects very different from those known in any other reptiles. Presumably, of course, they are approximated in other members of the Family Diadectidae. They appear to set this family well apart from any other well understood reptilian stocks.

As far as the supposed relationship of *Diadectes* to turtles is concerned, this now seems out of the question. The apparent resemblances are superficial and due to convergence. This appears to apply as well to the rather vague similarities of *Diadectes* and some of the reptiles grouped as sauropsids by Watson (1954). It is true that some features of the otic and quadrate regions of *Diadectes* are of the pattern considered characteristic of sauropsids by Watson. In fact, they were strongly involved in the formulation of the diagnosis. The more or less vertical quadrate, with its concave posterior margin and exposed lateral surface, and the high position of the stapes fall within this category. The preponderance of otic and cranial features of *Diadectes*, however, conforms neither to the patterns of the so-called sauropsids nor theropsids. The massive stapes, with its two foramina, is a far cry from the slender stapes of sauropsids. Most features seem to be strictly diadectid. Resemblances to one or another group of reptiles are due to convergence, related largely, it would appear, to similar adaptive modifications of the masticatory apparatus.

The vast morphological difference between *Diadectes* and any of the reptiles grouped as "sauropsids" clearly removes it from any close taxonomic association with them. A cornerstone of the concepts of dichotomy of the reptiles, either as sauropsids or theropsids or as parareptilians and eureptilians (Olson, 1947) is thus removed. Watson (1957) softened his views on the intimate relationship of *Diadectes* to other reptiles, suggesting that it might be quite isolated. Parrington (1958) made a strong case against the sauropsid-theropsid

dichotomy. Removal of *Diadectes* from its role as a supporter of concepts of dichotomy, necessary in view of the new evidence on its cranial morphology, seriously weakens the already tottering framework of dichotomy and leaves both the sauropsid-theropsid concept (Goodrich, 1916; Watson, 1954) and the parareptilian-eureptilian concept (Olson, 1947) with little or no support as far as the evidence of osteology is concerned.

The current study has added nothing to an understanding of the possible relationships of *Diadectes* to procolophons and pareiasaurs, often grouped with diadectids in the Diadectomorpha. As far as is known, the special features of the basicranium, otic region, and brain case of *Diadectes* do not occur in either of these two groups. Only a detailed analysis of skulls of representatives of each of these groups would permit the necessary comparisons. As things now stand, it seems probable that there is no very close relationship of *Diadectes* to either of them.

Of the well known tetrapods of the late Paleozoic only *Seymouria* has structures in the basicranium brain case and middle ear that are at all similar to those of *Diadectes*. Both *Diadectes* and *Seymouria* are late and fairly specialized members of their respective groups. As would be expected under such circumstances, even though there was a fairly close relationship, there are many marked differences between the two.

It seems probable that *Diadectes* and *Seymouria* stemmed from a common stock in which the unusual features shown in both were at least incipient.[1] The stock that each represents had a fairly long history, dating back at least into the early part of the upper Carboniferous. Both had radiations in the upper Carboniferous, known, however, only from rather fragmentary remains. *Seymouria, Kotlassia,* and *Lanthanosuchus* are representatives of the better known Permian radiation of the seymouriamorphs or batrachosaurs. All seem to have had a pattern of otic and cranial features similar to that best known from *Seymouria, Diadectes, Diasparactus*; perhaps *Bolosaurus, Stephanospondylus,* and *Phanerosaurus* represent the diadectid radiation near the end of its history. From these repre-

[1] Since this was written, Vaughn (1964) has described a new reptile from the Cutler Group, *Tseajaia campi* Vaughn. The skull has both diadectid and seymourid features. This new creature seems to offer support to the proposed relationship of *Diadectes* and seymouriamorphs. Also, as noted in the introduction, Romer (1964), suggested that *Diadectes* was an amphibian, which may cast additional light on the discussion in this section.

tatives it is clear that the adaptive patterns in the diadectids and seymouriamorphs were very different.

At present it seems reasonable to think of diadectids and seymouriamorphs as two early stocks that evolved into the reptilian habitus from a common amphibian ancestry, each along somewhat different lines. Some Seymouriamorphs had larval stages and thus are technically amphibians. Nothing is known of the ontogeny of *Diadectes*. It is possible that other reptilian groups arose from one or both during the early phases of their radiations. There exist, however, no actual data which can either confirm or deny this. Almost certainly no known reptilian lines descended from either group as represented by the end members of their radiation.

LIST OF ABBREVIATIONS

A.AMP.	anterior ampulla of inner ear
AMP.	ampulla of inner ear
ART.	articulation of quadrate and periotic
A.ST.	stapedial artery
A.V.S.C.	anterior vertical semicircular canal
BO.	basioccipital bone
BPT.	basipterygoid process
BS.	basisphenoid bone
C.FA.A.	canal for facial artery
CH.T.	chorda tympani, part of cranial nerve VII
C.I.C.	canal for internal carotid artery
CNHM UR.	collection designation, Chicago Natural History Museum, University Reptiles
EPIPT.	epipterygoid bone
EXO.	exoccipital bone
Ex.St.	extrastapedial (extracolumella)
F.F.	facial foramen, for cranial nerve VII
F.I.C.E.	external foramen for internal carotid artery
F.I.C.I.	internal foramen for internal carotid artery
FI.MET.	metotic fissure
F.JU.	jugular foramen
F.OV.	fenestra ovalis
F.ST.	stapedial foramen
H.S.C.	horizontal semicircular canal
HY.	hyoidean branch of cranial nerve VII
I.A.M.	internal auditory meatus
I.C.	internal carotid artery
JU.C.	jugular canal
LAG.	lagena
N.	notch in ossified plate of stapes

O.C.	otic canal
O.P.	ossified plate of stapes and tympanic membrane
OPISTH.	opisthotic bone, posterior part of periotic
PA.	parietal bone
PAS.	parasphenoid bone
PER.	periotic bone
PI.	pineal opening
PL.SPH.	pleurosphenoid bone
PR.CUL.	cultriform process
PRO.INC.	prootic incisure
PT.	pterygoid bone
P.V.S.C.	posterior vertical semicircular canal
QJ.	quadratojugal bone
QU.	quadrate bone
QU.P.ST.	quadrate process of stapes
QU.T.	quadrate tubercle
REC.	secondary recess in central parasphenoidal recess in *Diadectes*
R.PAS.	parasphenoid recess: C, central part; D, dorsal part; M, mesial part
R.SAC.	saccular recess
R.SC.T.	recessus scala tympani
SE.T.	sella turcica
S.PERI	sinus perilymphaticus, the extracapsula perilymphatic sinus in Chelonia
St.	stapes
ST.(FT.)	foot of stapes
ST.C.	stapedial canal
S.ST.	shaft of stapes
S.UT.	sinus urticulus
TY.	tympanic
TY.M.	tympanic membrane
USNM.	collection designation, United States National Museum
V.C.L.	vena capitis lateralis, the lateral head vein
VII	the seventh cranial nerve, the facial
XII	the twelfth cranial nerve, the hypolossal

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