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REINTERPRETATION OF THE TEMPORAL AND OCCIPITAL REGIONS IN *DIADECTES* AND THE RELATIONSHIPS OF DIADECTOMORPHS

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ABSTRACT—New materials from the Permo-Pennsylvanian of north-central New Mexico permit a new description of the temporal and occipital regions of the diadectomorph *Diadectes.* The important issue of the fate of the intertemporal bone is resolved by demonstrating its absence and apparent incorporation into the parietal as a lateral lappet. Four cranial autapomorphies of *Diadectes* are recognized: 1) loss of contact between postparietal and tabular; 2) supratemporal greatly enlarged with well-developed occipital process; 3) tabular no longer exposed on skull roof, but greatly reduced and incorporated into occipital plate, with a coarse, posteromedially facing surface; and 4) skull roofing bones thick and porous, with a consistent network of U-shaped grooves. The temporal–occipital region of *Diadectes* is compared with those of holotypic and recently collected specimens of *Limnoscelis* and *Tseajaia,* the type genera of the other two recognized diadectomorph families, Limnoscelidae and Tseajaiidae. On the basis of the literature the comparisons are extended to include certain late Paleozoic amniotes: synapsid Pelycosauria, Captorhinomorpha, and the primitive diapsid *Petrolacosaurus.* The results are subjected to a cladistic analysis, which supports the following hypotheses of relationships: 1) Diadectidae, Tseajaiidae, and Limnoscelidae form a natural group, the Diadectomorpha; 2) *Diadectes* and *Tseajaia* share a more recent common ancestor than either does with *Limnoscelis*; 3) Diadectomorpha, Pelycosauria, and their descendants form an unnamed, primitive sister clade to that consisting of Captorhinomorpha, *Petrolacosaurus,* and their descendants; and 4) the taxon Cotylosauria (sensu Heaton, 1980), consisting of Diadectomorpha and Seymouriamorpha, is paraphyletic and invalid. The third hypothesis dictates the assignment of Diadectomorpha to Amniota.

INTRODUCTION

WITH THE exception of the type genus *Diadectes,* taxa assigned to the late Paleozoic suborder Diadectomorpha have varied considerably through most of the last century (Watson, 1917; Olson, 1947; Heaton, 1980). Case (1911) made the initial attempt at determining the content and relationships of what he called the Diadectosauria,,but it was Watson (1917) who provided the most influential early working definition of the group. By recognizing several synonymies, Olson (1947) greatly clarified the number and validity of the diadectid genera. Recently, Heaton (1980) has defined the Diadectomorpha to include the families Limnoscelidae and Tseajaiidae, as well as the type family Diadectidae.

Regardless of criticism (Holmes, 1984) of the characters used by Heaton (1980) in his phylogenetic analysis and definitions of the Seymouriamorpha and Diadectomorpha, his designation of their content has been generally accepted in anticipation of a clearer understanding of the constituent taxa (Panchen and Smithson, 1988). Thus, although the Diadectomorpha is currently accepted as a monophyletic group (e.g., Panchen and Smithson, 1988; Gauthier et al., 1988), there are varying degrees of agreement (or disagreement) regarding both the validity of the characters used to unite the Diadectomorpha (Holmes, 1984) and the cranial morphology of *Limnoscelis* (Romer, 1946; Huene, 1956; Fracasso, 1983, 1987; Berman and Sumida, 1990) and *Diadectes* (Broom, 1910, 1914; Case, 1911; Huene, 1913; Gregory, 1946; Olson, 1947, 1950; Watson, 1954; Lewis and Vaughn, 1965), the best known and most important representatives of Limnoscelidae and Diadectidae. As yet, no one has challenged the only detailed description (Moss, 1972) of *Tseajaia campi,* the sole member of the Tseajaiidae.

Despite the diversity of the taxa that have been included in the Diadectomorpha and with the exception of the work of Carroll (1969a, 1969b, 1970), the consensus of a long series of studies (Case, 1911; Gregory, 1946; Olson, 1947, 1950; Watson, 1954; Heaton, 1980; Heaton and Reisz, 1986; Gauthier et al., 1988; Panchen and Smithson, 1988) is that the diadectomorphs are related to the more primitive seymouriamorphs on the one hand and the more derived amniotes on the other. The precise nature of the relationships, however, has been difficult to evaluate. Sutural patterns in the temporal region have played a pivotal role in determining the relationships of taxa involved in the origin and radiation of early amniotes. Both Parrington (1958) and Carroll (1969a) have pointed out that all amniotes lack an intertemporal bone. Whereas interpretation of most of the skull of *Diadectes* has been fairly consistent through the past century, the temporal and occipital regions have proven difficult to interpret due to the apparent fusion of the sutures and the spongy texture of the bone. The result, as noted by Olson (1950, p. 63), is that "every reasonable interpretation of the temporal region has been suggested at one time or another" for *Diadectes.*

In two influential studies Olson (1947, 1950) proposed the presence of a complete temporal series in the skull roof of *Diadectes* that included the intertemporal, as well as the supratemporal and tabular. For Olson (1947) the presence of an intertemporal barred *Diadectes* from close association with true amniotes, a group he termed the "eureptilia." The proposed presence of an intertemporal supported his contention that diadectids were better placed with turtles, pareiasaurs, and procolophonians as the "parareptilia." Olson (1966) has since modified his views of a close relationship between diadectids and turtles and has indicated that the parareptilia is better reserved as a conceptual term for amphibians close to the reptilian grade of organization, rather than as a taxonomic entity. Nonetheless, the presence of an intertemporal still ruled against grouping diadectids with amniotes. In contrast, Parrington (1958) argued that *Diadectes* appears to be similar to amniotes in, by his interpretation, lacking the intertemporal via its incorporation into the parietal to form a laterally directed lappet.

Among the diadectomorphs (sensu Heaton, 1980) the occipital elements of the braincase and the closely applied dermal postparietal and tabular bones are well known only in *Limnoscelis.* Fracasso's (1987) interpretation of the unusual structure of the occiput of *Limnoscelis* is, notwithstanding some errors

(Berman and Sumida, 1990), basically accurate. Fracasso pointed out what he believed to be significant features of the occipital region that he indicated were common to diadectomorphs and primitive synapsid mammal-like reptiles. At that time, however, the temporal–occipital region of *Diadectes* was very poorly understood and that of the only described specimen of *Tseajaia* poorly preserved (Moss, 1972). Therefore, a thorough understanding of the temporal and occipital regions of all three genera would be useful for assessing the phylogenetic relationships of the Diadectomorpha, as well as the interrelationships of its constituent families. Regardless of the general acceptance of the composition of the Diadectomorpha and the importance accorded it as the presumptive sister group of amniotes, its usefulness in determining amniote interrelationships is extremely limited until the member taxa can be clearly characterized. This study focuses mainly on reinterpreting the very poorly known sutural patterns of the temporal and occipital regions of the skull of *Diadectes*. For the purpose of analysis of diadectomorph relationships attention is also given to the reinterpretation of the same regions in *Limnoscelis* and *Tseajaia*, also a subject of some controversy.

MATERIALS

Specimens examined.—Although this study focuses on two previously undescribed specimens of *Diadectes*, CM 25741 and 38047, numerous additional specimens were also examined. Several of these were recovered from Lower Permian deposits of north-central Texas. Traditional schemes for dividing the terrestrial Lower Permian stratigraphic section of this region have recently been revised by Hentz (1988). Hook (1989) has provided a useful key to the appropriate formational nomenclature for well-known collecting localities. In the following list of materials examined not only is the most recent stratigraphic nomenclature applied, but previous formational names based primarily on the works of Plummer and Moore (1921) and Romer (1974) are also included parenthetically to aid in identification of specimens:

Desmatodon hesperis, CM 47665 (formally UCLA VP 1745), partial skull with braincase, Late Pennsylvanian, Sangre de Cristo Formation, Fremont County, Colorado.

Diadectes sanmiguelensis, holotype, MCZ 2989, complete skull with mandible and incomplete postcranial skeleton, Early Permian Cutler Formation, San Miguel County, Colorado.

Diadectes sideropelicus, AMNH 4839, nearly complete skull without lower jaws, AMNH 4532, partial skull without lower jaws, FMNH UR27 (formally MCZ 1105), nearly complete skull without lower jaws, presacral column, and pectoral girdle, Early Permian, Petrolia Formation (ex Belle Plains Formation) Wichita Group, Archer County; FMNH 1177, skull, pelvis, 15 dorsal vertebrae and ribs, Early Permian, Petrolia Formation (ex Belle Plains Formation) Wichita Group, Baylor County, Texas.

Diadectes sp., CM 25741, skull with right lower jaw attached, Permo-Pennsylvanian Sangre de Cristo Formation, San Miguel County, New Mexico.

Diadectes sp., CM 38047, partial skull consisting of numerous articulated and disarticulated elements of the skull roof and braincase, Premo-Pennsylvanian Cutler Formation, Rio Arriba County, New Mexico.

Diadectes sp., FMNH UC1078, nearly complete skull, Clear Fork Group (Arroyo Formation), Baylor County, Texas.

Tseajaia campi, holotype, UCMP 59012, complete, articulated skeleton, Early Permian, Organ Rock Shale of the Cutler Group, San Juan County, Utah.

Tseajaia campi, CM 38033, nearly complete, articulated skeleton, Permo-Pennsylvanian Cutler Formation, Rio Arriba County, New Mexico.

Limnoscelis paludis, holotype, YPM 811, complete, articulated skeleton, Late Pennsylvanian, Cutler Formation, Rio Arriba County, New Mexico.

Limnoscelis dynatis, holotype, CM 47651, disarticulated partial skull, lower jaw, and postcranial skeleton, Late Pennsylvanian, Sangre de Cristo Formation, Fremont County, Colorado.

Abbreviations used in text and figures.—The following abbreviations are used to refer to repositories of specimens: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard; YPM, Yale Peabody Museum, New Haven; UCLA VP, University of California, Los Angeles; UCMP, Museum of Paleontology, University of California, Berkeley.

Key to abbreviations used in figures for anatomical structures: BO, basioccipital; EO, exoccipital; F, frontal; F JU, jugular foramen; J, jugal; L, lacrimal; M, maxilla; N, nasal; OP, opisthotic; P. parietal; PF, postfrontal; PO, postorbital; PP, postparietal; PRF, prefrontal; PT, pterygoid; PTF, posttemporal fenestra; P FOR, parietal foramen; Q, quadrate; QJ, quadratojugal; SM, septomaxilla; SO, supraoccipital; SO-OP, supraoccipital–opisthotic complex; SQ, squamosal; ST, supratemporal; T, tabular; TM, ossified tympanic membrane.

DESCRIPTION OF NEW *DIADECTES* MATERIALS

The description presented here of the sutural pattern of the temporal and occipital regions of the skull of *Diadectes* is based on two previously undescribed specimens, CM 25741 and CM 38047, from the Permo-Pennsylvanian of north-central New Mexico. The principal specimen is an articulated skull, CM 25741 (Figures 1–4). The right side of the skull roof is preserved and the incomplete right lower jaw is exposed in lateral view. The occiput is nearly complete, though the condyle is hidden by elements of the atlantal vertebrae. The premaxillae are absent and much of the surface bone of the snout has spalled off. The posterolateral portion of the supratemporal is lost, but its extent is easily traced by either a remaining impression or a thin veneer of bone. Most of the ossified right tympanic region remains. There are indications that CM 25741 represents an immature specimen. All of the sutures of the skull roof are not only traceable but open, with some elements having even become slightly disarticulated. The high degree of relief of the skull roof created by well-developed, sharply defined prominences and channel-like grooves is apparently correlated with immaturity (see below). Its small size (skull length about 16 cm) is also consistent with immaturity. The second *Diadectes* specimen studied, CM 38047, consists of numerous articulated and disarticulated skull bones. This specimen is from an animal of approximately the same size as CM 25741 and can be judged as immature for similar reasons. Among the remains of this specimen important to this discussion are an articulated frontal, parietal, and postfrontal from the right side of the skull and an isolated left frontal that can be joined precisely to its mate (Figures 5, 6). A reconstruction of the skull roof and occiput of *Diadectes* based mainly on CM 25741 is presented in Figure 7.

The frontals are narrowly rectangular and border posteriorly the central portion of the anterior margin of the paired parietals. In CM 38047 a deep channel runs the anteroposterior length of the bone, with short side channels that create small, well-defined but irregular prominences. The paired parietals cover a transversely broad, subrectangular area except for a step-like emargination of the anterolateral corners for the postfrontals. The resultant rectangular, lateral extension of the parietal posterior to the postfrontal is the lateral lappet of the parietal. The entire lateral margin of the lateral lappet contacts the postorbital, whereas its posterior margin contacts the supratemporal. There is a posteriorly directed, spike-like jog in the parietal–supratemporal suture, which is also identifiable on skulls of mature individuals (AMNH 4839, FMNH UR27). The central portion of the posterior border of the paired parietals contacts an apparently single median postparietal. The parietal opening is very large, resulting in short fore and aft midline contacts of the parietals. In CM 25741 and 38047 an essentially identical pattern of five prominent grooves radiate from a point near the center of the parietal. One of these continues anteriorly on the postfrontal along its posteromedial contact with the parietal and gives off at least two grooves that extend a short distance laterally on the postfrontal.

The postparietal is a single, roughly trapezoidal element, with its breadth being nearly twice its midline length. It contacts the supratemporal laterally and the supraoccipital portion of the occiput posteriorly. Approximately the anterior two-thirds of the postparietal is positioned on the posterior portion of the skull table that slopes moderately posteroventrally to the occiput; the posterior third is incorporated into the occipital plate.

The postorbital is a large bone with extensive, mainly serrate contacts with the postfrontal anteriorly, the lateral lappet of the parietal dorsomedially, the supratemporal posterodorsally, and the squamosal posteroventrally. Ventrally and on the orbital margin the postorbital and jugal have a very narrow contact. The lateral lappet of the parietal and the squamosal are well separated by a broad postorbital–supratemporal contact.

The supratemporal is the most extensive element of the posterior skull table and is also very thick. In CM 25741 only the right supratemporal is well represented, lacking mainly only the posterior horn-like extension. The extent of the missing horn-like extension, which is clearly discernible in well-preserved skulls (AMNH 4839, FMNH UR27), can be traced by a combination of an impression and remaining veneer of bone on the underlying tabular. Anteroventrally the supratemporal has a broad, overlapping suture with the dorsal margin of the squamosal. Posterior to that suture the supratemporal narrows in breadth as it curves ventrally to form the posterior horn-like extension. The lateral margin of the horn-like extension forms the dorsal border of the temporal notch, whereas its medial margin arches dorsomedially to become the ventral margin of a thick, rectangular, medially directed occipital process. The occiptal process overlaps the dorsal margin of the supraoccipital–opisthotic complex, while contacting and probably also narrowly overlapping the ventral margin of the postparietal to reach within a short distance of the skull midline. In a specimen (CM 47665) of the somewhat more primitive and nearly identical Pennsylvanian diadectid *Desmatodon hesperis,* Vaughn (1972) reported the presence of paired fenestrae that are bordered dorsomedially and ventromedially by the postparietal and the supraoccipital-opisthotic complex, respectively. The complete left fenestra was shown as being bounded laterally by the tabular, which in turn is bordered laterally by the supratemporal; however, a thin groove was tentatively identified as the suture separating these two bones. The position of the fenestrae in *D. hesperis* corresponds exactly to the area occupied by the occipital process of the supratemporal in *Diadectes* CM 25741. The bone bounding the lateral margin of the left fenestra, therefore, quite likely represents only the supratemporal. Temporal depressions or openings have been described (Case, 1911; Huene, 1913) in a few specimens of *Diadectes.* Olson (1947) commented on these, noting that they do not correspond to normal reptilian temporal openings and represent poorly ossified or unossified areas of the skull. They also do not occupy the same positions as the occiptal fenestrae in *Desmatodon* or the occipital processes of the supratemporals in *Diadectes* CM 25741. It can also be noted that the occipital processes of the supraoccipitals correspond exactly in position to well-developed ridges that extend transversely across the occiput, except for a narrow midline gap, in mature specimens of *Diadectes* (AMNH 4839 and FMNH UR27 for example) and in reconstructions by Olson (1947) and Watson (1954). It is quite likely that the presence of occipital fenestra in the *Desmatodon* specimen described by Vaughn (1972) is indicative of immaturity. According to Vaughn (1972, p. 20), the partial skull (CM 47665) in which this feature is described very probably belongs to an immature individual, judging from the almost complete lack of ossification in the region of the otic labyrinth and by its close association with a juvenile maxilla.

Only the right tabular is preserved in CM 25741 and except for possibly slight weathering is essentially complete. As it appears in Figures 1 and 2, the lateral half of its exposure is the result of loss of the overlying posterior horn-like extension of the supratemporal. Relative to other elements of the skull roof, the tabular has obviously undergone considerable reduction. As indicated in the skull reconstruction of Figure 7, the tabular has a somewhat lozenge-shaped, posteromedially facing exposure, medial to the distal end of the horn-like extension of the supratemporal. It is possible that the ventral margin of the tabular was visible in lateral view of the skull. The medial margin of the tabular narrowly overlaps the lateral margins of the paroccipital process and the supraoccipital portion of the occiput. The tabular has the appearance of being incorporated into the lateral margin of the occipital plate of the braincase in that its exposed surface has the same coarse texture as the plate and faces posteromedially.

No suture demarking the supraoccipital–opisthotic contact can be found in CM 25741. There is a very small opening on either side near the lateral margins of the supraoccipital–opisthotic complex; that on the right is crescent-shaped and apparently within the complex, whereas that on the left does not appear to be bounded laterally by the complex. These openings occupy the precise position normally identified in more primitive vertebrates as the posttemporal fenestrae, and it is presumed that they would be lost in the adult stage of development. The contacts between the exoccipitals and the probable opisthotic portions of the occiput are quite clear, revealing that the probable supraoccipital portion of the occiput formed the dorsal margin of the foramen magnum. The dorsal processes of the exoccipitals not only bound the lateral, but their bases seemingly also formed the ventral margins of the foramen magnum. It is presumed that the supraoccipital–opisthotic suture would have occupied the standard amniote position, extending dorsolaterally from the dorsolateral margin of the foramen magnum just above the contribution of the exoccipital and ending at or near the medial margin of the presumed posttemporal fenestrae. If true, then the reduced tabular has contacts with both occipital elements.

PREVIOUS INTERPRETATIONS

Several interpretations of the sutural pattern of the temporal and occipital regions of the skull of *Diadectes* have been published and are depicted here in Figure 8. Olson's (1947, 1950) are among the most recent, focus specifically on the interpretations of the temporal–occipital region, and are more widely accepted. His analyses, based on 15 specimens, were in his view severely hampered by four characteristics he perceived in the skull roof of *Diadectes*: 1) a remarkable variability in the relative sizes, shapes, and sutural patterns in the skull bones; 2) variable prominences and flutings of the skull surface that obscured the positions of sutures; 3) the thick, porous nature of the skull bones that obstructed tracing sutures through the bones; and 4)

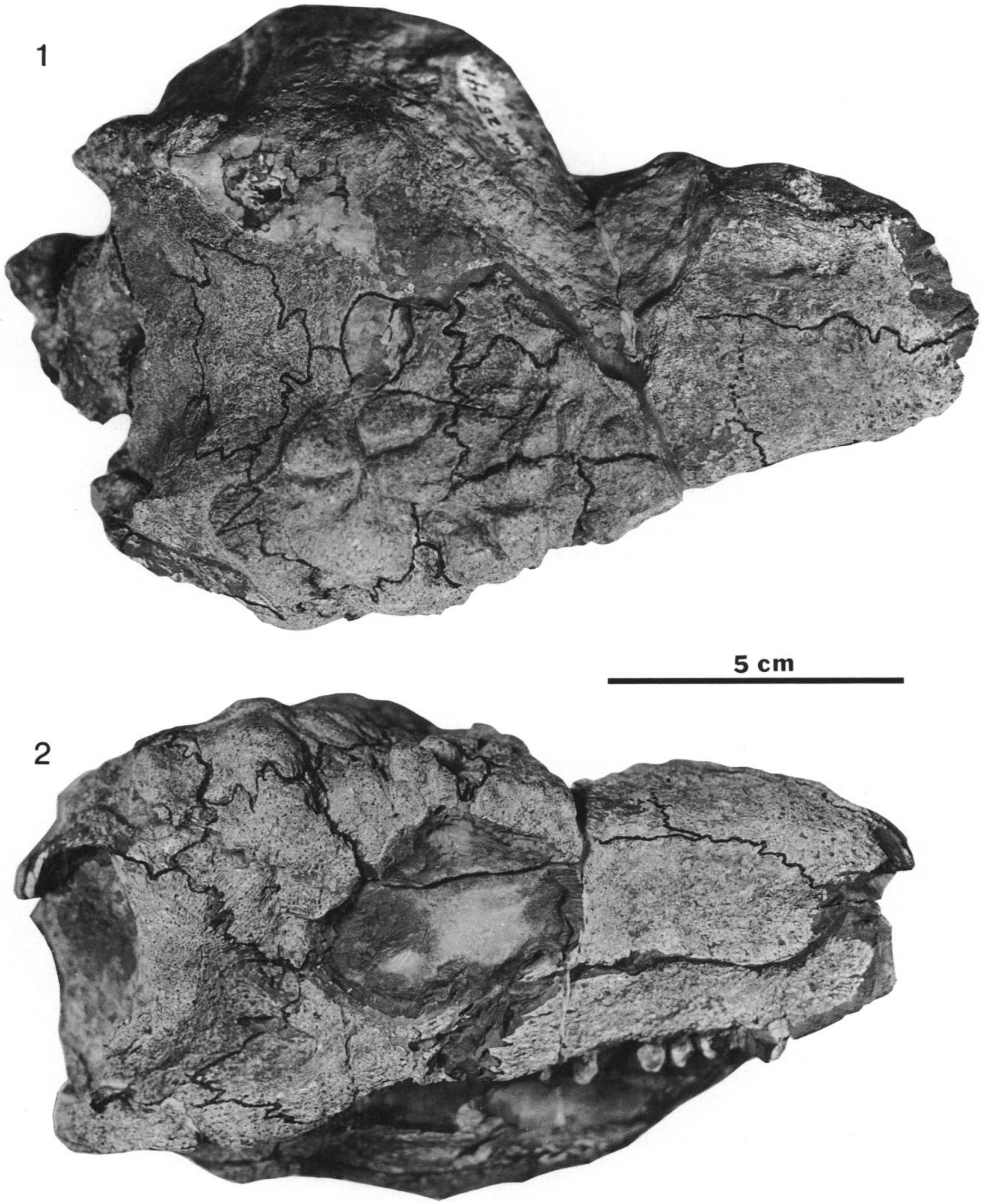


FIGURE 1—Skull of *Diadectes* sp., CM 25741, in *1*, dorsal and *2*, lateral views.

the fusion of sutures initiated at an early stage of development that progressed from the inner to the outer surface of the skull so that in advanced stages sutures were often represented by matrix-filled grooves or channels on the skull surface. The material described in the present paper indicates that Olson's observations 2 and 3 appear to be generally true, whereas 1 and 4 are erroneous.

The material used in the present study indicates that the

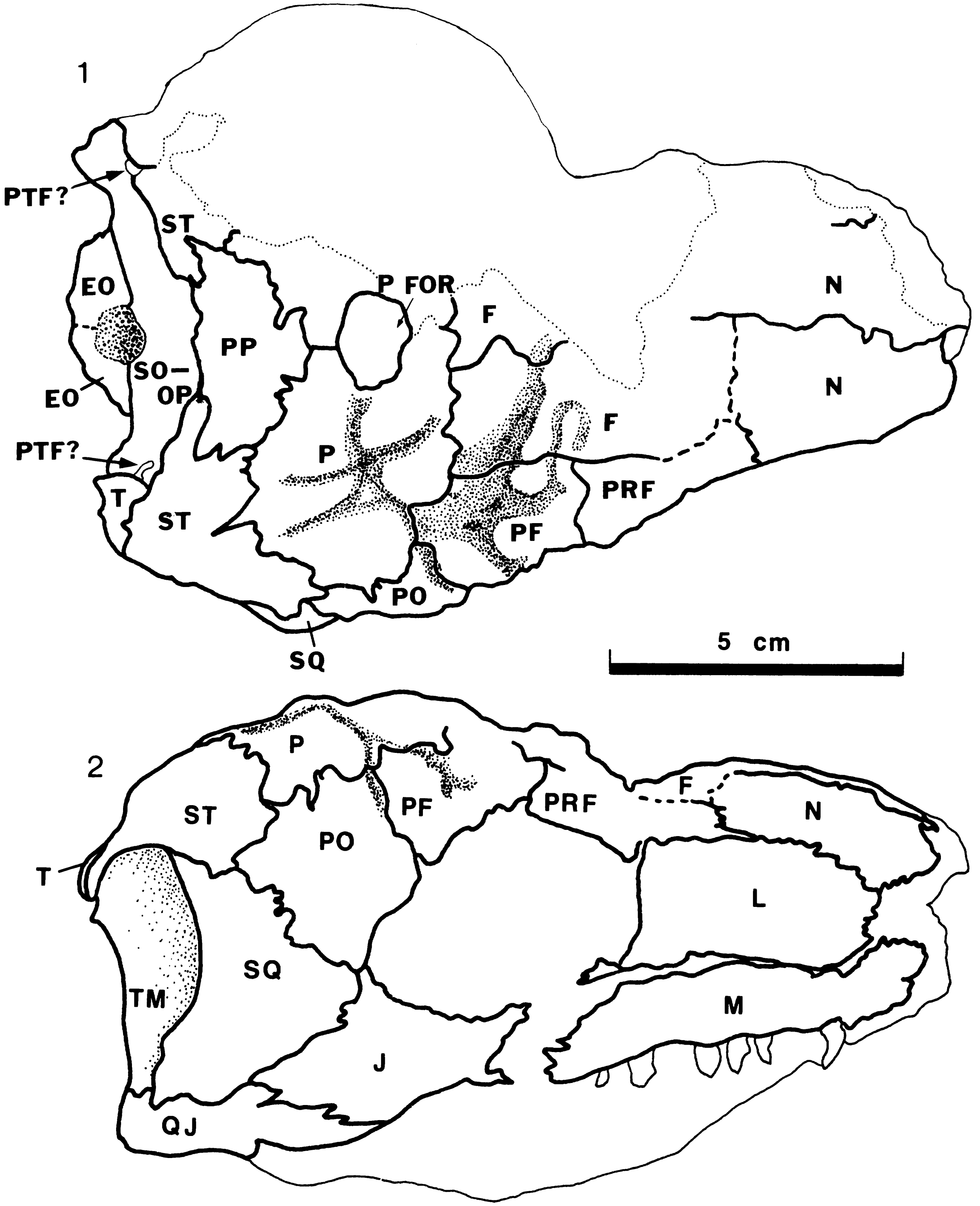


FIGURE 2—Outline sketches of *Diadectes* sp. CM 25741 as seen in Figure 1 showing sutures and channel-like grooves on skull roofing bones.

grooves of the skull roof are not related structurally to the sutures, and can be characterized by three general observations: 1) the positions of the major grooves are bilaterally symmetrical and fairly constant; 2) the walls are for the most part smooth and distinctly U-shaped in cross section; and 3) they are more pronounced in juvenile individuals. The great width, absence of serial foramina for sensory neuromasts, and unique distribution pattern of the grooves is ample evidence that they do not represent remnants of a lateral line organ.

In several specimens Olson (1950) recognized two elements

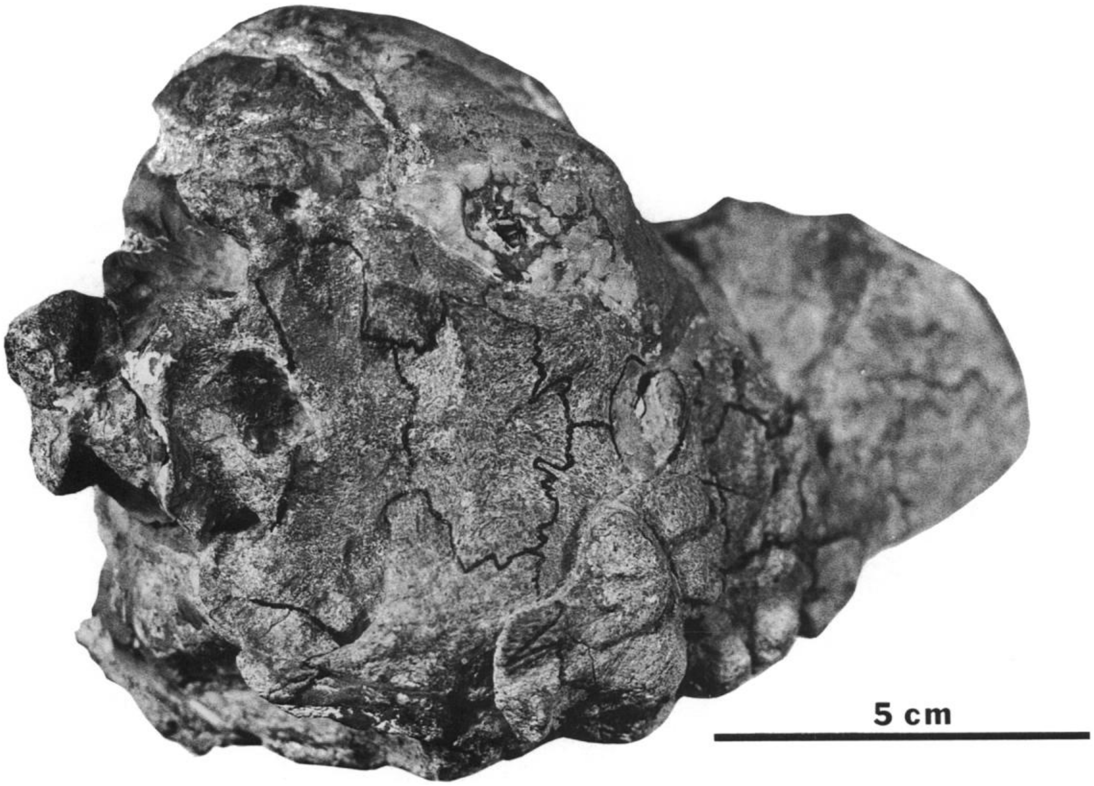


FIGURE 3—Skull of *Diadectes* sp., CM 25741, in posterodorsal view.

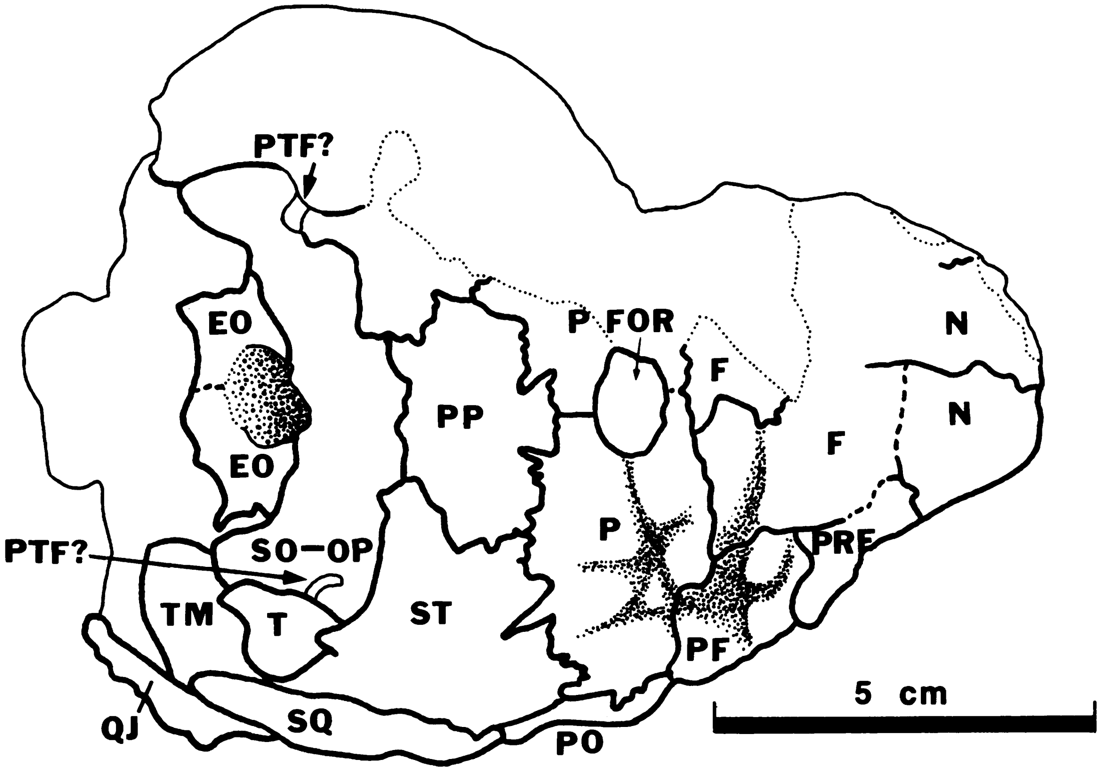


FIGURE 4—Outline sketch of *Diadectes* sp. CM 25741 as seen in Figure 3 showing sutures and channel-like grooves on skull roofing bones.

FIGURE *5*—Portion of skull roof of *Diadectes* sp. CM 38047.

lying between the lateral margin of the parietal and the dorsal margin of the squamosal, an anterior intertemporal and a posterior supratemporal. Together they formed a greatly thickened area he termed the supratemporal prominence. The area he recognized as the intertemporal is clearly what is identified here as the lateral lappet of the parietal. The suture he showed as delimiting the lateral edge of the parietal from the intertemporal and supratemporal corresponds exactly in position with two of the well-formed anteroposteriorly oriented grooves radiating from the center of the parietals in CM 25741 and 38047 (Figures 1, 2, 5, 6). These grooves were misinterpreted by Olson as a partially closed suture. The intertemporal–supratemporal suture identified by Olson (1950) does not follow a groove as indicated by him, but actually separates the posterior margin of the parietal lappet from the anterior margin of the supratemporal. Olson's material did not permit him to recognize that this suture continues medially from the anteroposteriorly aligned grooves he believed marked the separation of the parietal from the temporal series and ends at the lateral margin of the postparietal.

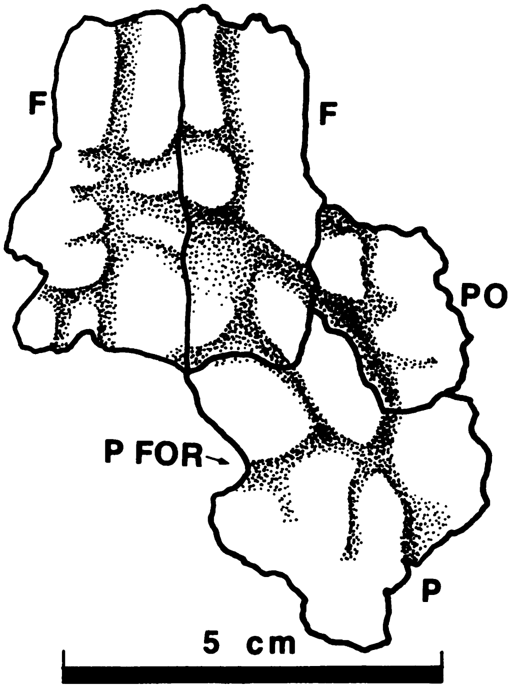


FIGURE *6*—Outline sketch of *Diadectes* sp. CM 38047 as seen in Figure 5 showing sutures and channel-like grooves.

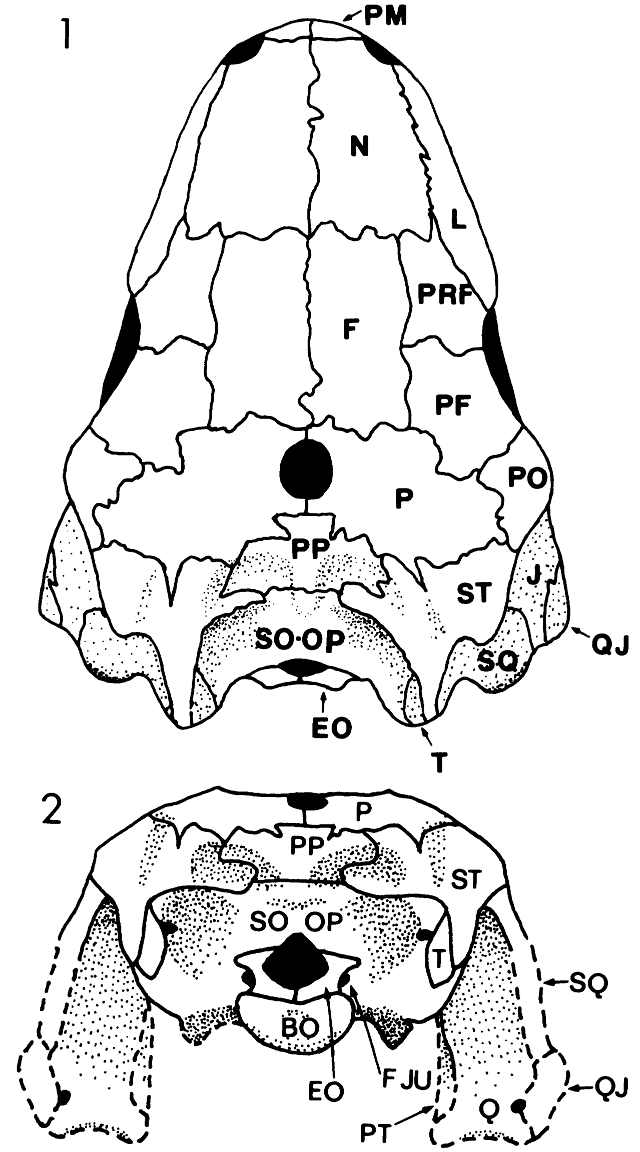


FIGURE *7*—Diagrammatic reconstruction of the skull of *Diadectes* in *1*, dorsal and *2*, occipital views. Sutural pattern based primarily on CM 25741 and skull outline on reconstruction by Olson (1947).

Olson (1950, p. 76) was unable to define clearly the tabular in any of the specimens he studied and on the basis of very tenuous evidence from two skulls incorrectly described it as "lying in contact with the interparietal [=postparietal] and the parietal and forming the dorsal margin of the posterior part of

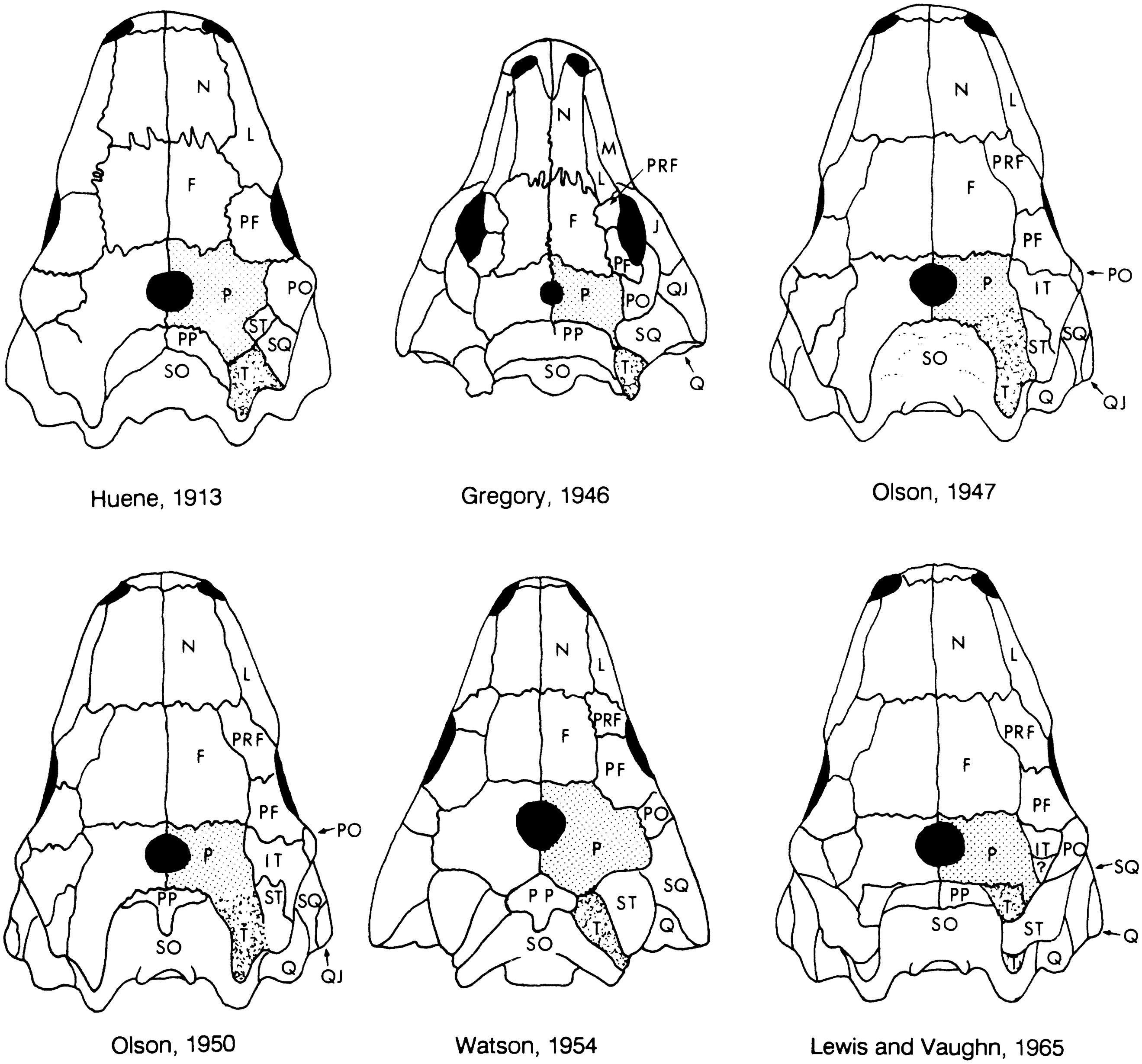


FIGURE 8—Previous interpretations of the skull sutural pattern of *Diadectes*.

the otic notch." As he noted, his interpretation is virtually identical to that shown in every published figure in which a tabular is identified and he considered that this position is logical because "it corresponds to that well documented in various labyrinthodont amphibians and in *Seymouria*." Olson reasoned that the absence of sutures defining the tabular in the other specimens he studied was probably due to coalescence with the parietal and the interparietal; he was unaware of the extremely large size of the supratemporal. Contrary to our description, Olson (1947) illustrated the exoccipitals meeting above the foramen magnum. It is worth noting that we have examined nearly all of the specimens studied by Olson (1947, 1950), and in no instance did we find any evidence that would contradict the anatomical description reached here on the basis of CM 25741 and 38047. In fact, a few of his specimens, such as FMNH UC1078, provide evidence of a lateral lappet of the parietal replacing a distinct intertemporal bone.

Olson's (1950) restudy of the temporal sutural pattern of *Diadectes* was probably prompted in great part by Gregory's (1946) reconstruction of the skull that depicts the absence of an intertemporal and a large postorbital contacting the lateral margin of what could be considered a lateral lappet of the parietal. However, a supratemporal is not indicated in Gregory's reconstruction, and in its position is shown a large tabular that fails to reach the postorbital, allowing a parietal–squamosal contact.

In a detailed description of the skull of *Diadectes*, Watson (1954) correctly described the parietal as having a lateral lappet that occupies the area normally held by the intertemporal; however, he misinterpreted the lappet as reaching the dorsal margin of the squamosal and excluding the supratemporal and postorbital from contact. Watson's interpretation of the shape and sutural relationships of the tabular is essentially identical with that of Olson (1947, 1950) and therefore is incorrect for the same reasons. Watson believed the tabulars to be indistinguishably fused with the paroccipitals and to have substantial contacts with the supratemporal and parietal bones. Watson, as well as others discussed here, also failed to recognize the extraordinary medial expanson of the supratemporal, which brings it into contact with the postparietal and greatly reduces the tabular. In his interpretation the postparietal has a strongly pointed anterior margin that penetrates deeply between the midline union of the parietals. He correctly showed the exoccipitals as not completely bounding the foramen magnum dorsally.

The small, juvenile, holotypic skeleton of *Diadectes sanmiguelensis* (MCZ 2989) was described by Lewis and Vaughn (1965, fig. 7) as exhibiting a sutural pattern of the skull roof that, though having open sutures due to immaturity, is unclear in the temporal region because of imperfect preservation. Although they expressed considerable doubts in indicating the presence of an intertemporal bone, some aspects of their interpretation of the temporal region of the skull roof are accurate and differ in important ways from those of Olson (1947, 1950) and Watson (1954). They correctly showed the anterolateral margin of the supratemporal contacting a much shorter dorsal margin of the squamosal. In addition, they correctly depicted the postorbital as a large element, having a much greater posterior extent that contacts the supratemporal narrowly and thereby barely prevents the parietal lappet and squamosal from meeting (at least externally). Lewis and Vaughn's description of the nature of the contacts of the disputed part of the temporal region of the skull studied by them can be reinterpreted to agree perfectly with that given here. What they labeled as the questionable intertemporal is a portion of the postfrontal. Behind the questionable intertemporal is a triangular fragment labeled by them with a question mark that is undoubtedly a portion of the lateral lappet of the parietal, giving the lappet a broad contact with the postorbital. Lewis and Vaughn reasoned that the alternatives to interpreting the disputed temporal area as the intertemporal are to regard it as either part of the parietal or the postorbital.

Lewis and Vaughn (1965) described the position of the tabular in *D. sanmiguelensis* as obscure, noting (p. 17) two areas of the skull where it may be represented. One is "a fragmented area of bone immediately posterior to the posterolateral part of the parietal and medial to the supratemporal, from which it is demarcated by what seems to be a suture." This would give the tabular a position like that described by previous authors (Olson, 1950; Watson, 1954). However, they also noted as perhaps representing the tabular "a small fragment of bone ventral to the posterior tip of the right supratemporal." This position agrees precisely with that described in this study.

There are several lesser accounts of the skull roof of *Diadectes*. Huene's (1913) descriptions of several skulls of *Diadectes* did not indicate the presence of an intertemporal, and there is considerable confusion as to the extent and position of the supratemporal, tabular, squamosal, and bones of the occiput. In one of the specimens (AMNH 4352, figs. 15, 17) he interpreted the lateral margin of the presumed left lateral lappet of the parietal as contacting the squamosal, whereas that of the right parietal contacts the supratemporal. Other studies (Broom, 1910, 1914; Case, 1911) of *Diadectes* included only very superficial treatments of the skull roof sutural patterns.

DIADECTOMORPH RELATIONSHIPS

To date there has been no in-depth analysis of the ingroup relationships of Diadectomorpha. The reinterpretation presented here of the temporal and occipital regions of the skull roof of *Diadectes* permits a limited analysis of the interrelationships of Diadectomorpha. Of broader significance, however, is that a better understanding of the diadectomorphs is central to resolving the interrelationships of primitive late Paleozoic amniotes, since they are widely accepted as the primitive sister group of all amniotes (Brinkman and Eberth, 1983; Gauthier et al., 1988; Panchen and Smithson, 1988). In the following analysis, therefore, we include also key late Paleozoic amniotes to test not only their interrelationships, but their relationships to the diadectomorphs.

Two important contradictory hypotheses for the relationships of primitive late Paleozoic amniotes have been proposed. Carroll and co-workers (Carroll, 1964, 1969a, 1969b, 1969c, 1970, 1982, 1986; Carroll and Baird, 1972; Clark and Carroll, 1973) have argued strongly that the order Captorhinomorpha (families Protorothyrididae [Romeriidae of some authors] and Captorhinidae) includes the most primitive known reptiles (protorothyridids in particular) and are the sister group to all other amniotes. In contrast, others (Kemp, 1980; Reisz, 1980; Heaton and Reisz, 1986; Gauthier et al., 1988) have proposed that the early mammal-like synapsids, order Pelycosauria, are the sister group to all other amniotes. Kemp (1980) demonstrated that on the basis of anatomical and functional grounds the cheek and occipital regions of captorhinomorphs could not be ancestral to those of primitive synapsids. Using a different approach, Reisz (1980) listed several synapomorphies of captorhinomorphs and diapsids that are present in the primitive state in pelycosaurs. From this he reasoned that pelycosaurs and their descendants are the sister group of all other amniotes (captorhinomorphs, diapsids, and their descendants). Heaton and Reisz (1986) demonstrated that the Captorhinidae, Protorothyrididae, and Diapsida, as represented by the genera *Eocaptorhinus, Paleothyris,* and *Petrolacosaurus,* form a natural group and that the captorhinomorphs are not the sister taxon of all other amniotes but are advanced relative to pelycosaurs, with the protorothyridids and diapsids sharing a more recent common ancestor than either does with the captorhinids. This hypothesis was strengthened by Gauthier et al. (1988) employing a large-scale cladistic analysis of amniote relationships that places synapsids as the sister taxon of all other amniotes.

Diadectomorph taxa.—As in the other families of the Diadectomorpha, the Diadectidae is best represented by its type genus, *Diadectes.* Allied genera include *Desmatodon* (Case, 1908; Romer, 1952; Vaughn, 1969, 1972) and *Diasparactus* (Case and Williston, 1913), neither of which is represented by much skull material. *Diadectes,* on the other hand, is represented by a large suite of skulls exhibiting a wide range of completeness and quality of preservation. Similarly, the other two diadectomorph families Tseajaiidae and Limnoscelidae are best or solely represented by the type genera *Tseajaia* and *Limnoscelis.* Excellent skulls of both genera are available and have been examined for this study.

The monotypic Tseajaiidae (Vaughn, 1964) is based on a single species, *Tseajaia campi,* until recently represented by a single complete skeleton (UCMP 59012). The only detailed description of *T. campi* was by Moss (1972). More recently several additional specimens, including a nearly complete skeleton with skull (CM 38033), were collected in New Mexico (Berman and Reisz, 1980). The new material, as well as examination of the holotype, has revealed some important errors in Moss's (1972) description of the skull roof. The two known skulls of *Tseajaia* (Figures 9, 10) together illustrate the sutural pattern of the skull roof (Figure 11). In both specimens, particularly CM 38033, the occiput is too poorly preserved to be useful for most comparisons. Although the skull roof of CM 38033 is badly fractured, making most of the sutures difficult or impossible to trace, the unusual tabulars are well preserved and defined very clearly. In contrast to the description by Moss (1972), the dorsal exposure of the tabular is limited to a very small thumb-like process that extends posteriorly and slightly ventrally from beneath the tip

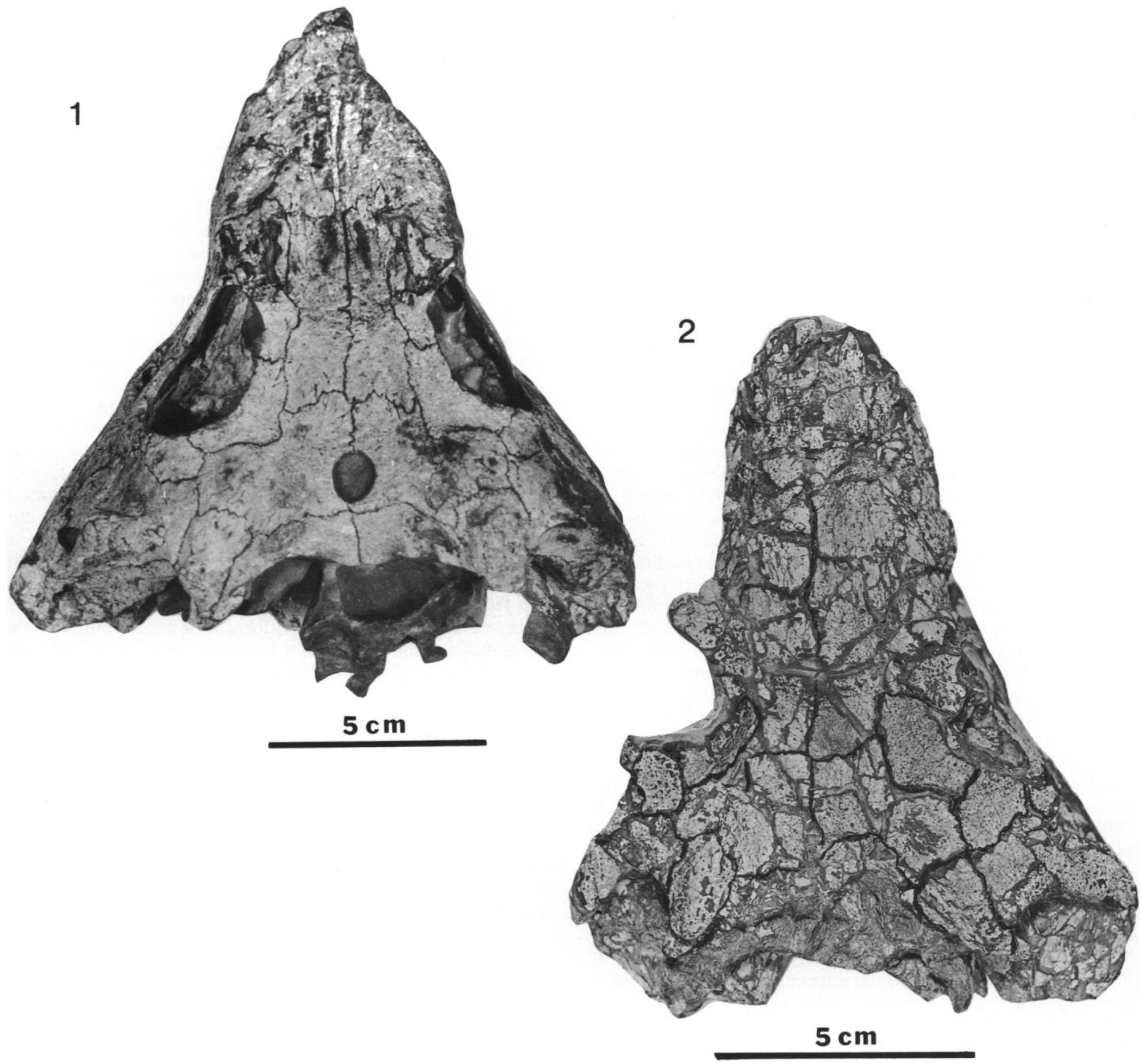


FIGURE 9—Skulls of *Tseajaia* in dorsal view. *1, Tseajaia campi,* holotype, UCMP 59012. *2, Tseajaia* sp. CM 38033.

end of the horn-like posterior extension of the supratemporal and contributes minimally to the posterodorsal border of the temporal notch in lateral view of the skull. The tabular is about 4 mm in dorsoventral thickness and at least 10 mm long, with about the anterior half of this length being covered dorsally by the supratemporal and postparietal. The dorsally exposed portion of the tabular is sculptured strongly and can be considered as part of the dorsally exposed skull table. Also, in contrast to the description of UCMP 59012 by Moss, *Tseajaia* possesses paired postparietals that extend along almost the entire medial length of the supratemporal to contact narrowly the tabular. The tabular, therefore, is widely separated from the parietal. Further, judging from CM 38033, it is clear that Moss (1972) misinterpreted the general shape of the skull in dorsal view as being broadly triangular with a sharply pointed snout. More correctly, the snout was rather narrow and tapered slightly to its bluntly rounded tip. In both specimens the cheeks are splayed outward due to dorsoventral crushing and were undoubtedly inclined steeply in life. In general shape the skull of *Tseajaia* is very similar to that of *Limnoscelis* (Figure 11).

The cranial anatomy of *Limnoscelis paludis* has recently been described at great length by Fracasso (1983). The basis of Fracasso's description was the holotype (YPM 811) and only known skull. The description by Berman and Sumida (1990) of a new species of *Limnoscelis, L. dynatis,* based almost entirely on disarticulated skull and postcranial elements of a single specimen

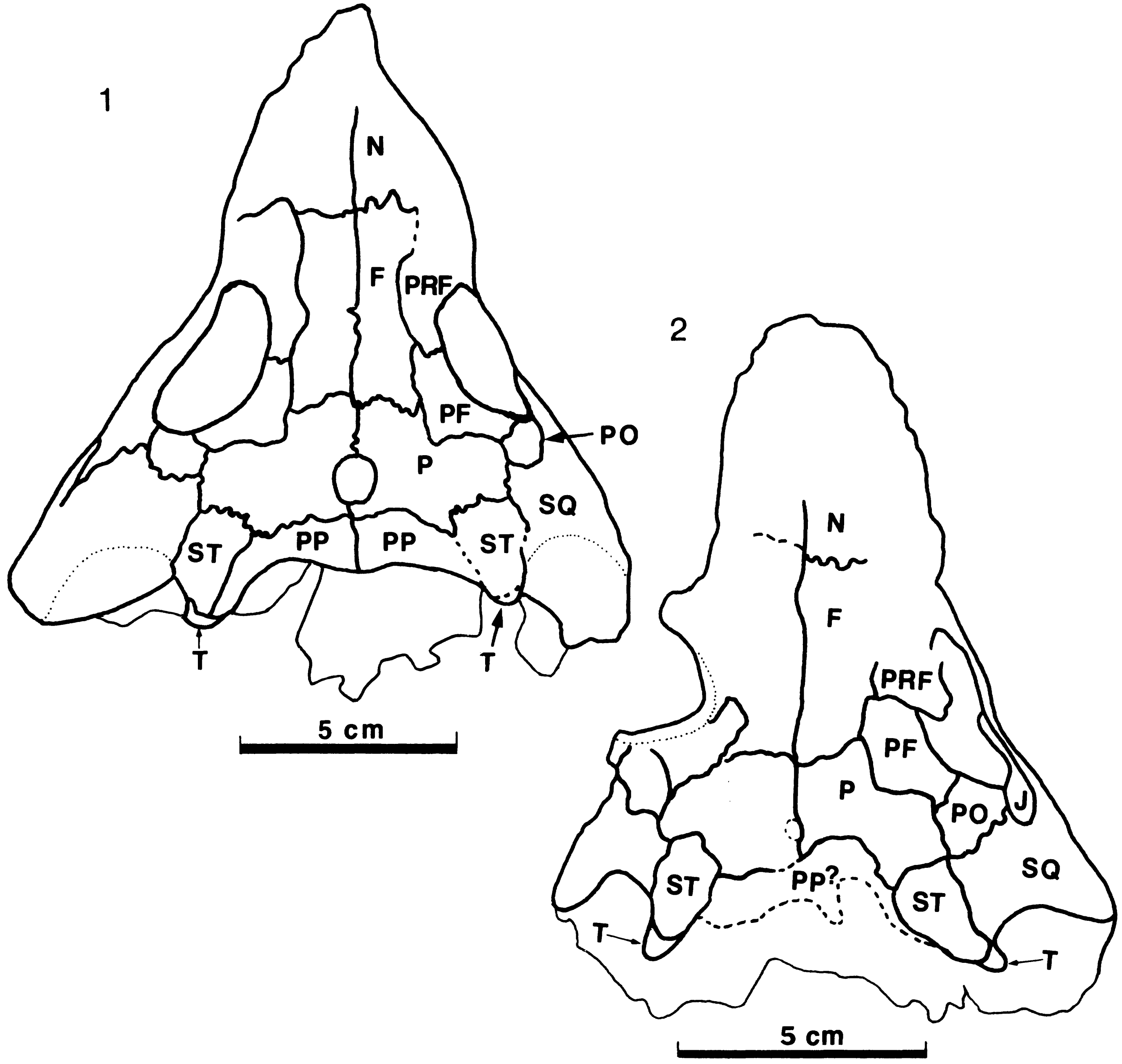


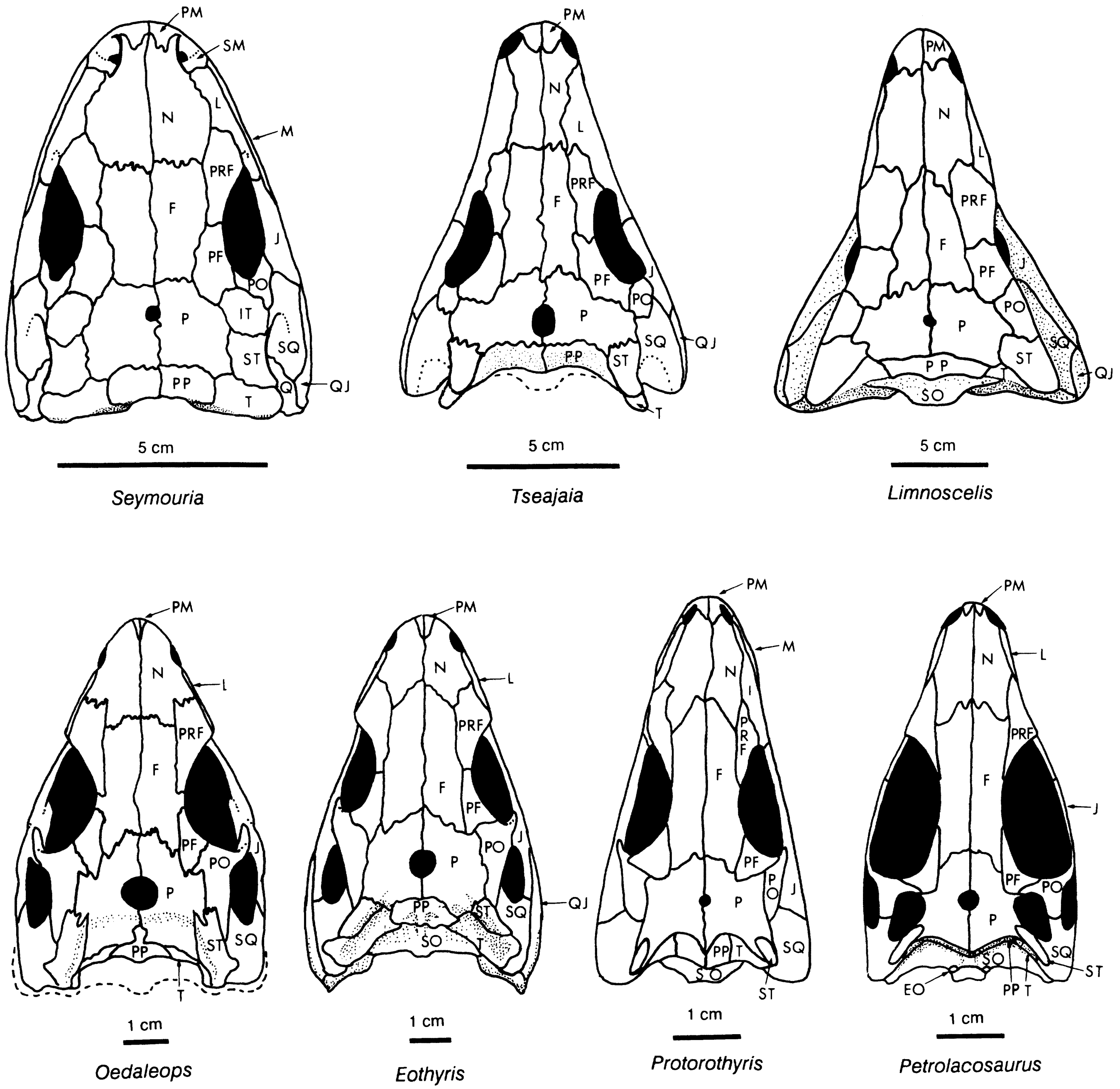
FIGURE *10*—Outline sketches of *Tseajaia campi* UCMP 59012 and CM 38033 as seen in Figure 9 showing sutures.

(CM 47653), as well as additional preparation of the holotypic skull of *L. paludis,* has allowed a more precise account of some aspects of Fracasso's description. He falsely attributed unique features to the occiput, including misidentifying the course of the supraoccipital–opisthotic suture, the extent of the exoccipitals, and the position of the jugular and hypoglossal nerve foramina. In all cases these structures are of standard primitive amniote form and position (Berman and Sumida, 1990).

Five other species in four genera of limnoscelids (*Limnosceloides dunkardensis* Romer, 1952; *Limnoscelops longifemur* Lewis and Vaughn, 1965; *Limnosceloides brachycoles* Langston, 1966; *Limnostegis relictus* Carroll, 1967; *Romeriscus periallus* Baird and Carroll, 1967) have been described, but all are based on fragmentary (or in some instances nondiagnostic) specimens and provide little or no basis for comparisons.

Other taxa.—In accordance with previous analyses (Gauthier et al., 1988; Panchen and Smithson, 1988), the Seymouriamorpha, as represented by *Seymouria,* was chosen as the primitive outgroup for this analysis. Other anthracosaurs, such as *Anthracosaurus, Archeria,* and *Proterogyrinus,* are identical for the characters analyzed. Evaluation of phylogenetic relationships of the Diadectomorpha is limited to comparisons with well-known representatives of the Pelycosauria, Captorhinomorpha, and Diapsida.

Comparisons made with Pelycosauria are based primarily on members of its primitive suborder Caseasauria, which includes



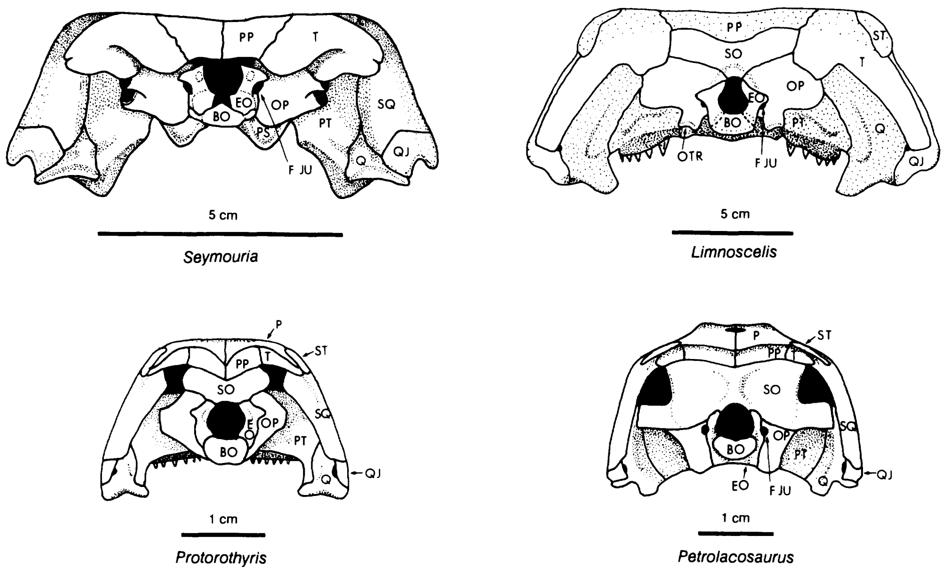
Seymouria Tseajaia Limnoscelis

Oedaleops Eothyris Protorothyris Petrolacosaurus

FIGURE *11*—Skulls in dorsal view. *Seymouria* (after Berman et al., 1987); *Tseajaia* reconstructed on basis of UCMP 59012 and CM 38033; *Limnoscelis* (after Romer, 1946); *Oedaleops* (after Langston, 1965); *Eothyris* (after Reisz, 1986); *Protorothyris* (after Clark and Carroll, 1973); and *Petrolacosaurus* (after Reisz, 1981).

the families Eothyrididae and Caseidae, whereas comparisons with the more advanced suborder Eupelycosauria, which includes all other pelycosaurs (Reisz, 1986), are more limited. The best known and therefore most useful caseasaurs with regard to this analysis are the eothyridids *Oedaleops* and *Eothyris* and the caseid *Casea* (Langston, 1965; Reisz, 1986). In addition, the well-known eupelycosaur *Ophiacodon,* widely interpreted as one of the most primitive members of the suborder, is frequently cited as illustrating primitive states for the order. An understanding of the detailed anatomy of the captorhinomorphs is provided by several publications (Carroll, 1969a; Carroll and Baird, 1972; Clark and Carroll, 1973; Heaton, 1979). The analysis presented here is, for the most part, not affected by which of the captorhinomorph families, Protorothyrididae or Captorhinidae, is considered the more primitive (Heaton and Reisz, 1986). In this analysis the well-known diapsid reptile *Petrolacosaurus,* the only member of Petrolacosauridae, has been chosen to represent the Diapsida. This follows other analyses in which Petrolacosauridae is recognized as the most primitive diapsid family and the sister group of all later diapsids (Benton, 1985; Heaton and Reisz, 1986). The anatomy of *Petrolacosaurus* was described in detail by Reisz (1981).

Character-state analysis.—The characters discussed below are assigned consecutive arabic numbers, whereas their states are



Seymouria *Limnoscelis* *Protorothyris* *Petrolacosaurus*

FIGURE *12*—Skulls in occipital view. *Seymouria* (after White, 1939; Berman et al., 1987); *Limnoscelis* (after Fracasso, 1987; Berman and Sumida, 1990); *Protorothyris* (after Clark and Carroll, 1973); and *Petrolacosaurus* (after Reisz, 1981).

indicated by parenthetically enclosed arabic numbers. This allows direct reference to Tables 1 and 2, where the characters and their states are described and coded, and their taxonomic distributions are designated in a taxon-character state matrix, respectively. In addition, reconstructions of the skulls of *Seymouria, Tseajaia, Limnoscelis, Oedaleops, Eothyris, Protorothyris,* and *Petrolacosaurus* in dorsal and occipital views are given in Figures 11 and 12 in order to illustrate certain states in these taxa.

Character 1. Intertemporal bone. The absence of an intertemporal bone and the correlated presence of a distinct lateral lappet of the parietal found in all diadectomorphs is derived (1) relative to *Seymouria,* as well as all anthracosaurs, which possess an intertemporal bone and lack a lateral lappet of the parietal (0). Pelycosaurs, captorhinomorphs, and *Petrolacosaurus* also lack an intertemporal bone, but only in pelycosaurs is the configuration of the parietal such that a lateral lappet can be confidently identified. The one possible exception of note among the primitive pelycosaurs is *Eothyris* (Reisz, 1986). In captorhinomorphs and *Petrolacosaurus,* on the other hand, there is no distinct lateral lappet of the parietal. It seems very probable that an expansion of the posterior lateral margin of the parietal, so that the paired parietals now occupy almost the entire subrectangular area of the skull table, has disguised the presence of a lateral lappet. In *Petrolacosaurus* the lateral extent of the parietal has been somewhat reduced by the lateral emargination of the parietal by the upper temporal fenestra. The parietals of captorhinomorphs and *Petrolacosaurus* are, therefore, interpreted in this analysis as possessing a lateral lappet.

Character 2. Posterolateral corner of skull table. All three diadectomorphs discussed here exhibit the derived feature of an expansion of the supratemporal and concomitant reduction of the skull table exposure of the tabular, so that the supratemporal forms the entire, or almost the entire, posterolateral corner of the skull table and ends posteriorly in a horn-like extension (1). The primitive state is well exemplified in *Seymouria* and all anthracosaurs, where the dorsal exposure of the tabular is large and subequal to that of the supratemporal and forms the posterolateral corner of the skull table (0).

As in the diadectomorphs, the supratemporal in the primitive pelycosaurs *Oedaleops* and *Eothyris* is large and forms almost the entire posterolateral corner of the skull table. This is also the condition in some of the more advanced pelycosaurs, such as *Edaphosaurus* (Romer and Price, 1940; Reisz, 1986). Therefore, some pelycosaurs and diadectomorphs are judged as possessing the same derived state 1 of this character. It should be noted, however, that in the majority of the advanced pelycosaurs the posterolateral corner of the skull table is further derived. In those pelycosaurs in which the supratemporal dominates the posterolateral corner of the skull table the parietal has a relatively greater longitudinal length that exceeds or is subequal to its transverse width. In addition, the parietal either lacks a posterolateral, wing-like extension or it is short and transversely very broad. In the more advanced eupelycosaurs the main body of the parietal becomes greatly shortened in longitudinal length and develops a long, transversely narrow, posterolateral, wing-like extension. As a result, the parietal secondarily becomes the dominant element of the posterolateral corner of the skull table. There is also a concomitant marked narrowing of the supratemporal, which lies on the parietal wing and contacts medially the tabular.

In contrast to the condition in diadectomorphs and primitive pelycosaurs, the parietal in captorhinomorphs and *Petrolacosaurus* forms almost the entire posterolateral corner of the skull table as an apparent result of an expansion of its posterior lateral margin (2). Further, this typically results in the parietal extending along the medial margin of the supratemporal, reducing its exposure on the skull table to a narrow elliptical bone. In some captorhinomorphs and in *Petrolacosaurus* a secondary embayment of the occipital margin of the parietal falsely gives it the appearance of having a posterolateral, wing-like extension as in the advanced pelycosaurs and reduces its contact with the medial margin of the supratemporal.

Character 3. Sutural patterns of temporal region of skull roof. Two patterns of sutural contacts of the lateral margin of the lateral lappet of the parietal with the postorbital and squamosal can be identified in the diadectomorphs. In the primitive state, exhibited by *Tseajaia,* the postorbital is very short in posterior extent and does not contact the supratemporal, allowing the lateral margin of the parietal lappet to contact broadly both the postorbital and the squamosal (0). In the derived state, seen in *Diadectes* and *Limnoscelis,* the postorbital has a long posterior expansion that contacts the lateral margin of the lappet and also gains substantial contact with the supratemporal to separate widely the parietal and squamosal (1).

Although the history of the temporal bones is controversial, our analysis is based on the simple assumption that the parietal lappet in diadectomorphs had originally the same spatial and sutural relationships as the intertemporal bone in such forms as *Seymouria* and most primitive anthracosaurs. Loss of the contact between the lateral lappet of the parietal and the squamosal is due mainly to a large posterior expansion of the postorbital and possibly some anterior expansion of the supratemporal. This analysis, therefore, does not depend on determining whether the loss of the intertemporal is due to fusion to the parietal or true loss with concomitant invasion by the postorbital. Gauthier et al. (1988, p. 111) stated, presumably referring to Lewis and Vaughn (1965), that in some (?subadult) specimens of *Diadectes* there is sutural separation between the lateral lappet and the body of the parietal (discussed above). Heaton (1980) and Fracasso (1983) argued that in *Limnoscelis* the intertemporal is lost through fusion to the supratemporal. Yet, except for a possible slight encroachment by the supratemporal into the posterolateral corner of the parietal in *Limnoscelis,* the outlines of the parietals of all three diadectomorphs discussed here are virtually the same, and alternative theories to explain the loss of the intertemporal are, therefore, not necessary. Gauthier et al. (1988) also concluded that the parietal lappet represents the intertemporal fused to the parietal.

In the primitive pelycosaurs *Oedaleops* and *Eothyris,* as in *Diadectes* and *Limnoscelis,* there is a substantial postorbital–supratemporal contact that prevents the lateral lappet of the parietal from contacting the squamosal. Even in most pelycosaur species, where the posterolateral wing of the parietal is well developed, a narrow postorbital–supratemporal contact persists. Species of *Ophiacodon* exhibit both conditions, with the postorbital and supratemporal having either a very narrow contact or a narrow separation (Romer and Price, 1940). The loss of a postorbital–supratemporal contact in some pelycosaurs (caseids, ?*Edaphosaurus*) may be accounted for by an increased size of the temporal fenestra (Heaton and Reisz, 1986). In captorhinomorphs and *Petrolacosaurus* the expansion of the posterior lateral margin of the parietal and the reduction of the supratemporal to a small, elliptical element on the occipital margin of the skull table has, however, allowed the parietal to regain contact with the squamosal (2). Although the parietal–squamosal contact in captorhinomorphs is broad, in *Petrolacosaurus* it has become greatly reduced by the development of the upper temporal fenestra, and the remaining portion of the contact is hidden from dorsal view by the overlying supratemporal. It is important to note that, whereas a parietal–squamosal contact is achieved in some pelycosaurs on the one hand, and captorhinomorphs and *Petrolacosaurus* on the other, both groups retain a long posterior expansion of the postorbital.

Character 4. Parietal–tabular contact. The presence of a contact between the parietal and tabular in *Limnoscelis,* although quite narrow, is recognized as the retention of the primitive state seen in *Seymouria* and all anthracosaurs (0). Although *Diadectes* and *Tseajaia* exhibit the advanced state of a wide separation between the parietal and tabular, it is accomplished in a unique manner in each. In *Tseajaia* the lateral margin of the postparietal becomes greatly extended posterolaterally as a long, narrow exposure along the medial margin of the supratemporal to contact narrowly the greatly reduced tabular at the tip end of the horn-like posterior extension of the supratemporal (2). In *Diadectes,* on the other hand, the supratemporal is greatly expanded medially in the form of a large occipital process that not only separates widely the parietal and tabular, but also the postparietal and tabular (1).

In pelycosaurs, protorothyridid captorhinomorphs (captorhinids lack a tabular) and *Petrolacosaurus* the primitive state of a contact between the parietal and tabular is retained. Although the contact is retained in *Petrolacosaurus,* it is very narrow, probably as a result of the deep embayment of the occipital margin of the parietal.

Character 5. Otic trough. The possession of a stout, rectangular flange of the opisthotic that projects ventrolaterally from the posterior border of the fenestra ovalis and exhibits a deep trough-like basin on its anterior surface, termed an otic trough (Fracasso, 1987), is believed to be present in all diadectomorphs and is judged a derived state (1) relative to *Seymouria* and all anthracosaurs in which this structure is absent (0). This contradicts Fracasso's (1987) identification of this structure in *Seymouria.* Examination of the *Seymouria* specimens studied by White (1939) reveals that the posterior lip of the fenestra ovalis formed by the opisthotic does not project ventrally in a distinct flange-like process that is comparable to the well-developed otic trough in *Diadectes* and Limnoscelis. In his description of the otic trough in *Limnoscelis,* Fracasso (1987) mistakenly described it as being continuous with the basioccipital. Berman and Sumida (1990), however, demonstrated that this structure is formed entirely by the opisthotic. The presence of an otic trough in *Tseajaia,* however, is questionable. In the specimen described by Moss (1972) a bluntly pointed process projects ventrolaterally from the ventrolateral margins of the occiput that forms the posterior margin of the fenestra ovalis and is formed undoubtedly by the opisthotic. The processes, which were not commented on by Moss (1972), are too poorly preserved to be compared in detail with the otic troughs of *Diadectes* and *Limnoscelis.* Yet, they have the same orientation and relationships to neighboring structures as those in *Diadectes* and *Limnoscelis,* and *Tseajaia* is, therefore, tentatively considered to have possessed a structure comparable to an otic trough.

Among the caseasaurs it is not known whether an otic trough is present in *Oedaleops* or *Eothyris* due to poor preservation, but it appears to be present in *Casea.* A well-developed otic trough formed by the opisthotic that is identical in detail to those of *Diadectes* and *Limnoscelis* is known to be present in some eupelycosaurs (e.g., *Dimetrodon* and *Edaphosaurus*; Romer and Price, 1940). An otic trough is, therefore, considered to have been ancestrally present in pelycosaurs. An otic trough is primitively absent in all captorhinomorphs and in *Petrolacosaurus.*

Character 6. Temporal notch. We accept the view that a temporal notch (Godfrey et al., 1987) between the cheek and skull table is primitive for anthracosaurs (Bolt and Lombard, 1992). Presence of a notch does not imply the presence of a tympanic ear. Two derived states of the temporal notch are recognized relative to the primitive state of a small, dorsal notch (0) in *Seymouria* and all anthracosaurs: state 1, the absence of a notch, as characteristic of *Limnoscelis,* pelycosaurs, captorhinomorphs, and diapsids; and state 2, a greatly expanded notch that occupies most of the posterior margin of the cheek dorsal to the jaw joint, which characterizes *Diadectes* and *Tseajaia.*

Character 7. Tabular–opisthotic contact. The absence of a contact between the tabular and opisthotic in protorothyridid captorhinomorphs (captorhinids lack a tabular) and *Petrolacosaurus* is undoubtedly a derived state (1) that sets them apart from *Seymouria* and anthracosaurs, diadectomorphs, and pelycosaurs, in which this contact is primitively present (0). Only in *Tseajaia* and *Ophiacodon* is there some question as to the state of this character. In the only two known skulls of *Tseajaia* (Figure 9) the occiputs are, unfortunately, poorly preserved, with no visible suture to indicate the supraoccipital and opisthotic portions. Despite this, there was obviously an extensive contact between the tabular and the dorsolateral margin of the occiput (Moss, 1972), though much of this contact was certainly hidden by the posterolateral extension of the postparietal over the tabular. A narrow tabular–opisthotic contact, therefore, very likely existed in *Tseajaia.* Reisz (1980) has presented the other possible exception in which he reconstructed the tabular and opisthotic of the occiput of *Ophiacodon* as being widely separated by a lateral expansion of the supraoccipital. This was done, however, without comment, and the sutures were drawn as dashed lines.

The loss of the tabular–opisthotic contact in captorhinomorphs and *Petrolacosaurus* is very likely related to the development in these forms of an enormous occipital opening commonly, but not necessarily correctly (Panchen and Smithson, 1988), referred to as the posttemporal fenestra. Primitively, as in *Seymouria* and primitive anthracosaurs, the posttemporal fenestra, if present at all, is very small, and large occipital flanges of the tabular make broad contact with the opisthotic, including that portion of its dorsal margin occupied by the supraoccipital in more advanced forms. With the development of the very large posttemporal fenestra in captorhinomorphs and *Petrolacosaurus* there may have been a concomitant loss of the occipital flanges of the tabular that contacted not only the opisthotic, but the supraoccipital. A narrow tabular–supraoccipital contact may be present in some captorhinomorphs and in *Petrolacosaurus,* but it involves only the small remnant of the skull-table portion of the tabular. Pelycosaurs, which have a small posttemporal fenestra, retain the primitive condition of a tabular with extensive occipital flanges that contact broadly the supraoccipital and opisthotic.

All three genera of diadectomorphs discussed here are considered to lack posttemporal fenestrae as adults, yet the extent and pattern of the occipital exposures of their tabulars vary dramatically. The tabular of *Limnoscelis,* which undoubtedly most closely approaches the primitive state, has been described (Huene, 1956; Fracasso, 1983, 1987) as a very complex element consisting of three major portions: 1) a dorsal portion extending onto the transitional sloping area between the skull table and the nearly vertical occiput and referred to by Fracasso (1983, 1987) as the tabular dorsal plate; 2) an entirely occipital, dorsomedial portion contacting medially the supraoccipital and opisthotic paroccipital process and referred to by Fracasso as the tabular cone; and 3) an elongate, rectangular portion extending ventrolaterally below the posterior end of the horn-like extension of the supratemporal along the posterior margin of the cheek to over half the distance to the jaw joint and referred to by Fracasso as the tabular occipital plate. The great length of the tabular occipital plate portion in *Limnoscelis* probably represents an autapomorphy. In *Diadectes* there has been a loss of the occipital plate portion and a great reduction of the cone portion of the tabular. The dorsomedial cone portion of the tabular also exhibits the unique feature of being incorporated into the lateral margin of the occipital plate of the braincase and having a coarsely textured surface that faces posteromedially. In *Tseajaia,* on the other hand, the occipital plate portion of the tabular exhibits the unique features of being reduced to a small thumb-like process that projects posteriorly beyond the end of the horn-like extension of the supratemporal and acquiring secondarily a sculptured skull-table exposure. In addition, the dorsomedial cone portion of the tabular in *Tseajaia* has also been greatly reduced, though it is also covered partially by the posterolateral lengthening of the postparietal along the medial edge of the supratemporal. The possession of a greatly expanded temporal notch would seem to be the only obvious, plausible explanation for why the occipital portions of the tabulars of *Diadectes* and *Tseajaia* are so reduced compared to that of *Limnoscelis.*

Character 8. Occipital exposure of supraoccipital. This character and character 9 below are derived from an analysis of the relationships of captorhinomorph reptiles by Heaton and Reisz (1986) and pertain to features of the supraoccipital. An ossified supraoccipital is present in diadectomorphs, pelycosaurs, captorhinomorphs, and *Petrolacosaurus,* whereas *Seymouria* and all other anthracosaurs appear to lack this element. When present the ossified supraoccipital contributes to the dorsal area of the occipital plate of the braincase, occupying a position between the exoccipitals ventrally and the postparietal and parietal bones of the skull table dorsally. In those forms lacking an ossified supraoccipital the element may be present as a much reduced cartilaginous tectum posterior (Heaton, 1980); however, part or all of the area of the absent supraoccipital is occupied by a more greatly expanded posterodorsal region of the opisthotic. If a supraoccipital were present in *Seymouria* and other anthracosaurs, even as a cartilaginous element, it would have occupied only a very narrow width on the occiput.

The presence of a narrow occipital exposure of an ossified supraoccipital, as seen in primitive pelycosaurs, captorhinomorphs, and *Petrolacosaurus,* is therefore considered a derived state (1) relative to its primitive absence (0) in *Seymouria* and anthracosaurs. In *Diadectes* and *Limnoscelis* the supraoccipital is further derived in being greatly expanded laterally well beyond the otic capsule and joining with the opisthotic to form a complete bony barrier between the chamber for the mandibular adductor musculature and the occipital musculature of the cervical region (2). Though the supraoccipital–opisthotic suture cannot be identified in *Tseajaia,* its large, ossified occipital plate strongly suggests the presence of a large supraoccipital. A laterally expanded supraoccipital does occur in the advanced eupelycosaurs, where it typically forms well-developed lateral processes which encroach partially on the area otherwise occupied by the opisthotics. In the primitive caseasaur pelycosaur *Eothyris* and probably in *Ophiacodon,* however, the supraoccipital is narrow and lacks lateral processes, and the opisthotics are relatively larger. For this reason the derived state 1 is considered to be ancestral for the pelycosaurs.

Character 9. Anterior cristae alares of supraoccipital. Heaton and Reisz (1986) noted that *Eocaptorhinus,* the protorothyridid *Paleothyris,* and *Petrolacosaurus* possess the shared-derived feature of anteroventrally directed cristae alares of the supraoccipital that separate the chamber for the mandibular adductor musculature from the cranial cavity (1). In contrast, the supraoccipitals in diadectomorphs and pelycosaurs, regardless of their lateral development on the occiput, primitively lack cristae alares, and the adductor chamber and cranial cavity are separated by the otic capsule, primarily the prootic portion (0).

Results and discussion.—The above character analysis allows the assessment of the phylogenetic relationships among the Diadectomorpha and its constituent families Diadectidae, Tseajaiidae, and Limnoscelidae, Pelycosauria, Captorhinomorpha, *Petrolacosaurus,* and their descendants. A cladistic analysis utilizing the branch and bound algorithm of the computer program PAUP (Swofford, 1984) was used to determine the most parsimonious tree(s), as defined by the data matrix of Table 2. Shared derived characters were determined using *Seymouria,* as well as all anthracosaurs, as the basis for outgroup compar-

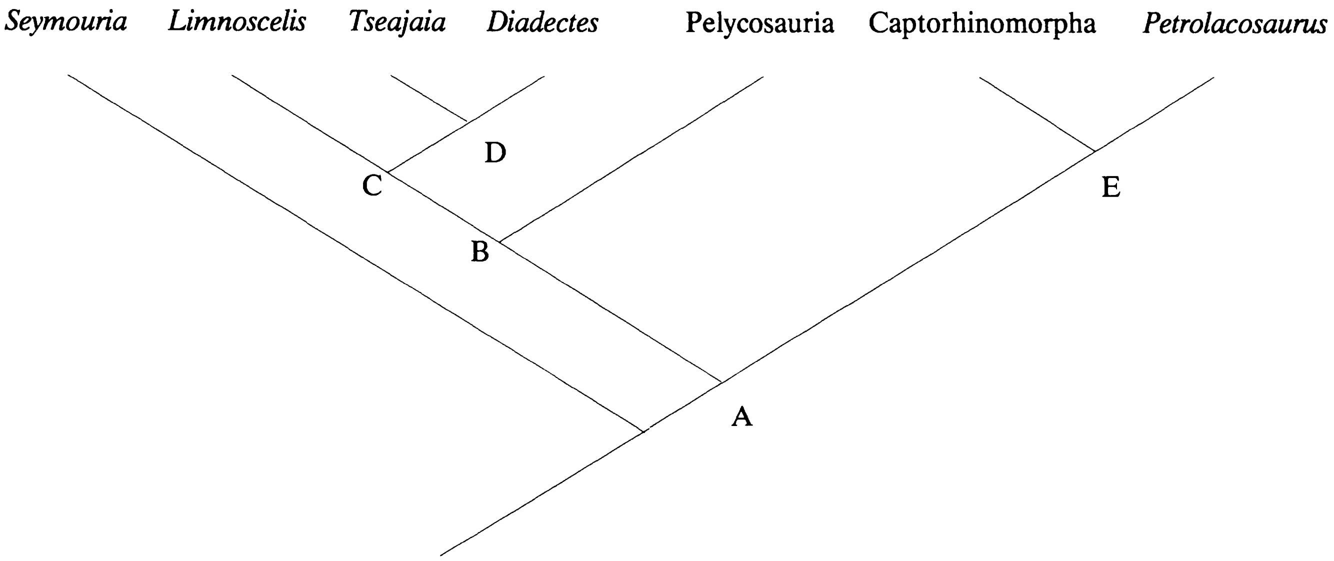


FIGURE *13*—Cladogram illustrating hypothesis of phylogenetic relationship among the diadectomorph genera *Diadectes, Tseajaia,* and *Limnoscelis* (representing the families Diadectidae, Tseajaiidae, and Limnoscelidae), Pelycosauria, Captorhinomorpha, and *Petrolacosaurus* (representing Diapsida). Upper-case letters indicate character-states supporting each node: A, loss of intertemporal bone, presence of ossified supratemporal, parietal lappet excluded from contacting squamosal (reversal in *Tseajaia*); B, otic trough present; C, supraoccipital extending beyond margin of otic capsule; D, temporal notch large and occupies entire posterior margin of cheek; E, long posterior expansion of postorbital does not contact reduced supratemporal and allows parietal–squamosal contact, posterolateral corner of skull table formed almost entirely by parietal, loss of tabular–opisthotic contact, presence of anterior cristae alares of supraoccipital.

isons. Whereas other characters bearing on the interrelationships of these taxa have been proposed by a number of authors (Heaton, 1980; Heaton and Reisz, 1986; Gauthier et al., 1988), only characters derived from the temporal–occipital region of the skull are used here (Table 1). Consideration of postcranial anatomy is best postponed until thorough restudies of the entire skeletons of the diadectomorphs now in progress are completed. The data were processed without a predefined topology. The tree was rooted using a hypothetical ancestor possessing all primitive character states. All multistate derived characters were entered as unordered data.

The most parsimonious tree obtained in this analysis is presented in the cladogram of Figure 13. It requires 16 steps and has a consistency index of 0.875. Although the consistency index is quite high, it must be remembered that the data matrix includes a small number of characters. The association of *Diadectes, Tseajaia,* and *Limnoscelis* conforms to Heaton's (1980) definition of Diadectomorpha. However, the Diadectomorpha synapomorphies listed by Heaton (1980) are now generally considered to be plesiomorphic or invalid (Holmes, 1984; Smithson, 1985; Panchen and Smithson, 1988). In the present analysis the diadectomorphs are united by the common possession of a greatly expanded supraoccipital that extends well beyond the margin of the otic capsule (character 8, state 2). *Diadectes* and *Tseajaia* are depicted as being more closely related to one another than either is to *Limnoscelis* on the basis of a single synapomorphy, the possession of a greatly expanded temporal notch (character 6, state 2).

For several reasons the implication that the Diadectomorpha share a more recent common ancestor with the Pelycosauria and their descendants than with any of the other taxa analyzed is of considerable interest. Shared derived characters supporting this relationship are: 1) posterolateral corner of the skull table formed nearly entirely by the supratemporal (character 2, state 1); 2) long posterior expansion of postorbital contacts supratemporal to exclude parietal lappet from contacting squamosal (character 3, state 1); and 3) possession of an otic trough (character 5, state 1). This relationship, however, is not without at least one serious difficulty. It requires the reversal of state 1 to state 0 of character 3 in *Tseajaia,* which is the reduction of the long posterior expansion of the postorbital to allow the re-establishment of the contact between the lateral lappet of the parietal and the squamosal. An important implication of a common ancestry of the diadectomorphs and pelycosaurs is the recognition of the former as amniotes. Although the placement of the Diadectomorpha within the Amniota has to be considered tentative given the limited number of characters utilized, such a relationship is not unprecedented (Watson, 1917; Romer, 1946, 1956; Fracasso, 1983, 1987). Additionally, Olson (1947) recognized the essentially reptilian grade of organization of *Diadectes.* With the inclusion of the Diadectomorpha, Amniota is supported by three derived features: 1) loss of the intertemporal bone (character 1, state 1); 2) absence of a temporal notch (character 6, state 1); and 3) presence of an ossified supraoccipital (character 8, state 1). Although the term Amniota is used here, it is understood that the assignment of the Diadectomorpha to that clade is based on characters that in themselves have no apparent relationship to reproductive strategies. Amniota is recognized here as the only currently accepted term to classify taxa sharing a common ancestor with synapsids exclusive of members of "Reptilia" as recently redefined by Gauthier et al. (1988).

Also of interest here is the indication that the derived state of the greatly expanded temporal notch (character 6, state 2), characterizing *Diadectes* and *Tseajaia,* was derived from the notchless, derived state 1 rather than from the primitive state 0 in which the notch is moderate sized and located at the dorsal margin of the cheek. Lastly, if the diadectomorphs and pelycosaurs and their descendants form a natural group or clade, then the status of the taxon Cotylosauria, recently redefined by Heaton (1980) to include Diadectomorpha and Seymouriamorpha, must be considered paraphyletic and therefore invalid.

The analysis here indicates that Captorhinomorphs, *Petro-*

TABLE *1*—Characters and their states. The numbers of the character sets and the designation of the primitive or ancestral condition as state 0 and the derived conditions as states 1 and 2 correspond to those used in the character-state analysis in text. The numbering scheme of the multistate characters does not imply that the states are ordered.

Character 1. Intertemporal bone
  0. Present and lateral lappet of parietal absent
  1. Absent and lateral lappet of parietal present
Character 2. Posterolateral corner of skull table
  0. Formed entirely by tabular
  1. Formed entirely or nearly entirely by supratemporal
  2. Formed almost entirely by parietal and partly by greatly reduced supratemporal
Character 3. Sutural patterns of temporal region of skull roof
  0. Small postorbital does not contact supratemporal, allowing lateral margin of either parietal lappet or intertemporal to contact squamosal
  1. Long posterior expansion of postorbital contacts supratemporal to exclude parietal lappet from contacting squamosal
  2. Long posterior expansion of postorbital does not contact greatly reduced supratemporal, allowing parietal to contact squamosal
Character 4. Parietal–tabular contact
  0. Present
  1. Posterolateral extension of postparietal contacts medial margin of supratemporal to exclude parietal-tabular contact
  2. Occipital process of supratemporal contacts supraoccipital to exclude parietal–tabular contact
Character 5. Otic trough
  0. Absent
  1. Present
Character 6. Temporal notch
  0. Small and located at dorsal margin of cheek
  1. Absent
  2. Large and occupies entire posterior border of cheek
Character 7. Tabular–opisthotic contact
  0. Present
  1. Absent
Character 8. Occipital exposure of supraoccipital
  0. Ossified supraoccipital absent
  1. Present, but narrow and not extending beyond lateral margin of otic capsule
  2. Present, and greatly expanded laterally and extending well beyond margin of otic capsule
Character 9. Anterior cristae alares of supraoccipital
  0. Absent
  1. Present

TABLE *2*—Distribution of the character states among the taxa discussed in text and included in cladogram of Figure 12. Description of characters and their states given in Table 1.

Taxon	Characters								
	1	2	3	4	5	6	7	8	9
	Character states								
Seymouria	0	0	0	0	0	0	0	0	0
Diadectes	1	1	1	1	1	2	0	2	0
Tseajaia	1	1	0	2	1	2	0	2	0
Limnoscelis	1	1	1	0	1	1	0	2	0
Pelycosauria	1	1	1	0	1	1	0	1	0
Captorhinomorpha	1	2	2	0	0	1	1	1	1
Petrolacosaurus	1	2	2	0	0	1	1	1	1

lacosaurus, and their descendants are more closely related to one another than either is to any other taxon of the analysis. This relationship is in agreement with the taxon defined as "Reptilia" by Gauthier et al. (1988). The derived states supporting this association are: 1) posterolateral corner of the skull table is formed almost entirely by the parietal and greatly reduced supratemporal (character 2, state 2); 2) long posterior expansion of the postorbital that does not contact the greatly reduced supratemporal and allows the parietal to contact the squamosal (character 3, state 2); 3) tabular does not contact the opisthotic (character 7, state 1); and 4) presence of anterior cristae alares of the supraoccipital (character 9, state 1).

In addition to generating an alternative hypothesis of relationships of diadectomorphs and primitive amniotes, the temporal and occipital characters analyzed here can also be used to test the two other competing hypotheses of relationships discussed at the beginning of this section. Two predefined topologies representing the previously suggested phylogenetic schemes were imposed on the same taxa and characters used in the analysis presented here. They differ only in whether captorhinomorphs or pelycosaurs and their descendants are chosen as the most primitive amniote taxon, and in both diadectomorphs and *Seymouria* are represented as successively more primitive outgroups. If captorhinomorphs are considered as the most primitive amniotes, then 21 steps are required, which yield a consistency index of 0.667. The lower consistency index reflects the requirement of parallel derivation of the large supratemporal dominating posterolateral corner of skull table, otic trough, loss of the tabular-opisthotic contact, and anterior cristae alares of the supraoccipital (characters 2, 5, 7, and 9, respectively). In this analysis the node from which the captorhinomorphs, on the one hand, and the Pelycosauria and *Petrolacosaurus* on the other diverge cannot be defined from one another, thus requiring the recognition of an unresolved trichotomy. The diadectomorphs, however, still share the loss of the intertemporal and presence of an ossified supraoccipital (characters 1 and 8, respectively) as syanpomorphies uniting them with amniotes.

If the predefined topology of the cladogram depicts pelycosaurs and their descendants as the most primitive amniotes, then 17 steps are required, which yield a consistency index of 0.824. Though the results may not be significantly different from those of the single most parsimonious tree arrived at in the present study, this hypothesis of relationships exhibits some serious difficulties. A large supratemporal dominating the posterolateral corner of the skull table would have to have been derived twice or derived in the ancestors of the diadectomorphs and lost again to account for the condition in captorhinomorphs and diapsids. A similar series of events would be required to explain the character-state distribution of the otic trough. On the other hand, this hypothesis of relationships not only supports a close relationship between the diadectomorphs and pelycosaurs, but also between the captorhinomorphs and *Petrolacosaurus,* since they have in common the shared derived states of a loss of the intertemporal and possession of an ossified supraoccipital (characters 1 and 8, respectively). Acceptance of diadectomorphs as the sister group of all amniotes, however, does not require nor rule against assignment to Amniota.

Because the phylogenetic hypothesis proposed by this study is based solely on temporal and occipital characters, it may not be considered strongly documented. However, the number of supporting characters is sufficient to judge it a reasonable alternative to previous hypotheses.

From the descriptions and character-state analysis above it is possible to note four autapomorphic characters of *Diadectes* not previously recognized in the literature: 1) loss of contact between the postparietal and tabular; 2) supratemporal possesses well-developed occipital process that contributes to the occiput; 3) tabular greatly reduced and incorporated into occipital plate of braincase, with a coarsely textured surface that faces posteromedial; and 4) skull roofing bones thick and porous, with network of deep, smooth, U-shaped channels or grooves. These and other unique cranial characters of *Diadectes,* such as its dentition and middle ear structure (Olson, 1966), clearly indicate that it is the least appropriate member of the Diadectomorpha to be used as the sole outgroup for analysis of amniote interrelationships (Brinkman and Eberth, 1983).

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ALCIDEDORBIGNYA INOPINATA (MAMMALIA: PANTODONTA) FROM THE EARLY PALEOCENE OF BOLIVIA: PHYLOGENETIC AND PALEOBIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT—*Alcidedorbignya inopinata* Muizon and Marshall is a primitive pantodont from the Early Paleocene of Tiupampa, Department of Cochabamba, in the "Cordillera Oriental" of south-central Bolivia. It is known by almost complete upper and lower dentitions, which are described in detail. The occurrence of abundant juvenile specimens allows a study of tooth replacement. The molars of *Alcidedorbignya inopinata* are primitive for a pantodont but they show the characteristic synapomorphy of the group, which is the presence of a V-shaped ectoloph of P3-4. However, the paracone and the metacone of *A. inopinata* are separated at their bases, a feature absent in the Bemalambdidae and *Harpyodus*, which have connate to semi-connate paracone and metacone. Because of this character, *A. inopinata*, although the oldest, is not the most primitive pantodont. However, *A. inopinata*, as in bemalambdids and *Harpyodus*, does not have a mesostyle on M1-2/ or a strongly V-shaped centrocrista, which are found in all other pantodonts. For this reason, *Alcidedorbignya inopinata* is removed from the Pantolambdidae (which are too specialized) and referred to the new monotypic family Alcidedorbignyidae. The family Wangliidae Van Valen, 1988, is not accepted here and the genus *Wanglia* is regarded as a junior synonym of *Harpyodus*; the latter includes the two species *H. euros* and *H. decorus*. Analysis of pantodont origins leads to the conclusion that didelphodontines constitute the best potential sister-group; however, no synapomorphy could be found to substantiate this hypothesis. *Alcidedorbignya inopinata* is the first pantodont known from a southern continent and, being the oldest, it raises a discussion on the paleobiogeographic history of the group.

INTRODUCTION

AN INTRIGUING and controversial issue in vertebrate history is the origin and biogeographic history of the land-mammal fauna of South America. The earliest undisputed record of mammal life on that continent was long restricted to knowledge of fossils from rocks presently regarded as Middle Paleocene age in Argentina and Brazil (Marshall, 1985, and references therein). Groups belonging to what Simpson (1980) called Stratum 1 (i.e., marsupials, edentates, condylarths, astrapotheres, xenungulates, notoungulates, litopterns) were first recorded in these faunas. However, the phylogenetic relationships of these groups among themselves and with groups of similar and earlier age elsewhere in the world were either unknown or only tenuously established. It was not known if some or all these groups evolved in situ in South America from long-established Cretaceous stocks, or if some or all came from stocks that dispersed to South America from elsewhere (i.e., North America, Africa, or Australia via Antarctica) in Early Paleocene time. It was long