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THE TEMPORAL REGION OF THE PERMIAN REPTILE DIADECTES

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INTRODUCTION

A review of the literature reveals considerable diversity in interpretation of the temporal region in the skulls of the genus *Diadectes*, a large, Early Permian genus of the Parareptilia. In 1947, I published an interpretation that differed from others in the recognition of a complete series of temporal elements, including tabular, supra-temporal and intertemporal. Questions as to the validity of this suggestion have prompted a restudy of a series of skulls of the genus with the results reported in this paper.

The rather remarkable variability of the skulls of *Diadectes* was emphasized in my 1947 review of the genus. It is important in a consideration of the temporal region to recognize that this variability extends to the relative sizes and the shapes of the skull bones and the nature of the junctions of adjacent elements. Three additional factors, moreover, make interpretation of the temporal structure difficult. The surfaces of the skulls are marked by variable prominences and flutings that tend to obscure the positions of sutures. The thick and porous nature of the skull bones makes it difficult to trace sutures through the bones. Fusion of adjacent elements in the occipital and temporal regions appears to have been initiated at an early stage and to have progressed from the inner to the outer surface of the skull. These factors probably account for much of the confusion that has attended analyses of the temporal region.

REVIEW OF PREVIOUS WORK

Every reasonable interpretation of the temporal region has been suggested at one time or another. Case (1911, fig. 20) figured a skull of *D. phaseolinus*, A.M.N.H.4839, showing the squamosal as

a large element in contact with a broad parietal, which occupied much of the posterior dorsal surface of the skull. He tentatively identified a tabular overlying the posterior margin of the otic notch but did not show either a supratemporal or an intertemporal. In his figure (fig. 32) of A.M.N.H.5347 (identified by him as *Chilonyx rapidens*, but referred to *Diadectes* by me in 1947) a distinct tabular was shown.

Von Huene (1913) figured the skulls of A.M.N.H.4352, 4370, 4378, 4559 and 4839. In A.M.N.H.4352 (fig. 15) he indicated the presence of two temporal elements, the supratemporal and the tabular. The supratemporal is shown to lie between the parietal and the squamosal. The dorsal and medial extent of this element suggests that it would occupy a part of the area identified as parietal in A.M.N.H.4839 by Case. The tabular lies back of the supratemporal essentially as a continuation of the interparietal (dermo-supraoccipital of von Huene). In A.M.N.H.4378 (von Huene, op. cit., fig. 19) the tabular is shown to be lateral to the parietal, which, in part, separates it from the interparietal. The details of the temporal regions are not shown for the other figured skulls.

Williston (1925, fig. 22) illustrated the skull of *Diadectes*, basing the inferred sutural pattern primarily on C.N.H.M.-U.C.1075. A very broad parietal is shown to lie in contact with the squamosal without intervening bone. A tabular is indicated at the posterior termination of the interparietal (dermosupraoccipital of Williston). Romer (1933, fig. 111A, and 1945, fig. 134A, respectively) figured *Diadectes* after Williston. The drawing resembles the cited figure of Williston very closely except for the presence of a supratemporal between the squamosal and the parietal. I have studied with care the skull that appears to have been the basis of Williston's figure. At best the sutures on the posterior part are difficult to make out and I have been unable to determine the limits of any bones in the temporal region.

Gregory (1946, fig. 6A) presented a lateral view of the skull of *Diadectes*, based primarily on A.M.N.H.4839. The parietal and the squamosal are shown to be in contact, without any intervening bone, and a tabular is indicated over the posterior termination of the otic notch. In contrast to the determination of Case, the parietal is shown to be rather narrow posteriorly and the marginal parts of the bone as shown by Case are interpreted as squamosal. In figure 13A of the same paper, a dorsal view, the boundaries of the tabular are shown by a broken line.

I showed (1947, figs. 1 and 2) the tabular fused to the parietal and lying over the posterior termination of the otic notch in much the same position as indicated in the other cited figures. Two elements were shown between the parietal and the squamosal, an anterior intertemporal and a posterior supratemporal, which formed the supratemporal prominence. It was noted that the full extent of the suture between these two bones had not been traced. The discussion (Romer, 1948, and unpublished) occasioned by this paper concerns the existence of two elements, rather than one, between the parietal and the squamosal. In order to clarify the situation, the results of studies of fifteen skulls from the collections of Chicago Natural History Museum, the American Museum of Natural History, and the Museum of Comparative Zoology at Harvard University are here reported on in detail.

SIGNIFICANCE OF THE TEMPORAL REGION

Before proceeding to these analyses, a word upon the bearing of this region on the phylogeny of the reptiles is in order. In 1947, I suggested that reptilian evolution was dichotomous and that the two major lines be designated as subclasses Parareptilia and Eureptilia. The former was believed to include the order Diadecta, comprising the Seymouriamorpha, Diadectomorpha, Procolophonina and Pareiasauria, and the order Chelonia. The Eureptilia included the remainder of the reptiles. It was noted that the Seymouriamorpha and Diadectomorpha were characterized, among other common features, by the possession of the tabular, the supratemporal and the intertemporal, but that the representatives of the other major categories of the Parareptilia lacked one or more elements of this primitive series. A relationship of the Seymouriamorpha and Diadectomorpha somewhat closer than usually conceived was suggested, as well as the interpretation of the supposed supratemporal of *Triassochelys* as intertemporal. The evidence of the temporal region was, of course, but a small part of the total evidence presented and the structure of the otic and basicranial regions was considered to be of primary importance. It seems clear, in view of the probable rhipidistian ancestry of both lines of reptiles, that each underwent a reduction in the number of temporal elements so that the cited evidence is concerned basically with the time of loss of one or more elements and with the homology of the temporal elements in advanced stocks of the Parareptilia. If the condition in *Diadectes* was correctly interpreted, it tends to confirm the more important evidence of the basicranium and otic region. The case

for the suggested dichotomy would be but little weakened, however, were the interpretation to be proven incorrect.

ANALYSES OF THE TEMPORAL REGION IN DIADECTES

Because of the great variability in the skull it seems preferable in this case to discuss the specimens individually rather than to give

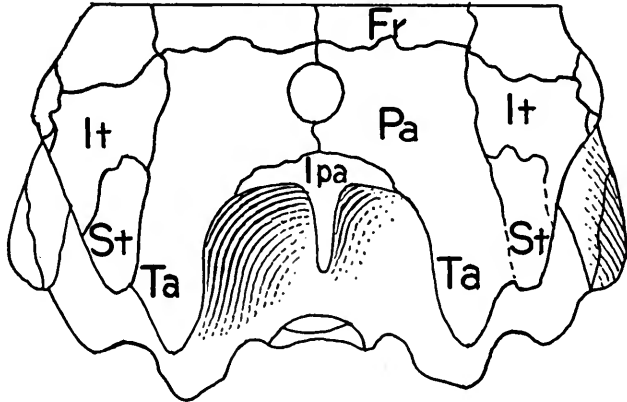


FIG. 27. C.N.H.M.-U.R.27 (formerly M.C.Z.1105). Dorsal aspect of skull, showing posterior skull platform. *Fr*, frontal; *Ipa*, interparietal; *It*, intertemporal; *Pa*, parietal; *St*, supratemporal; *Ta*, tabular.

a general account based on features seen now in one, now in another. Such treatment brings out the nature of the evidence clearly and should facilitate future work by others.

The following skulls were examined in the course of the present study: C.N.H.M.: U.C.675, U.C.706, U.C.1075, U.C.1078, U.C.1177, U.C.1659, U.R.27, U.R.28. A.M.: 4352, 4357, 4378, 4675, 4838, 4839. M.C.Z.: 1106.

C.N.H.M.-U.R.27 (fig. 27): The skull of this specimen (obtained by exchange from Harvard University and formerly designated as M.C.Z.1105) is the one upon which the restoration I figured (Olson, 1947) was based. It is a complete skull, modified only slightly by dorso-ventral crushing. Sutures are clearly shown in some areas, being represented by matrix-filled grooves in the skull surface. Even where best developed, where there can be no doubt of identity in view of close correspondence to sutural patterns in comparable areas of other skulls of *Diadectes*, sutures cannot be traced far into the bone in cross section. Fusion has progressed to an advanced stage, apparently starting at the inner surface of the skull and

progressing outward. Sutures in the occipital and temporal regions are only partially visible.

The suture between the parietal and more lateral bones may be traced posteriorly, medial to the supratemporal prominence, for

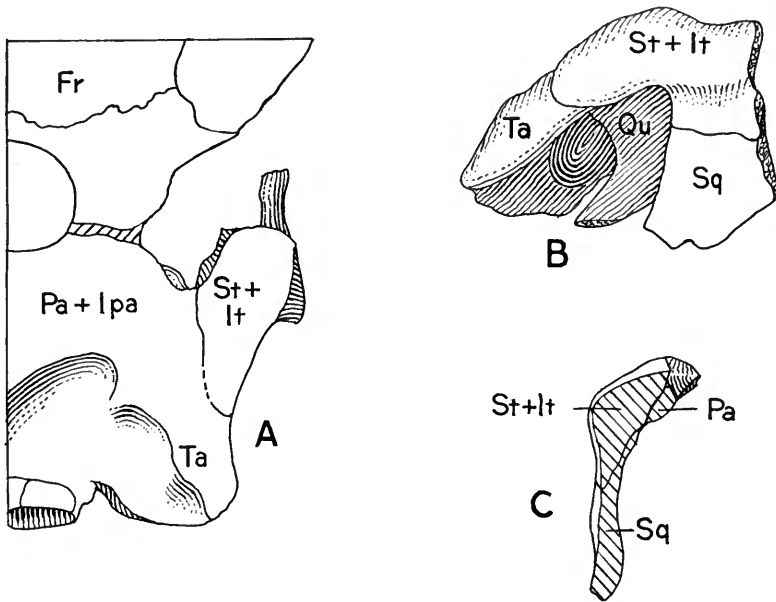


FIG. 28. C.N.H.M.-U.C.1078. A, dorsal; B, right lateral; C, transverse section through postorbital region of skull in anterior aspect. *Fr*, frontal; *Pa+Ipa*, parietal and interparietal in anterior aspect; *Qu*, quadrate; *Sq*, squamosal; *St+It*, compound bone representing fused supratemporal and intertemporal; *Ta*, tabular.

about one-half the length of the prominence on the right side of the skull and for the full length on the left. On both sides of the skull a strongly developed suture passes forward from the anterodorsal margin of the otic notch. This and the suture lateral to the parietal isolated an area of bone between the squamosal below and the parietal medial to the supratemporal prominence. About three-fourths of an inch forward from the notch along the squamosal-supratemporal suture, another suture may be seen passing anterodorsally and then dorsally. The full extent of this suture has now been observed on the left side of the skull, more detailed study having revealed a part not evident when the 1947 restoration was made. On the right side of the skull, fully cleaned in the course of the current study, the antero-medial part of the suture is well

shown, but the posterior end cannot be made out. It is this suture that separates the area of bone between the squamosal and the parietal into two parts, called supratemporal and intertemporal in 1947.

Neither of these two elements occupies the normal position of the tabular, which usually overlies the posterior margin of the otic

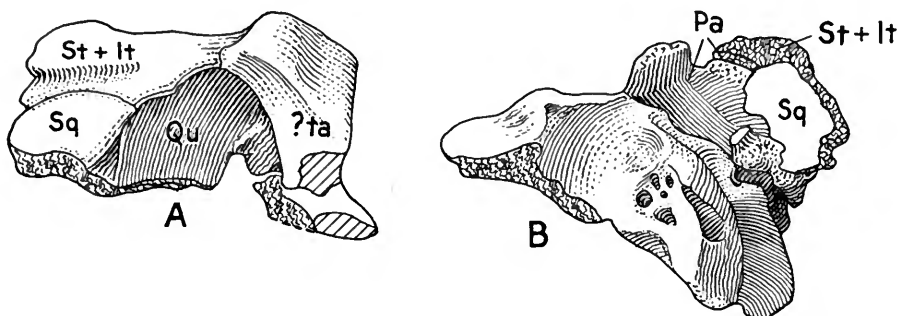


FIG. 29. C.N.H.M.-U.R.28. A, lateral; B, ventral, showing contact of parietal and squamosal under supratemporal and intertemporal. *Pa*, parietal; *Qu*, quadrate; *Sq*, squamosal; *St+It*, supratemporal and intertemporal; *ta*, tabular.

notch. No separate tabular element can be identified on the skull, although it is reasonable to assume that one was present over the posterior portion of the otic notch between the notch and the occipital plate.

C.N.H.M.-U.C.1078 (fig. 28): Sutures are well shown on most parts of this skull. In right lateral aspect there is a clear separation of the squamosal and a more dorsal element that is in turn separated from the parietal. This element occupies the position of the supra-temporal and the intertemporal of C.N.H.M.-U.R.27. There is, however, in C.N.H.M.-U.C.1078, no evidence of a separation into two elements. There is an open break at the position of the supra-temporal-intertemporal suture as seen in C.N.H.M.-U.R.27 but no definite evidence that this break is along a suture. The left temporal region of the skull is not preserved.

C.N.H.M.-U.R.28 (fig. 29): This specimen consists only of the back part of a skull and some postcranial fragments. The separation of the squamosal and the parietal by a large intermediate element is clearly shown, but there is no evidence that this element is separated into two parts. There is considerable cracking and breakage in the area but it seems improbable that they are sufficient to have masked an open suture had one been present.

M.C.Z.1106 (fig. 30): This specimen includes the dorsal surface and the posterior part of a skull in fair condition as well as other badly crushed and broken skull and postcranial elements. Sutures are moderately well shown and there has been a strong tendency for sutures to be opened in the course of crushing. On the right side,

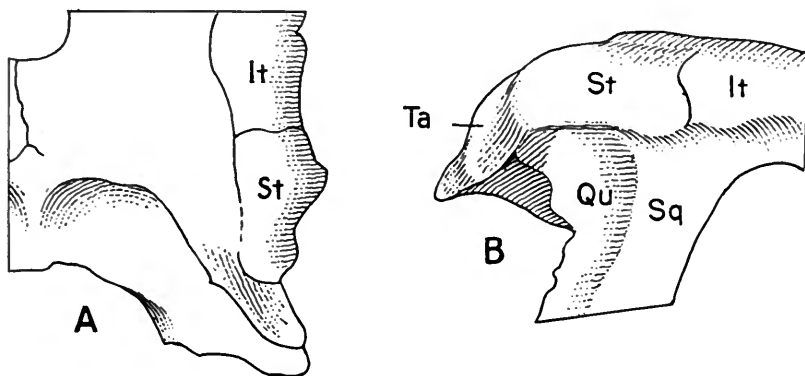


FIG. 30. M.C.Z.1106. A, dorsal; B, right lateral. *It*, intertemporal; *Qu*, quadrate; *Sq*, squamosal; *St*, supratemporal; *Ta*, tabular.

in the temporal region, a suture between the squamosal and a pair of overlying bones is clearly visible. It has been opened by crushing but is shown to represent an authentic junction of bones in cross section.

The junction of the overlying pair of bones and the parietal is indicated by a well-developed groove that, followed forward, occupies the normal position of the suture lateral to the parietal. Its identity can hardly be doubted. The elements lying between the squamosal and the parietal form a supratemporal prominence posteriorly and carry forward to about the level of the anterior end of the pineal foramen. Passing dorso-medially from the suture that marks the dorsal limit of the squamosal is a slightly open, matrix-filled structure that is precisely like the open sutures in other parts of the skull. It occupies much the same position as the suture between the supposed supratemporal and interparietal in C.N.H.M.-U.R.27. At this junction the posterior element overlaps the anterior one for several millimeters. Such overlap is characteristic of the sutures throughout the skull of *Diadectes*. It appears quite certain that this structure represents a sutural junction of two elements that correspond to the bones identified as supratemporal and intertemporal in C.N.H.M.-U.R.27.

The opposite side of this skull illustrates the sort of difficulties that have resulted in confusion in interpretation. This side has not been subjected to the tensional stress that has affected the other, and the sutures have not been opened. The squamosal-supratemporal suture, so clear on the right side, is seen only with difficulty on the left and the squamosal-intertemporal part is not to be seen at all. Yet this suture can be identified in a considerable number of skulls of *Diadectes* and its existence cannot be doubted. There is a transverse break passing through the squamosal and proceeding dorsally along a line that is almost a mirror image of the suture between the supratemporal and the intertemporal on the right side of the skull. Were the left side alone preserved there would be little basis for believing that the upper part of the break was along a sutural junction. Very careful examination reveals that there has been a slight infiltration of matrix in the upper part of the break, not present in the squamosal part, but this in itself would hardly be sufficient for determination.

As in other skulls discussed to this point there is no separation of the parietal and the area presumed to be occupied by the tabular. No sutures are shown in the occipital region or on the posterior part of the parietal shelf.

C.N.H.M.-U.C.675 (fig. 31): This specimen, unlike the rest, which are from the Wichita and Clear Fork beds of Texas, comes from the Permian of New Mexico. It is rather badly distorted and large areas have been reconstructed in plaster. Part of the left temporal region is preserved and what is shown is rather difficult to interpret. Ossification is much less complete than in most skulls of *Diadectes* and the temporal region is characterized by very deep grooves and recesses. It appears that these occur along bone junctions. If this interpretation is correct, and there seems to be no other plausible explanation, the following bone pattern may be inferred. The squamosal, which is but partially ossified dorsally, is separated by a deep, broad recess from an overlying element. The dorsal part of the latter forms the supratemporal prominence. Passing dorsally from the junction of the squamosal and the overlying element is a narrow groove that passes just anteriorly to the supratemporal prominence. About midway in its dorsal course the groove expands posteriorly to form a deep V-shaped incision in the bone posterior to it. The groove continues to the inner margin of the supratemporal prominence where it terminates against a faintly shown suture that appears to mark the lateral margin of the parietal. Anterior to the groove there is preserved a small

fragment of bone that must be considered a separate element if the groove represents a suture. This fragment is in the area occupied by the intertemporal in C.N.H.M.-U.R.27 and M.C.Z.1106 and by the anterior part of the large element that intervenes between the squamosal and the parietal in other skulls described to this point.

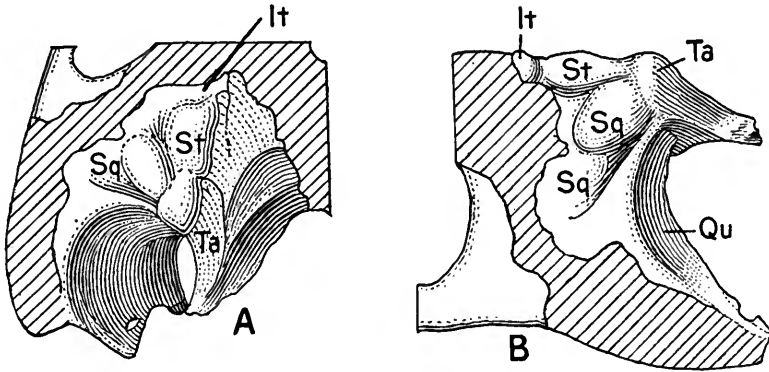


FIG. 31. C.N.H.M.-U.C.675. A, dorsal; B, left lateral. *It*, intertemporal; *Qu*, quadrate; *Sq*, squamosal; *St*, supratemporal; *Ta*, tabular.

Thus there seems to be evidence of both an intertemporal and a supratemporal in this skull.

There is also some evidence concerning the position of the tabular. A poorly developed groove passes medially from the supratemporal prominence and swings posteriorly to meet the lateral margin of the occipital plate. It is in the position in which a suture between the tabular and the interparietal (see discussion of A.M.N.H.4839, p. 72) is to be expected.

Conditions in this skull suggest a condition similar to that in C.N.H.M.-U.R.27 and M.C.Z.1106, but the interpretation has been based on grounds somewhat different from those used for other skulls.

C.N.H.M.-U.C.1659: This skull possesses well-developed sutures in areas anterior to the pineal foramen and in the region just back of the orbit, but almost no detail can be made out in the posterior parietal, occipital, or temporal areas. Between the parietal and the squamosal there is a large area occupied by a separate element. The limiting sutures are difficult to trace and, although there is a groove passing across the area, there is no real evidence of separation into two parts. The particular importance of this skull with respect

to the matter under discussion is that it illustrates the degree of difference in fusion that may occur between different areas of the same skull.

C.N.H.M.-U.C.706, -U.C.1177, -U.C.1075: These three skulls, although promising for study upon cursory examination, prove to be of little value either because sutures are not well shown or because of damage in the critical areas.

A.M.N.H.4378: Sutures are fairly evident in this specimen, but part of the area critical to the current study is missing. The relationship of the parietal and a more lateral element is well shown, with the former shelving well under the latter. This latter element must be either a squamosal or a bone lying between the parietal and the squamosal. In view of the condition in several other skulls, the latter interpretation seems more probable. If this be the case, the squamosal is missing. There is no clear evidence of separation of the element into an anterior and a posterior part.

A.M.N.H.4839 (fig. 32): This is probably the most figured skull of *Diadectes*. There have been various interpretations, that of Case (1911) and of Gregory (1946) being the most important. The sutures are clear in places but in other areas pass into grooves and become more difficult to follow. The skull also has a number of cracks that make for confusion. After I had examined a rather large series of skulls of *Diadectes*, the pattern seemed very clear, especially on the left side of the skull. The presence of a suture separating supratemporal and intertemporal is, of course, the critical point. There is a matrix-filled structure in the position illustrated in the figure. It corresponds in the nature of its development to other sutures in the area, but cracks also are filled with a similar matrix. The parietal suture swings laterally to form a slight V-shaped apex at the point of junction with this structure, as is common at many sutural junctions. The position and pattern of the line correspond very closely to the conditions shown in C.N.H.M.-U.R.27 and M.C.Z.1106. These facts strongly support the interpretation that this structure is actually a suture separating the supratemporal and the intertemporal.

This skull gives some indication of the probable position of the tabular and its relationships to the parietal and the interparietal. It has been supposed that the tabular lay over the posterior margin of the otic notch and, as shown in my illustration (Olson, 1947), continued posteriorly from the parietal. This skull shows the parietal and the interparietal well and indicates that the tabular is

more nearly a posterior continuation of the interparietal-tabular suture, as shown in figure 32.

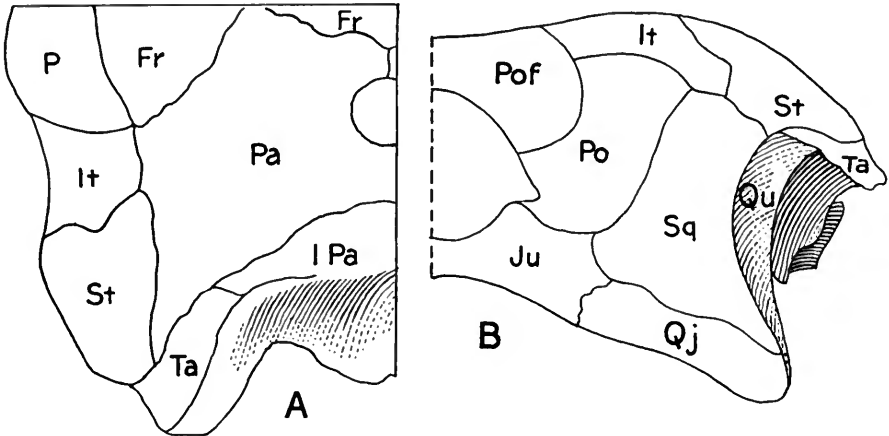


FIG. 32. A.M.N.H.4839. A, dorsal; B, left lateral. *Fr*, frontal; *Ipa*, interparietal; *It*, intertemporal; *Ju*, jugal; *P*, postfrontal; *Pa*, parietal; *Po*, postorbital; *Pof*, postfrontal; *Qj*, quadratojugal; *Qu*, quadrate; *Sq*, squamosal; *St*, supratemporal; *Ta*, tabular. These drawings were made from freehand sketches designed to show sutural relationships and may be slightly in error in proportions and precise bone outlines.

A.M.N.H.4352: This skull shows some sutures but is damaged and restored over much of the critical area. Fusion, furthermore, has obliterated sutures in areas that might prove helpful.

A.M.N.H.4838: The ventral surface of the skull roof is available with an excellent sutural pattern but it does not extend back to the critical area. Even were this the case it is doubtful that an intertemporal-supratemporal suture would be evident, for the parietal shelves well under these elements laterally and the squamosal passes under them medially. In C.N.H.M.-U.R.28, among others, the two elements are known to make contact under the single large element that occupies the supratemporal-intertemporal region (fig. 29, B).

A.M.N.H.4357: This is a highly grooved partial skull with some of the sutures completely open in the postorbital region. Unfortunately, the condition in the temporal region is not clear because of poor preservation and considerable plaster reconstruction. The situation with respect to the supratemporal and the intertemporal cannot be determined.

A.M.N.H.4675: A skull roof and part of the back of the skull are preserved in rather poor condition. The presence of an element

between the parietal and the squamosal is clearly shown and on the inner surface of the skull the parietal-squamosal suture can be seen. No certain evidence of a separation of the supratemporal and the intertemporal is apparent, although there is a break just anterior to the supratemporal prominence that may have followed such a suture for part of its length.

DISCUSSION

The conditions determined in the fifteen skulls with respect to the sutures critical to this study are summarized in the table (p. 75). Six of the fifteen prove to be of no value because of damage or the lack of sutures. Of the remaining nine all but one show that the parietal and the squamosal fail to make contact on the dorsal surface of the skull. Two, however, show a contact of these two bones on the under surface of the roofing bones. It seems safe to conclude that one or more bones lie between the parietal and the squamosal on the outer surface of the skull.

Four specimens show the presence of a suture separating into two parts the bone that intervenes between the parietal and the squamosal. The nature of the suture and the bases for interpretation are outlined in the descriptions of the individual skulls. Four other skulls, in which preservation is good or fair in this region, do not show such a suture. The absence may be attributed either to a real lack of one of the elements or to its loss by coalescence with the adjacent bone. All of the skulls may be referred to one genus, *Diadectes*. Three species, *D. phaseolinus*, *D. tenuitectis* and *D. lentus* are represented. It seems improbable, even with the high variability within the genus, that a bone of major proportions would be present in one of the species and absent in another. It may be of some interest, however, to note the distribution with respect to species. Three of the skulls (C.N.H.M.-U.R.27, M.C.Z.1106 and A.M.N.H.4839) that show the suture may be referred to *D. phaseolinus*. The other in which the suture occurs (C.N.H.M.-U.C.675) is *D. lentus*. Thus no skull of *D. tenuitectis* shows the suture. C.N.H.M.-U.R.28, C.N.H.M.-U.C.1659, and possibly A.M.N.H.4675 belong to this species and in each the preservation is such that a suture might be shown. On this basis there might seem to be justification for believing that the difference, whether resulting from fusion or from actual absence of the bone, might have a taxonomic significance. C.N.H.M.-U.C.1078, which lacks the suture, however, is a specimen of *D. phaseolinus*. Presence and absence in the same species seems quite certainly to point to fusion as the reason for the difference and

CONDITION OF TEMPORAL REGION IN FIFTEEN SKULLS OF DIAECTES

Sutures	CNHM	CNHM	MCZ	CNHM	CNHM	CNHM	CNHM	CNHM	AM	AM	AM	AM	AM	AM	
	UR27	UC1078	UR28	1106	UC675	UC1659	UC706	UC1177	UC1075	4878	4839	4352	4838	4357	4675
Parietal and lateral element...	P	P	P	P	P	P?	U	U	U	P	P	U	U	U	P
Squamosal and dorsal element.	P	P	P	P	P	P?	U	U	U	P	P	U	U	U	P
Intertemporal and supratemporal.....	P	A	A	P	P	A	U	U	U	A	P	U	U	U	A
Tabular.....	A	A	A	A	A	P?	U	U	U	A	P?	U	U	U	U
Parietal and squamosal..... (ventral surface)	U	U	P	U	U	U	U	U	U	U	U	U	U	U	P

P = present.

A = absent but area present.

U = condition uncertain because area is poorly preserved or absent.

? following letter = indication of presence of suture but evidence not conclusive.

while the tendency toward fusion may differ in species, it cannot be said to be confined to *D. tenuitectis*.

If the existence of the pair of elements be considered demonstrated there still remains the problem of determining homologies. It seems evident that the two bones are members of the temporal series, but whether they represent intertemporal and supratemporal or supratemporal and tabular may be open to question. There is some evidence, from two of the skulls studied, of a separate tabular element lying in contact with the interparietal and the parietal and forming the dorsal margin of the posterior part of the otic notch. In neither skull is the separation so well developed that it can be identified as a suture beyond any doubt. The position shown for the tabular in virtually every published figure in which a tabular is shown at all, is that suggested by these supposed sutures. It is the logical position for the bone, for it corresponds to that well documented in various labyrinthodont amphibians and in *Seymouria*. If the evidence of the supposed sutures is neglected, other explanations might be that the tabular has disappeared completely, that it has fused with adjacent elements, or that the posterior element of the pair of bones between the parietal and the squamosal is the tabular. With respect to the last suggestion, only rather drastic modification of an otherwise very primitive skull pattern could have resulted in the development of a tabular well forward between the squamosal and the parietal, with a concurrent elongation of the interparietal to a position over the posterior margin of the otic notch. The probabilities of such a series of changes without major modifications in related parts of the skull seem so slight that I feel justified in dismissing this suggestion as untenable.

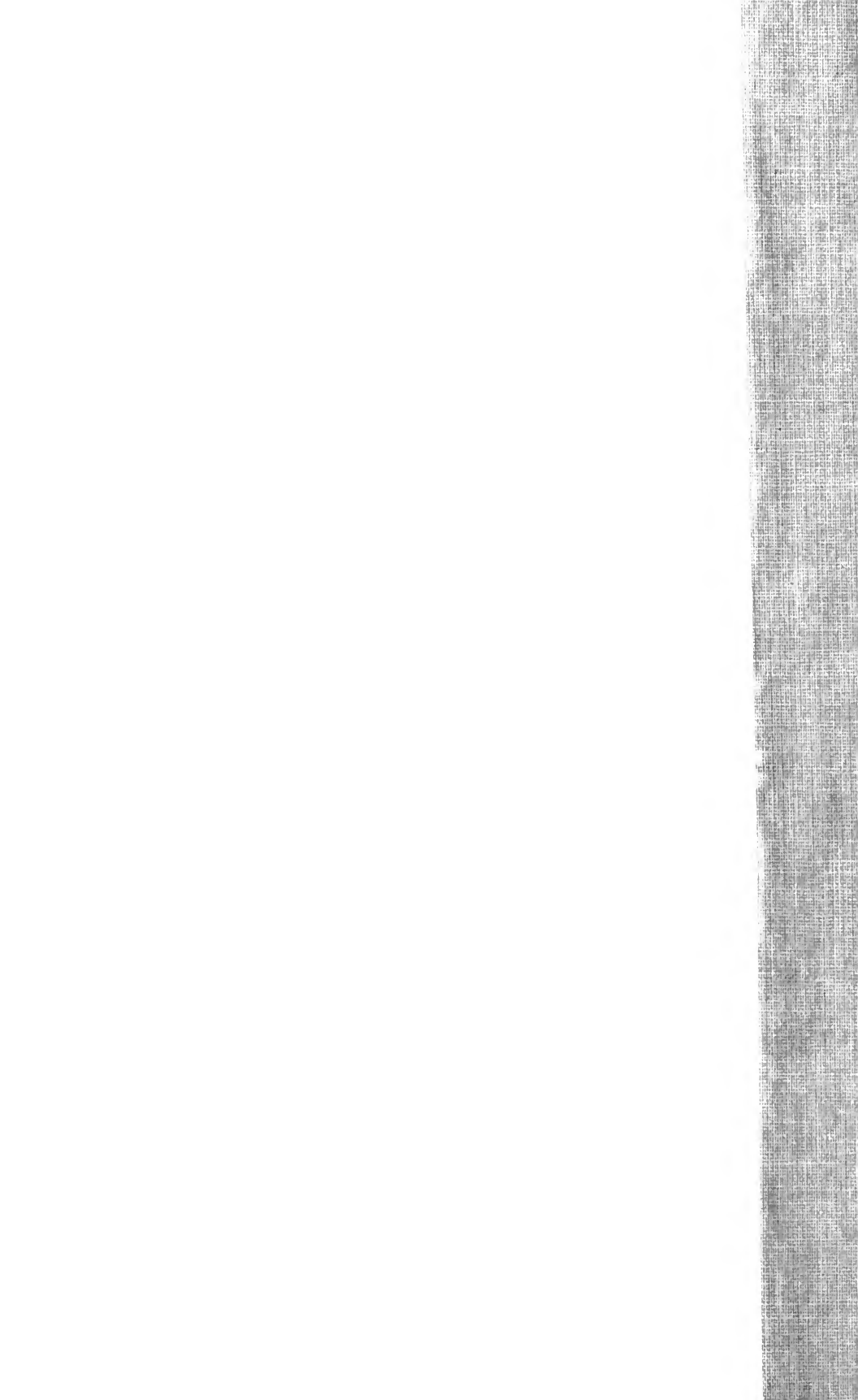
Either the tabular has been lost or it is usually obliterated by fusion. The fact that there are suggestions of a suture in two skulls and the fact that the tabular tends to be a persistent element in the line of evolution that led to the diadectids make it probable that coalescence with the parietal and the interparietal is the correct explanation.

If the more posterior of the two elements between the parietal and the squamosal is not tabular, it must then be supratemporal. The position is that which the supratemporal normally occupies in amphibians and primitive reptiles, although it may lack contact with the squamosal in animals with very deep otic notches. The remaining element, which lies anterior to the supratemporal, between the parietal and the squamosal and in contact with the postorbital and the postfrontal anteriorly, must be the intertemporal.

It was this sort of evidence and reasoning that led me in my earlier review of the family Diadectidae (Olson, 1947) to the conclusion that there was a complete series of temporal elements in *Diadectes*. More complete and thorough study seems to offer no basis for revision of this contention.

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