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Article XXXI.—ON THE STRUCTURE OF THE BRAIN-CASE IN CERTAIN LOWER PERMIAN TETRAPODS.

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During the last ten years the work of E. C. Case and S. W. Williston has enormously extended our knowledge of the Lower Permian tetrapod fauna of Texas and New Mexico, making us acquainted with the whole skeleton of many forms. This extended knowledge shows that there is on the whole a great similarity in the skeletons of all these early types, so much so that the quite lengthy diagnoses of the "Orders Cotylosauria and Theromorpha" given by Williston in 1911 differ practically solely in the possession of a perforated temporal region of the skull in the latter forms.

During the last few years I have been able to examine the structure of the cranial cavity and brain-case generally in the following types of Permian and Triassic reptiles:—*Dicynodon, Endothiodon, Lystrosaurus, Kannemeyeria, Scymnognathus, Diademodon, Dimetrodon, Pariasaurus, Procolophon, Erythrosuchus, Belodon, Plateosaurus, Nothosaurus.* In very many more forms I have been able to see the general structure of the occipital region but not to examine the cranial cavity.

These studies have shown me that there is a great family resemblance between the cranial cavities of *Erythrosuchus, Belodon, Plateosaurus, Iguanodon* and Crocodiles, depending on the following features, and many more not listed:—

1. The separation of the inner ear from the brain cavity by bone.
2. The excessive narrowness of the cranial cavity between the ears.
3. The anteroposterior compression of the paroccipital process and the opening of the fenestra ovalis and the ductus fallopii on its ventral surface.
4. The enclosure of the anterior part of the brain by the bones usually but incorrectly called alisphenoids in crocodiles.

These characters are found in combination in no other groups of reptiles which I have been able to examine and seem to tie very closely together the Thecodonts, Deinosaurs and Crocodiles, groups which have long been recognized as allied. The fact that an extremely similar occipital region should characterize an obviously natural group of this kind, when considered in the light of the very considerable range of structure of this part found in others of the more modern reptiles, raises the hope that study of it would throw light on the interrelationships of the earlier reptiles. I purpose in this paper to examine certain early Tetrapods in this connection.

Eryops.

Occiput. The occiput of *Eryops* has been described by several authors; Branson, Broili, Broom, Case and v. Huene have given somewhat divergent accounts of it. By removing the matrix from the specimen in the American Museum (No. 4314e) which gave Dr. Broom much of his information, a task of no difficulty, I have been able to examine a perfectly preserved brain-case of this type. Study of it renders it certain that some of Dr. Broom's statements are not quite correct.

Basioccipital. The basioccipital is a small bone of spongy texture almost

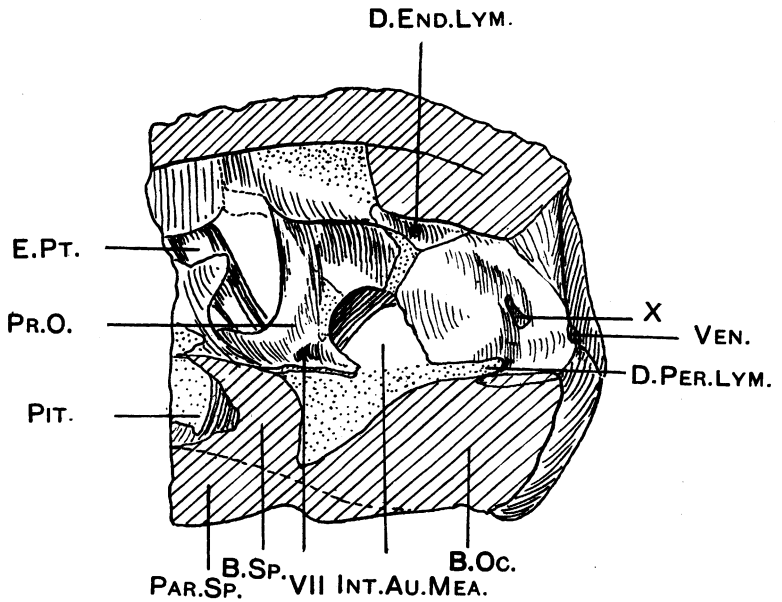

Fig. 1. Brain-case of *Eryops* sp. in median section. Amer. Mus. No. 4314e. × 1½.
B. Oc., basioccipital; *B. Sp.*, basisphenoid; *D. End. Lym.*, foramen for the ductus endolymphaticus; *D. Per. Lym.*, notch for ductus perilymphaticus; *E. Pt.*, epipterygoid; *Int. Au. Mea.*, internal auditory meatus; *Par. Sp.*, parasphenoid; *Pit.*, pituitary fossa; *Pr. O.*, proötic; *Ven.*, venous foramen; *VII* and *X*, exits of cranial nerve.

completely surrounded by other elements. As Dr. Broom has correctly represented it, it forms the lower part of the triple condylar surface supporting the exoccipital condyles above. The exoccipitals send in thin plates over its dorsal surface which apparently exclude it from participation in the formation of the cranial cavity.

The lateral faces of the bone are in contact with the exoccipitals behind

and the opisthotics in front. The anterior end of the bone thins rapidly and was obviously continued by cartilage.

The lower surface of the bone is exposed as a small triangular area just in front of the condyle; the lateral portions of the ventral surface are covered posteriorly by the exoccipitals and the remainder by the parasphenoid.

Basisphenoid. The basisphenoid is a small bone, which resembles the basioccipital in being only rather incompletely ossified. Posteriorly it nearly meets the basioccipital, its surface rising rapidly so as to leave a wide

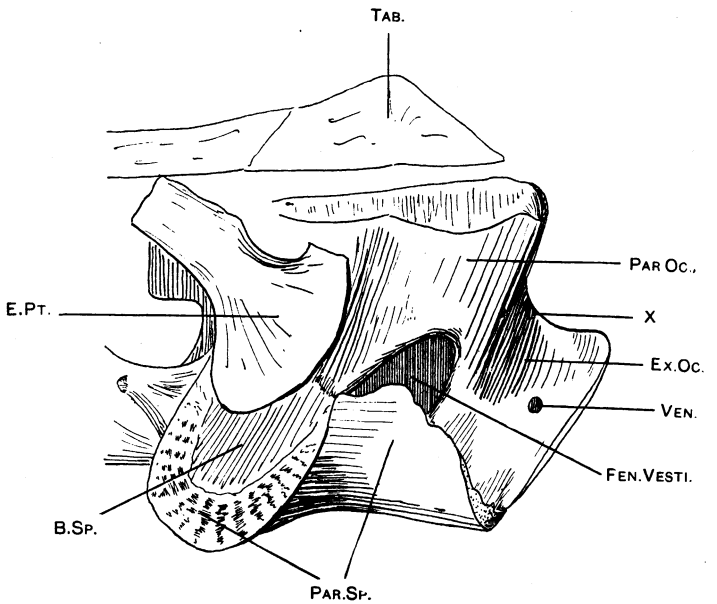

Fig. 2. Brain-case of *Eryops* sp. Lateral aspect. Amer. Mus. No. 4314a. × 1.
Reference letters as before with *Ex. Oc.*, exoccipital; *Fen. Vesti.*, fenestra vestibuli; *Par. Oc.*, paroccipital (opisthotic); *Tab.*, tabular.

transverse groove of triangular section, filled during life by cartilage. This surface continues until it terminates in the thin dorsum sellæ. Much of the dorsal surface of the bone in this region is covered by the proötics. Further forward the upper surface is depressed to form the deep sella turcica, which is divided into two halves by a low rounded median ridge on its posterior face. Just behind the sella the basisphenoid is produced into the basipterygoid processes which articulate with the pterygoids.

The whole ventral surface of the basisphenoid is covered by the parasphenoid.

Exoccipital. The exoccipital is a remarkable bone. It forms the large exoccipital condyle on the posterior surface of the skull, in front of which the great mass of the bone lies; this mass is split, the upper portion forming the floor of the braincase and meeting or nearly meeting its fellow of the opposite side above the basioccipital. The lower part underlies the postero-lateral corner of the basioccipital, which is here nearly surrounded by it. Above the condyle the exoccipital is continued to the roof of the skull, as Dr. Broom has described it, being overlapped posteriorly by special lappets of the postparietals. It is uncertain whether these two bones really meet above the brain.

The anterior surface of the exoccipital is covered by the paroccipital, the suture being plainly visible on the outer surface and from within the ear cavity or rather the space formerly filled with cartilage in connection with it, although not on the endocranial surface.

On the posterior surface of the exoccipital above the condyle and only just lateral to the foramen magnum is a small foramen which as it seems to be sometimes absent can only be for a blood-vessel. On the same level as this but further from the middle line is another somewhat larger foramen, through which the suture between the exoccipital and paroccipital seems invariably to pass, although it lies almost wholly in the exoccipital. On the lateral surface of the condylar portion of the exoccipital is another very small and inconstant foramen.

Behind the paroccipital on the endocranial surface four or fewer foramina leave the brain cavity; one of these presumably lies in the suture between the paroccipital and exoccipital and is constant; it leads to the outer of the two foramina on the occipital surface above the exoccipital condyle.

The other three foramina lie one above the above described opening, this being inconstant, another and very small one below, and the third only just within the foramen magnum; all pass merely into the body of the bone and must be for blood-vessels.

Paroccipital. The paroccipital is a large bone closely united with the exoccipital; it has a large process extending out beyond the exoccipital, when viewed from behind, to articulate with the tabulare in a manner Broom has already described. This process passes down into a part of the bone which lies immediately in front of the lowest (condylar) part of the exoccipital, which terminates anteriorly in a smoothly rounded border of the large fenestra ovale. On the inner aspect the suture separating the paroccipital and exoccipital is not visible but consideration of the position of the semicircular canals and the inner opening of the foramen, the external opening of which lies in the suture, renders it possible to fix its position, with some certainty. The paroccipital on its endocranial face

is a large bone, the visible portion being a very thin plate of bone which divides the posterior part of the vestibular cavity from that for the brain. This sheet passes backward into a mass of spongy bone which lies in front of the exoccipital and passes outwards into the paroccipital process and to the fenestra ovale. Its lower border is articulated with the basioccipital and its anterior face forming the posterior wall of the vestibular cavity is perforated by a hole which leads directly into the posterior ends of the horizontal and posterior vertical semicircular canals, which are quite distinctly shown although their walls are not composed of very compact bone.

The vestibular cavity is open to the brain through a special notch between the plate of bone which forms most of the endocranial exposure of the paroccipital and that process of the basisphenoid which floors the cranial cavity. The anterior edge of the paroccipital on the endocranial

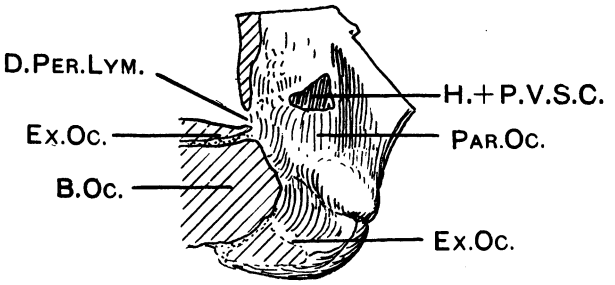

Fig. 3. Brain-case of *Eryops*, same specimen as Fig. 1, Amer. Mus. No. 4314e, left side, cut vertically through the vestibule whose hinder wall is shown and the Fenestra ovale. × 1½.

Reference letters as before with *H. + P. V. S. C.*, opening leading to the posterior ends of the horizontal and posterior vertical semicircular canals.

surface is separated by an open suture from the proötic and by a somewhat less distinct, though I think certain one, from a supraoccipital; below the suture with the proötic it forms the posterior margin of the large internal auditory meatus, from the posterior lower corner of which the special slit already described passes backwards.

Proötic. The proötic is a large bone applied to the front face of the paroccipital. Although the suture on the paroccipital process is not visible its continuation within the fenestra ovalis renders it certain that the whole anterior part of the process is proötic. Below the two bones are separated by the large fenestra ovalis, above which the proötic is continued to articulate with the skull, mostly with the parietal but probably in part also with the "supratemporal." This portion of the proötic is pierced by a venous foramen passing upwards. Internally the proötic is produced inwards and

forwards by a process which overhangs the incisura proötici and extends forwards to meet what is apparently the posterior end of the sphenethmoid.

Below and in front of the fenestra ovalis the proötic is in contact with the basipterygoid region of the basisphenoid from which it is not separated by suture externally. On the inner surface the proötic has a distinct suture with the supraoccipital and with the paroccipital, the three bones meeting in the familiar triradiate suture, and more ventrally forms the anterior border of the large internal auditory meatus, medially and anteriorly to which it expands into a horizontal sheet forming much of the floor of the brain cavity. This floor just internal to the internal auditory meatus is depressed into a shallow pit from the anterior part of which the aquæductus fallopii for the VIIth nerve opens. The flooring portion of the proötic extends forward in advance of the incisura proötici overlapping the lateral portion of the dorsum sellæ and forming a distinct processus anterior inferior from which rises an extremely delicate plate forming a wall to the brain cavity and extending up almost to the posterior end of the sphenethmoid so as to convert the incisura prootici into a foramen. The external opening of the "aquæductus fallopii" is not known but it is seen in sections to pass straight down through the bone.

The portion of the inner ear which lies within the proötic has not been cleared but something is seen of its structure in sections.

Supraoccipital. The supraoccipital is a small bone apparently continuous across the middle line and with the exoccipitals. It unites with the proötic and paroccipital of either side in a triradiate suture and obviously, from the known structure of the paroccipital and proötic, must contain the upper parts of the vertical semicircular canals, and is pierced on each side by a very small foramen for the ductus endolymphaticus.

Parasphenoid. The parasphenoid is a very large bone, with a long anterior stem, a channel, the upper surface of which receives the sphenethmoid. Posteriorly the bone expands, covering the whole lower surface of the basisphenoid and much of that of the basioccipital. It extends out so as to sheath the lower surface of the basipterygoid processes, having sutures with the pterygoids. Behind this it reaches up by special flanges outside the basisphenoid to form the lower margins of the fenestra ovalis. Its extreme postero-lateral corners are drawn out into low muscular processes over the meeting place of the paroccipital, exoccipital and basioccipital; these are typical tubera basisphenoidales.

On the lower surface of the parasphenoid passing round from the back of the basipterygoid process is a deep groove which leads to a foramen, plunging into the rostral portion of the bone and apparently (though not certainly) opening on its dorsal surface in advance of the sella turcica.

Another foramen enters the upper surface of the basipterygoid from near the front and a third enters its front face.

Stapes. A very well preserved stapes is present in position in a fragment of an *Eryops* skull (Amer. Mus. No. 4200). It is a rather massive bone considerably curved dorso-ventrally but straight in the other plane. At the outer end it is about 8 mm. deep and through anteroposterior compression about 4 mm. thick. Proximally the bone deepens and is pierced anteroposteriorly by a rather large foramen, immediately medial to which it separates into two stout branches, the upper being much the larger and lying in the fenestra ovalis. The lower is much smaller and is quite widely separated by a broad and shallow notch from the upper; it is a little difficult to see how it could have articulated with anything and it may be a muscle insertion.

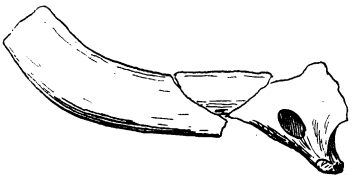

Fig. 4. Stapes of *Eryops*. Amer. Mus. No. 4200. × 1. Accidentally broken into three pieces.

Discussion of the Eryops Brain-case. The position and to some extent the structure of the inner ear being known there can be no doubt that the internal auditory meatus and fenestra vestibuli (seu ovalis) are correctly identified; the occurrence of a stapes still in situ in the latter adds further proof if any should be needed. It is apparently to the fenestra vestibuli that Broom refers as "a large oval foramen for the IXth, Xth, and XIth nerves" (p. 587). It is therefore necessary to seek a new opening for the vagus. The peculiar notch running back from the internal auditory meatus reminds one of the internal opening of the jugular foramen in certain types; as, however, it runs directly into the inner ear and there is no opening out of that cavity on the external surface except the fenestra vestibuli, it cannot be for any nerve and it appears probable to me that it transmitted the ductus perilymphaticus to the cranial cavity.

The only opening behind the ear which leads from the cranial cavity to the outside is that foramen whose outer opening though lying almost entirely in the exoccipital is cut by the suture between that bone and the paroccipital in all cases. This foramen must therefore be for the vagus which always leaves between the exoccipital and the paroccipital. As there is no other foramen further back which pierces the exoccipital there is no evidence in this form of the presence of a hypoglossal nerve.

The other foramina, that for the ductus endolymphaticus in the supraoccipital and for the VIIth nerve in the proötic, are identified with certainty.

The outer opening of the facial nerve has not yet been seen, and I am

inclined to consider that it lies above the basipterygoid process, the nerve immediately after its exit entering that process and passing through it to leave by the foramen on its front face; this point, however, must remain subject to very grave doubts. What the grooves round the lower surface of the basipterygoid processes are for if they be not for the internal carotids I do not know, but they seem to reach the dorsal surface of the basis cranii somewhat forward for those vessels.

Seymouria.

The brain-case of *Seymouria* is represented solely by that of the badly preserved type specimen of *Conodectes favosus* Cope (Amer. Mus. No. 4342). This specimen shows very little of the exoccipital, nothing of the basioccipital and only the lateral border of the basisphenoid.

Exoccipital. The extreme dorsal tip of the exoccipital ends in a rounded surface, presumably formerly continued by cartilage. This surface lies immediately below the ventral border of a lappet formed almost equally by the postparietal and tabular. This scrap of exoccipital is separated from the paroccipital by a large groove, the upper part of the foramen jugulare.

Paroccipital. This is a large bone stretching out to the tabular which sends a special process down its posterior and upper surface.

Proximally the paroccipital is separated from the proötic by the apparently large fenestra ovalis but distally these two bones meet in suture.

Proötic. The proötic is a large bone which covers the front face of the paroccipital and stretches at its lateral corner up to the skull roof where it articulates with the "supratemporal." The flat front face of the bone is pierced by a large venous foramen and its anterior border is continuous with that flange of the basisphenoid which passes back to form the tuber basisphenoidale.

Endocranial cavity. The endocranial cavity is extremely badly preserved, but shows that the internal auditory meatus was very large and that there was something in the nature of a supraoccipital.

Sphenethmoid. There is a large sphenethmoid which has not been sufficiently cleared for description.

Diadectes.

The brain-case of *Diadectes* has been described by Cope and v. Huene, both of whom have figured a "brain cast" now in the American Museum (No. 4843). v. Huene's account of the external surface of the brain-case is fairly accurate but the brain cast taken from a specimen in which the whole basis cranii had been lost before burial and a good deal of the proötic removed since is extremely misleading. The following account is drawn up mainly from No. 4843 in the American Museum which is uncrushed and well preserved and has been very completely cleared of matrix both inside and out by the author. All the other material in the Museum has been used for comparison and the whole gives an almost complete knowledge of the region under discussion.

Basi- and Exoccipitals. The basi- and exoccipitals are fused and no specimen shows a clear suture between them. The three bones form an almost circular condyle which is generally flat but has a somewhat steep walled notochordal pit towards the upper edge. The basioccipital extends forward, most of its lower surface being covered by the basisphenoid or more probably by a parasphenoid indistinguishably fused with that bone.

On the lateral face near the back is a facet for the opisthotic behind which lies the groove which forms the lower part of the foramen jugulare. A good deal of the dorsal surface of the basioccipital posteriorly is covered by the exoccipitals which may indeed meet below the brain. The exoccipitals bear strong upstanding processes which form the walls of the cranial cavity and unite with the opisthotic by a small face in front of the jugular foramen and by a very large flat facet with the opisthotic and supraoccipital above. The side wall of the exoccipital just at its base is pierced by a single foramen for the XIIth nerve and further forward a foramen enters the bone on the floor of the brain cavity and has no visible exit.

Basisphenoid. The basisphenoid of *Diadectes* is a large and very characteristic bone. Its body lies in front of the basioccipital, and it overlaps the lower surface of that bone, there being no definite tubera at the junction. The lower surface in this region has a median ridge and powerful muscular insertions for the recti capitis on each side of it. Further laterally it is provided with two processes which form the lower border of the fenestra vestibuli. These muscle insertions are shaded by two large flat processes forming the lateral borders of the bone and extending down so as to form pockets in which the insertions of the muscles lie. These processes are of very varied sizes; in No. 4239 (an old individual) they are comparatively small, whilst in No. 4843 (which is younger) they are very large, meeting in

the middle line and extending back about to the basisphenoid-basioccipital suture. The pocket formed by these flaps gradually reduces in size as it is traced forward until it ends in a single minute foramen which cannot possibly be for the carotid because it does not pass through the bone (No. 4378). In advance of these pockets the bone is rather narrow and bears the short basipterygoid processes which have a distinct groove for the entocarotid on the lower surface. In some specimens, but as Case has already stated not in all, a small foramen opens into the lower surface of the basisphenoid between the processi basipterygoidei.

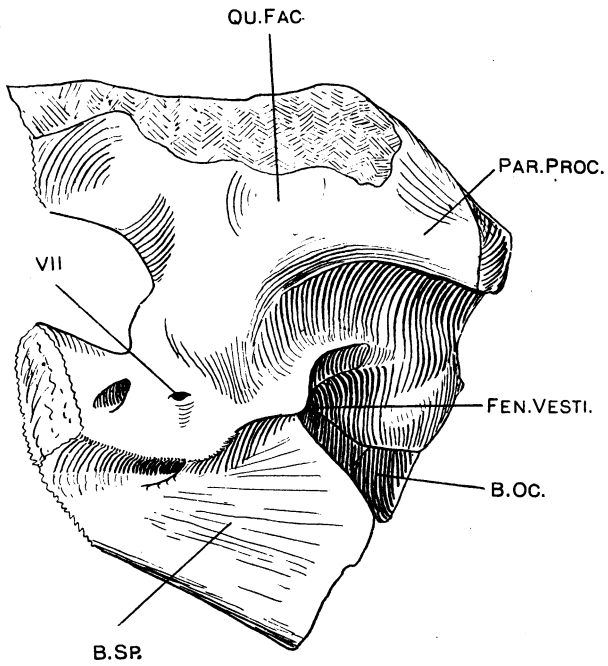

Fig. 5. Posterior part of the brain-case of *Diadectes*. Amer. Mus. No. 4843. Lateral aspect. × 1.

Reference letters as before with *Par. Proc.*, paroccipital process; *Qu. Fac.*, facet with which the mass of bone surrounding the top of the quadrate articulates.

The front end of the basisphenoid is continued by a long and powerful parasphenoidal rostrum above which is the sella turcica. This is a large and deep cavity tunnelling backwards horizontally into the bone and overhung by a rather massive dorsum sellæ. The posterior end of the sella is divided by a median septum and ends blindly. On the lateral surface somewhat behind the level of the posterior end of the sella a large foramen

opens forward; this leads from a cavity which in the bony skull is continuous with that for the vestibule and its meaning is quite obscure.

Otic capsule. The bones of the otic capsule are indistinguishably fused even in quite young individuals, but the regions can be easily distinguished.

Paroccipital. The paroccipital (opisthotic) has two facets, a small lower and a large upper one for the exoccipital and just meets the basioccipital. Its front face is in contact with the proötic, the two together forming a very short but massive paroccipital process which is covered dorsally by the overlapping tabular and which seems to have a small contact with the squamosal distally. No. 4378 seems to show that the "supratemporal"

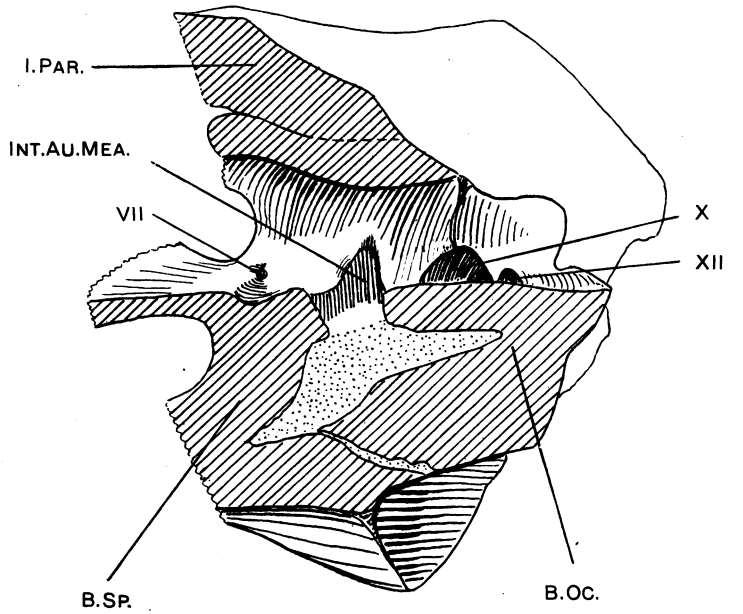

Fig. 6. Posterior part of the brain-case of *Diadectes* in median section. Amer. Mus. No. 4843. × 1.

Reference letters as before with *I. Par.*, interparietal.

does not meet the paroccipital process. The fenestra vestibuli lies on the snterior face of the process somewhat anterior to its distal end and only just above the lower border.

The opisthotic can have only a very small exposure on the endocranial surface, mainly represented by the triangular area and narrow ridge between the very large internal auditory meatus and the large foramen jugulare. There is a distinct notch in this ridge which represents the fenestra rotunda.

Proötic. The proötic forms the anterior part of the fenestra vestibuli from which its long suture with the basisphenoid runs forward. Its outer surface has a shallow depression just over the paroccipital process in the region where it is fused with the parietal, which seems to have abutted against the mass of bones sheathing the head of the quadrate. The contact with the roof of the skull is a prolonged one and in some specimens at any rate a special process runs laterally to articulate with the lower surface of the "supratemporal." On the inner surface the proötic forms the anterior margin of the internal auditory meatus from which a marked short groove runs forward at the anterior end of which lies the foramen pro nervo faciali. There is a large deep incisura proötici.

Supraoccipital. The supraoccipital cannot be clearly distinguished from the other bones but, judging from the position of the vertical semicircular canals whose upper parts always lie within it, must form a good deal of the roof of the brain cavity running forward from the top of the foramen magnum nearly to the parietals. It is not pierced by any foramina.

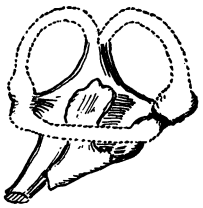

Fig. 7. The bony labyrinth of *Diadectes*. Amer. Mus. No. 4843. × 1.

Inner ear. The inner ear cavity is in very wide communication with the brain cavity through the large internal auditory meatus. There is a large triangular vestibular cavity from which three processes lead to the roots of the semicircular canals. The anterior has the forward end of the horizontal canal cleaving, and then runs forwards before turning upwards to the anterior semicircular canal. The posterior is a rather narrow and lengthy process whose splitting is only just indicated. The upper is short and divides into two equal branches. The actual canals visible in No. 4441 are slender and pass round as segments of circles in a very simple way.

On the outer side of the vestibular cavity is a long tube which leads to the fenestra vestibuli. This tube is very remarkable because an oval foramen opening into its dorsal surface leads into a very large and irregular cavity lying within the semicircular canals. This feature is so far as I know quite unique, and no explanation of it suggests itself.

The inner ear is in connection with a large recess lying between the dorsal surface of basisphenoid and the proötic, from which a foramen opens forward to the exterior of the basisphenoid.

The anterior part of the brain is surrounded by a bone which rests on the dorsal surface of the parasphenoid and, except that it is not continuous above the brain, has all the appearance of the sphenethmoid of *Pariasaurus* or *Eryops*.

It is not possible to be certain of the number and position of the foramina leading through this bone.

Discussion of the Diadectid Brain-case. All the nerve exits of *Diadectes* are identified without any difficulty since they agree with the ordinary reptilian arrangement in general plan. The question of the identification of the vascular foramina is, however, at present insoluble, as it seems certain that the blood supply of the head differed considerably from that of known living reptiles and indeed from that of fossil reptiles also.

The vein which in some individuals pierces the proötic high up is paralleled in many early reptiles and perhaps represents an early condition of a branch of the vena capitis lateralis.

Captorhinus.

No account of the brain-case of a Captorhinid which is at all detailed has been published, but Broili, Williston and Branson have given short accounts, mainly of its occipital surface.

The material at my disposal (Amer. Mus. No. 4315) is not of a very satisfactory character, but does enable me to add a few facts to those already recorded.

Captorhinus and *Labidosaurus* differ in details but are essentially similar and the followng description founded mainly on *Captorhinus* is completed from *Labidosaurus,* portions so introduced being specially mentioned.

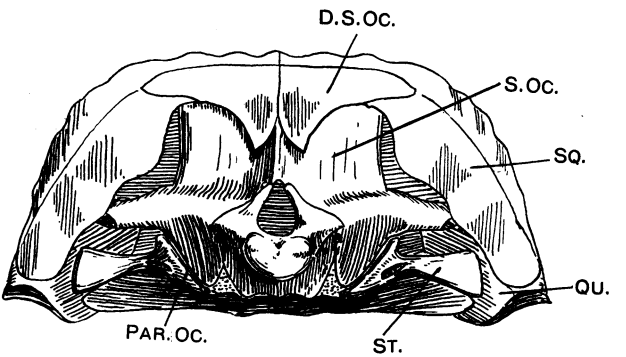

Fig. 8. Occipital view of skull of *Captorhinus* sp. Amer. Mus. No. 4315. × 1½.
Reference letters as before with *D. S. Oc.*, dermosupraoccipital (postparietal); *Qu.*, quadrate; *S. Oc.*, supraoccipital; *Sq.*, squamosal; *St.*, stapes.

Basioccipital and Exoccipital. The basi- and exoccipitals are fused but the suture separating them is seen indistinctly in No. 4876, *Labidosaurus.*

The condyle is large, rounded and very markedly tripartite, the upper half of it being formed by the exoccipitals which are separated by a deep notochordal pit, but meet in the middle line to form the floor of the brain-case. The basioccipital is a somewhat short bone and its lower surface towards the front is produced into distinct processes for articulation with the tubera basisphenoidales. These are much more marked in *Labidosaurus* than in *Captorhinus*. The lateral borders of the joint basi- and exoccipitals form an almost flat surface terminated above by the notch which forms the posterior border of the foramen jugulare, above the opening the exoccipital is produced as a small angular process. The exoccipital ends dorsally in a large flat surface for articulation with the supraoccipital and paroccipital. The exoccipital is pierced at the level of the base of the brain cavity by a small foramen for the XIIth nerve.

Basisphenoid. The basisphenoid is a large bone articulating with the basioccipital behind and continued in front by a strong parasphenoidal rostrum. The lower surface of the bone bears a pair of strong ridges which in front form the bottom of the basipterygoid processes and posteriorly overlap processes on the basioccipital to form the tubera basisphenoidales; the outer edge of the bone in the latter region is continued upwards by a somewhat faintly distinct border which forms some of the rim of the fenestra vestibuli.

Paroccipital. The paroccipital is a comparatively small bone which articulates with the exoccipital and basioccipital behind, with the supraoccipital above and with the proötic in front.

The paroccipital process is a short and rather slender rod, the paroccipital part of it being grooved on its anterior and lower edge. Below the process the paroccipital is continued downwards as a large area of bone lying in contact with and immediately outside of the tuber of the basioccipital. The lateral margin of this region of the bone forms the posterior border of the fenestra vestibuli.

Proötic. The proötic is not well known; it is a comparatively small bone covering the front face of the paroccipital and extending out into the paroccipital process. It forms the front border of the fenestra vestibuli below which it articulates with the basisphenoid. Dorsally it articulates with the supraoccipital and ends in a notch for a venous exit from the brain cavity. The anterior border has a shallow incisura proötici.

It is specially to be noted that the proötic does not nearly reach up to the roof of the skull.

Supraoccipital. The supraoccipital forms the upper part of the foramen magnum and articulates by a small surface with the exoccipitals and by large ones with the proötics and opisthotics. Above its contact with these

bones it widens and is converted into an anteroposteriorly flattened plate with a slender ridge running down to the top of the foramen magnum behind and a much more powerful one in front. The lower ends of the postparietals overlap the posterior surface of the bone being separated by this ridge ventrally.

The opening for the anterior and posterior vertical semicircular canals are very plainly shown in No. 4705, *Labidosaurus*. The two genera are very similar in this regard.

I have been unable to obtain a satisfactory preparation of the cranial cavity which is, however, very high and short behind the incisura proötici.

Stapes. The stapes is a large bone having an enormous foot plate which articulates with the paroccipital, basisphenoid and proötic round the border of the fenestra vestibuli. Immediately distal to the foot the stapes is perforated by a large foramen which runs from below and behind, upwards and forwards. Beyond this region the bone has a narrow shaft which expands to a head lying in a special groove in the quadrate.

The brain-case of this form is still so incompletely known that it does not call for any detailed discussion in this place.

Theropleura.

The brain-case of a member of this genus is very well shown in Cope's type specimen of "*Diopeus leptocephalus*" (Amer. Mus. No. 4155) which is excellently preserved, the bones being disarticulated, largely free from matrix and uncrushed.

The basi- and exoccipitals are fused as are the paroccipitals, proötics and supraoccipitals, but the basisphenoid, postparietals and tabulars are disarticulated.

Basi- and Exoccipitals. The basioccipital and exoccipitals of *Theropleura* are fused but the sutures separating them are visible through most of their course. The three bones form a tripartite condyle of which the lower three-quarters are provided by the basioccipital which is a rounded knob. The exoccipital regions of the condyle are separated by a deep pit and lie in a level anterior to that of the basioccipital. The basioccipital is a short bone whose anterior lower margin is articulated with the basisphenoid presumably through a pad of articular cartilage. The lower surface is produced into long and strong processes which with the corresponding flange of the basisphenoid form the tubera, the outer face of this process being a distinct articular facet for the stapes.

The exoccipitals cover the whole dorsal surface of the basioccipital,

meeting in the middle line. From this region in each bone a strong process rises which forms the side of the foramen magnum and is pierced by a single foramen for the twelfth nerve. This process terminates dorsally in a large nearly flat articular face directed upwards, outwards and forwards which

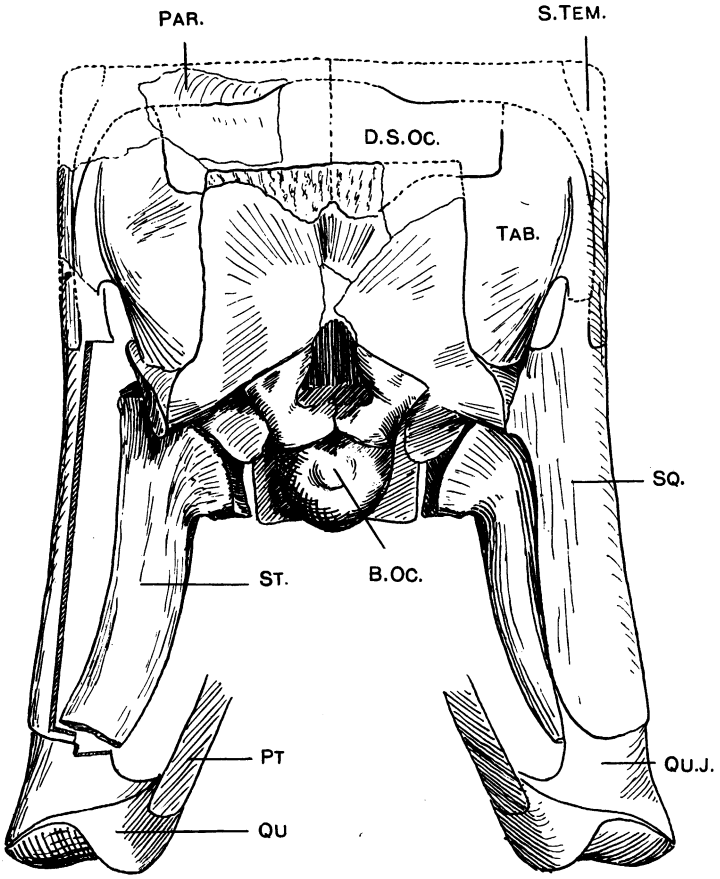

Fig. 9. Occipital view of the type skull of *Diopeus leptocephalus* Cope. Amer. Mus. No. 4155. × ⅔. Each side restored from the other. Regions in dotted outlines hypothetical.

Reference letters as before with *D. S. Oc.*, dermosupraoccipital = postparietal; *Par.*, parietal; *Pt.*, pterygoid; *Qu.*, quadrate; *Qu. J.*, quadratojugal; *S. Tem.*, supratemporal; *Sq.*, squamosal; *St.*, stapes.

joins the supraoccipital and paroccipital. The anterior face of this process has a small notch which forms the back of the foramen jugulare.

The lateral surface of the exoccipital has a facet continuous with one on the upper end of the process of the basioccipital which helps to form the

tubera, with which the lower end of the paroccipital articulates. In front of the facet there is a deep depressed area on the lateral aspect of the bone which forms the inner wall of the vestibular cavity.

Basisphenoid. The basisphenoid articulates posteriorly with the basioccipital, being produced into powerful processes which join with the cor-

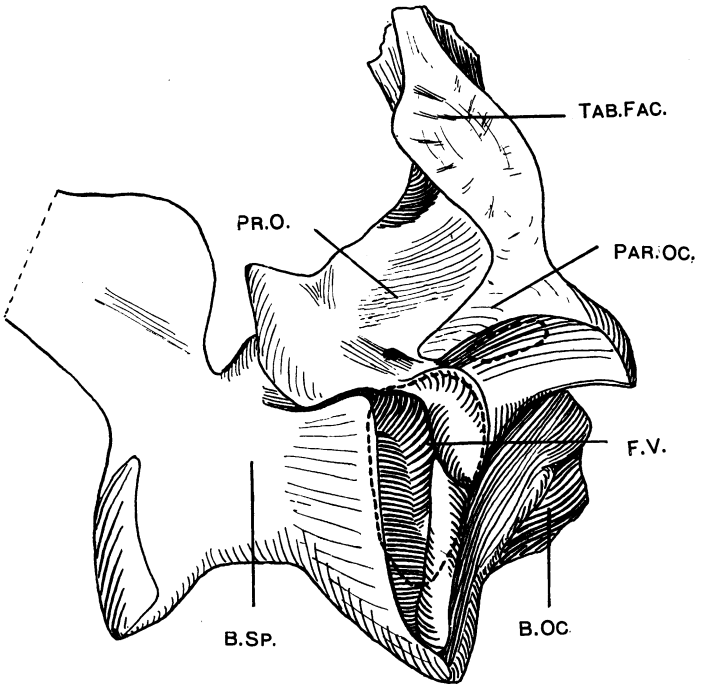

Fig. 10. Brain-case of the type specimen of *Diopeus leptocephalus* Cope. Amer. Mus. No. 4155. × 1. Lateral aspect.

Reference letters as before with *F. V.*, fenestra vestibuli; *Tab. Fac.*, tabular facet on the supraoccipital.

responding parts of the basioccipital to form the tubera. Lateral to the articulation the posterior margin of the basisphenoid spreads out into a wing which forms the front border of the fenestra vestibuli, and dorsally articulates with the proötic. This process and wing is continued forwards by a ridge on the lower surface of the bone which terminates in the powerful downwardly produced processus basipterygoideus. From there the bone is continued forwards by a long straight parasphenoidal rostrum.

The sella turcica lies immediately above the basipterygoid processes, forming a deep pit whose lateral walls articulate with the proötic dorsally.

Between the posterior end of these walls and the wing which articulates with the proötic posteriorly is a small notch which may be the lower border of a foramen similar to that which pierces the side of the basisphenoid in *Diadectes*. There is no ossified dorsum sellæ on this specimen.

Although the proötic, opisthotic and supraoccipital are fused it is easy to distinguish approximately the various regions.

The paroccipital articulates with the exoccipital by two facets separated

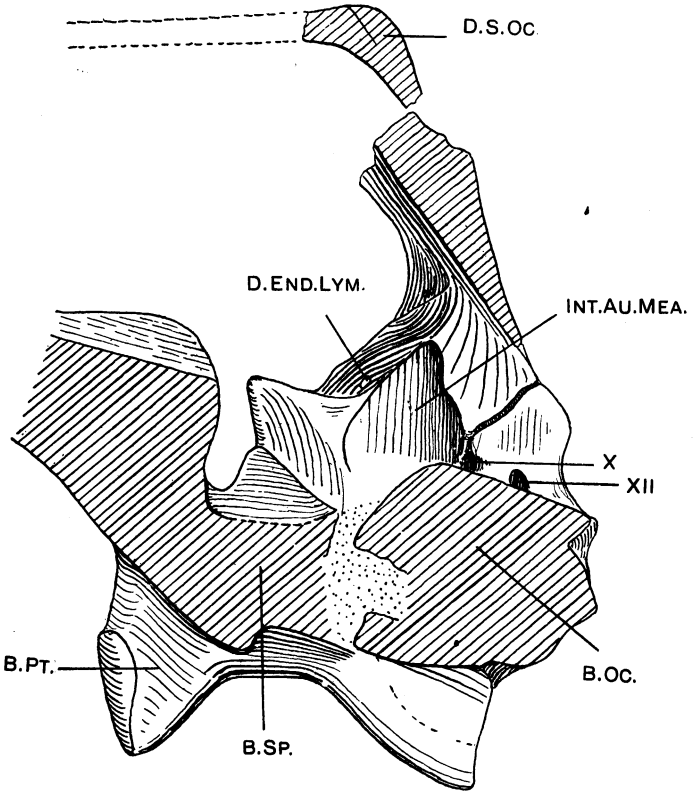

Fig. 11. Brain-case of the type specimen of *Diopeus* in sagittal section. Amer. Mus. No. 4155. × 1.
Reference letters as before.

by the notch which forms the front border of the foramen jugulare. Immediately lateral to this notch the bone forms an extremely short paroccipital process which articulates with the squamosal. The ridge which forms the lower border of this process is continued inwards and is terminated

by an articular face for the stapes immediately in front of which the bone forms the posterior margin of the fenestra vestibuli.

Dorsally the bone articulates with the supraoccipital and in front is covered by the proötic. On the inner surface the foramen jugulare is confluent with the internal auditory meatus owing to the depression of the ridge which separates them below the general level of the endocranial surface. The notch so formed represents the fenestra rotunda.

Supraoccipital. The supraoccipital is a large bone, expanded at the top so that its lateral border and that of the paroccipital form a single slightly concave area with which the tabular articulates, so that the suture between them on the occipital surface is nearly straight and stands vertically.

The upper part of the supraoccipital forms a thin sheet whose posterior surface is overlapped by the postparietals and which does not reach the parietals. Ventrally on each side the bone thickens and articulates with the proötic and paroccipital, so as to form the upper border of the very large internal auditory meatus; a groove for a blood-vessel runs outwards from the front face of the supraoccipital passing dorsal to the proötic. A small foramen for the ductus endolymphaticus issues on the inner surface of the bone.

Proötic. The proötic is probably a rather small bone. It covers the anterior face of the paroccipital and articulates below with the basisphenoid. It contributes to the paroccipital process and forms the anterior margin of the upper part of the fenestra vestibuli. Above this opening it is pierced by the foramen for the VIIth nerve, which is overhung by a short crista proötica.

Stapes. The very remarkable stapes has been already described by Cope and Case; it is an immensely heavy rod with two distinct faces separated by a deep notch at its proximal end and perforated by a rather large foramen. The larger of the two heads articulates with the margin of the fenestra ovalis having quite distinct and closely fitting articular faces with the paroccipitals, basioccipital, basisphenoid and proötic. The smaller head articulates with the under surface of the paroccipital process.

Nerve exits. The determination of the nerve exits and other openings of the brain-case present no difficulty and it does not require a separate discussion.

General Discussion of the Brain-case of Early Tetrapods.

The primary object of Palæontology as of taxonomic Zoölogy is the development of a "natural" classification of animals, one that is which shall express real blood relationships between divers types. Such a classification may be either a vertical one, in which divisions founded on the divergent groups of the terminal members of a stock are carried down as far as possible, until in fact the various lines merge, or a horizontal classification in which all those members of a group, belonging to different phyla, which are in the same degree of advance in structure are associated.

Both of these methods are valuable, expressing as they do different aspects of the subject and both, if they are to be valuable, must be founded on a similar type of study; involving a search for those slowly changing palæotelic characters, usually inconspicuous and hard of access, which are the only real guide to affinities.

In discussing any animal or group of animals, it is essential clearly to realize what characters displayed by it are merely specializations, either of the apparently non-adaptive kind which often characterize species, or else adapting it for some special mode of life; such specializations tend to obscure relationships whilst emphasizing differences. After the rejection of these characters there remains another series which may themselves be divided into two groups, those which are common to groups known to be not closely allied, and are hence probably derived from very distant ancestors, and those which obviously represent advances on their ancestral condition, which when once acquired change very slowly and usually in a similar way in the diverse phyla of the group.

In discussing the brain-case of early reptiles it is therefore necessary to discover what features may be expected in a presumed ancestral type and then to discover how the known brain-cases of Permian reptiles are structurally related to one another.

To my mind the whole structure of the post-cranial skeleton of the Lower Permian reptiles of Texas as it has been gradually shown to us by Professors Williston and Case demands a derivation of the group from temnospondylous amphibians.

The complete structural identity of the primitive shoulder-girdle, arms, pelvis and hind leg of a reptile, arrived at by comparing what are obviously the more primitive features of these regions in *Seymouria*, *Diadectes* and *Limnoscelis* with the similar parts in *Eryops* and its allies, when taken in connection with the extraordinarily close resemblance between the juvenile vertebræ of *Seymouria* and embolomerous vertebræ of Amphibia seem to me to place this conclusion almost beyond dispute.

It is therefore possible that the *Eryops* brain-case may give a morphologically ancestral stage to that of Cotylosaurs.

The only other Permian Amphibian in which the brain-case is known is *Trimerorachis* described by Broom, but I have examined satisfactory material of two genera of Embolomerous Amphibia from the British Coal Measures. The chief features in which *Trimerorachis* differs from *Eryops* in this region are, that there is a XIIth nerve, that the exoccipitals do not reach up to meet over the foramen magnum, that the supraoccipital remains cartilaginous, that the inner ends of the paroccipital and proötic are so very incompletely ossified that the impressions of the outer surfaces of the semicircular canals lie on the outer wall of the bony endocranial surface and that owing probably to its incomplete ossification the proötic does not articulate with the "supratemporal" at its inner and upper corner as it seems to do [1] in *Eryops*.

Professor Williston has shown us that *Trimerorachis* is a highly specialized, secondarily aquatic form and these differences depending as they do to a large extent on defective ossification may be entirely and certainly are to some extent due to the general degenerate ossification due to its aquatic life. The primitively aquatic and infinitely more primitive *Pteroplax* of Carboniferous age resembles *Trimerorachis* in the general lack of ossification of the inner ends of the paroccipital and proötic and in the exoccipitals not meeting over the foramen magnum, but resembles *Eryops* in the strong antero-internal upper corner of the proötic reaching the skull roof and coming into close relation with the posterior end of the sphenethmoid.

Trimerorachis resembles *Eryops* in the fact that the parasphenoid forms the lower border of the large fenestra vestibuli and in the large size and perforation of the stapes which also seems to have a special articulation with the parasphenoid in both forms.

Comparing these types and evaluating their resemblances and differences so far as the very meagre material allows, leads me to believe that a morphological ancestor of the primitive temnospondyl stem would have the following characters:—

(1) Basioccipital large and fairly well ossified.

(2) Basisphenoid with a well defined sella turcica and small basipterygoid processes.

(3) Parasphenoid covering all the lower surface of the basisphenoid including the basipterygoid processes and lapping up behind them onto the sides of the bone, the upper edges in this region forming the lower border of the fenestra ovalis.

[1] "Seems to do" because it is possibly really the parietal with which it articulates.

(4) Exoccipitals of moderate size, forming a small part of the tripartite condyle and with their dorsal ends in contact with the lower edges of the descending processes of the postparietals.

(5) Paroccipital (opisthotics) articulating with the exoccipital and basisphenoid, leaving a foramen jugulare. Distal end of the paroccipital articulating with the tabular (in advanced types this sends a process down the dorsal surface of the cartilage bone but does not do so in the primitive embolomerous forms *Pteroplax* and *Cricotus*). Proximal end of the bone not very well ossified so that the bony internal auditory meatus is very large.

(6) Proötic articulating with the anterior face of the paroccipital, with the basisphenoid below and with the tabular and supratemporal or parietal above. Pierced by a foramen for the VIIth nerve in front of the large internal auditory meatus.

(7) Inner ear placed entirely in the side wall of the brain cavity so that the vestibule lies almost or entirely above its floor and the summits of the vertical semicircular canals nearly reach to the roof of the skull. Fenestra ovalis large and stapes heavy and perforated.

The modern Amphibia both Urodeles and Anura show many resemblances to the theoretical primitive large amphibian brain-case. They are degenerate as far as concerns the basioccipital and basisphenoid, but the large parasphenoid still forms the lower margin of the fenestra vestibuli. The paroccipital and proötic still reach up to the very degenerate skull roof, the proötic of *Cryptobranchus* resembling that of *Eryops* very closely. The ear still lies entirely in the side wall of the cranial cavity and the semicircular canals still reach very nearly to the top of the skull. On the other hand in frogs and in some urodeles such as *Amphiuma* the inner ends of the pro- and opisthotic bones have ossified and separate the inner ear from the cranial cavity in the bony skull, except for the very small foramina for the VIIIth nerve and the ductus perilymphaticus and endolymphaticus.

On the whole the resemblances are such as to suggest some distant relationship between the living Amphibia and the Temnospondyls whilst the differences are to a large extent obviously due to the degeneracy and high specialization of the living forms.

Seymouria is on the whole the most temnospondyle in appearance of all known reptiles, and this resemblance extends to the incompletely known brain-case. This resembles the primitive amphibian type restored above:

(1) in the relations of the upper end of the exoccipital to the postparietal.

(2) in the connection of the tabular to the paroccipital by a process running down the dorsal surface of that bone,

(3) in the connection of the distal end of the proötic with the skull roof,

(4) in the widely open internal auditory meatus, and apparently

(5) in the position of the inner ear.

It differs, however, in the retraction of the internal anterior and dorsal corner of the proötic from the skull roof.

So far as they go these resemblances show that the primitive temnospondyl brain-case arrived at in the above discussion does really represent a morphological stage in the development of the reptilian ear, and shows that we are justified in using it, at any rate till something better is offered, as a term of comparison with which to compare other reptiles.

Diadectes though far more modified than *Seymouria* resembles the temnospondyl type in many features. These are:—

(1) that the exoccipitals meet below the brain over the upper parts of the tripartite condyle;

(2) that the paroccipitals are in contact with the tabulars;

(3) that the proötic articulates with the tabular? and with the supratemporal by its anterior inner and dorsal corner;

(4) that the internal auditory meatus is widely open;

(5) that the inner ear lies almost entirely in the side wall of the brain-case;

(6) that the semicircular canals reach nearly up to the skull roof.

The brain-case of *Diadectes* differs from the temnospondyl type in:—

(1) not having the exoccipitals reaching the postparietals;

(2) the complete closure of the posttemporal fossæ by a bending down of the postparietals and tabulars onto the occipital surface; and

(3) by the long and low form of the cranial cavity.

Although I quite recently described and discussed the braincase of *Pariasaurus* it seems advisable to refer to it again in the light of the new knowledge of this region of Texas animals recorded in the present paper.

Pariasaurus resembles the temnospondyl type only in having the inner ear in the side wall of the brain-case, in the paroccipital meeting the tabular and in having the tabulars and postparietals only on the top of the skull.

It differs from them in the following features:

(1) The exoccipitals do not reach the skull roof.

(2) The proötic does not touch the skull roof.

(3) The internal auditory meatus is closed by bone leaving only a small foramen.

(4) The supraoccipital is a large bone forming a powerful process reaching to the parietals and postparietals.

(5) The fenestra vestibuli is entirely bounded by the paroccipital and proötic

(6) and in the long low form of the cranial cavity.

It is thus in this region far more advanced than *Diadectes*. The *Pari-*

asaurus brain-case resembles that of *Diadectes* in the long low form of the cranial cavity but differs widely from it,

(1) in the reduced proötic,

(2) in the mode of articulation of the neuro-cranium with the skull roof,

(3) in the form of the paroccipital process, and

(4) in the non-development of the flanges from the basisphenoid which cover the recti capitis muscles.

At the same time an accurate knowledge of the brain-case of *Diadectes* shows that the differences are not so considerable as I had formerly supposed on the evidence of the brain cast figured by Cope, Case and v. Huene which is extraordinarily misleading and should never have been published without a statement of the actual extent to which it is "restored."

The captorhinid brain-case so far as it is known resembles the temnospondylous type:

(1) in having the parasphenoid (or basisphenoid?) forming a large part of the border of the fenestra vestibuli,

(2) in the fact that the upper part of the tripartite condyle is formed by the exoccipitals which meet below the brain, and

(3) in the heavy stapes.

It differs from the amphibian type

(1) in not having the exoccipitals reaching the postparietals.

(2) in the complete absence of any connection between the proötic and skull roof,

(3) in the position of the postparietals entirely on the occipital surface,

(4) in the high wide plate formed by the supraoccipital, and

(5) in the high short brain-case behind the Vth nerve exit.

The brain-case of *Theropleura* resembles that of an amphibian:

(1) in having the exoccipitals meeting below the brain,

(2) in the widely open internal auditory meatus, and

(3) in the part played by the para-basisphenoid in the fenestra vestibuli, and

(4) in the heavy stapes.

It differs from this type very markedly:

(1) in the method in which the broad supraoccipital articulates with the postparietals and their position on the occipital surface,

(2) in the proötics and exoccipitals not reaching up to the skull roof,

(3) in the lower position of the inner ear where the vestibule lies to a considerable extent below the floor of the brain-case and the semicircular canals do not nearly reach the skull roof, and

(4) in the high short brain-case behind the Vth nerve exit.

The brain-case of *Theropleura* on the whole resembles that of *Dimetrodon* very strongly. The differences are:

(1) The mode of articulation with the tabulars which in *Theropleura* have a powerful articulation with the sides of the brain-case whilst in the more specialized genus they are thin splints overlapping the posterior surface.

(2) The production of the paroccipital processes backwards in *Dimetrodon* and their extreme shortness in *Theropleura*.

(3) The exceptional length of the process of the basioccipital for the tubera basisphenoidales.

In all the important features of this region the two forms agree; for example

(1) in the high and short brain-case and the position of the inner ear and fenestra ovalis,

(2) in the very remarkable way in which the foramen jugulare leaves in the closest connection with the internal auditory meatus,

(3) in the broadened supraoccipital and

(4) in the small proötic with a venous notch passing dorsal to it.

It must be noticed that all these are advanced structures not derived from Stegocephalia and not in any way paralleled by *Seymouria*, *Diadectes* or *Pariasaurus*.

The whole series, however, appear in a quite characteristic form in the South African Therapsids. The completely known brain-cases of *Dicynodon*, *Endothiodon* and *Lystrosaurus* agree quite closely with *Dimetrodon* and *Theropleura* in the features listed above and the primitive Gorgonopsid *Arctops* is as I have already shown singularly like *Dimetrodon* in the structure of its basicranial and otic region. In fact *Dimetrodon* differs from *Theropleura* in very much the same way in which *Arctops* differs from it. In the advanced Cynognathids the anterior margin of the proötic at its upper end has grown forward and upward so that it meets the parietal. *Theropleura*, *Dimetrodon*, *Scymnognathus* and *Diademnodon* form a structural series showing this gradual growth forward so that there is no doubt that the connection of the proötic with the parietal is purely secondary and has nothing to do with the primary connection in *Eryops* and *Diadectes*.

The complete differences between *Theropleura* and the Cotylosaurs *Diadectes*, *Pariasaurus*, *Seymouria* and *Procolophon* in the region of the brain-case will be obvious from the above descriptions and in all cases except *Seymouria* this difference is due to the different character of their advances; *Seymouria* differs solely in its very unadvanced nature, differs in fact in exactly the same way that *Eryops* does.

Captorhinus, however, differs very much less from *Theropleura*, in fact the only visible difference of importance is that the supraoccipital is not quite so wide; the types resemble one another not only in the general shape

and structure of the brain cavity but also in very many minor details such as the mode of articulation of the stapes with the edges of the fenestra vestibuli. These resemblances add much weight to the view that the Captorhinids are allied to the Cotylosaurian stock from which the Therapsids arose, which has already been suggested by Professor Williston and supported by the present author.

Comparison of the brain-case of the Cotylosaurs with one another shows that *Seymouria* differs from the others in that this region has retained almost unmodified the temnospondyl condition, that *Diadectes* and *Pariasaurus* resemble one another in the length and lowness of their cranial cavity but differ in the persistent temnospondyl position of the tabulars and postparietals on the top of the skull in *Pariasaurus* and in the obliteration of the posttemporal fossæ in *Diadectes* as well as in the different arrangements of the basisphenoid and fenestra vestibuli.

Captorhinus differs in its short high brain cavity and in the condition of the fenestra ovalis, *Procolophon* in its quite *Sphenodon*-like occiput.

In conclusion I wish to express my gratitude to President Osborn and the staff of the Department of Vertebrate Palæontology in the American Museum for the generosity with which they placed the whole of their magnificent collections of early reptiles at my disposal, allowing me to prepare them at my pleasure, and for the many suggestions which I owe to the stimulating mental atmosphere of the Museum.

London, Mar. 12, 1916.