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Article XXXII.— RECONSTRUCTIONS OF THE SKULLS OF THREE PELYCOSAURS IN THE AMERICAN MUSEUM OF NATURAL HISTORY.

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There are in the collections of the American Museum three skulls of Pelycosaurs which, although they are somewhat disarticulated, crushed and fragmentary, show the sutures with clearness. As they represent rare types, very incompletely known, and of special interest, it is desirable to make reconstructions of them.

This paper explains in some detail the methods I adopt in treating such material and the resulting figures will I hope be useful because by the method of reconstruction on which they depend no errors of morphological importance can be introduced, that is the contacts and relations of the individual bones will be correctly represented, although the general shape of the skull may not be very accurately reproduced.

(1) Edaphosaurus pogonias *Cope.*

Cope's famous type specimen of *Edaphosaurus* has been the subject of restorations by Case and Broom and has recently been described by v. Huene, but the accounts of these authors differ so considerably that it seems advisable to rediscuss it, especially as the new skull described by Professor Williston does not show the sutures clearly although being uncrushed it gives a perfect knowledge of the shape. The very different proportions of the parietals and interorbital widths which can be directly measured on the top of the skull in these two specimens show that they belong to different species.

Professor Williston's specimen shows that we shall not be far out in regarding the interorbital surface as flat. In our specimen there is a slight concavity between the lateral edges of the parietals and some evidence that they formed a rounded surface anteroposteriorly passing smoothly into the interparietal on the occipital surface.

The sutures separating the parietals, frontals, postorbitals, postfrontals, nasals and prefrontals are quite plain on the specimen.

The whole supraorbital border is preserved on the left side and the upper border of the temporal fossa on the right; there is, therefore, no difficulty in making a reconstruction of these regions.

The next point to determine is the width of the skull. There are three places where this can be done.

a. The left premaxilla is present, complete and to all appearance undistorted. This gives the contour of the anterior end of the skull and a width on the palate by direct measurement.

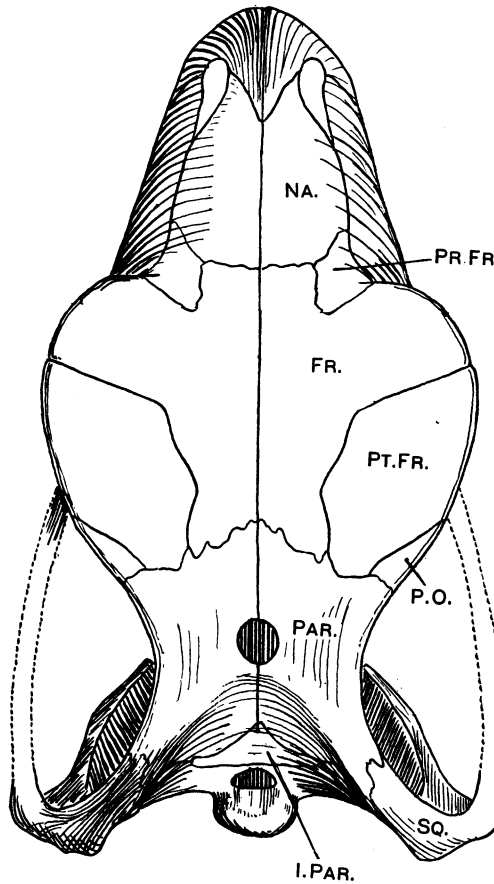

Fig. 1. *Edaphosaurus pogonias* Cope. Reconstruction of the type skull. Dorsal aspect. × ⅛. *Fr.*, frontal; *I. Par.*, interparietal; *Na.*, nasal; *P. O.*, postorbital; *Par.*, parietal; *Pr. Fr.*, prefrontal; *Pt. Fr.*, postfrontal; *Sq.*, squamosal.

b. On the right side the inner edge of the pterygoidal part of the "dentigerous plate" is clearly a sutural face which must have articulated with its fellow. As this plate is in close connection with the maxilla and as the two sides give identical measurements we have fixed

the width of the palatal surface of the skull in the region of the middle of the orbit.

c. The occiput is present, displaced and somewhat although obviously not much distorted, it gives with certainty the width beween the ends of the paroccipital processes. As the right squamosal is present and well preserved we have obtained, with only small possible error, another width on the extreme back of the skull.

By measuring with a flexible strip of paper the widths of the maxillæ, lachrymals, prefrontals and nasals in the same transverse plane in front of the orbits, it is easy to obtain the distance between the dentigerous edges of the maxillæ measured over the snout. The measurements of the two

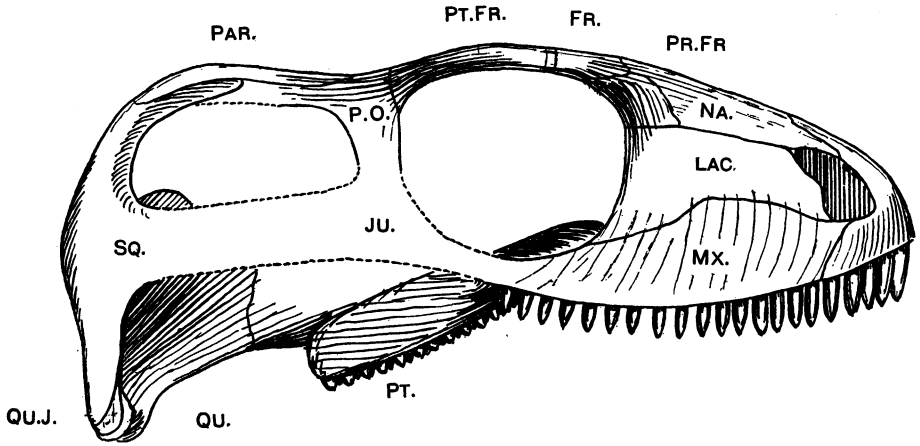

Fig. 2. *Edaphosaurus pogonias.* Reconstruction of the type skull. Lateral aspect. × ⅛.
Reference letters as before with *Ju.*, jugal; *Lac.*, lachrymal; *Qu.*, quadrate; *Qu. J.*, quadratojugal *Pt.*, pterygoid.

sides obtained in this way agree closely and as they are differently crushed we have assurance that the total measurement is probably very nearly right.

As the width between the lower edges of the maxillæ is known by bending the strip of paper on which the measurements were taken we can obtain possible cross sections of the snout. The height of the orbital margin of the lachrymal which runs nearly up to the strongly overhanging supraorbital margin of the frontal gives us a minimum height for the snout, and the width between the ends of the fronto-prefrontal sutures on the orbital rim gives a near approximation to the width of the dorsal surface. The cross section of the snout just in front of the orbit is hence fixed within rather narrow possible limits.

By making projections from this section onto dorsal and lateral views of the skull, we get fixed points which with the curve shown in the apparently only very slightly crushed premaxilla and the known edges of the various bones concerned, enable us to reconstruct the face with some confidence.

As the left pterygoid is in natural articulation with the maxilla and the

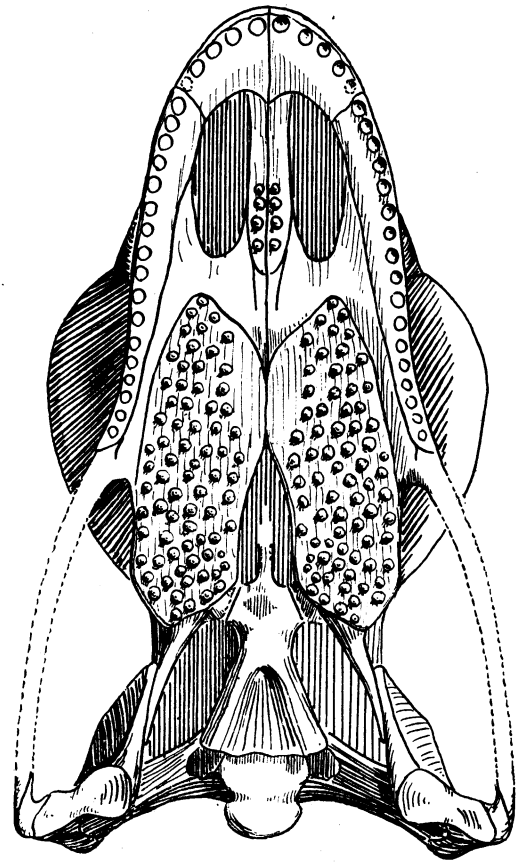

Fig. 3. *Edaphosaurus pogonias.* Reconstruction of the type skull. Palate. × ⅓.

right with the basisphenoid, which has its natural relations with the basioccipital, the position of all these bones is fixed with regard to the face.

As the right pterygoid is in natural articulation with the quadrate, we have the distance of that bone from the basipterygoid process fixed and as we already know the position of the squamosal at its articulation with the

end of the paroccipital process and the mode of articulation of this bone with the quadrate is clear, we have the width between the quadrates and their anteroposterior position fixed with a possible error of certainly not more than one centimetre.

Having these points fixed by measuring with a strip of paper the distance from the middle line to the quadrate condyle we get the contour of

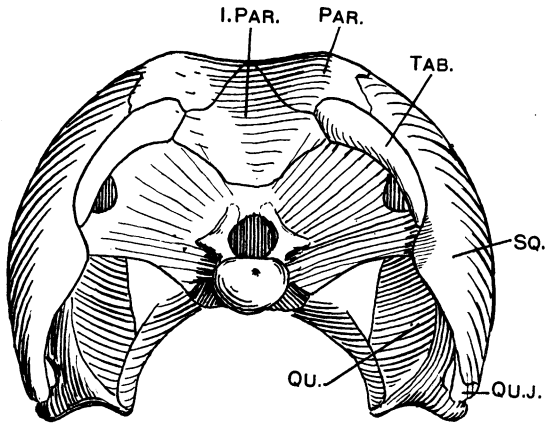

Fig. 4. *Edaphosaurus pogonias.* Reconstruction of the type skull. Occiput. × ⅔. Reference letters as before with *Tab.*, tabular.

the occipital view and as the interparietal and tabulars are well preserved and clearly shown this gives us the whole structure. With all these points fixed by independent means the reconstruction of the rest of the skull is merely a matter of filling in checked by measurements and projections onto dorsal, ventral and lateral planes and hypothetical cross sections.

(2) Diopeus leptocephalus *Cope.*

The type skull of *Diopeus leptocephalus* Cope (Amer. Mus. No. 4155) is one of the most interesting pelycosaur skulls in existence and deserves fuller treatment than it has received.

Some time ago the various fragments were fitted together and restored in plaster by Mr. O. Falkenbach under the direction of Dr. W. D. Matthew. This restoration is apparently very good so far as concerns the preorbital region, but certain changes seem necessary in the hinder part.

The whole occiput is readily articulated, the bones fitting excellently. It has been described and figured in the preceding paper.

The left tabular is nearly complete and a small mass of bone is articulated with its outer edge; this is clearly divided by sutures into three parts, two of which restricted to the anterior part of the fragment are clearly the posterior ends of the postorbital and parietal. The other runs back in contact with the outer margin of the tabular and is incomplete posteriorly.

The complete, uncrushed and very well preserved left squamosal is present in the material. It shows on its inner face a facet for the end of the paroccipital process, which fixes its relations to the tabular and attached piece of temporal region. The upper end of the squamosal is truncated

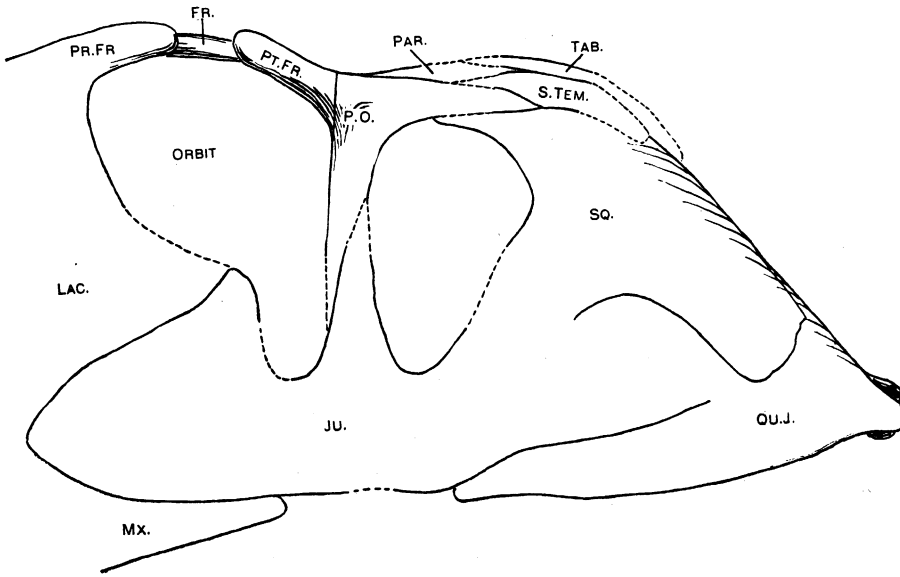

Fig. 5. *Diopeus leptocephalus* Cope. Reconstruction of the posterior part of the type specimen. × ½.
Reference letters as before, with *S. Tem.*, supratemporal.

obliquely by a ridge, above which is a sutural surface rather distinctly divided into two parts, an inner for the parietal and an outer for the postorbital, which have quite correct relations with the pieces of those bones attached to the tabular.

Behind the fragment on the posterior surface of the squamosal are two much less well marked articular areas, the inner of which is obviously for the continuation of the tabular, which is shown by it to reach down to the paroccipital process outside the temporal fossa; whilst the other is for the continuation of the outer bone, the "supratemporal" which stops

dorsally to the lower end of the tabular. The specimen thus gives certain evidence of the presence of a supratemporal in exactly the position in which it was found by Case and later by v. Huene in *Dimetrodon*.

The upper part of the left tabular has attached to it the outer corner of the postparietal and another fragment with a poor fit retains much of the rest of that bone with the hinder edge of the parietal articulated with it.

The nearly complete right parietal has articulated with it parts of both frontals, giving the middle line, and nearly all of the right postfrontal. The left postorbital is preserved, and its position is fixed by that of the parietal and postfrontal. The postorbital bar of the left jugal and the whole of its anterior part in natural articulation with the lachrymal and prefrontal are preserved, giving with considerable certainty the structure and shape of the orbit and the relations of all the circumorbital bones.

The postorbital bar and part of the posterior ramus of the right jugal are preserved, and both quadrates and quadratojugals, the left with some of the posterior part of the jugal in connection.

These various connections make the restoration of the top of the skull and the temporal region fairly easy and certain.

"Theropleura."

The last skull (Amer. Mus. No. 4604) is more completely preserved than the type of *Diopeus*. It is somewhat distorted and crushed, the quadratojugals and part of the face between the orbit and the premaxillæ are missing. Its reconstruction is easy following the methods used in the preceding cases and it does not seem worth while to describe the details.

Discussion of the Skulls of Diopeus (Amer. Mus. No. 4155) and "Theropleura" (Amer. Mus. No. 4604).

These two skulls represent closely allied but no doubt generically distinct animals; in all important features of their osteology they agree closely and are clearly members of the same family.

In the general structure of the skull they resemble *Varanosaurus* and even more closely Williston's recently described *Mycterosaurus*.

The skull of *Diopeus* is of very great interest because on it Cope founded his view of the presence of two temporal arches in Pelycosaurs, subsequent extension of which has created great confusion in reptilian classification.

One other specimen, the magnificent skeleton of *Ophiacodon* in the Walker Museum, is now held by Professors Williston and Case to show two

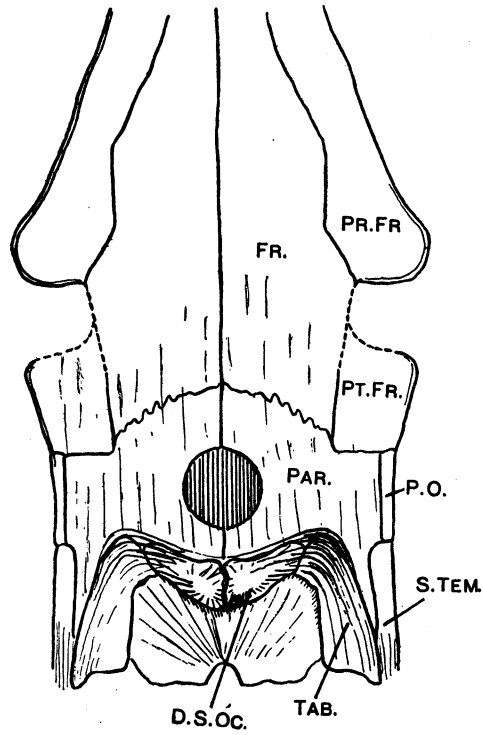

Fig. 6. "*Theropleura*" No. 4604, A. M. N. H.
Reconstruction of posterior part of skull. Dorsal aspect. × ⅔.

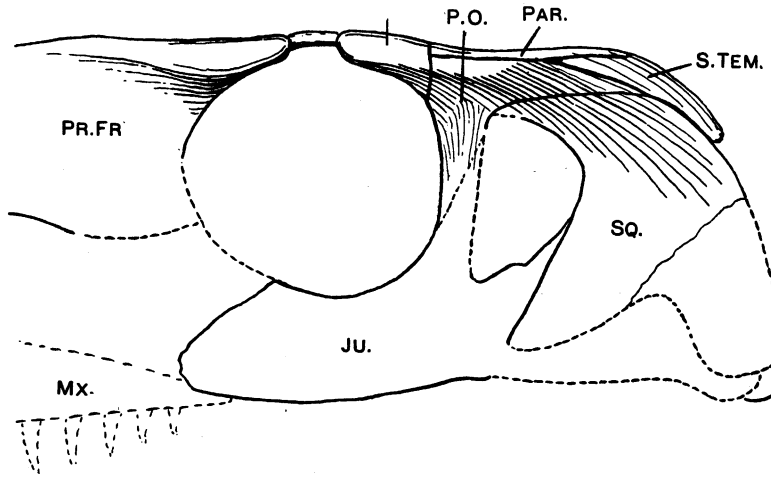

Fig. 7. "*Theropleura*" No. 4604, A. M. N. H.
Reconstruction of posterior part of skull. Lateral aspect. × ⅔.

temporal vacuities. Through the kindness of Professor Williston I had an opportunity of examining this skull, and am convinced as everyone must be of the actual occurrence of the very small upper temporal vacuity. The skull seems to me to show the structure more completely than was recognized in the original description, and leaves no doubt that the foramen lies between the postorbital and squamosal below and the parietal and supratemporal above, the latter bone not being distinguishable but from the evidence of the nearly allied *Diopeus* certainly present. It is quite certain from the evidence given by the small mass of bone still connected with the tabular in the type specimen of *Diopeus*, which is referred above, that there is in that animal no fenestra in a similar position. It will be noticed that this opening lies in the position of the "Upper Temporal Vacuity" reported by Baur and Case in *Dimetrodon*. That this opening is purely the result of post mortem dislocation is I think now recognized by all authors; in the original specimen where it is undeniably really present its sides show clearly sutural surfaces facing one another, and the numerous well preserved skulls since found show no trace of it. It is therefore extremely probable, to say the least, that the similar opening in *Ophiacodon* is also the result of crushing after death.

The remaining fenestra in *Ophiacodon* is surrounded by the postorbital, squamosal and jugal, being obviously homologous with that in *Dimetrodon* and in the South African Therapsids.

The large fenestra in *Diopeus* and "*Theropleura*" (4604) has exactly similar relations.

Cope's lower temporal fenestra in *Diopeus* is of very doubtful occurrence; nothing of the kind occurs in *Ophiacodon*, and its presence depends entirely on the evidence afforded by the single T-shaped squamosal and the apparently natural edge of a bit of jugal connected with one of the quadratojugals in the type specimen. These edges are polished by preparation and there is no evidence to show how much bone has been removed; 5 cm. added to each edge would close the putative infratemporal fossa.

It thus seems that the occurrence of two temporal openings in a Pelycosaur is still unproved, and from the material I have examined, by far the greater part of that so far collected, it cannot in my opinion be proved.

In his 'Revision of the Pelycosauria' Case held that *Diopeus* represented a morphological ancestor of *Dimetrodon*. My new studies have shown that this view has a fundamental basis of truth, although the animal is really somewhat specialized in a divergent direction. The feeble ossification shown in the brain-case and the limb bones suggests that the animal was aquatic and some of the peculiarities of its skull may depend on this mode of life.

Diopeus resembles *Varanosaurus* in the following in addition to common pelycosaur characters:—

1. In the great length of the face.
2. In the straight tooth row.
3. In the arrangement of the bones above the temporal fossa.
4. In the presence of a notch in the skull top above the orbit.
5. In the large quadratojugal on the side of the skull.
6. In the general build of the occiput.
7. In the short paroccipital process.
8. In the non-laterally compressed quadrate.
9. In the powerful parasphenoid.

Diopeus differs from *Varanosaurus* in the following advances and specializations:—

1. In the reduction of the quadrate ramus of the pterygoid which no longer approaches the squamosal.
2. In the carrying down of the quadrates far below the basi cranii.
3. In the great reduction of the quadrates.
4. In the articulation of the stapes with the paroccipital process by a special head.
5. In the non-production of the lachrymal to the nostril.

These resemblances and differences show that *Diopeus*, although it must have been derived from a *Varanosaurus*-like ancestor, is far more modified in many directions; some of these alternations (1, 2, 4, 5) are apparently of the nature of advances common to several stocks, others (3 and some not listed) are apparently specializations restricted to this stock.

Dimetrodon differs from *Diopeus* in the following characters, which are advances and specializations:—

1. The increased differentiation of the dentition and deepening of the maxilla.
2. In the curved tooth row.
3. In the obliteration of the supraorbital notch.
4. In the small quadratojugal.
5. In the fusion of the postparietals.
6. In the lengthening of the paroccipital processes in connection with the drawing back of the quadrate region.
7. In laterally compressed quadrate with a deeply grooved trochlear condyle.
8. In the reduced and upturned parasphenoid.
9. In the much reduced size of the basisphenoidal tubera and neig boring regions of the basioccipital and basisphenoid.
10. In the much smaller fenestra vestibuli.

11. In the different arrangement of the stapedial apparatus, and in the following preservation of a more primitive feature.
    (1) The rather large quadrate ramus of the pterygoid.

Dimetrodon is thus a more advanced and specialized type than *Diopeus*, which except for certain peculiarities such as the mode of articulation of the tabulars with the neural cranium does, as Case believed, afford a morphological ancestor for it.

Edaphosaurus.

Certain features in the type skull of *Edaphosaurus pogonias* which were left doubtful by the previous investigators may be referred to here.

The interparietal and tabulars are just as they were recognized by Case; they lie on the posterior surface in a typical Therapsid way.

The specimen shows that the squamosal is continued forward and the postorbital backward below the parietal for a long way; it seems most probable that they met as they do in other Pelycosaurs, but the imperfection of the postorbital prevents confirmation of this view.

There seems to be no supratemporal, the apparent sutures in the squamosal being cracks.

There is a quadrate foramen, the quadratojugal articulating with the quadrate just above the outer condyle, then separating from it and finally articulating with its posterior edge just as in *Dimetrodon*. The quadratojugal is a small bone nearly the whole of whose outer and posterior surfaces is covered by the squamosal.

The skull of *Edaphosaurus* resembles that of *Dimetrodon* in fundamental features more than it does that of any other Pelycosaur, and such differences as do separate the two genera are largely dependent on their totally different adaptive specializations.

As is universally the case amongst animals with crushing teeth, *Edaphosaurus* has a very short face which preserves the primitive feature of a lachrymal reaching the nostril, lost in *Dimetrodon* and most other Pelycosaurs.

The palate is easily derived from that of *Diopeus* or even *Dimetrodon* by the exaggeration of the small teeth with which the pterygoids of each of these genera are beset.

The more vertical suspensorium, and lack of that pulling back of the quadrates and paroccipital processes which occurs in *Dimetrodon*, are also directly dependent on the development of the powerful palatal dentition.

The resemblances between *Dimetrodon* and *Edaphosaurus* are best seen

in the brain-case and quadrate. Both have brain-cases differing in the reduction of the tubera basisphenoidales of the fenestra vestibuli, when compared with *Diopeus*.

As Case has already recognized the quadrate of *Edaphosaurus* is singularly like that of *Dimetrodon* in its lateral compression, the thrusting back of the outer condyle, and its relations to other bones.

Another very striking and important similarity is in the bone called "stapes" which is the same remarkable wing-like bone in both, differing very markedly from the stapes of *Diopeus*.

These resemblances between the skulls go with considerable similarities in the vertebral column in the development of the transverse processes and rib articulations, and in the deep, short, and wedge-shaped centra in the pectoral region.

These resemblances show that *Edaphosaurus* and *Dimetrodon* stand on the same level of evolutionary advance, and it seems not improbable that the adaptive differences may have been rapidly acquired.