**Article XVIII.**—THE SKULL ELEMENTS OF THE PERMIAN TETRAPODA IN THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK.

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Translated by William K. Gregory.

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Preface.

In the spring and summer of 1911 I had the opportunity to spend several months in the United States. It had long been my desire to become familiar by personal observation with the rich treasures of fossil Sauropsida in the collections there. I was especially interested in the structure of the Permian Tetrapoda, which had not yet been worked over connectedly. The preliminary reports by Case and Williston caused very high expectation. At that time Case had just published his "Revision of the Pelycosauria," and Williston’s book on the Permian Vertebrates had not yet appeared. So with the highest anticipations I first came to New York. I cannot describe the friendliness with which everything was shown to me in the American Museum of Natural History, where every facility for investigation was given. I owe the warmest thanks to Prof. Osborn, Dr. Matthew, Dr. Gregory and Mr. Granger. Mr. Charles Falkenbach assisted me in examining the Permian collection, with which he is very familiar, and Mr. Charles Christman with great patience and skill prepared for me the brain case of Eryops. The whole four weeks available in New York were devoted to making observations, drawings and notes; the general review ¹ could only be written at home, after comparison with observations made in other places. This was made easier by the photographs which were most liberally placed at my disposal. A number of negatives were also very kindly made at my suggestion. My warmest thanks are due to Dr. W. K. Gregory for translating this paper from the German and for reading the proofs.

With the feeling of gratitude I submit especially to my American colleagues the observations recorded below, for their criticism and for their service.

(Signed) Friedrich von Huene.

Tübingen, Nov. 1, 1912.

¹ 120 species of Amphibians and reptiles from the red Permian and Upper Carboniferous of North America have been described up to the present time.
Abbreviations used in figures.

Adl. Adlacrymal (lacrymal auct.).
A. g. Articular facet for basipterygoid process.
Ang. Angular.
Art. Articular.
Bo. Basioccipital.
Bs. Basi-.
B. sph. Basisphenoid.
Bst. Basipterygoid process.
car. Entrance for carotis interna.
Ch. Choanae (internal nares).
C. i. Canalis intertyinpanicus.
Co. Complementare (coronoid).
C. Cond. Condyle.
Co.
D. Dentary.
Dso. Dermo-supraoccipital.
Eo. Exoccipital.
Ept. Epipterygoid.
F. Frontal.
F. m. Foramen magnum.
F. ov. Fenestra ovalis (vestibuli).
F. p. Foramen parietale.
F. q. Foramen quadrati.
Hyp. Fossa for the hypophysis.
J. Jugal.
L. Lacrymal (prefrontal auct.).
lat. lateral (external).
Md. Mandible.
M. Maxilla.
Med. medial (internal).
N. Nasal.
N. o. Nasal opening.
Opo. Opisthotic (paroccipital).
O. Orbit.
P. Parietal.
P. art. Prearticular (Goniale).
Pf. Postfrontal.
Pl. Palatine.
P. m. Premaxilla.
P. Postorbital.
Po. Paroccipital (opisthotic).
Pro. o. Prootic.
Pt. Pterygoid.
Q. Quadrate.
Qi. Quadratojugal.
r. C. Right condyle.
Sa. Supraangular.
Sm. Septomaxillary.
So. Supraoccipital.
Spl. Splenial.
S. t. Sella turcica.
Spt. Septum interorbitale.
Sq. Squamosal.
St. Supratemporal.
Stp. Stapes.
T. teeth.
Tb. Tabulare.
Temp. Temporal Opening.
Tr. Transverse (ectopterygoid).
V. Foramen for a vein.
V. Vomer.
I. W. First vertebra.
I. Exit of olfactory nerve.
II. Exit of optic nerve.
V. Exit of trigeminus.
VI. Exit of abducens.
VII. Exit of facial nerve.
VIII. Entrance of auditory nerve.
IX–XI Exit of "vagus group."
X. Exit of vagus.
XII. Exit of hypoglossus.

Hatched parts in some of the figures (e. g. Fig. 15) are restorations in plaster.
I. DESCRIPTIVE SECTION.

**Eryops megacephalus** Cope.

Figs. 1-6.

So much has been written on the skull of *Eryops*, by Cope, Case, Branson, Broili and others, that one would scarcely think it possible to contribute any new facts and yet in several not unimportant points it seems to be. Our present knowledge is best presented and summarized by Case in his "Revision of the Amphibia and Pisces of the Permian of North America," published December, 1911.

The presence of septomaxillaries, which I am enabled to confirm, can be seen in all of the numerous skulls in the American Museum that have been prepared to any extent. Nor is the parietal foramen ever absent. In adult skulls it is about 5 mm. in diameter.

The back of the skull appears to me to differ from previous representations of it, especially as regards the exoccipital and basioccipital. The posterior corner of the upper border of the cranial roof between the auditory notches is formed by two pairs of bones: the dermo-supraoccipitals in the middle,
and the tabularia on the two sides. Below the tabulare on the occiput is the long paroccipital (= opisthotic), plainly separated from the exoccipital. I refer especially to skull No. 4272 (Amer. Mus.). Below the dermo-supraoccipitals there is in this skull a somewhat depressed, triangular bony surface which extends to the foramen magnum. This must be the supraoccipital. A horizontal suture separating it from the dermo-supraoccipitals is not visible, but the depression of the bony surface is uniform throughout and is not divided in the middle, while the dermo-supraoccipitals, extending back beyond the posterior edge, are separated by a very distinct and suddenly ending suture. Thus lying in a typical manner upon the primary cartilage bones, supraoccipital and paroccipital, are their associated dermal covering-bones, the dermo-supraoccipital and the tabulare. The exoccipitals are of considerable extent. They flank the foramen magnum and bound the supraoccipital below, but they also bound the foramen below and form both condyles. In skull 4272 there is a break through the right exoccipital just above the condyle, which must not be confounded with a suture.

On the left the bone is undivided.

*Base of the cranium.* The basioccipital is only visible as a narrow band between the condyles. It appears as a small triangle on the ventral surface of the base of the skull, and anteriorly is bordered in normal manner by the large basisphenoid. The latter, as shown in longitudinal sections, for some distance forms a scale-like overlap covering the basioccipital beneath it, so that the true extent of the basioccipital is much greater than its apparent extent. No doubt the ligaments of the articular capsule of the joint between skull and neck were inserted also on the hinder ventral border of the exoccipitals, so that the participation of the exoccipital betokens only a
gradually increasing ascendency. The basisphenoid imperceptibly passes forward into the long and stout parasphenoid; although the former is a cartilage bone and the latter a covering bone a boundary between them cannot be seen. The basisphenoid has stout and long lateral basipterygoid processes, on to the facets of which the pterygoid is attached. The hind process of the pterygoids and the front one of the quadrate together form a vertical, backwardly directed thick wall of bone, which makes it very difficult to see the lateral wall of the brain case and its perforations; the latter may best be seen with the aid of a small mirror.

**Brain case.** An examination of the outer and inner sides of the brain case (made possible by two longitudinal sections which Mr. Ch. Christman prepared) resulted as follows: first, that the twelfth pair of cranial nerves (hypoglossus) is lacking; secondly, that the whole auditory capsule buds off laterally and is almost constricted off in a separate bony chamber. Issuing from the auditory chamber of the brain case in a postero-anterior series appear first the perilymphatic vessels and above them probably a vein (not the jugular); in front follows the great fenestra ovalis, in which (in skull No. 4188 and 4272 and according to Case also in a skull in the University of Michigan) rests a stapes about 4 cm. long. A little in front of the otic opening lies the aperture of the Fallopian canal, through which the facial nerve passes. Behind the above-named openings and quite close to the condyles lies the exit of the vagus group (IX–XI). Possibly the
Fig. 5. *Eryops megacephalus*. Lateral wall of brain-case. A, with the pterygoid in place; B, with the pterygoid removed. P, foramen for perilymphatic vessels, V, foramen for a vein. V, foramen for trigeminus. Amer. Mus. 4188. X 4.

jugular vein also emerges here, or else together with the perilymphatic vessels. On the inside and in front of the otic diverticulum, obliquely above the sella turcica, are seen two entrances for the branches of the trigeminius, and these two also appear on the outside in front of the insertion of the vertical flanges of the pterygoids. Three centimeters further forward and somewhat lower is the opening for the optic nerve. The exits of the third and fourth nerves I could not see, nor was I certain of the foramina for the abducens which are to be sought in the floor of the brain, directly behind the sella turcica.

Lysorophus tricarinatus.

Figs. 7–10.

*Lysorophus* also has given rise to an extensive literature by Cope, Case, Broili and Williston. The description and interpretation of this little skull have undergone great changes and for that reason especially it is still well worthy of study. I studied 9 skulls in New York and 24 in Tübingen; these (in Tübingen) vary in length between 12 and 40 mm. (actually 37, but in this skull a portion was missing).

It is at once noticeable that the *sides of the skull* are scarcely ossified; the orbit is not surrounded by bones and the skull roof and palate are connected only at the tip of the snout, and not on the base of the skull. The premaxillae are small and in No. 4761 give off anteriorly only quite short ascending processes. In a specimen in Tübingen they bear about 6 narrow sharp little teeth; in the same specimen the maxillae bear about 10 similarly compressed, but somewhat larger, teeth. The maxilla is narrow and long. It reaches forward to the nasal opening and according to Case is in contact with the tip of the lacrymal.

On the *roof of the skull* the paired nasals, frontals and parietals follow in sections of almost equal length; the parietals, however, being a little longer than either of the others. A parietal foramen I could not distinguish. The median suture between the parietals is now strongly and irregularly jagged, now almost straight and only finely notched, but the hinder borders of the parietals always have some deep lateral zig-zags, which become stronger laterally. The parietals form the lateral margins of the skull roof,
but next to the frontals and nasals a long narrow lacrymal intrudes, and extends to the nasal opening, as Case assumes, and as I can verify in a Tübingen specimen. The parietales are bounded behind by three bones, the median one of which is the supraoccipital. This is almost as long as the frontal; behind the parietales it begins moderately broad, is then considerably constricted and then attains its greatest breadth, again becoming narrow and bounding the foramen magnum at its highest point. The broad hinder half of the supraoccipital bears a median sagittal crest. The pair of bones that flank the supraoccipital behind the parietales I regard as supratemporals. Anteriorly, next to the parietales, they form long, deep zig-zags; the outermost one especially in many skulls is long and finger-like.

Next to these the parietal forms a backwardly directed spur, thus bounding a small part of the lateral border. Next to this the squamosal, forming a small zig-zag, encroaches upon the supratemporal. The latter is bounded posteriorly by the supraoccipital and exoccipital.

*Temporal region.* Since the whole periphery of the orbits remains unossified, there appear on the side of the skull only two bones: the large, long, rod-shaped quadratojugal, directed obliquely forward, and a small squamosal covering the attachment of the quadratojugal. The squamosal consists of two branches, one on the skull roof, directed forward, and one on the quadratojugal, directed backward. In form it may be compared with a sharply bent sickle. As a narrow strip it follows the lateral margin of the skull roof from the supratemporal to the mid-length of the parietal. The squa-
mosal is pointed below and overlies the quadrate for half its length, lying chiefly on the outer border, if it is not displaced, as it very frequently is. The quadrate is broader above than below. In No. 4761 the squamosal is displaced backward and so the quadrate shows the surface usually covered by the squamosal; this surface bears a depression in which the squamosal fits. The lower end of the quadrate bears a gracefully arched trochlea. The length of the quadrate is about two-fifths to one-half of the skull-length. The quadrate is inclined forward at an angle of about 45°.

The back of the skull is interesting and until now has never been accurately described in detail. Some of it can be made out in one of the New York skulls, but it can best be seen in some of the skulls in Tübingen which I have worked out of the matrix myself.\(^1\) The foramen magnum is bounded above entirely by the supraoccipital and laterally by the exoccipitals, which form the greater part of its margin. The large condyle is crescent-shaped; its outer two thirds project strongly, they are formed from the exoccipitals; the deeper depression is formed from the basioccipital. This condyle is intermediate between the true reptilian condyle and the true amphibian condyle; as compared with that of *Eryops* the basioccipital is here a little more prominent, but in principle they do not differ. However, the structure of the condyle also shows a great resemblance to that of Theromorphs and of Turtles. Where the exoccipital, the supraoccipital and the supratemporal meet well preserved skulls (3) show a vacuity in the bone which I assume to be the homologue of the post-temporal opening of other Amphibia and Reptilia; this serves for the exit of the veins. Coalesced without suture with the exoccipital (a condition also frequent elsewhere) is what I take to be the opisthotic (= paroccipital). Since these elements cannot be separated, I shall speak here only of the exoccipital. From that part of the exoccipital which belongs to the condyle, a long process passes obliquely outward and forward; between it and the upwardly directed part of the exoccipital there is a deep insinking of the surface of the bone and I suspect that in the deepest part of this were the exits of the vagus group and of the perilymphatic vessels. Higher up, right near the border of the supratemporal, behind the upper posterior corner

\(^{\footnote{The figures of this Tübingen skull are not given here but elsewhere (Anatom. Anz. 43, 1913, p. 393).}}\)
of the squamosal and the origin of the quadrate, one finds a circular, deep and sharply bordered insinking which I take to be the fenestra ovalis (vestibuli).

Base of the cranium. The basioccipital on its lower surface is almost completely covered by the basisphenoid. In one of the New York specimens the basisphenoid shows a small short embayment in the middle of the hinder border; in another, behind the border of the basisphenoid, which has a similar embayment, one sees the basioccipital appearing as a narrow strip. In a Tübingen specimen the same embayment of the basisphenoid is discernible, and in it also the basioccipital is visible; for the rest the basisphenoid here reaches to the border of the condyle, but on both sides of the border of the basisphenoid and below the exoccipital part of the condyle occurs a quite small tuber of the basioccipital; between this and the lower lateral process of the exoccipital is a deep groove on either side, which I identify as the entrance for the carotids.

The palatal side of the skull is not quite completely preserved in any of the specimens examined by me. One of the New York skulls shows a broad basisphenoid, and in front an equally broad-based parasphenoid which becomes narrower anteriorly and extends to near the inner nasal openings. The same skull shows two large, elongate internal nares, separated by a narrow bridge; also, on the right side the dentition. Case mentions the vomerine teeth arranged in the form of a horseshoe. One of the Tübingen skulls (the one with the well preserved occiput) shows the broad basisphe-
noid and parasphenoid, yet without discernible boundary between them. On both sides the quadrate articulation appears somewhat lower than the palate and on the better preserved right side, on the longitudinal border of the skull-base and between the latter and the quadrate, one sees a narrow, anteriorly broadening band forming a steep bony flange, which I hold to be the hinder end of the pterygoid; its hinder end is attached to the quadrate.

In several examples the lower jaw is preserved. Corresponding to the forward inclination of the quadrate, it [the jaw] is considerably shorter than the skull itself. The two halves meet in a point at the symphysis, whereas the tip of the skull is broad and blunt. The right ramus of No. 4761 in New York and three specimens in Tübingen show good side views. In front of the articular region the lower jaw, in the region of the supraangular, forms a moderately ascending part, which regularly decreases in height anteriorly. Below the highest point, in the middle of jaw, is a great oval perforation, bounded above by the supraangular and below by the angular; the anterior tip of this perforation reaches even in front of the dentary. The articular forms a postarticular process in which the angular also participates. The latter does not quite reach to below the toothed part of the dentary. I am in doubt whether to interpret a weak line on the highest part of the New York jaw as a suture or not. In the Tübingen specimens I have no definite confirmation of it. Several skulls show in the view from below a stout and long splenial, which also participates in the symphysis. The dentition of the dentary is limited to the front half and does not extend as far back as does that of the maxillary.

The hyobranchial apparatus is well known. It consists of a series of four pairs of little rods with thickened ends, as described and figured by Williston, and as also shown in the Tübingen specimens.

**Gymnarthus willoughbyi** Case.

Figs. 11–14.

This form is known from two small skulls 16 millimeters long, both in very good preservation, which have been satisfactorily described by Case and by Broom. It is only in regard to the occiput that I have something to add, and I interpret the temporal region somewhat differently. In contrast to *Lysorophus*, the circumorbital region is here ossified.

**Roof of the skull.** The premaxillæ are small and provided with short ascending processes; they bound the nasal openings anteriorly and on the lower half. In No. 4892 the extreme tip of the snout is damaged, but the
hinder half of the premaxillae is still preserved; from this I estimate that the entire premaxilla bore 4 teeth. In No. 4673 the tip of the snout is wanting. The nasals, frontals, parietals, are not very different from each other in length. Their limiting sutures all run from the median line obliquely backward. The nasals and frontals are equal in breadth, the latter do not extend to the orbits. The parietals are broader. They enclose in their midst a small oblong parietal foramen. Toward the rear the parietals are bounded by two large dermo-supraoccipitals meeting in the mid-line. On

the outer side of these and on the hinder half of the parietals adjoin the supra-temporals, forming the postero-lateral corners of the skull.

Side of the skull. The orbit is surrounded normally. The long low maxilla (in No. 4892) is beset with 8 broad, pointed, anteroposteriorly compressed teeth. Above it follows a long adlacrymal, which forms the whole front border of the orbit and extends to the nasal opening. Above the orbits the lacrymal and postfrontal meet, the lacrymal reaching to the middle of the distance between the orbits and the nasal opening, while the long narrow postfrontal extends back to the supratemporal. Below this follows

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a small postorbital, the rest of the orbital boundary being formed by a sharply angulate, narrow jugal, which, however, is not fully preserved in either of the two skulls. Between the jugal and the quadrate is a deep high excision in the bony surface, somewhat similar to that of lizards. In both

Fig. 12. Gymnarthrus willoughbyi. A, Side of skull. Amer. Mus. 4892. Temporal region and orbit. Amer. Mus. 4892. C, Side of skull. Amer. Mus. 4673. $\times \frac{1}{2}$.

skulls, especially on the left side of No. 4673 and on the right side of No. 4892, one finds within this excision and below the supratemporal and postorbital a long, fragmentary piece of bone. Case, whose "prosquamosal" is the same as our squamosal, his "squamosal" being equivalent to our supra-
temporal, considered it to be the squamosal of our terminology, and Broom took it to be a continuation of the jugal. I also think it most probable that it belongs to the jugal and in No. 4673 perhaps partly to the postorbital. Of a quadrato-jugal there is no trace.

The quadrato is long and rod-shaped, much as in *Lysorophus*, but less sharply inclined forward. As in *Lysorophus* the quadrato in its upper half is covered by a small hammer-shaped squamosal, which, however, in No. 4892 is unfortunately incomplete. This in its upper broad part touches the supra- and especially the dermo-supra-occipital. The anterior tip is broken off; probably it extended along the border of the supratemporal to the jugal; for this no great length was required. Here and in *Lysorophus* the squamosal is still clearly revealed as the primitive covering-bone of the quadrato, a fact which once misled even Gaupp into applying the name paraquadratum in certain groups, until he admitted its identity with the squamosal.

Very interesting is the occiput. Behind the dermo-supraoccipitals there is a median acute-angled space, bordered by a narrow band of the supraoccipital. But even this does not border the foramen magnum; on the contrary, the exoccipitals send up narrow off-shoots which surround the fora-

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**Fig. 13. Gymnarthrus willoughbyi.** Occiput. A, Amer. Mus. 4673. B, Amer. Mus. 4892. × 1/2.
men magnum and unite above it, so that the supraoccipital is separated from it. Paired condyles are present, in form like those of *Eryops*. The processes surrounding the foramen start out from either condyle. Although no sutures are discernible around the condyles, I assume that these are chiefly formed from the exoccipitals. A long process beginning next to each condyle and directed outward and downward as a concave arch I regard as the paroccipital. Behind the lateral posterior corner of the dermo-supraoccipital and in particular behind the supratemporal, there is a small bony element which from its position can only be identified as the tabulare. Below the latter is a large circular fossa which I regard as the auditory fossa with the fenestra ovalis.

The *under side of the skull* shows a great broad basisphenoid overlapped by a narrower, but still relatively broad, parasphenoid, which is sharply pointed both in front and behind. Posteriorly the basisphenoid of No. 4892...
shows a small pointed median embayment, as in *Lysorophus*; in No. 4673 it even shows a blunt, backwardly pointed median tip. In this specimen the condyles are very well preserved and on the mid-line a most reach the tip of the basisphenoid. I suspect that the basioccipital as in *Eryops* is located here, but is quite small and does not share much in the formation of the condyles, but since the sutures are not discernible the question remains open.

In No. 4892 the condyles, especially in their lower half, are badly preserved, and I think that matrix still adheres between them so that the real distance between the basisphenoid and the inferior angle between the condyles is much less than it seems; compare No. 4673. Accompanying the parasphenoid anteriorly is a broad pterygoid with a narrow process (No. 4892) directed toward the quadrate. In front of it lies the palatine, on either side of the tip of the parasphenoid. Its anterior and lateral limits, as well as the internal nares, are covered by the lower jaw.

The lower jaw in the region of the supraangular has a rather high, steeply ascending process. On the lower border, extending from behind forward to the region below the highest part of the ascending process, appears the angulare, in the lateral view of the lower jaw; in front of the angulare, in the same view, the splenial is visible for a short distance. The greatest part of the lower jaw is formed externally from the dentary. The lower jaws of both skulls are also visible from below, and they show that the splenials participated in the symphysis.

**Diadectes.**

Figs. 15–18, 20–29.

*Top and Side of the Skull.* The fine skull No. 4839 (*D. phascolinus*) shows on the outside no clearly discernible sutures, so that Broom's figures remain hypothetical. On the other hand, a skull of *D. molaris* (No. 4352) shows very clear sutures.

The premaxillaries, which extend to the middle of the nares, send upward rather short, pointed median processes (to be seen only on the left side, since the right side has been repaired with plaster). The maxillary is not very high and extends to a point below the middle of the orbit, where it unites with the jugal in a deeply interdigitating suture. It [the maxillary] is pushed away from the border of the orbit by the adlacrymal and the jugal. The adlacrymal is fairly narrow and reaches from the orbit to the nasal opening, cutting into the nasal above in the form of an arch. The nasals are separated at their tips by the premaxillaries and border on the frontals...
with a very acutely zig-zag suture. The median suture of the frontals in its hinder half is regularly and deeply serrate, in its anterior half it runs an asymmetrical course. The frontals are separated from the orbits by the

Fig. 15. Diadectes molaris. Skull-top. Amer. Mus. 4352. Coffee Creek, Baylor Co., Tex. X 4.

rather small lacrymals and postfrontals. The most medial part of the suture between frontal and parietal is here not discernible. But on this point aid is rendered by the inside of the skull roof in another skull of the same species
The difference in the more precise course of these sutures in the two skulls may be explained by the fact that one observation is made on the external surface, the other on the internal surface. The parietals enclose the very large parietal foramen (2 cm. in diameter). The parietals are much broader than long. They give off obliquely in a postero-lateral direction a long process. Behind the parietals the large dermo-supraoccipitals still lie on the upper side. In No. 4352 they are incomplete and on both sides they are bounded by holes which have been filled up with plaster. Behind the dermo-supraoccipitals follows the large, gable-like supraoccipital.

Anteriorly, next the frontals, the parietals are bounded by the postfrontals. Behind these and next to the parietals and their long posterior prolongations is the large postorbital. It has a narrow border on the orbit, surrounds the posterior part of the postfrontal, and grows wider posterosuperiorly. Posteriorly it touches the supratemporal and squamosal. The suture between these two begins at the end of the parietal processes. The squamosal is narrow and long. Superiorly it adjoins the small scale-like supratemporal and tabulare. Behind the parietal process and supratemporal a sharp axial ridge runs back, separating the tabulare, which is lateral to it, from the dermo-supraoccipital and supraoccipital. The tabulare is thus bounded by the two last named bones, by the supratemporal and by the squamosal. Behind and below it is the paroccipital.
In the well preserved skull No. 4352 a great part of the temporal region with the quadratojugal. The upper border of the quadratojugal, separating it from the squamosal, I can not see. A depression is present where Broom indicates the suture, but the latter is not demonstrable. In No. 4352 at the lower broken surface of the squamosal one can see in the cross section that the squamosal embraces the upper end of the quadrate with a deep postero-internally directed concavity. This glenoid-like relation of the squamosal to the quadrate is shown in a horizontal cross section through the quadrate in No. 4675 (Fig. 18). The contact of the pterygoid with the inner wing of the quadrate is also clearly seen.

Especially important is a part of a skull roof (No. 4378) which strongly suggests Nothodon lentus Marsh (Fig. 19). The short, broad parietals surround a fairly large parietal foramen. The sharply bordered hole for the epiphysis widens below in the thick bone; at the same time the epiphysial concavity on the inner side of the bone is prolonged forward to the borders of the parietals and is also probably continued forward into the frontals. Anteriorly the parietals extend more than 1½ centimeters under the frontals. At their hinder borders the parietals are so coalesced with the dermo-supraoccipitals that it is hard to find the suture; internally it is easy to recognize, but it does not correspond completely with the outer suture on account of the thickness of the
bones. Posteriorly the parietal is prolonged into a long, laterally pointed process which on the right side is surrounded by a finely serrate suture. Lateral to this is the supratemporal.


*Dorsal openings in the temporal region.* A peculiar fact which has also been noted by Case is that in quite a series of normal skulls two openings
in the hinder half of the skull roof are indisputably present. *Diadectes molaris* skull No. 4370, 18 centimeters long, shows two symmetrically placed round openings, about 3 centimeters in diameter, 1 cm. behind the parietal foramen, and 2½ cm. distant from each other. The borders in some places are so clear that one cannot doubt their existence and the under side of the skull shows a well preserved palate with complete dentition, so that one cannot doubt its reference to *Diadectes*. It is scarcely possible to assume, there-

![Fig. 20. *Diadectes molaris*. Skull showing openings in the temporal region. A, skull-top. B, Under side of skull. Amer. Mus. 4370. Wichita Basin, Tex. × ½.](image-url)
are two deep grooves which however, apparently do not quite pierce the bone. Skull 4839 also shows something of this. But in the two first-named positions true temporal openings could not occur. One must therefore con-

Fig. 21. *D. molaris*. Underside of skull. Amer. Mus. 4352. Coffee Creek, Baylor Co., Tex. × 4.

ceive them as probably unexplained vacuities in the ossification of the skull top. Case has also come to the same conclusion. They are probably too large for auditory openings like those of *Cyclotosaurus*. 
That irregularities occur in this region is shown in the well preserved skull No. 4352; on both sides of the parietal foramen are little abnormal places, on the right a rugose thickening, on the left a small sharply defined hole. It is clear that these occurrences in several examples of Diadectes have nothing to do with true temporal openings.

Underside of the skull. The palate has been well described by Case, especially in No. 4839, and I have nothing important to add. Broom assumes the presence of a transverse and I think I can verify this on skull 4352 (right) but toward the jugal I can find no suture. According to Case, however, it is present in skull 1078 (Chicago Univ.). In skull 4352, in front of the transverse, between the right pterygoid and palate there is a small round postpalatine vacuity about 13 to 16 mm. long.

A few other items may also be noted.

The premaxillaries send back into the palatal surface small median processes which form the beginning of the narrow bridge separating the opposite internal nares; this is continuous with the narrow toothed vomers. According to Case and Broom this bony bridge or isthmus is formed in its whole length by the vomer, but this does not agree with my observations on skull 4352. The vomers extend back to the level of the seventh maxillary tooth; they bear an anteroposterior row of 11 conical denticles. In No. 4350 (figured by Cope in Proc. Amer. Phil. Soc., 1880, XIX, pl. v) the vomerine teeth extend back to near the fifth molar from the rear. At the places thus designated the opposite vomers separate and their divergent branches embrace the antero-medial processes of the pterygoids. These prolong uniformly the median bridge and after a short interval bear an antero-posterior row of denticles. Behind the widest part of the pterygoids they are prolonged into thin lamellæ lying on the anterior processes of the quadrate, and extending back almost to the jaw articulation (No. 4398, 4675). The palatines form a projecting collar (flange) alongside the maxillæ, and medially end freely on a plane lower than that of the vomers and anterior processes of the pterygoids. The palatine lamellæ appear to send back a branch reaching to the higher plane of the pterygoids, so that the two palatine lamellæ lie one above the other and are connected behind by a vertical bridge. The same is true also in the palatines of the Parasuchia.

Occiput and base of the skull. The cartilage bones (Ersatzknochen) of the base of the skull together with the parasphenoid, etc., are not yet known in all details. The supraoccipital appears in No. 4352 as a large, broad triangular bone on the outer surface, anteroposteriorly bounded by the dermosupraoccipital. It does not end here, however, but extends forward beneath the latter (as shown especially in No. 4378) and in the median line it reaches a point only 1 cm. behind the parietals. Externally the supr-
occipital is excluded from the foramen magnum by the exoccipitals (cf. No. 4839) but internally (No. 4378) it reaches the foramen magnum at one point. Laterally the supraoccipital abuts on the tabulare and paroccipital, inferiorly on the exoccipitals. The exoccipitals extend from the condyle, forming its upper border and surrounding the foramen magnum, above which they give off projections which may best be compared with the zygapophyses of vertebrae. The boundary separating the exoccipitals from the paroccipital is evident in No. 4378. The basioccipital, with its concave articular surface, forms the principal part of the condyle. Seen from below it forms, directly behind the condyle, a raised triangular surface, with the apex directed forward, and thus strongly suggests the basioccipital of *Eryops*, only there it is entirely covered by the basisphenoid.

The basisphenoid is a stout bone rounded below. It narrows anteriorly, giving off on both sides the stout basipterygoid processes, which are provided with articular facets. The hinder borders of the basisphenoid are produced into lamellae which widen, funnel-like, behind, and are inflated, especially on the sides. They also project over a part of the basioccipital. Both branches of the carotid run forward into the basisphenoid about 2 cm. apart and under the projecting border (cf. Nos. 4378, 4839, 4352). Between the basipterygoid processes on the lower side is a median foramen which Case has identified as the carotid foramen but which from its location can only be an intertympanic air passage (cf. Crocodilia, Saurischia, Parasuchia). The sella turcica and fossa for the hypophysis is well preserved in No. 4378; to this part a parasphenoid is attached in Nos. 4839 and 4352; in the latter it is about 3½ cm. long. The posteriorly widening and divided basisphenoid is very characteristic of the Cotylosaurs.
The skull-base of No. 4675 shows a well preserved sella turcica, in front of this the fossa for the hypophysis. In front of the latter is the insertion of the parasphenoid, next follows the paired basipterygoid processes with attached parts of the pterygoid. Behind the sella turcica at the base of the brain one sees plainly the exits of the abducent nerves. In skulls 4839, 4352, 4378 the side walls show something of the foramina for the nerves and blood vessels. In the first-named skull on the right side, I can distinguish five pits with foramina, from behind forward. The hindmost pit near the condyle must be the exit for the hypoglossus, but whether in one or more foramina cannot be positively distinguished. The next pit is almost circular with at least two foramina, and here the vagus group, with the jugular vein and the perilymphatic vessels, may have passed out. Still further forward and now no more visible directly from the rear, may be sought the fenestra ovalis and the canalis falopii (facialis) in the foramina located there. Directly behind the epipterygoid is the place to look for the exit of the trigeminus. A slight depression at the upper corner of the condyle is probably a foramen for the hypoglossus; the latter may indeed have consisted of several branches. The upper halves of the canals and gutters leading from the foramina, in which the nerves and vessels ran and branched, can be seen in skulls 4352 and 4378.

**Intraorbital region.** The innermost parts of the skull yield but few observations. Through the orbits of skull 4839 one can see resting on the right basipterygoid process an epipterygoid, which is plate-like on the pterygoid, and columnar above. In front of this is the broad upper surface of the pterygoid and just behind the adlacrymal is the similar surface of the palatine with three foramina for blood vessels. In the adlacrymal, where it meets the lacrymal within the orbits, is the entrance of the nasolacrymal duct. In the same skull, deep within the orbits is the interorbital septum, which is a vertical lamella, thicker below than above, extending down from the middle of the orbits to the pterygoid and further forward to the vomer; anteriorly it becomes thinner. It is designated by Case as ethmoid.

![Fig. 24. Diadectes. A, Fragment of brain case viewed from above. B, The same from in front. Amer. Mus. 4675. × ½.](image-url)
Brain cast. There is a brain cast of the fragmentary skull No. 4441 but as some of the openings in the original have not been cleared out the cast is thus incomplete. On the side of the skull is the great opening for the trigeminal and above this is probably the sunken area of the aqueductus vestibuli (right side). Behind this follows a damaged region and a stalk which perhaps pertains to the seventh and eighth nerve group; still further to the rear follow three stalks one above the other, of which I regard the lowest as the vagus group, the upper two

Fig. 26. Diadectes sp. Imperfect brain cast. Amer. Mus. 4441. \( \times \frac{1}{4} \).
as openings for vessels. The hypoglossus foramen has obviously not been worked out, for its corresponding projection on the cast is not seen. The fossa for the hypophysis also appears not to have been opened as the cast shows nothing of it. Further forward, in the region of the exit of the optic nerve, are small but incomplete projections.

Lower jaw. Good lower jaws are present in specimens 4353 and 4684. The articular portion of the lower jaw is low. In front of it rises vertically

![Diagram of lower jaw]

Fig. 27. Diadectes. Lower jaw. Amer. Mus. 4684. Godkin Creek, Archer Co., Tex. X 1.

a high pointed coronoid process. A postarticular process is not present, though an intraarticular process may be, formed from the articular itself. Beneath the articular the angular begins; it is continued half the length of the jaw. As it appears to me the angular rises high up on the outserside, highest beneath the coronoid process; there, half way up it is deeply invaded
Fig. 28. *Diadectes*. Lower jaw. Amer. Mus. 4353. Big Wichita River, Tex. × 1.
by the dentary, but it is also possible that the part lying above this projection of the dentary belongs to the supraangular; but here I am not sure of one of the sutures. On the inner side the angular does not reach so high and ends below the projection of the prearticular. The complementare [coronoid] reaches from the tip of the coronoid process to nearly the last tooth and on the outer side is visible only in narrow strips, while internally it reaches down somewhat further. The supraangular is not very large. Externally, below the complementare, it interlocks (verzahnt sich) with the dentary and thus forms chiefly the surface of the coronoid process; internally it extends further down and covers the wall of the mandibular cavity. The opposite wall below the medial border of the cavity is formed by the prearticular (= goniale Gaupp) which ends in an oblique laterally directed tip; in front of this there is occasionally a vacuity which is surrounded by the splenial and angular. The splenial covers the whole breadth of the dentary and also shares in the symphysis. It is remarkable how much the lower jaw recalls that of Placodus both in form and tooth structure, but this is indeed only a superficial resemblance.

**Bolodon tenuitectus** Cope.

Fig. 30.

Skull 4375 shows the very well preserved right side. The sutures as a whole can be clearly followed; but in a few places they could be completed conformably with the inner side. The upper tip of the premaxilla appears to encroach upon the nasal, so that the nasals are pressed between the ascending processes of the premaxillae. Within the nasal opening and near its hinder border lies the small septomaxillary. The maxilla does not reach
the orbit. The adlacrymal extends with a fairly uniform breadth from the front border of the parietals. The parietal gives off a process postero-laterally as in Diadectes. Lacrymal and postfrontal form the upper boundary of the orbit in a broad surface which is pointed in front and behind. The postorbital is very large and broad, as in Diadectes. The jugal is short, the quadratojugal extends far forward, if what I regard as the suture is really such. Above the long squamosal lies a small scale-like tabulare, just as in Diadectes. Behind the parietals come the dermo-supraoccipitals, preserved as a little piece on the right side. The limits of the supratemporal which separate it from the postorbital, I could not fully distinguish. The supratemporal is near the parietal process and encroaches somewhat upon the upper front border of the squamosal. The opposite side shows that there were 17 upper teeth, of which 4 are in the premaxilla. The vomers with small conic denticles are also recognizable. The occiput shows nothing.

**Chilonyx rapidens** Cope.

Skull 4357 is a large incomplete skull-top and a part of the occiput. The surface of the superficial bones is strongly sculptured. The sutures are partly distinct. As the parietal foramen is filled with plaster the skull-pattern at first sight is somewhat obscured. The hinder border of the right nasal opening is still present, as also the natural front border of the maxilla;
whether the latter reached the orbit is not clear. The nasals are extraordinarily broad, but whether they came in contact with the nasal opening is not apparent. The adlacrymal very probably extended from the orbits to the nasal opening. The lacrymal encroaches upon the floor of the frontal.

In \textit{Chilonyx} (in contrast to \textit{Diadectes} and \textit{Bolbodon}) the postfrontal lies near the parietal rather than near the frontal. The postorbital reaches the supratemporal as in \textit{Diadectes} and \textit{Bolbodon}. The supratemporal as in those genera is small and separates the parietal and squamosal. Behind the
parietal process and the supratemporal lies the fairly large tabulare, which forms the hinder corner of the skull and lies above the paroccipital. The dermo-supraoccipitals are very narrow. The parietal foramen is relatively smaller than in the two above named forms and it lies behind the mid-point of the parietals. The tabulare in its hinder half forms a thick horn-like peak and two somewhat smaller ones. Below the long squamosal the quadratojugal is separated off by a long clear suture. Between the quadratojugal and the quadrate is the foramen quadrati. The quadrate extends far upward, medially it is covered by the pterygoid; the articular surface is large and bipartite. The supraoccipital is broad and pointed like an arrow-head below. Whether or not it reaches the foramen magnum at one point is not quite clear. Its chief boundaries are formed by the exoccipitals which extend pretty widely on the sides and below. The paroccipitals are separated from them by clear suture; they lie directly below the tabularia.

**Captorhinus** div. sp.

Figs. 32–35.

Of *Captorhinus angusticeps* Cope, *isolomus* Cope (= *Ectocynodon incisivus* Cope) there are a number of good skulls in New York and many other col-

![Diagrams of skulls](image_url)

Fig. 32. *Captorhinus angusticeps*. Skull. **A**, Amer. Mus. 4334. × 1. **B**, Amer. Mus. 4437. West Coffee Creek, Baylor Co., Tex. × 1.
scarcely anything to add, but will give here accurate figures with some explanatory words.

*Top and sides of the skull.* The premaxilla, which embraces the front half of the nasal opening, sends two projections up to the nasals and on the palatal side has a fairly long branch which covers the front end of the vomer and so reaches back a little further between the internal nares. In the interior of the hinder half of the external nasal opening lies the septomaxillary, as shown for example in *C. angusticeps* No. 4334, 4457; in the middle

![Diagram of skull](image)

Fig. 33. *Captorhinus angusticeps.* A, Skull top. Amer. Mus. 4334. W. Coffee Creek, Baylor Co., Tex. × \(\frac{1}{4}\). B, Top of occiput. Amer. Mus. 4340. Baylor Co., Tex. × \(\frac{1}{4}\).

(of the septomaxillary) a process projects forward. The maxilla is low, bears several rows of teeth and is very far separated from the orbit by the adlacrymal and jugal. The frontal touches the orbits only at one point and is almost excluded by the lacrymal and postfrontal. The medial borders of the latter two form together an almost directly anteroposterior line. The parietal foramen lies in the front half of the large parietals which are nearly like a right-angled triangle and possess no posterior processes like those of the Diadectidae and *Chilonyx*. Behind the parietals follow the dermo-supraoccipitals, but on the upper side they appear only in a very
narrow strip near the posterior ridge of the skull-top; their surfaces extend chiefly on the hinder side of the skull as sickle-shaped undulating bands; on both sides of the sharply pointed supraoccipital (which is pushed in between the dermo-supraoccipitals) one always finds a perforation. Over the lateral end of the dermo-supraoccipital and at the postero-lateral angle of the parietal one finds on the hinder edge of the skull-top a very small bony element, with its point turned toward the parietal. When I found this element in the New York skulls at the end of March 1911 neither Branson’s work nor Case’s Revision of the Cotylosaurs had appeared. I then identified this element as the supratemporal and I still maintain this view against Case and Branson. A tabulare should be looked for lateral to the dermo-supraoccipital and not in front of it. Comparison with the Diadectidae plainly supports this: the tabulare has already vanished phylogenetically, the supratemporal holds on longer, but in Labidosaurus even the supratemporal is gone and only vestiges of the dermo-supraoccipital remain. These completely dermal elements which in the most primitive forms still have a broad surface on the upper side of the skull roof in course of phylogeny were displaced more and more on to the hinder edge of the skull roof and there gradually vanished, beginning at the lateral end.

This rule holds for the dermo-supraoccipital and the tabulare, but seldom for the supratemporal which is an inconstant element varying in position and scarcely appearing at all except in relatively primitive forms. I suspect that its vanishing is not due to gradual decline, as in both the above named elements, but to fusion with the squamosal.

Temporal region.—The squamosal is the greatest element on the side of the skull; it also forms the ascending posterior edge of the skull and on each side of the same it forms a broad occipital band, which produces the surface of the dermo-supraoccipitals down to the quadrate.
That this surface is really to be regarded as squamosal is shown by the direction of the bone-fibres which radiate from a center on the ridge, both in front and behind. Below the squamosal is a narrow and fairly long quadratojugal, which is prolonged into a small triangle and on each side of the ridge, on the occiput. The small quadrate is not seen in lateral view of the skull but only from the rear.

Occiput and base of the cranium. The supraoccipital, which forms the whole upper border of the foramen magnum, is roof-shaped and is produced far back. The exoccipitals form the whole lateral border of the foramen magnum. The basioccipital is short. The basisphenoid is remarkably produced anteriorly; toward the rear it bifurcates and broadens, bears evident basipterygoid processes and just behind these is usually constricted. In No. 4338 on either side lies in situ a perforated stapes.

Palatal region. From the basisphenoid a narrow long parasphenoid arises. Around the parasphenoid the pterygoid leaves a lancet-like open space. On the border of this space and on the hinder border of the downwardly directed oblique wing (of the pterygoid) the pterygoid bears teeth. A transverse I could not note. The palatine extends from near the axial tooth-row of the pterygoid to the hinder end of the internal naris. The narrow, posteriorly broadening bridge between the elongate internal nares is formed by the vomers which diverge somewhat posteriorly and embrace the ends of the pterygoids. In front the vomers dip under the hinder processes of the premaxillae.

Of the lower jaw nothing new is to be noted. The articular possesses a small pointed postarticular process and a short, broad intraarticular process. A prearticular is present. The splenial shares in the symphysis. The angular is broad and extends for half the length of the jaw. The dentary bears several rows of teeth, as does the upper jaw. The supraangular occupies only a narrow space.

**Labidosaurus hamatus** Cope.

Figs. 36, 37.

*Labidosaurus* is extremely like *Captorhinus* in its skull, only it is somewhat larger, and lacks the supratemporal. The arrangement and relative dimensions of the elements is exactly the same and their form differs only in quite unimportant details. The septomaxillary is present. The dermo-supraoccipital reaches more to the upper side and on both sides of the occipital ridge it is about equally broad. The squamosal likewise extends down on the hind side of the ridge and the long fibres radiate in all directions
from a point on the ridge. That which Williston has designated as "epiotic" (in his paper 'The Skull of Labidosaurus.' Amer. Jour. Anat., 10, 1910. Pl. 3, fig. 4) is no other than this hinder surface of the squamosal. Supraoccipital, exoccipital and paroccipital, as best represented in Williston's figures (l. c.) show the same arrangement as in Captorhinus. Stout epi-

Fig. 36. Labidosaurus hamatus. Amer. Mus. 4427. Coffee Creek, Baylor Co., Tex. A, border of occiput. × 1. B, skull-top. × 4.

pterygoids, according to Williston are present. Also like those of Captorhinus are the palate and the lower jaw, the latter possessing likewise a small ascending process in which the complementare [coronoid] shares; a prearticular and an anterointernal perforation below its tip are also present.
Of this form Case has given very good figures. The teeth refer *Bolosaurus* to the Diadectidae and with equal certainty the skull-base indicates the same group; only the parasphenoid is longer, the basi-sphenoid is higher and has evident tubers. In the original I can see nothing of the great posttemporal opening which Case assumes in his paper on *Bolosaurus* (1907, Fig. 5), but of course the specimen is badly preserved and much compressed in this region. Skulls 4685, 4686, 4327, 4461 are also present. Such small Diadectids would be especially interesting and it is to be hoped that better specimens will be found.

**Pariotichus brachyops** Cope.

The type, No. 4328 is so badly preserved that one can see nothing really important in it. No. 4760 is better preserved. The temporal region and occiput are lacking. The preserved part of the skull in the arrangement of its elements shows a general correspondence with *Captorhinus*. The form of the snout, of the nasal opening and orbits differ from *Captorhinus*, the hinder part of the jugal is less high, the small parietal foramen lies further back. It is practically certain that the two genera are distinct but nearly related.

**Isodectes megalops** Cope.

This is a very small skull, No. 4329, which shows only something of the left and upper sides. The frontals are separated from the orbits by the
lacrymals and postfrontals. It is not quite certain whether the maxilla borders the orbit or whether it is separated from it by a very narrow branch of the jugal. The postorbital is remarkably small and placed far down. In the parietals I cannot see the parietal foramen, no doubt because of the poor preservation. Behind the parietals appear the dermo-supraoccipitals in a not very narrow band which is still on the upper surface of the skull. Next to the parietal and along its entire length I think a broad supratemporal must be differentiated; Case gives this suture as doubtful. The squamosal is at this place completely separated from the parietal. Behind the jugal only a small quadratojugal is present. The lower jaw shows an ascending process and a dental pavement.

If the presence of the large supratemporal is to be accepted as certain Isodectes must be placed not with the Pariotichidae but near Pantylus. For the two bones, which in Pariotichus brachyops Case designates as squamosal and prosquamosal are to be regarded as squamosal and quadratojugal, as is very clearly shown in Figure 36 and others in Case's Revision of the Co-tylosauria (1911, p. 92). Moreover what Case in Captorhinus calls prosquamosal I hold as surely the quadratojugal. Captorhinus and Labidosaurus according to Case's conception would be far separated and could scarcely be brought together in the same family or even suborder; yet Case puts both genera in the same family. In the relations of the frontal and orbit also Isodectes is similar to Pantylus.

Pantylus cordatus Cope.

Figs. 40, 41.

By close examination with a magnifying glass in skull 4330 one can distinguish all the bony elements of the skull-top. The premaxillae are small; they send off short medial ascending processes between the nasals. Each premaxilla contains two teeth. According to Mehl's observations on a Chicago specimen the premaxillae do not extend far on the palate between the internal nares. The nasals are extraordinarily wide and not long. The frontals are rectangular and remain far removed from the orbits. The lacrymal reaches from the middle of the upper border of the orbit to near the beginning of the nasal. The adlacrymal extends from the orbit to the nasal opening. The maxilla is very low and remains far separated from the orbit. The jugal behind the orbit has a broad and high expanse.
The postfrontal is small and the considerably larger postorbital is pushed far upward. The parietals are considerably broader than the frontals and so far as preserved are rectangular in form. The parietal foramen lies near the frontal border. Next to the parietal is a large and broad supratemporal, which suggests *Isodectes*. It separates the squamosal from the parietal in its whole length. Below the squamosal is a fairly broad and wide quadratejugal extending forward in a point. The quadrate does not appear in side view but can only be seen from the rear. On the inner surface beneath the squamosal it sends upward a high process which reaches to below the supratemporal. This process is covered behind by the pterygoid which extends down to the articular surface of the quadrate and to the border of the squamosal. Of the palatal surface Mehl has described: the elongate inner nasal opening, the interpterygoid opening extending to between the internal nares, the anterior processes of the pterygoids, covered with small denticles, the small vomer and the broad palatines covered with a pavement of teeth.

The *lower jaw* I was enabled to study in Nos. 4330 and 4331. The anterior half has been made known by Mehl. The articular is short and thick, and appears to lack posterior or medial process; from the articular a broad prearticular (= goniale Gaupp) takes rise, but after a short distance is covered by the splenial. The splenial is very stout and bears a dental pavement near the teeth on the dentary, it also shares in the symphysis.
The angular on the lower side is quite broad; it lies on the under side and in a narrow surface also on the inner side. The supraangular, on the outside, is considerably narrower than the angular. Supraangular and angular lengthwise, and splenial anteriorly, surround the large internal mandibular opening. I have not been able to observe a complementare [coronoid],

yet more favorable material may well reveal this element. Each ramus of the lower jaw is triangular in section with a wide inner concavity. The element which Mehl figures in the interior of this concavity may well be the tip of the prearticular, which is covered by the splenial and in the course of maceration has bent up toward the dentary. The two remaining elements are the angular and the supraangular.

**Dimetrodon incisivus** Cope.

Figs. 42–47.

The skull of *Dimetrodon* has lately been discussed several times by Case, then also by Broom and by the author, basing his discussion on the literature. The distribution of the bony elements is on the whole sufficiently well known, but in respect of the temporal region and the quadratojugal there are still differences between the three above named authors.

Temporal region. Case had correctly figured and designated the quadratojugal of *Dimetrodon incisivus* and *Theropleura* in his “Revision of the Pelycosauria” in 1907, and even in a work of ten years earlier. However, on the lateral side of the skull he did not find the boundary between the jugal and squamosal (which as is well known he calls prosquamosal). But
this suture I have been able to see plainly in several places, for example on the left side of No. 4034 towards the jugal. Although in certain specimens Case has several times correctly figured the quadratojugal as lateral to the foramen quadrati, yet very recently he commits the inconsistency of seeking the quadratojugal behind the foramen and above the quadrate. In the occipital aspect of Captorhinus (Bull. Am. Mus. Nat. Hist., Vol. XXVIII, 1910, p. 194 and Revision of the Cotylosauria, 1911, p. 93, fig. 19, C.) and in a photograph of a skull of Dimetrodon in the collection of the University in Ann Arbor, Michigan, which Dr. Case sent me to New York in April, 1911, he has inscribed certain sutures and names of bones, from which it is evident that he makes the jugal and quadrate directly contiguous and makes the quadratojugal run up behind (medial to) the foramen quadrati as far as the supratemporal (which he calls squamosal). Broom has correctly viewed the quadratojugal and its limits against the jugal and squamosal

![Diagram of Dimetrodon incisivus](image-url)
(Case's prosquamosal) but he gives the course of the suture somewhat inexactely; the foramen which he indicates in this suture, between the squamosal and quadratojugal is surely not present. In his figure 4 (l. c. 1910, p. 193) he quite correctly indicates the right quadratojugal as viewed from behind, but on the left on account of unfavorable preservation he has not been able to follow the suture and consequently makes it run up near the end of the paroccipital, behind (medial to) the "prosquamosal." According to my investigations on all the New York skulls and skull-parts the quadratojugal is placed laterally to the quadrate. The foramen quadrati is bounded by both these bones. Superiorly the quadratojugal is bounded by the squamosal (Case's prosquamosal). At its hinder end it sends up a short sharp ascending process which Case has plainly figured (l. c. 1907, pl. 3, fig. 1 and l. c. 1910, fig. 4 right). The forepart of the quadratojugal is lower and is fairly long and produced foward, it connects by a serrate suture with the jugal.

As this position of the quadratojugal makes untenable the earlier representation of the temporal region by Case a re-examination of this region was needed; Case and Broom did this in 1910; the writer, in his work on Erythrosuchus, in the winter of 1909–10 did the same thing, so far as it could be based on the literature. In the spring of 1911, I was also enabled to study personally the whole material in New York. The temporal opening is bounded below by the jugal, behind by the squamosal (prosquamosal Case); the upper border is formed by the postorbital (on which account the opening corresponds to an infratemporal fossa). The postorbital is accompanied above by the parietal, both bones run back in downwardly directed projections; between these is inserted a long narrow bone, which further down accompanies the squamosal but does not extend down to the quadratojugal. This is the supratemporal (Case in his last work consistently calls it "squamosal"). In skulls 4034 and 4636, these relations are clearly shown. In the same skulls, behind the supratemporal and beginning behind the tip of the parietal lies a long narrow element, which Case has attributed (l. c. 1910, p. 193) to the supraoccipital. This I regard as improbable, but would rather discuss it in connection with the posterior side of the skull. The long posterolaterally directed process of the parietal recalls the Diadectidæ.

The posterior side is best shown in the two above mentioned skulls. The condyle is formed from the basioccipital. To the latter are attached the narrow exoccipitals, which project like zygapophyses and completely sur-

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*Fig. 43. Dimetrodon incisivus.* Oblique rear view of left quadrate and quadratojugal. Amer. Mus. 4636. ×4.
Fig. 44. *Dimetrodon incisivus*. A, occiput. B, the same viewed obliquely from above. Amer. Mus. 4636. Wichita Basin, Tex. × ½.
round the foramen magnum. On both sides extend the long narrow paroccipitals which are sharply bent backward; it seems possible that a small part of the medial portion of these processes belongs to the exoccipitals and that the suture is obliterated. Two specimens in the Tübingen University Collection show the same thing, only in one of them the exoccipitals are narrowly compressed above and extend to the foramen magnum. In the New York skulls the supraoccipital, which is surrounded by suture only, shares in the occipital surface above the foramen magnum and is divided by a median crest into two roof-like contiguous surfaces. Above it is pointed and sends off on each side a sharp corner. Now the question rises, of what is the large remaining part of the occipital surface formed? The supraoccipital at most does not reach to the posterior (lateral) ridge of the skull. Is it formed by the parietals which extend down on the supraoccipital? They would be the nearest but they belong to the (lateral) crest of the skull, the suture can be seen and one can follow it laterally from the middle of the crest: it ascends to the summit of the crest near the parietal process, keeping close to the summit, then turning away and reaching the supratemporal, under the border of which it (the suture) is continued. Thus the long narrow piece that is medial to the supratemporal is bounded both by this suture (which ends below in a tip) and by the lateral occipital crest. At the crest, however, I find no sutural limits between the supraoccipital and parietal. According to its position this part is probably formed from the dermo-supraoccipitals and the tabularia, the latter form-

![Fig. 45. Dimetrodon incisivus. Right pterygoid, etc., outer side view. Amer. Mus. 4636. X \( \frac{1}{2} \).](image-url)
ing the portion between the paroccipitals and the supratemporal. These two paired dermal bones must therefore be very firmly coalesced. This is a conclusion resulting from the fact that between the parietals and the supraoccipital there is a bony surface which I cannot otherwise explain. The above described suture I regard as certain.

On the brain-wall and base of the skull are shown the foramina for the nerves and vessels, which I shall discuss further in another place.1 From the hypoglossus to the trigeminus one can observe them all, both from without and from within. A large and broad perforated stapes is present, as

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Fig. 46. *Dimetrodon incisivus*. A, palatal region as preserved. B, reconstruction of palatal region. Amer. Mus. 4636. × 1.

represented by Case and Broom. The basisphenoid is not as long as in Cotylosaurs but is still of similar form: broadening sharply behind, divided below in the mid-line, constricted near the front end and provided in front with two short but plainly differentiated basipterygoid processes. In front is attached a fairly long, somewhat upwardly directed parasphenoid, consisting of a thick, high, vertical plate, pointed anteriorly.

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1 See Anatom. Anz. 43, 1913, pp. 519–523.
The palate lacks the transverse; in this I can confirm Case and Broom. On the pterygoid broadly rests an epipterygoid, narrowing above. In *Dimetrodon* the epipterygoid bears on its medial basal surface the deep articular sockets for articulation with the basipterygoid processes. In *Theropleura* on the contrary these facets are found on the pterygoid itself. The appearance of the pterygoid and epipterygoid, as also the connection with the quadrate recalls, in a surprising way, the Parasuchia. In skull 4636 the left and right halves of the palate have been torn apart. By close examination one can easily discern how far the interpterygoid space extended and where the (opposite) bones in the midline again came together. The interpterygoid space reached nearly to between the internal nares, that is, considerably further forward than as represented by Broom. Case has not correctly represented the suture between the pterygoid and palatine. In the front half it runs forward parallel to the border of the interpterygoid space and further forward than as given by Broom, to the hinder angle of the internal naris, so that for a short space the latter is bounded medially by the pterygoid. Next the two pterygoids are shoved in, arrow-like, between the vomers. The narrow fore part of the [median] bridge between the internal nares is formed solely by the vomers; the latter meet the pre-maxillae at the front end of the bridge. These relations of the pterygoids and the mode in which the internal nares are bounded again strongly recall the Parasuchia. Without going into details it may also be said that the base of the cranium and the arrangement of the cranial nerve-exits likewise correspond extensively with the Parasuchia.

In the descriptions of the lower jaw the complementaré (coronoid) has hitherto not gained recognition, but I was able to observe it as a small narrow strip on the highest part of lower jaws 4034 and 4636. The long prearticular (= goniale Gaupp), which Case gives, I can verify.
Naosaurus (Edaphosaurus) pogonias Cope.

Figs. 48, 49.

Edaphosaurus (No. 4009) is a highly interesting but, unfortunately, strongly crushed skull. Case has discussed it thoroughly and Broome has given a reconstruction of it. Although the latter indicates the skull sutures very clearly, I cannot indeed see them all, yet I can in many points confirm his views.

Top and sides of the skull. Both external nasal openings are preserved.

Fig. 48. Naosaurus (Edaphosaurus) pogonias. Crushed skull, upper surface. Amer. Mus. 4009. Coffee Creek, Baylor Co., Tex. × 4.

In front of and between them are the premaxillae which are appressed and cuneiform between the nasals. Of the suture between nasals and frontals I can only see something at one place, in the middle, between the front borders
of the orbits. A narrow long adlacrymal can be traced on the right, from the orbits to the external nasal openings. The septomaxillary I can not surely establish, but I think I can see a small triangle in the upper front border of the adlacrymal, so that the latter could only have touched the nasal openings with its lower process. The long maxilla is notably low and is far separated from the orbits, especially by the jugal. The jugal borders the orbit with uniform breadth from below and to the middle of the front border, there meeting the notably broad surface of the adlacrymal. Below the rear border of the orbit the transverse process of the pterygoid bends down with an obtuse angle and continues down as a vertical piece. Here Broom's reconstruction seems uncertain. The beginning of a process that ran up to the hinder border of the orbit is present. Of the right lacrymal I can find in front only a small bit of the suture separating it from the nasal. It is possible that the frontal bordered a part of the upper rim of the orbit. The postfrontal begins in the middle of the upper border of the orbits and extends widely toward the middle of the skull-top, narrowing next to the hinder part of the frontals. Of the postorbital only the upper half is preserved; it runs beside the postfrontal and surrounds a small part of the temporal fossa. Below and behind it are broken surfaces. The parietals are pretty narrow, because the temporal fossae reach so far upward. Between them on the mid-line is a small parietal foramen. From below the supraoccipital intrudes between the parietals like a sharp arrow-point, appearing with its tip on the upper side of the skull. Pos-

![Image of Naosaurus (Edaphosaurus) pogonias. Crushed occiput. Amer. Mus. 4009. × 4.](image-url)
hinder corner of the skull, extending to near the foramen quadrati, without actually reaching it, and ending in a gentle expansion in a thick serrate suture. The bow-shaped bony piece only forms the border of the orbit in its upper half, from below upward as far as its middle; it is accompanied by a very narrow process from another bony element, which broadens near the lower end of the former and forms the beginning of a forwardly directed bony surface, ending in a broken surface and reaching either to or near the foramen quadrati. On account of their mutual relations I regard the latter as the squamosal and the former as the supratemporal. Behind the foramen quadrati lies the fairly long quadrate with its articular surface, but only above the foramen and up to the supratemporal are its lateral limits visible; below it is obviously fused with the quadratojugal; also the suture between the quadratojugal and the squamosal is not shown. Yet I do not doubt the presence of the quadratojugal, for without it a foramen quadrati would not be present. Between the squamosal and postorbital there must have been a bony bridge as the broken surfaces indicate.

Through crushing the originally high occiput has been disorganized: the exoccipitals with the base of the cranium have broken loose from the supraoccipital and on the right side are pushed under the right parietal process. The supraoccipital was very high. The exoccipitals meet above the foramen magnum.

To the right of the supraoccipital and separated from it by suture one finds below the parietal process and below the beginning of the supratemporal a vertically ascending bony strip, the longitudinal fibers of which beneath the parieto-supratemporal suture clearly change their direction; therefore this strip may consist of two elements of which the medial one may be the right dermo-supraoccipital and the lateral one the right tabulare. The latter would then lie in a normal manner above the paroccipital. The right stapes in fine preservation is still present in situ. The large fenestra ovalis is visible. The basisphenoid is similar to, but longer than, that of *Dimetrodon*. The appearance of the pterygoid with its anterior processes, and of the palatine, together with the dental pavement on both bones recalls *Dimetrodon*, only the transverse processes of the pterygoids are not bent so sharply downward. The lower jaw has the splenial dentition as in *Pantylus*. 
SHORT NOTES ON SOME OTHER SKULLS.

**Diplocaulus limbatus** Cope.

Fig. 50.

The skull of *Diplocaulus* has been frequently figured, most recently by Moodie (*D. magnicornis*). The species which I was enabled to study in New York differs a little from Moodie's representation of the elements between the orbits and the tip of the snout. There the short and broad paired nasals lie in front of the united frontals. Moreover the lacrymal and adlacrymal is present. And from Tübingen specimens of the same species I can add that paired and very low and broad premaxillaæ are also present. Postfrontal and postorbital can be distinguished above the jugal. Between the latter and the parietal lies the supratemporal. Between the parietals is seen a small parietal foramen. Next to the hinder half of the parietal follows the squamosal and quadratojugal. The long posterior horns are formed by the tabularia and behind the parietals are found the pair of large
dermo-supraoccipitalia. The supraoccipital I have not been able to distinguish since this part of the skull is always squeezed together. The two condyles are formed from the exoccipitals.

The palate is best known from Moodie's description. One of the lower jaw rami in Tübingen shows, besides the 26 teeth on the dentary, a second row of conical teeth near the symphysis; three of them nearest the symphysis are visible; I suspect that they rest on the splenial which reaches the symphysis. The same jaw shows a very large angular nearly reaching the symphysis, also the prearticular (= goniale), extending half the length of the jaw, and the great internal mandibular fenestra.

**Cricotus crassidiscus** Cope.

Fig. 51.

Concerning this species I can only confirm Case's description. A slight difference will only be found in the form of the postfrontal and postorbital. The skull of *Cricotus* shows very clearly the lateral line of the mucous canals. Skull 4551 shows this especially well. It runs up on the squamosal, then behind the hinder border of the orbits, downward and along the border of the jaw forward to below the nasal opening. Thence another canal branches backward at a sharp angle, running up on to the upper side of the skull, then again it turns somewhat laterally and vanishes above the upper border of the orbit.

The side view of the same skull No. 4551 shows posteriorly a deep otic notch which recalls *Dissorophus (= Otocelus), Aspidosaurus novo-mexicanus* Williston and especially *Seymouria (= Conodectes favosus* Cope).

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Seymouria (= Conodectes favosus Cope).

Fig. 52.

The skull of Conodectes favosus No. 4342 shows no sutures on the upper side. Yet it appears of interest to figure here, because according to Williston (Science, N. S., XXXIII, 1911, p. 631) the genus Conodectes is probably identical with Seymouria. The figure shows the characteristic deep otic notch.

The under-side shows the closed palate with widely extended pterygoids and the internal nares, which are separated by the vomers.
**Dissorophus mimeticus** Cope sp.

Fig. 53.

Although skull 4376 shows no sutures its form is well preserved. It is somewhat broader than long. Of special interest is the peculiar appearance of the otic notch, that is, the upper posterior corner of the skull (probably the tabulare), sends down a process which meets the quadrate and so by forming a shut off space simulates a temporal opening. But with such a fenestra the opening in question naturally has nothing to do. The same thing holds in *Cacops*. In the left otic notch one sees a long rod-shaped structure stretching from above and forward obliquely downward to the quadrate; this is probably the stapes. Something of this is also shown on the right side.
**Zatrachys microphthalmus** Cope.

Fig. 54.

Skull 4873 shows best the whole form of the *Zatrachys* skull, although no sutures are recognizable, because of a hard incrustation covering the whole surface. One sees the nasal openings, the orbits, the otic notches and the concave middle surface of the skull roof.

**Acheloma cumminsi** Cope.

Fig. 55.

Skull 4205 shows but very few sutures. The front half of the skull is restored in plaster to the border of the jaws. In the hinder half I can recognize only a few sutures which are reproduced in Figure 55. One may recognize the hinder end of the very low maxilla, the broad jugal below the orbits, the limits of the fairly small squamosal on the posterior corner of the skull and the upper border of the obviously very large quadratojugal, the full length of which is not evident. Above, on the hinder edge of the
skull appear the short, very broad dermo-supraoccipitals in a band running along the crest; the median suture is visible and one can also recognize the small parietal foramen.

Fig. 55. *Acheloma cumminsi*. Side and top of skull. Amer. Mus. 4205. Coffee Creek, Baylor Co., Tex. X 3.
Trimerorhachis.

Figs. 56, 57.

*Trimerorhachis insignis* Cope and *mesops* Cope show in skulls Nos. 4557, 4570, 4568, the conditions represented by Case, only with some supplementary data. The premaxillae are low and broaden and quite without median ascending processes; the broad nasals are inserted between them. *T. mesops*, No. 4568, shows very clearly the septomaxillaria on the hinder border of the nasal opening, with a forwardly directed tip. A small lacrymal and a large adlacrymal are present. The maxilla is extraordinarily low and very long. Still longer and broader is the jugal. A large postfrontal and a large postorbital are present. The frontals appear to be long and narrow. An oblique suture between the orbits, which I entered in my sketches in New York on the 4th of April, 1911, must be erroneous. Next to the parietals follow the supratemporal, squamosal and quadratojugal and behind them the dermo-supraoccipital and tabularia, as Case has indicated. The palate strongly recalls *Eryops*. The basisphenoid has broad basipterygoid processes. The lower jaw possesses prearticular and splenials which share in the symphysis. The great angular reaches to the middle of the jaw.

II. Remarks on Taxonomy.

**Lysorophus.**

*Lysorophus* is referred by Case and Williston to the Amphibia, and especially by Williston, in a convincing and positive manner, to the Urodeles. He says: “That *Lysorophus* is not a reptile requires no argument — the unpaired supraoccipital, the absence of pineal foramen, quadratojugals, jugals, postfrontals, temporal arches, the evidently large parasphenoid, the double occipital condyles, paired branchials, neurocentral single-headed ribs, etc., are positive evidence that the animal is not only not a reptile, but that it is related to the modern urodele amphibians.” Broili wished to put *Lysorophus* with the most primitive Rhynchocephalia; later he considered relationship with *Amphibisæna.*
Fig. 57. *Trimerorhachis insignis*. Top and underside of skull. Amer. Mus. 4570. Slippery Creek, Wichita Basin, Tex. × 1.
The earlier descriptions, together with the details which I have been able to contribute to our knowledge of the skull of *Lysorophus*, have established in my mind the definite conviction that *Lysorophus* belongs with the Amphibia in the neighborhood of the Urodeles. Although in external appearance the skull of *Amphisbaena* at first sight shows a certain resemblance to that of *Lysorophus* yet the base of the skull, with its large basi-occipital, which also forms the entire condyle is fundamentally different from that of *Lysorophus* described above; here the difference between Amphibian and Reptile is particularly decisive. When one compares Lysorophus with certain Urodele skulls the striking similarity and extended correspondence are immediately shown. For example *Amblystoma mexicanum* has the same form of skull, it also lacks the lateral ossification surrounding the eye. The maxilla is only connected with the upper skull roof by the tip of the lacrymal, otherwise it projects freely behind, only connected with the pterygoid by connective tissue. Also the rod-like forwardly directed quadrate is similar. Even the squamosal which adjoins the parietal and reaches down far upon the quadrate occurs in similar fashion in many Urodeles, as in *Sieboldia maxima*, *Menopoma*, *Siren* and *Triton*. The condyles in *Lysorophus* as in all the above named genera are formed from the exoccipitals and between them appears the basioccipital, mostly indeed only as a small cartilaginous piece. (Compare W. K. Parker: 'On the structure and development of the Skull in the Urodeles.' *Trans. Zool. Soc. London*, Vol. XI, Pt. 6, 1882). The large basi- and parasphe- noid are shown in all. In *Siren lacertina* there appears in the middle above the foramen magnum a triangular cartilaginous piece which probably corresponds to the supraoccipital, which in *Lysorophus* in contrast to most Urodeles, is still large and osseous. Through the presence of the large bony supraoccipital and of the supratemporal *Lysorophus* is distinguished from the recent Urodeles; but these are marks that stamp *Lysorophus* as a more primitive form, such as one would expect to find in ancient times.

A more precise grouping of the Lysorophidae within the Urodeles cannot be undertaken, since in all the great time interval between the Permian and the early Tertiary (except the Wealden) nothing is known of the Urodeles doubtless then existing, nor of their evolution and embranchment at that time. Moreover according to Williston, *Lysorophus* did not have a proatlas and whether it was limbless or provided with limbs is still not quite settled, since the extremities in Chicago and Tübingen might belong eventually either to *Lysorophus* or to the accompanying forms (*Gymnarthus*, *Cardiocephalus*, *Diplocaulus pusillus*); but from their association and size I regard it as probable that they really belong to *Lysorophus*.

With the Temnospondyli the Permian Urodele *Lysorophus* has still greater resemblances than it has with the modern Urodeles, on account
of the base of the cranium and of the greater number of posterior surface bones in the skull roof. The basioccipital in *Eryops* according to my representation is very nearly comparable with that of *Lysorophus*; also there is still present a paroccipital process as in the Stegocephala. The presence of the supratemporal indicates the relatively short road which the Permian Urodeles had travelled away from the branching place of the Stegocephala. The lack of the hypoglossus (see the description above) they share in common with the Stegocephala (*Eryops*) and with all Amphibia.¹

**Gymnarthus.**

On account of the base of the skull above described I also regard *Gymnarthus* as an Amphibian; but that is no reason for placing it in the order of Urodeles. Also the side of the skull around the eye is ossified as in *Cardiocephalus*. Although I have not seen the original of the latter I believe with Case that the two forms are nearly related. The quadrate and squamosal strongly recall *Lysorophus* and especially the Urodeles, but the great number of bones in the skull-roof, the circumorbital ossification, the dentition, the coronoid process of the lower jaw, find no equivalents among the Urodeles. Ossification has not only invaded the temporal region, but even the primary supraoccipital is largely covered by two dermo-supraoccipitals, so that the former only remain visible immediately above the foramen magnum and slightly below the latter. The whole arrangement of the skull bones is to be compared most closely with the Stegocephala or with the Cotylosaurs, which have much in common with each other. The principal distinction is found in the base of the skull and here (in *Gymnarthus*) the same thing is also true.

The systematic position of the Gymnarthridae within the Amphibia in the present state of our knowledge can unfortunately not be exactly defined. Only this can be said that they stand considerably nearer to the point of divergence of the Stegocephala and the Urodeles than do the Lysorophidæ.

**Diadectosauria.**

This group, proposed by Case, I can only confirm, not only from the forms of which I have studied the skulls (*Diadectes, Bolodon, Chilonyx, Bolosaurus*), but also from Williston’s description and figures of *Nothodon lentus* Marsh. *Nothodon* is the nearest relative of *Diadectes*. *Bolosaurus*, on account of its small size stands apart from the rest. Thus the two families Diadectidæ and Bolosauridæ appear to be natural divisions of the larger and equally natural group.

¹ More recently my view on the phylogeny is expressed in the article “Stegocephala” (1913) in “Handwörterbuch der Naturwissenschaften,” edited by Gustav Fischer, Jena.
Pareiasauria as limited by Case.

Here again, I rely chiefly on the American forms, the skulls of which I have studied. First we must premise that the South African Pareiasaurus according to Seeley possesses the entire assemblage of skull bones, as do the Diadectosauria. This, however, among the American forms referred by Case to the Pareiasauria is true only of Seymouria (including Conodectes). Isodectes by its large supratemporal is distinguished from all other forms except Pantylus. Since in the remaining skull structure Isodectes shows no important differences from Pantylus I would regard the two forms as probably nearly related. Of Pariotichus I have seen only indifferent skull parts which do not essentially distinguish it from Captorhinus, so that I would conceive these two genera as probably not widely removed from each other. In Captorhinus the dermo-supraoccipitals are limited to a narrow strip on the hinder border of the skull and the tabularia have vanished, the supratemporals are only present as small vestiges. That is very different from Pareiasaurus.

Captorhinus belongs on the limits of the Carboniferous in the Wichita beds and Pareiasaurus occurs on the other side of the ocean in formations of at least middle and upper Permian age; that is, the large animal, although provided with all the primitive skull elements, is not older, but on the contrary even somewhat younger, than the small animal which has almost entirely lost them; it follows that Captorhinus cannot belong in the natural phyletic series of the Pareiasauria. I would on the contrary infer that the Pareiasauria stand considerably nearer to the Diadectosauria than to the Captorhinidæ. Labidosaurus in a very natural way is connected with Captorhinus, for it is a more recent form (Clear Fork beds) of larger size and has lost the supratemporal rudiment, while the skull otherwise is quite like that of Captorhinus. The Pareiasauria are doubtless separate from the Diadectosauria as Case indicates, but so also are the Captorhinidæ. In the temporal region the latter have but one bone, the Pareiasauria have two; the Captorhinidæ have several rows of teeth in the upper and lower jaws, the Pareiasauria have only one; in the skeleton of the Pareiasauria no abdominal ribs are so far known; but the Captorhinidæ have them. There are also still other differences.

There yet remains Seymouria (= Conodectes) which by the deep otic notch, the differently constituted palate, cleithrum, etc., is essentially different from the Pareiasauria, so far, indeed that the two cannot be brought together in a natural genetic group.

So it appears to me that the suborder of Pareiasauria is not represented in North America by any of the genera included in it by Case, and that in the Permian period it remained limited to the old world.
PANTYLOSAURIA.

From the evidence already given, I would provisionally group here Isodectes and Pantylus.

PELYCOSAURIA.

The Pelycosaurs, which Broom and Williston unite with the South African Therapsida, collectively designating them as Thermorpha, no longer appear so unified as Case represented them five years ago. This is the result of the new discoveries by Williston (compare among others, Science, XXXIII; 1911, 632). To the Pelycosaurs in the narrower sense (Dimetrodon) one can no longer refer Edaphosaurus (= Naosaurus). Thus one may hold fast to Williston's procedure in treating the Edaphosauridae (= Naosauridae) as an equal group with the Pelycosaurs. According to Williston the Poliosauridae also (including Varanosaurus), the Caseidae and perhaps the Aëroscelidae are similar suborders. Multiplicity grows, but coherence also grows with equal pace. This knowledge we owe in recent years to no one more than to Williston.

III. MORPHOLOGICAL RESULTS.

1. Skull-base and occiput.

The foregoing investigations have resulted as follows: that in the Urodele Lysorophus, in the Amphibian incertae sedis Gymnarthus and in the Temnospondyl Eryops, the pair of condyles are formed by the exoccipitals; that nevertheless there is between them a small basioccipital, which is so covered by the hinder border of the basisphenoid that only a very small triangle on the ventral side is still visible. This is also the case (as in Eryops) in the frequently figured occiput of Mastodonsaurus robustus from the Lettenkohle (middle Trias) of Gaildorf in Württemberg, which is in the Tübingen collection. It would be desirable, therefore, to examine other well preserved Stegocephala, to see whether (as I suspect) a small basioccipital is always present, and likewise whether it is visible on the ventral surface or covered by the borders of the basioccipitals or exoccipitals. In the Cotylosaurs the exoccipitals have withdrawn further dorsal so that the condyle is formed from the basioccipital. The basioccipital is larger than in Eryops but nevertheless relatively small and the lamelliform hinder border of the basisphenoid covers it widely, especially on the sides.
In *Diadectes* itself the triangular surfaces are elevated, in *Eryops* they alone are the only part of the whole bone visible.

In the Pelycosauria (*Dimetrodon*) the basioccipital also is of considerable size; it forms only a spherical condyle; although it does not quite attain the size of the basisphenoid it is relatively larger than in the Cotylosauria.

The basisphenoid, in all the Temnospondyls, Cotylosaurs and Pelycosaurs that I have examined, is provided with fair sized or often even long basipterygoid processes. In the Temnospondyls the basisphenoid has increased chiefly in breadth, in the Cotylosaurs it has been greatly elongated. In the Cotylosaurs the basisphenoid is almost always constricted immediately back of the pterygoid processes. Among the Cotylosaurs the Diadectosauria are distinguished by the greatly broadened hinder part of the basisphenoid, while in the Captorhinidae the same is enormously elongate and relatively narrow. In the Pelycosaurs the hinder part is likewise strongly broadened; in front the whole bone narrows and the basipterygoid processes are directed not sideways but directly forward and there is no broadening of the bone.

The parasphenoid is lacking in none of these forms; as well known it contributes largely to the formation of the palate. This is the case to an extraordinary degree in *Lysorophus* and *Gymnarthrus*. In the Cotylosaurs and Pelycosaurs the parasphenoid is a vertically placed lamella of lesser length than in the above named Amphibians and Stegocephala.

The exoccipitals, which in the Urodeles and Temnospondyls form the paired condyles, extend upward near to and even quite above the foramen magnum, so that they nearly or quite come in contact above it in *Diadectes*, *Chilonyx* and *Dimetrodon*, although in the latter three only as small processes which lie on the lower border of the supraoccipitals. They (the exoccipitals) are frequently but not always united without suture with the paraoccipitals. In the exoccipitals of Pelycosaurs the last aperture for the paired cranial nerves forms the exit of the hypoglossus. In the Temnospondyl *Eryops* such an exit is surely lacking, as I was enabled to establish beyond doubt by the preparation of three brain-cases. It is also lacking in *Lysorophus* and *Gymnarthrus* as in all Amphibia. In *Diadectes* the hypoglossus foramen appears to me to be present, yet I can not affirm this with the positiveness with which I have stated the conditions in Amphibia and in Pelycosauria. As stated in the above mentioned description I think I can recognize in *Diadectes*, right near the border of the foramen magnum, a foramen, which if it really is a foramen, can be no other than that of the hypoglossus; moreover the brain cast shows the last lateral offshoot so far removed from the foramen magnum that it is almost certain that the last foramina present in the original must have been nearer the border of the foramen magnum,
only it could not have been cleared or worked out in this skull, and thus it would be exactly where one would look for the hypoglossus.

The stapes is present in the Temnospondyls, Cotylosaurs, Pelycosaurs (also in the South African Theromorphs, as recently admitted by Broom, who formerly regarded it as the tympanic); it is often of considerable size and with proximal perforation or deep notch.

The supraoccipital, a median primary cartilage bone, is present in *Lysorophus, Gymnarthrus, Eryops*. In the second it is excluded from the periphery of the foramen magnum by the exoccipitals and projects only in a narrow margin below the covering-bones. In the first and third of the named genera it narrowly touches the foramen magnum with its lower angle.

In *Diadectes* and *Chilonyx* there is a relatively small supraoccipital, broad above and plainly separated by suture, similar to that in the Pelycosaur *Dimetrodon*; in both there are specimens in which one can hardly if at all perceive the lateral and superior limits and the bone seems to fuse easily with the paroccipital. In *Captorhinus* and *Labidosaurus* the supraoccipital is narrow and pointed above; in *Edaphosaurus (= Naosaurus)* it is similar.

2. The covering (derm) bones of the hinder skull crest.

Here are included the dermo-supraoccipitals and the tabularia. The former name originated with Miall in 1878; in the last few years Broom calls them postparietals; they are often conceived as a paired supraoccipital but the latter is a cartilage bone and here we have to do with derm bones. The tabularia were formerly often falsely named epiotics, but the epiotics are cartilage bones and the tabularia are derm bones. Cuvier and Cope called this pair of bones intercalare, but the designation is ambiguous, because intercalary pieces are distinguished in the vertebral column and because Dreyfuss (1893) so named a cartilage piece of the middle ear ('Beitr. z. Entwicklungsgesch. d. Mittelohres u. d. Trommelfells d. Menschen u. d. Säugetiere.' Morphol. Arbeiten herausgeg. v. Schwalbe, 2, 1893); Cope finally used the name tabulare.

In the Temnospondyli these two pairs of bones, as is well known, are constantly present, in the middle of the hinder crest of the skull. They are sculptured like the other derm-bones. The tabularia often form angles or spine-like processes, which border medially on the otic notch. In the same manner they are found according to Broili and Williston in *Seymouria* as well as in *Aspidosaurus novomexicanus* and in *Trematos, Dissorophus, Cacops*, only in the last three genera peculiar processes are given off toward the quadrate of which nothing further is known. In *Eryops* the dermo-supraoccipitals can be distinguished from the supraoccipitals.
Both these pairs of bones are, however, not limited to the Stegocephala but are also found in many reptiles. All Cotylosaurs possess at least the middle pair. The Diadectosaurus possess large dermo-supraoccipitals which are also flanked externally by the great tabularia. The hinder limit of the dermo-supraoccipitals is completely clear in Diadectes, Nothodon (according to Williston), Chilonyx and also, according to Williston, in Limnoscelis. Considerably smaller in Captorhinus and Labidosaurus, the dermo-supraoccipitals are pushed back as narrow bands to the hinder crest of the skull, extending far over the same down on the posterior side of the skull. Here also they meet the unpaired true supraoccipital but are clearly defined from it. Here they appear to overlap each other only at their borders, but in the Diadectosaurus they lie one above the other, that is the scale-like dermal elements cover the supraoccipital with the greatest part of their surfaces; while the supra-occipital reaches nearly to the edge of the parietals and is actually considerably larger than it appears from the outside; this condition I have been able to verify in four skulls, so there can be no question of illusory appearances. Labidosaurus has no tabulare, but neither has Captorhinus, for I regard the small elements on the posterior corner of the skull as the supratemporal, for reasons given below. Seymouria (=Conodectes) has dermo-supraoccipitals and tabularia similar to those of Temnospondyls; in Isodectes the former are narrow bands on the posterior edge, the latter are wanting. In Parciasaurus both pairs of bones are known, of considerable size as in the Temnospondyls. From these indications the Captorhinidae appear less primitive than all the other Cotylosauria of the Permian; on the other hand the covering of the supraoccipital by the dermo-supraoccipitals in a flat overlap is probably not as primitive as the rectangular conjunction of these elements in Seymouria and the Temnospondyls. In the latter the occipital segment of the skull is still connected with the surface frame-work of the skull in such a way that metakinetin movement (Versluijs) of the skull is possible.

As more closely set forth above in the descriptive part, both pairs of bones are also present in the Pelycosaurs (Dimetrodon) and in Edaphosaurus (=Naosaurus). In Dimetrodon the tabulare still takes its normal position on the hind corner of the skull and above the paroccipital. The dermo-supraoccipitals which are shoved down on the back of the skull, as far as one can judge presumably cover the supraoccipital as flat scale-like elements, much as in the Diadectosaurus. Just as in Captorhinus and Labidosaurus the paired dermo-supraoccipitals are placed vertically on the hinder skull-crest and at a projecting angle between the parietals, so also the “inter-parietal” is placed in some of the South African Theromorphs. This, I hold, is the fusion-product of the paired dermo-supraoccipitals of the more
primitive Theromorphs; and that is a very satisfactory explanation of this otherwise strange element. The further conclusions which follow from the presence of the "interparietal" in certain mammals are likewise of a simple character.¹

A few words on Gymnarthrus and Lysorophus may be appended. In Gymnarthrus and Cardiocephalus a pair of dermo-supraoccipitals clearly follow behind the parietals; concerning the identity of these there can be no doubt; tabularia are wanting in Lysorophus but not in Gymnarthrus. In Lysorophus the median unpaired true supraoccipital extends forward narrowly in the median line, to the parietals; but on either side of it elements broaden out which not only lie entirely behind the parietals but also reach down from above to the roof-like part of the supraoccipitals; nevertheless I regard them as supratemporal-like part of the supraoccipital; nevertheless I regard them as supratemporal; because the undoubted squamosals in Lysorophus are pushed far back, while these elements (the supratemporal) lie at the sides of, and articulate with the squamosals, as well as with the parietals, although they also lie behind the parietals and bound the abnormally prolonged upper part of the supraoccipital.

3. Temporal Region.

Between the parietal, postfrontal, postorbital and quadrate in most of the forms here treated two temporal bones are interpolated; of these two the lateral one is the squamosal, the medial is the supratemporal. (The reasons in favor of this and against the reversed application of these names I have given elsewhere.) Only in a few forms is the supratemporal nearly as large as the squamosal: here belong among the Temnospondyls Tri-merorhachis, Zatrachys and Tersomius, among the Cotylosaurs Isodectes and Pantylus. Equal size of the two elements may be assumed as somewhat primitive, since it is apparent that the supratemporal in course of phylogeny has a tendency to disappear. In the majority of the Temnospondyls and Cotylosaurs the supratemporal is a small squamous element, which is situated on a line between the tabulare and the postfrontal and where the tabulare has vanished, it appears on the hinder crest of the skull next to the dermo-supraoccipital, and in front of its outer end. (The latter is never the case with the tabulare, since as a derm-bone covering the paroccipital it is fastened exclusively to the corner of the skull.) The squamosal, as the derm-bone covering of the quadrate, forms not only the long, often posteriorly directed, lateral ascending part of the hinder edge of the skull but also a broad surface toward the postorbital. The upper end of the quadrate in

*Diadectes* is articulated below the squamosal in a glenoid-like depression of the latter.

It is only in *Seymouria (= Conodectes)* among the Cotylosaurs and in a few Temnospondyls that one finds between the supratemporal and the postorbital still a third bone in the temporal region, namely the intertemporal of Broili. This is much rarer and more inconstant than the supratemporal. Possibly one may conceive this bone as the remnant of a second osseous ring around the orbit; I do not at any rate regard it as a temporal bone. In those forms in which the derm-bones lying behind the parietals are beginning to diminish and disappear, the squamosal increases at the expense of the supratemporal; in *Captorhinus* the squamosal covers the whole temporal region and the supratemporal has sunk to a minute vestige: in *Labidosaurus* even this is lacking. That the little ossicle in *Captorhinus* is really the supratemporal and not as Case and Branson assume the tabulare, follows from this, that it lies not right next to but principally in front of, the lateral end of the derm-supraoccipital. These vanishing elements push their way back to the hinder skull crest and there become lost; the supratemporal follows; the reverse case according to my knowledge does not occur. The intertemporal, which is probably of another origin, does not follow this road.

In *Lysorophus* and *Gymnarthrus* the squamosal is revealed with special clearness as primitively the derm-bone that covers the quadrate. The upper end of the quadrate lies beneath the same; this is true in both genera. *Gymnarthrus* and *Lysorophus* still possess besides the squamosal large supratemporals; because of their position between the squamosal and the parietal this identification is practically certain. It is true they are lateral to the dermosupraoccipitals in *Gymnarthrus*, but they push their way so far between the two above named pairs of bones, that they cannot possibly be tabularia. Hence it follows that *Gymnarthrus* is considerably more primitive than *Lysorophus*, for *Gymnarthrus* also has the dermo-supraoccipitals in their normal position which is not the case in *Lysorophus*, and the same is true of the tabularia.

In the zygodactyphous Pelycosaurs and Edaphosaurs (Naosaurs) the temporal region is important because of the forms of the temporal arches, consisting of long narrow connecting pieces. In *Dimetrodon* directly behind the processes of the parietal and postorbital is the supratemporal and below that the squamosal, which shares in the boundary of the infratemporal fossa. The latter stands in relation with the jugal and through the quadratojugal, with the quadrate. There is no need at all to assume an abnormally placed quadratojugal or bones which are otherwise not present ("prosquamosum") on the contrary everything is explained quite naturally and with-
out disregarding the relations with other groups. The small quadratojugal, on which part of the differences of opinion have turned, was first figured by Case, but was later contested, then it was observed by Broom and afterward I thoroughly convinced myself from a number of skulls in more than one collection and could definitely establish its individuality in all. In Dimetrodon and Edaphosaurus (= Naosaurus) supratemporal, squamosal and quadratojugal are certainly present, in the manner described above, as the sutures could be followed all the way around. Not on the same plane of certainty is the participation of the tabulare in the hind corner of the skull, since I could not follow the suture all around; yet I am convinced of its presence in that neighborhood.

In Naosaurus (Edaphosaurus) the enclosed temporal opening is somewhat differently bordered than in Dimetrodon. Postorbital and supratemporal do not occur on the upper border, on the contrary they do not reach it, so that the parietal intrudes between them and the border of the temporal opening.

The temporal arch, which bounds the temporal opening below, is indeed broken off, but is not difficult to reconstruct as follows: on the hinder end of the arch the squamosal is just beginning, therefore it probably formed the entire arch; at the other end the arch met the postorbital; however, as this has a piece extending far upward, we no longer look for the opposing process of the squamosal. Such an arch is customarily called the upper arch, yet the postorbital is directed away from the temporal arch, upward. Similar conditions obtain in Tapinocephalus. Moreover, Naosaurus (Edaphosaurus) has a sharply down-turned jugal, a quadratojugal (from the presence of the foramen quadrati this may be inferred with certainty, although the suture is not recognizable).

This condition in Naosaurus (Edaphosaurus), which an upwardly turned postorbital (a character which I once held as decisive for the recognition of a lower temporal opening) have convinced me that in the monозygocrotaphous forms one can not indisputably distinguish those with only an upper arch from those with only a lower arch, which I once thought with Broom I could do (cf. Erythrosuchus, 1911). Tapinocephalus would not have convinced me of this, as its postorbital is directed upward. There are, however, other forms such as Diademodon in which the postorbital gives off equally long processes upward and backward to the squamosal. The form of the postorbital shows plainly that the temporal opening arises now higher, now lower, but it now seems to me that this relativity does not suffice to homologize the single opening with either the upper or the lower one. The fact remains that there are forms so constituted, as if they possessed only one lower or only one upper temporal opening.
and which thoroughly support such a proposed homology (for example the temporal opening of Dimetrodon is without question constituted like a lower one while that of Deuterosaurus, in case my reconstruction of 1911 is correct, is an upper one). And yet I am coming to Williston’s opinion that this difference is not of phylogenetic importance and thus that two groups of zygocrotaphous forms were not separated off from the primitive ste gócrotaphous forms, nor did the two later go through a separate phyletic history.

It has already been set forth above that the openings in the hinder lateral halves of the skull roof in some specimens of Diadectes (which, however, are surely lacking in other individuals) should not be regarded as temporal openings, since they do not lie between the postfrontal and postorbital on one side and the supratemporal and squamosal on the other, but far behind these. So no matter how alluring the idea would be, these structures do not give us the first beginnings of these temporal vacuities.

4. Lacrymal and Adlacrymal.

Next I may refer again to the fact that I here use the designation lacrymal for the bones hitherto called prefrontals and adlacrymal for those hitherto called lacrymal. E. Gaupp has shown the identity of the reptilian prefrontal with the mammalian lacrymal (Anatom. Anz., XXXVI. 1910, p. 529–555). He says in summing up: “Both bones arise as derm-bones on the hinder portion of the nasal capsule and the naso-lacrymal duct lies essentially outside of them. In Sphenodon and in most lizards and birds the duct simply remains in position on the external surface throughout life; but in the mammals there follows a more or less complete overgrowth of the duct by the bone, from within, a process also observed in some Sauropsida (snakes, Ascaloba (Geckos), Dromæus, Casuarius). That this constitutes a pure convergence phenomenon is certain. In this connection we note the circumstance that the prefrontal in the Sauropsida is a very constant element of the skull, while the so-called lacrymal of the Sauropsida is limited to certain groups: among recent forms to a number of families of lizards and to the crocodilia. It would be, if not impossible, at least remarkable, if the element which is constant in all Sauropsida should vanish in the mammals, and the inconstant element should have attained so general a distribution among them. This view, however, is completely refuted by the topographic relation of the Sauropid lacrymal to the nasolacrymal duct and to the nasal capsule.” The now free element which Cuvier identified with the mammalian lacrymal must be named anew. Jaekel (1905) has named it postnasal, but this designation is very misleading since the bone certainly never lies behind the nasals, so Gaupp has proposed to call it adlacrymal. Against
this later change of name (1910) there is no objection, since the principle of priority has never been applied unconditionally to technical terms, and in consequence of the misleading etymology the exception is thoroughly justified.

It can be established that with one exception in all the forms here studied the adlacrymal reaches from the orbits to the nasal opening and that the lacrymal is always limited to the vicinity of the orbit and always remains far removed from the nasal opening. Only in the gymnocrotaphous Urodele *Lysorophus* is an adlacrymal wanting and here the lacrymal reaches to the nasal opening and restores the bony connection of the maxilla with the skull roof.

5. *Setpomaxillary.*

The presence of the septomaxillary has been shown among the Temnospondyls in *Eryops* and *Trimerorhachis*, in the Diadectosauria *Bolbodon*, in the Captorhinidæ *Captorhinus* and *Labidosaurus*, in *Dimetrodon* and in *Naosaurus* (*Edaphosaurus*.) It appears accordingly to belong in the fixed osteological inventory of the primitive reptiles.


The pterygoid in *Diadectes*, *Dimetrodon* and *Naosaurus* (*Edaphosaurus*) extends much further forward than has previously been supposed. The antero-median processes which form the ascending lamellæ in the two last named genera extend to a point between the internal nares, and to the same processes in *Diadectes* belong two-fifths of the part formerly ascribed to the vomers. The presence of teeth on these median lamellæ in *Diadectes* is the rule. The transverse and a postpalatine perforation are shown in *Diadectes*.

7. *The lower jaw.*

In Temnospondyls, Cotylosaurs and Pelycosaurs, the lower jaw without exception consists of articular, prearticular (= goniale Gaupp), angular, supraangular, dentary, splenial and complementare (coronoid). The Meckelian groove is always large. The splenial reaches the symphysis and in many cases bears teeth. A coronoid process is more or less strongly developed. In the Cotylosaurs there is a medial perforation between the front ends of the prearticular and of the angular. The lower jaw is similarly constituted in the Microsaur *Diplocaulus* and in the Urodele *Lysorophus* so that one can say that this is the most primitive form of the lower jaw.
IV. Bibliography.

The three works at the head of the following list are on the whole the most important and contain the chief bibliographic resources; the present list includes only works of later date.


Branson, E. B. Notes on the osteology of the skull of Pariotichus. Journ. of Geol., March, 1911, XIX, pp. 135–139, pl. i.


