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Article XX.— A COMPARISON OF THE PERMIAN REPTILES OF NORTH AMERICA WITH THOSE OF SOUTH AFRICA.

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Historical — South African Permian Reptiles.

The first discovery of fossil reptiles in South Africa was made by A. G. Bain in 1838, when he found the large skull which in 1876 became the type of *Pareiasaurus serridens*. Bain, who is regarded as the Father of South African geology not only gave the first detailed account of the South African formations — an account which the latest work has proved to be surprisingly accurate — but it is to him that the discovery of most of the Karroo fossil reptiles in the British Museum is due. Almost all his specimens he sent to Owen by whom they were ultimately described and the indebtedness of Science to Bain has been fully acknowledged.

To Owen is thus due almost all that has been known of South African Permian forms till comparatively recent times. In 1845 he described two species of *Dicynodon*, and in 1855 another species. In 1859 he founded the order Anomodontia for the reptiles with an anomalous dentition, including under it the "families" Dicynodontia for *Dicynodon*, Cryptodontia for *Oudenodon* and Gnathodontia for *Rhynchosaurus*. In 1860 he described two reptiles with a mammal-like dentition, *viz*: *Galesaurus* and *Cynochampsa*, and in the same year three species of *Oudenodon* and two of *Ptychognathus*. The following year he added the "family" Cynodontia to the Anomodontia for the reception of *Galesaurus* and *Cynochampsa*. In 1876 Owen published his large catalogue of the South African fossil reptiles in the British Museum which is the most important work that has appeared on the Karroo reptiles. He gives descriptions of *Pareiasaurus* and *Procolophon*, of *Tapinocephalus*, and of the imperfect skulls of a large number of mammal-like reptiles. Among the Anomodonts in addition to a large number of new species of *Dicynodon*, *Oudenodon* and *Ptychognathus*, he describes the new genera *Endothiodon* and *Cistecephalus*. In one or two respects later work has shown that his classification in unsatisfactory. Thus *Tapinocephalus* and *Pareiasaurus* he regards as types of two new "families" of the Dinosauria, while all the reptiles with mammal-like dentition are grouped together under the new order Theriodontia. *Procolophon* is also included in the Theriodontia, and

Saurosternon is placed with the Labyrinthodonts. Notwithstanding these defects almost all subsequent work has been merely a further building on the foundation laid by Owen.

Seeley came out to South Africa in 1889 and obtained, principally through Mr. T. Bain, Dr. Kannemeyer, and Mr. A. Brown a fairly large collection of fossil reptiles. Most of these and a number of specimens belonging to the South African and Albany Museums were described by him between 1889 and 1895. His most important work on the Permian reptiles is a description of a fairly good skeleton of *Pareiasaurus*. He described *Delphinognathus* from a skull in the South African Museum and founded for it the suborder Dinocephalia. He contributed a good deal to our knowledge of the Anomodont skeleton and described a number of new genera, including *Eunotosaurus, Cryptocynodon* and *Pristerognathus*. The most important part of Seeley's work, however, deals with the Upper Triassic types such as *Cynognathus* and *Gomphognathus*. He suggested various new classifications but these have not been generally accepted.

In any historical sketch of the South African reptiles must be mentioned the name of Lydekker, who in 1890 published a new catalogue of the specimens in the British Museum. He described very few new forms, and was more impressed by resemblances than differences. His revision of Owen's types has led to the elimination of a considerable number of doubtful species and to a clearer understanding of the early types.

During the last ten years I have been enabled to throw some further light on the structure of the Permian reptiles and have described a considerable number of new forms. As regards classification, I have thought it well to retain the name "Anomodontia" for the *Dicynodon*-like forms, as originally intended by Owen, and it has been found necessary to divide Owen's Theriodontia into two, as the Permian forms have among other characters a Rhynchocephalian palate, while the Triassic forms have a secondary palate like mammals. For the earlier group I have proposed the name "Therocephalia," and for the latter group Owen's name of 1861 "Cynodontia" should be retained. The name "Theriodontia" becomes unnecessary and should be dropped. The various orders or suborders of mammal-like reptiles — Dromasauria for *Galechirus*, Dinocephalia for *Delphinognathus*, etc., Therocephalia for *Scylacosaurus*, etc., Anomodontia for *Dicynodon*, etc., and Cynodontia for *Galesaurus*, etc.— I have proposed to group under a single superorder or order, the "Therapsida."

Historical — American Permian Reptiles.

Our knowledge of the American Permian reptiles is mainly due to Cope, who first described them, and who between 1878 and 1894 published many papers dealing with the structure, affinities and classification of the groups. Case, in his recent memoir on the Pelycosauria gives a full historical account of Cope's work, and of the frequent modifications of his opinions as his investigations proceeded. None of his numerous attempts at classification appear to have long satisfied even himself, and one can fully sympathise with his difficulties. When he first examined such types as *Clepsydrops, Dimetrodon, Diadectes,* and *Pariotichus,* he was apparently struck by the fact that while in many ways they seemed related to each other, they also showed affinities with the Rhynchocephalia on the one hand and the South African Theriodonts and Anomodonts on the other. In all his proposed classifications we see an endeavour to express these affinities, while at the same time differentiate the groups. The order Pelycosauria was primarily established for reptiles resembling *Clepsydrops* and *Dimetrodon,* but for a time genera such as *Pariotichus* and *Diadectes,* and the South African Theriodonts, were also included in it. Later on *Diadectes* was placed in a new group, the Cotylosauria, which though temporarily abandoned was ultimately extended to include all the Permian reptiles with a roofed temporal region. Very early Cope was struck by what appeared to be the mammalian affinities of most of the Permian types and proposed the name Theromorpha, afterwards changed to Theromora, for all the mammal-like forms.

Between 1889 and 1897 Zittel, Lydekker, Seeley, and Haeckel supported the view that the order Pelycosauria was probably identical with the Theriodontia of Owen and allied to the Anomodontia, and the name "Theromorpha" or "Theromora" was very generally used to include almost all known Permian reptiles.

In 1897 Baur and Case believed they discovered in *Dimetrodon* two temporal arches, and argued that the Pelycosaurs were more nearly related to the Rhynchocephalians, and should be removed from association with the mammal-like Theriodonts and Anomodonts. Since then most writers, including Smith-Woodward, Hay, Zittel, Osborn, McGregor, Boulenger, Case, and Broom, have agreed in separating the Pelycosaurs from the South African type. A few however — Gadow, Broili, and v. Huene — still favour the older view.

In 1904 Broili published a most important account of the Permian reptiles of Texas. Besides giving descriptions of a number of new types he added much to our knowledge of the structure of others, especially *Labidosaurus.*

Case, in 1907, issued his 'Revision of the Pelycosauria of North America,' in which he critically re-examines all Cope's specimens and most of those more recently obtained. Besides giving a complete systematic revision of all the known genera and species, he deals at length with the structure and morphology of the different types. His figures of complete restorations of *Naosaurus* and *Dimetrodon* give a better idea of the general appearance of the Pelycosaurs than was previously possible.

South African Permian Fauna.

Before comparing the North American and the African Permian faunas it will be necessary to examine in some detail the structure of the most typical and best known genera of each continent.

South Africa during the whole of Permian times was almost completely covered by a large fresh water lake or series of lakes or marshes. Enough is not yet known of the geology of the Karroo to say definitely what the conditions of deposit were, but the shales which are found over the greater part of the country were probably formed by the mud brought down by some huge river or rivers and deposited in a shallow lake. Irregular beds of sandstone are found throughout the whole formation, varying in thickness from a few inches to many feet. The sandstone beds often abruptly pass into shale, and they usually show signs of false bedding. Possibly the sand was wind-blown over the dry banks of mud during periods of drought. However the sandstone may have been formed it is interesting to note that reptilian remains are usually found in the shale immediately below a bed of sandstone and sometimes in the sandstone itself, but very rarely in the middle of a very thick bed of shale. Most probably the reptiles lived and died on the banks of the swamps or lagoons, and their bones became preserved in the mud and sand.

In Upper Carboniferous and Lower Permian times the climatic conditions were unfavourable for land animals and though the geological conditions were ideal for their preservation few land forms are met with till we reach beds which are probably Middle Permian. The first forms we find are two large imperfectly known Dinocephalians, one of which has been named *Archæosuchus*, and a huge Diaptosaurian, *Eccasaurus*. Other small animals are only known by fragmentary vertebræ and limb bones. In the north of the colony, on a horizon which at present cannot be correlated with certainty with those of the southern Karroo but probably of Middle Permian age, we find remains of *Galechirus*, and *Galepus*, primitive Therapsidans, *Heleosaurus* and *Heleophilus*, two possibly semiaquatic Diaptosaurians, and a small species of *Oudenodon*.

In the south, at a horizon probably 2000 feet above that in which the Dinocephalians first appear, we begin for the first time to get an abundant fauna. *Pareiasaurus,* of which at least two species are known, is not uncommon. The gigantic *Tapinocephalus* and the smaller but allied *Delphinognathus,* the large imperfectly known *Titanosuchus* and the small *Gorgonops* represent the Dinocephalians. A few small species of *Dicynodon* and *Oudenodon* are met with, and a large number of rather small Therocephalians. From the same horizon only one Stegocephalian genus is known, *Rhinesuchus.*

In the Upper Permian beds the Anomodonts become abundant. Many species of *Dicynodon* and *Oudenodon* are found, some fairly large. Besides these, are many other Anomodonts which though unknown in the older beds are clearly of a more primitive type. These are included in the family Eudothiodontidæ and differ from *Dicynodon* and *Oudenodon* in having molar teeth. A considerable number of genera are known. Numerous Therocephalians are found in the Upper Permian beds, but their structure is imperfectly known. A small reptile, *Saurosternon,* is found which is now known to be allied to *Procolophon. Pareiasaurus* is no longer met with but two allied genera, *Propappus* and *Anthodon,* are known.

As in the present paper I only wish to show that the South African fauna is distinctly related to that of the Permian of North America I shall confine myself mainly to the consideration of the skulls of a number of the more important types and endeavour to show that the American types are in many ways singularly like those of the South.

Pareiasaurus.

Though four fairly good skeletons of *Pareiasaurus* have been discovered which reveal most of the general structure of the skeleton there are many details of which we are still ignorant.

The skull is large with the temporal fossæ completely roofed over, but the detailed structure of the roof is still doubtful. There appears, however, to be little doubt that there is a quadrato-jugal. The bones are pitted somewhat like those of Stegocephalians. There is a distinct septomaxillary. The palate is fairly well known and as shown in the figure (Fig. 1) has the typical structure met with in most primitive reptiles. There are paired prevomers bearing teeth, paired palatines probably also bearing teeth, and apparently small transpalatines. The pterygoids are fairly large and have rows of small teeth.

The occipital condyle is flat.

The vertebræ are large and massive and have intercentra. The zygapophyses are very broad. The ribs for the most part are single-headed.

The shoulder girdle has a large scapula with a well developed acromion, large precoracoid and fairly large coracoid. There is well developed cleithrum, fairly large clavicles and a massive T-shaped interclavicle.

The humerus is very massive and has a large deltopectoral ridge. The ulna has an olecranon process.

The carpus, so far as known, appears to be similar to that of most early reptiles.

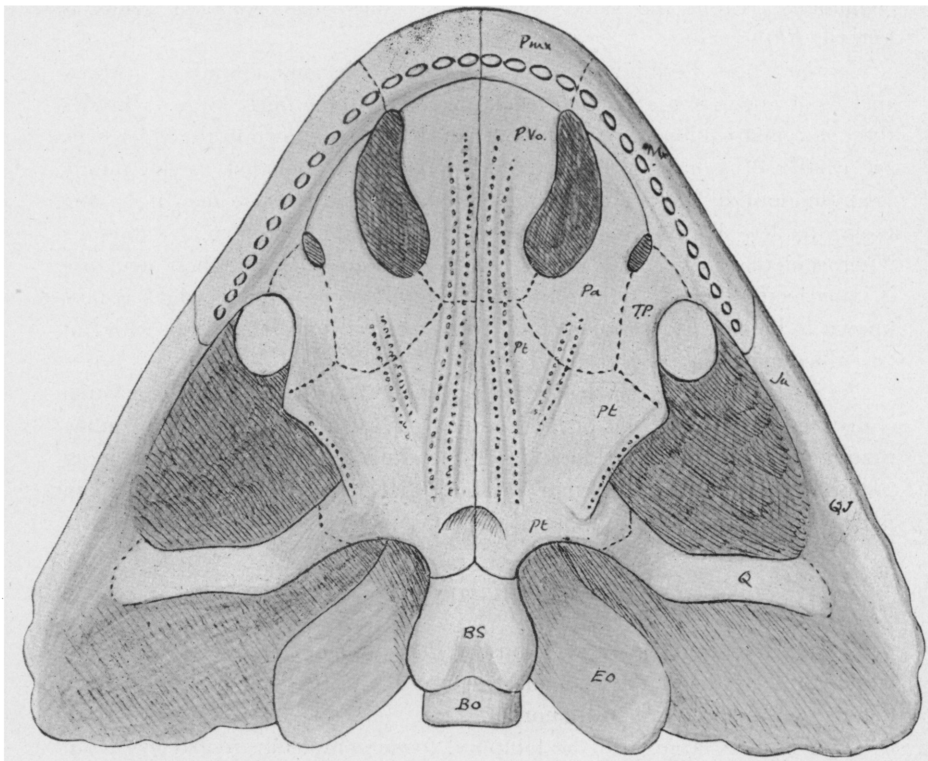

Fig. 1. Under view of skull of *Pareiasaurus*. Slightly restored.

The digital formula is unknown. It has been stated to be 2, 3, 3, 4, 3, but in the closely allied *Propappus* it is most probably 2, 3, 4, 5, 3, two digits having certainly more than 3 phalanges.

There are apparently no abdominal ribs.

The pelvis is remarkable for having the ilium large and directed forward as in Mammals and the higher Therapsida.

The teeth are peculiarly specialised. Externally they are markedly convex, the inner side being nearly flat. Round the edges are 7 or 9 large cusps arranged in a semicircle.

Procolophon.

Procolophon is a small lizard-like reptile with a large broad head and comparatively short limbs, which, though only known from the Middle Triassic beds of the Karroo, may be considered as a Permian type which has survived. *Saurosternon,* which undoubtedly occurred in Permian times, is apparently pretty closely allied, but is less perfectly known.

The skull, which forms the type in the British Museum, though very fine has been somewhat injured in preparation and much of the bone removed. This has resulted in two small lateral temporal vacuities having been artificially produced. In all specimens where the temporal region is perfectly preserved there are no vacuities. Though *Procolophon* has been somewhat specialised in one or two respects the skull shows most of the features that must have been present in the ancestral Diaptosaurian. The premaxillary and maxillary are well developed. There is a small septomaxillary. The nasals are large. There are distinct lachrymals, prefrontals, postfrontal and postorbitals. The squamosal is small and there is a large quadrato-jugal which in many skulls, probably males, forms a large lateral horn. There is a well developed superficial bone doubtless corresponding to the so called "epiotic" of the Stegocephalians but which had probably better be called posttemporal. The temporal roof is narrow owing to the very large size of the orbit, but it is interesting to note that it is formed by the very same bones as in *Sphenodon,* viz., squamosal, quadrato-jugal, jugal and postorbital, the chief difference being that in *Procolophon* the bones are close together, whereas in *Sphenodon* they are pushed apart by the development of two large temporal vacuities.

The palate is a modification of the Rhynchocephalian type. The premaxillaries have large palatine processes. The prevomers are large and have a number of teeth as shown in the figure (Fig. 2). The palatines are small and have a few teeth. The pterygoids do not extend so far forward as in the typical Rhynchocephaloids. They meet the prevomers in front and the quadrates behind. They bear a few teeth. There is a small but distinct transpalatine which with the pterygoid forms a well marked pterygoid process. There are feeble, very lizard-like epipterygoids. The parasphenoid (true vomer) is present but small. The occipital condyle is single and rounded.

There is a distinct proatlas; and the body of the atlas is already united to the axis to form an odontoid process. There are well developed intercentra, and both the cervical and dorsal ribs are single-headed.

The shoulder girdle has a short scapula, and well developed coracoid and precoracoid which remain distinct throughout life. There are no cleithra, but well developed clavicles and interclavicle.

The digital formula is 2, 3, 4, 5, 3–4.

The pelvis has plate-like pubis and ischium.

There are numerous small abdominal ribs.

There has been much discussion as to the systematic position of *Procolophon*, but if we recognize that on the one hand it comes near to the primitive Rhynchocephalians and on the other retains characters of the

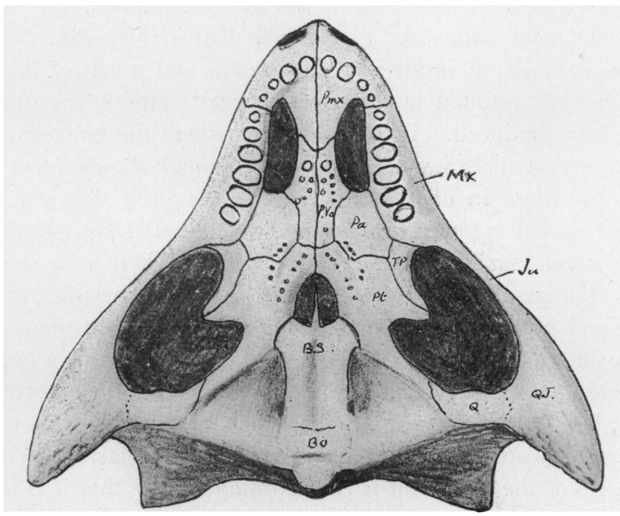

Fig. 2. Under view of skull of *Procolophon trigoniceps* Owen. Supposed male. Nat. size.

primitive roofed types it matters little with which division it is placed. It certainly seems to me nearer even to the living *Sphenodon* than it does to *Diadectes* or *Pareiasaurus*.

There are a number of other primitive Diaptosaurians or advanced Cotylosaurs in South Africa but they are imperfectly known. The best known are *Mesosaurus, Heleosaurus, Heleophilus,* and *Saurosternon.*

Dromasauria.

This suborder was proposed by me for the small primitive mammal-like reptile *Galechirus*, which though essentially allied to the more typical Therocephalians shows a number of more primitive characters. Though most of the skeleton of *Galechirus* is known, unfortunately we know little of the skull. Just recently however, a new specimen has been discovered of an allied genus in which the skull is well preserved. This new animal I propose to call **Galepus jouberti**. It is about the same size as *Galechirus scholtzi* but differs in a number of respects.

The skull is extremely interesting. In general shape the snout is somewhat lizard-like and the orbit is very large (Fig. 3). The temporal fossa is about half as large as the orbit. The parietal region is broad with a large pineal foramen. As in the Anomodonts, the postorbital meets the squamosal, and the squamosal is large and extends down by the side of the occiput a

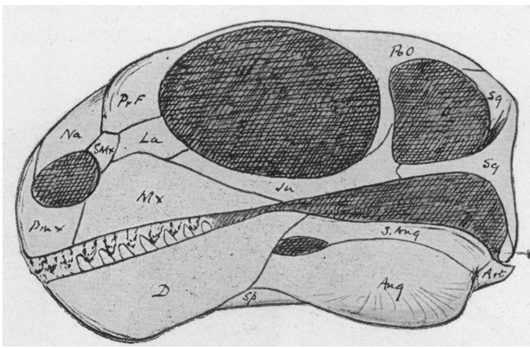

Fig. 3. Skull of *Galepus jouberti* Broom. × $\frac{5}{3}$. Slightly restored.

considerable distance below the jugal arch. There is no quadrato-jugal. The lower jaw has the angular and surangular together as large as the dentary, and there is practically no coronoid process. The canines are not enlarged.

The shoulder girdle is of the ordinary Therapsidan type, but it is doubtful whether there is any cleithrum.

The digital formula is 2, 3, 3, 3, 3.

There are abdominal ribs in both *Galechirus* and *Galepus*.

In the possession of abdominal ribs, the simple plate-like pelvis, the generalised dentition and the separation of the maxilla from the nasal by the septomaxillary and the lachrymal, the Dromasauria are more primitive than any of the other Therapsida.

Dinocephalia.

The order or suborder Dinocephalia was proposed by Seeley for reptiles of the type of *Delphinognathus* and *Tapinocephalus*, and though when it was proposed it was impossible to characterise it satisfactorily there is little doubt that these genera can very conveniently be placed in a distinct suborder. The other genera which seem to fall into the same group are *Titanosuchus*, *Scapanodon*, *Pelosuchus*, *Archæosuchus* and *Gorgonops*. It is possible that the Russian forms *Deuterosaurus* and *Rhopalodon* also belong to the *Dinocephalia* but at present they are only very imperfectly known.

In *Tapinocephalus* and *Delphinognathus* the skulls are fairly well known, and as they are closely allied, between them we have revealed most of the points of structure.

The bones of the upper cranial wall are enormously thickened and the pineal foramen is very large (Fig. 4). There is a single temporal fossa bounded by the squamosal, parietal, and postorbital. The squamosal is very large and the descending part passes so far forward as to carry the

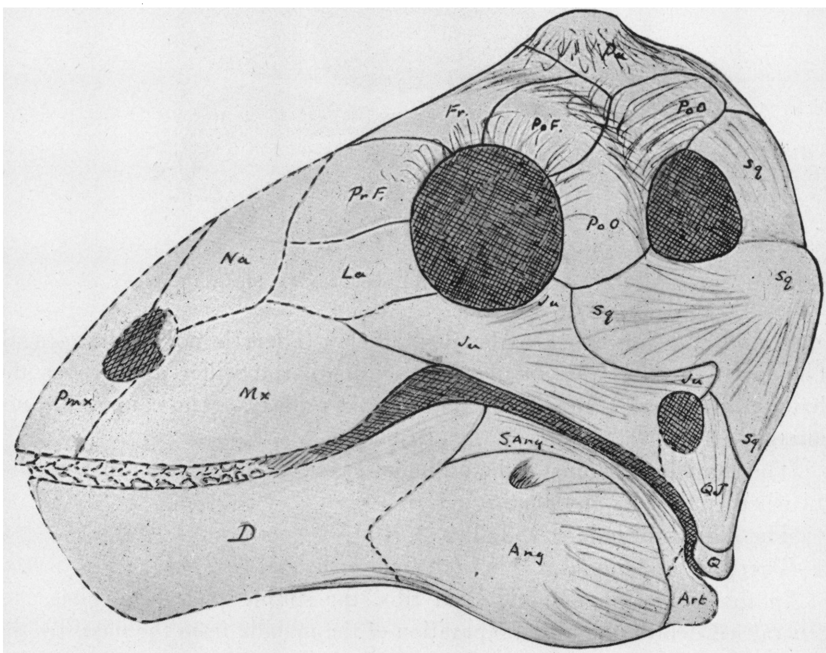

Fig. 4. Skull of *Delphinognathus conocephalus* Seeley. About ⅓ nat. size. Restored in front.

quadrate almost under the orbit. A well developed quadrato-jugal is present in *Delphinognathus*.

The palate is a little like that of *Procolophon* but differs in there being no teeth on any of the bones and in the absence of a transpalatine.

The occiput is very wide, the lateral portions being formed as in the Anomodontia by the squamosals. The condyle is single and rounded.

The lower jaw has a large angular and surangular and a very large articular which together form more of the jaw than the dentary. There is no distinct coronoid process formed by the dentary. The teeth are not, in *Delphinognathus* at least, differentiated into incisors, canines or molars; but in *Titanosuchus, Gorgonops, Archæosuchus* and *Scapanodon* there are specialised canines.

The vertebræ are remarkable for the great development of the transverse processes which resemble those of the Pelycosaurs, the spines are, however, by no means unusually large.

The shoulder girdle has a large scapula, coracoid and precoracoid. There is a feeble cleithrum, powerful clavicles, and a large interclavicle.

There is no evidence of abdominal ribs.

Therocephalia.

This suborder of the Therapsida was proposed by me in 1903 for those mammal-like reptiles which have differentiated incisors, canines, and molars, and a palate of the Rhynchocephalian type.

For long the Permian mammal-like forms with the open palate were grouped with the upper Triassic forms which have a secondary palate, under the name Theriodontia. When it was recognised that the Permian types differed greatly from the Triassic the name Therocephalia was proposed for the primitive group and, as had been previously done by Seeley, Owen's older name of Cynodontia was applied to the higher forms. This adoption of the name Cynodontia is all the more justifiable since the first animal described by Owen with mammal-like teeth was *Galesaurus,* which is a typical Triassic form.

Most of the early described Therocephalians were too imperfect to reveal much of the essential structure and even now little is known of the skeleton except the skull, and that is only fairly well known in four genera, *Scylacosaurus, Lycosuchus, Aloposaurus,* and *Scaloposaurus.*

Scylacosaurus sclateri is known by a nearly perfect skull, and by an imperfect one which, however, shows the palatal structure. In general proportions the skull is fox like (Fig. 5). The maxillary is large, the premaxillary rather small, and there is a distinct septomaxillary. The jugal arch is fairly strong. The frontals are long but narrow. There is a distinct postfrontal and a small postorbital. The pineal foramen is large, but relatively smaller than in the Dinocephalia or Dromasauria. The squamosal is large and the quadrate small. There is no quadrato-jugal.

The palate has a pair of very long prevomers without teeth, and a pair of large palatines, also without teeth. The pterygoids pass forward between the palatines to meet the prevomers. They have an external process which meets the transpalatine, and a posterior process which extends to the quadrate. There are a number of small teeth on the pterygoid. There is a well developed distinct transpalatine which stretches from the jugal and palatine to the external process of the pterygoid and forms the wall of a large posterior palatine vacuity (Fig. 6).

The lower jaw is long and slender, two thirds of the length being formed by the dentary. There is a fairly large coronoid process. The angular is large, and the surangular, as displayed externally, is small, and the articular is also small.

The occiput is small and slopes downward and backward. On the inner side of the descending part of the squamosal is a prominent ridge which forms the inner wall of the external auditory meatus and divides off the occiput proper from the squamosal. The condyle is single and rounded.

Lycosuchus vanderrieti is a fairly near ally of *Scylacosaurus* but differs in a number of minor details. There does not seem to be a distinct postfrontal,

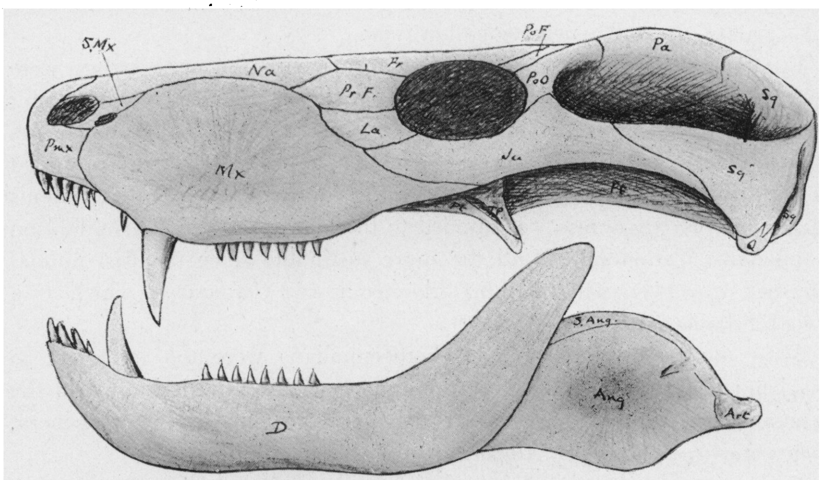

Fig. 5. Skull of *Scylacosaurus sclateri* Broom. × 4/7.

though the post-orbital is well developed. The squamosal shows the same auditory groove.

Aloposaurus gracilis is much smaller than most of the other known Therocephalians but agrees fairly closely with the majority of types. The skull (Fig. 7) is relatively much narrower and deeper than that of either *Scylacosaurus* or *Lycosuchus*. The premaxillary is small and carries five incisors which have a number of vertical ridges. There is a large septo-maxillary. The maxillary is deep, and has a slender portion which extends backwards some distance below the orbit. The lachrymal is rather small, and the prefrontal of fair size. The nasal is narrow but broader behind. The frontal is much longer than broad, and a slight median ridge is formed by the two. The parietal region is unusually broad and formed mainly by the parietals and post-orbital. Whether there are distinct postfrontals is not clear. The jugal is a large deep bone. The squamosal is not well shown but appears to be fairly like that of *Scylacosaurus*.

The lower jaw is long and slender and the dentary forms about three fifths. There is a well developed coronoid process. The angular and surangular are similar to those in the other known genera but are of less vertical depth.

The greatest length of the skull is 120 mm.

The dental formula is apparently i $\frac{5}{4}$, c $\frac{1}{1}$, m $\frac{?5}{?}$. The double condition of the canine is due to one replacing an older.

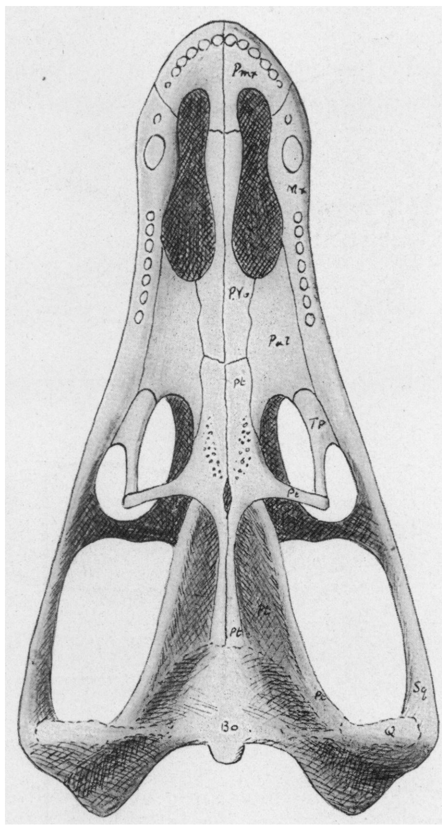

Fig. 6. Under side of skull of *Scylacosaurus sclateri* Broom. Slightly restored.

Scaloposaurus constrictus. This is the smallest known Therocephalian and one of the smallest of the Therapsida. It has been argued that the mammal-like reptiles are all too large for any of them to have been the mammalian ancestor, but *Scaloposaurus, Galechirus* and *Galepus* show that some at least were quite small. Unfortunately nothing but the type skull has ever been discovered.

The maxillary is large and has many small teeth, perhaps the first three of which may be looked upon as canines. The premaxillary is not well preserved but was probably as restored in the figure (Fig. 8). The lachrymal and prefrontals are large. The jugal is long and slender and apparently does not meet the postorbital arch. The squamosal is of the usual Therocephalian type but more slender and there does not seem to be a specialised auditory groove. The parietal region is nearly as broad as the frontal, and there is at least a distinct postorbital which forms a feeble incomplete postorbital arch.

The lower jaw has a very long slender dentary with a small coronoid process. The angular is large and the surangular probably small.

The dental formula is probably i^6, c^3, m^9.

In some respects *Scaloposaurus* is the most primitive of the Therocephalians and approaches the Dromasaurian genera *Galechirus* and *Galepus*.

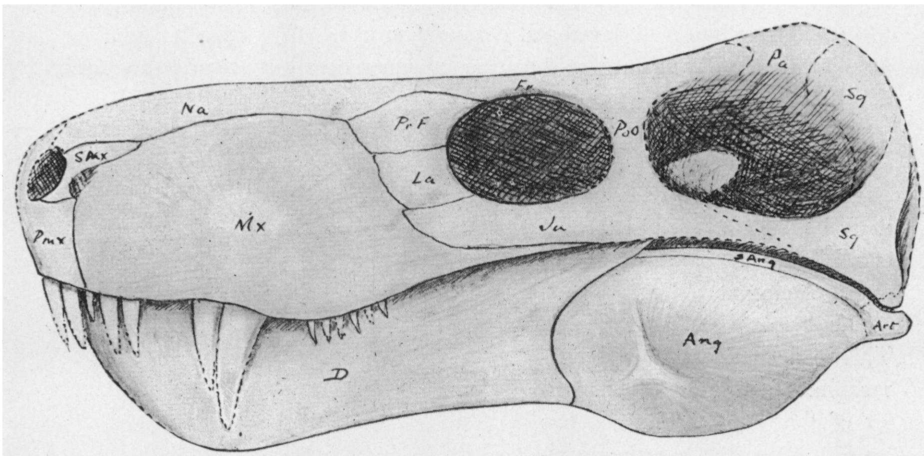

Fig. 7. Skull of *Aloposaurus gracilis* Broom. Nearly nat. size.

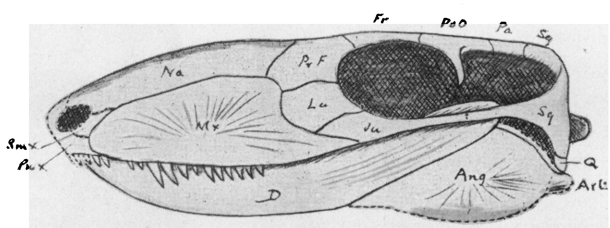

Fig. 8. Skull of *Scaloposaurus constrictus* Owen. $\times \frac{3}{2}$.

Anomodontia.

The Anomodonts form a very well defined group of highly specialised Therapsidan reptiles which are perhaps the most striking and characteristic members of the Karroo fauna; and they are certainly the most abundant.

The most typical and the first discovered genera are the tusked *Dicynodon* and the tuskless *Oudenodon*. Whether or not *Oudenodon* may be the female of *Dicynodon* is still an unsettled point. Owen, Lydekker and Broom have all considered the suggestion and come to the conclusion that the probabilities are rather in favour of the genera being distinct. As time goes on, however, the evidence seems to be getting stronger in favour of *Oudenodon* being but the female *Dicynodon*. Certain it is that wherever *Dicynodon* occurs *Oudenodon* is also to be met with. Until recently only *Dicynodon* was known to occur in the Upper Beaufort Beds (Upper Triassic) but *Oudenodon* is now also known to occur. Further, while many of the species of *Oudenodon* seem to differ markedly from the known species of *Dicynodon* others are so similar that it is impossible to say to which genus some specimens belong till the presence or absence of the tusk has been determined. Further, among the Endothiodonts, the genera seems to run in pairs, the tuskless *Esoterodon* and the tusked but otherwise very similar *Cryptocynodon,* and the tuskless *Opisthoctenodon* closely allied to the tusked *Pristerodon.* While all these facts seem in favour of the tusked Anomodonts being the males and the tuskless the females, both males and females of *Lystrosaurus* must have been tusked, for though many skulls of *Lystrosaurus* are known, no skull the least like *Lystrosaurus* but tuskless has ever been discovered; and again all the specimens of *Cistecephalus* are tuskless so far as known. The two specimens in the British Museum with tusks are unquestionably wrongly referred to *Cistecephalus* and are really fragmentary skulls of small Dicynodons.

Though the Anomodonts form such a well defined group they do not differ from the more primitive Therapsidans nearly so much as would appear at first sight. The large toothless beak with the modification of the arches and palate to suit it are the most striking specialisations. The Endothiodonts, with molar teeth, to some extent connect the Dicynodonts with the lower forms, but except for the presence of molars they agree closely with *Dicynodon.*

Dicynodon and *Oudenodon* are the least known Anomodont genera, nearly every detail of the structure being known of both the skull and postcranial skeleton.

The powerful beak is formed by the peculiarly developed premaxillaries and maxillaries (Fig. 9). In no Anomodont genus is there any evidence of incisors and the premaxillaries are further remarkable by being anchylosed at a very early period. The maxillary is relatively short and has either a tusk or a tusk-like bony process. In *Dicynodon* the tusk is usually very powerful and directed mainly downward, the mandible passing between the two tusks. On the palatal surface the premaxillaries show largely, forming most of the hard palate. The maxillaries form a rudimentary secondary palate. Hitherto no evidence of a septomaxillary or of paired prevomers has been obtained in any Anomodont. The nasals are usually to some extent separated by the median process of the premaxillaries. The prefrontals, lachrymals and jugals are pretty much like those of more normal Therapsidans. The vomer is, as in mammals, an unpaired median bone. There are well developed palatines, which also help in the formation of the rudimentary secondary palate, but there are no transpalatines. The pterygoids are large, with long anterior processes which pass forward and slightly outward, and long posterior processes which extend to the quadrates. There is a pair of long slender epipterygoids. In *Dicynodon* postfrontals are usually absent but occasionally small ones are present in other Anomodonts. The postorbitals, on the other hand, are always very large and usually form the whole inner wall of the temporal fossa. The parietals are small, and in front of the pineal foramen is a median preparietal bone. The squamosal is of very large size, stretching, from the postorbital and parietal above, downwards by the side of the occipital to support the quadrate and forwards to form the zygomatic arch with the jugal. In some Anomodonts it even extends forward to meet the maxilla *e. g.*, *Lystrosaurus*. The quadrate is a fair sized bone which lies in front of and below the descending portion of the

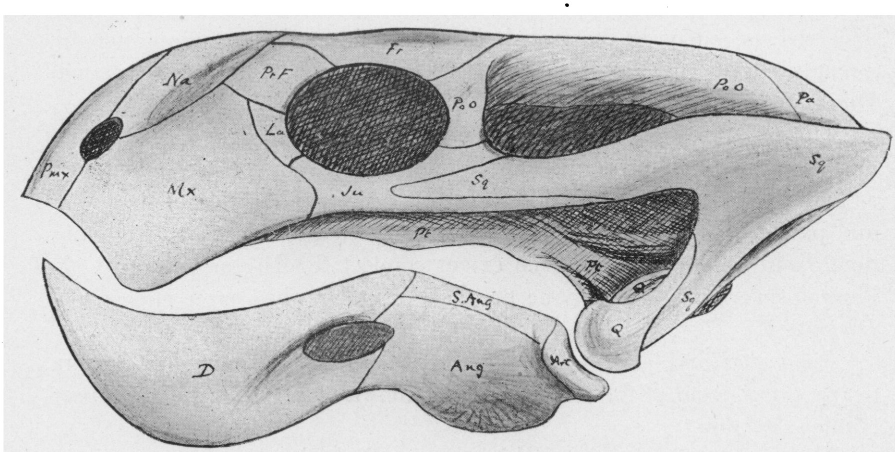

Fig. 9. Skull of *Oudenodon gracilis* Broom. Nat. size.

squamosal. The occiput is large and massive, formed by a small basioccipital and two very large exoccipitals. Above these is a median bone which may be either supraoccipital or interparietal, probably the former. Inferiorly the exoccipital has two short descending processes supported in front by two processes from the basisphenoid. Between this basioccipital process and the quadrate lies a short dumb-bell shaped tympanic bone.

The lower jaw is composed of a large dentary, which becomes anchylosed with its neighbor as age advances, well developed angular, surangular and articular bones with a smaller splenial. There is no coronoid process and no coronoid bone.

The post-cranial skeleton is very mammal-like. The shoulder girdle is interesting from the fact that the cleithrum is still retained. The digital formula is 2, 3, 3, 3, 3. The pelvis is like that of the mammal in the forward direction of the ilium and the presence of a small obturator foramen. There are no abdominal ribs and no ossified prepubis.

There are a few specialisations of the Dicynodont type. *Lystrosaurus,* which first appears in beds which are probably Lower Triassic, is an aquatic modification where the head is twisted to bring the eye and nostril as near the

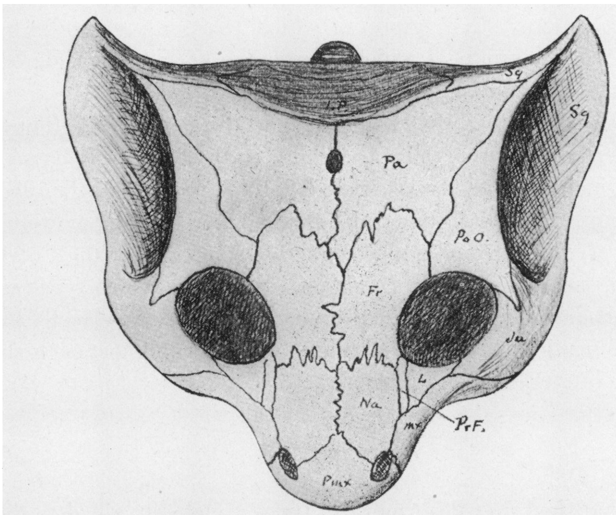

Fig. 10. Skull of *Cistecephalus microrhinus* Owen. Nat. size.

upper surface of the water as possible. The limbs are short and feeble and the joints cartilaginous.

Cistecephalus is a small Anomodont which only occurs in beds which are believed to be Upper Permian (Fig. 10). It is never tusked and the beak is small. The chief peculiarity is the great breadth of the parietal region which to a large extent roofs over the temporal fossa. The arrangement of the bones is seen in the figure given.

North American Permian Fauna.

The Permian Fauna of North America is, like that of South Africa, of the very greatest interest. Professor Williston has recently written on the relationships of this fauna and concludes that it has been evolved in isolation from the rest of the world and that it has no near affinities with other faunas. The South African fauna belongs mainly to Middle, and Upper Permian and Triassic; the North American is mainly a fauna of the Lower Permian and to some extent Upper Carboniferous.

The principal types of Amphibians and Reptiles may be placed in seven groups or orders. The Amphibians belong to: (1) The Temnospondyli, a group of Stegocephalian Amphibia characterised by the vertebræ having large intercentra and small paired pleurocentra. *Eryops, Trimerorachis* and *Acheloma* are the best known types. *Cricotus,* though having in certain regions large centra alternating with disc-like intercentra, is usually also placed in this group. (2) A group of which *Diplocaulus* may be regarded as the type. (3) A group of which *Lysorophus* may be considered as the type. And (4) a division of which *Gymnarthrus* is the type.

The Reptiles are much better known than the Amphibia. They belong to three orders or groups. The best known are the (1) Pelycosauria, of which the principal types are *Dimetrodon, Naosaurus* and *Edaphosaurus.* The next group is (2) the Cotylosaurs, of which the best known type is *Diadectes.* The (3) third group is also sometimes included in the Cotylosauria but is not very nearly related to *Diadectes.* It contains such types as *Pariotichus* and *Labidosaurus.* A number of genera are too imperfectly known to admit of classification with much certainty, but possibly most of them can be placed in one of these three groups.

Temnospondyli.

I am not satisfied that the American types are closely allied to the European, such as *Archegosaurus,* but the American seem to be of a considerably higher type. The vertebræ, however, are typically rhachitomous. They are best known in *Eryops, Trimerorhachis* and *Acheloma.*

Cricotus differs in having many of the vertebræ of the embolomerous type.

Trematops, which has recently been described by Williston, is a most remarkable type of temnospondylous Amphibian which has a temporal fossa. In most other respects it seems allied to *Eryops.*

Diplocaulus.

Diplocaulus is placed by Williston among the Microsauria, as the vertebræ are completely ossified, but he admits that it represents a more highly organised type than that seen in the ordinary Microsauria.

Lysorophus.

There has been considerable difference of opinion as to the affinities of this little snake-like form. There can, however, be no doubt that it is an Amphibian; the only question being whether it can be placed in any of the known groups.

The skull, as shown by Williston, agrees with the Urodela and differs from the Gymnophiona and most primitive groups in having the orbits open and in the structure of the suspensorium. Even in many minor details it approaches the Urodela and is remarkably like that of *Amphiuma.* Doubtless in one or two points *Lysorophus* is more primitive but there seems better reason for placing it with the Urodela than with any other recent or extinct group. The living Urodeles present a considerable variety of type, and are evidently the somewhat degenerate descendants of a large and varied order, and *Lysorophus* seems to be one of the specialised but less degenerate early members.

In a recent paper Moodie criticises this conclusion and on account of the presence of ribs and the snake-like character prefers to place *Lysorophus* in the Gymnophiona. A snake-like character is apparently fairly easily acquired in many groups, and among recent lizards we can see all the stages, and it is remarkable to note in how many different orders it has been independently acquired. Even in living Urodeles we get a very near approach to the snake-like character in *Amphiuma.* The presence of ribs in *Lysorophus* is a more important character, but ribs are so generally present from fishes upward that when one finds a group of animals where they are generally rudimentary, as in the Amphibia, the more natural conclusion seems to be that short ribs is a degenerate character rather than a primitive. Long ribs are characteristic of the Microsauria, and though they are short in the Branchiosauria the evidence seems to me rather in favour of the long rib being the primitive condition.

Diadectes.

Diadectes is one of the best known of the primitive Permian reptiles and one of the most interesting. In some respects it is much specialised, in others it is very primitive. The teeth are large and broad, and the lower jaw powerful, and for its suspension the quadrate is of very large size.

The maxilla is powerful, but is completely divided from the nasal by the lachrymal extending forward to the nostril (Fig. 11). The jugal is deep and articulates with the post-orbital, squamosal and quadrato-jugal. The postorbital is large. The postfrontal and prefrontal form the whole upper margin of the orbit. The squamosal extends from the parietal down to the quadrato-jugal and jugal and forms most of the support for the very large quadrate. The quadrato-jugal supports the lower part of the quadrate and forms the lower part of the back of the temporal wall.

The quadrate is very large and extends nearly as far up as the squamosal. It also has a large inferior process which passes forward to meet the pterygoids. The pterygoids are small quadrangular bones which meet the prevomers, palatines, and transpalatines in front. They form small pterygoid processes (Fig. 12). The palatines are small and form an imperfect secondary palate. There appear to be a pair of small transpalatines. The prevomers are long and narrow and have each a longitudinal row of teeth.

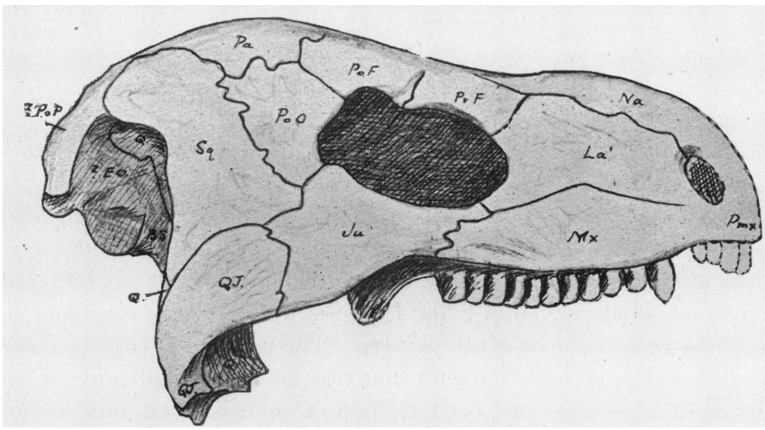

Fig. 11. Skull of *Diadectes phaseolinus* Cope. About ⅓ nat. size.

The occiput is massive. The condyle is large and flat. The elements are so anchylosed that the limits of each cannot be made out. A distinct suture however is present between the basioccipital and the basisphenoid.

The vertebræ are massive, and a number of the anterior ribs are expanded into broad bony plates.

The limb girdles are large and heavy, though the limbs are rather feeble.

Pariotichus.

Pariotichus is one of the best known of the American Permian reptiles. It is a small form with a roofed temporal region, and though in many respects it is primitive in others it is pretty highly evolved. It is very slightly generalised[1].

Cope placed it in the Cotylosauria, but though it agrees with *Diadectes* in having the temporal region roofed, it differs from it so greatly that unless the term Cotylosauria is used in a very wide sense it cannot well include the two genera. All confusion is avoided however if *Pariotichus* is considered as a type by itself.

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[1] [The word " generalised " is here apparently a *lapsus* for " specialized ".— Ed.]

The skull is broad and flat, and the bones sculptured. The bones of the upper side are well seen in the figure given (Fig. 13). The upper surface is mainly formed by the nasals, frontals and parietals. There are distinct and well developed prefrontals, postfrontals, and postorbitals. The lachrymal is very large and extends to the nostril. The maxilla, on the other hand, is very narrow and forms but a small part of the side of the snout. There is a well developed septomaxillary. The jugal is very large, and posteriorly meets the squamosal and the quadrato-jugal. The squamosal is a large

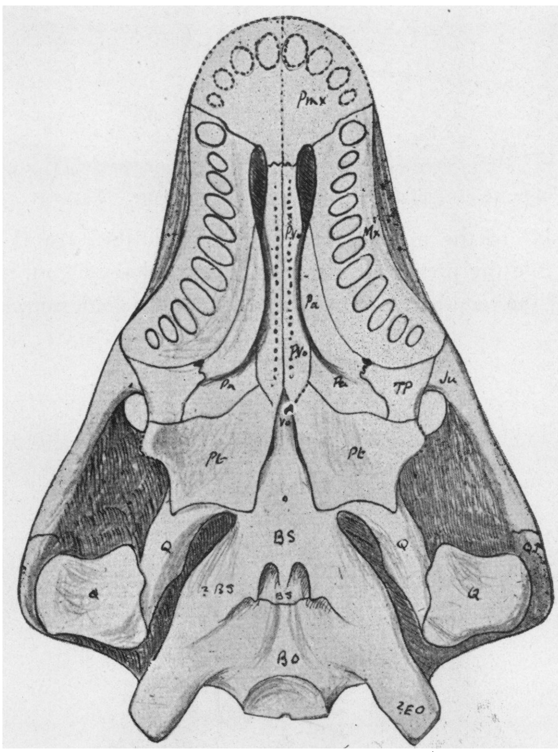

Fig. 12. Under view of skull of *Diadectes*. Slightly restored.

square bone which articulates broadly with the parietal above and with the quadrato-jugal below. It forms part of the back of the skull and has a groove for the auditory canal. The quadrato-jugal is about a third of the size of the squamosal. There is no evidence of a distinct prosquamosal in *Pariotichus*, though there appears to be in *Pantylus*, though whether this latter is allied is at present unknown and rather doubtful. The quadrate shows to some extent on the side view. Behind the parietal at its outer corner is a small distinct ossification which probably corresponds to the so called "epiotic" of the Stegocephalians and may be preferably called the post-temporal.

The palate is fairly well known. The prevomers are well developed and

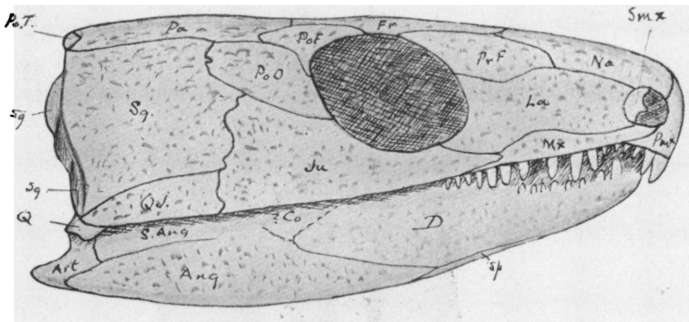

Fig. 13. Skull of *Pariotichus angusticeps* Cope. Nat. size.

lie on the inside of the internal nares. The palatines are also fairly well developed; while the pterygoids are very large and send long processes forward inside of the palatines. They form large pterygoid processes and pass

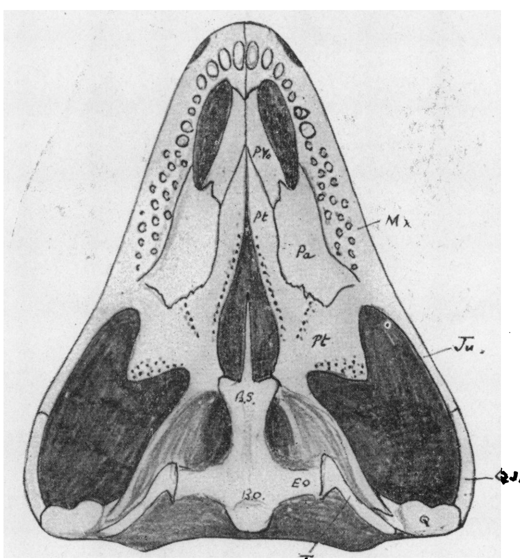

Fig. 14. Under view of skull of *Pariotichus angusticeps* Cope. Slightly restored.

back to meet the quadrates. Teeth are developed on the pterygoids in three groups, as seen in the figure (Fig. 14). A small median vomer — the so called parasphenoid — is present. Between the quadrate and the basi- or exoccipital process lies a slender little bone which seems to articulate with the bones at either end. This is the bone which I believe to be the tympanic. The occipital condyle is single and rounded.

The lower jaw has a large dentary and a large angular, a smaller surangular, apparently a distinct coronoid, and a small articular. A narrow splenial lies inside the dentary.

As the result of the work of Cope, Broili, Case and Williston the post-cranial skeleton of *Pariotichus* and its allies is fairly well known. The girdles are well developed but the limbs rather feeble and short. Abdominal ribs are present in at least some members of the group. The digital formula is doubtful but Williston says that "quite surely it was not that of the modern lizards and Sphenodon, 2, 3, 4, 5, 3. In much probability it was 2, 3, 3, 4(3), 2."

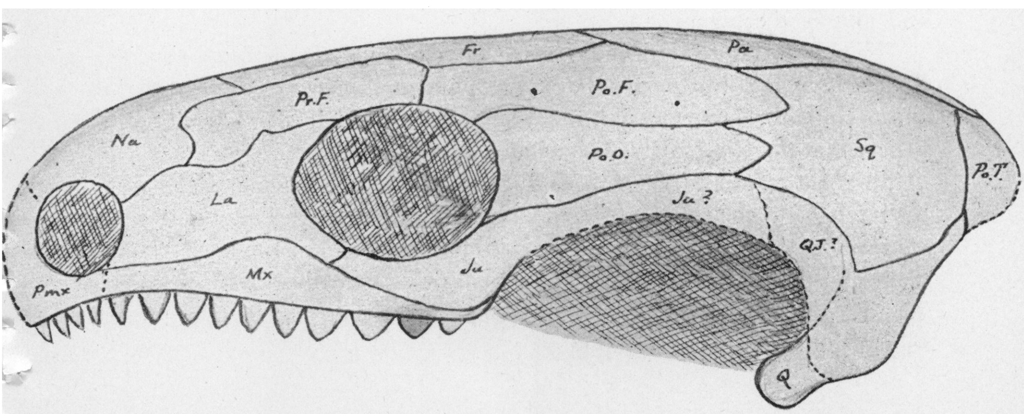

Fig. 15. Skull of *Gymnarthrus* Case. Restored. Much enlarged.

Gymnarthrus.

During my short stay in New York Dr. Case kindly allowed me to examine a small skull which he had recently discovered, and which he is describing under the name *Gymnarthrus*. Though Case is elsewhere[1] describing the specimen it is of such great interest and its affinities so difficult to decide that I have his kind consent to give an independent opinion.

The skull (Fig. 15) is very small, but fortunately well preserved. Judged by the upper and even by the side view one would incline to the opinion that *Gymnarthrus* is a near ally of *Pariotichus*. The nasals, frontals, parietals,

[1] See *antea*, p. 177.

prefrontals, postfrontals, postorbitals and squamosals are all strikingly like those of *Pariotichus*. Further, the lachrymal is very large and extends to the nostril, and the maxilla is a narrow bone which forms little of the side of the snout; and behind the squamosal there is a post-temporal. In all these characters *Gymnarthrus* agrees with *Pariotichus*. But when one examines the palatal aspect of the skull one finds a condition of affairs very unlike that of the reptile. The occipital condyle appears to be double, and the pterygoids do not meet in the middle line. There is in the middle line either a single very large vomer (or parasphenoid) or a large basisphenoid and a fairly large true vomer or parasphenoid in front. I rather incline to the former alternative. The palatines and prevomers are not displayed but they can be restored with considerable probability.

The quadrate is long and in the specimen extends free much below the squamosal. I incline, however, to suspect that a quadrato-jugal is missing and part of the jugal.

Though owing to the condition of the palate and the occipital condyles I prefer to regard *Gymnarthrus* as an Amphibian, it must be admitted that it shows so many characters also found in *Pariotichus* that it is difficult not to believe that there is a fairly close relationship between them.

In some respects *Gymnarthrus* suggests the Gymnophiona, and if it is really an Amphibian it raises a number of very interesting questions *e. g.*, whether the reptiles may have sprung from more than one group of Amphibians and not, as is generally supposed, all from some ancestral Cotylosaur. The discovery of the Amphibian *Trematops* with a temporal vacuity, further suggests unsuspected possibilities.

Pelycosauria.

The Pelycosaurs are in many ways the most interesting of the North American fossil reptiles. In the strange specialisation of the vertebral spines they are unique and they will always be interesting as among the first discovered reptiles which seemed to have some close affinity with the ancestors of the mammals. As has been already shown, opinions have differed greatly as to whether Cope was right in believing the Pelycosaurs to be related to the South African mammal-like reptiles, and even as to whether the wonderful mammal-like appearances presented by many of the African types in any way represented affinities. Before discussing the question it will be well to examine the structure of the Pelycosaurs.

In view of Case's recently published magnificent work on the Pelycosaurs it might well seem wiser to wait till further specimens had been obtained.

So much, however, depends on a solution and the interpretation of the already known specimens is a matter of such difficulty that a further examination seems permissible.

The types which I have been able to study have been the skulls of *Dimetrodon* in the American Museum, including the very fine one recently found by Case, and Cope's type of *Edaphosaurus.*

Edaphosaurus.

Though the type skull of *Edaphosaurus pogonias* is very badly crushed and somewhat imperfect it is in some respects the most important Pelycosaur skull known.

In making restorations of the skull I started with the mandible, which is nearly perfect and practically uncrushed. As the symphysis is perfect the other mandible can be restored and we can determine with much certainty the width of the palate, the inclination of the pterygoid plates, the distance of the quadrates from each other, and the relative position of the quadrates to the upper jaws. As we have the bony arch complete from the parietal, down the squamosal to the quadrate we can obtain the height of the parietal region. And having obtained the relative positions of the quadrates, parietals, premaxillæ and maxillæ with considerable certainty the fitting in of the remaining parts is not a matter of much difficulty.

In like manner the palate can be restored. We can fix the position of the premaxillary and maxillary teeth, the pterygoid plates and the quadrates, and as most of the other structures are preserved their restoration in position is comparatively easy.

The figures given (Figs. 16–18) show my restoration of the side, upper, and under views. The premaxilla is fair sized, and of the usual type. The front of the specimen is too imperfect to show whether there may have been a septomaxillary. The maxillary is long and narrow and appears to be completely separated from the nasal, as in *Pariotichus,* by the forward development of the lachrymal. The shape of the nasals and frontals is shown in the figures. The frontal has a peculiar outward development which with the postfrontal forms a very prominent supra-orbital ridge. The prefrontal is wedged in between the outer part of the frontal and the nasal. The postfrontal is large, and the postorbital small. The shape and relations of almost all the bones of the upper surface of the skull can be made out with certainty. The parietals are well preserved. They are broad and have a large pineal foramen. There is a large temporal fossa bounded above by the postorbital and parietal, and posteriorly by the squamosal. Most of the squamosal is well preserved, but the zygomatic portion is lost and the structure of the zygoma cannot be made out with certainty. There is a quadrato-jugal, which apparently takes some part in the formation of the zygoma, but there is little evidence as to what extent. There seems to have been a small fenestra between the quadrato-jugal and the squamosal, and in the restoration given an attempt is made to show what are the probable relations of the bones. The quadrate is well developed and fairly well preserved.

The palate is well preserved and can be restored with much probability, the prevomer, palatine and pterygoid of the right side being preserved with the bones in almost their natural relations to each other and to the maxilla.

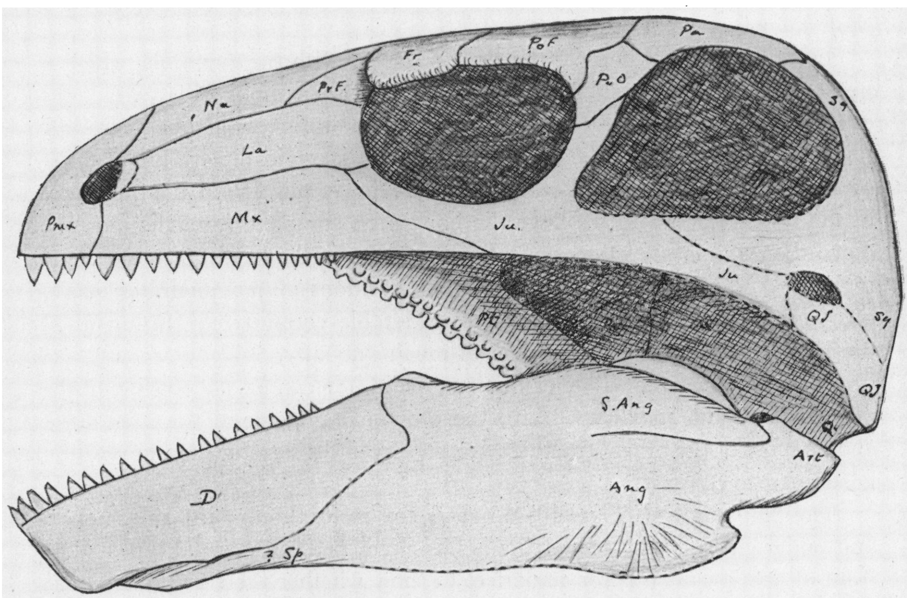

Fig. 16. Skull of *Edaphosaurus pogonias* Cope. Restored.

The prevomers are small and narrow and lie between the internal nares. Each has a row of small rounded teeth. The palatine and pterygoid together form a large plate covered with small rounded teeth. The shape of the bones and the arrangement of the teeth will best be understood from the figure given. The anterior third of the plate is in my opinion formed by the palatine, and in the specimen there is a slight displacement along the suture. There is apparently a rather large postpalatine foramen, but there does not appear to be a transpalatine bone. The basisphenoid is well developed and supports the pterygoids. There is a distinct vomer (parasphenoid). The occipital condyle is single and rounded. The bone which Cope, Case, and others have regarded as the stapes I regard as the tympanic. It bears the same relations to the basioccipital and quadrate as does the tympanic in *Dicynodon,* differing mainly in fact that, as in *Edaphosaurus,* the quadrate is large and flat, the tympanic has its outer half flattened out to lie on the quadrate. I am not satisfied that there is a bone behind the parietal which might be looked upon as a postparietal.

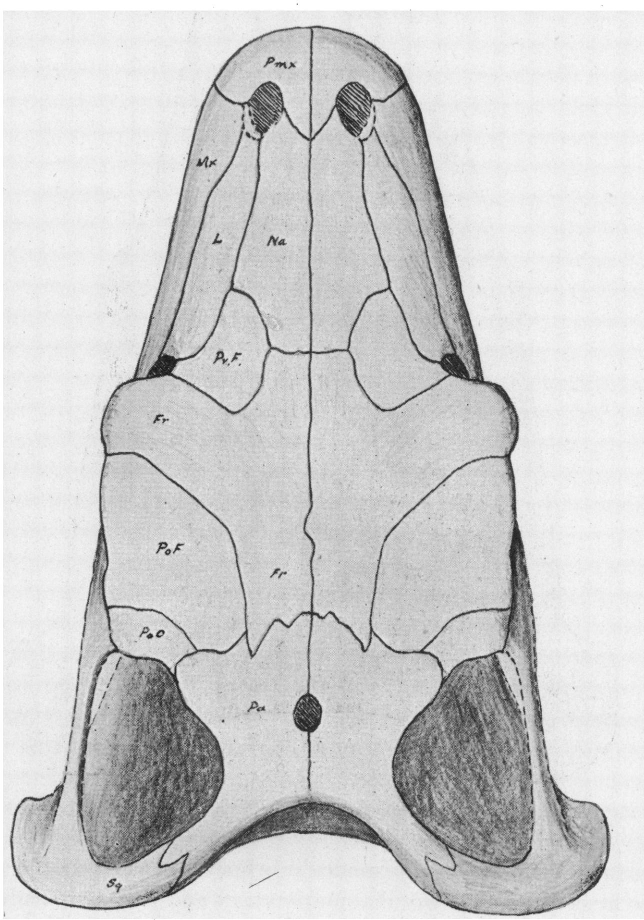

Fig. 17. Top of skull of *Edaphosaurus pogonias* Cope. × ⅔. Restored.

The dentary forms less than half of the mandible. The angular and surangular are both well developed, and the articular is distinct. The splenial appears to be large.

In my restoration I have shown the teeth different from what is shown in both Cope's and Case's figures, or even from what appears to be the condition from an examination of the specimen. The large maxillary teeth appear

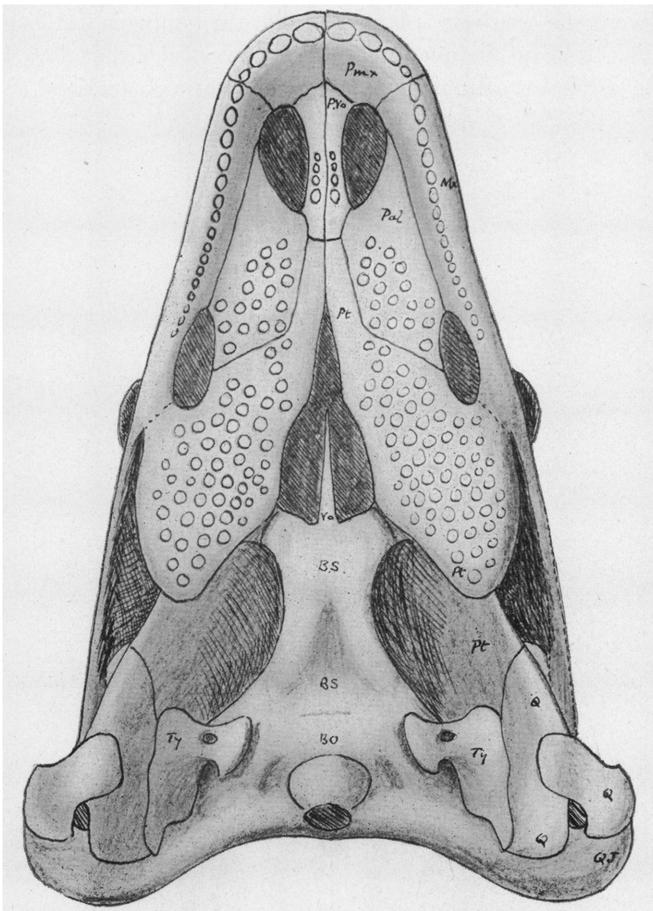

Fig. 18. Lower view of skull of *Edaphosaurus pogonias* Cope. Restored.

to me to have been artificially made by whoever developed the specimen. From the alveoli the teeth are manifestly small and rounded, and like those in the lower jaw.

Dimetrodon.

Dimetrodon is known by a considerable number of pretty well preserved skulls and by practically all the postcranial skeleton. It is a much larger animal than *Edaphosaurus,* and it is less specialised, there being no crushing plates of teeth. As it is from the restorations of the skulls of *Dimetrodon* that the conclusion has been arrived at that the Pelycosaurs are allied to *Sphenodon,* and that the temporal region has two fenestræ as in the Rhynchocephalians the determination of the exact structure is a matter of the utmost importance. The skulls in the American Museum enable one to decide with certainty on all points in the structure of the skull with the exception of two and these we can decide with some probability.

The snout is pretty well known and my restoration (Fig. 19) agrees

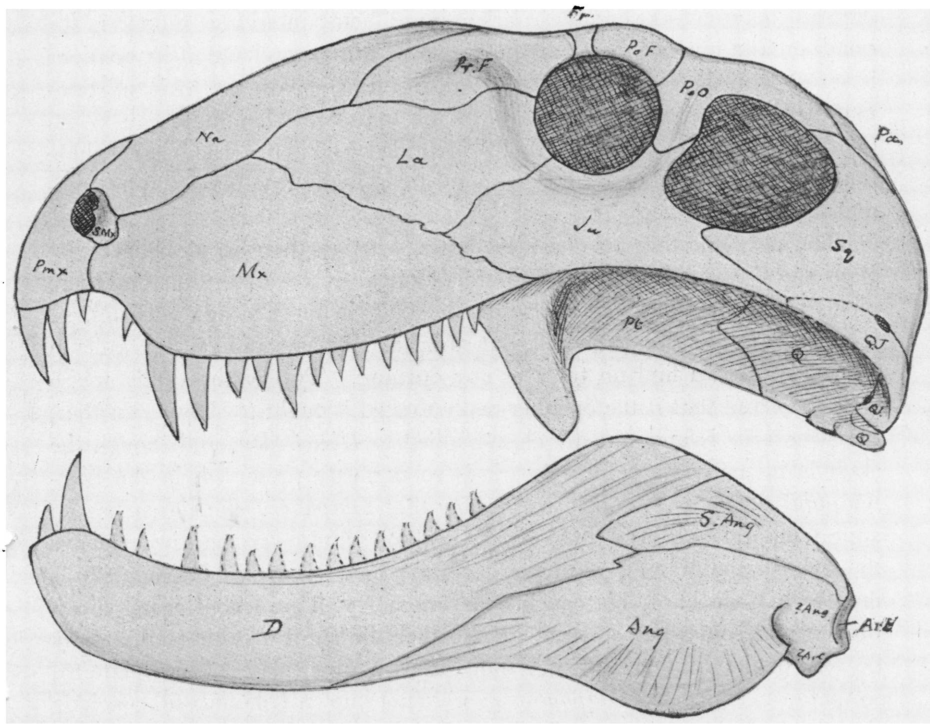

Fig. 19. Skull of *Dimetrodon incisivus* Cope. About ⅓ nat. size.

pretty closely with that of Case. The only point where we differ is in the matter of the relative sizes of the lachrymal and prefrontal. I regard the former as large and extending well forward, but not, as in *Edaphosaurus,* extending to the nostril. We are also in close agreement as to the jugal and postorbital, but in the structure of the posttemporal region we differ entirely. In none of the specimens I have examined is the region perfectly preserved, but the principal bones can be made out I think with certainty.

There is a large temporal vacuity, rather larger than the orbit. It is bounded in front by the postorbital arch which is formed by the postorbital and the jugal. The upper margin is also formed by the postorbital. Posteriorly the fenestra is bounded by a large flattened bone concerning which there is difference of opinion. Baur and Case believe it to be a prosquamosal, but in my opinion it is the squamosal. There is no doubt whatever about the parietal and the postorbital, and they bear exactly similar relations to each other as they do in the Therocephalians and Anomodonts. Posteriorly they both unquestionably meet the upper part of the large bone under consideration in exactly the same way as they meet the squamosal in the African mammal-like reptiles. The large bone inferiorly supports the quadrate and in front meets the jugal: so that in every detail of its relations it agrees with the squamosal of the African forms. Now the African Mammal-like forms approach so nearly to the mammals that there can be no question that the squamosal is rightly identified, and hence we must conclude that the large bone behind the temporal fossa is the true mammalian squamosal.

The next question for consideration is whether there is, as believed by Baur and Case, a small supra-temporal fenestra. Case assures me that there seems to be a distinct one in one of the skulls in the Chicago museum. I regret I have not seen this skull, but so far as I have examined the skulls in New York I can find no trace of any opening. Two of the skulls are so well preserved that if the opening really existed it ought to show. Further, *Edaphosaurus* is undoubtedly closely allied to *Dimetrodon,* and though the skull is in many ways imperfect it is so perfectly preserved, in the post-temporal region as to conclusively show that *Edaphosaurus* at least has no supratemporal fossa, and that being so it would require very positive evidence to establish a supratemporal fossa in *Dimetrodon.* Now the Chicago skulls on which Case bases his conclusions are not well preserved being much broken and somewhat crushed, and further the sutures cannot apparently be very distinctly seen, judging from Case's figures (plate 17 and plate 8), so that even supposing *Edaphosaurus* were not known I should still conclude that the evidence of the New York specimens against a supra-temporal fossa was much stronger than the evidence of the Chicago specimens for a supra-temporal fossa, and until a good uncrushed specimen is discovered showing a supra-temporal fossa I shall conclude that there is no supra-temporal fossa in the Pelycosaurs. Whether there be a small superior fossa or not there is no question that the large fossa is the homologue of the temporal fossa in the African Mammal-like reptiles.

Below the large squamosal there is a distinct quadrato-jugal. In no skull of *Dimetrodon* is it well preserved and there seems to be some doubt concerning its extent forward and its relations to the squamosal and the jugal. From the evidence obtained from specimen 4034, and to a less extent from other specimens, I incline to regard the quadrato-jugal as passing forward to meet the jugal and forming a small fenestra with the squamosal, as I have shown in the restoration. It must be clearly understood, however, that the restoration of this region is largely hypothetical.

The quadrate is a large bone which has a large flat plate passing forward to meet the pterygoid. The palate is well known and my restoration (Fig. 20) agrees pretty closely with Case's, differing mainly in the proportions of certain of the bones. The pterygoids I regard as narrower than Case does, and I think there is a distinct post-palatine foramen. The basisphenoidal and basioccipital region I regard as flatter, and I have placed in position the bone which I regard as tympanic.

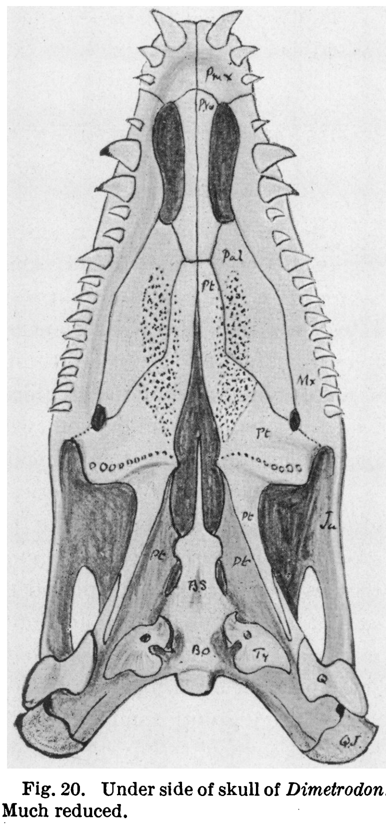

Fig. 20. Under side of skull of *Dimetrodon*. Much reduced.

Concerning the occipital region there is some doubt. There is unquestionably a well developed exoccipital which sends a process outward to meet the descending squamosal. This is the process called paroccipital by Case. I should rather restore it as passing about as much downward as outward (as shown in Case's fig. 7, plate 11). Above the foramen magnum there is a broad flat plate which may be supraoccipital, but no sutures can be made out. The exact structure behind the large squamosal must remain for the present in doubt. In some specimens one might persuade oneself that there was a distinct postparietal bone and also an elongated post-temporal. In others it is by no means certain that such bones can be made out. The parietal unquestionably has an outward and backward process by the side of the postorbital, which meets the squamosal. Behind the inner part of the parietal there is probably a bone separating it from the supraoccipital. Then behind the outer process of the parietal there is also some bony element above the supra- or exoccipital. Whether, however, this is a post-temporal or a part of the squamosal I cannot determine in the New York specimens.

The mandible is well preserved. The dentary is large and forms about two thirds of the jaw. There is no developed coronoid process to the dentary though the coronoid region is occupied by this bone. There is no coronoid bone. The angular is large and forms a rounded angle to the jaw. The surangular is comparatively small. The articular is largely hidden by the membrane bones. In Case's fig. 4, plate 9, the parts marked articular and prearticular I regard as parts of the angular, the true articular being the part behind and scarcely seen from the outer side.

To Case's very full description of the post-cranial skeleton I have nothing to add.

The apparent resemblance of the American types to the South African.

Though it is many years since Cope first called attention to the resemblance between some of the American and African types, of later years zoölogists have been more impressed by the differences. Like most others I had regarded the resemblances as more due to a parallel development than to affinity and I was a little surprised to find that the resemblances were of a more fundamental nature than had been supposed. Not only do certain American types resemble, somewhat remotely of course, African forms, but the whole fauna has got an African look about it that is very striking.

Williston regards the American Permian reptiles as belonging to three groups — the Pelycosaurs, the Cotylosaurs proper, and the Pariotichus group; and it certainly is very remarkable that some years ago writing of the reptiles of South Africa I placed them in the groups Procolophonia, Pareiasauria, Therocephalia, Anomodontia and Cynodontia. If we unite the allied mammal-like groups Therocephalia and Anomodontia under the Therapsida and omit the Triassic Cynodontia, we get our principal Permian reptiles also in three groups, and further, the three groups correspond in many ways to the American. The Pelycosaurs resemble the Therapsida, the Cotylosaurs the African Pareiasauria, and the Pariotichus group the Procolophonia. A short comparison will show that there is a fundamental affinity between the faunas.

The Pelycosauria compared with the Therapsida.

While the Pelycosauria differ from the Therapsida sufficiently to justify their being kept in a distinct order they are nevertheless in my opinion closely related. Let us compare the various parts of the skeleton in each.

The skull of the Pelycosaur resembles that of the Therapsida and differs from that of all other reptiles in having a single temporal fossa bounded by the postorbital, squamosal and jugal. In Cynodonts, Therocephalians, and some Anomodonts the parietal forms part of the fossa wall through the postorbital and the squamosal failing to meet, but most Anomodonts, Dinocephalians and Dromasaurians show what is manifestly the primitive condition where the parietal does not touch the margin of the fossa. The general arrangement of the bones of the snout and orbit is similar in the typical Therapsidans and Pelycosaurs. The occipital region in both is fairly similar though possibly the Pelycosaurs retain a primitive postparietal and posttemporal which certainly are lost in the Therapsidans. The suspensory arch is in both formed by a huge squamosal, the Pelycosaurs differing from most only in retaining the quadrato-jugal which is lost in all Therapsidans except the Dinocephalians. But in these latter the arrangement of jugal, squamosal and quadrato-jugal is strikingly like that of the Pelycosaurs.

The palate in the Pelycosaurs is distinctly Rhynchocephalian. So it is in the Therocephalia. In the retention of the transpalatines the Therocephalian type is more primitive, but in having the prevomers toothed the Pelycosaurs are the earlier type. In the Therapsida the palate varies greatly. The Anomodonts, Dinocephalians, and Cynodonts have, like the Pelycosaurs, all lost the transpalatines.

The lower jaw of the Pelycosaurs agrees very closely with that of the Dinocephalians and Dromasaurians and fairly well with that of the Anomodonts. The Therocephalian jaw differs in the great development of a coronoid process, and the Cynodont in the greatly increased size of the dentary and the relative reduction of the other elements.

The vertebræ of the Pelycosaurs agree pretty closely with those of the Dinocephalia, less closely with those of the Anomodonts and Therocephalians. The sacrum of the Pelycosaur has 3 vertebræ while in the Dinocephalia and the Anomodontia 4 is the number in those types where it is known.

The shoulder girdle is exactly of the same type in the Pelycosaurs and the lower Therapsidans. A cleithrum certainly occurs in the Dinocephalia and the Anomodontia and probably in the Therocephalia. In the Therocephalia, the Dinocephalia and the Dromasauria the scapula is flat without a specialised acromion. The Dinocephalia have a large interclavicle very similar to that of the Pelycosaurs.

The humerus in the Therapsida varies considerably. In the Anomodonts the delto-pectoral ridge is very large, and it is also large in the Dinocephalians, but in the Dromasauria and the Therocephalia the humerus is long and the ridge only moderately developed. The Pelycosaur humerus resembles the

Therapsidan in having an entepicondylar foramen and in the well developed delto-pectoral ridge and on the whole it is pretty like that of the Dinocephalians and differs less from this latter type than do most of the other Therapsidans.

The ulna in the Pelycosaur is like that of the Therapsidan in having a well developed olecranon process.

The carpus, so far as known in the Pelycosaurs and Therapsidans, agrees fairly closely as regards elements, both belonging to the generalised Rhynchocephalian type.

The Pelycosaur manus has the metacarpals increasing in length from the first to the fourth and the digital formula is 2, 3, 4, 5, 3. In the Dromasauria and Therocephalia, and to a slight extent in the Cynodontia, there is the same increase in the length of the metacarpals in passing outward, but in all the Therapsida the digital formula so far as known is 2, 3, 3, 3, 3. In the Anomodonts the metacarpals are subequal.

The pelvis in the Pelycosauria is of the plate-like type. In the Anomodontia and the Cynodontia the type is much modified by the forward extension of the ilium and by the formation of an obturator foramen, but in the Dromasauria and apparently also in the Dinocephalia and the Therocephalia the pelvis is essentially similar to that of the Pelycosaur.

The tarsus is not sufficiently well known in the Therapsidan types to admit of comparison with the Pelycosaurian. For the hind limb the digital formula of the Therapsidan is 2, 3, 3, 3, 3, and of the Pelycosaurians 2, 3, 4, 5, 4.

From these points of comparison I think one must conclude that the Pelycosauria are allied to the Therapsida. In some respects the former are more specialised but in most they are more primitive. The skull while essentially similar in the two types is more primitive in the Pelycosaur than the Therocephalia in the retention of the quadrato-jugal and perhaps of a postparietal and posttemporal. It is less primitive in the loss of the transpalatine. The Dinocephalia alone among the Therapsida retain the primitive quadrato-jugal. The Dromasauria alone have the primitive character of the lachrymal meeting the septomaxillary, a character also seen in *Edaphosaurus,* and the possession of abdominal ribs, also present in some Pelycosaurs.

In retaining the typical Diapsidon digital formula the Pelycosaur is more primitive, but though the Therapsida have acquired the mammalian formula of 2, 3, 3, 3, 3, to suit the placing of the feet under the body and to bring the toes into line, we can see from the condition of the metatarsals and metacarpals in the Dromasauria that this formula has probably only been recently acquired and that the feet are not yet completely suited to the new mode of walking.

The conclusion to which I come is that the Pelycosaurs and the Therapsida had a common ancestor in the Upper Carboniferous times, which was characterised by having the typical Diapsidan digital formula, abdominal ribs, a single temporal fossa, a quadrato-jugal bone, and a Rhynchocephalian palate. Such an ancestor could be so near the ancestral Rhynchocephalia or Diaptosauria that though it only had a single temporal fossa corresponding to the lower one in *Sphenodon* it ought to be regarded as a Diaptosaurian, and though the Pelycosauria are specialised in a number of respects I should still keep them in the Diaptosauria.

The South African Therapsidans have sprung from the same ancestor but have evolved in a different way. By a change of habit the limbs have become more powerful and by the adoption of the habit of walking with the body off the ground the digital formula has been changed from 2, 3, 4, 5, 3, to 2, 3, 3, 3, 3. The changes in the skull are of less importance, the only marked one being the loss of the quadrato-jugal. The Dromasauria are perhaps quite as near to the common ancestor as are the Pelycosaurs, but as they are on the Mammalian line I should keep them in the mammal-like phylum and regard them as the most primitive division of the Therapsida.

Diadectes compared with Pareiasaurus.

Though the resemblance between *Diadectes* and *Pareiasaurus* is less striking than between the Pelycosaurs and the Therapsidans it is nevertheless pretty marked.

If a vertebra of *Diadectes* had been found in South Africa and submitted to me for determination I should have had little hesitation in referring it at least to some Pareiasaurian, even though *Pareiasaurus* itself has not the zygosphenal articulation. The arrangement of the zygapophyses and the transverse processes and the mode of articulation of the head of the rib are all typically Pareiasaurian.

The skull appears to differ considerably. *Diadectes* has a highly specialised type of palate and dentition; *Pareiasaurus* has a more primitive palate and dentition specialised in a different direction. Still in essentials the palates are similar. Further, there is probably a close agreement in the structure of the upper part of the skull. The quadrate is much larger in *Diadectes* but so far as is known the arrangement of the bones of the temporal region is similar. The occiput in *Diadectes* is more highly developed and more completely ossified but probably the elements are as in *Pareiasaurus*. Both genera have a flat condyle.

The limbs and limb girdle appear to be fairly similar except that the limbs of *Diadectes* are feeble, those of *Pareiasaurus* relatively very large and powerful.

Both may have had a common ancestor which resembled *Diadectes* in the limbs and *Pareiasaurus* in cranial structure. *Diadectes* has a very specialised skull and teeth, *Pareiasaurus* a more primitive skull but greatly developed limbs.

Pariotichus compared with Procolophon.

The resemblances of *Pariotichus* to *Procolophon* are in many ways striking.

The skull is very similar in the two genera, practically all the elements agreeing except in relative development. *Pariotichus* is much more primitive in having the lachrymal extending to the nostril and in the feeble development of the maxilla, also in retaining the broad temporal region and the postparietal bones. *Procolophon* has the temporal region much reduced, and the quadrato-jugal highly specialised. It further retains the transpalatine which appears to be lost in *Pariotichus*. The palatal structure in each is similar, and both have a rounded occipital condyle.

The vertebræ are fairly alike in the two genera and the limbs bear a considerable resemblance. The digital formula differs, *Procolophon* having the typical Diapsidan formula and *Pariotichus*, according to Williston, probably the formula 2, 3, 3, 4(3), 2. There is also a considerable difference in the structure of the carpus and tarsus.

On the whole *Pariotichus* is a primitive member of some reptilian group of which *Procolophon* is a late representative — more highly evolved in some respects, considerably specialised in others, and degenerate in a few.

Comparison of the American Permian Stegocephalians with those of South Africa.

Unfortunately so little is known of the South African Permian Stegocephalians that it is difficult to compare them with those of America. Only one genus is known at present from the lower Karroo beds, namely *Rhinesuchus*, and this one very imperfectly. It is, however, very interesting to note that many years ago Lydekker believed that the African animal belonged to the American genus *Eryops*. Though in this he was apparently wrong, *Rhinesuchus* is apparently closely allied to the American form and pretty certainly belongs to the Temnospondyli. In the Upper Karroo beds, which are of Triassic age, a number of Stegocephalians are known, and some may perhaps be allied though remotely to the American Permian types. *Batrachosuchus* was, when described by me some years ago, thought to perhaps come nearer to *Diplocaulus* than to any other previously known form. *Bothryceps* is a small temnospondylous form.

Conclusions.

Taking all the facts into consideration it seems to me probable that in Upper Carboniferous times there appeared in the northern part of South America a primitive land vertebrate fauna comprising among other types temnospondylous amphibians, primitive Cotylosaurians, and primitive ancestral Pelycosaurs. Before the conclusion of the Carboniferous period this South American fauna invaded North America and almost immediately afterwards the northern group became isolated. The isolation continued during at least the whole of the Lower Permian times and these isolated types became greatly specialised in their struggle with some adverse conditions. What the conditions were we do not know and no satisfactory explanation has, I think, been given of the development of the enormous spines of the vertebræ in the Pelycosaurs. Nor do we know what caused the extinction of the whole fauna about Middle Permian times, but most likely some change in climatic conditions.

In South Africa the first Karroo reptile to appear is *Mesosaurus*, which is found in beds a little above the Dwyka tillite. It is certainly generically similar to the *Mesosaurus* of Brazil and closely allied specifically. This occurrence of *Mesosaurus* on both sides of the Atlantic, as well as a series of plants which are specifically identical in Brazil and South Africa, renders it practically certain that there was a land connection between South America and South Africa in Lower Permian times and that animals might have migrated from what is now the one continent to the other. There is, however, no evidence that any reptiles other than *Mesosaurus* arrived in South Africa till some considerable time after the origin of the Permian. Perhaps the reason for this may be that about the beginning of the Permian period South Africa and probably much of South America, Australia and India was, from some cause or other, largely covered by glaciers, and possibly for long afterwards the climate was too severe to allow the more northern or equatorial types to invade the south. In beds which are called Ecca we get the earliest immigrants — a large carnivorous reptile called *Archæosuchus* which may have been a Dinocephalian, and evidence from a tooth of a large undoubted Dinocephalian which was a herbivore. It is, however, not till Middle Permian times that the fauna becomes rich. Then there appear

Pareiasaurians, a considerable variety of Dinocephalians, many Therocephalians, a few Anomodonts, the only known Dromasaurians and a temnospondylous amphibian. Where this great collection of forms came from is of course unknown. They can hardly have originated in South Africa, because though the lower Permian beds are lithologically exactly similar to those of later Karroo times, they are almost entirely unfossiliferous.

It seems to me, however, probable from the general resemblance of the African fauna to the North American Permian that both have come from the common source which I believe must have lived in the northern part of South America. After the invasion of North America in Upper Carboniferous times all connection between North and South America ceased for a very long period. The near relatives of the ancestors of the North American Permian forms left in South America evolved on quite other lines. For long they were probably confined to the Brazilian region owing to the cold prevailing in the South, but ultimately they spread down and across the South Atlantic into Africa where they for the most part arrived during Middle Permian times.

If this conclusion be correct we may regard the American and South African Permian faunas as derived from a common origin but having evolved in quite different directions. The American types undergo many curious specialisations; the African, or more preferably the South Atlantic type, is chiefly remarkable for the great development of the limbs. The Pareiasaurians, the Dinocephalians, the Therocephalians and the Anomodonts have all developed powerful limbs, and not improbably all independently of each other. What may have been the cause we cannot at present tell, but it was a most fortunate thing for the world. It was the lengthened limb that gave the start to the mammals. When the Therapsidan took to walking with its feet underneath and the body off the ground it first became possible for it to become a warm-blooded animal. All the characters that distinguish a mammal from a reptile are the result of increased activity — the soft flexible skin with hair, the more freely moveable jaws, the perfect four chambered heart, and the warm blood. It is further singularly interesting to note that the only other warm-blooded animals, the birds, arose in a similar fashion from a different reptilian group. A primitive sort of Dinosaur took to walking on its hind legs, and the greatly increased activity possible resulted in the development of birds. Birds are reptiles that became active on their hind legs, mammals are reptiles that acquired activity through the development of all four.