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Article IX.— A FURTHER COMPARISON OF THE SOUTH AFRICAN DINOCEPHALIANS WITH THE AMERICAN PELYCOSAURS.

By R. Broom.

When in 1878 Cope first described an example of the American Pelycosaurs he regarded them as belonging to the Rhynchocephalia, but very shortly afterwards he recognized affinities with two other groups — the forms with a roofed temporal region which we now group under the name Cotylosauria, and the South African Permian reptiles placed by Owen in the orders Anomodontia and Theriodontia, and soon he came to regard the Theriodont affinity as stronger than the Rhynchocephalian.

From 1878 till now many different views have been expressed as to the affinities of the Pelycosaurs. For years most were inclined to agree with Cope in recognizing a close affinity with the South African mammal-like types. Then from 1897 onwards almost all palæontologists followed Baur and Case in believing that the affinities were more marked with the Rhynchocephalians.

In 1910 I endeavored to show that there was a distinct genetic relationship between the Pelycosaurs and the South African mammal-like reptiles, and especially with the Dinocephalians. Yet though all the additional evidence tends the further to strengthen this view it must not be thought that the earlier views of Cope, Baur, and Case, had no truth in them. The relationship of the Pelycosaurs with the Cotylosaurs is very manifest and there can be little doubt that the former is descended from the latter. With the Rhynchocephalians there are also many marked affinities. Both have doubtless had a common ancestry in the Cotylosaurs and though they have branched off in different directions they still each retain a good many common characters.

With the South African Dinocephalians the affinities are much more close as I hope to show, and while some of the points of agreement may be due to convergence others I feel convinced are due to a fairly close genetic relationship.

In my paper of 1910 on "A comparison of the Permian Reptiles of North America with those of South Africa" I showed that the bones of the skull of *Dimetrodon* so far as can be seen from the outside agree closely with those of the S. African Dinocephalian *Delphinognathus*. In the figure I gave the front of the *Delphinognathus* skull was restored from the nearly allied genus *Moschops*. The sutures shown are from the S. African Museum type speci-

men of *Delphinognathus conocephalus* where they can be clearly traced. Though one or two skulls of *Moschops* and other Dinocephalians, are known, no skull shows the sutures so clearly as the specimen which I have figured. Though the Dinocephalians were presumably planteaters and *Dimetrodon* a carnivorous type, and the skulls like every other part of the skeleton modified to suit very different habits the strikingly close agreement of the bones of the skulls as regards their relations to each other is remarkable.

The Dinocephalians have the bones of the top of the skull enormously thickened, yet all the bones around the orbit and the temporal fossa closely agree with those in *Dimetrodon.*

The structure of the occiput is not certainly known in any Dinocephalian. It is beautifully preserved in quite a number, but it is extremely

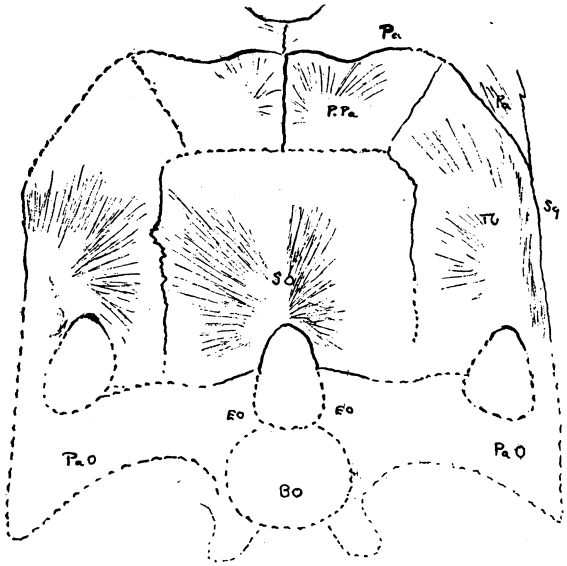

Fig. 1. Occiput of *Theropleura retroversa* Cope, slightly reduced. The parts shaded and the sutures in line are shown in the specimen.

difficult to trace all the sutures, though some can be made out clearly. There is certainly a transverse suture above which there appear to be a large interparietal or fused postparietals and a pair of tabulars. Between the transverse suture and the large foramen magnum there appears to be a supraoccipital. The exoccipitals are small, and the paroccipital very large. If the structure has been correctly interpreted it will be seen to agree closely with that of the Anomodonts and Cynodonts.

The occiput in the Pelycosaurs has never yet been very satisfactorily

made out. In 1909 I examined the best specimens of *Dimetrodon* in the Am. Mus. but as there were one or two points on which I felt doubt I did not publish my drawings. V. Huene has recently gone over the same specimens, and come to much the same conclusions as I did, namely that there is a pair of dermo-supra-occipitals or post parietals, a pair of tabulars, a median supraoccipital, small exoccipitals, and large opisthetics (paroccipitals). Fortunately I have come across in the collection of the American Museum a crushed but fairly good skull of apparently *Theropleura retroversa* Cope. While the occiput is somewhat crushed much of the structure can be made out without question. There are behind the parietals a pair of postparietals, with on each side a large tabulare. The tabulare articulates with the posterior process of the parietal and also with the squamosal. Below the pair of post parietals is a large median supraoccipital. Though the occipital condyle and exoccipitals are present in the specimen they are displaced and crushed, and have been restored in the drawing in dotted line. In some other Pelycosaurs e. g. *Edaphosaurus*, the postparietal is a single median bone, and the tabulars are narrow.

It will be seen that the occiput agrees essentially with the type found in the African types. It also agrees fairly closely with the type found in *Diadectes* which may be regarded as the primitive reptilian type.

The lower jaw has not hitherto been fully described in either the Dinocephalians or Pelycosaurs, though Case, v. Huene, and I have figured the outer side of the jaw of *Dimetrodon*, and Case has given drawings of the bones of the inner side in which an attempt is made to delimit the various bones. Prof. Williston has recently sent me a drawing of the jaw of *Dimetrodon* which is the most satisfactory of the inner side yet made, and in a note in "Science" 10th Oct., 1913, gives a brief description of it.

The structure of the Dinocephalian mandible though fairly well shown in the type of *Moschops capensis* Broom is shown in practically every detail in an allied form which may be called *Moschognathus whaitsi*.

On the outer side of the jaw the dentary forms about the interior $\frac{2}{3}$, the back third being formed by the articular, angular and surangular. On the inner side the dentary forms most of the symphysis and most of the upper half of the anterior third. There is no precoronoid bone present. The splenial forms the lower corner of the symphysis as indicated in the figure and occupies most of the lower half of the anterior portion of the jaw. It does not pass round to the outer side. The prearticular posteriorly lies underneath the articular and passes forwards forming the lower margin of the Meckelian fossa and passing between the splenial and the coronoid reaches the posterior part of the dentary. The coronoid is a fairly well developed bone which lies in front of the Meckelian fossa and passes forwards

some distance resting on the dentary. It is more flattened than usual, and though the jaw has a Meckelian fossa it is very narrow and differs considerably from the wide fossa seen in the Cotylosaurian jaw. The angular forms about the lower third of the posterior half of the jaw. At its posterior lower border the angular forms a thin fan-like expansion which

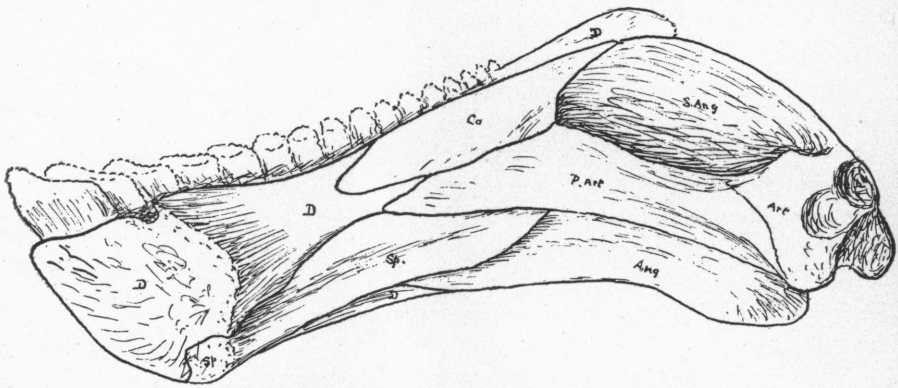

Fig. 2. Inner side of Mandible of *Moschognathus whaitsi* Broom. $\frac{2}{5}$ nat. size.

passing down from near the middle of the back part of the outer surface forms a deep narrow hollow such as is also seen in the Pelycosaurs and most Therapsids. The articular has two rounded articular pits which look backwards and a little inwards. There is a short postarticular process.

The structure of the outer side of the Pelycosaur jaw as has been known for some years is almost exactly similar to that of the Dinocephalian. The structure of the inner side has not hitherto been fully known.

The following description is based on the beautifully preserved jaw in the National Museum, Washington. It is there labelled *Dimetrodon cruciger*, but whether it is the jaw of a species of *Dimetrodon* or of *Naosaurus* or of some other Pelycosaur need not for the present concern us. It is certainly

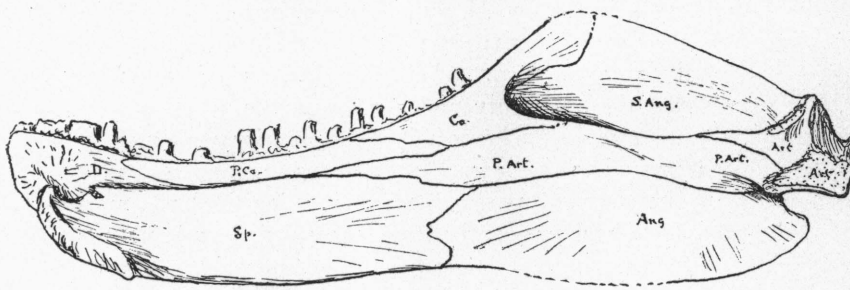

Fig. 3. Inner side of mandible of *Dimetrodon* sp. About $\frac{2}{5}$ nat. size.

the jaw of a near ally of *Dimetrodon* if not a species of that genus and certainly of a Pelycosaur. The inner side of the jaw shows the following bones: dentary, splenial, angular, prearticular, articular, surangular, coronoid,

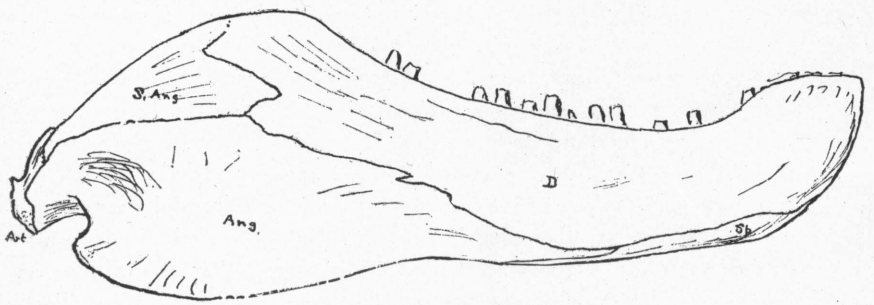

Fig. 4. Outer side of mandible of *Dimetrodon* sp. About $\frac{2}{5}$ nat. size.

and precoronoid. The dentary only shows at the symphysis and a little behind and to a slight extend along the alveolar border. The splenial forms most of the inner side of the anterior half of the jaw. Above it is a small supposed precoronoid bone. Williston has recently discovered this element in the *Dimetrodon* jaw but was not certain whether it is continuous with the coronoid. The coronoid is a fairly large element which forms the anterior border of the Meckelian fossa and has a firm articulation with the upper

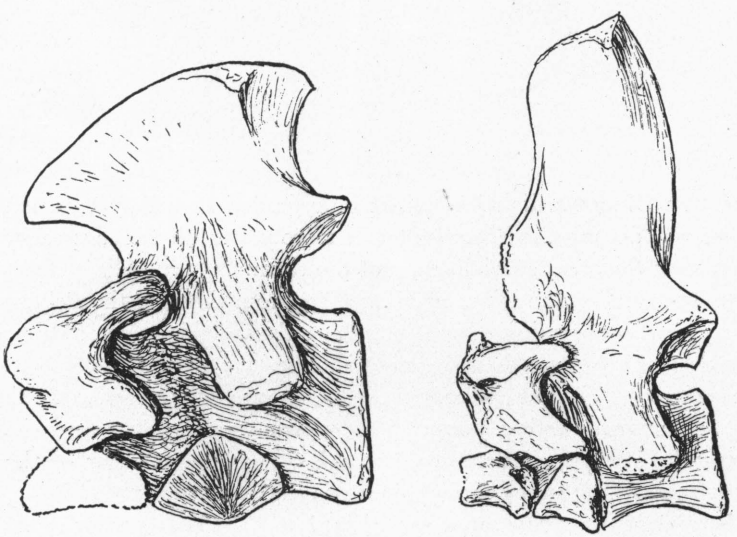

Fig. 5. Atlas and axis of *Moschops capensis* compared with atlas and axis of *Dimetrodon* sp. Both reduced.

part of the surangular. Below it has a long articulation with the prearticular. In front it has a long articulation with the precoronoid. Williston describes the coronoid in *Dimetrodon* as lying "at the summit of the coronoid eminence, extending about two inches back of the teeth. It is covered on the outer side by the dentary, and in inserted in a pit in the surangular... If it is continuous with the alveolar bone [my precoronoid], as it seems to be the connection must be very narrow." As will be seen in the drawing I give the condition in the Washington specimen is very different. The angular, surangular prearticular and articular will be readily understood from the figure given.

A comparison of the jaws of the Pelycosaur and the Dinocephalian shows that though the jaws are specialized as regards the dentition in quite different ways the essential structure is almost identical. The only difference of importance is the loss of the precoronoid bone in the Dinocephalian.

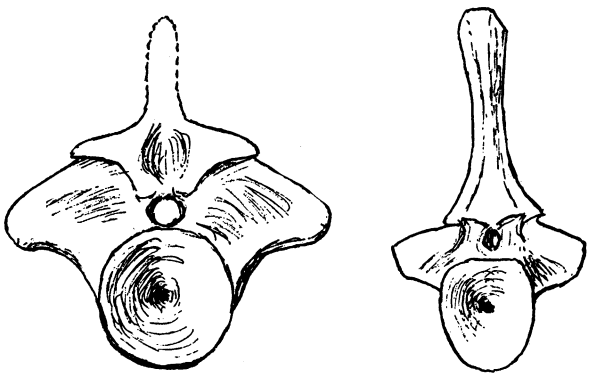

Fig. 6. Cervical vertebræ of *Moschops capensis* and of *Ophiacodon mirus*. The former original; the latter after Williston and Case. Both figures reduced.

In fact the Dinocephalian jaw might be regarded as a Pelycosaurian jaw in which the dentary had become much more powerfully developed in connection with the great specialization of the teeth.

The vertebræ of the Dinocephalian differ from those of the Pelycosaurs in being much more massive and in lacking the specialization of the spines, but in general structure the agreement is close.

A comparison of atlas and axis in the two groups will be seen in the figures given. Though doubtless many of the characters are common primitive features the striking similarity of the atlas, and the relations of the axis transverse process to the centrum seems to suggest affinity.

The cervical vertebræ are seen in Fig. 5 to be closely similar in the two groups.

The dorsal and later cervical vertebræ of the Pelycosaur are very re-

markable in the peculiar specialization of the transverse processes. Fig. 6 shows that the Dinocephalians have an exactly similar specialization.

The limbs in the Dinocephalians differ from those of the Pelycosaurs in being relatively much more massive. The Pelycosaurs were crawling animals with feeble limbs: the Dinocephalians heavy bodied walking animals, and the differences in the girdles and limbs are readily accounted for by the differences of habits.

Case objects to my comparison of the South African forms with the America, stating that "Broom's summary of evidence only cites as common

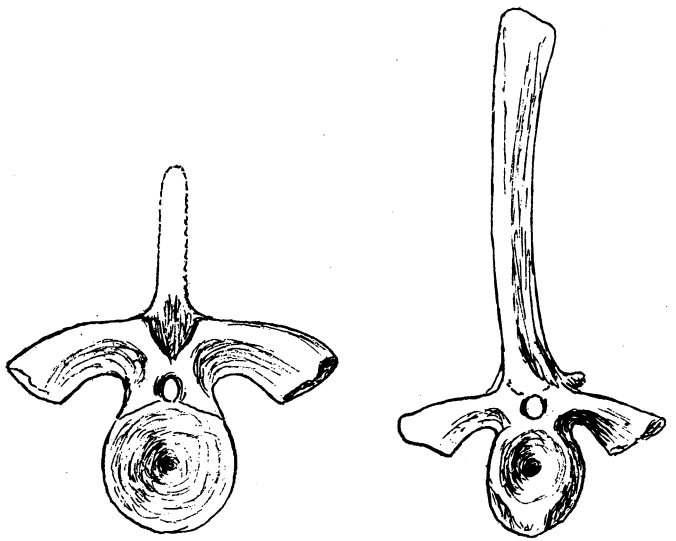

Fig. 7. Dorsal vertebra of *Moschops capensis* and posterior cervical vertebra of *Sphenacodon ferox*. The latter after Case and Williston.

characters the most primitive features, which all date from the time when the reptiles separated from the amphibians. Such a relationship of the two groups must be admitted, but it can only be very remote." The characters of the jaw, to take only a single point, seen in the two groups are not amphibian characters, and either we must assume that we have a marvellous case of convergence or a striking affinity. What seems to me the most remarkable thing about the Dinocephalian jaw is that notwithstanding the striking specialization of the front part the back half remains so typically Pelycosaurian as to be practically indistinguishable.

The later South African Therapsids have all taken on further specializations of the skull and jaw and though they can be readily compared with the Dinocephalian for the most part the Dinocephalian structure is nearer to the Pelycosaurian than to the Anomodont or Therocephalian.