17. On the Gorgonopsia, a Suborder of the Mammal-like Reptiles. By R. Broom, M.D., D.Sc., C.M.Z.S.

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(Plates XXXVI. & XXXVII.*)

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When *Gorgonops torvus* was described by Owen in 1876 he regarded it as the type of a distinct group, partly on account of the apparent peculiarity of the nose, and also because the temporal region was believed to be roofed. Lydekker in 1890 and Seeley in 1895 both agreed that the temporal region was roofed, and Seeley proposed the name Gorgonopsia as a distinct order for the reception of *Gorgonops*. A re-examination of the type in 1909 convinced me that though the parietal region is wide, *Gorgonops* has temporal openings like the other Therapsida, and the discovery by the Rev. J. H. Whaits of a nearly perfect skull of *Gorgonops torvus* shows that my observation was correct.

Still one has long had the feeling that *Gorgonops* differed considerably from the typical Therocephalians. For a time I inclined to place it with *Titanosuchus* and others in the Dinocephalia. Later on I put it back among the Therocephalians. Now the discovery of one or two perfect skulls shows that the difference from the Therocephalians is sufficient to warrant the re-establishment of Seeley's group—the Gorgonopsia—as a distinct suborder of the Therapsida. I am well aware that the formation of so many new orders and suborders of reptiles as have been made in recent years has been criticized ; but it seems to me wiser to separate into distinct groups forms that are manifestly distinct than to group into one order animals that are markedly different ; and one can now say without any fear of contradiction that *Gorgonops* differs from the typical Therocephalians more than does a Carnivore from a Marsupial. As will be seen from the present paper, the skull in many ways approaches more nearly to that of the Anomodont.

Skull.

Though nearly perfect skulls are known of *Gorgonops torvus* and *Scymnognathus whaitsi*, in neither species can the sutures be very clearly made out. The discovery by Mr. S. H. Haughton of two fine skulls from the *Cistecephalus* zone, and of a good skull obtained by the Rev. J. H. Whaits from the *Pareiasaurus* zone, gives us material which reveals practically every point in the structure of the skull.

* For explanation of the Plates see p. 230.

Scylacops capensis (Pl. XXXVI.).

Broom, Annals S. African Mus. 1913.

Scylacops capensis is pretty closely allied to *Gorgonops torvus*. The figures given show most of the cranial characters. The most noteworthy features seen in the figure of the side view (fig. 1) are the large septo-maxilla, the large prefrontal which meets the postfrontal and shuts out the frontal from the orbital margin, and the great forward extension of the zygomatic portion of the squamosal.

The upper view of the skull (fig. 2) shows some much more remarkable characters. The large size of the prefrontal is again seen. The frontals, though fairly large, do not reach the orbital margins. Behind the frontal is a large postfrontal bounded by the prefrontal, the frontal, the parietal, and the postorbital. Between the back parts of the frontals and in front of the parietals is a well-developed median preparietal. Though a preparietal has long been known in most Anomodonts, it has not hitherto been detected in any other group. It is certainly absent in typical Therocephalians such as *Scylacosaurus* and *Lycosuchus*, and is apparently not present in Dinocephalians, while no trace of it exists in Cynodonts, nor has it been detected in Pelycosaurs. A careful re-examination of the skull of *Galepus jouberti* seems to show evidence of a small but distinct preparietal round the front of the large pineal foramen. We may thus regard the presence of a preparietal as a character of the Anomodontia. the Gorgonopsia, and the Dromasauria. In Anomodonts and in *Galepus* the preparietal always forms at least the anterior wall of the foramen. In the Gorgonopsia the foramen is between the parietals, and the preparietal is some distance in front. The parietals are large, and each has a process which extends far back and forms an important part of the bony wall which separates the temporal fossa from the occiput. The end of the posterior process is clasped by the squamosal. Posteriorly the parietals are mainly bounded by the large interparietal. The postorbital is very large. It forms the greater part of the postorbital arch and the whole of the upper margin of the temporal fossa.

Whatever may be the case with the temporal fossa in the Plesiosaurs, the condition of the bones in this skull will, I think, convince everyone that the fossa in the Therapsida is the homologue of the inferior fossa of the Rhynchocephalia, as I have for a number of years maintained.

The occipital view (fig. 4) of the skull shows the great development of the squamosals and the large interparietal. The suture between the basioccipital and the exoccipitals cannot be made out, nor is there any evidence of a distinct supra-occipital. The condyle is single.

The palatal view (fig. 3) shows many features of great interest. The front part of the palate cannot be seen, and is restored from other specimens. Though the skull of *Scylacops capensis* shows

only the general appearance of the palatal elements when viewed from below, our knowledge of the morphological structure has been gained mainly by the skulls of *Scymnognathus tigriceps* and *Scylacognathus parvus*. The settling beyond question of the nature of the palate, and especially of the vomer, was a matter of such importance that I have not hesitated to break up the skulls of both of these types. As museum specimens they are none the worse for having been broken across in various directions and internally dissected, and, as a result, every detail of the internal anatomy is now known.

For many years I have known that the type of *Gorgonops torvus* showed an apparently undivided median vomer, but whether it was a true vomer or a pair of prevomers fused as we get in *Ornithorhynchus* it was impossible to tell. In typical Therocephalians there are two prevomers as in Lizards and Rhynchocephalians. In Anomodonts and Cynodonts there is a single unpaired vomer as in Mammals. A good many years ago (1895) I endeavoured to maintain that the mammalian vomer was not homologous with the reptilian paired vomers, but that these latter were the homologues of the dumb-bell bone of *Ornithorhynchus*. The question has been discussed by Gaupp, Versluys, Fuchs, Osborn, Williston, and others, but may be said to be still unsettled. As the Gorgonopsia stand between the Therocephalians on the one hand and the Anomodontia and Cynodontia on the other, it is in this suborder that we must look for a solution of the vomer problem. Unfortunately, the skulls examined still fail to give us the solution, as both *Scymnognathus* and *Scylacognathus* agree with the Anomodonts, Cynodonts, and Mammals, and differ from the Therocephalians in having a median impaired vomer and, so far as can be seen, no trace of paired vomers.

Scymnognathus tigriceps (Pl. XXXVII.).

Broom, Annals S. African Mus. 1913.

In *Scymnognathus tigriceps* the basisphenoid is very large. It has two greatly developed thick descending processes, which pass down a considerable distance below the level of the condyle. In front there is a deep but thin median keel, which passes forwards and meets the median keel formed by the united pterygoids. Above, the sphenoid passes between the pterygoids, and forms a large median plate that extends forwards and upwards as far as the plane of the front of the orbit.

The pterygoid is a huge bone which more closely resembles the pterygoid of the Pelycosaurs than that of the other South-African Therapsid suborders. The descending pterygoid process is very large, but the most remarkable feature is the enormous development of the ascending plates. These pass upwards and clasp the front of the median sphenoid. In front of the sphenoid they become ankylosed, and form a median plate which extends forward to meet the vomer. Whether this large, thin, median

plate is entirely made up of the fused pterygoids, or whether there is a median basi-cranial element as well, cannot be made out in the specimen. Certainly it is largely composed of the pterygoid plates. In *Scylacognathus* the pterygoid plates are separate from one another, and a median cartilaginous element might have been between them. Further forward the median plate in *Scymnognathus* is clasped by the ascending plates of the palatines. In front of the median plate we meet with the vomer. In *Scymnognathus* it clasps the front of the median plate, but in *Scylacognathus* it is seen clasping a median element which is not the fused pterygoids but may be regarded as ethmoid, a fact which suggests that not improbably there is in *Scymnognathus* an ethmoid element between the pterygoid plates, though no sutures can be detected. There can, I think, be no question that the vomerine bone is the true mammalian vomer. I can find no evidence of paired prevomers. The relations of the palatine bones, as viewed from underneath, can best be understood from the figure of the condition in *Scylacops* (Pl. XXXVI. fig. 3).

The mandible is beautifully preserved in *Scymnognathus*, and the condition is thus better known than in any of the Therapsidan suborders. The outer aspect, of course, and something of the internal relations of the bones, are known in all; but there are gaps in our knowledge even of the Anomodont mandible, and only of the Gorgonopsian jaw is our knowledge practically complete. Full detailed figures are thus given for later comparison with the other types (figs. 6 & 7).

The dentary is large and powerful. The front of the jaw is deep and formed by the dentary, except the base, which is splenial. About two-thirds of the outer aspect of the jaw are made up of the dentary, and there is a well-developed coronoid process. Only a little of the dentary shows on the inner aspects, as in front the inner side of the jaw is mainly splenial, and further back most of the dentary is hidden by the angular, gonial, and coronoid. The relations of these elements to the dentary will best be understood by the section and figures. The splenial extends backwards to opposite the point where the angular begins to replace the dentary on the outer side. The angular is the second largest bone in the jaw, and extends nearly the whole length. In front it is fitted in between the dentary and splenial. Posteriorly it forms the main part of the jaw. As will be seen in the drawing, there is a curious doubling of the back part, forming a deep groove for some structure. A very similar condition is seen in Pelycosaurs, though, so far as known, not in other Therapsida. There is a distinct coronoid bone, as shown in the figures, lying on the inside of the back part of the dentary. The surangular is of fair size and, with the angular, forms most of the back third of the jaw. The articular is large but short. It forms the articulation. It is clasped by the angular and the gonial. It has a peculiar posterior process which curves downwards and forwards. The gonial clasps the

inner side of the articular in front, and extends forwards between the coronoid and the angular to a little beyond the posterior end of the splenial.

Postcranial Skeleton.

The upper cervical vertebræ are very similar to those in other Therapsidans. The proatlas is large, and the upper portion of the atlas is very similar to that in Anomodonts and Dinocephalians; and the condition further resembles that of these suborders in the two halves being free and not forming a single arch as in Cynodonts.

The shoulder-girdle has a large scapula without any distinct acromion process. The coracoid and precoracoid resemble those of the Therocephalians. There is a distinct cleithrum (at least in *Scylacops*), a large clavicle and interclavicle, and an ossified sternum.

The carpus has a large radiale and ulnare and a small intermedium. There are two centralia, of which the outer is the smaller. There are four distal carpalia, but the fourth is very broad and, I believe, formed of the ankylosed fourth and fifth.

The digital formula is 2, 3, 4, 5, 3; the third toe having a small phalanx and the fourth two small phalanges as in the Therocephalia.

Very little is known of the posterior half of the body.

Affinities of the Gorgonopsia.

Till we know more of the structure of the Therocephalia it is impossible to say how far the Gorgonopsia differ. The differences in the skull may be tabulated as follows:—

Gorgonopsia.	*Therocephalia.*
1. Parietal region broad.	Parietal region narrow.
2. A preparietal bone.	No preparietal bone.
3. A large postfrontal.	Postfrontal small or absent.
4. Postorbital large, forming the upper temporal margin and meeting squamosal above.	Postorbital small, not extending far back and not meeting squamosal above.
5. A single median true vomer.	A pair of prevomers.
6. Transpalatine closely united to pterygoid.	Transpalatine separated from pterygoid by large foramen.
7. Mandibles united by powerful symphysis.	Jaws loosely articulated.
8. Angular with deep groove.	Angular perforated.

Most of the characters in which the Gorgonopsia differ from the Therocephalia are characters in which they agree with the Anomodontia. The Therocephalia are unquestionably the more primitive group, but there are some early characters in the Gorgonopsia and also in the Anomodontia. Of course we only know well one or two of the later Gorgonopsians, and we have good reason to believe that the group is very early—earlier in

South Africa perhaps than the Therocephalia, and pretty certainly earlier than the Anomodonts.

As so many of our types are founded on imperfect snouts, it will be some time, probably long, before it will be possible to divide the Gorgonopsians from the Therocephalians. All we can do at present is to give a list of the known Gorgonopsians and of those that are probably members of that group.

The known Gorgonopsians are *Gorgonops torvus* Owen, *Scymnognathus whaitsi* Broom, *Scymnognathus tigriceps* Broom & Haughton, *Scylacops capensis* Broom, and *Scylacognathus parvus* Broom.

The following are probably Gorgonopsians:—*Titanosuchus ferox* Owen, *Titanosuchus cloetei* Broom, *Scapanodon duplessisi* Broom, *Archæosuchus cairncrossi* Broom.

Besides these there are quite a number of supposed Therocephalian genera which, on further investigation, may prove to be Gorgonopsians, such as *Inostransewia*, *Eriphostoma*, *Lycosaurus*, *Cynosuchus*, *Arctognathus*, *Ictidosaurus*, and a number of others.

Archæosuchus occurs in beds which are Lower Permian. *Scylacognathus* and a number of other probable Gorgonopsians occur in the Middle Permian or *Pareiasaurus* zone. *Gorgonops* and *Scymnognathus whaitsi* are from the *Endothiodon* zone; while *Scymnognathus tigriceps* and *Scylacops capensis* are from the *Cistecephalus* zone or top of the Permian. From the very top of the *Cistecephalus* beds a small undescribed Gorgonopsian has just been discovered, so that we can confidently affirm that the Gorgonopsia extend throughout the Middle and Upper Permian beds, and that they probably extend from Lower Permian to Lower Trias.

EXPLANATION OF THE PLATES.

Ang. Angular. *Art.* Articular. *B.o.* Basioccipital. *B.s.* Basisphenoid. *Co.* Coronoid. *D.* Dentare. *E.o.* Exoccipital. *Fr.* Frontal. *I.P.* Interparietal. *Ju.* Jugal. *L.* Lachrymal. *Mx.* Maxilla. *Na.* Nasal. *P.A.* Prearticular or Gonial. *Pa.* Parietal. *Pal.* Palatine. *Pmx.* Premaxilla. *Po.F.* Postfrontal. *Po.O.* Postorbital. *P.P.* Preparietal. *Pr.F.* Prefrontal. *Pt.* Pterygoid. *Q.* Quadrate. *S.Ang.* Surangular. *Smx.* Septomaxilla. *Sq.* Squamosal. *St.* Stapes. *V.* Vomer.

Plate XXXVI.

Scylacops capensis.

Fig. 1. Side view of skull. About ½ nat. size.
2. Top view of skull. A little over ½ nat. size.
3. Palatal view of skull. About ½ nat. size.
4. Occiput. About ½ nat. size.

Plate XXXVII.

Scymnognathus tigriceps.

Fig. 5. Side view of skull. Nearly ½ nat. size.
6. Inner aspect of mandible. Nearly ½ nat. size.
7. Sections across jaw at the places indicated in fig. 6.