3. The Bases of Classification of the Theriodontia.

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(Text-figures 1–29.)

Among the first series of reptiles from the Karroo system of South Africa sent home by Andrew Geddes Bain were a few poor fragments of animals with a heterodont carnivorous dentition. Later collections from the same rocks included more satisfactory remains of these animals, which were described by Owen, who recognised their mammalian appearance and despite his ante-evolutionary views even suggested that they were mammalian ancestors. Prof. Seeley's visit to South Africa marked a turning-point in our knowledge of these reptiles, because he showed that their remains were found in rocks of widely different ages, and that the latest assemblage—*Diademodon*, *Cynognathus*, and *Trirachodon*—were more mammal-like in their dentition than were their earlier forerunners. He showed also that they possessed a mammal-like secondary palate, but failed to arrive at a satisfactory interpretation of that region in the less complete remains of the earlier forms known to him. Neither Owen, Seeley, nor Lydekker was able to draw up any useful classification of these reptiles on account of the paucity of material, and the first definite step in so doing was made by Broom, when in 1904 he showed that *Scylacosaurus sclateri*, a form from the lowest zone of the Beaufort beds, differed from the "Cynodonts" of the highest zone of that formation in lacking any trace of a secondary palate.

Subsequent work by Broom added many new generic types to those included with *Scylacosaurus* in that primitive division of the carnivorous Therapsids whose members lacked a secondary palate and had uncusped molar teeth. This division Broom made into an order and called Therocephalia.

No further important additions were made to our knowledge of the skull of any of these reptiles till, in 1911, the writer gave a very detailed account of the skull of *Diademodon* and Broom a more general description of the skull in all the Cynodonts. The first important addition to our knowledge of the earlier Theriodonts was the description by the present author of the posterior half of a skull from the *Cistecephalus*-zone, which agreed with *Gorgonops* in having a broad parietal region, the parietal bone being excluded from the margin of the temporal fossa. In the same paper some of the more salient features of the palate of *Gorgonops* were described, and it was indicated that the form showed the beginnings of the Cynodont secondary palate, the skull known as *Arctognathus curvimola* showing an intermediate condition. Whilst I was writing this paper in

London, Broom in South Africa was describing two very complete Gorgonopsid skulls, one associated with the anterior part of a skeleton. Of these skulls Broom gave a good description, bringing out the whole structure of the face and parietal region, but not giving us so satisfactory an account of the palate and occiput. Broom, sometimes in conjunction with Haughton, subsequently added many new and often strange forms to the Gorgonopsidæ—on the whole, emphasizing rather their resemblance to the Deinocephalia and Dicynodontia and even Pelycosauria than those which they show to the "Cynodontia." In 1914 I was able to show that known Gorgonopsids could be arranged as a morphological series giving a gradual passage in the structures of the occiput, and of the basicranial and otic regions between *Dimetrodon* a Pelycosaur and *Diademodon* a "Cynodont." In the same paper I described the palate of the "Cynodont" *Bauria*, showing that it differed much from the Cynognathids and resembled the non-Gorgonopsid Theriodonts with a primitive palate more than the Gorgonopsids. In consequence, purely as a temporary measure, I revived the order Theriodontia and divided it into four sub-orders—the Therocephalia, the Gorgonopsia, the Bauridæ, and the Cynodontia. Since that paper was written, Haughton has published descriptions of certain new forms and made important new additions to our knowledge of the brain-case of the earlier Theriodonts. In his most recent paper he uses provisionally my 1914 classification, emphasizing its insufficiency.

In revising a paper on the relative ages of the Palæozoic and Triassic reptile-bearing rocks, which has occupied me at intervals for some years, I was forced to deal with the problems presented by the fauna of the copper-bearing Permian sandstones of the Orenburg district of the Urals. One of the most noteworthy forms from this locality is *Rhopalodon*, an animal whose skull, which alone is certainly known, presents many resemblances to the Gorgonopsids. The necessity of discussing the systematic position of this form led me to an examination of all the Theriodont material available, with the results which are set out below.

It is convenient to begin with a description of the material at my disposal, then to discuss the morphological results which arise from it, and, finally, consider the evolution of the group and the relationship of *Deuterosaurus* to it.

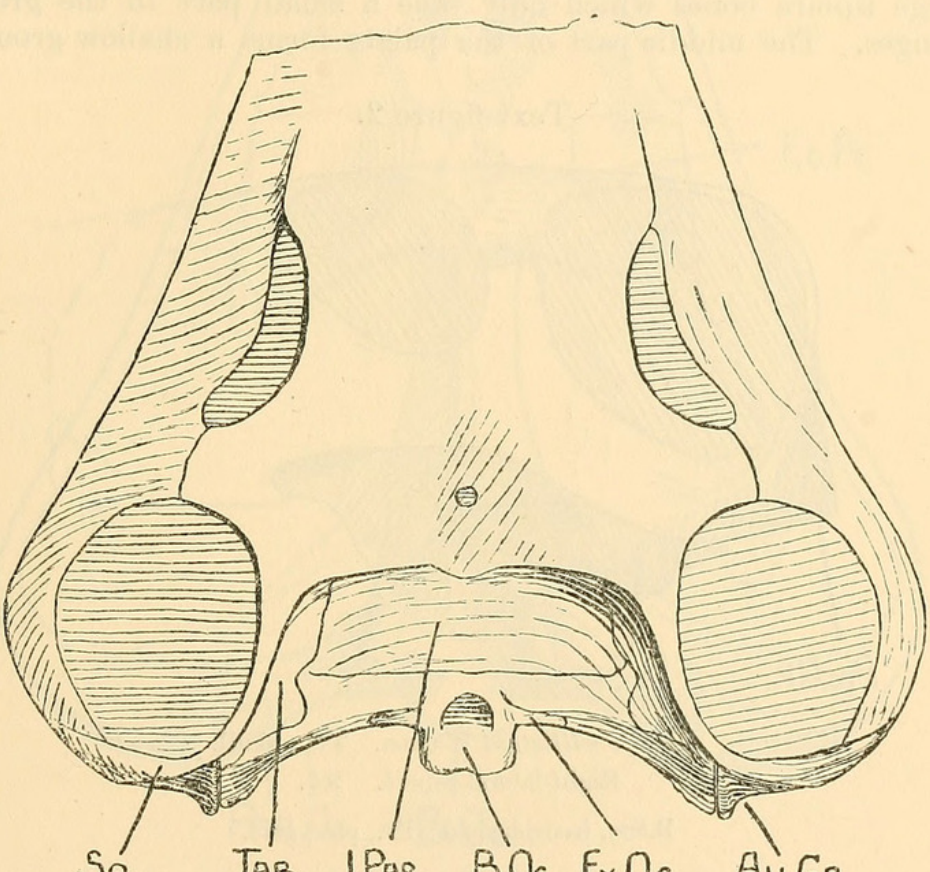
Arctops willistoni Watson, Proc. Zool. Soc. 1914, p. 1026.

Type and only known material: a skull lacking the anterior part of the snout, the quadrates and quadrate rami of the pterygoids, otherwise complete and practically undistorted. From Howse Post, near Fort Beaufort, S. Africa, not improbably Endothiodon zone.

I described and figured the occiput and basicranial region in the original description.

Arctops has a depressed and very massive skull, the snout, when broken off about 5 cm. in advance of the orbit, being rectilinear in section, bounded by a straight dorsal surface which passes somewhat abruptly into straight, nearly vertical, lateral surfaces. The orbit is small, placed high in the skull, and nearly laterally directed; its upper margin is continued forward by a ridge separating the dorsal surface from the lachrymal region, which is excavated into a shallow depression. The interorbital region is very wide, forming a flat surface bounded laterally by shallow bays over the orbits.

Text-figure 1.

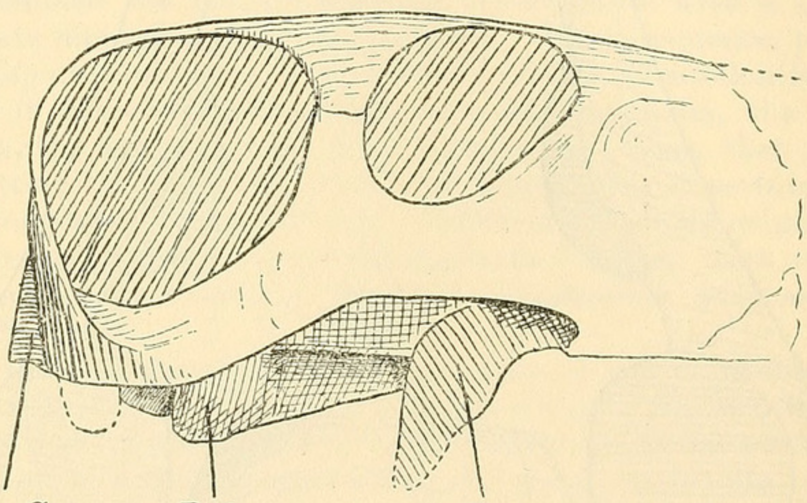


Arctops willistoni Watson. Type-skull.
Dorsal aspect. ×⅔.
B.Oc., basioccipital; I.Par., interparietal; Sq., squamosal; Tab., tabular.

The parietal region, also flat, is even wider than the interorbital surface; it separates the very small temporal fossæ which face more largely laterally than dorsally. The occipital surface is very wide and is separated from the parietal by a sharp corner. The squamosal is small, consisting mainly of a vertically standing plate passing directly outward from the end of the massive paroccipital process. The posterior surface of the bone at this articulation is produced backwards into a ridge which forms the inner wall of the auditory groove. Sutures over the outer surface are not clearly recognisable.

I have already described the basicranial region, but would again call attention to the flat, laterally directed, plate-like basi-pterygoid processes. The narrow ridged girder formed by the parasphenoid and pterygoids extends forward to the front of the orbit, where it suddenly passes into the wide posterior end of the palate. The pterygoids pass outward to form thick downwardly directed flanges, not very deep when compared with later forms, but of great antero-posterior extent. The middle region of the posterior part of the palate forms a slightly raised area separating two concavities, whose surface lies mainly on the ectopterygoids, large square bones which only take a small part in the great flanges. The middle part of the palate forms a shallow groove

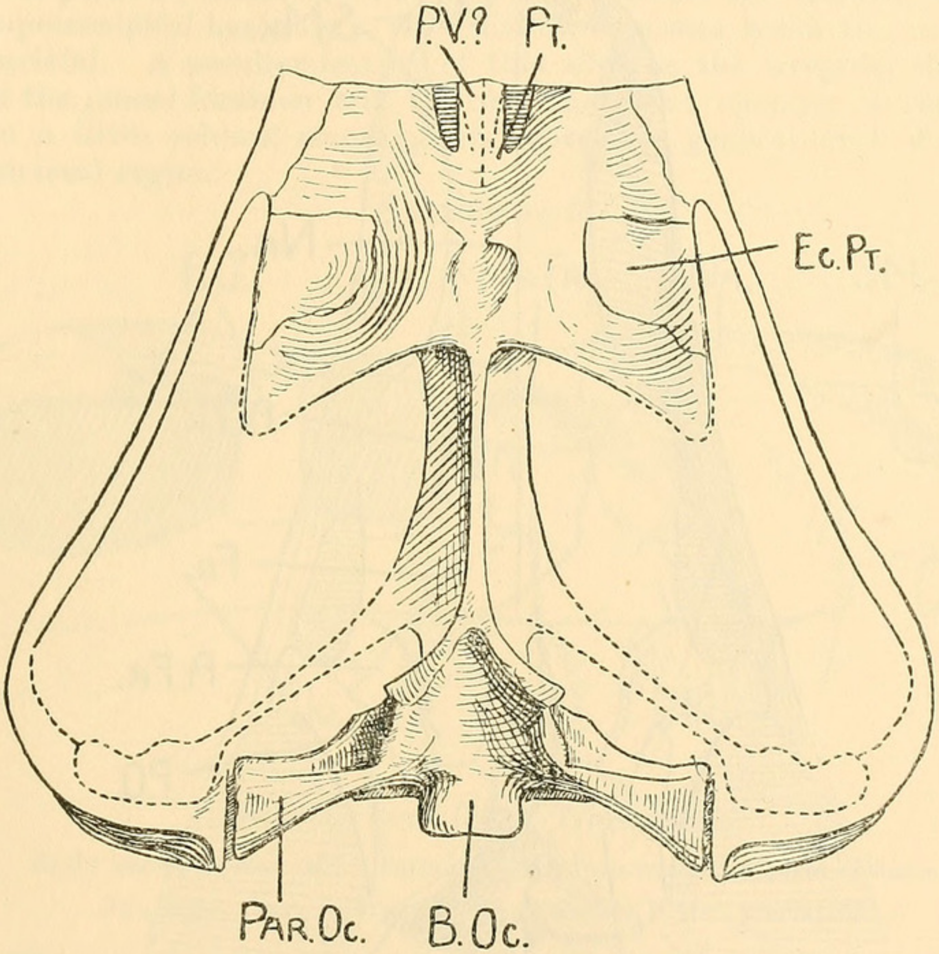
Text-figure 2.



Arctops willistoni Watson. Type-skull.
Right lateral aspect. ×⅔.
B.Sp., basisphenoid; Pt., pterygoid.

beginning at the extreme posterior end and running forwards to the posterior nares. At about the level of the anterior end of the ectopterygoid, this groove is overhung by a pair of small processes rising from the pterygoids. Further forward the floor of this groove is cut into by the narrow slits which represent the posterior ends of the posterior nares. These are separated by a narrow bar of considerable vertical depth. The structure of this bar is not quite certainly determinable, but on the curved fracture which forms its present front termination it is certain that its upper surface consists of a pair of ridges separated by a parallel-sided cleft not more than a millimetre wide and nearly a centimetre deep. From this slit a suture seems to be continued on to the palate. Further back two lateral ridges are added to the original pair, the gaps between them being also apparently continued as sutures on to the palate. Thus the posterior part of the bar separating the internal nares seems to be built up of two pairs of bones, of which the outer terminates not far in front of the posterior ends of the nares. It is probable that the inner pair are prevomers and the outer the anterior ends of the pterygoids, which hence form a part of the border of the posterior nares.

Text-figure 3.



Arctops willistoni Watson. Type-skull.

Palatal aspect. ×⅔.

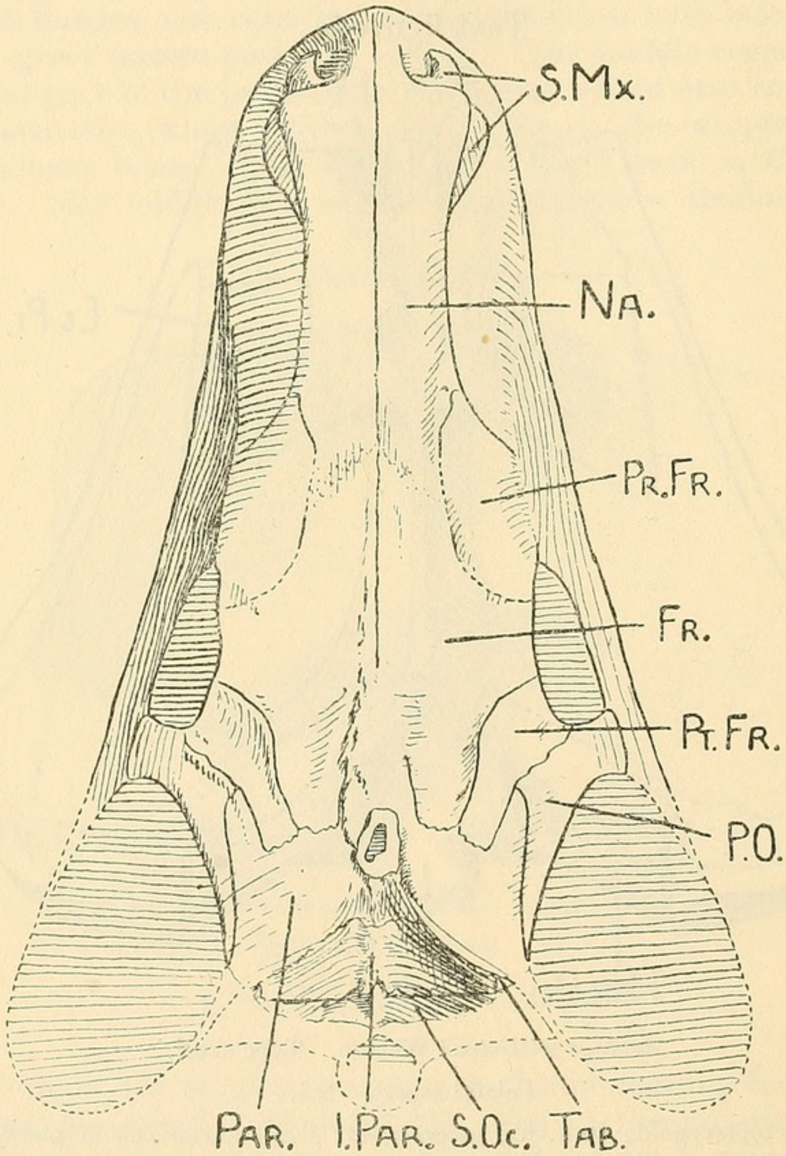
Ec.Pt., ectopterygoid; Par.Oc., paroccipital; Pt., anterior end of pterygoid; P.V. ?, prevomer, posterior end of internarial bar. Parts in broken lines restored without evidence.

Gorgonops torvus Owen, Cat. S. Afr. Rept. 1876.

Type: a skull with the zygomatic arches broken away, the basis cranii only represented by a fractured surface passing horizontally through the basisphenoid. The paroccipital processes only represented by the impression on the matrix of the anterior face of that of the right side, the posterior part of the palate represented only by the impression of its dorsal surface.

Otherwise the skull is complete and, on the whole, extremely well preserved. It is represented by beautiful and most accurate lithographic drawings in Owen's Catalogue. From Mildenhals, Fort Beaufort. Another more complete, but less well-preserved, skull from the *Endothiodon*-zone of Beaufort West is in the American Museum of Natural History.

Text-figure 4.



Gorgonops torvus Owen. Type-skull.

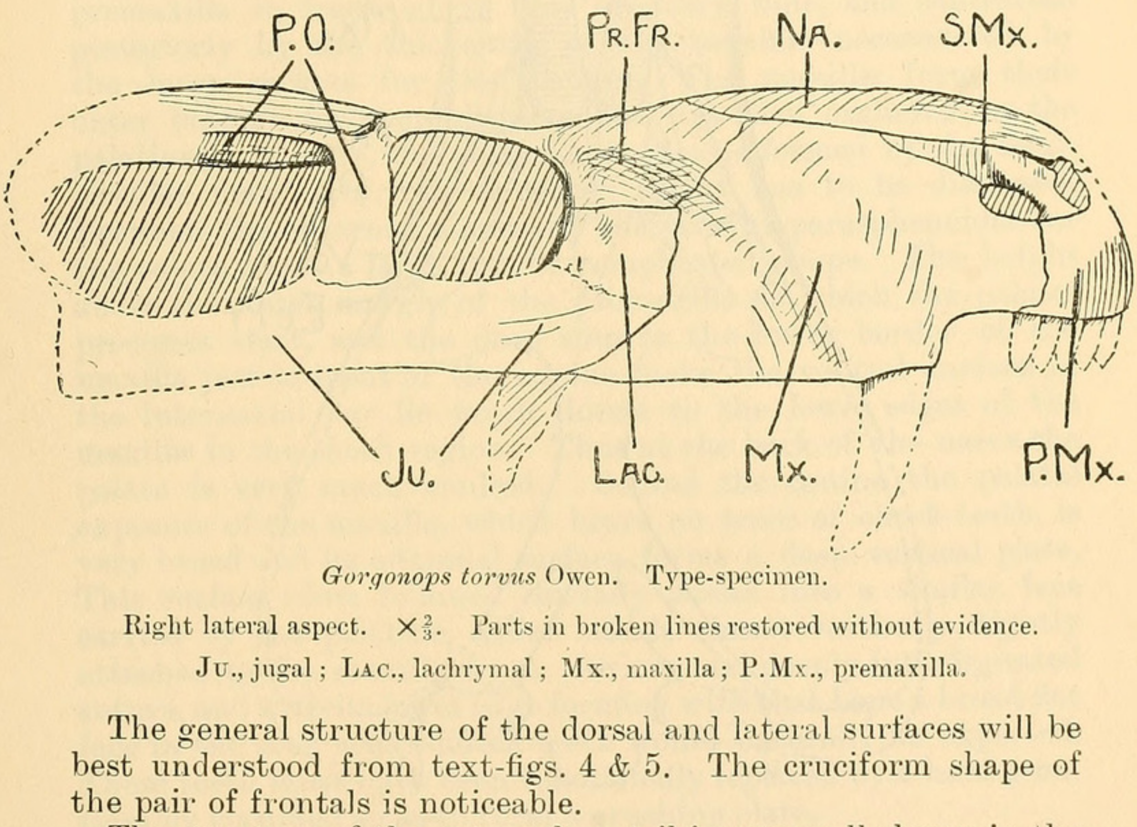
Dorsal aspect. ×⅔. Parts in broken line restored without evidence.

Fr., frontal; I.Par., interparietal; Pr.Fr., prefrontal; P.O., postorbital; Pt.Fr., postfrontal; S.Mx., septomaxilla; S.Oc., supraoccipital.

The skull of *Gorgonops* has a flat dorsal surface, which passes through a chamfered corner into the nearly vertical sides of the snout. The orbit is large, directed almost entirely laterally and of considerable depth. Immediately in front of it the snout is nearly square in section, the lachrymal region being excavated into shallow hollows overhung by a thickening of the prefrontal, which forms the lateral border of the flat dorsal surface. Further forward the snout becomes deeper, the nearly flat lateral surface passing by a rounded corner into the dorsal surface. There is a long broad swelling on the maxilla over the root of the canine.

The interorbital and parietal regions are both very broad, the latter passing smoothly into the broad occipital surface. The part of the occiput preserved consists mainly of the very broad interparietal, whose sutures with the tabulars are shown. The supraoccipital has only a very shallow exposure below the interparietal. A peculiar feature of this skull is the irregular shape of the pineal foramen and the fact that that opening is raised on a little column standing up above the general level of the parietal region.

Text-figure 5.



Gorgonops torvus Owen. Type-specimen.

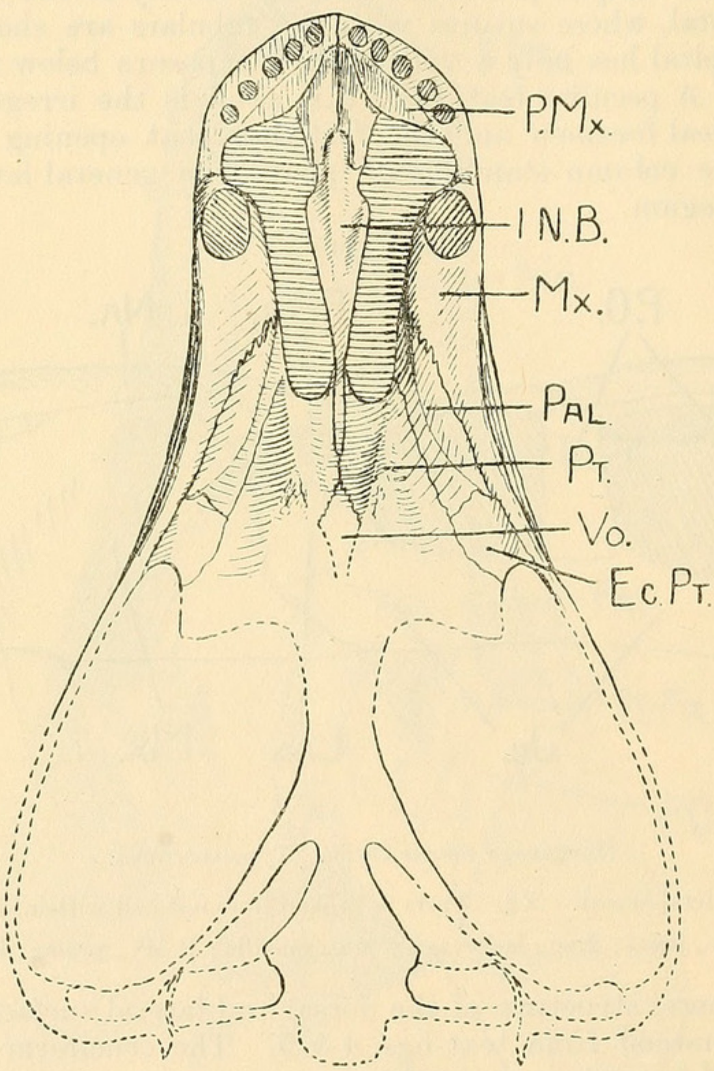
Right lateral aspect. ×⅔. Parts in broken lines restored without evidence.

Ju., jugal; Lac., lachrymal; Mx., maxilla; P.Mx., premaxilla.

The general structure of the dorsal and lateral surfaces will be best understood from text-figs. 4 & 5. The cruciform shape of the pair of frontals is noticeable.

The structure of the external nostril is very well shown in the specimen. The dentigerous part of the premaxilla is deep, and articulates directly with the anterior end of the maxilla, which overlaps on to it. The dorsal surface of the two bones is the lower margin of the nostril and forms the emplacement of the septomaxilla. Behind the nostril the maxilla rises to a long suture with the facial part of the septomaxilla; behind this bone it reaches the nasal. The nasals form a slightly coved roof to the olfactory chamber and reach forward almost to the end of the nose, where they terminate in a nearly straight margin, from the middle of which arises the narrow process which articulates with the facial processes of the premaxilla. The facial part of the septomaxilla articulates with the lower margin of the nasal, but the two bones separate before the nasal terminates, so as to leave that bone overhanging the nostril like the eaves of a roof. After its separation from the nasal the septomaxilla passes downwards and gives off a process from its anterior border, which passes inwards towards the middle line, following the curve of the

Text-figure 6.



Gorgonops torvus Owen. Type-specimen.

Palatal aspect. ×⅓. Unshaded areas surrounded by continuous lines present but mutilated, broken lines parts restored without evidence.

P.V. ?, internarial bar, ? prevomers ; Pal., palatine ; Vo., "vomer."

anterior border of the nasal. The lower part of the septomaxilla is a rounded column, swelling out to a base which rests on the premaxilla.

I have already (1912) given an account of the general features of the palate of *Gorgonops*, but, as further study of the specimen in the light of other material has enabled me to make out some interesting features not previously recorded, I give here a more detailed description. The premaxilla has a narrow dentigerous surface, with five sockets for the roots of the incisors; above the border the bone thickens, forming a deep wall, from whose admedian half the palatine process arises: this is at first a flat expansion, but soon becomes a rounded, backwardly directed tubercle, separated from its fellow and resting in a groove on the lower surface of the "prevomer." The internarial bar is a narrow rod which anteriorly is comparatively wide. Anteriorly its palatal surface bears a median ridge which separates two channels bounded by other lower ridges, which form the lateral borders of the bone. Further back the lower surface of the bar becomes flat, and the whole of the posterior part is only represented by a broken surface, which probably originally supported a deep median ridge.

The internal nares are very large openings bounded by the premaxilla in front, where they are very wide, and contracted posteriorly by the thickening of the maxillæ necessitated by the large sockets for the canines. The maxillæ form their outer borders for some distance and are then excluded by the palatines. Finally, the posterior border is formed by the semicircular margin of a bone whose nature has to be discussed. Between the internal nares and the pterygo-parasphenoidal bar the palate forms a large area of complicated shape. The height above the lower margin of the premaxilla at which the palatal processes start, and the deep step in the lower border of the maxilla just in front of the canine make the ventral surface of the internarial bar lie much dorsal to the lower edges of the maxillæ in the cheek-region. Thus at the back of the nares the palate is very much vaulted. Behind the canine the palatal exposure of the maxilla, which bears no trace of cheek-teeth, is very broad and its admesial surface forms a deep vertical plate. This surface when followed caudally passes into a similar face carried by the palatine, which stands almost vertically, tightly attached to the maxilla by an obvious and deeply interdigitated suture, and with its lower edge forming with that bone a broad flat face in the area where cheek-teeth would naturally be expected. These teeth must have been functionally replaced by a hard gum, possibly cornified so as to form a crushing plate.

The wide groove formed by the palate at the posterior end of the internal nares is rapidly divided into three, each groove of the lateral pair is deep and narrow and cylindrical; it shallows rapidly when traced backwards, finally becoming flat when it reaches the ectopterygoid. The bottom of the lateral groove has a suture running the whole of its length, which is completely exposed on the right side, but concealed by matrix except for its anterior end on the left side of the type-skull. This suture, which seems to be truly a suture and not a crack, unites the palatine with the pterygoid, which bone hence forms the posterior margin of the posterior nares.

The middle groove of this part of the palate becomes narrower as it is traced backward, but remains deep. Its hinder end is separated from the lateral grooves by triangular raised areas, which are roughened, but seem not to bear teeth.

The internarial bar is continued back into this part of the palate as a narrow slip separated from the pterygoids by a pair of open and very obvious sutures. These sutures rapidly approach and fuse, being continued backwards by an obvious median suture for about 5 mm. This open suture, with a visible strip of matrix in it, then suddenly ends and is with certainty not continued backward in the middle line. It is, however, apparently replaced by a pair of much less obvious sutures, between an overlapping median bone and the pterygoids, which pass outward to the margins of the median groove and seem then to be continued backward by still less obvious sutures running along these borders. Further back the wide, essentially flat palate gives origin to the descending flanges. The ectopterygoids are separated by obvious sutures and are comparatively small bones not taking any large part in the flange.

The palate of *Gorgonops* thus seems to show large pterygoids reaching forward to the posterior nares and widely separating the palatines, which are small bones simply continuing the ectopterygoids forward. In that part of the palate which lies in front of the transverse flanges the pterygoids do meet each other for a very small distance in the middle of their length, but posteriorly are separated by a median vomer and anteriorly by the posterior end of the internarial bar which is clasped between their distal ends. There is no evidence to show whether or not these two median bones are really separated, but as the anterior passes dorsal to the pterygoids, whilst the other overlaps their ventral surface, there is great probability that they do not represent parts of the same element.

SCYMNOGNATHUS WHAITSI Broom, Proc. Zool. Soc. 1912, p. 861.

Type: a figured skull, nearly complete, but considerably crushed and showing little of the structure. Other imperfect skulls and other bones.

The individual of which, under the name of *Scymnognathus whaitsi*, I described the lower jaw (1912) and the brain-case and occiput (1914), does not belong to this species, and is described in this paper as a new genus and species. There are in the British Museum three specimens of *S. whaitsi*:—R. 4053 collected by the Rev. J. H. Whaits, as a very large number of small fragments which, fitted together, form a skull from the front of the orbits backwards with the pro-atlas and atlas in position, the anterior end of the snout and a mass of separate fragments representing the major part of the face; of these a small bit of the posterior part of the palate is of great morphological interest. The back of the skull built up from these remains is quite undistorted and has been very completely developed, now showing the whole lateral surface of the brain-case, the structure of the zygomatic arches and roof of the skull and occiput with great perfection. It is in many ways the best Gorgonopsid skull known.

R. 4052. A skull retaining a well-preserved and only slightly sheared snout, with a much crushed posterior part, permitting the definite identification of R. 4053.

49369. A snout, somewhat distorted and not very well preserved which has been cut into slabs. It agrees well with the corresponding part of R. 4052.

All the material of *Scymnognathus whaitsi* comes from the *Endothiodon*-zone of Beaufort West. The skull, as a whole, is remarkable for the marked distinction between the relatively narrow snout and palate and the wide postorbital region. Owing to this shape, the orbits look as much forward as outward. The temporal fossæ are very large and face more upwards than outwards. The parietal region is, in consequence, narrow and the occiput deeply cupped, owing to the backward swing of the squamosals from their union with the postorbitals.

The snout is much more rounded than in *Gorgonops* or *Arctops*, although towards the orbits it is still somewhat "square-cut." The external nares closely resemble those of *Gorgonops*, and there is the same step between the lower edges of the premaxilla and maxilla.

The structure of the dorsal and lateral surfaces of the skull are obvious from text-figs. 7 & 8, but it is necessary to give some account of the brain-case and palate.

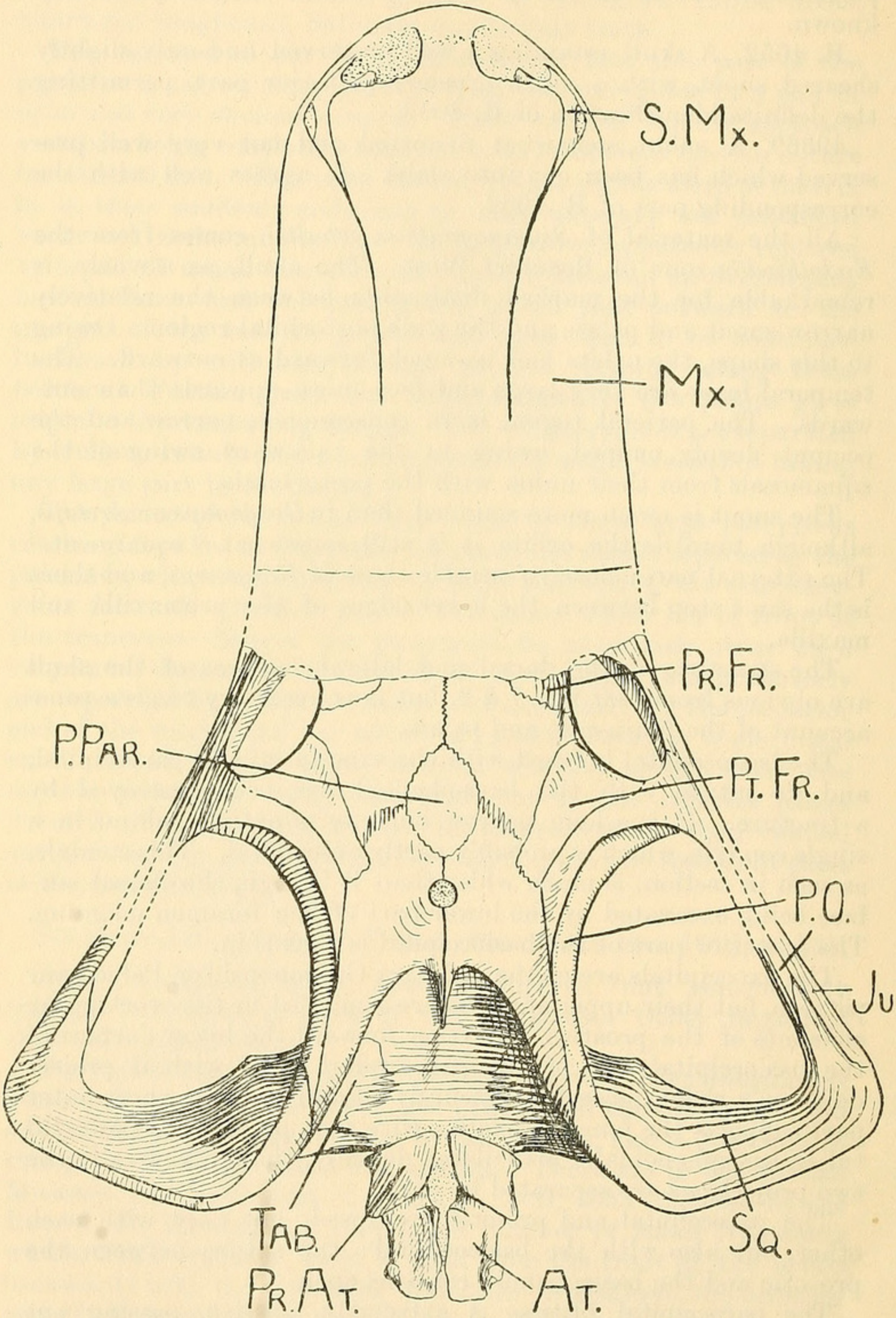
The basioccipital is fused with the exoccipital and paroccipital, and its suture with the basisphenoid has been destroyed by a fracture. It is a long narrow bone, terminating behind in a single condyle, which is probably partly exoccipital. This condyle, as seen in section, is much wider than it is high, the dorsal surface being excavated by the lower part of the foramen magnum. The posterior part of the basioccipital is thus thin.

The exoccipitals are of the ordinary Gorgonopsid or Pelycosaur pattern, but their upper surfaces are concealed by the overlapping elements of the proatlas. Further forward the lower surface of the basioccipital and of the paroccipital fused with it project down as a short, powerful, obscurely bilobed process, whose outer part supports the fenestra ovalis; with this process the powerful tuber basisphenoidalis articulates dorsally, though ventrally the two projections are separated by a gap.

The paroccipital and pro-otic are fused, not only with each other, but also with the basioccipital; the suture between the pro-otic and the basisphenoid remains open.

The paroccipital process is extremely massive, passing out from the side of the basioccipital on the lower surface of the skull to its broad abutment on the squamosal. The anterior and lower faces of this process are excavated by a groove which leads inward to the large irregular opening, which is the fenestra ovalis. The

Text-figure 7.

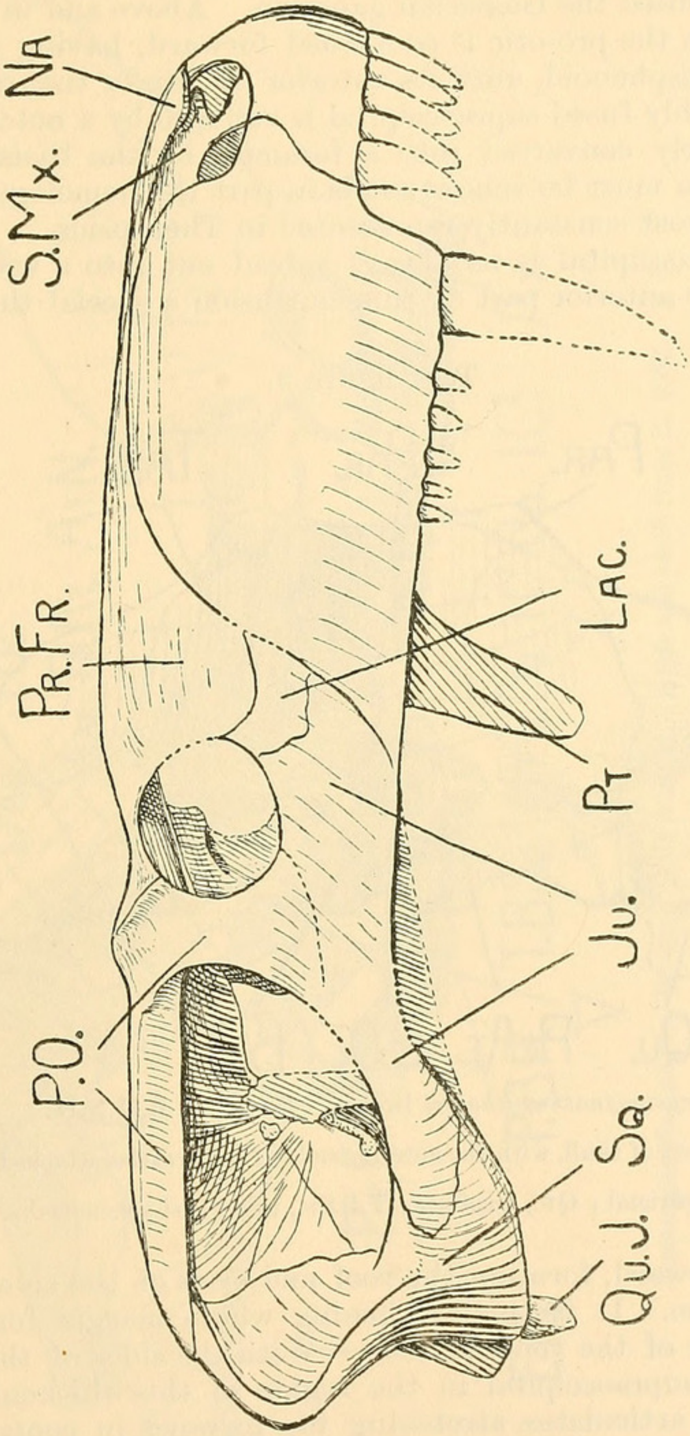


Scymnognathus whaitsi Broom. Back from R. 4053. Snout from R. 4052.
B.M.N.H. Dorsal aspect. × 4/9.

At., atlantal neural arch ; Ju., Jugal ; P.Par., preparietal ; Pr.At., pro-atlas.

paroccipital process is bounded above by the small oval post-temporal fossa, which lies at the level of the floor of the foramen magnum.

Text-figure 8.



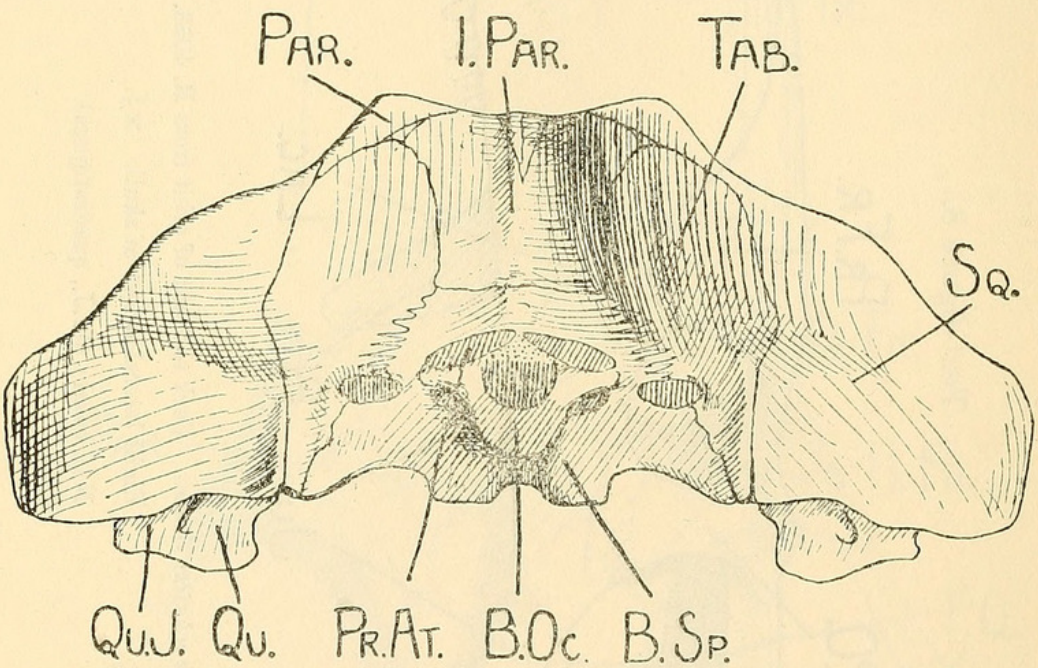
Scymnognathus whaitsi Broom. Back to front of orbit from R. 4053. Snout from 4052.
Right lateral aspect of skull. × $\frac{1}{5}$.
Na., nasal; Qu.J., quadratojugal.

In the pro-otic on its front face, above, and in front of the fenestra lies the outer opening of the foramen for the facial nerve. This opens downwards and has below it a little hollow for the geniculate ganglion.

Immediately above and a little in front of the facial is another much larger foramen opening directly forward; its outer margin is carried by a spout-like projection from the pro-otic, its inner border is basisphenoid. That bone immediately in advance of the foramen has a deep depressed groove. There can be no doubt that this foramen is for the fifth nerve, the cavity before it having housed the Gasserian ganglion. Above and in front of this foramen the pro-otic is continued forward, having a suture with the basisphenoid, until its anterior margin or that of the indistinguishably fused supraoccipital is cut into by a notch, which is very nearly converted into a foramen by the basisphenoid. This foramen must be venous; it is in part the homologue of one which is almost constantly represented in Therapsids.

The supraoccipital is as always spread out into a wide plate, but from the anterior part of this expansion a special thickening

Text-figure 9.



Scymnognathus whaitsi Broom. R. 4053. B.M.N.H.

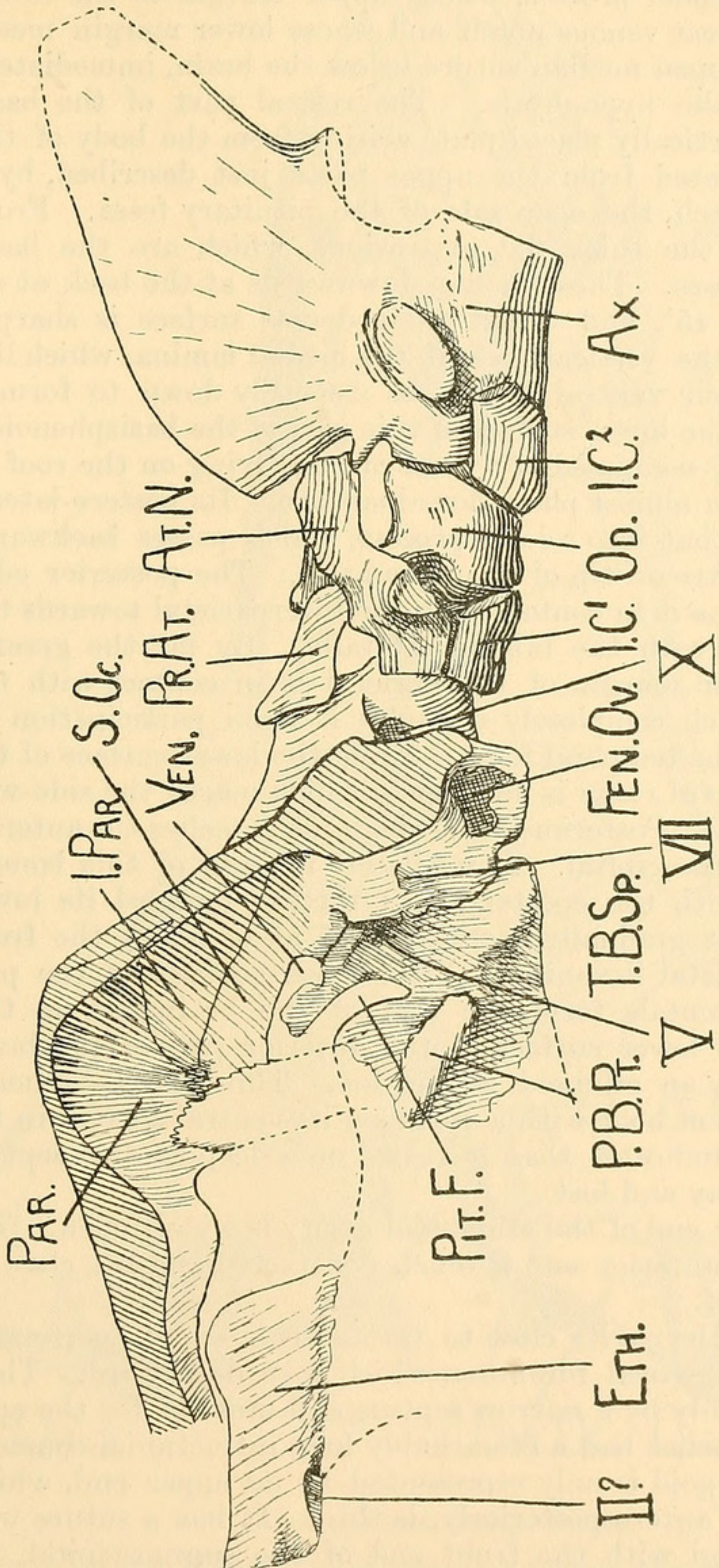
Occipital aspect of skull, with the anterior ends of the proatlas attached. $\times \frac{1}{5}$.

Par., parietal; Qu., quadrate; T.B.Sp., tuber basi-sphenoidalis.

is carried forward, forming the roof and part of the side-wall of the brain-case. It is this thickening whose margin forms the dorsal border of the venous notch. With the sides of the upper part of the supraoccipital in the region of this thickening the interparietal articulates, stretching far forward in contact with the parietal above and the supraoccipital below, and widely exposed in the outside view of the brain-case.

The basisphenoid is a remarkable bone, which in the specimen is broken off in front. As far as it is preserved, however, it consists of a body which is articulated with the front of the basioccipital largely through the intermediary of the two massive downward projections, which are its tubera. Above this articulation the bone becomes narrower where it is attached to the

Text-figure 10.



Scymnognathus whaitsi Broom. Axis from R. Atlas and skull from R. 4053. × ⅔.

Left lateral aspect of the brain-case as seen when the left side of the skull is removed by a parasagittal cut just medial of the post-temporal fossa, with the atlas and axis in position.

Reference letters as before, with :—At.N., atlantal neural arch; Ax., axis; E.Pr., epipterygoid; Eth., "ethmoid"= orbito-sphenoid; Fen.Ov., fenestra ovalis; I.C., 1st and 2nd intercentra; Od., odontoid; V., VII., X., foramina for the exit of those nerves.

pro-otic. Its lateral face here bears the groove for the Gasserian ganglion, above which the bone again widens to the continuation of its suture with the pro-otic. Above and in front of the termination of this suture the basisphenoid is still continued upward as a slender process, whose upper margin is the lower border of the great venous notch and whose lower margin meets its fellow in an open median suture below the brain, immediately in advance of the hypophysis. The rostral part of the basisphenoid is a vertically placed plate arising from the body of the bone and separated from the upper parts, just described, by a deep narrow notch, the open side of the pituitary fossa. From its sides arises the thick flat expansions, which are the basipterygoid processes. These incline downwards at the back at an angle of about 45°, and whilst their dorsal surface is sharply separated from the vertical face of the medial lamina, which lies above them, their ventral faces pass smoothly down to form a blunt ridge on the lower surface of this part of the basisphenoid.

The parietal is composed of a plate of bone lying on the roof of the skull with an almost plane dorsal surface. Its postero-lateral corner is drawn out into a long process, which passes backwards to touch the extreme tip of the squamosal. The posterior edge of the whole bone is in contact with the interparietal towards the middle line and with the tabular laterally. By far the greater part of the outer margin of the parietal is in contact with the postorbital, which completely excludes it from participation in the margin of the temporal fossa. From the lower surface of the parietal a powerful ridge is developed, which marks the side-wall of the brain-case. Posteriorly this ridge just touches the anterior end of the supraoccipital. Immediately in front of this bone it has a suture with the epipterygoid; further forward its lower edge is free, but gradually declines, until at or about the front end of the parietal it vanishes. The lower surfaces of the preparietal and frontals form the roof of the brain-case in this region, and the lower surface of the anterior part of the brain is supported by an ethmoid ossification. This is a thin hemicylindrical shell of bone with a rib along its ventral surface in the middle, which indicates that it rested on a deep median septum now broken away and lost.

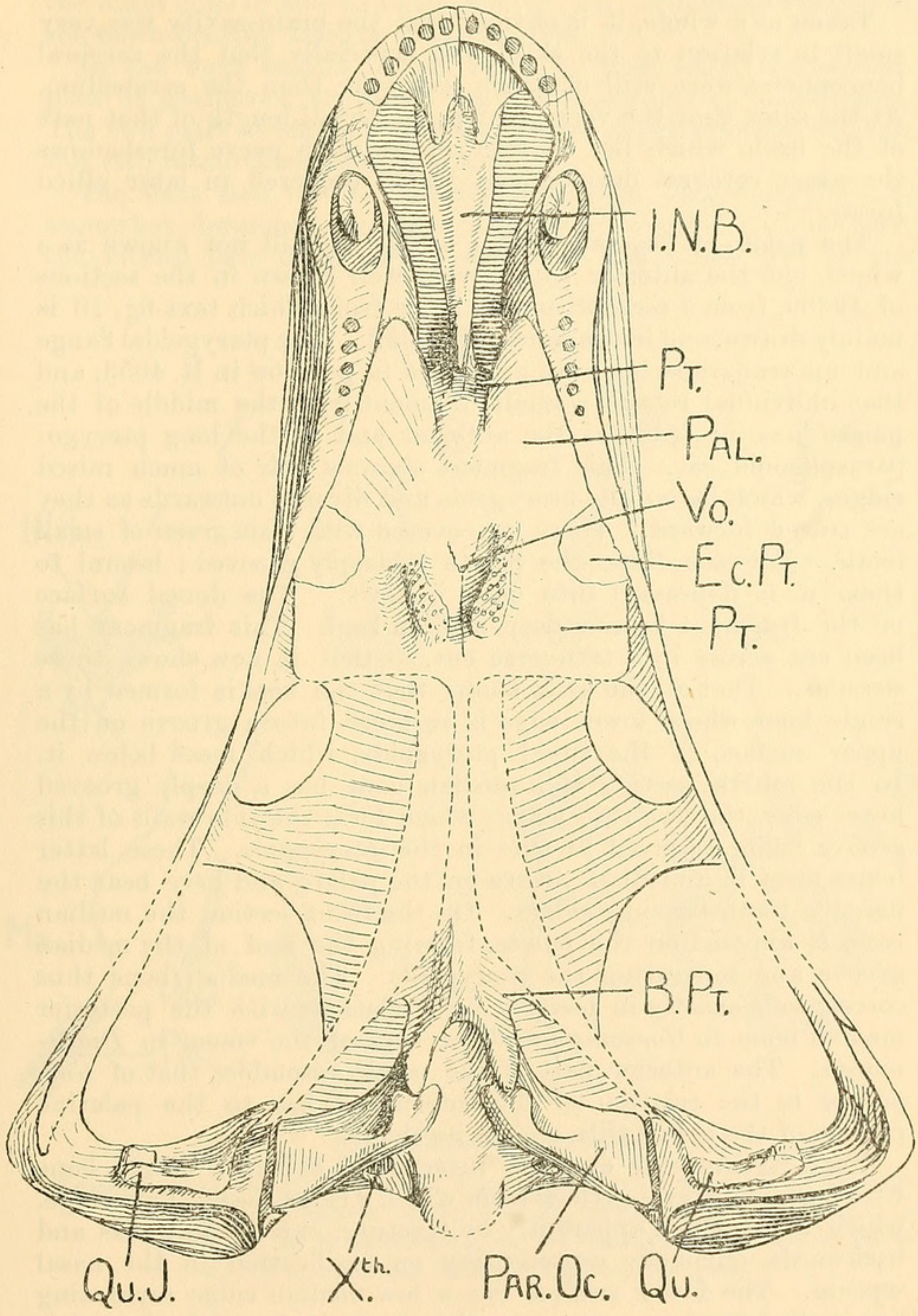
The posterior end of the ethmoidal cavity is widely open. The opening of the anterior end is much contracted and lies close up to the skull-roof.

The floor of the cavity close to its anterior end is perforated by a pair of large oval foramina, which face downward. These are separated only by a narrow septum and must be for the optic nerves, which hence had a remarkably long intracranial course.

The epipterygoid is only represented by its upper end, which, though narrow antero-posteriorly, is thin. It has a suture with the parietal and with the front end of the supraoccipital, the latter connection being of considerable morphogenetic importance.

There is a medium-sized foramen for the Xth nerve, opening downwards and backwards below the exoccipital well above the

Text-figure 11.



Scymnognathus whaitsi Broom.

Posterior part from R. 4053. Snout reconstructed from a series of transverse sections of 49369 completed from R. 4052. Ectopterygoid region + detached area including the vomer R. 4053. ×⅘. B.Pt., basipterygoid process.

bottom of the skull. There is a single hypoglossal foramen in the usual position.

Taken as a whole, it is obvious that the brain-cavity was very small in relation to the skull, and especially that the cerebral hemispheres were still of much less bulk than the cerebellum. At the same time the very great proportional length of that part of the brain which lies in front of the fifth nerve foreshadows the great cerebral development which occurred in later allied forms.

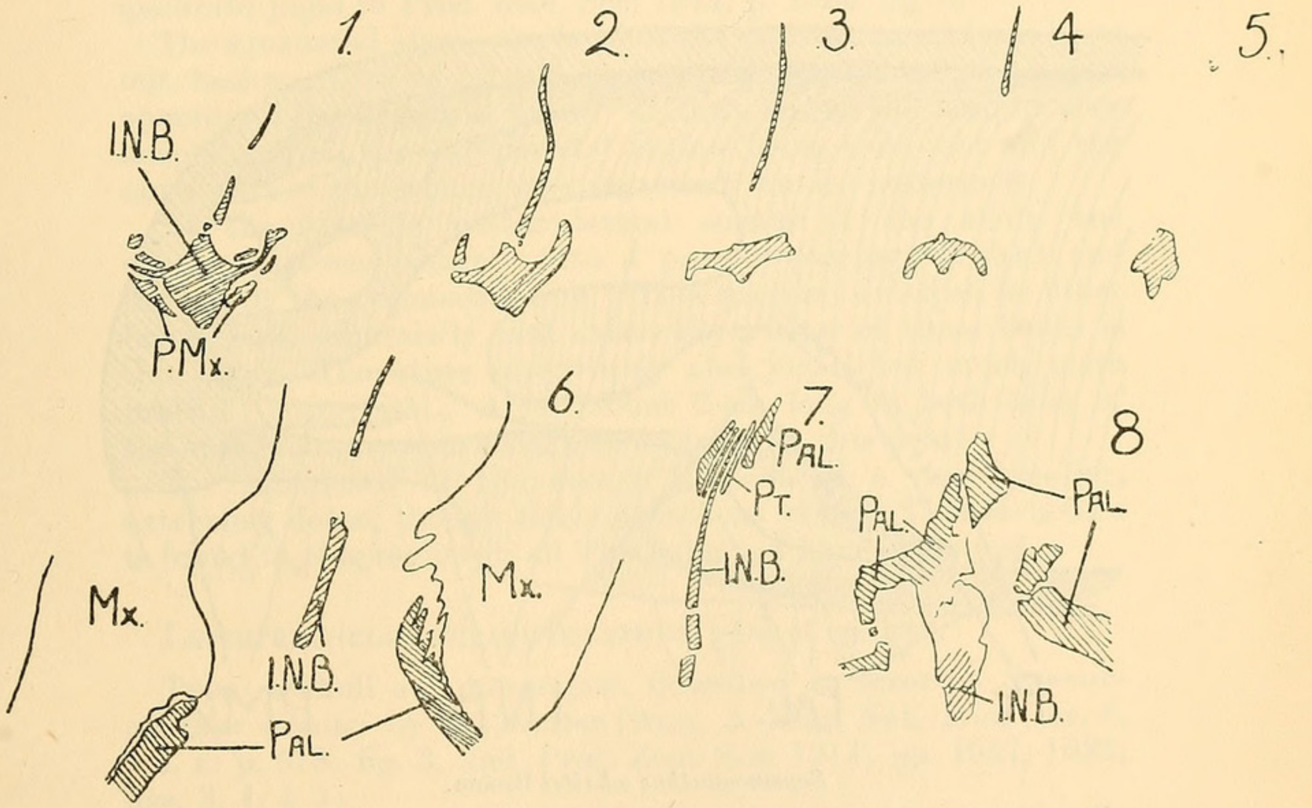
The palate of *Scymnognathus whaitsi* is still not known as a whole, but the anterior part is very well shown in the sections of 49369, from a reconstruction made from which text-fig. 10 is mainly drawn, and in the solid in R. 4052. The pterygoidal flange and one transverse bone are preserved in position in R. 4053, and that individual retains a small fragment from the middle of the palate just in front of the anterior end of the long pterygo-parasphenoid bar. This fragment shows a pair of much raised ridges, which lie on the pterygoids and diverge outwards as they are traced forward. These are covered with a shagreen of small teeth. Between these the palate is deeply grooved ; lateral to them it is depressed into deep hollows. The dorsal surface of the fragment bears a deep median keel. This fragment has been cut across by a tranverse cut, so that it now shows three sections. That at the back shows that the keel is formed by a single bone whose lower edge is received into a groove on the upper surface of the fused pterygoids, which meet below it. In the middle section this median bone has a deeply grooved lower edge, the two thin ridges which form the side-walls of this groove being received in slits in the pterygoids. These latter bones meet in a median suture on the palate and here bear the massive tooth-bearing ridges. On the front section the median bone is exposed on the palate, forming the roof of the median groove and separating the pterygoids. The median bone thus corresponds exactly in position and relations with the posterior median bone in *Gorgonops* and the back of the vomer in *Diademodon*. The anterior part of the palate resembles that of *Gorgonops* in the relation of the internarial bar to the palatine process of the premaxillæ and in its shape.

Near its anterior end the internarial bar is a single bone with a convex dorsal surface from which a ridge rises. This ridge, which is detached, apparently by fracture, extends upwards and backwards, obviously representing an ossification in the nasal septum. The lower surface has a low median ridge separating two well-defined grooves. As this bone is traced backward it gradually becomes narrower from side to side until in the region of the first molar tooth, where it is seen in section (text-fig. 12), it has become converted into a plate 35 mm. in depth and only two millimetres thick at the lower edge, where it is widest. The dorsal centimetre of this narrow septum is clasped between two thin films of bone, whose outer surfaces are in contact with another pair of similar slender processes. Even in this region the lower edge of the median bone still lies considerably dorsal of the tooth-bearing margin of the maxilla.

In the next section, about 1 cm. further back, the median plate is shallower, its dorsal margin being curved downwards. The two pairs of plates which support its upper edge are thicker, but still retain their same relations.

The next slab has fortunately been split longitudinally and somewhat developed, so that it gives conclusive evidence that the lateral pair of processes described above are part of the

Text-figure 12.



Scymnognathus whaitsi Broom.

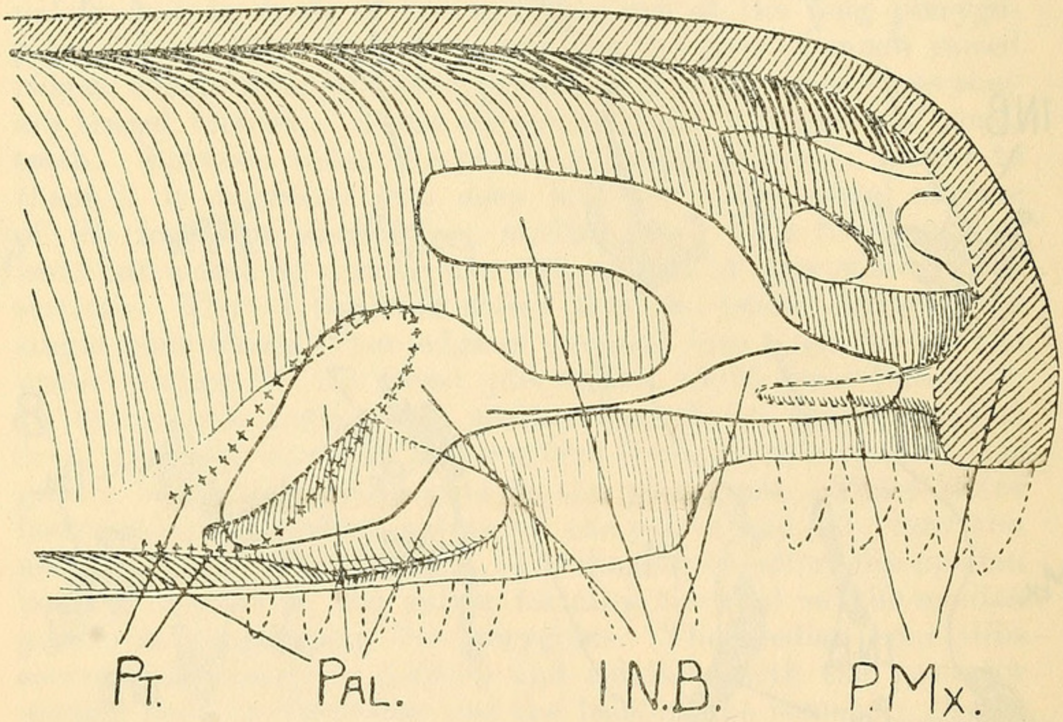
Series of transverse sections at about 1 cm. interval, across the snout of No. 49369. B.M.N.H. 1, anterior section; I.N.B., internarial bar; in 2–5 only the internarial bar is represented; in 6 the maxillæ and palatines are shown; in 7 only the anterior ends of the palatines and pterygoids. × $\frac{2}{3}$.

palatines. The inner pair pass down to the ventral surface and there form a little boss on the palate, which separates the two deep grooves on the palatines. These grooves are so overhung by the more ventral parts of the palatines that their floor can scarcely be seen in a direct ventral projection No sutures can be seen in the little median boss, and it is probable that the median element of the internarial bar has terminated in it.

The vertically standing part of the palatine, which forms the side-wall of the groove just described, descends to the level of the lower border of the maxilla, where it passes into a flat, thick, horizontally lying plate, which extends outward to the lower edge of the maxilla with which it has a suture.

This horizontal part of the palatine forms the greater part of that bone, and extends backward and forward in contact with the maxilla, until by narrowing and increasing in depth it becomes converted into a mainly vertically disposed plate, which forms part of the side-wall of the posterior part of the very large internal nares. It then terminates.

Text-figure 13.



Scymnognathus whaitsi Broom.

Reconstruction of internal aspect of the left side of the snout cut through in the middle line. Internarial bar and ossification in the nasal septum unshaded and surrounded by a thick continuous line; anterior end of the pterygoid represented by a line of small crosses. Parts of palatine seen through other bones in broken line. Reconstructed from the sections of 49369, checked by R. 4052. × $\frac{2}{3}$.

Thus the anterior part of the palate is essentially a flat plate of bone, whose middle part is cut out by a narrow but gradually widening groove which plunges steeply downward to the deeply sunk posterior margin of the posterior nares. This groove is divided into two by a narrow vertical septum, which descends nearly to the level of the general plane of the palate.

There can be little doubt, especially when the conditions in *Arctops* and *Gorgonops* are considered, that the inner pair of processes which support the internarial bar are the anterior ends of the pterygoids. It remains to be shown by other material whether the median internarial bone and the median vomer in the back of the palate are parts of the same bone or are, as is more probable, separated.

The strange way in which the median internarial bar rises as a thin but very deep septum from the much sunk posterior nares, nearly to the general level of the palate, seems to be only explicable if its ventral border supported the middle of a small soft secondary palate stretched between the maxillæ and the palatines.

I have already described the mode of articulation of the squamosal with the brain-case and with the fused quadrate and quadrato-jugal in Proc. Zool. Soc. 1914, p. 1034, fig. 6.

The squamosal above the level of the post-temporal fossa bows out backward, so as largely to increase the size of the dorsal opening of the temporal fossa. It thus makes the occiput very deeply cupped, the interparietal region being narrowed and the outer part of the tabular running nearly antero-posteriorly.

At the extreme postero-lateral corner of the skull, the squamosal turns sharply into a process passing forward and inward in the zygomatic arch. This process is clasped by other bones both admesially and externally. One of these bones is the jugal. The other conceivably also jugal, but much more probably postorbital. A gap about 2 cm. long in both sides of the specimen prevents a definite decision on this point.

The squamosal at the corner is made of a very peculiar, extremely dense, though finely cancellous bone. This structure is found in this region in all Theriodonts I have examined.

LEPTOTRACHELUS EUPACHYGNATHUS, gen. et sp. nov.

Type: a skull and lower jaw, described in error as *Scymnognathus whaitsi* by the writer (Ann. & Mag. Nat. Hist. ser. 8, vol. x. p. 578, fig. 3, and Proc. Zool. Soc. 1914, pp. 1027, 1032, figs. 3, 4, & 5).

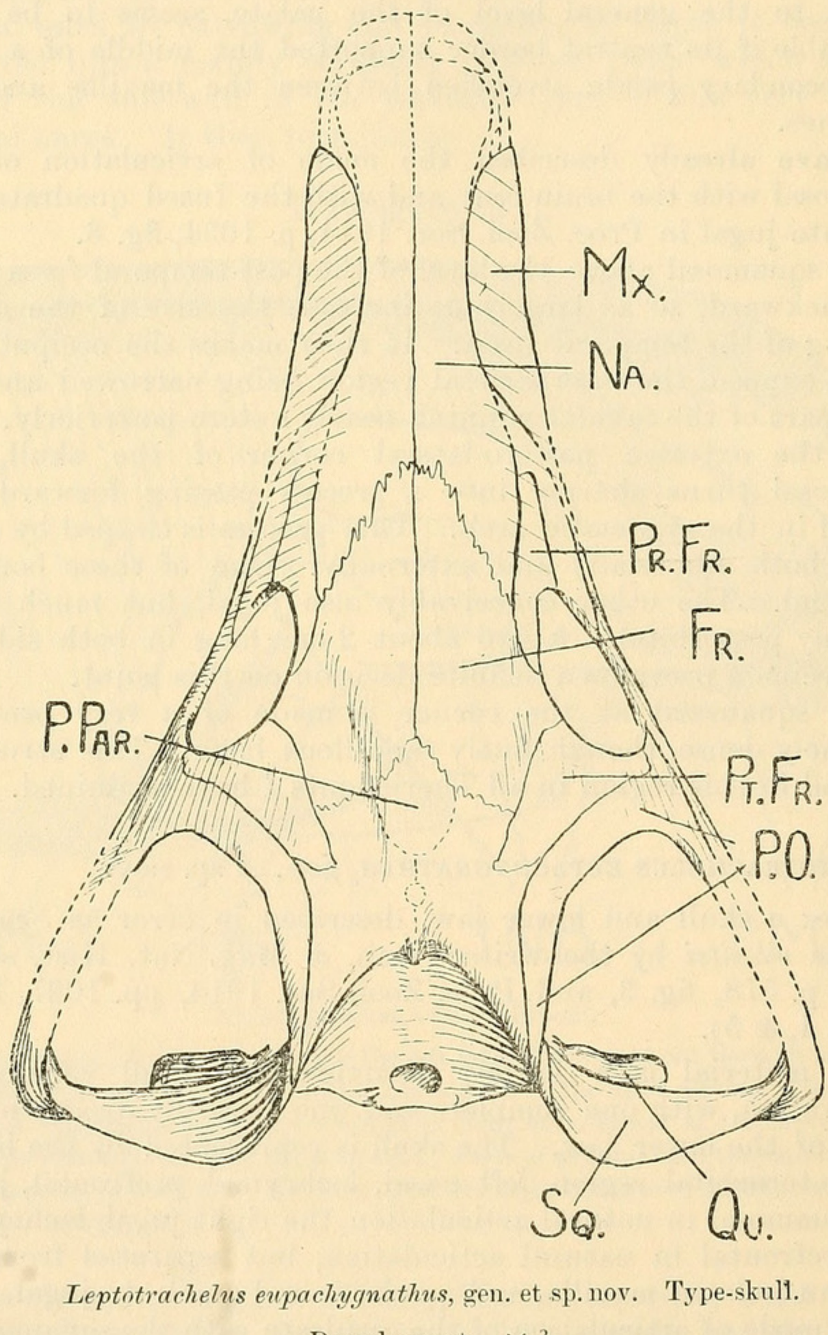
The material is a largely disarticulated skull varying in preservation, with one complete and one partially disarticulated ramus of the lower jaw. The skull is represented by the brain-case, interorbital region, left nasal, lachrymal, prefrontal, jugal, and squamosal in natural articulation, the right jugal, lachrymal, and prefrontal in natural articulation, but separated from the skull, an isolated maxilla, and quadrate and quadrato-jugal.

The mode of articulation of the quadrate with the squamosal is clear, and with the perfect lower jaw gives the length of the skull and the position of the maxilla. The large articulated part of the skull gives practically all the dorsal and the posterior part of the lateral surface directly. The occiput is essentially completely preserved. All the sutures except those of the parietals with each other and the preparietal are well shown.

In text-fig. 14 it is probable that the anterior part of the snout is made a little too narrow.

I have already described and figured the basicranial and otic regions, the occiput, and the interior of the brain-case.

Text-figure 14.

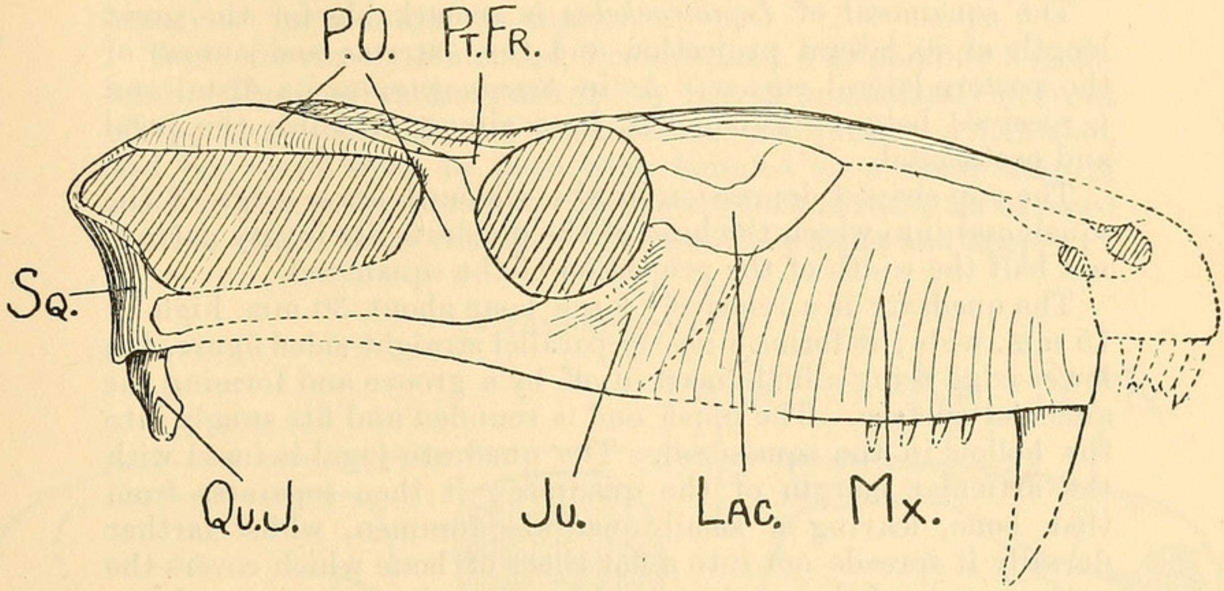


Leptotrachelus eupachygnathus, gen. et sp. nov. Type-skull.

Dorsal aspect. × ⅔.

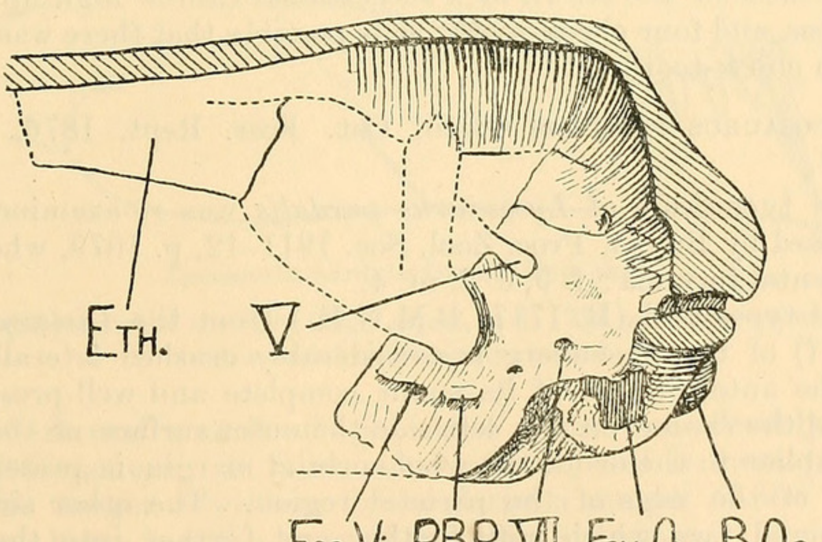
The outside of the brain-case is illustrated in text-fig. 16. The foramen for the VIIth nerve lies just above and in front of the fenestra ovalis, opening downwards through the pro-otic. The trigeminal "foramen" lies considerably forward and is more dorsal in position. It lies at the end of a long slit and is presumably really only an incision and not a foramen. The length

Text-figure 15.



Leptotrachelus eupachygnathus. Type-skull.
Right lateral aspect. × ⅔.

Text-figure 16.



Leptotrachelus eupachygnathus. Type-skull.

Left lateral aspect of brain-case, the parts of the skull lateral to the post-temporal fossa being removed as in text-fig. 10.

of the slit is rendered uncertain by the fracture of the anterior end of this part of the brain-case. In the part of the brain-case preserved there is no evidence of the large venous foramen described above in *Scymnognathus whaitsi.* There is no trace of the great anterior projections of the basisphenoid which in *Scymnognathus* meet in median suture in advance of the pituitary.

There is an ethmoid, which, so far as its very incomplete exposure allows it to be seen, does not differ from that of *Scymnognathus.*

The squamosal of *Leptotrachelus* is remarkable for the great length of its lateral projection and the extreme suddenness of the postero-lateral corner. As in *Scymnognathus* its distal end is received between two bones, here almost certainly the jugal and postorbital.

The cup-shaped depression in the widened lower edge of the squamosal into which the head of the quadrate fits is very narrow, not half the width of the projection of the squamosal.

The quadrate is a relatively large bone about 30 mm. high by 15 mm. wide; it forms a nearly parallel straight-sided figure, the lower edge being a little marked off by a groove and forming the articular surface. The upper end is rounded and fits snugly into the hollow in the squamosal. The quadrato-jugal is fused with the articular margin of the quadrate; it then separates from that bone, leaving a small quadrate foramen, whilst farther dorsally it spreads out into a flat sheet of bone which covers the outer margin of the quadrate and laps over its posterior surface.

When articulated with the squamosal the quadrate and quadrato-jugal are largely visible from behind.

The maxilla of *Leptotrachelus* shows a single canine in use, with traces of the crown of a successional canine high up in the alveolus, and four cheek-teeth; it is possible that there was really a fifth cheek-tooth.

Lycosaurus pardalis Owen, Cat. Foss. Rept. 1876, p. 15, pl. 14.

The type-skull of *Lycosaurus pardalis* was re-examined and discussed by Broom, Proc. Zool. Soc. 1911–12, p. 1079, who gave it a dental formula: i. 5, c. 2, m. 4.

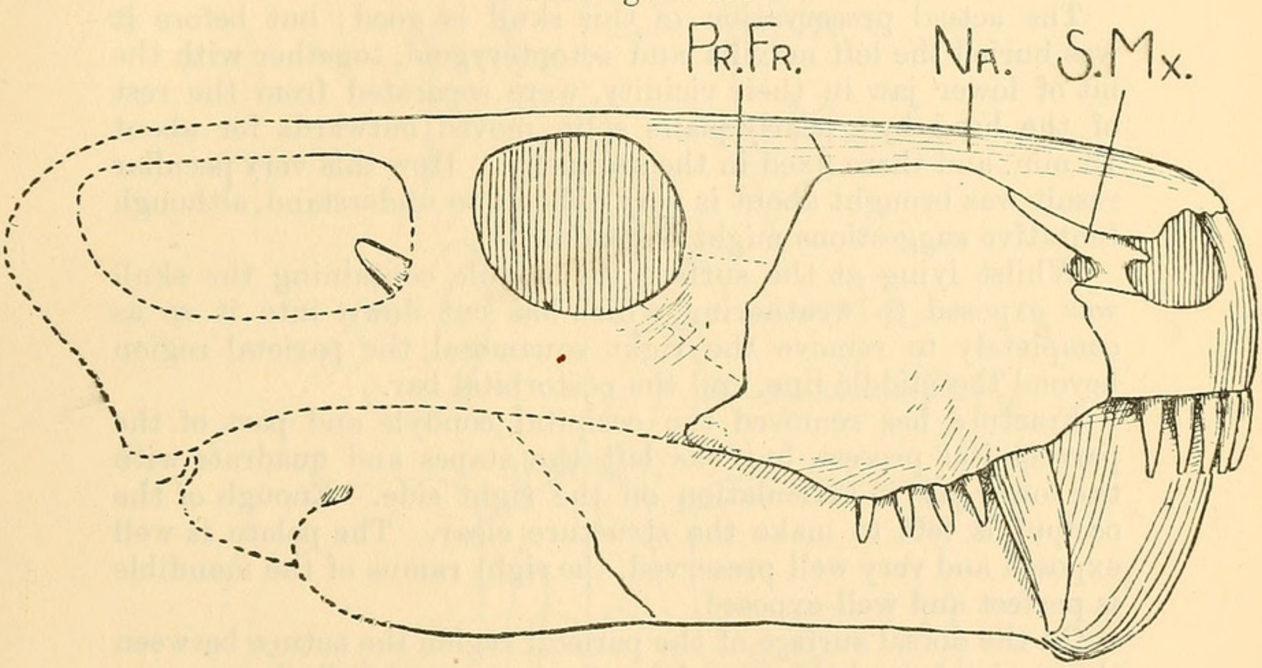
The type-skull (R. 1717, B.M.N.H.) from the *Cistecephalus*-zone (?) of the Sneeuberg is considerably crushed laterally, but has the anterior end of its snout complete and well-preserved; behind the canine on the left side the outer surface of the skull is complete to the orbit, the whole orbital margin is present and a bit of the edge of the parietal region. The other side is a weathered face which cuts further and further into the skull until it so far crosses the middle line as to expose the admedian surface of the left epipterygoid and completely to remove the brain-case. The squamosals are completely destroyed. The right lower jaw is, however, nearly perfect, having suffered only the loss of the posterior part of the angular so as to expose the articular—the position of the quadrate is thus fixed. The parts of the skull remaining are quite well-preserved and show many sutures.

It is obvious that the snout is short, high, and narrow, with no trace of the square section which occurs in all the Gorgonopsids described above.

The tooth-bearing edge of the maxilla is curved and passes gently into that of the premaxilla without the step of *Gorgonops* or *Scymnognathus*. There is, however, a diastema between the closely-set incisors and the canine.

There are clearly 5 incisors, 1 canine, and 4 or possibly 5 molar teeth. The small canine recorded by Broom immediately in front of the large one does not exist on the well-preserved left side, and his views seem to have been founded on a small strip of tooth in this position on the right side, which is really an exposed portion of the lower canine. The maxilla is short and deep.

Text-figure 17.



Lycosaurus pardalis Owen. Type-skull.
Reconstruction of the right lateral aspect, × ⅔. The parts represented in broken lines hypothetically restored.

The external nostril of *Lycosaurus* differs considerably from that of *Gorgonops*. It faces more laterally and is much larger; it is no longer overhung by so large a corner of the nasal, although there is still a trace of the older structure.

The facial part of the septomaxilla is much smaller, and the foramen between that bone and the maxilla is not only smaller but opens more directly outward. The septomaxilla in front of it seems to be rounded and grooved. Finally, the internarial process of the premaxilla is longer and stands more vertically, so that the end of the snout is deeper and less rounded in side-view.

The interorbital region is narrow, the postfrontal being a narrow pointed strip, as in the skull of *Arctognathus curvi-*

mola subsequently described (text-fig. 18). The parietal region is obviously of the Gorgonopsid type and cannot be very wide, although its width cannot be determined with any pretence to accuracy.

ARCTOGNATHUS CURVIMOLA (Owen), Cat. Foss. Rept. 1876, p. 71, pl. 68.

The skull (No. 47339 B.M.N.H.) described by Owen as *Lycosaurus curvimola* was found with *Dicynodon tigriceps* in the *Cistecephalus* beds of the Kagaberg, near Bedford, S. Africa. Its palate was developed by Mr. Hall and described by Prof. Seeley, Phil. Trans. B. 185. The skull was then examined by Dr. Broom, who noted that the parietal region seemed to be broad, and made for it the genus *Arctognathus*.

The actual preservation of this skull is good; but before it was buried the left maxilla and ectopterygoid, together with the bit of lower jaw in their vicinity, were separated from the rest of the head by a nearly plane split, moved outwards for about 15 mm. and there fixed in the sediment. How this very peculiar result was brought about is very difficult to understand, although tentative suggestions might be made.

Whilst lying at the surface the nodule containing the skull was exposed to weathering, which has cut down into it so as completely to remove the right squamosal, the parietal region beyond the middle line, and the postorbital bar.

Fracture has removed the occipital condyle and part of the paroccipital process, but has left the stapes and quadrate with the lower jaw in articulation on the right side. Enough of the occiput is left to make the structure clear. The palate is well exposed and very well preserved, the right ramus of the mandible is perfect and well-exposed.

On the dorsal surface of the parietal region the suture between the parietals and the pineal foramen are very well shown on a weathered face, which lies a little below the original dorsal surface; the right side of this region retains its natural surface and shows the structure clearly.

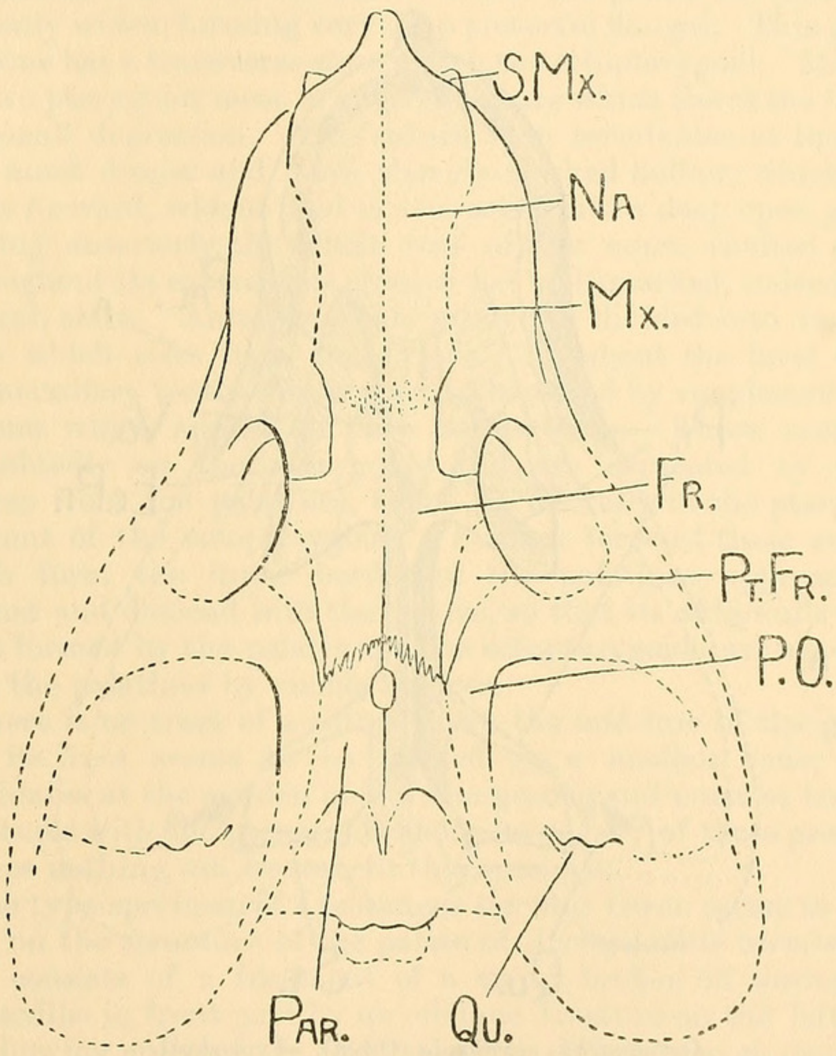
The skull is short, broad, and deep. The snout is rounded in section and terminates in front in the internarial premaxillary processes, which form the extreme front end of the skull overhanging the oral margin.

The very large nostril faces largely outward and is not overhung by an outstanding corner of the nasal. The septomaxilla is small, and the foramen between it and the maxilla very small.

The interorbital width is considerable, but the orbits look upward and forward as largely as outward. The frontal does enter into the orbital margin, but only through a short distance The postfrontal is a narrow strip of bone wedged in between the frontal and the postorbital.

No trace of a preparietal is to be seen on the parts preserved, the median suture is clearly shown from the front of the pineal foramen to a point between the frontals, and the well-marked suture between the frontal and parietal passes very little in advance of the pineal opening. These sutures are, however, exposed at a plane below the orginal dorsal surface, and there is a remote possibility which cannot, although very improbable, be entirely excluded, that the preparietal was represented by a

Text-figure 18.



Arctognathus curvimola Owen. Type-skull.

Restoration of the dorsal aspect, the parts in broken lines being hypothetically restored.

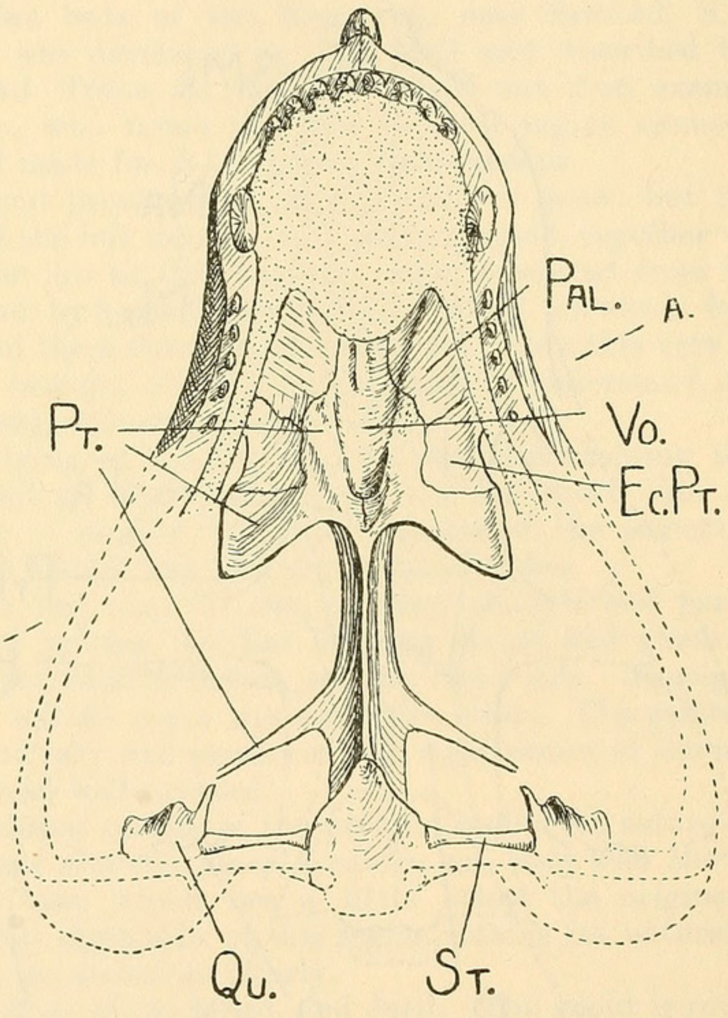
minute scale of bone lying on the dorsal surface. The parietal region is about as wide as the interorbital.

The maxilla is short and deep, its tooth-bearing margin is much curved and passes smoothly with no trace of a step into that of the premaxilla. The canines appear not to be completely erupted, and the four small cheek-teeth are also not very firmly planted. The four incisors, though powerful, are not so disproportionately large as they are in earlier Gorgonopsids.

The palate of *Arctognathus* is very well-preserved, but its anterior end and two strips along the maxillæ are concealed by unremoved matrix and by the lower jaw.

The basioccipital is broken off through the vagal foramen, where it is thin and not very wide. The posterior part of the

Text-figure 19.



Arctognathus curvimola (Owen). Type-skull.

The palate, × ⅔. Stippled area covered by matrix and the lower jaw. Parts in dotted lines hypothetical.

A......A, direction of the section of "*Lycosaurus tigrinus*," text-fig. 20.

ST., stapes.

basisphenoid forms a triangular area with raised lateral margins, representing the tubera of earlier forms. Above the edges the sides of the bone are flat and vertical, posteriorly they terminate in the region of the fenestræ ovales, these openings being concealed by the foot of the stapes. Anteriorly these vertical sides of the basisphenoid approach together until they are only separated by a narrow ridge which runs forward to the palate proper. From the vertical sides of the basisphenoid horizontal processes arise ; these basipterygoid processes support the pterygoids. From their articulation with the basisphenoids the pterygoids pass backward towards the quadrates, but do not articulate with those bones, as they appear to terminate in free points before reaching them. The pterygoids pass forward, forming with the median ridge which continues the basisphenoid a bar whose ventral surface is almost cylindrical, broken only by the median fillet. At the hinder end of the palate the pterygoids suddenly widen, forming very deep powerful flanges. This part of the bone has a transverse suture with the ectopterygoid. Medially the two pterygoids meet in a visible suture which lies at the bottom of a small depression. This suture soon terminates at the brim of a much deeper and more sharply-marked hollow, which, as it passes forward, widens and is converted into a deep open groove forming anteriorly the whole roof of the much vaulted palate. Throughout its extent this groove has well-marked, indeed often vertical, sides. Anteriorly this groove is divided into two by a ridge which rises from its surface. At about the level of the last maxillary tooth this groove is bounded by roughened areas of bone, which appear to have borne teeth. These areas are undoubtedly on the pterygoids and are separated by visible sutures from the palatines, which lie laterally to the pterygoids in front of the ectopterygoids. Further forward these sutures, which form the inner border of the palatines, approach one another and descend into the groove, so that its side-walls are in front formed by the palatine. The ectopterygoids are separated from the palatines by visible sutures.

There is no trace of a suture down the mid-line of the groove, and its roof seems to be formed by a median bone, which terminates at the sudden end of the groove and must be bounded by sutures with the pterygoids along its edges ; of these presumed sutures nothing can be seen in this specimen.

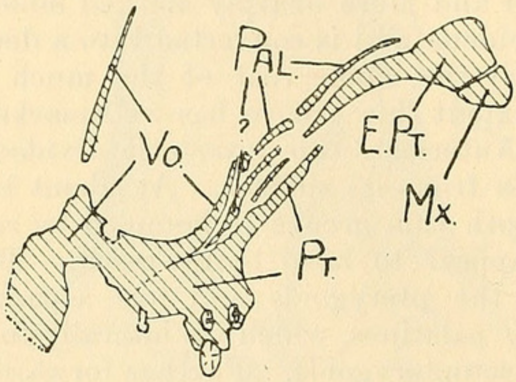
The type-specimen of *Lycosaurus tigrinus* Owen seems to throw light on the structure of the palate of *Arctognathus curvimola*.

It consists of a fragment of a snout, broken off through the premaxillæ in front and by an oblique fracture on the left side, but showing much of the right maxilla. It has been so developed as to show a small strip of the surface of the right palatine and shows a section of the palate on the hinder end. This species is referred by Broom to a new genus *Arctosuchus*, and said to have a dental formula, i. 5, c. 1, m. 4 or 5, representing a much more primitive type of Theriodont than *Arctognathus*. The type-specimen only shows two incisors, a canine, and a few cheek-teeth, and it seems certain that Broom examined and used for his description a snout of *Scymnognathus whaitsi* which Lydekker had referred to *L. tigrinus*.

Except in the larger size and somewhat different direction of its canine, the type-specimen of *L. tigrinus* seems to agree exactly in size and every point which can be compared with *A. curvimola.* The section of the palate shown on its posterior fracture is represented in text-fig. 20.

There is a median element bearing a high dorsal ridge, now detached, with a very deep groove on its mid-ventral surface and carried out laterally in a long wing, which is overlapped by the pterygoid. This bone bears a powerful irregular roughened projection carrying small teeth: laterally its surface is smooth, and is continued to the hinder end of the maxilla by that of the ectopterygoid. The two bones scarcely meet, but are joined together by a thin film of bone, undoubtedly the palatine, which covers their dorsal surfaces.

Text-figure 20.



Arctognathus. Type-specimen of *Lycosaurus tigrinus* Owen. × $\frac{?}{?}$.

Obliquely transverse section as a plane corresponding to A......A in text-fig. 19.

If this section be compared with that which the palate of *Arctognathus* would present if cut along the line A–A, there can be no doubt of the close affinity—indeed, specific identity—of the two forms, for even the possible measurements are in very close agreement.

Thus we have confirmation for the view that the roof of the median groove in the palate of *Arctognathus* is formed by a median vomer.

The epipterygoid of the type-specimen of *A. curvimola* is shown to meet the parietal in a long suture, exactly as does that of *Diademodon.*

The preceding series of description is based on the more complete and satisfactory remains of Gorgonopsids in the British Museum, largely *Endothiodon*-zone forms. Of recent years Broom and Haughton, either independently or together, have described many complete Gorgonopsid skulls, chiefly from the *Cistecephalus*-zone. They have, however, never given so complete an account of any form as that of *Scymnognathus* included in this paper, and it is seldom that they have given more than one or, at most, two drawings of any one skull. Thus it is difficult to carry out any detailed discussion of the mutual relations of the known Gorgonopsids.

In order to discuss with any satisfaction the classification of a group, it is necessary to know the main outlines of its history, to understand the direction of the advances which make the structure of all late members of it differ from their ancestors, and to work out any adaptive modifications which characterize its different branches.

It is now generally agreed that the Gorgonopsids include the ancestors of the Cynognathidæ, and that the Pelycosaurs are a group which includes self-contained lateral branches springing from the very base of the stem of the mammal-like Reptiles. Thus by comparing the two extreme terms, *Varanosaurus* and *Diademodon*, we can gain at once a knowledge of the advances in structure which have occurred in the Anomodonts, and on the assumption that these changes have proceeded regularly we can determine the trend of advance during the evolution of the group. Discussion of intermediate forms will then enable us to decide whether this trend really expresses a true view of the mode of evolution, or whether the actual observed differences between the extremes represent the result of a series of fortuitous changes of indeterminate direction.

The work of Broili, of Case, of Williston, and the present writer has led to the view that *Varanosaurus* is the most primitive known Pelycosaur, forming a morphological ancestor to *Dimetrodon*, through a *Deiopeus*-like form. The view that *Diademodon* or *Trirachodon* is the most advanced of known Anomodonts results from the work of Seeley and Broom.

The differences between the skull of *Diademodon* and *Varanosaurus* are:—

In General Shape.

In *Varanosaurus* the snout is very long, square-cut in section, and roomy, compared with the rest of skull, with lateral nostrils and a long straight tooth-row. The large orbits are entirely laterally directed. The small temporal fossa lies entirely on the side of the skull and is almost hidden from above by the very broad parietal region. The occiput slopes forward, but is not deeply cupped. The sides of the skull are nearly straight. The skull is higher than wide.

In *Diademodon* the snout is short, small in volume, rounded in section, with nostrils looking more forward than laterally. The tooth-row is short and curved The orbit is comparatively small and looks very largely forward. The temporal fossa is very large, lies entirely on the top of the skull, and is not visible from the side, the parietal region being drawn up into a narrow crest. The occiput slopes a little forward and is deeply cupped. The sides of the skull gradually approach one another to the orbits but their direction is then changed as they form the slender snout. The skull is much wider than high.

In the Brain-case.

[The structure of the anterior face of the pro-otic and supra-occipital is not known in *Varanosaurus* and other regions are not very well shown. The following account of the Pelycosaurs is based on *Deiopeus* and *Dimetrodon.*]

In Pelycosaurs the basioccipital is thick, ending in a large rounded condyle. The large fenestræ ovales are placed on the bottom of the skull, far out at the side of the deep well-developed tubera. The paroccipital process is short and slender, supporting the squamosal and touching the tabular; it lies well above the lower surface of the skull. The pro-otic is small, its anterior face in no way overhanging the notch for the fifth nerve. The supra-occipital is entirely plate-like, not forming a roof over the brain in advance of the Vth nerve. The basisphenoid is massive, forming a sloping floor to the posterior part of the brain-case. It bears definite *Sphenodon*-like basipterygoid processes, anteriorly it is in *Varanosaurus* continued forward by a long channel-shaped parasphenoid.

The parietal does not form any part of the side-walls of the brain-case. The epipterygoid is a slender rod of circular section.

The whole brain-cavity is very small in comparison with the size of the skull.

In *Diademodon*, on the other hand, the basioccipital is small and plays at most a subsidiary part in the pair of occipital condyles. The small fenestræ ovales are placed on the bottom of the skull, not very far separated. Basisphenoidal tubera are represented merely by the edges of the triangular lower face of the basisphenoid. The paroccipital is a long powerful process supporting the squamosal and touched by the tabular; it lies on the lower surface of the skull.

The pro-otic is large, being carried forward by a great process which completely overhangs the trigeminal foramen.

The supraoccipital is produced forwards by two wings, which cover and form side-walls to a great deal of the brain-cavity in advance of the Vth nerve.

The basisphenoid is a small bone forming a nearly horizontal floor to the brain-case. It has small lateral basipterygoid processes with the pterygoids attached to their flat lower surfaces; anteriorly it is carried forward by a slender process which reaches the palate and there spreads out into a broad vomer in the roof of the posterior part of the naso-pharyngeal ducts.

The parietal forms a good deal of the side-wall of the brain-case. The epipterygoid is a flat plate forming the side-wall of the brain-case for some distance and articulating with the anterior edges of the pro-otic. The brain-cavity is relatively very large.

The ear of a Pelycosaur, so far as can be inferred from the bone which housed it, lies low down on the side of the brain-case, has small simple semicircular canals, and has a cochlea which leaves no evidence of its existence on the bones. The fenestra rotunda is represented by a notch on the ridge, which in the bony skull separates the vestibular cavity from the vagal foramen, and thus opens inside the brain-cavity. The stapes is always very large and is perforated, the fenestra ovalis being a large irregular hole. There is no groove for the external auditory meatus.

In *Diademodon* the inner ear retains its original position low down on the side of the brain-case and still shows only simple semicircular canals. It has, however, a well-defined cochlea housed in a crypt passing forward and inward, and curved forward through about a quadrant of a circle. The fenestra rotunda is a complete foramen, which opens indeed into the vagal foramen, but does so on the outer surface of the neural cranium, exactly as it does in the young *Ornithorhynchus*.

The stapes, although still of good size, is much smaller than in Pelycosaurs, and the fenestra ovalis is a neat round hole of small size. The external auditory meatus is housed by a deep groove.

The nose of *Diademodon* occupies a smaller space than that of *Dimetrodon*, but the area of its sensory epithelium seems to have been increased by a great development of turbinal cartilage, now only represented by a series of ridges, on the inner surface of the nasals and prefrontals which once supported them. Nothing of the kind occurs in Pelycosaurs.

Many other features in the nose of the Anomodonts can only be discussed in connection with the septomaxilla, palate, etc., and then only in a detailed discussion of individual forms.

The Roof of the Skull.

In *Varanosaurus* the parietals are short, very broad, and with the pineal foramen very far back. Their edges are separated from the temporal fossæ by a union of the postorbital and squamosal. There is a large postfrontal lying on the roof of the skull. The frontal is a large bone always entering into the orbital margin. The prefrontals are large bones, almost equally divided between the dorsal and lateral surfaces of the skull, each bearing a depression on the outer face just in front of the orbit. The nasals are narrow slips of bones. There is a small supratemporal.

In *Diademodon* the parietals are long, very narrow, and with the pineal foramen between their anterior ends. They form the inner margins of the temporal fossæ for a very long way, the squamosal and postorbital being widely separated. There is no postfrontal. The frontal is a small bone, not entering the orbital margin. The prefrontals are small bones on the rounded snout, with no depression in front of the orbit. The nasals are wide, especially posteriorly. There is no supratemporal.

In side-view the skull of *Varanosaurus* shows a long shallow maxilla, completely separated from the nasal by the long lachrymal extending from the orbit to the septomaxilla. There is no very marked specialization of the dentition, all the teeth from the premaxilla backward being similar in form and not very dissimilar in size. The quadrato-jugal is exposed on the side-wall of the skull and the jugal stops considerably before the quadrate.

Diademodon has a short deep maxilla reaching the nasal in a long suture. The lachrymal is a small short bone. The dentition is fully divided into incisor, canine, "premolar," and "molar teeth."

The quadrato-jugal no longer appears on the surface of the skull and the jugal extends back to its extreme hinder end.

The suspensorium of *Varanosaurus* consists of a large quadrate with a definite pterygoid wing, whose posterior surface is covered by the pterygoid. The outer edge of the quadrate is attached to the quadrato-jugal, there being no quadrate foramen. The upper part of the posterior surface of the quadrate is covered by the squamosal, that bone passing so far inwards as to touch the pterygoid.

In *Diademodon* the quadrate is a very small bone, either with or without a pterygoid wing, but in no case articulating with the pterygoid. The outer edge of the quadrate is fused with the quadrato-jugal, from which it is separated only by a small foramen, the articular surface being formed about equally by either bone. The whole posterior surface of the joint bone is covered by the very large squamosal, which extends down to the condylar edge.

The primitive Pelycosaur palate has the following characters:—The pterygoid is a triradiate bone, articulating by a movable facet with the basipterygoid process, from which point the quadrate ramus rises and runs backward as a vertically placed sheet of bone, passing behind the quadrate. The lateral wing of the pterygoid passes directly outward from the region of the basipterygoid and terminates in the usual flange.

The anterior part of the pterygoid forms a large part of the essentially flat palatal surface and articulates with the prevomer. It meets its fellow in median suture in *Varanosaurus*. The dorsal surface of the pterygoid is raised into a ridge near the middle line of the skull. In later forms (*Dimetrodon*, e.g.), the ridge is much exaggerated and its median surface passes smoothly into the ventral surface. The palatines are small flat bones. The prevomers are distinct. The anterior end of the palate is not known in any primitive Pelycosaur, but from the conditions in later forms there is no doubt that the posterior nares were small and lay in the general plane of the rest of the palate, which was essentially flat. In such later Pelycosaurs as *Dimetrodon*, owing to the step in the lower edge of the maxilla, the palate is considerably vaulted, and the posterior nares lie above the level of the cheek-teeth.

In *Diademodon* the pterygoid articulates by a rigid suture with the lower surface of the basipterygoid process, and there is no quadrate ramus, the bone terminating at its attachment. The transverse ramus does not arise from the basipterygoid region, but very much further forward, the posterior part of the bone being a slender strip, which is united with its fellow and the parasphenoid to form a slender bar.

The transverse ramus arises very suddenly from this bar, the bone being drawn downward into deep and very powerful flanges.

There is no anterior ramus, the bone ending in a transverse suture with the palatine at the region where it joins the jugal.

The transverse bone is very small and is not included in the flange at the foot of which it lies.

The palatine is a very large bone, forming a great deal of the posterior part of the palate, then turning downward to form the lateral wall of the posterior part of the nasopharyngeal duct, and, finally, developing a secondary plate, which forms a floor to that passage.

The two palatines are separated by a median vomer, which forms the roof of the nasopharyngeal passage, apparently terminating behind in a pointed slip separating the anterior ends of the pterygoids, but really passing backward to the basisphenoid.

The prevomers seem to have vanished entirely.

The maxillæ send inward secondary plates, which continue those of the palatine forward. The premaxillæ have palatal processes, which pass dorsally to the secondary plates of the maxillæ and touch the anterior end of an ossification in the nasal septum, viz., a mesethmoid.

In *Varanosaurus* the epipterygoid is a slender rod rising vertically from the dorsal surface of the pterygoid just in advance of the basipterygoid articulation.

In *Diademodon* the epipterygoid is a large flat sheet of bone forming a side-wall to the brain-case and articulating by a very long suture with the parietal and frontal above, having a suture with the pro-otic behind, articulating with the basipterygoid process below, and ending in a suture with the pterygoid. Behind the basipterygoid and below the point of exit of the maxillary, mandibular, and motor portions of the fifth nerve, the epipterygoid is continued backward by a process occupying the position of a quadrate ramus of the pterygoid. The ramus in certain species articulates with the front face of the quadrate.

The preceding pages record the more important differences between the most primitive and the most advanced known Anomodont; they bring out the direction of the evolutionary advances and show how enormous is the structural gap between them, a gap represented in time by the relatively small interval between the bottom of the Permian and the middle of the Triassic system.

It remains to show how completely this morphological gap can be bridged by the material available. Although, as Case and Williston have repeatedly and emphatically pointed out, the Pelycosaurs are a self-contained group dying out with *Dimetrodon* and

Edaphosaurus, they show evolutionary changes which are in the main in the same direction as those which lead from *Varanosaurus* to *Diademodon*, coupled, of course, with many individual specializations. Although it is not essential for the purpose of this paper, it is, I think, useful to point out certain of the more striking of these advances, using *Varanosaurus*, *Deiopeus*, and *Dimetrodon* as the series of forms. These animals lived side by side, and this series is only a morphological one.

In general shape *Dimetrodon* shows an advance on *Varanosaurus* in that the snout is much deepened, is square in section only immediately in front of the orbit, and is, in general, wedge-shaped with a rounded dorsal edge. The parietal region is narrower, and leaves the temporal fossæ visible from above. The occiput is more vertical. In the brain-case *Dimetrodon* shows an advance over *Deiopeus* in that the basioccipital is thinner, the basisphenoidal tubera smaller, and the paroccipital process larger. The anterior margin of the pro-otic lies further in advance of the internal auditory meatus. The brain-cavity is considerably deeper and wider posteriorly. The fenestra ovalis of *Dimetrodon* is smaller than that of *Deiopeus* and the stapes lighter. The roof of the skull of *Dimetrodon* differs from *Varanosaurus* in the following ways:—the parietals are less wide and the pineal foramen further forward. The postorbital is visible from above. The pair of frontals have acquired a cruciform shape owing to a widening of the interorbital surface. *Deiopeus* provides an exact intermediate, the increased width of the interorbital surface having arisen by an increase in size of the pre- and post-frontals, so as to leave a gap which is filled up by a special process of the frontal.

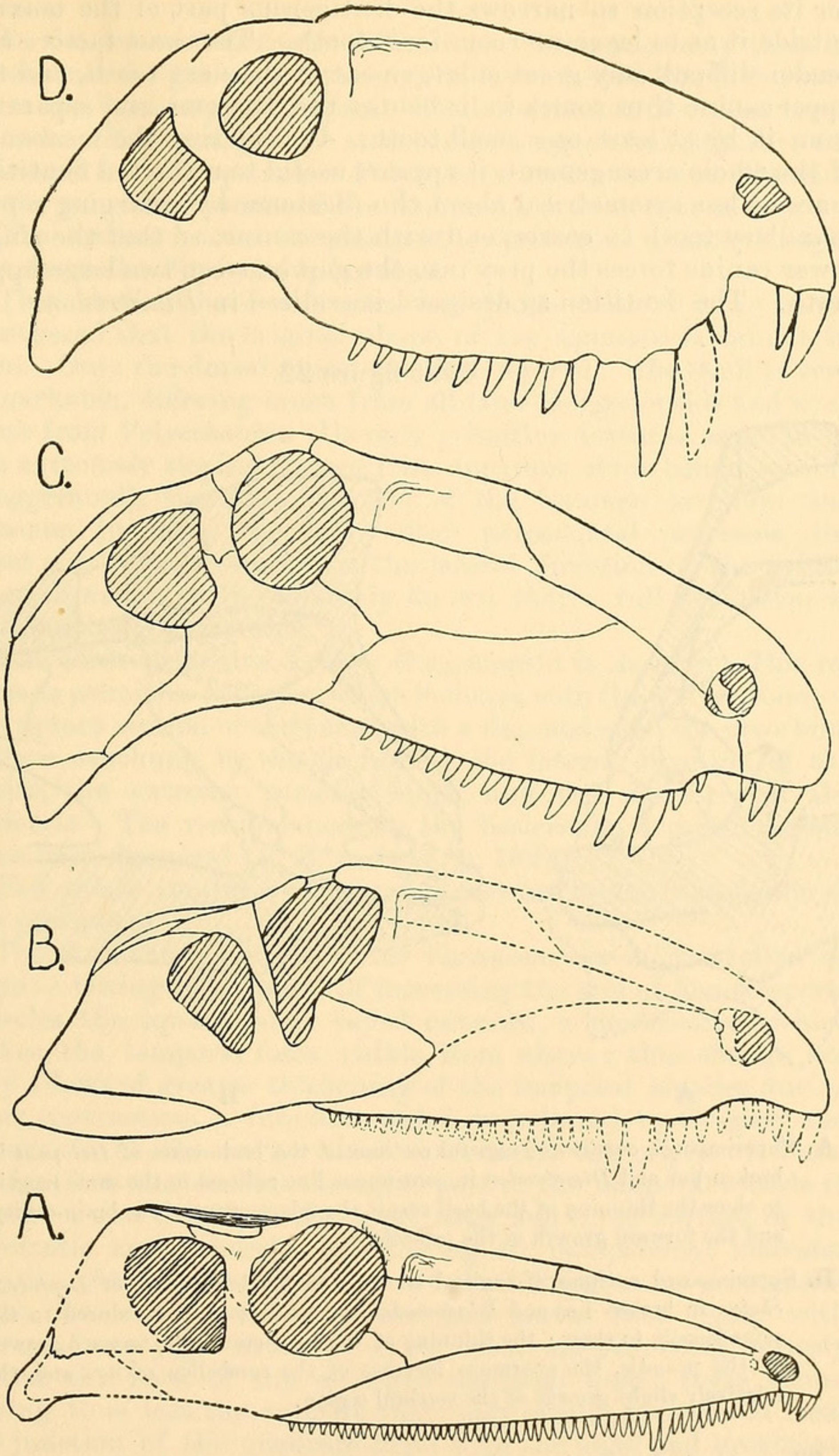
In side-view the skull of *Dimetrodon* shows a shortened and deepened maxilla touching the nasal in a short suture. The dentition is sharply divided into incisors and cheek-teeth by a diastema. The third maxillary tooth is much larger than the first two, and the lower border of its socket lies well below the dentigerous border of the premaxilla.

The lachrymal does not reach the septomaxilla. The orbit is placed high up in the skull.

It seems probable that the deepening of the maxilla and the "step" depend on the necessity of finding room for the roots of, and the development of, replacing teeth for the greatly lengthened maxillary teeth.

The condition of the canine may depend on the following considerations:—A large canine in the upper jaw presupposes a similar tooth in the lower jaw; such teeth, which are designed for killing animals, are most useful in the front of the mouth. The lower jaw, as a whole, bites inside the upper jaw. The first tooth of the lower jaw cannot be much enlarged, because of the difficulty of making a pit for its reception near the middle line in the palatal process of the premaxilla; hence the lower canine cannot be quite at the end of the jaw. A large lower canine almost involves a diastema in the upper jaw for it to bite into, because

Text-figure 21.

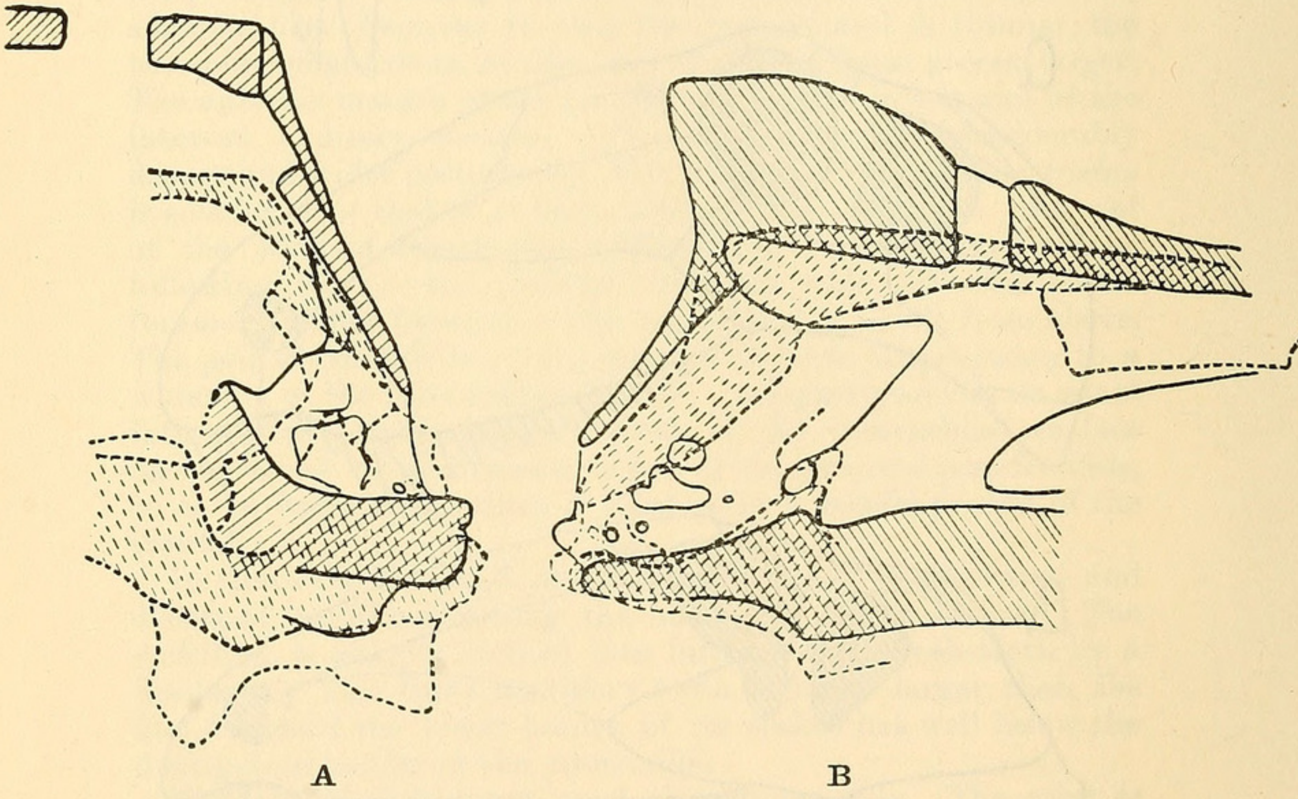


Series of drawings of the right lateral aspect of Pelycosaur skulls, reduced to the same length.

A. *Varanosaurus acutirostris* Broili, restored from the type-skull in Munich, partly after Broili. B. *Deiopeus leptocephalus* Cope, restored from the type-skull in the American Museum. C. *Sphenacodon ferox* Marsh, after Williston. D. *Dimetrodon gigas* Case, from a photograph published by Case.

being laterally placed, the formation of a pit in the palate for its reception so narrows the dentigerous part of the maxilla outside it as to leave no room for a tooth. The same factors will render difficult any great enlargement of the next tooth, and the upper canine thus comes to lie behind the diastema and separated from it by at least one small tooth. Considering the mechanics of the whole arrangement, it appears useful to make the dentition more or less symmetrical about the diastema by enlarging a pre-maxillary tooth to correspond with the canine, so that the single lower canine forces the prey into the gap between two large upper teeth. The dentition so designed is realized in *Dimetrodon*.

Text-figure 22.



A. Superimposed outlines of sagittal sections of the brain-cases of *Deiopeus* in broken line and *Dimetrodon* in continuous line reduced to the same length, to show the thinning of the basis cranii, the enlargement of the brain-cavity, and the forward growth of the pro-otic.

B. Superimposed outlines of sagittal sections of the brain-cases of *Leptotrachelus* in broken line and *Diademodon* in continuous line reduced to the same length, to show: the thinning of the basis cranii, the forward growth of the pro-otic, the enormous increase of the cerebellar cavity, and the relatively slight growth of the cerebral region.

The great deepening of the maxilla demanded by the canine automatically squeezes out of existence the anterior part of the lachrymal.

Deiopeus and *Ophiacodon* provide an exact intermediate between

Varanosaurus and *Dimetrodon* in dentition, as Case has already shown.

In the palate *Dimetrodon* differs from *Varanosaurus* in that the transverse flanges of the pterygoids have moved much forward from the basipterygoid region. The condition in *Deiopeus* is not known. Thus many of the structural changes which separate the advanced from the primitive Pelycosaurs are in the same direction as the general advances of the Anomodonts from first to last.

The earliest known Gorgonopsid is *Galesuchus gracilis* Haughton, from the *Tapinocephalus*-zone.

This skull I have not seen, but judge that it is so much weathered that the original shape of the squamosals cannot be seen. Only the dorsal aspect has been figured. The skull is very remarkable, differing much from all later Gorgonopsids and even more from Pelycosaurs. Its only primitive features seem to be the extremely sloping occiput (the apparent slope being possibly exaggerated), the high position of the foramen magnum and foramen jugulare, the large deep paroccipital processes, the great size of the frontal, and the lateral direction of the orbits. It is, however, so incompletely known that a full discussion of its affinities is impossible.

The most primitive known Gorgonopsid is *Arctops*. This retains as primitive features, which it shares with the Pelycosaurs:—the square section of the snout with a depression on the preorbital surface overhung by the prefrontal, the lateral direction of the orbits, the extreme parietal width, and the shortness of the parietals. The resemblances in the basicranial and otic regions have been discussed (P. Z. S. 1914, p. 1027).

The palate retains a primitive structure in the non-fusion of the prevomers.

The skull shows advances over *Varanosaurus* in the following ways:—Owing to the need of increasing the size of the temporal muscles the squamosal is bayed outward, a modification which makes the temporal fossa visible from above; this change not only allows of greater thickening of the temporal muscles during their contraction, a function which is believed by Gregory and Adams to be the factor which determines the origin of fenestration, but also enables the outer part of the temporal muscle to acquire a new origin on the upper edge and inner surface of the zygomatic arch, thereby establishing an independent masseter muscle. At the same time this widespread zygomatic arch passes much laterally to the quadrate and leaves that bone, with the quadrato-jugal attached to its outer margin, lying entirely within the back of the enlarged temporal fossa; these bones, having thus lost the support that they originally received from the junction of the quadrato-jugal with the jugal and squamosal by sutures, can only be adequately supported by a more powerful abutment on the paroccipital process and by an extension of the squamosal down their posterior surface.

At the same time the lateral extension of the squamosal renders the back of the skull much wider than the neck, and makes the tympanic membrane lie much nearer the middle line than the side of the skull. As it is necessary to keep this membrane exposed to the outer air, any swelling of the neck will automatically lead to the formation of an external auditory meatus; the beginnings of this passage are seen in *Arctops* in a groove on the posterior surface of the squamosal, just outside the end of the paroccipital process.

On the ventral surface *Arctops* has advanced over *Varanosaurus* in the shift forward of the great pterygoidal flanges to a position far in advance of the basipterygoid processes; this change results in a further great enlargement of the cavity for the temporal muscles, and allows the development of great pterygoidal muscles with an insertion on the dorsal surface of the palate.

This shift forward of the flanges has occurred in *Dimetrodon*, but the conditions in *Arctops* differ from those in the earlier form in the fusion of the posterior parts of the pterygoids and parasphenoid into a massive ridged girder. This change adds greatly to the strength and rigidity of the skull, but its details cannot readily be explained by mechanical considerations; the most important of these is the replacement of normal basipterygoid processes by the laterally directed flat lappets which occur in all Theriodonts.

In the palate itself the more important changes are the development of a median groove, a necessary preliminary to the establishment of a secondary palate, which is brought about by that change in the dentition involving the development of a "step" between the maxillary and incisor teeth which has been discussed under *Dimetrodon*, and the extreme posterior position of the hinder ends of the posterior nares; this latter change is itself probably to be associated with the incipient secondary palate, leading as it does to a longer air-passage whose posterior end is not so easily closed by the presence of food in the anterior part of the mouth.

Another advance in *Arctops* is the more vertical position of the occiput.

Gorgonops is in some ways as primitive as *Arctops*, with which it shares very broad parietal and interorbital regions and a square sectioned snout. The orbit faces laterally in both forms, and each has a remarkably broad interparietal, a feature in which they resemble Deinocephalians.

Gorgonops has a pair of large frontals, which are cruciform in plan exactly as in the later Pelycosaur.

The prefrontal is a large bone which overhangs a well-marked depression on the preorbital surface.

Gorgonops shows advances over *Varanosaurus* which, so far as the parts are known, include all those which occur in *Arctops*, with the following additions:—The external nostril in *Gorgonops* is much complicated by the great development of the septomaxilla and the foramen behind it. This foramen, first recognised by

Case in *Dimetrodon*, occurs in all the more primitive Anomodonts and is still of uncertain function. In all Pelycosaurs the septomaxilla is a small bone resting on the maxilla and premaxilla at the back of the nostril, being touched by the nasal and forming with the other bones the foramen, which I propose to call the septomaxillary foramen.

In *Dimetrodon* the lower edge of the septomaxilla, where it rests on the maxilla, is turned inwards and forms a partial floor to the nasal passage. The anterior border of the septomaxilla is provided with a process which partially divides the external nostril into a lower and an upper part.

It is probable that the process on the anterior edge of the septomaxilla is associated with the original turbinal, simply forming the anterior end of that ridge. In the living lizards and snakes, the septomaxilla lies inside the nostril as it does in the Captorhinids, the collateral ancestors of the Pelycosaurs; it has in them a characteristic and uniform situation, in that it is ossified in the membrane dividing the main nasal cavity from Jacobson's organ, running nearly horizontally from the maxilla to the cartilaginous nasal septum.

In Anomodonts I have only heard one possible suggestion for the function of the septomaxillary foramen, that it served as an outflow for the ductus naso-lachrymalis, the liquid poured out from it serving to keep the muzzle wet as in Artiodactyls. This view is in harmony with the known position of the duct in early amphibia and reptiles. It, however, does not afford any satisfactory explanation of the great size of the foramen in *Gorgonops*.

The very peculiar conditions in the Deinocephalian *Mormosaurus* (Proc. Zool. Soc. 1914, p. 757, figs. 1 & 2) suggest another explanation. In this animal the ordinary external nostril, which in early reptiles always lies between the premaxilla, the septomaxilla, and nasal, appears to be represented by a minute foramen between the septomaxilla and the nasal. The large opening which is the functional nostril seems to be really a septomaxillary foramen, as it lies between the premaxilla, the maxilla, and septomaxilla, a situation which is never occupied by the ordinary nostril in early reptiles, but agrees with that of the septomaxillary foramen in the earlier Theriodonts. Thus this foramen must be of the nature of a nostril. The characteristic position of the septomaxilla in *Squamates* suggests that the foramen leads into Jacobson's organ, and it will follow that that organ was the functional olfactory organ of *Mormosaurus*; the shallowness and small size of the upper part of the nasal cavity, which distinguishes *Mormosaurus* from such Deinocephalia as *Moschops* with a normal septomaxillary foramen and nostril, can thus be accounted for.

The advances over *Varanosaurus* which are shown in the nose of *Gorgonops* are:—(1) the direction of the nostril forwards instead of laterally, a change which renders the appreciation of odours coming from the direction in which the animal is proceeding more delicate, because owing to a Pitot effect more air will be driven into the nasal cavity; (2) a great increase in the size of the septomaxillary foramen, possibly associated with a further elaboration of Jacobson's organ; (3) a great increase in the size of the facial part of the septomaxilla—this may be due to purely mechanical reasons.

Another advance very clearly shown in *Gorgonops* is a great deepening of the maxilla and a concurrent reduction of the lachrymal, the prefrontal showing little reduction.

The palate of *Gorgonops* is advanced in the great size of the internal nares, in the width, depth, and backward extension of the median groove, in the internarial bar being single, and in the occurrence of a median vomer in the back of the palate.

The very large size of the pterygoids and the forward position of the roughened and possibly tooth-bearing areas on these bones are primitive features.

The basicranial region shows no structural detail.

Scymnognathus whaitsi shows many resemblances to *Gorgonops* in its snout.

It shows advances over *Arctops* in the thinner basioccipital, smaller basisphenoidal tubera, and less massive paroccipital processes.

The brain-case is advanced over that of the Pelycosaur *Dimetrodon* in the great forward extension of the pro-otic and supraoccipital and the junction of the latter bone with the epipterygoid; a remarkable feature is the forward process of the basisphenoid, which forms a floor to the brain-case in advance of the pituitary fossa.

The most striking advances over *Arctops* are the great reduction in width of the parietal region, the lengthening of the parietals, and especially the enormous increase in spread of the squamosals. The turning backward of the upper part of the squamosal at the posterior margin of the temporal fossa makes that opening even larger, and increases the length of certain fibres of the temporal muscles.

So far as known, similar differences separate *Scymnognathus* from *Gorgonops*, the latter genus having much larger frontals than the former.

By the great expansion of the width of the back of the skull, the orbits of *Scymnognathus* are made to look partly forward.

Another small but important advance in *Scymnognathus* is that certain fibres of the temporal muscle have secured an origin from the dorsal surface of the parietal region.

Scymnognathus is probably less advanced than *Arctops* and *Gorgonops* in its less vertical occiput. In the palate *Scymnognathus* is probably less advanced than *Gorgonops* in the small size of the median groove, and its restriction to the anterior part of the palate and to a narrow space round the hinder end of the posterior nares.

The incompletely known *Leptotrachelus* shows an important stage in the advance in structure of the basicranial region, already discussed in P. Z. S. 1914, p. 1027, figs. 3 & 4; it is in this region more advanced than any other known *Endothiodon*-zone Gorgonopsid. It retains as primitive features the very large quadrate, large postfrontal and frontal, and a sloping occiput.

Thus the *Endothiodon*-zone Gorgonopsids show definite advances over the Pelycosaurs in the direction of *Diademodon*. Each form is advanced in certain features whilst retaining a more primitive structure in others, so that an imaginary animal, built up by throwing together the most advanced features found in all the actual animals, would be far more advanced than any one is on the average; although in no point would it be more advanced than a known form. In fact, the evidence existing here, small though it is, suggests that there is a limit to the total amount of advance possible to the members of a group in a given time, and that these changes may be distributed either over the whole animal or concentrated on a definite region, which will then present a structure of much more advanced type than is found in allied contemporaneous forms. A somewhat similar conclusion seems to have been reached by W. D. Matthew from the study of the more abundant material of fossil mammals.

Discussion of the Gorgonopsids of the *Cistecephalus*-zone is rendered difficult by two factors—the incomplete descriptions and insufficient figures of many of the perfect skulls in S. Africa and New York, and the fact that the *Cistecephalus*-zone is a long one and that we do not know the relative ages of the Gorgonopsids from it. It will appear from the evidence to be brought forward in this paper that the forms from Dunedin and Nieuweveld localities are early, those from New Bethesda and the Kagaberg which are associated with *Dicynodon tigriceps* considerably later in time. There is, however, no stratigraphical evidence that this is so.

From the *Cistecephalus*-zone Broom and Haughton have described several forms as species of *Scymnognathus*—*S. tigriceps* B. & H., *S. parvus* Br., *S. minor* Br., *S. angusticeps* Br., *S. serratidens* Hau., are all from the Nieuweveld. These forms may very possibly be congeneric; they agree with *Scymnognathus* in having i. 5, c. 1, m. 4–5, but quite certainly do not belong to that genus. They differ from *Scymnognathus whaitsi* in the following characters:—

The snout is very much deeper, its anterior end instead of being rounded is vertical (*cf.* Broom, P. Z. S. 1913, p. 225, pl. 36), the external nostril is much larger, the septomaxillary foramen smaller. The anterior end of the nasal does not fully overhang the nostril. The top of the snout may be ridged, and the square section with a preorbital depression overhung by the prefrontal is entirely lost (cf. *S. serratidens*, Ann. South Afr. Mus. vol. xii. p. 89, pl. xiii.). The snout is much shorter and the prefrontal in consequence smaller.

There is no step in the upper jaw, the curved tooth-bearing edge of the premaxilla passing smoothly into that of the maxilla. In *S. tigriceps* thé squamosals are not nearly so much spread, the skull being much deeper in proportion to its width. If we may trust the existing description of a not very satisfactory preparation, the palate of *S. tigriceps* differs from that of *S. whaitsi* in the loss of the anterior projection of the pterygoid and the great extension of the palatines. On the other hand, judging from the description by Haughton of its endocranial surface, the brain-case of *S. tigriceps* may have greatly resembled that of *S. whaitsi.*

Thus the *Cistecephalus*-zone animals referred to *Scymnognathus* do not belong to that genus, but differ from it by a series of advances which will be seen to be all in the direction leading to *Diademodon.* Certain of these species appear to resemble *Lycosaurus pardalis* considerably, agreeing with that animal in dentition, the short high snout with a rounded dorsal surface, the large nostril, the vertical internarial bar, the small exposure of the septomaxilla, the absence of a step in the upper jaw, the short and deep maxilla, and the small prefrontal. All of them, however, seem to retain a large postfrontal bone.

Two other remarkable forms, apparently from the lower part of the *Cistecephalus*-zone, *Scylacops capensis* and *Gorgognathus longifrons*, are of interest because they strongly recall *Endothiodon*-zone forms.

Gorgognathus with its immensely long low snout somewhat resembles *Scymnognathus whaitsi*, and its very broad interorbital and intertemporal surfaces agree with *Gorgonops.* It is, however, advanced in the following characters :—The loss of the step in the jaw, the rounded snout, and especially the vertical occiput. Haughton has pointed out another advanced feature in the structure of the basicranial region. *Scylacops* is a small unusual form with a low broad snout: it is advanced in the exclusion of the frontal from the orbital margin, in the rather vertical occiput, in the loss of the step in the upper jaw, and especially in the loss of the anterior ramus of the pterygoid : it appears to retain a rather primitive *Gorgonops*-like nose and has only small temporal fossæ. Broom's figure of the occiput suggests that it is advanced in the shallowness of the paroccipital processes. [It is probable that the fragment of a Gorgonopsid skull which I described (Ann. & Mag. Nat. Hist. 1913, vol. xi. p. 65, figs. 1-4) belongs, if not to *Scylacops*, at any rate to a closely allied form.]

Arctognathus curvimola is a far more advanced form than any so far discussed in this paper ; it presumably comes from a higher horizon in the *Cistecephalus*-zone than *Gorgognathus*, etc. It shows advances in the following features :—The snout is short, narrower than the orbital region, rounded over the mid-line. The nostrils are very large and the septomaxillary foramen small. The nasals do not overhang in front. The interorbital and intertemporal surfaces are narrow, the orbits facing outwards, upwards, and a little forwards. The postfrontal is very small, the preparietal is absent. The maxilla is very short and deep, there is no step in the upper jaw. The prefrontal is short and probably small. I have already shown that the basicranial and otic regions are very advanced (Proc. Zool. Soc. 1914, p. 1028). The epipterygoids are widened and flat, very much as in *Diademodon*. The posterior end of the quadrate ramus of the pterygoid no longer reaches the quadrate. The pterygo-parasphenoidal girder, instead of having a flat ventral surface from which a deep median crest rises, is rounded, with the crest represented by a low fillet.

The palate is most conveniently compared with that of *Gorgonops*, which represents an earlier stage leading to it.

The great median groove is deepened and its roof is entirely formed by a median vomer, which presumably represents a forward growth of the posterior median bone of the *Gorgonops* palate. Anteriorly the ridge rising from the vomer in *Arctognathus* suggests that there was a soft secondary palate into which a secondary bony plate may have grown out in the concealed part of the palate.

The tooth-bearing roughened area of the anterior ramus of the pterygoid lies much further back than in *Gorgonops*, and the pterygoid no longer reaches the posterior nares.

The quadrate of *Arctognathus* is much smaller than that of *Scymnognathus*.

The conversion of *Arctognathus* into a "Cynodont" like *Cynognathus* demands only the following changes:—Still further thinning of the basis cranii, further reduction of the quadrate wing of the pterygoid, the development of a connection between the quadrate wing of the epipterygoid and the paroccipital; further retraction of the anterior ramus of the pterygoid, so as to reduce the roughened areas to a pair of small knobs on each side of the posterior end of the median groove; a little reduction of the ectopterygoid; the development of secondary plates from the maxillæ and palatines in the existing soft secondary palate; the conversion of the narrow intertemporal area into a sagittal crest, to increase the length of the temporal muscles; the loss of the postfrontal, and a further reduction of the frontal and prefrontal, leading to an increase in size of the posterior part of the nasals. These changes are all in the same direction as those which convert a Pelycosaur like *Varanosaurus* into a Theriodont like *Gorgonops*, and an animal like *Gorgonops* into a form like *Arctognathus*, and are, on the whole, smaller than those which are necessary to carry out the earlier improvements; in fact, *Arctognathus*, which is technically a Gorgonopsid, is structurally closer to *Cynognathus* than it is to *Gorgonops*.

Amongst other advanced forms allied to the Gorgonopsids and coming from the *Cistecephalus*-zone are *Cynosuchus* and *Whaitsia*, which have both been excellently described, though not completely figured, by Haughton.

Whaitsia is a remarkable form with a somewhat primitive basicranial region, and a palate which in general agrees with *Gorgonops*, but differs in the development of a special process passing out on each side of the internarial bar so as to divide each posterior nostril into two. [The meaning, morphology, and function of this arrangement are quite uncertain, the anterior vacuities are not exactly homologous with the anterior palatine incisions of mammals and Cynodonts, because the posterior border of these incisions is always formed by the anterior edge of the secondary plate of the maxilla.] *Whaitsia* is very advanced in the reduction of the wide parietal region to a narrow sagittal crest, which characterizes it, and in the extreme reduction of the dentition.

The preceding discussion shows that the Gorgonopsids include a series of forms which exhibit in their skulls a gradual series of changes by which so primitive an animal as *Arctops* passes insensibly into a Cynognathid. It establishes clearly the existence of a series of evolutionary trends, which persist without change from the beginning of the Anomodonts in *Varanosaurus* to their end in *Diademodon*, and indeed to lead on to mammals. It remains to discuss the other primitive Theriodonts included in Broom's order Therocephalia and the Deinocephalia, to see how far these evolutionary trends apply also to them, and to consider the relation of these forms to the Gorgonopsids, which are plainly the central group of the Theriodonts.

No Therocephalian is at all well known, despite the very large number of forms which have been described. We know the dorsal and lateral surfaces of the skull in a good many forms (*Scylacosaurus*, *Lycosaurus*, *Scaloposaurus*, etc.), the palate is known more or less completely in others (*Scylacosaurus*, *Scymnosaurus*, *Scaloposaurus*, etc.). The basicranial region is known in no Therocephalian, neither has any occiput been figured. Haughton has described the brain-case of *Alopecognathus*, but his figure is not in all points (*e.g.*, the character of the supraoccipital and the relations of the interparietal and parietal) very convincing.

The most important materials of Therocephalia in the British Museum are the more or less complete skulls of *Scaloposaurus* from the *Cistecephalus*-zone and *Scylocosaurus* and *Scymnosaurus watsoni* from the *Tapinocephalus*-zone.

Scymnosaurus watsoni Broom, Proc. Zool. Soc. 1915, p. 169, fig. 6.

Lycosuchus? Watson, Proc. Zool. Soc. 1914, p. 1036, fig. 7.

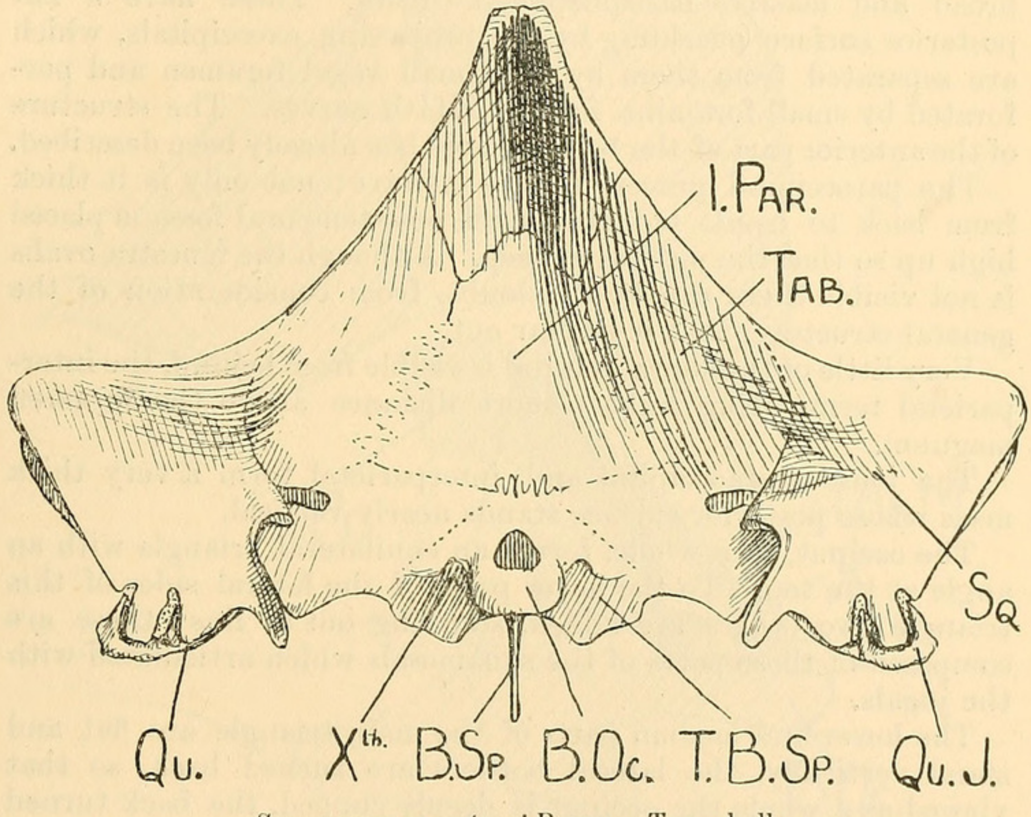
Type: a skull with seven cervical vertebræ in natural articulation, other vertebræ and fragmentary limbs doubtfully associated. *Tapinocephalus*-zone, Uitkyk, Dist. Prince Albert, Cape Province.

The skull of the type is curiously preserved: it is embedded in a calcareous nodule, which breaks with a conchoidal fracture and is so loaded with a very fine siliceous mud as to be glass-hard, completely blunting a carefully hard-tempered chisel after a single blow.

The skull is broken through along the plane of the palate, part of that structure adhering to each block. The skull is then broken through by a split which passes through the brain-cavity and removes the whole left posterior corner of the skull behind the orbit. Finally, another split traverses the occiput, part of that region adhering to each surface.

Where weathering has softened the matrix, very good preparations are easily made, and in these regions, especially where

Text-figure 23.



Scymnosaurus watsoni Broom. Type-skull.

Occipital aspect. × ⅓.

the bone has been cleaned by weathering, the preservation is extraordinarily good. Development of the unweathered regions is a very difficult and extremely slow and tedious process. Nevertheless, I have been able to make a satisfactory preparation of the inner surface of the cranial cavity.

The occiput now shows nearly every detail of its structure, although a direct view of its posterior surface cannot be seen. Its outline is well shown and the posterior surfaces of the quadrates and squamosals are clean.

Dr. Broom's figures give a good idea of the general shape, the structure of the dorsal and lateral aspects not being shown.

My former figure gives a good idea of the palate, whose structure is well shown. It, however, does not clearly illustrate the exact mode of articulation of the quadrate to the squamosal and the structure of the extreme postero-lateral corner of the skull and the auditory groove. This inaccuracy, which is not of a very serious nature, was due to a misunderstanding by about 30° of the orientation of the detached left corner, which was at that time the better exposed.

The basioccipital condyle is largely concealed by the attached atlas, but is partly exposed from below and cut by fractures which give sections through it. It is rounded and nearly twice as wide as it is deep. It is short and immediately in front of it, at a plane a little in front of the general occipital surface, lie the very broad and massive basisphenoidal tubera. These have a flat posterior surface overhung by the projecting exoccipitals, which are separated from them by the small vagal foramen and perforated by small foramina for the XIIth nerves. The structure of the anterior part of the basisphenoid has already been described.

The paroccipital process is very massive; not only is it thick from back to front, but the small post-temporal fossa is placed high up so that the process is deep. Although the fenestra ovalis is not visible there can be no doubt, from consideration of the general structure, that it lies far out.

Very little of the supraoccipital is visible from behind, the interparietal terminating only a short distance above the foramen magnum.

The joint supraoccipital and interparietal form a very thick mass whose posterior surface stands nearly vertical.

The occiput, as a whole, forms an equilateral triangle with an angle at the top. To the lower parts of the lateral sides of this triangle two others are added, standing out as fins; these are composed of those parts of the squamosals which articulated with the jugals.

The lower and median parts of the main triangle are flat and stand vertically, the lateral borders are turned back, so that viewed as a whole the occiput is deeply cupped, the back-turned margins gradually approach one another and, finally, fuse to form the very deep sagittal crest.

The extreme upper part of the occiput is formed by the parietals, the interparietal terminating far below the summit.

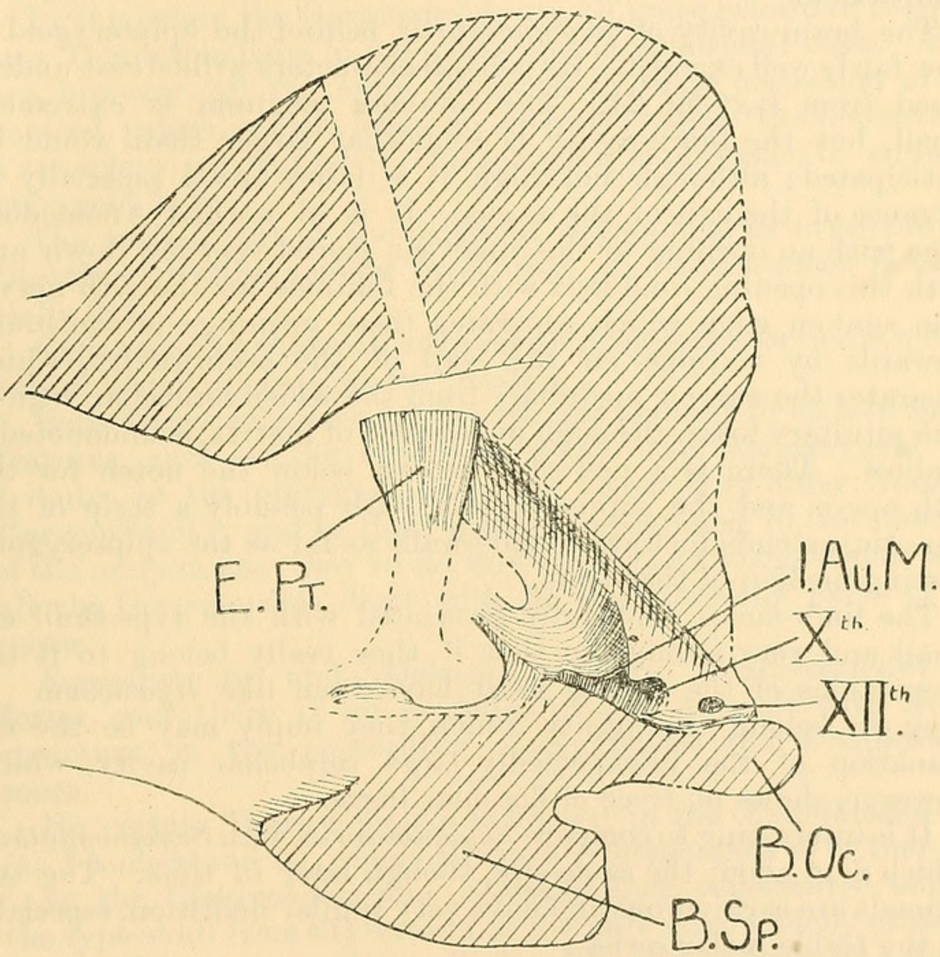
Laterally the parietals are covered by the tabulars, which form the margin of the occiput for some distance, strengthened by production of the parietals along their anterior faces and more laterally by a similar covering of squamosals, which, indeed, overlap onto the parietals.

The squamosals articulate, as just described, with the parietals and tabulars, and then extend outward into powerful processes, their upper parts being turned backward so as greatly to increase the size of the dorsal opening of the temporal fossæ.

The ventral halves of their posterior surfaces are vertical, continuing the plane of the paroccipital processes, with whose ends they are rigidly articulated. The posterior surface of the lower part of the squamosal is separated from that of the paroccipital by the usual ridge, which borders a groove for the external auditory meatus.

This ridge continues upwards until, just below the level of the post-temporal fossa, its hinder margin is turned inwards as a scroll with a thickened edge in a very unusual manner, not understood by me when I published my figure of the palate.

Text-figure 24.



Scymnosaurus watsoni Broom. Type-skull.

Brain-case in sagittal section seen from the left side. Epipterygoid of left side seen in outer view. × $\frac{2}{3}$.

I.Au.M., internal auditory meatus.

This scroll overhangs the occiput, but very rapidly subsides into the general surface of the squamosal, just at the point where that bone begins to bend backward.

The lower edge of the squamosal is thin and is split by two notches associated with the attachment of the quadrate.

The quadrate, or in all probability the fused quadrate and quadrato-jugal, is relatively small, nothing of its hinder surface being visible except the extreme articular edge and the two processes which interlock with the squamosal. There is evidence that it is no higher than the paroccipital process, but its upper edge and front face are not seen. The bone extends only very slightly laterally of the outer process, forming the extreme end of the lower margin of the occiput. Above its end the border of the squamosal runs upward and slightly outward, its front face being supported by the jugal.

The plan of this very remarkable occiput is repeated in a less exaggerated form in *Scylacosaurus sclateri*, so far as the still very incomplete preparation of the British Museum skull allows of a comparison.

The brain-cavity of *Scymnosaurus* behind the epipterygoid is now fairly well exposed. Its general characters will be best understood from text-fig. 24. The foramen magnum is extremely small, but the brain-cavity is somewhat larger than would be anticipated; although not high it is fairly broad, especially in advance of the exit of the vagus. It is of normal Anomodont type with an opening to the inner ear placed very low down and with this opening confluent with the foramen for the Xth nerve. The sunken edge which separates these openings is continued upwards by a ridge on the wall of the brain-cavity, which separates the narrow medullary from the wider cerebellar region. The pituitary fossa, although not cleared of matrix, is undoubtedly shallow. There is a powerful process below the notch for the Vth nerve, and the supraoccipital, with possibly a strip of the pro-otic, extends forward as side-walls as far as the epipterygoid, passing median of that bone.

The limb-bones doubtfully associated with the type-skull are small and very slender, so that if they really belong to it the proportions of the animal must have been like *Hyænodon*. If they do belong the agility which they imply may be the explanation of the unexpectedly large cerebellar cavity, which, however, shows no trace of floccular fossæ.

It is interesting to compare *Scymnosaurus* with *Scymnognathus*, which is of about the same size, though later in time. The two animals are carnivorous and have very similar dentition, especially in the feeble molar series.

The Therocephalian is the more advanced in the following characters:—

1. The reduction of all parts lying below the base of the brain, the basioccipital, basisphenoid, and especially the quadrates.
2. The reduction of the intertemporal region to a narrow sagittal crest.
3. The shortening of the snout.
4. The lengthening of the temporal fossæ.

Scymnosaurus rather recalls *Scymnognathus* in its square-cut snout, *Scylacosaurus* is much more advanced in the rounding of the dorsal surface of the nose, in both forms the extreme lowness of the face in early Gorgonopsids is lost, the maxilla being deep and the anterior part of the skull in general high.

The incisor-teeth in *Scylacosaurus* are small and the premaxilla shallow below the nostril.

There is no step between the canine and the incisors, the teeth forming a curved row like that of the latest Gorgonopsids and the Cynognathids.

A preparietal appears to be lacking in Therocephalia, otherwise the interorbital region does not differ greatly from that of Gorgonopsids.

In the palate the Gorgonopsids are all more primitive than the two Therocephalians in not possessing a suborbital fossa. They are, however, all far more advanced in their possession of the vaulted palate, which leads so directly to the development of a secondary palate, and in the complete suppression of an inter-pterygoid fossa.

The median part of the palate of *Scymnosaurus* even projects slightly above the general level, that of *Scylacosaurus* is essentially flat.

Scymnosaurus shows an advance on *Scylacosaurus* in the median vomer which appears on the palate.

Both Therocephalians agree with one another in certain special features, such as the extent to which the ectopterygoid contributes to the pterygoid flange (in which they differ from the Gorgonopsids); and in their general appearance, in the structure of the occiput, etc., they in no way recall the Cynognathids, as do all the Gorgonopsids dealt with in the preceding parts of this paper.

Scymnosaurus and *Scylacosaurus* are *Tapinocephalus*-zone forms, and there is no evidence of any animals with similar structure in the succeeding *Endothiodon*- and *Cistecephalus*-zones.

No certain Therocephalian is known in the *Endothiodon*-zone (as I understand it), unless Broom's *Ictidognathus* is of that age.

In the *Cistecephalus*-zone *Scaloposaurus*, represented only by the type-skull from Stylkrantz, is the only satisfactorily preserved form. It has been well described and figured by Owen and Broom, whose accounts should be referred to. The little skull differs exceedingly from *Scymnosaurus*, the temporal fossæ are short, there are no pronounced sagittal and lambdoid crests, the squamosals are not expanded, and the postorbital apparently does not reach the jugal behind the orbit. [This may be only on account of weathering of the surface.]

On the palate there is evident a wide interpterygoid vacuity, agreeing with the much narrower opening in *Scymnosaurus*; there are large suborbital vacuities as in that form. Nothing is shown of the anterior part of the palate, nor are the details of the basis cranii well displayed.

Thus the extant material of Therocephalia sheds no light on the evolution of that group, and the known forms are so few that no classification is possible.

It is, I think, reasonable to assume that the Therocephalia have sprung from the Gorgonopsid stock, and that they represent a series of distinct branches which display a much more rapid advance in structure than the conservative main stem. These advances are, on the whole, along the trends of Gorgonopsid evolution, quite early Therocephalians thus agreeing in certain features with Cynognathids. It is, as I have already shown, probable that *Bauria* and its allies are descendants of Therocephalia, representing the product of a parallel series of changes to that which resulted in *Cynognathus* imposed on a different ancestor.

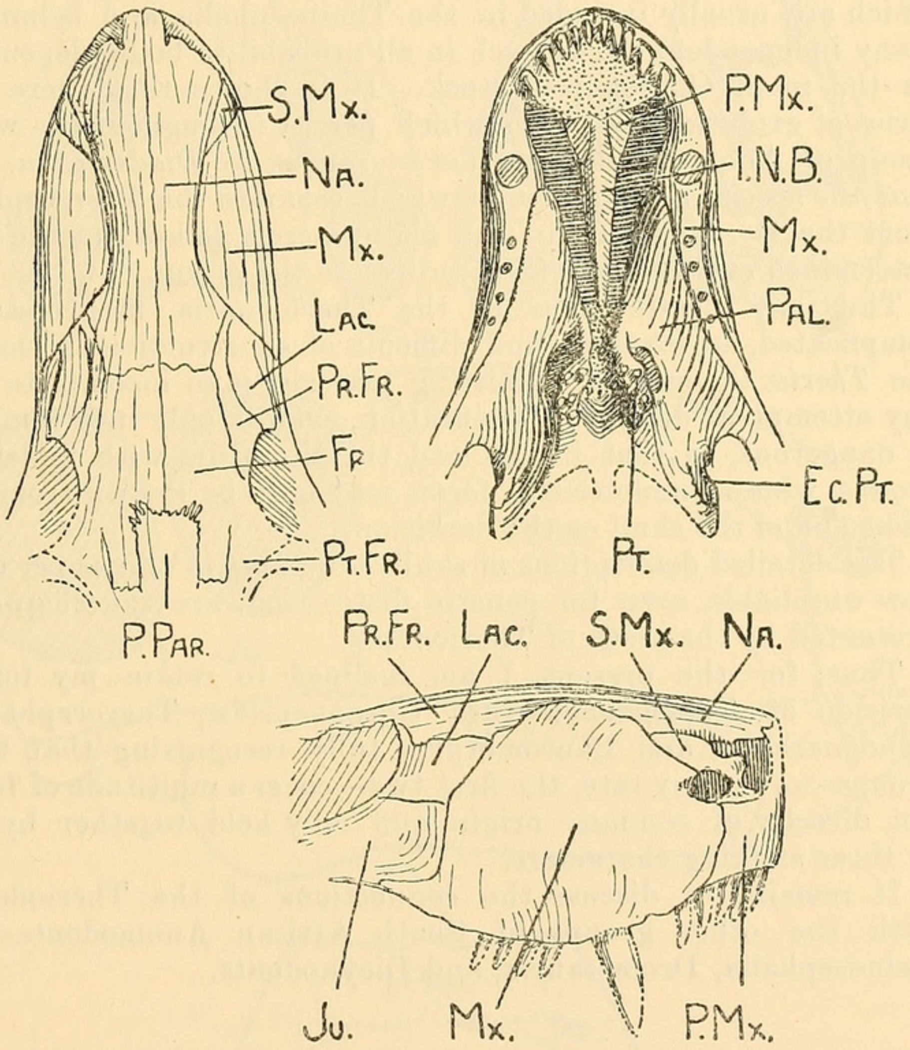
In the preceding part of this paper, I have dealt only with a selected series of Gorgonopsids which present resemblances to the Cynognathids, and have tacitly assumed that these forms are the main stock. There are, however, many other Gorgonopsids which appear to represent side-branches, displaying either accelerated evolution of certain features or else individual specialisations.

Of these forms the earliest and one of the best known is *Æluro-saurus felinus* Owen. This form was first described by Owen, Q. J. G. S. vol. xxxvii. p. 261, pl. ix., Seeley subsequently figuring an incompletely prepared palate. Broom later corrected certain features of Seeley's description of the side of the skull.

The British Museum includes, in addition to the type, two snouts which were regarded by Lydekker as *Æ. felinus*. Broom left manuscript-labels concurring in the identification, and a detailed examination which I made of them showed that the external surface and dentition are in complete agreement. One of the specimens had no lower jaw attached and the palate has been developed, with the remarkable result that it is shown to differ very considerably from the type, being probably generically distinct. The whole circumstance is of importance, because it shows that a specimen showing only the outer surface of the snout and dentition of a Gorgonopsid may be an inadequate type. In text-fig. 25 I give three slightly reconstructed views of the snout of B.M.N.H. R. 855 from the *Endothiodon*-zone? of Beaufort West. This type is very advanced in the depth and rounded section of the snout, in the supression of a step in the maxilla before the canine, and in the relatively slight overhang of the anterior border of the nasal. It retains a very large septo-maxillary foramen and a large facial exposure of the septomaxilla. The palate unfortunately shows no sutures, but gives a good view of the general form. In general form this palate differs very considerably from that of *Arctops*, *Gorgonops*, *Scymnognathus*, etc. The median region is excavated into a very narrow groove bounded laterally by massive processes, whose palatal surfaces bear small teeth in sockets. Lateral to the process is a small fenestra or possibly a very deep pit with a well-defined margin;

further laterally the palatine forms a deep groove, flattening out as it is traced forward until it becomes the nearly vertical surface of that anterior part of the bone which bounds the outer side of the posterior nares. The pterygoid flanges are powerful, but differ from the ordinary Gorgonopsid type in that the ecto-pterygoids extend down to their summits. There is a single inter-narial bar whose ridged lower surface lies far above the lower edge of the maxilla.

Text-figure 25.



Ælurosaurid, ? gen. et sp.

Dorsal, right lateral, and palatal views of the anterior part of a skull. R. 855, B.M.N.H. × ¾.

The palate is of the same type as that of *Ælurosaurus felinus*, but differs in the much smaller development of tooth-bearing areas and in the much more caudal position of the hinder ends of the posterior nares.

An analysis of the structure presented by a series of animals belonging to the Theriodontia thus suggests that that group is a natural one, the conservative main stem which leads on to the Cynognathids being represented by a series of Gorgonopsids of which *Gorgonops* itself is one of the most primitive members. From this stem side-branches arise, which retain the broad parietal region and other primitive features, but present either an accelerated development of certain regions or are individually specialised. From still earlier members of the main stem arose the groups of animals, resembling one another in the precocious conversion of the broad intertemporal region into a sagittal crest and in the acquirement of suborbital vacuities, which are usually included in the Therocephalia and belong to many independent stirps, each in all probability being dependent on the main Gorgonopsid stock. It is shown that there is a series of evolutionary trends which persist throughout the whole group of Anomodonts from *Varanosaurus* to *Diademodon*, and that the special rapid advances which separate the Therocephalia from the Gorgonopsids, in the main, merely follow out the predetermined evolutionary track proper to the group.

Thus any classification of the Theriodontia is necessarily complicated, as involved and difficult of construction as that of the *Theria* themselves. Existing material is so incomplete that any attempt at detailed classification, even if only into families, is dangerous, in that it will load the literature with undefined groups, whose characteristic forms may only be known from the front end of the skull or the dentition.

The detailed descriptions of skull-structures in this paper show how unreliable, even for generic distinction, are the characters presented by the teeth of Theriodonts.

Thus, for the present, I am inclined to retain my former division of Theriodontia into Gorgonopsidæ, Therocephalidæ, Cynognathidæ, and Bauromorpha, fully recognising that these groups—or, at any rate, the first two—cover a multitude of forms not directly of common origin and only held together by two or three striking characters.

It remains to discuss the connections of the Theriodontia with the other groups of South African Anomodonts—the Deinocephalia, Dromosauria, and Dicynodonts.

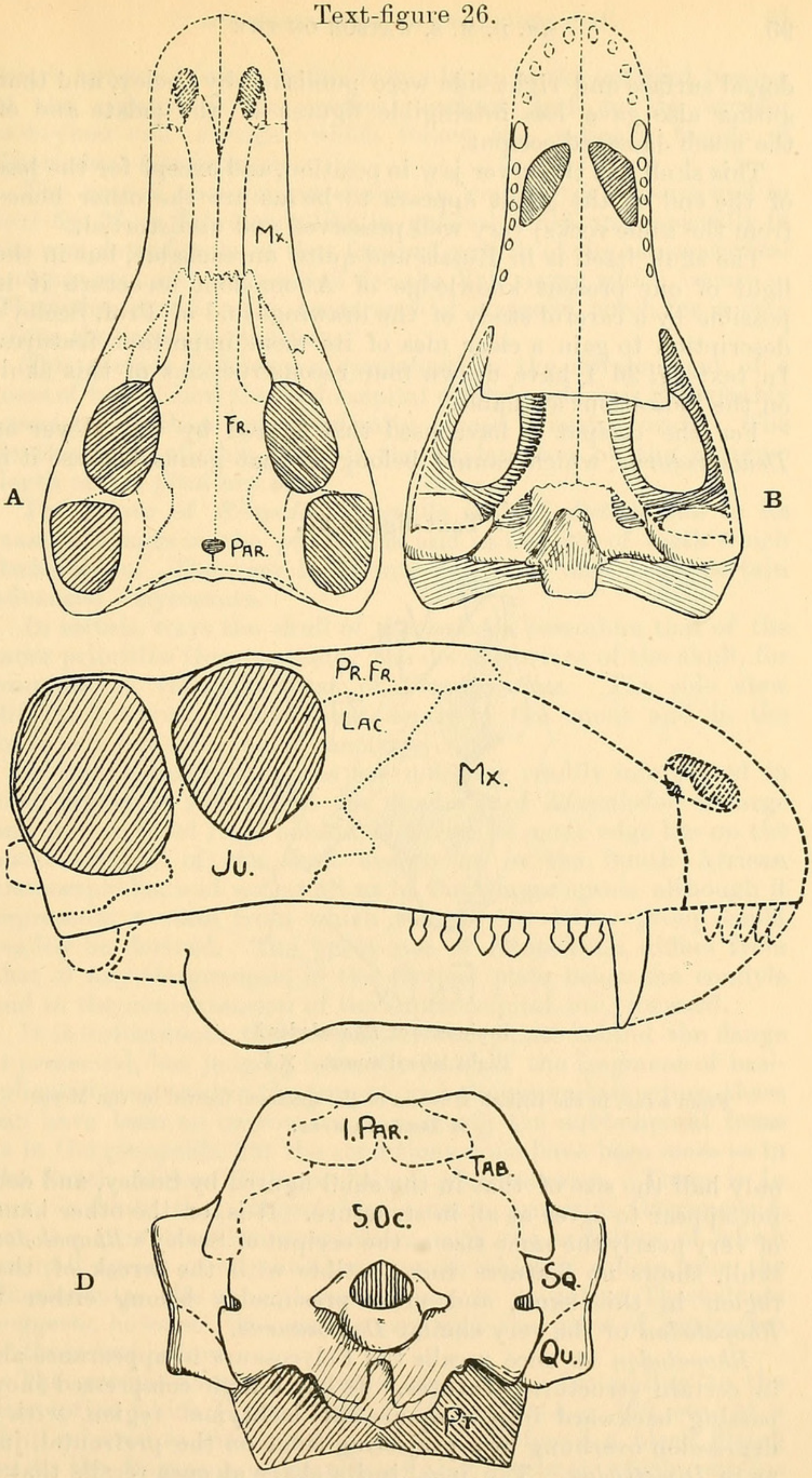
In the copper-bearing sandstones and associated limestones of the Ural Mountains, which immediately succeed the Artinsk beds and are shown by a comparison of reptile and amphibian faunas to be slightly older than the *Tapinocephalus*-zone, are found three types of Anomodonts, each represented by skulls or jaws: of these *Deuterosaurus* is clearly a Deinocephalian of the Tapinocephaloid group recalling many South African forms.

Deinosaurus (= *Cliorhizodon*) is represented by jaws, in one case associated with a palate whose dorsal surface is well exposed.

Rhopalodon is a name covering not only several jaw-fragments but also a complete skull, which was described by Prof. Seeley.

Of this skull, remarkably beautiful lithographic drawings of the

Text-figure 26.



Rhopalodon fischeri Kutorga.

Restoration of skull from the figures published by Seeley, Phil. Trans. B. 185, 1894. and the brain-case figured by von Meyer, 'Palæontographica.'
Parts in broken lines hypothetical, sutures in dotted line suggested by the original figures.

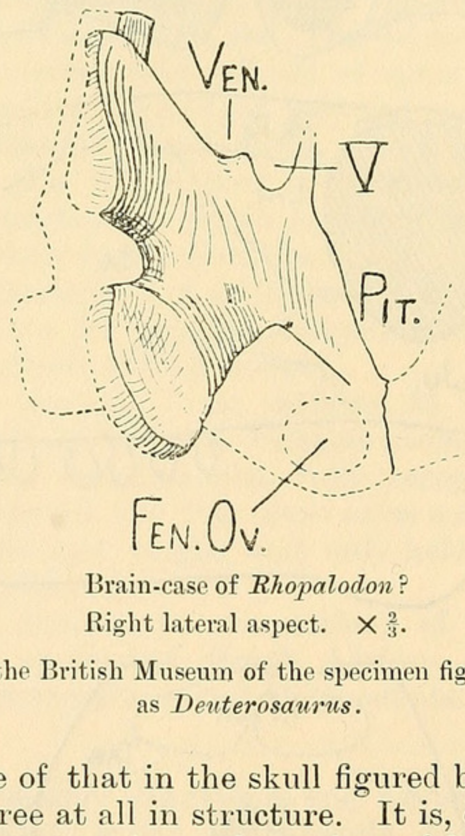
dorsal surface and right side were published by Seeley, and that author also gave less intelligible figures of the palate and of the much damaged occiput.

This skull has the lower jaw in position, and except for the loss of the end of the snout appears to be (as are the other bones from the same rocks) very well preserved and undistorted.

The skull itself is in Russia and quite unreachable, but in the light of our present knowledge of Anomodont structure it is possible by a careful study of the drawings and of Prof. Seeley's description to gain a clear idea of its more important features. In text-fig. 26 I have drawn four reconstructions of this skull on the indications available.

For the occiput I have used that figured by von Meyer as *Deuterosaurus*, which cannot belong to that genus because it is

Text-figure 27.



Brain-case of *Rhopalodon*?
Right lateral aspect. × $\frac{2}{3}$.

From a cast in the British Museum of the specimen figured by von Meyer as *Deuterosaurus*.

only half the size of that in the skull figured by Seeley, and does not appear to agree at all in structure. It is, on the other hand of very nearly the same size as the occiput of Seeley's *Rhopalodon*' skull, shows no features incompatible with the wreck of that region in this skull, and must presumably belong either to *Rhopalodon* or the very similar *Deinosaurus*.

Rhopalodon at once recalls the Pelycosaurs in appearance and in certain structural features. It has a high compressed snout passing backward into a square-cut lachrymal region, with a depression overhung by a projecting ridge on the prefrontal, just as in *Dimetrodon*. The jugal in its shape at once recalls that of the earlier genus. It differs from *Dimetrodon* in the much larger temporal fossæ, visible from above, in the outward bowing of the zygoma, in the vertical occiput, and in the smaller lachrymal—all changes which follow the ordinary trends of Theriodont development.

The neural cranium, as shown in von Meyer's figures and in text-fig. 27, is Pelycosaur-like in general build, and especially in the complete absence of that forward growth of the supraoccipital and pro-otic above the notch for the Vth nerve which occurs in Theriodonts, and in the occurrence of a special notch for a vein above the incisura prooticis.

This occiput is, however, specialised in the development of a mass of bone below the basioccipital condyle, which is presumably associated with a very vertically placed fenestra ovalis. The development of this plate is the explanation of the extreme depth of the pituitary fossa.

The palate of *Rhopalodon* recalls that of *Dimetrodon* in its massive flanges on the pterygoids and in the row of teeth which decks them. The very large internal nares also recall certain advanced Pelycosaurs.

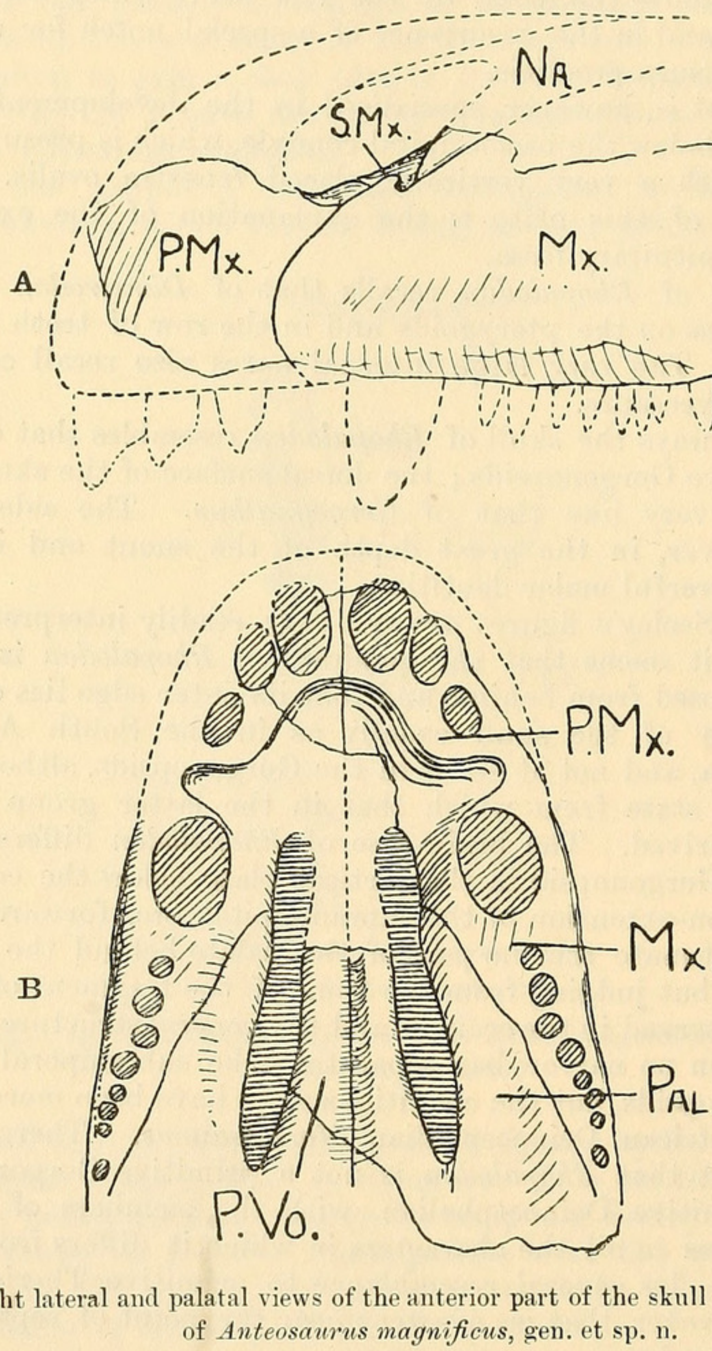
In certain ways the skull of *Rhopalodon* resembles that of the more primitive Gorgonopsids ; the dorsal surface of the skull, for example, is very like that of *Gorgognathus*. The side view differs, however, in the great depth of the snout and in the relatively powerful molar dentition.

Although Seeley's figures are not very readily interpreted in that region, it seems that the quadrate of *Rhopalodon* is large and well exposed from behind, and that its outer edge lies on the outer surface of the skull exactly as in the South African Deinocephalia, and not at all as in the Gorgonopsids, although it represents a state from which that in the latter group could readily be derived. The brain-case of *Rhopalodon* differs from that of any Gorgonopsid in the vertical plate below the condyle and in the non-extension of the supraoccipital, etc., forward.

It is unfortunate that no part of the palate behind the flange is preserved, but judging from the front of the fragment of basisphenoid preserved in the occiput, and the general structure, there can have been no narrow bar separating the subtemporal fossæ as in Gorgonopsids, but the conditions must have been more as in the South African Deinocephalian *Mormosaurus*. There is, in fact, no doubt that *Rhopalodon* is not a primitive Gorgonopsid, but is a primitive Deinocephalian, with the members of which group it agrees in all the characters in which it differs from the Theriodonts. Its general resemblance to primitive Theriodonts suggests, however, that we are very near the point of separation of these two orders.

The present seems a suitable opportunity for adding to the description which I gave (Proc. Zool. Soc. 1914, p. 770, etc.) of a skull referred to *Titanosuchus*. I recently found a block fitting on to the fragment of maxilla of that specimen which contains the anterior end of the maxilla, parts of the premaxillæ, septomaxilla, etc. This addition shows that there are only three premaxillary teeth, that the end of the snout is longer than in the original figure, and that it is rounded. Thus the skull belongs to a new genus and may be called *Anteosaurus magnificus*, gen. et sp. nov., holotype R. 3595, B.M.N.H.

Text-figure 28.



Right lateral and palatal views of the anterior part of the skull of the holotype of *Anteosaurus magnificus*, gen. et sp. n.

Parts in broken lines restored, areas surrounded by thin irregular lines present in the specimen. × $\frac{1}{3}$.

The general structure will be best understood from text-fig. 28. The septomaxilla is a small bone lying within the nostril, to which it forms a floor, passing inward nearly to the middle line.

It articulates with the nasal posteriorly, with the maxilla in the middle, there being apparently no septomaxillary foramen, and with the premaxilla in front.

The palatine extends forward to the middle of the canine tooth, forming the greater part of the outer wall of the long narrow posterior nares; at the hinder end of the opening it has a suture with the prevomer, which appears to form the whole inner border of the nostril.

The prevomers are unfused, each provided with a high, thin dorsal ridge, similar flanges from the pterygoids passing between and separating those of the prevomers.

The whole structure is like that of the Tapinocephaloid *Mormosaurus*, and especially like that of the detached nose which seems to belong to *Lamiasaurus*.

The structure of these palates raises doubts as to the formation of the internarial bar in Gorgonopsids by the fusion of a pair of prevomers, because in the Deinocephalia the pterygoids separate the posterior ends of the prevomers, whilst in Gorgonopsids they clasp the outer sides of the posterior ends of the internarial bar. The difficulty is not, however, an insuperable one.

The relation of the Dicynodonts to other Anomodonts is a subject on which there has been much difference of opinion, but which can be more satisfactorily discussed now that many details of Gorgonopsid structure are known.

The characteristic features of all Dicynodonts are:—

1. The occipital condyle is triple, the exoccipitals forming its upper parts.
2. The supraoccipital is only slightly drawn forward to form side-walls to the brain-case.
3. The fenestra ovalis lies at the end of a long tube communicating with the vestibule.
4. The temporal fossæ are very large.
5. The face is short.
6. The premaxillæ are edentulous and the maxilla is carried out laterally to the molar teeth, if any be present, and its margin is a sharp ridge covered by a horny sheath.
7. There is a rudimentary secondary palate.
8. The prevomers are fused, forming a roof to the depressed median part of the palate.
9. There are no definite pterygoid flanges.
10. There is an interpterygoid vacuity reaching back to the basipterygoid process and forward to the prevomer.
11. Both quadrate and quadrato-jugal form the articular condyle for the lower jaw.
12. The squamosal is of characteristic shape with a wide flat zygomatic part rising from the upper part of a flat body, the lower part of whose front face is covered by the quadrate and quadrato-jugal.
13. The dentaries are fused and extremely massive.

When the structure of the skull of a Gorgonopsid was discovered, Broom and I independently pointed out the many resemblances which it presented to Dicynodonts in the intertemporal, basicranial, and other regions.

These resemblances are real, but, with the exception (?) of the occurrence of a preparietal, lie entirely in the common possession of primitive Anomodont characters, such as the broad parietal surface and the main features of the basis cranii. When considered in more detail, the structure of such a Dicynodont as *Endothiodon* seems to show no such resemblance to that of a Gorgonopsid as to imply any closer connection between the two groups than either of them bears to the Deinocephalia or Dromosauria. The secondary palate of *Endothiodon* is different in type from that of *Diademodon* and all the forms of Gorgonopsids leading up to it. In them, as in mammals, the original vaulting of the palate is brought about by a downgrowth of the tooth-bearing edge of the maxilla below that of the premaxilla; the internarial bar remains attached to the ends of the palatal processes of the premaxillæ, and when the secondary plates of the maxillæ grow out they lie ventral to the palatal parts of the premaxillæ. In fact, the original surface of the palate lies on the roof of the naso-pharyngneal duct, the sides of the palate growing down below it.

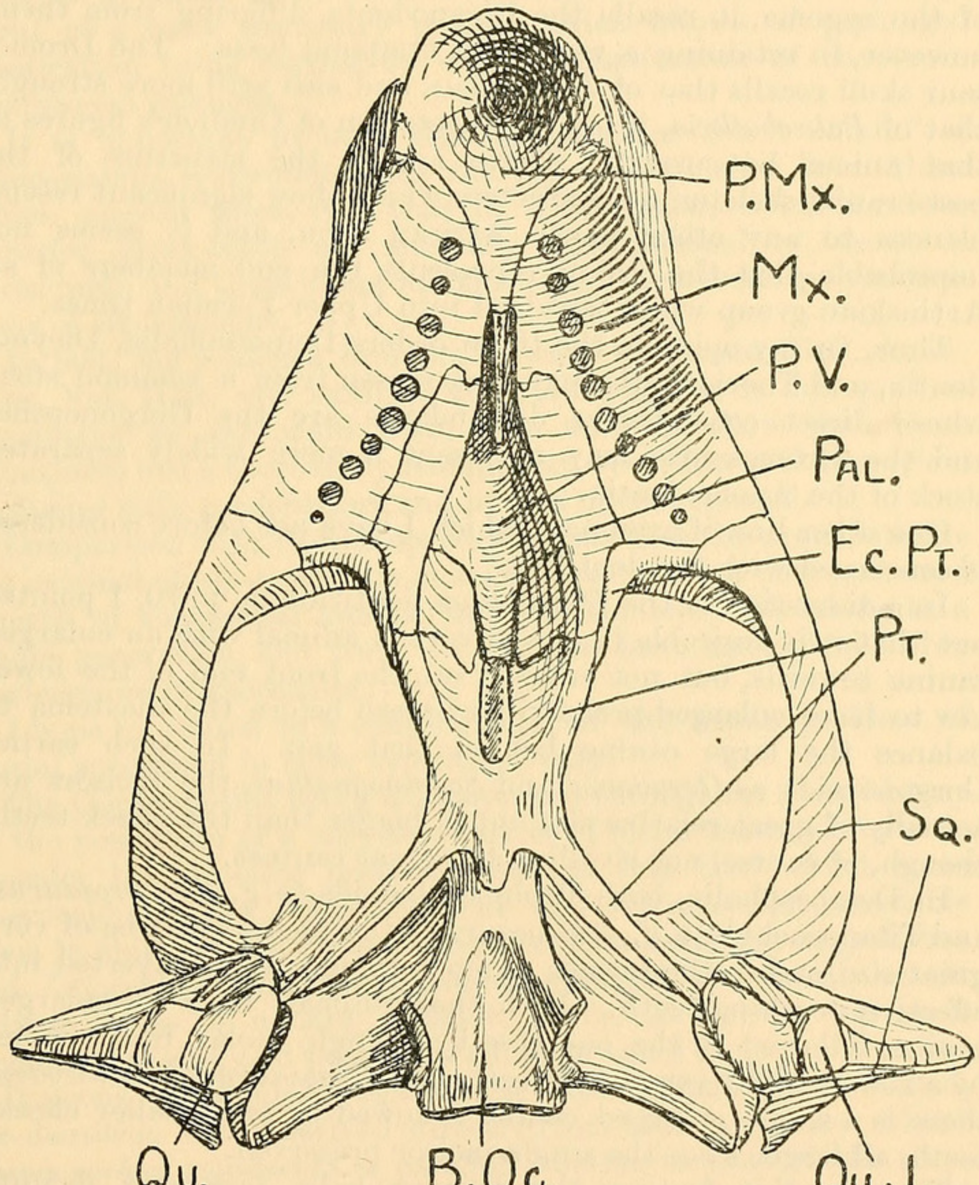
In *Endothiodon* (text-fig. 29), on the other hand, the palatal surface of the premaxillæ lie in the same plane as that of the maxillæ and transverse bones, the posterior nares open into a deep groove, excavated in the original palate, which is roofed by a great forward growth of the prevomers over the region formerly occupied by the large posterior nares.

Thus it appears that the palate of Dicynodonts does not present a real resemblance to that of Gorgonopsids, but represents a different mode of development of a secondary palate, identical with that of a Chelonian. One of the most striking features of the Dicynodont palate is the loss of the pterygoid flanges, which are only represented by slight eminences on the edge of the narrow posterior part of the palate over the pterygo-transverse suture. This loss seems to be due to the very great expansion of the temporal muscles squeezing them out of existence, their presence not being necessary to insure accurate closure of the mouth in an animal without a closely-fitting dentition—in some cases their function being taken over by the long canines, which often present wear-faults on their inner sides in large Dicynodonts.

When allowance is made for the changes resulting from the development of the horny covering of the edges of the jaws and the extension of the crushing palate, it is readily seen that the main plan of the anterior part of the *Endothiodon* palate is reducible to that found in Therocephalia, except for the absence of suborbital fenestræ.

Posteriorly, however, there is in Dicynodonts no trace of the long narrow girder which in the Theriodonts extends from the basipterygoid processes to the flanges of the pterygoids, and it is therefore probable that the Dicynodonts separated from the Theriodonts before the establishment of this feature—that is, at about the same time as the Deinocephalia. At the same time, in

Text-figure 29.



Palate of *Endothiodon* ? *microps* Broom.

Drawn from R. 4044, B.M.N.H.; the quadrates, quadrato-jugals and jugals, and quadrate rami of the pterygoids, from other material.

the Dicynodonts as in the Deinocephalia and all other S. African Anomodontia in which the facts are known, the descending flanges of the pterygoids lie well in advance of the basipterygoid processes, a position which is markedly different from that found in all non-mammal-like reptiles, but which has arisen within the group, as it does not occur in *Varanosaurus*.

The relation of the Theriodontia to the Dromosauria is obscure, because of our very slight knowledge of the detailed skull-structure of the members of that group. In general build the Dromosaur skull differs from that of the Theriodonts and also of the Pelycosaurs in the extreme shortness of the face. In this feature, and also in the depth of the squamosal below the root of the zygoma, it recalls the Dicynodonts, differing from them, however, in retaining a very short temporal fossa. The Dromosaur skull recalls that of *Bolosaurus*, and also still more strongly that of *Palæobathria*, if my interpretation of Credner's figures of that animal be correct. There are in the structure of the post-cranial skeleton no characters which show significant resemblances to any other South African form, and it seems not improbable that the group represents the end members of an Artinskian group which survived into Upper Permian times.

Thus, in my opinion, the three orders Deinocephalia, Dicynodontia, and Theriodontia may have arisen from a common stock whose direct conservative descendants are the Gorgonopsids, and the Dromosauria may represent a more widely separated stock of the Anomodontia.

One other line of argument which I have not before considered is concerned with the dentition.

In a discussion of the *Dimetrodon* dentition on p. 70, I pointed out that it is desirable in a carnivorous animal with an enlarged canine towards, but not actually on, the front end of the lower jaw to have enlarged premaxillary teeth before the diastema to balance the large canine behind that gap. In such earlier Gorgonopsids as *Gorgonops* and *Scymnognathus*, the incisors are actually of great relative size, much bigger than the cheek-teeth, though, of course, not rivalling the great canines.

In Deinocephalia, both Tapinocephaloids (e.g., *Deuterosaurus*) and Titanosuchids (e.g., *Anteosaurus*), the incisors may be of very great size, and in the former group very curiously converted into effective crushing-teeth. Both these animals have an enlarged canine, followed in the one case by a single molar, in the other by a row of eight very small teeth; in *Deinosaurus* (*Cliorhizodon*) there is a single enlarged canine followed by ten smaller cheek-teeth, all larger than the single incisor preserved.

Thus in this feature the Deinocephalia present a definite resemblance to the Gorgonopsids, one which is shared also by *Dimetrodon*.

In later Gorgonopsids, as I have shown above, the incisors become relatively smaller, and the " molars," although not increased in number above the original five, become relatively larger.

There is some evidence of an irregular replacement of all the teeth of a Gorgonopsid.

When the Cynodontia are reached we find a still further decrease in the relative importance of the incisors, together with an increase in the number of cheek-teeth in *Cynosuchus* to 8, all still much smaller than the incisors, in *Nythosaurus* to 8, all larger than the incisors, *Galesaurus* ? 10, *Cynognathus* 9, *Diademodon* ? 12, *Trirachodon* 9. This sudden increase in the number of cheek-teeth seems to be associated with the development of a bony secondary palate, which allows of prolonged mastication being carried on without obstruction of the naso-pharyngeal passages.

It is important to note that the anterior five "molars" of *Cynognathus crateronotus* are sharply distinguished from those which succeed them, and that in *Diademodon*, when the four anterior cheek-teeth are similarly distinguished by structure, these teeth and these alone amongst the cheek-teeth give indications of replacement.

In fact, the evidence brought forward by Broom (Bull. Amer. Mus. Nat. Hist. vol. xxxii. p. 465), although it is not quite so conclusive as one could wish, does tend to show that these Cynodonts had a thoroughly mammalian dentition with premolars replacing milk-predecessors and molars never replaced.

Comparison with Gorgonopsids suggests that the premolars are the original cheek-teeth, the molars representing a new backward growth of the dental lamina, in which the teeth all belong to a single generation, and from their origin have never had either predecessors or successors.

I hope to return to a consideration of the whole problem of dental succession in early reptiles shortly.

The Gorgonopsids being characterized throughout their history by the possession of a very short series of molar teeth, we have to consider the problem presented by the fact that whilst some Therocephalia, e.g., *Scymnosaurus* and *Hyænosuchus*, resemble them in this feature, others, *Alopecodon* etc. amongst large forms and *Icticephalus* and *Scaloposaurus* amongst the small, retain a large series of molars, without, so far as known, having a secondary palate, and possess in addition small incisors.

It seems reasonable to regard these latter animals as unmodified, the dentition being derived directly from their ancestors, whilst *Hyænosuchus* represents a parallel reaction to that of the Gorgonopsids to similar feeding habits. All detailed discussion of the dentitions of Theriodontia are rendered nugatory by our complete absence of knowledge of the postcranial skeleton, for only by a study of the whole structure is it possible seriously to consider the habits and adaptations of an animal, and teeth react perhaps more quickly than any other structures to external impressions.

In any case the occurrence of these Therocephalians with a long tooth-row and small incisors, and of a similar structure in *Cliorhizodon*, shows that the heavy incisors of Gorgonopsids and Deinocephalia have been independently acquired by these two groups.

The study of Theriodont structure and evolution, which is the content of this paper, thus leaves us still without any satisfactory classification of that group, but in its establishment of a series of evolutionary trends, which persist throughout the history of the Anomodontia, has I hope laid a solid foundation on which a natural arrangement may in future be built up when increased knowledge allows an examination of the "adaptive radiation" of the order to be entered on. Meanwhile, the forms whose skulls are well known fill in with considerable completeness the great morphological gap which exists between the Lower Permian Pelycosauria and the Lower and Middle Triassic Cynodonts, and in this way enable us to understand the material steps in the evolution of almost all the structures of a Cynodont skull from those in so primitive a reptile as *Seymouria* or, indeed, in the still more primitive Embolomerous amphibia. Dealing as it does with many diverse faces of the subject with which it is concerned, this paper does not lend itself to summarisation, but the point of widest interest brought out in it is undoubtedly the demonstration of the occurrence of the same evolutionary trends in so many allied branches in the Pelycosaurs, Gorgonopsids, Therocephalia, and Deinocephalia; and the fact that the changes brought about in accordance with these trends often serve an adaptive purpose and appear to depend on mere mechanical necessities.

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