Some Features of the Cranial Morphology of the Tapinocephalid Deinocephalians

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BULLETIN

OF

THE AMERICAN MUSEUM OF NATURAL HISTORY

VOL. LXXII, ART. II, pp. 75–98

New York

Issued August 21, 1936

Article II.—ON SOME FEATURES OF THE CRANIAL MORPHOLOGY OF THE TAPINOCEPHALID DEINOCEPHALIANS

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Plates V to VIII; Text Figures 1 to 11

In the collection of The American Museum of Natural History there are a number of skulls of the tapinocephalid deinocephalians, all of which have been purchased from Dr. R. Broom during the period 1913–1935. These skulls have been described by both Broom and Gregory and my only excuse for presenting these new descriptions is that further preparation has exposed quite a number of additional features, whose study adds appreciably to our knowledge of the cranial structure.

Moschops capensis Broom

Plates V and VIA; Figures 1 to 3

Broom, R., 1911, P. Z. S., p. 1073.

Gregory, W. K., 1926, Bull. Amer. Mus. Nat. Hist., LVI, p. 179.

Broom, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 43.

Type.—Amer. Mus. No. 5550. Spitzkop, Moordenaar's Karroo, *Tapinocephalus* zone.

In 1911, Broom described the type skull. Only the external features of the skull and the lower jaw were described and in one illustration the right side is figured.

In 1926, Gregory published a full account of all the *Moschops* material in The American Museum of Natural History. This account is mainly devoted to the postcranial skeleton, although the known cranial material of the tapinocephalids was compared in detail. Unfortunately, Gregory only figured the lateral view of the skull and the anterior part of the palate. After considerable labor I have exposed many features of the dorsal, palatal and occipital surfaces and also the outer surface of the brain-case and I believe that a description with accompanying figures of these features of the skull of *Moschops* will supplement the accounts of Broom and Gregory and facilitate comparisons with other cranial material of the deinocephalians.

The dorsal surface (Pl. V and Fig. 1) shows the main joints of structure in a topotype skull, No. 5552, and Fig. 1 is based mainly on it, but also includes features determined in the type, No. 5550, and in another topotype, No. 5553.

The premaxillaries form the internasal bar and are then continued

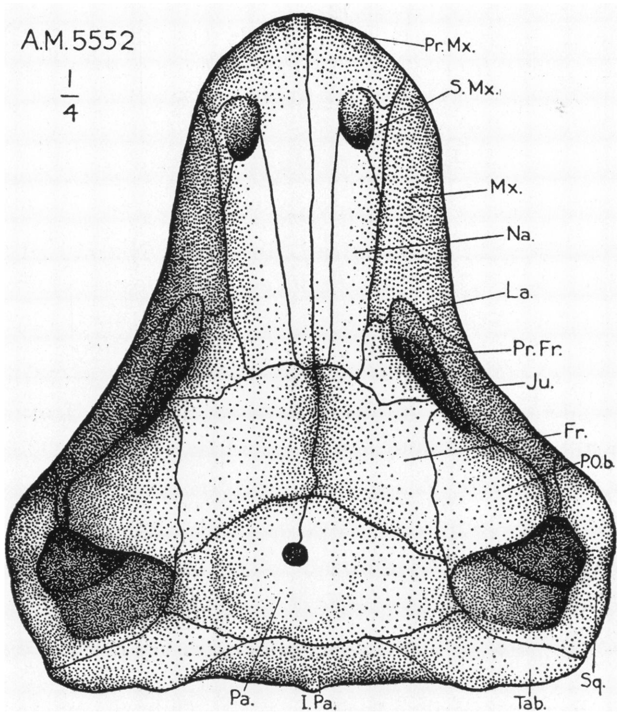

Fig. 1. *Moschops capensis.* Dorsal view, based mainly on the topotype, Amer. Mus. No. 5552, but including some features determined in the type, Amer. Mus. No. 5550 and another topotype, Amer. Mus. No. 5553. $\times 1/4$.

in posterior direction for a very great distance and finally end as an intercalation between the prefrontals and meet the frontals. This elongation of the premaxillaries is common to all the deinocephalians, but it varies considerably in degree. The maxillaries are not deep, and due to the general shortening of the snout, the maxilla is comparatively short.

The nasals do not meet each other in the median line owing to the intercalation of the premaxillaries.

The septomaxillaries have a small facial exposure, although the part within the nostril is extensive, forming a floor to the nostril. I cannot locate a septomaxillary foramen as Watson found in *Mormosaurus* and *Lamiasaurus*. The prefrontal is a medium-sized element forming the antero-dorsal part of the orbital border. The bones anterior to the prefrontal are not greatly thickened but all the dorsal bones posterior to it are greatly thickened. As Broom and Gregory have pointed out the bone-thickening is in part dependent on age and sex.

The lacrymal, although not of great antero-posterior length, is a large bone, which forms the whole anterior border of the orbit and passing ventrad to the prefrontal forms a large part of the inner surface of the upper orbital border. I have not located any lacrymal foramen. The greater antero-posterior length of the lacrymal in *Mormosaurus* (Watson) and particularly in *Moschosaurus* (Haughton) indicates that in this character these two forms are more primitive than *Moschops*.

The frontal is a large, greatly thickened element; it has a very narrow lateral tongue, which just enters the supraorbital border; anteriorly, the premaxillaries reach the edge of the frontals.

I have not been able to determine the presence of a distinct postfrontal, although this element has been recorded as present in a number of the deinocephalians, viz., *Moschosaurus* (Watson), *Keratocephalus* (Huene), *Jonkeria, Delphinognathus* and *Tapinocephalus* (Broom).

The postorbital is a massive element, which forms the whole postorbital bar, but extends posteriorly for only a very short distance along the lateral face of the parietal; ventrally, it has a squamous suture with the jugal.

The parietals together form the thickest part of the cranial roof; where they are perforated by the pineal foramen they form a raised mound of bony tissue; curving round the temporal opening the parietal is firmly wedged in between the postorbital, squamosal and tabular. In the type the pineal foramen is much longer than in the two topotype skulls; this is probably due to the lesser degree of bone-thickening in the type.

The interparietal forms the posterior edge of the dorsal surface and is supported from below by the supraoccipitals.

The tabular is a large bone forming the postero-lateral corner of the dorsal surface; it has a large face on the occipital surface and supports the posttemporal squamosal bar; its mesial border is clasped by the interparietal.

The squamosal forms the infratemporal bar and then rises up in the skull to form the posterior border of the temporal fossa and meets the parietal; laterally, the squamosal overlies the jugal and sends flanges ventrally to clasp the quadrate along its lateral and posterior face; posteriorly, the squamosal carries an everted scroll-like flange, which forms the mesial face of the auditory groove; this part of the squamosal is supported by the strong paroccipital.

The quadratojugal is a medium-sized elongated bone, which, laterally, supports the quadrate.

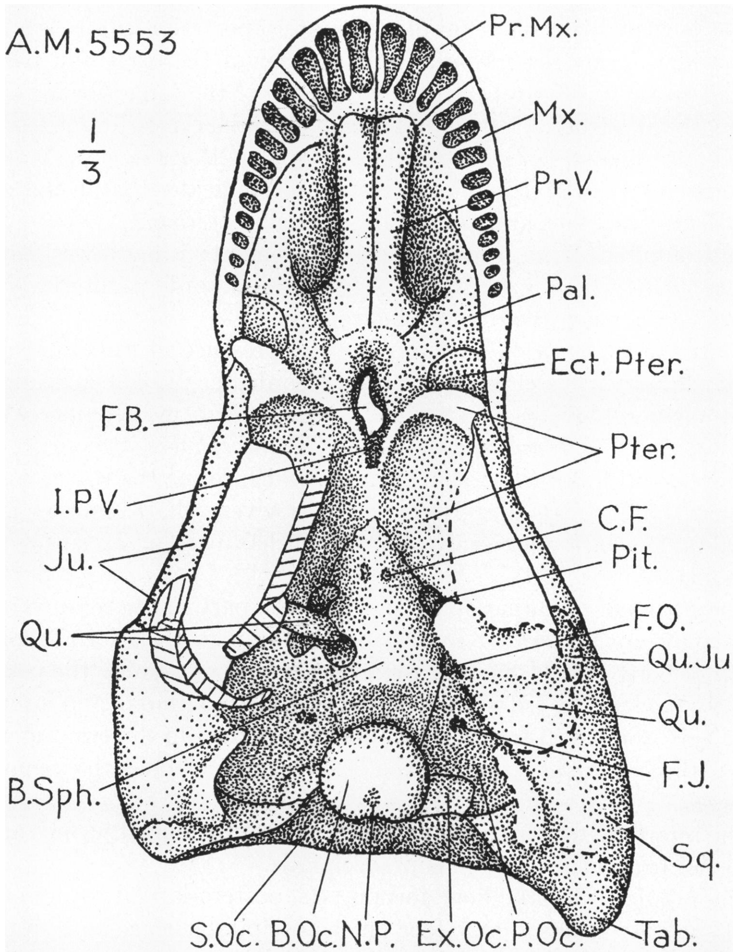

Fig. 2. *Moschops capensis*. Amer. Mus. No. 5553. Ventral view. The distortion is not corrected. The left quadrate and quadratojugal is drawn from the type, Amer. Mus. No. 5550. On the right these structures are seen in section.

F.B., foreign bone wedged in the interpterygoid vacuity. $\times ^1/_3$.

The jugal is small and forms the whole infraorbital bar.

The palatal surface has been exposed in the topotype, No. 5553. This skull has suffered from postmortem distortion and in Fig. 2 the palatal structure is shown, without correction of the distortion.

The prevomers form a stout interchoanal bar; anteriorly they underlie the posterior edges of the premaxillaries and, posteriorly, underlie the palatines; the prevomers resemble those of the cotylosaurus and pelycosaurus and approach the therocephalian condition, but differ from the gorgonopsian in the widened posterior end.

The palatines are short antero-posteriorly; they overlie the posterior ends of the prevomers and curve round the choanae to meet the maxillaries in a long suture; posteriorly, they meet the ectopterygoids and are here pierced by a small foramen; in the median line the palatines apparently form the anterior part of a heart-shaped thickening, but here the sutures between the palatines and the pterygoids cannot be traced. This thickening on the palatines and pterygoids resembles the dentigerous ridges present in all the known gorgonopsians; here, however, there is no evidence of teeth.

Postero-lateral to the palatines lies a small ectopterygoid, which descends along the anterior face of the lateral pterygoid ramus.

There is no large suborbital vacuity between the palatines, ectopterygoids and pterygoids as in the pelycosaurs and therocephalians.

The pterygoid is a bone of complex shape, but is fundamentally triradiate with an anterior, a lateral and a quadrate ramus; ventrally, the anterior ramus carries a short median ridge and, a little lateral to these, two ridges continue on to the thickening, whose anterior part has been mentioned as being apparently formed by the palatines; dorsally, the anterior ramus has a very high keel, which applied to its fellow forms the median septum in the facial part of the skull; I have not been able to determine whether this septum continues dorsally of the prevomers (Watson, 1914) or whether it is here confluent with a prevomerine septum. The lateral ramus forms a deep ridge across the palate; anteriorly, it is supported by the ectopterygoid and posteriorly, a ridge from it curves inwards and then sweeps backwards and outwards as the guadrate ramus; on the right side in No. 5552, a flat piece of bone applied to the dorso-lateral surface of the pterygoid is probably a remnant of the epipterygoid. Due to the anterior position of the quadrate the quadrate ramus is short; it passes on to the anterior face of the quadrate (in *Mormosaurus* Watson stated that it passes on to the posterior surface of the quadrate). In the median line the pterygoids underlie the anterior end of the basisphenoid and (parasphenoid ?) and, forming the anterior border of the pituitary fossa, curve outward and continue posteriorly as the quadrate ramus.

The basisphenoid is not shown very well; there are low basipterygoid processes or tubera; in the middle line it carries a keel (parasphenoid ?); anteriorly, on either side of this keel there are two slit-like foramina (carotid foramina); laterally, the edge of the basisphenoid is scooped out and then widens to form the anterior edge of the *fenestra ovalis;* an anterior notch leads into the pituitary fossa; on the dorsal surface there are vertical sheets of the parasphenoid anterior to the pituitary fossa, which continue upwards to meet the sphenethmoid.

The basioccipital forms the large rounded condyle; the posterior surface of the condyle is pierced by a deep V-shaped notochordal pit

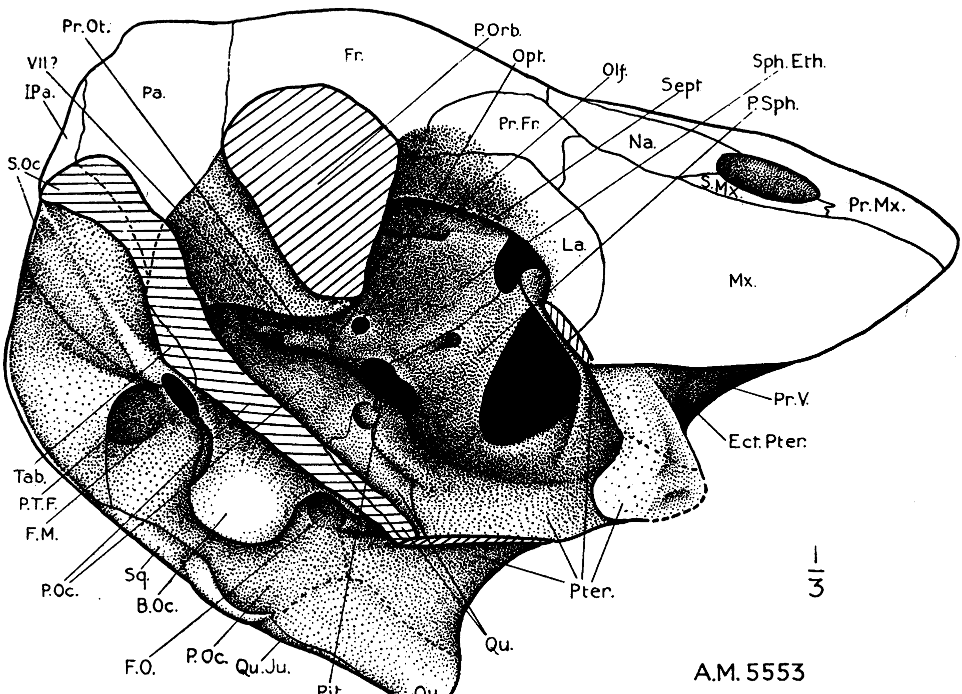

Fig. 3. *Moschops capensis.* Amer. Mus. No. 5553. Lateral view of the skull with the postorbital, infraorbital and infratemporal arches and part of the occipital plate removed to show the outer surface of the brain-case from the right side. $\times 1/3$.

and its dorsal surface is grooved for the reception of the medulla; anterior to the condyle the basioccipital has a narrow vertical face, which descends to meet the basisphenoid; the limits of the interparietal and supraoccipital are not distinctly shown; together they form the greater part of the occipital plate; a median ridge separates two large areas for muscular insertion.

The quadrate is a large element with its condyles placed well forward in the skull; laterally, it is flanked by the quadratojugal and squamosal and, anteriorly, a process from the quadrate is applied to the quadrate ramus of the pterygoid; the quadrate ascends very high in the skull (cf. cotylosaurs and pelycosaurs), where it finally merges into the anterior face of the paroccipital; the condyle is bipartite.

In the topotype, No. 5553, the brain-case has been exposed on the right side (Fig. 3). Due to the shape of the skull the posterior part of the side-wall formed by the proötic is compressed so that it is very difficult to determine the position of the various nerve foramina, which pierce the proötic. A small foramen under the postorbital bar may be that of the seventh cranial nerve.

Anterior to the lateral opening leading into the pituitary fossa there rises a vertical sheet of bone, which rests on the basisphenoid and pterygoid; this is the parasphenoid, which has the same relations as in the anomodonts and gorgonopsians; dorsally, the parasphenoidal edge bifurcates and carries the sphenethmoid. The sphenethmoid presents a large lateral surface; in its posterior part it is pierced by a large rounded foramen; this has the same relations as the foramen in the gorgonopsian, *Arctognathus*, identified as the foramen for the opthalmic branch of the fifth cranial nerve; dorsally, the sphenethmoid meets the median septum sent down by the frontals; between the median septum and the postero-dorsal edge of the sphenethmoid there is a groove, which opens anteriorly and is posteriorly connected with the fore-brain; this groove housed the olfactory lobe.

Anteriorly to the sphenethmoid and parasphenoid the median septum is unossified in parts and there are thus large fenestrae; anterior to these fenestrae the median septum is formed by the dorsal keel on the anterior ramus of the pterygoid.

Taurocephalus lerouxi Broom

PLATES VIB, VII, AND VIIIA; FIGURES 4 TO 7

BROOM, R., 1928, Ann. S. Afr. Mus., p. 436.

BROOM, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 41.

TYPE.—Amer. Mus. No. 5655. Abraham's Kraal, Prince Albert district, *Tapinocephalus* zone.

This specimen was first described by Broom in 1928 when he figured the dorsal and lateral surface. When I first saw the skull it had not been prepared—the dorsal, lateral and most of the occipital surfaces were fairly well exposed through natural weathering. On both sides the frontal-postorbital-postfrontal region was weathered away so that the greater part of the thick bone in these regions is missing—the contours surrounding this weathered region and the fact that on the median line some surface is preserved makes a reconstruction of the missing surface fairly certain.

The extreme tip of the snout and the anterior third of both dentaries are missing. I have thoroughly cleared all the dorsal and lateral surfaces and have determined the limits of all the bones except in the weathered supra-orbital region where the sutures are seen in section, but their position on the surface is of course not quite certain. The occiput was completely freed of matrix and I was successful in exposing the whole palate.

In general appearance and the proportions of the various structures *Taurocephalus* shows many points of similarity to the herbivorous forms, *Struthiocephalus*, *Mormosaurus* and *Tapinocephalus*. The thickening of the bones in the posterior half of the dorsal surface is, however, less than in *Mormosaurus* and *Tapinocephalus* and approaches the condition shown in the largest of the topotype skulls of *Moschops*. The snout is, however, much longer and the quadrate and occipital plate are not bent so far in anterior direction as in *Moschops*. The remaining form which *Taurocephalus* resembles most closely is thus *Struthiocephalus* but in this form the snout is relatively much longer and shallower.

In dorsal view (Fig. 4, Pl. VIB) it is seen that the skull is twice as long as wide; the part of the skull posterior to the orbits is one-third of the total length and appears very square; the muzzle forms two-thirds of the length, but, although long appears less so because of its width; but as its dorsal surface is rounded the muzzle is less massive than its outline conveys. The temporal fossa is large; in dorsal view the orbits are largely obscured by the overhanging thickened edges of the prefrontal, frontal (+ postfrontal) and postorbital; latero-dorsally, there is a large though shallow preorbital depression; the premaxillaries stretch posteriorly to the plane of the orbits; the nostrils have a peculiar posterior subdivision; the septomaxilla has a large and long facial exposure; I have not been able to locate the limits of the postfrontal; the parietal is small and dorsally it meets the squamosal, although it is possible that the postorbital reaches the squamosal at a lower level; the interparietal has a great part of its surface exposed on the dorsal surfaces; the lacrymal is large but does not extend far anteriorly.

In lateral view (Fig. 5, Pl. VIIA) the shallowness of the snout, the overhang of the postorbital and frontal over the orbit, the thickening

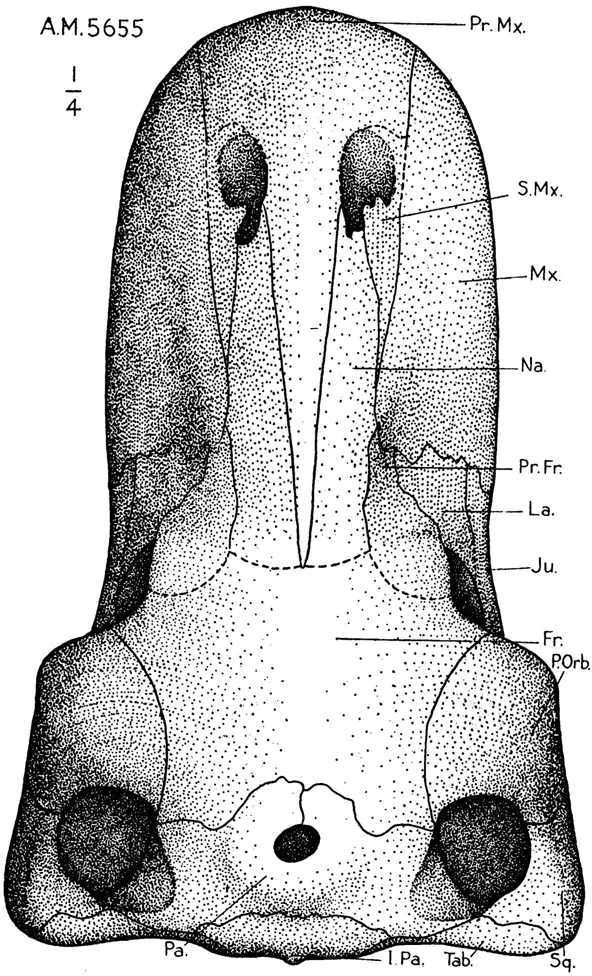

Fig. 4. *Taurocephalus lerouxi*. Type, Amer. Mus. No. 5655. Dorsal view. Drawn so that features on the one side supplement what is determined on the other. $\times^1/_4$.

in the frontal and parietal regions and the antero-posteriorly compressed temporal opening are well seen. The lacrymal does not extend much anteriorly; the quadratojugal has a small outer exposure; the postorbital forms a greatly thickened postorbital bar, which reduces the size of the temporal opening; the septomaxilla has a long narrow facial exposure; the nostril has a peculiar posterior slit-like prolongation.

The occiput (Fig. 6, Pl. VIIIA) is nearly circular in outline; in proportion to the massiveness and size of the skull it is small, having no greatly developed lateral flanges. The greater part is formed by the large supraoccipital, which is roughly rectangular in shape and has a thick swollen median ridge in its dorsal part which is confluent with the swollen mass of bone formed by the interparietal. The interparietal has more than half of its surface exposed on the occipital surface.

The tabular is a thick sheet of bone applied to the squamosal—

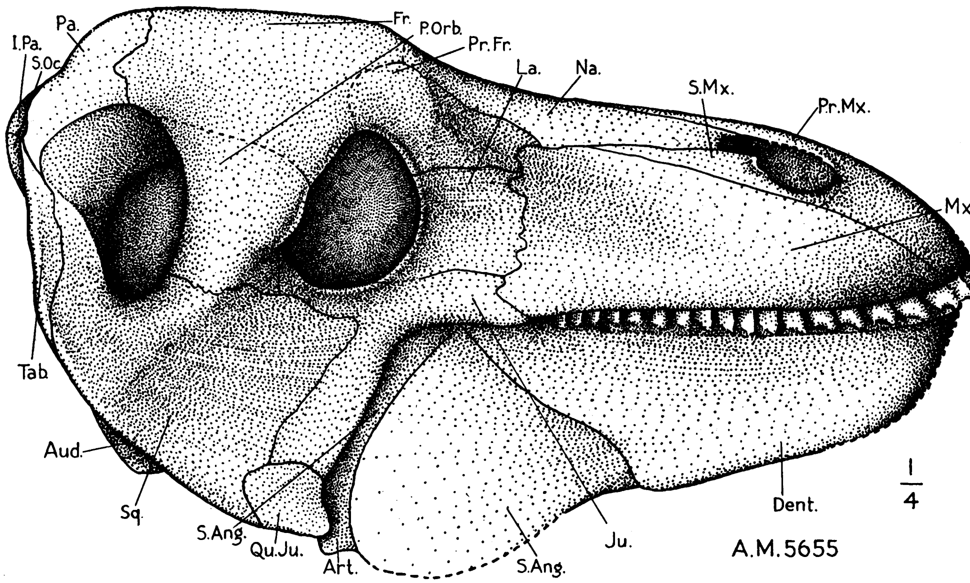

Fig. 5. *Taurocephalus lerouxi*. Type, Amer. Mus. No. 5655. Lateral view. Some features of the left side are incorporated. The crowns of the teeth are reconstructed. $\times 1/4$.

in effect it strengthens that part of the squamosal which forms the posterior bar of the temporal fossa.

Only a small part of the squamosal curves round on to the occipital surface; lateral to the small posttemporal fossa the squamosal carries a high curved ridge which forms the inner border of the auditory groove; this is mesially supported by the paroccipital.

The basioccipital condyle is only partly preserved—it is a massive knob of bone to which, dorso-laterally, the exoccipital is firmly fused.

Stretching laterally, the exoccipital extends as a tongue of bone applied to the posterior surface of the supraoccipital.

The paroccipital forms a massive bar, which laterally, abuts against the auditory ridge on the squamosal and latero-ventrally, overlaps on the posterior quadrate surface; medially, the paroccipital meets the exoccipital, basioccipital and basisphenoid; here it is pierced by the *foramen jugulare;* medio-anteriorly, the paroccipital forms part of the rim of the *fenestra ovalis* and forms the posterior border of the fossa which dorsally leads into the pituitary fossa from the side.

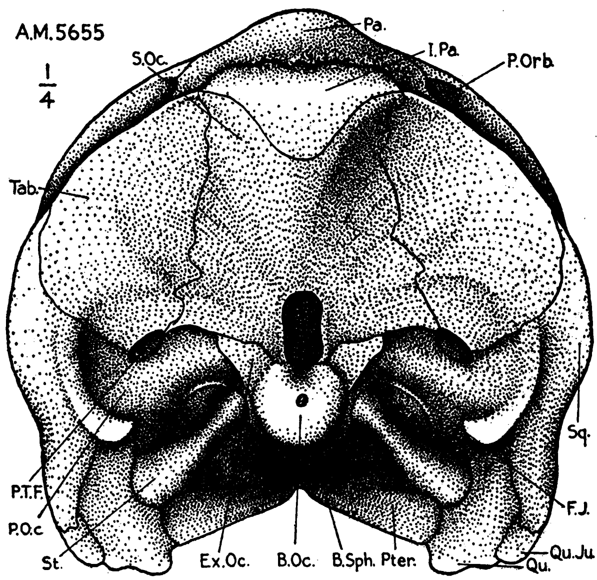

Fig. 6. *Taurocephalus lerouxi.* Type, Amer. Mus. No. 5655. Occipital view. The figure has been drawn symmetrical by supplementing features on one side with others determined on the other side. $\times 1/4$.

The quadrate has a large occipital exposure; from the condyle it stretches dorsally to the plane of the auditory groove, where it is overlapped by the paroccipital and squamosal which extend nearly to the plane of the condyle. The quadratojugal is a small element flanking the quadrate, ventral to the tip of the squamosal. The quadrate ramus of the pterygoid meets the quadrate; a process of the quadrate extends a short distance anteriorly and lies lateral to the quadrate ramus of the pterygoid.

The stapes is a short massive rod with expanded ends; medially it fits firmly in the *foramen ovale* and laterally is received in a pit in the inner quadrate surface. The stapes appears to be practically immovably fixed between the depression in the quadrate and the *fenestra ovalis*, no stapedial foramen has been determined.

The quadrate and lateral rami of the pterygoids are at a level considerably below the basioccipital so that they are visible in occipital view.

The raised boss on the parietal pierced by the pineal foramen and the postorbital bar formed by the postorbital are also visible in occipital view.

The palate (Fig. 7, Pl. VIIB) has been completely freed of the very hard matrix. As in all the lower therapsids the constituent bones are—prevomers, palatines, ectopterygoids, pterygoids, basisphenoid, parasphenoid, basioccipital, quadrate, paroccipital and stapes.

The prevomers are massive but much shorter than in *Jonkeria;* lateral to the median line there are two ridges on the posterior part of the bones enclosing a median groove, whereas in therapsids generally there is a median keel; posteriorly, the prevomers underlie the palatines. The palatine is a fair-sized bone which, anteriorly, is applied to the inner maxillary surface; it then curves round the posterior border of the internal nares; it does not reach its fellow in the middle-line, the prevomers and pterygoids being intercalated.

The limits of the ectopterygoids are not shown by definite sutures but the direction of the bone-fibres indicate that their form is as indicated in the figure.

The pterygoid is, as is usual in the therapsids, a triradiate bone with an additional anterior ramus. The transverse ramus does not descend so far down below the dentigerous border as in nearly all the other deinocephalians. A long slit-like interpterygoid vacuity separates the two pterygoids for a considerable distance. There are no deep ridges lateral to this vacuity as in the various species of *Jonkeria*. As the quadrate is situated far anteriorly the quadrate ramus of the pterygoid is short; it is applied to the inner face of the short anterior flange of the guadrate. Medial to the quadrate ramus proper, the pterygoid has a web of bone, which, lying at a higher plane, meets the basisphenoid.

The basisphenoid is a large bone with a low median keel; in its anterior part it is pierced by a pair of carotid foramina; laterally, it carries a thickened ridge, which forms the ventral rim of the *fenestra ovalis;* posteriorly, it is intimately confluent with the basioccipital and, postero-laterally, meets the paroccipital in a very firm suture.

The basioccipital condyle is only partly preserved; it was manifestly a large rounded knob laterally supported by the exoccipitals.

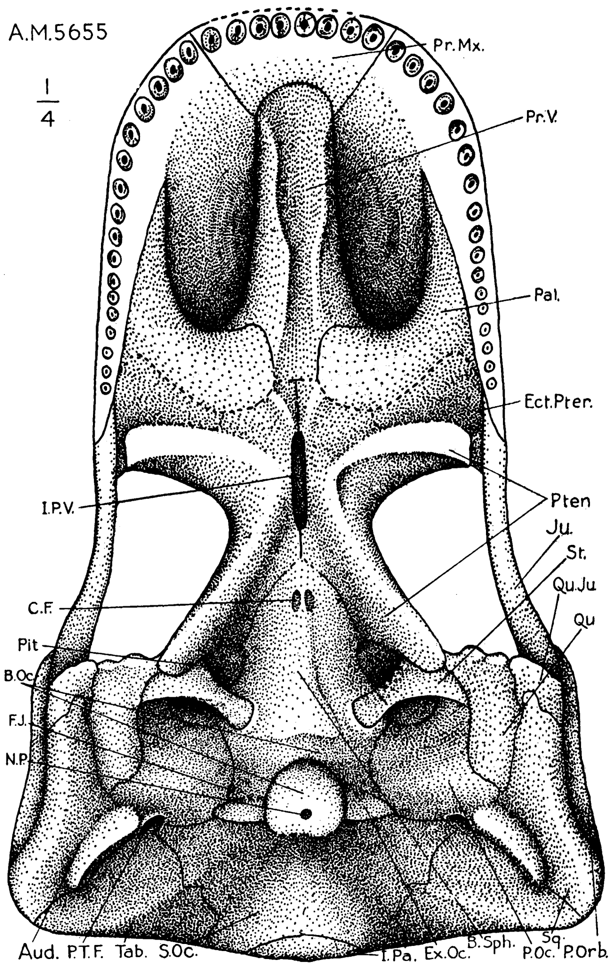

Fig. 7. *Taurocephalus lerouxi*. Type, Ber. Mus. No. 5655. Ventral view. Supplementary features on the two sides has made it possible to draw a symmetrical figure. $\times {}^1/_4$.

The teeth are badly preserved; in none of the teeth is the crown present; the roots show that the dentition was not differentiated except that the anterior teeth are the largest and that the series progressively decreases in size in posterior direction; the premaxilla housed 4 teeth; the first tooth on the maxilla is not differentiated as a canine and is of the same size as the last tooth on the premaxilla; the maxilla carried at least 17 teeth. The undoubted affinity of *Taurocephalus* to *Struthiocephalus, Mormosaurus, Moschops* and *Tapinocephalus*, in addition to the direct evidence afforded by the teeth, points to the conclusion that this form was herbivorous.

Tapinocephalus atherstonei Owen

PLATE VIIIB; FIGURES 8 TO 11

BROOM, R., 1928, Ann. S. Afr. Mus., p. 427.

REFERRED SPECIMEN.—Amer. Mus. No. 5626. Gans Kraal, Prince Albert district, *Tapinocephalus* zone.

Among the number of deinocephalian specimens sold to the American Museum in 1928 by Dr. Broom there is included the greater part of a skull of *Tapinocephalus atherstonei*. When the specimen came under my observation the posterior part of the dorsal and lateral surfaces were exposed by weathering. Mr. J. Walsh has succeeded in exposing the occiput and the lateral surface of the brain-case from the left side. The snout, most of the palate, squamosals, quadratojugals and quadrates are missing.

Although described and figured by Broom, I give a figure of the dorsal surface (Fig. 8, Pl. VIIIB) because in using a pantograph I have obtained a quite different outline. The relations of the constituent bones are readily understood from the figure and Broom's description—all the sutures being beautifully weathered out. The slit-like temporal opening has an antero-posterior measurement even less than in *Taurocephalus, Moschops* and *Struthiocephalus*. This is due to the fact that the thickening of the frontals, parietals, postorbitals and postfrontals is much greater than in the other forms mentioned. Just anterior to the frontonasal suture there is a sharp drop onto the dorsal surface of the snout. This is greater than in *Mormosaurus* and much greater than in *Struthiocephalus, Taurocephalus* and *Moschops*. Only the dorsal edge of the interparietal is exposed on the dorsal surface.

In occipital view (Fig. 9) the ventral part of the squamosal, the quadratojugal and the quadrates are missing; for the rest it is well preserved. The interparietal extends much further ventrally than in *Taurocephalus* and only its edge is exposed on the dorsal surface. As a result the supraoccipital is a shallow bone.

The tabulars form a large part of the lateral surface of the occipital plate and curve down laterally of the posttemporal fenestra to meet the paroccipital.

The paroccipital forms a very massive bar and is pierced by a small jugular foramen. Medially, the paroccipital is overlain by the exoccipital, which abuts against the basioccipital condyle and overhangs the jugular foramen.

The basioccipital condyle is large; its dorsal surface is grooved for the reception of the medulla; posteriorly it carries a notochordal pit. Except that the basisphenoid does not lie at a level much below the condyle the occipital aspect of the skull of *Tapinocephalus* is very similar to that of *Mormosaurus* as figured by Watson.

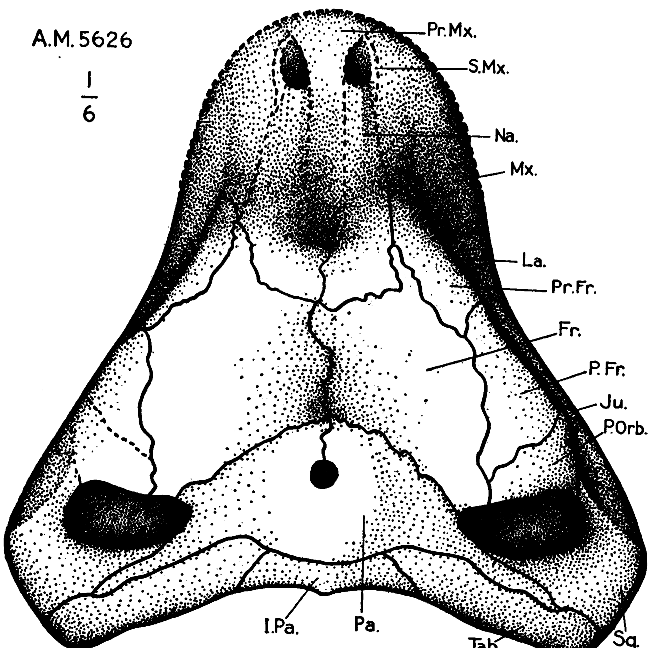

Fig. 8. *Tapinocephalus atherstonei.* Type, Amer. Mus. No. 5626. Dorsal view Parts of the left side, which are not preserved, are restored from the right side. $\times 1/6$.

Only the posterior part of the palatal aspect of the skull is preserved. The basioccipital forms the large rounded single condyle and then extends forward to meet the basisphenoid at the level of the *fenestra ovalis;* the basioccipital forms a small part of the border of the *fenestra ovalis;* laterally, the basioccipital meets the paroccipital and exoccipital. The exoccipital merely abuts against the side of the condyle and there is no evidence of its ever reaching on to the condylar surface; the exoccipital overhangs the small jugular foramen, which pierces the paroccipital. The paroccipital is a massive bone which is distally scooped out to receive the quadrate; laterally, it meets the basioccipital and forms most of the posterior border of the large *fenestra ovalis*. The proötic is applied to the anterior face of the paroccipital and forms the whole anterior border of the *fenestra ovalis*.

In lateral view (Fig. 10) it is seen that the posterior part of the brain-case is compressed into a very small space. Dorsal to the limits of the proötic, flanges of the supraoccipital, tabular, interparietal and parietal form part of the lateral surface of the brain-case, but their exact limits cannot be determined. A large venous foramen, found in

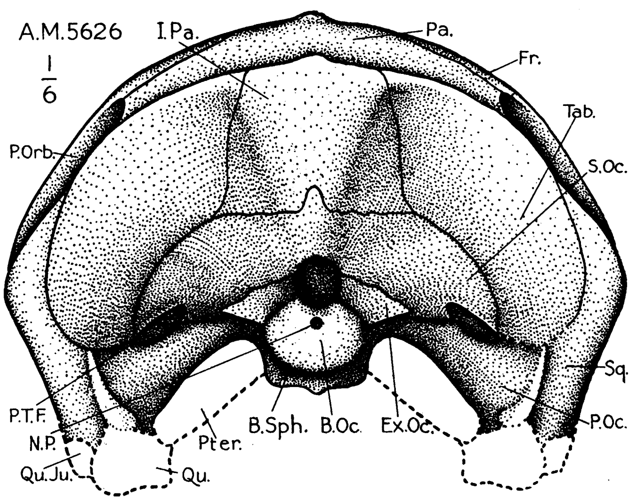

Fig. 9. *Tapinocephalus atherstonei*. Amer. Mus. No. 5626. Occipital view. The left side is restored on the basis of the right side. $\times {}^1/_6$.

all therapsids, pierces the side-wall above the proötic. The proötic forms the posterior border of the lateral opening into the pituitary fossa; posterior to this edge I have not been able to locate the foramina for the Vth and VIIth cranial nerves, which in the other therapsids occupy this position. The anterior border of the pituitary fossa is formed by the basisphenoid and the median parasphenoidal septum. The parasphenoid rests on the basisphenoid and ascends in the skull as a fairly thin median septum and has the same relation as in the anomodonts and gorgonopsians; on its postero-dorsal edge it supports the large sphenethmoid; this bone is pierced by a foramen just above the pituitary fossa, apparently for the opthalmic branch of the Vth cranial nerve; as is evident from the section (Fig. 11), the sphenethmoid is a solid bone not housing any part of the fore-brain; the olfactory lobe lies in a recess above the sphenethmoid and is separated from its fellow by a median bony septum; the connection of the olfactory lobes with the posterior part of the brain must be by a thin string of nervous tissue which penetrates the median septum by a small foramen.

The whole structure of the brain-case thus appears to be very similar to the less specialized therapsids, such as the therocephalians, gorgonopsians and anomodonts, but the fundamental pattern they have in common is greatly obscured by changes in proportion produced by the enormous thickening of nearly all the constituent bones. A more detailed study of this region in better preserved material will undoubtedly produce very interesting facts on the adaptative features forced on the brain

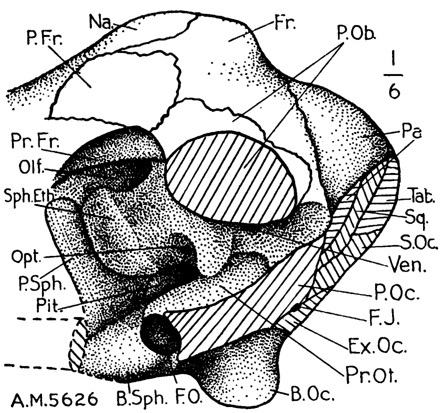

Fig. 10. *Tapinocephalus atherstonei*. Amer. Mus. No. 5626. Lateral view of the posterior half of the skull with the occipital plate and postorbital seen in section to show the outer surface of the brain-case. $\times {}^1/_6$.

by the intense pachyostosis, but I do not believe that such a study will show anything contrary to the view here advanced, viz., that the structure of the brain-case of the deinocephalians shows that this group of animals arose from a stock which also produced the gorgonopsians and therocephalians and thus also the cynodonts and bauriamorphs.

Taurops macrodon Broom

Broom, R., 1912, P. Z. S., p. 859.

Gregory, W. K., 1926, Bull. Amer. Mus. Nat. Hist., LVI, p. 235.

Broom, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 46.

Type.—Amer. Mus. No. 5610. Boesmanshoek, Laingsburg, *Tapinocephalus* zone.

This specimen consists of a snout, which only shows some interesting features of the anterior teeth and has been adequately described by Broom and Gregory.

Moschognathus whaitsi Broom

Broom, R., 1914, Bull. Amer. Mus. Nat. Hist., XXXIII, p. 137.
Broom, R., 1914, Phil. Trans. Roy. Soc., p. 42.
Gregory, W. K., 1926, Bull. Amer. Mus. Nat Hist., LVI, p. 191.
Broom, R., 1932, 'Mammal-like Reptiles of South Africa, p. 44.
Type.—Amer. Mus. No. 5602. Beaufort West, *Tapinocephalus* zone.

The mandibles and parts of the upper jaws have been fully described by Broom and Gregory and it is evident that this form is closely related to *Moschops*.

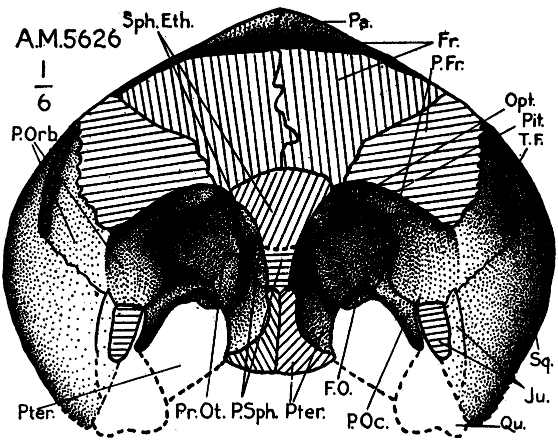

Fig. 11. *Tapinocephalus atherstonei.* Amer. Mus. No. 5626. Cross-section through the skull at a plane just anterior to the posterior border of the orbit to show the median septum, the sides of the brain-case and the anterior surface of the occipital plate. $\times 1/6$.

DISCUSSION

In South Africa the first fossiliferous bed of the Karroo is the *Tapinocephalus* zone of the Lower Beaufort. It is to this zone that the deinocephalians are confined. No deinocephalian has as yet been found in younger beds in South Africa, or elsewhere, and it would appear that they died out before the commencement of *Endothiodon*-zone times, being a phylogenetically sterile group of therapsids. Of their origin also practically nothing is known. When first encountered the order is already fully established. Hitherto, the preceding Ecca beds in South Africa yielded no undoubted deinocephalians; beds of the same age elsewhere have also yielded no ancestral forms.

It has been suggested that the tapinocephalids arose from a pre-gorgonopsian stem of which a form like *Anningia* may be a representative and it would appear that this view is not without foundation. Before, however, discussing this matter further it may be profitable first to analyze the suborder, Tapinocephalia, itself. Hitherto the following tapinocephalids are known from cranial material: *Moschosaurus, Tapinocephalus, Delphinognathus, Moschops, Moschognathus, Pnigalion, Mormosaurus, Struthiocephalus, Taurops, Taurocephalus, Keratocephalus, Criocephalus* and ? *Lamiasaurus.*

The first step in our analysis will be an attempt to subdivide the suborder into a number of groups:

MOSCHOSAURIDAE.—In the only known skull the following characters can be enumerated: skull small, long and narrow; snout long and moderately deep; no thickening of any of the cranial bones; postorbital bar narrow and slender; temporal fossa small and rounded; intertemporal region laterally somewhat bayed; parietal apparently excluded from supratemporal border; no clear differentiation into incisors, canines and molars........................*Moschosaurus.*

MOSCHOPIDAE.—The members of this group are very similar—three of the genera may even be cogeneric. Skull fairly small, short and moderately wide; snout short and fairly deep; fairly strong thickening of the cranial bones; postorbital bar thickened and fairly massive; temporal fossa fairly small with the antero-posterior diameter less than the dorso-ventral; intertemporal region only slightly laterally bayed; parietal just entering the supraorbital border; no differentiation into incisors, canines and molars.....*Delphinognathus, Moschops, Moschognathus, Pnigalion,* and ? *Lamiasaurus.*

TAPINOCEPHALIDAE.—The skull of only one member of this group is at all adequately known. Skull large, short and broad; snout short and shallow; very strong thickening of the cranial bones; postorbital bar greatly thickened and very massive; temporal fossa small and slit-like with the antero-posterior diameter greatly reduced; no lateral baying of the intertemporal region; parietal enters supratemporal border; no differentiation into incisors, canines and molars.............*Tapinocephalus, Taurops,* and *Keratocephalus*.

MORMOSAURIDAE.—Three of the four known forms have adequately preserved skulls and they form a fairly homogeneous group. Skull large, long and moderately wide; snout long or fairly long and shallow; cranial bones strongly thickened; postorbital bar thick and massive; temporal fossa fairly small with the dorso-ventral diameter not very much greater than the antero-posterior; intertemporal region laterally slightly bayed; parietal entering supratemporal border; no differentiation into incisors, canines and molars.

Mormosaurus, *Taurocephalus*, and *Struthiocephalus*.

The mormosaurids are not very clearly differentiated from the tapinocephalids—*Mormosaurus* approaching *Tapinocephalus* fairly closely. The snout in this group is, however, definitely longer than in the tapinocephalids and the pachyostosis not so excessive.

Do these four groups represent morphological stages and can one determine the evolutionary tendency?

Moschosaurus is undoubtedly the most primitive of the tapinocephalids. As it comes from high up in the *Tapinocephalus* zone it cannot be a direct ancestor, but it does appear to represent a morphological stage more primitive than that of any other tapinocephalid. Moreover, from it one can derive the three other groups.

The mormosaurids (*Mormosaurus*, *Struthiocephalus*, and *Taurocephalus*) can be derived as follows: increase in size; retention of the long snout but shallowing; thickening of the cranial bones; postorbital bar becomes wider and more massive; reduction of antero-posterior diameter of temporal fossa; incipient obliteration of baying of temporal region; loss of connection between postorbital and squamosal; increase of intersquamosal width.

The moschopids can be derived: shortening of skull with increase of intersquamosal width; slight reduction in snout depth; bone-thickening and increased massiveness of postorbital bar; reduction of antero-posterior diameter of temporal fossa; connection between postorbital and squamosal just lost; obliteration of baying of temporal region.

The tapinocephalids can be derived: increase in size, shortening, widening and shallowing; great thickening of cranial bones (postorbital); antero-posterior diameter of temporal fossa greatly reduced; obliteration of baying of temporal region; loss of connection between postorbital and squamosal.

This analysis seems to indicate two evolutionary tendencies (which, however, have the following factors in common: varying degree of thickening of cranial bones, increased massiveness of postorbital bar; separation of postorbital and squamosal; obliteration of baying of temporal region): in the mormosaurids the snout retains its length, whereas in the moschopids and tapinocephalids it is shortened and in the latter two groups the skull widening is much greater. Moreover, it is apparent that the tapinocephalids differ from the moschopids only in that here the degree of change is greater. Accepting this bifurcation of the tapinocephalid stem from a form like *Moschosaurus* one may now institute an enquiry into the relations of the tapinocephalids to the other therapsids (including *Pelycosaurus*).

Titanosuchids.—That the titanosuchids are intimately related to the tapinocephalids admits of no question. They represent subdivisions of equal value of the order DEINOCEPHALIA and I have recently shown that the styracocephalids must be considered as a third suborder. These suborders exhibit the same tendency to pachyostosis; same bone texture; large quadrate and quadratojugal; no preparietal; structure of occiput identical, though differing in shape; same general arrangement of all the cranial bones; auditory groove similar; brain-case compressed into dorso-posterior corner of skull; premaxillaries identical and different from all other therapsids; septomaxillaries similar; palate built on identical plan, etc. This close similarity undoubtedly indicates a recent divergence from the same ancestors. In fact, both the titanosuchids and tapinocephalids can very well be derived from a form like *Moschosaurus*, although the following derivation is perhaps nearer the truth: the tapinocephalids arose from a form like *Moschosaurus*, the titanosuchids arose from a form like *Rhophalodon* and *Moschosaurus* and *Rhophalodon* sprang from a common pre-deinocephalian. Moreover, a detailed comparison of the tapinocephalids and titanosuchids reveals the presence of a form like *Taurocephalus* which incorporates in itself features of both suborders. The features in which the titanosuchids diverge from the tapinocephalids can be enumerated: elongation and narrowing of snout; reduction in the intertemporal width and tendency to formation of parietal crest; no reduction of the antero-posterior diameter of the temporal fossa; pachyostosis of dorsal roof bones and postorbital bar not intensive; quadrate not shifted so far forward and longer quadrate ramus; posterior sweep of squamosals and accompanying concavity of occipital plate; carnivorous dentition with accompanying increased gape of jaws.

Pelycosaurs.—Broom, Watson and Gregory have argued for a close affinity of these two groups. Incorporating their findings the similarities in structure can be enumerated: close general agreement as to the topographic relations of the cranial elements (the changes in the tapinocephalids due to pachyostosis); a supratemporal, however, not present in tapinocephalids; occiput essentially identical; mandible similar—no coronoid process in either and the articulation though farther posterior in pelycosaurs, essentially similar; attachment of distal end of stapes to quadrate similar; brain-case compressed into dorso-posterior corner of the skull; parasphenoid and sphenethmoid identical; high dorsal keel on pterygoids and prevomers; extremely deep lateral pterygoidal flanges; relations of squamosal, quadratojugal, quadrate and pterygoid; no preparietal.

The main differences are: the basicranium of pelycosaurs more primitive, e.g., primitive basisphenoidal tubera, basipterygoidal processes and *processus cultriformis* visible through posteriorly elongated interpterygoid vacuity; primitive greater anterior extent of lacrymal, even reaches nostril in *Edaphasaurus;* specialized anterior position of quadrate in tapinocephalids; frontal long in pelycosaurs; postorbital partly excluded from temporal fossa in tapinocephalids; no reduction of size of temporal fossa in pelycosaurs; in no pelycosaur does premaxilla extend as posteriorly directed V between nasals; posterior part of palate at a level far above the quadrate ramus in pelycosaurs; primitive teeth on pterygoid and palatine in pelycosaurs; pelycosaur teeth carnivorous.

The foregoing remarks clearly indicate that the pelycosaurs and tapinocephalids are derived from common ancestors; the pelycosaurs are in many respects nearer their common point of origin, whereas the tapinocephalids are encumbered by some rather intensively specialized characters, probably induced by an adaptation to a peculiar vegetable diet.

Gorgonopsians.—Watson (1914) stated, " . . . it is legitimate to assume that Deinocephalia and the gorgonopsids arose from a not very distant common ancestor, but that they subsequently pursued quite different paths." Gregory (1926) went even farther: ". . . I have yet to find a character which will definitely exclude the Deinocephalia from derivation from the more primitive gorgonopsians." In view of these rather definite expressions of opinion it may serve some purpose to enumerate some points of difference: the gorgonopsian preparietal is unknown in the tapinocephalids; the strong coronoid process of the dentary in gorgonopsian is absent in tapinocephalids; the basisphenoidal tubera of gorgonopsians are present only in a very reduced condition in the tapinocephalids; no gorgonopsian has the large slit-like interpterygoid vacuity found in all tapinocephalids; in no gorgonopsian is there a web of bone connecting the lateral and quadrate rami of the pterygoid; no gorgonopsian has the elongated premaxillaries intercalated between the nasals found in all the tapinocephalids; in the gorgonopsians the prevomers do not meet the pterygoids but are wedged in between the palatines, which meet in the median line, whereas in the tapinocephalids the palatines do not meet in the median line and the prevomers do not taper posteriorly so that in this respect the tapinocephalid condition is closer to that obtaining in the therocephalians; in the gorgonopsians the palatines and pterygoids carry dentigerous ridges, whereas no such teeth are known in any tapinocephalid—a slight thickening is met with in this region in all tapinocephalids, but only in *Moschops* are definite, albeit edentulous, ridges preserved; the specialized anterior location of the tapinocephalid quadrate is not found in the gorgonopsians; in the gorgonopsians there is a tendency toward an increased size of the temporal fossa, whereas in the tapinocephalids there is a reduction; the mandibular mentum is square in the gorgonopsians but sloping in the tapinocephalids; the median keel on the prevomers and basispehnoid is not present in the tapinocephalids; the postorbital loses its connection with the squamosal in most tapinocephalids; the gorgonopsian dentition is differentiated into incisors, canines and molars; the quadrate and quadratojugal are reduced in the gorgonopsians.

The above list of differences clearly shows that we know of no gorgonopsians which could have given rise to any known tapinocephalid, but these differences are not so fundamental as to invalidate Watson's opinion. In fact, when one compares such a tapinocephalid as *Moschosaurus*, to the gorgonopsians of the *Tapinocephalus* zone, it is manifest that their common ancestor cannot be very remote. They agree in both having large facially exposed septomaxillaries, the same primitive slender epipterygoids, wide intertemporal regions, no palatal fenestra between the palatine, pterygoid and ectopterygoid, the relations of the sphenethmoid, parasphenoid and pterygoid are essentially similar and the telescoping of the proötic in the tapinocephalids is simply due to the pachyostosis, which obscures a fundamentally similar structure, which is common to all therapsids (in primitive gorgonopsians the proötic has no great anterior extent and it is possible that the smallness of the tapinocephalid proötic represents a retention of a primitive character rather than a secondary reduction). Moreover, many of the points of difference can be explained as losses or acquisitions due to a specialized mode of life in two groups of the same origin but evolving on divergent lines.

Therocephalians, etc.—No profitable results can be expected from a comparison of the tapinocephalids to the therocephalians, anomodonts, bauriamorphs, cynodonts, etc., as the points of structure in which they agree are simply those fundamental characters common to all the therapsids. Unfortunately, the dromosaurians are not well known; there is nothing known of their cranial structure which precludes the view that they are primitive therapsids; the arrangement of the dermal cranial bones, the quadrate-articular joint, the intertemporal region, the mandible and the dentition suggest a condition one would expect in the ancestors of the deinocephalians and possibly also of the gorgonopsians. Broom (1932) has recently suggested *Anningia* as representing a possible ancestral type. Here again the skull is very inadequately known. If Broom's figures are correct, *Anningia* possesses the following features one would expect in an ancestor of the tapinocephalids: broad intertemporal region, postorbital meeting squamosal, large quadrate and quadratojugal, interparietal on occipital surface and single basioccipital condyle.

All that the foregoing analyses enable us to do is to state that the tapinocephalids are very closely related to the titanosuchids and with them are typical therapsids. Among the therapsids their nearest allies are the gorgonopsians, dromosaurians and *Anningia;* the common ancestors of these forms could not have lived very long before *Tapinocephalus*-zone times since the divergence at the beginning of the *Tapinocephalus*-zone is not yet very marked. As previously pointed out by Broom and Watson, the American pelycosaurs represent a branch which sprang from the same stem as the therapsids, but apparently somewhat earlier than the separation of the tapinocephalids from the gorgonopsians, dromosaurians and *Anningia.*

In the preparation of this paper I am indebted in various ways to the following: the South African Museum for study-leave; the University of Stellenbosch for a stipendium; to the officers of the Department of Vertebrate Palaeontology at The American Museum of Natural History for all the facilities put at my disposal during the course of my work; and to my wife, Esmé E. Boonstra, for the execution of all the drawings which illustrate this paper.

PLATES V TO VIII

PLATE V

Moschops capensis. Topotype. Amer. Mus. No. 5552. Dorsal surface $\times {}^{1}/_{2}$.


A.M.
5552
1/2

PLATE VI

A.—*Moschops capensis*. Topotype. Amer. Mus. No. 5553. Lateral surface $\times ^1/_5$.

B.—*Taurocephalus lerouxi*. Type. Amer. Mus. No. 5655. Dorsal surface $\times ^1/_5$.

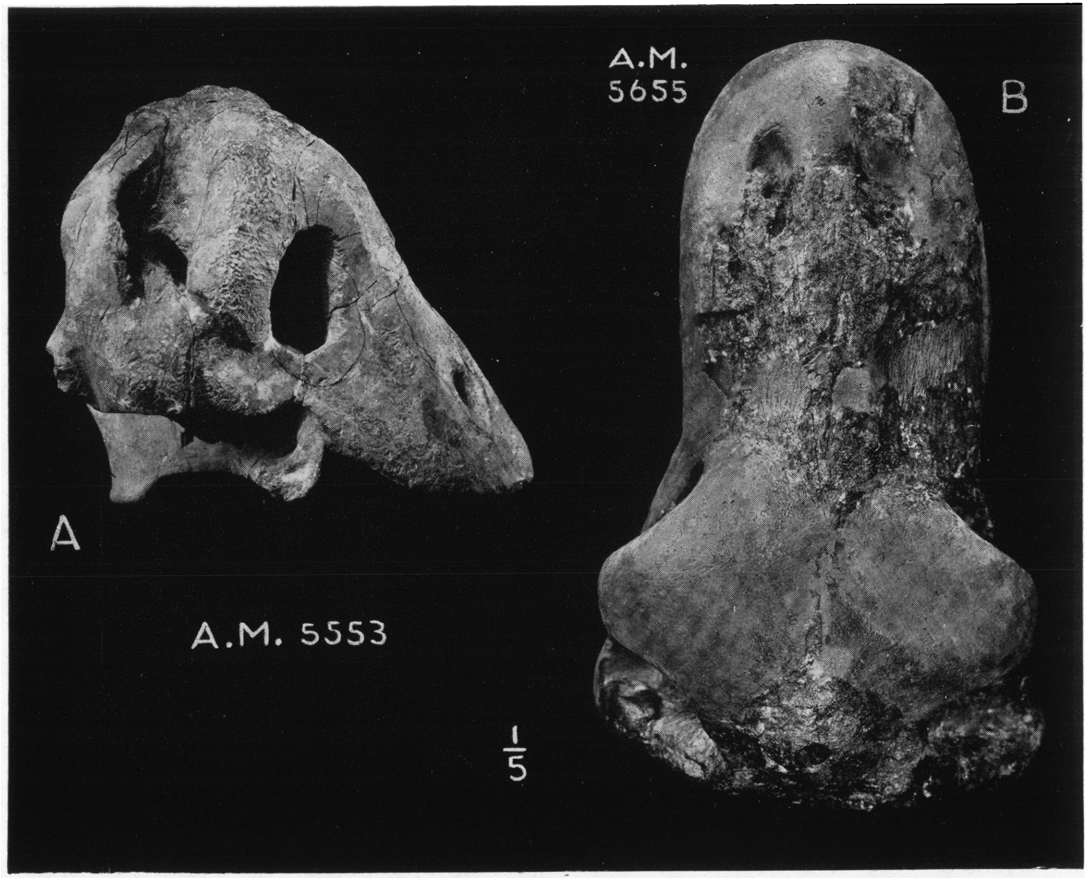
A.M. 5655
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PLATE VII

Taurocephalus lerouxi. Type. Amer. Mus. No. 5655. A.—Lateral surface $\times \frac{1}{5}$. B.—Palatal surface $\times \frac{1}{5}$.

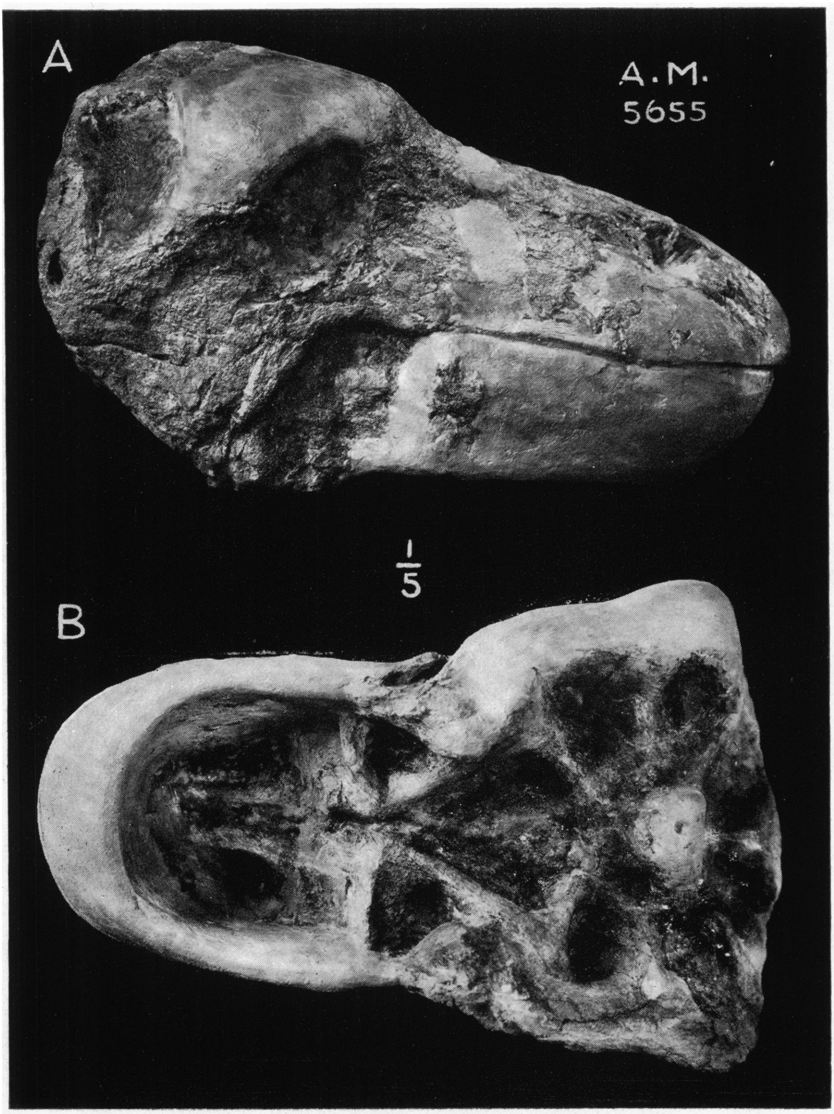
A
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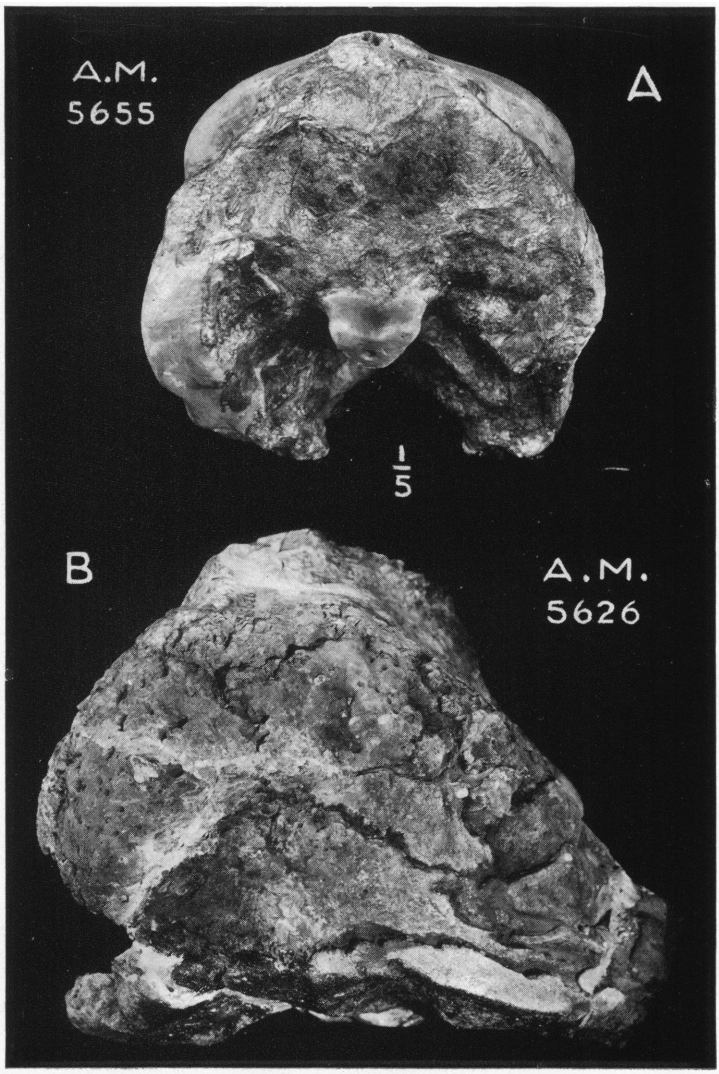
PLATE VIII

A.—*Taurocephalus lerouxi.* Type. Amer. Mus. No. 5655. Occipital surface $\times {}^{1}/_{5}$.

B.—*Tapinocephalus atherstonei.* Referred specimen. Amer. Mus. No. 5626. Dorsal surface $\times {}^{1}/_{5}$.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