The Cranial Morphology of Some Titanosuchid Deinocephalians

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Article III.—ON THE CRANIAL MORPHOLOGY OF SOME TITANOSUCHID DEINOCEPHALIANS

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Plates IX to XVII; Figures 1 to 11

In the collection of The American Museum of Natural History there are a number of skulls and lower jaws of titanosuchid deinocephalians which were purchased from Dr. R. Broom in 1928. In all there are four skulls, one good lower jaw and parts of the skull of another specimen, which have been described by Dr. Broom under the following names: *Dinophoneus ingens*, *Jonkeria vanderbyli*, *J. pugnax*, *J. crassus*, *Phoneosuchus angusticeps*, and *Anteosaurus minor*. As will be fully shown in the sequel, *Dinophoneus* and *Phoneosuchus* are synonyms of *Jonkeria*.

When these specimens came under my notice they were uncatalogued and as they were for the greater part still unprepared it was difficult to identify them by means of Broom's reconstructed and partly hypothetical figures. With the assistance of Mr. J. Walsh, who was detailed to help in the development work, I was able to free these specimens from the intractable matrix in a little over a month, so that we now have four practically complete skulls and one complete mandibular ramus, which show nearly all the morphological features.

My thanks are due to the officers of the Department of Vertebrate Palaeontology for all the facilities that have been put at my disposal and, in particular, to Mr. J. Walsh for his perseverance when faced with such intractable matrix. As in all my recent papers the figures which illustrate this account were done by my wife.

Jonkeria ingens (Broom)

Plates IX to XIII; Figures 1 to 6

Broom, R., 1923, P. Z. S., p. 666.

Broom, R., 1929, Ann. Trans. Mus., p. 33.

Broom, R., 1932, 'Mammal-like Reptiles of South Africa,' pp. 27, 30.

Type.—*Dinophoneus ingens*. Amer. Mus. No. 5634. Kookfontein, Prince Albert District, C. P.

Referred Specimen.—*Jonkeria pugnax*. Amer. Mus. No. 5608. Kookfontein, Prince Albert District, C. P.

In 1923, Broom described two skulls under the name *Dinophoneus ingens* and published composite drawings based on both specimens.

In 1929, Broom removed his topotype specimen from this genus and placed it in the genus *Jonkeria* to form a new species: *J. pugnax*.

When these two skulls came under my observation the type specimen of Broom's *Dinophoneus ingens* consisted of a number of pieces, which when fitted together formed the major part of a skull in which the palate was nearly complete and fairly free of matrix, the snout missing, the postorbital and posttemporal bars nearly all weathered away, the part of the outer surface preserved much weathered and the whole skull distorted by postmortem deformation. The type specimen of Broom's *Jonkeria pugnax* consisted of a muzzle encased in matrix and not joined to the rest of the skull; the posterior part of the skull had the parietal and frontal regions exposed by natural weathering, the left squamosal and postorbital arches missing and the right enclosed in a mass of matrix which also included a massive scapular blade.

After spending some considerable time on these two skulls we now have No. 5634 showing most of the palatal structure, some features of the occiput and the parietal region and, as the postorbital arch and the adjacent bones were weathered away, it was possible to expose the brain-case from the left side. In No. 5608 we were successful in exposing most of the palate, the right side with a nearly complete lower jaw, the dorsal surface with the left squamosal and postorbital missing and, in addition, a fracture made it possible to expose the *basis cranii* from above, i.e., expose the floor of the brain-case.

When both these skulls were freed of matrix it was immediately evident that Broom's original inference was correct and that they are cospecific, and that both are undoubtedly referable to van Hoepen's genus, *Jonkeria*, but represent a distinct species. Broom's *Dinophoneus* is thus a synonym of *Jonkeria* and his *J. pugnax* a synonym of *J. ingens*. In the type specimen the palate shows most of the features (Fig. 1).

The prevomers form a long stout internarial bar; along the median line they are grooved, whereas in practically all the other therapsids the prevomers carry a ventral keel; posteriorly, the prevomers meet the pterygoids and overlie the palatines; in the gorgonopsians the palatines are intercalated between the prevomers and the pterygoids, whereas, in the therocephalians, the prevomers reach the pterygoids but underlie the palatines; in this deinocephalian there thus seems to be a mixture of therocephalian and gorgonopsian characters.

The palatines form most of the posterior and lateral borders of the internal nares; laterally they abut against the inner face of the maxilla and from there narrow somewhat and proceed medially to form a spatulate sheet of bone underlying the posterior end of the prevomers. There is no vacuity between the palatine, ectopterygoid and pterygoid; in this

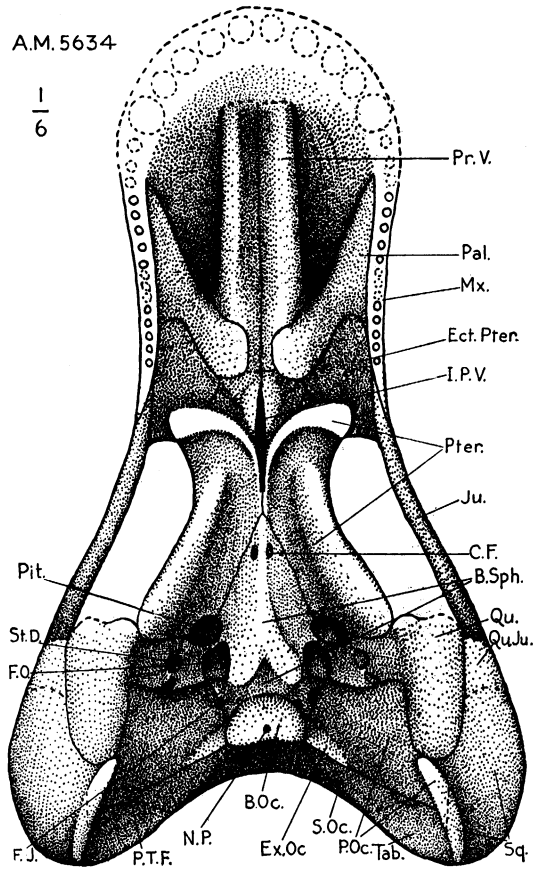


Fig. 1. *Jonkeria ingens.* Type, Amer. Mus. No. 5634. Ventral view. The skull is considerably distorted. In the drawing the right side was taken as basis and the resultant symmetrical figure shows the posterior part flattened out and much wider than the skull would be in actual life. $\times 1/6$.

respect it agrees with the gorgonopsians and differs from the therocephalians, cynodonts and bauriamorphs.

The ectopterygoid is a fairly large element, which descends halfway down the anterior face of the lateral pterygoidal ramus; no perforating foramen has been located.

The pterygoid is a large element which is, along the median line, nearly completely separated from its fellow by a long interpterygoid vacuity; anteriorly, it meets the prevomers and overlies the palatines

and ectopterygoids; the lateral flanges are of great depth, viz. as deep as the lower jaw; anterior to the lateral flanges there are grooves which lead on to the under face of the ectopterygoids; from the transverse flange the quadrate ramus sweeps backward as a wide sheet of bone to overlap the quadrate; the outer edge of the quadrate ramus is turned downward to form a vertical edge which lies on a plane considerably ventral to the inner part of the bone which meets the basisphenoid; the postero-median edge of the quadrate ramus is notched and together with the basisphenoid it forms the border of the opening leading into the pituitary fossa; dorsally, the pterygoids carry a high thin sheet of bone forming a median septum. Neither pterygoid, palatines, prevomers or ectopterygoid carry teeth; just posterior to the prevomers the pterygoids are raised into two mounds as usually found in the therocephalians and gorgonopsians but there is no evidence, whatsoever, of any teeth.

The basisphenoid has a large ventral exposure; anteriorly, it is intercalated between the two quadrate rami of the pterygoids as a V-shaped bone; near its anterior extremity it is pierced by a pair of carotid foramina; in the median line it carries a low ridge, which posteriorly bifurcates to form two low tubera; laterally, the basisphenoid is notched twice—the anterior being for the lateral opening leading into the pituitary fossa and the posterior one for the large *fenestra ovalis;* posteriorly, the basisphenoid and basioccipital are intimately fused so that the junction of the two bones cannot be determined externally.

The basioccipital forms a large but low kidney-shaped single condyle which carries a notochordal pit.

The paroccipital is a large bone; laterally, it overlaps the quadrate and abuts against the squamosal to form about half of the auditory ridge; medially, it is applied to the side of the basioccipital and is overlapped by the exoccipital; the paroccipital curves up on to the occipital surface to the plane of the posttemporal fenestra.

The exoccipital is a small element lying on the paroccipital and abutting against the basioccipital; ventral to it lies the *foramen jugulare.*

In ventral view the quadrate has a large exposure; it is clasped by the quadratojugal, squamosal and paroccipital; it lies obliquely in the skull and at the plane of the condyle is flanked by the quadrate ramus of the pterygoid; the stapes is not preserved and it can now be seen that the quadrate ascends high up in the skull and continues dorsal of the *fenestra ovalis;* on its inner face, some distance above the condyle, a large, deep depression received the distal end of the stapes.

The occiput is not very well preserved although it is possible to de-

termine that it is composed of interparietal, tabulars, squamosals, supraoccipital, paroccipitals, exoccipitals and basioccipital. The *foramen magnum* is large and the posttemporal fenestra small. In contour the occiput is kidney-shaped. Broom's figure (1923) of the occiput, if it was based on this specimen, which to me is inconceivable as the little that is preserved was not freed of matrix until I developed the skull, is a sample of good hypothetical reconstruction.

As most of the arches and some of the dorsal surface was lost it has been feasible to expose part of the brain-case from the left side (Fig. 2).

Due to the shape of the skull the part of the side-wall of the brain-case

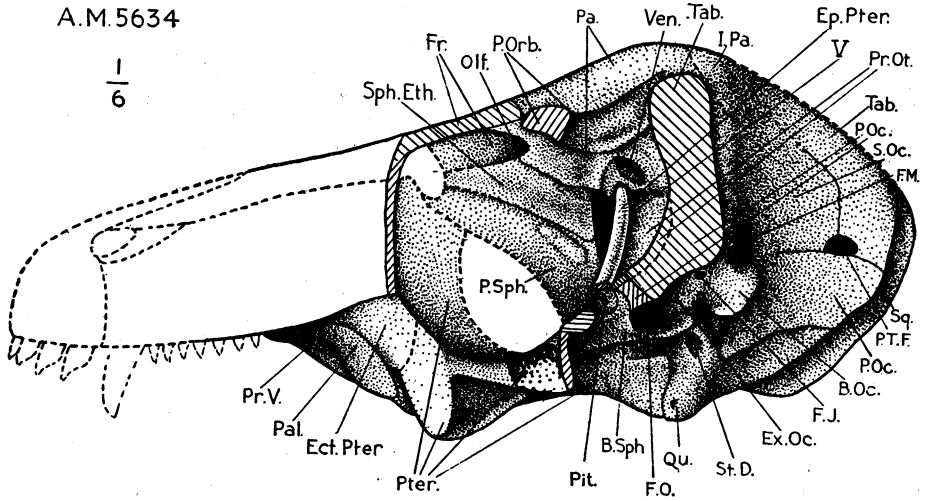


Fig. 2. *Jonkeria ingens.* Type, Amer. Mus. No. 5634. Lateral view. The occiput and postorbital bar are shown in section in order to present the outer surface of the left side of the brain-case. $\times 1/6$.

between the occipital plate and the lateral opening of the pituitary fossa is greatly reduced, when compared with the other therapsids. The proötic has a very small lateral surface and its antero-posterior extent is greatly reduced; anteriorly, it forms the margin of the lateral opening of the pituitary fossa and is pierced by a small foramen for the Vth cranial nerve; I have not been able to locate the perforation for the VIIth nerve; dorsally, the proötic meets a flange of the parietal and is here pierced by the large venous foramen found in all therapsids; posteriorly it is applied to the anterior face of the paroccipital. In this exposure it is seen that the large *fenestra ovalis* is surrounded by the paroccipital,

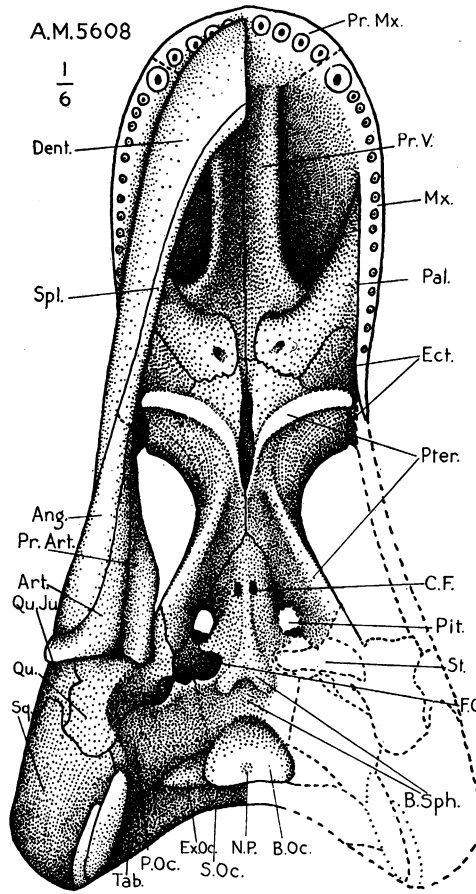


Fig. 3. *Jonkeria ingens.* Amer. Mus. No. 5608. Ventral view of the skull, with the right mandibulary ramus nearly in natural relations. The left side is restored on the basis of the right side. This figure shows the proportions of the palate more truly than the figure of the type specimen (Fig. 1). $\times 1/6$.

basisphenoid and basioccipital. The basisphenoid extends anterior of the *fenestra ovalis* to form the border of the lateral opening of the pituitary fossa and, anterior to this, it serves as a base for the parasphenoid, which rises vertically in the skull to form a high median septum, which, dorsally, is grooved in order to receive the sphenethmoid.

The sphenethmoid has a relatively flat outer surface; dorsally, it meets a descending flange of the parietal and anterior to this it forms the

ventral border of a groove in which the olfactory lobes were apparently housed; a median septum separates the two lobes. I can find no perforation in the sphenethmoid for the optic nerve.

The median septum formed by the pterygoids ascends in the skull and apparently supported the anterior edge of the parasphenoid.

The epipterygoid is an extremely slender rod, which rests on the quadrate ramus of the pterygoid and meets the descending flange of the parietal; it does not lie far lateral of the outer surface of the brain-case so that the *cavum epiptericum* was not over spacious.

No incisors or canines are preserved, as that part of the snout is missing; a part of the maxillary alveolar border is preserved and shows the roots of a number of molars; in all there were certainly not less than 16 fairly small conical molars.

In the topotype specimen, No. 5608, the palate is beautifully exposed (Fig. 3). As figured the width over the squamosals is less than in the type; this is, however, due to the fact that in the type postmortem pressure has forced the sides outwards. The structure, as shown in the figure, is as in the type; in addition it is seen that a nutritive foramen pierces the palatine; the mounds on the anterior pterygoidal ramus, reminiscent of the dentigerous ridges of the gorgonopsians, are well preserved.

The right mandibular ramus is preserved in its natural relations and is included in the figure in ventral view. The inner flange of the prearticular is noteworthy.

In lateral view (Fig. 4) the lower jaw has a large exposure of the dentary, which manifestly had a sloping mentum; the splenial is applied to the inner face of the dentary and forms the posterior corner of the symphysis; the angular has a large outer surface, which exhibits no particular features as, for instance, the ridge-pattern found in all the therocephalians; in outer view the surangular is exposed as an arch which meets the articular in a firm articulation.

The lateral surface of the skull appears very therocephalian-like, except that the lower-jaw-articulation is situated far forward and very low down. The preorbital portion is greatly elongated, but is fairly high, although it appears low on account of the relatively great length. The septomaxilla has only a small facial exposure. The anterior extent of the lacrymal is very small, which would imply that it had already lost its relation with the nostril before the lengthening of the snout took place.

The circumorbital bones are jugal, lacrymal, prefrontal, frontal, post-

frontal and postorbital; the entry of the frontal and postfrontal in the orbital border is small; the postorbital forms the whole postorbital bar and then proceeds backward as a thin flange applied to the parietal and it just meets the squamosal, which thus agrees with the gorgonopsian condition and differs from all the other therapsids. The squamosal is a large element forming the subtemporal bar and most of the posttemporal bar and, posteriorly, has a prominent ridge developed, which together with a ridge of the paroccipital forms one side of the auditory groove. The parietal is greatly thickened and is laterally pinched in so that it forms a high fairly narrow parietal crest and in this region thus differs

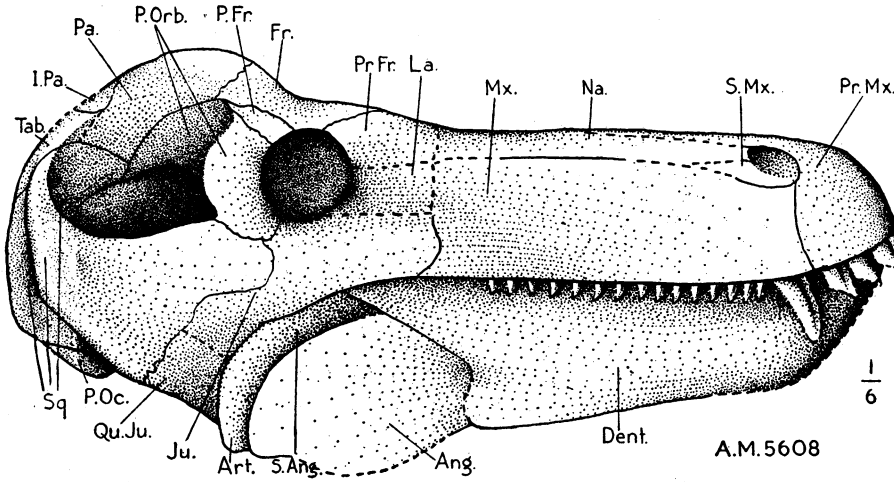


Fig. 4. *Jonkeria ingens.* Amer. Mus. No. 5608. Lateral view of the skull with the right mandibulary ramus in position. $\times 1/6$.

from the gorgonopsians and approaches the condition seen in nearly all the other therapsids. The quadratojugal overlaps the outer surface of the quadrate and when the lower jaw is in position the quadrate is not visible in lateral view.

The temporal opening is quite large and its antero-posterior diameter is not reduced so as to form a transverse slit as in the tapinocephalids.

In dorsal view (Fig. 5) nearly all the structure is shown except that in the preorbital portion most of the surface of the bone has been weathered away.

The most conspicuous feature is the mound formed on the parietal by the thickening of the bone; it is only in the parietal region that the titanosuchids have any excessive bone-thickening, which in the tapino-

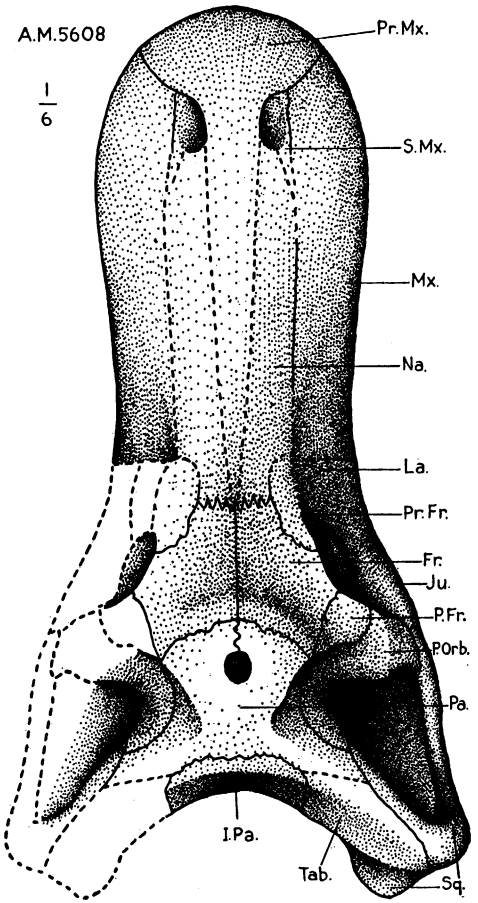


Fig. 5. *Jonkeria ingens.* Amer. Mus. No. 5608. Dorsal view. The left postero-lateral corner is restored on the basis of the preserved right side. $\times 1/6$.

cephalids embraces practically every bone in the skull; since the post-orbital bar and the posttemporal bar are relatively slender the temporal fossa consequently retains a relatively great antero-posterior diameter, whereas in the tapinocephalids the thickening of these two bars produces a dorso-ventrally elongated slitlike posttemporal fenestra. In these features the titanosuchids are much less specialized than the tapinocephalids.

The intertemporal width is slightly greater than the interorbital width, but due to the fact that the parietal is raised and is laterally

bayed it has an appearance of lesser width. The parietal region, incorporates features of both the gorgonopsians and therocephalians, and it would appear that it could be derived from a condition similar to that of the gorgonopsians and proceeding in a direction, which, in some respects, converges with that followed by the therocephalians.

The parietal mound is pierced by a large circular pineal foramen.

The interparietal enters the dorsal surface.

Posteriorly the tabular is applied to the squamosal and parietal and these three bones form the posttemporal bar.

The postfrontal forms the antero-dorsal corner of the postorbital bar.

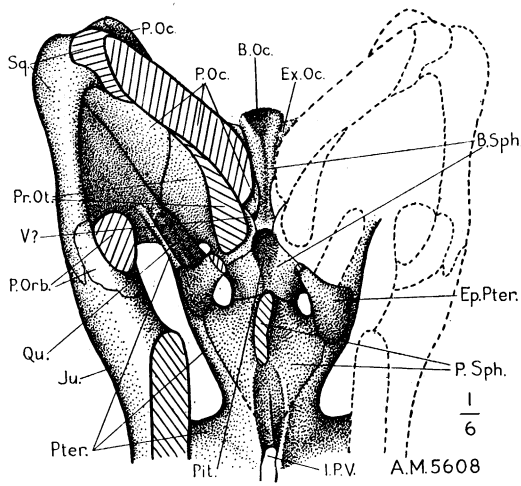


Fig. 6. *Jonkeria ingens.* Amer. Mus. No. 5608. View of the dorsal surface of the floor of the brain-case with the occipital plate, sides and median parasphenoidal septum shown in section. $\times 1/6$.

The two frontals present a cruciform figure with a fairly large entry into the supraorbital border. The prefrontal forms a low ridge, which forms a slight overhang over a shallow preorbital depression.

The occiput is not fully preserved; it does, however, show the massive paroccipitals very well; the paroccipital sweeps in latero-posterior direction to end with a thickened protruding edge, which together with a ridge of the squamosal forms the side-wall of a deep auditory groove. The presence of the large *foramen magnum*, a small posttemporal fenestra, exoccipitals overhanging the *foramen jugulare* and supporting the basioccipital, a large supraoccipital and tabulars can be determined, but

if figured would imply a certain amount of reconstruction. The posterior part of the brain-case and *basis cranii* has been prepared from above (Fig. 6).

The epipterygoids are preserved on both sides; the slightly expanded base, is applied to the lateral face of the quadrate ramus of the pterygoid, and the bone then ascends in the skull, being applied to the proötic and meeting the parietal. In dorsal view it is seen that the quadrate ramus of the pterygoid extends posteriorly far beyond the plane of the quadrate.

The dorsal surface of the basioccipital is scooped out for the reception of the medulla; anteriorly, the floor is formed by the slightly grooved surface of the basisphenoid, which extends anteriorly to form the posterior rim of the large pituitary fossa; the floor of the pituitary fossa is also formed by the basisphenoid; laterally, the exoccipital abuts against the basioccipital and basisphenoid to form the postero-ventral corner of the side-wall of the brain-case; anterior to the exoccipital, the supraoccipital meets the side of the basisphenoid and forms part of the side-wall anterior to that formed by the exoccipital; the proötic is applied to the anterior face of the supraoccipital and paroccipital and, anteriorly, abuts against the basisphenoid; a foramen (Vth cranial nerve?) pierces the side-wall at the junction of the proötic and basisphenoid. Resting on the basisphenoid, anterior to the pituitary fossa, the high parasphenoidal septum rises obliquely in the skull; anteriorly its base, which is an extensive horizontal sheet of bone, rests on the pterygoids. Anteriorly to the parasphenoidal septum a deep hollow lies in the floor of the pterygoids; anteriorly, this hollow opens on to the palatal surface through the interpterygoidal vacuity. I can offer no suggestion as to what was housed in this depression. At this point it is of interest to recall the large size of the pituitary fossa; the hypertrophy of the pituitary gland is undoubtedly connected with the pachyostosis and general skeletal massiveness of the deinocephalians. Unfortunately, the size of the pituitary fossa is not known in the unspecialized *Moschosaurus*.

Only the roots of some of the teeth are preserved; these were 4 incisors, 1 canine and at least 15 molars; above the functionary incisors some replacing teeth can be seen.

Jonkeria vanderbyli Broom

Plates XIV–XVI; Figures 7 to 9

Broom, R., 1929, Ann. Trans. Mus., p. 23.

Broom, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 24.

Type.—Amer. Mus. No. 5620. Jan Willemsfontein, Prince Albert District, C. P., *Tapinocephalus* zone.

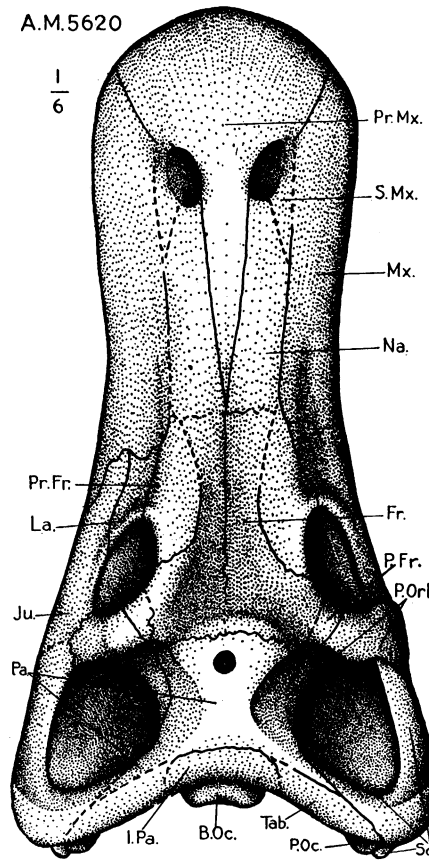


Fig. 7. *Jonkeria vanderbyli.* Type, Amer. Mus. No. 5620. Dorsal view of the skull. $\times 1/6$.

This species is based on a very good skull, which lacks only the lower jaws, parts of the quadrates and quadratojugals and the dorsal edge of the posttemporal bars. Broom has figured the dorsal and lateral surfaces but without indicating the relations of the constituent bones. When this skull came under my notice the dorsal and lateral surfaces had been weathered out to show the general contour but there was still a thin film of matrix covering most of the bone. A long continued process of alternately grinding and etching has exposed the majority of the sutures. In addition I have been successful in developing the whole palatal surface, which now shows practically all the structural features.

In dorsal view (Fig. 7) the figure shows that this skull is very similar to *J. truculenta.* The condyle is visible as in the genotype, whereas in dorsal view it is not visible in *J. ingens.*

In lateral view (Fig. 8) the great similarity to the genotype is again evident, but the number of points mentioned by Broom do appear to warrant his distinguishing this skull by name from *J. truculenta.* The structural details are evident from the figure; a number of nutritive foramina open on the maxillary surface; the great depth of the transverse pterygoidal flange and the contiguous bones are strikingly evident in lateral view.

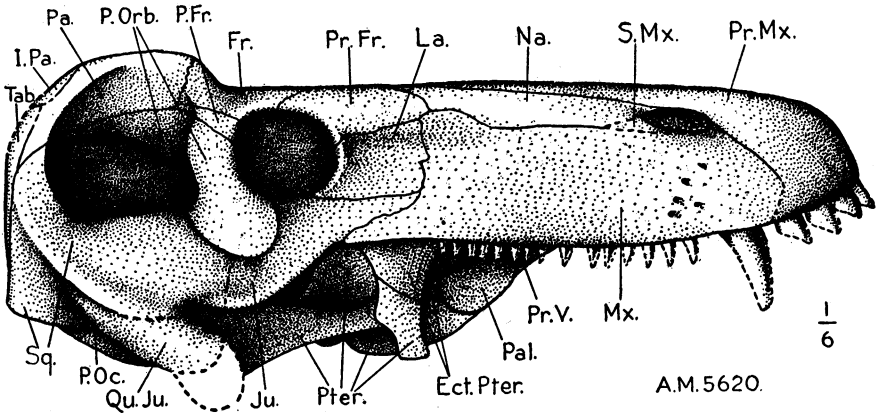


Fig. 8. *Jonkeria vanderbyli.* Type, Amer. Mus. No. 5620. Lateral view of the skull. $\times 1/6$.

In palatal view (Fig. 9) the essential structural details are as described above for *J. ingens,* but the detailed proportions differ appreciably—the quadrate rami of the pterygoids are not so divergent in posterior direction, the prevomers are more slender, the median pterygoid keel posterior to the large interpterygoid vacuity is much deeper and the condyle is relatively situated farther posteriorly. The stapes are preserved in their natural relations and it is evident that they are nearly immovably fixed in a depression on the inner face of the quadrate; they are short, massive rods with expanded ends.

The roots of 4 incisors with a replacing set in the premaxilla, 1 enlarged canine and at least 14 conical molars are present.

Jonkeria crassus Broom

Broom, R., 1929, Ann. Trans. Mus., p. 26.

Broom, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 27.

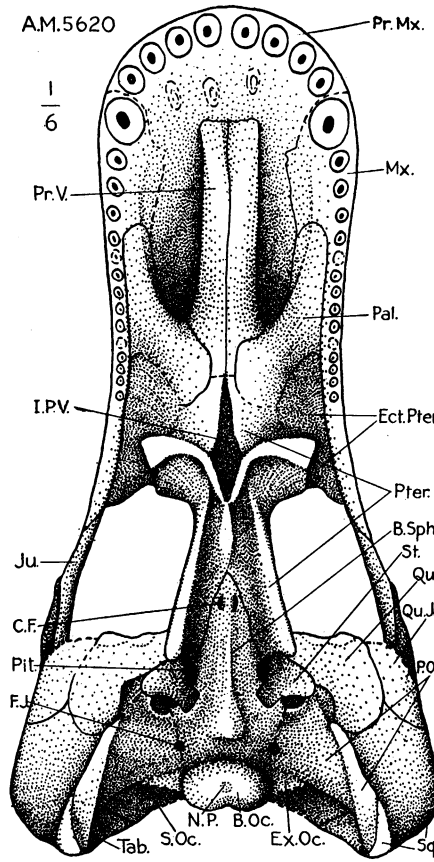


Fig. 9. *Jonkeria vanderbyli.* Type, Amer. Mus. No. 5620. Ventral view of the skull. The quadrates are restored. $\times 1/6$.

TYPE.—Amer. Mus. No. 5577. Kruidfontein, Prince Albert District, C. P., *Tapinocephalus* zone.

The only cranial material of this specimen is some parts of the dentaries, which are undoubtedly titanosuchid and appear to be correctly referred to the genus, but whether it is specifically distinct from the other species of *Jonkeria* cannot, I think, be determined on the basis of the dentaries.

Jonkeria angusticeps (Broom)

Plates XVI, XVIIIA; Figure 10

BROOM, R., 1923, P. Z. S., p. 676.

BROOM, R., 1929, Ann. Trans. Mus., p. 31.

BROOM, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 29.

TYPE.—*Phoneosuchus angusticeps*, Broom. Amer. Mus. No. 5633. Abraham's Kraal, Prince Albert District, C. P., *Tapinocephalus* zone.

This specimen consists of a nearly perfect right mandibular ramus (Fig. 10). Since Broom described the specimen I have thoroughly cleared the matrix away with the result that the limits of the constituent bones are not quite as figured by Broom, although he was right in all the essential points of structure.

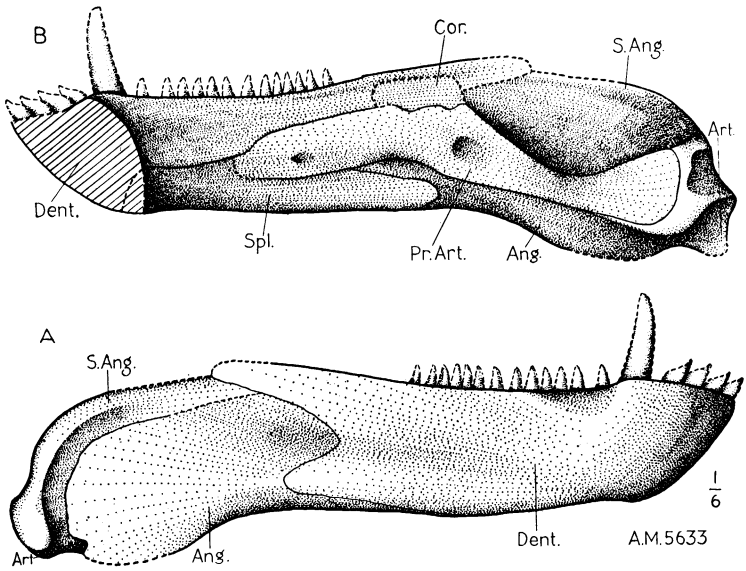


Fig. 10. *Jonkeria angusticeps* (Broom). Amer. Mus. No. 5633. A, outer, B, inner, view, of the right mandibulary ramus. $\times 1/6$.

Broom first described the mandible under the name *Titanosuchus cloetei* and then, in 1929, made it the type of the new genus and species *Phoneosuchus angusticeps* and in his description stated that it differed from the jaw of *Jonkeria*—meaning *Jonkeria truculenta*. Since I have exposed the lower jaw in *Jonkeria ingens* (Amer. Mus. No. 5608) it is now evident that this specimen agrees very closely with it and although there may be some doubt as to its specific identity it is undoubtedly referable to the genus *Jonkeria*. Broom's *Phoneosuchus* thus becomes a synonym of van Hoepen's *Jonkeria*.

Anteosaurus minor Broom

Plate XVIIB; Figure 11

BROOM, R., 1929, Ann. Trans. Mus., p. 35.

BROOM, R., 1932, 'Mammal-like Reptiles of South Africa,' p. 35.

REFERRED SPECIMEN.—Amer. Mus. No. 2224, Van der Byl's Kraal?, Prince Albert District C. P., *Tapinocephalus* zone.

This specimen was sent for sale to the American Museum and, in his covering letter, Broom stated that this skull is a topotype of the type specimen in the British Museum. In his original description Broom only mentions one specimen. I have examined the type in the British

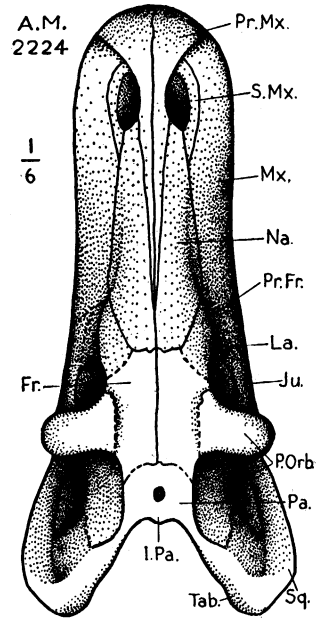


Fig. 11. *Anteosaurus minor.* Amer. Mus. No. 2224. Restored dorsal view of a considerably distorted skull. $\times 1/6$.

Museum (Natural History) but found that I could make very little of it. The specimen now under consideration is undoubtedly an *Anteosaurus* and as there appear to be no characters preserved in the fragmentary type which would prevent the inclusion of this skull in the species, *minor*, it will be convenient to do so.

The skull is considerably distorted by postmortem crushing and the greater part of the arches and most of the palate are missing.

I am including a figure of the dorsal surface (Fig. 11) in which an at-

tempt has been made to restore the skull to its original shape and proportions.

The bulbous supraorbital swelling, the vertical occipital plate and the great posterior extension of the posttemporal arches are undoubted characters of Watson's genus *Anteosaurus*. This specimen is two-thirds as large as Watson's *A. magnificus* and the supraorbital bosses are relatively less developed so that it is specifically distinct, unless it is an immature skull of *A. magnificus*.

DISCUSSION

In my account of the tapinocephalid deinocephalians I have shown that the titanosuchids and tapinocephalids are two branches of the deinocephalians which had diverged from each other when the evolutionary development was more or less at a stage represented by the two forms, *Moschosaurus* and *Rhopalodon*.

The titanosuchids do not possess, or show to a lesser degree, the remarkable specialization of the tapinocephalids; they show less general bone-thickening; no reduction in the antero-posterior diameter of the temporal fossa; no secondary widening of the intertemporal region; no shortening of the snout; quadrate not so anteriorly situated; occiput remains concave; less widening across the squamosals; no adaptation to herbivorous diet, etc. These characters seem to indicate that the titanosuchids exhibit a cranial structure, which approaches the ancestral condition more closely than does the tapinocephalids, whose basic structure is greatly obscured by superimposed specializations.

It has already been remarked that in general appearance the titanosuchids resemble the therocephalians. A comparison may serve some useful purpose. The titanosuchids resemble the therocephalians: long fairly narrow snout; the carnivorous dentition; unreduced temporal fossa; slender posttemporal and postorbital bar, but the postorbital meets the squamosal as in the gorgonopsians; the posttemporal bar extends posteriorly beyond the plane of the interparietal; the prevomers meet the pterygoids, because the palatines are not intercalated between them, but the relations of these bones are different from the therocephalian condition and it would appear that the two conditions have been arrived at by different ways; the mentum of the mandible slopes backward as in the therocephalians, but in the latter there is a strong coronoid process to the dentary (no therapsid mandible approaches the deinocephalian condition so closely as does that of some pelycosaurs); in the titanosuchids the parietals do form a crest and are pinched in laterally

but there is very slight similarity in the intimate relations of the bones in this region; a preparietal is absent; web of bone connecting the lateral and quadrate rami of the pterygoid as in some higher therocephalians.

It is thus evident that the few similarities in the titanosuchid and therocephalian skulls are mainly common therapsid characters together with some similar superficial adaptations. The differences in cranial structure are of far greater importance; in all the primitive and some higher therocephalians there is a large palatal fenestra between the palatine, pterygoid, prevomer and ectopterygoid, whereas this has not been found in any titanosuchid; the prominent basisphenoid tubera and median keel of the therocephalians are only weakly indicated in the titanosuchids; no primitive therocephalian has a web of bone connecting the lateral and quadrate rami of the pterygoid; in no therocephalian is the quadrate situated so far anteriorly; in no therocephalian does the postorbital reach the squamosal; in the titanosuchids, the epipterygoid is a weak rod-like element with an antero-posterior width less than in any therocephalian; in no therocephalian does the premaxilla extend so far posteriorly as it does in all the known titanosuchids; the prominent auditory ridge formed by the squamosal and paroccipital in the titanosuchids is entirely different from the therocephalian condition; in no therocephalian is there any evidence of a thickening of the cranial elements.

It would thus appear, as I have pointed out in my account of the tapinocephalids, that the deinocephalians are a quite distinct branch of therapsids and that their nearest relatives appear to be the gorgonopsians, but even from these they differ in a number of important characters so that one must postulate that these two groups must have split in lower Permian times if not even earlier.

PLATES IX TO XVII

PLATE IX

Jonkeria ingens. Type. Amer. Mus. No. 5634. Ventral view. $\times 1/4$.


1/4
A.M. 5634

PLATE X

Jonkeria ingens. Type. Amer. Mus. No. 5634. Lateral view. $\times 1/4$.

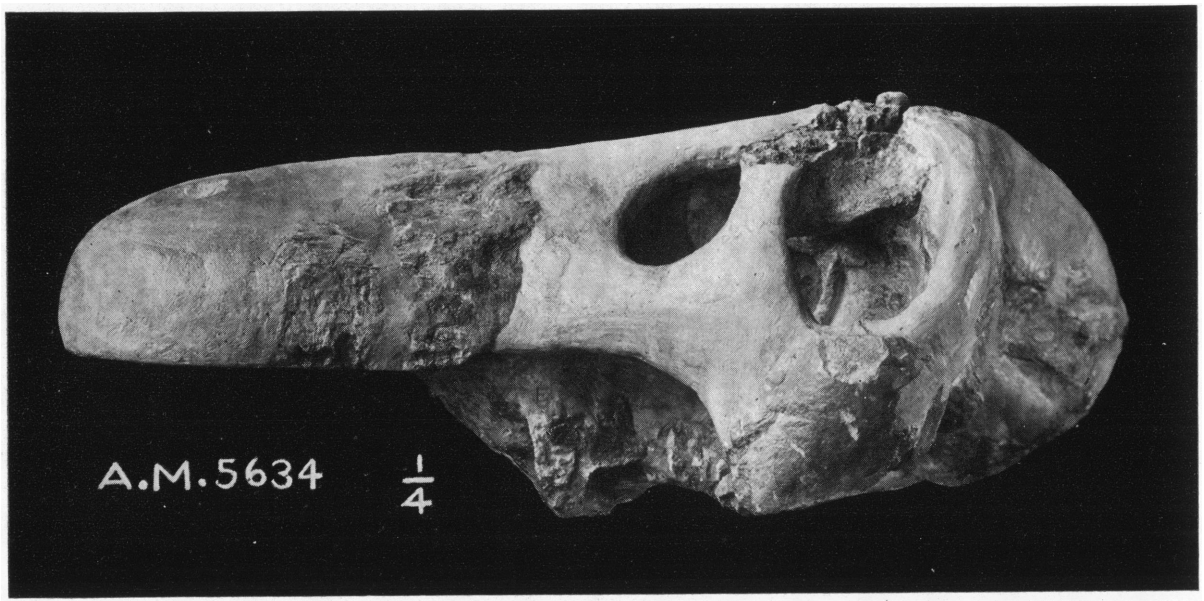

A.M.5634
1/4

PLATE XI

Jonkeria ingens. Amer. Mus. No. 5608. Ventral view. $\times 1/4$.


A.M. 5608
1/4

PLATE XII

Jonkeria ingens. Amer. Mus. No. 5608. Lateral view. $\times 1/4$.


1/4
A.M. 5608

PLATE XIII

Jonkeria ingens. Amer. Mus. No. 5608. Dorsal view. $\times 1/4$.


1/4
A.M. 5608

PLATE XIV

Jonkeria vanderbyli. Type. Amer. Mus. No. 5620. Dorsal view. $\times 1/4$.


A.M.
5620
1/4

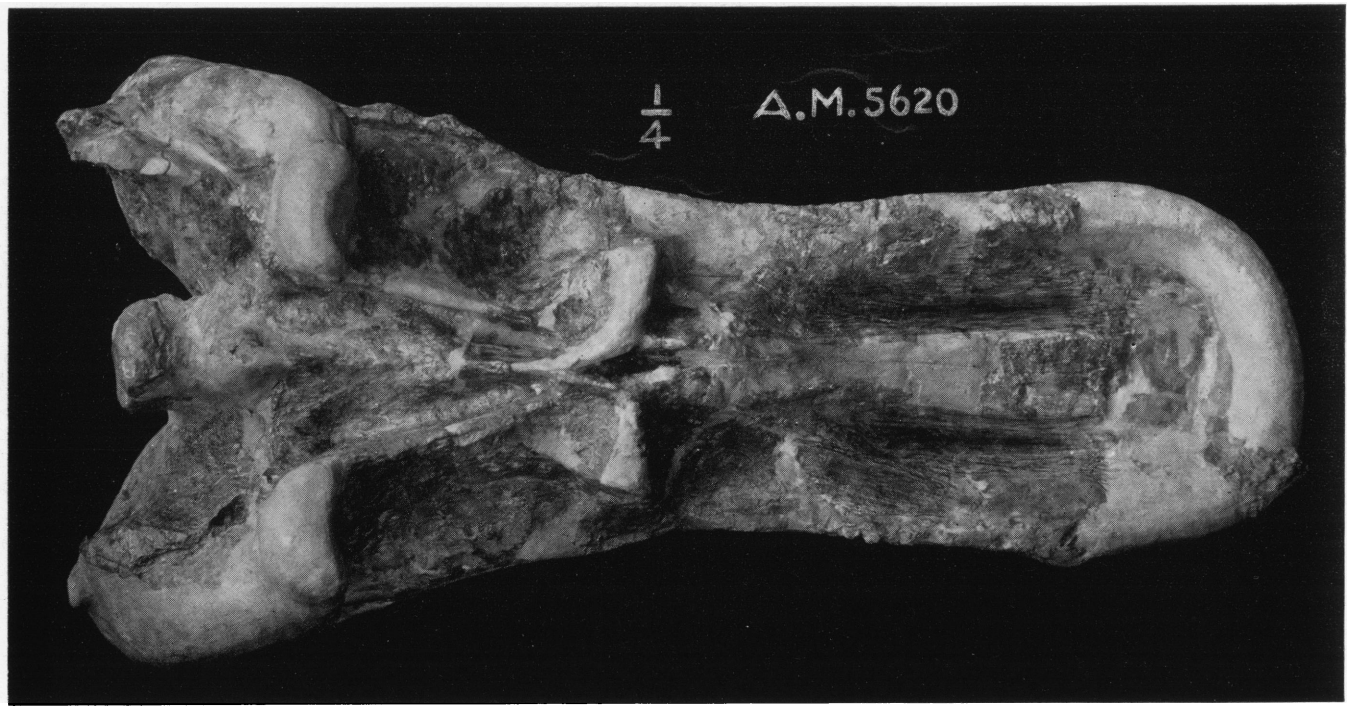
PLATE XV

Jonkeria vanderbyli. Type. Amer. Mus. No. 5620. Lateral view. $\times 1/4$.


A.M. 5620
1/4

PLATE XVI

Jonkeria vanderbyli. Type. Amer. Mus. No. 5620. Ventral view. $\times 1/4$.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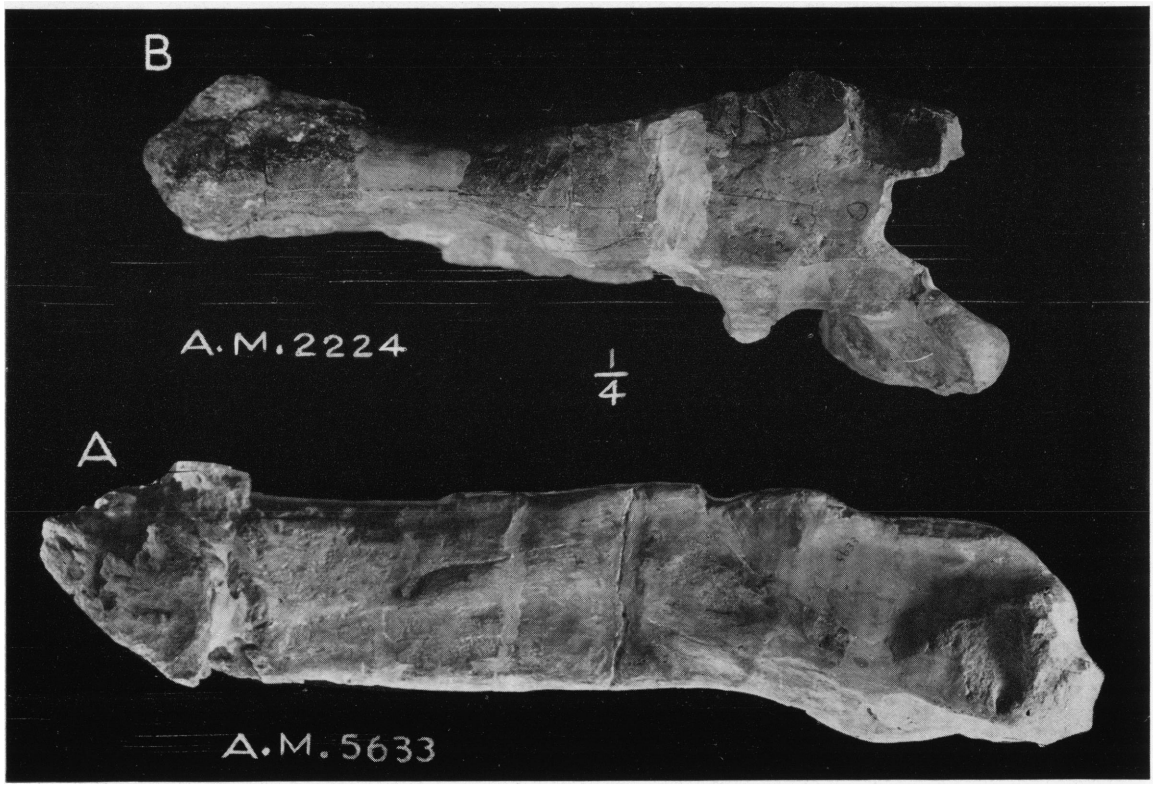
A.M.5620

Plate XVII

A. *Jonkeria angusticeps* (Broom). Amer. Mus. No. 5633. Inner view of right mandible. $\times 1/4$.

B. *Anteosaurus minor*. Referred specimen. Amer. Mus. No. 2224. Dorsal view of distorted skull. $\times 1/4$.


B
A.M.2224
1/4
A
A.M.5633