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UNIVERSITY OF MICHIGAN

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DESCRIPTION OF A SKULL OF *KANNEMEYERIA ERITHREA* HAUGHTON

BY
E. C. CASE

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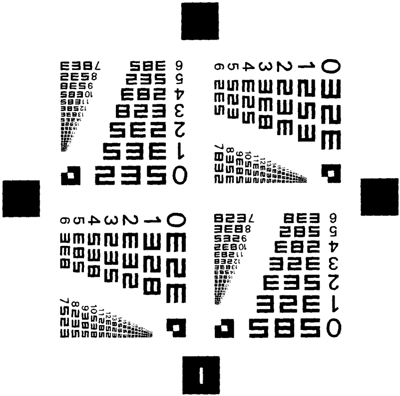

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CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

(Continuation of Contributions from the Museum of Geology)

UNIVERSITY OF MICHIGAN

Editor: EUGENE S. MCCARTNEY

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DESCRIPTION OF A SKULL OF *KANNEMEYERIA ERITHREA* HAUGHTON

By E. C. CASE

A SKULL of *Kannemeyeria erithrea* Haughton, No. 14530, was found in the Upper Beaufort (*Burghersdorf*) beds, about one mile north-northwest of Lady Frere, Cape Province, South Africa, by Mr. H. F. Donner, while collecting for the Museum of Paleontology of the University of Michigan. The whole specimen consisted of a large nodule inclosing the skull, with only the broken end of the left tooth and the tip of the nose exposed, several vertebrae, a right femur, and many fragments of ribs. The total length of the skull is 480 mm. Much of the matrix was removed from the bones of the axial skeleton by heating and plunging in water, after which the bones were easily cracked out of the loosening matrix. The preliminary cleaning of the skull was made by the use of an air hammer, but the final cleaning and the search for sutures were made by carefully chiseling with very fine points, largely under a binocular microscope.

The skull (Plates I–II) is nearly perfect; it lacks only the right tusk. The left quadrate and quadratojugal were detached, but were so little distorted that they fitted back into position very closely. The whole skull is slightly distorted, so that when viewed directly from above the lower part of the left squamosal and a part of the quadratojugal are visible. This distortion does not extend to the facial region.

The skull is that of an old individual, and this, with the rugose surface of the bones of the snout, makes the determination of some of the sutures difficult, but careful cleaning and search have revealed most of them in a satisfactory way. It resembles *Kannemeyeria erithrea* Haughton more closely than any other described

form of anomodonts, and since it comes from the same horizon and the same general locality it is referred to that genus and species.

In some places the specimen differs from the larger anomodonts already reported, but since most or all of these points have been uncertainly shown and tentatively described in the original specimens, and since there is so large a difference in the various forms, as revealed by the descriptions, the account given here is close to that of the apparent structure, even where it seems to depart

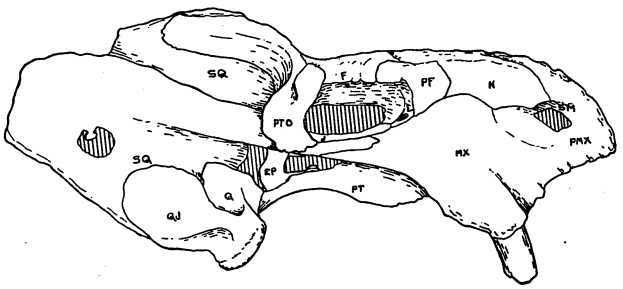

FIG. 1. Lateral view of the skull. × ⅙. EP, epipterygoid; F, frontal; J, jugal; L, lachrymal; MX, maxillary; N, nasal; PF, prefrontal; PMX, premaxillary; PT, pterygoid; PTO, postorbital; Q, quadrate; QJ, quadratojugal; SM, septomaxillary; SQ, squamosal

from the previously accepted form and relations of the various elements.

The *premaxillaries* (Plate I, Fig. 1,[1] and text Fig. 1) constitute the anterior part of the rostrum and terminate posteriorly in sharp processes between the nasals; the surface is rugose, and the suture lies in a decided groove. The prominent median ridge extends to the anterior end. The contact with the maxillaries beneath the narial opening is marked by a slight displacement, which can be followed upon the palatal surface. The suture can be traced backward and inward for a short distance; it then disappears in the

[1] The specimen was naturally colored in various shades of red; this made it impossible to bring out the details on a photographic plate. It was therefore covered with a fine-grained, water-soluble white paint, which accounts for the unusual appearance in the plates.

rugosities of the roof of the mouth. The premaxillary forms at least one half of the prechoanal area. The two prominent ridges are confined to the premaxillary part of the palatal surface.

The *maxillaries* meet the nasals and prefrontals on a line, slightly convex upward, which runs from the nares to the lachrymals; the surfaces are much roughened. Following the line of the socket of the large tooth there is a heavy prominence which gives the lower part of the maxillary a specious appearance of being an inner surface, whereas it is really outer, since it is entirely outside the cutting edge of the jaw.

The rugose condition of the palatal surface is continued to the anterior edges of the posterior nares. The median continuation of the vomer forms a prominent ridge on the posterior part of the bones. This ridge, with the adjacent parts of the maxillaries and premaxillaries, is marked by a peculiarly heavy and intricate rugosity; the surface, especially upon the ridge, has a worn, shiny appearance, as if it had been exposed and polished by use rather than covered by a horny sheath such as undoubtedly armed the edges of the maxillaries and premaxillaries. It is possible that this is a condition attained in old age, when the original horny covering had worn away.

The posterior part of the maxillary forms the anterior part of the suborbital arch, articulating with the squamosal and the jugal, and apparently with the lachrymal between the prefrontal and the jugal, though the exact outline of the lachrymal cannot be made out with certainty. On the lower side of the suborbital arch the maxillary extends as far back as the posterior edge of the orbit. On the lower surface the maxillary is in contact with both the palatine and the pterygoid and forms a good part of the periphery of the large lachrymal (suborbital ?) canal.

The *nasals* constitute the middle part of the rostrum; they are rugose and carry the extension of the median ridge. The articulation with the frontals lies in a decided groove which runs backward and inward on each side and forms an obtuse angle pointing to the rear. Anteriorly the nasal of each side overhangs the posterior part of the narial opening, so that the latter is not visible from above. The edge of the nasal, which is sharply in-

curved opposite the middle point of the nares, makes a distinct notch.

The *septomaxillary* is indicated on both sides as a small element on the under side of the overhanging part of the nasals, by obscure sutures seemingly in process of disappearance by anchylosis. It is set so far within the overhang of the nasal that it is visible only from below. It is broadest posteriorly and narrows to a point anteriorly. The posterior end is separated from the nasal-maxillary

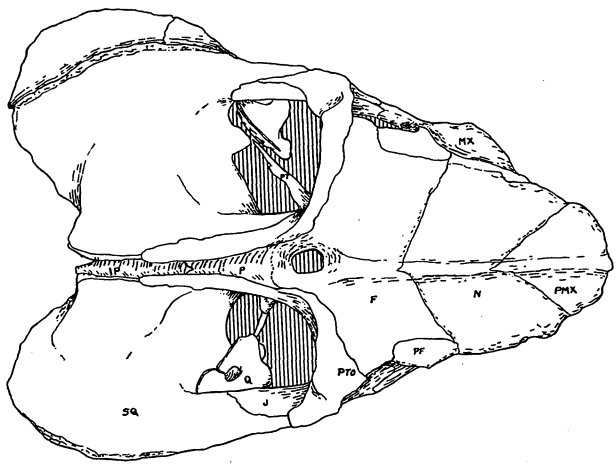

FIG. 2. Top view of the skull. × $\frac{1}{6}$. IP, interparietal; P, parietal. Other lettering as in Figure 1

junction by a distinct notch on the left side, but this area is filled with crushed bones on the right side.

The *frontals* (Plate I, Fig. 2, and text Fig. 2) form the posterior part of the snout and the posterior half of the upper rim of the orbit. The median ridge disappears at about the middle point and sinks into the depression which holds the pineal opening. Posteriorly the frontal is in broad contact with the postorbital; there is no evidence of a postfrontal. The whole surface is rugose. No suture can be found indicating a preparietal bone; the frontal is seemingly continuous around the large pineal depression and extends into the deep groove behind the point where it must join

the parietal. It is very possible that a preparietal exists and was distinct in the young skull, but that the sutures are obliterated in maturity or old age. Haughton [2] was unable to see the preparietal in the holotype genus and species, but believed that he could detect the sutures in a fragmentary specimen referred to the same genus. It is certain that the frontal extends backward on either side of the pineal pit between the prolongations of the postorbital.

The pineal pit is relatively large, with the sides nearly vertical. The walls are marked with a close and intricate, but not coarse, sculpture.

The *prefrontals* form the anterior half of the upper rim of the orbit and join the nasals, maxillaries, and lachrymals.

The *lachrymal* is a small bone lying almost entirely within the orbit and forming but a small part of the antero-inferior border of the rim. The outlines are not easily seen, partly because of the necessity for retaining a certain amount of the matrix to preserve the specimen. The lachrymal is entirely surrounded by the adjacent bones, being in contact with the prefrontals and maxillaries externally, the jugals posteriorly, and the palatine on the inner side. On the lower side of the suborbital bar they appear as small wedges between the palatines and the maxillaries. The large foramen leads directly downward, and the canal opens undiminished on the lower side of the bar. On the upper side the foramen is entirely within the lachrymal, but on the lower side it is bounded in front and on the sides by the maxillary, and posteriorly by the lachrymal and palatine. This canal is in the position and relations of the suborbital of the mammals rather than the lachrymal, for it is largely within the maxillary and really upon the outer side of the face. The prominence of the maxillary bone following the socket of the tooth gives the lower opening an apparent but false appearance of being on the lower or inner side. A true lachrymal canal leading to the nasal passage has not been located; possibly it is present as a branch of the larger one.

The *postorbital* follows the course commonly found in the larger anomodonts. It forms the postorbital bar, which expands at the

[2] Haughton, S. H., "On a Skull of the Genus *Kannemeyeria*," *Annals South African Mus.*, Vol. 12, pt. III, No. 8, p. 91, 1915.

lower end to overlap, on the outer side, a rising process from the jugal. This part of the bone is rugose on the outer and posterior face. At the level of the upper edge of the orbit it bends inward at right angles, joins the frontal by a close suture, and forms the anterior border of the temporal fenestra. Near the median line it curves backward, lying upon the parietal, interparietal, and squamosal and forming the side of the strong parietal crest.

The *parietal* and interparietal appear at the bottom of a deep groove between the postorbitals and squamosals which form the sides of the high and narrow parietal crest. These bones rise on the sides of the groove and appear irregularly at the crest of the ridge. They may be seen in places from the side, but only in very slender exposure. This condition must have varied with age and with different individuals. The anterior end of the short parietal cannot be distinguished by suture from the frontal and preparietal (?), but is clearly separated from the postorbital and interparietal.

The *interparietal* also appears on the upper surface for a short distance only, and within the groove. It is bifurcate posteriorly, continuing the groove upon the posterior surface of the skull. On the posterior face the bone spreads outward and downward in a fanlike shape between the squamosals, which overlap it on the crest, and the exoccipitals. Its lower two-thirds is covered by the narrow supraoccipital.

The *squamosals* are very large elements which form the greater part of the posterior half of the skull when seen from the sides or from above. The bone is, as a whole, relatively thin, but is expanded into three great flanges: an outer one supporting the quadrate (quadrate flange); an inner, forming part of the brain case (cranial flange); and a third, almost at right angles to the other two, uniting with the jugal and maxillary (zygomatic flange).

The zygomatic flange continues forward from the posterior edge of the skull to a point opposite the upper end of the quadratojugal, where it separates from the rest of the bone as the posterior end of the zygoma. It is shortly joined by the jugal, which lies along its inner side. Near its mid length the bar supports the

lower end of the postorbital and continues forward to end between the two points of the bifurcate posterior process of the maxillary.

The quadrate flange extends downward and forward and ends just above the articular condyles of the quadrate. The quadrate and quadratojugal lie upon the anterior face of this flange, which extends nearly halfway to its posterior edge.

A peculiarity of the specimen is the presence, in the right quadrate flange, of a perforation two or three centimeters in diameter. The nearly circular opening lies at the bottom of a depression on either side. The edges are paper-thin except where a small bit of bone extends into the opening from one side. The condition evidently resulted from injury sustained by the animal in life, which was partly or completely healed before death. The circular shape and the size of the opening suggest very strongly a blow from the tusk of some similar animal — perhaps, if the tusked anomodonts are the males, as seems very probable, a decisive thrust in some battle for a mate.

The anterior part of the cranial flange forms the side wall of the brain case, but the major part extends behind the foramen magnum. The articulations with the exoccipital and the opisthotic portions are clearly shown on the posterior face of the skull, but the adjustment to the proötic and epiotic elements is hidden. A small post-temporal fenestra lies in the angle of the juncture of the cranial and quadrate flanges.

The *quadratojugal* and *quadrate* bones are indistinguishably united at their lower ends, but are separate above. Broom [3] in his account of *Oudenodon kolbei* describes a fine suture that separates the two and runs across the face of the condyle, dividing it into two unequal parts. In this specimen no such suture can be found; the only indication of the union of the two elements is a rough line where the lower end of the quadratojugal joins the condylar part of the quadrate.

The condylar face is bipartite but complete; immediately above this the bone is divided into two oval plates of unequal size. The

[3] Broom, R., "On Some Points in the Structure of the Dicynodont Skull," *Annals South African Mus.*, Vol. 7, pt. V, No. 18, p. 337, 1912.

smaller, inner plate, the quadrate part, is nearly as broad, but only about one half as high, as the outer part. The larger, outer plate, the quadratojugal part, is applied closely to the anterior face of the quadrate flange of the squamosal, but the suture is very distinct. At its lower end it is separated from the quadrate by a circular opening of considerable size, about two centimeters in diameter. Above the opening the two plates come into close contact, but are not united. The quadrate stands at a slight angle to the squamosal, but is free from it. It is supported on the inner side by the posterior ramus of the pterygoid and the distal end of the opisthotic.

The two condyles of the deeply bipartite articular face of the quadrate are elongated antero-posteriorly, with their greater axis parallel to the main axis of the skull. They held the lower jaw to a strictly orthal movement and limited any preparation of the food to simple chopping, though this action was evidently a powerful one capable of cutting through very resistant material.

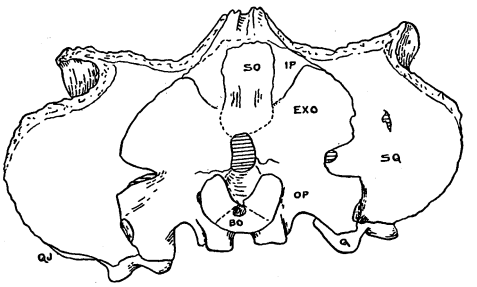

FIG. 3. Posterior view of the skull. × $\frac{1}{6}$. BO, basioccipital; EXO, exoccipital; OP, opisthotic process; SO, supraoccipital. Other lettering as in Figures 1 and 2

The posterior face of the skull (Plate II, Fig. 1 and text Fig. 3) is broad and inclined steeply forward and downward, owing to large development of the squamosals. The condyle is tripartite, with a deep excavation of the upper surface and a distinct notochordal pit.

The *basioccipital* forms the lower third of the condyle, which is set off from the remainder of the bone by a deep groove. The lower face carries two very prominent tubera of peculiar form and composition. Seen from behind, each process shows an irregular linear rugosity near the outer edge and extending down to the extremity of the process. This evidently marks the position of the suture with the opisthotic.

Seen from below, the face of the process has the outline of the letter C, with the points very nearly in contact; the main part of the surface is formed by the basioccipital and the outer, posterior, part by the opisthotic. The process is high and incloses a deep cavity that leads to the foramen ovale. The basisphenoid takes small part in the tubera and appears as only a thin plate overlapping the anterior faces of the processes.

The peculiar form of the tubera basioccipitalia and the part taken in them by the opisthotics explain the seeming anomaly in the position of the stapes as described by Broom.[4] The lower face of each process slants upward and outward, so that the deep inclosed pit opens as much outward as downward, thus permitting articulation with the nearly horizontal stapes.

The *exoccipitals* occupy a large part of the posterior face of the skull. The lower, opisthotic, portions are heavy processes which extend outward and downward to articulate with the quadrate, squamosal, and the pterygoid, for the quadrate ramus of the latter is wedged in between the opisthotic and quadrate for a short distance. The upper, outer corner of the opisthotic is developed into a stout prominence with a blunt end. The lower part of the inner end of the opisthotic is closely applied to — in the specimen anchylosed with — the basioccipital as described above. Just outside the condylar portion is the common opening for the IX–XII nerves and blood vessels. The upper part of the exoccipitals forms the base and the sides of the foramen magnum and comes in contact with the supraoccipital, interparietals, and the squamosals. Between this part of the postcranial surface and the opisthotics there is a deep notch, at the extremity of which lie the small post-temporal fenestrae.

The form of the *supraoccipital* is apparently different from that usually figured. It is a narrow plate which stands vertically in the skull and overlaps the interparietal, but which does not reach to the apex of the cranial ridge. Below, it fuses indistinguishably with the exoccipitals, but in youth apparently extended to the upper edge of the foramen magnum.

[4] Broom, R., "On the Structure of the Internal Ear and the Relations of the Basicranial Nerves in Dicynodon ...," *Proc. Zool. Soc. London*, 1912.

The *interparietal* appears on the posterior face of the skull as a narrow element on either side of the deep groove in the median crest, is overlapped on the sides by the squamosals, and then expands downward to its contact with the exoccipitals. The lower part of the median portion is covered by the narrow supra-occipital.

The lower surface of the skull (Plate II, Fig. 2, and text Fig. 4) begins with the basioccipital, although a very large part of the

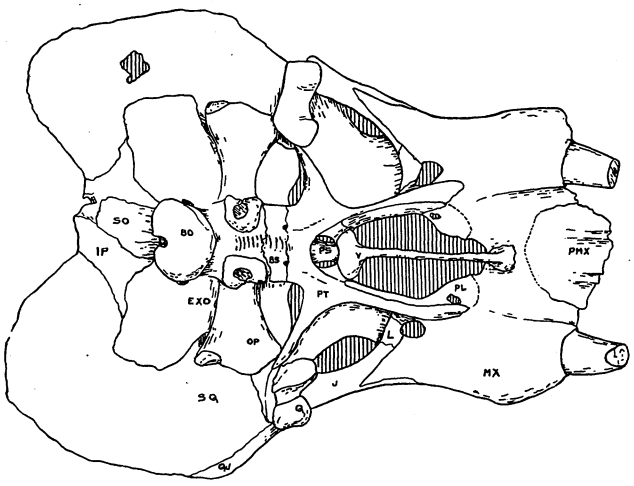

FIG. 4. Lower view of the skull. × $\frac{1}{6}$. BS, basisphenoid; PL, palatine; PS, parasphenoid; V, vomer. Other lettering as in previous figures

posterior face is visible from below because of its strong inclination backward.

The *basisphenoid* appears in a very narrow area, transversely; the posterior part turns sharply downward and overlies the anterior faces of the tubera, not reaching to the bottom of those processes. The remainder of the bone is hidden by the pterygoids and on the sides, in this specimen, by the epipterygoids and the matrix, which is necessarily retained to support that slender element. Just at the juncture of the basisphenoid and the pterygoids, but

largely within the former, are the foramina for the internal carotid arteries.

The *pterygoids* are complicated in structure and are best described in their several parts. The median part extends from the overlap by a straight transverse suture upon the basisphenoid, to the circular interpterygoid space. The posterior half of this part is marked by a depression which extends forward from between the tubera, across the basisphenoid; and ends on the pterygoid. All trace of the union of the two bones of the opposite sides has disappeared. The interpterygoid space is nearly circular. It is closed in front by two processes from the inner side of the anterior portions, meeting, or nearly meeting, behind the expansion of the posterior end of the vomer. At the top of this space can be seen the presphenoid process of the basisphenoid.

The quadrate processes rise opposite the interpterygoid space and curve backward to end between the quadrate and the opisthotic. They present a narrow face downward, but are expanded vertically. The anterior processes are narrower, but high, and curve forward around the posterior nares. The anterior end is somewhat expanded and articulates, by interlocking tongues, with the maxillary and rests upon the palatine.

The *palatines* lie above the pterygoids. They send backward the processes which lie upon the inner side of the pterygoids and form much of the outer walls of the choanae. Anteriorly they are expanded and heavier. On the inner side, opposite the anterior end of the pterygoid, there are roughened areas which extend into and partly close the anterior part of the choanae, but they do not meet in the median line or come in contact with the vomer. There is a foramen in this roughened space just at the contact of the palatine and the pterygoid, which is probably the palatine foramen. The palatine also appears on the outer side of the pterygoid that joins the lachrymal and the maxillary and forms part of the inner edge of the infraorbital foramen on the lower surface of the skull.

The *vomer* is high and narrow and is more or less roughened on its lower edge, but especially so at the anterior end. As mentioned in the description of the maxillary, its suture with that bone is

entirely closed or is indistinguishable in the rough sculpture. The posterior end is expanded and turned outward on each side in thin processes that overlap the parts of the pterygoids which close the interpterygoid space in front.

The *epipterygoid* lies in the normal position upon the upper edge of the quadrate process of the pterygoid and extends directly upward to articulate, probably, with the parietal, since it is too far back to join the frontal. The base is extended along the pterygoid from close to its junction with the quadrate nearly to its mid length. The rising portion is thin and rapidly narrows anteroposteriorly. It is broken at about its mid height on both sides, and on both sides there are strong suggestions that the separation is at the original union of an upper and a lower part. At the moment such a condition is not explainable.

The anterior extension of the base of the epipterygoid is low, not over a centimeter in height, and runs forward to beyond the front of the interpterygoid space. Near its front end there is a process about a centimeter long which rises abruptly, extends outward and upward, and ends bluntly. Careful search has revealed no conclusive evidence that this part is distinct from the base of the epipterygoid. The only suggestion of this continuation of the epipterygoid, or the presence of a separate element, is that it is the beginning of an orbitosphenoid bone; the notch behind the abruptly rising process is the point of exit of the optic nerve. The origin of the alisphenoid and orbitosphenoid bones has been variously explained, one suggestion being that they are developments from the epipterygoid, but the fact that the epipterygoid and the anterior structure are upon the outer edge of the pterygoid and hence well outside the brain case and any anterior extension of it seems to cast doubt upon such an explanation. However, as has been pointed out, they occupy the relative antero-posterior position of the sphenoidal elements, and it is possible that they have been drawn inward, in the process of development toward the mammalian skull, to build the anterior continuation of the primitive brain case.

Unfortunately the necessity for retaining some matrix to support the fragile epipterygoids has prevented any examination of

PLATE I

FIG. 1. Lateral view of the skull of *Kannemeyeria erithrea* Haughton. × $\frac{1}{6}$

FIG. 2. Top view of the skull. × $\frac{1}{6}$

PLATE II

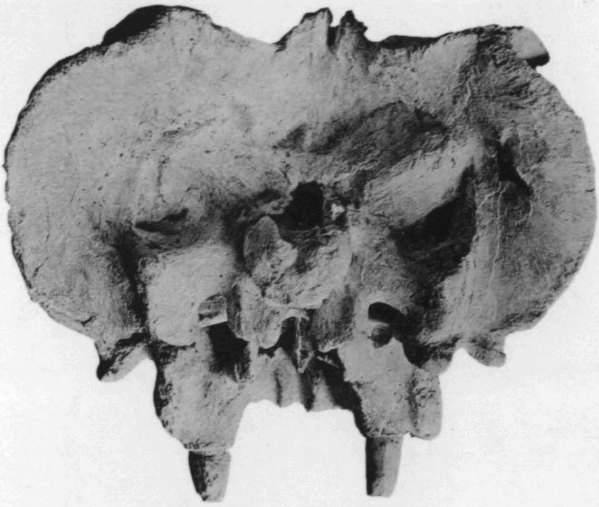

FIG. 1. Posterior view of the skull of *Kannemeyeria erithrea* Haughton. × $\frac{1}{6}$

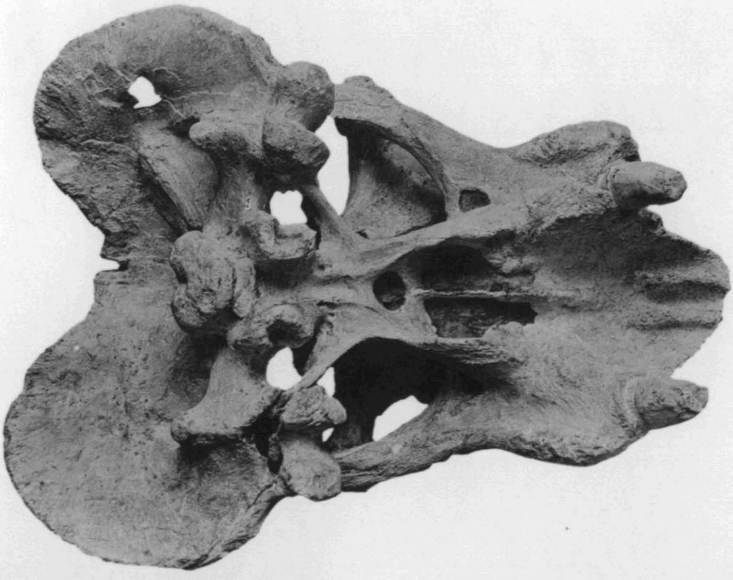

FIG. 2. Lower view of the skull. × $\frac{1}{6}$

the brain case, or of the proötic and epiotic bones, if such are present as distinct elements.

Careful preparation of the side of the brain case just above the base of the tubera revealed a fairly large foramen, evidently the one interpreted by Broom as the outlet for the VII nerve. The foramen for the V has not been located.

(*Continued from inside of front cover*)

of Michigan, by G. M. Ehlers and T. E. White. Pages 93–100, with 5 plates. Price, $.20.

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