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University of Michigan Studies

MEMOIRS OF THE UNIVERSITY OF MICHIGAN MUSEUMS

MUSEUM OF PALEONTOLOGY

VOLUME II

DESCRIPTION OF THE SKULL OF A NEW FORM OF PHYTOSAUR

DESCRIPTION OF THE SKULL OF A NEW FORM OF PHYTOSAUR

WITH NOTES ON THE CHARACTERS OF DESCRIBED NORTH AMERICAN PHYTOSAURS

BY

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ILLUSTRATIONS

PLATES

THE SKULL OF *BRACHYSUCHUS MEGALODON*

FIGURES IN THE TEXT

DESCRIPTION OF THE SKULL OF A NEW FORM OF PHYTOSAUR

WITH NOTES ON THE CHARACTERS OF DESCRIBED NORTH AMERICAN PHYTOSAURS

THE expedition from the Museum of Paleontology of the University of Michigan in 1927 to the Upper Triassic beds of western Texas recovered an almost complete skull, lacking the jaws, of a new form of phytosaur. This skull, number 10336 in the collection of the Museum of Paleontology, is the type of the genus and species *Brachysuchus megalodon.* The specimen was found near Otischalk in Howard County, Texas, about twenty miles southeast of Big Springs. The specimen, with many less complete and a large amount of fragmentary material, was found in a conglomerate of small clay pellets. The bones show no evidence of prolonged transportation or of exposure before burial; they are coated with a thin layer of very fine clay and there are frequently patches and seams of calcareous material. The dominant color of the fine clay which coats the bones is deep red, but there are patches of light green due to the reduction of the iron oxide. The clay pellets are frequently yellow from the hydration of the iron oxide, especially near the surface of the ground. The calcareous seams and incrustations, and the hydration of the iron in the pellets, are evidently secondary and the result of action at the place of burial of the bones, but the isolated position of the patches of clay pellets distributed through large areas of dominantly even-bedded and fine-grained clays, and the isolated and fragmentary character of the specimens, with no complete skeletons and rarely any associated parts of a skeleton, all tell of transportation to the place of burial. On the other hand, the bones rarely show evidence of erosion by movement; it is evident that the bones were buried in a soft slime of clay or in a mass of soft clay pellets and were afterward minutely fractured by movements of the clay in settling and compacting or in dessication, either before or after petrifaction. The abundance of sharply broken fragments on the surface is largely due to the minute fracturing *in situ,* for as soon as the specimens are exposed they fall to pieces along the old fractures. It is only when specimens are found shortly after exposure and removed in blocks of matrix that complete material can be recovered. Of the three complete skulls in the collection two were located by the exposure of the tip of the nose and the third was found completely buried in the process of excavating the lower jaw. Distortion of the individual bones is not common, but a skull may be distorted by slipping and displacement on the fractured surfaces.

The condition of the bones found in the clay is different from that of the bones found in the Shinarump conglomerate or its equivalents where the fragments all show evidence of prolonged transportation by water. The bones found in the clay can have been transported for a short distance only; the lack of complete skeletons of any considerable portion of a skeleton indicates either the decomposition of the cadaver before transportation, or decomposition and disintegration during transportation. The character of the matrix and the isolation of the skeletal elements indicate moving water so shallow that a swollen cadaver of any size would not be floated but rather dragged along the bottom. The fact that all the skulls are devoid of teeth would seem to bear out this suggestion; deeply rooted or even acrodont teeth would have been more likely to remain in position in a water-borne specimen. Supporting this idea of the dragging of the specimens is the fact that large quantities of coprolites, teeth, and other small débris are found in close association in restricted areas, as if they had been sorted by moving water acting on material of similar specific gravity. In addition to this, there is the great paucity of any remains of fish; a very few scales, three specimens of Dipnoan teeth, representing two species, a few fish bones probably belonging to a coelacanthid fish near *Macropoma* (*fide* A. S. Warthin, Jr.), are all that have been found by the collecting parties of several seasons. One or two beds of *Unio*-like pelecypods and a few scattered specimens of the same things, a few serpulid shells attached to larger specimens, and an unidentified specimen suggesting a large bivalved crustacean are the only invertebrates found. A few bits of charred wood, but no impressions of plants, make up the total record of life other than vertebrates.

In reviewing the evidence the author can only return to his own rather vague term of "flood wash" to describe the method of accumulation of the material, meaning by the term a sudden rush of water sweeping a large amount of débris, both organic and inorganic, from some adjacent higher area out upon a flat or into a depression, where there was a chance for the currents to assort and arrange their load. The suddenness of the rush of water would account for the undissolved clay pellets mixed with clay slime (just such deposits occur in the Big Bad Lands of South Dakota today) and for the deposition on areas where the absence of fossils of aquatic animals indicates that there was not usually a body of water. Just such a rush of water comes over the flats in the Bay of Fundy with the incoming tide, but the absence of marine or even fresh-water fossils precludes any direct comparison with tidal flats. That the same areas on which the vertebrate fossils were accumulated by sporadic waters were at other times under permanent bodies of water is shown by the heavy layers of evenly bedded, homogeneous clay both above and below and even laterally continuous with the fossiliferous clay pellet conglomerate. The bodies of water were singularly devoid of life if the absolute barrenness of the clays may be taken as an indication. The relatively few patches of fossiliferous clays and pellet conglomerates were probably formed by some sudden freshet or by the waters of some swollen stream which had burst its bounds, the waters rushing over an area of low elevation normally above water and sweeping the material along in the rapid current of the shallow flood, the quickly subsiding waters leaving the débris stranded. Such conditions would be found on a flood plain of a stream or, easily conceivable by one familiar with the violent storms of the arid regions, far above the usual level of the waters.

DESCRIPTION OF THE BONES OF THE SKULL

The skull here described was found in a small exposure of typical clay-pellet conglomerate, lying upon the ventral surface and with only the anterior extremity of the rostrum exposed. The exposed portion had already fallen apart, but the fragments were but little dispersed and almost all of them were recovered. As is usual, the teeth were nearly all lost; there is a single tooth near the middle of the series partly out of the socket and a few replacing teeth deep in the sockets. The bones were badly fractured, but the fragments had been re-cemented and held in place by the infiltering clay. The skull is only slightly distorted; the median portion has been forced downward crumpling some of the thin bones of the brain case. The bones are white when cleaned and the sutures, filled with the red matrix, are easily and definitely traceable in most places. Neither the lower jaw nor any other portion of the skeleton was found definitely associated with the skull; a large femur was found within a few inches of it, and, as it is of the proper size, may belong to the same individual as the skull, but as the whole of the small exposure was thickly strewn with isolated bones and fragments of bones the association is very uncertain. (See Figures 1, 2 and 3.)

Basioccipital.— The occipital condyle is very nearly hemispherical with the major portion of the articular surface on the lower side. There is a distinct and rather deep pit on the posterior face for the anterior end of the rudimentary notochord. A small portion of the outer upper angle on each side is formed by the exoccipital. The lower surface of the bone is short and set off sharply from the condyle; it is smooth except for a few small openings of nutrient vessels and some obscure longitudinal ridges. The anterior part of the lower face curves sharply downward and becomes strongly rugose where it joins the basisphenoid to form the rough, heavy prominence of the tubera basioccipitalia.

On the side, the suture between the basioccipital and the basisphenoid is a nearly straight line; at the upper end of the suture is the vertically elongate pit which held the upper end of the Eustachian canal. The canal apparently follows the suture between the two bones or lies very close to it. Posteriorly the basioccipital forms the lower border of the fenestra ovalis.

The upper face is visible only at the anterior end, well within the brain cavity, for the foramen magnum is entirely surrounded by the exoccipitals which exclude the basioccipital from any part in its floor. In all the specimens of the basicranial region in the collection, eight in all, the suture between the basioccipital and the basisphenoid is persistent and clearly visible, even on the irregular upper surface.

Basisphenoid. — This bone forms the greater portion of the floor of the brain case and is the strongest element in the cranial region. The posterior portion of the lower surface is the heavy descending process which is closely appressed to the similar, but much thinner, process of the basioccipital. This process is very rugose on the lower face and is the broadest part of the basicranium. The tubera are not distinct from each other or from the edge of the process as a whole. Anterior to the process the lower face is smooth and concave both laterally and antero-posteriorly; the concavity ends anteriorly in the low ridge which joins the bases of the slightly divergent basipterygoid processes. Near the lower edge on each side, about mid-way between the heavy descending process and the basipterygoid processes, are the lower openings of the canals for the passage of the internal carotid arteries. These canals extend upward and slightly forward and unite near their upper ends to open by a common foramen in the base of the sella turcia, different in this respect from specimen number 8409 of the Museum collection, in which they open by distinct foramina.

The basipterygoid processes are on the anterior end of the bone. They diverge as they descend, leaving a space between them in which the parasphenoid is attached. The outer face of each process is rounded and more prominent anteriorly than laterally. The lower half of the lateral face is smooth and flat, permitting free movement of the pterygoid upon it. These faces are shown distinctly in Mehl's figure of *Machaeroprosopus*.

Above the floor of the brain case the side of the basisphenoid extends upward and backward; the posterior edge of this portion forms the anterior border of the great foramen for the fifth nerve and joins the laterosphenoid above. The sides of the anterior edge, near the base of the sella, are low, smooth, and concave upward, marking the position of the foramen for the third nerve. This foramen is very close to the posterior end of the parasphenoid. Above the foramen for the fifth nerve there is another con-

Explanation of Lettering in Figures 1–3

BO, basioccipital

BS, basisphenoid

EXO, exoccipital

F, frontal

J, jugal

L, lachrymal

MX, maxillary

N, nasal

OP, opisthotic

P, parietal

PF, prefrontal

PL, palatine

PMX, premaxillary

PO, postorbital

PS, parasphenoid

PT, pterygoid

PTF, postfrontal

Q, quadrate

QJ, quadratojugal

SMX, septomaxillary

SQ, squamosal

TR, transverse

V, vomer

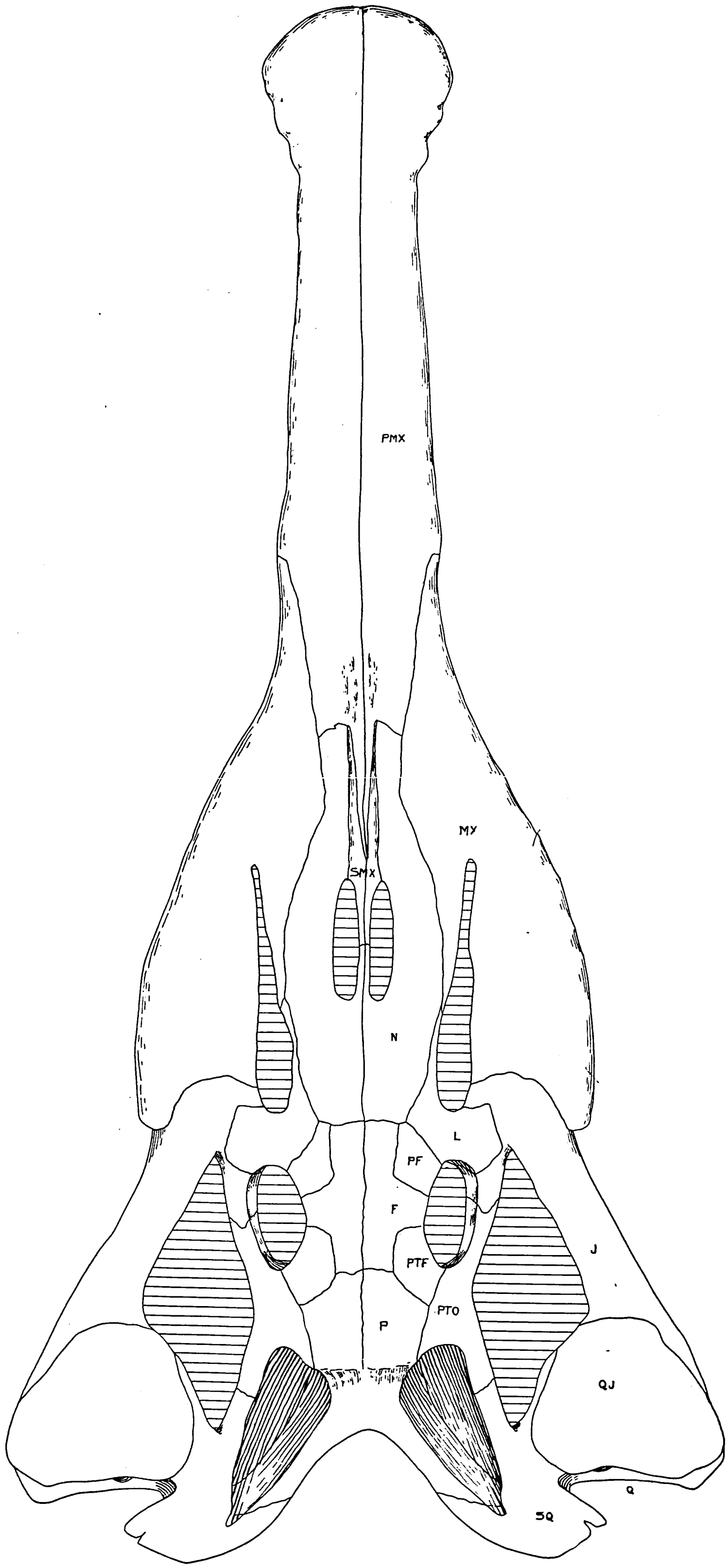


Fig. 1. Top view of skull of *Brachysuchus megalodon.* $\times \frac{1}{6}$

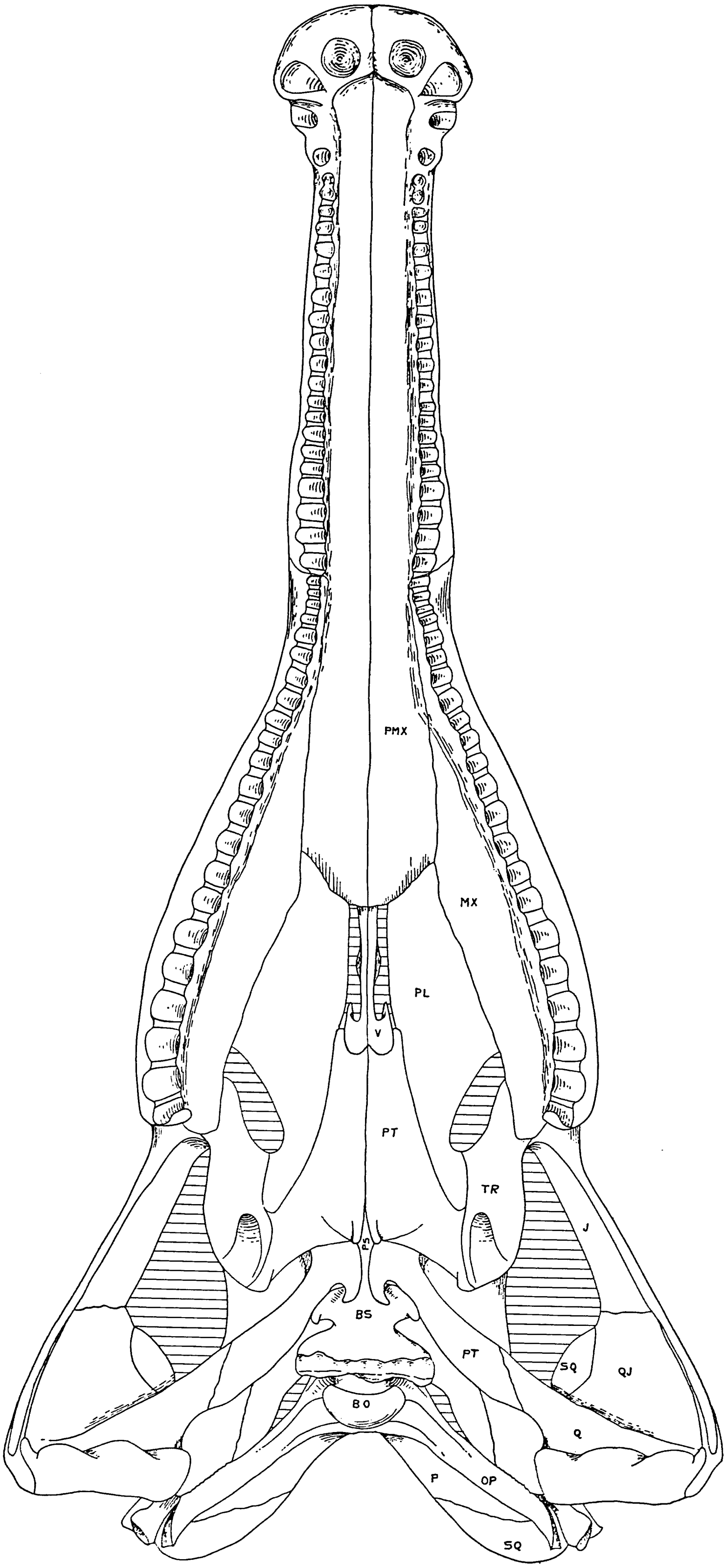


Fig. 2. Palatal view of skull shown in Fig. 1

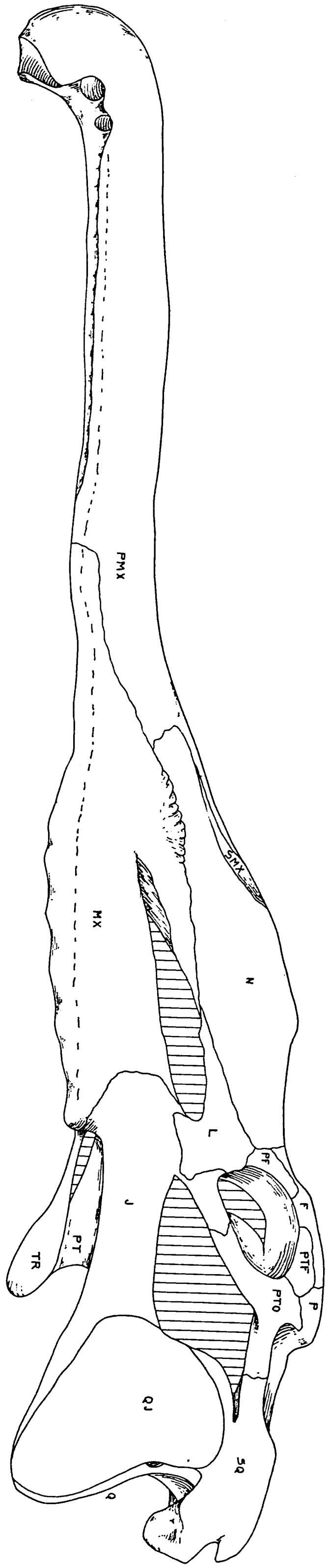


Fig. 3. Lateral view of skull shown in Fig. 1

cave space on the anterior edge which formed, with the cartilaginous extension of the cranial wall, the foramen for the second nerve.

The dorsum sellae rises obliquely backward; near its base, just behind the parasphenoid, is the single opening for the canals of the internal carotid arteries. On either side of this foramen there is a shallow pit on the face of the dorsum sellae. The dorsum is perforated on each side, somewhat above the middle, by the foramina for the sixth nerves. The upper edge is concave in the mid-line, but on either side is continued upward as a strong process which is free from the side of the basisphenoid and which joins by suture a similar process from the inner side of the laterosphenoid. The united processes form a pillar very similar to that seen in the same place in the skull of the alligator. The anterior face of the pillar is marked by a wide shallow groove which winds around it from without downward and inward. The outer face of the pillar is marked by a vertical groove and the laterosphenoidal portion is perforated by a foramen, probably for the passage of the fourth nerve.

Huene (1922), in describing this region in *Angistorhinopsis,* says: The orbitosphenoid (laterosphenoid of this paper) extends far forward and upward and (is characterized by the fact that it) has two upper processes, one extending forward and one laterally. The first appears in the orbit under the postfrontal and touching the frontal laterally and the second articulates bluntly beneath the postorbital. This description includes portions of both the laterosphenoid and the epiotic and it is possible that the two processes described are the divisions of the anterior edge of the laterosphenoid described in this specimen. It is also possible that the pillar-like process described above is the structure identified by Huene (1911) and Lees (1907) as the epipterygoid.

Laterosphenoid.—This name is used in preference to alisphenoid or orbitosphenoid because of the uncertainty of its morphological relationships. The contact of the laterosphenoid and the basisphenoid is shown on the inner surface of the left side of the brain case; here the outer edge of the dorsum sellae extends backward as a sharp point between the prootic below and the laterosphenoid above. No suture can be traced between the laterosphenoid and the epiotic, possibly because of the somewhat crushed condition of the bones in this region, but apparently there was complete union with all traces of the suture obliterated. The anterior portion of the laterosphenoid is bent sharply inward just below the roof of the skull in an apparently normal condition, since the curvature is the same on both sides and the edges meet or nearly meet, to form a short canal for the passage of the first nerve. This canal is described in *Paleorhinus* by Lees (1907). The somewhat crushed condition of the laterosphenoid makes the description of this region the least certain in the skull, but the author has satisfied himself by repeated examination and by the

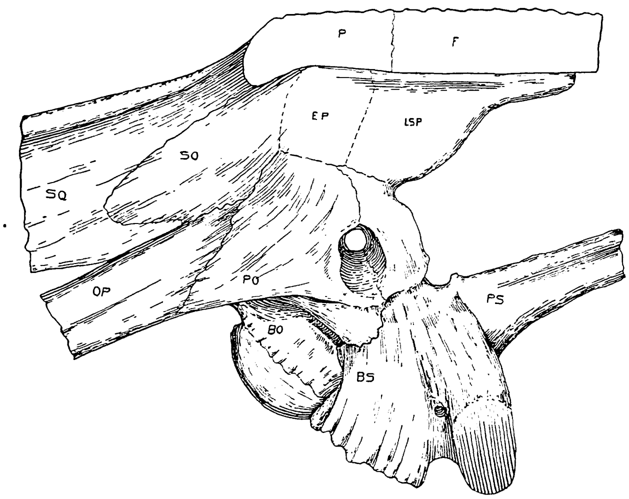


FIG. 4. Lateral view of right side of brain case; bones of temporal region removed. × ½

EP, epiotic; LSP, later osphenoid; PO, proötic; PS, parasphenoid; other lettering as in Figs. 1–3

criticism of others that the interpretation here offered is well founded. The restoration given in Figure 4 is the result of comparative measurements of this skull and of the uncrushed skull, number 7522 of the collection, and of measurements and replacements of fragments which have been forced into overlapping positions.

Parasphenoid. — The posterior end of the parasphenoid rises directly from the anterior end of the basisphenoid between the upper ends of the basipterygoid processes. There is no sign of a suture; the two bones are completely fused. The attachment of the parasphenoid is by the lower part of the posterior end and by a slender supporting ridge in the mid-line below. The upper part of the posterior end is free and forms the anterior vertical face of the hypophysial cavity. There is a shallow groove on this face which terminates below in a small canal which could be followed but a short distance with a fine probe. The parasphenoid becomes V- or boat-shaped in section almost at once. There is a long thin keel on the lower edge and the sides flare outward in equally thin edges. The upper surface is concave and the middle portion is rough and without surface as if it had given attachment to a strong cartilage. The bone extends forward in a horizontal line, becoming gradually and regularly smaller until it ends in a blunt point about opposite the vertical process of the palatine just posterior to the choanae. There is no detectable indication of a division into parasphenoidal and presphenoidal portions as reported by Huene (1911) in his specimen of *Mystriosuchus pleiningeri.* Mehl (1913) cites a longitudinal groove separating the two parts in *Angistorhinus;* it is probable that a downfolding of the slender sides produced the appearance of a double bone in both cases.

Epiotic. — This bone is indistinguishable from the laterosphenoid and the exoccipitals in the specimen; apparently the sutures were completely closed and obliterated. The key of the condition is found in specimen number 8409 of the collection, the one from which the endocranial cast was obtained (Case, 1928). In that specimen the sutures between the opisthotic, the epiotic and the proötic are visible in the cavity of the inner ear and can be traced from thence to the external surface of the bones. As shown in Figure 5 the three sutures meet in a triradiate manner in the space between the openings of the semicircular canals. The suture between the opisthotic and proötic passes almost directly downward, dividing the bridge over the horizontal canal into a lesser, anterior portion and a larger, posterior portion. This suture is continued in the stapedial groove. The suture between the opisthotic and the epiotic passes just anterior to the upper opening of the anterior vertical canal and from thence almost directly upward. The suture between the epiotic and the proötic passes forward to the posterior edge of the lower opening of the anterior vertical canal and thence upward; it is visible on the inner side of the brain case just within the opening for the fifth nerve. The epiotic is a slender element exposed on the inner surface of the brain case, but with the lower portion covered externally by the opisthotic and proötic. Huene (1911) describes the epiotic as appearing on the back of the skull between the squamosal and the parietal in *Mystriosuchus pleiningeri*. This is certainly not the case in this specimen where the squamosal joins the postorbital directly, and it is recorded for no other specimen of the phytosaurs.

Proötic. — This forms the posterior and lower borders of the foramen for the fifth nerve, overlaps the basisphenoid anteriorly, and covers the anterior part of the opisthotic. It meets the epiotic above and joins the

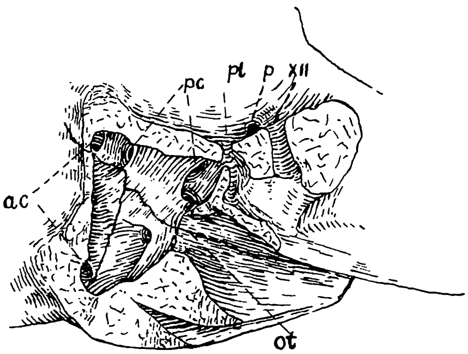


FIG. 5. View of the cavity of the inner ear of specimen number 8409, U. of M., showing the sutures between the proötic, epiotic and opisthotic. × 1

AC, anterior vertical canal; PC, posterior vertical canal; OT, otic-jugular opening and horizontal canal; PL, opening for perilymphatic duct; XII, opening for twelfth nerve

basisphenoid by a broad articular face above the foramen for the fifth nerve. These connections are in part visible on the inner surface of the brain case. Just posterior to the foramen for the fifth nerve, on the inner side of the brain case, is the common opening for the seventh and eighth nerves. The course of the canals for these nerves was described by the author (1928) in detail in the account of the endocranial cast taken from specimen 8409 in the Museum collection. The lower edge of the bone forms the anterior border of the stapedial groove and anterior to this is the deep groove in the bottom of which is the foramen for the escape of the seventh nerve. Huene (1922, p. 118) says that the foramen for the seventh nerve is on the border between the opisthotic and the proötic, but in all the specimens in the Museum collection which show this region, it is entirely within the proötic. Huene further says that the proötic reaches to the top of the epiotic and to the parietal. This does not seem to be the case in the present specimen.

Opisthotic.— This bone is overlain anteriorly by the proötic, as is shown in Figure 4. The posterior edge joins the exoccipital (without suture) and the squamosal, and the upper edge is in sutural contact with the supraoccipital-epiotic. The distal end extends outward and downward in a strong process which becomes spatulate just anterior to its extremity. There is a short, strong process on the inner side just short of the distal end for sutural connection with the quadrate. Huene (1911, p. 21) mentions a down-bent process or edge near the distal end of the opisthotic in *Mystriosuchus pleiningeri,* which he suggests may have been for attachment to the hyoid; this is evidently the process for attachment with the quadrate.

The distal extremity lies close to, but not in contact with, the posterior descending process of the squamosal. The posterior and lower edges of the proximal end join the supraoccipital and the exoccipital. The suture between the opisthotic and the proötic lies in the stapedial groove.

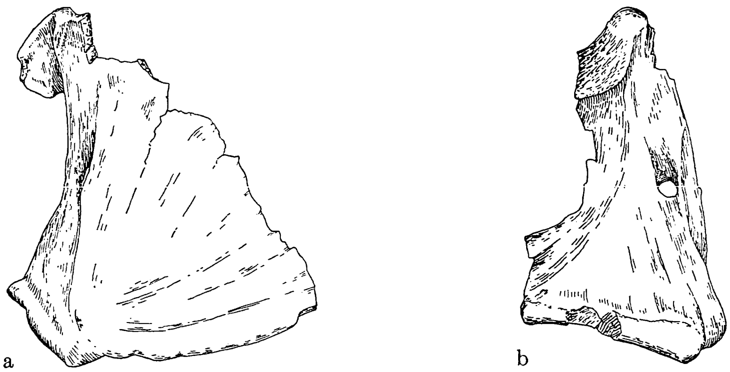
Viewed obliquely from behind, the opisthotic and proötic present three parallel grooves. The most anterior is the groove in the proötic into which opens the foramen for the seventh nerve. Behind this is the stapedial groove formed by both bones, and last is the large groove or opening through which escape the jugular vein and the ninth to the twelfth nerves. This posterior opening is separated from the one in front of it by a very thin partition of bone. The elongate pit which shelters the upper end of the Eustachian tube is practically a distal continuation of the posterior opening.

Exoccipital.— This bone is indistinguishable from the opisthotic by suture. The suture described and figured by Huene (1911) cannot be detected. As shown by this specimen and other specimens in the collection, numbers 8409 and 7522, the exoccipital completely encloses the foramen magnum. The lower ends of the bones form the upper outer portions of the condyle, joining the basioccipital by oblique faces which slant outward and downward. The inner edges of the lower portions meet in a suture in the median line in the floor of the foramen magnum. The upper ends send thin flanges inward which meet and fuse above the foramen magnum, excluding the supraoccipital from any part in the opening. The anterior edge of the outer side forms the wall of the large jugular opening, the third groove described above. The side wall is perforated by two canals, one, the posterior, for the twelfth nerve and the other, the anterior, for one or all of the ninth, tenth, and eleventh nerves, as described in the account of the endocranial cast from specimen number 8409 of the collection (Case, 1928). Just above the anterior foramen there is a deep pit on the inner side of the exoccipital, as described in the article just cited.

Supraoccipital. — This is a triangular plate which takes little, if any, part in the inner wall of the brain case. It lies upon the opisthotic and exoccipital and is excluded from the foramen magnum by the latter. It is not separated from the epiotic by suture, but is apparently excluded from any part in the inner wall of the brain case by the union of the epiotics in the median line above. It is loosely connected with the parietal, as noted elsewhere. Huene (1922) says that in *Angistorhinopsis* the two bones are closely united (*fest verwachsen*) and that the joint usually found between the roof of the skull and the brain case in primitive forms, as the *Parasuchia* are, is lost (*fortfallen*). As noted and described below, this is certainly not the case in the specimens in the Museum collection.

Quadrate. — The quadrate is but little exposed on the side of the skull, only the extreme lower end and a small portion of the posterior face being in sight. The remainder of the bone is concealed in lateral view by the quadratojugal and the squamosal. The posterior face is broad at the lower end and contracts to the apex. The quadrate foramen is located at about the middle of the outer edge. The upper end is the most interesting, as it reveals points in the morphology of the skull that have not previously been described. The upper end terminates in a smooth, almost hemispherical head which fits into a corresponding socket on the under side of the squamosal just at the point where the posterior descending process of the squamosal leaves the main part of the bone. This character is also shown in an isolated quadrate, number 8868 of the collection, Figure 6, and is visible on the type specimen of *Machaeroprosopus*. On the inner side of the quadrate, just below the articular head, there is a short, strong process which is closely united by suture with the lower, anterior, side of the opisthotic. The lower side of this process is concave, forming a wide groove or channel which leads to the stapedial groove of the opisthotic and the proötic.

The close union of the quadrate with the opisthotic and its free mobility on the squamosal, together with the movable articular faces between the basisphenoid and the pterygoid, and the pterygoid and the transverse indicate a very considerable degree of flexibility in the skull; it is decidedly



a b

FIG. 6. Right quadrate and quadratojugal, number 8868, U. of M. × ½. a, lateral view; b, posterior view

kinetic, as previously stated by the author (1922). The close union of the quadrate with the opisthotic, preventing all lateral movement of the former, necessitates a movable joint between the opisthotic and supraoccipital, and the parietal. To complete the flexibility of the skull, motion would be necessary between the bones of the temporal region; such motion is possible between the jugal and the quadratojugal where, as described below, the jugal fits into a groove in the lower edge of the quadratojugal with a smooth articular face visible in part on the inner side. To complete the possibility of movement there would have to be motion between the squamosal and the upper part of the quadratojugal or great flexibility of the bones at this point; this condition is not apparent in the specimen, but, as the union of the bones was by overlap, such an adjustment was possible.

The arrangement is such that a forward movement of the quadrate would elevate the strong descending processes of the pterygoids and make more room at the entrance of the throat, a mechanism that would aid materially in swallowing large bodies. Once the material had passed this point the descent of the processes would aid in forcing the mass further back until the constrictor muscles of the oesophagus could come into full play. The movement of the posterior part of the skull would be easily accommodated anteriorly by the peculiar arrangement of the vertical plates of the elements involved in the formation of the nasal passages (see pages 28–34 and Figures 12–16).

The process of the quadrate, which unites with the posterior process of the pterygoid, rises from the upper half of the inner edge and from the anterior face, and is supported by a strong buttress or ridge rising from the anterior face of the outer border. The process, strong at first, quickly changes to a thin nearly vertical plate and unites with the process from the pterygoid by a suture running downward and forward, at a point nearly half-way between the main body of the quadrate and the articulation of the pterygoid with the basisphenoid. There is no possibility in the three skulls in the collection that the pterygoid extends so far back as to appear on the posterior face of the quadrate, as described by Huene for *Mystriosuchus pleiningeri.*

The lower articular face of the quadrate is of nearly equal breadth throughout and is divided by a low oblique elevation into nearly equal saddle-shaped surfaces which are continuous across the elevation. The outer face is slightly the larger, with the main axis directed obliquely from without inward and backward; the inner face has the axis directed obliquely from within outward and backward, the two forming a close articulation which prevented any lateral motion of the jaws. The whole quadrate is peculiarly strong and formed to resist heavy stresses.

Quadratojugal.—This is a thin plate which overlaps the outer side of the descending process of the squamosal and covers most of the lateral face of the quadrate, overlapping the posterior surface slightly just below the quadrate foramen. The anterior edge takes small part in the formation of the border of the lower temporal fenestra. The lower edge is heavier and is bifurcate for the reception of the jugal, which reaches nearly to the posterior end of the skull, but is excluded from any contact with the quadrate (Figure 2). Huene (1922, p. 120) describes a similar condition in *Angistorhinopsis* when he says that just above the lower face of the quadrate there is a rugose thickening of the quadratojugal, and that 3 cm. anterior to the posterior end of the quadratojugal there is a notch into which fits the posterior end of the jugal. On the inner side the quadratojugal descends very nearly to the lower edge of the jugal and on this surface the smooth face between the two bones is visible. Huene (1922) says that the quadratojugal overlaps the jugal on the outer side and unites with it by an irregular suture in *Mystriosuchus pleiningeri.*

Squamosal.—The squamosal is a triradiate bone with a double anterior process, a descending process and a posterior descending process. The separation of the two parts of the anterior process takes place just above the point of articulation of the squamosal with the quadrate. One part, the upper, unites with the postorbital and is continuous with the descending process, which meets the quadratojugal and forms the posterior, and part of the upper, border of the lower temporal fenestra. The lower part articulates below with the distal part of the outer edge of the supraoccipital and joins the parietal anteriorly. Its upper, inner edge is thickened and the lower part is a thin plate resembling the part of the parietal with which it unites to form the outer edge of the supratemporal fenestra. There is no evidence in any of the skulls in the collection that the epiotic takes part in this edge as described and figured by Huene (1911) for *Mystriosuchus pleiningeri.* The squamosal is separated from the opisthotic by a narrow fissure; Huene (1911) describes it as lying upon the exoccipital but figures it as lying upon the opisthotic and supraoccipital. Mehl (1913) describes the squamosal of *Angistorhinus* as broadly connected with the opisthotic; it certainly is free from the opisthotic in this specimen.

Posterior to the point of articulation with the quadrate the two anterior parts unite to form the posterior descending process; this lies at an angle to the remainder of the bone and outlines the sharp otic notch. It it entirely free from the distal end of the opisthotic though the latter extends nearly to the extremity of the skull. The process is complicated by the presence of several minor processes and rugosities; the form is best

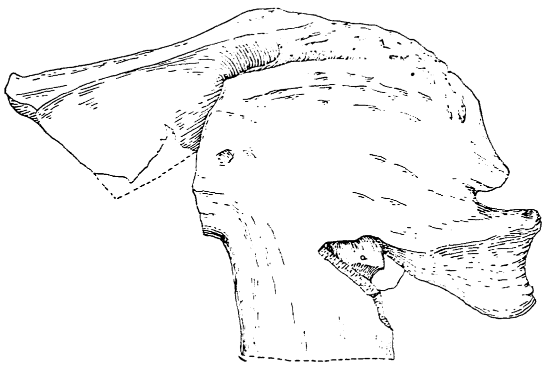


FIG. 7. Left squamosal and quadrate of *Brachysuchus*, showing the round head of the quadrate in position. × ½

appreciated from Figure 7. Seen from behind, the shape of the process makes clear the possibility of movement of the quadrate. The lower projection has a smooth upper face inclined inward and downward parallel to

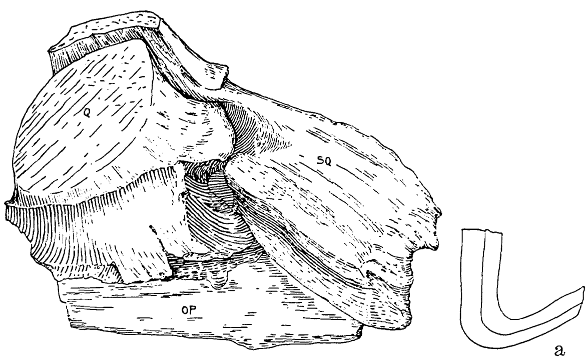


FIG. 8. Left squamosal, quadrate and opisthotic of *Brachysuchus* from behind and below, showing the head of the quadrate fitting into the socket in the squamosal and the groove on the quadrate into which the keel on the lower surface of the posterior process of the squamosal fits when the quadrate is thrust back. × ½

a, cross-section of groove in the quadrate

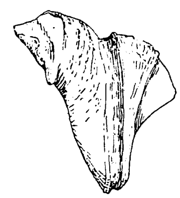


FIG. 9. Posterior view of the posterior process of the squamosal of *Brachysuchus*, showing how the lower edge is drawn into a keel to fit into the groove on the quadrate. × ½

the adjacent face of the opisthotic, but not coming into contact with it (see Figures 8 and 9). The two sides of the projection contract, sharply at first and then more slowly, to form a blunt ridge or keel. The lower edge slants downward and backward, increasing the depth of the keel toward the rear. This keel overhangs the groove or channel on the under side of the process of the quadrate, which unites with the opisthotic. In case the quadrate were thrown backward, the keel would fit into the depression exactly. It is obvious that the tympanic membrane was attached to this process and the postarticular process of the lower jaw and that it would have been relaxed when the jaws were opened and the quadrate thrown back in the act of swallowing, and tightened when the jaws were closed and the skull in an attitude of repose.

The otic foramen described by Williston (1904) and Lees (1907) is evidently a fracture of the squamosal permitting an imperfect view into the region of the quadrate-squamosal articulation. The more complete understanding of this region and the basicranial region, with a clear understanding of the position of the foramen ovale, made possible by more perfect specimens, makes the misinterpretation obvious. This was recognized by Mehl in 1915.

Stapes. — No stapes were found in this specimen or in the type specimen of *Leptosuchus crosbyensis,* number 7522 of the collection, but a very slender rod was found in the proper position in the type skull of *Promystriosuchus ehlersi,* number 7487 (Case, 1922).

Parietal. — The parietals have been broken across posterior to their junction with the supraoccipitals and the posterior portions dropped downward, but the replacement is simple. There was a distinct separation between the parietal and the supraoccipital, permitting anterior posterior movement of the supraoccipital-opisthotic-quadrate mass. The type specimen of *Leptosuchus crosbyensis* shows that the whole brain case was loosely attached to the roof of the skull by cartilage. Huene (1922, p. 119) says that the parietal is firmly attached to the supraoccipital in *Angistorhinopsis;* it certainly is not in any of the specimens in the University of Michigan collection.

The portion of the parietals above the supraoccipitals is flat and the bones of the two sides were closely united, but the position of the suture can still be traced. The flat surface continues back of the supraoccipital for a short distance, but the sides of the bone contract sharply, more on the inner side than the outer, and give the bone an irregular T-shaped section. The lower edge is in contact with the supraoccipital for nearly its whole length. On the lower surface there is a shallow indentation, probably marking the position of the epiphysial structures. Huene (1911) notes that there is a thickening of the suture between the bones of the opposite sides in *Mystriosuchus* which probably marks the former position of the parietal foramen.

Jugal.— As described above, the posterior portion of the jugal fits into a groove on the lower edge of the quadratojugal. It reaches nearly to the end of the skull, but is excluded from contact with the quadrate by the quadratojugal. The middle portion forms the lower edge of the lower temporal fenestra. Anteriorly the jugal joins the maxillary by a strong sutural attachment. The suture appears on the outer side in the deep notch at the posterior end of the dental series and then curves forward, upward, and backward, entering the lower edge of the antorbital vacuity some distance back of the middle point. It joins the lachrymal by a strong suture above, and the postorbital in the middle of the bar which separates the orbit from the lower temporal fenestra, and forms the anterior half of the border of the fenestra. At the posterior end of the antorbital vacuity the jugal is bipartite, a slender, smooth plate rising within the rough outer edge from which it is separated by a shallow groove.

On the inner side the jugal joins both the maxillary and the transverse. At the place of contact the bone is thickened and from this point a narrow buttress runs upward on the rising process which unites with the lachrymal. Between the jugal and the maxillary there is a large canal which leads forward and inward. Apparently the transverse does not take any part in the formation of this canal, from which it is excluded by a narrow contact of the jugal with the maxillary above. This canal has been observed in other specimens and was mentioned by Lees (1907) in his description of *Paleorhinus,* but its function is uncertain. In the skull of an alligator used in comparison there is a large foramen on one side, and two on the other, in approximately the same position, but entirely within the jugal and anterior to the transverse. These foramina lead into a cavity which soon breaks up into many small canals which open on the outer side of the maxillary just above the alveolar edge. In the skull of a Caiman, large openings of the same kind occur, also within the jugal but posterior to the transverse. It is probable that the large canal in the specimen allowed the passage of a large blood-vessel and nerves which ran forward on the upper surface of the palatal plate of the maxillary for a short distance and then entered the space between the roof of the mouth and the top of the skull, where they were broken up and distributed to the numerous small canals whose openings appear on the outer surface of the maxillary and premaxillary just above the alveolar border. Huene (1911, p. 10) describes the jugal of *Mystriosuchus* as excluded from the antorbital vacuity by the meeting of the lachrymal and the maxillary, and the lachrymal as meeting the postorbital under the orbit. The sutures are dotted in his figure, as if uncertain, and such relations do not occur in this specimen.

Maxillary.—The posterior edge of the maxillary is in contact with the jugal in the notch at the posterior end of the dental series. On the inner side there is a horizontal palatal plate forming part of the roof of the mouth and extending inward to meet the palatine and premaxillary. The lower surface of this plate is rugose at the posterior end. On the outer side the bone forms the greater part of the periphery of the antorbital vacuity. It meets the lachrymal above the vacuity by a very slender process, excluding the nasal from any part in the border of the opening. There is a line of small foramina on the outer side just above the alveolar border; one of these was followed as far as possible; it led almost directly upward between the outer surface of the bone and the wall of the alveolus. The surface of the bone is rugose, especially near the point where it joins the nasal; here the sculpture has a distinctly radial pattern.

The maxillary carries twenty-two alveoli on each side; the posterior ones are very large and the size diminishes regularly to the constriction of the rostrum at the anterior end of the bone. In the constriction there are four alveoli of exceptionally small size, especially as compared with the large alveoli of the posterior end of the premaxillary immediately in front of them. The reduction of the teeth and the constriction of the rostrum at the anterior end of the maxillary is apparently a very common character in the phytosaurs. It is indicated in many figures even when no mention is made of it in the description. It is apparently absent in *Mystriosuchus pleiningeri* and *M. planirostris,* and in *Angistorhinopsis* it amounts to a toothless space equal to two or three of the small alveoli and a constriction of the alveolar edge, but not of the rostrum as a whole, as figured by Huene (1922). The constriction in this region is much more obvious in the specimen of *Machaeroprosopus* than is shown in Mehl's figure (1916) and indicates a much shorter maxillary than he suggests.

The inner walls of the alveoli are very thin and apparently did not reach anywhere near so far downward over the roots of the teeth as on the outer side. The difference is 53 mm. in the third alveolus from the posterior end of the series. This character is very largely a natural one and not due to crushing or loss of the wall in fossilization, as the same character can be traced forward to the ninth or tenth alveolus from the anterior end of the whole series and is visible in two other specimens in the collection. This is the "bothriodont" type of dentition as defined by Jaekel. The horizontal palatal plate is separated from the alveolar edge by a shallow groove and is slightly elevated on the inner side of the groove.

Lachrymal. — The lachrymal forms the isthmus between the orbit and the antorbital vacuity. It joins the prefrontal above and sends a long process forward below the nasal to join the maxillary at about the middle of the upper border of the antorbital vacuity. It joins the jugal below by a thin overlapping plate. The heavier upper portion is perforated by the lachrymal canal. This opens by a large foramen in the inner border of the anterior portion of the lower edge of the orbit and is not visible from the side. The canal passes forward and upward and terminates on the inner side of the bone in the posterior upper corner of the antorbital vacuity; in both lachrymals of this specimen and in an isolated lachrymal in the collection, number 9602, the anterior end of the canal is obscure, but seems to end as an open groove on the inner side of the anterior end of the bone.

Prefrontal. — The prefrontal is a small bone roughly triangular in outline, meeting the frontal behind and mesially and the nasal in front and mesially. It forms a small portion of the orbit, but otherwise is entirely surrounded by bone. The surface is strongly rugose and is marked with deep pits, a character which is shown on both sides of the skull.

Frontal. — The frontal forms the middle portion of the upper edge of the orbit, meets the prefrontal and postfrontal by outer edges and the nasal and parietal by anterior and posterior edges. The bones of the two sides form a rough right-angled cross with the anterior and posterior arms longer than the lateral ones.

Postfrontal. — The postfrontal forms the upper posterior portion of the orbit and is otherwise surrounded by bones. It is roughly pentagonal in form, meeting the frontal by two surfaces and the parietal and postorbital by one each. The surface is rugose.

Postorbital. — This bone meets the postfrontal and parietal above and forms the posterior, and part of the lower, borders of the orbit. There is an anterior process or bar which joins the jugal to complete the lower border of the orbit. Posteriorly there is another bar which extends backward to meet the squamosal in the usual manner. The two bars meet at an obtuse angle just posterior to the orbit and their lower edges form the upper border of the lower temporal fenestra.

Nasal. — This bone is heavy posteriorly, where it meets the frontal, prefrontal, and lachrymal, and joins the bone of the opposite side for some distance forward. At about the middle of the length is the narial opening. The nasal sends a slender median bar forward which, with the bar of the opposite side, forms the posterior half of the septum of the nares. The anterior two thirds of the nasals are vertical, or nearly so, and the sides of the bones are convex outwardly, enlarging the nasal passage. The anterior end of the nares marks the highest part of the skull and from there forward the nasals descend in a gently sloping profile to the rostrum. In several specimens the authors have described an elevated rim to the nares; in others this is not mentioned. This seems an inconstant character, depending in large manner upon the condition of preservation of the specimen or the nature of the distortion. The same remark probably also applies to the breadth of the nares.

Septomaxillaries. — The septomaxillaries are slender elements standing vertically in the skull with only a very narrow exposure on the upper surface. The bones of the two sides meet posteriorly to form the anterior part of the upper septum. They diverge anteriorly where they are separated by slender posterior prolongations of the premaxillaries. The median portion of the septum is on the same level as the top of the skull but is not deep vertically, being entirely separate from the structures and septum of the choanae. Huene (1911) reports that in *Mystriosuchus pleiningeri* the septomaxillaries are separated by thin lamellae extending from the nasals and premaxillaries. This is not apparent in the present specimen; the septomaxillaries are in close, and in places in sutural, contact.

Premaxillaries. — The premaxillaries form the major portion of the rostrum. The upper surface is rounded and with minor rugosities. Some parts are almost smooth. There is an area of exceptional rugosity just anterior to the nares in the median line. This rugosity is shared by the nasals and the septomaxillaries and is the sole indication of the elevation of the rostrum anterior to the nares, which is so characteristic of some genera or species of the phytosaurs. Near the middle of the length of the premaxillary there is a slight convexity of the upper surface such as is present in almost all the described species, and is seemingly distinct from the elevation of the rostrum as a whole. This slight convexity can be seen in all the figures of the various forms described except *Phytosaurus kappfi, P. buceros,* and *Machaeroprosopus,* in which the elevation extends so far forward as to mask it. There are also certain specimens, as *Rhytiodon carolinensis* (Huene, 1911, Figure 30), an incomplete rostrum, number 7417 of the University of Michigan collection, and a specimen in the American Museum, described in a personal communication to the author by Mr. Walter Granger, in which the rostrum is devoid of the convexity, but is decidedly concave in profile; there is some slight suggestion of this character in *Mystriosuchus pleiningeri* and in *Angistorhinopsis;* it may come to be regarded as an important character as the phytosaurs are better known.

The elevation of the rostrum began at the posterior end and developed anteriorly, until in *Phytosaurus kappfi* and *P. buceros* it involved nearly the whole length. Attractive and suggestive as is the explanation of the elevation of the rostrum given by Abel (1922) and Nopsca (1926), the author is reluctant to admit the traumatic and pathological character of the elevation advocated by these writers. That such lesions did occur is shown in the specimen of *Leptosuchus imperfecta,* number 7523 of the collection, and has so been reported by the author (1924), and he cannot deny the cogency of the argument. Nopsca has supported the suggestion of Abel by showing that modern gavials frequently suffer from severe bites, and that if the bites are deep enough it gives rise to exostoses. He says (1926): " On the longi-rostral snout of the extinct gavial-like *Mystriosuchus* sometimes similar lesions occur. In some species of the genus *Mystriosuchus* the upper part of the rostrum is smooth, in other species of *Mystriosuchus* one or two excrescences are present, in other 'genera' the excrescences unite to form one big lump, and still other specimens ('genera') are known in which the excrescence deforms the whole facial region. In one case studied by an expert the outgrowths had a shape as if they had been formed by a tumour rather than an inflammation of the periostic layer.

" The gradual growth of the exostoses of the *Mystriosuchidae* shows that one is dealing with an inherited character, varying even within the same genus and species, but gradually growing during the history of the phylum. Considering what is known in the gavials, and that tumours are hereditary and due to repeated irritations, it is most tempting to look for the origin of the exostoses of the *Mystriosuchidae* in reiterated but individually acquired lesions."

Such statements have great weight but, on the other hand, it is not to be denied that incipient elevations are present in all known forms except *Mystriosuchus planirostris* (and perhaps *Rhytiodon*), and that the elevations increase in size in *Leptosuchus* and *Machaeroprosopus* without the suggestion of traumatic lesion. The author cannot concur with Nopsca's statement that there is a gradual phyletic growth in the size of the elevation. Such a series is not known, and if the recognizable pathologic forms are placed in a series, the series is not consistently borne out by other characters. Until more abundant evidence is obtained it can only be said that there was a tendency to the normal development of an elevation of the rostrum, and that there was susceptibility to injury in the same region. Nopsca's suggestion that repeated injuries resulted in a normal growth can only be regarded as an attractive but daring speculation.

The anterior part of the premaxillary is sharply expanded, bent downward, and developed into a nearly hemispherical prominence. The extremity is a little, but not much, more rugose than the rest of the bone. The lower surface, the roof of the mouth, is smooth, somewhat elevated in the median portion, and set off sharply from the alveolar edge by a distinct groove. The two anterior alveoli are much larger than any of the others of the series and are set, with the two of the opposite side, in a nearly transverse row across the end of the rostrum. The third and fourth alveoli are set in the side of the sudden constriction just back of the terminal expansion, and are much smaller than the anterior two, but indicate teeth still tusk-like in size and form. Behind these the twenty remaining alveoli are small at first and then increase gradually and regularly in size to the posterior end of the bone. The alveoli of all the teeth are remarkably deep, but this is peculiarly the case in the premaxillaries. In the posterior portion of the premaxillaries there is a cavity of considerable size between the roof of the mouth and the overarching roof of the rostrum. This cavity diminishes in size anteriorly until in the first third of the bone it is nearly or quite closed. The alveoli penetrate the outer wall of the cavity nearly to the mid-line; this character becomes increasingly prominent anteriorly. The alveoli of the tusks at the anterior end are closed by only a very thin wall of bone. The premaxillary teeth extend almost directly downward after escaping from the alveoli. This is a common character for all the heavier skulls. The teeth of *Mystriosuchus planirostris* extend outward at a considerable angle, as described and figured by McGregor (1906), and Huene (1922) says in one place that *Angistorhinopsis* has the teeth extended nearly lateral, but in another, that they are inclined at an angle of 25 degrees, and so figures them.

The posterior ends of the premaxillaries terminate in a blunt point in the middle line, which is strengthened by a thickening of the upper surface. In this thickened portion there is a socket which receives the anterior ends of the vomers. On either side of the mid-line the edge of the premaxillaries is complete and curves outward and backward forming the anterior edge of the lateral extension of the choanae. This edge passes above the anterior end of the palatine and unites with it some distance back by overlap, leaving a fissure-like opening between the two bones. This character has not been recorded in any other specimen of the phytosaurs, but it is very obvious on both sides in the present specimen.

Pterygoid. — The pterygoid extends from its contact with the quadrate behind, to its contact with the premaxillary in front of the choanae. It has the usual tripartite form with a posterior process, a lateral process, and an anterior process occupying the middle of the palate.

The posterior process is nearly vertical and extends backward and outward to join the quadrate. The contact with the anterior process of the quadrate is about half-way between the lower articular face of the quadrate and the point of articulation of the pterygoid with the basisphenoid. There is no possibility of the pterygoid extending to the posterior face of the quadrate, as figured and described by Huene (1911) for *Mystriosuchus pleiningeri;* indeed, his Figures 14 and 16 seem to indicate clearly that he has taken the anterior process of the quadrate for the posterior process of the pterygoid. Mehl (1913) observed the impossibility of such a posterior extension of the pterygoid in *Angistorhinus,* but seems to accept it in his description of *Machaeroprosopus* (1916), where, however, the region is partly broken away and a part, evidently the quadrate process for the opisthotic, is identified as the possible distal end of the pterygoid. Near the basisphenoid the posterior process is narrower vertically; the outer side is smooth, but on the inner side there is a low ridge rising from the upper edge and passing downward and forward, becoming stronger and heavier as it advances, until it develops into a smooth, flat face for contact with, and movement upon, the flat outer face of the basipterygoid process of the basisphenoid. The lower edge is thin in this region and is bent inward toward the basisphenoid as a thin flange, concave on the lower surface; this concavity is continued on the posterior face of the descending lateral process where it becomes a deep depression. Anterior to the flat articular face there is a sharp, recurved, hook-like process which fitted around the anterior face of the basipterygoid process of the basisphenoid, preventing any lateral motion of the pterygoid.

Immediately anterior to the hook-like process the pterygoid divides into the anterior and the lateral processes. The lateral process turns outward as it descends until the lower edge is almost at right angles to the mid-line of the skull. The upper part of the posterior edge is indented by the concavity mentioned above, but below, the edge contracts to a narrow plate lying upon and covering the posterior, upper, face of the transverse. Lees (1907) described the pterygoid of *Paleorhinus* as thickening distally; this was due to a lack of an understanding of the relation of the distal end of the pterygoid to the transverse. The large pit visible at this point is entirely within the transverse. The two bones meet with smooth surfaces which permitted motion in the direction of the main axis of the transverse, obliquely upward and downward. The direction of the motion was strictly limited by a raised edge on the inner side of the face on the pterygoid and a similar edge on the outer side of the face on the transverse. Above the transverse the pterygoid joins the palatine by a suture which runs at first upward and inward and then curves forward nearly parallel to the median line of the skull.

The anterior process is a portion of the skull which has been variously interpreted; its form and relationships are here described and further discussed in the description of the narial region. The palatine region of the skull is flat or slightly convex downward on the sides, but the middle portion is high and vaulted. This high vaulted portion is formed and roofed by the anterior process of the pterygoid almost entirely, a very important point in the study of the relationship of the phytosaurs to other groups.

The posterior portion of the anterior process is vertical or slightly inclined inward as it rises. The median edge is thickened and curved slightly outward at its posterior extremity. From the similarity in form of this curved edge to the part figured by Huene (1911) as the epipterygoid, it seems possible that he may have found a part of this edge detached and displaced and so misinterpreted it. The thickened median edges of the bones of the two sides are very close together even at the posterior end, leaving a very small interpterygoid space. The closely approximated edges run forward almost horizontally, forming the roof of the high vaulted median portion of the palate as far forward as the posterior end of the choanae. From the outer edge of the thickened median portion vertical plates pass both upwards and downwards, the combined bones of the two sides having an H-shaped cross-section (see Figures 10 and 17). The lower vertical plate rests upon the shelf formed by the strong ridge on the palatine and continues forward as far as the posterior end of the choanae. The upper plate rises part way to the roof of the skull and continues forward as far as the vertical plate of the palatine, opposite the posterior end of the choanae, where the median horizontal portion terminates and the vertical plate passes inside the palatine. Here the lower edges of the vertical plates come together and the upper edges drop down sharply, the plates of the two sides forming a V-shaped process which continues forward, as the inner of the two V-shaped processes which form the septum of the choanae, and comes to rest on the upper surface of the posterior end of the premaxillary (see Figures 16 and 17).

Transverse.— This is attached by a broad sutural surface to the maxillary and by a shorter one to the jugal. Above the distal articulation the shaft is contracted, but quickly enlarges again to a broad, heavy proximal end which has large contact with the pterygoid as described above. In the contracted portion the bone is twisted so that the plane of greatest expansion changes from nearly antero-posterior where it joins the maxillary and jugal, to nearly transverse where it is in contact with the pterygoid. The posterior end forms the outer corner of the descending process of the palate. Near the inner edge of this portion an opening marks the beginning of the large pit which penetrates far into the transverse. This cavity was at first considered to be a canal, but it has been impossible to follow it to an opposite opening. The direction of the pit is toward the center of the bone and there are no foramina where an exit might be expected; certain indications which were followed led into the sutural interspaces between the transverse and the pterygoid. It is possible that the pit broke up into small ramifications which it has been impossible to follow. The pit is in the position of the opening called the postpalatine foramen by Huene (1911) in *Mystriosuchus pleiningeri.*

The anterior edge of the distal portion of the transverse forms the posterior edge of the rather large palatine foramen; the proximal end, seen from above, seems to be wedged in between the palatines and the pterygoid.

Palatine. — The palatine is attached laterally to the maxillary as far back as the beginning of the palatine vacuity; the edge here turns inward and on the lower, posterior, side runs backward on the surface of the transverse as far as the opening of the deep pit in the latter. Mehl (1913) describes the palatine as not meeting the transverse in *Angistorhinus,* but as he speaks of the sutures as uncertain, and as the union of the palatine and transverse is a very persistent character in the phytosaurs, it is probable that the obscurity of the individual bones led to a very excusable misinter-

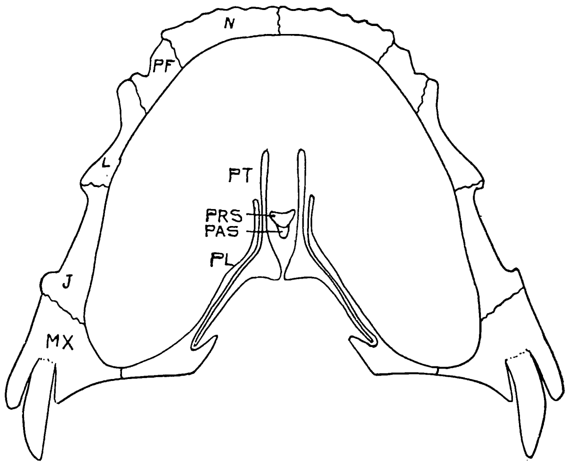


FIG. 10. Copy of Huene's figure, showing cross-section of the narial region in *Mystriosuchus pleiningeri* and his interpretation of the bones

PRS, presphenoid; other lettering as in Figs. 1–3 (pp. 6–7)

pretation. Just mesial to the opening of the deep pit the palatine joins the pterygoid and the suture runs inward at a little less than a right angle to the median line. On the same, lower, surface a ridge or angle starts from the posterior corner, near the opening of the pit in the transverse, and curves inward and forward, making the prominent rugose edge between the horizontal outer portion of the palatine and the vertical median portion which overlies the lower vertical plate of the pterygoid. Huene (1911) has shown this condition very well in his figure of the cross-section of the palate in *Mystriosuchus pleiningeri* (see Figure 10). Within, mesial to the ridge or angle, the palatine is concave, at first slightly and nearly horizontally, but as it advances toward the anterior end the concave face becomes more vertical and the inner edge rises as a thin plate applied to the outer, upper, surface of the lower vertical plate of the pterygoid. The edge of the lower vertical plate of the pterygoid rests upon the shoulder formed by the ridge on the palatine. The rising plate formed by the inner edge of the palatine is most amazingly thin, so thin that in this specimen it was at first considered that there must be a vacuity and in the type specimen of *Leptosuchus crosbyensis,* number 7522 of the collection, though the plates are complete and it is obvious that there was no vacuity, the

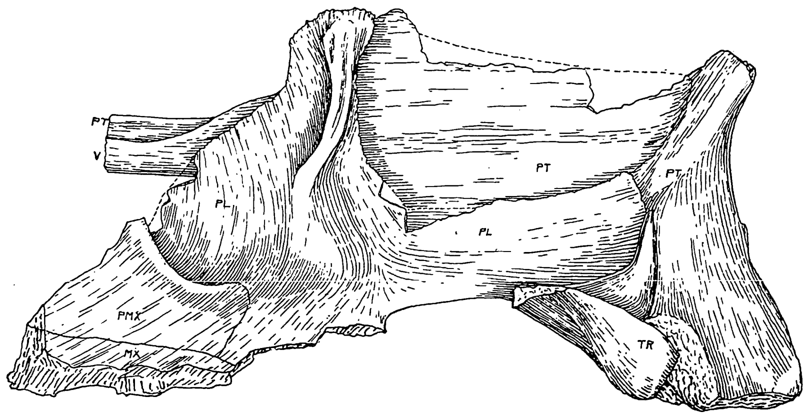


FIG. 11. Upper surface of the palate, left side, of *Brachysuchus.* $\times \frac{1}{3}$. Lettering as in Figs. 1–3 (pp. 6–7)

bones are translucent as prepared by the patient skill of Mr. W. H. Buettner. The upper edge of the plate runs forward nearly parallel to the edge of the pterygoid above them and at a point just opposite the posterior end of the choanae suddenly rise in a strong vertical process even higher than the pterygoids. The posterior edge of this rising process is nearly at right angles to the edge of the bone behind it. The anterior face of the process is concave and forms the posterior wall of the choana at this level. The outer edge of the concave face is formed by a strong ridge on the vertical process which grows stronger below and continues into the anterior edge of the palatine, which forms the lower edge of the lateral extension of the choana (see Figures 11 and 16). The inner edge of the concave face extends but a short distance forward and then descends rapidly to the level of the choanae; its anterior edge overlaps the posterior edge of the upper part of the vomer. This plate was wrongly interpreted by the author in his description of the type specimen of *Leptosuchus crosbyensis,* as is explained in the description of the narial region, below.

Vomers. — The vomers form the outer, lower, of the two V-shaped processes which make up the septum between the choanae. The anterior ends originate in a socket in the thickened median portions of the posterior ends of the premaxillaries. At first the vomers form a flattened oval, but soon change to very thin plates united by their lower edges and rising obliquely outward to form the outer V-shaped process. The anterior ends of the

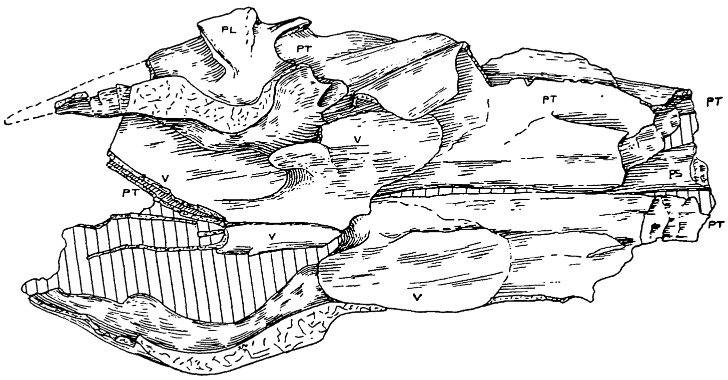


FIG. 12. Lower surface of the palate in the narial region of *Brachysuchus.* × $\frac{2}{3}$. Lettering as in Figs. 1–3 (pp. 6–7)

inner, pterygoid, V show above the vomers, but are soon concealed by the rising plates of the vomers. The posterior ends of the vomers rise to join the anterior ends of the inner plates of the anterior end of the palatine and so complete the septum. On the lower face each vomer passes beneath the anterior end of the inner process of the palatine, curves outward to form the posterior portion of the lower opening of the choana and sends a process downward which overlaps the line of contact of the anterior end of the lower plates of the pterygoid with the palatine (see Figure 12).

Epipterygoid. — No trace of this element has been found in any of the three very perfect specimens in the collection of the University of Michigan. Huene (1911) described it from *Mystriosuchus pleiningeri* and Lees (1907) from *Paleorhinus.* As mentioned, Huene may have mistaken a portion of the median edge of the pterygoid for the epipterygoid, or both authors may have detected and misinterpreted the pillar-like structure formed by the dorsum sellae with the inner edge of the laterosphenoid.

Narial region. — The structure of the narial region and the identification of the bones concerned in it have been matters of uncertainty. Both Huene (1911) and the author (1922) have given descriptions and interpretations from different specimens. The observations have been fairly consistent, but the interpretations have agreed less well. The study of the present specimen corroborates points in both interpretations and permits corrections in both. Fortunately the skulls in the collection of the University of Michigan have been slightly crushed in different planes, one from above downward and the other laterally; this has resulted in different presentations of the same bones which permits one specimen to be checked against the other. Below are reproduced the figures of the narial region given by Huene (1911) for *Mystriosuchus pleiningeri,* and by the author (1922) for *Leptosuchus crosbyensis* with a résumé of the original descriptions; this is followed by a description of the narial region in the present specimen and an attempt to bring the three into accord.

RÉSUMÉ OF HUENE'S DESCRIPTION OF THE NARIAL REGION IN MYSTRIOSUCHUS PLEININGERI

Palatine. — The palatine is a long, slender, thin bone ending posteriorly in a sharp point. The anterior end underlies the vomer for 4 cm. as a thin, flat plate and then joins the maxillary as far back as the palatine vacuity, where it is the broadest. Behind this it is bordered by the transverse to the extremity of its lateral border. In the middle of the suture between the palatine and the transverse is the posterior palatine vacuity. Medially the palatine is bordered by the descending process of the pterygoid. From the posterior end of the posterior palatine vacuity the palatine is marked by a sharp ridge; the portion of the palatine medial to this rises obliquely upward. Its median edge extends forward 13 cm. on the upper surface of the pterygoid. It then forms the lateral border of the choanae and continues to its union with the vomer.

The palatine has a much greater exposure on the upper surface of the palate than on the lower. Anteriorly it is overlain by the vomer and more posteriorly it overlies almost all the pterygoid anterior to the transverse. The suture between the palatine and the vomer runs in coarse serrations from the anterior lateral corner of the choanae obliquely backward and outward to a point opposite the alveolus of the fifth tooth from the rear, which exactly underlies the lower corner of the antorbital vacuity. At the posterior end the lateral edge of the transverse overlies the palatine for about 1 cm., with a coarsely serrate suture.

The extent to which the palatine covers the pterygoid is shown on both sides. On the left side a thin layer of sandstone separates a thin

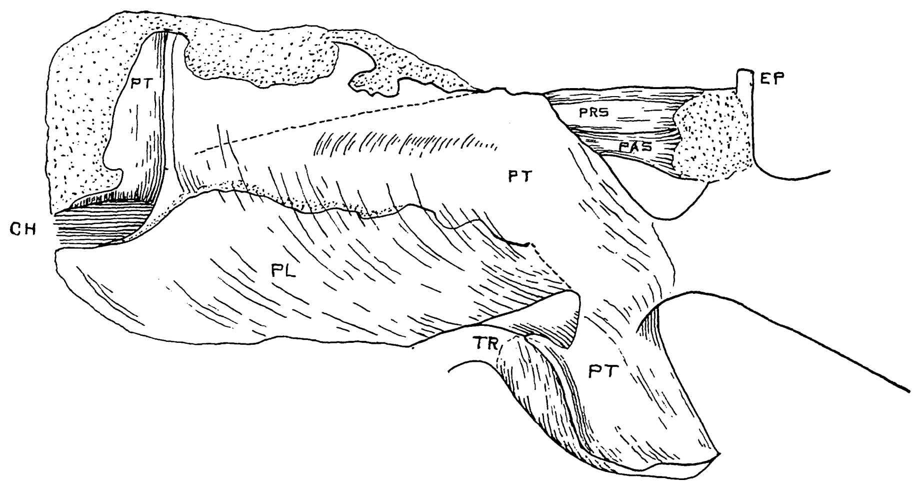


Fig. 13. Upper surface of left side of palate of *Mystriosuchus pleiningeri*, redrawn from Huene, showing his interpretation. $\times \frac{1}{2}$. EP, epipterygoid; PRS, presphenoid; CH, choana; other lettering as in Figs. 1–3 (pp. 6–7)

lamella of bone (the upper edge of the palatine) from the pterygoid to which the edge of the lamella is parallel (see Figures 13 and 14). This lamella forms a blunt point anteriorly and then the lateral border of the choana. This is unmistakable on the right side, but the region is lacking on the left side. The posterior border of the choana is formed by an outbending of the pterygoid entirely within the palatine. From this point back the palatine lies on the upper surface of the rising process of the pterygoid. The anterior lateral part of the broad plate which forms the lower surface of the palate is the pterygoid, but this is covered on the upper surface by the palatine.

Vomer.— The vomer forms the septum between the choanae, but expands laterally anterior to them. . . . The anterior half of the septum is formed by the vomers alone, but the posterior half is covered by the equally thin lamellae of the pterygoids. The specimen does not show how far back the vomer extends, but as the pterygoids come together somewhat posterior to the choanae the vomers reach at least to them and disappear in a point. Anterior to the choanae the vomers extend 7 cm. laterally and anteriorly. The vomer first unites with the palatine and is then bordered by the maxillary and the premaxillary. The posterior part of the premaxillary shows as far as the anterior end of the choanae, but there the two bones diverge and the vomer appears between them as a long,

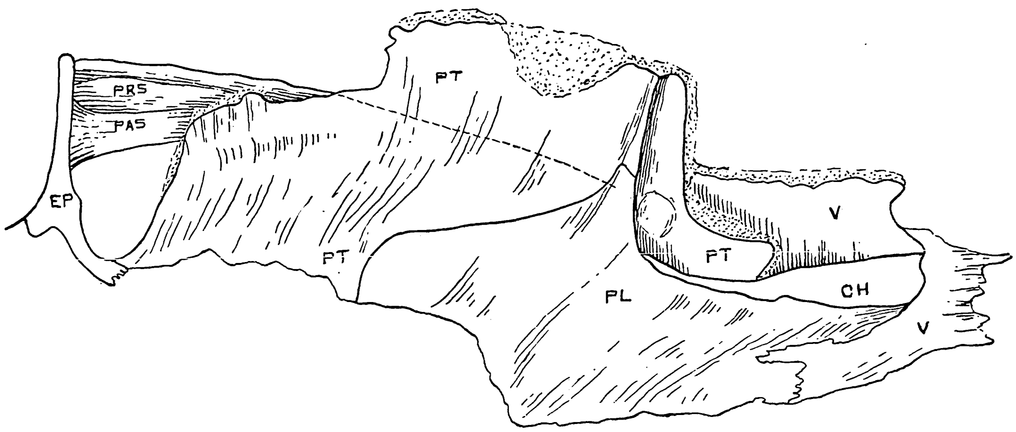


FIG. 14. Upper surface of right side of palate of *Mystriosuchus pleiningeri* redrawn from Huene, showing his interpretation. $\times \frac{1}{2}$. Lettering as in Fig. 13

slender process. The outlines of the vomer on the lower surface do not, however, reveal the entire extent, for on the upper surface it spreads widely over the palatine and the premaxillary. It has really a considerable breadth and terminates in broad undivided ends rather than in three points. It is exposed for only 4 cm. anterior to the choanae and here the premaxillary does not unite with it. The specimen does not show how high the median part of the vomer reaches, but it certainly does not touch the roof and there is apparently from 3 to 4 cm. between the septomaxillary and the vomer.

Pterygoid. — The pterygoids have a vertical rising process. . . . These form the high vaulted portion of the palate and take part in the choanae. The pterygoid has its greatest breadth in the region of the union of the transverse and the palatine; this whole surface is covered on the upper side by the palatine. The anterior ends form the posterior borders of the choanae; this, like the border formed by the palatine, is a vertical rising plate. From the lateral posterior corner of the choanae to the mid-height of the posterior border the pterygoid is covered by the palatine; above that point the posterior border is formed by the pterygoids alone. Below this point the pterygoids extend forward (on the vomer) for 4 cm. on the left side, i.e., about half the length of the choanae. From the posterior end of the choanae the rising vertical plate of the pterygoid extends back to the place, a few centimeters anterior to the basisphenoid, where the pterygoids separate (to form the interpterygoid vacuity). There is a space between the two vertical processes of the pterygoid within which the parasphenoid lies.

The complete anterior end of the pterygoid is exposed on both sides. Below is the process reaching forward (on the wall of the septum) 1½ cm. high and 2 cm. long; then the border rises at right angles directly upward 2 cm. anterior to the posterior border of the choanae. At a height of 6 to 6½ cm. above the lower edge of the choanae and 6 cm. below the wall-like posterior border of the outer nasal opening, the edge of the pterygoid bends sharply backward at a right angle. At a point 5 cm. posterior to this the edge, on both sides, is somewhat higher. The posterior portion of this edge is somewhat thickened and descends toward the root of the pterygoid, increasing in thickness as it descends. At the anterior end the edge has a different sort of thickening, not in the form of a broad, gradually flattening border, but a sharp vertical ridge extending from the choanae to the upper edge. Also on the lower surface the pterygoid is strengthened by a sharp ridge increasing in thickness toward the palatine. . . . The median edge is thickened most at the posterior end. It is on this border that the teeth are inserted in *Proterosuchus*.

RÉSUMÉ OF CASE'S DESCRIPTION OF THE NARIAL REGION IN LEPTOSUCHUS CROSBYENSIS

Palatine (see Figures 15 and 16). — The palatines are rather heavy posteriorly where they unite with the transverse, but soon become more thin and plate-like. The median portion of the palatine is thicker and this portion forms the characteristic ridge on the lower surface of the palate and the outer edges of the choanae. On the inner side of the heavier portion is the shoulder described and figured by Huene as supporting the lower edge of the pterygoid. The palatine sends out two very thin expansions: an upper, which overlies the pterygoid for a short distance, not nearly so far as figured by Huene, and an outer, which unites with the palatine plate of the maxillary. The upper plate forms the posterior and outer borders of the choanae. Near the middle of the plate there is a strong vertical process which ends upon a prominence upon the upper edge. Just anterior to this ridge the palatine divides into vertical plates. The upper edge of the inner plate descends rapidly and soon joins its fellow of the opposite side, leaving a shallow V-shaped channel on the upper surface; the two together form the septum which divides the choanae. The outer plate runs forward and joins the premaxillaries. The lower, or horizontal, plate of the palatine is deeply concave just below the heavier median portion, forming a channel which runs as far forward as the choanae.

Vomer. — The vomers do not appear on the lower surface. . . . In the V formed by the approximation of the anterior portions of the pterygoids there is evidence of a pair of very slender bones which have the same relations, i.e., they meet below to form a V; these are apparently the much reduced vomers.

Pterygoid. — The anterior process of the pterygoid extends forward and quickly becomes a thin vertical plate. In the specimen this plate lies directly in contact with the parasphenoid process and rises considerably above it, but not so high as figured by Huene. The upper edge of the pterygoid rises slowly, forward, from the median portion and passes above the outer edge of the parasphenoid process at about its middle point. The anterior portions of the pterygoids are joined at their lower edges, forming a V, which lies between the anterior portions of the palatines.

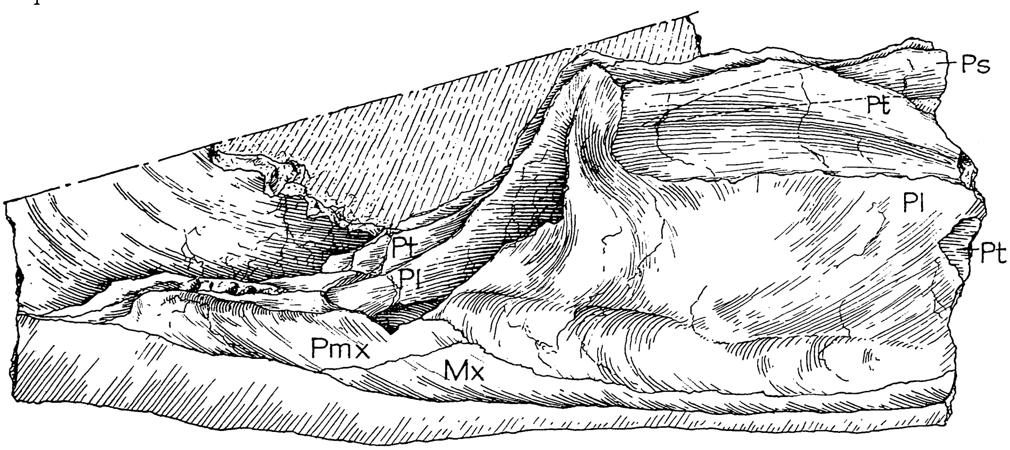


FIG. 15. Upper view of left side of palate of *Leptosuchus crosbyensis* as originally interpreted by the author. × $\frac{1}{3}$

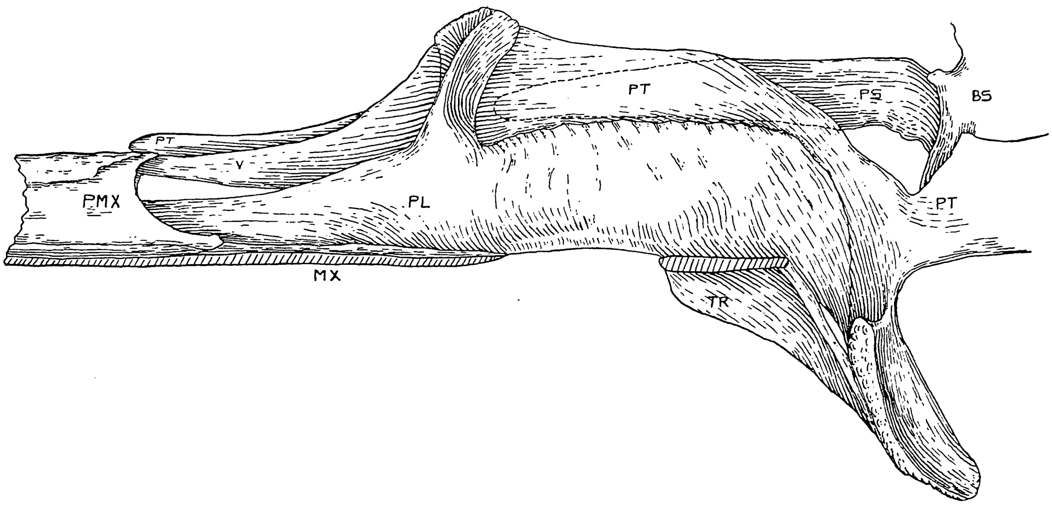


FIG. 16. Upper view of left side of palate of *Leptosuchus crosbyensis* as now interpreted by the author. Slightly diagrammatized. × $\frac{1}{3}$

Choanae.—The openings of the internal nares are separated by a bar composed of the palatines, pterygoids, and, probably, the vomers. There was a distinct space between the septum of the external nares and that of the choanae below. . . . The bar between the choanae is formed by three pairs of bones. The lower pair is the palatine portion. These bones gradually approximate; the posterior portion of the bar is V-shaped, the anterior portion a complete oval bar with a complete upper edge. Between the arms of the V formed by the palatines there is a second V formed by the anterior portions of the pterygoids, which retain their form to the anterior end. The lower part of the pterygoid V rests upon the upper edge of the palatine bar at the extreme anterior end. Between the arms of the V formed by the pterygoids there is evidence of a third V formed by the vomers.

DESCRIPTION OF THE NARIAL REGION IN THIS SPECIMEN, WITH AN ATTEMPT TO BRING THE THREE DESCRIPTIONS INTO ACCORD

The composition of the palate and narial region is shown in Figures 11, 12 and 16. Figure 16 is a correction of the one published by the author of the upper surface of the palate of *Leptosuchus crosbyensis* (1922). The changes to be noted are in the outline of the palatine, the recognition that the inner edge of the concave anterior face of the palatine descends abruptly and is joined by the vomer which forms the outer of the two V-shaped processes which make the septum. The inner V-shaped process is the extension of the pterygoid to join the premaxillaries. This figure differs from those of Huene in the recognition that the prominent vertical process is a part of the palatine, that the descending plate on the inner side of the choana is part of the palatine which meets the vomer, that the septum is formed by two pairs of bones, that the pterygoid extends forward as the inner of these to the premaxillary, and the different form of the vomer.

In Figure 17 are given cross-sections of the narial region taken from this specimen and checked by comparison with specimen number 7522, the type of *Leptosuchus crosbyensis,* and Huene's specimen of *Mystriosuchus pleiningeri.* At A, the anterior end of the septum, the vomers are slender and broader than high; immediately above them are the anterior ends of the pterygoids which end unattached in the space above the premaxillaries. At B, the middle of the septum, the vomers become thin plates meeting below and slanting outward and upward; they include within the V thus formed the similar plates of the anterior ends of the pterygoids. At C, opposite the rising process of the palatine and just anterior to the posterior end of the choanae, the palatines form the lateral walls of the choanae; the vomers and pterygoids retain their V shape and relative positions; the anterior end of the parasphenoid lies just behind this point. At D, just behind the posterior end of the choanae, the palatines overlap the pterygoids on the outside; the upper vertical plates of the pterygoids are as high as the palatine; the median processes of the pterygoids meet to

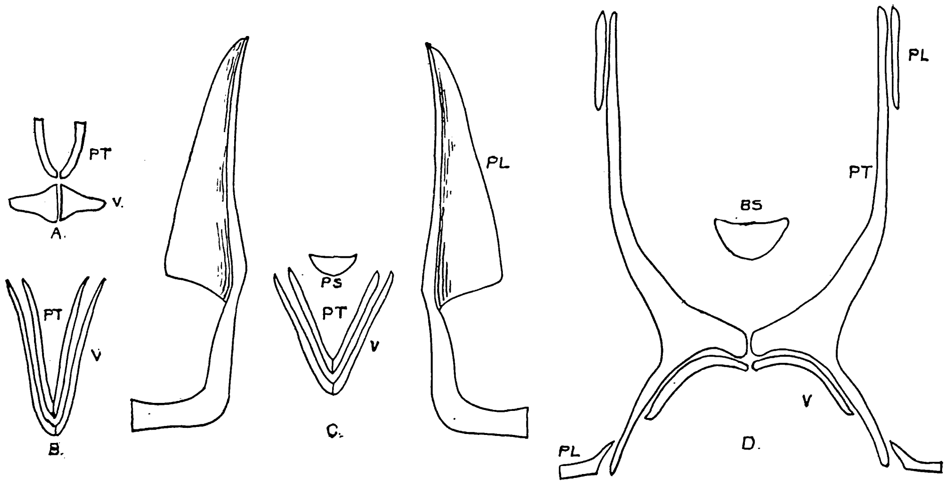


FIG. 17. Cross-sections of the narial region and the choanae in *Brachysuchus*. A, at the anterior end of the septum; B, at the middle of the choanae; C, at the posterior end of the choanae; D, a little posterior to the choanae

form the roof of the palate; and the descending plates of the pterygoids rest on the shoulder formed by the ridge on the palatines. The parasphenoid has assumed the wedge-like form which continues to the posterior end. Posterior to this point the upper vertical plates of the pterygoids decrease in height and merge into the median edges and the lower vertical plates are continued into the lateral processes.

Although the skeleton of the phytosaurs shows their complete separation from the Crocodilia, every suggestion of the body, either of the skeleton or of the soft parts in any possible restoration, and the habitat as revealed by the beds in which the remains are found, force the conclusion that the habits of life were very similar. Evidence from paleontology and embryology (Fuchs, 1908) shows that the peculiar character of the nasal passages and the choanae of the Crocodilia could not have been derived from the phytosaurs. Fuchs assumes the derivation of the Crocodilia from the phytosaurs, but his conclusions are based on an incomplete knowledge of the region in *Phytosaurus* and his own work proves the impossibility of the morphologic process he suggests. Because of the similar habits of the two groups, similar problems of structure had to be solved. In both the prey was seized and dragged beneath the water to drown. The Crocodilia are enabled to do this because the nares can be closed and the cartilaginous plate at the root of the tongue can be pressed against the vellum palati closing the air passage and preventing the water which fills the partially open mouth from entering the larynx. It is conceivable, at least, that the high vaulted portion of the palate of the phytosaurs served the same purpose as the naso-pharyngeal passage of the Crocodilia. Whether the phytosaurs held their prey by the premaxillary teeth or by the strong maxillary teeth, the mouth would necessarily be held partially open and would be flooded with water. Even if the prey were held far back in the mouth, the strong horizontal portion of the palatines would prevent any closure of the high vaulted part of the palate. Unfortunately we may not know whether this part of the palate was partially or completely cut off from the mouth by soft parts.[1]

We do not as yet know the method by which animals of such distinct groups but apparently similar habits arrived at equally efficient solutions of their necessities by such different routes. The phytosaurs were called upon to solve the problem before the mechanism of a naso-pharyngeal passage separated from the mouth by the closure of the palatines and pterygoids between them was developed. One would be tempted to see in the meeting of the pterygoids in the high vaulted portion of the palate an early instance of this process, did not the choanae open directly into the mouth and the parasphenoid occupy the space above the pterygoids. In the phytosaurs it is seemingly the adaptation of the more primitive condition to the same end.

Abel, in his *Paleobiologie,* ascribes the anterior position of the external

[1] Since this paper has gone into page proof the author has received from Doctor Mehl a description of a phytosaur from Arizona which he considers as showing the development of a secondary bony palate (Mehl, 1928).

nares in the Crocodilia to the fact the animals lie in the water in an inclined position which brings the nares soonest to the surface. There is nothing in the skeleton of the phytosaurs to indicate a different habit; the limbs are as well developed and the bones as weighty; the armor is fully as heavy. The nares were probably located upon the highest part of the skull for the same reason — that they would soonest reach the surface with the maximum of the body concealed in the water.

The author is thoroughly in accord with the ideas expressed by Branson and Mehl (1928), that our knowledge of the morphology of the phytosaurs is still far too incomplete to warrant more than a very tentative classification or to base any correlation of the beds upon known specimens. As the author has attempted to show, he believes that the remains of the phytosaurs found in the southwestern part of the United States are more or less closely associated with the Shinarump conglomerate and its equivalents, and even more closely with the environmental conditions indicated by the conglomerate and its associated beds. Whether this can be extended to the Popo Agie beds of Wyoming remains to be shown by future discoveries.

It is the author's opinion, coinciding with that of Branson and Mehl, that the known remains of phytosaurs in the United States indicate the presence of several stages of evolution, retarded as well as advanced, in the same beds. Huene (1926) has attempted to distinguish different stages, as Upper, Middle and Lower Triassic in the beds of the United States and to correlate them with the German beds, but some of his references of specimens to beds and to localities are faulty and his allocation of certain beds and localities to different horizons seems to the author to be unwarranted. So far as the author's knowledge of the Triassic beds of the Southwest, gained by considerable experience in them, permits, he is convinced that they are all of Upper Triassic age. This opinion is based on the stratigraphy and upon the vertebrate fossils contained in them, as there is no dependable evidence from either invertebrates or plants.

The known remains of vertebrate fossils, stegocephalians, phytosaurs, a single cotylosaur (Case, 1928), a few dinosaurs, and a very few fragments of fish, form a very incoherent collection of animals in various stages of evolution. There can be no doubt that the phytosaurs of North

America are closely similar to those of Germany and part of the same fauna, developed under very similar conditions of environment, but the morphology revealed by the specimen described in this paper shows how inadequately other specimens have revealed their structure, and until they can be made to do so by further preparation and study or until other specimens are discovered that will fully reveal their osteology, it is useless to attempt close correlations or phylogenetic series. Until a fairly complete skeleton shall be found with all parts associated it is useless to speculate on the relationships of skulls to isolated bones found in disassociated relationship or in other localities.

The author has spent many hours in careful review of the literature and has constructed many long series based upon isolated structures, associated structures, and upon laboriously compiled tables of comparative measurements and relative proportions of parts, and has failed to find a single series in which a satisfactory sequence of forms can be recognized.

Family and generic relationships and phyletic series have been based on the following characters:

1. The different height of the rostrum.
2. The different size of the post-temporal fenestra.
3. The different form of the vertebrae.
4. The different form of the interclavicle.
5. The different form of the ilium.
6. The different degree of curvature of the femur.
7. The different make-up of the carapace.
8. The different character of the teeth.
9. The different relative extent of the pre- and postnarial portions of the skull.
10. The different relation of the antorbital vacuity to the nares.

Abel (1922) and others have shown that most of these criteria must be rejected as inadequate because of intergradation or because they are not greater than individual or sexual differences might be.

So far as the author can determine from a careful study of the literature, but one fact seems to be well established. There are two types of carapace, one composed of irregular plates irregularly arranged, and another composed of regularly shaped plates arranged in definite rows. The first of these types is certainly associated with *Mystriosuchus* in one specimen from Germany, and in two specimens from eastern North America, *Rhytiodon carolinensis,* and an incomplete posterior portion of a skeleton referred to *Rhytiodon, R. manhattenensis.* No such satisfactory association has been found in Germany for a carapace composed of regular plates, but it is probable, from less definite association, that they belong with the type of skull called *Phytosaurus, P. kappfi.* In western North America no such association has been found except in the case of *Desmatosuchus* (*Episcoposaurus?*) where the regular type of plates was found with typical phytosaur vertebrae, but a skull that has no relationship to *Mystriosuchus, Phytosaurus,* or any other of the described skulls. The author has come to suspect that certain of the plates described by Cope as parts of his *Episcoposaurus* are very similar to certain of those in the carapace of *Desmatosuchus,* and that the latter name may have to be abandoned on the ground of priority, but as *Episcoposaurus* was described from roughly associated collections of limb bones and dorsal plates, with no trace of the skull in either species, this will be of no help in the systematic arrangement.

It seems very probable that there were at least two groups of the phytosaurs distinguished by the two types of carapace; Abel's suggestion that the carapace may be only a sexual character seems to stretch his point beyond credibility.

A second difference seems fairly definite. The skull of *Mystriosuchus planirostris,* as represented by Frass' photograph and McGregor's restoration, is characterized by the length and the slenderness of the rostrum and the slight development of the strong leaf-shaped maxillary teeth which are present in all the other known specimens. Also, there is no development of a hook at the anterior end of the rostrum and the tusks are relatively small. It is probable that *Rhytiodon* is the same as, or closely related to, *Mystriosuchus,* but it is to be noted that a group of the American phytosaurs have a slender concave rostrum which may be the distinguishing character separating *Rhytiodon* from *Mystriosuchus.*

All the other described forms have a heavier and proportionately shorter rostrum with very strong leaf-shaped teeth in the maxillaries, strong anterior tusks and a more or less well-developed hook at the anterior end of the rostrum. The forms *Mystriosuchus planirostris,* probably *Rhytiodon,* and possibly *Mystriosuchus pleiningeri* show evident adaptations to a fish-eating habit as evinced by the longer, less numerous premaxillary teeth, the weaker biting maxillary teeth, and the quicker snap of the long light jaws. This suggestion is borne out by the lighter limb bones associated with the skull of *Rhytiodon carolinensis.* The remaining forms show an equally evident adaptation to attacking and devouring much more resistant animals. The strong rostrum, the powerful anterior tusks, the closer set premaxillary teeth, and above all, the powerful cutting maxillary teeth were evidently fitted for seizing a powerful prey and piercing a strong armor, such as the head and thoracic plates of the great stegocephalians or the carapace of other phytosaurs. All these characters are shown in varying degree in the different forms. The specimen described in this paper is the most powerful yet discovered, but there is in the collection the posterior portion of a lower jaw which belonged to an even larger form.

Such a divergence in habits and form, adaptive radiation, may explain some of the other characters that have been used in attempted classifications. One such character is the relation of the nares to the antorbital vacuity. The vacuity has been supposed to have shifted from a position anterior to the nares, *Mesorhinus,* relatively backward until the nares lay over its middle point. While the various forms cannot be arranged in a series on this character, it is true that the two openings do occupy relatively different positions. The explanation may be found in the development of the biting power. The lower jaws are closed by two sets of muscles in the reptiles, a posterior mass, the capiti mandibularis, divided into an outer, a middle, and a deeper part corresponding more or less closely to the temporalis and masseter in the mammals, and a strong pterygoideus anterius (Adams, 1919). As the rostrum became heavier and the maxillaries proportionately shorter,[1] the pterygoideus anterius became longer, its origin extending well forward in the rostrum. As the antorbital vacuity is explainable only as a perforation of the side of the skull by the

[1] It has been impossible to work out a consistent series on these characters but the relation evidently exists.

swelling pterygoideus muscle, it is easy to see how the vacuity not only would become longer but would shift its position forward relative to the nares, as the muscle elongated.

Both the muscle masses are inserted on the lower jaw at about the same distance from the posterior end and share in the pull exerted in closing the lower jaws. The outer portion of the capiti mandibularis was attached to the jugal and the borders of the lower temporal fenestra while the middle and deeper portions were attached to the borders of the upper temporal fenestra. It is easy to imagine that some change in habit, as the development of biting, might alter this muscle mass so far as to determine whether the upper fenestra should remain on the top of the skull with well-developed borders or be depressed and open. It is far less easy to explain the method by which this was accomplished.

The size and the powerful proportions of the limbs associated more or less certainly with forms which had well-developed biting teeth indicate a development toward a terrestrial or semi-aquatic habit. That the biting habit was attained independently by different forms and in different degree is amply illustrated by the various specimens ranging from the small and slender *Promystriosuchus* to the very massive form described on this page.

MEASUREMENTS OF THE SKULL OF *BRACHYSUCHUS MEGALODON*

Extreme length	1260 mm.
Anterior end of the rostrum to the posterior edge of the condyle..	1105
Breadth across the quadrates	480
Extreme breadth just anterior to the quadrates	505
Breadth opposite the third from the last alveolus	375
Breadth of rostrum just anterior to the constriction	120
Breadth of articular face of a quadrate	115
Anterior end of rostrum to end of dental series	867
Anterior end of rostrum to anterior end of choanae	702

Size of the animal. — The skull of an alligator or crocodile is approximately one sixth of the total length; that of a gavial is approximately one fifth of the total length. Assuming the proportions of the phytosaurs to be similar to those of the gavial, the total length of *Brachysuchus* would be about 7.5 meters or 24 feet, 8 inches.

Characters of Brachysuchus.—The same series and sequence of characters are here used as were used in the author's previous lists of characters (see Case, 1922, pp. 68 and 69):

1. Post-temporal arch depressed.
2. Anterior end of antorbital opening just anterior to the nares.
3. Length of the prenarial portion of the skull to the postnarial as 10:7.
4. Post-temporal fenestra large.
5. Post-temporal bar depressed, lying on the opisthotic; long.
6. External nares without elevated rim; septum at upper border; internal nares directly under external.
7. Squamosal region extended posteriorly.
8. Orbits look more outward than upward.
9. Septomaxillary present.
10. Premaxillary and maxillary teeth 46; both oval and round in cross-section.
11. Inner edge of pterygoid (palatine of previous lists) elevated; palatine vacuity opposite middle of transverse.
12. Transverse underlies pterygoid.
13. Vomers on palatine surface dividing choanae.
14. Parasphenoid large, reaching nearly to posterior end of choanae.
15. Interpterygoid space short and narrow.

The most striking characters of the skull are the lack of any prenarial eminence and the breadth and heaviness of the rostrum. As the author has previously intimated, he is inclined to believe that many of the "genera" of the phytosaurs may properly belong in one or two and that the characters given may be only of specific value. Until this is determined the names are used to direct attention to particular specimens.

NOTES ON THE POSTCRANIAL SKELETON OF THE PHYTOSAURS

The author has long refrained from describing and figuring many isolated bones in the collection of the University of Michigan, which present interesting peculiarities in themselves, because he has been unable to bring them into profitable association with other material. Unfortunately no complete skeleton of a phytosaur has yet been recovered and many points in the morphology and systematic arrangement remain in doubt. As in the case of the skull, the various suppositious arrangements based on the postcranial skeleton fail of conviction when subjected to close scrutiny. Even the assignment of a dorsal armor composed of irregular plates to the genus *Mystriosuchus* and one composed of plates definitely and regularly formed and arranged to *Phytosaurus,* is, at best, highly probable. It is uncertain whether *Mystriosuchus* may not have had regular plates in certain parts of the armor and *Phytosaurus* may have had an abdominal armor of irregular plates which could easily, in the present state of our knowledge, be taken for those of the dorsal region of *Mystriosuchus.* The same difficulty exists with regard to the form and proportions of the limb bones and vertebrae that have been used as distinguishing characters.

The following notes record peculiarities of structure in certain elements of the postcranial skeleton which will be of value in systematic arrangements when they can be properly evaluated.

Cervical vertebrae.— The character of the axis and the atlas has been described by McGregor and specimens in the collection confirm his descriptions. No certainty exists as to the number of the cervical vertebrae and no series exists which shows the variations in different parts of the series. Two specimens in the collections show characters not previously noted. These vertebrae, numbers 7317 and 10191, are shown in Figures 18 and 19. The first consists of the neural arch with a complete spine of an, evidently, anterior cervical. The spine is weak with only a slightly expanded apex and rises from between the posterior zygapophyses, almost entirely posterior to the connection of the arch with the centrum. This specimen remained a complete puzzle in the collection until 1927, when specimen number 10191 was discovered. The latter specimen is nearly complete, lacking only the upper portion of the spine. The shape of the centrum and the position of the capitular and tubercular faces are ample evidence of the position in the anterior portion of the cervical series. Other cervical vertebrae in the collection show the gradual rise of the capitular face, the strengthening of the spine and the assumption of a horizontal position by the lower line of the centrum.

Dorsal vertebrae.— The author has been struck by one feature in the adjustment of the capitular and tubercular facets for the ribs on the dorsal vertebrae. It has been commonly assumed and mentioned that the adjustment is similar to that in the *Crocodilia* in that the face for the capitulum of the rib rises on the anterior edge of the centrum and then suddenly, at about the thirteenth vertebra, passes to the edge of the transverse process. So far this is correct, but the author has found no case described or figured, except that of *Desmatosuchus,* in which the capit-

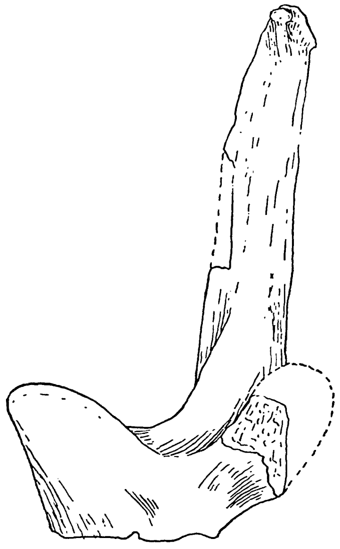


FIG. 18

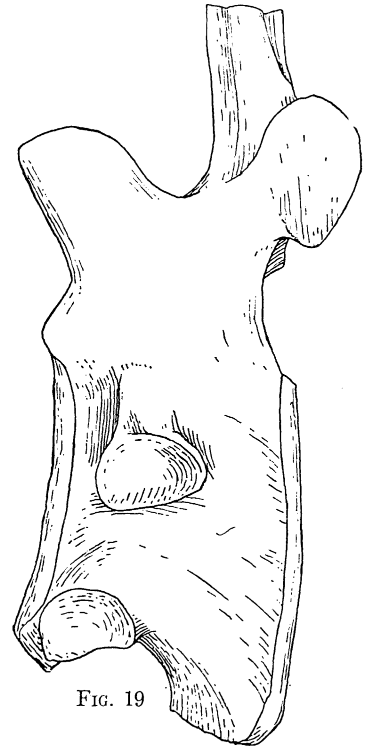


FIG. 19

FIG. 18. Neural spine and zygapophyses of an anterior cervical vertebra, number 7317, U. of M. × ½

FIG. 19. Centrum and part of neural spine of an anterior cervical, number 10191, U. of M. × ½

ular face assumes a position on the transverse process strictly comparable to the *Crocodilia.* In the figures and descriptions of *Mystriosuchus* and *Phytosaurus* by Von Meyer and Huene and of *Rhytiodon* by McGregor, the capitular face lies at the base of the transverse process or on the under side of the process, never, as in the *Crocodilia,* on the same horizontal plane. In *Desmatosuchus* the capitular face assumes the true crocodilian position on the anterior edge of the process early in the dorsal series and follows the same course as in the *Crocodilia,* i.e., the two faces originally far apart gradually approximate by the shortening of the tubercular portion. The same thing is seen in a specimen of a pelvis with several associated vertebrae and regular plates, number 7470. This character is certainly not shown by *Rhytiodon,* in which McGregor's figures show the inferior position of the capitular face throughout the series, and apparently from all figures and descriptions it does not occur in the European forms. It is very probably a character of considerable systematic importance, perhaps confined to *Desmatosuchus,* for in another specimen consisting of

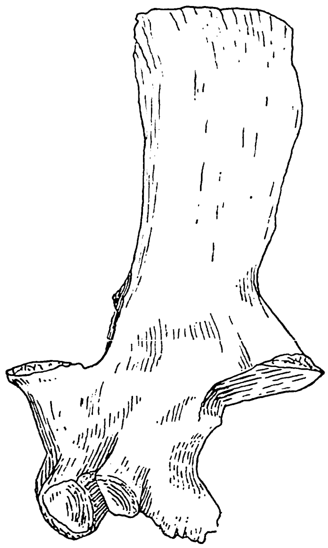


FIG. 20. Neural arch and spine of a posterior dorsal vertebra, number 9636, U. of M. × ½

two neural spines and a detached centrum, number 9636, shown in Figure 20, the two facets are very short, clearly distinct and the capitular face somewhat lower than the tubercular. These specimens are from the posterior part of the dorsal series, but are devoid of any expansion of the upper end of the spine, being thin, slightly broader antero-posteriorly at the apex, and terminating in a thin edge. This type of vertebra is radically different from any other in the collection; some have the thin distal end, but the transverse processes are typically those of the lumbars or anterior caudals without facets for rib attachment.

The author has been unable to satisfy himself that Huene's suggestion of a possible separation of *Mystriosuchus* and *Phytosaurus* by the proportions of the centrum and neural spine of the vertebrae is a usable character, as he has found in the University of Michigan collection all possible gradations and mixtures of the characters suggested by Huene. Such characters, or similar ones, may eventually prove of value, but not until we have a specimen sufficiently complete to show the associations in at least one genus.

Pelvis. — The author has published figures and descriptions (Case, 1922) of three types of ilia occurring in the Texas beds, but lack of asso-

FIG. 21. Right half of pelvis, number 7470, U. of M. Drawn to comparable size with Fig. 22

ciated material prevents any certainty of assignment to particular genera. The most common type is that shown by the author's figure (Case, 1922, Figure E, p. 71) and corresponds most closely to the form assigned by Huene (Huene, 1913, Figure 10) to *Phytosaurus kapffi*. Another type (Case, 1922, Figure C, p. 71 and Figure B, Plate 13) is nearer to that assigned by Huene to *Mystriosuchus planirostris* (Huene, 1913, Figure 9) though it was apparently associated with a *Phytosaurus* skull. Still a third type is represented in the collection by number 7322 (Case, 1922, Figure B, p. 71 and Figure A, Plate 13) and number 7470 (Case, 1922, Figure B, p. 73), which is not paralleled elsewhere. Of these two very similar ilia number 7470 is part of a nearly complete right half of a pelvis with the sacrum attached and associated with some posterior dorsal vertebrae and plates of the regular (*Phytosaurus*?) type. The peculiarity of this type of ilium is the relative shortness of the posterior process and the relative length of the anterior process, of the crest, so that the normal outline of the bone appears at first view to be reversed. In Figures 21 and 22 the outline of this pelvis is given with that of number 7244, assigned by association with a mass of fragments of a great skull to the genus *Phytosaurus* (Case, 1927). The vertebrae found with the pelvis, number 7470,

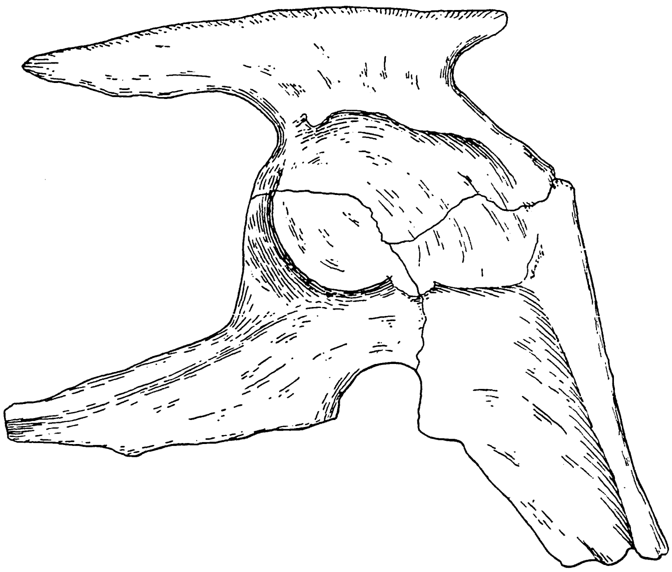


FIG. 22. Right half of pelvis of number 7244, U. of M. Drawn to comparable size with Fig. 21

have the typical crocodilian arrangement of the facets for the rib on the transverse process, a condition noted elsewhere only in *Desmatosuchus*. Unfortunately only a very imperfect portion of the pelvis was found with the type and only specimen of *Desmatosuchus*, so the association is suggestive but far from conclusive.

It is interesting to compare the pelvis, number 7470, with that of *Acompsosaurus wingatensis* Mehl and Schwartz (Mehl and Schwartz, 1916), especially if the distortion of the latter is corrected. The authors of *Acompsosaurus* describe the pelvis as follows: "The pelvis has been somewhat distorted, however, the essential features are readily determined. The left pubic bone has been broken and telescoped at its acetabular portion in such a manner that the posterior part overlies the ilium. The left ilium has been crushed in and back and the centra of the vertebrae are pushed somewhat to the right. . . . The acetabulum is exceptionally wide and deep."

The author has had an opportunity to study the specimen in the museum of the University of Wisconsin and made the following notes:

"*Acompsosaurus.* — A phytosaur pelvis like mine, number 7470. Badly distorted. Symphasis pushed to the right of mid-line. Crest of left ilium bent down. Anterior edge of ilium and pubis pushed back so acetabulum pinched together and presented obliquely to the rear. Neural spines heavy, expanded at top. Two sacrals not coössified. Peculiarities are due to crushing. Pubis had the sharp descending apron."

If correction is made for this distortion, the pelvis of *Acompsosaurus* is very like that of number 7470 and there can be no doubt that it is phytosaurian.

Femur. — There are in the collection five femora of the same type. One of these, number 10335, was found within a few inches of the great skull of *Brachysuchus,* but as the deposit in which they were found was a bit of river wash with thousands of fragments scattered over a small area, there is no reasonable assurance that the two belonged to the same individual. One of the femora, number 3395, has been figured (Case, 1922, Figure 29 B, p. 75). The following measurements are given to record the size and as a possible means of approximating the size to which the animals attained:

No. 10335, left femur	515 mm.
No. 10191, left femur	505
No. 10334, right femur, distorted slightly	505
No. 3395, right femur	315
No. 7330, left femur	73

Posterior foot. — There are in the collection some fragments of a small phytosaur, number 10604, found in Crosby County, Texas, which were badly rotted in the ground and only portions of most of the bones preserved. There are several isolated vertebrae, a sacrum with fragments of the pelvic bones, portions of both femora and humeri, some bits of the lower limb bones and bones of the tarsus and the foot. None of the limb bones are complete, so no full measurements can be made, but such as can be made show that the animal was of small size, about half that of the type specimen of *Episcoposaurus horridus* Cope, as figured by Huene (1915).

Length of the two sacral vertebrae	33	mm.
Length of another vertebral centrum	18.5	
Length of another vertebral centrum	17	
Length of another vertebral centrum	17	
Length of another vertebral centrum	17.5	
Width distal end of tibia	22	
Width distal end of fibula	13	
Right humerus (at least four fifths present)	45	

Most interesting is the presence of the left calcaneum and right tarsale IV, portions of the astragali of both sides, and portions of the metatarsals and phalanges.

The calcaneum and tarsale IV, with two badly decayed metatarsals, were closely cemented to the distal ends of the conjoined right tibia and

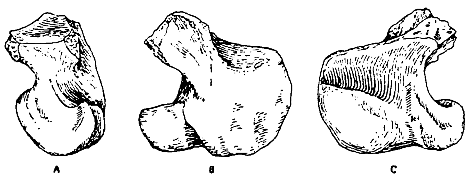


Fig. 23. Left calcaneum of number 10604, U. of M. A, front; B, posterior; C, outer. × 1

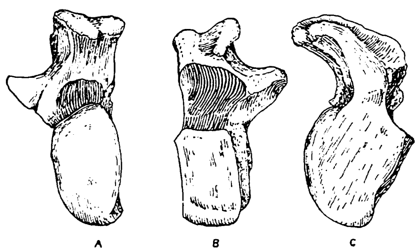


Fig. 24. Left astragalus, number 7445, U. of M. A, inner; B, posterior; C, anterior. × ½

fibula by the fine black, pyritized matrix. Careful preparation recovered the calcaneum and tarsale IV complete and the other bones in a determinable condition. The calcaneum, shown in Figure 23, is strikingly like that of the *Crocodilia,* so much so that the figure serves as an ample description. The only noticeable difference is the lack of a well-defined facet for articulation with the astragalus, and this may be due in part to the condition of the bone. There is a nearly perfect left astragalus, number 7445, from the same region and beds, which in combination with the two fragments permit a satisfactory description. The nearly perfect astragalus is shown in Figure 24; it is very similar to that of the *Crocodilia,* but also shows the lack of a facet for the calcaneum. It is evident from these bones that the specimen from the type material of *Episcoposaurus horridus* Cope, figured by Huene (1915), is not a left calcaneum, but an astragalus probably of the right side, but it is so incomplete or distorted that it is impossible to set up either the phytosaur astragalus, number 7445, or the astragalus of a crocodile to correspond with Huene's figures.

It is certain that the phytosaurs had a well-developed calcaneum and astragalus without, however, a good articular face between them, a fourth and very certainly a third tarsale. The tibia articulated by a well-developed face with the astragalus and the fibula touched the calcaneum. The metatarsals were long, relatively as long as in the *Crocodilia* and the distal ends had well-formed surfaces resembling those of the *Crocodilia.* It is as yet impossible to say anything concerning the possible reduction of the fifth digit or the claws, but it seems certain that the tarsus and the foot had a very close resemblance to those of the modern crocodiles.

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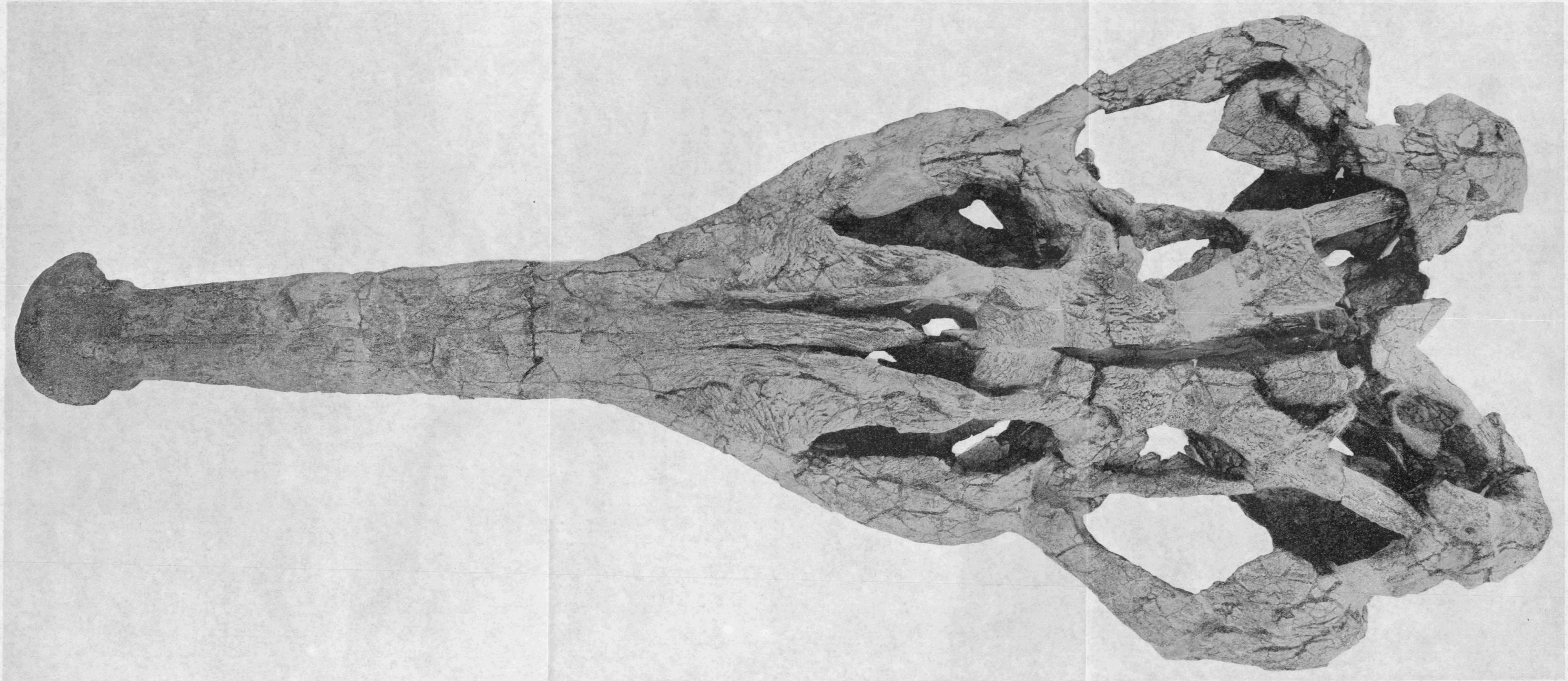

Plate I. Upper surface of the skull of *Brachysuchus*. $\times \frac{1}{3}$

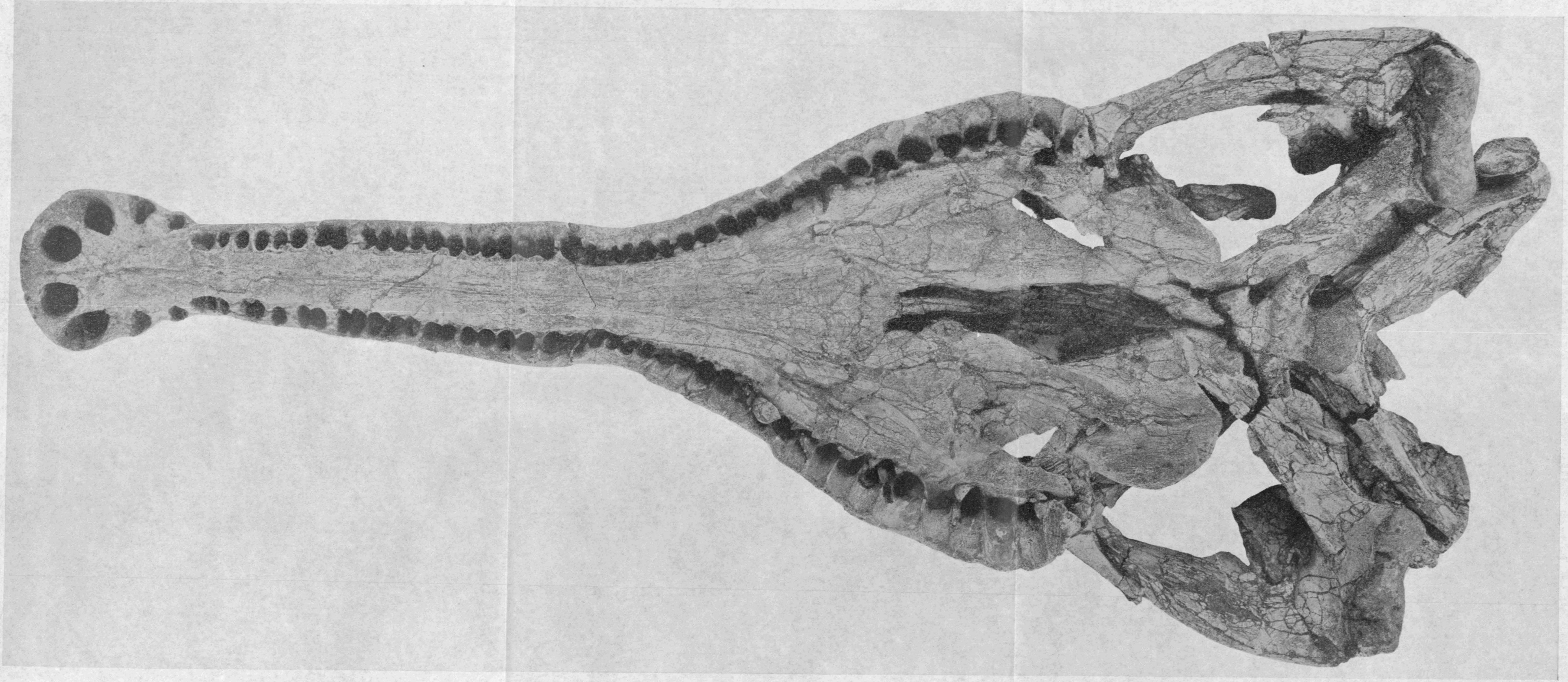

PLATE II. Palatal surface of the skull of *Brachysuchus*. $\times \frac{1}{3}$

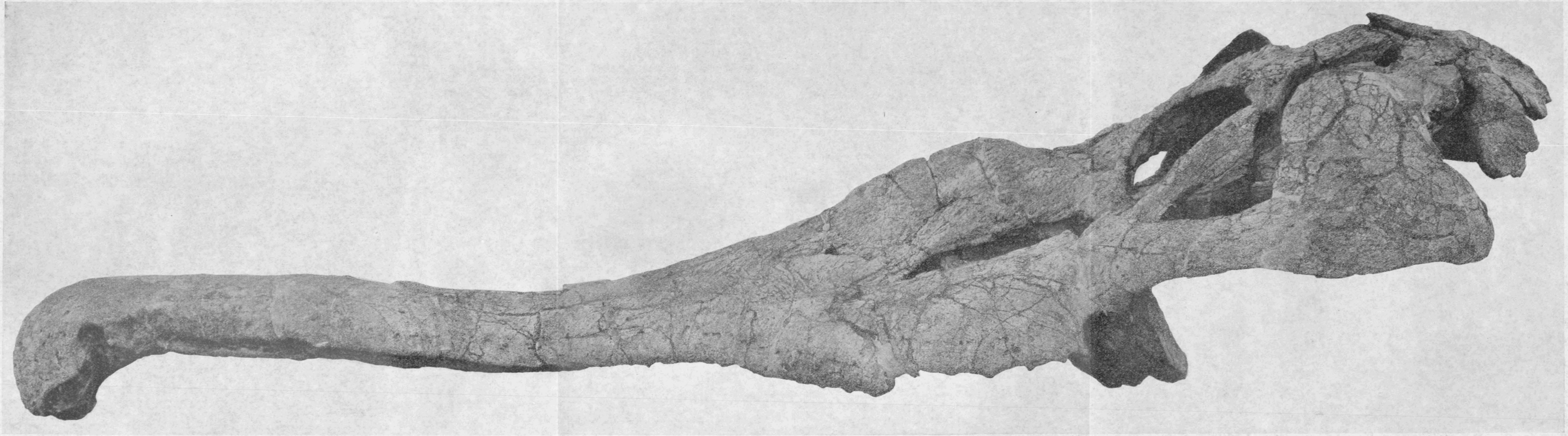

PLATE III. Left side of the skull of *Brachysuchus*. $\times \frac{1}{3}$

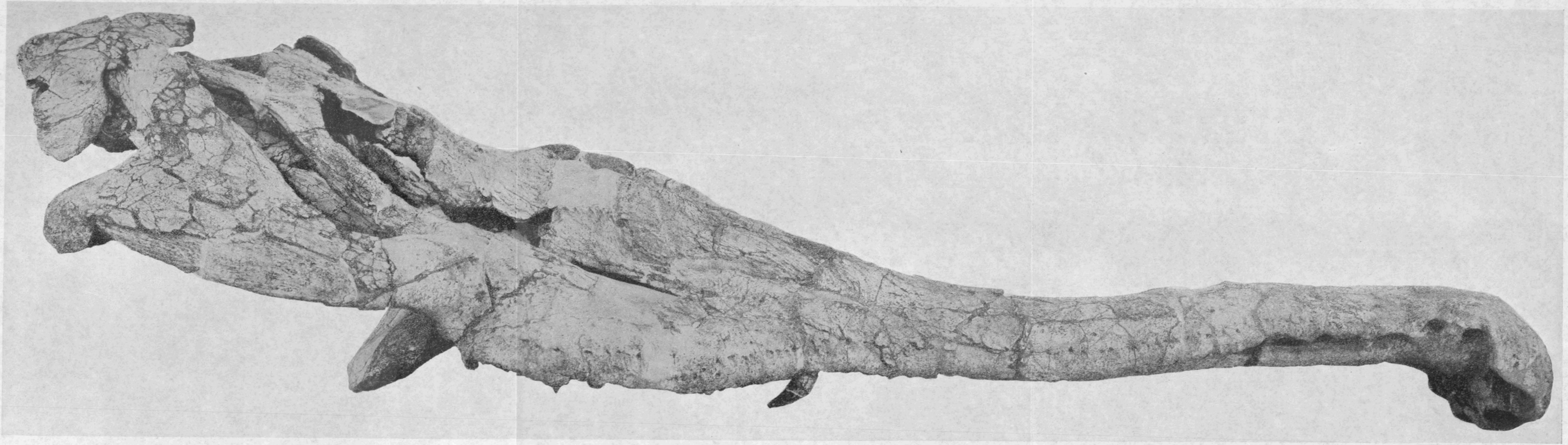

Plate IV. Right side of the skull of *Brachysuchus*. $\times \frac{1}{3}$

PLATE V

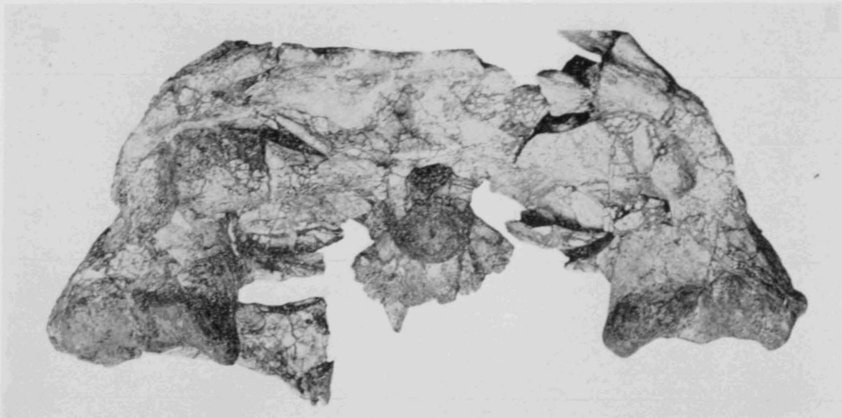

FIG. 1. Posterior surface of the skull of *Brachysuchus*

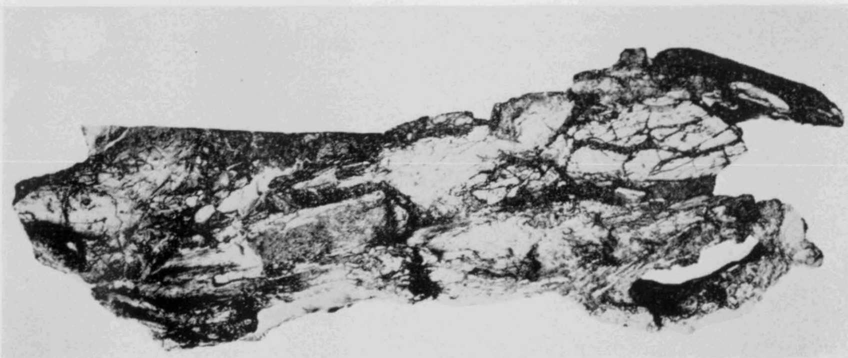

FIG. 2. Upper surface of the narial region

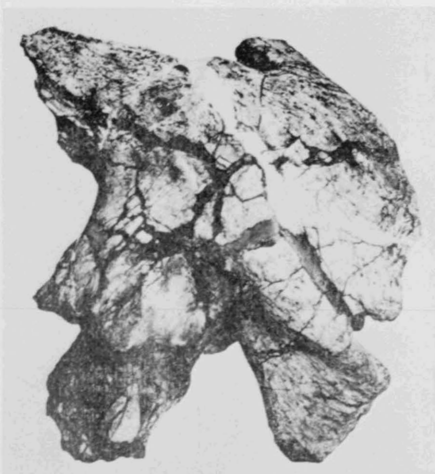

FIG. 3. Squamosal and quadrate of the left side, showing the head of the quadrate fitting into the socket in the squamosal. Compare text Figure 7

FIG. 4. Squamosal, quadrate and opisthotic of the left side seen from behind and below, showing head of quadrate in socket in squamosal and close attachment of the quadrate to the opisthotic. Compare text Figure 8

PLATE VI

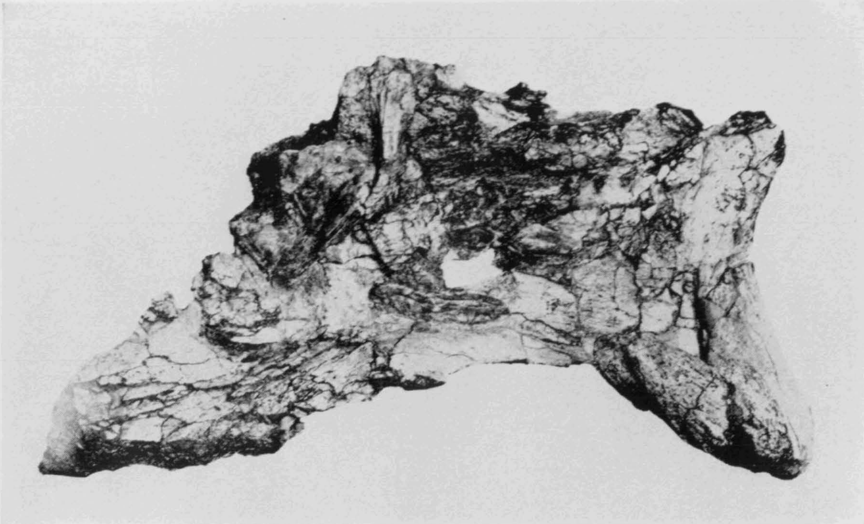

FIG. 1. Upper surface of the left side of the palatal region. Compare text Figure 11

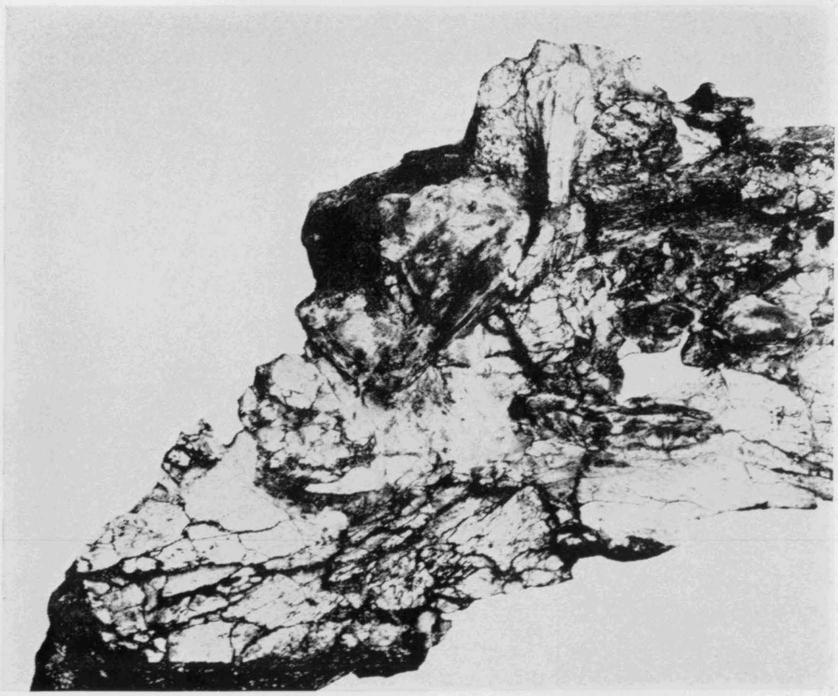

FIG. 2. Anterior portion of Figure 1 enlarged

PLATE VII

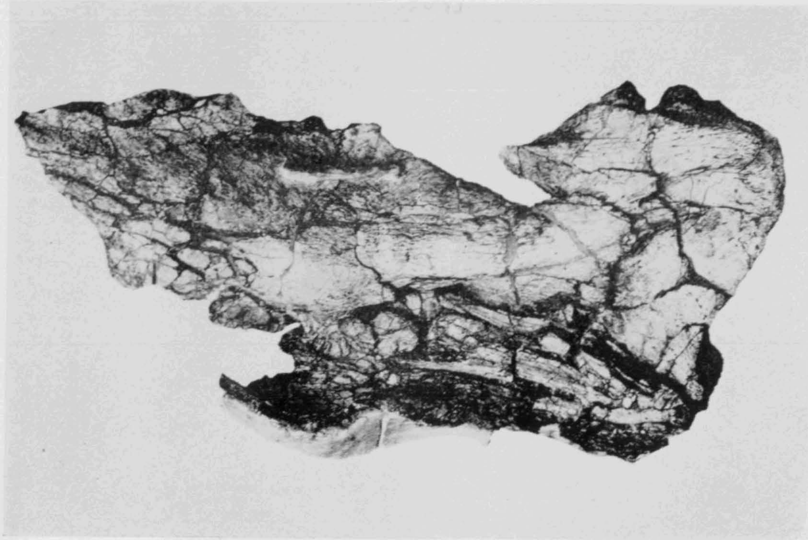

Fig. 1. Lower surface of the left side of the palatal region. Compare text Figure 12

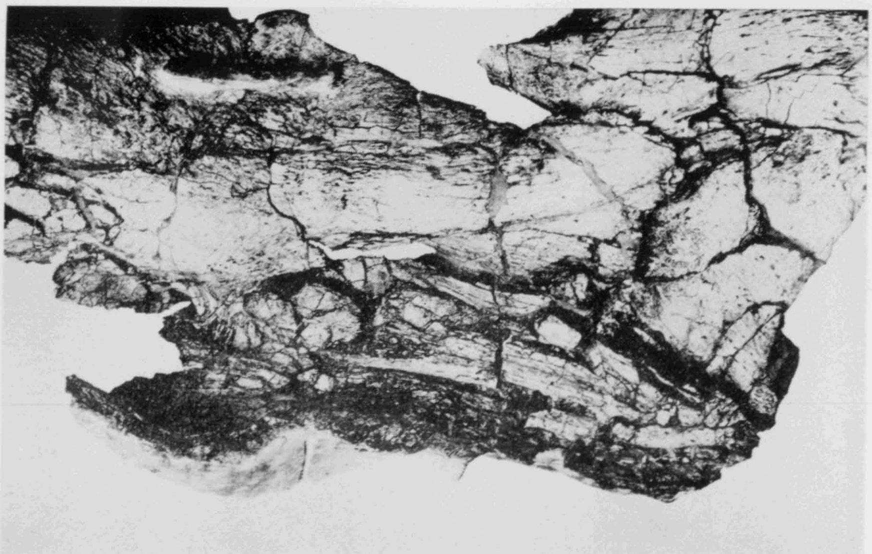

Fig. 2. A portion of Figure 1 enlarged

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