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(Continuation of Contributions from the Museum of Geology)

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TWO NEW SPECIMENS OF PHYTOSAURS
FROM THE UPPER TRIASSIC OF
WESTERN TEXAS

BY

E. C. CASE AND T. E. WHITE



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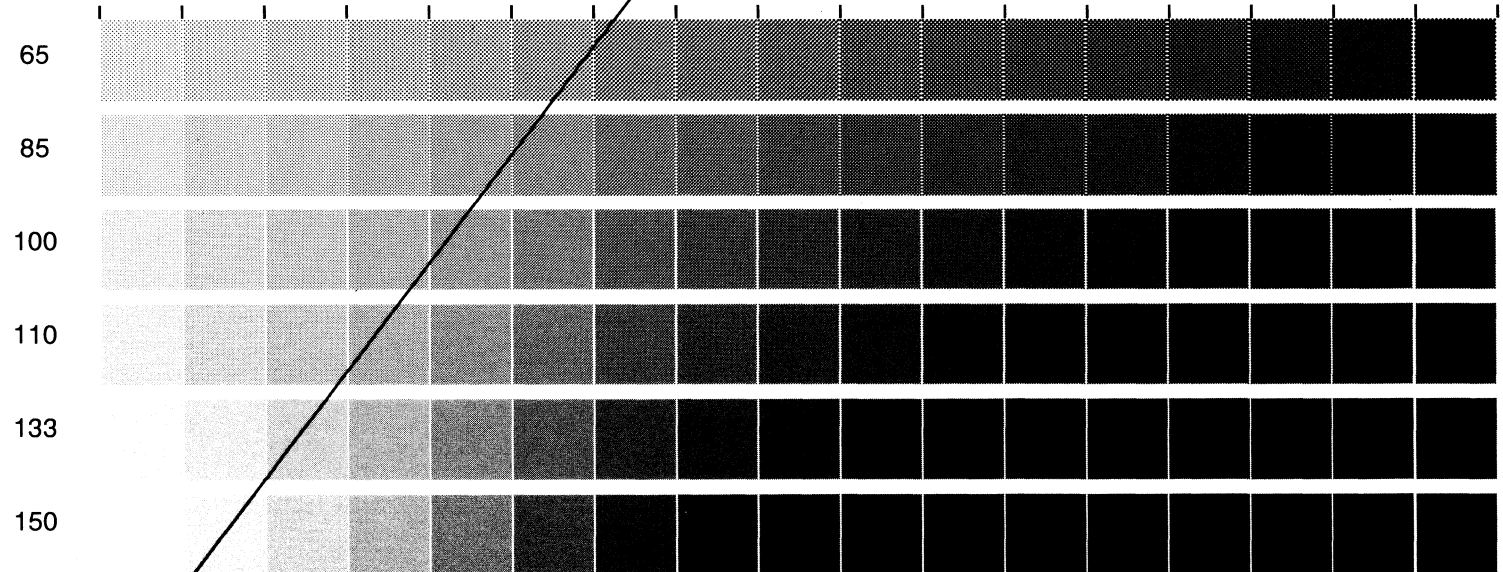
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CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

(Continuation of Contributions from the Museum of Geology)

UNIVERSITY OF MICHIGAN

Editor: EUGENE S. McCARTNEY

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(Continued on inside of back cover)

TWO NEW SPECIMENS OF PHYTOSAURS FROM THE UPPER TRIASSIC OF WESTERN TEXAS

By E. C. CASE AND T. E. WHITE

DURING the summer of 1931 an expedition from the Museum of Paleontology of the University of Michigan collected two nearly complete skulls of phytosaurs from the Upper Triassic beds of Potter County, Texas.

The first skull (Plates I-II) is sufficiently different from others to justify description as a distinct species. The specimen and holotype of the species is No. 14267 in the collection of the Museum of Paleontology in the University of Michigan. It is proposed to designate the specimen as *Leptosuchus studeri*, in recognition of the interest and the help afforded to the Museum of Paleontology by Mr. Floyd V. Studer, of Amarillo, Texas.

The skull was found in the breaks of Cerita de la Cruz ("Sweetly Cruz," of local parlance) Creek about twenty-three miles northwest of Amarillo, Texas. It was lying upon its left side, with the posterior part of the right side exposed and broken by weathering. Skillful preparation has replaced most of the fragments, so that but very little restoration was necessary. As is commonly the case, most of the teeth were dislodged, but a single tusk, evidently from the anterior end of the snout, was found lying less than an inch from its proper place. The skull is very slightly distorted; the rostrum is bent slightly to the left and the posterior part is slightly compressed from side to side.

The species is characterized by the convex contour of the lower edge of the rostrum, the prominent palatal ridges, the extremely large septomaxillaries, and the length of the prenarial elevation of the rostrum. The whole rostrum is narrow and elevated,

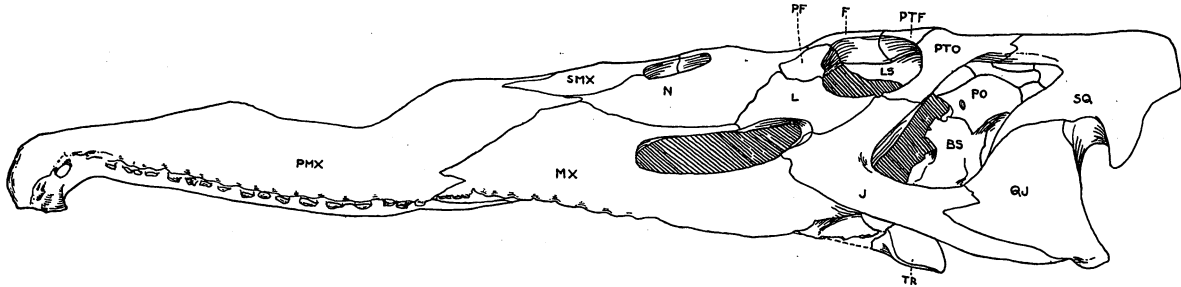


FIG. 1. Lateral view of the skull. $\times \frac{1}{6}$. BS, basisphenoid; F, frontal; J, jugal; L, lachrymal; LS, latero-sphenoid; MX, maxillary; N, nasal; PF, prefrontal; PMX, premaxillary; PO, prootic; PTF, postfrontal; PTO, postorbital; QJ, quadratojugal; SMX, septomaxillary; SQ, squamosal; TR, ectopterygoid

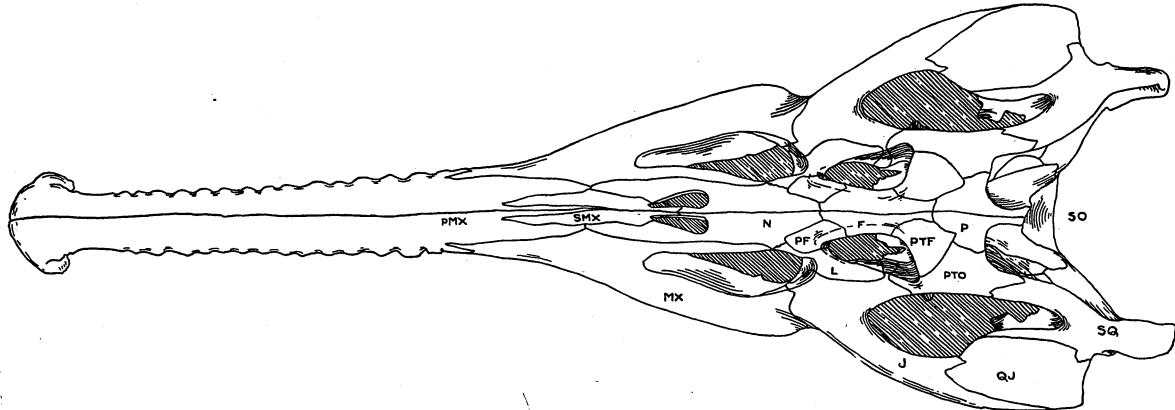


FIG. 2. Upper view of the skull. $\times \frac{1}{6}$. P, parietal; SO, supraoccipital. Other lettering as in Figure 1

characteristics which place the species in the Leptosuchan group as opposed to the Brachysuchan group with broader, depressed rostrum. It most closely resembles *Machaeroprotopus adamanensis* Camp, No. 26699 of the University of California collections, as figured by Camp.¹

In the general form and relationships of the various bones *L. studeri* does not depart greatly from other members of the group, as can be seen by comparing Figures 1, 2, and 3 with the published figures of other genera and species. In the following discussions only the points peculiar to the specimen are mentioned and described.

The *basisphenoid* does not extend upward to join the laterosphenoid and form a part of the anterior edge of the brain case, but is separated from the laterosphenoid by the

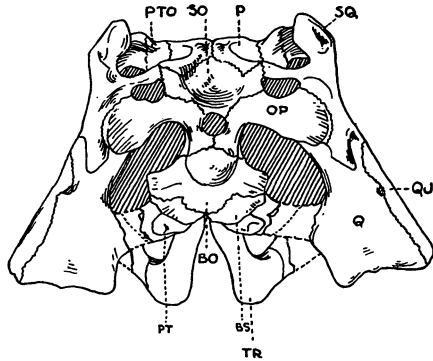


FIG. 3. Posterior view of the skull. $\times \frac{1}{8}$. BO, basioccipital; OP, opisthotic process; PT, pterygoid; Q, quadrate. Other lettering as in Figures 1 and 2

anterior extension of the proötic. This is as it is described by the senior author in *Leptosuchus crobsiensis* and by Camp for *Machaeroprotopus*. It is probable that the restoration of *Brachysuchus* is erroneous in this point, especially since the brain case of the type specimen of *Brachysuchus* is somewhat crushed. A small foramen lies on either side of the dorsum sellae on the suture between the proötic and the basisphenoid; it probably afforded exit for the VI nerve or a branch of the V nerve.

The presence of a presphenoid is not indicated or suggested in this specimen. The senior author² has previously given his

¹ Camp, C. L., "A Study of the Phytosaurs with Description of New Material from Western North America," *Mem. Univ. California*, Vol. 10, 1930.

² Case, E. C., *Description of the Skull of a New Form of Phytosaur, with Notes on the Characters of Described North American Phytosaurs*, *Mem. Univ. Mich. Mus., Mus. Pal.*, Vol. II, 1929.

reasons for believing that the parts thought by Huene and later by Camp to indicate the presence of this element are the thin upper edges of the troughlike parasphenoid broken down by pressure. The laterosphenoid does not extend greatly beyond the center of the orbit on the lower surface of the skull. Neither in this skull nor in any others of the collection of the University of Michigan is there any indication of an interorbital septum such as is figured by Camp in *Machaeroprotopus*. The lower edges of the laterosphenoids of the two sides are in contact, but this may be due to the slight lateral compression of the specimen. The groove on the outer surface running upward and forward from the foramen for the V nerve, described by Camp, is noticeable. Camp suggests that this carried a branch of the V nerve; it is in close association with the epipterygoid and may, in part, have received that bone.

The *proötic* completely surrounds the foramen for the V nerve and forms the upper half of the dorsum sellae.

The *epiötic* is fused with the supraoccipital, and the trace of the suture is visible only on the inner surface of the brain case. It is equally closely united with the exoccipital and must have ceased to exist as a distinct element of the skull early in the life of the individual. The same condition is found in all specimens of the phytosaurs in which this region can be examined.

The *exoccipital* (paroccipital process) has the dorsal edge rather deeply emarginate at about mid length, indicating a large post-temporal fenestra. In this it agrees with *Leptosuchus*, *Mystriosuchus*, and *Machaeroprotopus* and differs from *Promystriosuchus*, *Paleorhinus*, *Angistorhinus*, and *Brachysuchus*. On either side of the superior border of the foramen magnum there is an indentation formed by an overhang of the supraoccipital and adjacent parts of the exoccipitals. In specimens in the University of Michigan collection an indentation is present in *Leptosuchus*, but absent in *Brachysuchus* and *Promystriosuchus*, and in fragments of undetermined skulls showing the same region.

As in other specimens in the collection (five nearly perfect skulls in all), the authors have been unable to discover a suggestion of the presence of interparietal or tabulars such as are described by Camp in *Machaeroprotopus*.

The *squamosal*, with the whole parieto-squamosal arch, is depressed sharply below the surface of the skull. The posterior part of the squamosal is vertical and has no noticeable overhang over the supratemporal fenestra, a distinguishing character that places this specimen in the genus *Leptosuchus* as opposed to *Machaeroprotopus*. The sutural contacts between the squamosal and the quadrate and quadratojugal seem to have been more or less loose — a point in support of the kinetic condition of the skull suggested by the senior author.

The *quadratojugal* is closely articulated with the quadrate, but the attachment to the squamosal was more open and could have permitted some motion. The articulation of the jugal and quadratojugal is of the tongue-and-groove type, which would have permitted the forward-and-back movement of the quadrate-quadratojugal complex. Such a condition was suggested by the senior author in a previous paper in discussing the kineticism of the phytosaur skull, but the specimens at hand did not permit a complete demonstration. In the second specimen described in this paper, No. 14366 of the Museum of Paleontology collection, a fortunate break across the lower arch shows the relation perfectly (see Fig. 4). The jugal is thinned above and fitted deeply into the V-shaped groove on the lower surface of the quadratojugal.

The *jugal* extends posteriorly beneath the quadratojugal nearly to the quadrate. Anteriorly the jugal is almost excluded from the orbit by the close approximation of the postorbital and lachrymal. This condition is recorded in *Machaeroprotopus validus*, *Mystriosuchus pleiningeri*, and *Phytosaurus kapfii*. In other genera of the phytosaurs the jugal forms a large part of the lower border of the orbit.

In this specimen the jugal forms a part of the posterior border

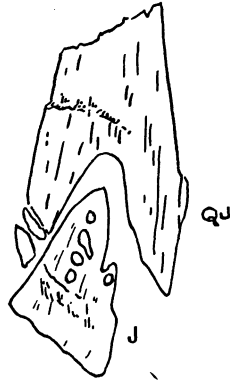


FIG. 4. Cross-section of the quadratojugal bar of the left side of *Brachysuchus megalodon*, No. 14366 U.M., showing the relation of the jugal (J) to the quadratojugal (QJ)

of the antorbital foramen, agreeing in this character with *Brachysuchus*, *Leptosuchus*, *Promystriosuchus*, *Angistorhinopsis*, *Angistorhinus*, *Mystriosuchus*, *Mesorhinus*, and *Machaeroprosopus validus*, and differing from *Phytosaurus kapfi*, *Machaeroprosopus gregorii*, *M. tenuis*, *M. zunii*, *M. adamanensis*, and *M. lithodendrorum*.

The *prefrontal* and *lachrymal* must be considered together. Just anterior to the border of the orbit there is a large elliptical pit on the inner side of the prefrontal; this extends for a short distance upon the lachrymal. Not far in front of and slightly below the pit is a small foramen, which leads into a canal directed toward the external naris. This canal is large in a small isolated lachrymal, No. 13723, of the collection. The pit and canal probably sheltered the lachrymal gland and duct.

The *lachrymal* meets the maxillary above the antorbital vacuity and excludes the nasal from any part in the border of the opening. In this it agrees with most of the recorded specimens of phytosaurs, but differs from most of the species of *Machaeroprosopus* described by Camp.

The *nasal* unites with the premaxillary by a suture of varying length in the different genera. In this specimen the connection is narrower than that of any form except *Pseudopalatus*, in which the two bones are described by Mehl as disconnected by the intervention of the septomaxillary.

The *septomaxillary* reaches the greatest proportional length and breadth on the surface of the skull observed in the known specimens of phytosaurs. Posteriorly it forms about one half of the nasal septum.

The *maxillary* carries twenty alveoli for teeth. The anterior four are smaller than those behind and smaller than the adjacent posterior premaxillary teeth, but there is no constriction of the rostrum in the region of the premaxillary-maxillary suture. The maxillaries do not meet in the median line of the palate, as figured by Camp for *Machaeroprosopus*.

The *premaxillaries* carry twenty alveoli for teeth. The two anterior ones held large tusks of the size of the single isolated tusk found close to the anterior end of the rostrum. The four posterior teeth are notably enlarged.

The major part of the rostrum is formed by the premaxillaries. It is decidedly triangular in section and noticeably higher than wide. One of the characteristic features of the specimen is the isolated elevation upon the rostrum. This begins 140 mm. from the anterior end, is 100 mm. long, and extends 15 mm. above the general level. The rostrum rises abruptly to the level of the posterior part of the skull, relatively far anterior to the nares; the beginning of the elevation is 240 mm. in front of the nares, and the prenasal length is 580 mm. The premaxillaries continue in contact for their full length on the lower face of the rostrum that separates the maxillaries. This is contrary to Camp's interpretation of the condition in *Machaeroprotopus adamanensis*, in which the maxillaries are figured as meeting in the posterior portion of the palatal surface, but he figures the maxillaries as separated in *M. gregorii*.

Posteriorly the premaxillaries apparently meet the united palatines, which by their union exclude them from contact with the prevomers. This is not the usual condition in phytosaurs and is not a normal occurrence in the primitive reptilia.

The *palatal ridges* are convex downward, in conformity with the curvature of the rostrum. They extend over a considerable part of the lower surface of both the premaxillaries and the maxillaries, appearing opposite the fifth tooth and disappearing opposite the twenty-eighth. The ridges rise rather abruptly and increase in height to a point opposite the last premaxillary tooth, the twentieth of the whole series, where they are 12 mm. above the rim of the alveolus. Posteriorly the ridges gradually decrease in height and become broader, fading into the general level of the palate. The ridges of the two sides are separated by a U-shaped trench which is deepest, 13 mm., opposite the twentieth tooth; at the twenty-eighth tooth the groove widens with the separation of the ridges and passes smoothly into the vault of the palate.

The *epipterygoid* is a very slender element which has not been found in any of the other specimens in the collection of the Museum of Paleontology, and the senior author has expressed his doubt of its presence in the skull of the phytosaurs, but it is distinctly present and in position on the left side of this specimen, though somewhat crushed. It rises from the pterygoid and passes upward

just anterior to the pituitary fossa and possibly did not reach contact with the laterosphenoid or the roof of the skull. The upper end is 5 mm. wide, the base probably twice as wide, and the total height about 60 mm.

The complex of bones, palatine, pterygoid, and prevomers, forming the vault of the palate and surrounding the nasal passage, is beautifully shown in its entirety, especially on the left side, and agrees in all major features with the various figures which have been published of this region of the skull, but the extreme thinness of the bones, with long and delicate squamous sutures, and the minute fracturing of the bones in place render any exact determination of the limits of various elements extremely difficult. The authors have examined the region most minutely and are inclined to believe that it corresponds with and confirms the last interpretation offered by the senior author.³

This specimen apparently belongs in the Leptosuchan group of the phytosaurs, including *Leptosuchus*, *Mystriosuchus*, *Phytosaurus*, *Rhytidon*, *Angistorhinus*, *Paleorhinus*, and certain forms described by Camp as species or age stages of *Machaeropsopus*, as *M. tenuis*, and the young of *M. adamanensis*. It is further characterized by the curvature of the rostrum, convex downward, seen also in *M. adamanensis*, No. 26699 of the University of California collection, *Mystriosuchus carolinensis* (*rostratus* Marsh), a specimen described as *Paleorhinus* (?) by Toepelman, a fragment of a rostrum, No. 7417 in the University of Michigan collection, and an incomplete skull, No. 6813 in the American Museum of Natural History. Like these specimens it also lacks the constriction of the rostrum at the junction of the maxillary and premaxillary bones.

	MEASUREMENTS	Mm.
Total length.....		920
Condylobasal length.....		900
Posterior end of parietals (mid line) to anterior end of snout...		880
Breadth across quadrates.....		340
Breadth across squamosals.....		210
Interorbital breadth.....		60
Height of skull at quadrate.....		190
Height of skull at nares.....		160
Vertical diameter of orbit.....		60
Antero-posterior diameter of orbit.....		85

³ Case, *op. cit.*

The second phytosaur skull discovered in 1931 has been identified as belonging to the genus and species *Brachysuchus megalodon*. It carries the number 14366 in the Museum of Paleontology of the University of Michigan.

This specimen was found in the same locality as the one described above and not far from it. The skull is complete, except for the extreme anterior end of the rostrum; it is accompanied by the left ramus of the lower jaw.

Because the skull and jaws of the genoholotype have been mounted in full relief ⁴ this skull has been prepared to show the palatal surface. As displayed (see Plate III), the anterior end of the rostrum has been restored. The part carrying the fourth and fifth teeth is bone, but back of this a short part of the lower surface, equivalent to the space occupied by seven tooth sockets on the right side and eight on the left, was not recovered; since the dorsal part of this region is complete, the exact position of the teeth on either side is determinable.

The skull is slightly smaller than the genoholotype — 1223 mm. instead of 1260 mm. Other proportions are comparable:

Posterior end of squamosal to anterior end of antorbital vacuity 582 mm.
Posterior end of squamosal to anterior end of external nares 595 mm.
Posterior end of squamosal to anterior end of internal nares 590 mm.

The specimen has suffered very little distortion. The maxillary of the right side is pushed slightly outward, but even if this is taken into account the sudden contraction in the breadth of the palate at the juncture of the maxillary and premaxillary parts of the skull is quite striking. There is a very slight increase of breadth in the middle of the premaxillary part.

As nearly as can be counted, there are forty teeth and sockets on the right side and thirty-seven on the left.

The internal nares are markedly unsymmetrical, that of the left side being shorter and broader in the posterior position. The broadening may be a part of the extension of the right maxillary region due to distortion in petrification, but the shortening can

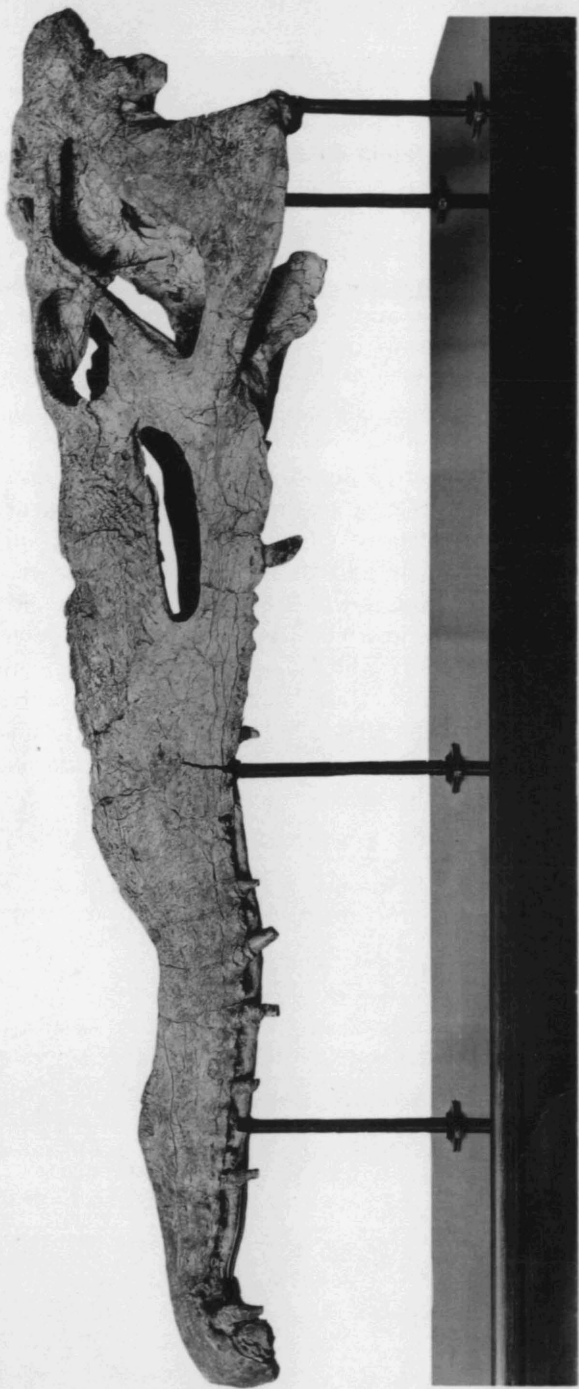
⁴ Case, E. C., "A Perfectly Preserved Segment of the Armor of a Phytosaur, with Associated Vertebrae," *Contrib. Mus. Pal.*, Univ. Mich., Vol. IV, pp. 78-79 and Plates VI-VIII, 1932.

hardly be accounted for in the same way. It seems to have been present in life as an individual variation, for no reptiles, aquatic or others, show a normal asymmetry of the narial or facial region such as occurs in some of the Cetacea.

In the genotype of *Brachysuchus* as previously described and figured by the senior author⁵ there is a distinct separation between the premaxillaries and the anterior end of the palatine, which is emphasized by the complete and rounded edge of the palatine. Apparently there was some sort of extension of the internal nares outward and forward which continued almost to the maxillary. In this specimen the condition is not the same. The region of premaxillary-palatine suture is minutely fractured, but there is no evidence that the anterior edge of the palatine was thickened or separate from the premaxillary. The contact was to all appearances by squamous overlap, and the suture runs backward and outward instead of forward and outward. This is the condition found in the known skulls in which the region has been described and figured. The condition in the genotype skull has been verified, and the senior author is at a loss to account for the apparent departure from the normal relations; it may be purely illusory, owing to some peculiarity of compression or petrification, but at the moment this seems improbable.

⁵ Case, as cited in note 2, Figs. 2 and 11.

PLATE I



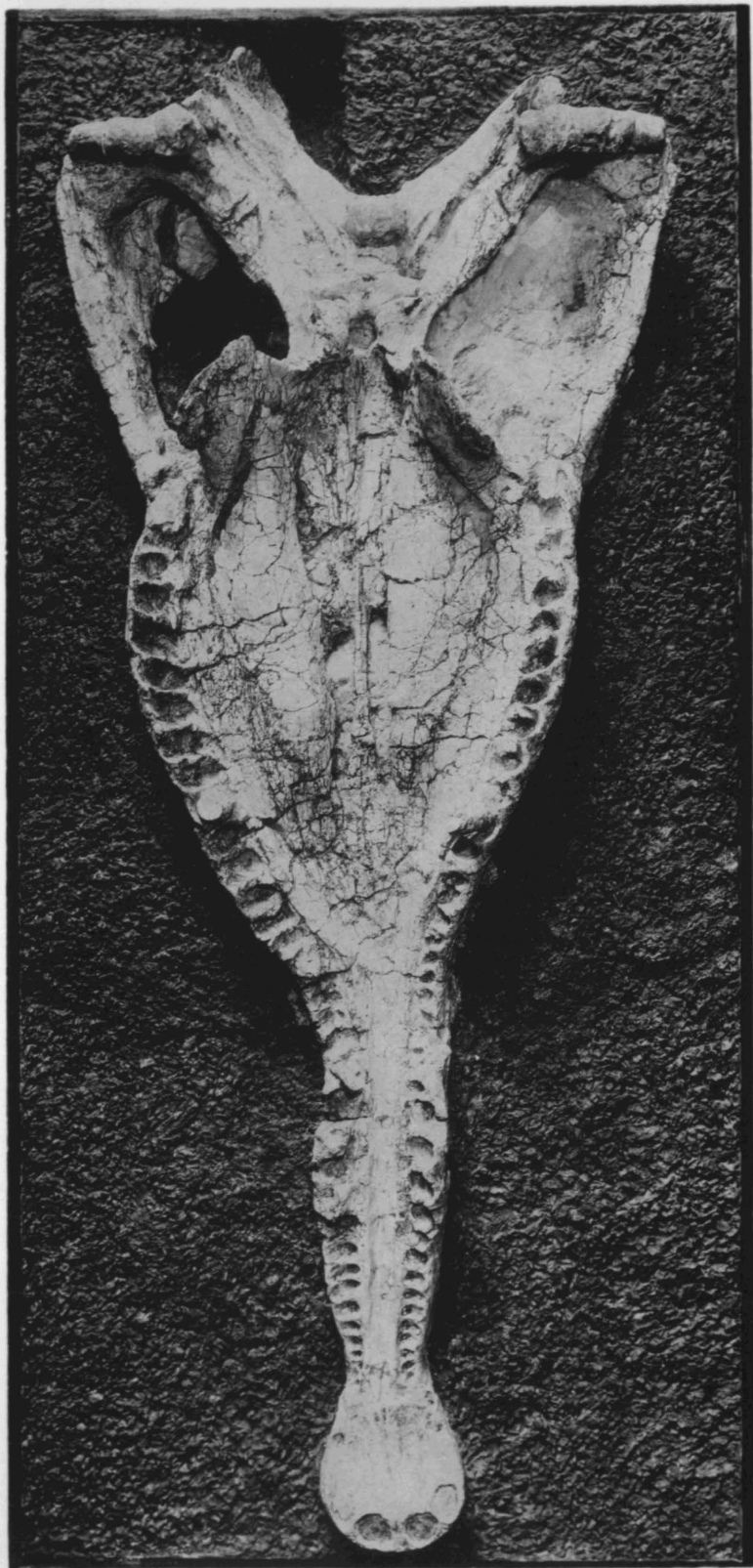
Lateral view of skull of *Leptosuchus studeri*. $\times \frac{1}{3}$

PLATE II



Top view of skull of *Leptosuchus studeri*. $\times \frac{1}{3}$. Photographed in strong side light to show the acute upper edge of the rostrum

PLATE III



Palatal view of skull of *Brachysuchus megalodon*, No. 14336 U.M. $\times \frac{1}{4}$

(Continued from inside of front cover)

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