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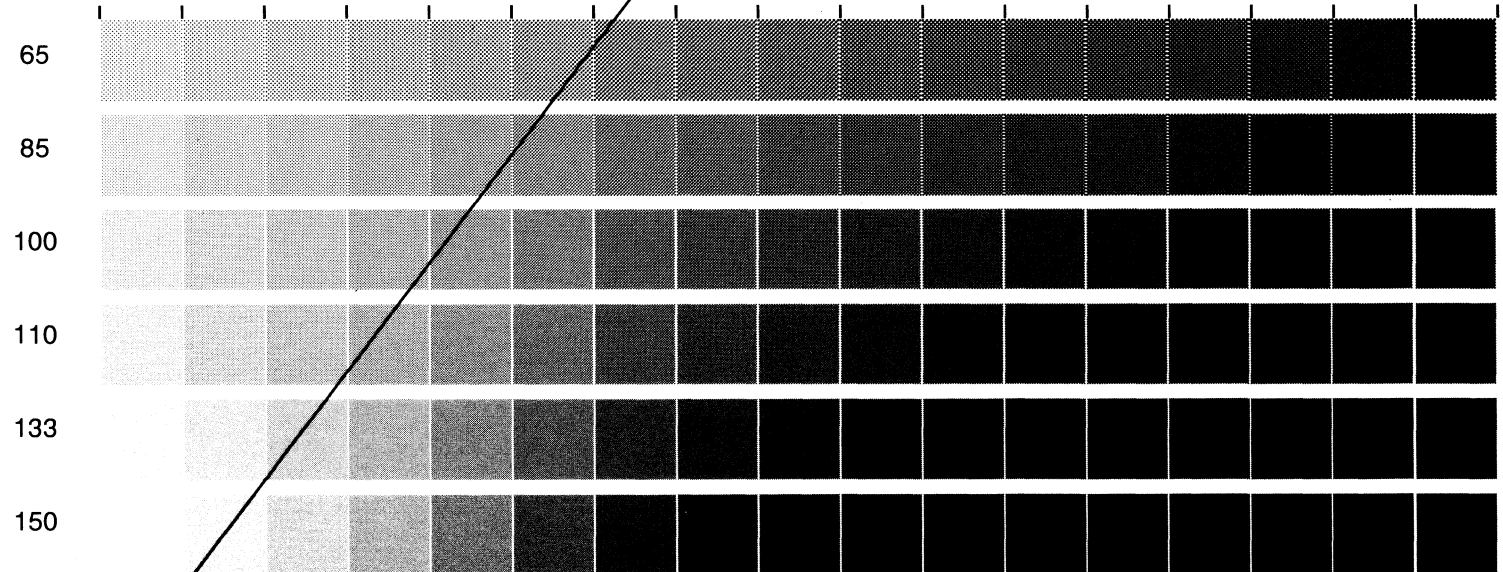
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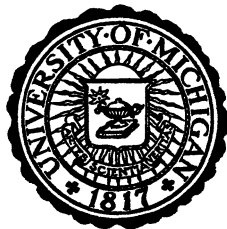
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DECEMBER 1, 1932

A PERFECTLY PRESERVED SEGMENT
OF THE ARMOR OF A PHYTOSAUR,
WITH ASSOCIATED VERTEBRAE

BY

E. C. CASE



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Editor: EUGENE S. McCARTNEY

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(Continued on inside of back cover)

A PERFECTLY PRESERVED SEGMENT OF THE ARMOR OF A PHYTOSAUR, WITH ASSOCIATED VERTEBRAE

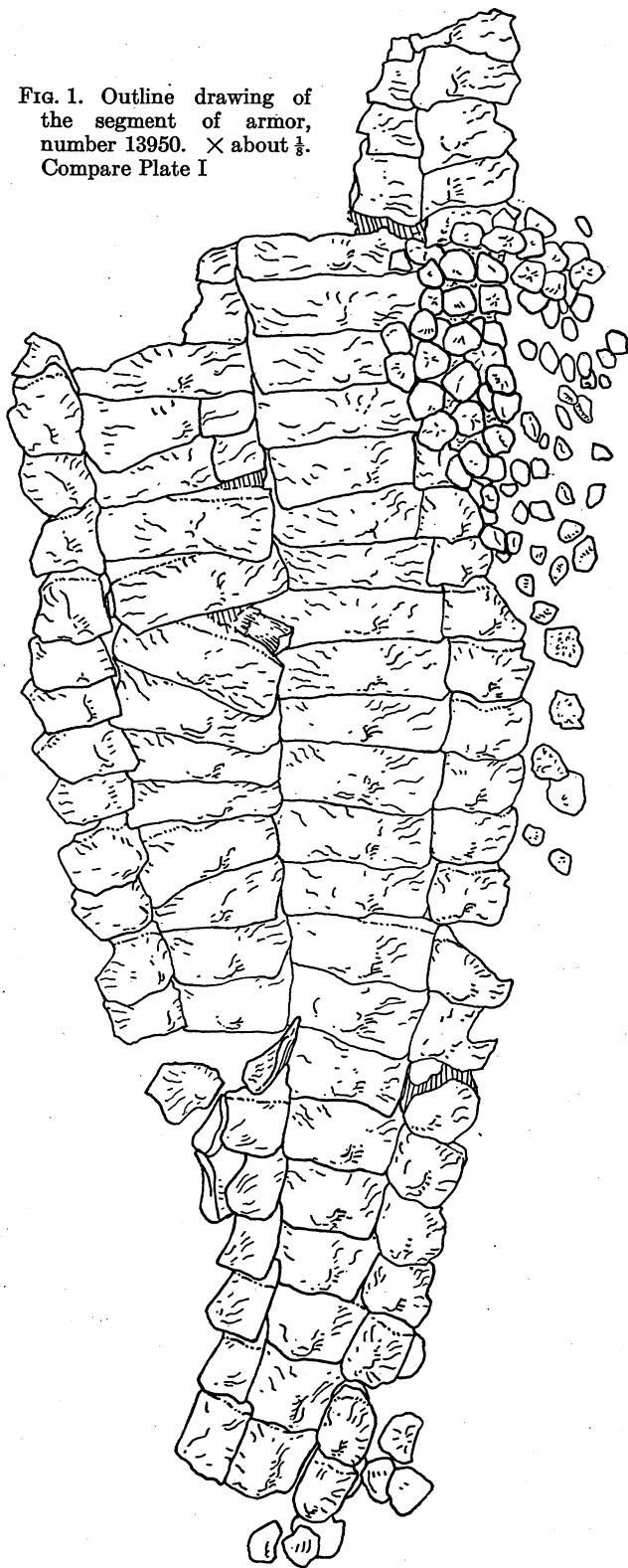
By E. C. CASE

THE expedition from the Museum of Paleontology of the University of Michigan to the Triassic beds exposed in the breaks of Cerita de la Cruz Creek northwest of Amarillo, Texas, in 1931, recovered a considerable portion of the armor of a phytosaur with the associated vertebrae. The segment of armor extended from the mid-dorsal to the mid-caudal region. The plates are in undisturbed position, except where the spine of the first caudal vertebra was forced through the carapace, displacing one of the plates, but serving to locate most effectively the plates with relation to the vertebrae. The vertebrae lay almost in position, but are slightly displaced at one or two points. The breaks are not sufficient to disturb the continuity of the series. Plate I and Figure 1 show the appearance of the upper surface of the specimen when cleaned and assembled. The anterior portion was weathered out, and the condition of the bone was such that the exposed parts broke into minute fragments. These were mingled with the débris in the gutter and much was hopelessly lost, but the centra of several vertebrae were recovered and can be arranged with fair certainty to extend the continuous series to the anterior dorsal region.

This specimen is of particular interest since it is the first in which any considerable portion of armor has been found associated with the axial skeleton and since it permits the allocation of the particular types of plates to particular types of vertebrae and pelvis.

The specimen was found with the dorsal surface down and the preserved parts in position. The vertebrae and plates were freed

FIG. 1. Outline drawing of
the segment of armor,
number 13950. \times about $\frac{1}{3}$.
Compare Plate I



from all loose matrix, hardened with shellac, covered with Japanese rice paper, and then with a heavy coating of plaster of paris. In the workroom the upper face was cleaned and then covered with a heavy layer of plaster and reversed. The first layer of plaster was cut away and the vertebrae were removed. Then the lower surface was again covered with plaster and the upper surface freed for permanent mounting and exhibition. In this way all parts were rigidly preserved in position.

The armor consists of two median rows and two lateral rows of well-shaped quadrangular plates, and an outer series of smaller plates varying in size and outline. The quadrangular plates have a more or less well developed knob at the center of the posterior edge and are marked by a rather shallow sculpture of radiating pits and ridges. The anterior edge of each plate is drawn out into an area or flange, permitting some movement at the juncture with the plate in front of it. The plates of a transverse series fitted closely together, but without sutural or articular surfaces.

The plates on the sides vary in form from those which are irregularly circular, three or four centimeters in diameter, with an obscure ridge or keel on the upper surface and a faint radial sculpture, to those very irregular in outline, with serrate edges and no distinct keel. Large numbers of such plates have been found isolated, and there has been much uncertainty as to their position, gular, caudal, or abdominal, and even as to the genus to which they should be assigned.

The specimen retains part or all of twenty-six transverse rows of plates. The first three, corresponding to the sixth, seventh, and eighth presacral vertebrae, are represented by the complete plates of the right lateral row and the outer halves of those of the right median row. The next two transverse rows are represented by the complete plates of the right side and the inner halves of the plates of the left median row. Posterior to this the transverse rows are complete.

The plates of the longitudinal median rows decrease in width (transversely) very slightly to the nineteenth or twentieth, posterior to which the decrease is more rapid. The twenty-sixth is less than one half of the width of the fifth. The knobs on the plates

become gradually higher, with a notable increase in height and sharpness beginning with the sixteenth or seventeenth. The posterior edge of each plate is slightly concave transversely, and overlaps about a centimeter upon the smooth flange of the succeeding plate. The character of the sculpture does not change materially throughout the series. The two sides of each plate meet at a very large angle, 150° or larger. The lower surface is smooth. The plates of the twenty-third and twenty-fourth rows are about equidimensional; anterior to this they are broader (transversely) than long, and posteriorly longer than broad.

The plates of the lateral rows are much narrower (transversely) than those of the median rows in the dorsal and anterior caudal regions. The knob is more prominent, and sharp; the sculpture is similar in kind and in pattern. These plates become narrower by a loss of breadth of the outer half, the inner half retaining its width throughout the series. The posterior edge is narrower than the anterior, so that the outer edge slants out and forward. As the outer half narrows in the caudal region the knob becomes higher and more spinelike, but never reaches the proportions found in *Desmotosuchus*. The angle between the two sides of each plate becomes smaller posteriorly, until in the mid-caudal region it approaches 120° to 130° . The twenty-third and twenty-fourth plates are about as long as broad. Anterior to this they are broader (transversely) than long and posteriorly narrower.

On the right side of the specimen there are a large number of smaller plates irregularly placed and of various sizes and forms. There were many more associated with the specimen, but because of the extremely fragile nature of the thin and rotten bone, only those most closely associated with larger plates could be held in position. Opposite the fifth to ninth transverse rows there is a cluster of plates, three to four centimeters in diameter, which are obscurely arranged in longitudinal rows. In different places along the right side of the specimen similar plates lie close to the lateral row. Outside these are numerous irregularly shaped plates of various sizes, approaching an oval in outline, and having more or less obvious keels and sculpture. Many plates of this kind were found on the under side of the vertebrae, and crushed tightly

against them. These were probably from the left side of the animal and were turned under in the desiccation of the skin or in the compression accompanying burial.

The measurements of certain plates showing the proportions are as follows:

RIGHT MEDIAN ROW

	Mm.
Sixth plate	
Breadth, anterior edge.....	195
Breadth, posterior edge.....	180
Antero-posterior length.....	76
Nineteenth plate	
Breadth, anterior edge.....	142
Breadth, posterior edge.....	129
Antero-posterior length.....	75
Twenty-fourth plate	
Breadth, anterior edge.....	89
Breadth, posterior edge.....	85
Antero-posterior length.....	75
Twenty-sixth plate	
Breadth, anterior edge.....	69
Breadth, posterior edge.....	67
Antero-posterior length.....	76

RIGHT LATERAL ROW

Second plate	
Breadth, anterior edge.....	106
Antero-posterior length.....	60
Fifteenth plate	
Breadth, anterior edge.....	83
Antero-posterior length.....	63
Twenty-first plate	
Breadth, anterior edge.....	66
Antero-posterior length.....	64
Twenty-sixth plate	
Breadth, anterior edge.....	46
Antero-posterior length.....	68

The breadth of the specimen is evidently greater than that of the animal in life, since the back has been pressed flat and the lateral plates pushed up and turned outward. If the plates are set with a slight convexity in the median line, the outer sides of the lateral plates would be almost vertical, as in *Desmotosuchus*, and the width of the body opposite the fourteenth transverse row, which is the greatest in the specimen, 537 mm., could not have exceeded 450 mm. Such dimensions must be approximate, since the angulation of the plates varies and the contour of the back is conjectural. There is considerable probability that the posterior portion of the tail was nearly inclosed by plates, but this cannot be verified.

Any estimate of the length of the animal must be an approximation. The specimen is 1,600 mm. long; if to this is added 560 mm. for the presacral vertebrae found in the débris and those not found, 700 mm. for the missing extremity of the tail, and 1,000 mm. for the head, if it was of the long-nosed phytosaur type, the total would be 3,600 mm., or about 12 feet. If, as is not impossible, the animal was of the *Desmotosuchus* type, the length of the head would be materially less.

The pelvis and vertebrae lay very little disturbed from their proper position, but since the specimen was buried with the dorsal surface down the axial skeleton was somewhat crushed and distorted. The bones have been separated from the plates, with the exception of the fourteenth and fifteenth caudals near the posterior end, which were so tightly cemented to the fragile plates that they could not be removed. The pelvis was crushed nearly directly downward, so that the two halves lay spread apart, with the sacral vertebrae against the inner side of the ischial symphysis and the apron-like pubes turned directly back and pressed down on the rest of the pelvisacral mass. The distortion and breakage resulting from this accident of fossilization made it rather difficult to interpret at first, but by comparison with a very similar pelvis and sacrum which is nearly complete and little distorted, number 7470 in the collection, a satisfactory restoration was finally accomplished.

Specimen 7470 from Crosby County, Texas, has been figured

and partly described by the author in previous papers (Case, 1922, 1929). The striking peculiarities are the shortened ilium, with a hooklike projection of the anterior end of the crest and a very much shortened posterior process of the crest. The specimen lacked the distal portions of the pubes, but from specimen 13950 can be added the characteristic shortening of these bones. Comparative figures of the two types of phytosaur pelvis have been given by the author (Case, 1929, Figs. 21-22). The pelvis as reconstructed is shown on Plate III.

The pubis formed an apron-like anterior face, as in the *Pseudosuchia* and *Parasuchia* generally, but did not descend greatly, if at all, below the level of the ischial symphysis. Neither the pubic foramen nor a pubo-ischiadic fenestra can be definitely outlined in either specimen, but they were in all probability present. In number 7470 there is a suggestion of a small pubic foramen on the outer edge of the bone near the articulation with the ilium.

The posterior ends of the ischia are stout and drawn out into a heavy spoutlike process. The crushing of the specimen, number 13950, forced the sacral vertebrae down into the cavity of the pelvis and dragged the sacral ribs with them. The articulation of the ribs with the ilia was so strong that the ribs have not been separated from them, but the pressure and distortion have stretched the ribs and pressed them so tightly against the inner side of the ilium that in spots it is difficult to distinguish the two. The ribs, as seen from this specimen and number 7470, were firmly attached to both the centra and neural arches of the sacral vertebrae and curved upward and outward to the ilia, but the articulation with the centra is still distinct. The anterior and posterior edges were drawn out into wings, which thickened and broadened at their distal ends to form the firm articulation with the ilia. The anterior sacral rib is much less expanded than the posterior one. In specimen 13950 it is the close application, almost fusion, of the expanded ribs with the ilium, due to pressure, which in places obscures the outline of the ilium and at first sight makes the anterior hook and the posterior process of the ilium appear to continue downward as thin plates.

The whole pelvis is stouter and more compact than in the more

common type, owing to the shortening of the distal portions of the ilium and the ischium and of the descending processes of the pubes. The acetabular portion is fully as heavy. The attachment of the sacral ribs is lower on the inner face of the ilium, in the lower half at least, and the crest of the ilium is heavier and more rugose.

VERTEBRAE

The vertebrae directly associated with the armor lay upon it in continuous series and in nearly normal position, but had been slightly displaced at two points (see Plate II). The caudals were

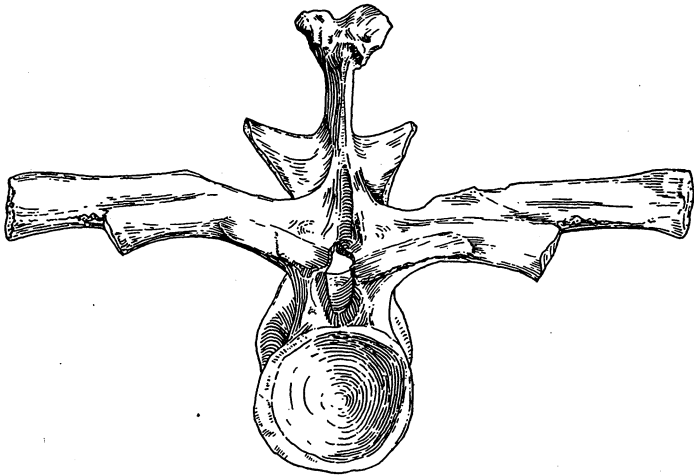


FIG. 2. Anterior view of a posterior dorsal vertebra, number 7470. $\times \frac{1}{2}$.

obscured in places by small plates from the sides or lower surface of the tail, which had been pressed down upon them. All were separated from the armor except the fourteenth and fifteenth caudals, which were so tightly cemented to it that their removal was impossible. A cast was taken of these before the final mounting, so that all proportions were preserved.

The spine of the first caudal vertebra was forced up between two plates of the left median row, the eleventh and twelfth, fixing the relative position of plates and vertebrae. There were twenty-two vertebrae preserved in continuous series from the fifth precaudal

to the seventeenth caudal, making, with the two sacrals, twenty-four in all. In the gutter eleven centra were found mingled with small fragments of plates and vertebral processes. Of these, nine can be arranged in a very satisfactory series, including the sixth to the fourteenth presacral, the thirteenth being an anterior dorsal. Another centrum with the diapophysis and parapophysis closely approximated must be the eleventh or twelfth from the anterior end, and another, represented by the lower half of the centrum, is an anterior cervical.

If twenty-five, the number found by Camp in *Machaeroprotopus adamanense*, is typical, there are eight vertebrae missing. These could hardly all have been present before the specimen was exposed, for the gutter was carefully searched and no more were found. The small size of the centra of the dorsals contrasted with the heavy lumbar, sacral, and anterior caudals might suggest a second specimen, but the free centra were all

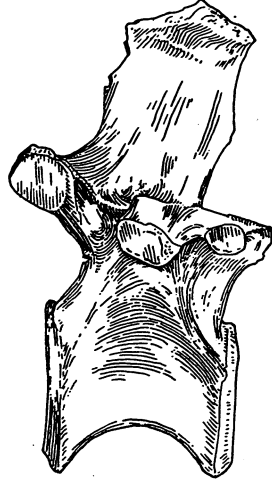


FIG. 3. Left side of the vertebra shown in Figure 2. $\times \frac{1}{2}$

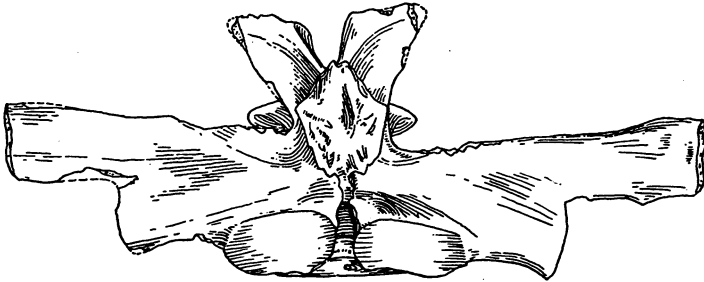


FIG. 4. Superior view of the vertebra shown in Figure 2. $\times \frac{1}{2}$

found directly below the exposure of the continuous series, and no indications of another specimen, fragmentary or complete, occurred in the small gully. The author has previously (Case,

1922, p. 35) given his reasons for believing that the presacral number in *Desmotosuchus* was probably twenty-seven or twenty-eight; this may be too high.

The following description begins with the first vertebra found in the continuous series and proceeds through the series. The less certainly placed vertebrae are described later (see Figs. 2-4, and Plate III).

Fifth presacral vertebra. — The faces of the centrum are nearly circular. The edges descend well below the body of the centrum. The lower face of the centrum is flattened and without keel. The sides are slightly concave. The transverse process rises from the neural arch nearer the anterior than the posterior face. The distal portion of the transverse process and the neural spine and the zygapophyses are missing.

Fourth presacral vertebra. — Very similar to the fifth.

Third presacral vertebra. — The centrum is very similar to those of the fourth and fifth. The transverse process curves upward and outward and shows the beginning of the lateral expansion. As illustrated in Plate IV, Figure 1, the transverse processes of the third, second, and first presacral vertebrae were expanded into very broad, thin plates, nearly or quite in contact at the distal ends. In the specimen the process of the right side lay in place, but the bone was so thin and so decayed, since it lay near the point of exposure, that it was preserved with difficulty. The photograph was made before the parts were removed in the necessary work of strengthening the armor.

The proximal portion of the transverse process of the fourth is preserved and shows little or no expansion of the edges. The process of the third has the anterior and posterior edges drawn out into thin plates; much more so on the anterior edge. This expansion continues to the extremity. The edges of the distal end were badly rotted, but the outline could be followed, and the whole was preserved by a cast in plaster. Both in this process and in that of the two following vertebrae there is a very suspicious appearance of a rib attachment with the tubercular and capitular faces offset, as in the *Crocodylia* and in *Desmotosuchus*. The evidence is not, however, decisive, and the vertebrae are so far posterior that it

seems improbable that ribs were present. If there were ribs, they formed at least half of the length of the part here called the transverse process and were fused with the process.

Second presacral vertebra. — The centrum shows little change. The transverse process has a strong convex thickening on the lower side running the full length; this is the body of the process. The anterior and posterior edges are drawn out into thin plates, gradually widening until the whole terminates in a broad leaflike expansion of very thin bone. This process was fortunately entire and has been preserved by a backing of plaster. The neural spines of this and the first presacral are complete, but distorted by pressure. They were short and strong, with well-developed distal tabular expansions.

First presacral vertebra. — The centrum is like those preceding it. The transverse process was badly injured by fracture and decay, but enough was preserved to show that it had an expansion similar to that of the second and third presacrals. The meaning of this peculiarity is not evident. The expanded processes (or ribs) were beneath a strong covering of dermal plates and were separated from the plates by a considerable space, five to eight centimeters. The plates were supported by the strong neural spines with expanded apices. The transverse processes could have had no supporting or strengthening value and certainly were not attached to the pelvis. They seem but one more of the problematical peculiarities of the specimen.

Two sacral vertebrae. — The centra are closely pressed together, but were not ankylosed; the zygapophyses connecting them are reduced in size, though still functional. The sacral ribs have been closely pressed against the ilia and somewhat injured, but can be traced in outline. The rib of the first vertebra is less expanded antero-posteriorly than that of the second. Both are strong and are attached to the body of the centrum as well as to the neural arch. The attachment to the ilium is strong and well down upon its inner surface, to the lower half, in distinction from the condition in the forms with an elongate ilium, in which the ribs are attached well up on the inner surface, within the upper half. The neural spines have been crushed obliquely forward, but show the full

length of the rather low spines and the very strong tabular development of the upper ends. The condition is much better seen in the undistorted specimen, number 7470, previously described in part (Case, 1922) and as noted in a later paper (Case, 1929); Mehl's *Acompsosaurus* is probably of the same type (Figs. 5-6).

First caudal vertebra. — The centrum is not unlike those of the lumbar and the sacrals. The transverse process rises from the



FIG. 5. Anterior view of sacral vertebrae, number 7470. $\times \frac{1}{2}$

neural arch and continues as a narrow blade to a blunt point. The neural spine terminates in a well-developed table.

Second caudal vertebra. — This is similar to the first, with some reduction in the size of the table on the neural spine. Neither of the first two caudals shows facets for the chevron bones.

Third caudal vertebra. — This has the terminal expansion of the neural spine smaller than on the second. The transverse processes originate lower, from the base of the neural arch. The lower face is flattened slightly, and the posterior half is divided into two low ridges which terminate in facets for the chevron bone.

Fourth, fifth, and sixth caudal vertebrae. — These show a slight but gradual change in the development of chevron facets, the elongation and increasing slenderness of the centrum, the shortening of the transverse process, and the loss of the tabular expansion on the apex of the neural spine.

Seventh caudal vertebra. — This has the centrum noticeably more elongate and slender. The lower surface of the centrum is

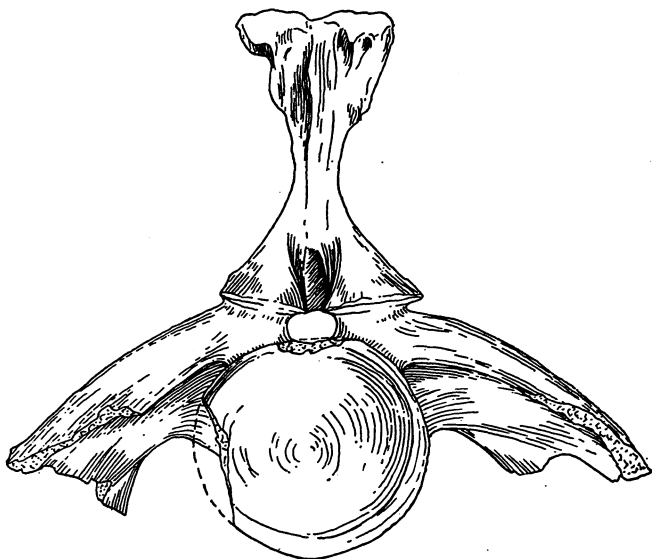


FIG. 6. Reconstruction of sacral vertebrae shown in Figure 5. $\times \frac{1}{2}$

flattened with well-marked and separate facets for the chevron. The transverse process rises near the midlength of the centrum, but still from the neural arch. The neural spine is widened antero-posteriorly and is so thin that it is probable that all apical expansion has disappeared.

Eighth to the tenth caudal vertebrae. — These show an increase in the length and slenderness of the centrum. The origin of the transverse process comes to be progressively nearer and nearer the midlength, but is still high up on the side of the centrum or on the neural arch.

There are remains of chevrons between the sixth and seventh, the seventh and eighth, and the eighth and ninth caudals. The first is represented by the distal end and the last by the proximal; the one between the seventh and eighth caudals is complete but compressed. The proximal faces are separate. The distal half becomes thin but expanded. The exact position with relation to the vertebrae is uncertain, but is shown in Plate III, as suggested by the facets on the vertebrae.

Eleventh, twelfth, and thirteenth caudal vertebrae. — These show the progressive reduction of the transverse process and antero-posterior elongation of the neural spine.

Fourteenth and fifteenth caudal vertebrae. — These could not be removed from the plates, but a cast of the exposed left sides was taken. The transverse processes are reduced to small projections from the middle of the centrum. The neural spine of the fifteenth is low and slender, but with considerable antero-posterior length. The chevron attached to the fifteenth is partly preserved; its proximal end is in place, but the distal portion, less than one half, is lost. The bone widened toward the distal end.

Sixteenth and seventeenth caudal vertebrae. — These show a groove on the lower surface of the centrum, shallow, but distinct. They carry nearly the last traces of the transverse processes as small projections from the side of the centrum. The neural spine of the seventeenth is very nearly complete; it is long and low, with no suggestion of an expansion of the upper end. A chevron between the sixteenth and seventeenth has an expansion toward the distal end, but is incomplete. The zygapophyses of these, the last vertebrae of the continuous series, are still functional, and the adjacent ones are still engaged.

It is probable that from a third to a half of the caudal series is missing.

From numerous isolated caudal vertebrae of the same type in the collection of the Museum of Paleontology, it is apparent that the caudals increased in length and slenderness, with an accentuation of the groove on the lower face and a gradual loss of the neural spines and zygapophyses.

As stated above, several incomplete vertebrae were found in

close association with the plates and the continuous series of vertebrae in such position and relations as to leave no room for doubt that they are parts of the same specimen. Owing to the nature of the preservation of the bones, these vertebrae are represented by the centra alone, all processes and associated plates having fallen into small pieces that could not be collected. They have been arranged according to size and character, and though the exact position of each one cannot be certain, they cannot be far from their proper place. Most notable about this series is the graduated but decided reduction in size toward the anterior end. All show a rounded lower surface of the centrum, without any trace of keel. The transverse process originated from well up on the sides of the neural arch. Extended description of the imperfect vertebrae is unnecessary, since their form is shown in Plate III.

Nine of the vertebrae can be arranged in series. This would make the most anterior one, the fourteenth presacral, an anterior dorsal.

Two other imperfect vertebrae were found. The more posterior has the proximal end of the rib attached in the normal position at the anterior edge of the centrum and neural arch. The capitular and tubercular heads are close together and are in the position assumed just anterior to the point where the capitular attachment is transferred from the edge of the centrum to the diapophysis in the *Crocodylia* and *Phytosauria*; it is probably the eleventh or twelfth in series from the front.

The lower half of another centrum carries the capitular facet almost at its lower edge. The lower face is broad, with a decided median ridge, which becomes wider and heavier toward the posterior end. It is evidently an anterior cervical. The striking decrease in size and the changing character of the mid-dorsal and anterior dorsal vertebrae is probably responsible for the assignment of much isolated material to distinct genera and species.

The discovery of this series of plates with the pelvis and vertebrae permits an association of parts of the phytosaur skeleton, found as isolated elements, hitherto impossible. The plates are of the regular quadrangular form, arranged in a definite pattern, with a subcentral knob or spine, a radial sculpture, and an articular

flange on the anterior edge. These are definitely associated by two specimens, numbers 7470 and 13950 in the University of Michigan collection, with a stouter type of pelvis having a short iliac crest.

The second type of plates, the irregular or irregularly triangular forms with a less fixed pattern, a keel, an irregular, rough sculpture, and no articular flange, are as definitely associated with the more slender type of pelvis having an elongate iliac crest (Camp, 1930).

The quadrangular plates have long been associated on very doubtful evidence with the European genus *Phytosaurus* and the irregular plates certainly with *Mystriosuchus*. Since the quadrangular plates in the European forms are associated, also doubtfully, with an ilium having an elongate crest, the evidence from European and American forms has previously been contradictory.

There is in the collection of the Museum of Paleontology a very large number of plates of various forms and sizes collected by several expeditions to the Dockum beds of western Texas. It has been assumed that certain different types of plates went with different forms, but it has hitherto been impossible to allocate these with any assurance, or even to be sure that they did not come from different parts of the body of very similar individuals. The discovery of plates in association with vertebrae and pelvis makes it certain that the armor was sufficiently fixed to assign isolated plates to distinct groups of phytosaurs.

There are in the collection at least four, probably five, distinct types of plates:

1. Heavy, approximately quadrangular plates; the plates of the median rows meeting those of the opposite side in thick sutural surfaces; the sculpture a series of pits and low ridges radiating from a subcentral prominence; the anterior edge a smooth beveled flange. The lateral rows with the outer side of each plate nearly vertical; a low radial sculpture from a spine-like prominence. Type of *Desmotosuchus*.

2. Thinner, approximately quadrangular plates; the plates of the median rows meeting those of the opposite side in thin or non-sutural edges; the sculpture a series of low pits or ridges radiating from a low subcentral prominence; the anterior edge a

smooth, beveled flange. The lateral rows with the two sides meeting at a larger angle; a low radial sculpture from a low prominence. Type of number 13950 U.M. (*Phytosaurus?*). (See Plate IV, Figs. 2-3.)

3. Thin, laterally elongate plates; the plates of the median rows meeting those of the opposite side in a thin or non-sutural edge; the sculpture a series of low ridges radiating from a low prominence nearer the median end; the anterior edge a smooth, beveled flange. The plates of the lateral rows unknown. Type of number 8859 U.M. (*Phytosaurus?*). (See Plate IV, Figs. 5-6.)

4. Heavy, irregularly triangular plates; the plates of the median rows meeting those of the opposite side in a thick sutural edge; the sculpture a series of deep pits and strong ridges radiating from a subcentral, antero-posteriorly elongated prominence or keel; the anterior edge continued as a roughened articular surface for nearly a third of the antero-posterior length on the median side. The lateral rows composed of thinner, irregular plates, with lower sculpture and keels, alternating with the plates of the median rows and overlapping the outer edges of two adjacent ones. Type of *Machaeroprotopus*, *Mystriosuchus*. (See Plate V, Fig. 3.)

5. A group of associated plates, number 13993 U.M., has the plates of the median row like those of type 4; with them are several smaller plates roughly quadrangular in outline which have thick sutural edges cutting obliquely across them. These plates would form a strong, closely fitted mosaic, with little possibility of movement between them. The inner surfaces of these plates, as of all of the group, show a peculiar textile-like arrangement of the fibers, even in unweathered specimens. These plates may have been developed on a small portion of the body; they are strongly suggestive of a heavy abdominal armor. These may be but a variant of type 4, or an as yet unrecognized distinct type. (See Plate V, Figs. 1-2.)

The plates of types 1 and 2 are similar in many respects, and an exaggeration of the characters of type 2 would increase the similarity. This is more striking if the posterior plates of *Desmotosuchus* are compared with specimen 13950. We know nothing of

the anterior dorsal and cervical plates of the latter; also the imperfect ilium of *Desmotosuchus* is strikingly similar to those of specimens 7470 and 13950. Another suggestion is worth considering in an attempt to bring some order into the classification of the phytosaurs. Specimen number 7470 was collected in Crosby County, Texas, by the author. A year or two later Mr. George Doughty of Post, Texas, and Mr. E. M. Brigham of Battle Creek, Michigan, secured from the same excavation a skull now in the possession of the American Museum of Natural History in New York, number 6813. Fossil material is so scarce and dispersed in the locality that the association of the two as parts of one individual is fairly certain. Dr. Walter Granger has been kind enough to examine this skull and to send a sketch to the author. His observation is that the rostrum is decidedly tilted upward and that the alveolar edge of the upper jaw is wavy in contour. Similar characters of the rostrum are shown in Huene's figures (Huene, 1911, Fig. 30) of *Rhytiodon* (*Mystriosuchus*) *carolinensis* and in two specimens in the collection of the University of Michigan, numbers 7417 (Plate IV, Fig. 7) and 14267. Dr. Granger assures the author that the contour of the specimen in New York is natural and not due to posthumous distortion, and this is certainly the case in the specimens of the University of Michigan.

If we may associate specimen 7470, in which the pelvis, sacral vertebrae, and plates are apparently specifically identical with those of 13950, with the skull 6813 of the American Museum, we have a second possibility of taxonomic arrangement. Opposed to this suggestion is the fact that Camp's type skull of *Machaeroprotopus adamanensis*, number 7038/26699, has a decidedly up-tilted nose and the wavy contour of the alveolar edge. Camp, however, considers this a distortion due to the crushing of the rostrum over the lower jaw (Camp, 1930, Fig. 10), and restores it with a straight rostrum. The correctness of his view is supported by the fact that the pelvis is of the better-known form, with an elongate posterior process on the ilium (his figure, 16). This specimen had associated plates of type 4 of this paper.

Plates of type 4 are associated with a skull and parts of the pectoral girdle in a specimen *Mystriosuchus planirostris*, and with

a good part of the axial skeleton and a pelvis with elongate ilium in a specimen described as *Rutiodon mahattensis* by Huene (Huene, 1913).

A variant of type 4 is shown in a single plate of a median row, number 13735, from Potter County, Texas (Plate IV, Fig. 4). The sculpture from the keel-like prominence is much more sharply defined than any other in the collection, and the whole has an imbricate appearance. This may be an individual variation, or may be part of the armor of a distinct genus or species; it is unique among the many plates recovered.

A group of plates, number 13695, from a small bone bed in Potter County, Texas, found with the limb bones, interclavicle, vertebrae, and ribs of a phytosaur, probably are to be associated with the other skeletal elements, since no duplicates were found in the small patch, though many stegocephalian bones were mingled with the phytosaur bones. The plates of the median row are of type 4, but those of the lateral rows are quite different from any others in the collection. The two sides meet at an angle of 45°, and the high prominence curves up and over the posterior edge (Plate V, Fig. 4). A similar plate occurs in number 7244 (Plate IV, Fig. 8), and one or two isolated plates are of the same form. It is impossible to place these plates exactly, but they evidently belong in the dorsal region and indicate a form with a relatively narrow back and high lateral edges to the armor.

The presence of smaller, diamond-shaped plates fitting next to the median row, in specimen 13984, suggests the possibility that in animals with plates of type 4 there were three dorsal rows with the lateral plates as in specimens 13695 and 7244. This suggestion is borne out by the fact that in specimen 7244 one of the large plates of the median row is coössified with one of the smaller plates, and the two are insufficient to account for one half of the normal breadth of the back. These plates were found so close to the complete pelvis with the elongate ilium, and are so similar in all characters of fossilization, especially a peculiar spotting due to very local conditions of decay, that they are included under the same number.

Plates of type 3 are very much less abundant in the collection.

They indicate an animal with a much broader back, and are similar to the plates found in the European Triassic and doubtfully associated with the genus *Phytosaurus*. No lateral plates and no skull or parts of the axial skeleton can be definitely associated with these plates in any of the collections from North America (Plate IV, Figs. 5-6).

From the evidence now before us we may recognize with certainty two groups of phytosaurs: those having quadrangular plates arranged in a definite pattern and with a stout pelvis having a short iliac crest, and those having irregularly shaped plates arranged in a less definite pattern and with a less stout pelvis having an elongate iliac crest.

The first group suggests relationships with the *Desmotosuchia* in the character of the plates and their pattern; in the ilium (the imperfect ilium of the holotype of *Desmotosuchus spurensis*); in the position of the facets for the tuberculum and capitulum of the ribs upon the transverse processes of the dorsal and lumbar vertebrae, which are upon a horizontal plane (specimen 7470 and the holotype of *Desmotosuchus*); and in that the neural spines of the posterior dorsal, sacral, and anterior caudals are expanded into a table at the apex.

There is also the suggestion that this group may belong to the *Phytosauria*, including forms with an uptilted nose and a wavy alveolar edge on the jaws. In this case it is probably necessary to assume parallel development of plates, pelvis, and rib articulation in two otherwise divergent lines.

The second group is of the *Mystriosuchus* (*Machaeropsopus*) type in the plates and their pattern of arrangement; in the elongate ilium; in the position of the facets for the capitulum and tuberculum of the ribs upon the transverse processes of the ribs, which are not upon a plane, but with the capitular facet below the tubercular facet (*vide* Camp, 1930); and in that the neural spines of the posterior dorsal, sacral, and anterior caudal vertebrae are not expanded at the apex.

The author has struggled with the numerous proposed classifications of the phytosaurs based upon various combinations of characters and has found them unsatisfactory, as have all other

workers. He does not believe it wise at this stage to go beyond the demonstrated facts.

The anatomy of the *Mystriosuchus* (*Machaeropsopus*) group is now pretty well known. How many subgroups may eventually be recognized and whether all forms now included in that group will be retained, is still uncertain.

Until a specimen showing skull, plates, and axial skeleton in association shall be recovered, the anatomy and taxonomy of the *Desmotosuchus* or *Phytosaurus* group (or both) must remain uncertain. Anything further must be based on assumptions and speculations, with a continuation of unsatisfactory results.

The author is compelled to disagree with Dr. Camp in certain of his conclusions, notably those as to sex and age. He cannot find any warrant for the assumption that size or prominence of orbital and narial borders can be correlated with sex, much less indicate the sex. In Camp's discussion the accidents of preservation and fossilization, as well as the unknown possibilities of individual and specific variation, seem to have been neglected.

Though it is very probable that the proportions of the skull changed in ontogenetic development, as in the modern gavials (a fact most kindly pointed out to the author by Dr. Nopsca of Vienna), in which the rostrum and teeth become heavier with age, the analogy is not a safe one, for an exact reversal of the process takes place in the long-nosed gars (*Lepidosteus*), in which the rostrum becomes elongate with age. It is hardly to be credited that such material changes as Dr. Camp suggests could be ontogenetic. The discovery of a group of skulls of varying size in the same layer, described as a delta deposit, cannot be a justification for assuming them to be individuals of the same species in various stages of development. The specific identification of fossil vertebrate material is too uncertain to warrant conclusions when the range of difference is so great. To the author it seems fully as plausible that the individuals may be different species as ontogenetic stages of a single species.

Within the group *Phytosauria* there were many different forms, and though some specimens described as different species and even genera may be age stages, still the difference between

such forms as *Rutiodon* and *Mystriosuchus* on the one hand and *Brachysuchus* on the other are sufficient to indicate radically different habits and possibly different phylogenetic relations. The excessively long and slender anterior teeth and light posterior maxillary teeth are such as could be used only in the capture and destruction of an unarmored or lightly armored prey, whereas the short, strong rostra of *Machaeroprotopus* and *Brachysuchus*, with powerful tusks and heavy posterior maxillary teeth, were adapted to a heavily armored prey. Camp's *M. adamanense* and *gregoryi* are to the author animals of different habit and adaptations from those of his *M. tenuis*. Certainly they are different enough to warrant generic distinction. Unquestionably there were intermediate adaptations.

THE MOUNTED SKULL AND JAWS OF *BRACHYSUCHUS MEGALODON*

In two previous papers the author has described separately the skull and lower jaws of a large phytosaur under the name *Brachysuchus megalodon*. More recently it was decided to mount the two parts in their natural position. The parts were found at the same locality and within a hundred feet of each other. This, with the fact that all comparable measurements correspond very exactly and that all features indicate the same form, seems ample warrant for considering the skull and jaws as belonging to a single individual.

The accompanying plates, VI-VIII, show the mount from various aspects. The skull is 4 feet, 1 inch in length (1,243 mm.). The region posterior to the nares is slightly depressed by crushing. Since it was found lying upon the palatal surface and had evidently been dragged some distance by currents of water, all the teeth but one had been displaced from the alveolae.

The lower jaw is complete, with the exception of the upper edge of the posterior end of the left ramus. The specimen was found in normal position, and most of the teeth are preserved in the alveolae. The anterior tusks and the oral surface of the symphyseal region had been injured in life, probably by a snap at some heavily armored form.

As previously discussed in figuring the restoration of this

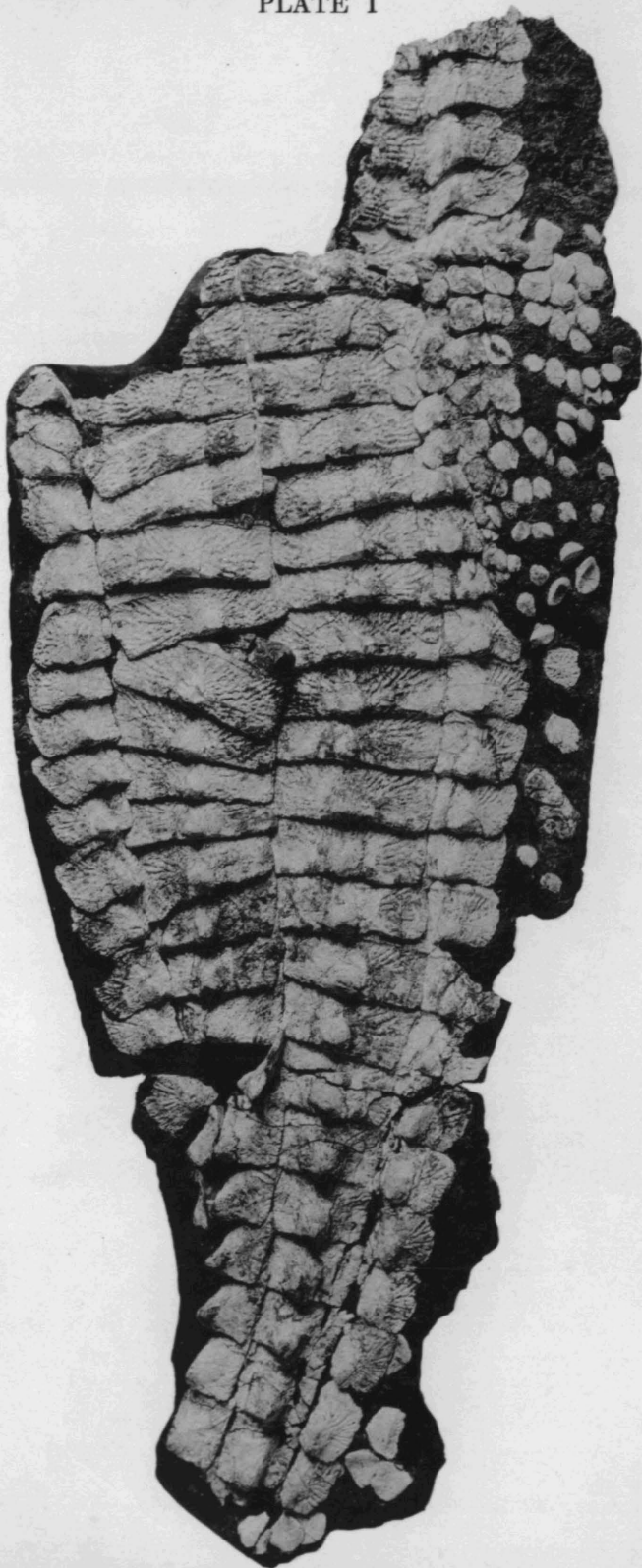
skull, the animal was of the heavy short-rostral type, with powerful posterior teeth in both jaws, evidently adapted to preying upon large and heavily armored forms.

The skull was probably close to one sixth of the length, giving a total length of approximately twenty-five feet.

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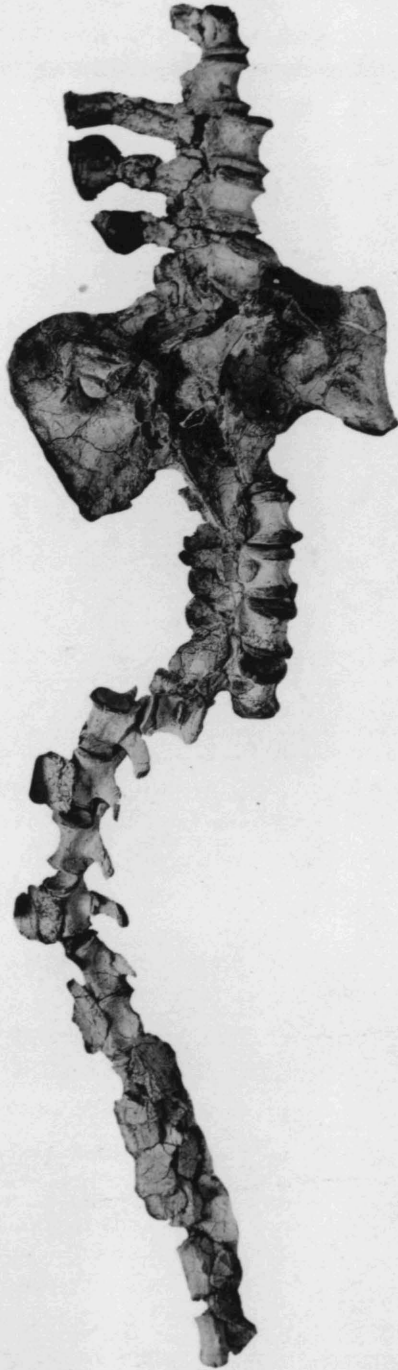
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PLATE I



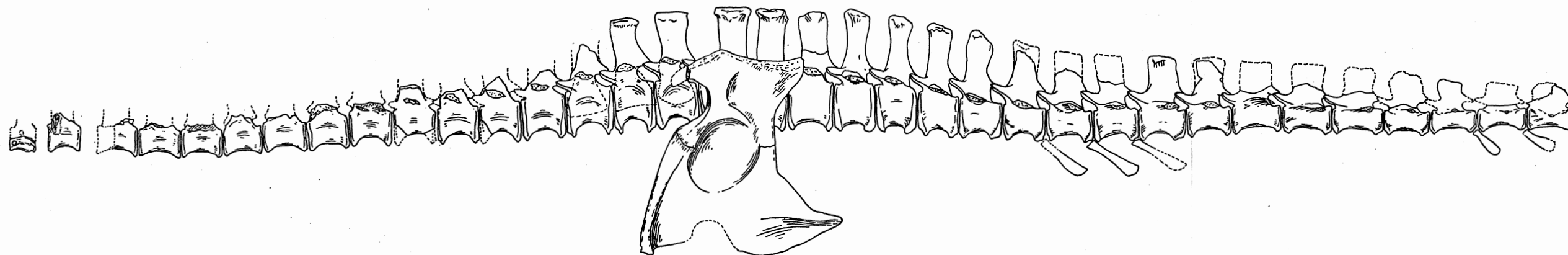
Dorsal surface of the segment of armor, number 13950.
× about $\frac{1}{4}$

PLATE II



The vertebrae in position before removing and straightening, number 13950. \times about $\frac{1}{2}$

PLATE III



Reconstruction of the vertebrae preserved in number 13950 (see Plate II). $\times \frac{1}{4}$

PLATE IV

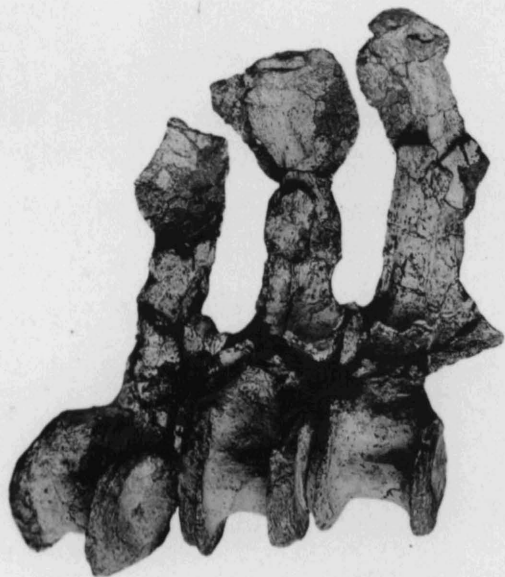


FIG. 1. The first three presacral vertebrae from below, showing the expansion of the transverse processes, number 13950. \times about $\frac{1}{3}$

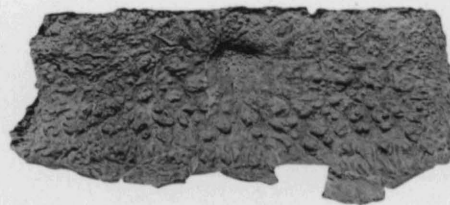


FIG. 2

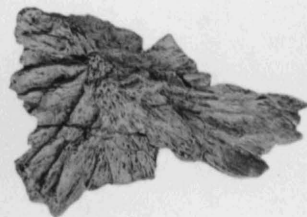


FIG. 4

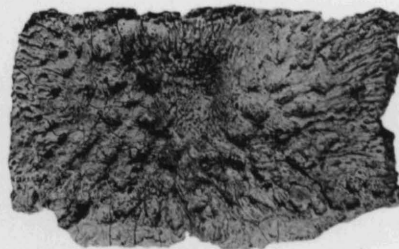


FIG. 3

FIGS. 2-4. Plates, numbers 9626, 13727, 13735. \times about $\frac{1}{3}$.
Figures 2 and 3 are type 2 of this paper



FIG. 5



FIG. 6

FIGS. 5-6. Plates, number 8859. \times about $\frac{1}{3}$.
Type 3 of this paper



FIG. 7. Rostrum of skull, number 7417. Slightly less than $\frac{1}{3}$.

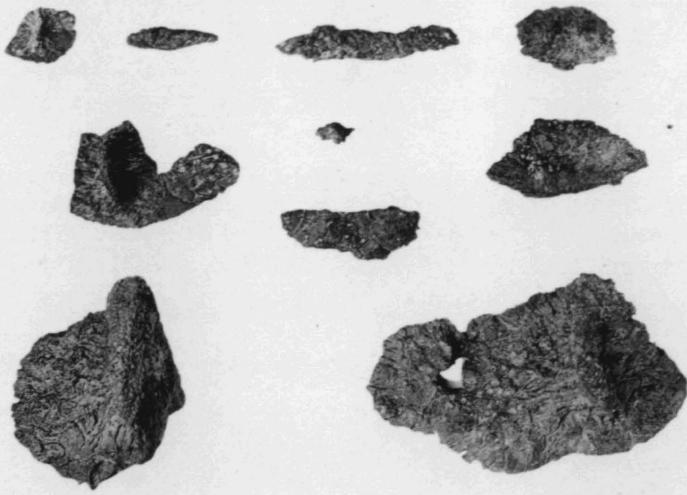


FIG. 8. Group of associated plates, number 7244, found close to pelvis of the same number. \times about $\frac{1}{3}$

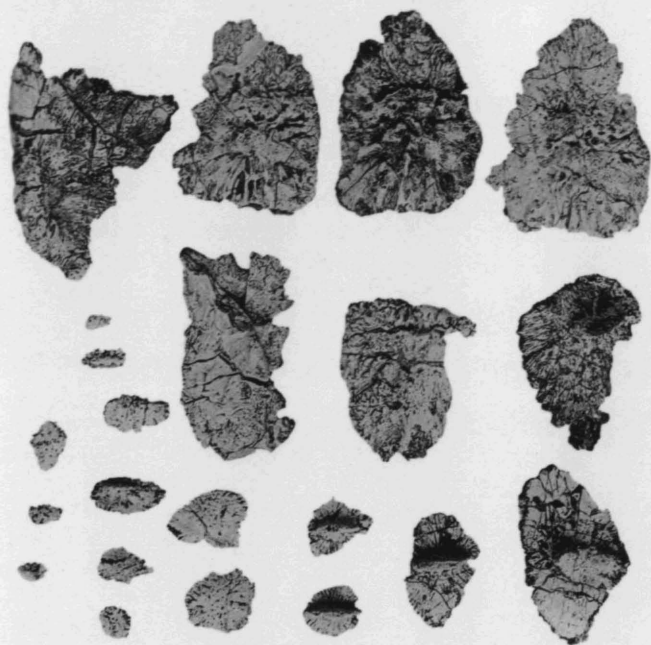


Fig. 4. Number 13695. \times about $\frac{1}{3}$

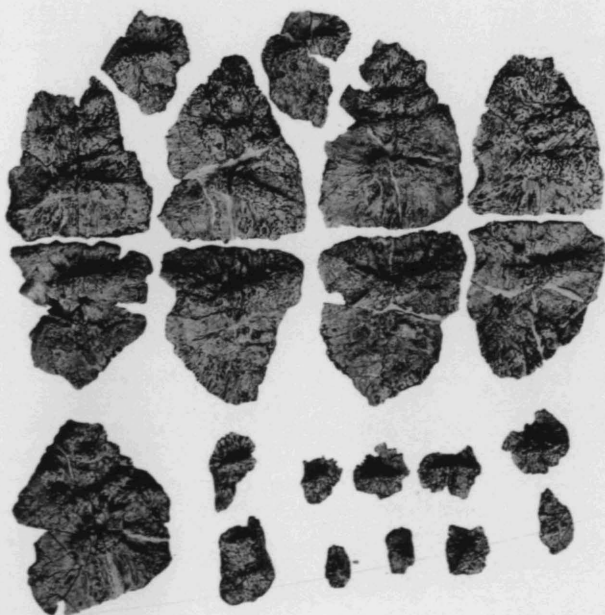


Fig. 3. Number 13894. \times about $\frac{1}{3}$. Type 4 of this paper

PLATE V

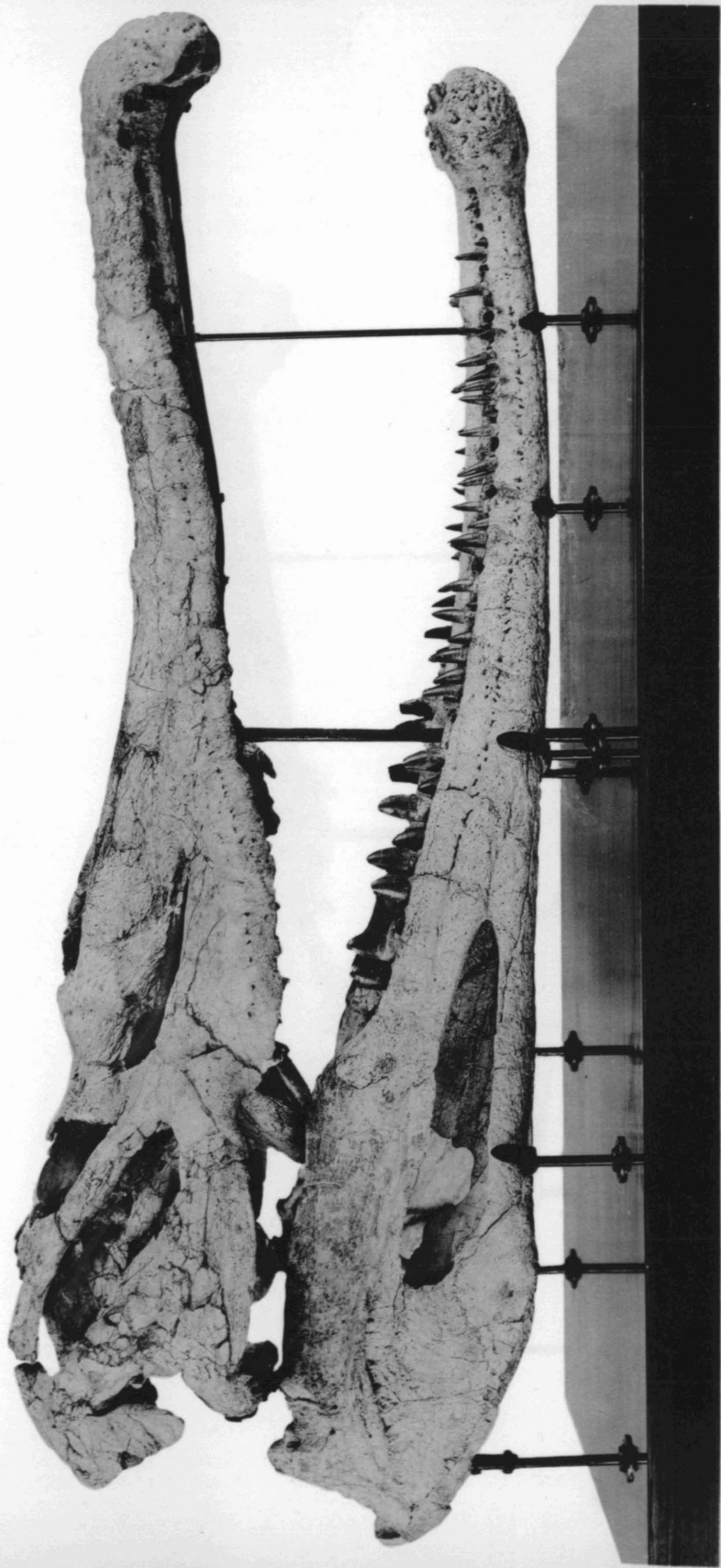


FIG. 1. Number 13993. \times about $\frac{1}{2}$



FIG. 2. Number 13993, showing the textile-like arrangement of the fibers on lower surface. \times about $\frac{1}{2}$

PLATE VI



Lateral views of skull and lower jaws of *Brachysuchus megalodon*, numbers 10366 and 10366B.
X about $\frac{1}{8}$

PLATE VIII

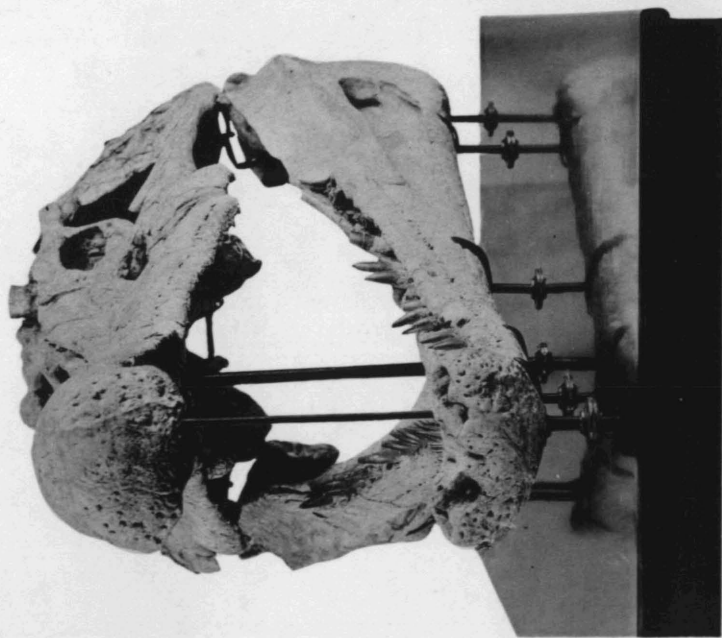


FIG. 1. Anterior view

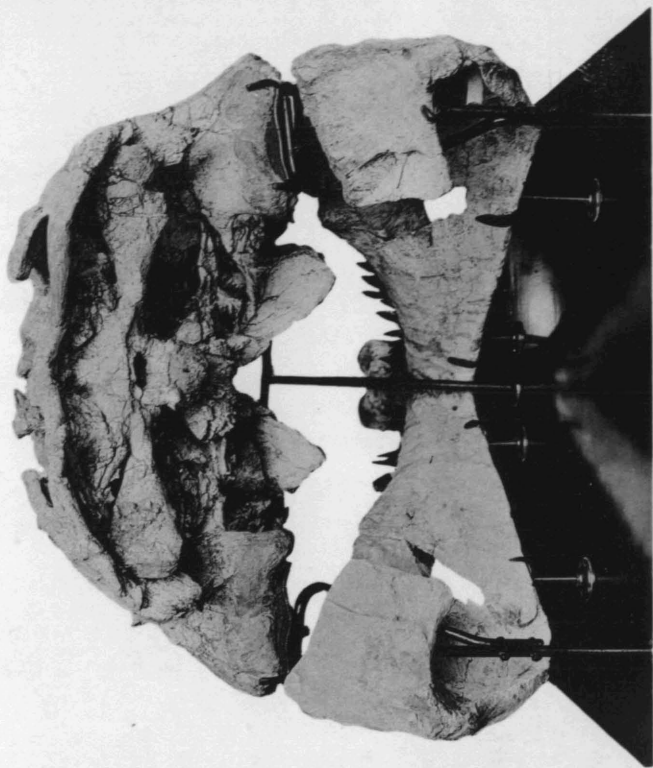


FIG. 2. Posterior view

Skull and lower jaws of *Brachysuchus megalodon*. \times about $\frac{1}{2}$

(Continued from inside of front cover)

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