ELASMOSAURID PLESIOSAURS WITH DESCRIPTION OF NEW MATERIAL FROM CALIFORNIA AND COLORADO

BY

SAMUEL PAUL WELLES

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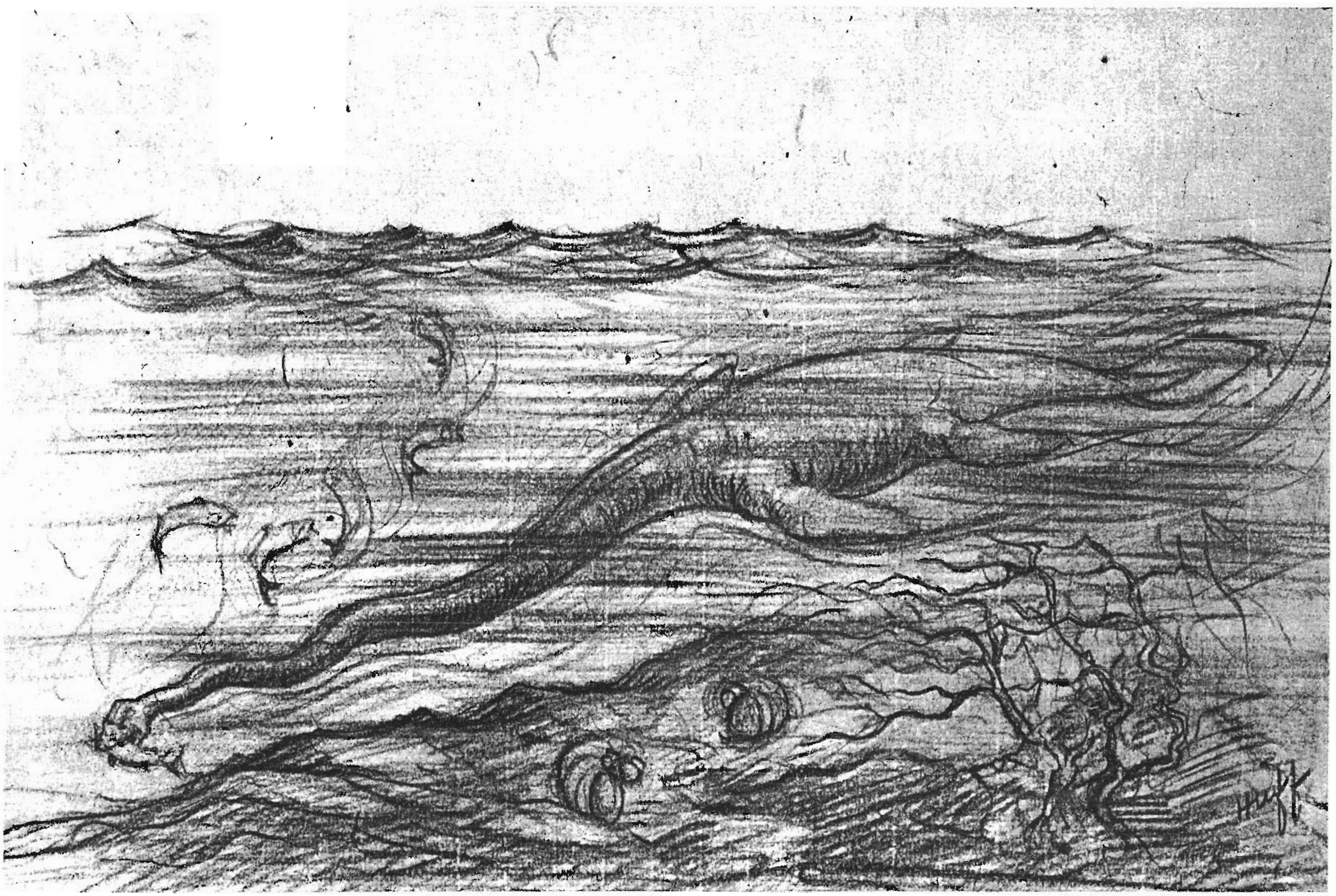

Hydrotherosaurus alexandrae. A restoration of the thirty-foot reptile by William Gordon Huff.

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CONTENTS

ELASMOSAURID PLESIOSAURS WITH DESCRIPTION OF NEW MATERIAL FROM CALIFORNIA AND COLORADO

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INTRODUCTION

THE MARINE REPTILES called plesiosaurs are first represented in the fossil record by small semiaquatic reptiles of the Trias of Europe. The limbs of the earlier forms were modified into paddles by a slight increase in the number of phalanges, and probably also by the development of connective tissue binding the digits together. The gigantic plesiosaurs of the Cretaceous exhibit a degree of hyperphalangy that is exceeded only by the Jurassic ichthyosaurs. Such paddles appear to have been admirable for swimming, yet they probably were incapable of supporting the animal on land. The later forms must therefore have spent their lives entirely in the water.

Along with the modification of feet into paddles went a major change in the proportions of head, neck, body, and tail, a dichotomous evolution resulting in two radically different types of plesiosaurs, one with a short neck and long head, the other with a long neck and short head. These specialized types flourished throughout the Jurassic and Cretaceous and their distribution became world-wide; but, like so many other dominant reptilian groups, they disappeared at the close of the Mesozoic.

Contemporary writers excepted, S. W. Williston was the last American paleontologist to work extensively on the plesiosaurs. He published several short papers but was unable to finish a contemplated monograph of the North American forms. He had good skeletons of the short-necked type, but poor material of the long-necked, short-headed plesiosaurs. The best specimen of the latter type known to Williston was *Elasmosaurus platyurus* Cope, which lacked the skull, pectoral and pelvic girdles, and limbs. The discovery of a complete skeleton of this type of plesiosaur in the Cretaceous of California has afforded me an opportunity to study these reptiles.

After the completion of this investigation, I learned of additional new material at the Colorado Museum of Natural History and at the California Institute of Technology. The authorities at both institutions kindly consented to the description of their specimens in the present paper. Although observations made during short visits are always somewhat incomplete, the study of this additional material has solved many of the problems arising out of the original work.

I wish to thank Miss Annie M. Alexander for making this work possible through her support of the Museum of Paleontology. Dr. C. L. Camp, Director of the Museum, has made constructive criticisms and suggestions during its progress.

I also wish to thank the President of the Colorado Museum of Natural History, Charles H. Hanington, and the Director, Alfred M. Bailey, for permission to describe the Denver specimen and for their many courtesies during the visit; I also wish to acknowledge the assistance and hospitality of Mr. and Mrs. I. N. Pruitt, who were hosts to the Denver collecting party. Dr. C. Douglas Chrétien, of the University of California Department of Public Speaking, suggested many of the new generic names. The assistance of Dr. Chester Stock and Mr. Eustace L. Furlong of the California Institute of Technology is gratefully appreciated. Most of the drawings were made by Owen J. Poe. Plates 17 and 18 were drawn by David P. Willoughby. Valuable assistance has been furnished by the personnel of the Work Projects Administration, Official Project No. 65–1–08–62, Unit A-1, and Works Progress Administration, Official Project No. 665–08–3–30, Unit A-1, in preparation, typing, and photography.

DESCRIPTION OF NEW GENERA

University of California Material

Hydrotherosaurus alexandrae n. gen. and sp.

In the spring of 1937 Dr. W. M. Tucker, Chairman of the Department of Geology of Fresno State College, brought some plesiosaur vertebrae to Berkeley. These were found by Mr. Frank C. Paiva on his property in the Panoche Hills, about fifty-five miles west of Fresno. A joint expedition of the Fresno State College and the University of California Museum of Paleontology was organized, and the specimen was collected and brought to Berkeley for preparation. We are indebted to Dr. Tucker for his active interest in the work, and to Mr. Paiva for his wholehearted coöperation.

The skeleton found by Mr. Paiva differs from other adequately known long-necked plesiosaurs and is therefore described as *Hydrotherosaurus alexandrae* n. gen. and sp. (*ὑδροθήρας*—a fisherman). The specific name is in honor of Miss Annie M. Alexander, who has contributed so much to the work on the vertebrates of the West.

Type.—U. C. Mus. Pal. no. 33912, a nearly complete skeleton, lacking only small parts of the skull, pectoral girdle, paddles, vertebral processes, and the last few caudal vertebrae.

Type locality.—U. C. V3735. In the Moreno formation, about 775 feet above the base, on the property of the Sun Ray Gypsum Mine, 2475 ft. S. 68° W. of the mine buildings and in the bottom of the S. fork of the first ravine S. of Moreno Gulch, 900 ft. E., 1500 ft. S. of NW. cor., Sec. 13, T 14 S., R 11 E., M. D. B. and M., U. S. G. S. Panoche Quadrangle. This locality is about 22 miles due west of Mendota, Fresno Co., Calif. (see figs. 1 and 2).

Diagnosis.—Teeth $\frac{14+}{13+}$; postfrontal extremely reduced, lying within the temporal fenestra; sagittal crest narrow (½ cm.), pineal foramen absent. Vertebrae 102, divided into 60 cervicals, 2 pectorals, 17 dorsals, 3 sacrals, and 20 (+10) caudals. Length of head, 33 cm.; neck, 471 cm.; body, 164 cm.; tail, 140 cm.; total length, 806 cm.+. Lateral longitudinal ridge on anterior 40 cervicals only. Arches fused to centra of all but posterior caudals. Cervicals depressed; posterior cervicals longest, anterior dorsals highest, pectorals broadest, in dimensions of centra. Atlas and axis completely fused. Median longitudinal bar absent in both pectrum (= pectoral girdle) and pelvis. Scapula with groove separating dorsal process from anterolateral border. Coracoid with slender posterior extension and posterior end expanded to over twice the width of the shaft. Intercoracoid vacuity narrow, acutely pointed anteriorly. Pubis rounded with concave posterolateral border and small concavity in convex anterior border. Ilium concave medially and strongly convex laterally. Humerus 70 per cent as broad distally as long, with concave facets for radius and ulna. Capitulum and trochanter of propodials partly separated by strong anterior and posterior grooves. Radius 28 per cent as long as humerus; ulna 22 per cent as long as humerus. Distal breadth of femur 65 per cent of length.

Occurrence and stratigraphy.—The Moreno formation (strike N. 25° W., dip 35° NE. at the plesiosaur locality) is a brownish gray, blocky shale that dries into angular frag-

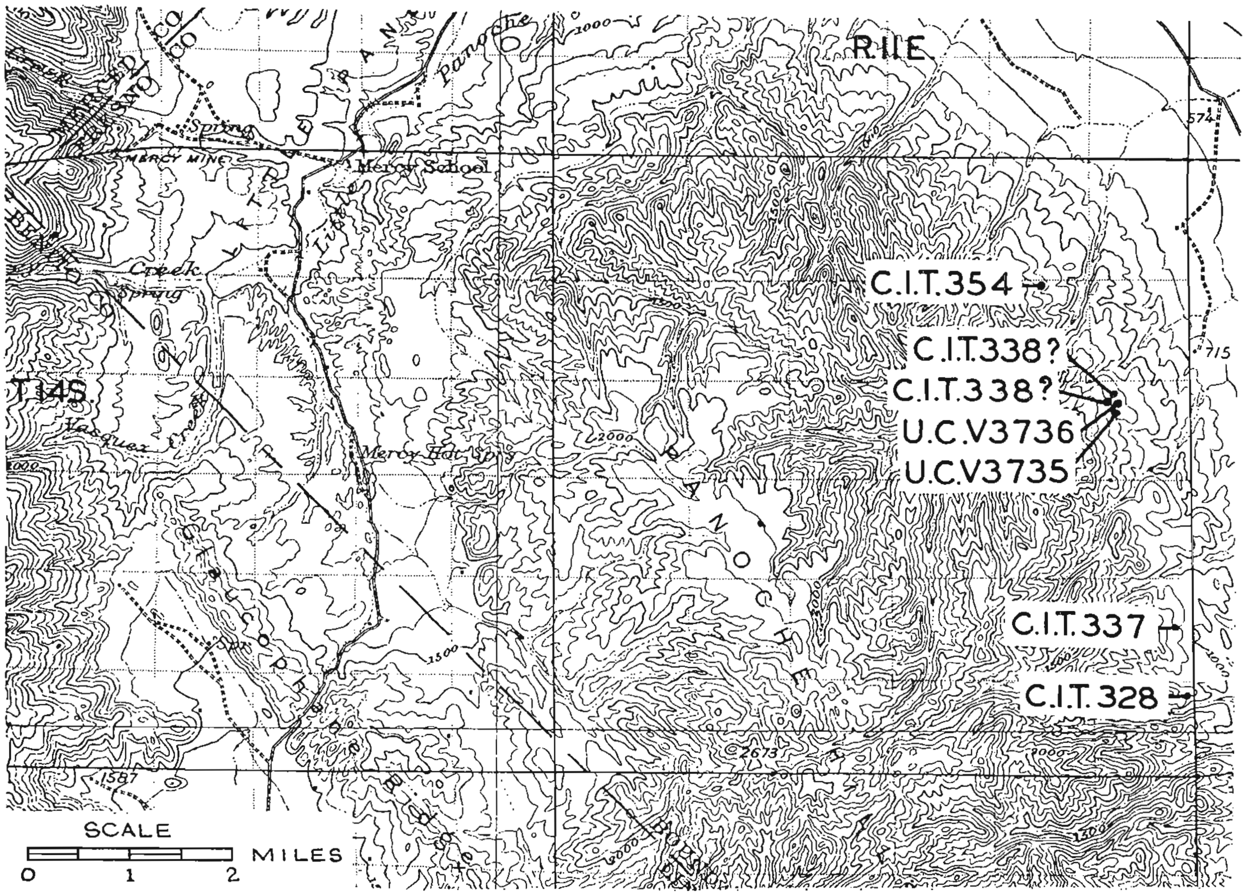

Fig. 1. University of California and California Institute of Technology reptile localities in the Panoche Hills, Fresno Co., Calif.

ments and dust. The fresh shale is velvety black, usually wet, and dries to a light chocolate color. The surface swells into a loose, brownish gray soil which supports little vegetation. Many sandstone dikes cut the Moreno, usually perpendicular to the bedding planes, but sometimes parallel to them.

There are changes in the lithology of the Moreno ranging through limestone and diatomaceous shale into the characteristic maroon shale which is at least locally foraminiferal. Gypsum is plentiful, sometimes as veins penetrating cracks and bedding planes, and sometimes as nodules. Barite nodules are found occasionally, as are limestone concretions, petrified wood, and poorly preserved mollusks. For a fuller description see Anderson and Pack (1915). Caudal vertebrae of a mosasaur, *Kolposaurus tuckeri* Camp (1942), were collected 55 feet above the plesiosaur.

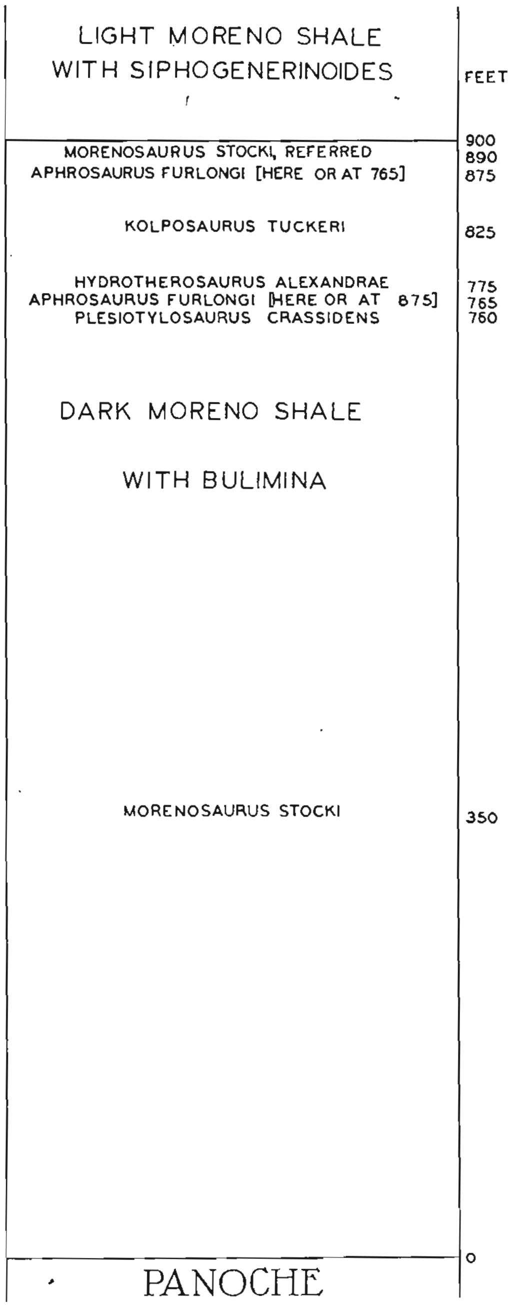

Fig. 2. Column through lower Moreno Shale showing relative levels of the Panoche Hills reptiles. (Data from Calif. Inst. Tech., and Mr. Max Payne, Richfield Oil Co.)

At the time of discovery, only a few posterior cervical vertebrae were exposed at the very bottom of a narrow V-shaped gully. The skeleton lay upon its right side along a bedding plane. The head and neck were upslope and covered by only a foot or so of matrix, but the body and tail extended 15 feet under the eastern bank.

The cervical ribs were lost from almost the entire upper (left) side, and the upper surfaces of the centra, except for the dorsal series, had been destroyed. The peripheral portions had been moved and disarticulated before burial, and there were indications in the disarranged jaw, phalanges, and caudal vertebrae that the carcass had been worried by scavengers. The right scapula and coracoid had been pulled out and turned ventral side up, and the left scapula, coracoid, and paddle were pulled around over the back. Teeth of sharks and shells of ammonites were collected a few feet from the skeleton, and these animals may have torn away bits of flesh and bone from the carcass. The right side was protected by the underlying mud and is well preserved.

A foraminiferal faunule contained in the matrix of the plesiosaur has been studied by Dr. A. S. Campbell, who supplies a list and note:

Anomalina pseudopapillosa (Carsey)
Bulimina obtusa d'Orbigny
Dentalina legumen (Reuss)
Flabellina pilulifera Cushman and Campbell
Frondicularia cf. *undulosa* Cushman
Gyroidina depressa (Alth)
Marginulina elongata d'Orbigny
Nodosarella (n. sp. Campbell) (?)
Nodosaria monile v. Hagenow
N. pomuligera Stache
N. spinifera Cushman and Campbell
N. (n. sp. Campbell)
N. spp. (fragments)
Robulus inornatus (d'Orbigny)
R. sp.
R. (n. sp. Campbell)

This faunule approximates that at Marsh Creek, U. C. loc. A1678. It is part of the general Bulimina obtusa zone which is pretty well distributed all over the [N. Amer.] continent and Europe. This is supposed to be equal to the Navarro of Texas. The same faunule occurs, in poorer form, at Corral Hollow, and in the hills near Tracy (= Maestrichtian).

It would not be too much to say that 99 per cent of the collection includes *Bulimina obtusa*. The other spp. are extremely rare, save *Flabellina pilulifera* which is not uncommon.

These protozoans might possibly have been attracted by the decaying carcass, yet the articulation of most of the skeleton indicates burial at least before the ligamentary connections were destroyed.

Age.—Maestrichtian, Upper Cretaceous. As noted above, Campbell, after a study of the foraminifera, correlated this with the Navarro of Texas. Dr. F. M. Anderson (in

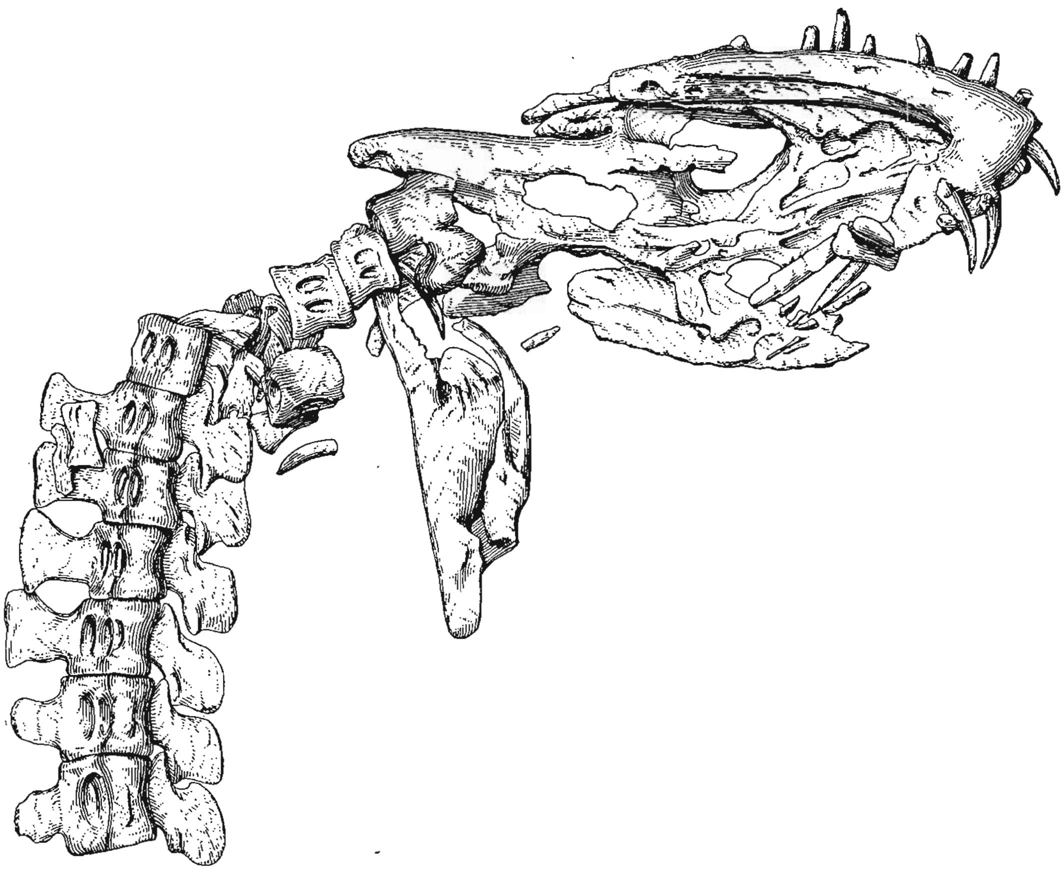

Fig. 3. *Hydrotherosaurus alexandrae*, type. Skull and anterior cervical vertebrae in position of burial. Palatal view of skull and jaws, ventral and left lateral view of vertebrae. U. C. Mus. Pal. no. 33912. × 2/9.

press) correlates the Moreno with the Maestrichtian. This correlation is based upon the mollusks. The resulting correlation is shown in table 15. It differs from that of the United States Geological Survey in lowering the Navarro to correspond with the Maestrichtian and Moreno. Evidence from the plesiosaurs places the Moreno above the Niobara and above the basal Pierre, but a more exact correlation is impossible because the reptiles in the Gulf and Mid-Continent regions are not directly comparable.

DESCRIPTION OF SPECIMEN

Skull.—The skull (pl. 12, and figs. 3 and 4) lay with the palate up, the side of the rostrum obscured by the lower jaws and the right quadrate region hidden by the articular. The palate was entirely eroded away. The occipital condyle was crushed out of position, the posterior part of the jaws shifted about, and some of the teeth drifted back as far as the seventh cervical vertebra.

The ventral surfaces of the median elements of the skull roof were exposed, but the sutures are not determinable. The length of the skull from premaxillary to condyle is estimated at 330 mm. The width from the midline to the alveolar border below the orbit is 85 mm., indicating a total width of about 170 mm.

There were originally at least 14 teeth in the upper jaw: 5 are still present in the right premaxillary; the 9 maxillary teeth are indicated by isolated teeth and empty alveoli. The number of premaxillary teeth is rather constant among the Elasmosauridae. Williston (1903) states that the premaxillary of *Cimoliasaurus snowii* contains 6 teeth, yet his figure shows but 5, as in *Muraenosaurus* and *Hydrotherosaurus; Brancasaurus* shows 6 alveoli.

The first premaxillary tooth is a tiny peg 4 mm. in diameter and 10 mm. long. The longest tooth is 46 mm., excluding the root, and lies in the maxillary below the naris. The teeth decrease in length behind the anterior border of the orbit.

The upper teeth are slightly less recurved than the lower, both being relatively straight. The upper teeth have a gibbous section; the long axis is in the direction of the jaw, the flat external surface facing a little more anteriorly than perpendicular to the curvature of the jaw.

A few isolated teeth show the enamel cap with fine longitudinal ridges. The ridges are sharp on the young teeth and smooth, probably because of wear, on the old. Enamel covers only the upper half of the teeth; below this they swell out into a bulbous root larger than the crown but not so swollen as roots of mosasaur teeth. The teeth were slender and delicate, but probably very effective in catching small fish or squid.

The jagged dentition (fig. 4, *b*) is remarkable for its irregularity, implying that the mortality of teeth was high. We may surmise that the crowding or spacing was dependent upon the presence or absence of an opposing tooth in the occluding jaw since the 3d and 4th, and the 7th and 8th, of the right maxillary have no lower tooth between them, and the 5th and 6th, and the 10th to 12th, of the right dentary are also contiguous.

Premaxillary.—The premaxillaries are fused into a solid rostrum that makes the front of the skull into a massive beak. Each premaxillary bears four large teeth and one small central tooth. The midline suture is perfectly straight for about 4 cm., and then is carried to the right about 1 cm. and runs parallel to its original course for about 5 cm., whence it continues in line with its anterior course for the rest of the skull's length. The result is to throw a part of the nasal region to the right. Some sort of rostral crushing is common among plesiosaurs, and the "jog" in the midline suture may therefore have occurred during life.

The suture with the maxillary can be traced with certainty, from the alveolar border just behind the fifth tooth, dorsally and posteriorly almost to the naris. On the right side the anterointernal border of the naris appears to be formed by a process from the maxillary; on the left the same process appears, with equal certainty, to be part of the premaxillary, and so here the suture is lost.

The posterior extent of the premaxillary cannot be determined. There appears to be a suture as shown in the figure, running anteromedially to the midline from the anterior corner of the naris, but I am not certain whether this is a suture or a break, even though it is the same on both sides. An additional complication lies in the "suture" described below between the nasal and frontal. In this there can be no question that the posterior element overlaps the anterior, but such an overlap could be produced by crushing the

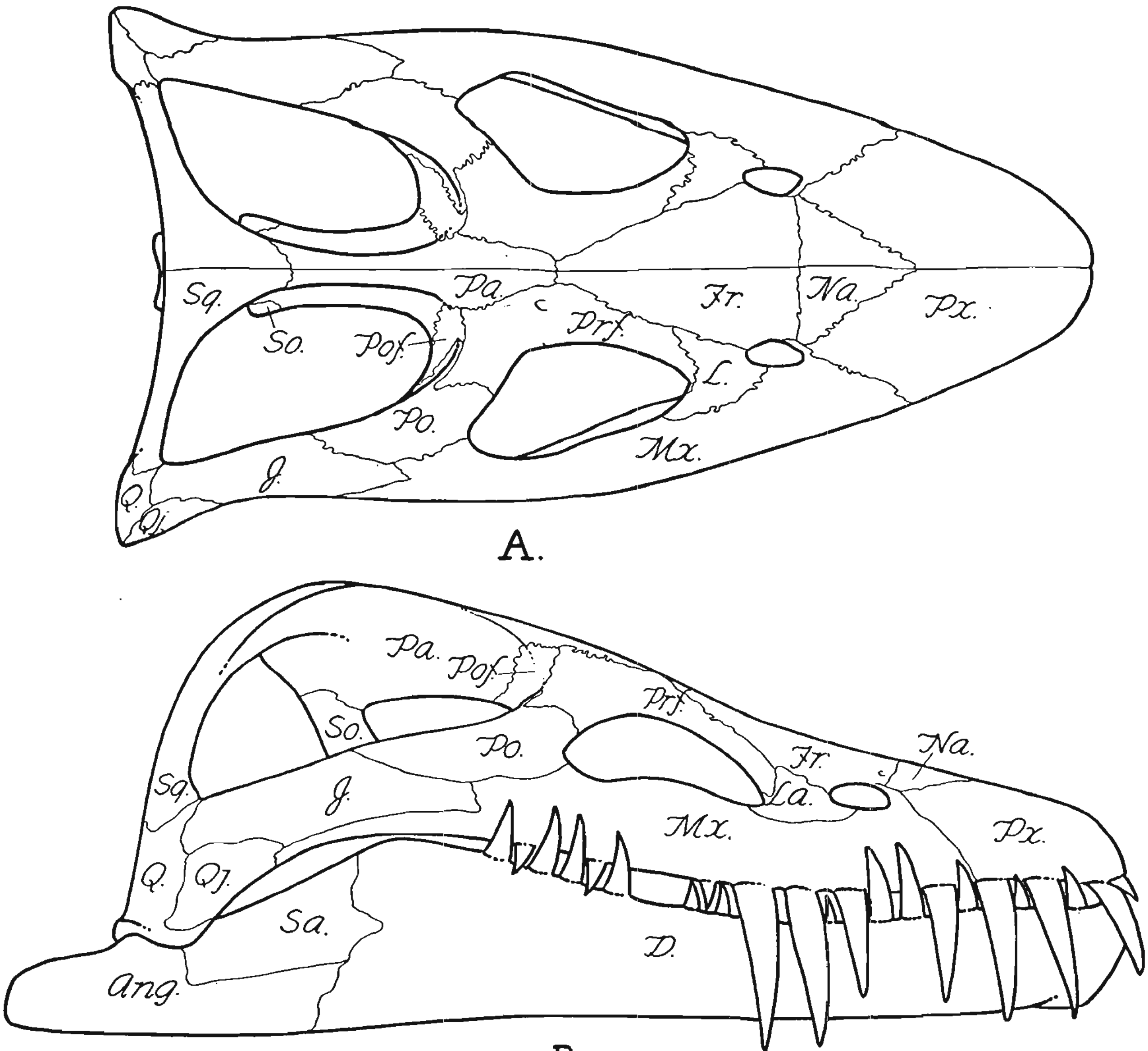

Fig. 4. *Hydrotherosaurus alexandrae*, type. Reconstruction of the skull made by Mr. William Otto, of the California Institute of Technology, under the writers' direction, to fit a pair of perfectly preserved C. I. T. mandibles. *a*. Dorsal view. *b*. Right lateral view. U.C. Mus. Pal. no. 33912. × 2/5 approx.

arch that presumably existed in this region. The shortening of the arch to the present nearly straight line could result in overlap, so that this "suture" might be a break and the premaxillary, or nasal, would continue posteriorly to meet the parietal! All this is perfectly possible and the premaxillary would include my "nasal" and "frontal." This, of course, would make my "prefrontal" a frontal and my "lacrimal" a prefrontal. The frontal would then occupy a more nearly normal position, but there would be nothing to represent a lacrimal. Any attempt to justify either alternative on theoretical grounds is fruitless, for this is a poorly known group of reptiles and nearly any arrangement can be found described in the literature.

The main argument in favor of the suture's lying where I have indicated is that the "crushed arch" explanation is hardly enough to account for the magnitude of the overlap. Furthermore, the ventral surface of the posterior element is smoothly excavated as though the nasal formerly extended farther under it posteriorly.

The reasons for placing the premaxillary nasal suture as I have in the figure are, first, the similarity on both sides of the skull, and second, the different direction of the grain of the bone on each side of the suture near the naris.

I therefore return to my original statement; the posterior extension of the premaxillary cannot be determined. It is thought to terminate as shown in figure 4, but this is a most unusual condition and I am not at all satisfied with my results.

Maxillary.—The maxillary extends from its suture with the premaxillary and nasal posteriorly below the naris, lacrimal, orbit, postorbital, and jugal. It probably terminates as an overlap on the quadratojugal as in the Denver specimen, but this is conjectural.

The suture with the nasal is questionable. It is indicated by a change in the direction of the grain of the bone on either side of an irregular depression. It is possible that all will prove to be premaxillary, yet I believe the interpretation shown in figure 4 is correct.

On the right side the anterior and part of the superior border of the naris is formed of a small projecting process of the maxillary. On the left this process seems to be part of the premaxillary. The lacrimal suture is not obvious, but can be followed with reasonable certainty under the binocular microscope.

Below the orbit the maxillary is marked by pits and grooves arranged in parallel rows that trend posteroinferiorly.

Nasal.—This is a short, broad bone. Although the premaxillary suture is questionable, the frontal suture can be seen on both surfaces of the skull, on both sides, as an overlap of frontal on nasal. The nasal is excluded from the naris by the dorsal process of the maxillary, or premaxillary—a most unusual relationship.

The premaxillary suture is discussed above under "*Premaxillary*," as is that between the nasal and frontal.

The nasal is apparently almost lost in *Pistosaurus*, although it is normal in *Nothosaurus;* it seems to be present and of large size in *Plesiosaurus guilelmi imperatoris*. It is not recorded in *P. macrocephalus*, *Brancasaurus*, or *Tremamesacleis*, but in these three forms it seems probable that the suture was closed or overlooked. The nasal of *Hydrotherosaurus* is different from any yet figured in its breadth and its transverse posterior termination.

Frontal.—The frontal forms the upper border of the naris. It meets the nasal in front, the maxillary or premaxillary at the naris, the lacrimal above the orbitonasal bar, the prefrontal above the orbit, and the parietal behind in the midline.

Under "Premaxillary" I mentioned the possibility that my frontal might be a part of the nasal or even premaxillary. Then my prefrontal would be the frontal lying in a more normal position. This would not affect the parietal, postfrontal, or postorbital, but I would then have to consider that either my lacrimal or prefrontal was absent, as there is definitely but one element in the lower part of the preorbital bar.

The frontal of *Thalassomedon* is a distinct bone lying medial to an element homologous with my prefrontal. I have been unable to find such a suture on *Hydrotherosaurus* and so solve the complexing problem.

The solution shown is not satisfactory, but is the best that I can offer with what sutures I can find.

Prefrontal.—The large size of this supraorbital element is evidently an advanced evolutionary character. Anteriorly it meets lacrimal, frontal, and parietal, and roofs the orbit. Behind, it meets parietal, postfrontal, and postorbital. A large nutrient foramen is situated near the midline about 1 cm. behind the parietal-frontal suture.

I am certain of the sutures that outline this element, but, as explained above, I am not certain that it is the prefrontal. Its posterior extent, to suture with the postorbital, is abnormal for this element and more like the frontal.

Postfrontal.—This element forms the anterior wall of the temporal fenestra. It is separated by distinct sutures from the prefrontal, postorbital, and parietal. Its dorsal surface is pitted where it undoubtedly formed part of the origin of the powerful temporal muscle.

The reduction of the postfrontal seems to have been an evolutionary feature of the Sauropterygia. Among the Triassic forms it builds a large part of the skull roof. In the Jurassic skulls it projects laterally from the frontal, still taking part in forming the skull roof and the postorbital bar. In both the California and Denver skulls, from the Cretaceous, it is reduced. In the latter it still lies on the skull roof but is excluded from the postorbital bar. In *Hydrotherosaurus* it has become excluded from both the skull roof and the postorbital bar, so that it lies entirely within the temporal fossa.

Parietal.—The parietal meets the frontal anteriorly and the pre- and postfrontals anterolaterally. It forms the central part of the skull roof and the wall of the temporal fossa behind the postfrontal. Posteriorly it is overlapped by the squamosal and below it meets the supraoccipital. The sagittal crest is missing but was probably low, not at all like that of *Cimoliasaurus snowii* Williston, or even that of the Denver skull.

There is no trace of a pineal foramen on the dorsal surface. On the ventral surface of the skull roof the posterior border of an almost obliterated and evidently closed "foramen" lies about 3 cm. behind the anterior tip of the parietal. The loss of the pineal foramen is evidently an advanced character.

Postorbital.—The postorbital forms the posteroinferior border of the orbit and most of the postorbital bar. It meets the prefrontal and the postfrontal above, the maxillary below in front, and the jugal behind. Evidence for this will be presented in discussing the jugal. The postorbital is typically elasmosaurian, its sutures distinct.

Jugal.—This element lies behind the postorbital and above the maxillary. Nearly all writers have called this the squamosal, or anterior bar of the squamosal, believing this bone to be triradiate. However, the left quadrate region shows an open suture that I suppose is for the posterior end of the jugal bar. The separation of jugal and squamosal is unquestionable on the Denver skull, and is suggested by many figures of plesiosaurs, pliosaurs, and nothosaurs. I therefore assume that this more normal relationship is the correct one.

In the Denver skull the jugal is underlain by a quadratojugal so that another open suture on the quadrate of *Hydrotherosaurus* is probably for the quadratojugal.

Lacrimal.—The lacrimal lies between the naris and the orbit, meeting the frontal and prefrontal above and the maxillary below. The bone is in the position of the element often called the prefrontal.

The upper sutures are distinct; the lower, less certain. If the "prefrontal" is really frontal (see above under "Premaxillary"), there is no way of determining whether this element is lacrimal or prefrontal, since I can find no trace of a lacrimal duct. However, if the dorsal element is prefrontal, as I think it is, this element must be the lacrimal.

Squamosal.—The squamosal has formerly been figured as a triradiate bone with its rays running forward as temporal bar, downward to the quadrate, and upward to the parietal. The whole posterolateral side of the skull was thought to consist of this one peculiar element, and for this reason the relationships of the whole order have been obscured.

On the right side the jugal has become separated from the squamosal and quadrate. On the left the jugal is missing, but there is an open suture on the quadrate for its main part, and the quadrate-squamosal suture is evident. This would not prove the existence of separate elements, were it not for the Denver specimen. Here the squamosal ends below against the quadrate in a fairly distinct suture, and meets its complement above the parietals in the midline.

The squamosal is thus restricted to the upper part of the posterior temporal bar.

On the posterior surface of the skull the squamosal apparently meets the parietal but not the supraoccipital.

Quadrate.—Only the left quadrate remains, and it is poorly preserved. As mentioned above, it evidently meets the squamosal above in a tight suture. The jugal suture is open, as is that for the quadratojugal. This latter element is definitely present on the Denver skull and the C. I. T. juvenile. I therefore feel justified in so positive an identification of the lower open suture in this form.

Mandible.—The symphysis is short, 5.3 cm., composed of the dentary and splenial. The right splenial extends posteriorly along the ventral border of the ramus at least 19.4 cm., where it is covered by the dentary. The latter is 3.3 cm. wide near the symphysis and narrows to 2.2 cm. below the posterior border of the orbit. Posteriorly the right ramus disintegrates into an indeterminate mass.

The left articular complex is a fragment 19 cm. long that was displaced and projects laterally from the 3d cervical. The postarticular process extends 4.2 cm. behind the deep articular fossa. This fossa measures 1.5 cm. anteroposteriorly and 2.2 cm. transversely, is convex posteriorly, and is strengthened by anterior and posterior buttresses. The articular region closely resembles *Tremamesacleis platyclis* (Andrews, 1910, fig. 48), but the sutures cannot be made out in *Hydrotherosaurus*.

The long postarticular process affords considerable leverage to the depressor muscles of the mandible, and the large temperal fossa is evidence of powerful temporal muscles. Fish vertebrae were found among the gastroliths, and these jaws must have formed an admirable device for the prehension of this type of prey.

The lower jaws must have been guided very accurately into the closing position, because the quadrate is fixed and the articular deeply notched. This type of hinge made certain that, should the animal miss its prey, it would not be possible for the teeth to mesh incorrectly and break or chip. Only through the protection afforded by some such close alignment of the jaws and teeth would it be possible for such an extremely prehensile dentition to develop.

It is interesting to compare this mechanism for occlusal alignment with that of other reptiles. The pelycosaur and therapsid pterygoid develops a massive vertical bar that guides the jaw into its proper position. A similar bar is developed in the crocodiles, but here the ectopterygoid also takes part in its formation. Anteroposterior alignment is not necessary in the pelycosaurs and therapsids since the lower teeth bite inside of the upper and do not mesh; but a lateral misalignment might be disastrous, and is prevented by the pterygoid bar. The anguid lizards (*Gerrhonotus*) have an analogous mechanism, but the guide is on the lower jaw—a high coronoid process which slides against the pterygoid.

Vertebrae.—In reviewing the literature, I found that isolated vertebrae often have been assigned to the wrong region of the column. As *Hydrotherosaurus* is complete, I thought that a list of characters might be compiled which would serve to separate the different regions. These characters are taken largely from the type specimen, but will apply throughout the long-necked plesiosaurs.

Anterior cervicals taper anteriorly and have hatchet-shaped ribs fused to the posterior part of the ventrolateral border of the centrum. The ventral face of the centrum is keeled and on either side of the keel is a nutrient foramen. There is sometimes a lateral longitudinal ridge on the lateral wall of the centrum about halfway between the base of the neural spine and the top of the rib. This ridge is usually bounded above and below by horizontal grooves. The neural spines are fused to the centra with a suture about as long as the centrum itself. Centra may usually be oriented by the anterior taper and by the rib facets, which are nearer to the posterior than to the anterior end.

Posterior cervicals have almost no taper and the centra are depressed. The ribs are longer and more slender posteriorly and become free from the centra. The rib facet is round, situated near the posterior end of the ventrolateral border, and faces ventrolaterally. It may be considerably modified in the last few cervicals, where it is usually compressed. The ventral keel is rounded and swollen, with the two nutrient foramina still present but much less prominent. The spines are still fused to the centra, with a suture as long as the centrum.

Following Seeley (1877) and most subsequent workers, pectorals are designated as vertebrae in which the rib facet is formed partly by the diapophysis and partly by the centrum. In *Hydrotherosaurus* there are three vertebrae in front of these that possess greatly compressed rib facets and are therefore highly modified. I would much prefer to label these pectorals but, for the sake of clarity, employ the customary terminology.

Dorsals are compressed, with smooth, concave sides. The ventral surface is smoothly rounded and all traces of the keel and the foramina have disappeared. The rib articulation lies entirely on the transverse process of the anterior and median dorsals, and the first dorsal rib facet is expanded to twice the area of the last pectoral. The anterior dorsals are larger than the median or posterior. On the posterior dorsals the rib facet is partly on the transverse process and partly on the centrum, and the spinous suture moves forward so that the pedicel rides partly on the centrum of the preceding vertebra. The rib facets on the posterior dorsals are largely on the centrum, but a small dorsal lip is formed by the diapophysis.

Sacrals are almost round in section. The rib facet faces laterally and is a large open crater with a rough bottom, a high rim, and a projecting lower lip. The facet is nearly as large as the centrum, about twice as large as that of the last dorsal, and still has a small dorsal lip formed by the diapophysis. The spinous suture is forward so that the pedicel overlaps the preceding vertebra.

Caudals taper posteriorly and the centra are depressed. The spines are fused to the anterior caudals, but posteriorly they are free. The exposed sutures are broader and nearer the front of the centrum on the anterior cervicals. The rib crater has a protruding rim, with a smooth concavity above between the rim and the suture for the neural spine. There are longitudinal ridges from the front of the crater to the articular face of the centrum. The crater is not round but V-shaped in longitudinal section, is nearly as long as the centrum, and is situated a little more anteriorly than posteriorly. The ventral surface usually shows one foramen and two ridges. The chevron facets are absent anteriorly but present distally, with the larger facet on the posterior end of the centrum.

There are 102 vertebrae present in *Hydrotherosaurus* with a total length, as preserved, of 775 cm. These may be divided into 60 cervicals, 2 pectorals, 17 dorsals, 3 sacrals, and 20 caudals. The tip of the tail is missing; but judging by the taper of the posterior caudals, and the Denver and Pasadena specimens, probably not more than 10 vertebrae have been lost. The total number of vertebrae was therefore about 112.

A summary of this and the other nearly complete vertebral columns from North America is given in table 13. The figures for *Elasmosaurus platyurus* Cope and *E. serpentinus* Cope must remain "estimated" until a reexamination of the original material can be made.

As shown by the table of measurements (table 1), the anterior cervicals are small. In fact, they seem absurdly small for so large an animal. The neural arches are fused to the centra on the cervical, pectoral, dorsal, sacral, and anterior caudal vertebrae. The arches of the posterior caudals are free.

The centra are always broader than high. This seems to indicate that dorsal and ventral flexion was greater than lateral. At least the former type of movement revolved about the long axis of the face of the centrum and therefore allowed greater freedom of action for a given intervertebral space. The cervicals back to the 44th are longer than high, and from the 48th on they are higher than long. The 40th to 43d cervicals are of distinctive length, this being their greatest dimension.

Cervical vertebrae.—The first and second vertebrae of *Hydrotherosaurus*, the fused atlas and axis, are partly obscured by the right squamosal. Their ventral surfaces are convex, in contrast to the other cervicals, which are pitted and concave below. The neural spines project 36 mm. above the centra, and are highest posteriorly. The anterior surface of the centrum is hidden, but the posterior is a depressed oval 33 $\times$ 43 mm., with a central concavity 4 mm. deep. The fusion of the elements is so complete that it is impossible to delimit the component bones.

The 3d cervical is short and compressed. Its proportions are typical of the next 37 or so anterior cervicals; centrum broader than long, and longer than high, with a concave ventral surface with two pits or longitudinal grooves separated by a median keel. The 3d vertebra is unique in having a single ventral nutrient foramen, which pierces the anterior part of the keel.

On the ventral border of each articular face, in line with the keel, is a broad, shallow notch. The notches of consecutive vertebrae form a broad groove along the ventral midline of the neck (fig. 5). The significance of this groove is not known. Bases of the cervical ribs remain fused to the ventrolateral ridges of the vertebrae.

The 4th cervical is heavier than the 3d, similarly proportioned, but with a much narrower keel than any other vertebra. The groove on either side is pierced by a nutrient foramen close to the keel. The concavity of the depressed oval articulating surface is 3.5 mm. deep.

The 5th cervical has the broad keel typical of the following cervicals. The neural spine is partly hidden, but its height is at least 23 mm. The pedicels are almost as long as the centrum and enclose a broad neural canal.

The 6th cervical (pl. 14, *a*) is the first of a consecutive series running back to the 98th vertebra, or the 16th caudal. As shown in the table of measurements (table 1) and in plates 14 to 17, the posterior centra become larger. The ventral keel becomes low and rounded, and in the posterior cervicals it is so swollen that it almost obscures the nutrient foramina. The lateral longitudinal ridge, quite prominent anteriorly, disappears at the 40th cervical.

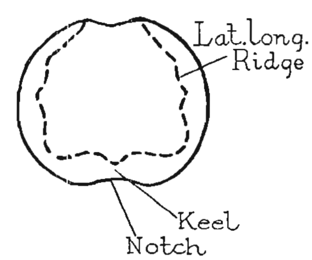

Fig. 5. *Hydrotherosaurus alexandrae*, type. Anterior view of centrum to show notch in articulating face, ventral keel, and lateral ridge. × ⅔.

This ridge, called a lateral angle by Cope (1877), was used by him to separate the species of *Elasmosaurus; platyurus* and *orientalis* having it on all the cervicals, and *serpentinus* on only the anterior cervicals as in the present specimen. Pravoslavlev (1919) considered this ridge to be an indicator of the muscular development and therefore the length of the neck. This is probably valid, as the ridge is absent in the short-necked forms.

The last three cervicals, 58, 59 and 60, are highly modified (pls. 16, *d* and 17, *a*, *b*). In the 58th the rib facet faces laterally for the first time, and is suddenly compressed to half the horizontal diameter of the large circular facet of the 57th. The facet is still on the ventrolateral border of the centrum, but it now occupies the posterior rather than the middle portion of this region. The 59th shows a strong ridge surrounding the deeply cupped rib facet. This facet is larger and opens lateroposteriorly. On both the 58th and 59th centra the border of the rib pits is buttressed by ridges running to the anterior and posterior articulating ends of the centra. The facet on the last cervical, 60, is still larger and buttressed, its upper border projecting 22 mm. from the centrum.

Pectoral vertebrae.—On the 61st, the first pectoral, the facet has shifted dorsally until it is about half on the transverse process and half on the centrum. The neural arch is now continuous with the rib facet and forms its dorsal lip. The rib facet on the 62d (pl. 17, *d*) is almost entirely on the expanded end of the diapophysis, but is still fused ventrally with the centrum. This rib facet is much larger than that of the first pectoral and bears the first long rib.

Dorsal vertebrae.—The 63d is the first vertebra with the rib facet clearly on the transverse process and is therefore considered to be the first dorsal. This process is short and close to the centrum, but expanded distally into a broad articulating facet with two distinct sulci for the rib articulation. These sulci are separated by a heavy dorsal rugosity that anchored the ligaments holding the rib head.

During this rather abrupt change in the position of the rib articulation, the two ventral longitudinal grooves with their foramina undergo a parallel change. On the 50th the grooves have become so small that only the two foramina remain. As the rib facet shifts dorsally from vertebra 58 to vertebra 63, the foramina disappear, and the ventral surface of the centrum becomes smoothly rounded. The sides of the centrum become slightly concave vertically up to the transverse process.

The dorsals are compressed, and the depth and breadth exceed the length of the centra. The transverse processes originate progressively higher on the centrum until on the 67th the process is entirely on the arch, a true diapophysis.

The centra increase in height to the 68th (the 6th dorsal), which is the largest vertebra and has the longest transverse process (13 cm.) as well as the longest rib. The transverse processes are directed posteriorly about 30° from the perpendicular, and the terminal rib facet is oblique to the process, facing about 45° posteriorly (fig. 12). The facets from 68 to 72 have a slight vertical cleft dividing them into an anterior and a larger posterior portion. The transverse processes decrease in length back through the sacrals, where they are mere remnants 2 cm. long, forming only the dorsal lip of the facet. From the 68th to the 79th or last dorsal, the vertebrae become smaller and less compressed. The 78th and 79th facets are small and are formed mainly by the centrum and only partly by the arch (pls. 18 and 19, *a*).

Sacral vertebrae.—The separation between dorsal and sacral vertebrae is based upon the ribs and rib facets. On the 80th, the first sacral, the rib facet is at least twice as large as on the 79th, although the stubby transverse process still forms about the same portion of the facet. The 80th facet (pl. 19, *a*) occupies almost the entire lateral wall of the centrum and has a large ventral lip and a strong, rugose cavity for the rib. This cavity is 56 mm. in vertical diameter and 55 mm. in horizontal.

The second and third sacral vertebrae, numbers 81 and 82, have equally large rib facets occupying almost the entire length of the centra and four-fifths of their height. These facets, like those of the succeeding caudal vertebrae, are craters with rough floors and elevated borders. They differ from the caudals in that the diapophysis forms a small dorsal part of the facet.

The sutures between the neural spines and the centra become increasingly plain behind the 76th vertebra, until on the 5th and succeeding caudals the spine is free and the suture on the centrum is open.

Caudal vertebrae.—The 83d vertebra is thought to be the first caudal because here the rib is flat rather than rounded and stocky as in the sacral vertebrae. Also the rib facet is appreciably smaller and is entirely on the centrum instead of having its dorsal lip formed by the transverse process.

The sutures for the neural spines, from about the 61st vertebra on, arise from the anterior border of the centrum and occupy almost its entire length. This is so pronounced in the caudal vertebrae that from the 83d to at least the 86th the pedicels lap over onto the preceding centrum and they have developed small, smooth facets from the friction of the overlap.

The caudals beyond the 87th are represented by a series of disarranged centra with open sutures for the spines and open facets for the ribs. Ribs and spines lie in approximate position but become more scattered posteriorly. The rib facet remains on the side of the centrum as far as the last caudal preserved. It still is almost as long as the centrum, but its vertical diameter has decreased so that posteriorly the rib crater is high on the side of the centrum.

Chevron facets are well developed on the posterior border of the 100th vertebra, and probably existed on some of the more anterior caudals. The posterior chevron facets are large and there is also a smaller anterior pair on the 101st and 102d. They are not present on the 86th, and the intervening vertebrae are too badly eroded to reveal just when the chevrons commenced; they probably did not begin until after the 90th. On some of the anterior caudals a peripheral groove separates the anterior articulating surface from the body of the centrum. This groove, apparently the character upon which Leidy (1851)

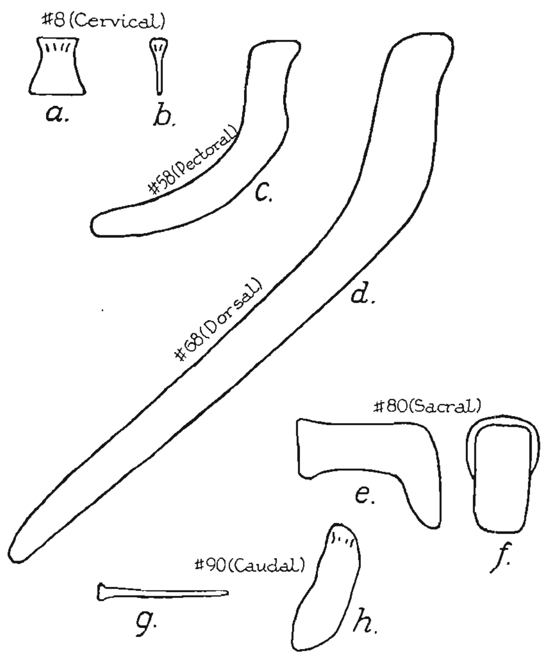

Fig. 6

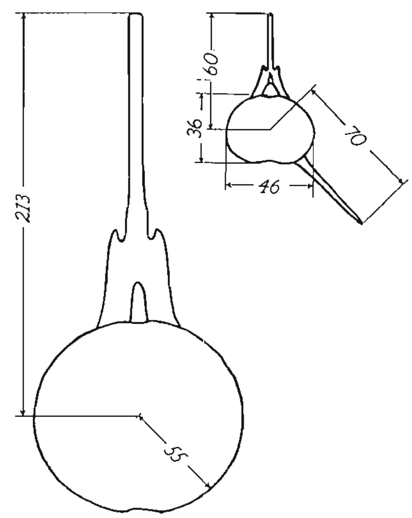

Fig. 7

Fig. 6. *Hydrotherosaurus alexandrae*, type. Rib variation. *a*. Lateral view of cervical. *b*. Anterior view of same. *c*. Anterior view of pectoral. *d*. Anterior view of dorsal. *e*. Anterior view of sacral. *f*. Lateral view of same. *g*. Anterior view of caudal. *h*. Dorsal view of same. U. C. Mus. Pal. no. 33912. × 1/6.

Fig. 7. *Hydrotherosaurus alexandrae*, type. Diagram of leverage of the ribs of 8th and 54th cervical vertebrae. Measurements in millimeters.

based his genus *Discosaurus*, is not constant and is therefore unreliable. A similar feature is shown in the specimen that Riggs (1939) refers to *Elasmosaurus serpentinus* as well as in the Denver specimen, and one of the specimens at Pasadena.

Neural spines.—The spines are all very narrow transversely, and their summits form a nearly continuous sagittal line. The cervical spines are almost as long anteroposteriorly as the centra, to which they are tightly fused. They increase in height from 23 mm. on the 5th cervical to 137 mm. on the 39th and 166 mm. on the 50th. There are gaps of about 1 cm. between consecutive anterior cervical spines, but posteriorly the spines are so close that they almost touch. This implies that the posterior neck region was more rigid than the anterior. The tallest spine rises about 20 cm. above the centrum and is on the 6th dorsal, the 68th vertebra. The fusion of spine and centrum continues through the pectoral, dorsal, sacral, and anterior caudal series until the 87th, or 5th caudal, where the spine is free.

Ribs.—The ribs (fig. 6) are all single-headed. The 8th, 9th, and 10th right cervical ribs are still fused to the centra, projecting ventrolaterally about 60° to the sagittal plane. They are about 45 mm. long, flat, with the distal end dilated so that its anteroposterior diameter exceeds the length of the centrum. Thus the distal ends of these cervical ribs actually overlap, the anterior border outside, and form a zygapophysis-like ventral brace to the neck. The problem of support for so long a neck is thus solved anteriorly by the triradial levers of the neural spines and cervical ribs.

The next vertebra having a well-preserved cervical rib is the 14th. The distal anteroposterior diameter of this rib is still greater than the length of the centrum. The cervical ribs decrease in anteroposterior dimension, not only relatively but actually, back at least to the 44th. The next 9 ribs have been destroyed, and the 54th is quite different. It is long (13 cm.), stout (4 cm. × 1 cm.), and not expanded distally. It is no longer fused to the centrum, but articulates in a round pit on the middle of the ventrolateral border.

Although this latter type of cervical rib is more usual among reptiles, it affords a much less effective lever than the fused rib of the anterior cervicals. If we assume the fulcrum to be the center of the articulating face of the centrum, a diagram (fig. 7) will show that the effective lever arm (5.5 cm.) is actually less on the very large 54th than on the small 8th vertebra, where it is 7 cm. long. In proportion to the linear dimensions of the faces of the centra, the 8th provides almost three times as much leverage. The 7-cm. lever was apparently sufficient for the anterior cervical series. No doubt the posterior neck muscles were larger and therefore stronger, so that less leverage was required in this region. This argument does not apply to the neural spines, as they increase from 6 cm. on the 8th to 21 cm. on the 54th and are even higher on the dorsals. Other factors, such as the proximally increasing compressive stress between adjacent vertebrae, must be invoked to explain the remarkable differences in the sizes of the cervical vertebrae.

The 60th rib, the last cervical, is 27 cm. long. The pectorals, 61 and 62, are 45 cm. and 48 cm. in length, about twice as long as the last cervical. The separation between pectoral and cervical regions is thus quite distinct. The anterior dorsal ribs measure 5 cm. × 2.5 cm. proximally, and they taper very gradually. The rib length increases to 57 cm. on the 69th, then gradually decreases to 21.5 cm. on the 75th, and 15 cm. on the 79th, which is the last free dorsal rib.

The 80th, or first sacral, is short and stout, projects laterally, and curves slightly downward; the 81st is similar, 13.5 cm. long. The 82d is also robust, projects 10 cm. laterally, then extends another 6 cm. after a sharp downward bend. The proximal end of the ilium lay in the angle thus formed, but in life it probably met the ends of the sacral ribs.

The flexion of the neck and the shape of the animal will be discussed under the heading, "Restoration."

Gastralia were present, but they have been too completely disrupted to permit an accurate restoration.

Pectrum and pectoral paddle.—Before burial the right paddle, scapula, and coracoid (pl. 13) were pulled out under the body, with the ventral side up. The left half of the girdle was pulled around to the back and the paddle was extended caudally along the vertebrae.

The left humerus and forearm still lie in approximately correct relation to the coracoid, but the scapula is slightly out of position.

The sutural surfaces of the scapula and coracoid are covered with small (1-cm.) cones which lie in depressions rimmed by the projecting surfaces of the bones. The scapula and coracoid therefore did not meet in a bony suture, but must have been separated by cartilage, possibly an indication of juvenility. The glenoid faces of the scapula and coracoid are relatively smooth depressions, but a considerable amount of cartilage must have been present in this region of the shoulder girdle.

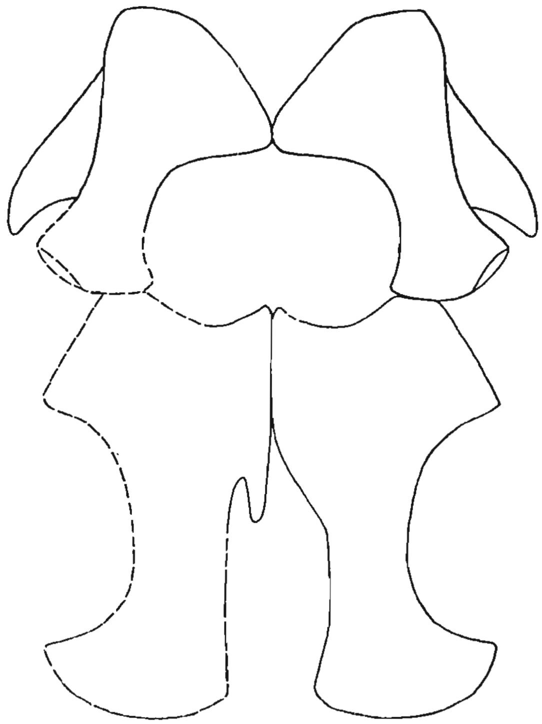

Fig. 8. *Hydrotherosaurus alexandrae*, type. Ventral view of pectrum. U. C. Mus. Pal. no. 33912. × 1/18. The coracoids have been interchanged; they are described correctly in the text.

Scapula.—The ventral plate of the scapula (fig. 8) forms almost a right-angled triangle, with the right angle pointed forward. The anterolateral border is arched outward in front, but is concave immediately ahead of the glenoid. The medial border is an arc whose center lies halfway out to the glenoid. The posterior border is concave, and a slender neck runs posterolaterally to the glenoid. The dorsal process rises from the anterolateral border and extends posteriorly and laterally to a point almost above the glenoid. The ventral surface of the scapula is plane anteroposteriorly but concave laterally. A reconstruction of the pectrum shows that the median bar joining coracoid and scapula, which is found in *Elasmosaurus platyurus* Cope, is absent in *Hydrotherosaurus*.

A prominent feature of the ventral surface of the scapula is the strong, rounded anterolateral shelf below the dorsal process. A concavity at the base of the dorsal process where it joins the ventral plate emphasizes this scapular shelf.

The two scapulae may have met in the midline, but they certainly were not fused. There is an open V, anteriorly between the two, that was probably occupied by the clavicles and interclavicle, but no trace of these bones has been preserved.

In general shape and in the absence of the median connection between scapulae and coracoids, this shoulder girdle is very close to the specimen figured by Williston (1914) as "*Elasmosaurus*" and later figured by Riggs (1939) as "*E. serpentinus*"; it is also close to *E. snowii* Williston (1906) and *Leurospondylus* Brown (1913) (figs. 29, 31, 36, this paper). None of these forms have a median pectoral bar, and all have been restored with the scapulae wide apart anteriorly and without any trace of clavicles or interclavicle. The absence of the pectoral bar is obvious, but in all of these forms the scapulae should be brought closer together anteriorly in order to widen the glenoid and make it capable of receiving the humerus. The discovery of clavicular arches in the Denver and Pasadena specimens indicates that they were present in all of the Elasmosauridae.

Coracoid.—The two coracoids (fig. 8) met in the midline with a suture 14 cm. long which represents a little over one-quarter of their length. This suture projects almost as far forward as the scapulocoracoid suture, that is, slightly beyond the glenoid. The critical midline region is missing from the right coracoid, but the extent of its anterior projection can be determined from the left. The coracoids are not widely separated posteriorly, but their posterior ends are broadly expanded. They are remarkable for the relative length and slenderness of their posterior projections. *Elasmosaurus snowii* Williston has much shorter and stouter coracoids, which project a little farther forward in the midline, as does *Leurospondylus*. "*E. serpentinus*," figured by Riggs (1939), is almost the same size as *Hydrotherosaurus*, but the coracoids are formed much more like the two former specimens. These resemble each other in the cardioid shape of the intercoracoidal vacuity. In *Hydrotherosaurus* this is a narrow, boat-shaped opening with an acute anterior termination. All that remains of the left coracoid (pl. 13) is the midline region. This, however, is well preserved and is asymmetrical with the right. The midline face of the left coracoid continues posteriorly 15 cm. farther than the right and must have met an intercoracoidal cartilage rather than the opposite coracoid.

Humerus.—The humerus (pl. 13) is massive, oval proximally, but broad and flat distally. Its anterior border is nearly straight, its posterior concave. The proximal end is partly separated into capitulum and trochanter by anterior and posterior vertical grooves. The distal end is divided into two equal concave facets for the radius and ulna. There is a large central rugosity for the insertion of the M. coracobrachialis brevis. Anterior to this, and separated by a smooth longitudinal groove, is a smaller roughening for the M. pectoralis. The scar for insertion of the M. deltoideus occupies the middle of the shaft, and in this respect it represents a distinct advance over any of the genera figured by Watson (1924), where the insertions are much more proximally situated. The humerus of *Tremamesacleis* figured by Andrews (1910, fig. 69) is similarly proportioned, but here again the muscle inserts nearer the proximal end of the shaft. The more distal insertion in *Hydrotherosaurus* provides a longer leverage than the proximal insertions of the more primitive forms. In this respect *Hydrotherosaurus* is farther advanced than other known dolichodires.

Compared with the "*Elasmosaurus serpentinus*" figured by Riggs (1939), the humerus of *Hydrotherosaurus* is longer and more slender, the distal breadths being 80 per cent and 70 per cent of the length, respectively. This is not merely an age difference, as the coracoids of the Chicago specimen are larger. Both specimens are much closer to *Tremamesacleis platyclis* of the Oxford Clay (Andrews, 1910) than to any other known Jurassic form. The Cretaceous humeri show changes in the more distal insertion of the muscles, in the concave faces for the epipodials, in the convex anterodistal border, and sometimes in the marked separation of capitulum and trochanter.

Epipodials et seqq.—The elasmosaur paddle is regularly composed of a row of 3 proximal mesopodials, followed by a row of 4, or, as in the Denver specimen, 5 distal elements. There has been universal agreement that the proximal mesopodials are radiale, intermedium, and ulnare, or their tarsal equivalents. The second row is customarily labeled carpale, or tarsale, 1, 2, 3 (or 1, 3, 4, Broom, 1921) and metapodial V.

It at first seemed unlikely to me that a metapodial, here the 5th, could shift entirely into the mesopodial row and assume the form and function of a mesopodial; yet a review of the ancestral forms shows that this has actually occurred in the elasmosaurs. Among the Triassic Sauropterygia, the proximal ends of the metapodials form a straight or nearly straight line regardless of the degree of ossification of the mesopodials. In *Ceresiosaurus* there are but three tarsalia (Peyer, 1931), yet there is no proximal shift of any of the metatarsals. In the beautifully preserved carpus of *Lariosaurus* (Peyer, 1933–1934, pl. 37, and fig. 1, *a*, pl. 38) there are five ossified carpalia and four tarsalia, but the proximal line of the metapodials is still straight. Another example (*loc. cit.*, figs. 6 and 7) shows but one distal carpal, and again the metapodial line is straight. Zangerl (1935) figured only two mesopodials in *Pachypleurosaurus*. His restorations moved the 5th metacarpal proximally although the other four formed a straight line. Peyer (1935) figured the pes of *Clarazia*, showing metatarsals I and V more proximally situated than is justified by the figure of the skeleton in his plate 47.

Thus among the Triassic Sauropterygia there are several well-preserved feet, none of which show a definite shift in the position of the 5th metapodial.

It is in the Liassic that the metapodial shift first appears. *Plesiosaurus rugosus* Owen (1840) of the Lower Lias has metapodial V in the mesopodial series, but it is still elongate. The same type of metapodium is shown in Owen's figure of *P. rostratus* and was apparently present in *P. dolichodeirus*. In *Thaumatosaurus* from the upper Lias, the front limb (Fraas, 1910, pl. 8) has reached the form typical of the Cretaceous elasmosaurs except that the epipodials are still elongated. Metacarpal V has shifted proximally, while the tarsus furnishes even better evidence. There is a space in the foot caused by the failure of the tibiale to ossify, yet there has been no proximal dislocation of the 1st tarsale into the gap thus formed. This indicates that the tarsus is relatively undisturbed. However, the 5th metatarsal has definitely shifted proximally half of its length. Here there can be little doubt that the element in question is metatarsal V, or that it has actually changed its position. It now occupies a place intermediate between that in the Triassic and in the Cretaceous Sauropterygia.

Plesiosaurus guilelmi imperatoris from the same beds (Fraas, *op. cit.*) is similar to *Thaumatosaurus*. Metacarpal V is restored here as having moved proximally half its length, although much space is left between elements. Even when a reconstruction is made with the elements placed closely together, the same proximal shift of the 5th metapodial is apparent.

Regarding the terminology of the distal mesopodials, the published alternatives are the accepted 1, 2, 3 and Broom's 1, 3, 4 (1921, fig. 25). The 4th carpale is the largest in most reptiles, and this is also the most persistent in the Triassic Sauropterygia as shown by a review of the forms just considered. Two species of *Lariosaurus* figured by Peyer (1933–1934, fig. 10, pls. 34 and 37) show the only ossified mesopodials to be radiale, intermedium, and three carpalia in the manus; and intermedium, fibulare, and two tarsalia in the pes. From their position, these are obviously carpalia 2, 3, 4, and tarsalia 3 and 4. In another example (*op cit.*, pl. 32), there is but one, the 4th distal mesopodial, in each foot. Other related forms show a persistent 4th mesopodial. This evidence is sufficient to determine that the mesopodial next to metapodial V is the 4th.

The terminology of the middle element is not so easily settled. A consideration of the same reptiles indicates that this element is the 3d and that Broom is correct. However, the Denver form has 4 tarsalia instead of the usual 3. Here the posterior is the largest, and is therefore the 4th. If so, the others must be the 3d, 2d, and 1st. It is of greatest interest that the 2d occupies the largest facet of the intermediale and completes the strong series, so characteristic of the elasmosaurs, directed anterodistally from the fibulare. The 2d tarsale is larger than the 3d. There are two alternatives: either the 3d distal mesopodial is lost in the forms with only three elements, or the 3d and 2d have fused. There seems to be no way of settling this question with the available evidence, so perhaps the simplest solution is to refer to this element as the 2d, bearing in mind that it may be 2d plus 3d.

The first distal mesopodial has had an interesting history: this element was lost, or at least failed to ossify, in many of the Triassic forms and yet was regained by the Jurassic plesiosaurs. This is explained through the change of function of the feet. The preaxial digit is always weak and relatively useless in land reptiles, yet in marine forms it is the preaxial side of the flipper, paddle, or fin that breaks the water, and this side is always the stronger. In the plesiosaurs the first digit becomes larger until in the Upper Cretaceous forms it is larger than the other digits.

Considering the foregoing evidence, the distal mesopodials will be referred to as carpalia, or tarsalia, 1, 2, and 4, the only known exception being the 1, 2, 3, and 4 of the Denver form. The 5th metapodial usually becomes a member of this series.

The epipodials of *Hydrotherosaurus* (pl. 21 and fig. 23) are broader than long and almost equal in size. The radius is convex anteriorly, concave posteriorly, and slightly convex proximally and distally. Both radius and ulna are slightly shorter and broader than those of the "*E. serpentinus*" figured by Riggs (1939); incidentally, as indicated by his table of measurements, he inadvertently reversed the labels on radius and ulna.

Radiale, intermedium, and ulnare are present in the proximal row, but the ulnare is displaced. The next row contains the three carpalia, 1, 2, and 4, one of which was lost in the right paddle. Only the first four rows of phalanges are preserved in the front paddle. These show broad metacarpals and proximal phalanges, with those of the 1st digit almost twice as broad as the others. Metacarpal V is missing, but apparently lay only half in the carpal row.

Both pectoral and pelvic paddles are well knit and powerful, and the bones fit together closely. Although the humerus is almost exactly the same length as the femur, the anterior epipodials are 1.2 times as long as the posterior. The most complete paddle, the left pelvic, has at least 11 phalanges on the 2d digit and a length of about 130 cm. from the proximal end of the femur. The ratio of 1:1.2 between pelvic and pectoral epipodials, if applied to the entire paddle, would result in a length of 156 cm. for the pectoral paddle.

However, in *Tremamesacleis*, although the humerus and femur are of different lengths, the rest of the paddles are about equal. The femur of *Hydrotherosaurus* is 36 cm. long, and the rest of the paddle measures 94 cm. The humerus is 39 cm. long, which, added to the 94 cm. for the distal part of the paddle, gives 133 cm. for the total length of the pectoral paddle, and this figure is used in the present reconstruction.

Pelvis and pelvic paddle.—The pelvic girdle (pl. 20 and fig. 9) is complete. The right pubis and ischia had been dislocated and turned ventral side up with the median borders laterad. In spite of this they still retained their relative position when buried. There was a weak median connection between the pubes and ischia, but no bar was formed as in *Elasmosaurus platyurus*.

Ilium.—The ilium is a short, stocky, curved rod, 23 cm. long, 5.5 cm. in diameter proximally, and 8 cm. distally. Its proximal end is sharply rounded and is now pressed

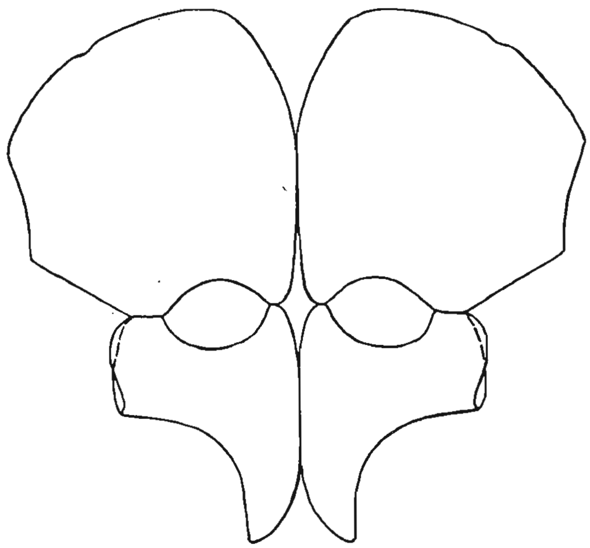

Fig. 9. *Hydrotherosaurus alexandrae*, type. Visceral view of pelvis. U. C. Mus. Pal. no. 33912. × 1/18.

into the angle of the rib of the 81st vertebra. It apparently projected forward, outward, and downward to meet the ischium, but not the pubis, at the acetabulum. The acetabular end is a cavity set with cones similar to the glenoid regions of scapula and coracoid, but the iliac cones are smaller and few in number.

Cope's figure of *E. platyurus* shows a nearly straight ilium, flattened proximally, which bears no resemblance to this. "*E. serpentinus*" is very much like *E. platyurus*. *Leurospondylus* has an arched ilium, but the bend is much weaker than in the Berkeley form. In short, the strong bow in the ilium sets *Hydrotherosaurus* apart from the other previously known dolichodirans. Strongly arched ilia are also found in the Pasadena and Denver specimens described below.

Pubis.—The pubis is longer anteroposteriorly (35.5 cm.) than broad (33 cm.). Its greatest breadth is anterior; it narrows to 28 cm. posteriorly. The median border is thick and straight, the anterior border convex, almost a semicircle, but with a small indentation 20 cm. from the midline. The posterior and external borders are concave. The result of these concavities is the formation of two broad necks, one of which extends anterolaterally, the other posterolaterally, to meet the ischium. Both pubes and ischia are thickest at the acetabulum. The pubis is more nearly circular than that in any of the elasmosaurs heretofore figured, the anterolateral neck being almost lost in the semicircle.

The necks are much thicker and less pronounced than in *E. snowii*. The anterior pubic border of "*E. serpentinus*" is reconstructed as in *Leurospondylus* and shows no anterior concavity, so the anterolateral neck is wanting.

Ischium.—The ischium is in the form of a right triangle, the right angle at the anteromedial corner. The median border is nearly straight, 39.5 cm. long, with a strong triangular thickening 9 cm. from the front. The posterior part of the median border is convex, turning outward 7 cm. and thickening so that a surface faces ventroposteriorly for cartilage attachment. Both the anterior and posterior borders are concave, and the shorter concavity is cephalad. The dorsal surface of the ischium projects slightly beyond the acetabulum.

It will be seen that this ischium is "short" along the midline. This feature was first noticed by Mehl (1912) in describing *Muraenosaurus* ? *reedii*: "Although there is no way of determining the length of the neck, it must have been long, for the ischia are short and the association of these two things, long neck and short ischia, seems to be a rule that can usually be depended upon."

The ischia of *Hydrotherosaurus* are similar to "*E. serpentinus*," but the process extending laterally to the acetabulum is more slender. Brown's restoration of *Leurospondylus*, as noted below, appears to have the ischia reversed, and they are of an even shorter type.

Femur.—The femur (pl. 20, *d*, *e*) is more slender than the humerus, especially in the proximal half of the shaft. The head is partly divided into two lateral halves, the internal or capitulum being a flattened, rounded, cartilage-capped surface similar to the head of an archosaur femur. The external, or trochanter, forms a smaller semicircular buttress that tapers distally into the shaft.

The anterior and posterior borders are concave, the greater concavity posterior. The distal end, like that of the humerus, is formed of two facets making an angle of 32°, but these facets are convex in the femur rather than concave as in the humerus. The femur also shows another character developed in the humerus—a convex "knee" on the anterior border just above the distal end. Earlier plesiosaurs have a smoothly concave anterior border extending to the distal articulation and they therefore lack this knee. It differs from *Tremamesacleis platyclis* in being more massive and having the trochanter form almost as much of the head as does the capitulum. In *Muraenosaurus*, *Brancasaurus*, and most earlier forms, the trochanter is smaller than the capitulum.

Epipodials et seq.—The tibia and fibula (pls. 20, 29) are smaller than the radius and ulna, but have about the same proportions of length to breadth. The total length of the paddle including the femur is 130 cm., of which 86 cm. lies distal to the fibula. The proximal half is articulated, but the distal portion is disarranged and many phalanges are missing.

The proximal row of tarsals consists of the usual three elements, the intermedium larger than tibiale or fibulare. The second row consists of the 5th metatarsal and 3 tarsalia. Metatarsals 1 to 4 form an even row, but the first phalanx of digit 5 begins opposite the middle of this row. Thus, the 5th digit is moved proximally a distance of one-half of a metatarsal.

There are 10 or 11 phalanges preserved in the 2d digit, but it seems probable that a few are missing at the tip. As nearly as can be estimated, the phalangeal formula was 10, 13, 11, 10, ?5. This estimate is too conjectural to warrant comparison with other forms.

Restoration.—Restorations of dolichodiran plesiosaurs have been trustworthy with respect to length of neck, body, and limbs, but the shape of the body and the flexibility

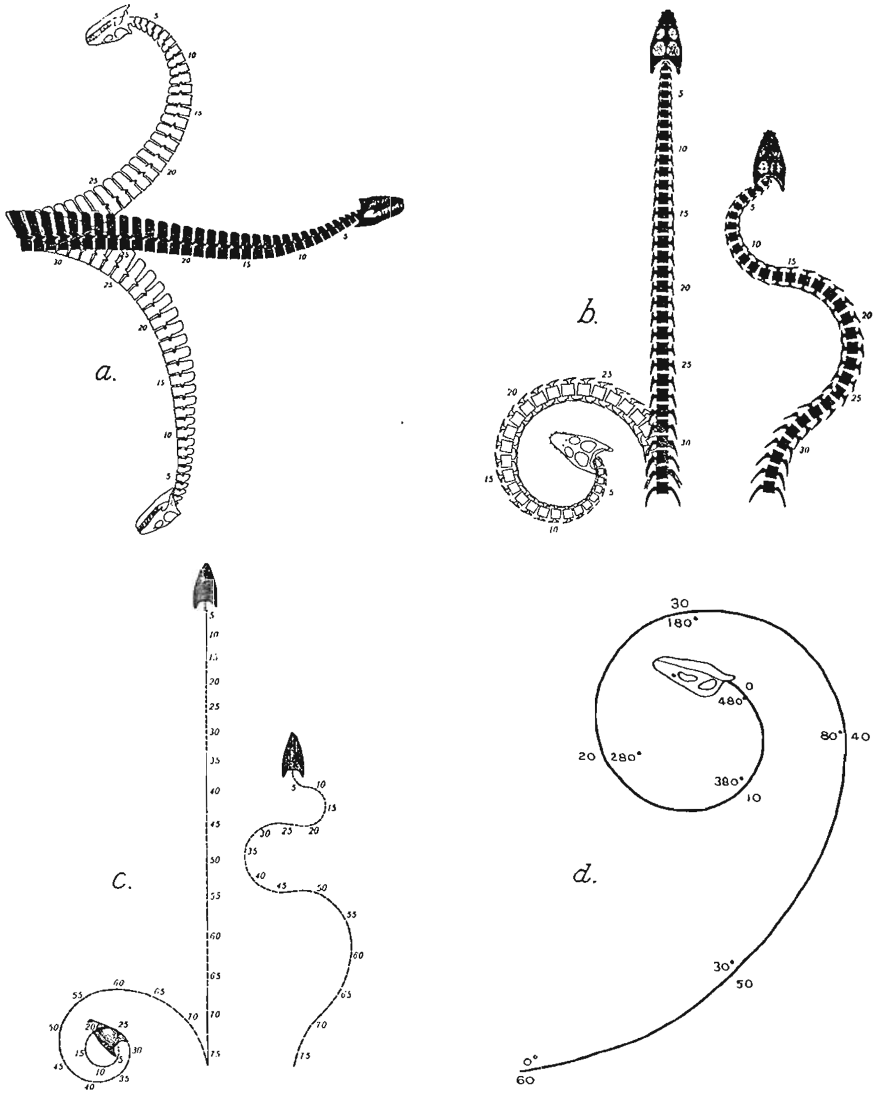

Fig. 10. Cervical flexibility of *Plesiosaurus*, *Elasmosaurus*, and *Hydrotherosaurus*. (*a*) *P. guilelmi imperatoris*. Dorsal and ventral flexion. (*b*) Same. Lateral flexion. (*c*) *E. platyurus*. Lateral flexion. (*d*) *H. alexandrae*. Dorsal flexion. (*a*, *b*, and *c* from Zarnik, 1926.)

of the neck have not been well understood. The neck has sometimes been arched like that of a swan or even coiled like a snake; at other times it has been restored straight and relatively stiff.

A mathematical solution has recently been proposed by Zarnik (1926), who, after a study of living sauropsida, derived estimates by measuring in degrees the movement possible between contiguous vertebrae. For the anterior cervicals of *Plesiosaurus bavaricus* he estimated a dorsal flexion of 6°, a ventral flexion of 5° 30′, a lateral flexion of

11°, and a torsion of 5°. For *P. guilelmi imperatoris* the estimates were: dorsal 5°, ventral 6° cervicals 11 and 12; dorsal 5°, ventral 5° 30′ cervicals 22 and 23. For *Muraenosaurus durobrivensis* the lateral flexion is 14°, anterior cervical, and 12°, posterior cervical; the torsion 6°, anterior cervical. His diagrams of the cervical flexion of *P. guilelmi imperatoris* and *Elasmosaurus* are reproduced here (fig. 10). These studies give us the maximum possible curvatures—the extremes which may never have been attained in the living animal. Although the estimates seem too high, they indicate a very flexible neck.

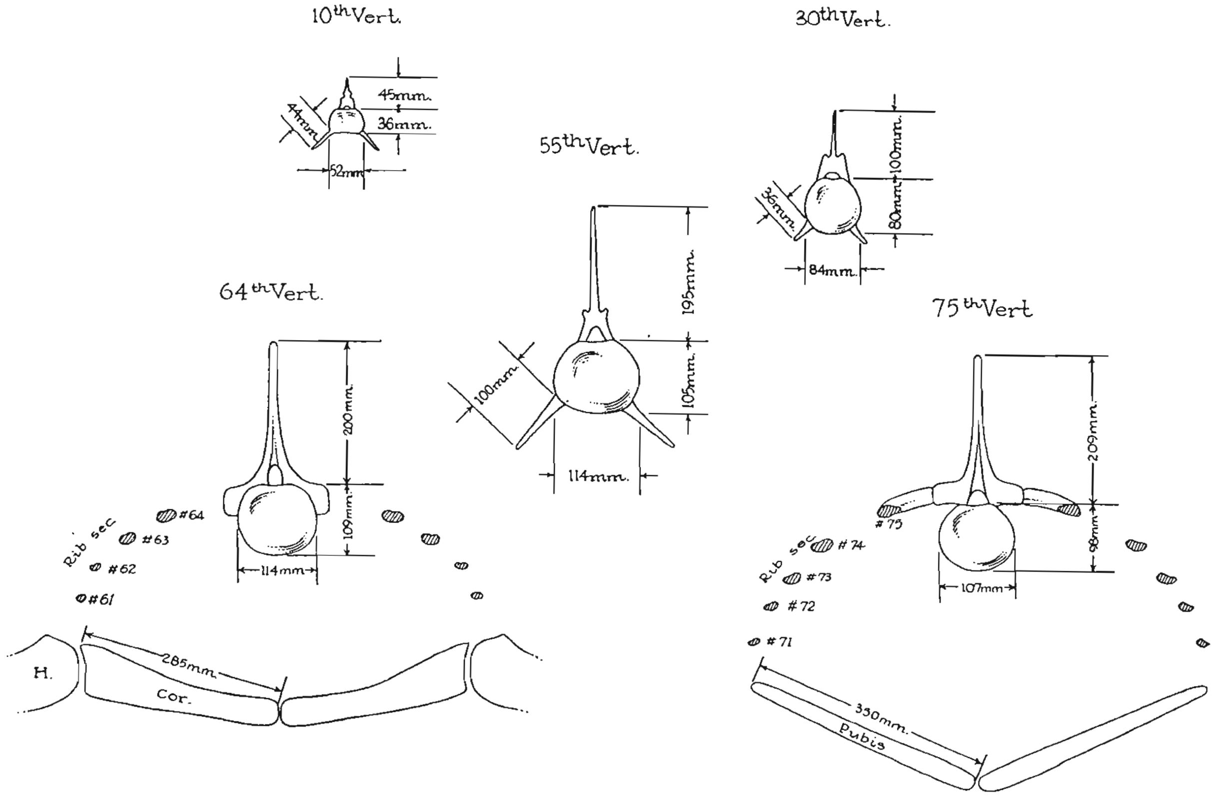

Fig. 11. *Hydrotherosaurus alexandrae*, type. Various transverse sections through the skeleton. U. C. Mus. Pal. no. 33912.

A similar study was made upon the dorsal cervical flexion of *Hydrotherosaurus*. The method was to place contiguous vertebrae together, flex them until the neural spines touched, and measure the angle of flexion. Since it was not convenient to move the vertebrae, wires bent to the configuration desired were substituted for the vertebrae to be moved. In this way it was found that the posterior ten cervicals were relatively inflexible, capable of bending only about 3°. From the 50th to the 40th, the dorsal flexion was about 5° between centra, while from the 40th forward the flexion averaged 10°. Thus the maximum curvature at the 50th centrum was about 30°; at the 40th, 30° + 50°, or 80°; at the 30th, 80° + 100°, or 180°; at the 20th, 180° + 100°, or 280°; at the 10th, 280° + 100°, or 380°; and at the 1st about 480°. These estimates are for dorsal flexion only; lateral and ventral movements were probably less restricted (fig. 10, *d*).

There is some difference between these figures and those of Zarnik, primarily because he estimated a 1-cm. intervertebral cartilage. Andrews (1922, p. 289) writes of *Leptocleidus superstes*, "In the posterior cervical and thoracic regions, the zygapophyses are large, and their articular surfaces are flat. . . . They project so far anteriorly and posteriorly that . . . there must have been a small interval between the articular surfaces of the centra. This interval is, in fact, shown in this specimen and it can be seen that it was partly occupied by a disc of hard substance which under the microscope seems to show some resemblance to calcified cartilage." He does not give the thickness of this disc, but in his figure 5, plate 14, it measures about 1 cm. Zarnik's spacing was similarly based upon the relative position of centra as determined by the overlap of their zyga-

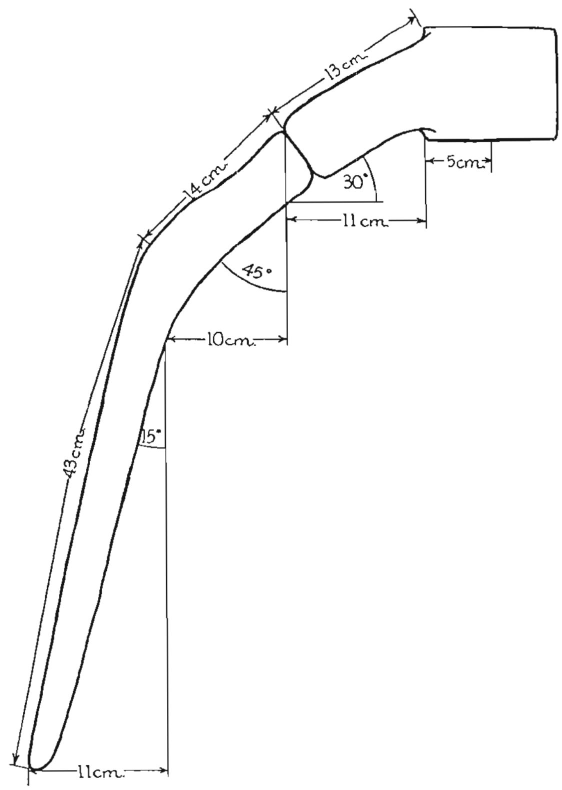

Fig. 12. *Hydrotherosaurus alexandrae*, type. Dorsal view of 65th vertebra and rib to show width of animal. U. C. Mus. Pal. no. 33912.

pophyses. This is probably justified for *Plesiosaurus* and *Muraenosaurus* because adequate material of these forms was studied, but the cervical flexion of *Elasmosaurus* must be questioned since here there is no direct evidence for intervertebral cartilages of this thickness. There is certainly no such evidence in *Hydrotherosaurus;* for when the zygapophyses are articulated, the centra practically touch, and the only space for cartilage was in the central cavities between the articulating faces of consecutive vertebrae.

Zarnik's total for *Elasmosaurus* is about 760°, or 180° greater than *Hydrotherosaurus.* Almost 90° of this increase is due to the longer neck of *Elasmosaurus,* but his estimate of 6° for the posterior cervicals is double that for the present specimen. There is admittedly little justification for comparing dorsal flexion of *Hydrotherosaurus* with lateral flexion of *Elasmosaurus,* but the reduction of the intervertebral cartilages of the latter form would certainly decrease Zarnik's estimate of the flexibility of the neck.

Further evidence may be derived from the attitude in which dolichodiran skeletons have been buried, but unfortunately this information has seldom been recorded. An

TABLE 1

HYDROTHEROSAURUS ALEXANDRAE, TYPE

MEASUREMENTS OF AXIAL SKELETON, IN MILLIMETERS. U. C. MUS. PAL. NO. 33912

	Centrum			Spine		Rib			Centrum			Spine		Rib	
	L	H	B	AP	H	AP	L		L	H	B	AP	H	AP	L
1 and 2	49	33	43	...	...	...	...	46.....	95	92	101	...	...	...	...
3......	34	...	45	...	...	...	...	47.....	94	93	103	...	...	...	...
4......	37	33	46	...	23	...	...	48.....	90	96	91	...	...	...	...
5......	39	33	38	...	...	...	...	49.....	89	94	110	...	...	...	...
6......	42	35	44	38	36	...	...	50.....	88	96	108	...	...	...	...
7......	41	36	...	39	41	...	...	51.....	96	93	95	...	...	...	...
8......	43	...	...	42	44	45	46	52.....	87	99	104	...	...	...	...
9......	43	36	...	39	45	50	46	53.....	99	99	108	...	...	...	...
10......	48	...	...	46	45	50	44	54.....	89	102	119	...	...	...	...
11......	47	...	...	44	45	...	...	55.....	86	105	114	...	...	...	...
12......	50	35	56	49	45	42	...	56.....	91	106	116	...	...	...	...
13......	53	38	55	50	47	...	34	57.....	91	103	118	...	...	...	...
14......	57	...	...	53	51	57	38	58.....	88	103	117	...	...	...	...
15......	58	48	60	50	46	...	...	59.....	87	102	116	...	...	...	220
16......	61	...	...	52	52	...	44	60.....	88	107	110	...	...	...	250
17......	63	41	...	55	53	...	...	61.....	89	98	120	...	...	...	440
18......	63	43	...	56	60	...	...	62.....	89	104	117	...	...	...	440
19......	64	...	...	57	61	...	...	63.....	92	109	114	...	...	...	500
20......	65	39	...	58	61	...	42	64.....	93	109	114	...	...	...	505
21......	68	...	...	59	68	62	41	65.....	90	117	114	...	...	...	570
22......	69	...	...	58	68	...	...	66.....	89	116	96	...	...	...	500
23......	73	50	74	65	72	...	44	67.....	92	121	120	...	...	...	500
24......	...	49	75	...	68	...	...	68.....	...	...	...	76	207	...	540
25......	76	...	79	67	78	...	...	69.....	82	104	...	80	186	...	520
26......	76	...	78	64	88	...	...	70.....	83	111	...	81	182	...	520
27......	73	...	76	73	88	...	...	71.....	88	116	...	90	172	...	490
28......	81	...	82	71	90	...	...	72.....	92	109	...	85	215	...	470
29......	78	...	...	72	94	...	...	73.....	88	108	...	...	...	...	410
30......	83	...	...	76	95	...	...	74.....	86	102	...	87	207	...	360
31......	83	...	...	...	96	...	...	75.....	80	98	...	76	209	...	300
32......	87	81	86	74	102	...	...	76.....	74	90	...	72	203	...	140
33......	87	88	95	...	...	...	...	77.....	81	90	105	64	189	...	140
34......	87	79	90	77	116	...	...	78.....	87	81	...	72	183	...	140
35......	88	79	80	76	118	...	...	79.....	83	87	...	...	179	...	...
36......	86	82	89	78	122	...	...	80.....	77	88	...	...	...	...	135
37......	87	82	94	83	132	...	...	81.....	77	83	...	65	165	...	165
38......	90	83	92	81	139	...	...	82.....	73	88	90	...	...	...	...
39......	91	87	96	85	137	...	...	83.....	68	87	99	...	...	...	...
40......	92	86	90	...	...	...	...	84.....	68	86	103	...	...	...	...
41......	89	86	87	...	...	...	...	85.....	62	85	96	...	...	...	...
42......	95	88	76	...	...	...	...	86.....	62	82	96	...	...	...	...
43......	94	89	92	...	...	...	...	87.....	60	77	100	...	...	...	...
44......	91	94	101	...	...	...	...	88.....	52	77	75	...	...	...	...
45......	93	91	93	...	...	...	...	89.....	55	...	...	...	...	...	...

TABLE 1—*Continued*

	Centrum L	Centrum H	Centrum B	Spine AP	Spine H	Rib AP	Rib L		Centrum L	Centrum H	Centrum B	Spine AP	Spine H	Rib AP	Rib L
90	55	...	...	...	...	...	...	97	46	...	...	...	...	...	...
91	60	...	...	...	...	...	...	98	45	...	...	...	...	...	...
92	57	...	...	...	...	...	...	99	48	70	81	...	...	...	...
93	51	...	...	...	...	...	...	100	48	68	85	...	...	...	...
94	48	...	...	...	...	...	...	101	53	66	80	...	...	...	...
95	38	...	...	...	...	...	...	102	49	60	73	...	...	...	...
96	50	72	85	...	...	...	...								

TABLE 2

HYDROTHEROSAURUS ALEXANDRAE, TYPE

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. U. C. MUS. PAL. NO. 33912

RIGHT SCAPULA

Greatest length	27
From midline to notch of dorsal process	28
Width of horizontal neck	7.8
Width of dorsal process	7
Length of dorsal process above notch	15
Greatest anteromedial diameter from coracoid suture	33.5
Glenoid portion	7.5
Length of coracoid suture	10

RIGHT CORACOID

Greatest length	50
Length of midline suture	14
Length of scapular suture	11.5
Glenoid portion	9
Greatest width	28.5
Width at anterior end of scapular suture	15
Width of posterior expansion	21.6
Width of shaft	10
Length from distal external border to anterior external border	28.1

RIGHT HUMERUS

Anteroposterior proximally	13.5
Same distally	27
Greatest length	39
Length of shaft	36.6
Anteroposterior of shaft	12.2

RIGHT RADIUS

Length	11
Width	14.6

RIGHT ULNA

Length	8.8
Width	12.3

RIGHT RADIALE

Length	7.3
Width	10.3

RIGHT INTERMEDIUM

Length	8
Width	9.7

RIGHT ULNARE

Length	7.5
Width	8

RIGHT ILIUM

Length	230
Anteroposterior proximally	50
Same distally	80
Width	45

RIGHT PUBIS

Anteroposterior length	36.5
Greatest width	35
Length of midline suture	24.5
Greatest diameter (anterolaterally)	39.5

(*Table 2 continued on p. 152*)

TABLE 2—*Continued*

RIGHT ISCHIUM			
Anteroposterior proximally	130	Same, shaft	8.7
Same distally	24.5	Transverse from midline	27
RIGHT FEMUR			
Length	36	Same distally	23.7
Anteroposterior proximally	12	Thickness proximally	10.5
Same, shaft	8	Same distally	6
RIGHT TIBIA			
Length	9	Thickness	5
Width	12		
RIGHT FIBULA			
Length	8.6	Thickness	4.6
Width	12		

articulated skeleton of *Plesiosaurus guilelmi imperatoris* (Fraas, 1910, pl. 6) was preserved with a 90° dorsal flexion for 18 of the anterior cervical vertebrae. This indicated a movement of 5° between consecutive vertebrae, as estimated by Zarnik, but only half of that estimated for *Hydrotherosaurus*. *P. conybeari* (Sollas, 1881, pl. 23) is flexed only 50° for the anterior 16 vertebrae, or 3° between centra. *P. brachycephalus* (*op. cit.*, pl. 24) bends 150° for 29 anterior cervicals, almost the entire neck, or again about 5° between centra.

The Denver specimen described below lay with the snout about 25 cm. from the 24th vertebra. The neck was smoothly flexed 180° in a dorsal direction for the 24 anterior cervicals, or 7½° between centra. *Hydrotherosaurus* was buried with a relatively straight neck, the total curvature being under 90°. The burial attitude has thus varied considerably, but it indicates that much flexion was possible.

The bodies of plesiosaurs have been compared to turtles. Perhaps this is because they have usually been found crushed out of shape and flattened. The restoration shown in the frontispiece was made by William Gordon Huff from measurements and cross sections of the restored skeleton (fig. 11). The widths of the girdles are probably accurate indications of the width of the animal, but a further check was made by a study of the ribs. Judging by the facets on the transverse processes of *Hydrotherosaurus*, the anterior dorsal ribs project backward about 30°, then, about 14 cm. out, they bend another 30° posteriorly and continue in a nearly straight line (fig. 12). The resulting animal is more slender and streamlined than is shown in older restorations.

Material in the Colorado Museum of Natural History

Thalassomedon haningtoni n. gen. and sp.

The Cretaceous elasmosaur now on exhibit in the Colorado Museum of Natural History is the finest and largest specimen of its kind. It is distinct from known forms and is therefore described as *Thalassomedon haningtoni* n. gen. and sp. (θαλασσόμεδον—lord of the sea). The specific name is in honor of Charles H. Hanington, president of the Colorado Museum of Natural History.

Type.—A nearly complete skeleton, C. M. N. H. no. 1588, consisting of skull, complete vertebral column, several ribs and gastralia; clavicular arch; anterior plate and dorsal process of the left scapula; left humerus, radius and ulna, both pubes, ischia, and one ilium, both femora, left tibia, fibula, and a complete pelvic paddle.

Type locality.—Quoted from a report by H. C. Markman, Curator of Geology, C. M. N. H., "On a small, intermittent and unnamed creek in northwestern Baca County, Colorado; E. ½ of Sec. 31, T 28 S., R 48 W.; 13½ miles N. of the town of Pritchett."

Age.—Graneros shales, lowest formation of the Benton Group, lower Upper Cretaceous.

Diagnosis.—A large elasmosaur, total length 11.6 meters, with large pineal foramen and small nares and orbits, the orbits in the anterior half of the skull. Mandibular symphysis sloping gently posteriorly; teeth, 8+ above and 16 below. Postfrontal greatly reduced, quadrojugal large, jugal excluded from orbit, prefrontal large, meeting postorbital. Parietal crest high and very narrow. Vertebrae, 114 divisible into 62 cervicals, 3 pectorals, 25 dorsals, 3 sacrals, and 21 caudals. Entire column strongly depressed, posterior cervicals and dorsals larger than any other known form. Pectorals without extremely compressed rib facets. Caudals with chevron facets only on posterior ends of centra. Interclavicle fused to clavicles, without clavicular foramen. Scapula with dorsal process broad below and narrow above; scapulae not fused in midline, but meeting with straight medial longitudinal borders. Coracoid not projecting anterior to glenoid, anterior border strongly concave. Pectoral and pelvic girdles without median longitudinal bar. Humerus slender, no groove separating capitulum and trochanter, distal breadth 66 per cent of length. Pubis convex anteriorly and with subequal lateral and posterior concavities, ischium very broad posteriorly, ilium with massive, subcircular base. Femur pendulous, distal breadth 58 per cent of length, no groove separating capitulum and trochanter, tibial facet twice as long as fibular. Second row of tarsal elements consisting of four tarsalia and metatarsal V.

Geology.—Quoted from report by H. C. Markman:

The skeleton was found near the top of the dark Graneros shales, lowermost formation of the Benton group in southeastern Colorado. Complete sections of the Benton formation are nowhere exposed in the Pritchett region and contacts usually are concealed. Typical Graneros shales, and outcroppings of the overlying Greenhorn beds, however, may be observed in several localities within a radius of a few miles surrounding the discovery site.

The skeleton rested 4 feet above the bed of the creek in a 20-foot cliff of shale showing little variation except in the matter of coloring due to iron oxide stains on weathered surfaces. When freshly exposed, the shales are mottled, bluish to brownish gray, streaked with brown and yellow. Occasionally interbedded are thin layers of white clay or bentonite, and small scales of selenite are more or less abundant at various levels.

Near the top of the cliff, there is a 1-foot bed of white clay, and above this, 10 feet of thinly bedded limestones with some sandy and shaly material irregularly intermingled.

The nearest exposure of undisturbed overlying rock lies 2,100 feet to the east, where thin limestones alternate regularly with slightly thicker beds of bluish gray shales. These beds are 52 feet above the rocks capping the cliff, and since there is no appreciable dip, this figure represents the approximate thickness of the intervening shales. The latter are weathered to a considerable depth and contain much sand. The gently sloping surface is an old one, part of which has been under cultivation, and is no doubt modified to some extent by drifting soil. The essential ingredient, however, is a bluish clay.

The uppermost limestones (referred to in the paragraph above) are bluish to brownish gray, weathering to almost creamy white, and showing a marked tendency to split vertically into small, clean-cut slabs. On Plum Creek, 10 miles south of the plesiosaur locality, there is a much larger exposure of similar limestones interbedded with shales. Here the uppermost 35 or more feet of the section contains prominent layers of thin limestones appearing at intervals of 2 to 3 or 4 feet, and forming terraced slopes on the local hillsides. Near the base of this series, the limestones become somewhat heavier, the thickest measuring 11 inches, with intervening shale beds measuring up to 6 feet or more. Vertical parting occurs in the thicker limestones. Under the lowest limestones and continuing below the creek bottom are 12 feet of paper-thin, gray shales.

It is evident that the Plum Creek exposure reveals most, if not all, of the Greenhorn beds (compare sections published in U. S. G. S. Folios 36 and 186, Pueblo and Apishapa quadrangles, respectively) as well as the upper shales of the Graneros. Thin limestones resting just above water level half a mile up the creek from the plesiosaur excavation check closely with some of the lower limestones of the Plum Creek locality and indicate a continuation toward the outcrop to the east of the quarry, which accordingly has been referred to the Greenhorn.

SECTION AT PLESIOSAUR EXCAVATION

FEET	
(?)	Thin limestones alternating with thin beds of clay, exposed for some distance over a low, rolling area, 2,100 feet east of the fossil diggings. (Base of the Greenhorn.)
52	Soil-covered slope consisting largely of bluish or grayish clay. (Upper shales of the Graneros.)
4	Thin layers of limestone, varying in purity and character of bedding, partly sandy and iron-stained, thinly and irregularly interbedded with light gray to yellow clays. This member is sufficiently durable to form a cap rock temporarily protecting the underlying wall of shales.
1	Thin-bedded, purplish gray limestone, weathering light brown.
4	Yellow and light gray shales.
1	White clay.
20	Bluish to brownish gray shales with yellowish, blackish, and white streaks irregularly distributed throughout the face of the cliff. The creek bed forms the base of the section and the probable total thickness of these shales could not be determined from any exposures examined elsewhere. (Plesiosaur skeleton 4 feet above creek bed.)

Preparation was carried on by Mr. Reinheimer and Mr. Landberg; the missing parts were restored and the mount was nearly completed at the time of my visit in May, 1940.

Skull.—The skull lay upon its left side, the neck flexed dorsally so that the tip of the snout was about 25 cm. from the 24th vertebra. Although well preserved, the skull was rather badly compressed, the dentaries broken just behind the symphysis. The palate is hidden, the quadrate regions broken, and the postorbital arch so crushed that many sutures are indeterminable. From the condyle to the alveolar border of the premaxillary, it measures 47 cm. As restored (fig. 13), it is 60 cm. long from rostral tip to quadrate, 19 cm. high from quadrate to parietal crest, and 21 cm. wide across the maxillaries. Its size and shape are similar to those of the skull figured by Williston (1890 and 1903) as *Cimoliasaurus snowii*, but Williston's specimen is smaller, the lower jaw being 48 cm. as opposed to 57 cm. in the Denver form. The orbit of the Denver specimen is smaller than Williston's form, and the parietal crest is lower and longer in the former.

The rostral region is depressed, and the orbital region is compressed and broken to the left. The skull is rather badly crushed and I have not been able to distinguish with certainty the breaks from the sutures. Two alternative interpretations are presented. I prefer the one shown in the complete restoration (fig. 13, *b*).

Premaxillary.—The premaxillaries are fused into a solid beak with a thin dorsal central ridge. The anterior tip bears no median teeth but is bent downward into a bony hook. The premaxillary certainly extends to opposite the front of the naris. Behind this an element reaches back almost half the skull length to meet the parietal above the center of the orbit. This element is either a nasal or a continuation of the premaxillary. I do not think it is premaxillary, because the premaxillary evidently extends above the naris between the lacrimal, prefrontal, and frontal, to be separated from the element in question by an anterior extension of the frontal. This, then, leaves a slender nasal lying along the midline between the frontals and extending from premaxillary to parietal.

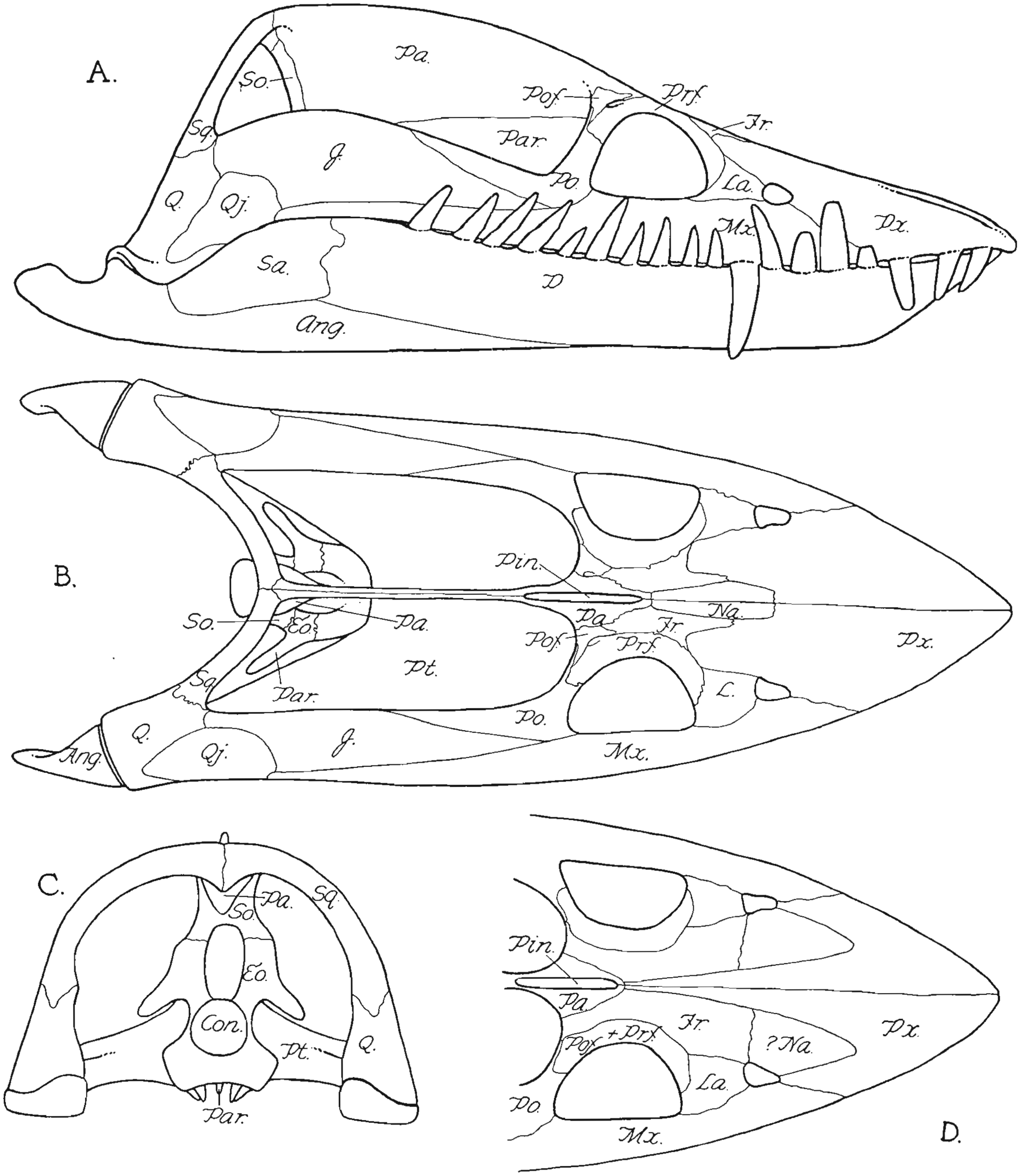

Fig. 13. *Thalassomedon haningtoni*, type. Reconstruction of skull. *a*. Right lateral view. *b*. Dorsal view. *c*. Posterior view. *d*. Possible alternative arrangement of sutures in front of skull. C.M.N.H. no. 1588. × ¼

The left maxillary is pulled away from the premaxillary, so the suture is open. The right suture is closed, but runs in a corresponding direction from a little in front of the naris to behind the fourth tooth.

In the alternative interpretation the premaxillary lies mediad to the frontal. It is improbable that the premaxillary could be excluded from the naris, yet the alternative is shown as a possibility.

Nasal.—I am still puzzled by a triangular depression above the naris. This depression is the real basis for the double interpretation of this region. It might consist of a nasal sunk into the skull, yet it would be more natural if it were formed entirely by the premaxillary, with the nasal restricted to a slender midline element. If the depression is all nasal, it separates the premaxillary from the naris—an unlikely condition. If premaxillary, it is separated from the frontal by a smooth round rim that seems to be a natural separation, and it forms the front and upper border of the naris.

This interpretation leaves the slender median element as nasal, and a more normal relationship results.

Frontal.—Separated from the midline by the nasal (or premaxillary), this element lies between the parietal, premaxillary, and fused prefrontal and postfrontal.

I am fairly certain of the sutures with ? nasal, parietal, prefrontal, and postfrontal, as they have a normal interdigitating pattern. That with the premaxillary is not typical, but is smooth and rounded in outline. It probably delimits the anterior border of the frontal, separating it from the premaxillary, yet this anterior element could be the nasal and the ? nasal the premaxillary.

Parietals.—The parietals form the posterior half of the skull roof. They meet the ? nasals in front of the long pineal suture, and the frontals and postfrontals in the upper anterior corner of the temporal fossa. Behind this they are fused into a long, high, very thin parietal crest. This crest is 3 mm. wide and 76 mm. high at its greatest height. Posteriorly the parietal meets the squamosal and the supraoccipital.

In posterior view the parietals appear as an inverted triangle between two projections (? of the supraoccipital) that run dorsally to meet the squamosals. The apex of the triangle lies about 3 cm. above the foramen magnum.

Squamosal.—The squamosal is not the triradiate bone shown in practically all previous reconstructions, but a curved bar that meets its opposite, the parietal, and the ? supraoccipital, in the midline above, and the quadrate and jugal below. Its lower end is expanded at the quadrate suture. Its upper and outer surface is rugose, its posterior surface smooth.

Lacrimal.—This is a small bone similar to that of *Hydrotherosaurus*. It rests upon the maxillary, and forms the posterior border of the naris and the base of the orbitonasal bar. Its dorsal margin is wedged between the premaxillary (or nasal) and the prefrontal.

Maxillary.—The maxillary meets the premaxillary in a suture running from naris to fourth tooth. It then underlies the naris, lacrimal, orbit, postorbital, and jugal, to terminate in a blunt process lateral to the anterior tip of the quadratojugal. It thus forms the lower border of the temporal arch.

Prefrontal.—The prefrontal rests upon the lacrimal in front and the postorbital behind. It may actually represent the fused prefrontal and postfrontal; yet lying between this and the posterior part of the frontal is another bone, which I take to be the postfrontal. The prefrontal meets the ? premaxillary and the frontal and forms the dorsal border of the orbit.

Postfrontal.—On the right side a small triangular element lies between the posterior end of the frontal and prefrontal. It extends down to the dorsal tip of the postorbital. If this element is a separate ossification it must be the postfrontal. If not, it could be a fragment of the frontal or the element I have called prefrontal. In this event my prefrontal would then represent the fused prefrontal and postfrontal. However, the element in question seems to be a distinct entity and therefore the postfrontal.

Postorbital.—This bone is typically elasmosaurian, forming the lower half of the postorbital bar and running posteriorly along the temporal arch. It meets the prefrontal and postfrontal above, the maxillary and jugal below.

Jugal.—The temporal arch is crushed on both sides. I have spent many hours with the dissecting microscope cleaning and studying this region, and I am fairly certain of all the sutures except that between the squamosal and the quadrate.

The jugal is a broad, thin bone wedged between the postorbital and maxillary anteriorly. Posteriorly it lies against the squamosal for most of its width. Below and behind lies the quadratojugal, while the posteroventral corner of the jugal may just reach the quadrate.

Quadratojugal.—Clearly inserted into a notch on the lower external side of the quadrate, the tip of the quadratojugal can be seen on both sides of this specimen and on the C.I.T. juvenile. The quadratojugal runs anterodorsally in front of the quadrate to meet the jugal and be overlapped by the maxillary.

Quadrate.—The broad, round condyle inserts deeply into the articular. Above lies the squamosal, separated by a suture that runs ventromedially from the thickened lower tip of the squamosal. The quadrate thus overlaps the squamosal, but it may also have a small internal process. If so, the squamosal inserts into a notch in the quadrate.

Internally the pterygoid forms a firm union and support just above the condyle.

The quadrate is sometimes found split into external and internal condyles; so, at least, in *Tricleidus seeleyi* and in the present specimen. As Andrews (1910, p. 156) suggested, I was at first inclined to consider these quadrate and quadratojugal, but the definite occurrence of the quadratojugal as outlined above precludes this possibility. The explanation apparently lies in the fact that the condyle is broad, and the articular has a sharp process projecting posteriorly into the sulcus, from the center of the anterior border of this sulcus. It also has a longitudinal ridge along the floor of the sulcus. Therefore any pressure, either vertical or anterior, upon the quadrate would cause the articular to wedge into it and split it into external and internal halves.

Posterior part of skull.—This region is crushed and partly covered and consequently cannot be described in detail. The condyle is nearly circular, but is not hemispherical as it is shallow anteroposteriorly. Below lie two short, massive tuberosities and below and in front of the center of these may be seen the ventral edge of the parasphenoid. I cannot find any suture with the exoccipital. The paroccipital process is short and tapers laterally. It is not very massive and could not have reached the squamosal.

The supraoccipitals are displaced with the parietals. They evidently were paired as in "*Cimoliasaurus*" *snowii* and *Dolichorhynchops* and roofed the high, narrow, foramen magnum. Each also sends a process dorsally lateral to the parietal to meet the squamosal.

This dorsal process is unusual and might be but the broken edge of the parietal, yet both sides are symmetrical. The beginnings of similar processes are shown on *Hydrotherosaurus*, but they do not meet the squamosals.

The exoccipitals form a long deep trough that is roofed by supraoccipital and parietals. The floor must be the basioccipital and basisphenoid, continued anteriorly by the parasphenoid. This latter may be represented by a large bone lying beneath the parietals. It terminates a little in front of the exoccipitals, but the anterior region just behind the orbits cannot be delineated.

Dentition.—Below the antorbital bar is a large caniniform tooth. In front of this the teeth are large and about equal in size in upper and lower jaws. Behind it both upper and lower teeth are considerably smaller. The upper teeth are practically confined to the anterior region, with but a few small remnants lying in the posterior part of the maxillary.

The posterior dentary teeth slant upwards and forwards as though to impale their prey by a forward thrust of the head.

In the premaxillary are four large teeth, but there is no central tooth. Instead, the bone curves downward into a rounded beak between the two anterior dentary teeth. If central teeth had been present, we would find the usual five premaxillary teeth. Here a reduction has obviously taken place. On the right side the maxillary teeth include the large caniniform tooth and but two small remnants behind it. There are thus but seven teeth on the right side of the upper jaw. The left premaxillary has two teeth and two empty alveoli. The maxillary has four teeth and at least three empty alveoli. The total for the right side of the upper jaw was therefore eleven teeth.

On the right dentary are fourteen teeth. The four in front of the caniniform tooth are large and they alternate with those in the premaxillary. The ten behind are smaller and evenly spaced without any intercalation of maxillary teeth.

As mentioned above in discussion of the dentition of *Hydrotherosaurus*, I believe that the spacing of the teeth, and perhaps their size, is determined by the occurrence of preëxisting occluding teeth.

The large caniniform tooth is interesting, for, as pointed out by Owen (1865), it is usually found only in the short-necked plesiosaurs.

Vertebrae.—The column (pl. 22) is complete; 11.3 meters long as mounted, consisting of 114 vertebrae. There are 62 cervicals including the fused atlas and axis, 3 pectorals, 25 dorsals, 3 sacrals, and 21 caudals, one of which was restored. The entire series is strongly depressed and the posterior cervicals and dorsals are larger than any known form, exceeding even *E. sternbergi* Williston.

The atlas and axis are so tightly fused that the sutures are obscured. They are higher than broad. There is no atlantal spine, but that of the axis slopes about 45° posteriorly, and the small, fused ribs of both slope backward about the same amount.

The anterior cervicals are strongly depressed and have a high neural canal. The pedicel is as high as the spine and the zygapophyses lie halfway up to the summit. The spine begins above the center of the centrum and slopes steeply backward. There is a prominent separation of the articulating face from the body of some of the centra, resulting in the "disc" that Leidy considered so distinctive. The lateral longitudinal ridge is prominent back to the 13th, but weakens posteriorly, disappearing on the 47th. As it vanishes it assumes a more ventral position. The sides of the centra are strongly concave so that on the 24th the breadth at the center is only half that of the articulating face. From the 17th to the 41st the centra are longer than broad, but they are never so elongate as in *E. platyurus* Cope. The other cervicals are broader than long and, except the last three, longer than high.

The spines of the median cervicals are farther forward on the centra. The pedicels are as high as those in front, but the spines have elongated so that their height above the zygapophyses is about equal to that of the centra. The spines project almost vertically and at the summits they incline forward. The summits are square and slope anteriorly.

The posterior cervicals have increasingly higher spines and rounder summits. The breadth relative to the height of the centra increases from 106:100 on the 39th to 153:100 on the 61st; yet the posterior centra are actually shorter. The 48th to 54th have the longest centra of the entire column.

The pectorals are not sharply differentiated, but are thought to be the 63d, 64th, and 65th. Here the rib facets climb from the ventrolateral border to high on the side of the centrum, and the facets seem to be formed partly by the diapophysis and partly by the centrum. The last pectoral has a slightly compressed rib facet, contrasting with the California forms in which the first pectoral facet is strongly compressed. There is no sign of the buttresses that are developed on the rib facets of *Hydrotherosaurus*. The centra are strongly depressed, the breadth to height being as 152 to 100. The spines are similar to those of the posterior cervicals, differing only in increased height.

The 1st dorsal is the broadest of the entire column, although the greatest height is attained by the 8th and 9th (73d and 74th). The transverse processes project upward about 30° and terminate in expanded knobs. Only in the median dorsals are the diapophyses free of the centra and even these are not entirely so. The transverse processes are short and almost round in section and not long and depressed as in the California forms.

The sacrals, 91, 92, and 93, have very large rib facets that occupy almost the entire lateral faces of the centra. They are only slightly different from the anterior caudals, and in these regions the breadth to length ratio becomes the greatest, 2 to 1. The spines become quite round on top and have concave posterior and slightly convex anterior edges.

The caudals are all very short and become less depressed posteriorly, until on the last two centra the height exceeds the breadth. Chevron facets begin on the 1st caudal and are situated only on the posterior end of the centrum. The last rib appears to be on the 8th caudal, or 101st vertebra, where it is a tiny knob fused to the side of the centrum.

Clavicular arch.—The elasmosaur interclavicle was first figured by Pravoslavleff (1916, pl. 16, fig. 49; and 1916*a*, pl. 1, fig. 1). It is represented as a weathered triangular element with a deep ventral keel that becomes shallower posteriorly. There can be no doubt that Pravoslavleff has correctly identified his specimen, but the outlines of the bone are lost. The Denver specimen (pl. 23 and fig. 14) is perfectly preserved and is very much like the Russian form, showing a concave dorsal surface and a strong keel on the ventral surface that projects anteriorly into a short, stout cone. The clavicles are tightly fused to the visceral surface of the interclavicle, but the separation is clear on the left side.

The clavicular arch was displaced in the skeleton, and the interclavicle pointed posteriorly. This I reversed and restored with the interclavicle forward.

Scapula.—This is represented only by the horizontal plate and dorsal process of the left side. The former has an anteroexternal angle of about 90° and a straight midline with no sign of fusion to the right scapula. There is no indication of a median bar joining scapulae and coracoids, nor is the ventral plate separated from the dorsal process by a projecting shelf as in *Hydrotherosaurus.* The dorsal process is very broad anteroposteriorly, its width decreasing sharply about halfway from the base to the summit. Since

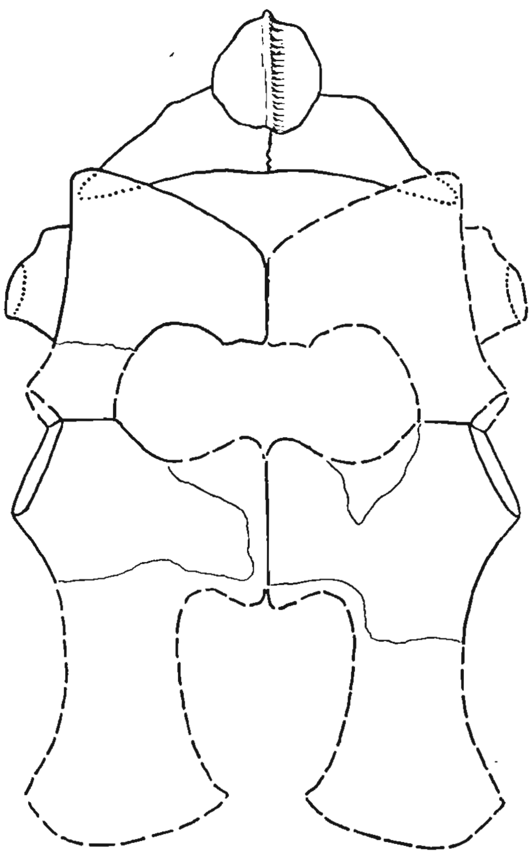

Fig. 14. *Thalassomedon haningtoni,* type. Ventral view of pectrum. C. M. N. H. no. 1588 × 1/12.

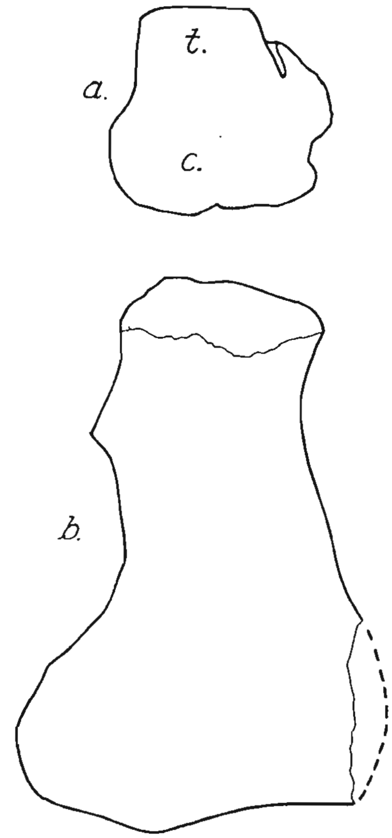

Fig. 15. *Thalassomedon haningtoni,* type. *a.* Proximal end of left humerus. *b.* Internal view of left humerus. C. M. N. H. no. 1588. × 1/6.

it is assumed that these broad dorsal processes must fit into the narrowing chest of the animal, the scapulae are restored close together in the midline.

Coracoid.—The critical posterior extension is missing, so the shape of the intercoracoid vacuity is unknown. The midline is massive and lies behind the glenoid; there is no indication of its continuation toward the scapula. There is a transverse ridge on the ventral surface which lies in the posterior half of the median plate. The anterior border is thin and concave. The articulating surface for the scapula is smooth, as is the glenoid portion, and devoid of the cones found in *Hydrotherosaurus.* This may mean that the Denver specimen is an adult and that the cartilage of this region had largely ossified.

Humerus,—The only brachial elements preserved are the left humerus, radius, and ulna (fig. 15). There is no groove on the humerus separating capitulum and trochanter as in *Hydrotherosaurus, Brancasaurus, Tremamesacleis platyclis,* and others. The antero-distal corner has been restored with a slight knee similar to that shown in Riggs' (1939) "*E. serpentinus.*" A prominent feature of the Denver specimen, setting it aside from the latter, is the great development of a posterior process (tuberosity of Andrews) one-fourth of the way down the shaft. The facets for radius and ulna are concave, that for the ulna being only three-fifths as large as the radial facet. In general proportion the humerus is slender, its distal breadth being only 66 per cent of its length.

Pelvis.—There are preserved the pubes, ischia, and one ilium (pls. 23 and 24). The pubis is convex anteriorly and slightly less so medially. It is about equally concave posterolaterally and posteromedially. There is no indication of a median bar joining pubes and ischia.

The median symphysis of the ischia is about the same length as that of the pubes. The anterior concavity is very pronounced and much stronger than the lateral. The outstanding feature of the ischium is the great lateral expansion posteriorly. The median sutures of both the pubes and the ischia indicate that the pelvis normally formed an open longitudinal trough. The ischial symphysis slopes upward posteriorly.

The acetabular end of the ilium is subcircular, its diameters 14 and 12 cm. (fig. 16). The larger diameter is anteroposterior. The proximal end is compressed longitudinally. The ilium is about as strongly convex laterally as that of *Hydrotherosaurus.*

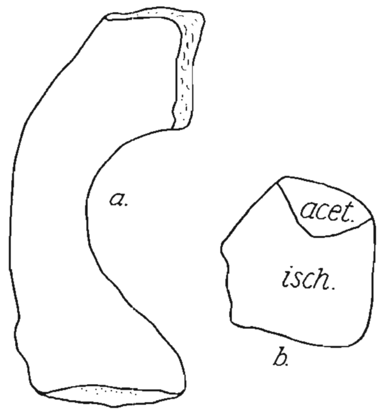

Fig. 16. *Thalassomedon haningtoni,* type. *a.* Posterior view of left ilium. *b.* Distal end of right ilium showing large ischial and small acetabular facets. C. M. N. H. no. 1588. × 1/6.

Pelvic paddle.—The left paddle (pl. 24) was perfectly preserved in complete articulation. The femur has an unusual shape for an elasmosaur, the trochanter being larger than the capitulum and without a separating groove. The anterior and posterior concavities of the shaft are almost equal, and although there is a well-developed anterior "knee," there is an almost equally developed posterior knee. The whole femur is thus almost symmetrical in a longitudinal plane, like that of a short-necked plesiosaur. The principal departure from this symmetry lies in the much greater size of the tibial facet as compared with the fibular, the former being twice as large. The distal breadth is about 58 per cent of the length, indicating a relatively slender femur.

The tibia and fibula are more elongate than in later forms. The tibiale, intermedium, and fibulare form the widest part of the paddle and there is no trace of supernumerary ossification. The tarsalia differ from all known elasmosaurs in being four in number. Posterior to these lies the 5th metatarsal, making 5 bones in this row rather than the usual 4. There can be no question about this, nor does it appear to be an abnormality, as it is the same in both tarsi. Metatarsal V has moved completely into the tarsal row and is but slightly longer than tarsal 4. There are 10 phalanges in the 1st digit, 12 in the 2d and 3d, and 11 in the 4th and 5th.

Comments.—This is the third longest known elasmosaur, exceeded only by the Kansan *Elasmosaurus platyurus* and the Russian *E. amalitskii.* The individual vertebrae attain a larger size than any previously recorded. *Thalassomedon* resembles the form described below as *Aphrosaurus* in lacking the separation of capitulum and trochanter of the propodials, but differs in lacking the small anterior concavity of the pubis and the grooved posterior cervicals. The skull of *Thalassomedon* is similar to *E. snowii* Williston, but the vertebrae of the Kansas specimen, although about 60 per cent as long as *Thalassomedon* in cervicals 3 and 4, increase to 100 per cent in cervicals 6 and 9, to 110 per cent in 14, and decrease to only 87 per cent in 27. Table 3 illustrates the different rate of increase of the cervical centra in the two forms.

TABLE 3

COMPARISON OF ANTERIOR CERVICAL CENTRA OF THALASSOMEDON (C.), AND THE SPECIMEN DESCRIBED BY WILLISTON AS ELASMOSAURUS SNOWII (K.)

[MEASUREMENTS IN MILLIMETERS]

	3		4		6		9		14		20		27	
	C	K	C	K	C	K	C	K	C	K	C	K	C	K
L	38	23	47	30	47	48	54	53	57	63	79	78	103	90
H	44	25	50	27	45	42	46	44	54	50	63	60	73	68
L:H index	115	110	107	90	96	87	85	83	93	79	80	77	70	76

TABLE 4

THALASSOMEDON HANINGTONI, TYPE

MEASUREMENTS OF AXIAL SKELETON IN MILLIMETERS. C. M. N. H. NO. 1588

	Centrum			Spine		Rib			Centrum			Spine		Rib	
	L	H	B	AP	H	AP	L		L	H	B	AP	H	AP	L
1 and 2	77	51	46	91	61	72	70	21	87	66	85	...	...	...	...
3	38	44	41	63	50	...	...	22	87	79	87	87	78	...	...
4	47	50	55	54	54	...	...	23	97	72	86	95	83	...	...
5	44	43	55	55	62	...	...	24	97	73	87	103	86	...	...
6	47	45	67	64	59	...	...	25	90	77	90	91	102	...	...
7	54	39	60	62	64	...	...	26	95	74	84	80	103	...	...
8	46	46	70	67	62	...	...	27	103	73	83	94	95	...	...
9	54	46	67	58	56	...	...	28	105	73	100	80	96	...	...
10	56	50	68	52	55	...	...	29	104	79	95	84	...	...	...
11	54	50	67	54	52	...	...	30	105	83	93	101	117	...	...
12	57	54	63	...	...	...	...	31	105	?85	?85	100	115	...	...
13	58	52	67	...	...	...	...	32	110	95	90	95	120	...	...
14	57	54	74	52	55	...	...	33	115	82	97	105	130	...	...
15	65	56	75	53	60	...	...	34	117	85	103	100	135	...	...
16	62	58	79	59	77	...	...	35	123	81	102	105	140	...	...
17	63	59	83	64	75	...	...	36	118	88	102	107	145	...	...
18	72	67	82	76	78	...	...	37	122	85	109	119	150	...	...
19	80	62	80	83	82	...	...	38	125	97	113	105	155	...	...
20	79	63	82	72	82	...	...	39	123	105	112	112	155	...	...

TABLE 4—*Continued*

	Centrum			Spine		Rib			Centrum			Spine		Rib	
	L	H	B	AP	H	AP	L		L	H	B	AP	H	AP	L
40	122	102	110	121	170	...	...	78	100	133	160	95	280	...	...
41	137	105	134	119	175	...	...	79	100	123	155	95	280	...	...
42	127	110	137	109	175	...	...	80	100	120	142	90	275	...	...
43	132	112	143	110	180	...	...	81	100	120	138	85	260	...	...
44	129	111	142	116	180	...	...	82	98	110	137	85	260	...	...
45	134	114	142	122	183	...	...	83	85	110	140	90	250	...	...
46	131	116	145	115	180	...	...	84	80	105	137	90	245	...	...
47	137	117	151	110	190	...	...	85	85	110	135	90	245	...	...
48	140	127	155	110	195	...	...	86	100	105	130	90	...	...	...
49	135	119	163	120	200	...	...	87	90	105	140	85	...	...	...
50	130	127	160	120	205	...	...	88	85	103	147	80	...	...	...
51	?	117	160	115	205	...	...	89	80	103	150	80	...	...	...
52	120	117	172	112	225	...	...	90	80	105	145	75	...	...	...
53	130	124	165	105	230	...	...	91	75	109	150	75	...	...	...
54	140	124	167	117	220	...	...	92	75	105	148	75	...	...	...
55	136	119	165	125	225	...	...	93	75	105	145	75	...	...	...
56	130	128	183	110	255	...	...	94	75	105	150	75	...	...	...
57	136	126	180	110	260	...	...	95	75	100	135	70	...	...	...
58	123	127	170	110	250	...	...	96	75	105	137	65	...	...	...
59	115	130	170	115	260	...	...	97	70	100	128	65	...	...	...
60	113	125	185	105	270	...	...	98	70	100	120	65	...	...	...
61	110	123	188	90	280	...	...	99	70	100	128	65	...	...	...
62	110	130	192	95	280	...	...	100	70	100	125	60	...	...	...
63	113	120	185	105	280	...	...	101	65	100	116	60	...	...	...
64	110	125	190	105	270	...	...	102	65	90	113	...	...	...	...
65	115	120	185	105	...	...	...	103	60	90	118	...	...	...	...
66	120	130	200	...	...	...	...	104	68	95	110	...	...	...	...
67	120	130	183	...	...	...	...	105	65	90	108	...	...	...	...
68	115	135	175	92	310	...	...	106	60	90	103	...	...	...	...
69	115	135	163	...	310	...	...	107	53	80	98	...	...	...	...
70	115	140	167	...	295	...	...	108	50	75	85	...	...	...	...
71	115	150	165	...	285	...	...	109	52	65	75	...	...	...	...
72	120	143	170	100	280	...	...	110	50	55	65	40	50	...	...
73	100	145	162	100	275	...	...	111	43	45	56	40	43	...	...
74	105	145	165	...	280	...	...	112	30	40	45	35	25	...	...
75	105	?	165	...	?	...	...	113	30	40	25	30	30	...	...
76	100	143	160	95	280	...	...	114	20	25?	13	...	...	...	...
77	107	143	165	100	285	...	...								

TABLE 5

THALASSOMEDON HANINGTONI, TYPE

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. C. M. N. H. NO. 1588

INTERCLAVICLE			
Length	18	Thickness at keel	7.5
Width	16		
CLAVICLES			
Total width of both	57	Length in midline behind interclavicle	8
Arch of posterior concavity	5.5		
RIGHT CORACOID			
Greatest length (reconstructed 65.5)	43	Length of midline suture	29
LEFT SCAPULA			
Length in midline	14	Width of horizontal neck	12
Width at front of midline border	33	Width of dorsal process	18
Width from midline to notch of dorsal process	34	Height of dorsal process above notch	24
LEFT HUMERUS			
Anteroposterior proximally	16+	Greatest length	44
Same distally	29	Anteroposterior of shaft	14.5
LEFT RADIUS			
Length	13	Width	16
LEFT ULNA			
Length	10.5	Width	12
RIGHT PUBIS			
Anteroposterior parallel to midline	49	Greatest diameter (anterolaterally)	57
Greatest width	48	Anteromedial diameter	53
Length of midline suture	25	Width of neck	23
RIGHT ISCHIUM			
Anteroposterior proximally	18	Same, shaft	13.5
Same distally	37	Transverse from midline	32
RIGHT FEMUR			
Length	44	Same, shaft	11.5
Anteroposterior proximally	17	Same distally	25.7
RIGHT TIBIA			
Length	11.5	Width	11.7

Material in the California Institute of Technology

The California Institute of Technology has collected additional reptilian remains from the Moreno formation near the *Hydrotherosaurus* locality (Stock, 1939). This material consists of parts of six skeletons; four are relatively complete, the other two are fragmentary. Three are juveniles, almost equal in size and about one-third as large as the remaining adults. Three genera and species may be recognized, all of which are apparently new. One specimen, C.I.T. 2754, is a series of adult vertebrae that is considered indeterminate.

The reference of a juvenile to the genus *Aphrosaurus* is almost certain, and its description is the first of the young of a determinable elasmosaur. The reference of another of the juveniles to the new genus *Morenosaurus* is not quite so certain, but seems best for the present.

Morenosaurus stocki n. gen. and sp.

The generic name refers to the formation yielding the fossils; the specific name is in honor of Dr. Chester Stock, who was responsible for their collection.

Type.—A fairly complete skeleton, C. I. T. no. 2802, lacking only the head, anterior part of the neck, and parts of the paddles.

Type locality.—C. I. T. 354, 2,400 ft. W. and 110 ft. S. of NE. cor. Sec. 11, T 14 S., R 11 E., M. D. B. and M. In the Panoche Hills, Fresno Co., 1½ mi. NNW. of U. C. loc. V3735 (see map, fig. 1).

Diagnosis.—2 pectorals, 17 dorsals, 3 sacrals, 30 caudals. Lateral longitudinal ridge on 18th and 17th prepectorals, vertebrae strongly depressed with deep median dorsal and ventral notches on the articulating faces, except in the dorsal series. Caudals with chevron facets equally developed on anterior and posterior ends of centra. Interclavicle weakly keeled and projecting slightly anteriorly. Clavicle with pronounced anterior shoulder, anterior border straight. Scapulae meeting in midline, projecting slightly posteriorly, but not meeting coracoids; dorsal process long and narrow, strong ridge separating ventral plate and dorsal process. Coracoids with long median symphysis projecting in front of glenoid; strongly concave anteriorly. Humerus with weak anterior knee and acute posterodistal border, distal breadth 78 per cent of length, radial and ulnar facets strongly concave, the radial larger; capitulum and trochanter completely separated by confluence of anterior and posterior grooves across head of humerus. Radius much larger than ulna, both concave medially. Anterior carpals and metacarpal with acute anteroproximal angles. Pubis broader than long, with slight posterior and shallower lateral concavities; anterior border with small central concavity. Ilium with subrounded acetabular region and sacral face transversely elongated. Ischium short and distally broad. Femur stocky, distal breadth 72 per cent of length, capitulum and trochanter almost separated by anterior and posterior grooves, trochanter inclining 65° to axis of shaft. Total length estimated at 8 meters.

The referred specimen indicates that the number of cervicals was 46 and the total vertebrae 99.

Vertebrae.—The vertebral column (pl. 25) consists of the 23 posterior cervicals, 2 pectorals, 17 dorsals, 3 sacrals, and 30 caudals. The first three of the series are the badly eroded 23d to 21st prepectorals. The 20th to 17th show a weak lateral longitudinal ridge which is absent on the last 16 cervicals. The centra are strongly depressed, the height of the articular face lessened by deep notches below the neural canal and above the ventral midline. Thus the height of the 11th, or 13th prepectoral, is 85 mm. in the midline and 98 mm. lateral to the notches. The lateral walls of the centra are deeply concave longitudinally, the rims of the articulating faces smooth. The rib facet is at the center of the ventrolateral edge in the anterior centra and assumes a more posterior position in the

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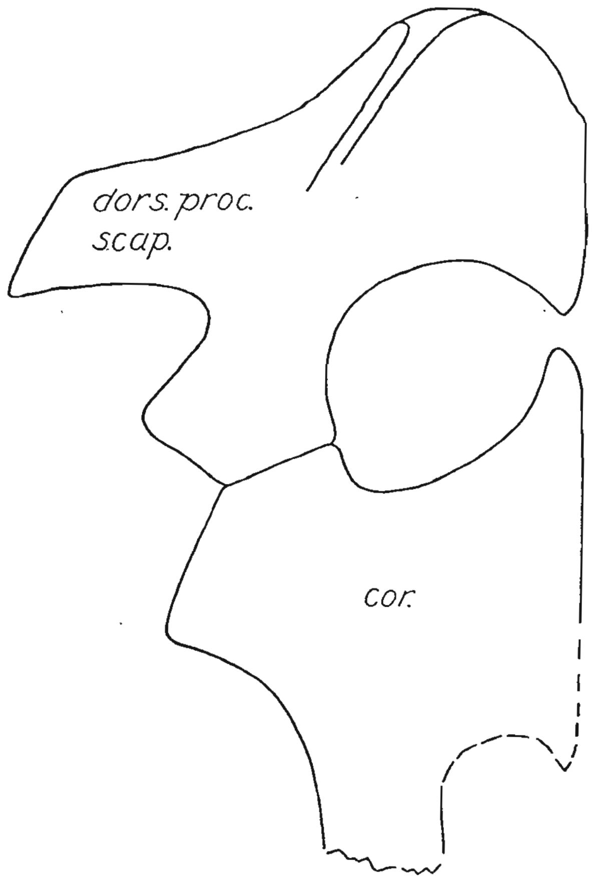

Fig. 18. *Morenosaurus stocki*, type. Ventral view of right scapula and anterior part of coracoid. C. I. T. no. 2802. × 1/6.

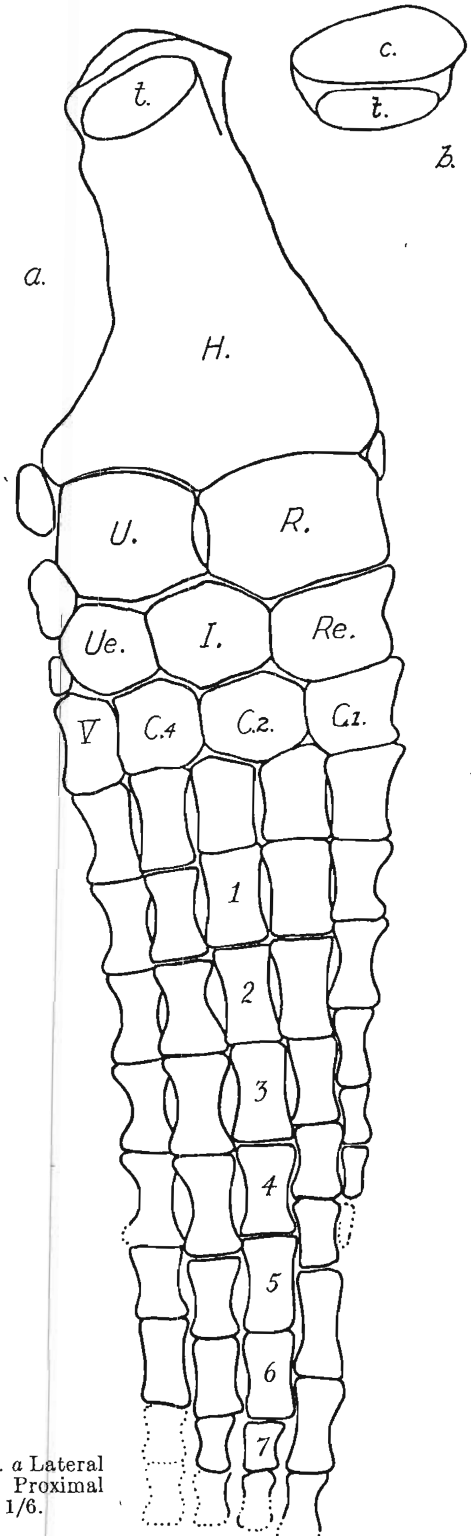

Fig. 19. *Morenosaurus stocki*, type. *a* Lateral view of right pectoral paddle. *b*. Proximal end of humerus. C. I. T. no. 2802. × 1/6.

it has a less well-developed anterior knee. The distal breadth is 78 per cent of the length. The radial facet is appreciably larger and less concave than the ulnar. The posterior distal expansion above the ulna is more pointed, sloping backward less steeply than in other forms. The trochanter is separated from the capitulum by the usual anterior and posterior grooves (fig. 19), but here the two grooves unite across the head of the humerus and effect a complete separation of the two articular surfaces. The face of the trochanter dips 15° posteriorly. A large rugosity, apparently for the insertion of the M. subscapularis, arises just below the capitulum on the posterior border of the shaft.

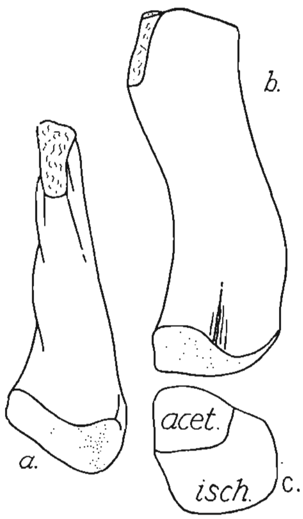

Fig. 20. *Morenosaurus stocki,* type. Left ilium. *a.* Internal. *b.* Anterior. *c.* Distal. C. I. T. no. 2802. × 1/6.

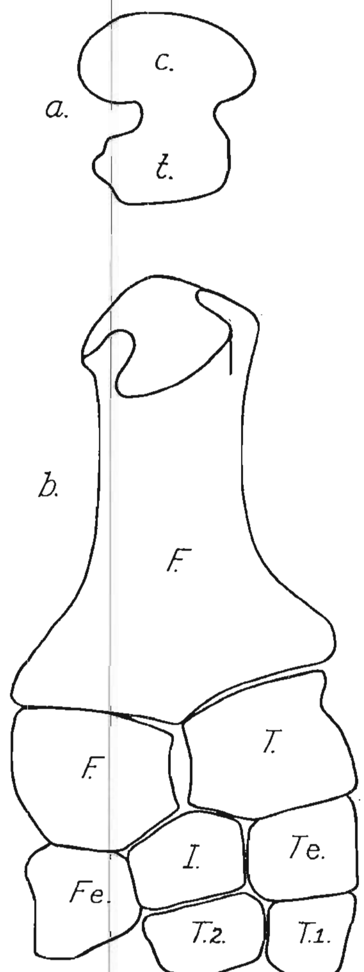

Fig. 21. *Morenosaurus stocki,* type. Right femur. *a.* Proximal view. *b.* Lateral view. C. I. T. no. 2802. × 1/6.

The radius is much larger than the ulna and both are concave medially, although less so than the Chicago specimen. Carpalia are of normal number and arrangement, but the anterior carpals and metacarpal are characterized by an acute anteroproximal angle. Supernumerary elements lie above and below the posterior border of the ulnare, and the ulna and the ulnare and 5th metacarpal have well-developed facets for their articulation. A tiny supernumerary ossicle lies between the anterior articulation of humerus and radius. The phalanges are articulated only proximally, their numbers being 6 on the 1st digit, and 4 on the 2d, 3d, 4th, and 5th. In addition, 3 phalanges are restored to the 3d and 4th, and 2 to the 5th digits. Even so, an almost equal number must have been lost. A characteristic feature is the great anteroposterior width of the elements of the first digit; and all the phalanges are extraordinarily wide.

Pelvis and pelvic paddle.—The pubes and ischia do not meet to form a midline bar (pl. 27). The pubis is broader than long, slightly concave posteriorly, less so laterally, and has a small anterior concavity. The anterointernal border is also concave, but this is probably due to crushing against an underlying centrum.

The ischium is short along the midline and widely expanded posteriorly as in the Denver specimen. The median symphysis is well preserved and indicates that the ischia met to form an open basin of 130°.

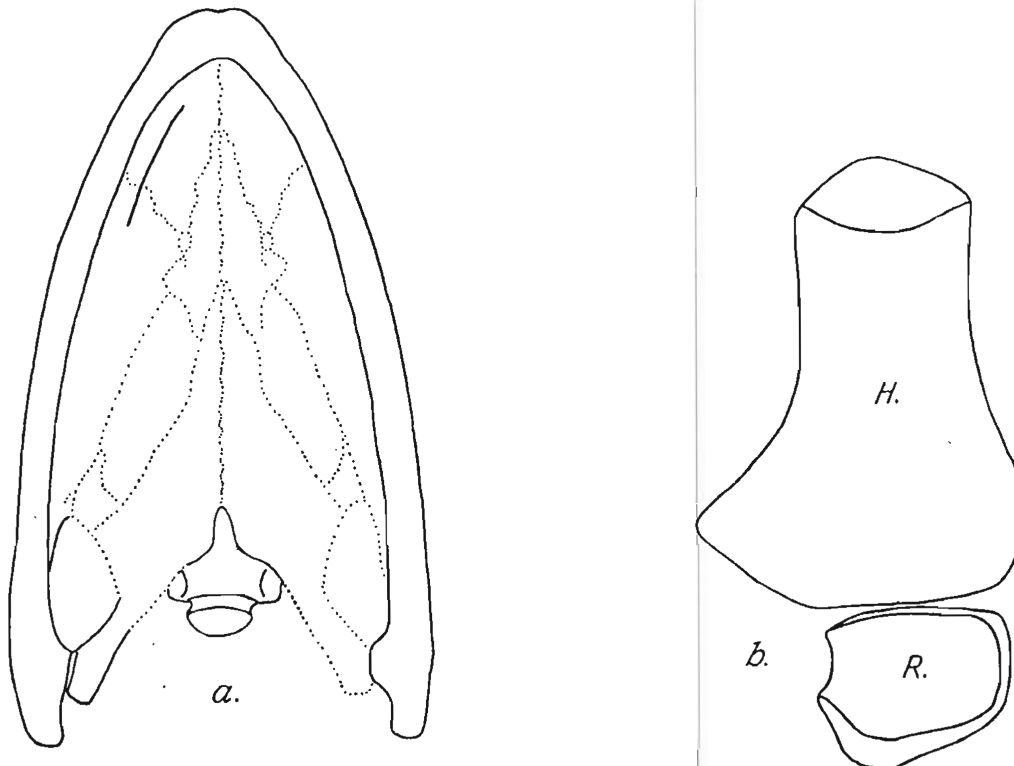

Fig. 22. *Morenosaurus stocki*, referred. *a*. Palate and jaws. *b*. Right humerus and radius. C. I. T. no. 2749. × ⅓. The palate was restored to show outline of jaws and position of condyle. It should also show vacuities.

The ilium (fig. 20) is uncrushed on the left side. Its distal end is subrounded, slightly wider than long. The greater part of its surface articulates with the ischium and but a small part, the narrower anterior portion, enters into the formation of the acetabulum. The proximal end is longitudinally compressed and the rough surface is carried across the head, then, after a right angle, down along the internal border of the shaft. The shape of the distal end indicates that the ilium sloped about 45° anteroventrally. The ilium is strongly arched laterally.

The femur (fig. 21) is characterized by the 30° posterior inclination of the trochanter, and by the deep grooves separating trochanter and capitulum. These grooves come within about 3 cm. of completely separating the articulating facets. The capitulum is almost hemispherical, but is elongate anteroposteriorly. The femur is massive and has a well-developed anterior knee. Its distal breadth is 72 per cent of its length. Facets for the tibia and fibula are slightly concave.

The fibula is larger in both dimensions than the tibia and both are slightly concave medially. The usual three proximal tarsals are present, while the distal row consists of the usual three tarsalia and the 5th metatarsal. A posterior supernumerary ossicle is indicated by facets on fibula and fibulare.

Referred specimen.—C. I. T. 2749, a juvenile consisting of a badly eroded skull, good jaws, the condyle, 46 cervical vertebrae, the first pectoral vertebra, the right pectoral paddle, and a scapular fragment (fig. 22).

Locality of referred specimen.—C. I. T. 337, 2500 ft. S. and 850 ft. W. of NE. cor. Sec. 25, T 14 S., R 11 E., M. D. B. and M. In the Panoche Hills, Fresno Co., Calif., 2¼ mi. SSW. of U. C. loc. V3735 (see map, fig. 1, p. 127).

TABLE 6

MORENOSAURUS STOCKI, TYPE

MEASUREMENTS OF AXIAL SKELETON IN MILLIMETERS. C. I. T. NO. 2802

	Centrum			Spine		Rib			Centrum			Spine		Rib	
	L	H	B	AP	H	AP	L		L	H	B	AP	H	AP	L
30......	94	77	127	...	...	...	...	65.....	...	...	...	...	207	...	...
31......	89	...	122	...	...	...	...	66.....	84	89	122	...	212	...	...
32......	91	...	127	...	...	...	...	67.....	80	89	121	...	...	...	162
33......	90	80	114	...	...	...	...	68.....	77	...	...	...	...	...	154
34......	92	80	127	...	...	...	...	69.....	73	75	137	...	...	...	150
35......	91	85	127	...	...	...	...	70.....	68	85	130	...	...	...	...
36......	93	83	128	85	180	59	60	71.....	69	81	127	...	...	...	...
37......	91	92	129	...	...	...	...	72.....	71	77	113	...	...	...	...
38......	88	...	136	...	...	...	...	73.....	71	80	114	...	...	...	...
39......	97	...	...	84	188	...	...	74.....	...	...	128	...	...	...	130
40......	...	94	...	...	...	...	...	75.....	66	75	123	...	...	...	...
41......	89	85	139	...	...	...	...	76.....	63	73	120	...	...	...	...
42......	87	87	147	80	200	47	141	77.....	61	...	...	53	...	...	125
43......	88	...	156	80	200	47	...	78.....	63	73	116	53	145	...	...
44......	88	...	...	80	200	47	150	79.....	64	75	112	55	139	...	...
45......	89	97	155	83	...	...	...	80.....	60	...	115	...	...	...	...
46......	87	106	144	83	223	...	150	81.....	64	77	117	...	...	...	...
47......	79	...	150	83	...	...	250	82.....	60	71	106	...	...	...	...
48......	83	...	155	83	..	...	300	83.....	62	68	107	...	...	...	...
49......	86	...	152	83	220	...	370	84.....	61	73	105	...	...	...	...
50......	86	95	147	83	...	...	425	85.....	61	69	100	...	...	...	...
51......	103	109	152	80	...	...	...	86.....	56	73	100	...	...	...	...
52......	93	104	137	...	273	...	...	87.....	59	61	95	...	...	...	...
53......	91	111	133	91	267	...	...	88.....	58	55	82	...	...	...	...
54......	97	105	136	79	274	...	...	89.....	56	59	75	...	...	...	...
55......	100	111	...	91	...	...	...	90.....	54	55	69	...	...	...	...
56......	96	111	141	87	248	...	...	91.....	50	50	69	...	...	...	...
57......	96	...	...	85	255	...	...	92....	46	...	60	...	...	...	...
58......	96	114	152	78	...	...	...	93.....	40	41	49	...	...	...	...
59......	96	110	148	...	248	...	...	94....	36	...	46	...	...	...	...
60......	102	...	125	89	...	...	...	95.....	32	36	43	...	...	...	...
61......	97	100	...	...	225		...	96....	30	...	36	...	...	...	...
62......	93	104	125	...	...	.	...	97.....	30	...	21	...	...	...	...
63.....	91	94	...	88	233	.	..	98..	30	..	13	...	...	...	.
64......	...	90	...	85	213	...	...	99.....	?21	...	12	...	...	...	...

TABLE 7

MORENOSAURUS STOCKI, TYPE

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. C. I. T. NO. 2802

INTERCLAVICLE			
Anteroposterior in midline	6.7	Thickness of keel	2.4
Width	17.6		
CLAVICLES			
Anteroposterior behind interclavicle	6.3	Greatest breadth of fused and eroded arch	30.2
SCAPULA			
Length in midline	19.1	Breadth at acetabulum and coracoid suture	15.1
Greatest posterolateral dimension	39.2	Height of dorsal process	19.5
Breadth of shaft	9.8	Breadth of anterior border of scapula to summit of dorsal process	35.2
Breadth in midline	29.6		
CORACOID			
Length of scapular suture	10.6	Width of shaft	9.3
Glenoid portion	13.3		
HUMERUS			
Anteroposterior proximally	14.3	Greatest length	37.4
Same distally	28.3	Length of shaft	28.4
RADIUS			
Length	11.6	Width	15.3
ULNA			
Length	11.1	Width	13.4
RADIALE			
Length	6.8	Width	7.0
ILIUM			
Length	28.6	Width proximally	8.1
Anteroposterior proximally	4.2	Same distally	10.7
Same distally	9.6		
PUBIS			
Anteroposterior length parallel to midline	35	Anterolateral diameter	43
Same from anterior notch	31	Ischial suture	11.5
Greatest width	43	Acetabulum	9
ISCHIUM			
Anteroposterior proximally	14.7	Transverse from midline	30.3
Same distally	34.3	Transverse posteriorly	15
FEMUR			
Length	36	Same trochanter	10
Length of shaft internally	29.3	Same distally	26.2
Anteroposterior proximally	13.4	Thickness proximally	14.8
TIBIA			
Length	9.6	Width	12.9
FIBULA			
Length	9.0	Width	12.1
TIBIALE			
Length	6.7	Width	8.7
INTERMEDIUM			
Length	7.6	Width	9.1
FIBULARE			
Length	8.5	Width	9.4

The jaws arch backward from a short symphysis and project 36 mm. behind the condyle. The angular width is 60 per cent of the length from tip of chin to condyle.

The first two cervicals are not fused, and the rib facet on the first pectoral is not compressed. The lateral walls of the centra are smooth as in the type, but without the wrinkled ends seen in the form described below as *Aphrosaurus*. The lateral concavities are less extreme than in the type and the centra are more depressed; but strongly depressed centra, as will be shown below, are common to the known juvenile elasmosaurs.

The humerus is stocky, its distal breadth being 74 per cent of its total length. The anterior knee is prominent and the posterior proximal muscle scars are well developed.

Although the humerus differs from the type humerus, it differs less than from the specimens described below as *Aphrosaurus*. The development of the anterodistal knee also excludes it from this genus and suggests *Morenosaurus*, although the capitulum and trochanter are poorly separated. Since none of the juveniles show a separation of the capitulum and trochanter, this character is applicable only to adults, and it is possible that in the present form such a separation would develop with age. It cannot be the young of *Hydrotherosaurus*, because the latter has 60 cervical vertebrae as opposed to 46 in the present specimen. If this reference to *Morenosaurus* be correct, this genus is a relatively short-necked dolichodire.

Aphrosaurus furlongi n. gen. and sp.

(**'Aφρόs**—sea foam). The specific name is in honor of E. L. Furlong.

Type.—Partial skeleton, C. I. T. no. 2748, consisting of pectrum, pelvis, paddles, and 10 posterior cervicals preceded by 11 indeterminate cervicals and followed by 17 crushed dorsals.

Type locality.—C. I. T. loc. 338, 1000 ft. E. and 900 ft. S. of NW. cor., or 650 ft. E. and 1000 ft. S. of NW. cor., Sec. 13, T 14 S., R 11 E., M. D. B. and M. This is either 750 ft. NW. or 1000 ft. NNW. of U. C. loc. V3735 in the Panoche Hills, Fresno Co., Calif. (see map, fig. 1, p. 127).

Diagnosis.—Posterior cervicals slightly depressed with almost circular articulating faces, weakly concave laterally with wrinkled borders on the lateral walls, and deep ventral trough running the length of the posterior cervicals, disappearing on the pectorals and dorsals. Interclavicle concave anteriorly and without keel. Clavicles short and blunt. Pectoral bar absent, scapulae almost touching in midline posteriorly, diverging 45° anteriorly, with blunt dorsal process. Coracoids with long median symphysis, projecting in front of glenoid, narrow posterior shaft ending in broad expansion extending as far laterally as glenoid. Intercoracoid vacuity cordiform. Humerus slender, distal breadth 59 per cent of length with poorly developed anterodistal knee. Trochanter only slightly separate from capitulum. Radius and ulna with flat internal faces, carpalia very thick. Pelvic bar absent, head of ilium transversely compressed. Pubis convex anteriorly with slight anterolateral concavity; posterolateral concavity shallow. Femur relatively more massive than humerus but still slender, distal breadth 61 per cent of length; trochanter continuous and almost level with capitulum, anterodistal knee well developed. Tibia and fibula slightly shorter than broad, with flat, internal faces, epipodial foramen absent. Mesopodials thick. From the referred juvenile come the additional characters, 57 cervicals, 3 pectorals.

Description of type.—The only determinable vertebrae are 10 posterior cervicals (pl. 26). They are broader than long and slightly longer than high. The cervical rib pit is on the ventrolateral border, near the caudal end of the centrum. The rib pit on the second from the last extends forward to the middle of the centrum. The next to the last shows a small anteroinferior buttress bracing the front of the rib pit. The posterior cervical vertebrae differ from any known form in having a semicylindrical groove about 1 cm. in diameter running the length of the ventral face of the centrum. The lateral walls of the centra are less concave than in *Morenosaurus* and are wrinkled terminally. The last cervical has a slightly compressed rib pit on the lateral wall of the centrum. Comparison with *Hydrotherosaurus* indicates that this is probably the third prepectoral vertebra.

Pectrum and pectoral paddle.—The clavicular arch (fig. 23, *b*) is about the same size as that of *Morenosaurus* but differs in having a concave anterior midline area and concave

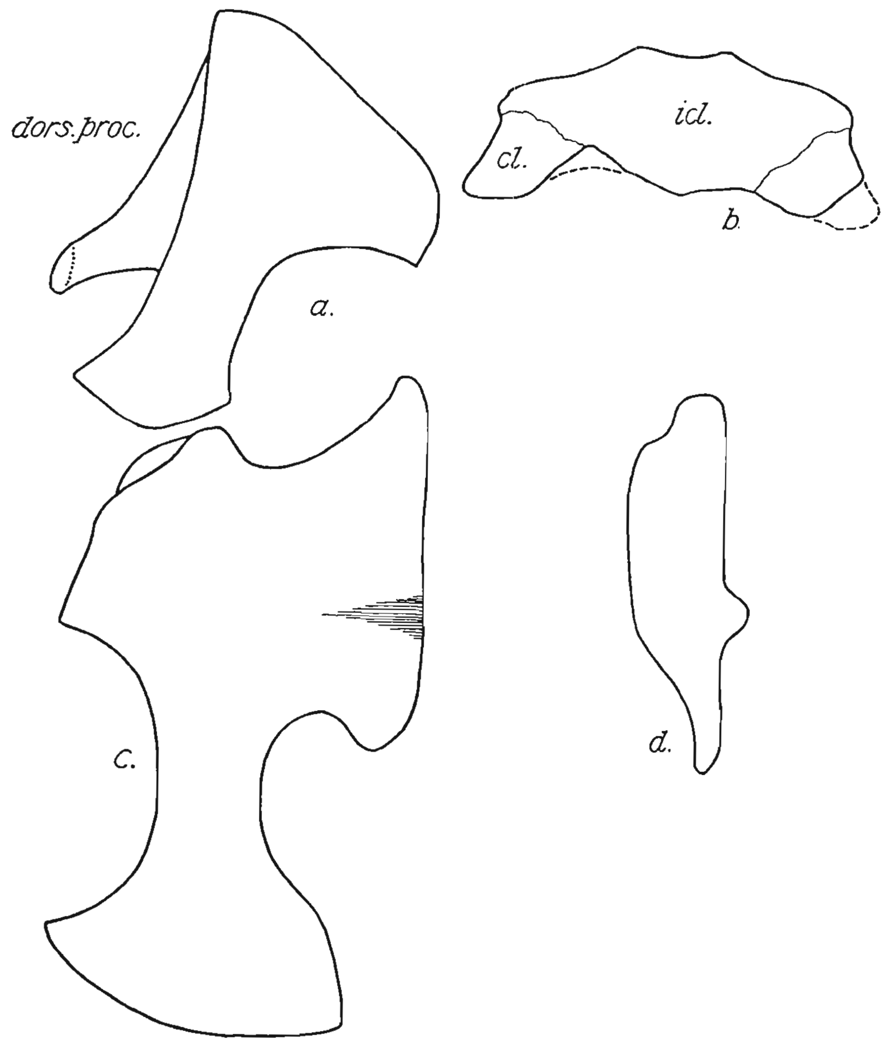

Fig. 23. *Aphrosaurus furlongi*, type. *a*. Ventral view of right scapula. *b*. Visceral view of clavicular arch. *c*. Ventral view of right coracoid. *d*. Midline face of same, ventral surface to right. C. I. T. no. 2748. × 1/6.

rather than straight anterior and anterolateral borders. It is remarkably close to the arch of *Eurycleidus arcuatus* from the Lias figured by Andrews (1922, p. 295). The interclavicle is a large bone anteriorly rounded and concave, with convexities lateral to the central concavity. The ventral and visceral surfaces are smooth, without a trace of a keel or the roughening seen in *Morenosaurus*. The clavicles are fused to the interclavicle and extend posterolaterally a comparatively short distance, ending in a rounded process.

The pectoral bar is absent. The left scapula is the better preserved and is in almost its normal shape except that the dorsal process has been crushed medially. The scapulae practically touched in the midline posteriorly. The anterior face is a cartilaginous surface 2 cm. thick, extending about 45° anterolaterally from the midline junction. The dorsal process is blunt, tapering rapidly to a rounded summit. The anterior edge of the dorsal process is sharply rounded.

The coracoids are well preserved on both the type and referred specimen. In the type the median symphysis is long (57 per cent of the total length) and projects forward beyond the glenoid. The ventral face of the median ramus has a sharp knob that thickens the central articulating surface. In other forms this extends laterally toward the glenoid, but in *Aphrosaurus* there is almost no such extension. The posterior ramus has a narrow shaft that is expanded posteriorly to three times the width of the shaft and extends laterally as far as the glenoid. The posterointernal border is convex, ending in a right angle distally. This is quite different from the usual concave, internally projecting distal end.

The intercoracoid vacuity is heart-shaped and its anterior excavation into the right coracoid is extreme.

The humerus (fig. 24) has a straight head and shaft that expands distally, with a blunt posterodistal border. The general proportions are primitive in having a distal breadth of only 59 per cent of the length; the humerus is thus quite slender in comparison with other elasmosaurs, even more so than in *Thalassomedon.* The anterior distal knee is poorly developed. The separation of the trochanter from the capitulum by the anterior and posterior grooves is only suggested, for though these grooves are outlined on the articular face, they are so slightly excavated as to be almost undiscernible. The anterior groove is slightly indented, the posterior not at all. The trochanter lies external to the capitulum and largely behind it.

The posterior part of the left ulna was crushed, as was the anterior part of the right fourth carpale. As a result the two paddles are asymmetrical and normal proportions are uncertain. Thus the radius–intermedium articulation is stronger in the right than the left, and although the left carpale 3 carries metacarpals II and III, as is customary, the right carries only metacarpal II, and metacarpals III and IV are borne by the crushed fourth carpale. The paddles are otherwise so normal that the crushing seems to have occurred during life and to have resulted in the readjustment of the carpal elements.

The radius and ulna are subequal, relatively square, and thick. Their mutual articulating surfaces are distinctive in being flat rather than concave. There is, therefore, no epipodial foramen.

Radiale, intermedium, and ulnare are massive, and the ulnare is concave posteriorly. There are 3 distal carpals, as usual, followed by the 5th metacarpal. The first carpale is unique in possessing an invagination on the distal quarter of the internal edge. The anteroproximal corner of metacarpal II fits into this invagination. The distal face of carpale 1 therefore projects below that of carpale 2. Metacarpal V has moved only three-quarters of the way into the carpal row and is unusual in being almost a half cylinder, the flat face being anterior. The phalangeal formula is 5, 11, 12, 9, 10, and is practically complete. The phalanges have their greater concavity posteriorly, this being more pronounced on the 5th digit. They are slenderer than in *Morenosaurus.*

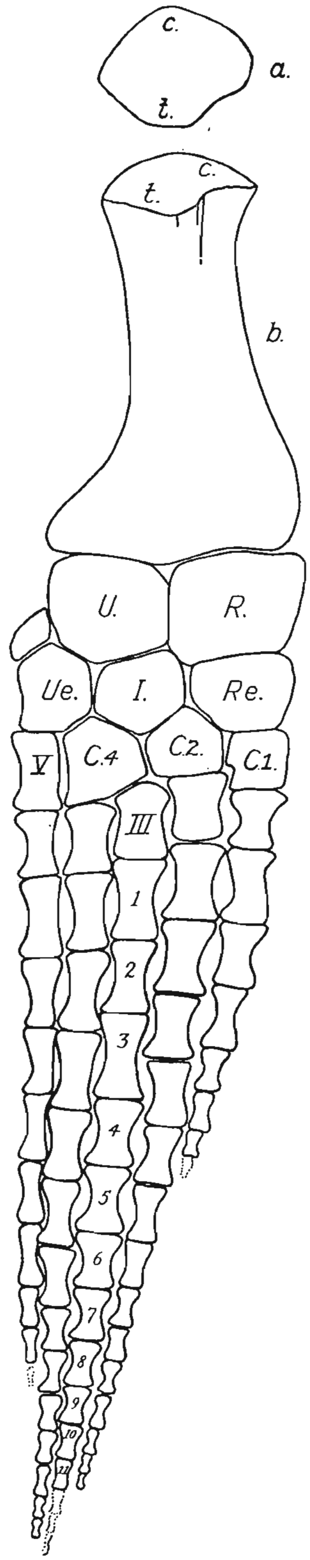

Fig. 24. *Aphrosaurus furlongi*, type. *a*. Proximal end of right humerus. *b*. Lateral view of right pectoral paddle. C. I. T. no. 2748. × 1/7.

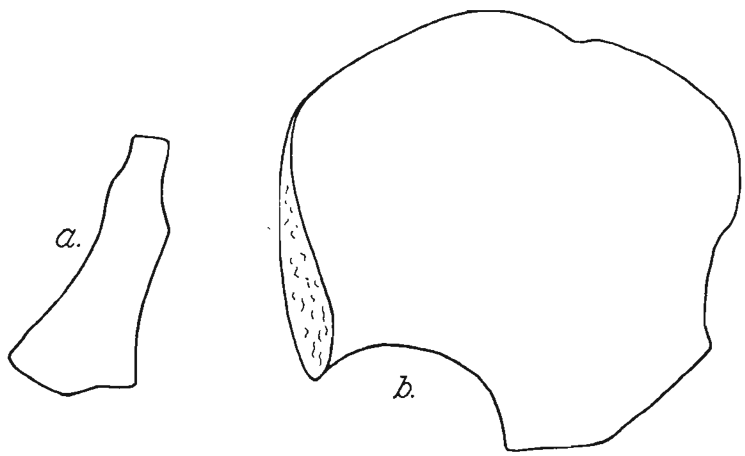

Fig. 25. *Aphrosaurus furlongi*, type. *a*. Lateral view of left ilium. *b*. Visceral view of right pubis. C. I. T. no. 2748. × 1/6.

Pelvis and pelvic paddle.—The ilium (fig. 25) is compressed anteroposteriorly at the sacral attachment, but a short distance down the shaft there is a strong thickening. This is rugose externally and has a large area for muscle attachment. From' this the shaft enlarges gradually to the acetabular end, which is nearly circular. This end is divided into two faces, the larger posterior face meeting the ischium, and the smaller forming a small part of the acetabulum. The ilium in life inclined forward, downward, and outward, but the forward slope was steeper than in *Hydrotherosaurus*.

The pubes did not meet the ischia in the midline; there was therefore no pelvic bar. The median face of the pubis is straight and thick posteriorly. The anterior, lateral, and posterolateral borders form almost a semicircle, indented by a slight anterolateral concavity and a longer posterolateral concavity which is shallow in comparison with other forms. The posteromedian concavity is strong.

Only the acetabular head of the ischium is preserved, and this is massive, with the pubic and acetabular faces meeting in almost a right angle.

The femur (fig. 26) is more massive than the humerus, its distal breadth being 61 per cent of its length. The trochanter is practically continuous with the capitulum, with no anterior groove, and with only a slight posterior groove to indicate the separation. The trochanter is almost level with the capitulum and slopes (dips) only 15° posteriorly. The anterodistal knee is well developed.

Tibia and fibula are almost equal in size and slightly broader than long. They are as distinctive as radius and ulna in having flat internal surfaces and no epipodial foramen. The fibulare is oddly shaped with the facet for tarsale 4 only slightly smaller than that for the fibula and with a straight posterior edge that is broadly rounded. The tarsalia are thick. Tarsale 1 is like carpale 1 in its posterodistal invagination and extension below tarsale 2. Metatarsal V resembles metacarpal V in its semicylindrical shape and its position three-quarters of the way into the mesopodial row. The nearly complete phalangeal formula is 9, 10, 11, 11, 9.

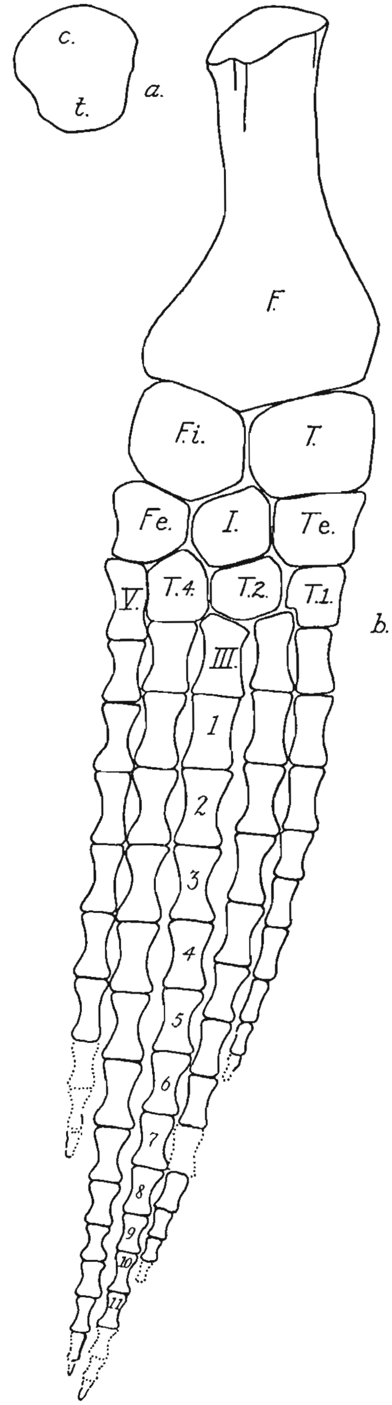

Fig. 26. *Aphrosaurus furlongi, type. a.* Proximal end of right femur. *b.* Lateral view of right pelvic paddle. C. I. T. no. 2748. × 1/7.

Referred specimen.—C. I. T. no. 2832, a very young individual consisting of the articular region of the lower jaws, a few skull fragments, a series of 68 vertebrae including 57 cervicals, 3 pectorals, and 8 dorsals, pectrum without clavicular arch, and most of the right pectoral paddle (pls. 27 and 28).

Locality of referred specimen.—C. I. T. loc. 316, Moreno Cretaceous, Panoche Hills, Fresno Co., Calif. Exact locality unknown.

Description of referred specimen.—The vertebrae apparently begin with the 2d cervical and continue through the 8th dorsal. They are all strongly depressed. The vertebral column is rather characterless in this young specimen, but it is of value in giving us the numbers 57 (plus atlas) cervical, 3 pectoral, and 8+ dorsal vertebrae. The cervical rib facets have a right-angled interior with the short, steep face in front. The anterior spines have square summits, but they become rounded from the 26th posteriorly. The lateral longitudinal ridge is present on the anterior 40 cervicals only. The lateral walls of the centra are less concave than in *Morenosaurus* and they show the same wrinkled ends as in the type of *Aphrosaurus*. In the pectoral vertebrae the position of the rib facet changes abruptly from the centrum to the transverse process.

The shoulder girdle illustrates a stage in which the forward growth of the ventral plates of the scapulae is incomplete, although the coracoids have assumed practically their adult proportions. The scapulae approach each other to within about 4 cm. in the midline and terminate in rounded projections. The dorsal process is clearly developed but not sharply separated from the ventral plate.

The coracoids have a long median suture projecting in front of the glenoid and forming an open notch anteriorly as though for a cartilaginous continuation toward the scapulae. On the ventral surface a sharp ridge begins at the midline, at the center of the sutural surface, and runs laterally toward the posterior border of the glenoid, fading into the smooth body of the coracoid in about a third of this distance. This ridge forms a conspicuous thickening of the median sutural face of the coracoid. The median face of the coracoid is 60 per cent of the entire length. The anterior and lateral borders of the coracoid are strongly concave. The intercoracoid vacuity is heart-shaped, the posterior continuation of the midline extending posterolaterally into the vacuity. The posterior bar of the coracoid is slender, about the width of the scapular suture, and points directly toward it. Distally, this bar expands to almost three times the width of the shaft.

The pectoral paddle has humerus, radius, ulna, radiale, and ulnare in place, but the position of the other elements is conjectural. All the elements are distinctly juvenile in their lack of character. The distal breadth of the humerus is 65 per cent of the length. Its general form and lack of separation of capitulum and trochanter are similar to the type.

TABLE 8

APHROSAURUS FURLONGI, TYPE—MEASUREMENTS OF VERTEBRAE IN MILLIMETERS. C. I. T. NO. 2748

	Centrum		
	L	H	B
49	90	87	111
50	94	...	...
51	...	...	112
52	95	...	110
53	93	91	109
54	...	90	106
55	87	...	...
56	89	...	116
57	86	..	119

TABLE 9

APHROSAURUS FURLONGI, TYPE

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. C. I. T. NO. 2748

INTERCLAVICLE			
Length	11	Anterior breadth	28
CLAVICLE			
Length	8.2	Anterior breadth	7.5
SCAPULA			
Posteromedial from anteroexternal corner to posterior tip of midline	25.5	Length of coracoid facet	6.7
Anteromedial from glenoid face to midline	32	Same, glenoid	7.4
Anteroposterior, top of dorsal process	5	Thickness, glenoid	7.5
		Width of horizontal shaft	7.3
CORACOID			
Length from center of anterior concavity	45	Same, at center of midline surface	8.3
Same, midline suture	29.8	Width from midline to posterior corner of glenoid	28.7
Same, scapular suture	8.6	Same, shaft	8.2
Same, glenoid	11.9	Same, distal expansion	25.5
Thickness of glenoid	9		
HUMERUS			
Length	39.4	Same distally	23.4
Anteroposterior proximally	14.7	Same, shaft	11
RADIUS			
Length	9.2	Width	13
ULNA			
Length	10	Width	10.5
RADIALE			
Length	6.8	Width	10
INTERMEDIUM			
Anterodistal length	8.4	Width	8.4
ULNARE			
Length	8.3	Width	7.0
ILIUM			
Length anteriorly	21	Same distally	8.5
Anteroposterior anteriorly	3	Width proximally	4.5
Same, 6 cm. down shaft	6	Same distally	7.5
PUBIS			
Length, parallel to midline	35	Thickness at midline posteriorly	6.7
Same, midline suture	23	Same laterally	2
Width	35	Length of ischial facet	8
Posterolateral diameter	37.3	Same, acetabulum	10.5
ISCHIUM			
Length of pubic facet	7.7	Width (anteroposterior) of shaft	8.9
Same, acetabulum	9.2		
FEMUR			
Length	37.3	Same, shaft	9
Anteroposterior proximally	12	Same distally	23
TIBIA			
Length	9.4	Width	11.7
FIBULA			
Length	9.7	Width	11.5

TABLE 9—*Continued*

	TIBIALE		
Length	6.6	Width	8.4
	INTERMEDIUM		
Length	6.6	Width	7.6
	FIBULARE		
Length	7.7	Width	6.4

TABLE 10

APHROSAURUS FURLONGI, REFERRED

MEASUREMENTS OF VERTEBRAE IN MILLIMETERS. C. I. T. NO. 2832

	Centrum			Spine			Centrum			Spine	
	L	H	B	AP	H		L	H	B	AP	H
3	20	18	26	..	..	37	48	39	69	..	..
4	20	..	28	..	..	38	47	40	69	41	85
5	22	..	32	..	32	39	47	..	70	..	..
6	25	21	33	19	..	40	51	..	72	..	..
7	23	..	34	20	..	41	48	..	74	..	..
8	25	18	36	..	..	42	49	..	74	43	96
9	26	19	37	..	..	43	49	..	..	..	..
10	27	..	39	..	..	44	50	..	76	..	..
11	27	..	40	24	37	45	49	..	76	..	..
12	27	22	41	..	..	46	46	..	76	..	..
13	30	22	42	..	..	47	49	..	76	..	..
14	30	..	44	..	..	48	49	45	77	45	..
15	..	..	45	..	..	49	49	..	..	..	110
16	33	..	..	..	..	50	48	..	..	..	..
17	33	..	..	..	..	51	48	..	77	..	..
18	35	..	..	..	..	52	50	..	..	..	..
19	35	..	48	..	..	53	49	..	80	..	..
20	37	26	51	..	..	54	52	..	77	47	127
21	..	27	51	..	..	55	49	..	..	..	..
22	38	..	53	..	..	56	50	..	..	..	..
23	36	..	54	..	..	57	51	..	..	..	..
24	39	..	55	32	..	58	48	..	..	48	..
25	41	..	56	..	..	59	49	..	..	..	129
26	41	..	56	..	..	60	49	..	81	..	..
27	42	..	57	..	..	61	..	..	..	..	..
28	43	32	58	36	70	62	47	52	80	..	..
29	45	33	61	..	70	63	52	..	..	..	..
30	43	..	62	..	..	64	..	..	80	..	..
31	..	..	63	..	..	65	54	..	76	..	..
32	..	..	..	..	..	66	..	..	..	..	..
33	..	..	..	..	..	67	..	..	73	..	..
34	..	.	..	38	76	68	53	..	73	..	..
35	45	..	66	..	..	69	52	..	73	..	..
36	47	..	67	..	..	70	52	..	73	..	..

TABLE 11

APHROSAURUS FURLONGI, REFERRED

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. C. I. T. NO. 2832

SCAPULA			
Posteromedial breadth of ventral plate	20.4	Width of shaft	4.4
Greatest diameter anteromedially from glenoid	18.5	Length of coracoid suture	4.3
		Same of glenoid	2.7
CORACOID			
Greatest length from scapular suture	26.8	Greatest breadth from midline	15.6
Length of midline suture	14.1	Breadth of shaft	4.8
Same of scapular suture	5.5	Same of distal end	12.3
Same of glenoid	7.3	Thickness at midline expansion	4.9
HUMERUS			
Length	16.7	Same distally	10.9
Anteroposterior proximally	6.0		

Fresnosaurus drescheri n. gen. and sp.

This, the third juvenile in the Pasadena collection, is of much more massive proportions than either of the others and is designated as *Fresnosaurus drescheri* n. gen. and sp. The generic name is derived from the county of the locality, and the specific name is in honor of Mr. Arthur Drescher, who was in charge of collecting the Pasadena plesiosaurs.

Type.—A fragmentary skeleton, C. I. T. no. 2758, consisting of coracoids, humerus, pelvis, femora, and disarticulated paddle bones.

Type locality.—C. I. T. loc. 346, Moreno Cretaceous, Panoche Hills, Fresno Co., Calif. Exact locality unknown.

Diagnosis.—Coracoid short, broad, and thick, weakly concave anteriorly, not projecting in front of glenoid in midline, and with short posterior shaft only slightly expanded posteriorly. Intercoracoid vacuity cordiform and broad. Humerus with slight development of shaft and round anterodistal and distal border. Ilium not compressed anteroposteriorly at proximal end, with large posterior rugosity one-third the way down the shaft. Pubes convex anteriorly, with posterointernal concavity much longer than postero-external, not projecting posteriorly in midline to form pelvic bar. Ischium short anteroposteriorly. Femur with only slight posterior expansion and no contraction into shaft.

Pectrum and humerus.—The coracoids (fig. 27) are all that remain of the pectoral girdle. They are massive and short. The midline suture is over half the total length and terminates about 1 cm. posterior to the front of the glenoid. The posterior process is short and only slightly expanded posteriorly. The intercoracoid vacuity is heart-shaped and broad.

The distal breadth of the humerus is only 62 per cent of the length, yet the bone is massive, for it does not thin to a shaft, but tapers gradually to the head. There is no development of a trochanter separate from the capitulum, and therefore no anterior or posterior grooves. In this respect it resembles *Aphrosaurus;* yet this may be merely a juvenile lack of development. The most distinctive feature of the humerus is the anterior border, which is straight, or slightly concave, proximally and rounded distally into almost a semicircle that continues around the distal face. There is no separation of the smoothly convex distal end into facets for radius and ulna.

Pelvis and femur.—The ischia are arched laterally and have a large rugosity on the posterior margin about one-third the distance down the shaft. The proximal end is slightly compressed, but, instead of being compressed anteroposteriorly as in *Morenosaurus* and *Aphrosaurus*, the compression is lateral and weaker. The distal end is broadly expanded but does not show separation into ischial and acetabular facets.

The pubes have a short midline suture that ends some 3 cm. anterior to the ischial facet. The anterior border is convex, the posterolateral concavity is about one-half as long and deep as the posteromedial.

The ischium is most remarkable for its extreme anteroposterior shortness near the midline. In this respect it resembles *Hydrotherosaurus*.

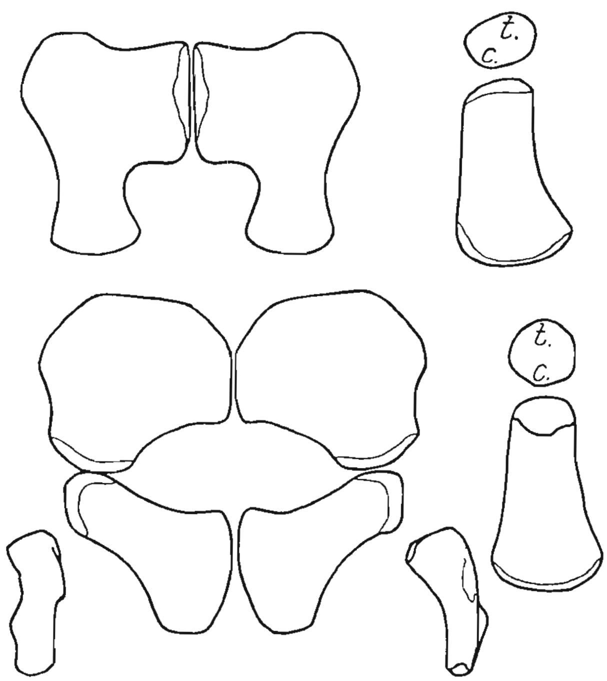

Fig. 27. *Fresnosaurus drescheri*, type. Visceral view of coracoids and pelvic girdle, internal and proximal views of right humerus and femur, anterior view of right ilium, lateral view of left. C. I. T. no. 2758. × 1/6.

The femur is pendulous with a heavy cylindrical shaft and only a slight distal expansion and a faint indication of an anterior knee. The head is hemispherical and shows no sign of development of a trochanter. The distal breadth is but 57 per cent of the length, which is almost the same as *Ogmodirus*, yet greater than *Leurospondylus*.

Comments.—The humerus of this juvenile differs from *Ogmodirus* in having a convex anterior border, a relatively narrower head, and a much narrower distal end that is more convex. The femora of the two have similar proportions, but *Fresnosaurus* has a hemispherical proximal end that is not so sharply separated from the shaft as that of *Ogmodirus*. *Fresnosaurus* has a thicker shaft and a more convex distal end.

Leurospondylus is quite different in shape and proportions of pectrum, pelvis, and propodials. *Aphrosaurus* has a concave anterior border of the humerus and a stronger concavity on the posterior border, as well as a much slenderer and better developed shaft. The head of the humerus of *Fresnosaurus* is sharply separate from the shaft as in

Ogmodirus, not rounded and confluent as in *Leurospondylus* or the Pasadena juvenile tentatively referred to *Morenosaurus*. The extreme shortness of the ischia and the youthfulness of the specimen, indicated by the complete absence of propodial facets, coupled with the large size of the specimen, indicate that *Fresnosaurus* was the young of a very large adult.

TABLE 12

FRESNOSAURUS DRESCHERI, TYPE

MEASUREMENTS OF APPENDICULAR SKELETON IN CENTIMETERS. C. I. T. NO. 2758

	CORACOID		
Greatest length from scapular facet	17.1	Width to posterior border of glenoid	13.1
Length of transverse plate	8.8	Same of shaft	5.1
Same of midline suture	9.7	Same of distal expansion	7.5
	HUMERUS		
Length	14.7	Width proximally	4.5
Anteroposterior proximally	5.7	Same distally	3.8
Same distally	9.2		
	ILIUM		
Length medially	11.4	Width proximally	2.1
Anteroposterior proximally	3	Same distally	4.1
Same distally	4		
	PUBIS		
Length of midline suture	8	Anterolateral diameter from posterior concavity	11
Greatest posterolateral diameter	16	Width of posterolateral neck	8.3
	ISCHIUM		
Greatest anteroposterior diameter near midline	11	Perpendicular to midline	13.4
		Length of pubic facet	3
Anteroposterior neck	4.5	Same, acetabulum	4.3
	FEMUR		
Length	15	Width proximally	5.1
Anteroposterior proximally	5.1	Same distally	4.2
Same distally	8.5		

REVISION OF THE PREVIOUSLY DESCRIBED NORTH AMERICAN ELASMOSAURS

Evidence from *Hydrotherosaurus* and the other genera described above, applied to a review of the literature, has convinced me that the genus *Elasmosaurus* as it now stands is heterogeneous. All of the cercidopleuran dolichodires have been placed in this genus, and yet none is a form which should be referred to the same genus as the type species. Williston had premonitions of this, as shown by his plans to revise the group and by his frequent suggestions that certain forms might represent new species or genera. It is now possible to redefine the family Elasmosauridae to include all the Cretaceous dolichodiran plesiosaurs, while the genus *Elasmosaurus* includes only the type species.

FAMILY **Elasmosauridae** Cope, 1870

Plesiosauria with greatly elongated neck of 40 to 60 vertebrae; head small; ribs single-headed throughout; fused, "hatchet-shaped" anterior cervical ribs; lateral longitudinal ridge on the anterior cervical centra; clavicular arch large and fused; scapulae with large flat ventral plates; coracoids separated posteriorly; pubes expanded into subrounded plates; ischia triangular and short; humerus as large as femur or larger; epipodials as broad as long, or broader.

GENUS **Elasmosaurus** Cope, 1868

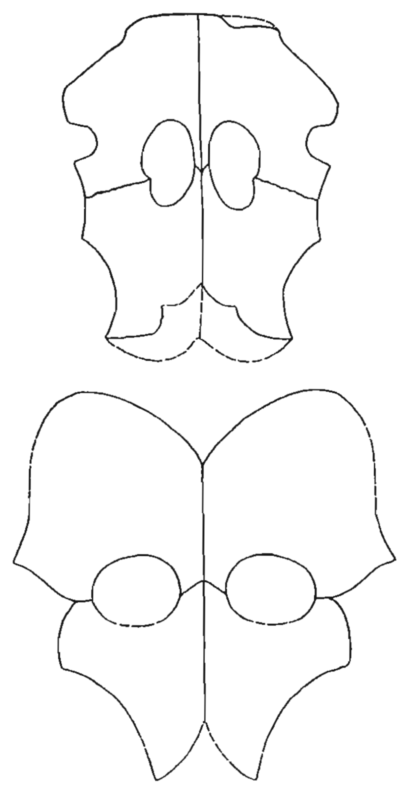

Fig. 28. *Elasmosaurus platyurus* Cope. Pectrum and pelvis. (Modified from Cope, 1870.)

Type.—*E. platyurus* Cope, 1868. A. N. S. P. no. 10081, a skeleton lacking only the skull and paddles. The girdles have since been lost.

Type locality.—*Fide* LeConte (1868, p. 11): ". . . in a ravine 15 miles NW of the post [Fort Wallace, Kansas]. The ravine debouches into the Smoky by the Henshaw Springs . . ."

Diagnosis.—Mandibular symphysis 6.6 cm. long. Vertebrae 132+ divided into 74 cervicals, 3 pectorals, 26 dorsals, 3 sacrals, and 26 caudals; lateral longitudinal ridge on all cervicals, cervical centra strongly compressed; anterior caudals with prominent ventral ridges. Median bar present in both pectrum and pelvis; posterior borders of scapulocoracoid vacuities opposite center of glenoid; pubis with convex anterior border (fig. 28). Total length, 12.7 meters.

Age.—Given by Cope as Niobrara, corrected by Williston (1903) to basal Pierre, Upper Cretaceous.

Synonym.—*Discosaurus carinatus* Cope, 1868. Cope thought the small anterior cervicals represented a distinct genus. The complete skeleton proved that all were the same individual; *E. platyurus* has page priority.

Comments.—This is the only known elasmosaur with compressed cervicals, and I suspect that the compression is due to crushing. Cope estimated the total length at 45 feet and Williston (1906) reduced this to 42. At either length, it is still the largest known elasmosaur. It is followed closely by *E. amalitskii* Pravoslavlev, 40 feet, *Thalassomedon*, 39 feet, and *E. serpentinus* Cope, 37 feet.

Cope's description and figure of the pectrum are acceptable for outline, but the scapulocoracoid suture at the glenoid must be altered. In all known forms the scapula forms the anterior portion, almost half, of this cavity. The restoration shown here in figure 28 illustrates this correction.

Hydralmosaurus n. gen.

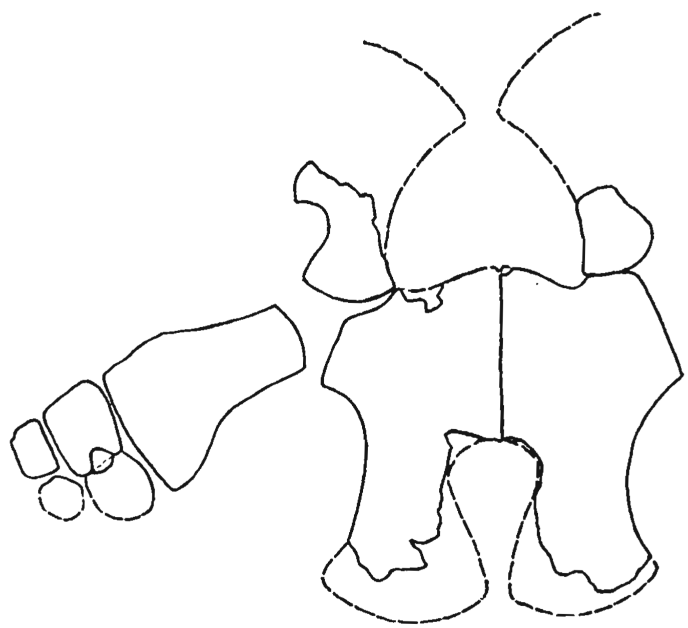

Fig. 29. *Hydralmosaurus serpentinus* (Cope) n. gen. Pectrum humerus and mesopodials. (After Watson, 1924.)

The specimen described by Cope (1877) from Nebraska is thought to exhibit generic distinctions, and for it this name is proposed, derived from the Greek ὑδράλμη—salt water.

Type.—*Elasmosaurus serpentinus* Cope (1877). The type specimen consists of "the entire vertebral column, with the exception of a few anterior cervical and distal caudal vertebrae; the pectoral arch, with the clavicles a good deal broken; the greater part of the anterior limb of one side; the greater part of the pelvic arch, with a large part of both posterior limbs."

Type locality.—Fide Cope, *op. cit.:* "A bluff of blue shale in Nebraska on the southwest side of the Missouri River between Yankton, [S.] Dakota, and Sioux City, Iowa."

Age.—Cretaceous No. 3 (Niobrara or possibly Pierre Shale).

Generic diagnosis.—No midline bar in pectrum or pelvis. Lateral longitudinal ridge absent on posterior cervicals. Intercoracoid vacuity cordiform. Pubis with concave anterior border, the anterolateral and posterolateral necks well developed. Capitulum of humerus separated from trochanter by grooves. Epipodial foramen well developed.

Specific diagnosis.—118 vertebrae divided into 63 cervicals, 3 pectorals, 19 dorsals, 3 sacrals, 17+ (probably 13 more) caudals (see table 13); posterior cervicals broad; posterior 25 cervicals without lateral ridge; obtuse ridge extending anteriorly from chevron facet reaches anterior articulating surfaces only on median caudals, *et seqq.* Coracoid (610+ mm.) long. Humerus massive, distal breadth 78 per cent of length; distal end of humerus convex and rounded. Distal breadth of femur 70 per cent of length. Total length 11.3 meters.

Comments.—The type is the only specimen certainly referable to this genus and species, and the only figures available are some drawings of the shoulder girdle made for Watson (1924) by W. K. Gregory, reproduced here in figure 29. The coracoids probably terminated anteriorly much like those of *Hydrotherosaurus* and the specimen figured by Riggs (1939) as "*Elasmosaurus serpentinus,*" instead of projecting forward as shown in Watson's figure. The specimen should be redescribed and figured.

The comments on this and the other elasmosaurs are based upon the literature, without benefit of autoptic investigation. My conclusions must be evaluated accordingly.

Alzadasaurus riggsi n. gen. and sp.

The specimen from Montana recently described by Riggs (1939) is also thought to be generically distinct, and for it this new name is proposed. The generic name is derived from the place of discovery, Alzada, Montana. The specific name is in honor of Mr. E. S. Riggs, Curator of Paleontology of the Field Museum of Natural History.

Type.—"Elasmosaurus serpentinus." Fide Riggs (1939): "Field Museum no. 12009, consisting of sixty or more vertebrae, both scapulae and both coracoids, the left paddle almost entire, the left pubis, and both ischia and ilia."

Age.—Fide Riggs, *op. cit.*: "Benton Cretaceous of southeastern Montana."

Diagnosis.—Scapula with narrow ventral plate and broad, smoothly tapering dorsal process. Coracoids with long median symphysis projecting anterior to scapular suture. Intercoracoid vacuity broadly cordiform. Humerus 80 per cent as broad distally as long, shorter than *H. serpentinus*, yet thicker proximally; distal end of humerus with distinctly concave facets for epipodials; radial facet much larger than ulnar; capitulum and trochanter separated by anterior notch. Ulna as broad as long. Ilium as long as ischium. Epipodial foramen large and round.

Comments.—This specimen was figured first by Williston (1914, fig. 39) and later by Riggs (1939, fig. 111). Williston's figure does not extend the coracoids far enough forward in the midline. In both, the scapulae are wide apart anteriorly and as a result the glenoid is squeezed into an acute angle. If the scapulae are brought closer together as in *E. snowii* (Williston 1906, fig. 2), the glenoid is widened and is made capable of receiving the head of the humerus. Riggs apparently figured the visceral view of the scapulae and the ventral view of the coracoids. The pubis was restored in Riggs's figure with a convex anterior border. This could be justified by a comparison with *E. platyurus*, *E. ischiadicus* (Williston, 1906, pl. 1), *Leurospondylus ultimus* (Brown, 1913), or *Thalassomedon*; yet in the lateral flare of the preacetabular plate Riggs's specimen is close to the specimen referred

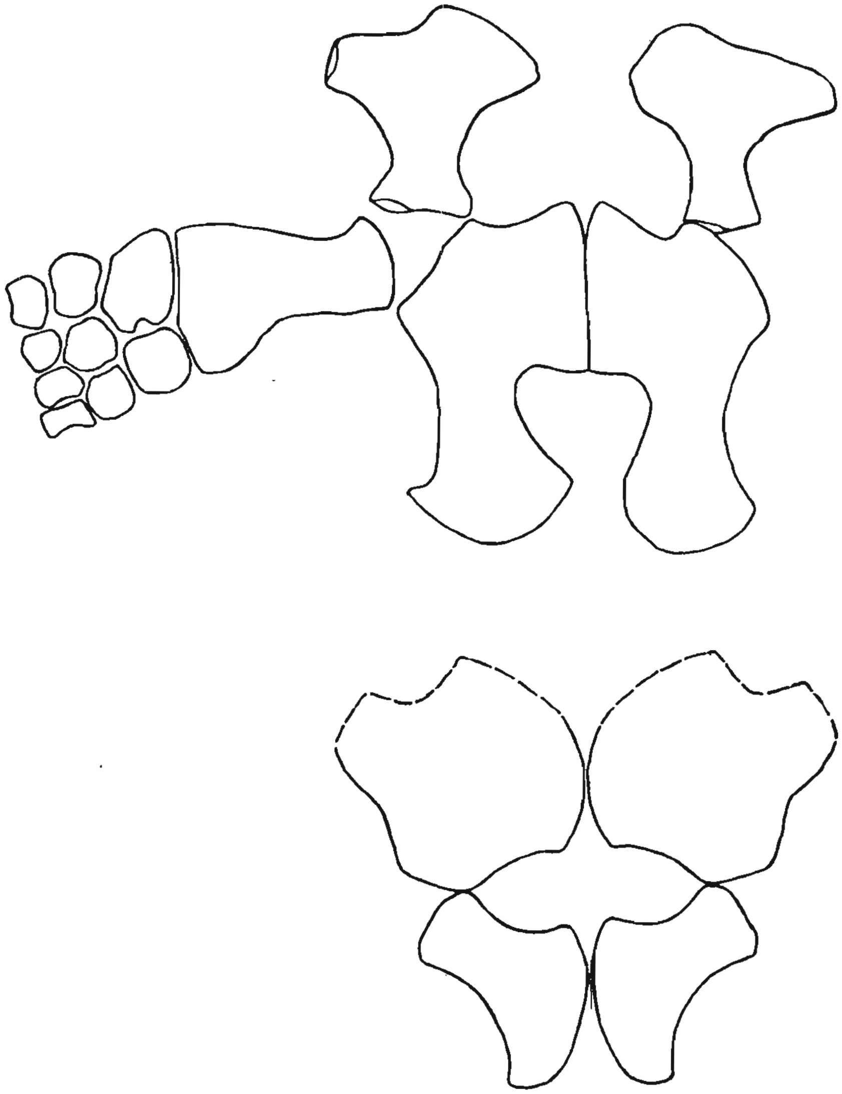

Fig. 30. *Alzadasaurus riggsi* n. gen. and sp. Pectrum, upper pectoral paddle, and pelvis. Field Museum no. 12009. (Modified from Riggs, 1939.)

by Williston (1906) to *Elasmosaurus snowii*, and this form shows a concave anterior pubic border. I prefer the latter restoration, as shown here (fig. 30), but this of course is a matter of judgment and not of proof, and it must be admitted that the ischia of *H. riggsi* and *E. ischiadicus* are similar. As shown below, it is possible that this variation in the anterior pubic border may be due to age or sex of the individual.

The ulna and ulnare both have well-developed facets for a supernumerary element, as in *Morenosaurus*. This element is apparently accidentally lost in *Alzadasaurus*.

Styxosaurus n. gen.

The Kansas specimen described by Williston (1890, 1903, 1906) also exhibits characters of generic value, and for it the name given above is proposed. The name is derived from the type locality.

Type.—*Elasmosaurus snowii* Williston (1906, p. 228). A skull and 28 cervical vertebrae.
Type locality.—Hell Creek, Plum County, Kansas.
Age.—Niobrara Cretaceous.

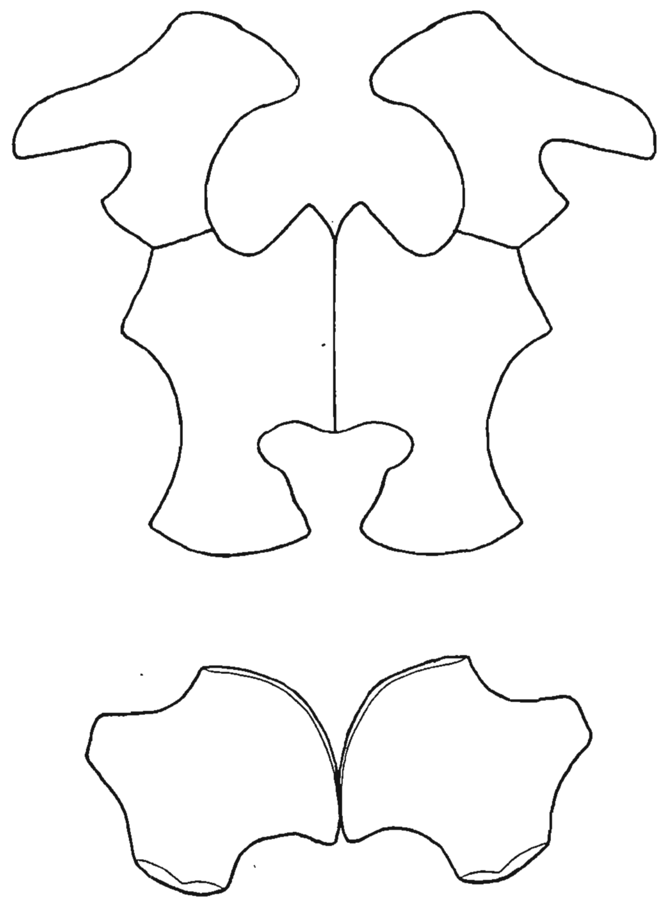

Fig. 31. *Styxosaurus snowii* (Williston) n. gen. Pectrum and pubes of referred specimen. (After Williston, 1906.)

Diagnosis.—Skull about 48 cm. long and 23 cm. high. Anterior cervical vertebrae, excluding the fused atlas and axis, increase in size rapidly. Coracoids with long median symphysis, 66 per cent of coracoid length, and consequently with short posterior processes; anterior border of coracoid markedly concave, with median border projecting in front of glenoid fossa. Intercoracoid vacuity cordiform. Femur pendulous and nearly symmetrical, distal breadth 62 per cent of length. Pubis with narrow anterolateral neck and the anterior, lateral, and posterior concavities subequal.

Referred specimen.—Scapulae, coracoids, pubes, and vertebrae, Yale no. 1644 (Williston, *loc. cit.*). Dr. Lewis has informed me that Williston figured this specimen under the accession number Yale 636 instead of the specimen number Yale 1644. This specimen (fig. 31) was collected in 1874 by Mudge and Williston, on Plum Creek, in western Kansas.

Comments.—The skull and cervical vertebrae must be regarded as the type of this species, and characters derived from the scapulae, coracoids, pubes, and femur referred here by Williston must be considered tentative until more material can be found to prove the specific identity. The propodial that Williston figured (1906, pl. 3) is probably a femur and not, as labeled, a humerus.

Thalassonomosaurus n. gen.

The shoulder girdle of the specimen which Williston (1906, p. 229) described as "*Elasmosaurus* ? *marshii*" is too distinct to be included in any of the known genera. It is therefore

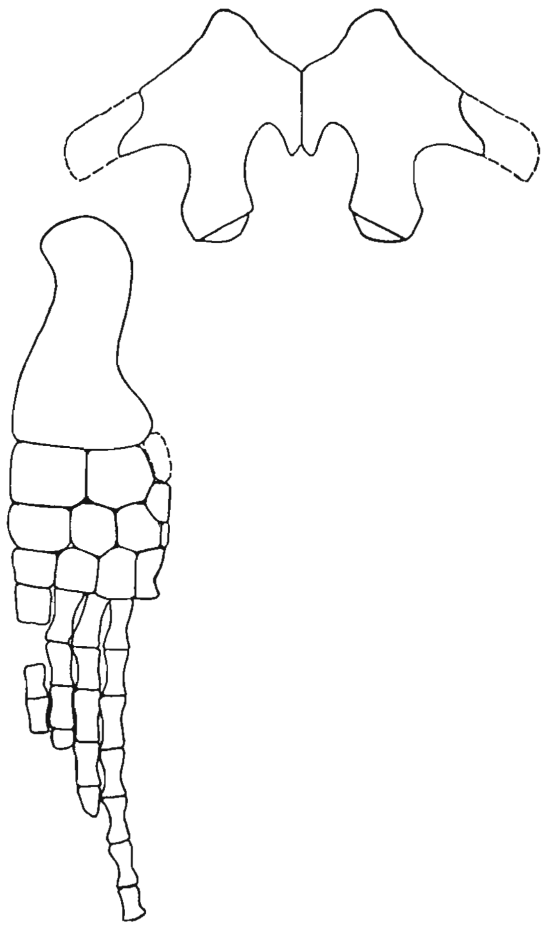

Fig. 32. *Thalassonomosaurus marshii* (Williston) n. gen. Scapulae and pectoral paddle. Yale Museum no. 1645. (After Williston, 1906.)

made the type of a new genus, the name of which is derived from the Greek θαλασσονόμος —living in or deriving nourishment from the sea.

Type.—"*Elasmosaurus* ? *marshii*" Williston, 1906. Yale Museum no. 1645, scapula, 32 vertebrae, and nearly complete fore limb.

Type locality.—Logan County, Kansas.

Age.—Niobrara Cretaceous.

Diagnosis.—Scapulae meeting in midline and projecting a short distance backward toward the coracoids. Distal width of humerus 58 per cent of length; humerus distinguishable by sigmoid curvature and with additional facet for supernumerary epipodial. Ulna approximately equal in size to radius; ulna with three distal facets. Large supernumerary carpal element behind and between ulna and ulnare; supernumerary bone behind lower half of ulnare. Metacarpal V entirely in carpal row and equal in length to carpale 4; metacarpals II, III, and IV slender, II articulating only with carpale 3, III articulating equally with carpalia 3 and 4, IV articulating only with carpale 4.

Comments.—Williston (1906, p. 231), in describing the peculiarities of the forearm, wrote, "These characters are, I believe, of generic value, but until the structure of the coracoid is known, I leave the species provisionally in this genus." To me, the characters shown by the scapulae and humerus require the erection of a new genus. In giving the dimensions of the humerus Williston called it "femur," but since the only material mentioned in the type is "thirty-two vertebrae, a scapula, and a nearly complete fore limb," and since the paddle figured is pectoral, this designation was obviously an error.

This genus (fig. 32), with its serial supernumerary carpal bones, appears to show the beginning of hyperdactyly—a condition never attained by the Sauropterygia.

Watson (1924) wrote that the scapulae failed to meet the coracoids because of the youth of the individual and that an adult would have a well-developed pectoral bar. If

Fig. 33. *Thalassonomosaurus nobilis* (Williston). Femur. Yale Museum no. 1640. (After Williston, 1906.)

so, we should have to reëxamine the relation to *Elasmosaurus platyurus*. Since the limbs are unknown in the latter, it might be difficult to separate the two. However, when one reviews Andrews' (1910) growth series of *Cryptocleidus oxoniensis*, it is apparent that the median bar develops along with the expansion of the ventral plate of the scapula. Furthermore, the coracoids grow forward before the scapulae grow backward to meet them. If the growth of the present form is similar to that of *Cryptocleidus*, we should expect that by the time the scapulae had grown backward as far as shown in *T. marshii*, and had developed so broad a ventral plate, the coracoids would have grown forward to a firm union with them. Although I am inclined to consider *T. marshii* an adult individual, and a form which did not develop the pectoral bar, it must be admitted that with our present material it is impossible to disprove Watson's contention.

Williston, *fide* Lewis *in litt.* figured this specimen under the accession number Yale 2062 instead of the catalogue number 1645.

Thalassonomosaurus nobilis (Williston)

Type.—*Elasmosaurus nobilis* Williston, 1906. Yale Museum no. 1640, represented "originally by a considerable portion of a skeleton." Williston figures femur, ilia, dorsal and sacral vertebrae, and mentions a massive fragment of a scapula and coracoid.

Type locality.—Jewell County, Kansas.

Age.—Fort Hays limestone, basal Niobrara.

Comments.—The femur (fig. 33), ilia, and vertebrae described by Williston as *Elasmosaurus nobilis* are tentatively referred to this genus because the femur shows a large facet for a supernumerary epipodial. The limbs of *E. platyurus* are unknown and when found might prove identical with *T. nobilis.* Yet it seems unlikely that *Elasmosaurus,* still retaining the primitive median bar of pectrum and pelvis, would have a specialized paddle containing supernumerary epipodials, and the pectoral paddle of *T. marshii* does show this specialization. It might not seem advisable to consider the two species *T. nobilis* and *T. marshii* distinct, yet Williston examined the material and separated the species. For that reason they are separated here. Additional characters may be quoted from Williston (*op. cit.*):

A massive fragment of the scapula shows a broad and firm union with its mate in the middle line. The posterior projection of the coracoid is very long and much constricted before its extremity, its distal width being a little less than twice that of its least width; the outer posterior angle is acute and not much produced. The femur shows facets for but two epipodial bones.

Length of femur, 337 mm.

Greatest width distally, 206 mm.

In spite of the foregoing statement about the two epipodial bones, the femur (*op. cit.*, pl. 4, fig. 3) shows a distinct facet for a third epipodial. The proportions of the femur are the same as in *Aphrosaurus,* the distal breadth being 61 per cent of the length, but the shaft is slenderer and the trochanter less inclined. Williston's description of the coracoids indicates a similarity to *Hydrotherosaurus alexandrae.*

Thalassiosaurus n. gen.

Williston (1903, p. 26) described a pair of ischia which he provisionally referred to *Polycotylus* as *P. ischiadicus.* Later (1906, pl. 1 and pl. 2, fig. 1) he figured a pelvis and femur that he considered conspecific with the above, but here he referred the species to

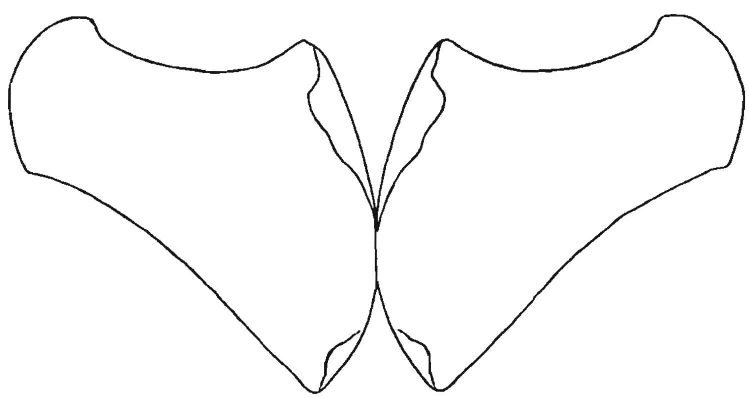

Fig. 34. *Thalassiosaurus ischiadicus* (Williston) n. gen. Type ischia. Univ. Kan. specimen. (After Williston, 1906.)

the genus *Elasmosaurus.* As defined in the present paper, *Elasmosaurus* cannot include the species *ischiadicus,* so it is made the type of a new genus, *Thalassiosaurus* (θαλάσσιος)—marine).

Type.—*Elasmosaurus ischiadicus* Williston. The original specimen, described in 1903, consisted of ischia, ilia, sacral vertebra, and other bones (fig. 34) in the University of Kansas Museum.

Age.—Niobrara Cretaceous.

Diagnosis.—Pubis convex anteriorly as in *E. platyurus,* but without median bar; posterolateral concavity feebly developed. Ischium short, as in *Hydralmosaurus serpentinus*, but more massive and with less concave anterior and posterior borders. Femur with distal breadth 60 per cent of length, proportioned as in *Hydrotherosaurus* but more massive, and with tibial and fibular facets in a nearly straight line.

Referred specimen.—Yale no. 1130, pelvis and pelvic limb described and figured by Williston (1606).

Remarks.—The Yale specimen (fig. 35) may prove to be a distinct species because of the greater concavity of the anterior ischial border and its slightly different proportions. However, it seems better to accept Williston's judgment and consider the two specimens conspecific until more material can be found. This species may also be identical with *Alzadasaurus riggsi*, but the parts that would establish the identity are missing. *A. riggsi* lacks the anterior pubic border and the femur, while *T. ischiadicus* lacks the pectrum.

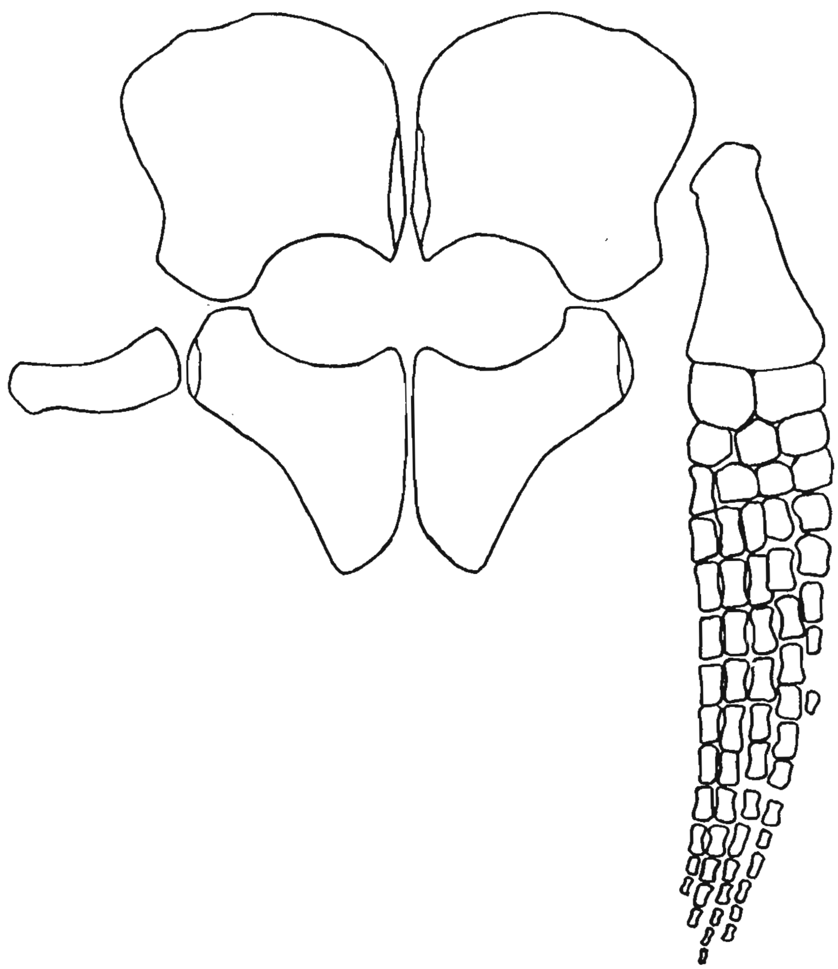

Fig. 35. *Thalassiosaurus ischiadicus* (Williston). Referred specimen. Pelvis and pelvic paddle. Yale Museum no. 1130. (After Williston, 1906.

Pravoslavlev (1916, p. 274) expressed the opinion that the vertebrae illustrated (Williston, 1903, pl. 10) are too short to belong to an elasmosaur, and that the ischia are like those of the brachydiran *Polycotylus donicus*, although the ilia differ. The vertebrae are probably not cervical as labeled, but caudal because the large rib facets face laterally instead of ventrally. If so, we may overrule Pravoslavlev's objection, because the proportions are then elasmosaurian. The ischia, pubes, and femur seem to me to be typically elasmosaurian.

Ogmodirus martinii Williston and Moodie

Type.—Fide Williston and Moodie (1917): "fifty-one consecutive cervical vertebrae, eighteen caudal vertebrae, humerus, femur, many carpal and phalangeal bones, the right ilium, part of a pubis and various fragments of ribs and neural spines."

Type locality.—"Cloud County, Kansas."

Age.—"Ft. Hays ls. of the basal Niobrara, or possibly uppermost Benton."

Diagnosis.—At least 51 cervicals, probably about 60. Humerus stocky, distal breadth 67 per cent of length; anterior border nearly straight, without knee; shaft sharply separated from relatively flat head, distal end rounded, without facets. Phalanges of digit 1 broad. Femur slender, distal breadth 59 per cent of length; head flat and sharply separated from shaft.

Comments.—This genus was mentioned in 1913 by Williston and Moodie, but was not characterized until four years later (Williston and Moodie, 1917). In this second paper the authors wrote, "The only other long-necked genus with which it can be compared is *Leurospondylus* Brown [1913] recently described. So far as the description and figures of that genus apply to the present material, the two genera cannot be distinguished." If this were true we should have to suppress *Ogmodirus*, for it was not characterized until Williston and Moodie described it more fully in 1917, while *Leurospondylus ultimus* Brown was described and figured in 1913. However, the vertebrae show proportional differences that are sufficient to permit the retention of both genera. In *Ogmodirus* all the vertebrae, except the 3d, are almost twice as long as *Leurospondylus*, yet the first thirty cervicals of *Leurospondylus* are actually broader than in *Ogmodirus*; and from 30 to 47, as nearly as can be determined, those of *Ogmodirus* are broader than *Leurospondylus*. Even though age might account for the differences in length, it could scarcely cause the reversal in the breadth measurements noted above.

Williston and Moodie (1917) reproduced Brown's (1913) figures of the girdles of *Leurospondylus* to illustrate their own genus, yet they gave no reasons for doing so. If the girdles were too badly broken to be reconstructed, it is unlikely that Williston and Moodie could have identified them as *Leurospondylus*. I suspect that a careful reconstruction of the girdles of *Ogmodirus* would reveal important differences.

The three juvenile specimens at Pasadena have made it apparent that the differences in the propodials of *Leurospondylus* and *Ogmodirus* are significant. *Ogmodirus* has a much more massive humerus with a less rounded distal end. The femur of *Ogmodirus* is also more massive but nearer the proportions of *Leurospondylus*. In *Ogmodirus* the heads of the propodials are rounded and almost confluent with the shafts, while in *Leurospondylus* they are sharply separated by distinct borders. The length : breadth ratios of the propodials of *Ogmodirus* are exactly the same as in *Thalassomedon*, and it is possible that these forms are identical.

The proportional differences of the vertebrae of the two juveniles and the differences in the propodials lead me to believe that each is a valid genus, and so both are retained. Of further significance is the stratigraphic separation of the genera. One is from the Benton, the other from the Edmonton. This, of course, is emphasizing stratigraphic occurrence rather than comparative osteology, yet in a group evolving as rapidly as the elasmosaurs a generic distinction would be expected with such a stratigraphic difference. Both are young individuals, possibly immature specimens of previously described species. Only more material can settle their true relationships.

Leurospondylus ultimus Brown, 1913

Type.—Amer. Mus. Coll. no. 5261, comprising, *fide* Brown (1913): "35 vertebral centra and 16 spines of which there are 12 cervicals, 18 dorsals and 5 caudals; 30 ribs, 7 abdominal ribs, coracoids, scapulae humeri, ilia, ischia, pubes, femora, 3 epipodials, 7 meso- and metapodials, and 15 phalanges."

Type locality.—"Alberta, Canada, high up in the Edmonton beds, uppermost Cretaceous."

Diagnosis.—Vertebrae exceedingly broad and short. Coracoid broad, projecting in the midline only slightly in front of the scapular suture; posterior ramus broad; distal end moderately expanded; midline

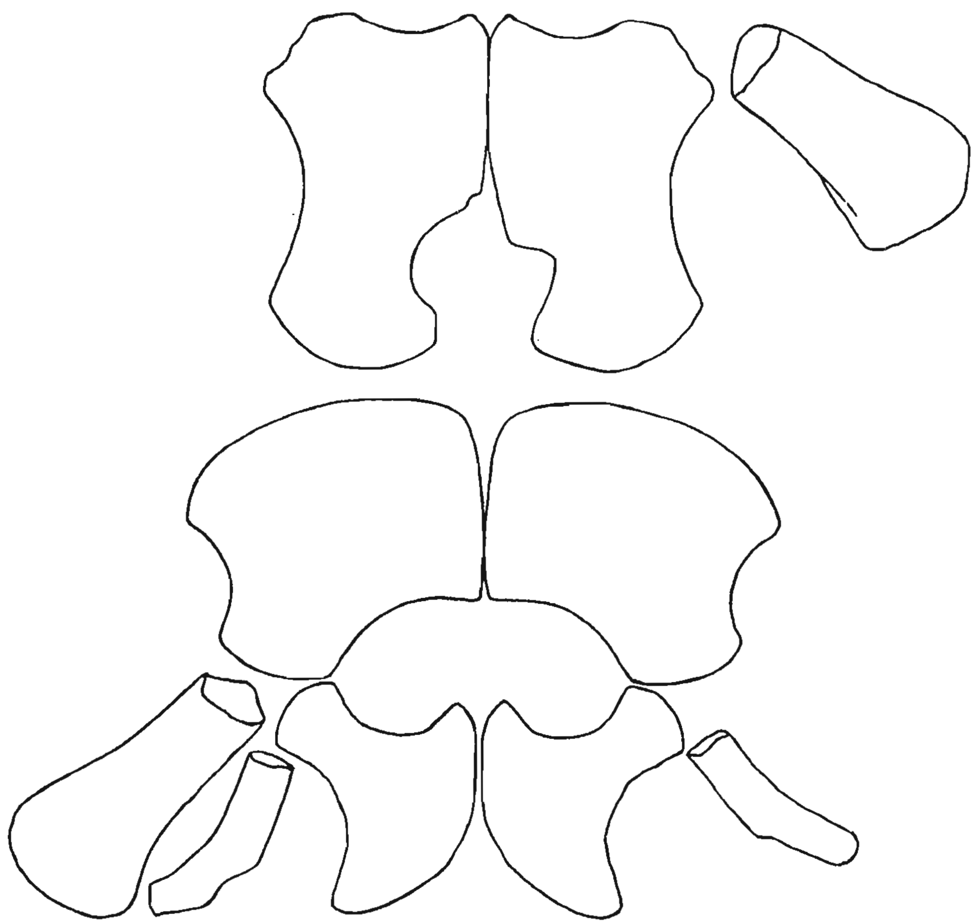

Fig. 36. *Leurospondylus ultimus* Brown. Scapulae, humerus, and pelvis. Amer. Mus. Coll. no. 5261. (After Brown, 1913. Pelvis modified.) × 1/4.

suture long, intercoracoid vacuity cordiform. Humerus slender, distal breadth 58 per cent of length; head highly arched and confluent with shaft; distal end rounded, without facets. Pelvic bar absent. Ilium only slightly expanded distally, and weakly arched. Pubis convex anteriorly; the posterolateral concavity shorter and deeper than the posteromedial. Ischium short along midline; deeply concave anteriorly. Femur slender and almost symmetrical, the posterior border slightly more concave; distal breadth 53 per cent of length.

Comments.—This specimen is well characterized and figured, although it is an immature animal, probably about half grown. The coracoids are much like *Styxosaurus snowii* (Williston) in their long median symphysis and stubby proportions; but it is useless to compare juvenile and adult proportions until the changes can be established in an adequate series of growth stages. The pubes of the two species are distinct, *Leurospondylus* having a convex anterior border. As mentioned above, this might be adequate reason for restoring *Alzadasaurus riggsi* similarly.

The ischia are apparently reversed in Brown's photograph and in the Williston and Moodie figure, as the short concavity should face the pubes. This is true of all of the dolichodires, and, since the short ischia and the "elasmosaurian" coracoids place *Leurospondylus* in this group, a reversal of the ischia as shown here in figure 36 seems more logical.

Neither Woodward (1933) nor Kuhn (1935) gives reasons for including *Leurospondylus* and *Ogmodirus* in the Polycotylidae. Perhaps this was because of the short, broad centra, but, as shown below, this is a juvenile character and not necessarily diagnostic. Nopcsa (1928) groups them with *Elasmosaurus*. This follows Williston (1925) and is apparently carried through his "Osteology" from the paper on *Ogmodirus* (Williston and Moodie, 1917) in which the authors considered *Leurospondylus* and *Ogmodirus* inseparable.

In spite of the differences just indicated, both genera probably belong in the Elasmosauridae. *Leurospondylus*, because of its coracoids, certainly belongs in this family, and probably had about twice the number of cervical vertebrae that were assigned to it. On the basis of length of neck *Ogmodirus* also belongs here, and no known characters of the propodials conflict with this assignment.

The vertebral columns of North American Elasmosauridae are summarized here in table 13.

TABLE 13

VERTEBRAL COLUMNS OF NORTH AMERICAN ELASMOSAURIDAE

	Total length	Cervicals	Pectorals	Dorsals	Sacrals	Caudals	Total
	m.						
Aphrosaurus furlongi	....	57[a]	3	..	..	..	...
Elasmosaurus platyurus	12.7	74[b]	3[b]	26[b]	3[b]	26[b]	132[b,c]
Hydralmosaurus serpentinus	11.3	63[b]	3[b]	19[b]	3[b]	30[b]	118[b]
Hydrotherosaurus alexandrae	8.0	60	2	17	3	30[b]	112[b]
Morenosaurus stocki	8.0?	46[a]	2	17	3	30[b]	99[a]
Thalassomedon haningtoni	11.8	62	3	25	3	21	114

[a] Cervicals based on referred specimen.
[b] Estimated by writer.
[c] Cope, 1870, listed 103 and figured 162.

CLASSIFICATION OF THE SAUROPTERYGIA

Before considering the classification of the plesiosaurs it may be well to review Boulenger's (1917) reasons for discarding the term Sauropterygia in favor of Plesiosauria. Conybeare's original term (1821, p. 562) was "*Enalio-Sauri.*" This was to include his previously described *Ichthyosaurus* and the new *Plesiosaurus*. According to Boulenger, De Blainville in 1835 named and defined the order Plesiosauria; Owen continued to unite Ichthyosauria and Plesiosauria in the Enaliasauria, but called the former the Ichthyosauri and the latter, Plesiosauri. The nothosaurs he later included in the Plesiosauri. This should have established the order as Plesiosauria. However, Owen in 1859 dropped the term Enaliasauria and proposed Ichthyopterygia and Sauropterygia for the groups already named, defining the Sauropterygia as long-necked marine reptiles with finlike limbs and not more than five digits; *Plesiosaurus* was made the type. Boulenger concludes that "the earlier name Plesiosauria, also the better for its non-committal meaning should stand for the order in its widest sense; and that the name *Sauropterygia* should only be applied, in accordance with Owen's definition and express designation of the type, as well as with its etymology to the suborder including the *Plesiosauridae*, *Pliosauridae* and *Elasmosauridae*, in which the limbs are transformed into hyperphalangeal fin-like paddles."

The ordinal name Plesiosauria may thus be historically preferable, but the term Sauropterygia as an ordinal name has become thoroughly imbedded in the literature (Williston, 1925, Romer, 1933, Kuhn, 1934, Camp and VanderHoof, 1940). The accepted usage of the order Sauropterygia includes the suborders Nothosauria, Plesiosauria, and Placodontia, with the possible addition of the Pistosauria if its validity be established. This usage is widespread and, since priority need not apply, confusion can be avoided by admitting the correctness of Boulenger's argument but rejecting his resurrection of the ordinal name Plesiosauria.

In classifying the (suborder) Plesiosauria, Owen (1840) relied upon characters of the vertebrae, girdles, and limbs and considered the greatest change to have been in the length of the neck. In 1865 he correlated large "canines" with a short neck and a long head. He recognized three groups characterized by long, intermediate, and short cervical centra. Seeley (1874) and Sauvage (1879) stressed the presence or absence of an interclavicle; Kipriianov (1882) used the length of the neck; Cope (1887) relied upon the proportions of the epipodials; Lydekker (1889) lumped all of the genera into the Plesiosauridae, but was one of the first to employ a suite of characters. His genera were based primarily on skull type, but length of neck, character of rib head, and structure of pectoral arch were given full consideration; in fact, he mentioned practically every character that has been used by subsequent workers. Later, Seeley (1892) also used many characters. He stressed the type of rib head, with secondary divisions based upon the length of neck, degree of ossification, and type of interclavicle. His attention was centered on the dicranopleurans to the exclusion of the cercidopleurans and he introduced the terms Dolichodeira and Brachydeira for the long- and short-necked groups. Williston (1903) listed many characters but did not commit himself concerning their relative value until later. Bogolubov (1912) relied upon the length of neck; Mehl (1912) did not present a scheme of classification, but established the correlation of a long neck with short ischia;

Linder (1913) correlated two atlas types with long and short skull; Pravoslavlev (1916) relied entirely upon vertebral indices; in 1919 he correlated the lateral ridge on the cervical vertebrae with a long neck and attempted to demonstrate relationships through proportions of length to height to breadth of the centra. Watson (1924) recognized phyletic lines of long-necked and short-necked plesiosaurs ranging from the Lower Lias to the Upper Cretaceous and considered these forms genetically related. In Williston's "Osteology of the Reptiles" (1925) there is no evaluation of the characters that he listed in 1903, but it is noteworthy that the first two plesiosaurian families are dicranopleuran and the last four cercidopleuran, and this separation takes precedence over the length of skull even though the latter is listed first among the family characters. In his major division he thus agrees with Seeley. Nopcsa (1928) returns to the length of neck as a primary character, but uses new group names; Woodward (1933) repeats Williston's scheme of listing two dicranopleuran families first, followed, however, by only two cercidopleuran families. Kuhn (1935) follows Woodward with but minor changes. White (1940) bases his separations primarily upon the shoulder girdle, with lesser emphasis upon length of head and shape of rib head, although he regards this shape as an ontogenetic character. The later authorities, except White, have recognized about the same number of families comprising about the same genera, but have not agreed whether to lay primary emphasis upon the nature of the rib head or upon the length of the neck.

An evaluation of the status of *Plesiosaurus guilelmi imperatoris* will have an important bearing upon plesiosaur classification. This form was described by Dames (1895) upon a complete juvenile skeleton, now in Berlin, from the Upper Lias of Holzmaden. Watson (1909) declared this to be a new genus close to *Microcleidus*, but he refrained from naming it until he could see the specimen. Fraas (1911) accepted the genus and species and refuted what he thought was Watson's reference of the specimen to *Microcleidus*. Fraas at the same time described an adult skeleton from the same locality, only 15 cm. below the Berlin type, and thought that his specimen was the adult of the Berlin juvenile. White (1940) believed the two specimens to be distinct and established a new genus and species for Fraas's specimen.

White regarded the absence of the interclavicle and the narrower skull in the type as important differences, yet he based his primary emphasis upon the pectoral bar in the adult form.

Watson (1924) pointed out that the pectoral bar is ossified in old, but not in young or even young adult individuals of *Plesiosaurus dolichodeirus*, *Microcleidus*, and *Muraenosaurus*. Andrews (1910) showed the same in *Cryptocleidus*. We therefore could regard the presence of the pectoral bar as an indication of old age in Fraas's specimen and not of taxonomic value. On the other hand, the elasmosaurs include six specimens with adequate pectra, and only one of these, *E. platyurus*, has developed the median bar. Nevertheless, the Liassic and Jurassic forms apparently developed bars in old adults and the taxonomic importance of this character among the earlier plesiosaurs is questionable at best.

The relative length and breadth of the skulls is almost impossible to determine. Fraas (1910, p. 108) states that both were crushed but the Berlin form was depressed and the referred specimen compressed. His plate 7 is sufficient to show that skull measurements are useless.

The absence of the interclavicle is another questionable character, especially as

Dames (1895, p. 46) suggests that it might be fused with the clavicles into a sutureless plate, and Fraas (1911, p. 116) states that in the type the broad face of the clavicle joined the interclavicle. This element was probably accidentally lost and not absent.

The characters used by White are thus of questionable value. Further characters, not mentioned by White, are the pelvic bar in the referred specimen and the concave anterior borders of its pubes. The development of the bar may be dismissed through the same arguments that apply to the pectrum.

The concave anterior pubic border is a character that is more difficult to evaluate. It could be an age or sex difference. If the latter, I am unable to explain its value. If it is merely an age difference, then the juvenile is convex, the adult concave as in *Cryptocleidus*. The Upper Cretaceous juveniles *Fresnosaurus* and *Leurospondylus* support this, yet the adults may have only a small indentation, as in *Hydrotherosaurus* and *Aphrosaurus*, or may be convex as in *Elasmosaurus*, *Thalassomedon*, and *Morenosaurus*. This at least indicates that the juvenile condition is convex as in the type of *P. guilelmi imperatoris*. It also seems to show that among the Upper Cretaceous forms there is a tendency to retain this juvenile convexity and lose the concavity that is developed in earlier adult forms such as *P. rugosus* and *Brancasaurus*. I have attempted to use this character taxonomically, and yet I am not convinced of its value.

Opposed to the separation of the two specimens are the facts that each is a similarly proportioned dolichodire; each has the same number of cervicals, pectorals, dorsals, and probably caudals; the juvenile type measures 2.7 m., the referred adult, 3.2 m. in total length; the humeri are very similar, the juvenile 23 cm. long, its distal breadth 46 per cent of this, the adult 26 cm. long, its distal breadth 49 per cent (the adult is thus slightly more massive as might be expected); the femora are similarly proportioned, the type measuring 22 cm., its distal breadth 49 per cent, while the adult is 26 cm., its distal breadth being 48 per cent (the decrease of one per cent in the adult is negligible). And finally Fraas, in recent years and with modern concepts, carefully studied both specimens and concluded that both were the same species.

The more conservative course at present seems to be to follow Fraas in considering his specimen to be the adult of the type. If so, we may conclude that, at least in the Jurassic forms, the presence of pectoral and pelvic bars are indications of old age and the concave pubic border is either an age or sex difference. Although it is quite likely that many dolichodires never develop pectoral and pelvic bars, we may feel almost certain that specimens exhibiting this character are old individuals.

The characters available for classification are numerous and are tabulated below; credit is given to particular workers for emphasizing particular features:

1. General size increases (1 m. to 12 m.).
2. Skull elongates or remains short (60 cm. to 3.7 m.). Williston (1903, p. 5) wrote, "Teeth may be irregular in size and large, or small and nearly uniform; prefrontals and postorbitals separated or suturally united; the parietals with a high thin crest, or without such a crest; the palatines widely separated or broadly contiguous; the supraoccipitals paired or single (?)."
3. Cervical vertebrae increase in number (76), or decrease (13).
   a. Increase and lengthen and depress.
   b. Decrease and shorten and round.
4. Cervical vertebrae with two or one rib facet.
5. (Linder, 1913).

a. Atlas centrum forms most of the support for the condyle.

b. Atlas intercentrum and arches ring the centrum and may exclude it from the condyle.

6. Arches may remain free or may fuse to centra.
7. Ventral vascular foramina present and prominent, or absent.
8. Neural spines high or short.
9. *a.* Interclavicle remains large and is overlapped with a squamous suture by the clavicles.
   b. Interclavicle lost and clavicles meet in midline.
   c. Interclavicle triangular and clavicles lost.
10. Pectoral bar present or absent (?).
11. Ventral plate of scapulae may be relatively broad or narrow.
12. Coracoids may be convex, straight, or concave in the midline.
13. Coracoids may project laterally or remain relatively slender.
14. Ilia become narrow proximally or remain broad.
15. Pelvic bar present or absent.
16. Pubes become platelike and elongate, or relatively round, may become convex anteriorly or concave.
17. Ischia elongate or remain short along the midline.
18. Propodials become massive, the humerus larger than the femur, or pendulous, the femur the larger.
19. Capitulum and trochanter of propodials may remain connected or show changes leading up to complete separation.
20. Epipodials shorten to less than their breadth and may or may not retain the foramen. They may remain two in number or increase.
21. Mesopodials vary in number and the distal row may include none, part, or all of metapodial V.
22. Phalanges increase in number and vary in relative strength.

What Williston wrote in 1903 is true today: "Certainly among all these characters, and probably not a few others, there will be no dearth of material for classification. Unfortunately there are yet many forms in which we do not know what relations these different characters bear to each other, and until we do, any classification must be provisional."

The main problem is to correlate and evaluate the available characters and then establish a classification based upon all of the skeletal features. It is useless to set up facile schemes based upon single characters, or even several characters. Any useful phylogeny must utilize all of the available evidence.

Some of these characters are of an evolutionary nature and, as such, apply equally to the entire suborder. These include general increase in size, reduction of cervical rib heads from two to one, shortening and broadening of the epipodials, and progressive hyperphalangy.

Other characters are of opposing natures and are more useful in classification. Thus there are tendencies to shorten or lengthen the neck and the individual vertebrae, to lengthen or shorten the head, to shorten or lengthen the pelvis along the midline, etc.

When enough of these characters are associated in one or more specimens, it is customary to group these specimens taxonomically, and if certain groups of characters show continuous variation through a stratigraphic sequence of specimens, the case for calling such a group "natural" becomes convincing. Obviously, those forms which possess the greatest number of similarities must be regarded as the most closely allied.

The brief review of the literature shows that the main tendencies among previous writers have been to classify the plesiosaurs either upon the nature of the rib head or upon the length of the neck. The first is a horizontal scheme and has the disadvantage of grouping under the Cercidopleura (single cervical rib head) such diverse forms as

Trinacromerum, *Kronosaurus*, and *Thalassomedon*. The second is a vertical scheme, and seems to me to be much more logical. It involves only direct relationships, whereas the horizontal scheme, by the mere grouping of diverse forms, necessarily implies their connection through some "common ancestor" and therefore indirectly depends upon the vertical, although pretending to ignore this dependence. The difficulties inherent in the vertical scheme are, first, the separation of similar "ancestral forms" into distinct categories; and second, the grouping of diverse end forms into the same category. The first objection has been entirely overruled by the largest taxonomic groups, which are entirely vertical.

The second difficulty is much better solved with the vertical than with the horizontal system. Furthermore, the time range of a particular form of life can be more concisely stated with the vertical scheme of classification.

Seeley's primary division was based upon the nature of the rib head. It is a horizontal classification, and by Dicranopleura he refers to early forms, both long- and short-headed. Williston approached this problem from Kipriianov's viewpoint, and although he had often urged the importance of vertebrae in taxonomy, and therefore was inclined to follow Seeley, he wrote (1903, p. 5), ". . . forms very closely allied to *Pliosaurus*, a dicranopleuran, have single-headed ribs throughout. *Polycotylus* is a short-necked type with single-headed cervical ribs. . . ." This enigma he solved as follows: ". . . elongation of the neck is a specialized character in the plesiosaurs [paralleling the dolichosaurs]. . . . It seems also evident that monocranial ribs are a specialization, not only in these, but in other aquatic air-breathing vertebrates, such as the cetacea, some ichthyosaurs and the mosasaurs, due to environmental causes. It is true that all the Squamata show the same single-headedness of the ribs, brought about by similar conditions—the lack of the necessity of support of the abdominal organs by the ribs in animals resting prone upon the ground, or in a medium of nearly the same specific gravity as the creatures themselves.

"It is a singular fact that, in many plesiosaurs, vestiges of dicranial ribs have been retained in the neck, though such have disappeared elsewhere in the vertebral column; and this character has been retained in both the long-necked and the short-necked types. . . . Did the long-necked forms become differentiated before the dicranial character was lost, and have they continued as a distinct phylum until the character was wholly lost? If so, the short-necked Pliosaurs must represent a distinct branch of the order which has also undergone the same change." He reiterated this opinion in 1907.

I heartily agree with Williston and believe that the primary division of the plesiosaurs can be based upon the tendencies either to lengthen or shorten the neck. All of the early plesiosaurs are Dicranopleura and the Cercidopleura appear only in the Upper Jurassic and Cretaceous, yet the separation into Brachydeira and Dolichodeira was apparent in the Lower Lias, and perhaps even in the Triassic. The division into Brachydeira and Dolichodeira thus has the added advantage of stressing the first structural trends to appear.

The first dolichodires are moderately long-necked animals of the Triassic. Here, as with the brachydires, they are dicranopleures. But the cercidopleures appear earlier in this group than in the short-necked types, with *Picrocleidus*, *Tricleidus*, and *Cryptocleidus* of the Oxfordian. The Cretaceous plesiosaurs are all cercidopleures.

The brachydiran dicranopleures begin in the Lias and continue until the Portlandian, when *Pantosaurus* appears as a brachydiran cercidopleure. There are two possibilities here: either *Pantosaurus* is an offshoot of the normally dolichodiran cercidopleures that again became short-necked, or it represents an advanced brachydiran dicranopleure that has lost the double rib articulation. The second alternative seems to be the more probable, as one would scarcely expect a group that was already specializing in the direction of increase in the length of the neck to reverse that trend and produce a short-necked form. It would be more logical to expect the brachydires to develop cercidopleury and thus parallel the dolichodires.

Associated with brachydiry are an elongate skull; irregular dentition with large caniniform teeth; enlarged atlantal intercentrum and arches which ring the odontoid; shortened vertebral centra; loss of the clavicles and reduction of the interclavicle, or enlargement of the clavicles and reduction and notching of the interclavicle; broad distal extremities of the coracoids; pendulous propodials, the humerus equal in size to or smaller than the femur; broad anterolateral projections of the pubes; pubes and ischia elongate in the midline.

With dolichodiry are associated a short head; small, relatively uniform teeth, reduction of the part taken by the atlantal intercentrum and arch in forming the articulation for the occipital condyle; elongate and usually depressed cervical vertebrae; loss of the interclavicle, and median junction of the clavicles, or squamous suture of the clavicles beneath an interclavicle which may be concave anteriorly or pointed anteriorly and keeled; excavation of the coracoids along the posterior midline; massive propodials, the humerus larger than the femur; pubes and ischia short anteroposteriorly in the midline, the pubes either round or concave anteriorly.

The discovery of specimens which are more complete will undoubtedly add to these characters, especially in the development of the scapula. However, these associations of characters seem adequate to justify the major division of the plesiosaurs into Plesiosauroidea and Pliosauroidea. It is possible that these branches will carry back through the Nothosauridae and Pachypleurosauridae, but if the distinctions break down in these ancestral groups it may be necessary to recognize a third category of mesodirans, as was indirectly suggested long ago by Owen (1865, p. 35). Before this can be determined more work must be done upon the earlier forms, especially those of the Lias referred to *Plesiosaurus*.

The terms Brachydeira and Dolichodeira are satisfactory in a descriptive sense, but they do not fit into our modern taxonomic terminology. Therefore the superfamily terms Pliosauroidea and Plesiosauroidea are used here.

If the evolution into Pliosauroidea and Plesiosauroidea be accepted, and especially if this evolution be progressive, we may attempt further separation of these lines. On this principle, we would expect to derive increasingly shorter-necked forms from ancestors in which the trend is established. Thus *Pliosaurus* with 20 cervicals might come from *Thaumatosaurus* with 27, but *Polycotylus* with 26 cervicals could not be derived from *Peloneustes* with 19 or *Simolestes* with 20.

Among the Pliosauroidea there seems to be one line that early develops gigantism and becomes extinct in the Lower Cretaceous. In these forms the cervical centra are about twice as broad and high as long. This group includes *Kronosaurus, Pliosaurus, Peloneustes* and possibly *Thaumatosaurus*.

Another line, less specialized in that the centra were relatively longer, culminated in *Trinacromerum*. This may have originated in *Macroplata*, or possibly in *Thaumatosaurus*.

These two lines may have been more closely allied than their clavicular arches now indicate. It is possible that *Peloneustes*, etc., actually possessed large triangular clavicles similar to *Trinacromerum*, but that the clavicles of the former have simply not been preserved.

A questionable third line of brachydires seems to include *Brachauchenius* and *Simolestes* and has an origin near or through *Thaumatosaurus*. For the present this third line is better included in the other two.

Following this principle of progressive evolution, we find the Plesiosauroidea also divisible into two major lines. One apparently culminates in *Elasmosaurus* and includes *Thalassomedon*, perhaps *Colymbosaurus* and possibly *Tremamesacleis* or *Muraenosaurus* to originate through or close to *Plesiosaurus dolichodeirus*.

Aphrosaurus and *Hydrotherosaurus* are shorter-necked forms that may be derived from *Mauisaurus*.

Morenosaurus, *Leurospondylus*, *Fresnosaurus*, *Styxosaurus*, and *Alzadasaurus* are of uncertain ancestry.

If the concave anterior pubic border has a phylogenetic significance, a line could be drawn to include *Seeleyosaurus*, *Brancasaurus*, *Alzadasaurus*, *Styxosaurus*, and *Hydralmosaurus*.

Cryptocleidus, including *Apractocleidus*, seems to constitute an aberrant branch that did not survive the Jurassic. The paddles are too highly specialized to have been ancestral to any of the later known forms.

Still another line seems to have evolved *Leptocleidus* from *Tricleidus*, but the ancestors of the latter are unknown.

Most of the plesiosaurian lines of evolution lead back to the genus *Plesiosaurus*, *sensu lato*. Much recent work has been done upon this genus, and the tendency has been to establish new genera on the old species. More work is needed and should be done by someone having access to the specimens as well as the literature.

The greatest gaps in dolichodiran phylogeny now lie in the Lower Cretaceous and in the Liassic. The plesiosaurs described in this paper add appreciably to our knowledge of the Upper Cretaceous types, but they comprise a variety of end forms whose ancestry is not established. For the present, the phylogeny shown here (fig. 37) represents an attempt to correlate all of the known characters. Increased knowledge will undoubtedly alter it considerably.

This is not the place for a detailed study of the difficult problem of the possible ancestry of the nothosaurs to the plesiosaurs. Nevertheless, after a rather brief review of the literature I am of the opinion that plesiosaurian ancestors will be found among the nothosaurs. Closely similar skulls can be found in both groups; for example, *Pistosaurus* and *Plesiosaurus rostratus; Ceresiosaurus* and *Plesiosaurus hawkinsii; Simosaurus* and *Plesiosaurus dolichodeirus*. These are either remarkable examples of convergence or they imply true relationship. If similar skull shape indicates relationship, it seems that the plesiosaurs and nothosaurs are both polyphyletic groups and that the plesiosaurs should be derived not from a nothosaur but from various nothosaurs.

The classic objection to this view is that the nothosaurs have a closed palate and this is considered to be an advanced character, while the plesiosaurs have an open palate and this is considered to be a more primitive character.

The discovery of an open palate in *Pistosaurus* led Miss Edinger (1935) to propose a

PHYLOGENY OF JURASSIC AND CRETACEOUS PLESIOSAURIA

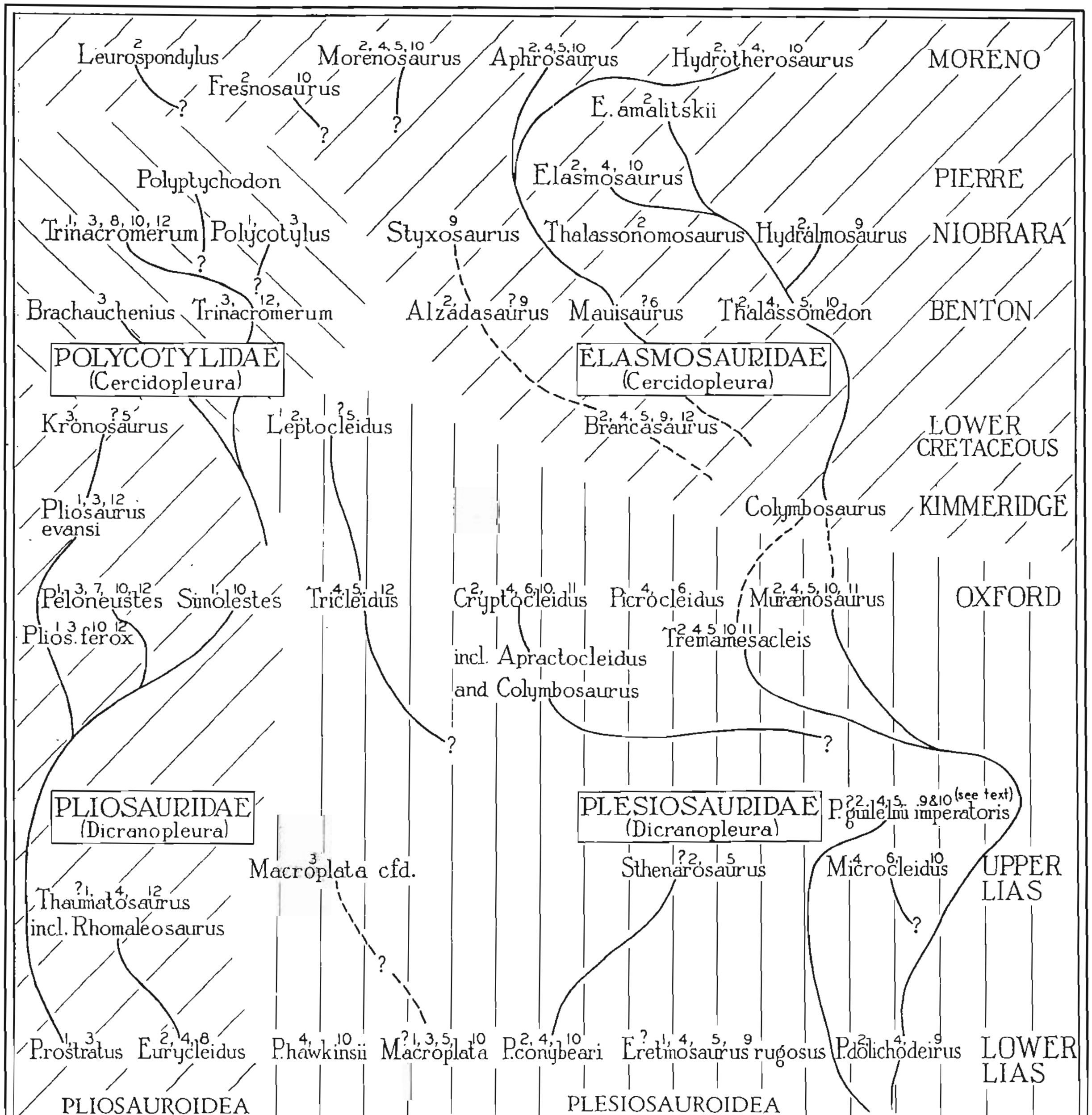

Fig. 37. Phylogeny of the Jurassic and Cretaceous Plesiosauria:

(1) Coracoids, pubes, and ischia long, scapulocoracoid vacuity small, humerus smaller than femur. (2) Coracoids, pubes, and ischia short, scapulocoracoid vacuity large, humerus larger than femur. (3) Long headed. (4) Short headed. (5) Interclavicle large, joining clavicles in squamous suture. (6) Interclavicle lost, clavicles meeting in midline. (7) Interclavicle triangular, clavicles lost [?]. (8) Interclavicle reduced, clavicles large. (9) Concave anterior pubic border. (10) Round anterior pubic border. (11) Odontoid large, intercentrum and arch reduced. (12) Odontoid ringed by large intercentrum and arches.

TABLE 14

Comparison of Genera of Elasmosauridae

	Vertebrae	Pectrum	Pelvis	Paddles
Alzadasaurus	Unknown.	Median bar absent. Scap. close to midline ant. Cor. long, projecting in front of scap. sut. Intercoracoid vacuity cordiform.	Median bar absent. Ant. border pubis concave (?).	Hum. massive; B. 80% of L. Capit. and troch. separated by at least ant. notch. Circular epipodial foramen.
Aphrosaurus type	Deep trough along ventral surface of post. cerv. 3 pect.; 17+ dors.	Icl. concave ant., without keel. Median bar absent. Cor. project in front of scap. sut. Intercor. vac. cordiform. Scapulae meet in midline.	Median bar absent. Ant. border pubis convex with small concavity.	Hum. straight and slender; B. 59% of L.; carp. 1 concave int.; mc. V hemicylindrical. Fem. B. 61% of L.; capit. and troch. united, no knee. No epipodial foramen.
Aphrosaurus referred	Lat. long. ridge on ant. 43 cerv.; all depressed. 57 cerv.; 3 pect.	Median bar absent. Scapulae meet in midline. Cor. project in front of scap. sut. Intercor. vac. cordiform.	?	Hum. B. 65% of L. Capit. and troch. united. No knee.
Elasmosaurus	Lat. long. ridge on all cerv. Ant. cerv. compressed. 76 cerv.; 3 pect.; 19 dors.; 2 sac.; 26 caud. =126	Median bar absent.	Median bar present. Ant. border pubis convex.	Unknown.
Fresnosaurus	Unknown.	Median bar absent. Coracoids short, wide, and massive, not reaching to scap. sut. in mid. Intercoracoid vacuity broad and cordiform.	Median bar absent. Ant. border pubis convex. Lateral concavity weak. Head of ischia narrow.	Hum. B. 62% of L. Capit. and troch. united (juvenile). Fem. B. 57% of L.
Hydralmosaurus	Lat. long. ridge on ant. cerv. only. Ant. cerv. less elongate than *Elasmosaurus*. 63 cerv.; 3 pect.; 19 dors.; 2 sac.; 17+8 caud. =112	Median bar absent. Scapulae wide apart anteriorly. Intercoracoid vacuity cordiform.	Ant. border pubis concave. Post. border pubis concave.	Hum. B. 78% of L. Very massive. Epipodials and mesopodials normal. Fem. B. 70% of L. Epipodial foramen present.
Hydrotherosaurus	Lat. long. ridge on ant. 40 cerv. only. All cerv. depressed. 60 cerv.; 2 pect.; 17 dors.; 3 sac.; 20 + 10 caud. =112	Median bar absent. Intercoracoid vacuity narrow ?	Median bar absent but pubes meet ischia. Ant. border pubis with small concavity; post. concavity strong.	Hum. B. 70% of L.; massive with "knee" on ant. distal border. Capit. and troch. partly separated. 1 supernumerary epipodial in brachium. Fem. B. 65% of L. Epipodial foramen present.
Leurospondylus	? 17+? dorsals.	Median bar absent. Cor. short, rel. broad, project barely beyond scap. sut. Intercoracoid vacuity roughly cordiform.	Median bar absent. Ant. border pubis convex; lateral concavity strong. Head of ischia wide.	Hum. B. 58% of L.; capit. and troch. united (juv.). Fem. B. 53% of L.

Morenosaurus	Lat. long. ridge absent on 15 post. cerv. Cerv. strongly depressed and with deep dorsal and ventral notches. 47 cerv.; 2 pect.; 17 dors.; 3 sac.; 30 caud. =99	Icl. weakly keeled. Median bar absent. Scapulae meet in midline. Intercor. vac. cordiform.	Median bar absent. Ant. border pubis convex with tiny concavity. Post. weakly concave. Isch. very short and massive.	Hum. B. 78% of L.; pointed post. dist. Capit. and troch. strongly separate. Fem. B. 72% of L.; hemisph. capit. and inclined troch. Epipodial foramen present.
Ogmodirus	15+ cerv. 18+ caudals.	?	?	Hum. B. 67% of L.; capit. and troch. united (juvenile). Fem. B. 59% of L.
Styxosaurus	28+ ? cerv.	Median bar absent. Scap. separated ant., vent. plate narrow. Cor. with long med. suture, proj. ant. to scap. sut. Intercoracoid vacuity cordiform.	Median bar absent. Ant. border pubis strongly concave.	Femur pendulous; B. 64% of L. Capit. and troch. united.
Thalassiosaurus	Unknown.	Median bar absent. Scapulae wide apart anteriorly.	Median bar absent? Ant. border pubis convex; post. border weakly concave. Ischia very short and massive.	Fem. B. 60% of L.
Thalassomedon	Lat. long. ridge on ant. 47 cerv. only. All cerv. and dors. depressed. 62 cerv.; 3 pect.; 25 dors.; 3 sac.; 21 caud. =114	Icl. strongly keeled. Median bar absent. Scapulae meet with long contact. Cor. post. to glenoid.	Median bar absent. Ant. border pubis convex, pubis symmetrical. Ischia very broad posteriorly.	Hum. B. 66% of L.; capit. and troch. united. Fem. B. 58% of L. 4 tarsalia. Epipodial foramen absent.
Thalassonomosaurus	Unknown.	Median bar absent. Scapulae meet in midline.	Median bar absent? Pubis unknown.	Hum. sigmoid; B. 58% of L. Supernumerary epipodials. [*T. nobilis* Fem. B. 61% of L.]

new suborder which she considered directly ancestral to the plesiosaurs. The palatal problem was thus solved. However, I believe that the early plesiosaurs are already so diverse that their origin cannot be confined to so narrow a "group" as the *Pistosauria.* Nor do the Jurassic and Liassic plesiosaurs show the convergence that would indicate a common origin in the Triassic.

To return to a consideration of the palatal relationships; in the first place we do not know the type of palate possessed by the ancestors of the nothosaurs. If they came directly from cotylosaurs, the closed palate could be derived from such a form as *Seymouria* by a simple posterior growth of the pterygoids along the midline. The fenestrated plesiosaur palate could then be considered an advanced type much as the fenestrated skull is an advance over the anapsid. In the second place, if we are forced to admit that the nothosaur palate is more specialized, we might then suggest that the plesiosaurs secondarily developed the interpterygoid vacuities. I see no reason why the attainment of a closed palate should fix this character permanently in the phyletic line.

In short, I do not believe that the nothosaur palate bars them from ancestry to the plesiosaurs.

The ancestry of the Sauropterygia has been sought by some, including Romer, among the Protorosauria, particularly *Araeoscelis*. Others, including Huene and Williston, derive the Sauropterygia from the Synapsida, while the Protorosauria are considered ancestral to the Squamata. Another group, including Baur, Boulenger, and Andrews, derive the plesiosaurs from the Rhynchocephalia.

Many complications are involved in either of the first two views, and the third has been abandoned by recent workers. In the first place, I believe that *Araeoscelis* has no direct relationships with the Protorosauria. In the second place, the Squamata are now known to have come from the Eosuchia; while the Synapsida, in the retention of a septomaxillary, the development of a massive vertical pterygoidal mandibular guide, and other characters, seem to me to exhibit a fundamentally different skull pattern.

Still another group, the Mesosauria, has been proposed as ancestral to the Sauropterygia. Unfortunately, the skull structure of the mesosaurs is still too poorly known to establish their exact systematic position.

Williston's interesting conclusion was based upon his conviction that the Squamata are directly descended from *Araeoscelis* and not from the diapsids. Furthermore, he united *Araeoscelis* with *Protorosaurus* and *Kadaliosaurus* into a group called Araeoscelidia or Protorosauria. After examining the figures of *Protorosaurus* and *Macrocnemus*, I am of the opinion that these are eosuchians, and therefore probably ancestral to the lizards and rhynchocephalians. Peculiarly enough, I therefore agree with Williston's conclusion that the "Protorosauria" are ancestral lizards; but my reasons are based on *Protorosaurus* and not on *Araeoscelis*. *Araeoscelis* I would remove to a place near the pachypleurosaurs, and I would place the other members of the "Protorosauria" in the Eosuchia, thus eliminating the group entirely.

Except that the temporal fossa is relatively larger in *Araeoscelis* than in *Pachypleurosaurus*, I see no grave objection to deriving the latter from the former. As for the remaining Nothosauria, I know of no Paleozoic reptiles that might be suggested as ancestors.

A review of the literature has shown that many species of plesiosaurs were based upon isolated vertebral centra. Vertebrae, because they are the most common remains, have thus assumed an unnatural taxonomic importance.

I have made a thorough attempt to use vertebral measurements and indices in classification, but since the results were unsatisfactory and largely negative, they will be presented here only in summary.

1. Vertebral proportions are ontogenetically variable, juvenile elasmosaurs having relatively broader centra.
2. Comparisons are therefore only valid between animals of similar size.
3. Cretaceous forms have relatively broader and higher centra than Jurassic.
4. Much more data is needed before significant results can be expected.

ELASMOSAURIDAE INCERTAE SEDIS

Many of the Cretaceous Plesiosauroidea from North America, and practically all of the foreign forms, have been described on isolated centra or short series of vertebrae. These, as indicated above, are indeterminate. Owen, Hector, and others have described the New Zealand material; Kipriianov, Bogolubov, Pravoslavlev, and others, that from Russia; yet no material warrants closer identification than to family. The evidence points to a world-wide distribution of the Elasmosauridae, but much more material is required to establish the ranges and relationships of the various genera. Until it is collected, the forms discussed below cannot be placed in smaller groups than the family Elasmosauridae.

Brimosaurus grandis Leidy, 1854

This form was based on four vertebrae from Greenville, Clark County, Arkansas. The vertebrae were never figured, and even if they had been it would be impossible in the present state of our knowledge to establish their taxonomic position without additional parts of the skeleton. Leidy referred in his original description to material collected by Albert Koch and sent to Berlin. This, Leidy wrote, came from the same state and probably the same individual.

In an attempt to trace this material and see if it would be possible to determine Leidy's specimen, I wrote to Dr. W. Janensch of the University of Berlin. He very kindly gave me all the pertinent information and also sent photographs. It will be seen in the following quotation from Dr. Janensch's letter that the Berlin specimen came not from Clark County, but from Hempstead County, and must therefore belong to a different specimen:

"Die Stücke sind aus der Sammlung des berühmten Physiologen und Anatomen Johannes Müller in unser Museum gelangt. Gesammelt sind sie von Koch in Arkansas; sie fanden sich 1–3 Fuss tief unter der Oberfläche an der Seite eines Hügels, der aus einem grau-grünen Kreidemergle besteht. Als Fundort is genamert: Arcansas Hemstad County. Es sind vorhanden 30 Wirbel oder Wirbelkörper, 8 unvollständige Rippen und zahlreiche Rippenfragmente, Fragmente von Neuralbögen, zahlreiche isolierte Querfortsätze, der distale Abschnitt einer Scapula (?), einige Phalangen . . ."

The upturned transverse processes of the dorsal vertebrae and the general proportions of the vertebrae are similar to *Dolichorhynchops osborni* Williston (1903). The Berlin specimen therefore seems to represent a short-necked form, but it is indeterminate.

Janensch notes further, "Unter den Wirbeln weicht No. 17 und ein zweiter, kleinerer, ähnlicher, durch seine gestreckte Form von den übrigen völlig ab; J. Müller charakterisiert diese beiden Wirbel als ähnlich dem *Plesiosaurus constrictus* Owen, was wegen der gestreckten Gestalt auch zutrifft. Alle übrigen Wirbel sind vom gleichen Typ. Unter diesen werden 19 als zusammengehörig bezeichnet . . ." This observation is apparently correct. Number 17 does represent a distinct type, probably an elasmosaurian as it is certainly dolichodiran.

This investigation, instead of clarifying *Brimosaurus*, uncovered evidence of three indeterminate Arkansas saurians, Leidy's *Brimosaurus* from Clark County and the two Berlin specimens from Hempstead County.

Cimoliasaurus Leidy

The genus *Cimoliasaurus* has been a "catch-all" from the start, reaching a climax Lydekker's "*Cimoliosaurus.*" Here 28 species were referred to this genus, yet a b examination of the type description will show that the genus is not determinab Leidy (1851) founded the genus and species *C. magnus* on 13 vertebrae from Burlingt County, New Jersey. These he figured later (1865) along with others from Monmouth County. All were referred to the same species. However, an examination of the measurements of the two series of vertebrae reveals proportional differences that are at least specific.

We must therefore restrict the species and the genus to the type specimen from Burlington County. Only 3 vertebrae of this specimen were ever figured and they are indeterminate.

Cope (1870) figured a series of cervicals, apparently *Cimoliasaurus*, to contrast them with his *Elasmosaurus*. He pointed out characters that separated the two genera, and might even have established the genus *Cimoliasaurus* if it were possible to identify the description with the type. It is dismaying to find that at least 34 species (Kuhn, 1935, lists 22) have been referred to this indeterminate genus! Most of this material is referable to the Elasmosauridae, but some of it, possibly including the type, may be placed in the Pliosauroidea.

Elasmosaurus sternbergi

This species was described by Williston (1906) because of the giant size of the vertebrae. The largest centrum measured 80, 140 and 165 mm. in length, height and breadth, and Williston estimated the total length at 60 feet (18 meters). The largest corresponding vertebra of *Thalassomedon* (table 3) measured 115, 145, and 170 mm., and the skeleton has a total length of 38.8 feet or 11.8 meters. Williston therefore considerably overestimated the size of his specimen and this has been perpetuated by various authors. This species is mentioned here to show that size of centrum is not an adequate character and to destroy the myth of a 60-foot elasmosaur.

No attempt is made to list all of the references to indeterminate forms, to compile lists of synonyms, or to include a complete bibliography, as these are already available in the literature (Kuhn, 1935; Camp and VanderHoof, 1940; Camp, Taylor, and Welles, 1942). Even though aided by the excellent skeletons at hand, I have been unable to identify many of the North American dolichodires from the literature. After a careful review, I now believe that 13 genera containing 14 species are determinable, and that the remainder are of value only in establishing the occurrence of a member of the Elasmosauridae (table 14). Topotype material may identify some of these fragmentary specimens, but until diagnostic parts of the skeleton are obtained it is useless to recognize many of the old genera and species. Such names as *Piratosaurus*, *Orophosaurus*, *Discosaurus*, *Piptomerus*, *Brimosaurus*, *Embaphias*, and *Cimoliasaurus* may be ignored until diagnostic material is collected from the type horizons. The accompanying table (table 15) shows the stratigraphic occurrences of North American Elasmosauridae.

TABLE 15

APPROXIMATE CORRELATION OF AMERICAN AND EUROPEAN UPPER CRETACEOUS

Europe	North America		
	Mid-Continent	Gulf	West Coast
Danian	Lance Laramie		
Maestrichtian	Fox Hills Pierre *Elasmosaurus platyurus*	Navarro	Edmonton (may = Moreno) *Leurospondylus ultimus* Moreno *Hydrotherosaurus alexandrae* *Aphrosaurus furlongi* *Morenosaurus stocki* *Fresnosaurus drescheri*
Campanian		Taylor	
Santonian	Niobrara *Hydralmosaurus serpentinus* *Thalassonomosaurus marshii* *Styxosaurus snowii* *T. nobilis*	Austin (Elasmosauridae, exact horizon unknown)	
Coniacian (Emsherian)	Benton *Alzadasaurus riggsi* *Ogmodirus martinii* *Thalassomedon haningtoni*	Eagle Ford	
Turonian	Dakota	Woodbine	

Elasmosauridae are known in Europe from the Upper Jurassic throughout the Upper Cretaceous.

SUMMARY

Four new genera of elasmosaurian plesiosaurs from the Upper Cretaceous Moreno formation of the Panoche Hills, Fresno Co., Calif., are described as follows:

1. *Hydrotherosaurus alexandrae* n. gen. and sp. A long-necked form with sixty cervicals and a 33 cm. skull; a narrow intercoracoid vacuity and long, distantly expanded coracoids; dorsal process of the scapula separated from the ventral plate by an anteriorly projecting shelf on the latter; large subrounded pubes and short ischia; propodials with the capitulum and tuberculum partly separated. This form was an active piscivore with long, flexible neck.

2. *Morenosaurus stocki* n. gen. and sp. A relatively short-necked dolichodire with 46 cervicals; a fused clavicular arch; a cordiform intercoracoid vacuity and relatively short posterior rami that are broadly expanded posteriorly; pubes broader than long; ischia short and very broad distally; propodials with capitulum and tuberculum completely separate. This reptile, to judge by the development of the propodials, was very active.

3. *Aphrosaurus furlongi* n. gen. and sp. A long-necked form with 57 cervicals; a deep median trough on the ventral side of the posterior cervicals; a fused clavicular arch, the interclavicle concave anteriorly; coracoids with long median symphysis, narrow posterior rami, and extreme posterior expansion; propodials slender, trochanter and capitulum continuous; epipodial foramen absent. This was a less active but longer-necked form than *Morenosaurus*.

4. *Fresnosaurus drescheri* n. gen. and sp. Length of neck unknown, but probably long; coracoids short, broad, and thick; wide cordiform intercoracoid vacuity; propodials massive; pubes subcircular and ischia extremely short anteroposteriorly.

5. *Thalassomedon haningtoni* n gen. and sp. A new plesiosaur from the Graneros shales, lower Benton Cretaceous of Colorado. A very large elasmosaur with a long neck of 62 cervicals and a 47-cm. skull; a fused clavicular arch with a keeled, anteriorly pointed interclavicle; scapulae meeting in midline and with broad dorsal process; pubes convex anteriorly, ischia widely expanded posteriorly; propodials relatively slender, the capitulum and trochanter confluent; epipodials relatively long; distal row of mesopodials consisting of four tarsalia and the fifth metapodial. This appears to have been a relatively inactive, gigantic plesiosaur.

6. *Elasmosaurus platyurus* Cope. Added knowledge gained from this new material makes it advisable to restrict the genus *Elasmosaurus* to the type species. The previously described elasmosaurs are therefore revised. The longest-necked plesiosaur known, with 74 cervicals, each of which bears a lateral longitudinal ridge; pectrum with median bar and broad dorsal processes of the scapulae; pelvis with median bar and convex anterior borders of the pubes.

7. *Hydralmosaurus serpentinus* (Cope) n. gen. A long-necked elasmosaur with 63± cervicals, lateral longitudinal ridge on anterior cervicals only; intercoracoid vacuity cordiform, the pectrum without the median bar; pubes concave anteriorly, without median bar; humerus very massive with capitulum and trochanter separated by grooves; epipodial foramen large.

8. *Alzadasaurus riggsi* n. gen. and sp. A medium-sized elasmosaur, length of neck unknown; scapulae narrow anteriorly, with broad dorsal processes; intercoracoid vacuity

cordiform and broad, coracoids relatively short; ischia with massive acetabular rami; humerus massive, capitulum and trochanter separated by anterior notch; ulna as broad as long, epipodial foramen large and round.

9. *Styxosaurus snowii* (Williston) n. gen. Skull about 48 cm., but length of neck unknown; anterior cervical vertebrae increase in size rapidly; coracoids with long median symphysis and short posterior processes; intercoracoid vacuity cordiform; pubes concave anteriorly; femur pendulous and slender.

10. *Thalassonomosaurus marshii* (Williston) n. gen. Scapulae with broad ventral plates meeting in midline and projecting toward the coracoids; humerus sigmoid and slender with distinct facet for supernumerary epipodial; ulna equal to radius.

11. *T. nobilis* (Williston). Femur slender, with facets for 3 epidopials.

12. *Thalassiosaurus ischiadicus* (Williston) n. gen. Pubes convex anteriorly but without the median bar; ischia short, as in *Hydralmosaurus serpentinus*, but more massive and with less concave anterior and posterior borders; femur slender, tibial and fibular facets in a nearly straight line.

13. *Ogmodirus martinii* Williston and Moodie. This juvenile has a neck of more than 51 vertebrae with relatively long centra; humerus stocky; femur slender; the head flat and sharply separated from the shaft.

14. *Leurospondylus ultimus* Brown. This is also a juvenile, but the centra are relatively broad and short; coracoids broad with cordiform intercoracoid vacuity and broad, moderately expanded posterior rami; humerus slender with head highly arched and confluent with shaft; pubes convex anteriorly, ischia short along the midline and deeply concave anteriorly; femur slender and almost symmetrical.

15. An evaluation of skeletal characters shows that relationships must be based upon a consideration of all possible features. The suborder Plesiosauria, of the order Sauropterygia, may thus be primarily divided into long-necked and short-necked groups, and these in turn may be divided into the more primitive Plesiosauridae and Pliosauridae, with double cervical rib heads and elongate epipodials, and the advanced Elasmosauridae and Polycotylidae, with single cervical rib heads and broad epipodials:

Suborder PLESIOSAURIA

Superfamily PLIOSAUROIDEA (= Brachyderia; short neck, long head, long ischia, pendulous propodials)
  Family Pliosauridae (dicranopleurous, long epipodials, Jurassic)
  Family Polycotylidae (cercidopleurous, short epipodials, Cretaceous)
Superfamily PLESIOSAUROIDEA (= Dolichodeira; long neck, short head, short ischia, stocky propodials)
  Family Plesiosauridae (dicranopleurous, long epipodials, Jurassic)
  Family Elasmosauridae (cercidopleurous, short epipodials, Upper Jurassic and Cretaceous)

16. The genera discussed above are all placed in the family Elasmosauridae, defined as follows: Plesiosauria with neck elongated to about 60 vertebrae; head small; ribs single-headed; anterior cervical ribs hatchet-shaped and fused to centra; clavicular arch fused; scapulae with broad flat ventral plates; coracoids separated posteriorly; pubes expanded and subrounded; ischia triangular and short; propodials massive; epipodials at least as broad as long.

Museum of Paleontology, University of California
Berkeley, California, February 1, 1941

LITERATURE CITED

Anderson, R., and Pack, R.

1915. Geology and oil resources of the west border of the San Joaquin Valley north of Coalinga, California. U. S. Geol. Surv. Bull. 603, 220 pp., 4 figs., 14 pls.

Andrews, C. W.

1896. On the structure of the plesiosaurian skull. Quart. Jour. Geol. Soc. London, 52, 246–253, 2 figs., 1 pl.

1910. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part I. London, xxiii + 205 pp., 94 figs., 10 pls.

1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). Quart. Jour. Geol. Soc. London, 78, 285–298, 1 fig., 2 pls.

Bogolubov, N. N.

1912. Note sur les plésiosaures du Jura Superieur de la Russie. Ann. Geol. Min. Russie, 14, 4–7.

Boulenger, G. A.

1917. On the use of the names Plesiosauria and Sauropterygia. Proc. Zoöl. Soc. London, parts 3 and 4, 221–222.

Broom, R.

1921. On the structure of the reptilian tarsus. Proc. Zoöl. Soc. London, no. 10, 143–155, 27 figs.

Brown, Barnum

1913. A new plesiosaur, *Leurospondylus*, from the Edmonton Cretaceous of Alberta. Bull. Amer. Mus. Nat. Hist., 32, 606–615, 7 figs.

Camp, C. L.

1942. California mosasaurs. Mem. Univ. Calif., 13:1, pp. vi + 68, 26 figs., 7 pls.

Camp, C. L., and Hanna, G. D.

1937. Methods in Paleontology. Univ. Calif. Press, xxiii + 153 pp., 58 figs.

Camp, C. L., and VanderHoof, V. L.

1940. Bibliography of fossil vertebrates 1928–1933. Geol. Soc. Amer., Special Papers no. 27, 1–503.

Camp, C. L., Taylor, D. N., and Welles, S. P.

1942. Bibliography of fossil vertebrates 1934–1938. Geol. Soc. Amer., Special Papers no. 42, 1–663.

Conybeare, W. D.

1821. Notice of the discovery of a new fossil animal, forming a link between the *Ichthyosaurus* and Crocodile, together with general remarks on the osteology of the *Ichthyosaurus*. Trans. Geol. Soc. London, 5, 559–594.

Cope, E. D.

1868. Note on the fossil reptiles near Fort Wallace. In J. L. LeConte, 1868, *vide infra*.

1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Trans. Amer. Philos. Soc. (n.s.), 14, viii + 252 pp., 55 figs., pls. 1–14*a*.

1877. Report on the geology of the region of the Judith River, Montana, and on the vertebrate fossils obtained on or near the Missouri River. U. S. Geol. Surv. Bull., 3, art. 19, 565–597, pls. 30–34.

1887. The sea saurians of the Fox Hills Cretaceous. Amer. Nat., 21, 563–566.

Dames, W.

1895. Die Plesiosaurier der süddeutschen Liasformation. K. Akad. Wiss. Berlin, phys.-math. Klasse, Abh. 1–83, figs. 1–3, pls. 1–5.

Edinger, T.

1935. *Pistosaurus*. Neues Jahrb. Min. Geol. Pal., 74, Beil.-B., Abt. B., 321–359, 9 figs.

Fraas, E.

1910. Plesiosaurier aus dem oberen Lias von Holzmaden. Palaeontogr., 57, 105–140, 10 figs., pls. 6–10.

Kiprijanov, W.

1882. Studien über die fossilen Reptilien Russlands. II. Theil. Gattung *Plesiosaurus* Conybeare aus den Severischen Sandstein oder Osteolith der Kreidegruppe. Mem. Acad. Imp. St. Petersb., ser. 7, 30, no. 6, 1–55, 19 pls.

KUHN, OSKAR

1935. Fossilium Catalogus, Animalia, pars 69, Sauropterygia, 1–127.

LECONTE, J. L.

1868. Notes on the geology of the survey for the extension of the U. P. Ry., E. D. [Union Pacific Railway, Eastern Division], from the Smoky Hill River, Kansas, to the Rio Grande. Philadelphia: Review Printing House, 76 pp.

LEIDY, J.

1851. [Description of fossils.] Proc. Acad. Nat. Sci. Phila., 5, 325–328.

1854. [Remarks on extinct saurian from Greenville, Clark County, Arkansas.] Proc. Acad. Nat. Sci. Phila., 7, 72, 1 pl.

1865. Cretaceous reptiles of the U. S. Smithson. Contr. to Knowledge, 192, 1–135, 20 pls.

LINDER, H.

1913. Beiträge zur Kenntnis der Plesiosaurier—Gattungen *Peloneustes* u. *Pliosaurus*. Nebst Anhang: Ueber die beiden ersten Halswirbel der Plesiosaurier. Geol. Pal. Abh., 11 (15):1, 339–409, 40 figs., 4 pls.

LYDEKKER, R.

1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum. Part 2. Orders Ichthyopterygia and Sauropterygia. London: xxi + 307 pp., 85 figs.

MEHL, M. G.

1912. *Muraenosaurus ? reedii* sp. nov. and *Tricleidus ? laramiensis* Knight, American Jurassic plesiosaurs. Jour. Geol., 20, 344–352, 3 figs.

NOPCSA, BARON F.

1928. The genera of reptiles. Palaeobiol., 1, 163–188.

OWEN, R.

1840. Report on British fossil reptiles. Rept. Brit. Assoc. Adv. Sci., 9, 43–126.

1865. Monograph of the fossil Reptilia of the Liassic formations. Part first. Sauropterygia. Monog. Palaeontogr. Soc., 1–40, pls. 1–16.

PEYER, B.

1931. Die Triasfauna der Tessiner Kalkalpen. IV. *Ceresiosaurus calcagnii* nov. gen. nov. sp. Abh. Schweiz. Pal. Ges., 51, 1–68, figs. 1–31, pls. 18–24.

1933–1934. Die Triasfauna der Tessiner Kalkalpen. VII. Neubeschreibung der Saurier von Perledo. Abh. Schweiz. Pal. Ges., 53 and 54, pp. 3–130, figs. 1–14, pls. 31–41.

1935. Die Triasfauna der Tessiner Kalkalpen. X. *Clarazia schinzi* nov. gen. nov. sp. Abh. Schweiz. Pal. Ges., 57, 1–61, figs. 1–34, pls. 47–49.

PRAVOSLAVLEV, P. A.

1916. On the problem of the pectoral girdle in the *Elasmosaurus* Cope. Bull. Imp. Acad. St. Petersb., ser. 6, 10, no. 5, 327–343, 1 pl.

1916a. Restes d'un *Elasmosaurus* trouvés dans le Crétacé Superieur de la province du Don. Trav. Soc. Imp. Nat. Petrograd, 38, v + 153–334, 4 tables, 11 pls. (Russian, with French résumé).

1918–1919. Geological distribution of the Elasmosauri. Izvestiia Rosseeskoi Akademi Nauk, ser. 6, 12, part 2, 1956–1978, and 2325–2343.

RIGGS, E. G.

1939. A specimen of *Elasmosaurus serpentinus*. Field Mus. Nat. Hist., Geol. Ser., 6, no. 25, 385–391, 3 figs.

ROMER, A. S.

1933. Vertebrate paleontology. Univ. Chicago Press, vii + 491 pp., 359 figs.

RUSSELL, L. S.

1935. A plesiosaur from the Upper Cretaceous of Manitoba. Jour. Pal., 9, no. 5, 385–389, 3 pls.

SAUVAGE, H. E.

1879. Note sur quelques plésiosauriens de terrains jurassiques superieurs de Boulogne-sur-mer. Ann. Sci. Nat., (6), Zool. et Pal., 8, art. 6.

Seeley, H. G.
1874. Note on some of the generic modifications of the plesiosaurian pectoral arch. Quart. Jour. Geol. Soc. London, 30, 436–449, 13 figs.
1892. The nature of the shoulder girdle and clavicular arch in Sauropterygia. Proc. Roy. Soc. London, 51, 119–151, 15 figs.
Sollas, W. J.
1881. On a new species of plesiosaurs (*P. conybeari*) from the Lower Lias of Charmouth; with observations on *P. megacephalus*, Stutchberry, and *P. brachycephalus*, Owen. Quart. Jour. Geol. Soc. London, 37, 472–481, figs. 8–14, pls. 23, 24.
Stock, C.
1939. Occurrence of Cretaceous reptiles in the Moreno shales of the southern Coast Ranges, California. Proc. Nat. Acad. Sci. Phila., 25, no. 12, 617–620, 1 fig., 1 pl.
Watson, D. M. S.
1924. The elasmosaurid shoulder-girdle and fore-limb. Proc. Zoöl. Soc. London, 1924:2, 885–917, 12 figs.
Wegner, Th.
1914. *Brancasaurus brancai* n. g. n. sp., ein Elasmosauride aus dem Wealden Westfalens. Brancafestschrift. Berlin: Borntraeger, pp. 235–305, figs. 1–10, pls. 5–9.
White, T. E.
1940. Holotype of *Plesiosaurus longirostris* Blake and the classification of the plesiosaurs. Jour. Pal., 14, no. 5, 451–467, 13 figs.
Williston, S. W.
1890. A new plesiosaur from the Niobrara Cretaceous of Kansas. Trans. Kansas Acad. Sci., 12, 174–178, 2 figs.
1903. North American plesiosaurs. Part 1. Publ. no. 73, Field Columbian Museum, 3–77, 13 figs., 29 pls.
1906. North American plesiosaurs, *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. Amer. Jour. Sci., ser. 4, 21, 221–236, 5 figs., 6 pls.
1914. Water reptiles of the past and present. Univ. Chicago Press, vii + 251 pp., 131 figs.
1925. The osteology of the reptiles. Arranged and edited by W. K. Gregory. Harvard Univ. Press, xiii + 300 pp., 191 figs.
Williston, S. W., and Moodie, R. L.
1913. A new plesiosaurian genus from the Cretaceous of Kansas. Bull. Geol. Soc. Amer., 24, 120–121 (abstract).
1917. *Ogmodirus martinii*, a new plesiosaur from the Cretaceous of Kansas. Kansas Univ. Sci. Bull., 10, 61–73, 3 figs., 5 pls.
Woodward, A. S.
1932. In Zittel, Textbook of Paleontology, 2. Second English ed. revised, with additions by Sir Arthur Smith Woodward, F. R. S. London: Macmillan & Co., Ltd., St. Martin's Street, xvii + 464 pp., 533 figs.
Zangerl, R.
1935. B. Peyer, die Triasfauna der Tessiner Kalkalpen. IX. *Pachypleurosaurus edwardsi*, Cornalia sp. Abh. Schweiz. Pal. Ges., 56, 1–80, figs. 1–43, 2 pls.
Zarnik, B.
1926. K etologiji plesiosaurija, sa prinosima mechanici kraljeznice u. recentnik sauropsida. Soc. Scient. Natur. Croat. Glasnik, 38–39, 424–472, 22 figs., 1 pl. [with German summary].

PLATES

PLATE 12

Hydrotherosaurus alexandrae, type. Skull. U. C. Mus. Pal. no. 33912. × 1/2.

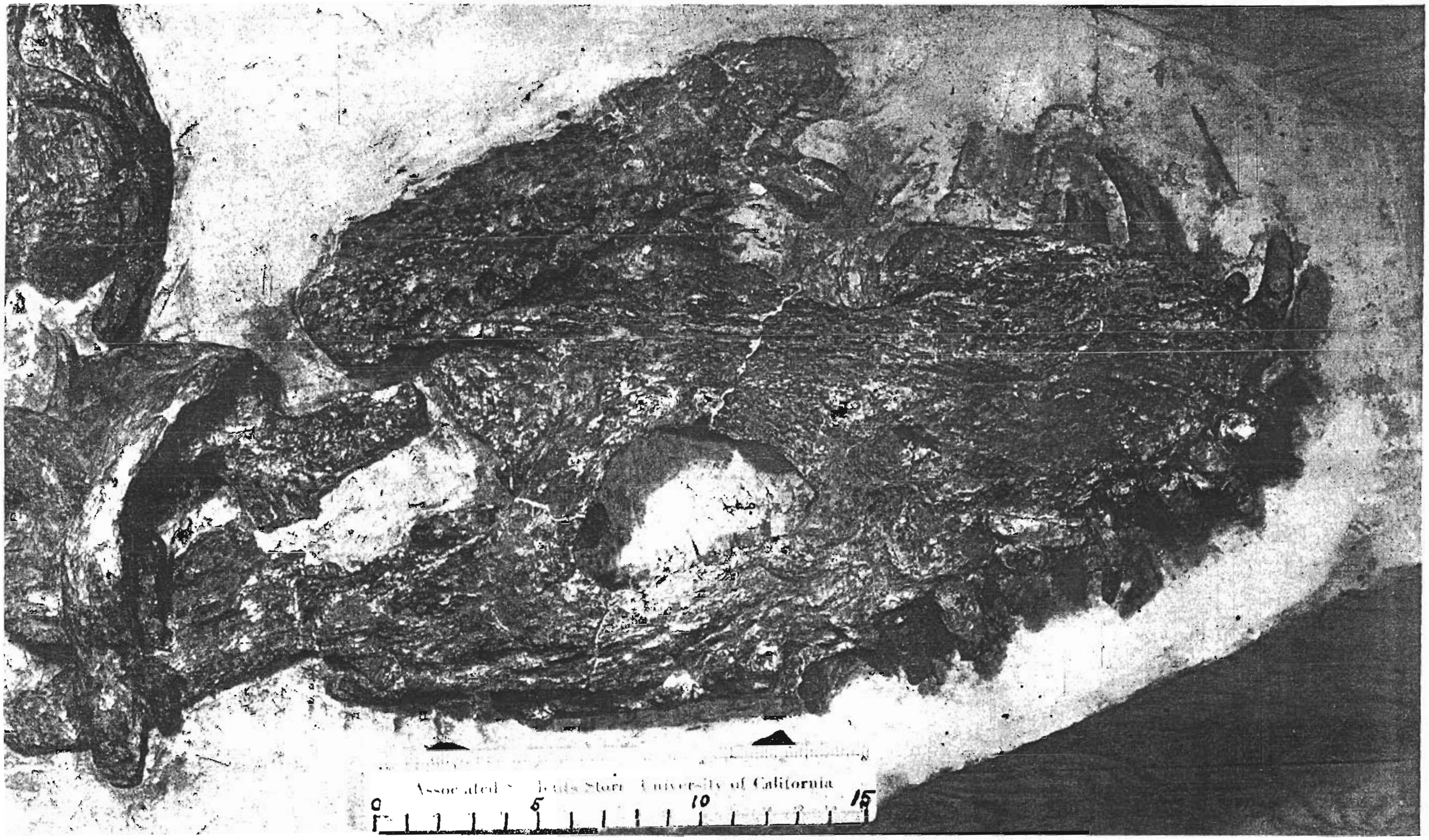
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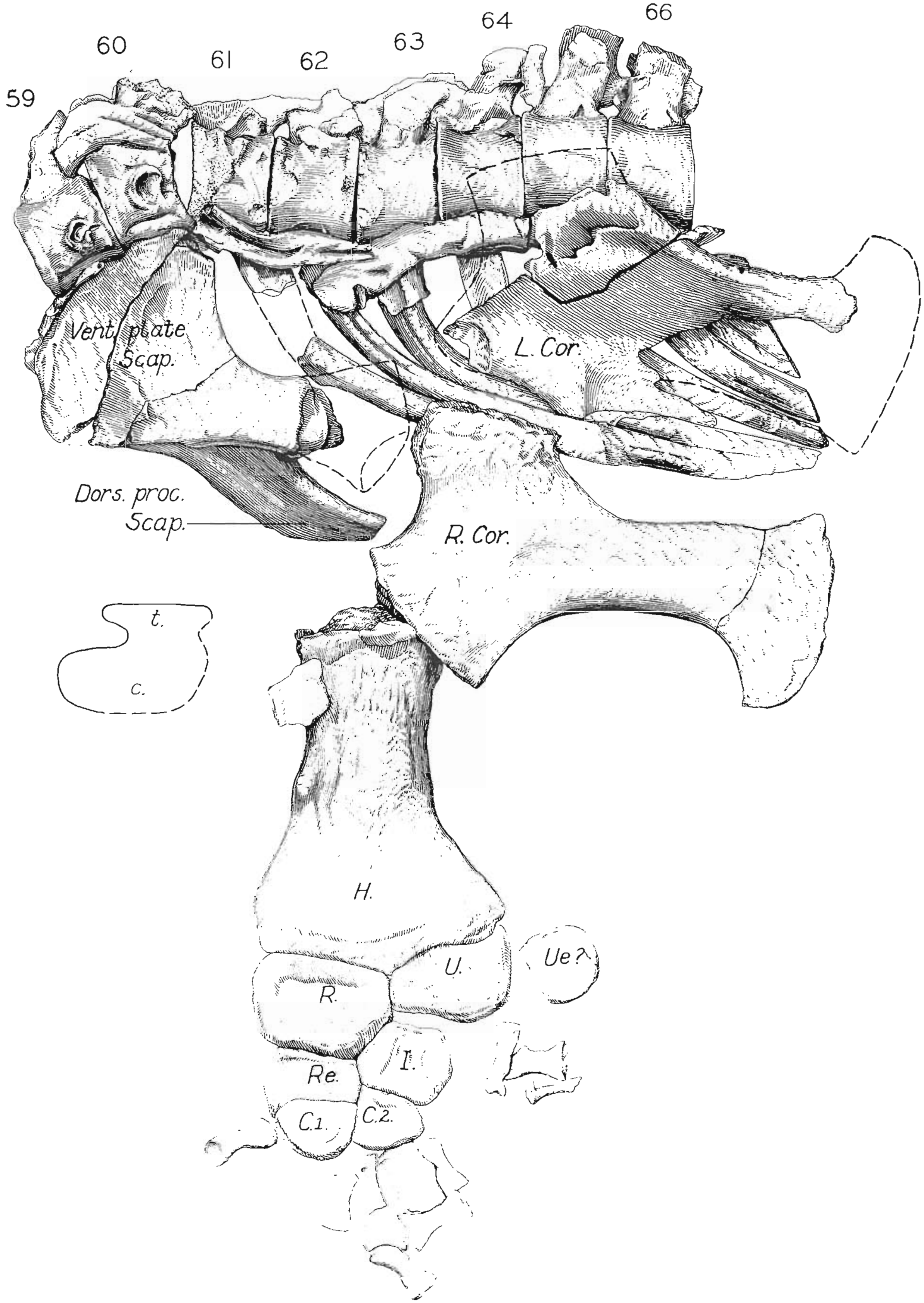
PLATE 13

Hydrotherosaurus alexandrae, type. Ventral view of shoulder region in position of burial. U. C. Mus. Pal. no. 33912. × 1/6.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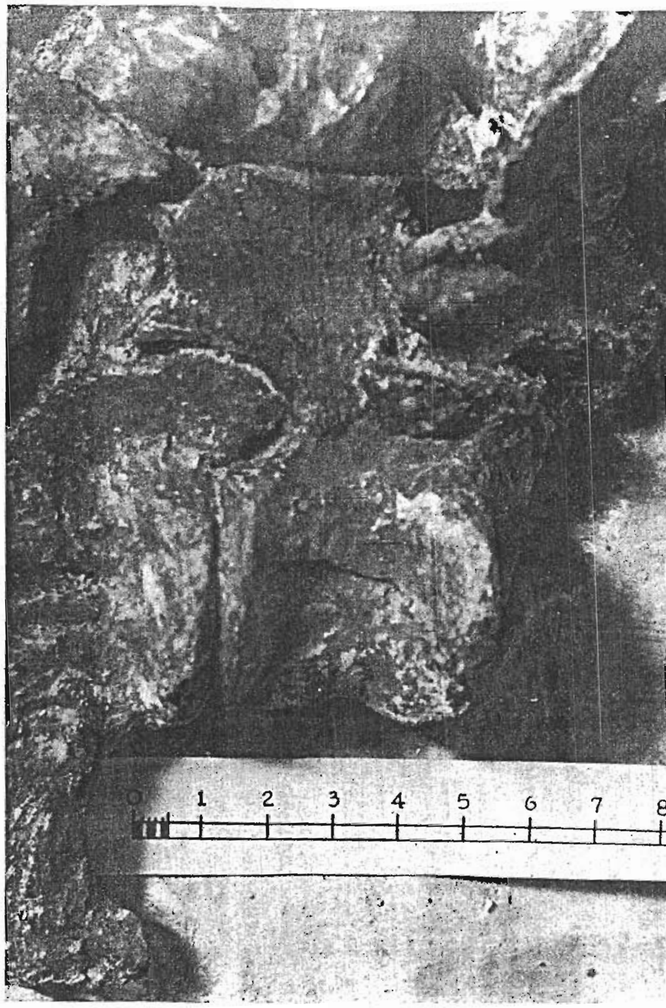
C.2.

PLATE 14

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. Right lateral views of anterior cervical vertebrae. *a.* Sixth. *b.* Tenth. *c.* Fifteenth. *d.* Twentieth.



a

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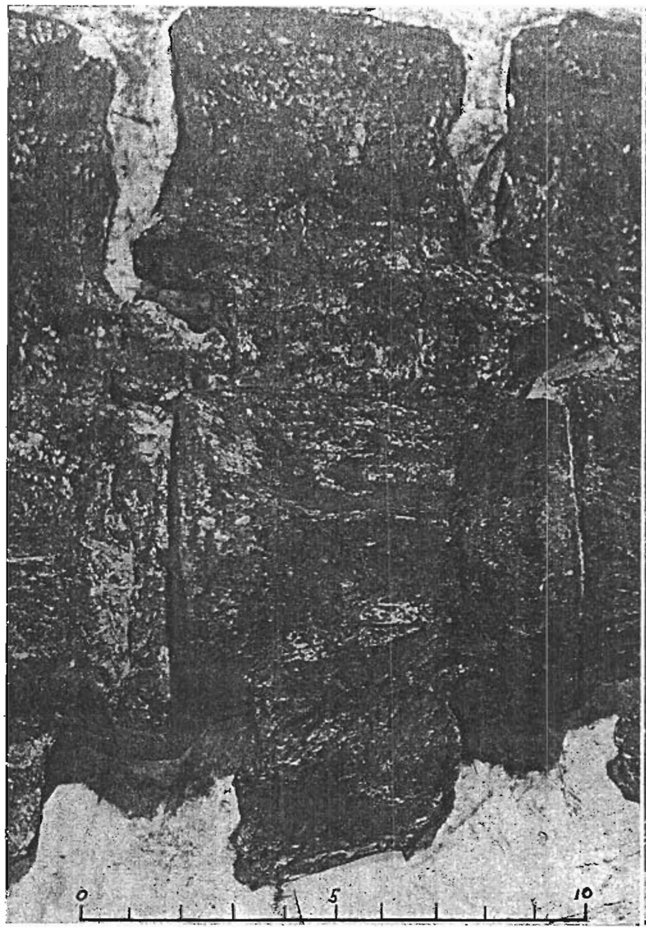
PLATE 15

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. Right lateral views of median cervical vertebrae. *a.* Twenty-sixth. *b.* Thirtieth. *c.* Thirty-fifth. *d.* Fortieth.



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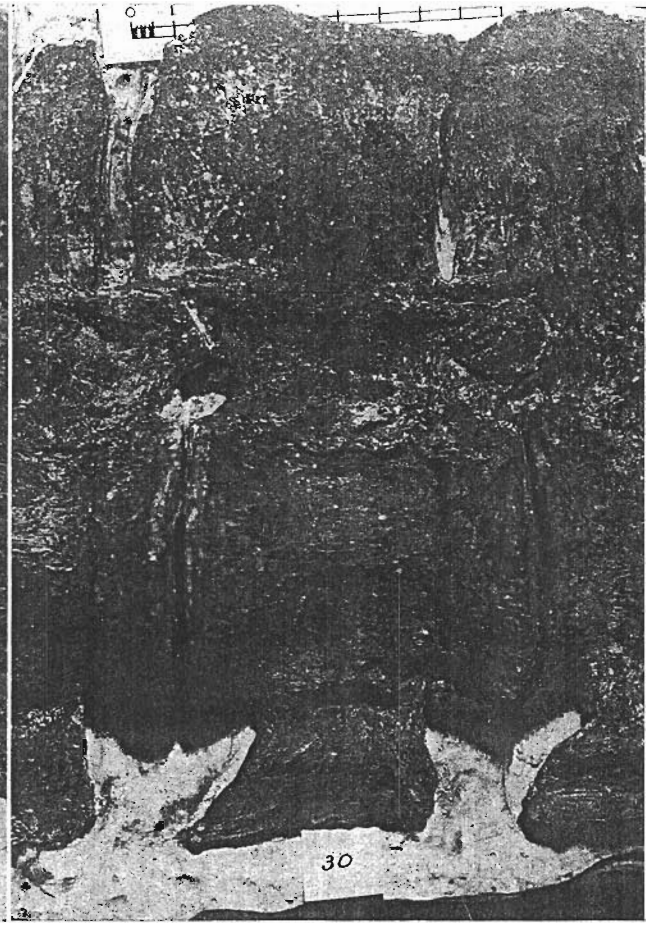

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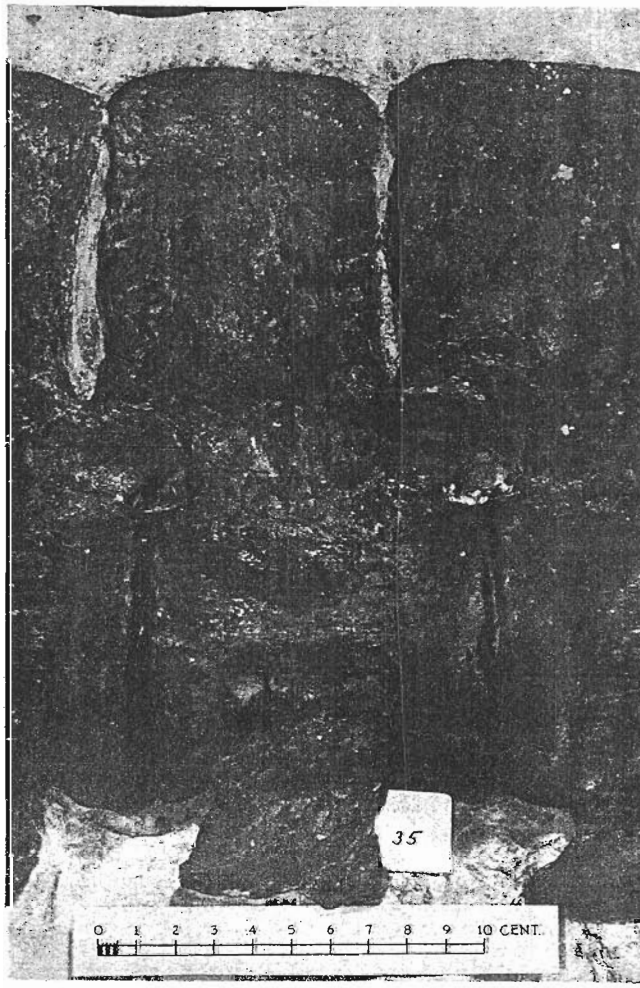

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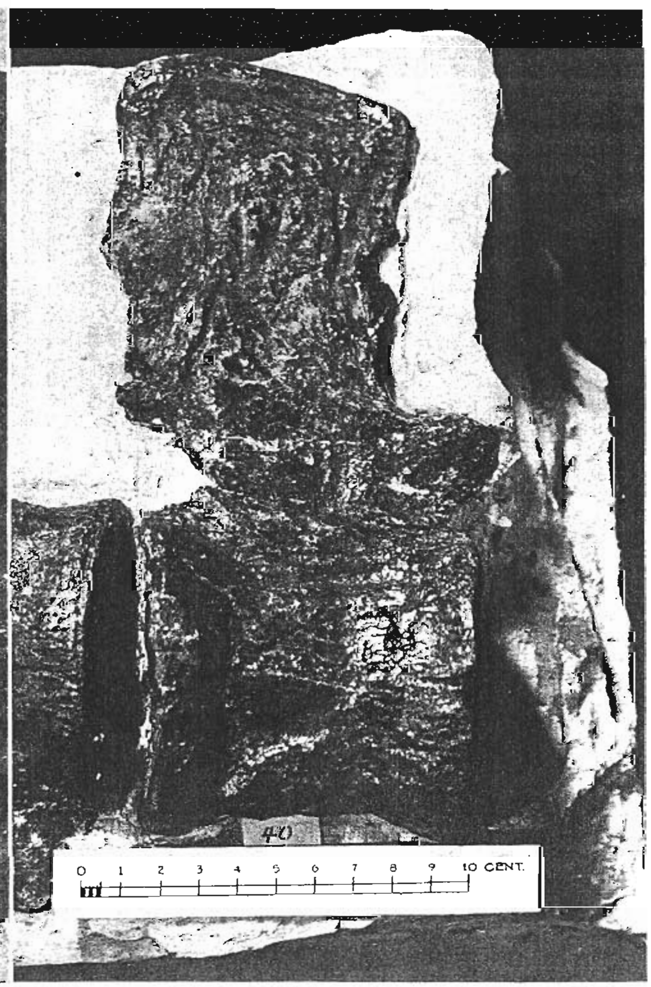

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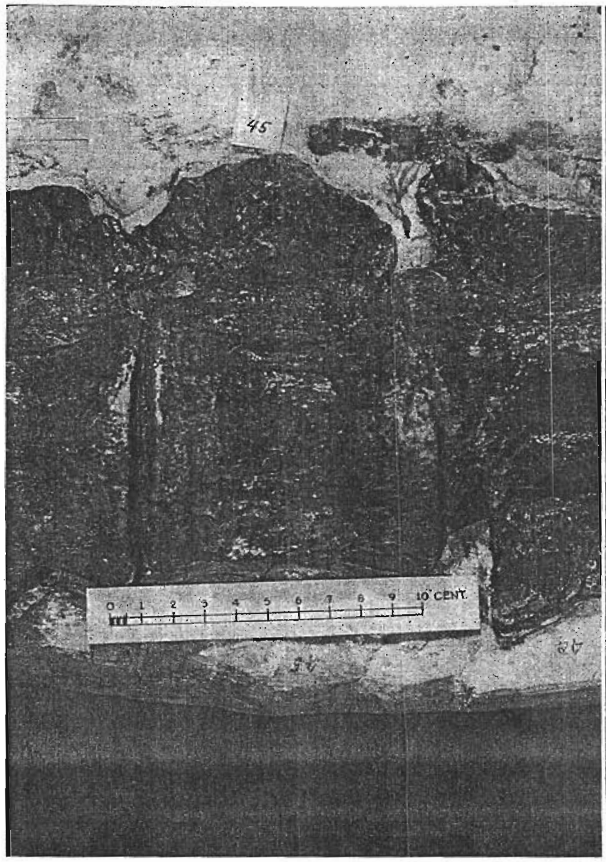
PLATE 16

Hydrotherosaurus alexandrae, Type. U. C. Mus. Pal. no. 33912. Right lateral views of posterior cervical vertebrae. *a*. Forty-fifth. *b*. Fiftieth. *c*. Fifty-fifth and fifty-sixth. *d*. Fifty-seventh and fifty-eighth.



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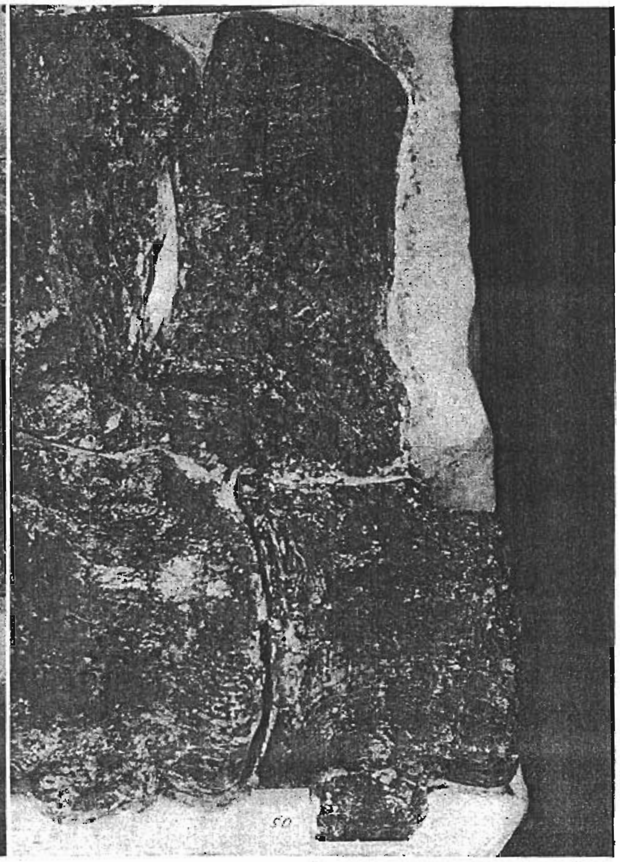

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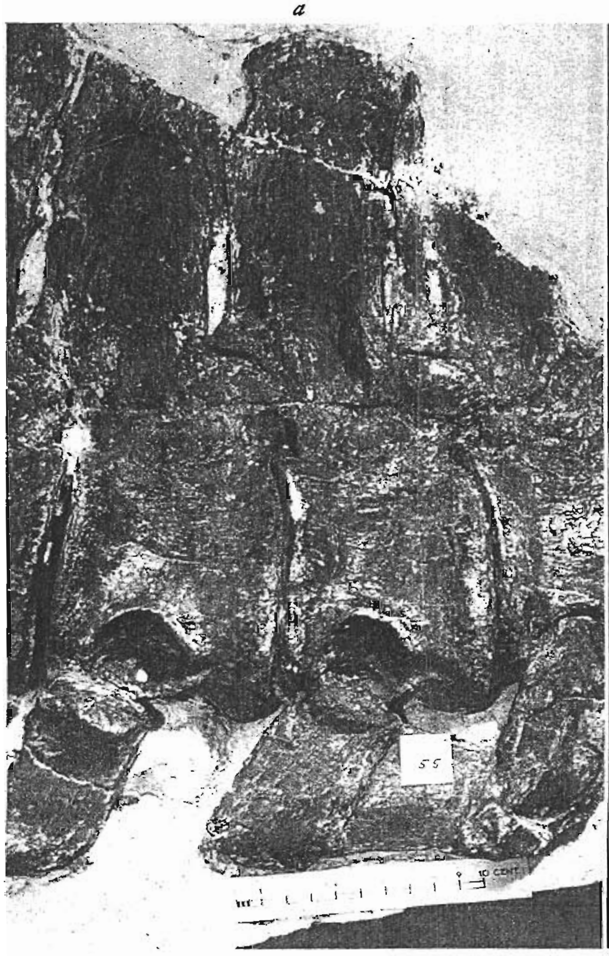
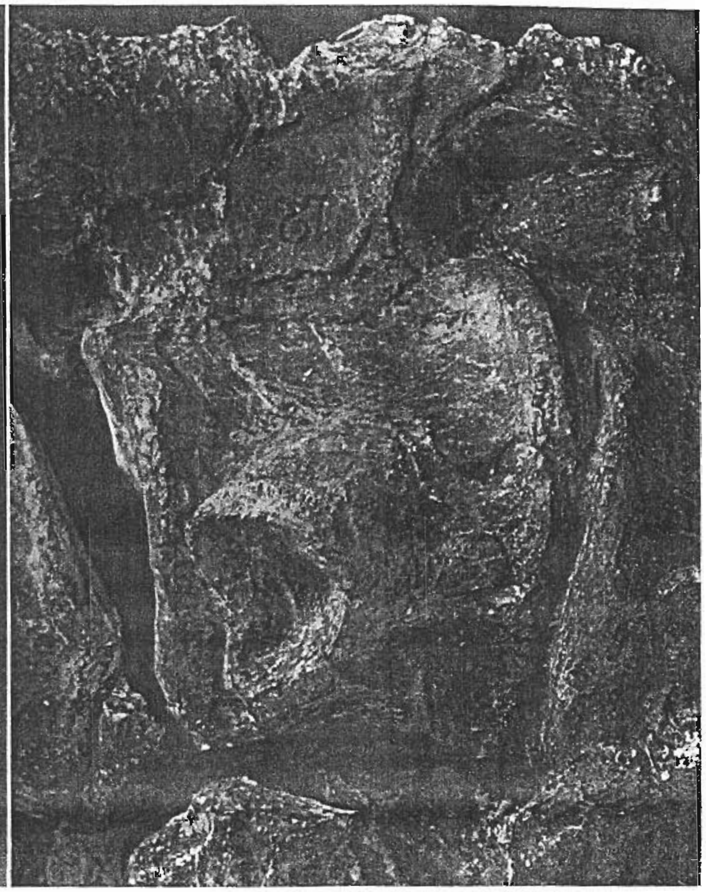


PLATE 17

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. Right lateral views of last two cervical and the two pectoral vertebrae. *a*. Fifty-ninth. *b*. Sixtieth (last cervical). *c*. Sixty-first (first pectoral). *d*. Sixty-second (second pectoral).

a



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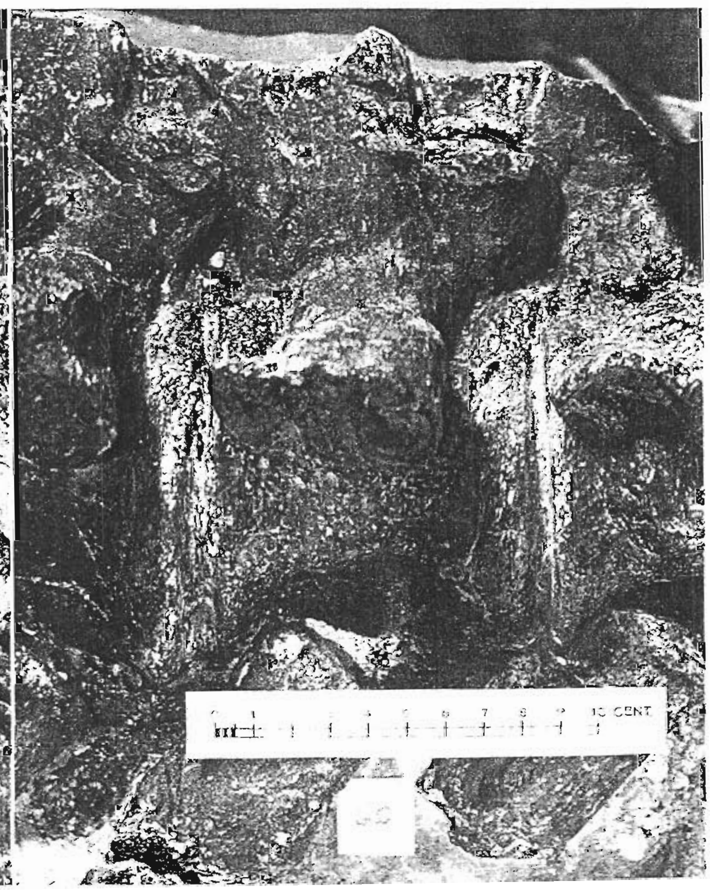

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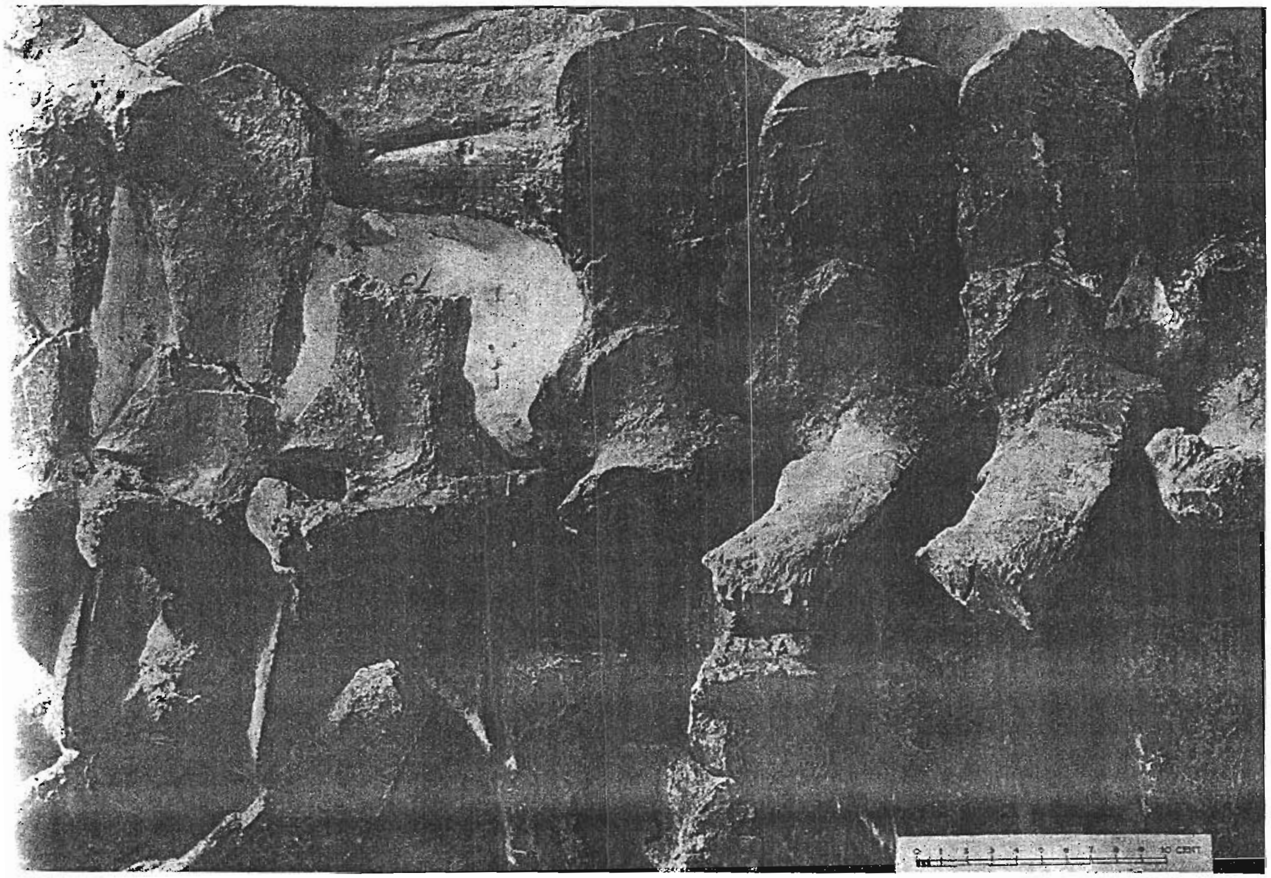
PLATE 18

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. Lateral views of dorsal vertebrae. *a.* Seventieth to seventy-fourth (eighth to twelfth dorsals). *b.* Seventy-fourth to seventy-eighth (twelfth to sixteenth dorsals).



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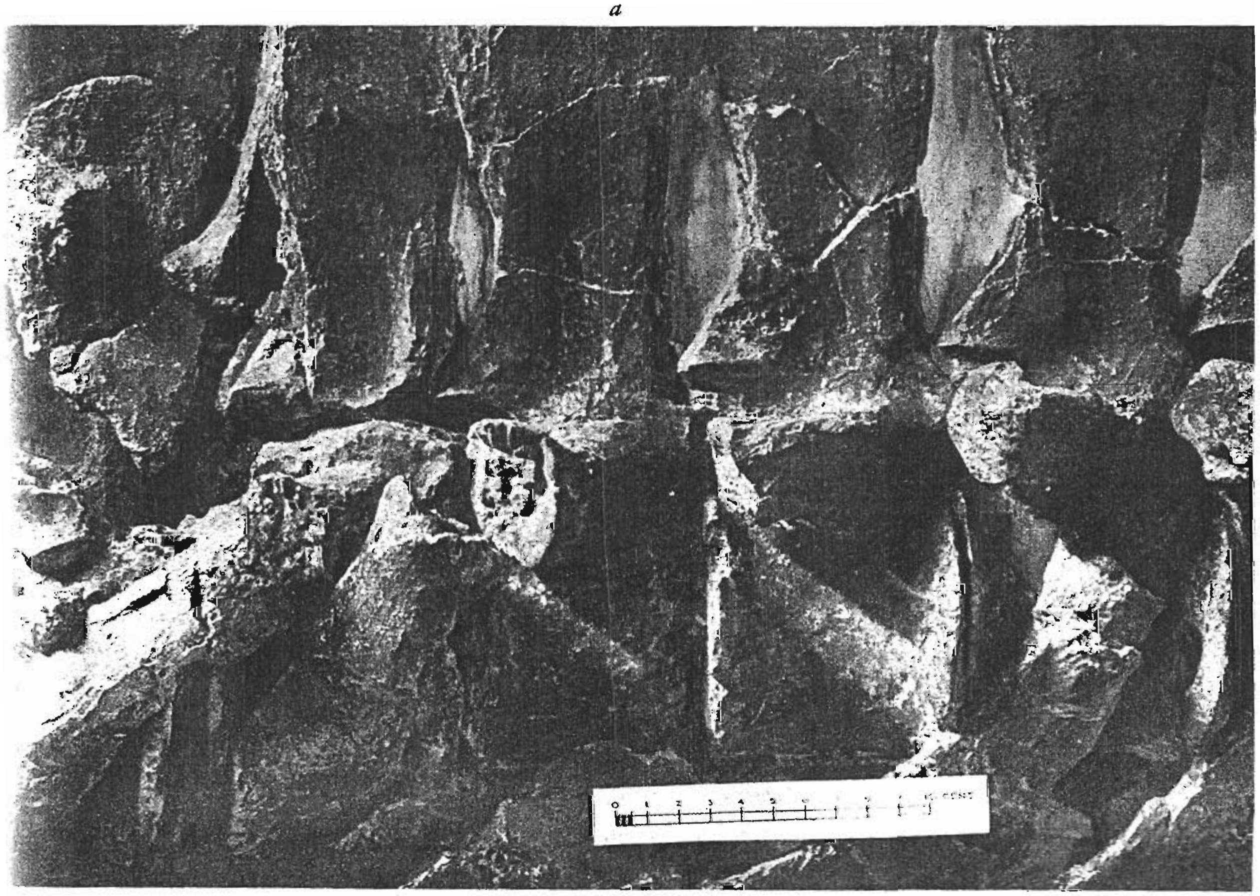

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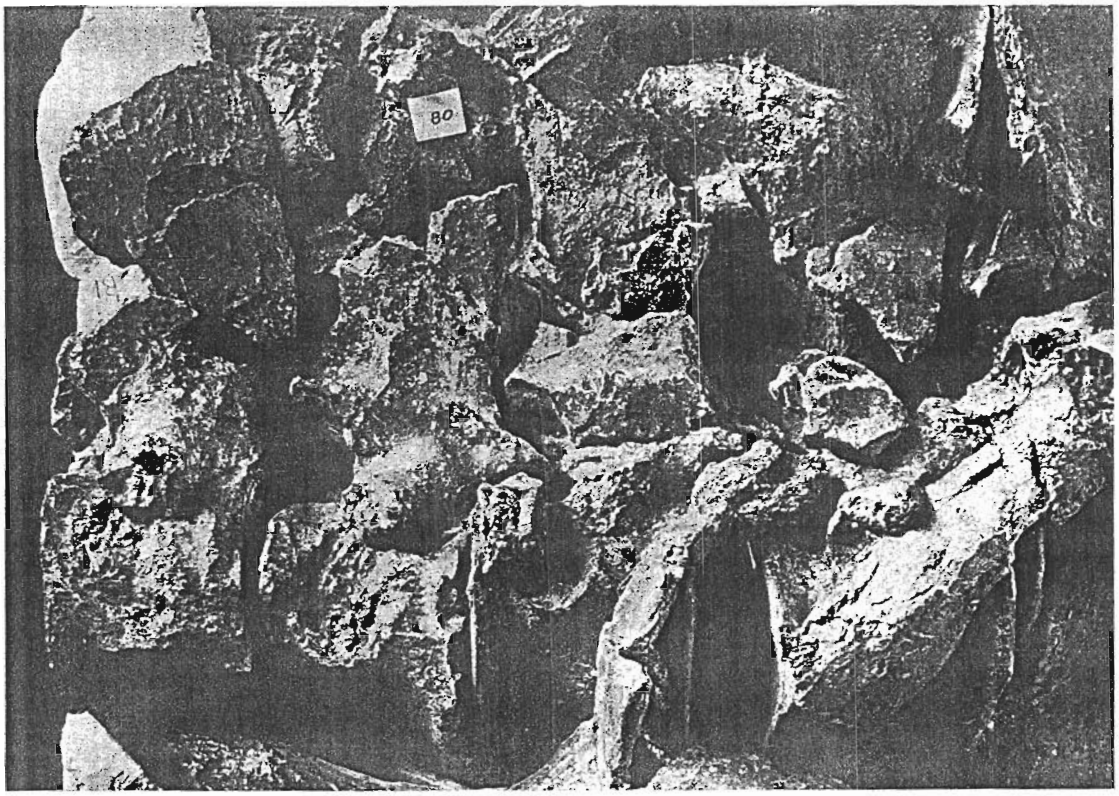
PLATE 19

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. *a*. Lateral view of vertebrae seventy-eight to eighty-one (sixteenth and seventeenth dorsals and the first two sacrals). *b*. Visceral view of right coracoid. *c*. Lateral view of right humerus and proximal paddle.



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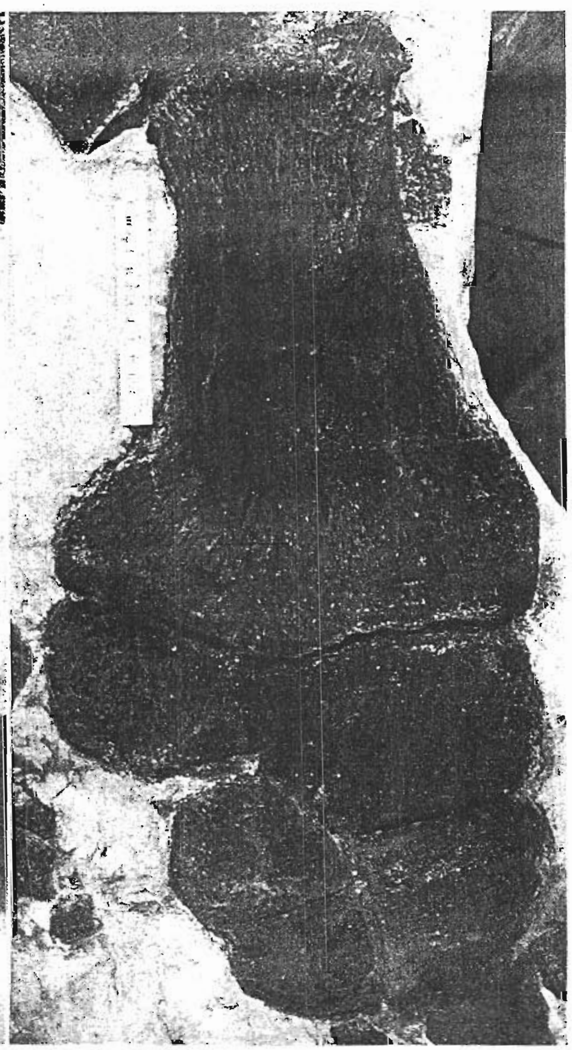

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PLATE 20

Hydrotherosaurus alexandrae, type. U. C. Mus. Pal. no. 33912. *a*. Lateral view of right ilium and two sacral ribs. *b*. Visceral view of left pubis. *c*. Lateral view of left pelvic paddle. *d*. Proximal end of right femur. *e*. Lateral view of same.

a

b

d

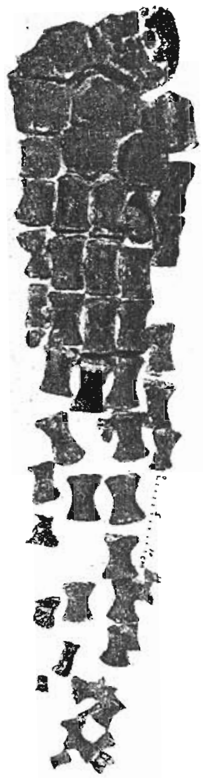

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PLATE 21

Hydrotherosaurus alexandrae, type. Skeleton in position of burial, but turned over upon left side during preparation. U. C. Mus. Pal. no. 33912. Length of specimen, 806 cm.

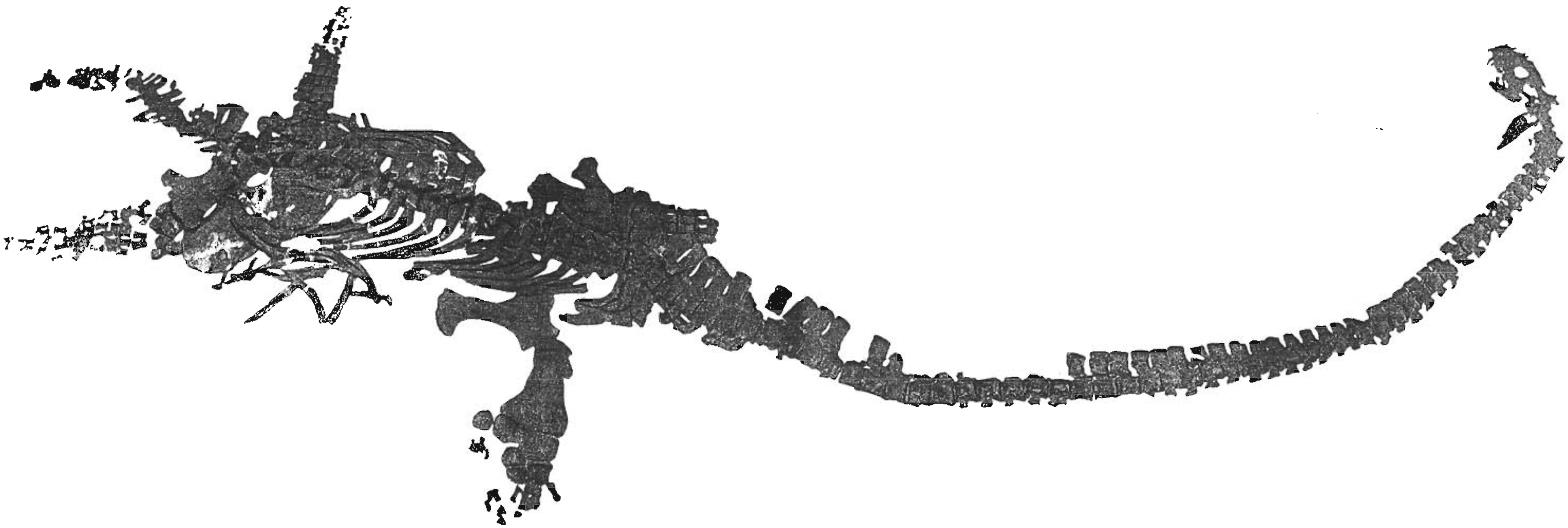
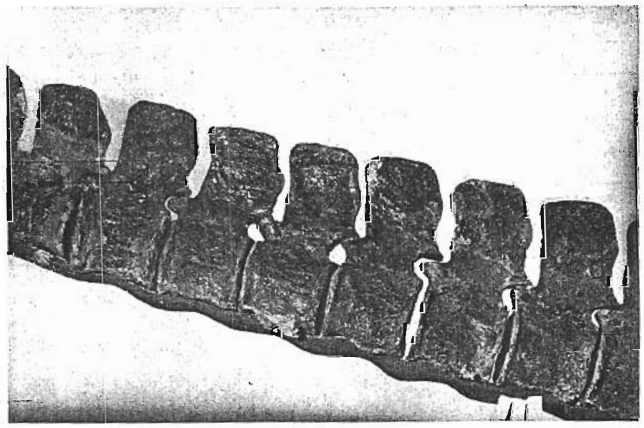


PLATE 22

Thalassomedon haningtoni, type. C. M. N. H. no. 1588. *a*. Left lateral view of fused atlas and axis. *b*. Left lateral view of 40th to 46th cervical vertebrae. *c*. Left lateral view of 62d to 67th vertebrae (last cervical, the 3 pectorals and the first 2 dorsals). *d*. Right lateral view of 70th to 77th vertebrae (5th to 12th dorsals). *e*. Left lateral view of 77th to 85th vertebrae (12th to 20th dorsals). *f*. Left lateral view of 102d to 114th vertebrae (9th to 21st caudals).

a



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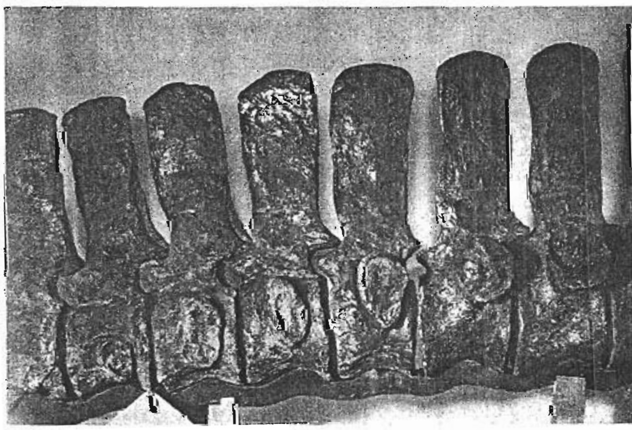

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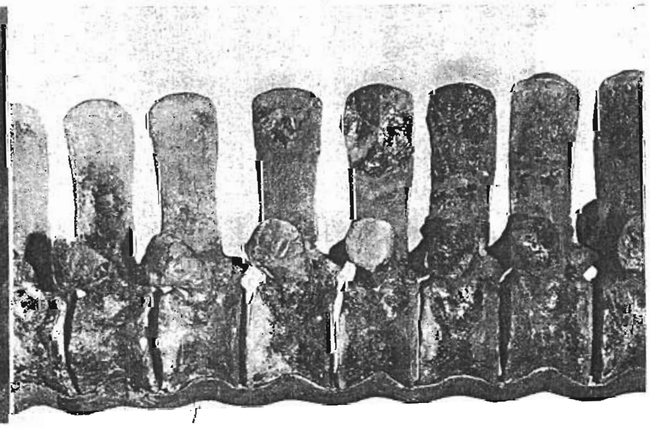

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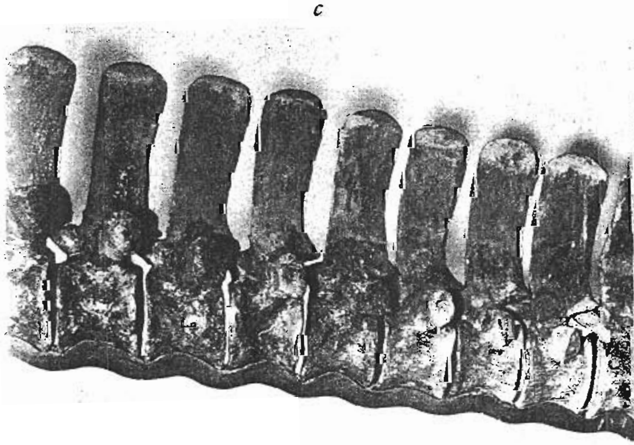

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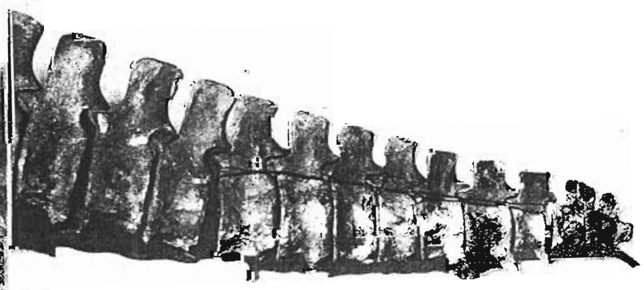
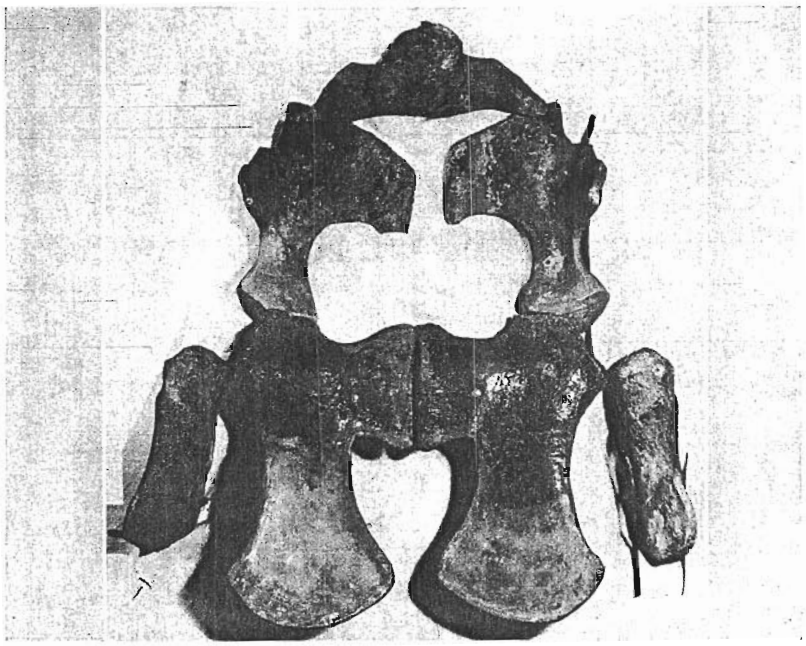


f

PLATE 23

Thalassomedon haningtoni, type. C. M. N. H. no. 1588. *a*. Visceral view of restored pectrum and humeri. *b*. Visceral view of pelvis, ilia extended laterally.



a

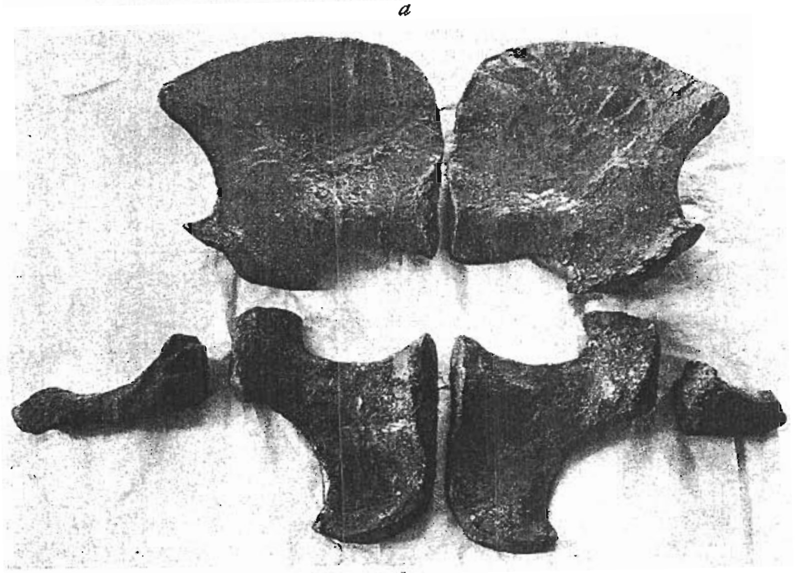


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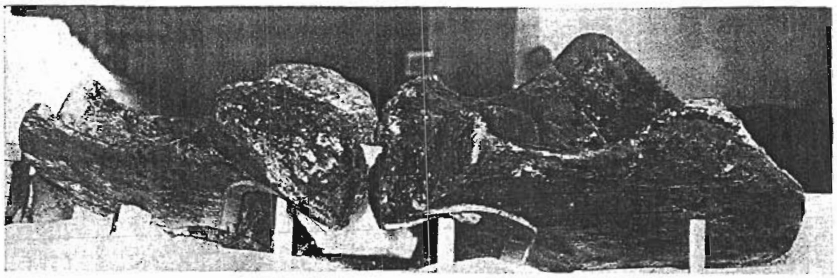
PLATE 24

Thalassomedon haningtoni, type. C. M. N. H. no. 1588. *a*. Right lateral view of pubes and ischia. *b*. Internal view of left pelvic paddle and vertebrae 95 through 102 (2d through 9th caudals). *c*. Lateral view of left pelvic paddle removed from matrix and articulated.



a

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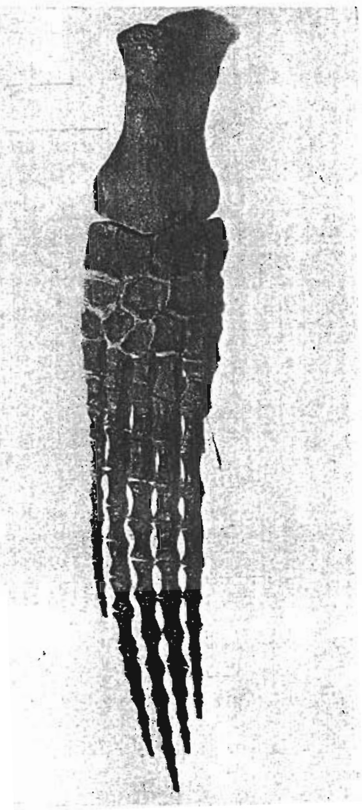


c

PLATE 25

Morenosaurus stocki, type. C. I. T. no. 2802. × 1/10. *a*. Left lateral view of 11th, 10th, and 9th prepectoral vertebrae. *b*. Left lateral view of last two cervicals and the two pectoral vertebrae. *c*. Proximal view of 8th dorsal vertebra. *d*. Proximal view of 11th dorsal vertebra. *e*. Left lateral view of last dorsal, 3 sacral, and 2 anterior caudal vertebrae. *f*. Ventral view of 7th caudal vertebra. *g*. Posterior view of 8th caudal vertebra. *h*. Left lateral view of 10th caudal vertebra. *i*. Left lateral view of 24th to 30th caudal vertebrae. *j*. Visceral view of pubes and ischia, internal view of left ilium and posterior view of right.

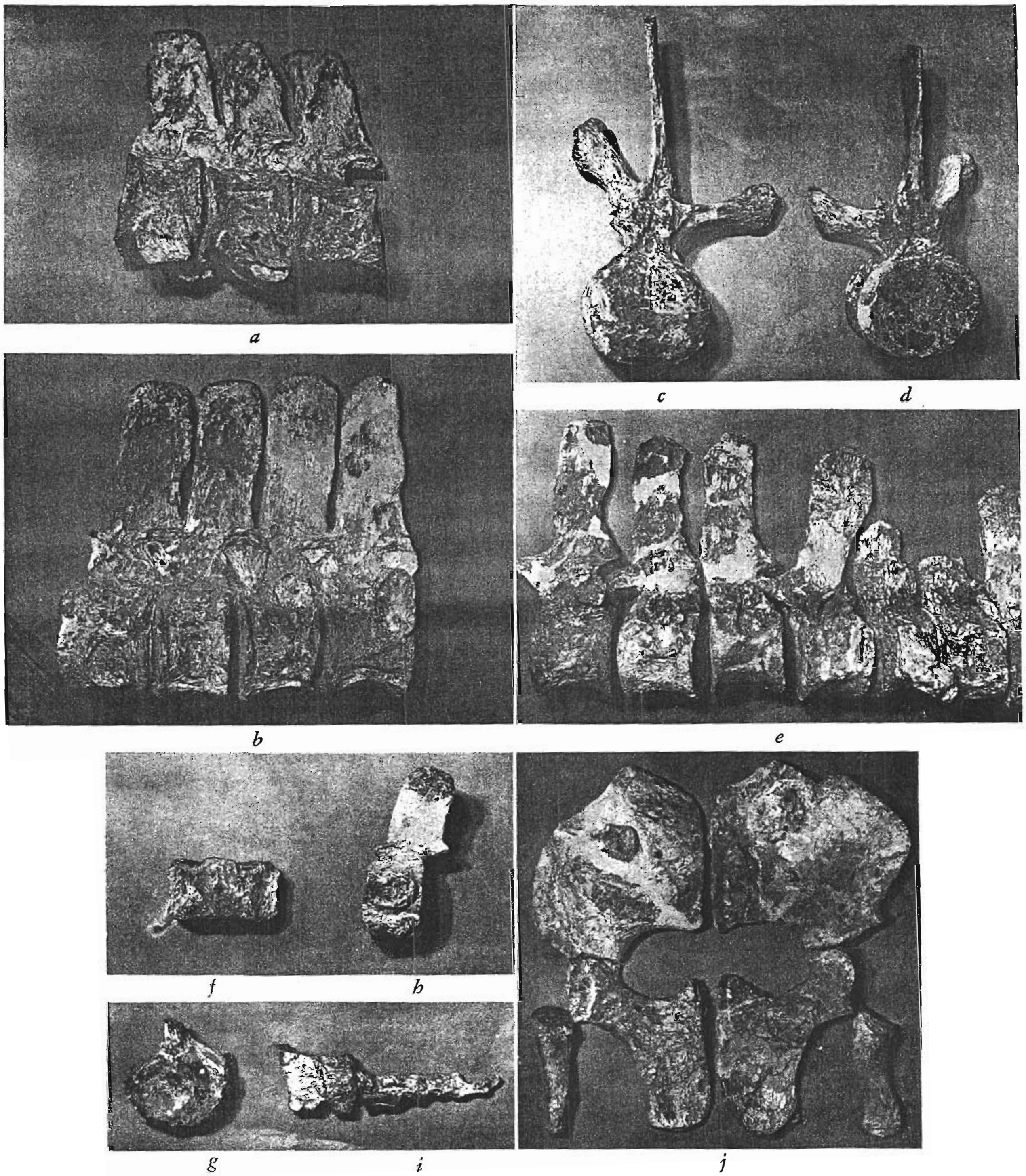
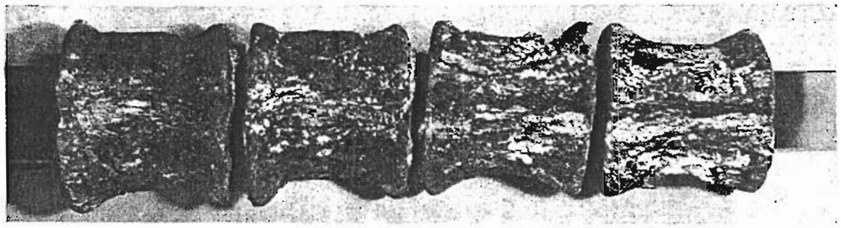
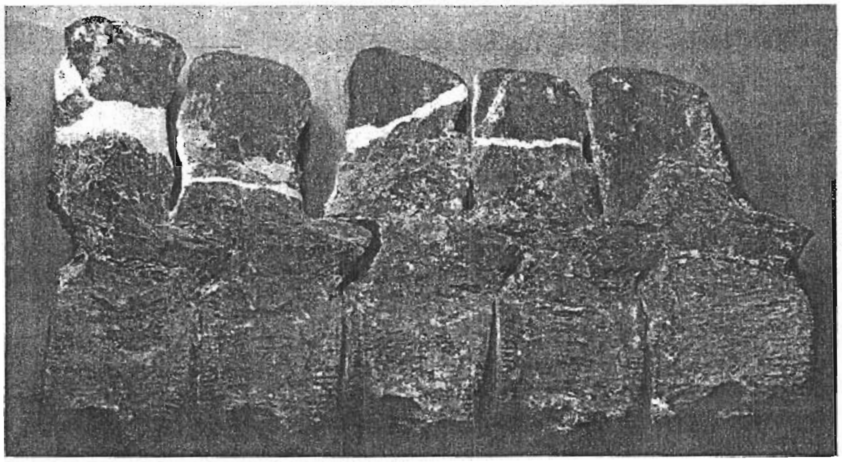

a
b
c
d
e
f
h
g
i
j

PLATE 26

Aphrosaurus furlongi, type. C. I. T. no. 2748. *a*. Ventral view of posterior cervical vertebrae. *b*. Right lateral view of same.



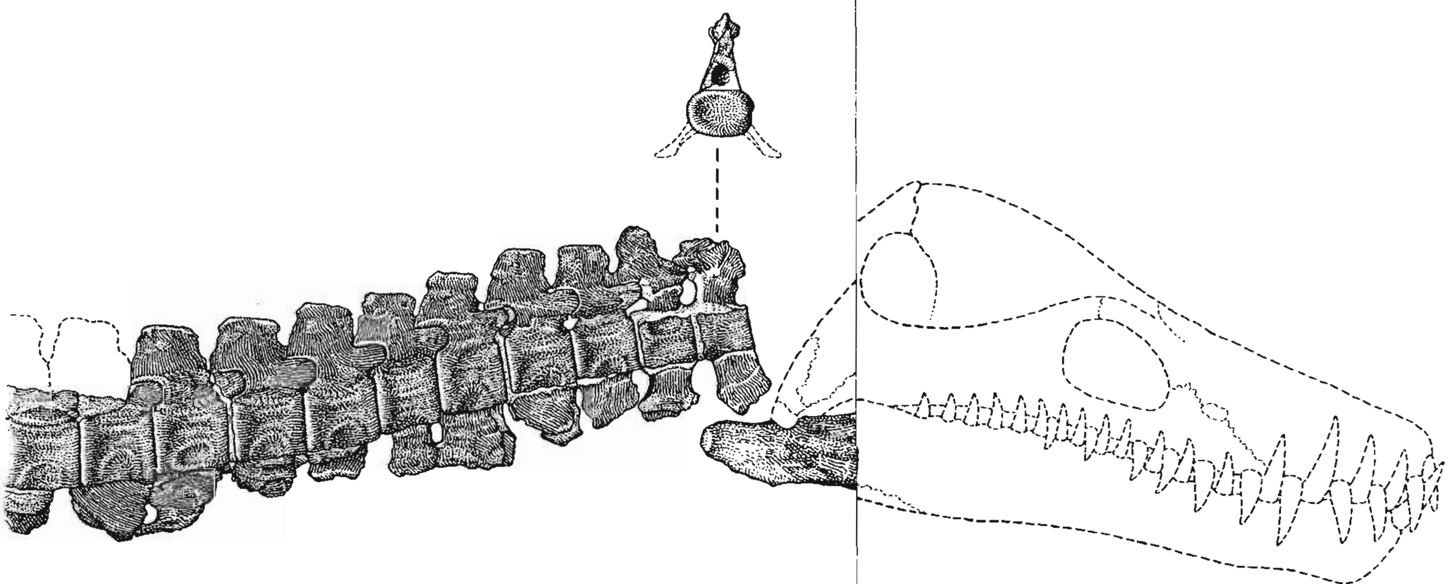
a

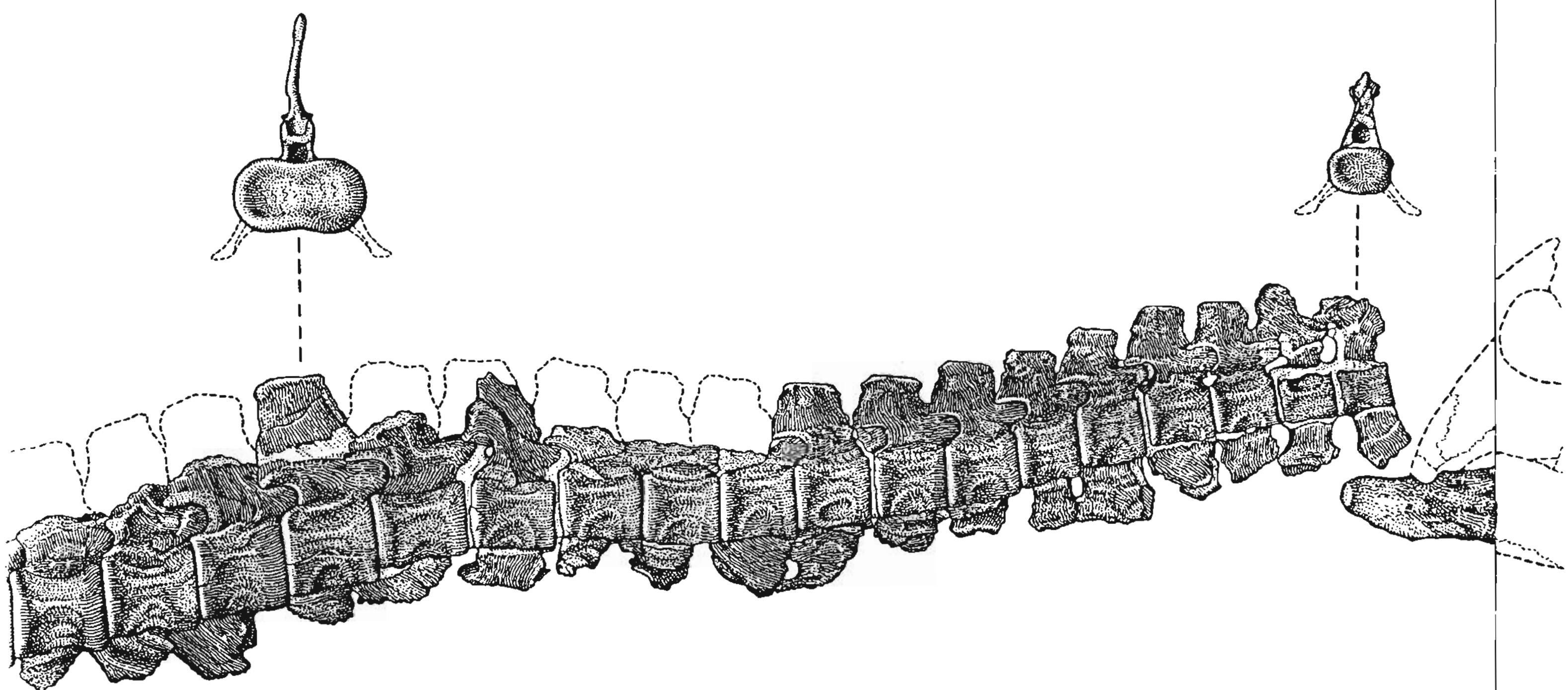


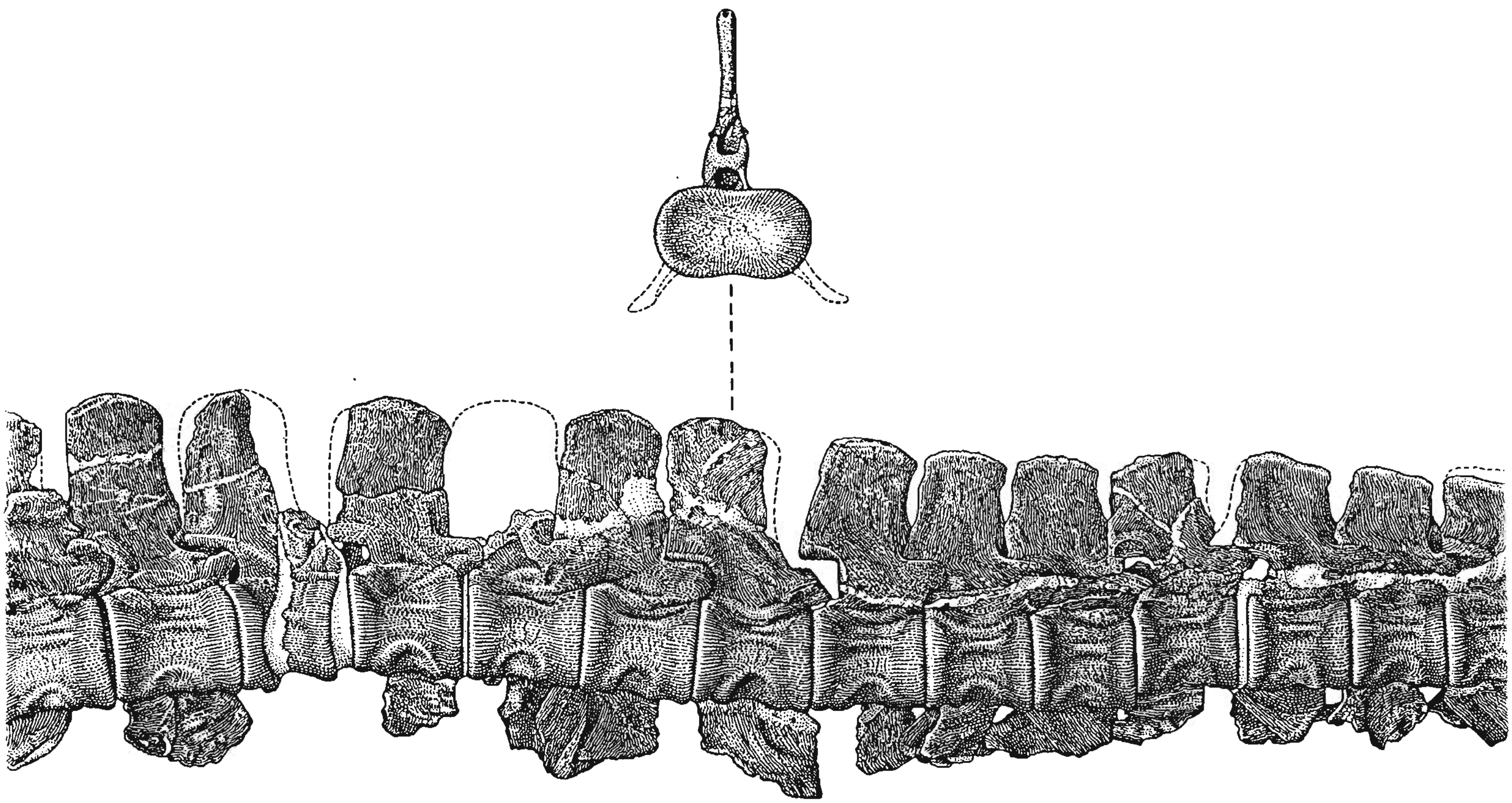
b

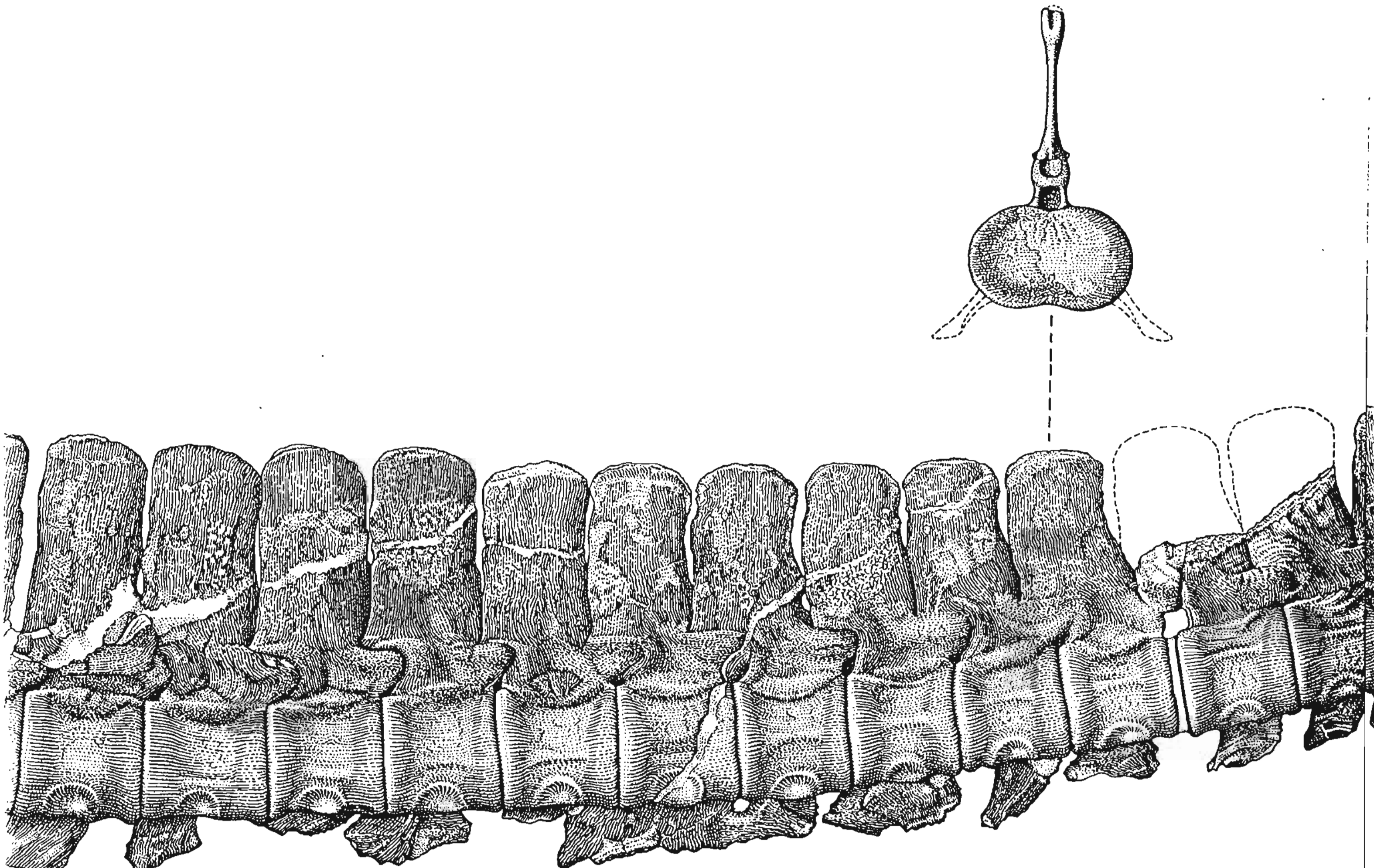
PLATE 27

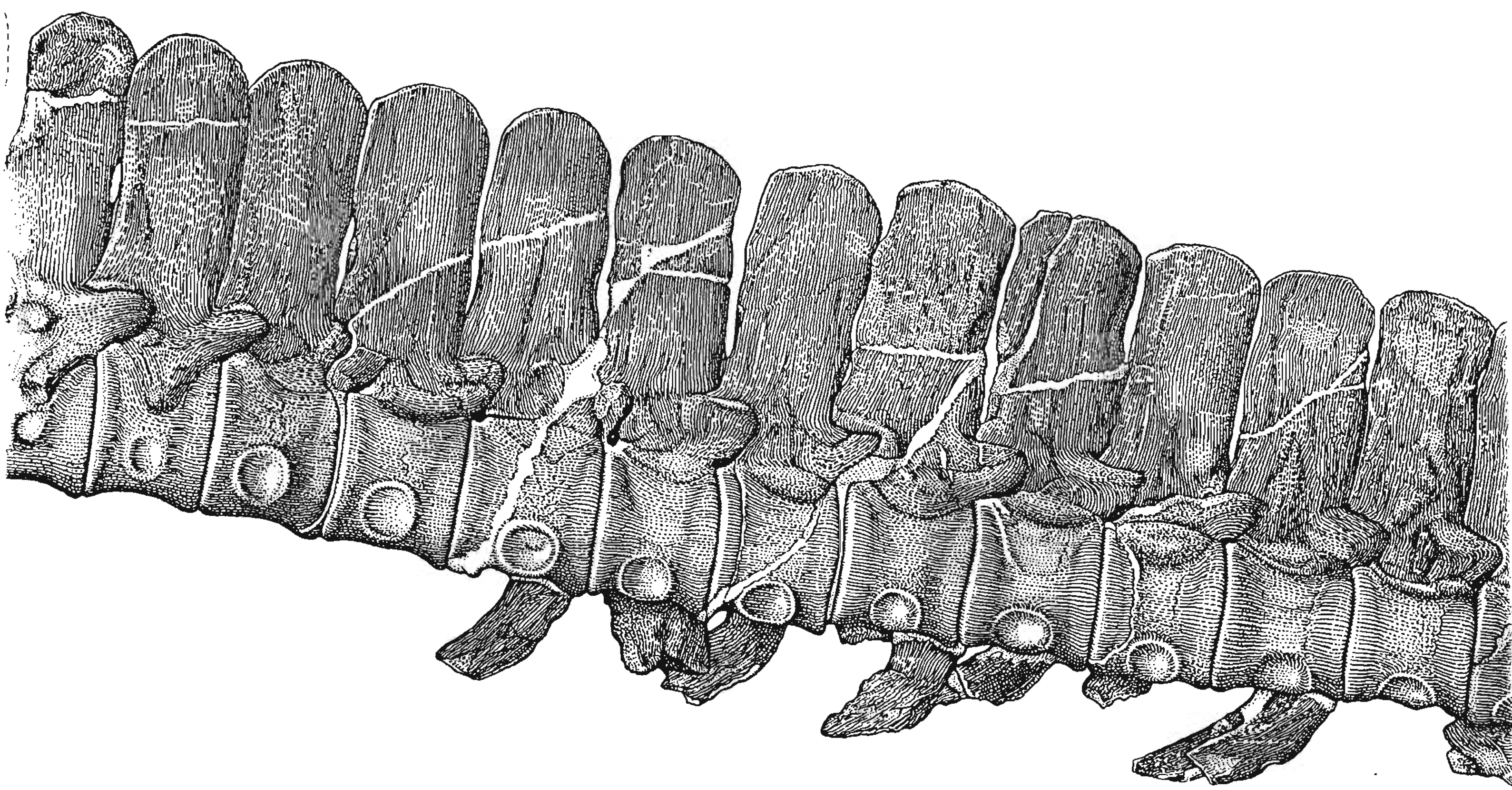
Aphrosaurus furlongi, juv. referred. Vertebrae. C. I. T. no. 2832. × 3/8.

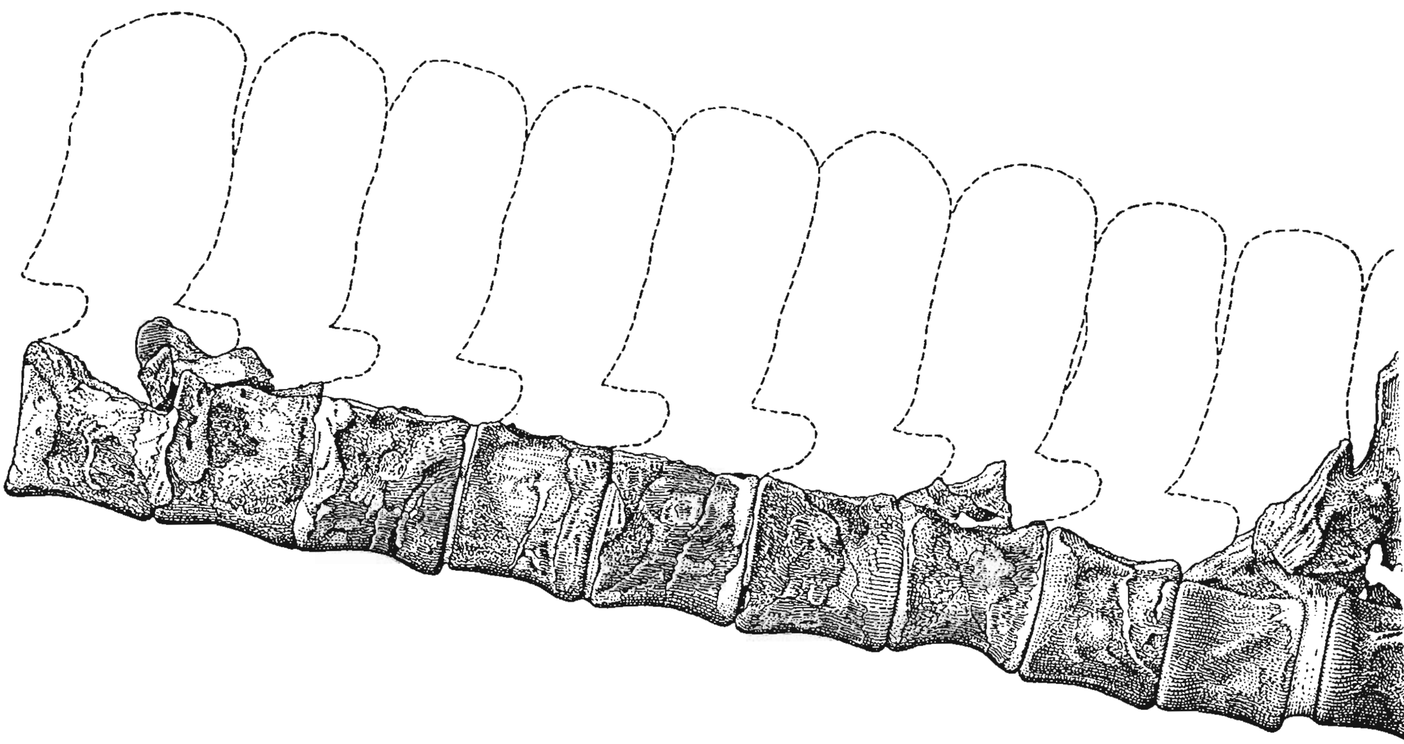


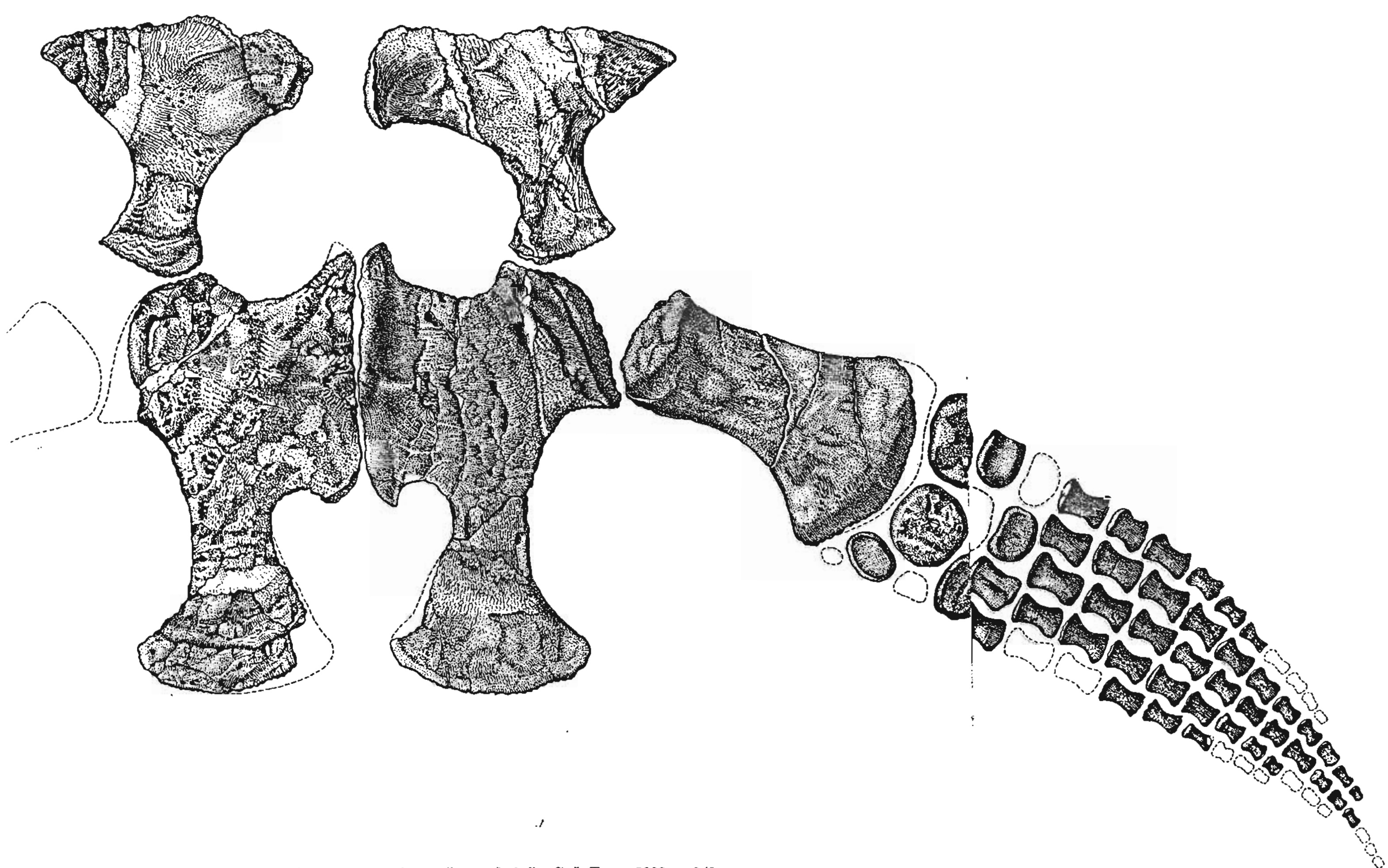




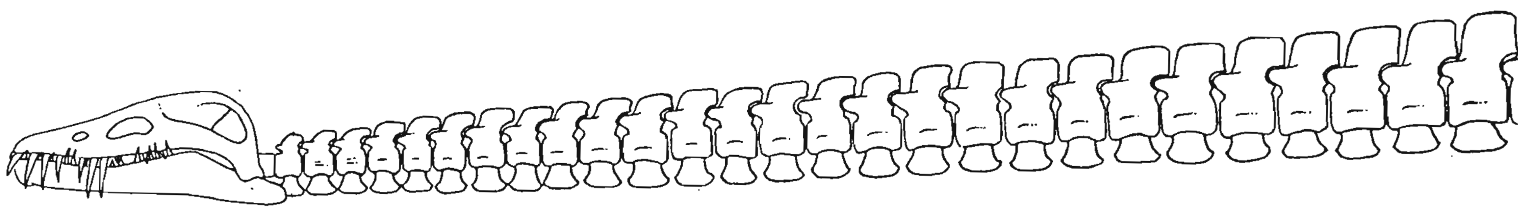








Aphrosaurus furlongi, juv. referred. Pectoral girdle. C. I. T. no. 2832. × 3/8.



Hydrotherosaurus alexandrae, type. Reconstruction of skeleton. U. C. Mus. Pal. no. 33912. × 1/15.