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A NEW SPECIES OF ELASMOSAUR FROM THE APTIAN OF COLOMBIA AND A REVIEW OF THE CRETACEOUS PLESIOSAURS

BY

S. P. WELLES

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN
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This work is dedicated to
Professor CHARLES LEWIS CAMP

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ABBREVIATIONS

<i>a</i>	angular	<i>P</i>	pubis
<i>bo</i>	basioccipital	<i>p</i>	parietal
<i>C</i>	coracoid	<i>pap</i>	paroccipital process
<i>c</i>	capitulum	<i>pf</i>	postfrontal
<i>Cl</i>	clavicle	<i>po</i>	postorbital
<i>d</i>	dentary	<i>prf</i>	prefrontal
<i>dp</i>	dorsal process of scapula	<i>ps</i>	parasphenoid
<i>eo</i>	exoccipital	<i>pt</i>	pterygoid
<i>ep</i>	epterygoid	<i>px</i>	premaxillary
<i>F</i>	femur	<i>q</i>	quadrate
<i>Fi</i>	fibula	<i>qj</i>	quadratojugal
<i>fr</i>	frontal	<i>R</i>	radius
<i>H</i>	humerus	<i>rp</i>	retroarticular process
<i>Hy</i>	hyoid	<i>S</i>	scapula
<i>I</i>	ischium	<i>sa</i>	surangular
<i>Icl</i>	interclavicle	<i>so</i>	supraoccipital
<i>ip</i>	interparietal	<i>sq</i>	squamosal
<i>j</i>	jugal	<i>T</i>	tibia
<i>l</i>	lacrimal	<i>t</i>	tuberosity
<i>m</i> or <i>mx</i>	maxillary	<i>tr</i>	trochanter
<i>n</i>	nasal	<i>U</i>	ulna

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BM	British Museum (Natural History)
CIT	California Institute of Technology
CMNH	Colorado Museum of Natural History
CNHM	Chicago Natural History Museum
KUMNH	Kansas University Museum of Natural History
MM	Manitoba Museum, Winnipeg
QM	Queensland Museum
SDSMT	South Dakota School of Mines and Technology
SMU	Southern Methodist University
UCMP	University of California Museum of Paleontology
USNM	United States National Museum
YPM	Yale Peabody Museum

Indices of vertebral centra are given by writing the absolute length in millimeters, followed by a comma; then the index of height to length ($H/L \times 100$), followed by a colon; then the index of breadth to length ($B/L \times 100$). Thus a centrum with L 47, H 35, and B 50 would be recorded 47, 74:106. Length is measured as a maximum from anterior to posterior ends of the centrum. Height is the maximum at the anterior end of the centrum, not diminished by the neural or haemal canal or the rounding of the edge of the centrum. Breadth is maximum across the end of the centrum, not that of a restricted disc. Such measurements are practical because they can be made on mounted specimens or on centra that are cemented together.

Other indices, such as the B:L index of the humerus, are maximum breadth divided by maximum length, and the quotient multiplied by 100. They indicate relative massiveness or slenderness of the elements concerned. This proportion is sometimes expressed as a percentage of the length, followed by the absolute length in centimeters as, B42%L28. The absolute measurement of length is important because it is necessary to be sure that the limb bones being compared are near enough in size to make the comparison meaningful.

A NEW SPECIES OF ELASMOSAUR FROM THE APTIAN OF COLOMBIA AND A REVIEW OF THE CRETACEOUS PLESIOSAURS

BY

S. P. WELLES

(A contribution from the University of California Museum of Paleontology)

ABSTRACT

All previously described plesiosaur remains from South and Central America are reviewed and are considered to be nondiagnostic. The names heretofore proposed are *nomina vana*. A new species of the elasmosaurian genus *Alzadasaurus* is described from two nearly complete skeletons from the Lower Aptian of Leiva, Boyacá, Colombia. This early elasmosaur is the basis for a revision of all Cretaceous plesiosaurs. Of the nearly 200 species named in the world-wide literature, only 24 are founded upon material that is here considered diagnostic, and the girdles and limb bones of these are refigured in this paper.

INTRODUCTION

IN 1945 A UNIVERSITY OF CALIFORNIA EXPEDITION to Colombia under Dr. R. A. Stirton collected a splendid, nearly complete elasmosaur skeleton. A second expedition in 1948, again under Dr. Stirton, collected another fine skeleton. Both are from the Lower Cretaceous (Lower Aptian) shales near Leiva, about 50 miles north of Bogotá. They were found about 100 yards apart and within a few feet of each other stratigraphically. The first was brought to Berkeley, and the second is on display at the Instituto Geológico in Bogotá.

The identification of these specimens has necessitated a review of, and comparison with, other Cretaceous plesiosaurs. The most impressive result of the review is the realization that out of more than 190 "species," or recombinations of these "species," only 24 have been founded upon material which is diagnostic. Most of these "species" can be identified as belonging to either the superfamily Plesiosauroidea or the superfamily Pliosauroidea, but the specimens usually consist of a very small part of a skeleton, often a single vertebra, limb bone, or girdle element. Such material cannot be identified on a specific, generic, or perhaps even family level. In most cases, "n. sp." means merely "new specimen," as Pravoslavlev (1918A, p. 60) so aptly noted.

How much of a specimen must we have in order for it to be diagnostic? This, of course, depends upon the level of identification that is attempted. A single centrum can usually be placed in the proper suborder, but, unless it exhibits unusual features, cannot be further categorized. Any attachment of a generic or specific name to such indeterminate material is not proper nomenclature, but merely the fixing of a handle to the specimen; this has been done many times by many workers. At the other extreme, even complete skeletons have been placed in the same species by one worker and in different genera by another as, for example, the two skeletons of *Plesiosaurus guillemi imperatoris* Dames (1895), and White (1940A), previously discussed by Welles (1943, p. 198).

At the present time we do not understand the variations in single bones in the

plesiosaurs. We do not know the growth changes of limb bones or girdle elements, nor do we know the range of variation to be expected in the individuals of a single species. Therefore isolated elements such as propodials, coracoids, pubes, and so on are not diagnostic for species. Furthermore, the skulls are so seldom associated with adequate skeletons, and are so similar among the members of each family, that even a good skull is not identifiable as to species.

The minimum requirements for a diagnostic specimen now include the better part of the vertebral column, the pectrum, the humerus, and the pelvis. The femur also is very desirable but not necessary for diagnosis. Even with specimens more complete than this there will always be some question about the identification, for, as our information increases, so does the complexity of the interrelations of morphological characters.

The questions of identification and diagnosis are always relative to the amount of knowledge, that is, the number of morphological characters and the level of identification. This is inherent in the growth of paleontological research. The first plesiosaur described was different from a crocodile and an ichthyosaur, as De la Beche and Conybeare (1821) recognized (hence the name *Pleisosaururus*). Conybeare's comparisons and many others in the next few decades were on a level that we now consider ordinal. Plesiosaur bones were compared with those of ichthyosaurs, crocodiles, and dinosaurs. Most of these descriptions are of specimens that differ among themselves, yet are not adequate to serve as types, or name-bearers on a specific level. Conybeare's original material included remains of both long and short-necked groups. However, all this early material is of a nondiagnostic nature when species names are applied. The isolated vertebrae and limb bones are not distinguishable from those of closely related species, and specific names founded upon nondiagnostic specimens are misleading.

Such "species" are briefly discussed in this paper and relegated to the *nomen vanum* category proposed by Simpson (1945I, p. 30; 1948E, p. 31) to designate a name that is properly described but is based upon nondiagnostic material. Additional specimens have often been referred to these *nomina vana*. This led to the addition to the original specific "diagnosis" of characters which might or might not pertain. In an attempt to clear up this confusion I have separated the references to type specimens from the references to referred specimens, and have retained only the names that are based upon identifiable material.

The nomenclatorial confusion surrounding the short-necked Upper Cretaceous plesiosaurs from North America has been resolved by eliminating the names *Piratosaurus* Leidy, *Polycotylus* Cope, and *Trinacromerum* Cragin as *nomina vana*. Our concept is based on the first adequately known genus, *Dolichorhynchops* Williston. This forces us to abandon the family name Polycotylidae and substitute Dolichorhynchopidae, but the change is long overdue and should stabilize our thinking. The host of *nomina vana* had best be dropped as taxonomic names, for they clutter our literature with misleading concepts. Specimens should be identified as closely as possible and named *Dolichorhynchops* sp., Dolichorhynchopidae indet., or Pliosauroida indet., as the material permits. Their value is in the record of the geographic and stratigraphic occurrence of a member of the group, not in being name-bearers for a name which is not significant in that it does not stand

for the assemblage of characters necessary to define a species, but stands only for some morphological peculiarity of the particular specimen.

CLASSIFICATION OF VALID SPECIES

Subfamily Plesiosauroidea
Suborder Plesiosauria
 Family PLESIOSAURIDAE (not discussed)
Family Plesiosauroidea
 Family ELASMOSAURIDAE

<i>Brancasaurus brancai</i>	<i>Styxosaurus browni</i>
<i>Alzadasaurus colombiensis</i>	<i>Hydralosaurus serpentinus</i>
<i>Thalassomedon haningtoni</i>	<i>Hydrotherosaurus alexandrae</i>
<i>Alzadasaurus riggsi</i>	<i>Leurospondylus ultimus</i>
<i>Alzadasaurus kansasensis</i>	<i>Aphrosaurus furlongi</i>
<i>Alzadasaurus pembertoni</i>	<i>Fresnosaurus drescheri</i>
<i>Elasmosaurus platyurus</i>	<i>Morenosaurus stocki</i>
<i>Elasmosaurus morgani</i>	

Superfamily PLIOSAUROIDEA

Family PLIOSAURIDAE (not discussed)

Family DOLICHORHYNCHOPIDAE ←

<i>Peyerus capensis</i>	<i>Dolichorhynchops kirki</i>
<i>Leptocleidus superstes</i>	<i>Dolichorhynchops osborni</i>
? <i>Kronosaurus queenslandicus</i>	<i>Brachauchenius lucasi</i>
<i>Dolichorhynchops willistoni</i>	? <i>Aristonectes parvidens</i>

These species are arranged stratigraphically in table 7.

Diagnoses of the suborder Plesiosauria and its subdivisions as recognized in this revision are as follows:

Suborder PLESIOSAURIA

Sauropterygia increasing in length to 45 feet, with sclerotic ring; sagittal crest narrow; paroccipital processes long and slender, meeting quadrate; posttemporal fenestrae large; fenestra ovale and stapes absent; thecodont with new teeth developing lingual to old and moving laterally to replace them; cervical, and often caudal, centra, with paired ventral nutrient foramina; anterior cervical ribs developing anterior processes, hence axiniform; coracoids, pubes, and ischia developing into large ventral plates; epipodials becoming broader than long; hyperphalangy increasing to 16 or 17.

Triassic through Cretaceous. Superfamilies included: Plesiosauroidea and Pliosauroidea.

Incertae sedis: *Aristonectes*, *Brachauchenius*.

Superfamily PLESIOSAUROIDEA

Plesiosauria with relatively small heads and long necks; teeth conical, no diastema; occipital condyle projecting, hemispherical, marked off by constricting groove; retroarticular process depressed, curving dorsally; cervical centra elongate, especially the median cervicals; vertebra pedicles flat; ventral plates of scapulae becoming very broad; ischia relatively short anteroposteriorly; anterior paddles larger than posterior; propodials massive; fibular facet of femur about equal to tibial facet.

?Triassic and Jurassic. Families included: Plesiosauridae and Elasmosauridae, with the Pistosauridae of doubtful validity.

Family PISTOSAURIDAE

Plesiosauroidea with primitive characters. Known only from two skulls and isolated skeletal elements. Perhaps should be included in Plesiosauridae.

Triassic. Genus and species not reviewed in this paper.

Family PLESIOSAURIDAE

Plesiosauroidea about 10 feet long; cervical ribs double-headed; maximum of about 40 cervical vertebrae; arches not fused to centra; epipodials elongate; metapodial v shifted proximally up to about half its length; maximum of about 10 phalanges in longest digit. Known from many skeletons.

Lower and ?Middle Jurassic. Genera and species not reviewed in this paper.

Family ELASMOSAURIDAE

Plesiosauroidea up to 45 feet long; cervical ribs single-headed; maximum of 71 cervical vertebrae; arches becoming fused to centra except for anteriormost, ventral plates of scapulae often meeting in midline, lying ventral to posterolateral ends of clavicles; intercoracoid vacuity becoming cordiform; propodials massive; epipodials short, becoming broader than long; metapodial v moving proximally entirely into distal mesapodial row; longest digit up to 17 phalanges. Known from many skeletons.

Upper Jurassic and Cretaceous. Subfamilies included: Elasmosaurinae, Alzadasaurinae.

Subfamily ELASMOSAURINAE

Elasmosauridae developing midline bar in pectrum and pelvis. Genera included: *Brancaesaurus*, *Elasmosaurus*.

Subfamily ALZADASAURINAE

Elasmosauridae without midline bar in pectrum and pelvis. Genera included: *Alzadasaurus*, *Aphrosaurus*, *Fresnosaurus*, *Hydralmosaurus*, *Hydrotherosaurus*, *Leurospondylus*, *Morenosaurus*, ?*Ogmodirus*, *Styxosaurus*, *Thalassomedon*.

Superfamily PLIOSAUROIDEA

Plesiosauria with relatively long heads and short necks; teeth often keeled; diastema between premaxillary and maxillary teeth; occipital condyle short and close to skull; retroarticular process compressed; cervical centra short; pedicles thick; ventral plates of scapulae narrow; ischia elongate anteroposteriorly; anterior paddles smaller than posterior; propodials slender and pendulous; fibular facet of femur larger than tibial facet.

Jurassic and Lower Cretaceous. Families included: Pliosauridae and Dolichorhynchopidae.

Family PLIOSAURIDAE

Pliosauroidae; cervical ribs double-headed; epipodials long. Poorly known.

Jurassic. Genera and species not reviewed in this paper (see Tarlo, 1958A, B, 1959A, B, C, 1960).

Family ~~DOLICHORHYNCHOPIDAE~~ *Polyclatylidae* (see p. 3)

Pliosauroidae with long mandibular symphysis; cervical ribs single-headed; epipodials short. Known from several skeletons.

Upper Jurassic and Cretaceous. Genera included: *Dolichorhynchops*, *Peyerus*, *Leptocleidus*.

This classification is phylogenetic in that it separates the two major divergent groups of plesiosaurs into the superfamilies Plesiosauroidea and Pliosauroidae.

This is an obvious division that even De la Beche and Conybeare recognized. It has long been known that the general lists of characters summarized here pertain to each superfamily. However, the division of superfamilies into families is not phylogenetic but horizontal, and is based on the development of features (cercidopleury, short epipodials, migration of metapodial v, increase in size and length of neck) which are common to all plesiosaurs. They represent grades of evolution rather than divergent specializations. Perhaps when additional material comes to light we may be able to recognize phyletic lines within the superfamilies and adjust our classification accordingly.

That this is not the ultimate in plesiosaur classification is demonstrated by the two forms *Brachauchenius* and *Aristonectes*, which do not fit into our present scheme. *Brachauchenius* has a short, rounded mandibular symphysis, as in elasmosaurs, but also has a short neck. *Aristonectes* has more and smaller teeth than other known plesiosaurs, and is not typical. A better understanding of plesiosaurian relationships must await the discovery of many more good skeletons.

Comparisons of the Colombian specimen with other plesiosaurs show this to be the first plesiosaur from South America which is complete enough to be diagnostic. It seems most closely related to the North American *Alzadasaurus riggsi*, but is more primitive and differs to the extent that it is given the new specific name *A. colombiensis*.

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HISTORICAL REVIEW OF THE SOUTH AMERICAN PLESIOSAURIA

The first plesiosaurian remains described from South America were three vertebral centra, some rib fragments, a "femur," and part of a "pelvis." These were found on the Island of Quiriquina, near La Concepción, Chile. This material was described by Gervais in Gay's great *Historia física y política de Chile*, where it was named *Plesiosaurus chilensis*. All subsequent writers acknowledged Gay's authorship until Colbert (1949A, p. 17, fn.) credited the name to Gervais. There seems little doubt that the bones were submitted to Gervais and that Gervais wrote the original description, as stated by Gay (1848, p. 132): "La que vamos a dar a conocer, segun la descripción que el Sr. Gervais ha tenido a bien hacer, es la única hallada en el Nuevo Mundo." Gervais (1859, pp. 432, fn., 479, 480) states that he described these fossils and had the figures made.

However, all of Gervais' 1859 references are to *Plesiosaurus andium*; so it seems likely that this was the name Gervais applied in his manuscript.

Since the original description appeared under the heading *Plesiosaurus chilensis*, it is reasonable to suppose that Gay substituted *chilensis* for *andium*, and did so without notifying Gervais, since Gervais in 1859 used the discarded term. I therefore assume that Gay was responsible for the publication of the name *P. chilensis* and I cannot agree with Colbert in crediting the name to Gervais.

Burmeister (1861, pl. 1, figs. 4-6), *vide* Huene (1927, p. 25), described and figured a vertebra from the Lias of Cerro Blanco, Argentina.

Blake (1862, p. 110) mentioned a caudal vertebra sent to him by W. Bollaert from San Vicente, near Talcahuano, Chile. Blake neither described nor figured this vertebra, but identified it as *Plesiosaurus chilensis* Gay.

Philippi (1887, p. 28) noted that the "femur" described and figured by Gay was 11 cm long and was juvenile. He mentioned several other occurrences of plesiosaurs, and collected a number of isolated skeletal elements from Quiriquina. A locality 250 miles to the north, at Algarrobo near Valparaiso, yield 23 vertebrae measuring 188 cm, a fairly large animal; another locality recorded is Hualpen. Philippi noted vertebrae 10.5-11 cm long, 12 cm high, and 16 cm broad, and figured (pl. 55) a tooth as belonging to a plesiosaur. He recorded a femur 38 cm long and 17 cm broad, a B:L index of 45.

Lydekker (1889C, p. 222) referred the species *chilensis* to the genus *Cimoliosaurus* [*sic!*] and described an additional caudal centrum (BMNH 38013) from San Vicente, near Concepción, Chile, noting its similarity to a caudal of *C. (Discosaurus) magnus*.

Woodward (1891, p. 316) described and figured a limb bone collected by Joseph Mawson in the Cretaceous beds near Bahía, Brazil. This, he said, "may probably be regarded as the left humerus of a typical marine plesiosaurian."

Deecke (1896) gave an excellent summary of the Chilean plesiosaurs, and described much additional material from Quiriquina Island. He noted that some of Gay's type is pliosaurian and some is "cimoliasaurian." He restricted the trivial name *chilensis* to the brachydiran material, placed it in the genus *Pliosaurus*, and listed as synonyms *Plesiosaurus chilensis* Gay and *P. andium* Sauvage. (I have not been able to confirm this reference, and assume it to be an error by Deecke for *P. andium* Gervais.) He referred the dolichodiran material to the genus *Cimoliasaurus*, with the new specific name *andium* [non *P. andium* Gervais, 1859]. He further pointed out that Gay's plate 1, figures 1-3, is a cervical vertebra, more anterior than any of Deecke's; Gay's plate 1, figures 6-10, represents a caudal vertebra, and Gay's dolichodiran material is without doubt the same genus and species as this new material. Deecke also described a coracoid (pl. 1, fig. 1) that Steinmann collected near the humerus.

The elasmosaurid material described by Deecke as *Cimoliasaurus andium* consists of three median cervicals, one posterior cervical, and some dorsals and caudals that are thought to be from a single individual. Limb bones are also described and assigned to this species; an isolated vertebra is considered to be a distinct, unnamed species. Deecke considered the tooth figured by Philippi to be mosasaurian rather than plesiosaurian.

Oliver (1921, p. 94, figs. 4, 5) described and figured a posterior cervical vertebral centrum and a tooth, both of which he referred to *Cimoliasaurus andium* Deecke. The vertebra has indices of 70, 150:216.

Von Huene (1927, p. 25) called attention to the fact that the vertebra from the Upper Lias of Cerro Blanco, valley of the Río Copiapo, described by Burmeister (1861, pl. 1, figs. 4-6) as *Crododilus neogaeus*, is a plesiosaur and should be named *Plesiosaurus neogaeus*. I have not seen Burmeister's figures, and so can add nothing to Huene's identification.

Broili (1930B, p. 498) described additional material collected by Dr. Wetzell at San Vicente, Quiriquina Island. This consisted of several blocks, each containing a number of vertebrae, and the central part of a paddle. Broili noted that the vertebrae differed from those of *Pliosaurus chilensis* Gay and therefore referred all to *Cimoliasaurus andium* Deecke [*sic!*].

Rusconi (1943, p. 1) announced the discovery of a Jurassic plesiosaur in Mendoza, Argentina, which he named *Namuncuranian malarguense*. This is based on parts of a vertebra and four ribs.

Rusconi (1948H, p. 328) described *Purranisaurus potens* from the ?Middle Jurassic of Mendoza, Argentina, on a well-preserved skull. This he later (1955A, p. 76) identified as a nothosaur.

Olsson (1944, p. 23) called attention to the Maestrichtian age of the Quiriquina beds, basing this in part on the close relation between the ammonites *Parapachydiscus quiriquinae* and *P. arkansasus* of the Texas Navarro. He considered the Quiriquina fauna most closely related to an equivalent fauna from New Zealand and rather close to faunas from Ariyalur and Pondicherry in India and also from the Nanaimo beds of Vancouver.

Osten (1948, p. 6) cites several unpublished occurrences of plesiosaurs in Venezuela, but gives no definitive information.

Colbert (1949A) gave a summary of the previous finds and described a new species, *Alzadasaurus tropicus* Colbert, from the lower Upper Cretaceous (Turonian) of Altagracia de Orituco, Monagas, Venezuela. Colbert's material was a partial skeleton with a posterior cervical, four pectoral and eight dorsal vertebrae, left scapula, part of a coracoid, humerus, and paddle.

Torre and Rojas (1949, p. 199) described a skull and some vertebrae from three Oxfordian localities in Viñales, western Cuba, between Laguna and La Palma.

Welles (1952, p. 84) made comparisons with *Alzadasaurus tropicus* Colbert, and this is the most recent publication on South American plesiosaurs.

TAXONOMIC REVIEW AND REVISION OF THE SOUTH AMERICAN PLESIOSAURIA

PLESIOSAURIDAE

Muraenosaurus leedsii Seeley, 1874

Referred material.—Torre and Rojas, 1949, described and figured two anterior cervical vertebrae which they named *Cryptocleidus ? cuervoi*. Similarly, a dorsal vertebra was named *C. ? cuervoi quesadai* and a skull was named *C. ? cuervoi caroli*. The localities are cited above.

Discussion.—Their first specimen, a split slab with two vertebrae and parts of two others, shows fused, hatchet-shaped ribs which are distinctive of anterior and median cervicals. The presence of both anterior and posterior projections on the ribs is characteristic of about the 15th in the series. This was made the type

TABLE 1

COMPARISON OF VERTEBRAL INDICES AND RIB CHARACTERISTICS OF OXFORDIAN PLESIOSAURS
(Estimates italicized)

Species	Median cervical	Anterior dorsal	Nature of cervical ribs
<i>Cryptocleidus ? cuervoi</i>	45, 85 : —	Hatchet-shaped, strong anterior projection, fused.
<i>C. ? cuervoi quesadai</i>	53, 100 : 100	?
<i>Cryptocleidus oxoniensis</i>	R 2860 32, 100 : 122	R 2412 48, 121 : 148	Straight, fused.
<i>Muraenosaurus leedsii</i>	Type R 2421 47, 81 : —	R 2421 56, 102 : 108	Strong anterior projection, hatchet-shaped, fused.
<i>M. durobriensis</i>	Type R 2428 50, 104 : 112	R 2428 55, 109 : 131 R 2863 56, 105 : 123	Less compressed, free.
<i>M. platyclis</i> , type.....	R 2678 50, 88 : 110	Weak anterior projection, weakly hatchet-shaped, fused, lat. keel.
<i>M. p.</i> , referred.....	R 2425 65, 92 : 118	R 2425 68, 112 : 124	
<i>Picrocleidus beloclis</i>	R 3698 26, 83 : 121	R 2429 <i>P. sp.</i> 40, 115 : 133	Strong anterior projection, hatchet-shaped, fused, lat. keel.
<i>Tricleidus seeleyi</i>	Type R 3539 29, 107 : 131	R 3539 37, 116 : 133	Weak anterior projection, hatchet-shaped, fused.
<i>Plesiosaurus dolichodeirus</i> ..	30, 71 : 106	40, 106 : 129	Strong anterior projection, hatchet-shaped, fused.

of *Cryptocleidus ? cuervoi* Torre and Rojas, and measurements and illustrations were given.

Since Torre and Rojas made no comparisons with other plesiosaurs, an attempt is made here to evaluate their material. The splendid descriptions and measurements published by Andrews (1910A) for the Oxford Clay reptiles provide a good basis for this, especially since the Cuban plesiosaur is of the same age. For the first Cuban specimen, the split slab which is the type of *C. ? cuervoi*, it is possible to get the L:H index and to note that the ribs have pronounced anterior projections. Compared with *Cryptocleidus oxoniensis*, the Cuban plesiosaur has

decidedly longer centra; although the ribs are fused to the centra as in *Cryptoclidus*, they are quite different in shape from the simple ribs of the British form. The indices of cervical centra of comparable plesiosaurs are listed in table 1; it is apparent that in proportions of centrum the Cuban plesiosaur is closest to *Muraenosaurus leedsii*, *Picrocleidus beloclis*, and *Muraenosaurus platyclis*. This means that all these plesiosaurs had necks of about the same length. Of these, *M. platyclis* has simple cervical ribs; both *Picrocleidus beloclis* and *Muraenosaurus leedsii* have hatchet-shaped cervical ribs.

The vertebrae of *P. beloclis*, however, are only about half the absolute size of the Cuban vertebrae. It has been my experience that larger individuals of the same or similar species develop more massive centra. Therefore, if *P. beloclis* were doubled in size we should find a less striking similarity of indices. The cervical vertebrae described as *Cryptocleidus* ? *cuervoi* seem to be quite different from *Cryptoclidus*, and very close to *Muraenosaurus leedsii*.

The second specimen, made the type of *C. ? cuervoi quesadai*, and described as thoracic, is an anterior or medial dorsal. Its indices are 53, 100:100. These are closest to *Muraenosaurus leedsii* and of similar size. Unfortunately, the dorsals of *Picrocleidus beloclis* are unknown, but the specimen (R 2429) which Andrews refers to *Picrocleidus* sp. has indices of 40, 115:133, indicative of a more massive animal with a shorter neck.

The third specimen is a skull, and is named *C. ? cuervoi caroli*. Skulls of long-necked Jurassic plesiosaurs are all very similar and I have not been able to distinguish the Cuban skull from other known forms. There seems to be no reason why the Cuban skull should be separated from *Muraenosaurus*.

This brief review of the Cuban material indicates that it is definitely not *Cryptoclidus*, and should be included in the genus *Muraenosaurus*. Furthermore, since it is inseparable from *M. leedsii* Seeley (1874), it is here referred to that species.

PLESIOSAURIDAE, gen. et sp. indet.

Plesiosaurus neogaeus (Burmeister) Huene (1927, p. 25). In 1861 Burmeister (*vide* Huene, *loc. cit.*) described and figured a vertebra under the name *Teleosaurus neogaeus*. This is from the Upper Lias of Cerro Blanco, Argentina, and was identified by von Huene as a dorsal of a plesiosaur and so renamed. I have not seen Burmeister's illustration, but a single dorsal vertebra is not diagnostic; so the name is a *nomen vanum*.

ELASMOSAURIDAE, gen. et sp. indet.

Gay (1848, p. 133, *Erpetologia fossil*, pl. 2, fig. 4) described and figured a "femur" from Quiriquina Island. This he called *Plesiosaurus chilensis*, and it is part of his hypodigm. He gave the total length as 4 pulgadas; however (p. 136), he also gave the distal breadth as 4 pulgadas. Philippi (1887, p. 28) recorded the length of this propodial as 11 cm and noted that it is juvenile. From this and Gay's figures we derive indices B71:L11, which are elasmosaurian rather than pliosaurian. It is certainly a very young individual, indeterminate as to species or genus.

Philippi (1887, p. 28), under the name *Plesiosaurus chilensis*, mentioned the

vertebral column of a small animal collected by Landbeck at Algarrobo near Valparaiso. This consists of 23 vertebrae with a total length of 188 cm, and is in the Museum of Santiago. Since the average length is about 80 cm, the specimen is probably elasmosaurian.

Philippi (1887, p. 28) also identified some vertebrae from Quiriquina Island as *Plesiosaurus chilensis*. These are evidently posterior cervicals of a large elasmosaur, and have indices 105, 114:154 and 111, 109:145.

Deecke (1896, p. 40, pl. 2, figs. 3, 4) described a propodium from Quiriquina as *Pliosaurus chilensis* (Gay). Indices from the measurements are B42%L21, and from the illustration B53%L19. It is massive as in elasmosaurids, and seems to be a femur. The tuberosity is well defined, but is broadly confluent with the capitulum without anterior or posterior grooves. It is certainly a juvenile, possibly the same species as Gay's humerus.

Deecke (1896, p. 42, pl. 2, figs. 1, 2) described as *Pliosaurus chilensis* (Gay) a beautifully prepared posterior paddle from Quiriquina. The propodium has indices B58%L26, is juvenile, probably a femur, and elasmosaurid in shape. The distal elements have all been rearranged and reversed with respect to the femur. The high B:L indices of the tibia (128) and fibula (110) confirm the late Cretaceous age of the specimen, as does the large number of phalanges, 16 in the second digit and 15 in the third. The capitulum and trochanter are broadly confluent, but on at least one border (?posterior) they are divided by a notch. It is indeterminate, but could be the same species as above.

Deecke (1896, p. 51, pl. 1, fig. 4; pl. 3, figs. 1-3) described and figured vertebrae from Quiriquina collected by Dr. Gärtner and now in the Kiel Collection. For these he used the name *Cimoliasaurus andium* Deecke, not as the same species Gervais had described, but as a new species. An "anterior cervical" (6) has indices 35, 126:129; a "median cervical" (13) 50, 116:120; a "posterior cervical" 63, 136:168; a dorsal 78, 114:115; and a caudal 55, 118:155. The vertebrae show prominent development of an epiphyseal-like disc at the end of the centrum—a character emphasized by Leidy (1851G, p. 326) for *Discosaurus vetustus*. However, this is not diagnostic, being found on cervical and caudal centra of many elasmosaurs. Deecke's illustrations of "cervical" vertebrae (*loc. cit.*) show an overlap of the arch and spine from one centrum onto the succeeding centrum. This is not a normal structure, but is characteristic of the caudals of elasmosaurs (*Hydrotherosaurus alexandrae* Welles, 1943, p. 138) where "the pedicles lap over onto the preceding centrum." This seems to be correctly oriented in Deecke's (pl. 4, fig. 3) anterior caudal. If his "cervicals" (pl. 3, figs. 1, 2) be regarded as caudals and properly oriented they become elasmosaurid. However, they are not diagnostic; so the name is a *nomen vanum*. They could be the adult of Gay's species.

Deecke (1896, pl. 1, fig. 5) described as *Pliosaurus chilensis* (Gay) two isolated cervical centra of a juvenile from Quiriquina. The rounded rib facets are rather high on the ventrolateral edges; so these are probably posterior cervicals. Their indices are 45, 113:151. An adult would have lower indices; hence, it is reasonable to believe that the animal is elasmosaurid even though there is no lateral keel. They are indeterminate.

Deecke (*ibid.*, p. 57, pl. 3, fig. 4) referred an anterior caudal vertebra to his

Cimoliasaurus andium. This is also in the Kiel Collection. It is an anterior caudal of an indeterminate elasmosaur, probably the same species as above.

Deecke (p. 56, pl. 1, fig. 7) referred a dorsal centrum in the Strassbourg Collection to the species *C. andium*. It is indeterminate.

Deecke (p. 58, pl. 1, fig. 6) referred a "humerus," B62%L35, to his *C. andium*. The capitulum seems to be crushed down into the shaft. Index and proportions are those of an elasmosaurid femur, and it could be the same species as above.

Deecke (p. 61, pl. 1, fig. 5) described and figured as *Cimoliasaurus* sp. two posterior cervicals with indices of 45, 113:151. These are in the Oldenburg Museum. They are of an indeterminate juvenile elasmosaur.

Colbert (1949A, pp. 1-15, figs. 1-9) described and figured as *Aladasaurus tropicus* some pectoral and dorsal vertebrae, and part of the pectrum of a single individual from the Querecual Islands near Monagas, Venezuela. This is probably Turonian in age (*vide* Hoffstetter *et al.*, 1956, p. 527). In a brief review of this (Welles, 1952, p. 84) I suggested that allocation to this genus was not certain. It is elasmosaurid, but is so incomplete that it is a *nomen vanum*.

DOLICHORHYNCHOPIDAE, gen. et sp. indet.

Plesiosaurus chilensis Gay, 1848, p. 133, *Erpetologia fossil*, pl. 1, figs. 1-3; Philippi, 1887, pp. 28, 29; *Pleiosaurus andium* Gervais, 1859, pp. 432, 480; *Pliosaurus chilensis* Deecke, 1896, p. 36; Kuhn, 1935C, p. 84; *Cimoliasaurus chilensis* Lydekker, 1889C, p. 222.

Gay (*loc. cit.*) based his original description upon material that is a composite of elasmosaurian and pliosaurian plesiosaurs, and no type was indicated. Deecke (*loc. cit.*) therefore selected the cervical centra as type; because these are of a short-necked form, he used the name *Pliosaurus chilensis*. Since there is no proof that even the cervical centra are from the same individual, the posterior cervical centrum (*Erpetologia fossil*, pl. 1, figs. 1-3) is hereby designated the type. Indices from Gay's measurements are 40, 138:273; from his illustration, 49, 136:265. Single cervical centra are not diagnostic; so the species is a *nomen vanum*. It is indicative of a pliosaur, as Deecke recognized, but, as Cabrera (1941, p. 126) pointed out, this centrum is cercidopleuran and hence cannot be included in the genus *Pliosaurus*.

Gay (1848, pl. 1, figs. 4-5) described part of the original hypodigm, consisting of a ?pectoral centrum with indices from measurements of 51, 125:174, and from the illustration of 52, 151:216. This is probably the same species as the type.

Gay (pl. 1, figs. 6-10, also part of the original hypodigm) described an anterior caudal centrum with indices from measurements of 38, 168:218 and from the illustration of 40, 177:240. It is from a short-necked plesiosaur and could be the same species.

Gay (pl. 1, fig. 1), under the name *Plesiosaurus andium*, figured a "coracoid" which I take to be a pubis. It could belong to this species.

Gay (pl. 2, fig. 3) figured a fragment of a "pelvis" which looks to me more like the middle of a coracoid with a median thickening or keel. Its narrowness indicates a juvenile, even though the pectoral bar is present.

Blake (1862, p. 110) mentioned a caudal centrum from San Vicente, near Talcahuano, Chile, that he said does not differ from the above.

Philippi (1887, p. 28) mentioned a femur from Quiriquina Island, B45%L38, which is probably pliosaurian and could be this species.

Lydekker (1889C, p. 222), under the name *Cimoliosaurus chilensis*, referred a caudal centrum from San Vicente. This had been mentioned earlier by Blake (1862, p. 110) under the name *Plesiosaurus chilensis*. Indices are 50, 148:200, which are probably pliosaurian, although the centrum is longer but lower and narrower than Gay's caudal. It is nondiagnostic.

Deecke (1896, p. 36, pl. 1, fig. 3, *a-d*) described as *Pliosaurus chilensis* a series of five cervical centra in the Oldenburg Museum from Quiriquina Island. He figured one centrum, and gave measurements which yield indices of 46, 184:239 and 50, 180:240. These are pliosaurian, probably this species.

Deecke (*ibid.*, p. 39, pl. 1, fig. 1) also described as *Pliosaurus chilensis* a "coracoid" from the same locality. This he restored, and I think correctly, from the outlines of a pubis. It is long, probably pliosauroid, and could be this species.

Oliver (1921, p. 94, figs. 4, 5) referred a centrum from Quiriquina Island to *Cimoliasaurus andium* Deecke. It is evidently a posterior cervical and has indices of 70, 150:216, which indicate a giant pliosaur.

Broili (1930B, p. 498, figs. 1-5) referred additional material from San Vicente, Quiriquina Island, to *Cimoliosaurus* [*sic!*] *andium* Deecke. This consists of three blocks containing vertebrae and part of an anterior paddle, collected by Professor Wetzel of Kiel and probably representing a single individual. The posterior cervical rips are on pedicles; the centra are short, low, and broad (indices 48, 115:200), with concave ends. The dorsals are deeply constricted around the centrum, and an anterior dorsal has indices of 60, 125:148. The fragment of a paddle includes the distal end of the humerus, epipodials, mesopodials, and a few distal elements. The humerus is so fragmentary that its proportions cannot be determined. The epipodials are very short and broad. All the material, vertebrae and paddle, is pliosauroid, but it is not adequate to diagnose a species.

NOT PLESIOSAURIAN

Plesiosaurus chilensis Philippi (1887, pl. 55, fig. 8), tooth, is probably mosasaurian, as indicated by Deecke.

Plesiosaurian, Woodward (1891, fig. 1), "humerus," is probably a radius of a terrestrial reptile.

Namuncurania malarguense Rusconi (1943, p. 2, figs. 1-3) was founded on an incomplete vertebra and some rib fragments from La Valenciana coal mine, 40 km from Malalhue, Mendoza (Dept. Pal. Mus. Hist. Nat. Juan C. Moyano, Mendoza, no. 123 P.V.). This is identified as a Jurassic plesiosaur, but the sharp angle made by the posterior and ventral faces suggests a strongly upcurved neck, which is not found among plesiosaurs. The material is indeterminate and the name a *nomen vanum*.

Rusconi (1948H, p. 328, figs. 1-13, pls. 1-2) described *Purranisaurus potens*, n. g., n. sp., from a fairly large part of a skeleton, including a good skull, from the Middle Jurassic of the valley of the Cajón Grande, south of Malalhue, Mendoza (Dept. Pal. Mus. Hist. Nat. Mendoza, no. 2060). Later (1955A, p. 76) Rusconi removed this genus from the Plesiosauridae and put it in the Nothosauridae.

Whatever its final determination, it is not a plesiosaur. The Middle Jurassic age of the associated invertebrates makes nothosaur relationship highly doubtful. The peculiar constriction above the orbits is suggestive of a mesosuchian crocodile, and the palate and basioccipital region are consonant with this interpretation, as are the vertebrae.

Family ELASMOSAURIDAE Cope, 1869

Genus *Alzadasaurus* Welles, 1943

Alzadasaurus colombiensis, n. sp.

Type.—UCMP 38349, a fine skeleton lacking only distal parts of paddles, ischia, ilia, and tail.

Hypodigm.—Type and second skeleton from 100 meters south and 10 meters stratigraphically below the type, now in Museo del Servicio Geológico, Bogotá, Colombia.

Locality.—Loma de la Catalina, 6 km west of Leiva, Boyacá, Colombia. About 300 meters north of road from Leiva to Chiquinquira. See fig. 1, UCMP loc. V-4540.

Horizon.—Lower Aptian, *fide* Bürgl (1954, p. 17), who lists the associated ammonites as *Deshayesites colombianus* Riedel, *D. sp. indet.*, *Prochelonicerias albrechti austriacae* (Hohenegger), and *Chelonicerias subnodosocostatum* (Sinzow).

Diagnosis.—A primitive *alzadasaur* with median cervicals not elongate; cervical spines with anterior tongue and posterior groove; median cervicals with convex enlargement of top posterior border of spine and corresponding concave anterior border; dorsal scapular process parallel-sided; coracoids with very long median suture, distal part of paddle inclined about 30° posteriorly from shaft of humerus; epipodials long.

Occurrence.—Most of the matrix is a gray-buff siltstone that scratches reddish; so the whole has a slight purplish cast. Casts of pelecypods and ammonites are common in the matrix near the bones, and a good Lower Aptian invertebrate fauna has been collected and determined (Bürgl, 1954, p. 16) from this general horizon. Red and yellow iron concretions are common, often more than 5 cm in diameter, with the hard red oxide forming a shell around the softer limonite. Gypsum occurs as veins in cracks and in crystals throughout the matrix surrounding the skull. A layer of gypsum 6 mm thick formed a shell around the skull, and other layers and crystals of gypsum penetrated the periosteal bone; so in many places it is very difficult to distinguish bone from matrix. Limestone formed concretions around some of the bones, especially the skull, and between the pectrum and vertebral column. This often adhered to the bone surface and was extremely difficult to chisel away. Red iron oxide coated much of the bone surface, and this was usually impossible to remove without damaging the bone.

The bones are brown to dark brown and weather to a lighter color. The neck is almost straight, with a dorsal flexion of only about 45° which is confined to the anterior 20 or so vertebrae. The animal lay upon its back, the lower jaws tightly closed. The vertebrae are articulated throughout the column, but rotated, with the left side down. The pectrum was flattened out, with the right coracoid crushed down over the anterior dorsals. The clavicular arch lies above the posterior cervicals, with the right clavicle crushed onto the 57th vertebra (the first pectoral). The right scapula is in almost normal position, its dorsal process downward, but the left scapula was turned completely over and then flattened out, with the dorsal process projecting medially.

Both pubes are in nearly normal position.

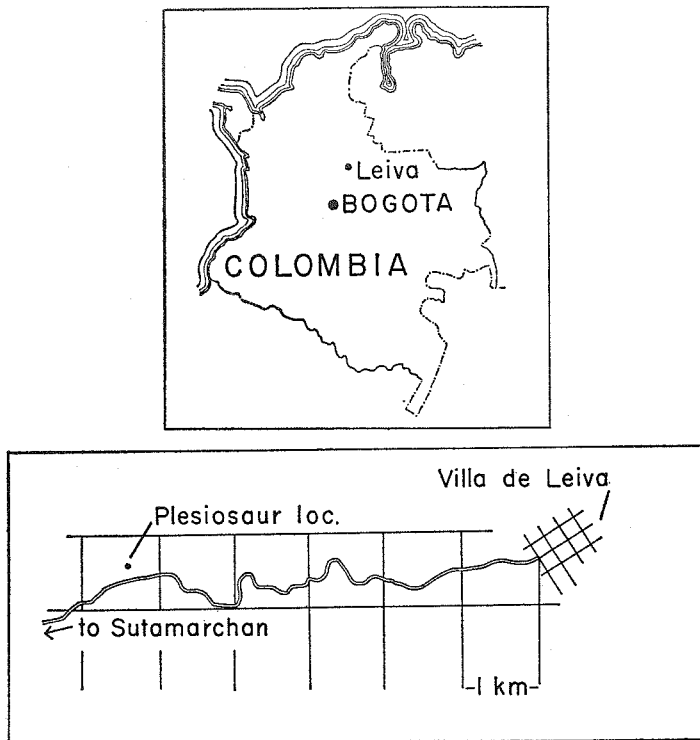


Fig. 1. Finding map of Colombian plesiosaur locality.

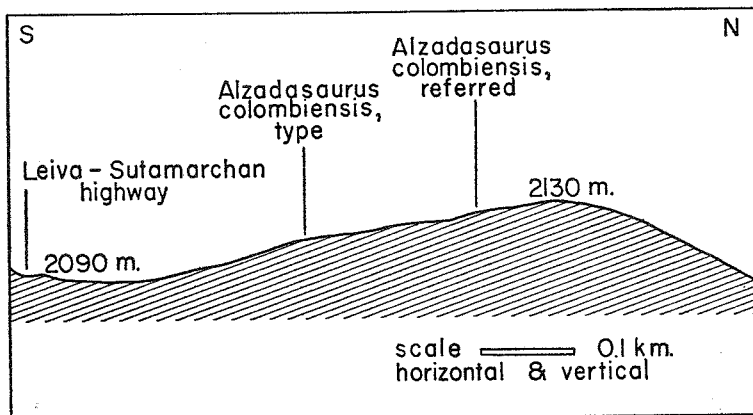


Fig. 2. Cross section of Colombian plesiosaur locality. From W. E. Denton, Tropical Oil Company.

The skeleton was probably complete when buried, but erosion removed ischia, tail, parts of the pelvic paddles, and the distal elements of the left pectoral paddle. The skull is well preserved, although the parietal crest and left jugal arch have been crushed to the right, their upper edges moved over. The left center of the snout has a large crushed pit; this crushing lowered the frontals and destroyed the bone surface over so much of the snout that sutures were obliterated. The left pectoral paddle evidently flattened out in the mud, its elements in normal position as far as preserved. The right, however, had epipodials displaced to lie above and behind the center of the humerus. A few of the proximal carpals are in proper position relative to the epipodials, but the distal elements and the metapodials and phalanges extend at right angles to their normal position, pointing posteriorly.

The left pelvic paddle stretched out in perfect alignment as far as preserved, which is through the proximal phalanges. The right, however, underwent a folding almost exactly like that of the right pectoral paddle. Both tibia and fibula were displaced to a position above and at right angles to the femur, pointing posteriorly. The fibula was simply pulled out of position and is in almost correct juxtaposition with the succeeding elements. The tibia, however, was not only pulled out alongside the fibula but was turned over, its lateral side up. The meso- and metatarsals are slightly twisted and moved about, but lie in their relative positions.

The spongiosa is still open and porous as in dried recent bone, indicating that the silts settling around the carcass formed an impervious blanket that prevented later infiltration by ground waters.

The occurrence of the skeleton indicates that the carcass of the plesiosaur settled gently to the muddy ocean floor. It came to rest upon its back, the left paddles flattening out, inner side up, alongside the body. The right paddles lay partially extended with the propodials alongside the body, but their distal parts were bent over the propodials and backward along the body. A plausible explanation for this disarrangement might be tugging and pulling by scavengers. However, the similar and parallel arrangement of the displaced parts might also be explained as resulting from a uniform force, such as a current, that lifted and folded back the partially decomposed paddles.

Since the skeleton was probably complete when buried, and nearly all articulated, it seems likely that deposition of sediments was rapid, and the carcass was not long exposed to scavengers.

According to Bürgl (1954, p. 11), the invertebrate fauna indicates a facies comparable with the Vocontian Fossa, or basin, of the western Alps and the Subbetic Fossa of central Spain, which was the deepest of the European Tethys. This is corroborated by the uniform fineness of the sediments.

Plesiosaur bones, in common with large marine vertebrates, have much spongiosa which would offer little resistance to crushing. Nevertheless, while there is some evidence of compression (e.g., the snout, left scapula, right coracoid, and a few limb elements), the skeleton as a whole is virtually uncrushed. Even the limb bones, often flattened in plesiosaurs, are nearly all intact, and the vertebrae are all uncrushed.

The bone surface is well preserved; measurements are trustworthy throughout.

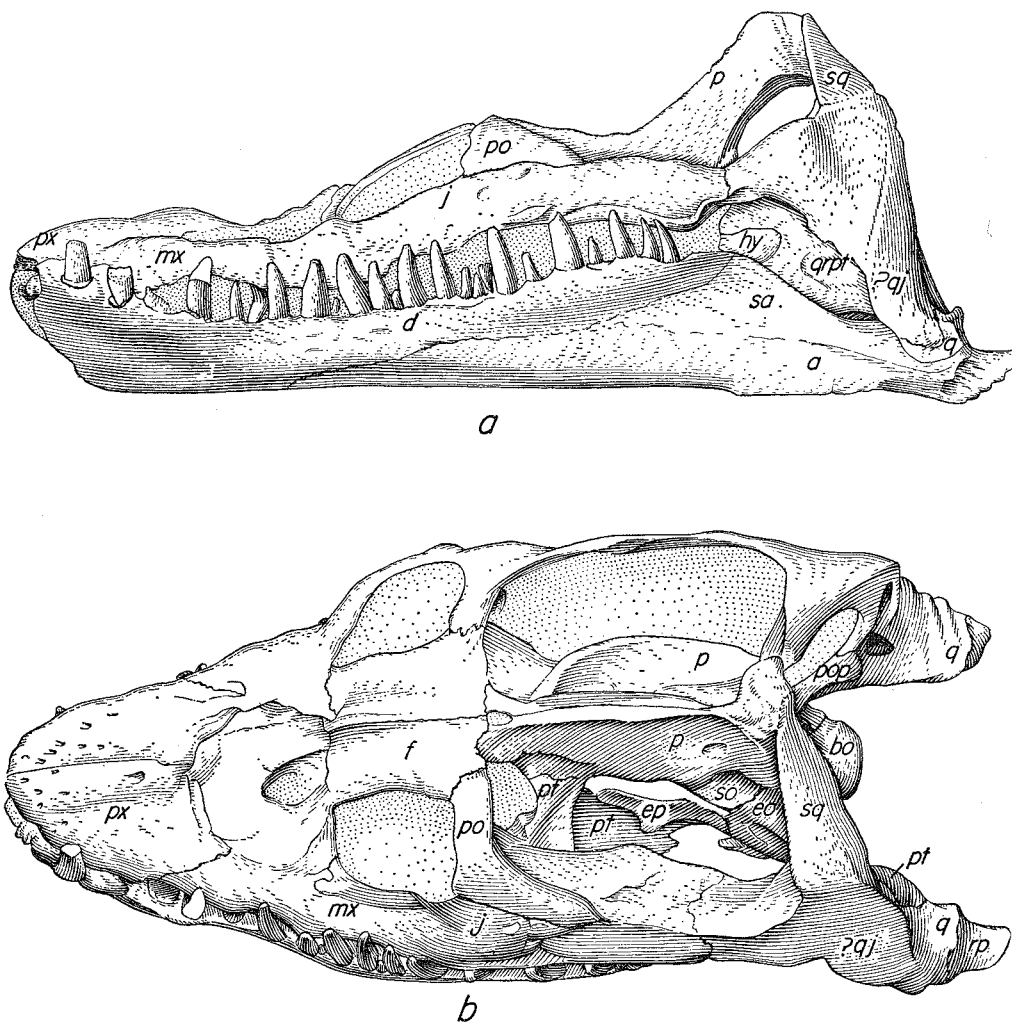


Fig. 3. *Alzadasaurus colombiensis* Welles, type specimen, UCMP 38349: *a*, left lateral, and *b*, dorsal views of skull. $\times 1\frac{1}{3}$.

There are many gastroliths in and around the rib-basket. Since these are the only pebbles in an otherwise uniformly fine-grained matrix, there can be little doubt of their authenticity.

DESCRIPTION OF THE BERKELEY (TYPE) SKELETON

SKULL

The skull measures 35 cm from snout to condyle and is only slightly distorted by crushing. The orbits are 13 cm behind the snout (beak index 37), and the breadth at the quadrates is 16.5 cm. The parietal crest and left temporal arch are dislocated by having their upper parts crushed to the right, and a circular

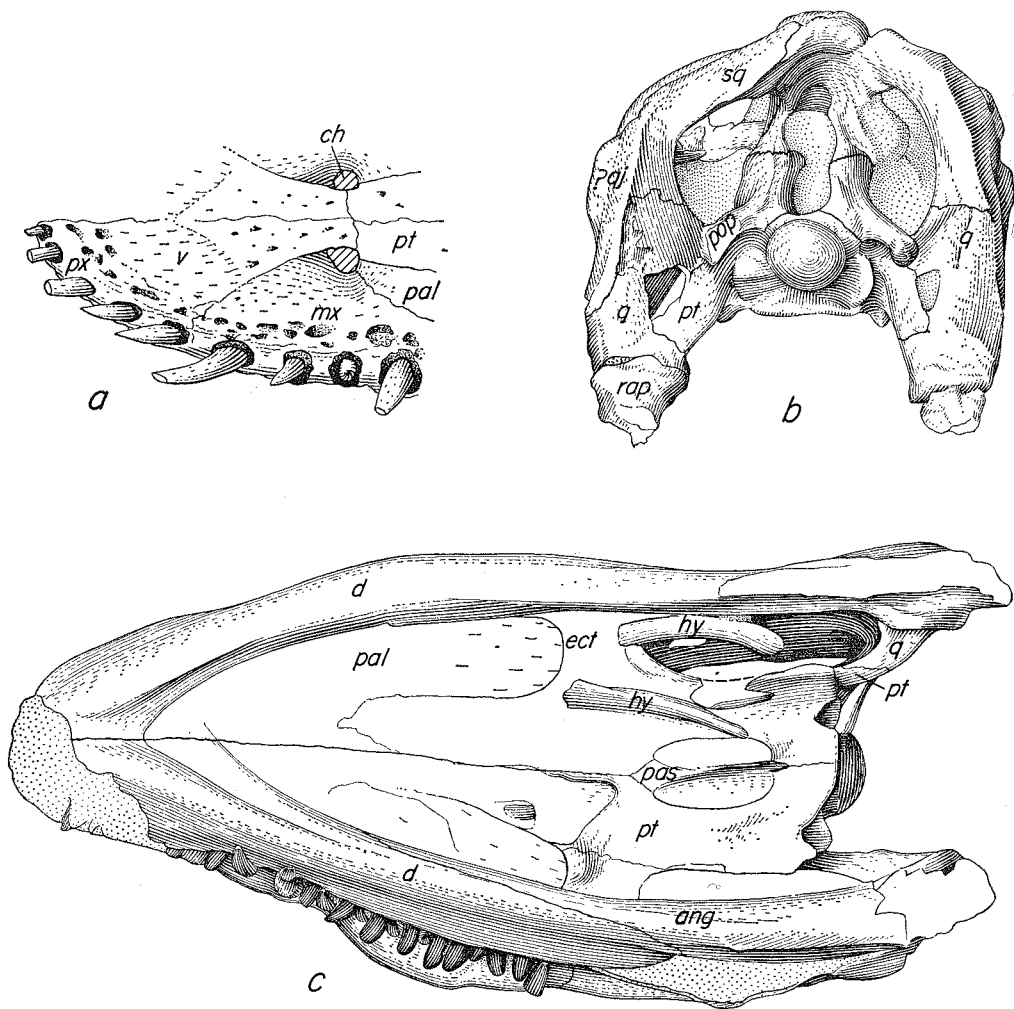


Fig. 4. *Alzadasaurus colombiensis* Welles: a, detail of front of palate of referred skull; b, c, posterior and ventral views of type skull. UCMP 38349. $\times \frac{1}{8}$.

pit 62 mm in diameter is crushed into the snout, centering at the nares. A similar crushing has occurred on the Bogotá skull. It seems unlikely that a predator could have injured both in the same manner, especially since no vital part is affected. It is more probable that a cavity immediately below the crushed area failed to fill with matrix and was subsequently collapsed by the weight of the overlying sediments.

The *premaxillary* joins its opposite in a thin, straight, noninterdigitating mid-line suture, or, in Owen's terminology, a harmonia. A rostrum is thus formed, which is rough-surfaced and pitted with many circular and longitudinally oval openings about 2 mm wide. These pits are concentrated at the tip of the beak, but extend posteriorly in a line along the maxillary to the orbit. The premaxillary

evidently extends posteriorly as a slender pointed projection that either lies median to, or more probably overlaps, the frontal. It seems to extend to the center of the orbit, although this region is crushed, and here I cannot be certain of sutures.

The *maxillary* suture also is obscured by crushing, but is traceable along the usual course posterodorsally from behind the fourth tooth to the naris. The maxillary immediately flares out, and so the skull width suddenly increases just below and in front of the orbits. The premaxillary suture is the only one that can be made out with certainty. The maxillary probably ends posteriorly below the middle of the jugal arch in a downcurved slender point. The facial surface of the maxillary bears numerous small pits and foramina similar to those on the premaxillary but smaller. The dentition is discussed below.

The *nasal* and *lacrimal* cannot be identified.

The *frontal* is crushed anteriorly, especially on the left side; hence the relationships with nasal, lacrimal, and prefrontal are not known, although in the midline the frontal seems to have the posterior projection of the premaxillary either lying upon it or wedged between the two frontals. The interorbital region is preserved as a unit and has nearly straight, parallel, orbital borders. A transverse section includes a ridge about 1 cm broad above the eye, a shallow groove about 1 cm broad medial to the ridge, and a narrow midline crest. The two frontals together form a nearly flat plate. Posteriorly the frontal forms the anterior border of the parietal foramen, and lateral to this forms the anteromedial border of the great temporal fenestra. It projects posterolaterally to meet the postorbital, then, anteriorly, forms the nearly straight supraorbital border. This border is slightly concave posteriorly and anteriorly and has a slight convexity near the center.

The *parietal* overlaps the frontal anteriorly, and forms the lateral and posterior walls of the parietal foramen and the long thin sagittal crest. This crest is crushed, but can be restored satisfactorily to rise steeply from the foramen to a little above the level of the top of the squamosal arch, convex from the foramen posteriorly. It is only 2 mm wide and about 9.5 cm long. Anterolaterally the parietal meets the postfrontal. Immediately behind this it forms the roof of the braincase, concave vertically about 4 cm across both parietals. There is a gap of 1 cm between epipterygoid and parietal. Posteriorly a lateral process extends 6 cm from the midline beneath the squamosal. This seems to be entire on the right side and broken free from the overlying squamosal.

On the occipital surface, below the squamosal process, the parietals form a narrow concave midline surface that slopes about 45° anteroventrally. The fused parietals overlap the supraoccipital. Although I have not been able to find a suture on the occipital surface, the suture is clear on the lateral wall within the temporal fenestra where the grain of the two bones makes an angle of nearly 90° . This difference in grain is accentuated by slight ridges on the lower part of the parietal parallel to its grain.

There seems to be no room for an *interparietal*, and I doubt that this bone is present in elasmosaurs.

The *postfrontal* cannot be delineated, but it seems to occupy the normal elasmosaurian position at the front of the great temporal fenestra lateral to the parietal.

The *postorbital* has a long base that overlaps the jugal from the orbit to about 7 cm behind the orbit, where it meets the ?quadratojugal. The contact is marked by a thickening of the temporal bar and an upcurving to the level of the postorbital. The upper end of the postorbital meets the frontal nearly at right angles and curves outward and downward. Its posterior border covers the lateral part of the postfrontal.

The *squamosal* overlaps the lateral process of the parietal, curving outward, downward, and backward to form the posterior arch. It terminates ventrally against the ?quadratojugal and quadrate, and curves downward, inward, and forward far enough to lie lateral to the paroccipital process for a distance of about 1 cm. The middorsal region is not clear, but the squamosal seems to cover the parietal dorsally and to wrap around the posterior border of the parietal. I cannot determine whether the two squamosals met in the midline dorsally, but it seems likely that they did.

The *jugal* probably forms the lower orbital border, meeting the maxillary anteriorly, although the suture with the maxillary is not clear. The jugal extends posteriorly above the maxillary and is overlain behind the orbit by the postorbital. It terminates against the ?quadratojugal in a nearly vertical suture directly above that which joins surangular and dentary. Its total length is about 15 cm, nearly half the length of the skull.

The ?*quadratojugal* meets the jugal and postorbital anteriorly, and extends posteriorly and ventrally as a thin plate lateral to the quadrate. None of the sutures is obvious. That between ?quadratojugal and squamosal is indicated on both the internal and external surfaces of the right side of the Bogotá skull, but even here is not beyond question. There is no trace of this suture on the Berkeley skull. This does not negate the arguments previously advanced (Welles, 1949, p. 11) for the existence of a separate quadratojugal, and I am therefore still indicating what I consider its likely presence by using the term "?quadratojugal" for this region.

The *quadrate* forms a condyle 3 cm broad, set deeply in the cup of the articular. From the condyle, the lower internal margin of the quadrate slopes about 45° anterodorsally to lie below and lateral to the quadrate ramus of the pterygoid. The suture between pterygoid and quadrate is parasagittal and plainly visible on the ventral surface. The anterior tip of this pterygoid ramus of the quadrate lies lateral to the vertically expanded pterygoid; although the suture can be traced around onto this lateral surface, it becomes obscure medially. The main vertical bar of the quadrate is convex laterally, slopes slightly forward and upward, and evidently fits into the lower end of the squamosal. A triangular foramen which could be an artifact, although it occurs on both sides, separates the pterygoid ramus from the vertical bar. The upper border of this ?foramen is formed by the lower end of the squamosal as it extends forward to meet the pterygoid. The suture between quadrate and ?quadratojugal cannot be delineated.

The *epipterygoid* has a narrow base which rests on the pterygoid just in front of, and immediately lateral to, the interpterygoid vacuity. The lower part is a vertical rod about 8 mm in diameter; this extends upward and expands into a broad blade nearly 5 cm long and 2 cm high that dips about 25° posteriorly.

This blade lies in a parasagittal plane below the lower edge of the parietal, and forms the lateral wall of the braincase.

The *basioccipital* forms the entire condyle, and slopes upward to form a suture with the opisthotic and exoccipital. The condyle is nearly round, slightly pointed, and set off from the anterior part by a ventral constriction that extends a short distance dorsally up the sides. The tuberous processes are short and stout and approach the pterygoids, but open posteriorly. There is no sign of a fenestra ovale on the end of the tuberous process. The ventral surface of the *basis cranii* between the tuberous processes is completely covered by the fused pterygoids.

The *basisphenoid* is not visible externally.

The *parasphenoid* is exposed between the pterygoids, where it forms the roof of the interpterygoid vacuity and extends ventrally into a sharp keel which reaches below the level of the pterygoids.

The *exoccipital* cannot be distinguished from the opisthotic on this skull, as the two are solidly fused. They rest upon the basioccipital on a suture dipping 30° ventrolaterally, and form the lateral wall of the lower half of the foramen magnum, rising 3 cm above the base. A vertical groove, 1 cm lateral to the foramen, separates the paroccipital process from the vertical moiety. The lateral wall of the exoccipital is convex anteroposteriorly. The long slender paroccipital process, so characteristic of plesiosaurs, arises at the level of the base of the foramen magnum and from here extends 3 cm posterolaterally to lie medial to the squamosal. The process is 1 cm high and is slightly expanded distally. It lies close to the quadrate ramus of the pterygoid, only 3 or 4 mm separating the two.

The exoccipital measures about 5 cm anteroposteriorly, is capped by the supraoccipital, and meets the posterior dorsal blade of the epipterygoid anteriorly. The exoccipital forms the lateral wall of the braincase and is about 1.5 cm thick.

The *supraoccipital* has a broad base where it joins the exoccipital. Above this it thins immediately and forms an open arch above the foramen magnum. This thinning results in a somewhat 8-shaped foramen magnum that has a lower, nearly parallel-sided opening between the exoccipitals and a broader, hemicylindrical opening within the supraoccipital. The upper opening, 23 mm in diameter, is constricted to about 20 mm between the exoccipitals. The supraoccipital-exoccipital suture dips forward about 30° , and the overlying parietal dips forward nearly 46° ; so the anterior end of the supraoccipital is shorter than the posterior.

The *palate* is so crushed and covered by a very tough gypsiferous matrix that the anterior part cannot be made out. In the basal part the two pterygoids separate to form an interpterygoid vacuity 5 cm long and 3 cm wide which is divided by a very thin parasphenoid. Lateral to the vacuity the pterygoids are concave transversely: their lateral edges extend below the general level and a cross section is slightly arched. This region is about 7.5 cm broad. Lateral to it lie the subtemporal vacuities, 9.5 cm long and 3.3 cm broad. Behind the interpterygoid foramen the pterygoids fuse to form a broad plate which projects backward below the basioccipital between its tuberous processes.

On its dorsal surface the pterygoid forms a thin vertical plate that extends from beneath the epipterygoid back beyond the horizontal plate of the pterygoid to meet the quadrate. The pterygoid-quadrate suture is visible on the ventral

surface as a straight parasagittal line. The vertical plate of the pterygoid, where it reaches back to the quadrate, lies below and close to the paraoccipital processes.

The *hyoids* lie nearly together on the left side of the palate, the left hyoid extending up into the subtemporal vacuity. They are rodlike, oval in cross section; the left, 7 cm long, is about 8 mm in diameter, and is convex downward along its length. The right hyoid is slightly smaller and nearly straight, but lies against the left pterygoid and was evidently crushed. These are presumed to be the first ceratobranchials (Romer, 1956, p. 420).

The *lower jaw* measures approximately 41 cm along the ramus, but the front of the symphysis and the posterior tip of the retroarticular processes are broken away; hence the estimated total is 43 cm. The mandible is shallowest, 3 cm, below the caniniform tooth and deepest, 6.5 cm, at the anterior border of the angular. The lower border is nearly horizontal from front to back, and the two rami arch laterally from the symphysis. The symphysis is massive and its lower surface bears a longitudinal groove formed by thin processes of the dentaries.

The quadrate articulation is typically elasmosaurian in that the articular and angular, or possibly prearticular, form a deep cup around the quadrate.

The only sutures that can be traced are those between dentary and prearticular, and between prearticular and angular. The former runs slightly forward and downward from the highest part of the jaw just below the jugal-?quadratojugal suture. The latter begins 26 mm above the lower border of the angular and can be traced posteroventrally to below the quadrate condyle, where it runs about 1 cm above the lower border.

The *teeth*, irregular in size and position, are thecodont, but they seem to have been rather loosely inserted because two teeth are out of their sockets and have been displaced. They now adhere to the skull along the outside of the maxillary and jugal.

Individual teeth are nearly round in section, with only a slight external flattening. The enamel crown is smooth externally, but the anterior and posterior edges are finely striated longitudinally.

In each premaxillary there were 5 teeth, now represented by empty alveoli or broken bases. In the right maxillary are indications of the presence, or formed presence, of 9 more. The left maxillary shows but 3. Thus the right side of the upper jaw seems to have held 14 teeth, the left but 8, and these extend only as far back as the center of the orbit.

The first premaxillary tooth is very small and peglike, 5 mm in diameter and projecting forward only about 10 mm. The tip of the upper jaw is thus armed with two tiny central teeth that extend forward between the large lower teeth at the front of each dentary. These are followed by the large premaxillary and maxillary teeth, which normally alternate and interlock with the lower teeth. The largest teeth occupy the region just below the orbitonasal bar, in a caniniform position. They are 10 mm in diameter and 45 mm long.

In the left dentary, 19 teeth remain, and there was probably one more anterior to these. All slant slightly forward. The first four measure 1 cm in diameter and are thicker than the others, but none is complete; so the length is unknown. Behind these the teeth are uniformly about 2.5–3 cm long and 7 mm in diameter.

The four large anterior teeth are below the premaxillary, the others below the maxillary, and they continue back to the middle of the jugal arch, at some distance behind the maxillary teeth.

AXIAL SKELETON

Many species of plesiosaurs are based on a few vertebrae or even a single vertebra; hence plesiosaur vertebrae have been described in greater detail than those of most other reptiles. Through his studies of plesiosaur vertebrae, Owen (1838, p. 64; 1840A, p. 56; 1840B, p. 516) gave us our modern concept and terminology of the parts of a vertebra: centrum, pedicles, neural arch and spine, pre- and post-zygapophyses, haemal arch, and facets for attachment of ribs and haemal spines. In the cervical and caudal regions of elasmosaurs the rib facet becomes a small crater with elevated rim and receives the convex single rib head. Of the many names that have been applied to this rib facet, the simplest is the newly coined "ripit" used throughout this paper. When the ripit is on the centrum it receives the capitulum of the rib, and is called a "parapophysis." In the dorsal region it may be close to the centrum, as it is in elasmosaurs, or on a pedicle that extends a few centimeters above the centrum, as in some of the pliosaurs. When the ripit develops on the arch it is known as a "diapophysis" and, in most reptiles, receives the tuberculum of the rib. However, in elasmosaurs the rib is always single-headed; so the ripit is single and may be on a parapophysis, a diapophysis, or a combination of the two. If it is a combination, the compound rib support is called a "transverse process."

The vertebral column is serially differentiated into cervical, pectoral, dorsal, sacral, and caudal regions. Owen (1840B, p. 523) attempted to define these regions by suggesting that "the vertebra in which the costal articular surface has first entirely left the centrum and passed upon the neurapophysis should be reckoned as the first dorsal."

Later, Owen (1851, p. 66) "selected the arbitrary character of the impression of the costal articular surface, or any part of it, upon the centrum, as the character of the cervical vertebrae in the *Plesiosaurus*." Seeley (1877, p. 545) refined this to restrict cervical vertebrae to those in which the rib articulated wholly with the centrum, and separated as "pectoral" those vertebrae with the ripit partly on the centrum and partly on the pedicle, or diapophysis. He then recognized as dorsals those vertebrae with the ripit entirely upon the diapophysis. Sacrals, like pectorals, again were characterized as having the ripit shared by diapophysis and centrum, like the pectorals, whereas caudals have the ripit entirely on the centrum. This separation of pectorals and sacrals has been accepted by most subsequent workers and was elaborated in my paper (Welles, 1943, p. 135). However, it is usually difficult and sometimes impossible to determine exactly where the facet leaves the centrum and is entirely on the diapophysis; so, although Seeley's categories are useful, they are not universally applicable.

The Berkeley skeleton contains 56 cervicals, 2 pectorals, 23 dorsals, and part of the 82d (? 1st sacral) in articulation, plus a single isolated proximal caudal centrum.

All centra lie on the left side and are uncrushed. They are nearly oval cylinders,

with only slight enlargements of the articular faces. The anteroposterior concavity of sides and bottoms decreases posteriorly until in the dorsal region it is barely noticeable. The ends are only slightly concave and have fairly sharp corners, but there is a slight angular truncation or beveling of the peripheries of the articular faces. This affects only the outer 2-3 mm and is pronounced only on the posterior cervicals.

The ends are nearly regular depressed ovals. There is no ventral groove; the neural canal forms only a flat top to the oval without descending into it to form a dorsal groove. In the center of the articular faces of the anterior and median cervicals is a shallow oval pit similar in outline to that of the articular face. This pit disappears by the 50th cervical and the articular face is slightly concave.

The lateral surface of each cervical is convex at the base of the fusion of pedicle and centrum. This low swelling is separated from the underlying lateral keel by a slight concavity. The lateral keel is faintly indicated and lies nearer the rhipit than in later elasmosaurs. The keel can be seen only as far back as the 38th centrum.

The ventral keel is smoothly rounded and poorly developed on the anterior cervicals. It widens at each end of the centrum where it joins the articulating face; so the ventral surface is fairly flat transversely at the ends of the centrum and but slightly convex in the middle of the centrum. An anteroposterior profile along the ventral keel of a cervical vertebra is only slightly concave. This profile is almost straight on the pectorals and dorsals. From the 30th centrum on, there is a nutrient foramen on each side of the ventral keel. No trace of this foramen can be seen anteriorly. The increase in size of the ventral nutrient foramina makes the ventral keel more sharply delineated as far as 46. From here on the foramina become more widely spaced and the keel broadens, partaking of the general curvature of the centrum. In the pectorals and anterior dorsals (57 on) the foramina are present only as indentations in the essentially cylindrical centra.

As Van Beneden (1882, p. 11) pointed out, since the anterior foramina are close together, and the posterior are far apart, the relative separation of these nutrient foramina can be of help in determining the position of a particular centrum in the column. The foramina are 11.5 mm apart on the 33d centrum, 14.7 mm on the 39th, 19.2 mm on the 50th, and 32.8 mm on the 59th. This increase is not entirely regular but nearly so.

The pedicles arise smoothly from the centra and are almost as long anteroposteriorly as the centra. In many plesiosaurs the arches are separate from the centra; in many others the arches and centra are fused, but the suture is easy to see. Here the fusion of centrum and arch is complete, and nowhere along the cervical, pectoral, or dorsal series is there any evidence of the suture. Anterior zygapophyses project slightly forward of the anterior face and stand above the centrum: 25 mm to the top of the zygapophysis anteriorly, 30 mm medial, 50 mm posteriorly, and 60 mm on the pectorals. The articular zygapophyseal facet is nearly horizontal on the first few cervicals, inclines inward at about 30° on 40, and has become vertical by 47. Posterior zygapophyses extend far backward; hence a plane projected upward from the posterior face of the centrum cuts through the middle of each zygapophysis. The normal overlap of anterior on pos-

terior zygapophyses is such that the centra are spaced an appreciable distance apart. This spacing is indicated also by the positions of the centra in the matrix. It averages 0.5 cm, sometimes only a few millimeters, for the first 20, 1 cm from 21 through 34, 1.5 cm through 46, 0.5 cm through 49, and about 1.5 cm through 54. From 55 through pectorals and dorsals, the centra lie closer together, only about 0.5 cm apart.

Arising from the lateral faces of the centra, the pedicles enclose a large round neural canal. Its diameter is 2 cm at the 10th centrum, 2.5 cm at 42, and 3 cm at 57.

Neural spines slope upward and backward to about the 30th cervical, curved like an overextended thumb. The plane of the posterior face of the centrum projected dorsally bisects not only the posterior zygapophyses but also the summit of the neural spine. This is true of all the cervicals, even from 31 on, where the spines become increasingly straight but still incline posteriorly. The summits of the anterior spines are rounded anteroposteriorly, but at about 28 they develop a flat summit for the anterior half, with the posterior half inclining downward posteriorly. On 33 a rounded expansion of the spine high on the posterior border fits a corresponding concavity excavated in the anterior border of the following spine. This structure is unique, and is found on about ten spines. From 42 on, the anterior border becomes straighter and a thickening of the summit of the spine is apparent. This thickening is directly above the posterior central face, and from 46 on at least to the pectorals a pronounced beveling or excavation marks the posterodorsal corner of the spine.

A peculiar feature, observable only after complete removal of the matrix, is a deep vertical groove in the posterior edge of the spine, running dorsally from between the posterior zygapophyses. Into this groove fits an anterior thinner part of the spinous process of the following vertebra. This tongue-and-groove arrangement is well developed on the posterior cervicals. The groove is first apparent on the 40th, whereas the anterior "tongue" is visible on all spines from the third centrum back to the first pectoral. Its continuation into the dorsal series cannot be determined until the specimen is further prepared. The anterior "tongue" seems to have developed as a response to the posterior extension of the posterior zygapophyses of the preceding vertebra. The posterior groove could be the result of mechanically adapting the posterior spinous border to the "tongue" of the succeeding spine, as the whole spinous system in this reptile is set far posteriorly with respect to the centra.

Owen (1850, p. 396) described the spine of *Plesiosaurus bernardi* as having a "rough shallow tract along the fore part and a wider, deeper, and smoother excavation behind." The posterior groove is similar to our form, but there is no anterior tongue. In *Plesiosaurus* sp. Owen (1851, p. 63) noted an "angular depression at the back part of the spine as in *P. bernardi* and many other species." Leidy (1865A, p. 24), in describing *Discosaurus vetustus*, stated that the spine "is deeply grooved behind at its root for an elastic ligament." Thus, although the posterior groove has been noted before, and its function suggested as attachment for an elastic ligament, the anterior tongue seems to be another unique feature of *Alzadasaurus colombiensis*.

Cervical ribs are fused to the centra back through 46, but on 47 the rib is an

oval crater on the ventrolateral border of the centrum, a little closer to the posterior end than to the anterior. The rib articulation faces slightly posteriorly and becomes vertically elongate on the last three cervicals (54-56). On the pectorals it has risen so high on the lateral wall of the centrum that the dorsal part is formed by a projection from the spine. By custom the pectorals are distinguished by this compound nature of the ripit. There are only two pectorals, 57 and 58. On 59, the first dorsal, the ripit is entirely on the diapophysis. From here through the middorsals, the diapophysis rises well above the centrum, and the ripit is an almost vertical surface facing slightly posteriorly. On 59 through 61 the ventral face of the diapophysis is divided into a sharp transverse ridge and a rounded anterior part, the two separated by a groove. From 62 on through the dorsal series the ventral surface of the diapophysis is single and smoothly rounded. The cervical ribs are exceptionally well preserved. From 4 at least through 9 they are broken away from the centra and collapsed, revealing the suture pattern of the ripit. From 10 through at least 14 there has been a slight separation at the ripit, but from 15 through 46 the ribs are fused to the centra and collapsing has been effected only by breaking the ribs a centimeter or so below their fusion with the centra. From 47 on the ribs are free from the centra.

The single caudal preserved is anterior, its indices 49, 130:151. The general shape is triangular, with large circular ripits 32 mm in diameter projecting on short pedicles low on the sides. The lateral surface of the centrum is convex above the ripit and is continued directly into the pedicle of the neural arch, which is as long as the centrum and inclines forward. The anterior end is slightly concave; the convex margin is set off from the lateral wall by a slight groove. This disc-like development of the articulating surface is common among elasmosaurs. The neural canal is small, the maximum breadth about 15 mm, and it is incised nearly half its diameter into the centrum.

The first few ribs consist of a short (4 cm) ventrolateral projection that is flattened laterally but is nearly as long as the centrum anteroposteriorly; the following ribs project slightly forward and are elongated posteriorly to at least the middle of the following centrum. In natural position the ribs underlapped each other posteriorly, the long posterior projection lying below the succeeding rib. The posterior projection of the rib (its original length) decreases posteriorly until, from 20 on, the anteroposterior dimension of the distal end is less than the length of the centrum and there is no underlap of ribs. By 47 the ribs are relatively elongate, having lost much of the anterior projection and "hatchet shape" of the more anterior ribs. From 54 on their length increases abruptly from 14 cm to 28 cm on 57, to 43 cm on 59, and to about 60 cm on 60. Thereafter they decrease gradually to a length of about 30 cm on 75.

The dorsal ribs lie in regular array beneath the girdles, but are obscured by matrix. However, on both sides the ribs lie closely parallel to each other and their distal parts are nearly sagittal.

The first two gastralia are dislocated. The first median gastralium is 55 cm long and has a small central prominence. There seem to have been eleven rows of gastralia between the coracoids and pubes. These are about the size of the dorsal ribs (3 cm in diameter) and formed a fairly complete ventral armor, but are now disarranged.

About 100 gastroliths lie between the ribs from vertebra 69 to 75. Some farther forward, but the concentration is rather near the pubes. The gastroliths are smoothed but not polished, usually ovoid, and all examined are of quartz. The largest found is 8 cm \times 3.5 cm, the smallest a 0.5 cm sphere.

TABLE 2
VERTEBRAL CENTRA OF ALZADASAURUS COLOMBIENSIS, N. SP., UCMP 38349

Vertebra number	Measurements (mm)			Vertebra number	Measurements (mm)		
	L	H	B		L	H	B
4.....	29	34		32.....	92		
5.....	34		43	33.....	80		
6.....	34			34.....	83		
7.....	33			35.....	87		
8.....	36			36.....	86		
9.....	39			37.....	86		
10.....	38	32	49	38.....	88	76	95
11.....	40	34	51	39.....	90		
12.....	41		52	40.....	89	79	96
13.....	45			41.....	88		
14.....	46	42	56	42.....	88	82	97
15.....	47	45	57	43.....	89		
16.....	52			44.....	94		
17.....	54			45.....	89		
18.....	56			46.....	88	88	100
19.....	60			47.....	88		
20.....	65	50	71	48.....	89		
21.....	65			49.....	89		
22.....	63			50.....	88		
23.....	67			51.....	99	92	107
24.....	65			52.....	85		
25.....	67			53.....	81		
26.....	63			54.....	87		
27.....	77			55.....	83		
28.....	78			56.....	78		
29.....	77			57.....	71		
30.....	84			58.....	79		
31.....	82	67	87	? Ant. cd....	49	64	74

PECTRUM AND PELVIS

The pectrum is complete, represented by the fused clavicles, both scapulae, and both coracoids. Clavicles, coracoids, and right scapula are but slightly displaced from their proper relative positions, but the left scapula is turned visceral side up: the anteromedial projection now faces anterolaterally and the dorsal process is crushed into the same plane as the ventral blade.

The *clavicular arch* is well preserved, lying opposite the 54th vertebra. The right clavicle has 14 cm of its lateral tip crushed down over centrum 56, and the posterior edge also is crushed for about 4 cm. Both clavicles meet in a 15 cm midline suture and narrow gradually laterally to about 5 cm. Since they are

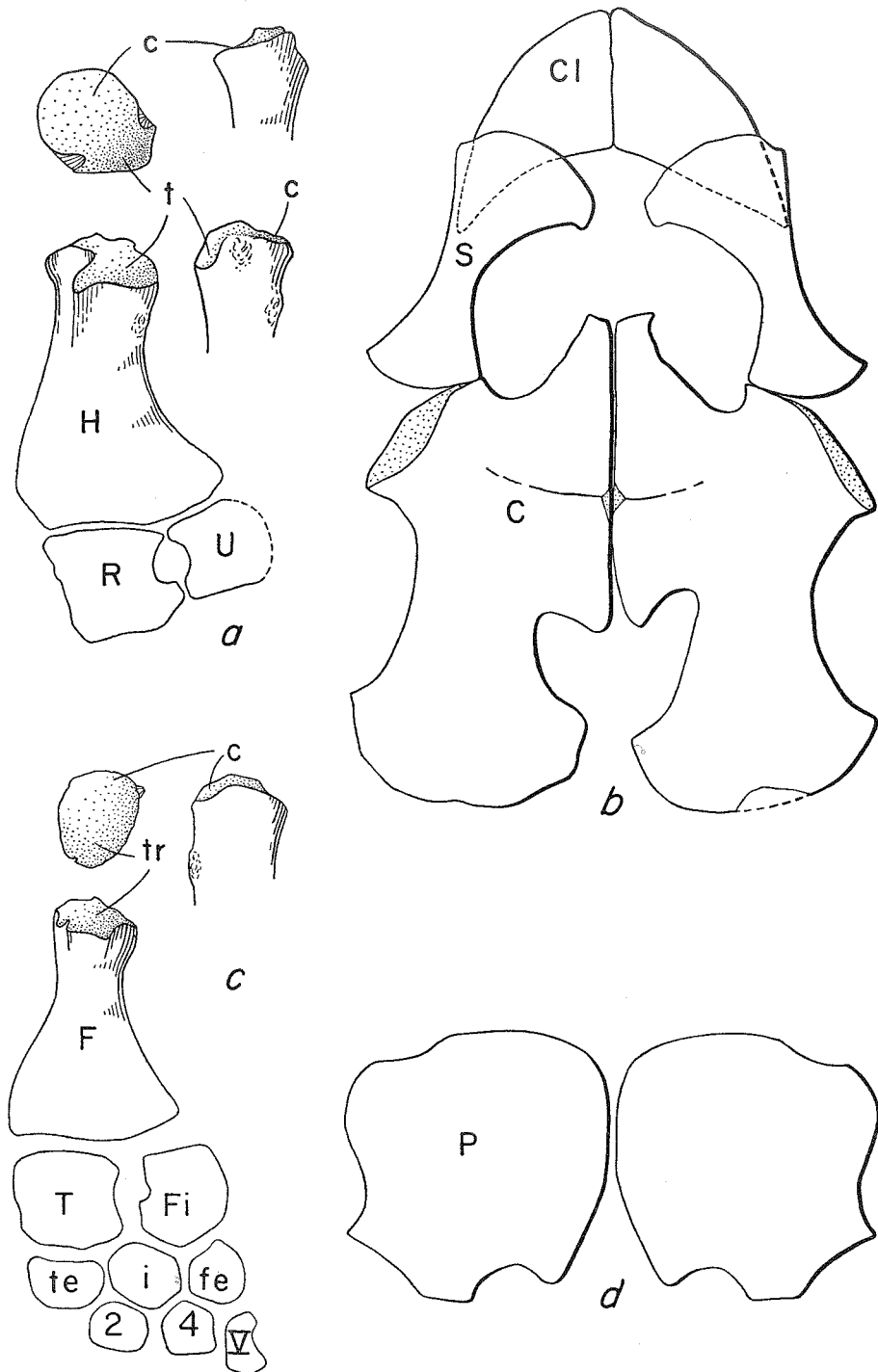


Fig. 5. *Alzadasaurus colombiensis* Welles, type specimen, UCMP 38349: a, lateral view of left humerus, radius, and ulna, and proximal, anterior, and posterior views of head of humerus; b, ventral view of pectrum; c, left lateral view of left femur *et seq.*, with proximal and anterior views of head of femur; pubes. $\times \frac{1}{10}$.

convex below, the anterointernal border slopes upward. The clavicles continue for at least 6 cm posteriorly, but this part is thin and has been crushed downward about 4 cm. The center of ossification is near the midline and near the center anteroposteriorly, of the clavicle. The grain of the bone is plainly visible radiating forward, backward, and especially outward from this center. The anteroposterior grain of the bone near the midline is thus evidently a part of the clavicle and not of the interclavicle. The clavicles were set, in life, to form a fairly sharp prow, at angles of about 120° to each other, with their midline suture inclining upward nearly 45° . The lateral wing of the clavicle measures 42 cm from the anterior midline. It is roughened distally where it overlies the scapula. Since the two clavicles meet in the midline, there is no room for an interclavicle, unless on the dorsal surface, and I judge the interclavicle to be absent.

The right *scapula* lies ventral side up, its dorsal process projecting downward at right angles to the ventral plate. The lateral surface of the dorsal process is concave just above the ventral plate. The dorsal process, 10 cm wide above, expands ventrally into a broad base as it joins the ventral plate. It ends dorsally in a surface 12.5 cm long and 4 cm thick that evidently formed the base for a cartilaginous continuation. The glenoid bar has a right-triangular cross section, the hypotenuse facing dorsointernally. Scapulae and coracoids were loosely attached and are now separate. The glenoid surface of both is very rough, covered with cones of about 1 cm base. A thick cartilage must have been present in life. The ventral plate of the scapula, about 20 cm wide and 3 cm thick, is concave along the anterointernal edge. This concavity is 1–2 cm deep, and was probably occupied by cartilage.

The ventral plates of the scapulae are flat. Heretofore I have assumed this to be their natural shape. However, this specimen is so well preserved that an accurate reconstruction can be made, and this demonstrates a very different condition. Three factors limit the position and shape of these scapular plates: the apposition of scapula and coracoid; the shape of the glenoid; and the overlap of the lateral clavicular wings.

At the scapula-coracoid contact, both surfaces are rough and there is no close osseous contact; so a considerable amount of cartilage must have been present. The best fitting of scapula to coracoid therefore gives only an approximation of their exact relationships and indicates an almost sagittal direction for the inner edge of the scapula immediately in front of the coracoid.

The minimum size of the glenoid can be reasonably ascertained by fitting it to the head of the humerus with considerable allowance for cartilage to smooth out the roughness of capitulum and glenoid. This estimate agrees with the position obtained by actually fitting scapula to coracoid.

However, the result of these two mutually corroborating factors is to throw the anterointernal blade of the scapula several centimeters from the midline into such a position that the clavicles are far out of contact. The dorsal (visceral) surface of the scapular blade bears a roughened area; as Professor D. M. S. Watson pointed out when he examined the specimen, this indicates a close overlap of the clavicle on scapula. The only method of fitting clavicles onto scapulae is to curve the scapulae. This, in turn, makes it necessary to fold the clavicles along the mid-

line, thus narrowing the distance between clavicular tips and bringing the scapulae almost together in the midline. The result of this fitting is a pectrum turned up in front and keeled like the prow of a rowboat. This is a natural reconstruction and the only one that fits all our requirements. With this reconstruction the scapulae nearly meet in the midline but do not project backward into a pectoral bar to meet the coracoids.

The *coracoids* are nearly together, but the right is shifted slightly backward. The right is entire; the left lacks only a little of the distal border. Both are broadly expanded posteriorly and are excavated to form a pronounced cordiform inter-coracoid vacuity just behind their symphysis. The coracoids are very thick between the glenoids, the midline suture being 9 cm deep. In front of the point of maximum thickness both coracoids have a dorsal flexion anteriorly and the bone thins to 7 cm. The result is a great concavity between the centers of the glenoids on the ventral surface of the coracoids, probably for pectoral muscles, and a thick plate, strengthened by its dorsal flexure, to take the centrally directed thrust of the head of the humerus. They extend far forward in the midline, 12 cm beyond the scapular suture, ending in a concave facet that was evidently for cartilage. The distal plate of the coracoid thins gradually to 2 cm in the midline and 0.5 cm laterodistally.

The right *pubis* is complete. It lies above centra 77–80 and has been slightly crushed laterally. The midline suture, approximately 16 cm, is so convex antero-posteriorly that much cartilage was probably present in life. The anterior border is convex.

Only a bit of the acetabular end of the left ischium remains; hence it is not possible to reconstruct the pelvis. Although the ischium, left pubis, and vertebral column are cleanly broken, a thorough search revealed only a few fragments. Further description can be supplied only from the Bogotá specimen.

LIMBS

Both *humeri* are present, the left complete, the right lacking only a bit of the anterodistal tip. The left humerus has two crushed places on the lateral face of the distal border, but otherwise both humeri are almost perfectly preserved. The right humerus is 39.5 cm long, 16 cm anteroposteriorly proximally, and probably 29 cm distally (B73%L39.5). Proximally it is 16 cm thick from inner edge of capitulum to outer edge of tuberosity. The distal end of the humerus is 7 cm thick across the radial facet and 6 cm across the ulnar. The left humerus is slightly longer, B71%L41, but is otherwise virtually identical with the right humerus.

Capitulum and tuberosity are nearly plane surfaces and meet at about 110°. They are partially separated by anterior and posterior grooves which narrow the upper surface of the tuberosity from 11 cm to about 6 cm. The anterior edge of the tuberosity is 5 cm behind that of the capitulum, measured in a plane perpendicular to the flat distal end of the humerus. The tuberosity is parallel to the radial facet, or, upon orienting the humerus with radial facet horizontal, the dip of the tuberosity is zero. The anterodistal knee is prominent, and a great rugosity for muscle insertion is developed about 8 cm below the rim of the capitulum on

the posterointernal border of the shaft. Above this rugosity the internal face of the humerus flares inward, meeting the capitulum at about 70° . The posteroproximal region of the internal face of the shaft is formed into two grooves by a sharp ridge running downward between capitulum and trochanter. The posterior groove thus formed seems to be the groove that normally separates the two heads of the humerus, but I have not noticed the development of the ridge and anterior groove in other elasmosaurs.

Radial and ulnar facets are 15 cm and 13 cm long, respectively. The radial facet is about 1 cm concave anteroposteriorly; the ulnar facet is nearly flat. In contrast, the radial facet is flat or convex laterally, and the ulnar facet is concave.

The epipodials *et seq.* were evidently in proper position in the left paddle but were displaced in the right. The radius fits loosely into the humerus, its proximal end much straighter than the facet on the humerus. Cartilage or connective tissue must have been nearly as thick as the 2 cm of matrix now present. The anterodistal corner of the radius is almost a right angle (95°). The posterodistal corner bends upward into a 3 cm facet for the distal end of the ulna. No proximal ulnar facet is developed, but the posteroproximal corner slopes downward at about 30° . The length barely exceeds the breadth: for the left, B92%L18; for the right, B86%-L17—a condition to be expected in so primitive an elasmosaur.

Both ulnae are preserved, but on the right the posteroproximal corner is crushed. The left has B122%L14; the right, B107%L14. The distal end curves dorsally to form a radial facet about 4 cm long. The proximal facet for the radius is very small, deflected 1 cm at the most. As a result the epipodial foramen is an ovoid about 6 cm long and 3.5 cm wide distally, narrowing proximally to about 1 cm.

The right forepaddle ends with the radius. An isolated piece, probably belonging to this paddle, contains a complete row of proximal phalanges. From 1 through 5 these measure 8.5 cm, 9 cm, 9 cm, 8 cm, and 6 cm in length. Above and below, these phalanges are separated from proximal and distal phalanges by spaces of 1.0–1.5 cm. There seems to have been no appreciable displacement of the elements, and I think that these gaps, like those between the vertebrae, represent the actual original cartilage and connective tissue. Both ends of the phalanges are slightly concave.

The right femur is 33 cm in maximum length, 12 cm anteroposteriorly proximally and 24 cm distally, therefore B73%L33. The trochanter is set well in front of the capitulum. The capitulum is slightly convex, the trochanter flat; both are confluent, with no indication of separation by anterior or posterior longitudinal grooves, although the surface area where the posterior groove is situated has been destroyed, and such a groove was probably present. The trochanter dips about 7° posteriorly relative to the plane of the tibial facet. The posteroproximal border is a sharp ridge that extends 5 cm down the shaft, ending just behind a large (4 cm \times 5 cm) rugosity for muscle insertion. This rugosity is on the posterointernal side of the shaft, corresponding in position to that on the humerus. Above this rugosity the capitular border is continued outward to form an overhanging edge, concave below, at the upper edge of the shaft. Elsewhere the internal and external surfaces of the shaft run almost straight up to meet the capitulum and trochanter at angles of about 140° .

The shaft is circular in section, 9 cm in diameter. It is composed of a very thin (about 2 mm) external shell of circumferential lamellae and a thick spongiosa. At about the middle of the shaft there is a marrow cavity 2 cm in diameter; the great mass of the bone is spongiosa. As with many other skeletal elements, much of the spongiosa is open and porous without permineralization. The tibial facet is 12 cm long; the fibular facet, 10 cm. The distal extremity is flattened to about 8 cm and this is natural, not due to crushing. The internal surface of the distal blade of the femur is more convex than the outer. This convexity is accentuated by a rugosity 12 cm above the inner distal border. A slight anterodistal knee is present 6 cm above the tibial facet. The distal part of the left femur is preserved, along with the articulated epi-, meso-, and metapodials, except for the proximal half of the fibula, tarsale 1, and metapodial 1.

The left tibia is 13 cm long near the fibular border and 14 cm broad proximally (B108%L13). The breadth was probably increased by crushing. The proximal end lies against the femur (?possibly crushed), but the distal end is separated by 1 cm of matrix from the tibiale and nearly 3 cm from the intermedium. The anterior border is crushed thin and projects forward beyond the femur, although there may have been a dislocation of femur and tibia. The posteroproximal corner is slightly inflected, but does not form a facet for the fibula.

The inner face of the posterodistal corner is strongly inflected, rounded for about 5 cm, and forms a strong distal facet for the fibula. On the lateral face this facet is very weakly developed. Above this the tibia is slightly excavated; a corresponding excavation in the fibula forms a long narrow epipodial foramen that narrows proximally.

The right tibia, which shows only the lateral surface, is a massive bone with a rounded proximal end and a distal end separated into facets for tibiale and intermedium. The distal surface is weakly inflected into a fibular facet. The tibia has only a shallow excavation for the epipodial foramen. The proportion of breadth to length (B118%L12.5) is higher than for the left.

The right fibula is 13 cm long and 11.5 cm broad (B88%L13). It is uncrushed and has a deep (2 cm) excavation for the epipodial foramen and a strong distal tibial facet about 4 cm long on the lateral face. There is no proximal tibial facet.

The left fibula is represented only by its distal two-thirds, which shows well-developed facets for intermedium and fibulare as well as a 5 cm facet for the tibia. Matrix now separates all these elements, indicating that they are preserved in approximately their original relative positions. The fibula is crushed; so its breadth is increased and its posterior border is very thin.

The left proximal tarsalia are evidently in correct position. The anterior border of the tibiale is in line with that of the tibia, and consequently the space between the two (now matrix-filled) widens anteriorly. The intermedium is rounded proximally and only slightly less so distally, where it is separated by 1.7 cm of matrix from centrale 3 and by 3 cm from centrale 4. The fibulare has a slightly concave posterior border with broadly rounded anterior and distal borders. It has no pronounced facet for metatarsal v and is well separated by matrix from all adjacent elements. Its greatest length (9 cm) is posterior and its greatest breadth (7 cm) is proximal.

In the left tarsus, tarsale 1 is missing but it evidently was proximal to, and supported, metatarsal I. Tarsalia 2 and 4 together form an open angle of about 130° into which is directed the distal end of the intermedium. The tarsalia are separated by about 1 cm of matrix that presumably represents the original spacing. The proximal end of tarsale 2 has a short anteroproximal facet and, diagonally opposite this, a short posterodistal facet. Tarsale 4 is slightly larger than 2, and its shorter facets are posteroproximal and anterodistal. Thus the two shorter distal facets of 2 and 4 form a notch that is directly above metatarsal III.

Left metatarsal I is missing. Metatarsal II is a stout element 8.5 cm long with a diameter of 4 cm in the central constricted shaft. Its anterior border is slightly straighter than its posterior, and it lies distal to the large facet of tarsale 2. Metatarsal III, which lies between tarsalia 2 and 4, has a rounded proximal end. It is 9.3 cm long and is constricted sharply just below the 5 cm head to a 3 cm shaft. Metatarsal IV lies distal to the large facet of tarsale 4. Its distal half is missing, but the proximal end is but slightly expanded. Metatarsal V is half in the tarsale row; this is, the distal border of tarsale 4 is even with the center of the shaft of the metatarsal. It is 9 cm long anteriorly, and the posterior border is strongly concave. The phalanges are missing.

DESCRIPTION OF THE BOGOTÁ (REFERRED) SKELETON

Referred skeleton.—A nearly complete skeleton in the Geological Survey Museum at Bogotá, Colombia.

Locality.—100 feet north and about 5 feet stratigraphically above type specimen.

Horizon.—Lower Aptian *vide* Bürgl (1954, p. 17).

Occurrence.—This reptile came to rest upon its back with jaws tightly clenched, but is spread out as though it had settled in a completely relaxed position. The neck is bent gently to the right and the cervicals are rotated, with their right side down. The pectoral paddles extend straight out from the body, and the girdles are centered above the vertebrae. The pelvic paddles extend posterolaterally about 45° . The phalanges are nearly complete in all four paddles, although most of the bone has rotted away, leaving only impressions in the limestone concretions.

These concretions formed around most of the bones and probably protected them from crushing, for they are as uncrushed as those of the Berkeley specimen. The skull also was enclosed in a limestone concretion which preserved the braincase intact. This limestone made it difficult for the collectors to be certain of the continuity of the cervical vertebrae, and there are two gaps in this series.

The natural articulation of the skeleton indicates that it was covered rapidly by sediments which hid it from scavengers. It was later protected from crushing by limestone concretions. The supine position of both skeletons (this and the type) suggests a buoyant force acting on the venter which caused both carcasses to settle on their backs. It is possible that gases of decomposition contributed to the positioning of the skeletons; yet disintegration had not gone far, since the skeleton is virtually complete.

The peculiar circular pit that was crushed into the snout of the Berkeley skull is duplicated in the Bogotá specimen. This makes it more probable that the cause of this peculiarity is a cavity in the snout which failed to fill with sediment and was therefore subject to crushing.

TABLE 3

APPENDICULAR SKELETON OF ALZADASAURUS COLOMBIENSIS, N. SP.

(Measurements in centimeters)

Measurements	Type		Referred
	Left	Right	
Scapula			
Greatest length (center of glenoid anteromedially) ..	38	40	35.5
Breadth of anterior end (from anteroexternal corner posteromedially)	18.5	20.5	18.5
Coracoid			
Greatest length inside scap. sut.	59	58.5	57.5
Length midline suture.	44	44	38
Greatest breadth (at post. end glenoid)	34.5	34.5	36
Breadth of post. expansion.	32+	40	33
Breadth of shaft.	16	17	15
Humerus			
Greatest length.	41	39.5	41
Anteroposterior proximally.	16	16	15
Anteroposterior distally.	29	29	28
Dip of tuberosity from radial facet.	0	0
Radius			
Length.	18	17.5	17
Breadth.	16.5	15	15.5
Ulna			
Length.	14	14	14
Breadth.	17	15	..
Ilium			
Length.
Pubis			
Length (from ischial suture to anteriormost point parasagittally)	34	33
Greatest breadth.	35	31
Ischium			
Length (parasagittally near midline).	25
Breadth (acetabular border to midline).	27
Femur			
Length.	33	36
Anteroposterior proximally.	12	10
Anteroposterior distally.	24	24	22
Dip of trochanter from tibial facet.	10° post.	..	15° ant.?
Tibia			
Length.	13	13	11
Breadth.	14
Fibula			
Length.	13	12.5
Breadth.	12	11.5	..

The presence of two complete articulated skeletons so close together is suggestive of a lethal environment, possibly a poisonous embayment, as has been postulated for Holzmaden by Drevermann (1931G, p. 473). We need collateral evidence from similar areas in which plesiosaur remains are common in order to arrive at the most probable explanation. Among these areas are Holzmaden and southern England in the Jurassic, the Panoche Hills of California, and parts of the Pierre shale in the Cretaceous.

Description.—Since this skeleton is similar to the type, there is no purpose in describing it in detail except where it differs or provides additional information.

The *premaxillaries* form a solid snout, very rough and with numerous small (up to 2 mm) foramina on the dorsal surface. This snout is constricted to 8 cm at the tip of the maxillaries. In each premaxilla are two small anteriorly projecting central teeth followed by four large teeth. The palatal continuation of the maxillary suture can be followed inward about 2 cm, where it turns anteriorly to separate premaxilla and vomer.

The *maxillary* has an interdigitating suture with the premaxillary just behind the fifth tooth. This suture can be clearly traced about 3 cm posteromedially, where it meets the vomer and continues to the internal naris. Another suture between maxillary and palatine must run posterolaterally from the naris, but it cannot be ascertained in this specimen. The dentigerous border of the maxillary contains large irregular alveoli with teeth close to the labial edge. Lingual to the alveoli is a ridge of cancellous bone about 1 cm wide. Replacement teeth develop within this ridge and then move laterally as they come into use.

The *vomers* form a thin plate, convex below and thickened dorsally in the midline. About 7 cm behind the snout they form a small median ventral ridge, and behind this a flat plate lower than the general level of premaxillaries and palatines. They meet the premaxillaries a few centimeters behind the snout in a suture hidden by matrix and the lower jaw. They measure 3 cm across anteriorly, widen to 6 cm at a distance of 8 cm behind the snout, then narrow to 1.8 cm between the nares, about 11 cm from the snout. The vomers form the median borders of the internal nares, which are about 1 cm in diameter and open posteroventrolaterally; the vomers probably continue posteriorly about 3 cm to meet the pterygoid and palatine, but sutures with the latter bones cannot be determined.

The *palatine* is convex transversely on its lower surface. It lies lateral to the internal naris. Here it meets the maxillary in an interdigitating suture that runs laterally from the middle of the choana and then bends sharply posteriorly. The anteromedial tip of the palatine is concave, and presumably formed a suture with the vomer. The posterior tip is rounded and overlaps the ectopterygoid with a squamous suture.

The *pterygoid* forms the center of the elongate palate. It measures 18.5 cm from the probable posterior tip of the vomer to the posterior midline edge, where it forms a ledge that fuses with the basioccipital but does not project back below the condyle as it does in the Berkeley skull. The suture with the basisphenoid is an overlap of only 1.5 cm, and the interpterygoid vacuity, split by the basi- and parasphenoid, is 5 cm long and 3 cm broad. Lateral to the interpterygoid vacuity the pterygoids are concave downward in transverse section; so the downcurved

lateral edge forms a longitudinal groove with the horizontal inner part. Here each pterygoid is about 2 cm broad. Each is bounded laterally by a large opening, the subtemporal vacuity, which has as its anterior border a lateral projection of the pterygoid and the ectopterygoid. The quadrate ramus of the pterygoid is a vertical plate 3 cm high that continues forward alongside the basisphenoid. The posterior suture with the quadrate runs parasagittally across the ventral surface of the ramus, its posterior extension lying 0.5 cm behind the palatal plate of the pterygoids. From here the suture runs anterodorsomedially to emerge on the dorsal surface. Thus the pterygoid portion of the quadrate ramus is very short, and almost four-fifths of it is quadrate.

The *ectopterygoid* evidently forms the anterior border of the subtemporal vacuity and lies lateral to the pterygoid behind the palatine. It is thickened along the edge of the subtemporal vacuity and its lower surface is convex from side to side and concave anteroposteriorly.

The basioccipital forms the slightly depressed condyle, 30×25 mm, which is set off by a ventral constriction in front of the ball. On its dorsolateral borders the basioccipital rises a few millimeters to form a base for the exoccipital, and the suture for the two bones dips forward at an angle of about 45° . It also slopes laterally. This suture was filled with limestone that dissolved out by acetic acid, revealing a gap of about 1 mm which was probably filled by cartilage in life. The dorsal border of the basioccipital is a shallow longitudinal groove that narrows anteriorly as the exoccipitals approach to within about 2 mm of each other. On the ventral side the basioccipital expands downward about 1 cm to form a flat surface that is underlain by the pterygoids. Lateral to the flat surface, 2.5 cm in front of the condyle, the basioccipital projects ventrolaterally into the tuberosities, which are about 2 cm in diameter. These approach to within a centimeter of the vertical plate of the pterygoid but do not meet it; hence they did not function as pterygoid supports, as suggested by Andrews (1910A, p. 79).

The *exoccipital* arises from an oval suture with the basioccipital and, with the fused opisthotic, forms the lateral wall of the braincase. This fusion is so complete that no suture can be seen. The internal surface is concave both anteroposteriorly and dorsoventrally, and is higher than long. The upper surface is capped by the supraoccipital; here, as with the lower suture, the acid has dissolved out 1-2 mm of limestone that presumably was formerly occupied by cartilage. The outer surface is convex and shows clearly the suture with supraoccipital above and prootic anterodorsally.

On the posterior surface a smooth groove extends dorsally from the union of the paroccipital process. At the base of this groove is a small foramen, about 3 mm in vertical diameter. This I take to be the exit of nerve XII. Just anterior to this, under the anterior edge of the opisthotic, is a large circular foramen, about 5 mm in diameter, that opens toward the overlying paroccipital process. This foramen lies near the anterior border of the fused exoccipital-opisthotic, and is probably between the two bones, although I have not been able to find the suture. A similarly situated foramen in *Iguana* and *Sphenodon* receives the foot of the stapes; although no stapes has ever been seen in a plesiosaur, this opening is evidently the fenestra ovale. Andrews (1910A, p. 82) describes a similar open-

ing which he calls the "jugal foramen," but the close correspondence with living forms makes it probable that Andrews' "jugal foramen" is actually the fenestra ovale.

The *prootic* can be seen in front of and between the supraoccipital and the opisthotic. It is a small bone, convex laterally, separated by about 5 mm from the underlying vertical plate of the pterygoid.

The *supraoccipital* has a broad base, anteroposteriorly oval, that rests upon the exoccipital-opisthotic at about the mid-height of the foramen magnum. The base of the supraoccipital is 15 mm broad, and above and below this the foramen magnum widens to 18 mm and 20 mm, respectively. Thus the foramen is constricted in the middle and is 8-shaped. Laterally the supraoccipital is convex and underlies the parietal with a suture sloping steeply anteroventrally. The posterior face of the supraoccipital forms an arch rising 3 cm to underlie the parietals. At the summit of the arch, immediately below the parietals, is an unfinished cancellous edge to the supraoccipital. This is notched and evidently housed a cartilage, perhaps the cartilaginous remnant of the interparietal.

The cervical vertebrae are on their right side and uncrushed, although they have been badly damaged by erosion. They are continuous except for gaps between numbers 12 and 13 and between 14 and 15. The ventral keel becomes increasingly prominent from 8 to 30 and disappears at 35. From here on the centra broaden and the lower surface flattens. Rib facets become more posteriorly situated; ribs are fused to the anterior centra and free from 32 on. There is no lateral keel. Neural spines, complete on 39 and 40, are 20 cm high from the centrum.

Anterior dorsals are circular and the caudal series extends, as indicated by rotted casts in the limestone concretions, 115 cm beyond the ischia.

The clavicular arch is eroded, as are the anterior ends of the scapulae, but their complete outlines are preserved in the limestone. The clavicles appear to be narrower and more sharply pointed anteriorly than in the Berkeley specimen. While it is not necessary to describe each bone in detail, the differences from the Berkeley skeleton are summarized herewith. The scapulae are longer and narrower; the coracoids have longer anterior projections and shorter midline suture, but show the same transverse ventral thickening and deep excavation in front of the buttress.

The humerus is a little less massive and shows a more oval tuberosity, but has about the same degree of separation from capitulum. The epipodials are longer than in the Berkeley specimen. The epipodials *et seq.* bend less sharply backward from the humerus; the lines along the anterior border of humerus and radius make an angle of 23° as opposed to 35° in the Berkeley paddle. Other paddle elements cannot be compared, but the Bogotá animal has more than eight phalanges, and the entire paddle, measured from the glenoid, is 150 cm. The left paddle measures 147 cm.

The pubes have a straighter midline suture than in the Berkeley reptile, and therefore are more nearly square in outline. The anterior concavity is stronger and the glenoid portion narrower. The femur has a more normal elasmosaur shape and the posterior dip of the trochanter is about the same as that on the Berkeley femur. The proximal extremity is quite different in the two: on the

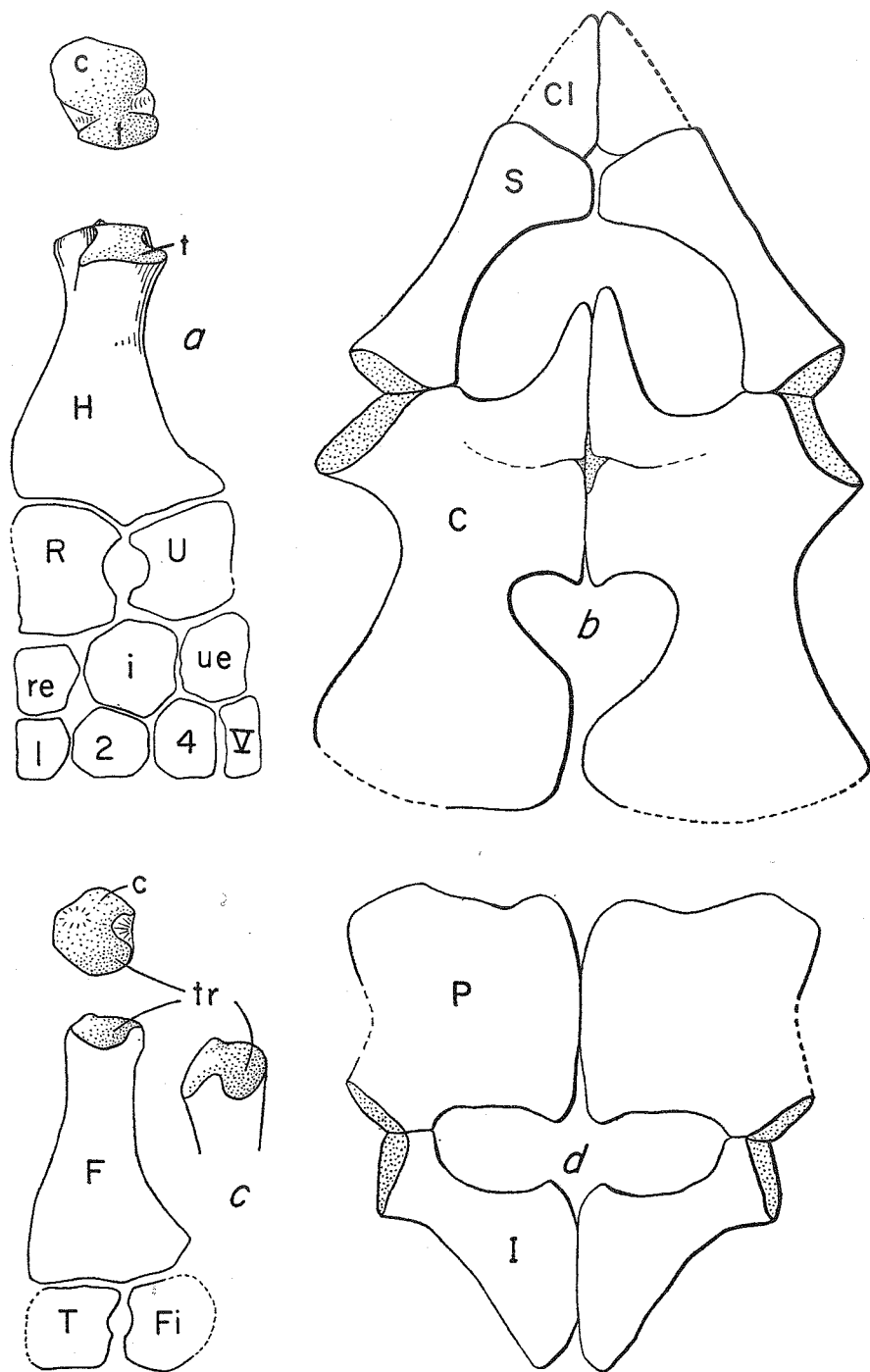


Fig. 6. *Alzadasaurus colombiensis* Welles, referred specimen: a, lateral view of left humerus *et seq.*, and proximal view of humerus; b, ventral view of pectrum; c, lateral view of left femur, tibia, and fibula, with proximal and posterior views of head of femur; d, pelvis. $\times \frac{1}{10}$.

Berkeley femur the heads are apparently (the posterior half of the trochanters is missing) confluent, without a posterior groove; the Bogotá femur shows well-developed posterior groove. The head is subrounded in outline, whereas the Berkeley femur is oval. As with the forepaddle, the distal elements bend less sharply backward from the femur than in the Berkeley paddle. The epipodials are slightly longer and the tibia has a more sharply excavated posterior border forming a well-rounded epipodial foramen.

EVALUATION OF DIFFERENCES

The skulls of the two reptiles are virtually identical, and the postcranial elements resemble each other very closely. Both are skulls of mature individuals; so it seems almost certain that they are the same species. They were found within a few feet stratigraphically and 100 yards geographically of each other, a distance of doubtful significance. The observable differences are therefore thought to be either individual variations or secondary sexual characters, although there might also be slight ontogenetic differences.

The Bogotá skeleton is less massive than the Berkeley one; yet propodials of the former are actually longer. This suggests sexual dimorphism. If in plesiosaurs the male is larger and heavier than the female we might hypothesize that the Bogotá specimen is female and the Berkeley specimen male. This would also explain the slightly more massive Berkeley coracoids. It might also explain the difference in the shape of the pubes. Such a difference led to difficulties in understanding the two skeletons of *Plesiosaurus guilelmi imperatoris* Dames, from Holzmaden. The type, described in 1895, was small and immature in the development of propodial heads, pectrum, and pelvis. The second specimen, from 15 cm below the type, described by Fraas in 1910, was considered an adult of the type juvenile. It is obviously a mature animal in that the propodials are well formed, the pectoral bar is well developed, and there is a pelvic bar. These enumerated differences could very well be ontogenetic, as Fraas indicated. In the opinion of White (1940A, p. 462), however, the differences were of such magnitude that he established a new genus and species, *Seeleyosaurus holzmadenensis*, for the larger reptile. He wrote (p. 463): "The extremely brachycephalic skull, the presence of an interclavicle, and the general form of the shoulder girdle show that this specimen cannot belong to the species to which Fraas assigned it." After discussing this concept at length (Welles, 1943, p. 197), and the characters of pelvic bar and shape of pubes, I finally concluded that the more conservative course was to follow Fraas in considering the two conspecific, the second specimen an adult of the type.

This close parallel between the two skeletons from Holzmaden and the two from Leiva lends support to the latter interpretation, and suggests furthermore, that the Holzmaden type is a juvenile male, and the second Holzmaden skeleton an adult female. The concave anterior border is therefore interpreted as indicative of a female in these two forms. However, the Holzmaden type pubis would certainly elongate posteriorly in the midline in ontogenetic growth; should it elongate anteriorly as well, a pubis similar to that of the referred skeleton would result, and sexual dimorphism need not be invoked to explain the different shape.

Ontogenetic development could not explain the differences in the Leiva skeletons in terms of those of Holzmaden, however, for the Berkeley specimen is more massive and, although the pectoral development is greater, the specimen has convex pubes like the Holzmaden juvenile. If we can interpret variations in either reptile through variations in the other, we revert to the conclusions reached above: the Holzmaden type is a juvenile male, the referred Holzmaden specimen an adult female, the Bogotá specimen an adult female, and the Berkeley specimen an adult male.

OTHER CRETACEOUS PLESIOSAURS

CRETACEOUS, UNDIFFERENTIATED

Brimosaurus grandis Leidy (1854B [1856], p. 72, pl. 2, figs. 1-3) is a *nomen vanum* based upon four centra from the ?Upper Cretaceous (?Benton *vide* Williston, 1903A, p. 8) near Hollywood, Clark County, Arkansas. The material is not diagnostic and the animal is probably pliosaurian.

Cimoliasaurus grandis (Leidy) Cope (1869A, p. 266) is a *nomen vanum* formed by the transfer to this genus of *Brimosaurus grandis*, *q.v.*

Cimoliasaurus planior (Leidy) Cope (1875E, p. 255) is a *nomen vanum*, a transfer to this genus of *Discosaurus planior*, *q.v.*

Cimoliasaurus vetustus (Leidy) Cope (1869A, p. 266) is a reference to this genus of *Discosaurus vetustus*, *q.v.*

Discosaurus grandis (Leidy) Leidy (1870I, p. 22) is a *nomen vanum* formed by transferring to this genus the species *Brimosaurus grandis*, *q.v.*

Discosaurus planior Leidy (1870I, pp. 20, 22) is a *nomen vanum* based upon a caudal centrum from the Cretaceous of Mississippi. It is not diagnostic. It is larger and longer than the Colombian reptile (indices 55, 120:155 vs. 46, 135:163), but it is not necessarily from a corresponding position in the column. Caudal centra decrease abruptly posteriorly, and vary more in the same individual than do other centra.

Discosaurus vetustus Leidy (1851G [1852] p. 326) is a *nomen vanum* for an anterior caudal centrum from the Cretaceous of Alabama. Its indices are 51, 108:130 vs. 46, 135:163 for the Colombian. It is thus lower and narrower, but such isolated centra are not diagnostic. It is probably pliosaurian.

Oligosimus grandaevus Leidy (1872E, p. 39) is a *nomen vanum* for a non-diagnostic single small caudal centrum from the ?Cretaceous of Henry's Fork of the Green River, Wyoming.

Polyptychodon patagonicus Ameghino (1893, p. 82) is a *nomen vanum* based upon isolated teeth from the ?Cretaceous of Santa Cruz Province, Argentina. Cabrera (1941, p. 125) considers them probably crocodilian. They are not diagnostic.

NEOCOMIAN

Cimoliasaurus valdensis Lydekker (1889C, p. 188) was based upon a large series of cervical, dorsal, and caudal vertebrae (BM R-609) from the Lower Wealden Wadhurst Clay (Lower Neocomian) of Hastings. The vertebrae of *C. valdensis* are less than a third the size of the Colombian reptile and are relatively higher

and broader. One of the type vertebrae (Lydekker, 1889C, fig. 61) is a posterior cervical because of the downcurving of the ventral surface. Indices are 23, 140:152 vs. 94, 97:114 for the Colombian form. The short, high, broad posterior cervical is pliosaurian, although Koken (1905, p. 688) transferred it to the genus *Plesiosaurus*. The material is not specifically diagnostic, and the name is a *nomen vanum*. It differs in proportions and in the shape of the spine from the Colombian reptile. Associated with the vertebrae was a right femur, B44%L17, much smaller and slenderer than the Colombian femur, B73%L33.

Leptocleidus capensis (Andrews) Andrews (1922A, p. 296) is a reference of *Plesiosaurus capensis* Andrews (1911B, p. 310) to this genus. Stromer (1935, p. 44) later placed it in the genus *Peyerus*, *q.v.*

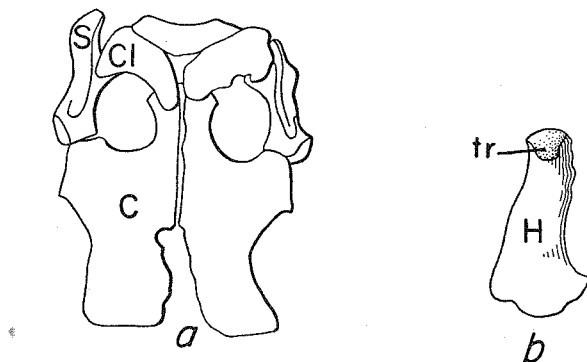


Fig. 7. *Leptocleidus superstes* Andrews, type: a, pectrum in dorsal view; b, lateral view of left humerus. From Andrews (1922A, pl. 15). $\times \frac{1}{10}$.

Leptocleidus superstes Andrews (1922A, p. 296, pl. 15) is based upon a partial skeleton, including the back of a skull, from the Upper Wealden (Upper Neocomian) of Sussex. This skull has the quadrate-squamosal arch tipped forward about 45° , whereas it is only about 80° in the Colombian skull. Consequently the quadrate projects far posteriorly, and the quadrate ramus of the pterygoid is greatly elongated. The temporal fenestra extends much farther in front of the parietal foramen, and the jugal is unusually long. In palatal view the interpterygoid vacuities are longer, reaching almost to the front of the ectopterygoid-ptyergoid bar. The lateral pterygoid fenestra is twice as long as the Colombian. The vertebrae are shorter, yet nearly as high and broad. Comparable indices are: anterior cervical 25, 120:152, posterior cervical 30, 146:155 vs. 34, 100:127 and 99, 93:105 for the Colombian form. The humerus is much smaller and slenderer, B50%L24.5 vs. B71%L41. The clavicles are entirely different, extending posteriorly in the midline to the coracoids, functionally supplanting the enlargement of the ventral scapular plate of the later elasmosaurid plesiosaurs. The pectrum is fundamentally different (Andrews, 1922A, pl. 15) in that the midline bar is formed by clavicles and coracoids rather than by scapulae and coracoids. The coracoids show an even greater anterior midline growth than those of the Colombian form, and the posterior processes are narrow. These differences indicate that *L. superstes* is a wholly unrelated form, probably an early dolichorhynchopid.

Peyerus capensis (Andrews) Stromer (1935, p. 44) was originally described by Andrews (1911B, p. 310) as *Plesiosaurus capensis*. Later Andrews (1922A, p. 296) referred it to the genus *Leptocleidus*, and Stromer (*loc. cit.*) made it the type of his new genus. The partial skeleton is from the Uitenhage beds, Upper Valanginian or Lower Hauterivian, of South Africa; hence it is older than the Colombian form. The skull is relatively broader posteriorly, a feature which may be due to crushing. Both have a similar slight development of a premaxillary rostrum, but the interpterygoid vacuities are relatively longer in *P. capensis*, where they extend forward well beyond the subtemporal fossa. The anterior cervical centra are quite different, being deeply amphicoelous, relatively shorter, and more nearly circular (25, 124:144 vs. 40, 80:101 for the Bogotá, and 34, 100:127 for the Berkeley, vertebrae). The neural canal is relatively smaller. Posterior cervicals have thumb-shaped spines, higher zygapophyses, and pedicles that are narrower anteroposteriorly, about the same breadth as the anterior zygapophysis. These features are markedly different from those of the Colombian form, wherein the spines are flat, actually bending forward dorsally, and have a posterior projection about halfway between posterior zygapophysis and summit. Only the distal end of the femur is known. It is very primitive in lacking any development of the anterodistal knee. The epipodials are similar in being apart proximally and articulating only distally, but are relatively longer. The tibia is B87%L6, the fibula B75%L6 vs. B108%L13 and B88%L13 for the Berkeley skeleton. The short vertebrae and narrow propodials indicate that *Peyerus capensis* is not an elasmosaur.

Plesiosaurus capensis Andrews (1911B, p. 310) was last transferred to *Peyerus capensis*, *q.v.*

Plesiosaurus mexicanus Wieland (1910, p. 359, pl. 52) is based on part of an interlocked dentary and maxillary from the Neocomian of Tlaxiaco, Mixteca, Oaxaca, Mexico. It bears 5/5 teeth in the 10 cm fragment, and in this respect is the same as the Colombian form. However, the fragment is not diagnostic; so the name is a *nomen vanum*.

Plesiosaurus nordmanni Eichwald (1869, p. 1276, pl. 39, fig. 5) is a *nomen vanum* based on an indeterminate fragment of a "humerus" from the Neocomian of Biassala, Russia. The specimen is not diagnostic, and Lydekker (1889C, p. 247) regarded it as purely a manuscript name.

Plesiosaurus valdensis (Lydekker) Koken (1905, p. 688) is a reference to this genus of *Cimoliasaurus valdensis*, *q.v.*

BERRIASIAN

Brancasaurus brancai Wegner (1914, pp. 235 ff.) is the only other Lower Cretaceous elasmosaur represented by a reasonably complete skeleton. It is from the Wealden (Berriasian) of Gronau, Westphalia, and is therefore older than the Leiva reptile and, as one would expect, considerably smaller: total length 3.26 vs. 7.36 meters.

The skull of *Brancasaurus* as reconstructed by Wegner is 26 cm from snout to parietal crest; the Colombian form is 34 cm (crushed to 33 cm). They are similarly proportioned except for a broader premaxillary region and a narrower frontal

region in *Brancasaurus*. The palate of *Brancasaurus* shows the internal nares less sharply delineated by the palatines, but otherwise similar. Both reptiles have very narrow parasphenoids, and, except for the much smaller size of *Brancasaurus*, there is nothing to indicate palatal differences. Both are typical elasmosaurs in palatal structure.

The dorsal surface of the skull roof is not preserved well enough in the Colombian reptiles to permit comparison.

Anterior cervical centra of *Brancasaurus* are more deeply cupped anteriorly and posteriorly, and the ends are more nearly circular. The spines slant more posteriorly and are narrower anteroposteriorly across the top.

Median cervical centra are similar in the development of concave ends, with horizontal oval depressions in their centers, but the depression is a mere slit in *Brancasaurus*. The ends are nearly circular and the spines are much shorter, slant more strongly posteriorly, and are narrower anteroposteriorly at the summits. They lack the anterior tongue, the spinous suture remains open, and the ribs are not fused.

Posterior cervicals have similarly concave ends but retain the central pit. They have a downturned anteroventral end. The spines slant more strongly, are a little shorter, and have an anterodorsal bevel. They are convex anteriorly and have an unbeveled posterodorsal corner. The base of the spine shows the beginning of the posterior groove, but has an equally developed anterior groove (hiatus of Wegner) rather than a tongue.

Pectorals are equal in number and differ about as do the posterior cervicals. The strong inflection of the anteroventral corner in this region indicates an up-curving of the column from neck to back.

Dorsals have more concave sides, and diapophyses which end in facets facing posteroventrally rather than in swollen knobs.

Further comparisons are not practical, but the smaller size, open sutures, simpler spines, and weaker development of the groove, without any tongue, indicate that *Brancasaurus* is a more primitive elasmosaur which in vertebral structure would make an ideal ancestor for the Colombian reptile.

The pectrum of *Brancasaurus* was incomplete, and Wegner restored it quite differently from that of comparable elasmosaurs. Andrews (1922A, p. 296) was evidently dissatisfied with this restoration, and I have attempted one of my own without having seen the specimen—always an unsatisfactory procedure. The distal extensions of the coracoids have always seemed to me to be inordinately long. There are two ways to check the length of the coracoids: by comparison of overall dimensions and proportions of elasmosaurian pectra; and by the average distance between coracoids and pubes. This space is occupied by gastralia.

Table 4 shows the length-breadth measurements of twelve comparable elasmosaurs wherein the B:L indices range from 48 to 62, with a mean of 55. Wegner's restoration yields an index of 38; mine, one of 52, which is close to the mean.

The two Colombian skeletons are preserved as buried, and the pectrum, pelvis, and dorsal (+pectoral+sacral) vertebrae can be measured. Corresponding measurements for *Cryptoclidus* and *Muraenosaurus* are shown in table 5. The Colombian skeletons demonstrate that the gastralia occupy considerably less space than the

TABLE 4
COMPARISON OF ELASMOSAURIAN CORACOIDS
(Measurements in centimeters)

Species	Length of coracoid to scapular suture	Breadth at posterior edge of glenoid	B:L index
<i>Brancasaurus brancai</i> (from Wegner).....	32.8	12.6	38
<i>B. b.</i> , present reconstruction.....	24.2	12.6	52
<i>Leptocleidus superstes</i>	25.3	15.6	62
<i>Muraenosaurus durobriensis</i> R 2428.....	36	19.5	54
<i>M. leedsii</i>	37.5	18.3	48
<i>Cryptocleidus oxoniensis</i>			
R 3538.....	37.2	20	54
R 2616.....	38.6	21.3	55
<i>Alzadasaurus colombiensis</i> , type.....	59	34.5	58
<i>A. c.</i> , referred.....	57.5	36	62
<i>Elasmosaurus morgani</i>	60	28	44
<i>Alzadasaurus riggsi</i>	53.7	32	60
<i>A. pembertoni</i>	62	31	50
<i>Hydralmosaurus serpentinus</i>	54.6	32.5	60
<i>Hydrotherosaurus alexandrae</i>	50	28.5	57

TABLE 5
COMPARISONS OF MEASUREMENTS AND SPACING OF PECTRUM, PELVIS,
AND RELATED VERTEBRAE OF ELASMOSAURS
(In centimeters; estimates italicized)

Species	Length of pectrum	Space for gastralia	Length of pelvis	Sum of pec- toral, dorsal, and sacral vertebrae and cartilages	Ratio ventral armor to pec- toral, dorsal, and sacral vertebrae	Anteropos- terior extent of ventral armor
<i>Alzadasaurus colombi- ensis</i> , type.....	114	61	59	207	113	234
<i>A. c.</i> , referred.....	111	64	59	207	113	234
<i>Cryptocleidus oxoniensis</i>	63	51	46	160	113	181
<i>Muraenosaurus durobriensis</i>	59	45	45	137	113	155
<i>Brancasaurus brancai</i> (from Wegner).....	52.5	10.5	27	80	113	90
<i>B. b.</i> , present reconstruction.....	38.3	24.7	27	80	113	90

pectrum and slightly more than the pelvis. The total of pectrum, gastralia, and pelvis is 13 per cent greater than the sum of pectoral, dorsal, sacral vertebrae, and intervertebral cartilages. The skeletons of *Cryptoclidus* and *Muraenosaurus* fit nicely into this pattern, but Wegner's restoration of the pectrum does not. In order to arrive at the restoration given here (fig. 8), the coracoids are shortened from 52 cm to 38 cm, the clavicular arch is moved back, and the scapulae brought together anteriorly so that the clavicles fit onto the dorsal surfaces of

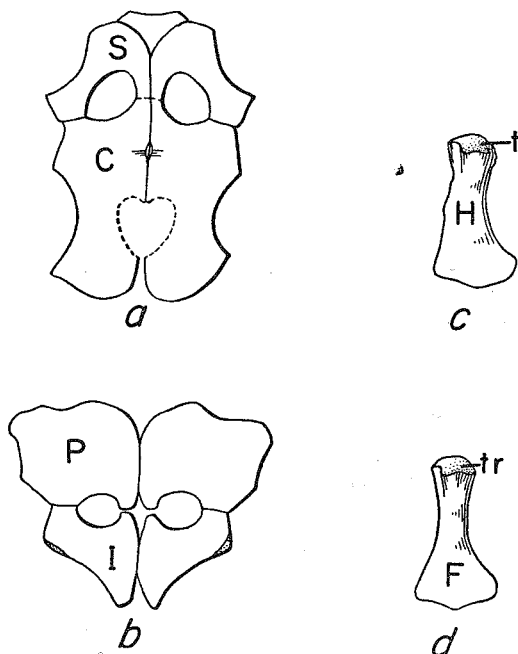


Fig. 8. *Brancasaurus brancai* Wegner, type: a, ventral view of pectrum; b, pelvis; c, d, lateral views of left humerus and femur. From Wegner (1914), coracoids shortened. $\times \frac{1}{10}$.

the scapulae. If the coracoids are restored with the usual cordiform vacuity, *Brancasaurus* then becomes a typical early elasmosaur. However, the intercoracoid vacuity in such an early form was probably poorly developed. It could, through loss of pectoral and pelvic bars, give rise to the Colombian forms, but a retention of these bars would lead directly to the genus *Elasmosaurus*, and is corroborating evidence for Cope's (1869M, fig. 7) illustration of a pelvic bar.

As here reconstructed, the pectrum of *Brancasaurus* is very different from the Colombian form. The clavicular arch is concave anteriorly, the scapulae are more strongly developed ventrally, and, although the specimen is only half as large, there is a solid pectoral bar. The coracoids are restricted in anteromedial growth by the scapulae. The intercoracoid vacuity is conjecturally somewhat cordiform.

The pelvis is almost unique in its complete midline bar, a feature elsewhere recorded only for *Elasmosaurus platyurus* by Cope (1869M, 1870W), and for the referred adult specimen of *Plesiosaurus guilelmi imperatoris* by Fraas (1910).

Neither pubes nor ischia of the Colombian form show growth into the pelvic bar.

Propodials are much smaller and are more primitive in having simpler ends and no development of anterodistal knees.

The foregoing comparisons indicate that *Brancaesaurus* is a different kind of elasmosaur. It is probably adult, although not an old individual, yet is but half the size of the Colombian form. In structure of vertebrae and propodials it is more primitive, but in pectrum and pelvis it is fundamentally different in possessing midline bars.

Cimoliasaurus limnophilus (Koken) Lydekker (1889C, p. 224, *Cimoliosaurus*) is a transfer to this genus of *Plesiosaurus limnophilus*, q.v.

Peloneustes kanzleri (Koken) Linder (1913, p. 341) is a reference to this genus of *Plesiosaurus kanzleri*, q.v.

Plesiosaurus degenhardti Koken (1887, p. 106) is from the Middle Wealden (Berriasian) of Bückeburg; the type consists of a sandstone block with impressions of 21 dorsal vertebrae in the Berlin Museum. It is an animal less than half the size of the Colombian reptile, with relatively shorter vertebrae and two fewer dorsals. Koken's figures (*ibid.*, pl. 9) show anterior dorsals in which the centra appear relatively shorter and have the lateral surfaces much more deeply concave. The diapophyses are similar: in both reptiles they terminate in rounded knobs. In *P. degenhardti* the spinous suture is still evident, but our specimen shows no trace of such a suture.

Later, Koken (1896, p. 123, pls. 3-4) referred additional material from Oberkirchen to this species, and his identification has been accepted by all subsequent workers. It consists of another sandstone block with impressions of vertebrae, this time a series of posterior cervicals, one pectoral, and several anterior dorsals. The rib facets are large, occupying nearly the entire length of the centrum, and the ribs do not increase in length appreciably from the cervical to the pectoral region. The rib ends are narrow and do not develop the anteroposterior expansion, or axiniform condition, of elasmosaurs. The anterior zygapophyses stand high above the cervical centra and descend on the anterior dorsals. The figures indicate but a single pectoral vertebra, although Koken reckoned three.

This species has been discussed by Lydekker (1889C, p. 224), Koken (1896), Wegner (1914, p. 296), and Andrews (1922A, p. 290). Lydekker considered it a synonym of *P. limnophilus* Koken, which he put in the genus *Cimoliosaurus* [*sic!*]. Koken's additional material described in 1896 proved the two species distinct, and Wegner recognized their separateness, yet Andrews follows Lydekker. Without going farther into the taxonomy of the species, a comparison of the cervical vertebrae shows that *P. degenhardti* is a short-necked and *P. limnophilus* a long-necked form, and that the two are very different. Since *P. degenhardti* is a pliosaur, it cannot be related to our Colombian reptile. It is actually based upon indeterminate material and is a *nomen vanum*.

Plesiosaurus kanzleri Koken (1905, p. 691, fig. 7) is a *nomen vanum* for a mid-dorsal vertebral centrum from the Wealden (Berriasian) of Gronau. Koken actually had two quite different vertebrae, according to Wegner (1914, p. 301); so the type is hereby designated the centrum illustrated by Koken (*loc. cit.*, fig. 7). This has indices 55, 104:124, and is not diagnostic.

Plesiosaurus limnophilus Koken (1887, p. 109) is a *nomen vanum* founded on three centra from two localities in north Germany, Ummeln and Kniggenbrinke. Koken (1896, p. 121) places this in the Upper Wealden. The figured specimen (pl. 9, fig. 5), from Ummeln, is hereby designated the type. It is evidently a median cervical, with indices 52, 88:100. Later materials referred here by Lydekker and by Koken are not significant; Lydekker (1889C, p. 224, *Cimoliosaurus*) referred the species to the genus *Cimoliasaurus*. Indices of a midcervical centrum of the Colombian reptile are 82, 82:106; hence *P. limnophilus*, although much smaller, is very slightly higher and narrower. Its articular face is similarly marked by a central pit, and the ends are about equally rounded. In ventral aspect the rib facets on *P. limnophilus* are farther under the centrum, the ventral keel is much sharper, and the nutrient foramina are closer together and set in grooves. The type represents an animal halfway between *Brancasaurus* and the Colombian beast in size and in proportions, but it is not diagnostic.

VALANGINIAN

Cimoliasaurus neocomiensis (Pictet and Campiche) Lydekker (1889C, p. 223, *Cimoliosaurus*) is a reference to this genus of *Plesiosaurus neocomiensis*, *q.v.*

Plesiosaurus neocomiensis Pictet and Campiche (1860, p. 42, pl. 6, fig. 1) was based upon three dorsal centra from the Valanginian of Switzerland. Since these centra are from different localities and horizons, I follow Lydekker (1889C, p. 223) in using as lectotype the centrum figured by the original authors (1860, pl. 6, fig. 1). This centrum is considerably shorter (46, 126:141) and relatively higher and broader than ours. I suspect that it is pliosaurian, but, in any event, single dorsal centra are not diagnostic and the name is a *nomen vanum*. The smaller "third dorsal" (*ibid.*, pl. 6, fig. 2, indices 37, 122:119) is narrower. The third centrum (*ibid.*, p. 46, pl. 5, fig. 2, *a-c*) is probably a sacral, since it is smoothly rounded below and lacks the keel and foramina of a pectoral; also, the posterior border dips downward. This has the same kind of boss in the center of the articular face and is probably the same species as the type, although from the Middle Neocomian. These indeterminate centra differ considerably from our Colombian form.

HAUTERIVIAN

Polyptychodon neocomiensis Schardt (1910, p. 355, figs. 1-2) is based on large teeth from the Hauterivian of Neuchâtel. It is named for indeterminate material that is pliosaurian rather than elasmosaurian, and is a *nomen vanum*.

APTIAN

Cimoliasaurus latispinus (Owen) Cope (1869A, p. 266) is a reference to this genus of *Plesiosaurus latispinus*, *q.v.*

Cimoliasaurus leucoscapelus Etheridge (1897, p. 19, pls. 5-7) is a *nomen vanum* for some short, deeply bicoelous centra from the White Cliffs, Western Division, New South Wales, of probable Aptian age. An anterior cervical, indices 25, 125:150, is pliosaurian in proportions. Persson (1960, p. 4) considers the material inadequate for specific determination and refers to it as *Dolichorhynchops* sp., in which I heartily concur.

Cimoliasaurus maccoyi Etheridge (1904, p. 312, *Cimoliosaurus*) is a *nomen vanum* based on 17 centra and fragments of poorly opalized bone from the White Cliffs, New South Wales, of Aptian age. The centra are slightly concave with a marked central boss, the ends oval to ellipsoid. The vertebral indices, although of a very much smaller specimen, are very close to the indices of *Cimoliasaurus magnus*. This species probably represents, as Persson considers, a form with plesiosauroidean affinities but with only a moderately long neck, and therefore is not related to the Colombian reptile. It is based upon material that is not diagnostic.

Plesiosaurus continuus (Owen) Eichwald (1869, p. 1274) is a reference to the genus of the species *Polyptychodon continuus*, *q.v.*

Plesiosaurus gurgitis Pictet and Renevier (1854, p. 5, pl. 1, fig. 1) is a *nomen vanum* for a single centrum from the Lower Aptian of Perte du Rhône. The illustrations and measurements yield indices of 51, 77:108, about half the size of the Colombian form and much more depressed. This is evidently a median cervical centrum of an elasmosaur, but the pedicle facets are unusually deep for a Cretaceous form and the rips are shallow and elongate. Its relation to the Colombian form cannot be determined.

Plesiosaurus latispinus Owen (1854, p. 63) is a *nomen vanum* based on the casts of two cervicals from the Lower Greensand (Aptian) of Kent. These were later redescribed and illustrated by Owen (1864, p. 14, pls. 7, 8, figs. 1, 2), but the material is not diagnostic. It does represent an early elasmosaur and differs in detail from the Colombian specimen.

Polyptychodon continuus Owen (1841, p. 19, pl. 72, fig. 3) was based on a single tooth from the quarry of Mr. Bensted in the *Trigonia* beds of the Shanklin Sand in the Kentish Rag quarries in the Lower Greensand, of approximately Aptian age. Similar teeth are found in younger rocks; so the reptile was undoubtedly a contemporary of the Colombian form. However, the teeth are of a decidedly different, more massive, pliosaurian type. The single tooth is not diagnostic; the name is a *nomen vanum* and should be dropped.

Polyptychodon mackesoni Owen (1884, I, vii) is a name for the "Gigantic Fossil Saurian" from the Lower Greensand at Hythe. This specimen is labeled "Saurian undetermined" (*ibid.*, II, vi) and the legend for plates 27 and 28 is "*Polyptychodon continuus*?" There are thus three names for the same specimen, which is not a plesiosaur and is not related to the Colombian reptile.

Woolungasaurus glendowerensis Persson (1960, p. 12) is founded on a specimen (QM D-6890) consisting of 46 vertebral centra and parts of the pectrum, pelvis, and limb bones. It is from the Aptian of Glendower, Prairie, Queensland, and is placed in the Elasmosauridae. Generic diagnosis is based on the fact that the anterior cervicals are longer than broad, and the posterior cervicals broader than long. "The narrowest portion of the scapula in line with the midmost part of the base of the dorsal scapular process. Coracoids not separated posteriorly; with a prominent ventral median keel. Humerus larger than femur" (*ibid.*, p. 11). Specific diagnosis includes: all cervicals longer than high; lateral keel back to 10th prepectoral; 3 pectorals and ?3 sacrals. Coracoid with fairly long antero-medial process. Humerus with capitulum and tuberculum confluent. Femur

slender, capitulum and trochanter confluent. The median cervicals have indices 63, 73:92; the posterior cervicals 73, 87:130 compared with 82, 82:106 and 99, 83:108 for the Colombian form. *Woolungasaurus glendowerensis* is thus smaller, with relatively lower and narrower median cervicals but slightly higher and considerably broader posterior cervicals. It is similar to the Colombian form in the lack of elongation of the middle cervical centra. The pectrum and limb bones are smaller. The glenoid rami of the scapulae are similar. The coracoids have similar anterior midline projections and thickenings to form a great ventral pectoral keel. Persson (*ibid.*, p. 14) assumed that the coracoids lacked an intercoracoid vacuity, basing this assumption on a referred specimen from the Albion of Richmond, Queensland (QM F-2634). The parts preserved of the type coracoids are so like the Colombian reptile that it seems possible that the posterior blades were also similar, and that an intercoracoid vacuity was present. The humerus (B67%L32) is smaller and slightly less massive than the Colombian (B71%L41, B73%L39.5, B68%L41). The tuberosity forms a shelf broadly confluent with the capitulum without the constriction that partially separates them in the Colombian humerus. The radial facet is similar, but the ulnar facet is at a much greater angle. The radius (B109%L10.2) is proportionately broader, hence more specialized, than in the Colombian form (B91%L18, B86%L17.5, B91%L17). The femur (B71%L27) is smaller, and the tibial facet is farther forward; so the anterior border of the femur is uniformly concave, and there is no anterodistal knee (B73%L33, B61%L36). The head is more hemispherical and not transversely elongate as in the Colombian form.

The many similarities and only slight differences indicate that *W. glendowerensis* is closely related to the Colombian form. However, the Australian reptile, although represented by a considerable amount of material, is still so incomplete that it is not really diagnostic. It is certainly elasmosaurian, but not specifically or generically determinable, and must therefore be considered a *nomen vanum*.

ALBION

Cimoliasaurus sutherlandi (McCoy) Etheridge (1904, p. 306) is a reference to this genus of *Plesiosaurus sutherlandi*, *q.v.*

Kronosaurus queenslandicus Longman (1924, p. 26, pl. 4) is a gigantic pliosaur from the Hughenden district of Queensland. Persson (1960, p. 4) dates it as Albion. At present it is a *nomen vanum* that should be established upon neotypic material at Harvard University.

Mauisaurus gardneri Seeley (1877, p. 541, pl. 23, fig. 2) from the Gault of Folkestone is a very large elasmosaur with elongate median cervicals that are less depressed than those from Colombia (B:H index 97 vs. 129 for the Berkeley skeleton). Seeley shows a posterior cervical which differs primarily in that the pedicle slopes posteriorly and the centrum is relatively broader (B:H index 126 vs. 117). The ripit is higher on the centrum, although this could be a positional feature in that the ripit moves dorsally near the pectorals in all plesiosaurs. The ends of the centra have a central depression with a circular swelling near the periphery. The humerus (B69%L33 vs. B73%L40) is smaller and less massive, as would be expected in an earlier plesiosaur. The material upon which this

species is based is indeterminate as to species; it is actually indicative only of elasmosaurian affinities, and the name is a *nomen vanum*.

Plesiosaurus gardneri (Seeley) Lydekker (1889C, p. 212) is a reference to this genus of *Mauisaurus gardneri*, *q.v.*

Plesiosaurus gouldii Williston (1897C, p. 57) is from the Comanche shale (?Albian) of Clark County, Kansas. The type is described as having a deep anterior excavation of the centrum, spoutlike anterior zygapophyses, and a peculiar cordate form of the centrum. The indices (79, 95:139) are of a slightly smaller plesiosaur with relatively broader centra. It could be pliosaurian, especially if it is the same species as the referred pectoral material. It is not closely related to the Colombian reptile, and the name is a *nomen vanum*.

Plesiosaurus macrospondylus McCoy (1867, p. 356) is a *nomen vanum* based on a single cervical centrum from Marathon, 40 miles down the Flinders River from Hughenden, Australia. The centrum has wrinkled ends and indices 76, 84:100, which are very close to those of a midcervical of the Colombian form, 82, 82:106. However, the material is not diagnostic, and no further comparisons are possible. This, as Persson indicated (1960, p. 18), is an elasmosaur, *Elasmosauridae*, *g. and sp. indet.*

Plesiosaurus mudgei Cragin (1894, p. 69, pl. 1, figs. 1-3) was founded on a small centrum from Kiowa County, Kansas. This is from the Fredericksburg division of the Comanche, approximately Albian in age. It is only about half as large (45, 98:100) as the Colombian specimen, and somewhat eroded. The absence of ripples indicates a dorsal centrum, as does the circular end. This specimen is not even generically determinable, and the name is a *nomen vanum*.

The referred propodial (*ibid.*, pl. 1, fig. 4) is long and slender and is probably pliosauroidean. It is also indeterminate.

Plesiosaurus sutherlandi McCoy (1867, p. 356) is a *nomen vanum* given to a single centrum from the Marathon beds, 40 miles below Hughenden on the Flinders River, Queensland. McCoy described it briefly; later, Etheridge (1892, p. 508) mentioned that the ends are nearly flat, and assigned it to the Rolling Downs formation of early Cretaceous age. Indices of 57, 111:167 and the flat ends indicate a posterior cervical of elasmosaurian relationships, but the specimen is indeterminate, although Chapman (1914, p. 278) referred it to the genus *Pliosaurus*. Persson (1960, p. 10) restudied the specimen and identified it as *Cimoliasauridae*, *gen. et sp. indet.* His measurements yield indices of 60, 105:157, and he placed it in the Albian. The B index is high for an elasmosaur and the vertebra is small. If it is a juvenile, we would expect a proportionately greater breadth.

Pliosaurus sutherlandi (McCoy) Chapman (1914, p. 278) is a reference to this genus of *Plesiosaurus sutherlandi*, *q.v.*

CENOMANIAN

Cimoliasaurus cantabrigiensis Lydekker (1889C, p. 183, fig. 60, *Cimoliasaurus*) is a *nomen vanum* for some cervical centra from the Cambridge Greensand (Cenomanian). He (p. 184) designated as type a posterior cervical, R461a, with indices 39, 88:105, moderately cupped ends with slight bevel, and a strong lateral ridge

running posteroventrally from anterior zygapophyses to posterior base of pedicle. The zygapophyses are wide apart and slant outward about 45° . There appears to be a groove on the anterior edge of the short flat spine. The indices are elasmosaurian, but the lateral ridge and the broad zygapophyses are pliosaurian. This species is not related to the Colombian reptile, but would make a good ancestor of dolichorhynchopid. The type specimen is not diagnostic.

Cimoliasaurus planus (Owen) Lydekker (1889C, p. 217, *Cimoliosaurus*) is a reference to this genus of *Plesiosaurus planus*, q.v.

Dolichorhynchops willistoni (Riggs, 1944, p. 78, figs. 1-8) is based upon the skull, 50 vertebrae, and most of the girdles (KUMNH 5070) from the Greenhorn limestone (Cenomanian) of Concordia, Kansas. Riggs described the specimen as *Trinacromerum willistoni*, but since the genus *Trinacromerum* is based upon nondiagnostic material, *T. willistoni* is here transferred to the genus *Dolichorhynchops*. It differs from *D. osborni* Williston in having a longer tooth row (34 teeth vs. 26), a larger interclavicle without an anterior notch, and the pubes projecting behind the level of the acetabulum. This is a valid pliosaur.

Elasmosaurus kurskensis Bogolubov (1911, p. 353) is a *nomen vanum* for vertebrae that Kiprijanoff (1882, p. 17, pl. 7, figs. 1-3; pl. 8, figs. 1-3) had referred to *Plesiosaurus helmersenii*. These are from the Upper Cretaceous Kursk sandstone of the Moscow basin, but from various localities. Bogolubov placed the age as Cenomanian, but did not select a type; so the type is here designated as the median cervical centrum (Kiprijanoff, 1882, pl. 8, fig. 2). This is elasmosaurian, but not specifically diagnostic. The indices are 73, 73:98, a bit lower and narrower than the Colombian form.

Lütkesaurus [no sp.] Kiprijanoff (1883, p. 35, pl. 17, figs. 1, 2) is a generic name applied to teeth and vertebrae from the Sewerisch Osteolite of the Kursk region. The teeth were diagnosed as being very finely striated. They are pliosaurian in form, but the striations are certainly different from those of related pliosaurs. The name is invalid because no specific name has ever been applied. Furthermore, it is unlikely that these teeth would be diagnostic. Regardless of the final taxonomic outcome, the specimen is not related to the Colombian elasmosaur.

Plesiosaurus cantabrigiensis (Lydekker) Wegner (1914, p. 302) is a reference to this genus of *Cimoliasaurus cantabrigiensis*, q.v.

Plesiosaurus cynodeirus Seeley (1869, pp. xvii, 41) is a *nomen nudum* founded upon vertebrae in the Cambridge Upper Greensand (Cenomanian) of England. There are no descriptions, measurements, or illustrations; hence no comparisons can be made.

Plesiosaurus eurypondylus Seeley (1869, pp. xviii, 41) is a *nomen nudum* for vertebrae from the Cambridge Upper Greensand. Since there is no description, illustration, or measurement, comparisons are impossible.

Plesiosaurus ichthyospondylus Seeley (1869, p. xvii) is a *nomen vanum* based on the vertebral centra that Owen (1864, pp. 7 ff.) referred to his *P. bernardi*. Although these vertebrae are all from the Upper Greensand of Reach, near Cambridge, none are associated. The posterior cervical figured by Owen (pl. 4, fig. 10; pl. 5, fig. 1) is well preserved and is hereby designated the lectotype. The centrum

(36, 133:122) is pliosaurian, shorter than *Cimoliasaurus cantabrigiensis*, but with a similar buttress running posteroventrally from the anterior zygapophysis. Bogolubov (1911, p. 320) placed the species in the genus *Polycotylus*, and Pravoslavlev (1915, p. 12) transferred it to the genus *Trinacromerum*. Although it is actually a *nomen vanum*, it is probably a short-necked form and should be referred to as *Dolichorhynchops* sp.

Plesiosaurus microdeirus Seeley (1869, pp. xviii, 40) is a *nomen nudum* for material from the Cambridge Upper Greensand. No comparisons are possible.

Plesiosaurus ophiodeirus Seeley (1869, pp. xviii, 44) is a *nomen nudum* for specimens from the Cambridge Upper Greensand. Comparisons are impossible.

Plesiosaurus pachyomus Owen (1840A, p. 74) is based upon a propodial, B47%-L24, remarkable for its thickness, 3.8 cm distally, with a transversely oval proximal end. It is from the Upper Greensand of Reach (Cenomanian) and is in the Sedgwick Collection at Cambridge. The index is pliosaurian, but the specimen is not diagnostic and so the name is a *nomen vanum*.

Plesiosaurus planus Owen (1864, p. 2, pls. 1-3) was based on a large number of waterworn centra from the Cambridgeshire Phosphatic Greensand (?Cenomanian). Since no type has ever been designated, the adult centrum (Owen, 1864, pl. 2, figs. 6-9) is hereby made the lectotype. There is no certainty that the vertebrae belong to a single species, though it seems likely that they do. Isolated centra are not diagnostic for species; so the name is a *nomen vanum*. Owen's figures indicate a small pliosaur with depressed centra, wholly unrelated to our Colombian reptile. Lydekker (1889C, p. 217) referred this species to *Cimoliosaurus*, but did not add to our knowledge. Hulke (1883, p. 59) mentions a pair of scapulae and some associated vertebrae in the British Museum under the name *Pliosaurus planus*. It is not clear whether he meant to transfer Owen's *Plesiosaurus planus* to this genus, had made an error, or was establishing a new species. These scapulae are certainly pliosaurian, but are not certainly this species. Even if they were of the same species, the material would not be diagnostic; so both names are *nomina vana*.

Plesiosaurus planus trigonalis Owen (1864, p. 6, pl. 3, figs. 1-4) from the Cambridge Greensand, has a more triangular face than that of *P. planus*. Owen evidently considered this to be of subspecific value, yet (*ibid.*, p. 7) he also thought it "merely indicative of a different position in the neck." I suspect that the latter is true, and that this variant could be included in the type and referred material that made up Owen's original hypodigm. It is so different in shape from the Colombian specimen that there can be no close relationship. It is not diagnostic, and the name is a *nomen vanum*.

Plesiosaurus platydeirus Seeley (1869, pp. xviii, 41) is a name for a series of vertebrae from the Cambridge Upper Greensand. There is neither description nor illustration; so the name is a *nomen nudum*. Furthermore, it is preoccupied by *P. platydeirus* Owen (1854, p. 59), which was proposed for a centrum from the Lower Lias of Lyme Regis (Royal College of Surgeons, no. 226).

Plesiosaurus poecilospondylus Seeley (1869, pp. xviii, 48) is a *nomen nudum* proposed for eight dorsal vertebrae from the Cambridge Upper Greensand in the Woodwardian Museum.

Pliosaurus planus Hulke (1883, p. 59) is a *nomen nudum* for a pair of scapulae in the British Museum from the Cambridgeshire Phosphatic Greensand.

Polycotylus brevispondylus Bogolubov (1911, p. 317, pl. 11, figs. 1, 2), from an unknown locality in Russia, is stated to be of Cenomanian age. The figured pectoral vertebra has indices 62, 148:178, vs. 84, 112:126 for the Bogotá specimen. It is thus significantly shorter and relatively higher and broader. It is dolichorhynchopid, but a single vertebra is not diagnostic; so the name is a *nomen vanum*.

Polycotylus epigurgitis Bogolubov (1911, p. 316, pl. 9, figs. 5, 6) is based on a posterodorsal centrum from the Cenomanian of Voronezhskaja, Russia. This centrum is not distinctive and the name is a *nomen vanum*.

Polycotylus ichthyospondylus (Seeley) Bogolubov (1911, p. 320) is a transfer to this genus of the species *Plesiosaurus ichthyospondylus* Seeley, *q.v.*

Polycotylus ichthyospondylus tanais Bogolubov (1911, p. 321, pl. 9, figs. 1-3) is based on a "posterior cervical" vertebra from the Cenomanian of Voronezhskaja, Russia. Indices of 39, 118:123 indicate a slightly higher centrum than that of the average elasmosaur, but well within elasmosaur range. However, the nearly circular end, not incised by neural canal or ventral groove, is pliosaurian; furthermore, the short neural spine is characteristic of anterior cervicals, and the indices and shape are dolichorhynchopid, not beyond the range of variation of the 8th or 10th cervical of *Dolichorhynchops osborni*. Here again we have a single vertebra which is not diagnostic for specific or perhaps even generic determination. Although Pravoslavlev (1915, p. 12) transferred the variety to the genus *Trinacromerum*, the name is a *nomen vanum*.

Stereosaurus cratynotus Seeley (1869, pp. xviii, 44) is a *nomen nudum* for undescribed vertebrae from the Cambridge Upper Greensand (?Cenomanian).

Stereosaurus platyomus Seeley (1869, pp. xviii, 43) is also a *nomen nudum* from the same horizon, as is *S. stenomus* Seeley (1869, pp. xviii, 43).

Thalassomedon haningtoni Welles (1943, p. 152, figs. 13-16, pls. 22-24) was based upon a nearly complete skeleton (CMNH 1588) from the Graneros shale (Cenomanian) of Baca County, Colorado. It differs in so many ways from the Colombian form that comparison is profitless. It is a giant, unrelated elasmosaur.

Trinacromerum ichthyospondylum (Seeley) Pravoslavlev (1915, p. 12, *ichthyospondylum*) is a reference to this genus of *Plesiosaurus ichthyospondylus* Seeley, *q.v.*

Trinacromerum ichthyospondylum tanais (Bogolubov) Pravoslavlev (1915, p. 13, *T. ichthyospondylum t.*) is a transfer to this genus of the variety *Polycotylus ichthyospondylus tanais* Bogolubov, *q.v.*

Trinacromerum willistoni Riggs (1944, p. 78, figs. 1-8) is in this paper transferred to *Dolichorhynchops willistoni*, *q.v.*

TURONIAN

Alzadasaurus riggsi Welles (1943, p. 186) was based upon most of a skeleton (CNHM 12009), lacking the skull and posterior paddles. Even though incomplete, the specimen is probably diagnostic. It came from the Benton (?Turonian) of Alzada, Montana. It is very much like the Colombian reptile in all comparable

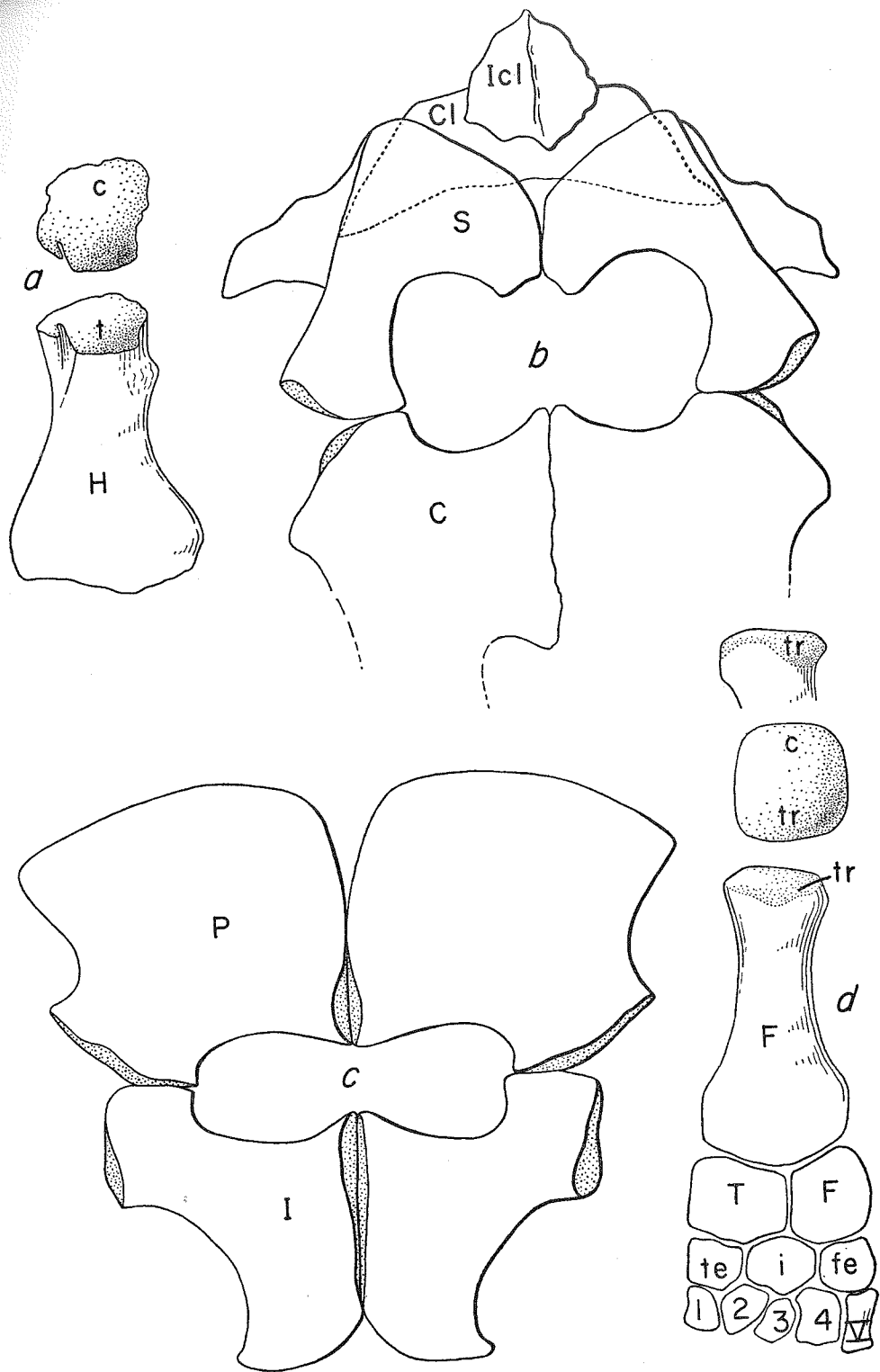


Fig. 9. *Thalassomedon haningtoni* Welles, type, CMNH 1588: *a*, lateral and proximal views of left humerus; *b*, ventral view of notum; *c*, ventral view of pelvis; *d*, lateral view of left femur.

parts. The ventral scapular plates are moderately developed and widely separated. The dorsal processes are broad ventrally and seem even broader because they are not parallel-sided dorsally. The clavicular arch is missing. The coracoids are alike in general shape and development of the ventral keel, but the midline suture is shorter in *A. riggsi*. The Colombian coracoids, therefore, project much farther both anteriorly and posteriorly. The humeri are alike proximally, although the capitulum of *A. riggsi* is higher anteriorly. Indices (*A. riggsi* B66%L30, Colombian species B71%L41) show the Montana reptile to be smaller, with a narrower distal end. The distal ends differ in the sharper posterior projection of the Colombian form and the steeper inclination of the ulnar facet. The antero-distal border slopes less sharply posteriorly, and this slope is continued by the anterior border of the radius; so the distal part of the paddle is inclined backward from the anterior border of the shaft of the humerus only about 15°, contrasted with the 30° inclination of the Colombian paddle. The Montana specimen is more advanced in having shorter propodials (RB115%L12 vs. B91%L18), and both species have relatively large epipodial foramina. The differences between the two species are of an evolutionary, or developmental, nature; hence the Colombian form is a suitable ancestor for the Montanan.

Alzadasaurus tropicus Colbert (1949A, p. 4, figs. 3-7, 8a, 9) was based on a shoulder region (AMNH 6796) from Altagracia de Orituco, Monagas, Venezuela. It is actually a *nomen vanum* and indeterminate. Whatever its relationships, it differs from the Colombian form in the shape of the pectoral ripits, which are round dorsally and have cylindrical dorsal surfaces. The Colombian reptile has anteroposteriorly compressed pectoral ripits with narrow dorsal surfaces. In the dorsal series, *A. tropicus* has high transverse processes which arise at a level with the top of the centrum and extend upward and backward, whereas the Colombian reptile has transverse processes arising lower on the pedicles and curving downward. The dorsal centra are more cylindrical and not constricted in the middle as are the Colombian centra.

Aptychodon cretaceus Reuss (1855, p. 86, pl. 15) was founded on a number of eroded teeth from the Turonian Pläner of White Mountain, near Prague. These are pliosauroidean and indeterminate, and the name is a *nomen vanum*, the genus invalid.

Brachauchenius lucasi Williston (1903A, p. 57, pls. 24, 25) was based upon a skull and vertebrae from the Benton (Turonian or Cenomanian) of Ottawa County, Kansas (USNM specimen, displayed in a wall case). The short neck and relatively long skull are pliosaurian, not related to the Colombian plesiosaur. It is distinctive in being a brachydiran with a short mandibular symphysis, and in lacking ventral or lateral keels on the cervicals, and lacking ventral nutrient foramina in the centra. Since we know nothing of the limbs or girdles, it is likely that the specimen is not specifically diagnostic, and will eventually become a *nomen vanum*.

Cimoliasaurus lissaensis Fritsch (1905, p. 15, pl. 6, figs. 6-8) is a *nomen vanum* based upon indeterminate fragments from a quarry behind the castle in Lissa, Czechoslovakia. The horizon is the Weissenberger shale of the Turonian Pläner. The propodial bears no resemblance to the Colombian form.

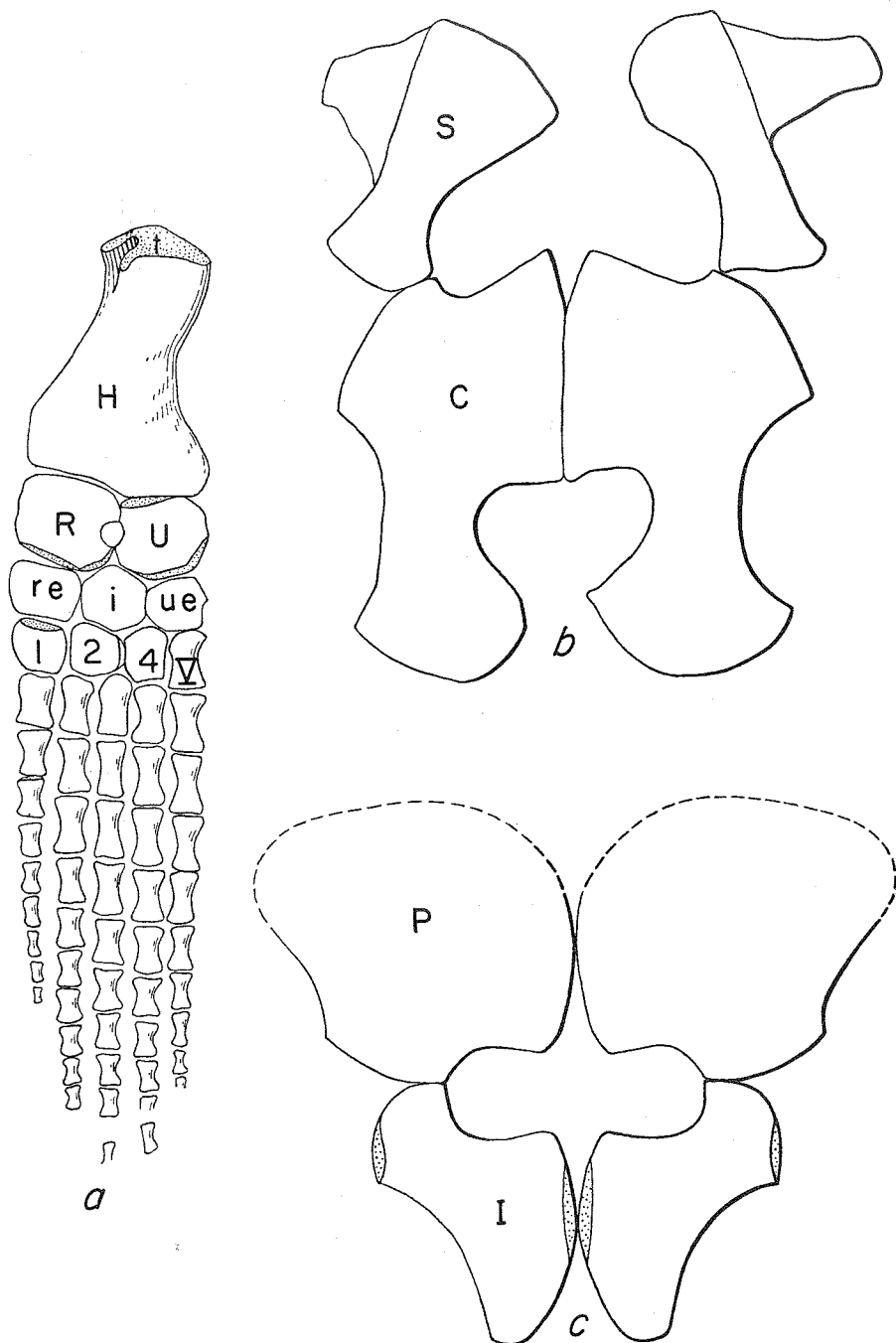


Fig. 10. *Alzadasaurus riggsi* Welles, type, CNHM 12009: a, lateral view of left pectoral paddle; b, c, ventral views of pectrum and pelvis. $\times \frac{1}{10}$.

Cimoliasaurus teplicensis Fritsch (1907, p. 3, figs. 3, 4) is a *nomen vanum* based upon generically indeterminate fragments from the Teplitz shales (Turonian) of Hundorf, Czechoslovakia. The single centrum illustrated seems to be the posterior cervical of a pliosaur.

Cimoliasaurus vicinus Fritsch (1907, p. 1, fig. 1) is based upon weathered fragments from the Iser shale (Turonian) of Chrast, Czechoslovakia. The centrum illustrated is pliosauroidean, but the material is indeterminate, and the name a *nomen nudum*.

Dolichorhynchops kirki (Russell, 1935D, p. 385, pls. 45, 46) is from the Assiniboine formation of Manitoba (?Turonian) and is founded on a fairly complete skeleton less the skull. It is a short-necked form, slightly more primitive than *Dolichorhynchops osborni* in having longer epipodials, and differs in its more slender propodials, outline of the pubis, and longer ischia. The species is based upon diagnostic material and is here referred to the genus *Dolichorhynchops*.

Elasmosaurus amalitskii Pravoslavlev (1916, pp. 315 ff.) was based on a large series of vertebrae of a single individual, described in great detail and well illustrated. The specimen is from the Turonian of the Liski River, Don Province, U.S.S.R. In spite of Pravoslavlev's careful comparisons, such a specimen is not diagnostic, and the name is a *nomen vanum*. Indices of anterior, medial, and posterior cervicals are 53, 58:94; 95, 58:88; and 114, 85:120 compared with 34, 100:127; 82, 82:106; and 99, 93:108 for the Colombian type skeleton. It is thus a bigger reptile with greatly elongated cervicals.

Elasmosaurus morgani Welles (1949, p. 7, figs. 1-3, pls. 1-6) was based on a skull, cervical and pectoral vertebrae, pectrum, and part of an anterior paddle (SMU Dept. Geol.). It is from the Upper Eagle Ford shale (Turonian) of Dallas County, Texas. The skulls are similar, but the Colombian form is smaller (42.5 cm vs. 35 cm). *Elasmosaurus morgani* has more elongate median cervicals and more depressed, though narrower, cervical centra. Indices for this and the Colombian form are: anterior cervical 37, 81:146 and 34, 100:137; medial cervical 95, 63:98 and 82, 82:106. It has 62 cervicals; the Colombian, 56. The pectra include similar clavicular arches, but the Texas species has a well-developed midline bar formed largely by posterior growth of the scapulae. The coracoids, even though they meet the scapulae in the midline, do not project as far forward. Their posterior blade is more slender, and the cordiform intercoracoid vacuity has convex sides. The humerus lacks the anterodistal knee and has a sharp posterodistal corner above the ulna. These differences are thought to be of generic significance.

Hunosaurus fasseli Fritsch (1905, p. 25) was based on vertebrae and other fragments from Hundorf, near Teplitz, Czechoslovakia. The material is indeterminate and the name a *nomen vanum*.

Iserosaurus littoralis Fritsch (1905, p. 20) was named for indeterminate fragments from the Iser formation near Lissa, Czechoslovakia. The name is a *nomen vanum*.

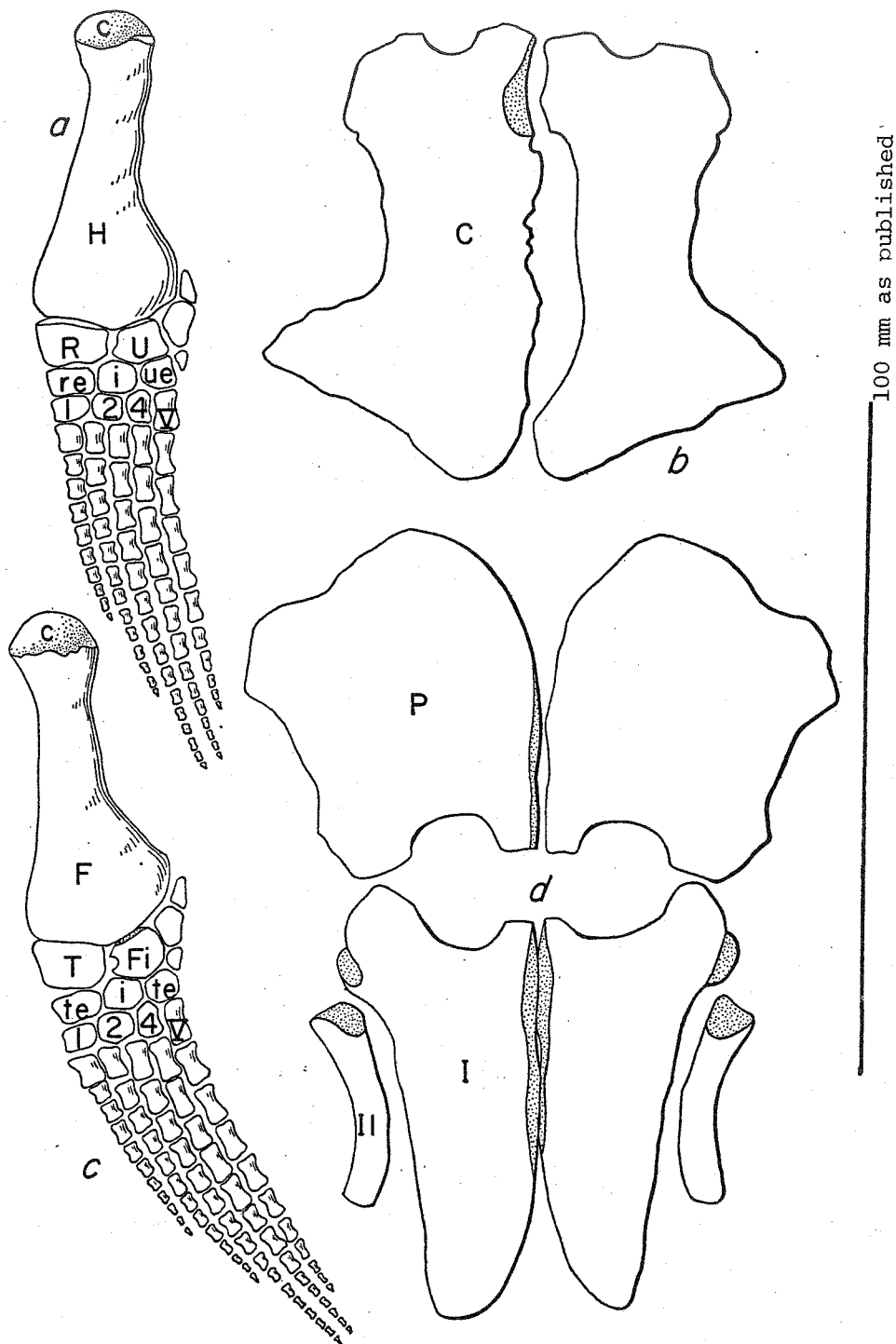


Fig. 11. *Dolichorhynchops kirki* (Russell), type, MM specimen: a, internal view of right pectoral paddle; b, ventral view of coracoids; c, internal view of right pelvic paddle; d, ventral view of pelvis. From Russell (1935). $\times \frac{1}{10}$.

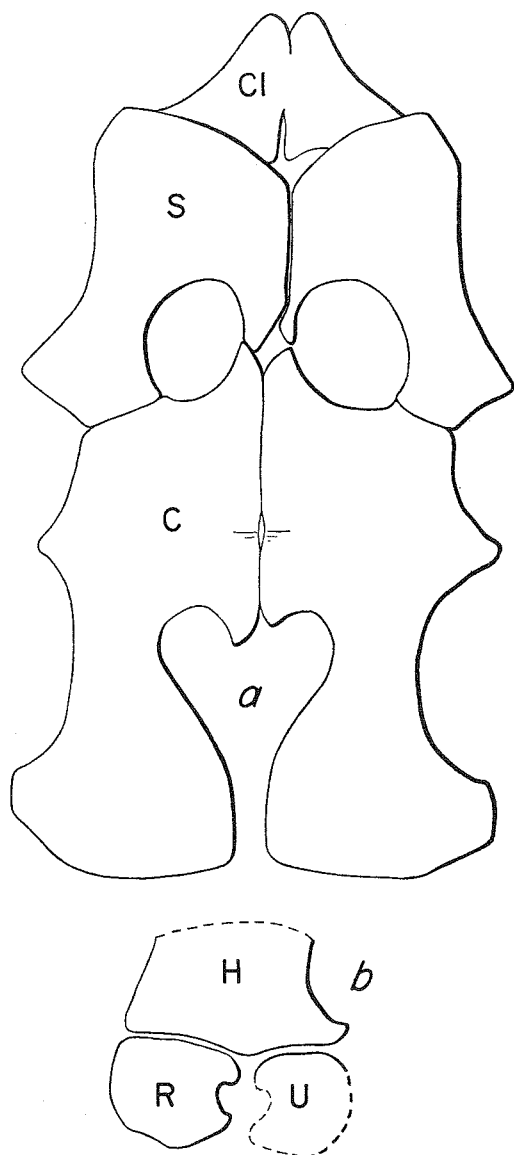


Fig. 12. *Elasmosaurus morgani* Welles, type, SMU specimen: *a*, ventral view of pectrum; *b*, lateral view of distal end of left humerus, radius, and ulna. $\times \frac{1}{10}$.

It is from the Upper Benton (*vide* Williston, 1908C, p. 729) of Osborne County, Kansas, and is approximately Turonian in age.

Trinacromerum bentonianum Cragin (1888A, p. 405) is the genotypic species.

p. 716, figs. 1, 2, 7, 8). It is not diagnostic, but is a short-necked plesiosaur. It is a *nomen vanum*, and, since the original material is lost, there is no possibility of validating the name by a new description. It can be referred to as *Dolichorhynchops* sp.

Trinacromerum kirki Russell (1935D, p. 385, pls. 45, 46) is referred in this paper to *Dolichorhynchops kirki*, *q.v.*

Trinacromerum latimanus Williston (1908C, p. 732, fig. 15) is based on a humerus with unusually broad distal end (B71%L35) from the Hailey shale (?Turonian) of Wyoming. This humerus is of a brachydiran plesiosaur and, even though it is quite broad, such a variation is not beyond expectation when we consider all the forms, including those described as *Polycotylus*. Actually, a single humerus is not diagnostic; so the name is a *nomen vanum*, and the specimen should be referred to as *Dolichorhynchops* sp.

SENONIAN

Cimoliasaurus bernardi (Owen) Lydekker (1889C, p. 185) is a reference to this genus of *Plesiosaurus bernardi* Owen, *q.v.*

Cimoliasaurus constrictus (Owen) Lydekker (1889C, p. 212) is a reference to this genus of *Plesiosaurus constrictus* Owen, *q.v.*

Cimoliasaurus magnus Leidy (1851G, p. 325) was based upon a series of 13 vertebrae from the Greensand of Burlington County, New Jersey (?Senonian). This material is not diagnostic, is probably pliosaurian, and is a *nomen vanum*.

Cimoliasaurus nazarowi Bogolubov (1911, p. 379, pl. 3, figs. 4, 8, 12) is a *nomen vanum* based on a nondiagnostic posterior cervical centrum from the Senonian of Verkhovia, Konoplianki, Orsk, U.S.S.R. It is very short and broad (indices 35, 114:171), and is probably pliosaurian.

Cimoliasaurus orientalis (Cope) Williston (1906B, p. 227) is a probable reference to this genus of *Elasmosaurus orientalis* Cope, *q.v.*

Cimoliasaurus smithii (Owen) Lydekker (1889C, p. 215) is a reference to this genus of *Plesiosaurus smithii* *q.v.*

Crymocetus bernardi (Owen) Cope (*barnardi*, 1869A, p. 266) is a reference to this genus of *Plesiosaurus bernardi*, *q.v.*

Discosaurus magnus (Leidy) Leidy (1870I, p. 22) is a transfer to this genus of *Cimoliasaurus magnus*, *q.v.*

Discosaurus orientalis (Cope) Leidy (1870I, p. 22) is a reference to this genus of *Elasmosaurus orientalis*, *q.v.*

Elasmosaurus constrictus (Owen) Cope (1869M, p. 42) is a transfer to this genus of *Plesiosaurus constrictus*, *q.v.*

Elasmosaurus helmersenii (Kiprijanoff) Bogolubov (1911, p. 359) is a reference to this genus of the species *Plesiosaurus helmersenii*, *q.v.*

Elasmosaurus orientalis Cope (1869M, p. 54, pl. 2, fig. 10) is a *nomen vanum* based on a single anteromedian cervical of an elasmosaur from Swedesboro, Gloucester County, New Jersey. It is thought to be from the Navesink formation (?Senonian). Such single centra are not diagnostic, and the indices (95, 80:113) are very close to those (82, 82:106) of the Colombian reptile. However, it differs in having fused ribs and elongate grooves for the ventral nutrient foramina.

Elasmosaurus orskensis Bogolubov (1911, p. 36, pl. 14, figs. 1-3) is named on a series of cervical centra, one of which is figured, from the Senonian of Kono-plianki, Orsk, U.S.S.R. It is a *nomen vanum*, an elasmosaur that has more depressed centra than those of the Colombian reptile.

Elasmosaurus serdobensis Bogolubov (1911, p. 374, pl. 14, figs. 4, 5) is a *nomen vanum* based upon a single anterior cervical from the Senonian of Serdoba, Petrovsk, U.S.S.R. It is an elasmosaur, not diagnostic, and larger than the Colombian form.

Plesiosaurus balticus Schröder (1885, p. 297, pl. 13, fig. 1; pl. 14, fig. 1) is a *nomen vanum* for a cervical and a dorsal vertebra from the Senonian of Marienburg, East Prussia. It is not diagnostic, and is probably pliosaurian.

Plesiosaurus bernardi Owen (1850, p. 396, pl. 40) is named for a single posterior cervical vertebra from the upper chalk pit (Senonian) at Haughton, near Arundel, Sussex. It is pliosaurian, generically and specifically indeterminate, and therefore a *nomen vanum*.

Plesiosaurus brevifemur Cope (1875E, p. 256) is a *nomen vanum* for the vertebra and femur from the Greensand (no. 5) of Barnesboro, New Jersey. The femur is smaller and slenderer than in the Colombian (B49%L25 vs. B73%L33 and B61%L36) specimen; the dorsal vertebra has transverse processes well above the centrum.

Plesiosaurus constrictus Owen (1850, p. 398, pl. 37, figs. 6, 7) is a *nomen vanum* for a single median cervical centrum from a chalk pit at Steyning, Sussex (Senonian). It is an elasmosaur, but is not diagnostic. The great constriction of the middle of the centrum is quite different from the Colombian form and is like *Elasmosaurus platyurus*.

Plesiosaurus helmersenii Kiprijanoff (1882, pp. 18, 21, pl. 11, figs. 1-3; pl. 12, figs. 1, 2; pl. 13, figs. 1, 2) was founded upon a series of centra from the Senonian of Serdoba, Petrov region, Saratov, U.S.S.R. These are from the same locality, possibly the same individual, and although Kiprijanoff added other specimens to his hypodigm, Bogolubov (1911, p. 359) restricted the type of this specimen. Persson (1959, p. 444) further restricted it to the original plate 11, figure 3, *d*. Bogolubov and later workers have referred the species to the genus *Elasmosaurus*. However, such specimens are not diagnostic and the name is a *nomen vanum*. Anterior and median cervicals have indices 78, 77:110 and 136, 69:93 compared with 34, 100:127 and 82, 82:106 for the Colombian reptile. It is much larger—in fact the largest elasmosaur known—and has relatively lower and narrower cervicals.

Plesiosaurus lockwoodii Cope (1869M, p. 40) is a *nomen vanum* based on a single dorsal vertebra from Monmouth County, New Jersey, which is not diagnostic. Its relation to the Colombian reptile cannot be determined.

Plesiosaurus smithii Owen (1884, I, viii; IV, iv, pl. 19) is a *nomen vanum* for a single ?pectoral vertebra from the chalk pit at Burham, Kent. It is crushed and not diagnostic.

Plesiosaurus vaccinsulensis (Cope) Hay (1930A, p. 116) is a reference to this genus of *Champsosaurus vaccinsulensis*. The specimen is very small (26, 112:173), is not at all like the Colombian reptile, and is nondiagnostic.

Pliosaurus gigas Schröder (1885, p. 322, pl. 16, fig. 1) is a *nomen vanum* based upon an indeterminate dorsal centrum from the Senonian of Altfelde near Elbing, Prussia. It has been variously identified by later workers and is probably elasmosaurian. Comparison with the Colombian reptile is meaningless.

Polycotylus balticus (Schröder) Bogolubov (1911, p. 337) is a reference to this genus of *Plesiosaurus balticus*, *q.v.*

Polycotylus donicus Pravoslavlev (1915, p. 17, pl. 1) is based upon a series of short cervical centra and part of a "pubis" from the ?Senonian of the Lysoff farm, north Don district, U.S.S.R. The vertebrae are not diagnostic, but are probably pliosaurian; the "pubis" seems to be the body of an elasmosaurian coracoid. The name is a *nomen vanum*, and there is no similarity to the Colombian elasmosaur.

Polycotylus orientalis Bogolubov (1911, p. 339, pl. 13, figs. 1-3, 5-7, 9-11) is a *nomen vanum* for vertebrae from the Senonian of Rosenberg, Prussia. These had been described by Schröder (1885, p. 317) and identified as *Plesiosaurus ichthyospondylus* Seeley. The vertebrae are not diagnostic and are probably pliosaurian.

Polycotylus ultimus Bogolubov (1911, p. 348, pl. 12, figs. 4-6) is a *nomen vanum* for two cervical centra from the Senonian of Petrovsk, Saratov, U.S.S.R. The specimen is nondiagnostic, probably pliosaurian. Bogolubov (*loc. cit.*) actually cites this as *Polycotylus* (*Trinacromerum*) *ultimus*.

Polyptychodon interruptus Owen (1841, p. 19, pl. 72, fig. 4) is named on a single tooth which is illustrated but not described. No locality is given; although Owen (1850, p. 378) credits Mr. Mackeson with finding it in the Greensand near Hythe, he later (1851, p. 56, figs. 1-3) refigures the specimen, and his legend reads: "from the Chalk of Sussex." It is pliosaurian, a *nomen vanum*, and not diagnostic.

Scanisaurus nazarowi (Bogolubov) Persson (1959, p. 447) is a reference to this genus of *Cimoliasaurus nazarowi*, *q.v.*

Taphrosaurus lockwoodii (Cope) Cope (1870D, p. 274) is a *nomen vanum* created for the nondiagnostic vertebra previously named *Plesiosaurus lockwoodii*, *q.v.*

Trinacromerum orientale (Bogolubov) Pravoslavlev (1915, p. 13) is a *nomen vanum* formed by altering Bogolubov's citation of *Polycotylus* (*Trinacromerum*) *orientalis*.

Trinacromerum ultimum (Bogolubov) Pravoslavlev (1915, p. 14) is a *nomen vanum* formed by this citation of Bogolubov's (1911, p. 348) original listing of *Polycotylus* (*Trinacromerum*) *ultimus*.

CONIACIAN

Elasmosaurus nobilis Williston (1906B, p. 232, pl. 4, figs. 1-9) is a *nomen vanum* based upon a fragmentary skeleton (YPM 1640) that is not diagnostic. It is from three miles west of Jewell City, Jewell County, Kansas, in the Fort Hays limestone, the basal member of Niobrara formation. The parts preserved do not differ greatly from the Colombian elasmosaur and several others, but the specimen is too incomplete to identify.

Ogmodirus martini Williston and Moodie (1913A, p. 120) was named for an incomplete juvenile skeleton (KUMNH 441) from the basal Niobrara (Coniacian)

of Cloud County, Kansas. The specimen is so young that its relationships are not determinable. It could be the young of any of the known adults; so the name is a *nomen vanum*.

Thalassonomosaurus nobilis (Williston) Welles (1943, p. 190, fig. 33) is a reference to this genus of the *nomen vanum*, *Elasmosaurus nobilis*, *q.v.*

SANTONIAN

Alzadasaurus kansasensis Welles (1952, p. 80, fig. 11) was based upon a series of cervical, pectoral, dorsal, sacral, and caudal vertebrae, and the pelvis and right pelvic paddle of a single individual (YPM 1130) from the Niobrara (?Santonian) of Wallace County, Kansas. The median cervical is longer, lower, and narrower than in the Colombian form; the posterior cervical is shorter, lower, and broader. Indices are 92, 66:76 and 84, 89:119 vs. 82, 82:106 and 99, 93:108 for the Colombian specimen. The increase in length of the median cervicals indicates a longer neck. This could be an evolutionary development, as could the increase in roundness of the centra. The pubes have narrow acetabular necks like the Bogotá specimen, but the anterior border is more like those at Berkeley. The femur is about the same size ($B60\%L31$ vs. $B73\%L33$ for the Berkeley and $B61\%L36$ for the Bogotá), but the anterior border is concave farther down; hence the antero-distal "knee" is lower and smaller. The posterior dip of the trochanter is 10° (not 25° as stated in Welles, 1952, p. 82), about the same in the two. The epipodials are much shorter, as would be expected, but they have straight contiguous borders with no trace of a foramen between them. This species is elasmosaurian, not directly related to the Colombian; the differences in shape of pubis and the lack of epipodial foramen make doubtful its assignment to this genus. There is now some question in my mind whether it is based upon diagnostic material.

Cimoliasaurus platyurus (Cope) Lydekker (1889C, p. 181, *Cimoliosaurus*) is a reference to this genus of *Elasmosaurus platyurus*, *q.v.*

Cimoliasaurus snowii Williston (1890A, p. 262, *Cimoliosaurus*) was later changed to *Elasmosaurus snowii*, *q.v.*

Discosaurus carinatus Cope (1868D, p. 68) was synonymized by Cope (1869M, p. 46) with *Elasmosaurus platyurus*, *q.v.*

Dolichorhynchops osborni Williston (1902D, p. 241) was based upon a complete skeleton from the Niobrara Chalk (?Santonian) of Logan County, Kansas. Now mounted at the University of Kansas, it is the first North American pliosaur to be founded upon adequate material. Williston (1903A, p. 13, figs. 3, 5, 8, 12, pls. 1-4, 6-17, 20, 22, fig. 5) later thoroughly described and illustrated the specimen. It is diagnostic and must be regarded as the real basis for our knowledge of this kind of plesiosaur. Since the genera *Polycotylus* and *Trinacromerum* are based upon nondiagnostic material, they must be abandoned, as well as families formed from these names. *Dolichorhynchops* therefore becomes the name-bearer, and the family name is hereby changed to Dolichorhynchopidae.

Elasmosaurus ischiadicus (Williston) Williston (1906B, p. 231) is a transfer to this genus of the specimen originally described as *Polycotylus ischiadicus*. It consists of a small part of the skeleton of a very young individual, and includes the ischia, ilia, proximal end of right femur, and 19 centra, from the Niobrara

(?Santonian) of Logan County, Kansas. It has been assigned to various genera by subsequent authors, but the material is juvenile, inadequate, and not diagnostic, except that the short ischia are elasmosaurian. It should therefore be considered a *nomen vanum*. Comparisons with the Colombian elasmosaur are meaningless.

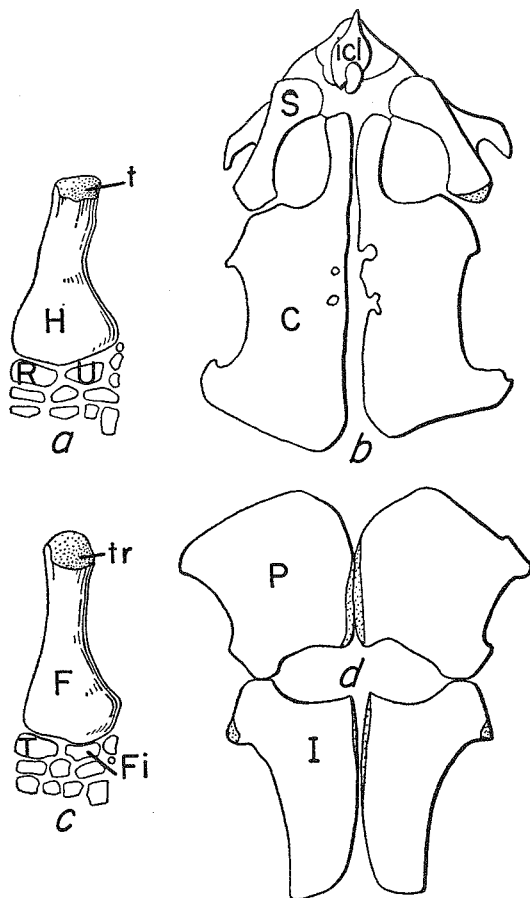


Fig. 13. *Dolichorhynchops osborni* Williston, type, KU-MNH specimen: *a*, lateral view of left humerus *et seq.*; *b*, ventral view of pectrum; *c*, lateral view of left femur *et seq.*; *d*, ventral view of pelvis. From Williston (1903). $\times \frac{1}{10}$.

Elasmosaurus marshii Williston (1906B, p. 229, fig. 4, pl. 2, fig. 2) was based upon a scapula, 32 vertebrae, and a front paddle with most of the phalanges missing. The specimen (YPM 1645) is from the Niobrara (?Santonian) of Logan County, Kansas. It is so incomplete that it is not really diagnostic; yet the known parts are so different that they probably represent a distinct species and genus, as the name indicates. However, the name is actually a *nomen vanum*. The scapulae could belong to a species of *Elasmosaurus*, and they differ from the Colombian scapulae in having a midline junction and posterior projection. The humerus

is more rounded posterodistally than the Colombian humerus, seeming to be quite different. The epipodials are more advanced in being shorter, but both species retain the epipodial foramen. *Elasmosaurus marshii* is also farther advanced in having supernumerary ossicles above and below the ulna. This specimen may be referred to as ?*Elasmosaurus* sp. until better material is found.

Elasmosaurus platyrus Cope (1868A, p. 92) was based upon a vertebral column, pectrum, and pelvis. It lacked skull and paddles. The specimen (ANSP 18001) is from the Niobrara (?Santonian) below *Polycotylus latipinnis*, which is in chalky limestone (Cope, 1868M, p. 36), although Williston (1902D, p. 242) wrote "basal Pierre." Much confusion has surrounded this specimen, primarily because Cope (1869M, pp. 46 ff.) first described it with the head on the end of the tail. Although this error was corrected, the revised text (Cope, 1870W) was largely a reprint of the original; the detailed description still applied to the reversed animal and are useless from a practical point of view. Furthermore, the girdles have since been lost. The discovery of *E. morgani* made it likely that Cope's restoration of the pectrum was correct in having a midline bar, even though he misinterpreted the dorsal processes of the scapulae and the scapulo-coracoid suture. Unfortunately, this skeleton was our first indication of these spectacular, gigantic marine reptiles, and it has become the basis for our idea of the group. It now consists of little more than a series of vertebrae, and is probably indeterminate, even though Cope illustrated the girdles, and the name is virtually a *nomen vanum*. If we accept the modified girdles (fig. 14; see also Welles, 1952, fig. 1) and the revised arrangement of the vertebrae (Welles, 1952, p. 54), we then have an elasmosaur that differs considerably from the Colombian form. The anterior and median cervicals are longer, lower, and narrower, but the posterior cervicals are broader. The pectrum and pelvis both have midline bars.

Elasmosaurus snowii Williston (1890D, p. 174, fig. 1) was first described as *Cimoliosaurus* (*Elasmosaurus*?) *snowii* on a skull and 28 cervical vertebrae of a single individual from the Niobrara (?Santonian) of Hell Creek, Logan County, Kansas. The skull is 42 cm, snout to condyle, and crushed nearly flat from side to side. The material is elasmosaurian but not diagnostic, and the name is a *nomen vanum*. The skull is 7 cm larger (20%) than the Colombian form, and is different in minor proportions; the cervicals are larger and lower.

Elasmosaurus sternbergi Williston (1906B, p. 232) is a *nomen vanum* for a few vertebrae and fragments from the Niobrara formation of Gove County, Kansas. These are not diagnostic and are probably pliosaurian.

Ogmodirus ischiadicus (Williston) Williston and Moodie (1917A, p. 61) is a reference to this genus of the species *Elasmosaurus ischiadicus*, *q.v.*

Piratosaurus plicatus Leidy (1865A, pp. 29, 116, pl. 19, fig. 8) is a *nomen vanum* for a nondiagnostic single tooth (USNM 1000) from the Upper Cretaceous near Red River Settlement, Manitoba, Canada. The tooth is probably pliosaurian (Williston, 1908C, p. 735) and unrelated to the Colombian elasmosaur. The name should be abandoned and the specimen referred to as ?*Dolichorhynchops* sp.

Polycotylus dolichopus Williston (1906B, p. 235, pl. 3, fig. 2) is a *nomen vanum* based upon a femur and part of the paddle from the Niobrara Chalk of Kansas (YPM 1642). Williston's hypodigm also included a humerus and part of a paddle,

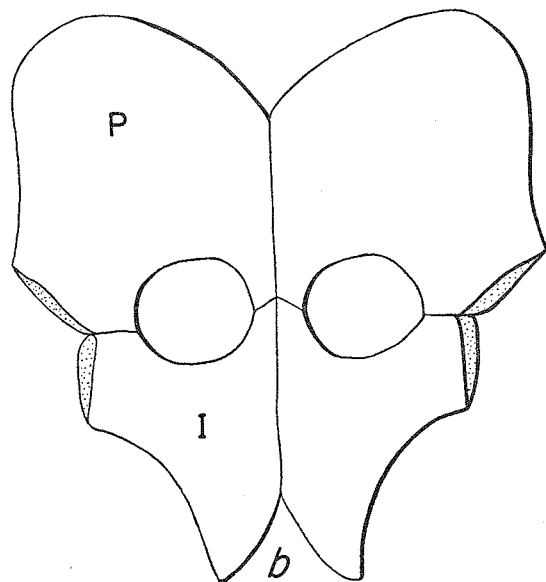
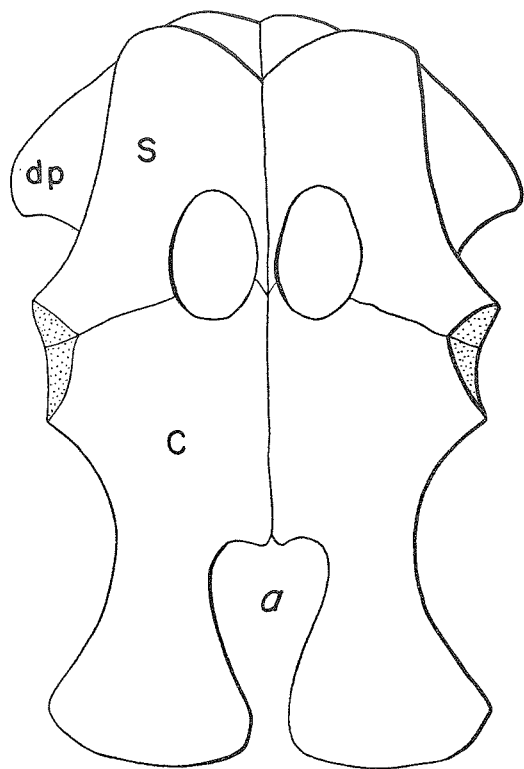


Fig. 14. *Elasmosaurus platyurus* Cope, type, ANSP 18001: a, b, ventral view of pectrum and pelvis. Modified from Cope (1869M). $\times \frac{1}{10}$.

but this is a distinct specimen (YPM 1646). Williston designated the latter as type, but the femur was illustrated and should be considered the type. The species is characterized by the slenderness of the propodials and their great distal expansion (humerus B54%L32, femur B50%L31) but such material is not diagnostic. It is very close to *Dolichorhynchops osborni* and should be referred to as *Dolichorhynchops* sp.

Polycotylus ischiadicus Williston (1903A, p. 72) is an elasmosaur. See *Elasmosaurus ischiadicus*.

Polycotylus latipinnis Cope (1869M, p. 36, pl. 1, figs. 1-13) was based upon 21 vertebrae and parts of the pelvis and pelvic paddle from the Niobrara (?Santonian) at Fort Wallace near the Smoky Hill River, Kansas. Cope compared his material with elasmosaurs, from which it is clearly distinct, but it is not diagnostic even though his descriptions are detailed. The name is a *nomen vanum*.

Styxosaurus snowii (Williston) Welles (1943, p. 188) is a *nomen vanum* formed by erecting a new genus for *Elasmosaurus snowii*, *q.v.*

Thalassiosaurus ischiadicus (Williston) Welles (1943, p. 191, fig. 34) is a *nomen vanum* formed by creating a new generic name for the *nomen vanum* *Elasmosaurus ischiadicus*, *q.v.* The generic name should be abandoned.

Thalassonomosaurus marshii (Williston) Welles (1943, p. 189, fig. 32) is a *nomen vanum*, an erection of a new genus for *Elasmosaurus marshii*, *q.v.* This generic name should be abandoned.

Trinacromerum osborni (Williston) Williston (1906B, p. 234) considers *Dolichorhynchops* a synonym of *Trinacromerum*, and later workers accept this as a transfer to this genus of *D. osborni*, *q.v.*

CAMPANIAN

Alzadasaurus pembertoni Welles and Bump (1949, p. 524, figs. 3-5, pl. 85) is based on a nearly complete skeleton (SDSMT 451) from the banks of the Missouri River, 11 miles northeast of Iona, South Dakota. The horizon is the basal Pierre formation (Campanian). The skull is 37 cm from snout to condyle, which is but 2 cm longer than the Colombian form. The South Dakota species is advanced in having five more cervicals, with the lateral keel prominent through cervical 58 instead of being restricted to the first 38. Anterior and median cervicals are longer, but the posterior cervicals are broader. The median cervicals are elongated, exceeding the other regions. Indices for anterior, median, and posterior cervicals for this and the Colombian species are: 45, 64:98; 108, 61:79; 106, 86:129 and 34, 100:127; 82, 82:106; 99, 93:108. The clavicular arch is greatly reduced; the anterior midline projection of the coracoids is absent, but the posterior blades are almost identical. The pubes are a compromise between the two Colombian specimens. The humerus has the tuberosity a little farther separated from the capitulum, and the epipodial facets more concave. The epipodials are a little shorter. The femur differs greatly in its completely separate, posteriorly inclined trochanter. Thus the Dakotan species differs in many advanced ways, and is a good linear descendant of the Colombian elasmosaur.

Elasmosaurus gigas (Schröder) Persson (1959, p. 445) is a transfer to this genus of the *nomen vanum* *Pliosaurus gigas*, *q.v.*

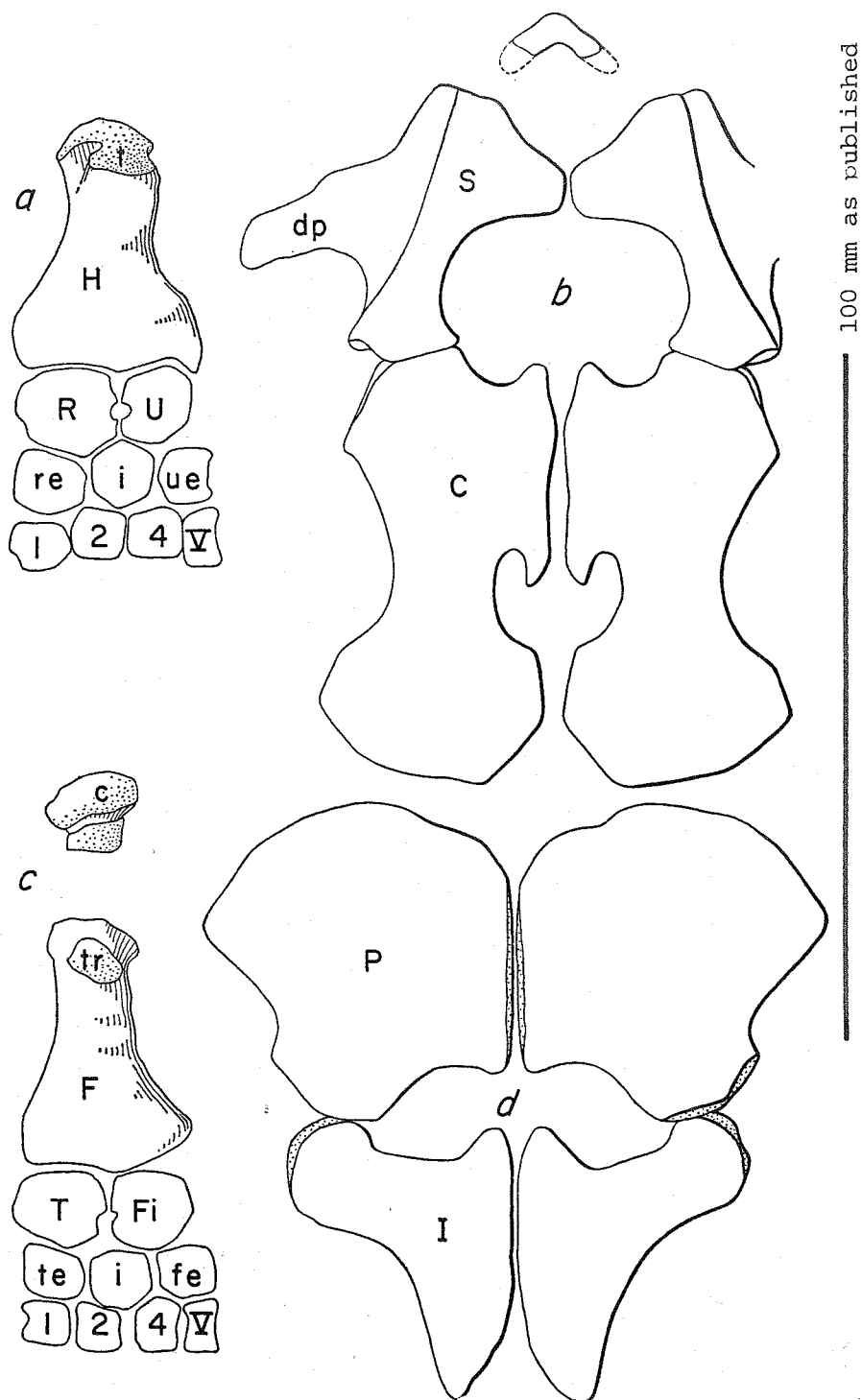


Fig. 15. *Alzadasaurus pambertoni* Welles and Bump, type, SDSMT 451: *a*, lateral view of left humerus *et seq.*; *b*, ventral view of pectrum; *c*, lateral view of left femur *et seq.*, with proximal end of femur above; *d*, ventral view of pelvis. $\times \frac{1}{10}$.

Elasmosaurus intermedius Cope (1894B, p. 112) is a *nomen vanum* for 19 vertebrae and the proximal end of a propodium from the Big Bend of the Missouri River, South Dakota. It is from the Pierre shale, is pliosaurian, and is non-diagnostic.

Elasmosaurus serpentinus Cope (1877G, p. 578) has been referred to the genus *Hydralmosaurus*, *q.v.*

Embaphias circulosus Cope (1894B, p. 111) is a *nomen vanum* for three vertebrae from the Big Bend of the Missouri River, South Dakota. They are from the Pierre shale, and are nondiagnostic and pliosaurian, unrelated to the Colombian elasmosaur.

Hydralmosaurus serpentinus (Cope) Welles (1943, p. 185, fig. 29) was named by Cope (1877G, p. 578) for a fairly complete skeleton without the skull (AMNH 1495) from a bluff of blue shale in Nebraska on the southwest side of the Missouri River, between Yankton and Sioux City. Cope listed this as Cretaceous no. 3, which would be Niobrara (?Santonian), but blue shale is more characteristic of the Pierre (Campanian) and this horizon seems more probable. It has 60 cervicals, 3 pectorals, and 19 dorsals compared with 56 cervicals, 2 pectorals, and 23 dorsals for the Colombian plesiosaur. The cervical vertebrae are regularly about 1 cm longer than the Colombian form and relatively lower. The anterior and median cervicals are narrower, but the posterior cervicals are broader. The lateral keel is restricted in both to the anterior 38 cervicals, and their ventral faces are similar. The scapulae lack comparable parts. The coracoids are massive with much greater midline thickening than the Colombian form, and in the midline do not project far in front of the scapular suture. The intercoracoid vacuity is more nearly circular. The pubes have a longer, straighter midline. The humerus is massive in both, but *H. serpentinus* has a more pronounced posterodistal expansion above the ulna. It also has the anterodistal knee ending nearly parallel to the shaft. The edge is continued into the radius and radiale: these are in line with the shaft, not sloped backward as in the Colombian elasmosaur. Radius and ulna are more nearly rectangular, but much shorter. The Colombian reptile would be a good ancestor for *H. serpentinus*, since the differences are more in degree than in kind, and as yet we know of no species better qualified. Even so, the backward sweep of the paddles in the Colombian form seems to be an aberrant development, indicating that it is really a specialized branch.

Plesiosaurus gigas (Schröder) Wegner (1914, p. 303) is a transfer to this genus of *Pilosaurus gigas*, *q.v.*

Plesiosaurus gulo Cope (1872BB, p. 127) is a *nomen vanum* for 11 cervical, 13 dorsal and other vertebrae, and parts of the pectrum and pelvis from the Niobrara (?Santonian) or Pierre (?Campanian) of Sheridan, Kansas. The material is non-diagnostic and inadequately described.

Pliosaurus gigas Schröder (1885, p. 325, pl. 16, fig. 1) is a *nomen vanum* for a nondiagnostic dorsal centrum from Altfelde, near Elbing, Germany. The indices (110, 118:126) are very close to those of an anterior dorsal centrum of *Elasmosaurus platyrus* (94, 112:128) and are also close to material described as *Pliosaurus*.

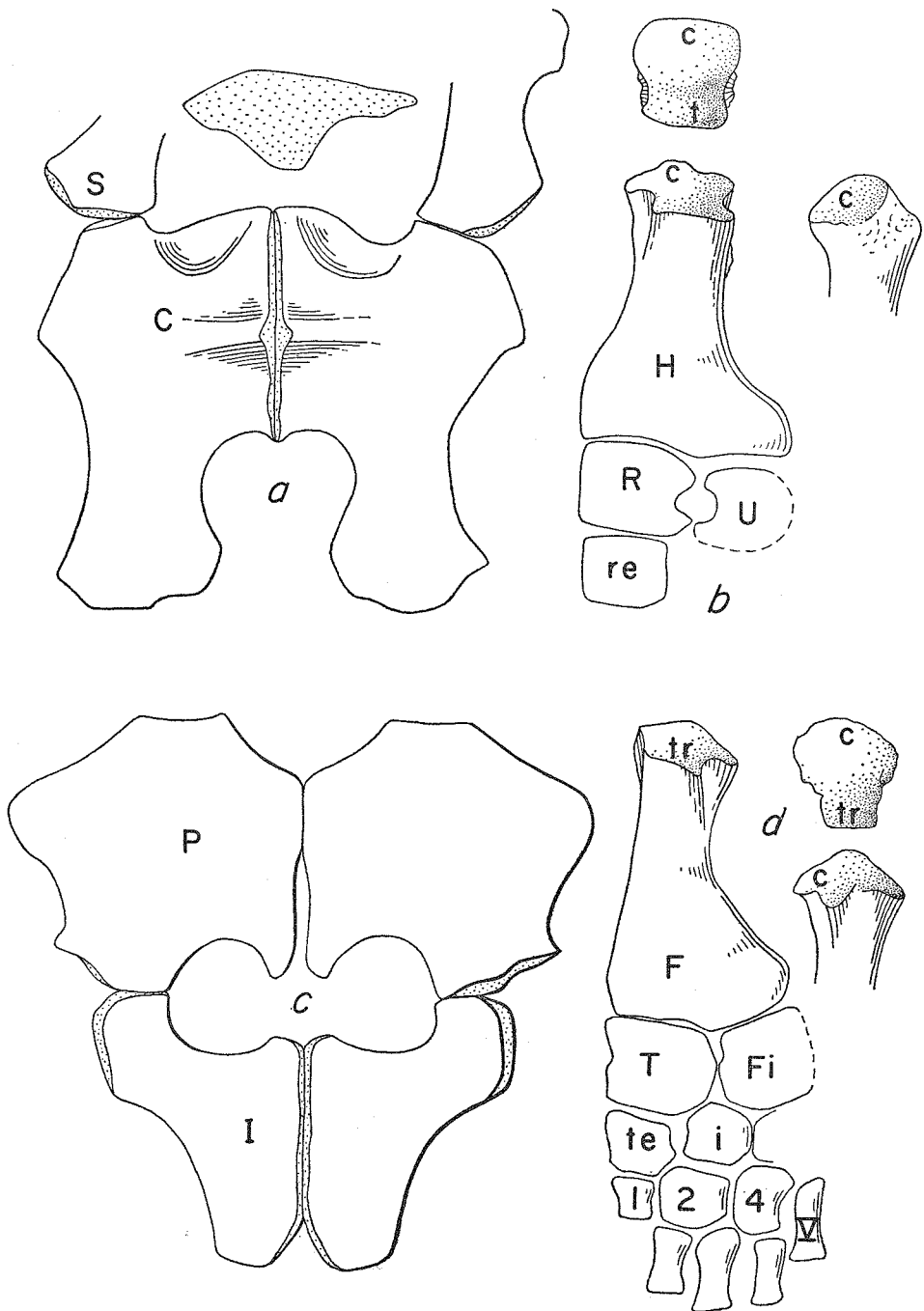


Fig. 16. *Hydralmosaurus serpentinus* (Cope), type AMNH 1495: *a*, ventral view of pectrum, with medial view of right coracoid above; *b*, lateral view of left humerus *et seq.*, with proximal view above, and anterior view of proximal end at right; *c*, ventral view of pelvis; *d*, lateral view of left femur *et seq.*, with proximal view above at right and anterior view of head of femur below. $\times \frac{1}{10}$.

Styxosaurus browni Welles (1952, p. 69, figs. 6-7) was based upon a skull, 75 vertebrae, pectrum, and front paddle of a single individual (AMNH 5835) from Mule Creek, 15 miles from Edgemont, South Dakota. The collector, Barnum Brown, placed the horizon as Niobrara, but the matrix is an adherent, hard, dark blue-gray shale that is more suggestive of the Pierre (?Campanian). Its differences from *Hydralmosaurus serpentinus* were pointed out in the original description; whether these will eventually be considered generic, specific, or even individual variations within the same species cannot be determined now. Both are large elasmosaurs, and they are closely related. Although the skull is nearly identical with the Colombian reptile, *S. browni* differs in having larger cervicals that are relatively much narrower in the anterior and median regions but considerably broader posteriorly, and in having about seven more cervicals and one more pectoral. The scapulae have a greater extent of midline contact; the coracoids end in the midline behind the level of the scapular suture. The humerus is similarly massive, but more expanded posterodistally. The epipodials are much shorter, as would be expected in a later form. *Styxosaurus browni* could very well be derived directly from the Colombian elasmosaur.

MAESTRICHTIAN

Aphrosaurus furlongi Welles (1943, p. 173, figs. 23-26, pls. 26-28) is based upon pectrum, pelvis, paddles, and about 38 vertebrae (CIT 2748) from the Moreno formation of the Panoche Hills, Fresno County, California. The posterior cervicals differ from the Colombian form in having a ventral midline groove and being a little lower and narrower. The clavicles are smaller and concave anteriorly; the scapular ventral plate is broader anteriorly; and the scapulae are about the same distance apart in the midline. The coracoids are less massive, do not have the central keel, and though they have an equally long midline suture, are more concave anteriorly. The posterior blade is much narrower, but the distal expansion is about the same. The pubis has a longer posterointernal border and a longer midline suture. The humerus is more slender, and lacks anterior and posterior grooves between the heads. There is no epipodial foramen, and the epipodials are much shorter. The femur is also more slender and the posterior epipodial foramen is absent. The two species are certainly distinct, and it is possible that the Californian species is descended from the Colombian.

Aristonectes parvidens Cabrera (1941, p. 114, figs. 1-5) is an enigmatic plesiosaur based upon a skull and cervical vertebrae from the Maestrichtian of Cañadon del Loro, northeast of Chubut, Patagonia. The head is large (73 cm, snout to condyle) and the neck short, as in pliosaurs, but the alveoli are very small and numerous (45/57) and the symphysis is very short. It seems to be an aberrant plesiosaur.

Cimoliasaurus andium Deecke (1896, p. 51, pl. 1, fig. 4; pl. 3, figs. 1-3) is a *nomen vanum* based upon caudals of an elasmosaur. They are not diagnostic, and comparison with the Colombian form is useless.

Cimoliasaurus australis (Owen) Lydekker (1889C, p. 220) is a transfer to this genus of *Plesiosaurus australis*, *q.v.*

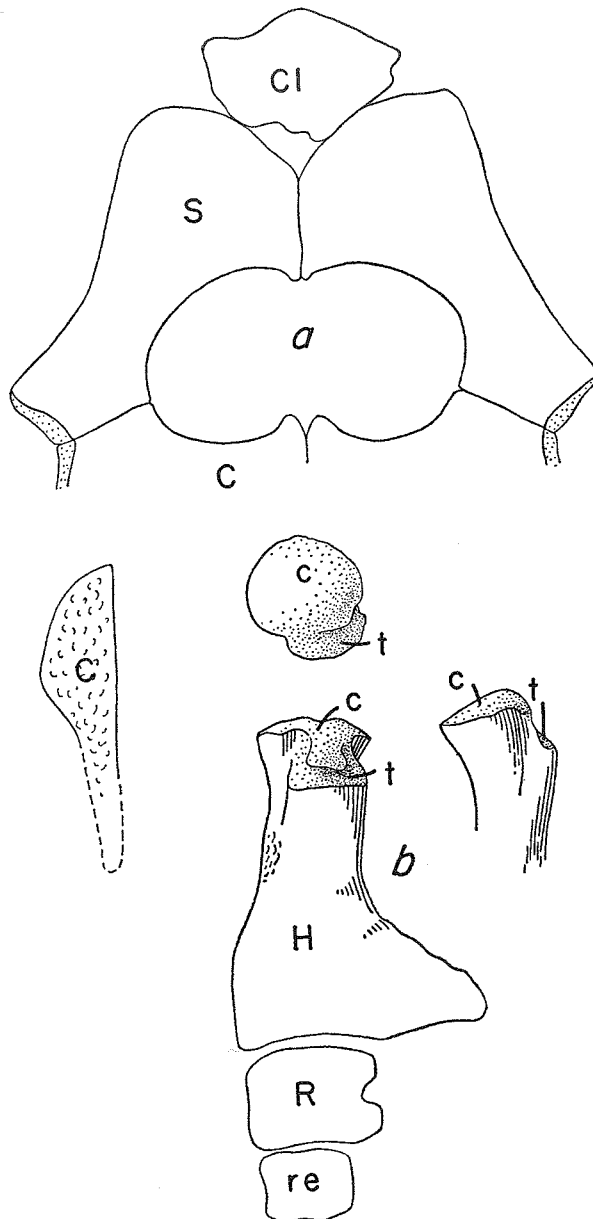


Fig. 17. *Styxosaurus browni* Welles, type AMNH 5835: *a*, ventral view of pectrum and, below to left, medial view of right coracoid; *b*, lateral view of left humerus *et seq.*, with proximal view above, anterior view to right. $\times \frac{1}{10}$.

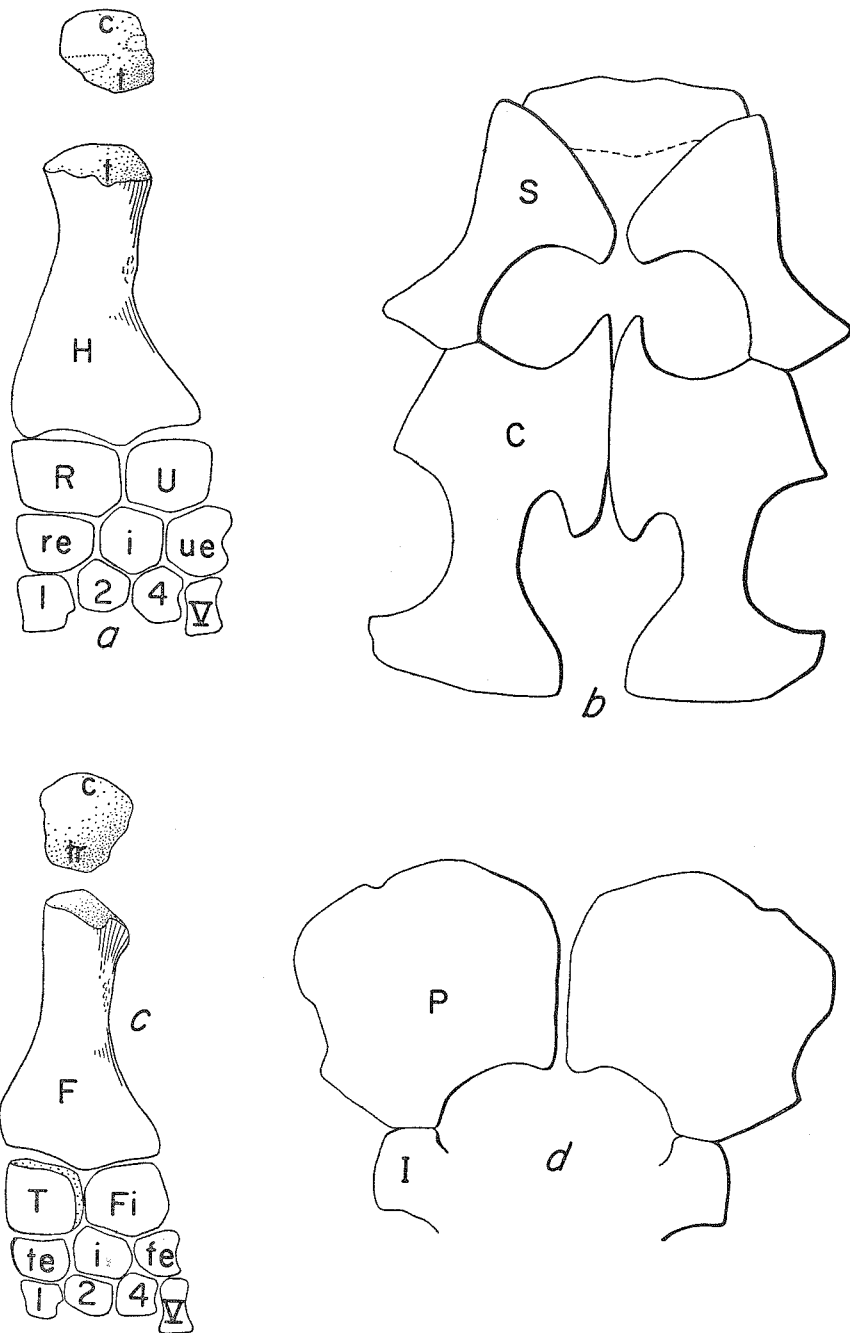


Fig. 18. *Aphrosaurus furlongi* Welles, type, CIT 2748: a, lateral view of left humerus et seq., proximal end above; b, ventral view of pectrum; c, lateral view of left femur et seq., proximal end above; d, ventral view of pubes. $\times \frac{1}{10}$.

Cimoliasaurus caudalis Hutton (1894, p. 356, pl. 42) is a *nomen vanum* based upon vertebrae and parts of the girdles from the ?Maestrichtian of Bobby's Creek, Waipara, New Zealand. The small size (8th dorsal, 48, 115:135) and the weak development of the coracoid blade are juvenile. It is elasmosaurian, but cannot profitably be compared with the Colombian elasmosaur.

Cimoliasaurus chilensis (Gay) Lydekker (1889C, p. 222) is a *nomen vanum* transfer to this genus of the species *Plesiosaurus chilensis*, *q.v.*

Cimoliasaurus haasti (Hector) Lydekker (1889C, p. 215) is a transfer to this genus of the species *Mauisaurus haasti*, *q.v.*

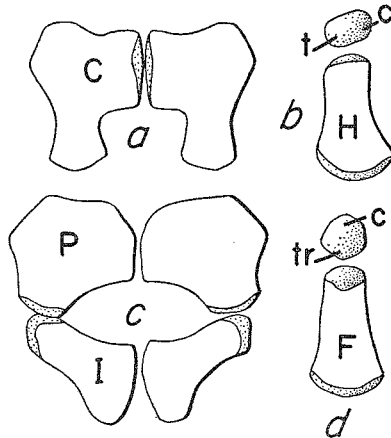


Fig. 19. *Fresnosaurus drescheri* Welles, type CIT 2758: a, dorsal view of coracoids; b, internal view of right humerus, proximal end above; c, dorsal view of pelvis; d, internal view of right femur, proximal end above. $\times \frac{1}{40}$.

Cimoliasaurus hoodii (Owen) Lydekker (1889C, p. 245) is a transfer to this genus of the species *Plesiosaurus hoodii*, *q.v.*

Cimoliasaurus tenuis (Hector) Lydekker (1889C, p. 188) is a transfer to this genus of the species *Polycotylus tenuis*, *q.v.*

Elasmosaurus haasti (Hector) Bogolubov (1911, pp. 84, 355) is a reference to this genus of *Mauisaurus haasti*, *q.v.*

Elasmosaurus hoodii (Owen) Pravoslavlev (1918, p. 1955) is a transfer to this genus of the species *Plesiosaurus hoodii*, *q.v.*

Fresnosaurus drescheri Welles (1943, p. 181, fig. 27) was based upon an incomplete juvenile skeleton (CIT 2758), consisting of coracoids, humerus, pelvis, femora, and paddle bones, from the Moreno formation (Maestrichtian) of the Panoche Hills, Fresno County, California. This very young reptile differs from the Colombian adult in lacking the anterior growth of the coracoids and in having narrow, short, broadly separated posterior blades. Other differences in shape of pelvis and propodials could be due to lack of development of the young individual, but the two do not seem to be closely related.

Hydrotherosaurus alexandrae Welles (1943, p. 126, front., figs. 3-9, 10, d, 11, 12, pls. 12-21, 29) was based upon a nearly complete skeleton (UCMP 33912)

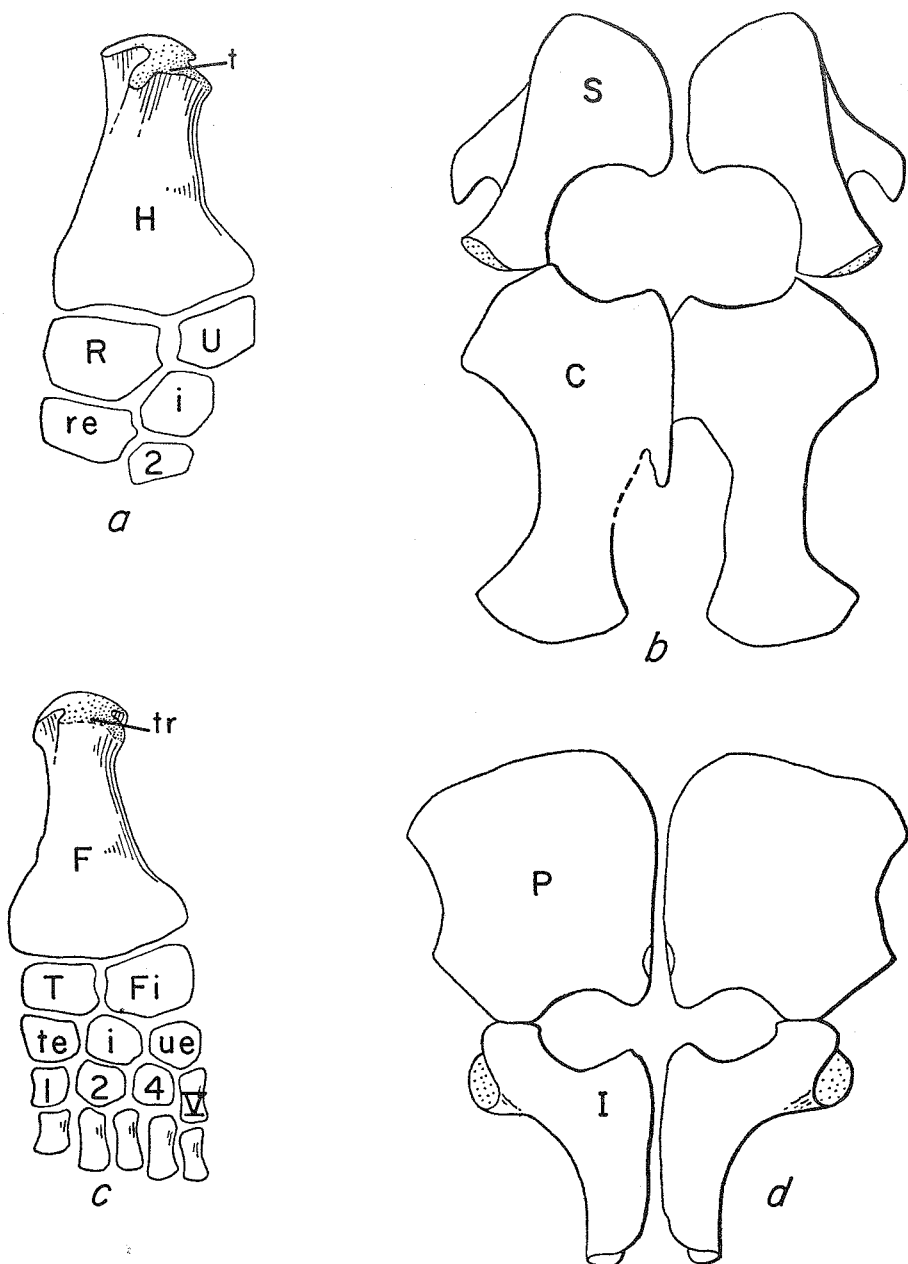


Fig. 20. *Hydrotherosaurus alexandrae* Welles, type, UCMP 33912: *a*, lateral view of left humerus *et seq.*; *b*, ventral view of pectrum; *c*, lateral view of left femur *et seq.*; *d*, dorsal view of pelvis. $\times \frac{1}{10}$.

from the Moreno formation (Maestrichtian) of the Panoche Hills, Fresno County, California. The skull length is 33 cm; the neck contains 60 cervicals, versus 35 cm and 56 cervicals in the Colombian elasmosaur. *Hydrotherosaurus alexandrae* thus has a slightly smaller skull but a longer neck. The cervicals are also differently proportioned, for the anterior cervicals are much lower and narrower; median cervicals are higher but narrower; and posterior cervicals are higher and broader. Cervical spines are vertical and rectangular, with horizontal summits, instead of inclining posteriorly with rounded tops and beveled posterodorsal corners. There is no tongue-and-grooving of the spinous edges. The lateral keel is more strongly developed, and the cervicals are thus quite different. The ventral scapular blades are a little larger; the coracoids have shorter anterior projections and much more deeply excavated lateral borders. The pubes have longer posterior borders. The humerus is similar in size, shape, and relative arrangement of heads, but the epipodials are much shorter and almost without the foramen. The femur has more pronounced grooves between capitulum and trochanter, but is otherwise similar. The tibia and fibula are shorter. Thus, while both are elasmosaurs, the Californian form differs in many respects. It could be descended from the Colombian reptile.

Leurospondylus ultimus Brown (1913C, p. 605, figs. 1-7) is a juvenile plesiosaur from the Edmonton formation of the Red Deer River, Alberta, Canada. It has a shorter anterior projection of the coracoids, as in many of the other North American forms. It could be the young of any of several of these, but additional material is needed to solve this problem. The cervical centra are very short, suggesting pliosaurian relationships, whereas the scapulae and coracoids seem to be elasmosaurian, as do the short pubes.

Mauisaurus brachiolatus Hector (1874, errata slip) is a *nomen vanum* for a fragment of a large humerus from the Amuri Bluff, New Zealand (Wellington Museum, no. 9a). It is indeterminate.

Mauisaurus haasti Hector (1874, p. 346, pl. 29) is based upon a composite hypodigm from several localities in New Zealand. The lectotype is here designated the pubes and pelvic paddle (Wellington Museum, no. 8a) from the Jed River, 20 miles south of Amuri Bluff, figured by Hector. The bones he describes as "coracoids" are pubes. They are narrow and long, and could be pliosaurian if his outline is correct. The "humerus" is evidently a femur, as it is very narrow distally. The bone is quite different from other plesiosaurs in having a hemispherical capitulum with a large trochanter that dips steeply posteriorly and is separated from the capitulum by a broad groove. Another unusual feature is the very small fibular facet. This is a unique plesiosaur. The narrow pubis and long narrow femur (B52%L44) suggest pliosaurian relationships, very different from the Colombian elasmosaur. As to the validity of the name, such small parts of a skeleton are

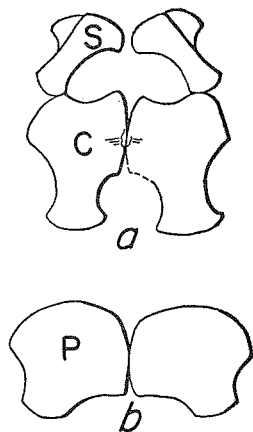


Fig. 21. *Leurospondylus ultimus* Brown, type, AM-NH 5261: a, ventral view of pectrum; b, pubes. $\times \frac{1}{10}$.

not normally diagnostic, but this femur is so different that we should perhaps suspend judgment on its status.

Mauisaurus latibrachialis Hector (1874, p. 350) is an error for *M. brachiolatus*, *q.v.*

Morenosaurus stocki Welles (1943, p. 165, figs 17-22, pl. 25) was based on a good skeleton, lacking the skull and the anterior cervical vertebrae (CIT 2802), from the Moreno formation of the Panoche Hills, Fresno County, California. Median cervicals are longer than posterior cervicals; both are higher and much broader than the Colombian form, as shown by the anterior and median cervical indices (94, 82:135 and 88, 102:177 vs. 82, 82:106 and 99, 93:108). The clavicular arch seems to retain an interclavicle; the scapulae have larger ventral blades that meet in the midline; the coracoids have short midline sutures. The pubes have longer posterior borders and convex lateral ones with a very broad anterolateral projection. The humerus has a complete separation of capitulum from a tuberosity which dips posteriorly. The radius and ulna are, expectedly, shorter. The femur has the trochanter nearly separate and nearly parallel to the tibial face. The anterior border is concave nearly to the bottom. Epipodials are very short. This animal seems to be only distantly related to the Colombian form.

Nothosaurops occiduus Leidy (1870U, p. 74) is a *nomen vanum* based upon an indeterminate single vertebra which might not even be a plesiosaur. It is from the Moreau River, South Dakota, of ?Cretaceous age.

Orophosaurus pauciporus Cope (1887G, p. 565) is a *nomen vanum* from the Fox Hills formation of New Mexico. The type is three anterior caudals of an indeterminate juvenile.

Piptomerus hexagonus Cope (1887G, p. 565) is a *nomen vanum* for an indeterminate juvenile ?pliosaur from the Fox Hills sandstone of New Mexico.

Piptomerus megaloporus Cope (1887G, p. 564) is a *nomen vanum* based upon nondiagnostic juvenile vertebrae and propodial from the Fox Hills sandstone, New Mexico.

Piptomerus microporus Cope (1887G, p. 565) is a *nomen vanum* for a few indeterminate juvenile centra from the Fox Hills sandstone of New Mexico.

Plesiosaurus andium Gervais (1859, pp. 432, 480) is a junior synonym of *Plesiosaurus chilensis*, *q.v.*

Plesiosaurus australis Owen (1862A, p. 123) is a *nomen vanum* based upon parts of several vertebral centra from the Maestrichtian of Waipara Gorge, Canterbury Province, New Zealand. This material is not determinate, and comparison with the Colombian elasmosaur is meaningless.

Plesiosaurus chilensis Gay (1848, p. 133, Erpetologia fossil, pl. 1, figs. 1-3) is a *nomen vanum* based on composite material from the Maestrichtian of Quiriquina Island, Chile. The lectotype is pliosaurian, unrelated to the Colombian reptile.

Plesiosaurus crassicostatus Owen (1870, p. 53, pl. 3, fig. 5) is a *nomen vanum* based on a block with seven cervicals from Bobby's Creek, Waipara, New Zealand. The specimen was more fully prepared and redescribed and refigured by Hector (1874, p. 341, pl. 28). It is juvenile, not diagnostic, and wholly unrelated to the Colombian elasmosaur.

Plesiosaurus holmesii Hector (1874, p. 344) is a *nomen vanum* based on eleven

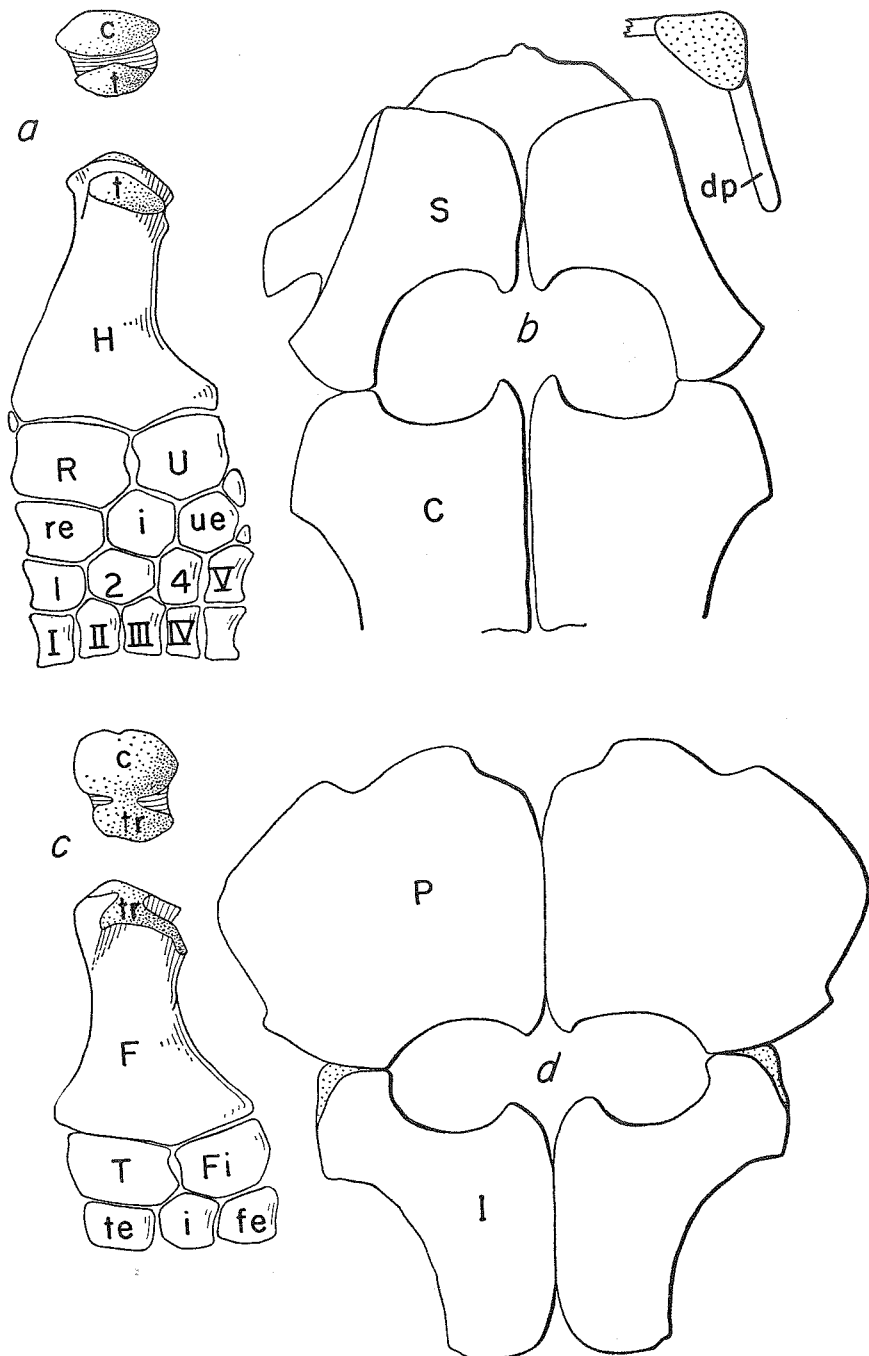


Fig. 22. *Morenosaurus stocki* Welles, type, CIT 2802: a, lateral view of left humerus et seq., proximal end above; b, ventral view of pectrum and posterior view of scapula to show angle of dorsal process; c, lateral view of left femur et seq., proximal end above; d, dorsal view of pelvis. $\times \frac{1}{10}$.

TABLE 6
VERTEBRAL INDICES OF TYPE SPECIMENS OF CRETACEOUS PLESIOSAURS, IN DESCENDING STRATIGRAPHIC ORDER
(Estimates italicized)

Species	Ant. Cerv.	Med. Cerv.	Post. Cerv.	Pect.	Ant. Dors.	Post. Dors.	Sac.	Cd.
<i>Aphrosaurus furlongi</i>			94	100
Welles.....	58	59	108 : 118	100 : 135
<i>Aristonectes parvidens</i>	81 : 114	59	61
Cabrera.....	39	102 : 158	135 : 189	77	60
<i>Hydrotherosaurus alexandriae</i>	85 : 97	83	96	89	89	80	114 : 125	128 : 150
Welles.....	96 : 99	117 : 128	110 : 135	130 : 108	91	80	68
<i>Morenosaurus stocki</i>	94	88	120 : 187	114 : 142	103 : 135	111 : 151	115 : 188
Welles.....	45	82 : 135	102 : 177	96	100	88	87	70
<i>Alzadasaurus pembertoni</i>	64 : 98	108	106	95 : 148	92 : 151	116 : 144	115 : 137	119 : 146
Welles and Bump.....	44	61 : 79	86 : 129	69
<i>Hydralmosaurus serpentinus</i>	77 : 114	98	111	122 : 162
(Cope).....	44	77 : 83	86 : 122	95	95
<i>Stygosaurus browni</i>	66 : 91	92	105	97 : 143	105 : 132
Welles.....	41	66 : 89	90 : 129	86	94	78	65
<i>Elasmosaurus platyurus</i>	76 : 93	98	105	111 : 134	112 : 128	108 : 128	111 : 157
? <i>Stygosaurus snowi</i>	40	62 : 61	91 : 125
(Williston).....	85 : —	90
<i>Alzadasaurus kansasensis</i>	76 : —	84	64	65	60	55
Welles.....	92	89 : 119	117 : 124	122 : 151	100 : 142	96 : 147
<i>Dolichorhynchops osborni</i>	28	66 : 76	26	25
Williston.....	107 : 125	51	146 : 172	160 : 160
<i>Brachauchenius lucasi</i>	117 : 130	50
Williston.....	— : 168
<i>Elasmosaurus morgani</i>	37	95
Welles.....	81 : 146	63 : 98
<i>Thalassomedon haringtoni</i>	44	105	123	113	115	90	75	70
Welles.....	98 : 125	78 : 89	103 : 138	111 : 164	117 : 143	115 : 156	145 : 200	143 : 172
<i>Alzadasaurus colombiensis</i>	34	82	99
Welles.....	100 : 127	82 : 106	93 : 108	40	34
<i>Brancasaurus brancai</i>	20	30	45	110 : 143	142 : 152	32	27
Wegner.....	100 : 125	100 : 111	98 : 112	141 : 151	142 : 156
<i>Leptocleidus superstes</i>	25	31
Andrews.....	120 : 152	146 : 155	155 : 178
<i>Peyerus capensis</i>	36	30
(Andrews).....	114 : 156	140 : 164

posterior cervicals (Wellington Museum, no. 4a). The specimen, presumably from Waipara, New Zealand, is not diagnostic.

Plesiosaurus hoodii Owen (1870, p. 53, pl. 3, figs. 1-3) is a *nomen vanum* based upon the drawings of a single anterior cervical vertebra from the Waipara Bluff, New Zealand. Indices are 53, 76:102, which are elasmosaurian, but such specimens are indeterminate. It is larger, lower, and narrower than the Colombian elasmosaur.

Plesiosaurus mackayii Hector (1874, p. 345) is a *nomen vanum* based on vertebrae, clavicle, fragment of coracoid, and a humerus (B59%L34) from the Amuri Bluff, New Zealand. This incomplete material is not diagnostic. The Colombian humeri average B71%L41; so *P. mackayii* is much slenderer, probably pliosaurian.

Plesiosaurus mauritanicus Arambourg (1952D, p. 275) is a *nomen vanum* based upon a single tooth (*ibid.*, pl. 40, fig. 13), which is not diagnostic. This and other material of Arambourg's hypodigm is from the Maestrichtian of Ouled Abdoun, Chichaoua, Djebel Tilda, Morocco. It cannot be distinguished from many other specimens, and comparison with the Colombian elasmosaur is not worth while.

Plesiosaurus occiduus (Leidy) Cope (1874C, p. 28) is a transfer to this genus of *Nothosaurops occiduus*, q.v.

Plesiosaurus traversii Hector (1874, p. 344, pl. 24H) is a *nomen vanum* based upon nine large quadrate centra (Wellington Museum, no. 5a) from the Amuri Bluff, New Zealand. Indices of one of the centra are 51, 174:200, and are pliosaurian.

Pliosaurus chilensis (Gay) Deecke (1896, p. 36) is a reference to this genus of *Plesiosaurus chilensis*, q.v.

Polycotylus tenuis Hector (1874, p. 345, pl. 37) is a *nomen vanum* based upon vertebral centra and a propodium from the Amuri Bluff (Maestrichtian) of New Zealand (Wellington Museum, no. 7a). It is certainly pliosaurian, but the vertebrae are not specifically or even generically diagnostic.

Polyptychodon patagonicus Ameghino (1893, p. 82) is a *nomen vanum* for some isolated teeth from the southern part of Santa Cruz Province, near Lake Argentina, Argentina. Cabrera (1941, p. 125) noted that they occurred with mammals and therefore are probably crocodilian.

Uronautes cetiformis Cope (1876I, p. 346) is a *nomen vanum* based upon vertebral centra (AMNH 5688) from the ?Fox Hills sandstone, west of Amell's Creek, Montana. The material is juvenile and not diagnostic.

TABLE 7

CRETACEOUS PLESIOSAURIA

PLESIOSAUROIDEA

PLIOSAUROIDEA

Maestrichtian		<i>Aphrosaurus furlongi</i>	<i>Fresnosaurus drescheri</i>	<i>Aristonectes parvidens</i>
		<i>Leurospondylus ultimus</i>	<i>Mauisaurus haasti</i>	
		<i>Hydrotherosaurus alexandrae</i>	<i>Morenosaurus stocki</i>	
Senonian	Campanian	<i>Styxosaurus browni</i>	<i>Hydralmosaurus serpentinus</i>	
	Santonian	<i>Alzadasaurus pembertoni</i>		
	Coniacian	<i>Elasmosaurus platyrus</i>		
Turonian		<i>Alzadasaurus kansasensis</i>	<i>Dolichorhynchops osborni</i>	
		<i>Elasmosaurus morgani</i>		
		<i>Alzadasaurus riggsi</i>	<i>Dolichorhynchops kirki</i>	
Cenomanian			<i>Brachauchenius lucasi</i>	
		<i>Thalassomedon haningtoni</i>	<i>Dolichorhynchops willistoni</i>	
Albian			<i>Kronosaurus queenslandicus</i>	
Aptian		<i>Alzadasaurus colombiensis</i>	<i>Leptocleidus superstes</i>	
Neocomian	Hauterivian		<i>Peyerus capensis</i>	
	Valanginian			
	Berriasian	<i>Brancasaurus brancai</i>		

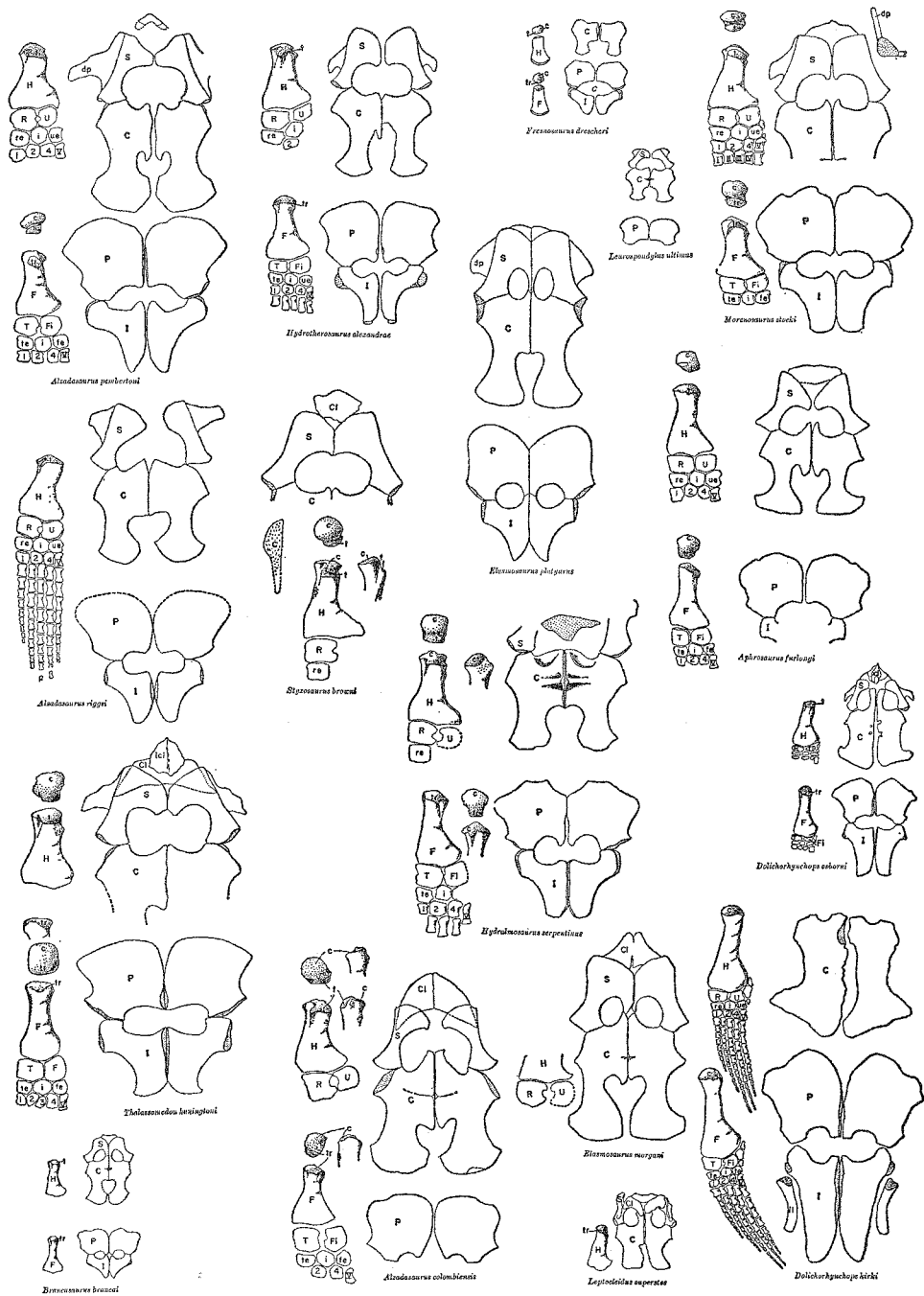


Fig. 23. Compilation of Plesiosaur girdles and limbs.

LITERATURE CITED

- AMEGHINO, FLORENTINO
1893. Sobre la presencia de vertebrados de aspecto mesozóico, en la formación Santacrucense de la Patagonia austral. *Rev. Jard. Zool. Buenos Aires*, 1:76-84.
- ANDREWS, CHARLES WILLIAM
1910A. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part 1. London: British Museum. xxiii + 205 pp., front., 94 figs., 10 pls. [Reviewed by E. T. N. in *Geol. Mag.*, (5) 7:564-567.]
1911B. On the structure of the roof of the skull and of the mandible of *Peloneustes*, with some remarks on the plesiosaurian mandible generally. *Geol. Mag.*, (5) 8:160-164, 2 figs.
1922A. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Geol. Soc. London Quart. Jour.*, 78:285-298, 1 fig., 2 pls., *Eurycleidus arcuatus*, n.g. et sp.
- ARAMBOURG, CAMILLE
1952D. Les vertébrés fossiles des gisements de phosphates (Marroc-Algérie-Tunisie). *Notes Mem. Serv. Géol. Maroc*, 92:1-372, 62 figs., 46 pls.
- BLAKE, CHARLES CARTER
1862. Plesiosaurus in Chile. *The Geologist*, 5:110.
- BOGOLUBOV, N. N.
1911. Iz istorii plesiosavrov v. Rossii. *Uch. Zap. Imperial Moscow Univ., Otd. Est-Ist.*, 29: viii + 412 pp., 16 pls. [Russian].
- BROILI, FERDINAND
1930B. Plesiosaurierreste von der Insel Quiriquina. *Neues Jahrb., Min. Geol. Pal., Abt. B.*, 63:497-514, 3 figs.
- BROWN, BARNUM
1913C. A new plesiosaur, *Leurospondylus*, from the Edmonton Cretaceous of Alberta. *Amer. Mus. Nat. Hist. Bull.* 32:605-615, 7 figs.
- BÜRGEL, HANS
1954. El Cretáceo inferior en los alrededores de Villa de Leiva, Boyacá. *Bol. Geol., Inst. Geol. Nac., Minest. Minas Petrol., Colombia*, 2:5-22, 4 pls.
- BURMEISTER, HERMANN
1861. Die Versteinerungen von Juntas im Tale des Rio Copiapo. *Abh. Naturf. Gesell. Halle*, 6 [not seen].
- CABRERA, ANGEL
1941. Un plesiosaurio nuevo del Cretáceo del Chubut. *Rev. Mus. La Plata, n.s.*, 2(8), Sec. Pal., pp. 113-130, 6 figs. [Spanish with English summary].
- COLBERT, EDWIN HARRIS
1949A. A new Cretaceous plesiosaur from Venezuela. *Amer. Mus. Nov.* 1420, 22 pp., 9 figs.
- COPE, EDWARD DRINKER
1868A. [On a new large enaliosaur.] *Proc. Acad. Nat. Sci. Phila.*, 20:92-93.
1868M. [Remarks on fossil vertebrates.] *Ibid.*, p. 313.
1869A. On the reptilian orders, Pythonomorpha and Streptosauria. *Proc. Boston Soc. Nat. Hist.*, 12:250-266.
1869M. Synopsis of the extinct Batrachia and Reptilia of North America. Part 1. *Trans. Amer. Phil. Soc., n.s.*, 14(1):1-235, 51 figs., 11 pls. [Advance separate copy; see 1870W].
1870D. On some Reptilia of the Cretaceous formation of the United States. *Proc. Amer. Phil. Soc.*, 11-271-274.
1870W. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Trans. Amer. Phil. Soc., n.s.*, 14:1-252 + viii, 55 figs., 14 pls. [This is a corrected reprint of Cope, 1869M, and is a second preprint of the whole volume, which was issued in 1871 without further changes. Line below title reads: "Read September 18, 1868 and April 2, 1869." Footnote p. ii Errata reads: "The present work was issued up to page 105 in August, 1869, and up to page 235 in April, 1870. The third part is issued in December, 1870."]
1872BB. [On some vertebrates from Sheridan, Kansas.] Plesiosaur above a *Chidastes* as though it had swallowed the mosasaur. *Proc. Acad. Nat. Sci. Phila.*, 24:127-129.

- 1874C. Review of the Vertebrata of the Cretaceous period found west of the Mississippi River. U. S. Geol. and Geog. Survey Terr. Bull., 1(2):5-48.
- 1875E. The Vertebrata of the Cretaceous formations of the West. U. S. Geol. Survey Terr. Rept., 2:1-303, 10 figs., 57 pls.
- 1876I. On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. Proc. Acad. Nat. Sci. Phila., 28:340-359.
- 1877G. 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. and Geog. Survey Terr. Bull., 3:565-597, 5 pls.
- 1887G. The sea-saurians of the Fox Hills Cretaceous. Amer. Nat., 21:563-566.
- 1894B. On the structure of the skull in the plesiosaurian Reptilia and on two new species from the Upper Cretaceous. Proc. Amer. Phil. Soc., 33:109-113, 1 fig., 1 pl.
- CRAGIN, FRANCIS WHITTEMORE
- 1888A. Preliminary description of a new or little known saurian from the Benton of Kansas. Amer. Geol., 2:404-407.
- 1894A. Vertebrata from the Neocomian of Kansas. Colorado Coll. Studies, 5:69-73, 2 pls.
- DAMES, WILHELM BARNIM
1895. Die Plesiosaurier der süddeutschen Liasformation. Abh. K. Akad. Wiss. Berlin, Phys.-Math. Kl., 1-83, figs. 1-3, pls. 1-5.
- DE LA BECHE, H. T., and W. D. CONYBEARE
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; from the observations of H. T. De la Beche, Esq., F.R.S., M.G.S., and the Rev. W. D. Conybeare, F.R.S., M.G.S., drawn up and communicated by the latter.
- DEECKE, WILHELM
1896. Ueber Saurierreste aus dem Quiriquina-Schichten. In Steinmann, 1896, pp. 32-63, pls. 1-3.
- DREVERMANN, FRITZ
1931. Ein jährlich wiederholtes Massensterben von Fischen und seine Bedeutung. Natur u. Museum, 61:468-474, 1 pl.
- EICHWALD, EDOUARD D'
1868. Lethaea Rossica ou Paléontologie de la Russie. 2:Période Moyenne, Sec. 2, pp. 641-1304.
1869. Atlas Période Moyenne, troisième partie, pls. 31-40.
- ETHERIDGE, ROBERT, JR.
1892. [Paleontology.] In Jack and Etheridge, 1892.
1897. An Australian sauropterygian (*Cimoliosaurus*) [*sic*] converted into precious opal. Rec. Australian Mus., 3:19-29, 3 pls.
1904. A second sauropterygian converted into opal, from the Upper Cretaceous of White Cliffs, New South Wales. *Ibid.*, 5:306-316, pls. 42-45.
- FRAAS, EBERHARD
1910. Plesiosaurier aus dem oberen Lias von Holzmaden. Palaeontogr., 57:105-140, figs. 1-10, pls. 6-10.
- FRITSCH, ANTON
1905. Neue Reptilien aus der böhmische Kreideformation. In Fritsch and Bayer, 1905, pp. 13-33. [Abstract in Sitz.-Ber. K. böhm. Ges. Wiss., Math.-nat. Kl., 1905(9):1-7, 3 figs.]
1907. Ueber neu Saurierfunde in der Kreideformation Böhmens. *Ibid.*, 1906(33):1-6, 4 figs.
- GAY, CLAUDIO
1848. Historia física y política de Chile. IV, part 2 [Zool., part 2] [Atlas, II, publ. 1866]. 372 pp.
- GERVAIS, PAUL
1859. Zoologie et paléontologie françaises. Paris: Arthus Bertrand, ed. 2. I, viii + 1-544; II, xii + 84 pls.
- HAY, OLIVER PERRY
- 1930A. Second bibliography and catalogue of the fossil Vertebrata of North America. Carnegie Inst. Wash. Publ. 390, part 2, xiv + 1-1074.

HECTOR, JAMES

1874. On the fossil Reptilia of New Zealand. Trans. Proc. New Zealand Inst., 6:333-358, 3 pls.
[Abstract by Hutton in *Geol. Mag.*, 30:378.]

HOFFSTETTER, ROBERT, *et al.*

1956. Lexique stratigraphique international. Vol. V, Amérique latine. Fasc. 3, Venezuela.
Paris. Cent. Nat. Rech. Sci., 740 pp.

HUENE, FRIEDRICH VON

1927. Beitrag zur Kenntnis mariner mesozoischer Wirbeltiere in Argentinien. Centralbl. Min.
Geol. Pal., Abt. B, pp. 22-29, 3 figs.

HULKE, JOHN WHITAKER

1883. The anniversary address of the president. Proc. Geol. Soc. London, 39:38-65, 18 figs.

HUTTON, FREDERICK WOLLASTON

1894. On a new plesiosaur from the Waipara River. Trans. Proc. New Zealand Inst., 26:354-358, 1 pl.

KIPRIJANOFF, VALERIAN ALEKSANDROVICH

1882. Studien über die fossilen Reptilien Russlands. II Theil. Gattung Plesiosaurus Conybeare aus dem Severischen Sandstein oder Osteolith der Kreidegruppe. Mém. Acad. Imp. Sci. St. Pétersbourg, 30:1-55, 19 pls.
1883. Studien über die fossilen Reptilien Russlands. III Theil. Gruppe Thaumatosauria N. aus der Kreide-Formation und dem Moskauer Jura. *Ibid.*, (7)31 (6):1-57, 21 pls.

KOKEN, ERNST

- 1887A. Die Dinosaurier, Crocodiliden und Sauropterygier des norddeutschen Wealden. Geol. u. palaeont. Abh., 3:311-420, 30 figs., 9 pls.
1896A. Die Reptilien des norddeutschen Wealden. *Ibid.*, Nachtrag, 7:117-126, 1 fig., 4 pls.
1905. Neue Plesiosaurierreste aus dem norddeutschen Wealden. Centralbl. Min. Geol. Pal., pp. 681-693, 7 figs.

KUHN, OSKAR

- 1935C. Fossilium catalogus. Part 69, Sauropterygia. 127 pp.

LEIDY, JOSEPH

- 1851G [1852]. [Description of fossils.] Proc. Acad. Nat. Sci. Phila., 5:325-328.
1854B [1856]. [Remarks on extinct saurian from Greenville, Clark County, Arkansas.] *Ibid.*, 7:72, 1 pl.
1865A. Cretaceous reptiles of the United States. Smithson. Contr. Knowledge, 192: v + 135 pp., 34 figs., 20 pls.
1870I. On *Discosaurus* and its allies. Proc. Acad. Nat. Sci. Phila., 22:18-22 [Abstract in Nature, 2:248 (also is Hay's 1870C)].
1870U. [Description of *Nothosaurops occidentus*.] *Ibid.*, 22:74.
1872E. [Remarks on some extinct vertebrates.] *Ibid.*, 24:38-40.

LINDER, HERMANN

1913. Beiträge zur Kenntnis der Plesiosaurier-Gattungen *Peloneustes* und *Pliosaurus*. Nebst Anhang: Ueber die beiden ersten Halswirbel der Plesiosaurier. Geol. Pal. Abh., 15:339-409, 40 figs., 4 pls. [Review by Huene in Neues Jahrb., 1913:2, 518-519.]

LONGMAN, HEBER A.

1924. Some Queensland fossil vertebrates. Mem. Queensland Mus., 8 (part 1):16-28, 4 pls.

LYDEKKER, RICHARD

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

MCCOY, FREDERICK

1867. On the occurrence of *Ichthyosaurus* and *Plesiosaurus* in Australia. Ann. Mag. Nat. Hist., (3) 19:355-356 [not seen].

OLIVER SCHNEIDER, CARLOS

1921. Contribución a la paleontología Chilena. Apuntes sobre el *Cimoliasaurus Andium*, Deecke. Rev. Chilena Hist. Nat., 25:89-95, 2 figs.

OLSSON, AXEL ADOLF

1944. The Cretaceous of the Paita region. Bull. Amer. Paleon., 28 (111):1-146, 3 figs., 17 pls.

OSTEN, ERIMAR VON DER

1948. Resumen de la paleontología vertebrada de Venezuela. Prim. Congr. Cien. Nat. Caracas, 18 pp., illus.

OWEN, RICHARD

1838. A description of Viscount Cole's specimen of *Plesiosaurus macrocephalus* (Conybeare). Proc. Geol. Soc. London, 2:663-666.
- 1840A. Report on British fossil reptiles. Brit. Assoc. Adv. Sci. Rept., 9:43-126. Birmingham, 1839.
- 1840B. A description of a specimen of the *Plesiosaurus macrocephalus*, Conybeare, in the collection of Viscount Cole. Trans. Geol. Soc. London, (2) 5:515-535, 3 pls.
1841. Odontography. Part 2. London: Bailliere. i-xl (of introduction), descr. of pls. 113-288, pls. 51-89. *fide* B. M. Cat. 3:1489 lxii a + b; lxiii a + b; lxiv a + b; lxv a + b; lxx a; lxxiii a; lxxx ix a.
1850. Description of the fossil reptiles of the Chalk formation. In Dixon, 1850, pp. 378-404, illus.
1851. A monograph on the fossil Reptilia of the Cretaceous formations. Mon. Palaeontogr. Soc., Part 1, 118 pp., pls. 1-37, +7a +9a.
1854. Descriptive catalogue of the fossil remains of Reptilia and Pisces in the Museum of the Royal College of Surgeons of England. Cat. Foss. Rept. Mus. Roy. Coll. Surg. xix + 184 pp.
- 1862A. On the remains of a plesiosaurian reptile (*Plesiosaurus australis*) from the oölitic formation in the Middle Island of New Zealand. Brit. Assoc. Rept., 1861 [1862]. Pp. 122-123.
1864. Monograph on the fossil Reptilia of the Cretaceous formations. Suppl. IV, 1-18 pp., pls. 1-9, Sauropterygia (*Plesiosaurus*), "issued in the volume for the year 1862." London: Palaeontogr. Soc.
1870. Notice of some saurian fossils discovered by J. H. Hood, Esq., at Waipara, Middle Island, New Zealand. Geol. Mag., 7:49-53, 1 pl.
1884. A history of the British fossil reptiles. London: Cassell & Co., Ltd. 4 vols., 1849-1884 [reprint of earlier papers].

PERSSON, PER OVE

1959. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). Ark. Min. Geol., 2:35, 431-478, 14 figs., 20 pls.
1960. Lower Cretaceous plesiosaurs (Rept.) from Australia. Univ. Lund Publ. Inst. Min. Pal. Quat. Geol., 80:1-23, 3 pls.

PHILIPPI, RUDOLPH AMANDUS

1887. Die tertiären and quartären Versteinerungen Chiles. Leipzig: F. A. Brockhaus. 266 pp., 58 pls.

PICTET, FRANÇOIS JULES, and G. CAMPICHE

1860. Description des fossiles du terrain crétacé des environs de Sainte-Croix. Matériaux pour la Paléont. Suisse. Genève, part 2. Pp. 29-580, 43 pls.

PICTET, FRANÇOIS JULES, and EUGÈNE RENEVIER

1854. Description des fossiles du terrain aptien de la Perte du Rhône et des environs de St. Croix. Matériaux pour la Paléont. Suisse. Genève, part 1. Pp. 1-7, 1 pl.

PRAVOSLAVLEV, PAVEL ALEKSANDROVICH

1915. Restes d'un jeune *Plesiosaurus* trouvés dans le crétacé supérieur du bassin de la rivière Liski, province du Don. Ann. Geol. Min. Russie, 17(1):1-18, 1 pl.
1916. Restes d'un *Elasmosaurus*, trouvés dans le crétacé supérieur de la province du Don. Trav. Soc. Imp. Nat. Petrograd, 38 (livr. 5), Sec. Geol. Min., v + 153-334, front., 11 pls.
- 1918A. Sur la question de "l'espèce" dan la paléontologie des vertébrés. Ann. Russ. Pal., 1: 43-60.
- 1918B. Geological distribution of the elasmosaurs. Bull. Acad. Sci. Russ. 12:1956-1978.

REUSS, AUGUST EMANUEL VON

1855. Paläontologische Miscellan. IV. Reptilienreste aus dem Pläner der Umgebung von Prag. Denkschr. K. Akad. Wiss. Wien, 10:84-87, 3 pls.

RIGGS, ELMER SAMUEL

1944. A new polycotylid plesiosaur. Univ. Kansas Bull. 30:77-87, 8 figs.

RUSCONI, CARLOS

1943. Presencia de un plesiosaurio en Mendoza. Bol. Pal. Buenos Aires, 15:1-4, 3 figs.

1948H. Plesiosauros del Jurásico de Mendoza. An. Soc. Cien. Argentina, 146:327-351, 13 figs., 2 pls.

1955A. Acerca del plesiosaurio "Purranisaurus" del Jurásico de Mendoza. *Ibid.*, 160:71-77, 4 figs.

RUSSELL, LORIS SHANO

1935D. A plesiosaur from the Upper Cretaceous of Manitoba. Jour. Paleon. 9:385-389, 3 pls.

SCHARDT, HANS

1910. Note sur deux dents de Polyptychodon du Hauteriviens supérieur. Bull. Sci. Nat. Soc. Neuchâteloise, 37:351-355, 1 pl.

SCHRÖDER, HENRY

1885. Saurierreste aus der baltischen oberen Kreide. Jahrb. K. preuss. geol. Landesanstalt, 1884:293-333, 5 pls.

SEELEY, HARRY GOVIER

1869. Index to the fossil remains of Aves, Ornithosauria, and Reptilia, from the secondary system of strata arranged in the Woodwardian Museum of the University of Cambridge. Cambridge: Deighton, Bell & Co. xxiii + 143 pp.

1874. On *Muraenosaurus leedsii*, a plesiosaurian from the Oxford Clay. Part 1. Geol. Soc. London Quart. Jour., 30(2):197-208, 1 pl.

1877. On *Mawisaurus gardneri* (Seeley), an elasmosaurian from the base of the Gault of Folkestone. *Ibid.*, 33:541-546, pl. 23.

SIMPSON, GEORGE GAYLORD

1945I. The principles of classification and a classification of mammals. Amer. Mus. Nat. Hist. Bull. 85:xvi + 350 pp.

1948E. The beginning of the age of mammals in South America. *Ibid.*, 91(1):1-232, 80 figs., 19 pls.

STEINMANN, GUSTAV

1896. Beiträge zur Geologie und Palaeontologie von Südamerika. Neues Jahrb. Min. Geol. Pal., 10:1-118, 12 figs., 7 pls.

STROMER, ERNST

1935A. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Aegyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 15. Plesiosauren. Abh. Bayer. Akad. Wiss., Math.-nat., Abt. (n.f.) 26:1-55, 19 figs., 1 pl.

TARLO, LAMBERT BEVERLY

1958A. The scapula of *Pliosaurus macromerus* Phillips. Paleontology, 1:193-199, 4 figs., 2 pls.

1958B. A review of pliosaurs. XVth Internat. Congr. Zool., Sec. V, Paper 9, pp. 438-442 [preprint of 1959B].

1959A. *Pliosaurus brachyspondylus* (Owen) from the Kimeridge Clay. Paleontology, 1:283-291, 2 figs., 2 pls.

1959B. A review of the pliosaurs. Proc. XVth Internat. Congr. Zool., pp. 438-442, 2 figs.

1959C. *Stretosaurus* gen. nov., a giant pliosaur from the Kimeridge Clay. Paleontology, 2:39-55, 6 figs., 3 pls.

1960. A review of the Upper Jurassic pliosaurs. Bull. Brit. Mus. (N.H.), Geol., 4:147-189, 9 figs., 9 pls.

TORRE, RICARDO DE LA, and LUIS E. ROJAS

1949. Una nueva especie y dos subespecies de Iethyosauria [Plesiosauria] del Jurásico de Viñales, Cuba. Mem. Soc. Cubana Hist. Nat., 19(2):197-200, 2 pls.

VAN BENEDEN, PIERCE JOSEPH

1882. Deux plésiosaures du Lias inférieur du Luxembourg. Mém. Acad. Roy. Sci. Lett. Belg., 43(2, art. 7):1-45, 4 pls.

WEGNER, THEODOR HUBERT

1914. *Brancaesaurus brancai*, n.g., n.sp., ein Elasmosauride aus dem Wealden Westfalens. In Brancafestschrift. Berlin: Borntraeger. Pp. 235-305, figs. 1-10, pls. 5-9.

WELLES, SAMUEL PAUL

1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Mem. Univ. Calif., 13:125-254, front., 37 figs., 18 pls.
1949. A new elasmosaur from the Eagle Ford shale of Texas. Fondren Sci. Ser., 1:1-28, 4 figs., 6 pls.
1952. A review of the North American Cretaceous elasmosaurs. Univ. Calif. Publ. Geol. Sci., 29:47-144, 25 figs.

WELLES, SAMUEL PAUL, and JAMES D. BUMP

1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. Jour. Paleon., 23:521-535, 5 figs., 1 pl.

WHITE, THEODORE ELMER

- 1940A. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. Jour. Paleon., 14(5):451-467, 13 figs.

WIELAND, GEORGE RIEBER

1910. *Plesiosaurus (Polyptychodon?) mexicanus* Wieland. Parergones Inst. Geol. México, 3:359-365, 1 pl.

WILLISTON, SAMUEL WENDELL

- 1890D. A new plesiosaur from the Niobrara Cretaceous of Kansas. Trans. Kansas Acad. Sci., 12:174-178, 2 figs.
- 1897C. A new plesiosaur from the Kansas Comanche Cretaceous. Kansas Univ. Quart., 6:57.
- 1902D. Restoration of *Dolichorhynchops osborni*, a new Cretaceous plesiosaur. Kansas Univ. Sci. Bull., 1:241-244, 1 pl.
- 1903A. North American plesiosaurs. Part 1. Field Columbian Mus. Publ. 73, Geol. Ser., 2:1-77, 13 figs., 29 pls.
- 1906B. North American plesiosaurs, *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. Amer. Jour. Sci., 21:221-236, 5 figs., 6 pls.
- 1908C. North American plesiosaurs: *Trinacromerum*. Jour. Geol., 16:715-736, 15 figs.

WILLISTON, SAMUEL WENDELL, and ROY LEE MOODIE

- 1913A. New plesiosaurian genus from the Niobrara Cretaceous of Nebraska [Abstract]. Geol. Soc. Amer. Bull., 24:120-121.
- 1917A. *Ogmodirus martinii*, a new plesiosaur from the Cretaceous of Kansas. Kansas Univ. Sci. Bull., 10:61-73, 3 figs., 5 pls.

WOODWARD, ARTHUR SMITH

1891. Evidence of the occurrence of pterosaurians and plesiosaurians in the Cretaceous of Brazil, discovered by Joseph Mawson, Esq., F.G.S. Ann. Mag. Nat. Hist., (6) 8:314-317, 2 figs.

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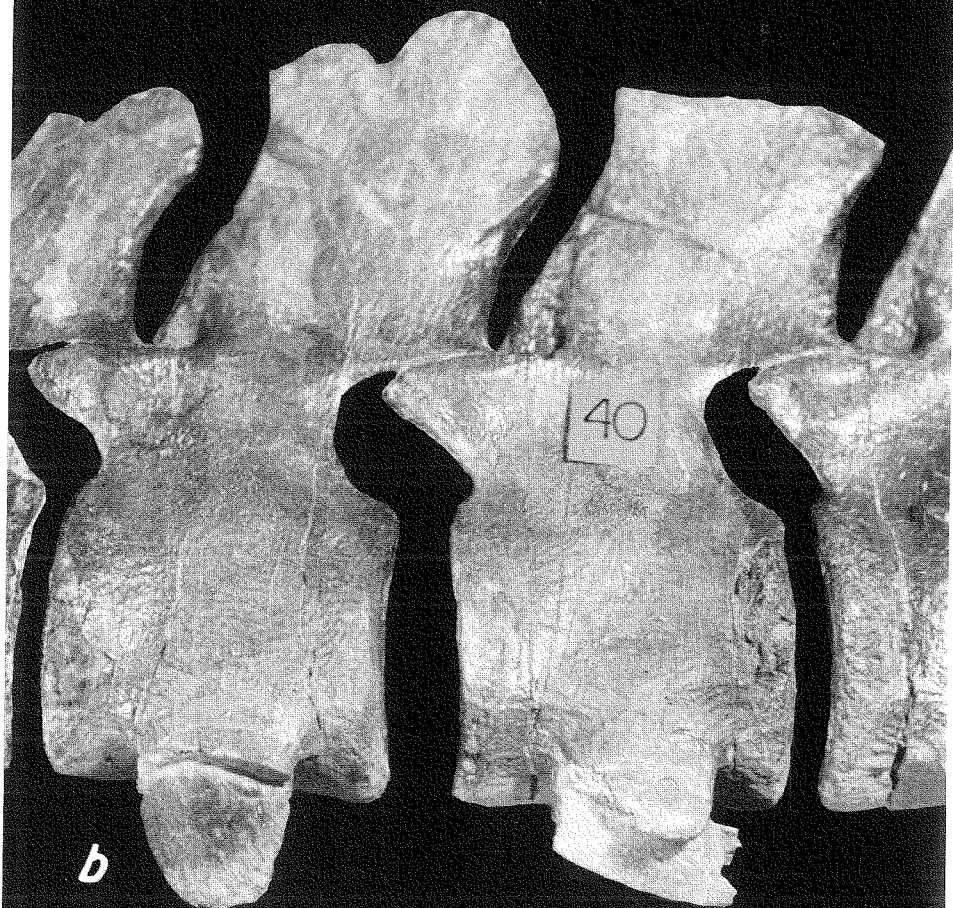
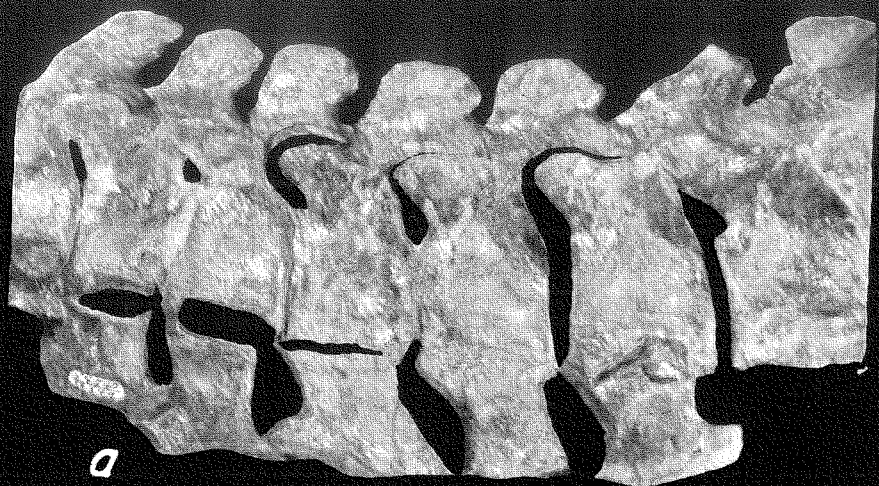
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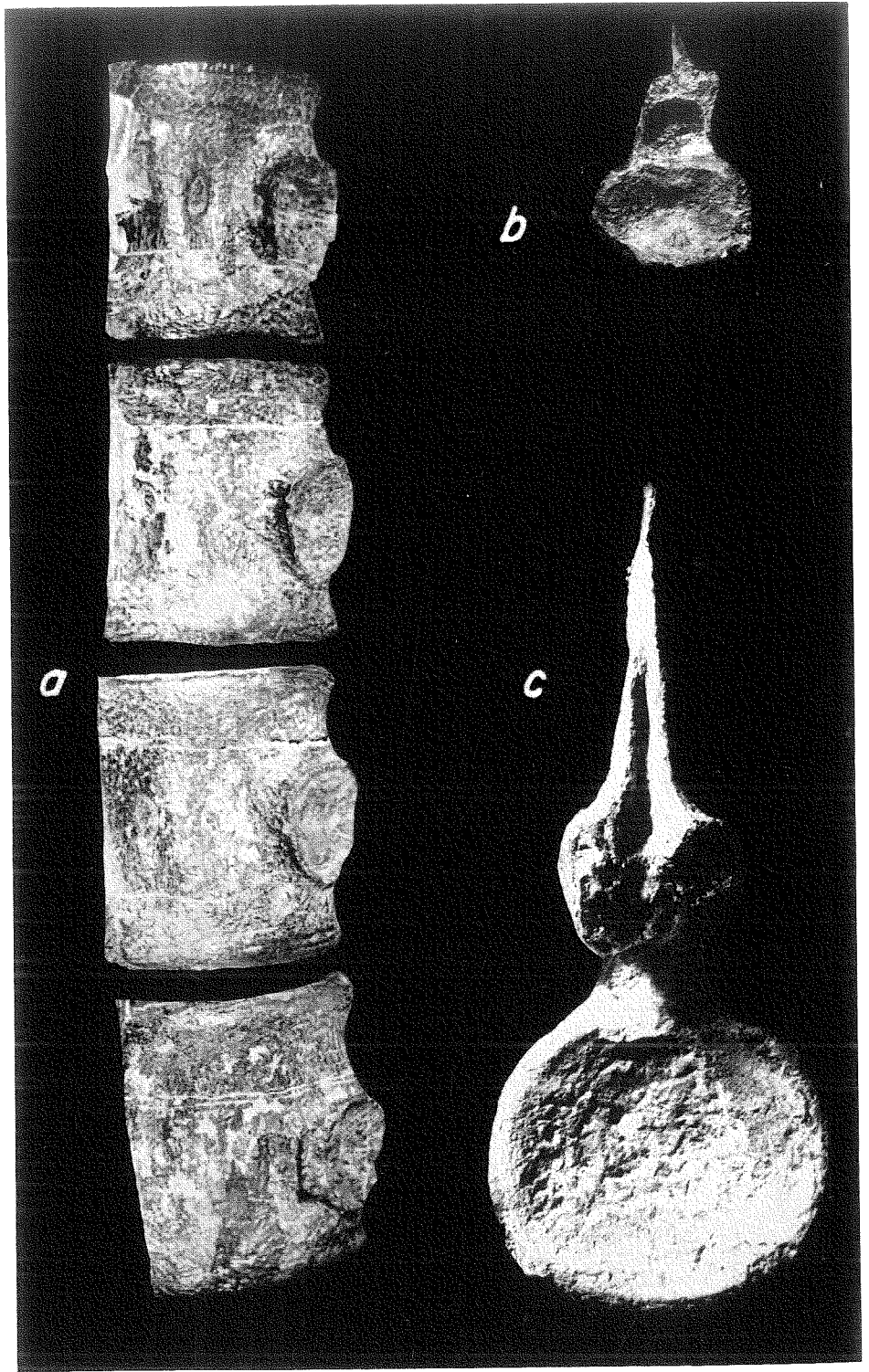
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Alzadasaurus colombiensis Welles, n. sp., type, UCMP 38349: a, ventral view of cervicals 47-50,

