

REVISION OF NORTH AMERICAN ELASMO SAURS FROM THE CRETACEOUS OF THE WESTERN INTERIOR

Kenneth Carpenter

Dept. of Earth Sciences, Denver Museum of Natural History, 2001 Colorado Blvd., Denver, CO. 80205

ABSTRACT

A review of North American elasmosaurs from the Cretaceous of the Western Interior recognizes only five valid genera and species: *Elasmosaurus platyurus*, *Hydralmosaurus serpentinus*, *Libonectes morgani*, *Styxosaurus snowii*, and *Thalassomedon hanningtoni*. *Alzadasaurus kansasensis*, *A. pembertoni* and *Thalassonomosaurus marshi* form an ontogenetic series of *Styxosaurus snowii* from the Smoky Hill Chalk and Sharon Springs Member of the Pierre Shale. The holotype of the genus *Alzadasaurus* is synonymized with *Thalassomedon*, leaving "*Alzadasaurus*" *columbiensis* without a generic name, therefore a new name is proposed. A preliminary phyletic analysis of *Pistosaurus*, Plesiosauridae, Cryptoclididae, and Elasmosauridae is presented.

INTRODUCTION

The first elasmosaurid plesiosaur from the Cretaceous of the Western Interior was named *Elasmosaurus platyurus* by E. D. Cope in 1869. Since that time, many other specimens have been collected, most notably from the Smoky Hill Chalk Member of the Niobrara Formation and Sharon Springs Member of the Pierre Shale., as well as from various Cretaceous strata in Texas, Nebraska and Colorado. These specimens were named or described by Williston (1890, 1903, 1906), Welles (1943, 1949, 1952), and Welles and Bump (1949). Revision of these elasmosaurs was undertaken by Welles (1962) and Persson (1963), nevertheless, elasmosaur taxonomy remains in disorder because of the inadequacy of type material and crushed skulls. The recent revision of English plesiosaurs by Tarlo (1960), Brown (1981), Taylor (1992), Taylor and Cruickshank (1993), and Storrs (1997) have shown the importance of ontogeny and dimorphism in plesiosaur taxonomy. Applying their methodology to the North American elasmosaurs shows considerably less diversity than recognized by Welles (1962), Persson (1963) and Kuhn (1964).

Traditional methods of elasmosaur taxonomy have relied primarily upon the postcrania, especially length, height and width indices of the vertebrae, presence or absence of the pectoral bar and shape of the distal end of the humerus (Welles, 1952). As Welles (1952, p. 50) admitted, however, vertebral indices change ontogenetically. Brown (1981) noted that the development of the pectoral bar, formed by contact

between the coracoids and scapulae along the midline, was ontogenetically controlled in some taxa of Jurassic plesiosauroids. This point may be illustrated with *Cryptoclidus eurymerus* (Figure 1), represented by the best ontogenetic series of any plesiosaur. However, in elasmosaurids, the presence or absence of this character may have some taxonomic utility as shown below. Finally, the shape of the humerus also changes ontogenetically, a point noted as early as Williston (1903), so it must be used with caution and only in adult individuals.

In his study of Upper Jurassic plesiosauroids, Brown (1981) evaluated 38 characters that had been used in plesiosaur taxonomy and divided them into four categories. Category A consisted of eight characters that were ontogenetic, but may have some generic and specific significance. Category B included six generic and specific characters. Category C included eight characters that had family-group significance and separated phyletic lineages into primitive and advanced grades. Finally, category D encompassed fifteen characters that had phyletic significance in determining plesiosaur evolution. Although Brown attempted to apply his analysis to some of the Cretaceous elasmosaurs from the Western Interior, he was limited to descriptions by Welles (1949, 1952, 1962), resulting in many errors. To rectify this handicap, a new analysis of some of these Cretaceous elasmosaurs was undertaken.

As Brown (1981) has observed, skulls have not been given equal consideration in plesiosaur taxonomy because they are seldom preserved well, as noted by

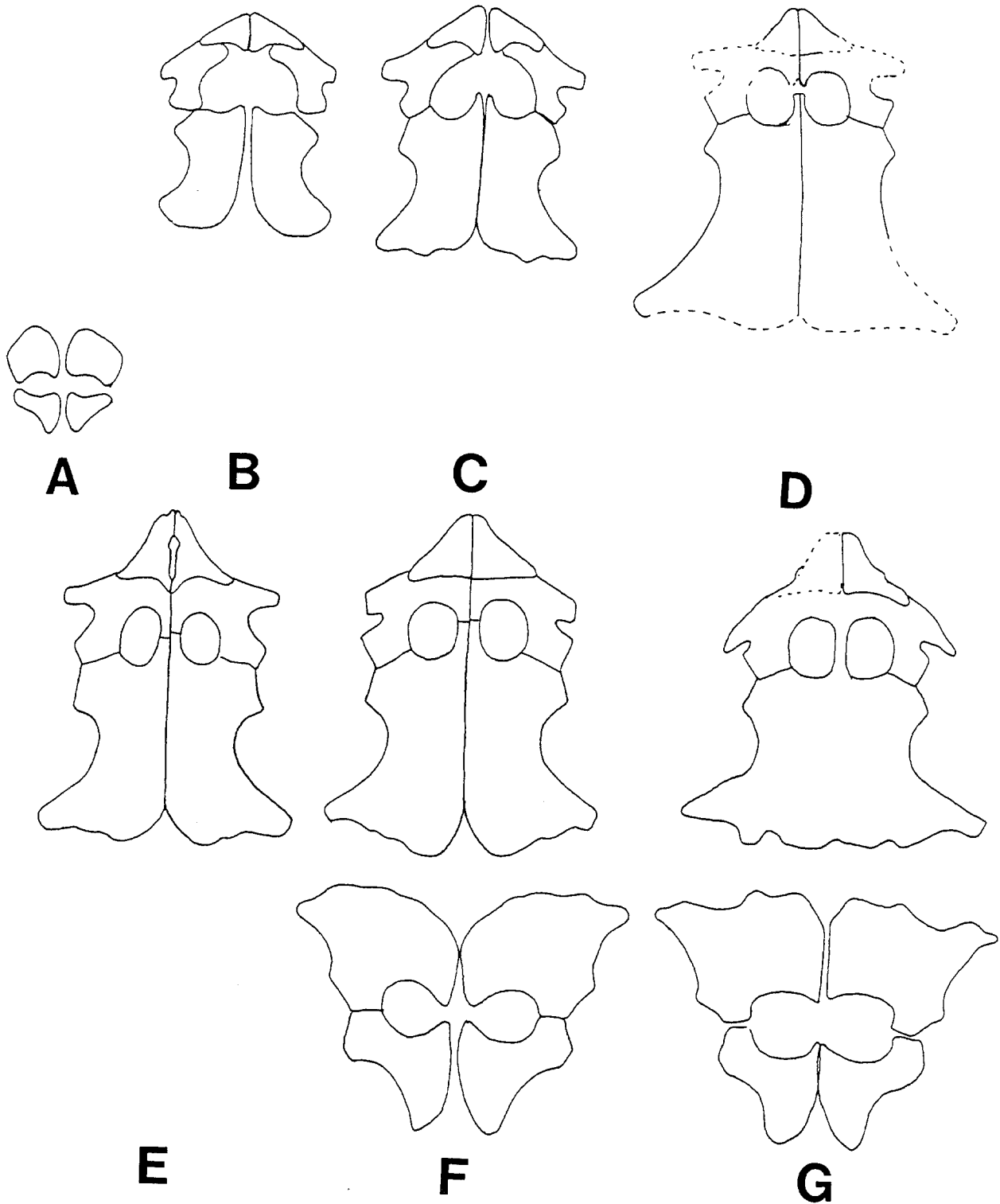


Figure 1. Pectoral and pelvic girdles of *Cryptoclidus eurymerus* showing four growth series: A, very young juvenile (BMNH R2417); B, older juvenile (BMNH R2416); C, subadult (BMNH); D, young adult (BMNH R2412) in which the pectoral bar is almost, but not quite complete; E, F, adult (BMNH R3538, R2616); G, old adult (HMG V1091). Note variation in adult specimens (E, F), including presence of an interclavicle and posterior extension of clavicles along the midline. See Brown (1981) for further discussions. Adapted from Andrews (1910), Seeley (1892), and Smellie (1917). To scale.

Welles (1952). The problem of identifying cranial sutures in elasmosaur skulls was first pointed out by Williston (1890) and reiterated by Cope (1894), Welles (1943, 1952, 1962) and Welles and Bump (1949). The problem is most often due to crushing which produces fractures that mask the sutures. This problem can be compounded by heavy gypsum encrustation in specimens from the Pierre Shale. Fortunately, Welles (1949) briefly described an uncrushed skull that he identified as *Elasmosaurus morgani*, but which was renamed *Libonectes morgani* by Carpenter (1997). Because the skull was preserved in a calcareous nodule, the skull was prepared by me using acetic acid. The skull was then studied with Computer Axial Tomography and X-ray without the problems associated with identifying differences between matrix and bone (Carpenter, 1997). The information thus obtained was used to interpret the crushed elasmosaur skulls below. The geographical location for all the specimens used in this study are shown in Figure 2, and geochronologically in Figures 3; the location for some measurements is shown in Figure 4.

In discussing the vertebral column, I have ceased using the term "pectorals" because it represents a subdivision of the vertebral column not recognized in modern reptiles (see Hoffstetter and Gasc, 1969). Seeley used the term as early as 1874, although it is not certain if he coined the term at this time. The term was used by Andrews (e.g., 1910), Williston (e.g., 1906), Welles (e.g., 1943), and Brown (1981) among others. The term was not used, however, by Sollas (1881) and Tarlo (1960); Swinton (1947) was inconsistent in its use. Neither Carroll (1981) nor Storrs (1991) used the term for nothosaurs, although Sues (1987) did for *Pistosaurus*, the closest sister group to the plesiosaurs. Pectorals have been defined nebulously as "the articulation for the rib is long and oblique, formed partly by the neural arch, partly by the centrum..." (Seeley, 1874), "...[on] one or two vertebrae the [rib-] facets are borne partly on the arch and partly on the centrum; the vertebrae on which this occurs are sometimes called the pectorals... (Andrews, 1910), "...the first pectoral, the [rib] facet has shifted dorsally until it is about half on the transverse process and half on the centrum. The neural arch is now continuous with the rib facet and forms its dorsal lip. The rib facet on the [next vertebra] is almost entirely on the expanded end of the diapophysis, but is still fused ventrally with the centrum. This rib facet is much larger than that of the first pectoral and bears the first long rib" (Welles, 1943).

The most consistent point of these definitions is that the rib facet bridges the centrum-neural arch suture. However, this condition is also seen today in *Sphenodon* (Hoffstetter and Gasc, 1969, Figure 28) and

lizards (DMNH uncataloged varanid skeleton); these animals also have single-headed ribs as in many plesiosaurs. Because these vertebrae are not referred to as "pectorals" in extant lepidosaurs, it seems pointless and disadvantageous to do so in plesiosaurs and puts undue weight on this character phylogenetically. Based on lepidosaurs, the last cervical in elasmosaurs may be defined as the vertebra in which the rib facet (formed by the combined parapophysis and diapophysis) extends across the centrum-neural arch boundary (i.e., the position of the neural arch-centrum suture located near the base of the neural canal). The first dorsal then is the vertebra in which the rib facet overlies the neural arch-centrum suture. Using the neural canal as a landmark, the suture can be approximated when fusion has obliterated all traces of it in mature animals.

Institutional abbreviations: AMNH American Museum of Natural History, New York, NY. ANSP Academy of Natural Sciences, Philadelphia, PA. BMNH British Museum of Natural History, London, GB. DMNH Denver Museum of Natural History, Denver, CO. HMG Hunterian Museum, Glasgow University, Glasgow, GB. KUVVP Kansas University, Vertebrate Paleontology, Museum of Natural History, Lawrence, KS. SMUSMP Southern Methodist University, Shuler Museum of Paleontology, Dallas, TX. SDSM South Dakota School of Mines, Rapid City, SD. UNSM, University of Nebraska State Museum, Lincoln, NE.

SYSTEMATIC PALEONTOLOGY

Superfamily Plesiosauroidea Welles 1943

Family Elasmosauridae Cope 1869

Genus *Elasmosaurus* Cope 1869

Elasmosaurus platyurus Cope 1869

Elasmosaurus platyurus Williston 1903

Elasmosaurus platyurus Williston 1906

Elasmosaurus platyurus Welles 1943

Elasmosaurus platyurus Welles and Bump 1949

Elasmosaurus platyurus Welles 1949

Elasmosaurus platyurus Welles 1952

Elasmosaurus platyurus Welles 1962

Elasmosaurus platyurus Persson 1963

Elasmosaurus platyurus Kuhn 1964

Elasmosaurus platyurus Wiffen and Moisley 1986

Revised Diagnosis--Longest neck of any elasmosaurid, with 72 cervicals, as compared with 63 in *Hydralosaurus serpentinus*, 62 in *Libonectes morgani*, *Thalassomedon hanningtoni*, and *Styxosaurus snowii*, 37 in *Brancaosaurus brancai*, 46 in *Morenosaurus stocki*, 56 in *Callawayasaurus columbiensis*; and 60 in *Hydrotherosaurus alexandrae*.

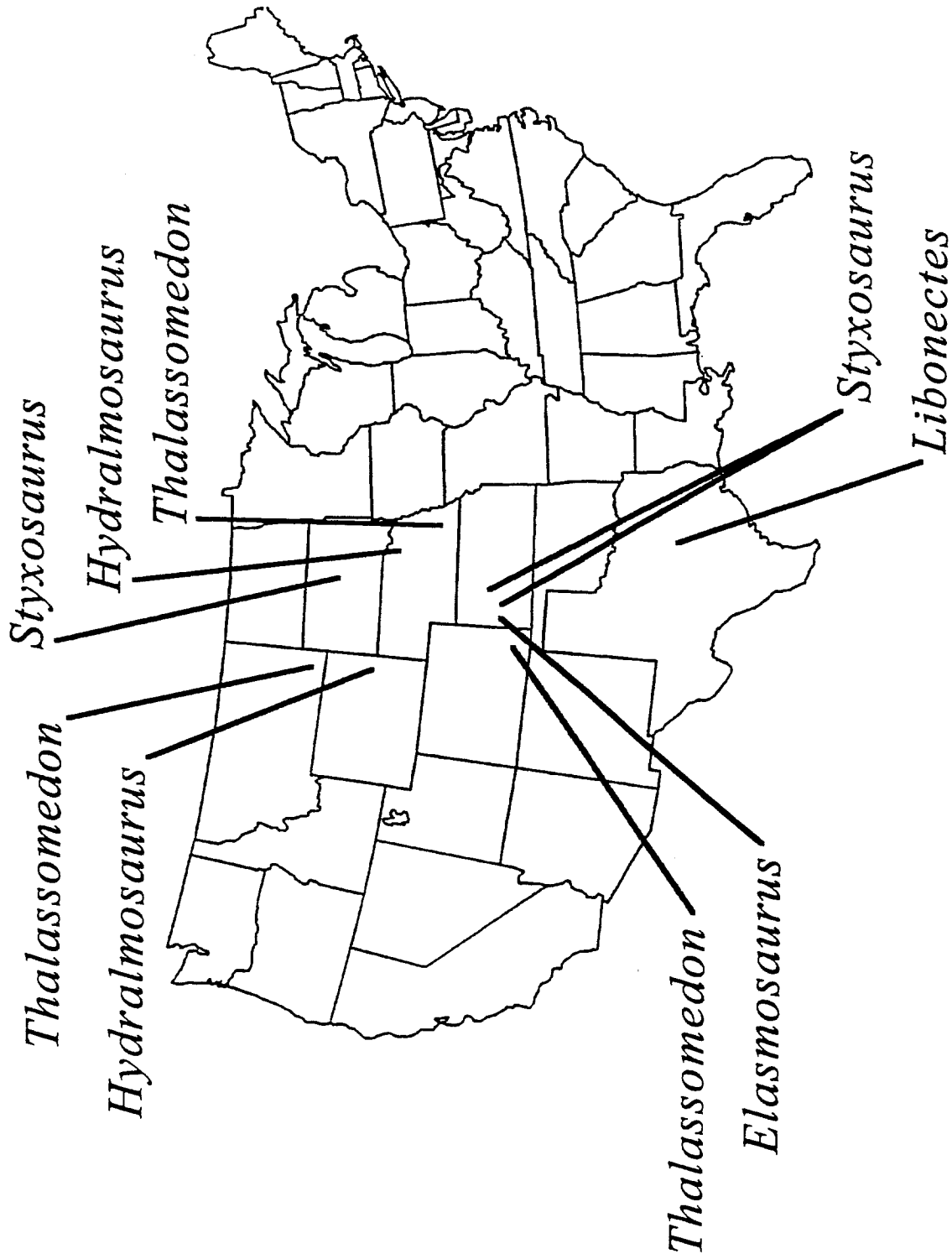


Figure 2. Geographical distribution of specimens from the Western Interior used in this study.

Maastrichtian	
Campanian	<i>Elasmosaurus</i> , <i>Hydralmosaurus</i> , <i>Styxosaurus</i>
Santonian	<i>Hydralmosaurus</i> , <i>Styxosaurus</i>
Coniacian	
Turonian	<i>Libonectes</i>
Cenomanian	<i>Thalassomedon</i>

FIGURE 3. Biostratigraphic distribution of specimens shown in Figure 2. *Elasmosaurus* from the mid-Campanian of Montana (Bearpaw Shales) were not used in this study because they lack skulls.

Atlas-axis long, low as in *S. snowii*, in contrast to short, deep in *L. morgani*, *T. hanningtoni* and *Tuarangisaurus keyesi*; axis postzygapophysis appears not to extend beyond posterior face of centrum as in *T. hanningtoni*. Prominent pectoral and pelvic bar in adult.

Holotype--ANSP 10081 (not ANSP 18001 as reported by Welles, 1952, 1962), tip of snout, occipital condyle, most of an articulated vertebral column.

Type Locality--Sharon Springs Member (lower Campanian), Pierre Shale at McAllister Butte, Logan County, Kansas.

Discussion--The history of the discovery of *Elasmosaurus platyrurus* by Theophilus Turner was presented by Almy (1987), with preservational comments by Cope (1875). Williston (1906) was the first to point out that the pectoral and pelvic girdles of the holotype were missing and recent attempts to relocate them have failed (Arnold Lewis, personal communications, 1984). It is possible that these elements were destroyed last century in New York City. Cope wrote to Turner on July 17, 1868, that Waterhouse Hawkins was going to reconstruct *Elasmosaurus* as part of the Paleozoic Park project (Almy 1987). Hawkins had previously been involved in the life restorations of prehistoric animals at Crystal Palace in England, and Paleozoic Park was to be America's version in Central Park, New York City. That project was brought to a violent end on May 3, 1871 (Colbert, 1959; Ryder 1988) with all of Hawkins' work destroyed and buried. It is possible that

the girdles were on loan to Hawkins at the time and suffered the same fate as the sculptures, although if true, it is interesting that Cope said nothing about the loss in his 1875 redescription of *Elasmosaurus*.

The pectoral girdles have played an important role in the taxonomy of *Elasmosaurus*. E.D. Cope (1969) presented the first version, that Welles (1952) noted was probably not correct, and over the years presented three different versions himself (Welles 1943, 1949, 1952). Cope (1869, p. 45) stated that the scapula forms about a third of the glenoid, but illustrated it (Cope 1869, Figure 7) as not contributing to it at all. In addition, Cope (1869, p. 45) stated that the "form of the glenoid cavity cannot be readily ascertained from the absence of the scapula. What we have of it..." implying that the element was not complete. Indeed, only a small portion of the right scapula is shown by Cope (1869, Figure 7 in ventral view). How Cope determined the shape of the left scapula, shown complete, is not known, unless it was based on an impression of the right scapula in the rock. Certainly the left coracoid is a mirror of the right, so the possibility that the left scapula is a mirror of the impression of the right is plausible. The problems with Cope's description and illustration of the pectoral girdle are contradictions that I am unable to rectify. Therefore, until the holotype girdles are found and their exact morphology re-examined, I have (Carpenter 1997) restricted the name, *Elasmosaurus platyrurus*, to the remaining parts of holotype ANSP 10081.

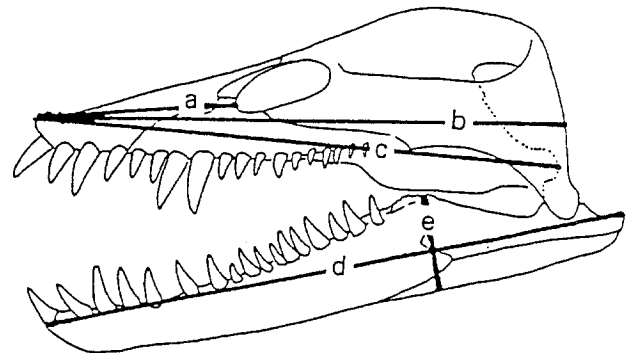


Figure 4. Location of measurements given in Table 1.

Welles (1949) based his diagnosis of *Elasmosaurus* on the pectoral girdle of "*E. morgani*" and on Cope's illustrations of the pectoral girdle of *E. platyrurus*. He defined the genus as having a pectoral bar along the midline joining the scapula to the coracoids, and later defined the subfamily Elasmosaurinae on this feature (Welles 1962). However, I do not accept it as a unifying character between the two specimens because the atlas-axis is

TABLE 1. Cranial comparative measurements (in cm) of elasmosaurs (see Figure 4 for location of measurements).

	a	b	c	d	e
<i>Hydralmosaurus serpentinus</i> (AMNH 5835)	13.5	40.4	-	-	7.5
<i>Libonectes morgani</i> (SMUSMP 69120)	18	45.9	46.6	-	7
<i>Styxosaurus snowii</i> (KUVS 1301)	17.5	-	42	48	7.5
(SDSM 451)	15	-	38.8	44	6.6
<i>Thalassomedon hanningtoni</i> (DMNH 1588)	18.8	51	48	62.5	7.5
(UNSM 50132)	50	-	-	-	-

short and deep in "*E.*" *morgani* and long and low in *E. platyurus* (Figure 5). As a result of this and other differences, "*E.*" *morgani* was renamed *Libonectes morgani* (Carpenter 1997).

The large size of the holotype of *Elasmosaurus platyurus* and complete fusion of the neural arches to the centra show that the specimen is of an adult. The apparent presence of the pectoral bar in this specimen (Figure 6A) based on Cope's statements, and its absence in the equally large holotype specimen of *Hydralmosaurus serpentinus* (Figure 6B) suggests that the bar is not totally ontogenetically controlled and that it has some taxonomic utility in elasmosaurs.

Hydralmosaurus Welles 1943

- Hydralmosaurus serpentinus* (Cope 1877)
- Elasmosaurus serpentinus* Cope 1877
- Elasmosaurus serpentinus* Williston 1903
- Elasmosaurus serpentinus* Williston 1906
- Elasmosaurus sergentinus* Watson 1924
- Hydralmosaurus serpentinus* Welles 1943
- Hydralmosaurus sergentinus* Welles 1949
- Hydralmosaurus serpentinus* Welles and Bump 1949
- Hydralmosaurus serpentinus* Welles 1952
- Styxosaurus browni* Welles 1952
- Hydralmosaurus serpentinus* Persson 196
- Hydralmosaurus serpentinus* Welles 1962
- Styxosaurus browni* Welles 1962
- Hydralmosaurus serpentinus* Persson 1963
- Styxosaurus browni* Persson 1963
- Hydralmosaurus serpentinus* Kuhn 1964
- Styxosaurus browni* Kuhn 1964

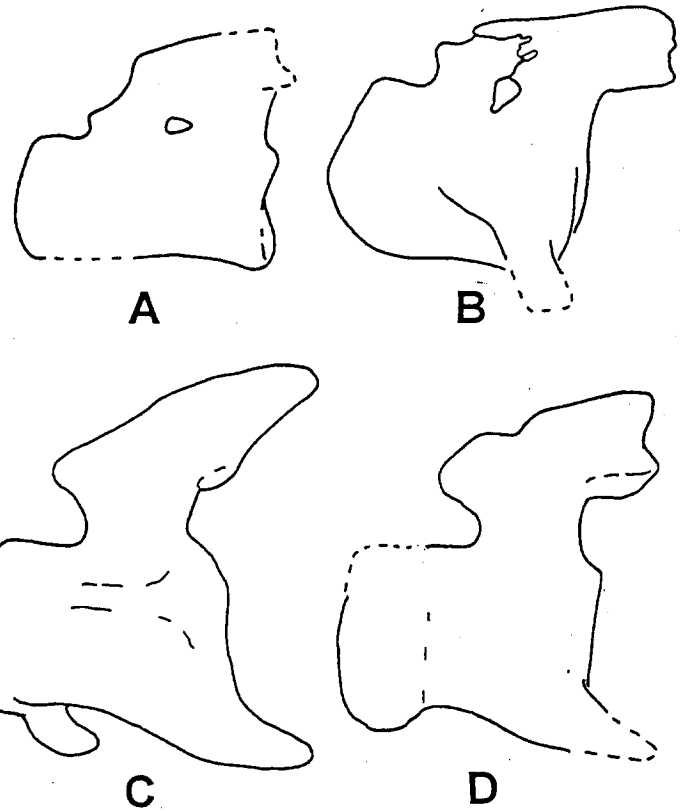


Figure 5. Comparison of the atlas-axis complex of A, *Elasmosaurus platyurus*, ANSP 10081; B, *Libonectes morgani*, SMUSMP 69120, C, *Thalassomedon hanningtoni*, DMNH 1588; D, *Tuarangisaurus keyesi* (from Wiffen and Moislley, 1986).

Revised Diagnosis--An elasmosaur with 63 cervicals compared with 62 in *Libonectes morgani*, *Thalassomedon hanningtoni*, and *Styxosaurus snowii*, 37 in *Brancaesaurus brancai*, 46 in *Morenosaurus stocki*, 56 in *Callawayasaurus columbiensis*, 60 in *Hydrotherosaurus alexandrae*, and 72 in *Elasmosaurus*

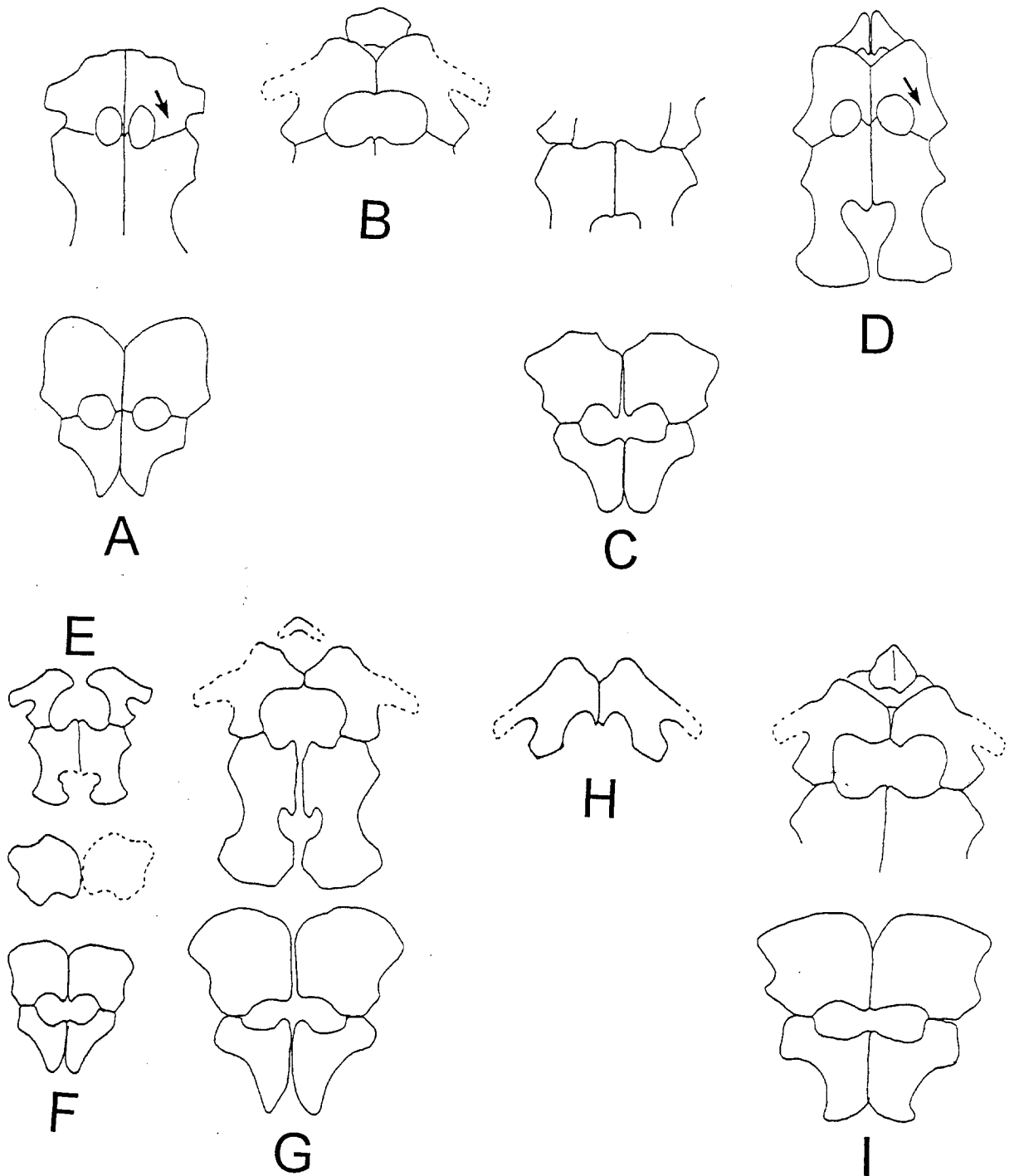


Figure 6. Comparison of elasmosaurid pectoral and pelvic girdles. A, *Elasmosaurus platyurus* pectoral (top) and pelvic (bottom) girdles as drawn by Cope (1865); B, *Hydralmosaurus serpentinus* adult pectoral girdle (AMNH 5835, holotype *Styxosaurus browni*); C, *Hydralmosaurus serpentinus* adult pectoral and pelvic girdles (AMNH 1495, holotype *Hydralmosaurus serpentinus*); D, *Libonectes morgani* pectoral girdle; *Styxosaurus snowii* growth series: E, juvenile pectoral girdle and pubis (YPM 1644 holotype of *Thalassiosaurus ischiadicus*); F, pelvic girdle (YPM 1130, holotype *Alzadasaurus kansasensis*); G, young adult pectoral and pelvic girdles (SDSM 451, holotype *Alzadasaurus pembertoni*); H, adult scapulas (YPM 1645, holotype *Thalassonomosaurus marshi*); I, *Thalassomedon hanningtoni* pectoral and pelvic girdles (DMNH 1588) To scale; modified from Welles 1952.

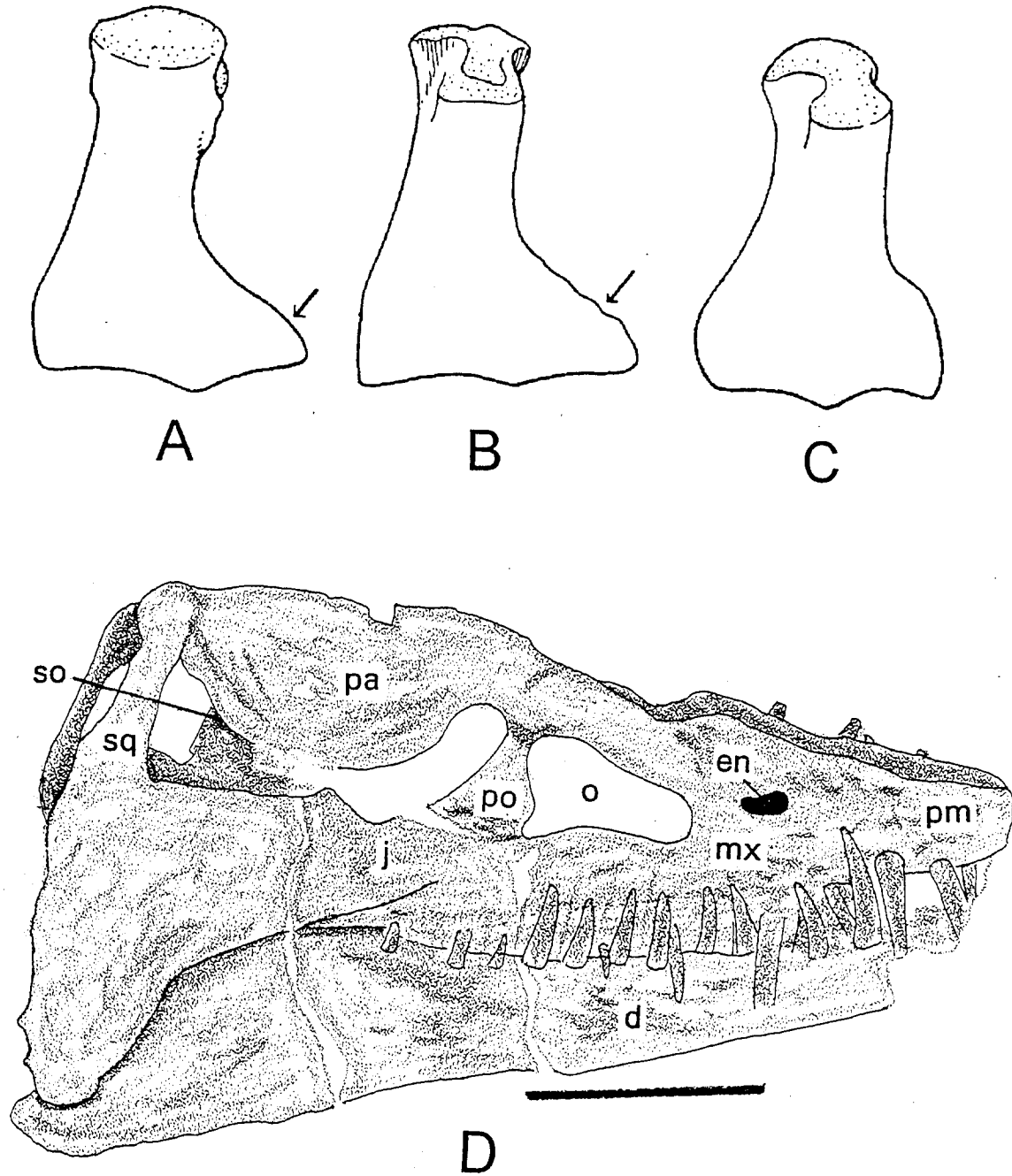


Figure 7. Comparison of humeri: *Hydralmosaurus serpentinus* A, AMNH 1495, B, AMNH 5835, and C, more typical elasmosaur humerus of *Styxosaurus snowii* SDSM 451. D, skull *Hydralmosaurus serpentinus* AMNH 5835. Abbreviations for this and other skull figures: a - angular; ar - articular; bo - basioccipital; bs - basisphenoid; cc - calcified cartilage; d - dentary; ec - ecompterygoid; en - external nares; ep - epipterygoid; f - frontal; fm - foramen magnum; j/ju - jugal; in - internal nares; ipf - interpterygoid fenestra; mx - maxilla; nf - nutrient foramen; o - orbit; oe - opisthotic; pa - parietal; pal - palatine; pf - prefrontal; pm - premaxilla; po - postorbital; pp - paroccipital process; pr - prootic; ps - parasphenoid; pt - pterygoid; q - quadrate; qpt - quadrate process of the pterygoid; ra - retroarticular; rt - replacement teeth; sa - surangular; so - supraoccipital; sof - suborbital fenestra; sp - splenial; sq - squamosal; sr - sclerotic ring; stf - subtemporal fenestra; tf - temporal fenestra; v - vomer; V - trigeminal foramen.

platyurus. Humerus of adult with pronounced posterior expansion on distal end unlike all other elasmosaurs. No pectoral or pelvic bar present in adults.

Holotype--AMNH 1495, partial skeleton, including most of the cervical column, pectoral and pelvic girdles, flippers.

Type Locality--Smoky Hill Chalk Member, Niobrara Formation (Santonian?), Cedar County, Nebraska.

Referred Specimen--AMNH 5835, anterior portion of a skeleton from the Sharon Springs Member (lower Campanian), Pierre Shale, Red Bird, Niobrara County, Wyoming (Barnum Brown, unpublished notes). Holotype of *Styxosaurus browni* Welles 1952, incorrectly reported as from the Niobrara Formation of Edgemont, South Dakota.

Description--The skull (Figure 7D) has five premaxillary teeth as with the skull of *Libonectes morgani*, not four as reported by Welles (1952). The number of maxillary teeth is difficult to determine owing to preservation and occlusion of the lower jaws. Welles (1952) reported 13 teeth, although I suspect that more were present (see below). At least 17 dentary teeth and alveoli are visible, but again, this number probably does not reflect the total number. The poor preservation makes it difficult to determine the maxillary tooth position over which the external nares lies. Skull measurements are presented in Table 1.

The holotype has a nearly complete cervical series of 56 vertebrae. Cope (1877) thought that two or three additional vertebrae may have been present at one time at the anterior of the series, although he gave no reason. Welles (1943), however, stated that originally there were 63 cervicals, but later modified this to possibly 58 (Welles 1952). As Welles (1952) noted, portions of the neck were disarticulated and the sequence of the vertebrae uncertain. Based on AMNH 5835, the number of cervicals was probably 63.

Welles (1952) used the presence of concavities on the lateral sides of the cervical centra as a diagnostic character for *Styxosaurus browni*. This feature, however, is most likely due to crushing of the cancellous bone based on observations of an articulated series of elasmosaur cervicals found in the same area as *Styxosaurus browni* (Carpenter, field notes). The vertebrae of this other elasmosaur contained in a septarian nodule, lack the lateral concavity, whereas those projecting into the surrounding shales showed this feature. Shuller (1950) illustrated thin sections of *Libonectes* elements showing the extremely well developed cancellous bone in elasmosaurs. It therefore appears that the presence of lateral concavities on the

cervical centrum of *Hydralmosaurus* have no taxonomic value, contrary to Welles (1952).

Other differences between the holotype and referred skeletons are most probably due to sexual dimorphism. Welles (1952) has noted that the cervicals of AMNH 1495 are proportionally broader than those of AMNH 5835, implying that the cervicals are more robust. As Welles (1962) has noted, sexual dimorphism in elasmosaurs is expressed by robustness. A similar condition is known among dinosaurs (e.g., Raath 1990, Carpenter 1990) and many extant reptiles (Fitch 1981). But unlike Welles (1962), I consider the robust form to be the female as in many extant reptiles. The girdles of *Hydralmosaurus* are shown in Figure 6B,C.

Discussion--Cope reported that the holotype was "discovered in the blue shale of Cretaceous No. 3, in a bluff in Nebraska, on the southwest side of the Missouri [River], between Sioux City, Iowa, and Yankton, [South] Dakota" (Cope 1877, p. 583). This information places the locality downstream of the type locality for the Niobrara Formation. Meek and Hayden (1861) had previously defined Cretaceous Number 3 along the Missouri River as the Niobrara Formation. The Smoky Hill Chalk along the Missouri River is a light gray (Condra and Reed 1959), giving it a bluish appearance when weathers. It is most probable, then, that Cope's "blue shale" is the Smoky Hill Member of the Niobrara Formation. Recently, Merewether and Cobban (1981) determined that the Niobrara at the type locality was Santonian in age.

The referred specimen, AMNH 5835, was incorrectly reported by Welles (1952) as coming from the Niobrara Formation of Edgemont, South Dakota. Field records by Barnum Brown show that the specimen actually comes from the Sharon Springs Member of the Pierre Shale at Red Bird, Wyoming. The specimen shares with the holotype the unusual posterior expansion of the distal end of the humerus (Figure 7A, B). This feature is not ontogenetic because it does not occur in any other adult-sized elasmosaur. This specimen also has a badly crushed skull (Figure 7D), which suffers from the deteriorating effects of gypsum as with many vertebrates from the Sharon Springs Member of the Pierre Shale. Only the right side of the skull has been prepared. I find no justification for most of the sutures shown by Welles (1952). Furthermore, my interpretation of the maxillary-jugal suture behind the orbits differs from that of Welles, being more like that seen in *Libonectes morgani*. Crushing has pushed the parietals up so that the lower border is visible (Figure 6D). Owing to poor preservation and incomplete preparation of the specimen, potential description of the skull is limited.

Libonectes morgani (Welles, 1949)

Libonectes morgani (Welles 1949)

Elasmosaurus morgani Welles 1949

Elasmosaurus morgani Welles 1952

Elasmosaurus morgani Welles 1962

Elasmosaurus morgani Persson 1963

Elasmosaurus morgani Kuhn 1964

Elasmosaurus morgani Wiffen and Moisley 1986

Diagnosis--Elasmosaurid with 62 cervicals as in *Thalassomedon hanningtoni* and *Styxosaurus snowii*, differs from 37 cervicals in *Brancasaurus brancai*, 46 in *Morenosaurus stocki*, 56 in *Callawayasaurus columbiensis*; 60 in *Hydrotherosaurus alexandrae*, 63 in *Hydralmosaurus serpentinus* and 72 in *Elasmosaurus platyurus*. Atlas-axis centrum short, deep as in *T. hanningtoni* and *Tuarangisaurus keyesi*, not long, low as in *E. platyurus*; neural spine of atlas-axis low as in *E. platyurus*, not tall as in *T. hanningtoni* and *T. keyesi*; axis postzygapophyses extending well beyond posterior face of centrum as in *T. keyesi*, unlike *E. platyurus* and *T. hanningtoni*. External nares over maxillary teeth 3 and 4 in *Libonectes morgani*, but over maxillary teeth 2 and 3 in *T. keyesi*, maxillary teeth 4 and 5 in *T. hanningtoni*, and maxillary tooth 6 in *S. snowii*. Pectoral bar present in adult.

Holotype--SMUSMP 69120: skull, most of the cervicals, gastralia, and gastroliths. The pectoral girdle and forelimb were apparently discarded long ago (Storrs 1981).

Type Locality--Britton Formation (lower Turonian), Eagle Ford Group, near Cedar Hill, Dallas County, Texas.

Description--The holotype skull of *Libonectes morgani* is the least crushed of any known specimen of elasmosaur skull (Figures 8, 9) and was described in great detail elsewhere (Carpenter, 1997).

There are 5 premaxillary teeth as in most plesiosaurs (Brown 1981). However, there are 14 teeth in each maxilla, not 9 in the right and 8 in the left as originally stated by Welles (1949). Furthermore, there are 18 teeth in the right dentary and 19 in the left, not 16 in the right and 15 in the left (Welles 1949). These differences in tooth count show that mechanical preparation alone may not reveal the correct number of teeth in a skull that has the lower jaws in occlusion. The preorbital region of the skull is formed by the large premaxillaries and large, triangular maxillaries. The dorsal process of the premaxilla separates the frontals

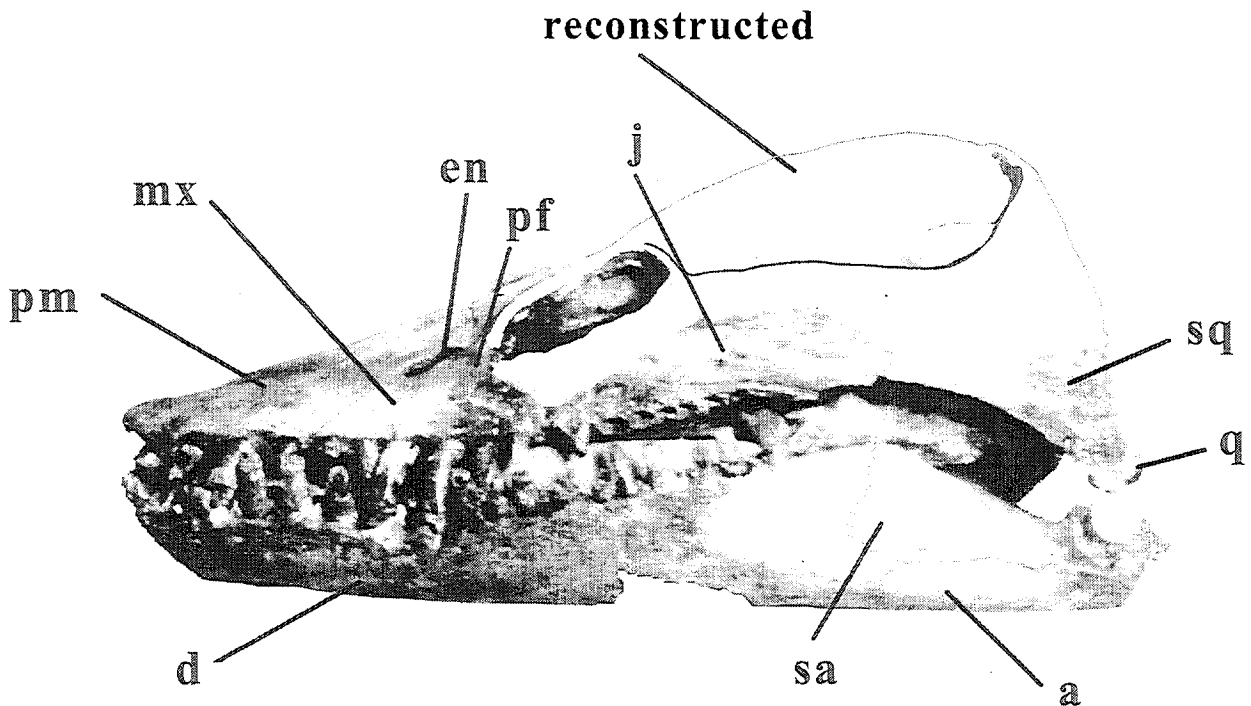


Figure 8. Skull of *Libonectes morgani*, SMUSMP 69120 in left lateral view. Scale 10 cm. See Figure 7 for abbreviations.

to contact the parietals above the orbits. In the primitive elasmosaur *Brancaesaurus brancai*, the frontals are apparently not separated (Wegner 1914), although this is not known for certainty because of fractures. The trend towards separating the frontals by the premaxilla occurs incipiently in *Plesiosaurus dolichodeirus* (Storrs, 1997).

The maxilla extends well posterior of the orbits and has alveoli for most of its length. The maxillary-jugal suture is oblique, and the jugals formed most of the lower edge of the orbits as they do in *S. snowii*. The sutural contact of the jugal with the squamosal is unknown in *L. morgani*, but in *S. snowii* it almost divides the temporal bar obliquely in half (Williston 1903) and vertically in half in *Thalassomedon*. The squamosal covers the quadrate laterally, having replaced the quadratojugal in this role. The quadratojugal is not present, having been lost with the elimination of the lower diapsid temporal bar (Carpenter, 1997). The top of the parietals is missing, so that the height of the sagittal crest is unknown. Welles (1949) identified a slit on the skull between the orbits as the pineal foramen. However, further preparation has shown this slit to be part of the premaxillary-parietal suture. The frontals are incomplete in the holotype but they apparently formed the dorsal rim of the orbit.

In palatal view, the premaxillaries form a V, with the large, diamond-shaped vomers between them. The palatines are rectangular plates that lay between the alveolar portion of the maxillae and pterygoids. The pterygoids are elongate and taper forwards to contact the vomer. Laterally, they contact the ecotpterygoids, which form the anterior edge of the subtemporal fenestrae. A detailed description of the braincase is given elsewhere (Carpenter, 1997).

Discussion--All that remains of the holotype specimen now is the skull, most of the cervicals, gastralia, and gastroliths (Storrs 1981). The pectoral girdle and forelimb were apparently discarded long ago, so discussion of these bones is confined to information provided by Welles (1949, 1962). The holotype specimen was originally described by Welles (1949) under the name *Elasmosaurus morgani*. Referral to the genus *Elasmosaurus* was based primarily upon the presence of a median pectoral bar. Welles (1962) later used this median bar to define the subfamily Elasmosaurinae but I find no justification for such a distinction and have abandoned it. Furthermore, because the genus and species name, *Elasmosaurus platyurus*, is restricted to the surviving holotype material as discussed above, the holotype of "*Elasmosaurus*" *morgani* (SMUSMP 69120) was left in need of a name, for which *Libonectes morgani* was proposed (Carpenter, 1997).

Styxosaurus Welles 1943

- Styxosaurus snowii* (Williston 1890)
- Cimoliosaurus snowii* Williston 1890
- Cimoliosaurus snowii* Cope 1894
- Cimoliosaurus snowii* Williston 1903
- Elasmosaurus ischiadicus* Williston 1906 (in part)
- Elasmosaurus snowii* Williston 1906
- Elasmosaurus marshi* Williston 1906
- Styxosaurus snowii* Welles 1943
- Thalassiosaurus ischiadicus* Welles 1943
- Thalassonomosaurus marshi* Welles 1943
- Styxosaurus snowii* Welles 1949
- Alzadasaurus pembertoni* Welles and Bump 1949
- Alzadasaurus kansasensis* Welles 1952
- Alzadasaurus pembertoni* Welles 1952
- Styxosaurus snowii* Welles 1952
- Thalassiosaurus ischiadicus* Welles 1952
- Thalassonomosaurus marshi* Welles 1952
- Alzadasaurus pembertoni* Welles 1962
- Alzadasaurus kansasensis* Persson 1963
- Alzadasaurus pembertoni* Persson 1963
- Styxosaurus snowii* Persson 1963
- Thalassiosaurus ischiadicus* Persson 1963
- Thalassonomosaurus marshi* Persson 1963
- Alzadasaurus kansasensis* Kuhn -1964
- Alzadasaurus pembertoni* Kuhn 1964
- Styxosaurus snowii* Kuhn 1964
- Thalassiosaurus ischiadicus* Kuhn 1964
- Thalassonomosaurus marshi* Kuhn 1964
- Styxosaurus snowii* Wiffen and Moisley 1986

Revised Diagnosis--Elasmosaurid with 62 cervicals as in *Thalassomedon hanningtoni* and *Libonectes morgani*, compared with 37 cervicals in *Brancaesaurus brancai*, 46 in *Morenosaurus stocki*, 56 in *Callawayasaurus columbiensis*; 60 in *Hydrotherosaurus alexandrae*, 63 in *Hydralmosaurus serpentinus* and 72 in *Elasmosaurus platyurus*. Atlas-axis centrum long, low as in *E. platyurus*, not short, deep as in *L. morgani*, *T. hanningtoni* and *Tuarangisaurus keyesi*. External nares over maxillary tooth 6-7, but over maxillary teeth 2 and 3 in *Tuarangosaurus*, maxillary teeth 3 and 4 in *L. morgani*, maxillary teeth 3 and 5 in *T. hanningtoni*. No pectoral or pelvic bar in adults.

Holotype--KUVF 1301, complete, laterally crushed skull with first 28 cervicals.

Type Locality--Hell Creek, Logan County, Kansas. *Spinapytychus sternbergi* or *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

Referred Specimens--KUVF 434 seven caudals, two ilia, two ischia, two sacral ribs, and partial femur (holotype of *Thalassiosaurus ischiadicus*, Welles

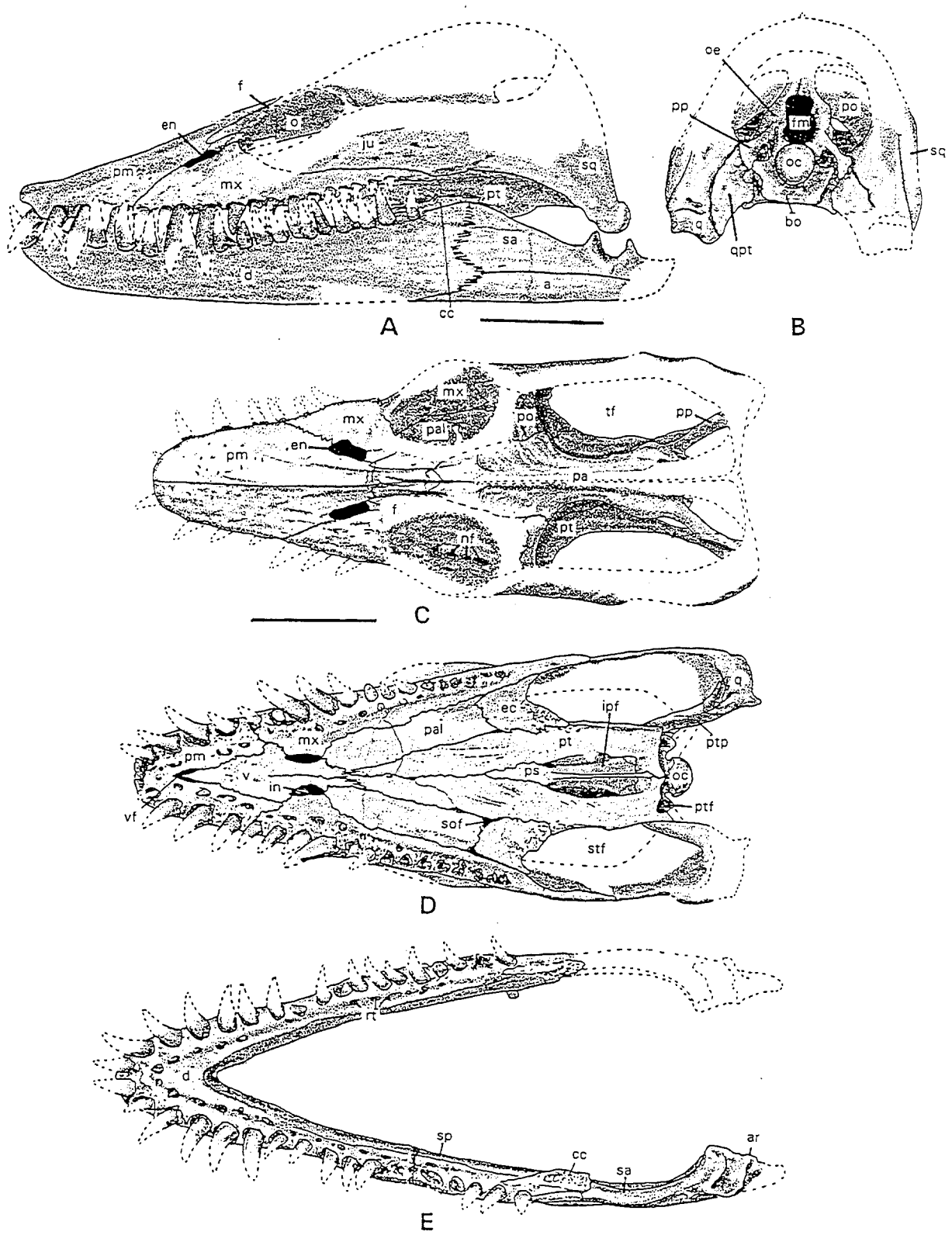


Figure 9. Skull of *Libonectes morgani*, SMUSMP 69120 in left lateral (A), posterior (B), dorsal (C), and ventral (D) views. Lower jaws in dorsal (occlusal) view (E). See Figure 7 for abbreviations.

1943). Plum Creek, Logan County, Kansas; *Spinaptychus sternbergi* or *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

SDSM 451 nearly complete skeleton (holotype of *Alzadasaurus pambertoni*); Sharon Springs Member (lower Campanian), Pierre Shale, Missouri River, Lyman County, South Dakota.

USNM 11910 posterior cervicals, dorsals, sacrals, caudals, and pelvis; Smoky Hill River, Logan County, Kansas; *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

YPM 1130 partial vertebral column, pelvic girdle, complete rear paddle (holotype of *Alzadasaurus kansasensis*; probably along the Smoky Hill River, Wallace County, Kansas; *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

YPM 1644 partial vertebral column, including cervicals and dorsals, pectoral girdles, humerus, and pubis; Plum Creek, Logan County, Kansas; *Spinaptychus sternbergi* or *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

YPM 1645 scapula, vertebrae and forelimb (holotype of *Thalassonomosaurus marshii*). Logan County, Kansas; *Spinaptychus sternbergi* or *Hesperornis* zone (Stewart 1990), upper Smoky Hill Chalk Member (basal Campanian), Niobrara Formation.

Description--The two skulls are shown in Figure 10. Except for possibly the premaxillary-maxillary suture at the tooth row, I am unable to find any sutures in the skull of SDSM 451 due to damage of the bone by gypsum. There is certainly no justification for the sutures shown by Welles and Bump (1949). Cranial measurements are given in Table 1. On the basis of the revised tooth count for *Libonectes morgani*, I doubt that Welles and Bump are correct that there are only four premaxillary teeth and eleven maxillary teeth. I suspect that there are five premaxillary teeth as in all other plesiosaurs, and more than eleven maxillary teeth. Welles and Bump reported 61 cervical vertebrae for SDSM 451, but I count 62; I am unable to account for this discrepancy. The atlas-axis complex is poorly preserved, nevertheless, it closely resembles that of *Elasmosaurus platyurus* in being long and low. However, it is doubtful that SDSM 451 is *Elasmosaurus platyurus* because it has fewer cervicals, and because the ventral process of the scapula is thinner (narrower) than in *E. platyurus* (Figure 4A, F). The validity of this latter character in taxonomy was discussed by Brown (1981).

Discussion--The skull of *Styxosaurus snowii* was the first of an elasmosaurid described (Williston 1890 as *Cimoliosaurus snowii*; see Figure 10A). The specimen has numerous fractures that make it difficult to delineate the sutures as can be seen by the different renditions of the skull by Cope (1894), Williston (1890, 1903) and Welles (1952). Welles (1952) proposed the genus *S. snowii* for the skull, but later concluded that the specimen was not diagnostic (Welles 1962). However, comparing the skull with *Libonectes morgani* does show some distinctive features. The external nares in *L. morgani* are above the two largest teeth (numbers 3 and 4) in the maxilla, whereas in *S. snowii*, it is considerably behind them (number 6). There may be more lateral expression of the quadrate in *S. snowii* than in *L. morgani*. This difference is based on Cope's and Williston's account of the left side of the skull which is not available to me because of the manner in which it is displayed.

Williston (1906) referred a partial, juvenile skeleton (YPM 1644) to *Elasmosaurus snowii*, that Welles (1952) later referred to *Thalassiosaurus ischiadicus*. However, I accept Williston (1906) as the first reviser under the Principle of the First Reviser (ICZN 1985, Art. 24) despite his work preceding 1931. Therefore, I accept his original designation because the holotype of *Thalassiosaurus ischiadicus* is of a very young animal that is most likely a juvenile of *Styxosaurus snowii* (see further discussions below).

A third specimen collected in the same general vicinity named *Elasmosaurus marshii* by Williston (1906), was placed in a new genus, *Thalassonomosaurus marshii*, by Welles (1952). Another specimen (YPM 1130) from near the top of the Smoky Hill Chalk was referred to *Elasmosaurus ischiadicus* by Williston (1906), but was named *Alzadasaurus kansasensis* by Welles (1952). Another species of *Alzadasaurus*, *A. pambertoni*, was named by Welles and Bump (1949) based on a skeleton (SDSM 451) with a very badly damaged skull (Figure 10B,C). The species *A. pambertoni* was referred to the genus *Alzadasaurus* primarily on the pectoral girdle and proportions of the humerus. I consider all of these specimens *Styxosaurus snowii* because none of the criteria used by Welles are valid based on the work of Brown (1981). The paratype and the referred specimens, including the holotypes of *Thalassiosaurus ischiadicus*, *Thalassonomosaurus marshii*, *Alzadasaurus kansasensis*, and *Alzadasaurus pambertoni*, are here considered to belong to *Styxosaurus snowii* on stratigraphic and morphological grounds. All of the specimens, except SDSM 451 (holotype of *Alzadasaurus pambertoni*), came from the *Spinaptychus sternbergi* and *Hesperornis* zones in the uppermost part of the Smoky Hill Chalk Member of the

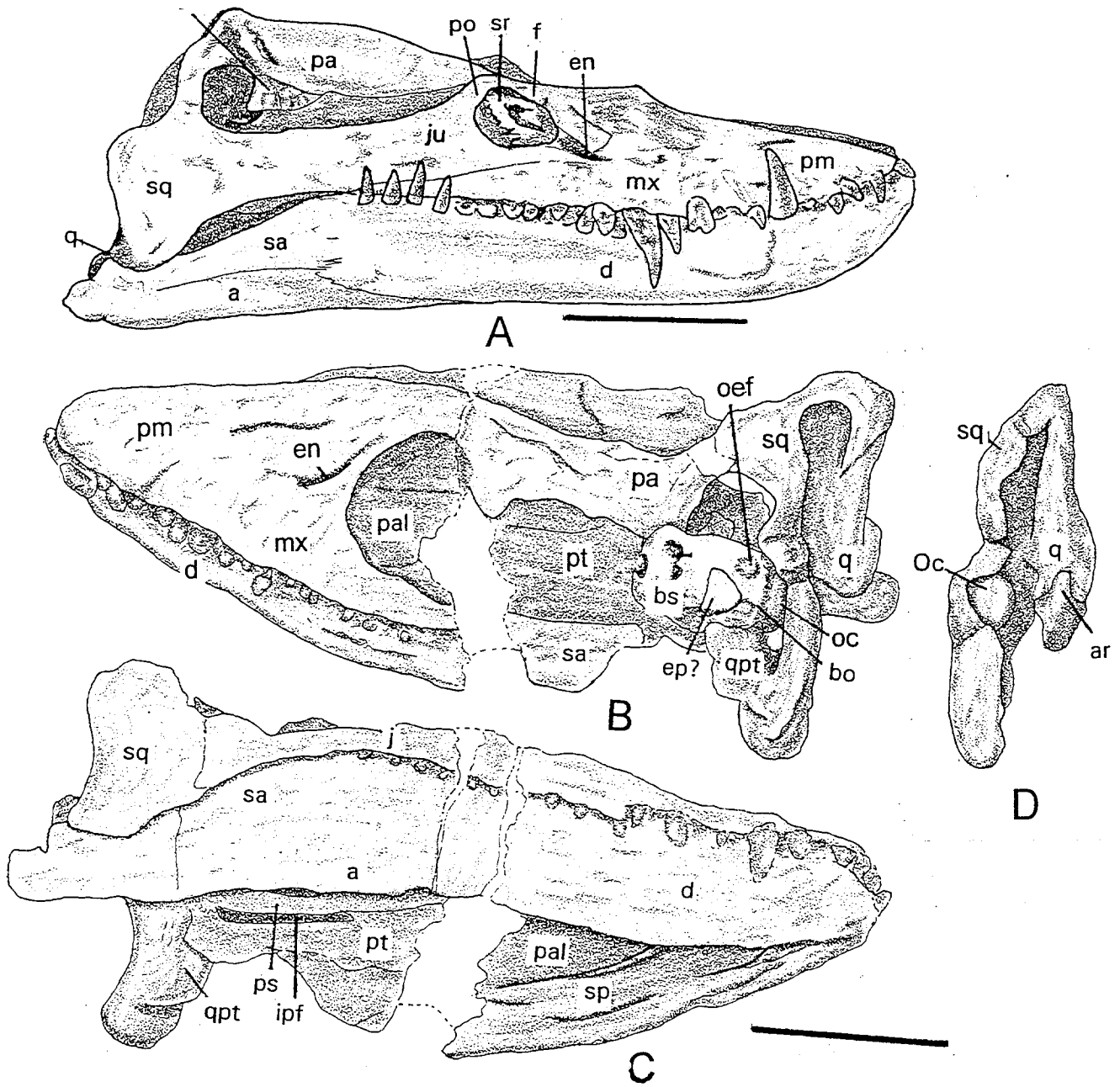


Figure 10. Skulls of *Styxosaurus snowii*: A, KUVP 1301 in right lateral view; SDSM 451 in B, left lateral, C right lateral and D, posterior views. Scale = 10 cm. See Figure 7 for abbreviations.

Niobrara Formation in Kansas; the holotype of *Styxosaurus snowii* is from there also. None of the specimens with propodials show the expanded distal end as in *Hydralmosaurus serpentinus*, and all probably represent a single distinct morph. The differences in size most likely reflect ontogenetic differences based on the work of Brown (1981). Ontogenetic changes in the pectoral and pelvic girdles of a plesiosaur can be illustrated by those of *Cryptoclidus eurymerus* for which a good growth series is known as discussed above. The same elements of the specimens referred to *Styxosaurus snowii* can be arranged by size into a similar ontogenetic series (Figure 6E-H).

The inclusion of SDSM 451 (holotype of *Alzadasaurus pambertoni*), into this growth series of *Styxosaurus snowii*, is justifiable because I find no differences, other than preservational, between its skull and that of the holotype, KUVF 1301 (see below). In addition, the postcrania more closely resembles that of the referred specimens than of *Hydralmosaurus serpentinus*; the propodials lack the distinctive distal expansion of *H. serpentinus*. Although SDSM 451 comes from the Sharon Springs Member of the Pierre Shale, whereas all the other specimens of *S. snowii* come from the top of the Smoky Hill Chalk, this does not invalidate placing it in the ontogenetic series. That is because there are greater changes between the different biostratigraphic zones of the Smoky Hill Chalk, than between the upper Smoky Hill Chalk and Sharon Springs.

Thalassomedon hanningtoni Welles 1943

Thalassomedon hanningtoni Welles 1943
Elasmosaurus serpentinus Riggs 1939
Thalassomedon hanningtoni Welles 1943
Alzadasaurus riggsi Welles 1943
Thalassomedon hanningtoni Welles 1952
Alzadasaurus riggsi Welles 1962
Thalassomedon hanningtoni Welles 1962
Alzadasaurus riggsi Persson 1963
Thalassomedon hanningtoni Persson 1963
Alzadasaurus riggsi Kuhn 1964
Thalassomedon hanningtoni Kuhn 1964

Revised Diagnosis--Skull differs from that of *Libonectes morgani*, *Hydralmosaurus serpentinus*, and *Styxosaurus snowii* in longer supratemporal fossa relative to skull length; external nares above maxillary teeth 3-5, over maxillary teeth 6-7 in *S. snowii*, over teeth 2 and 3 in *Tuarangosaurus keyesi*, and teeth 3 and 4 in *L. morgani*. External nares circular, not elongate as in *Hydralmosaurus* and *Libonectes*. 62 cervicals as in *S. snowii* and *L. morgani*, compared to 37 cervicals in *Brancasaurus brancai*, 46 in *Morenosaurus stocki*, 56

in *Callawayasaurus columbiensis*; 60 in *Hydrotherosaurus alexandrae*, 63 in *Hydralmosaurus serpentinus* and 72 in *Elasmosaurus platyurus*. Atlas-axis centrum short, deep as in *L. morgani* and *T. keyesi*, not long, low as in *E. platyurus* and *S. snowii*. No pectoral or pelvic bar in adults.

Holotype--DMNH 1588 nearly complete skeleton with crushed skull.

Type Locality--Graneros Shale (lower Cenomanian) near Pritchett, Baca County, Colorado.

Referred Specimens--FMNH 12009 mid-section of skeleton, including 60+ vertebrae, complete pectoral girdle, nearly complete pelvic girdle, complete fore paddle. Belle Fourche Formation (Early Cenomanian), near Alzada, Montana. Holotype of *Elasmosaurus serpentinus* Riggs 1939 and *Alzadasaurus serpentinus* Welles, 1943.

UNSM 50132 skull and cervicals. Graneros Shale, Seward County, Nebraska.

Description--Both skulls are crushed (Figures 11, 12), but not encrusted with gypsum as is the case with skulls from the Pierre Shale. The skulls differ from that of *Libonectes morgani* in their longer supratemporal fossa relative to skull length. The greater length is reflected in the greater distance between the coronoid process of the lower jaw and the articular glenoid, and in the greater length between the last tooth and the condylar end of the quadrate. The jugal forms less of the ventral border of the orbit than it does in *Libonectes*. Another possible difference is that the jaw below the coronoid process is shallower, although this is equivocal due to the crushed state of the skulls. Finally, the dentary teeth do not show as marked a decrease in size posteriorly. The atlas-axis complex is illustrated in Figure 5C. It is short and deep, being more similar to that of *L. morgani* than long and low as in *E. platyurus*.

Discussion--The holotype specimen was described in detail by Welles (1943) and illustrated with many of the sutures denoted. However, I am unable to follow many of these sutures with confidence owing to the numerous fractures caused by crushing. Another skull (UNSM 50132) is less damaged but is on exhibit and can not be studied very well. This specimen was very briefly described by Welles (1970) but not illustrated. Considering how well preserved the skull is, it is remarkable that Welles did not describe it in more detail. The external nares is almost circular, as it is in the holotype, rather than elongate as it is in *Hydralmosaurus* and *Libonectes* (Figure 12). The tip of the premaxilla is more blunt than seen in the holotype.

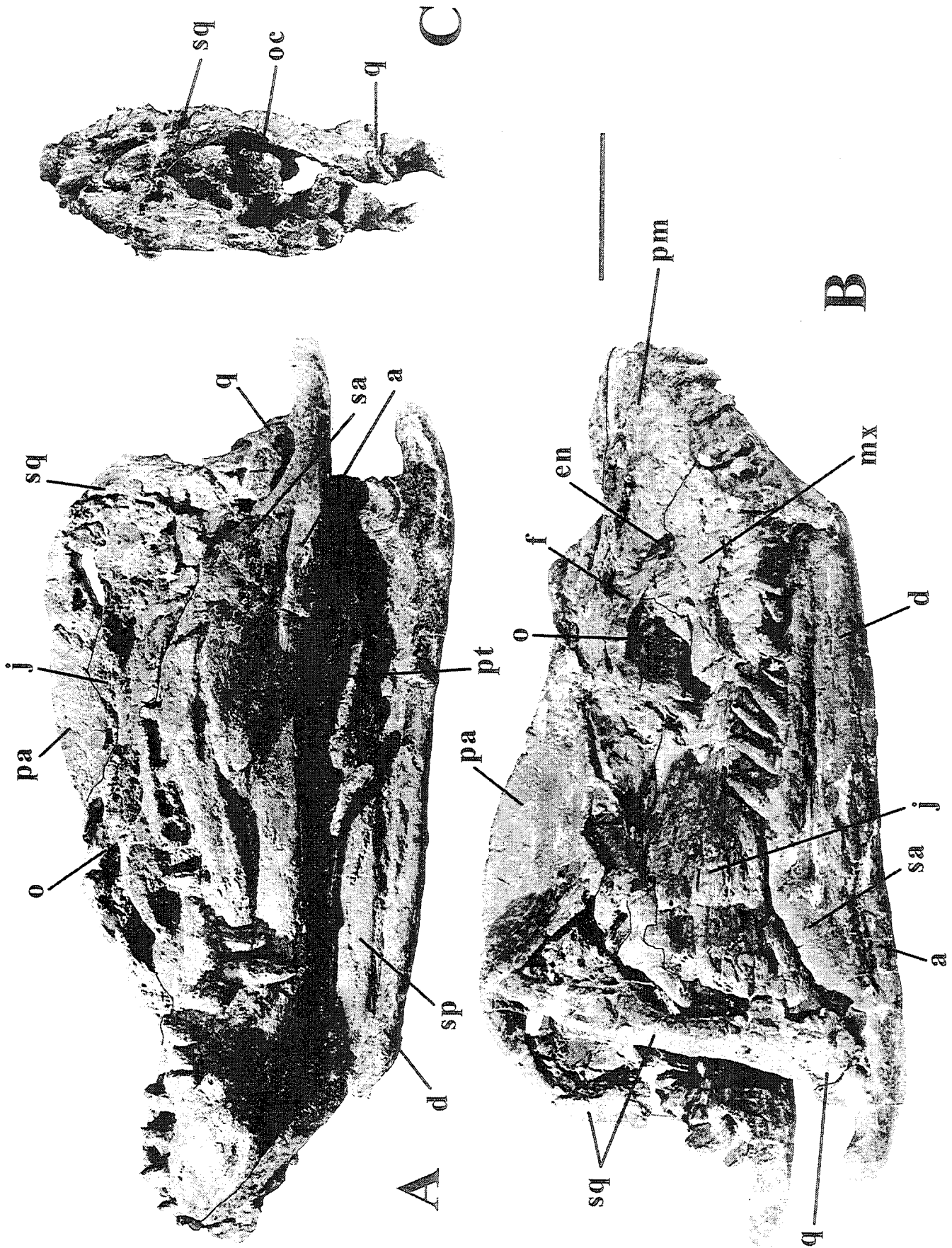


Figure 11 Skull of *Thalassomedon hanningtoni*, DMNH 1588, in A, right lateral and B, left lateral views. Scale=10cm. See Figure 7 for abbreviations.

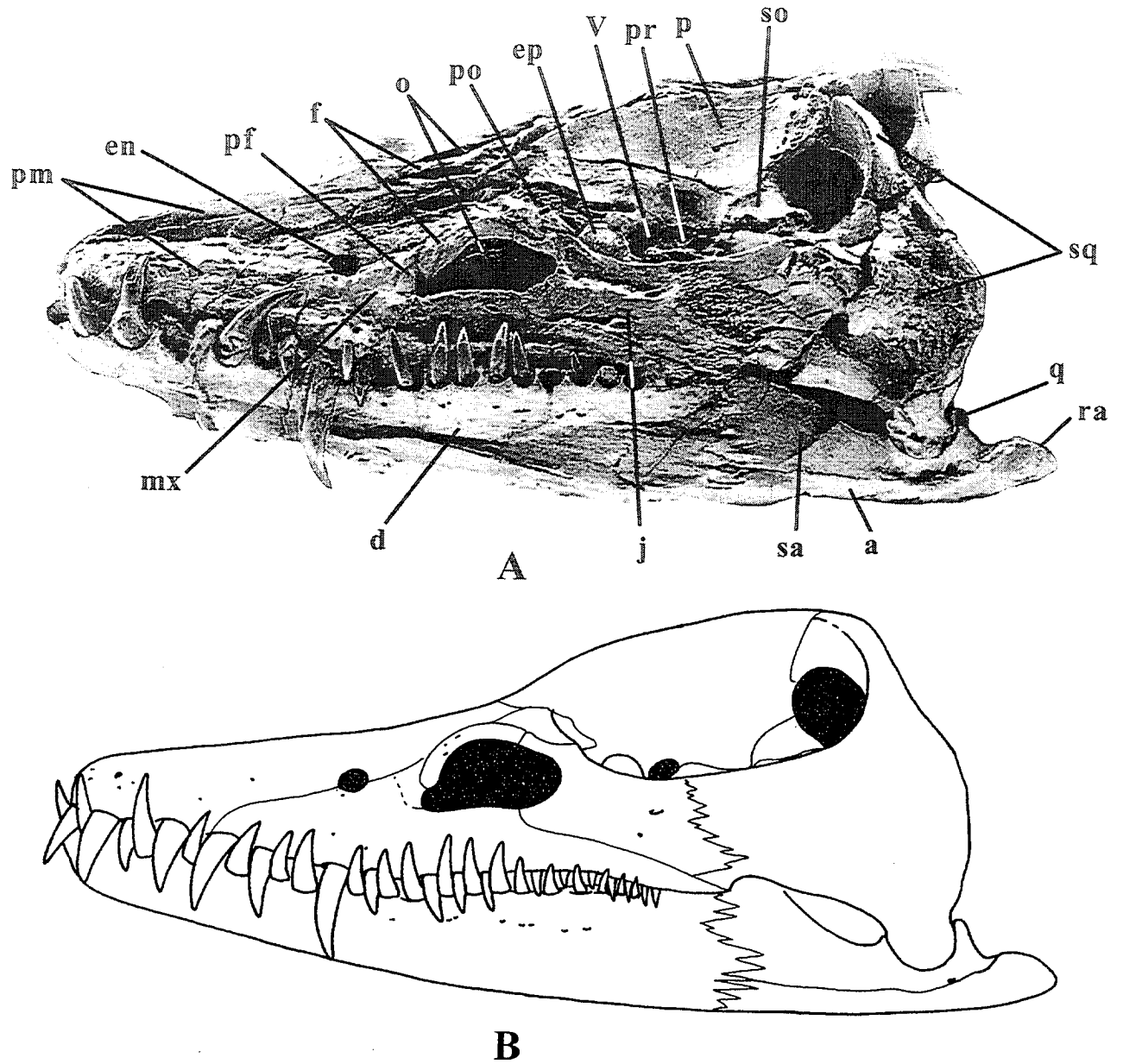


Figure 12. Skull of *Thalassomedon hanningtoni*, UNSM 50132, in A, left lateral view, and B, reconstructed. See Figure 7 for abbreviations.

DISCUSSION

Despite the wealth of plesiosaur specimens, especially from Europe, it is surprising that no attempt has been made to do a phyletic analysis. To rectify this situation and to stimulate further study, a preliminary phyletic analysis of elasmosaurs is presented. The core of this analysis is based on the review of the elasmosaurs from the Western Interior presented above. The analysis uses mostly taxa from skulls and postcrania (with the exception of *Elasmosaurus platyurus*), and ignores partial and fragmentary skeletons lacking skulls (e.g., *Morenosaurus stocki* Welles, 1943). The analysis does show that Late Cretaceous elasmosaurs are conservative, making it difficult to identify apomorphic characters.

Only the Plesiosauroidea (Cryptoclididae, Plesiosauridae, and Elasmosauridae) are considered in this analysis, with *Pistosaurus* as the outgroup (Sues, 1987; Rieppel, 1997). The Pliosauridae and Polycotyliidae are not considered in this analysis. The holotype of the genus *Alzadasaurus* is synonymized with *Thalassomedon* (above) leaving "*Alzadasaurus*" *columbiensis* without a generic name. *Callawayasaurus* is proposed and is diagnosed in Appendix I. The skull is illustrated in multiple views in Figure 13, and the skull of *Tuarangosaurus keysi* in Figure 14.

The data matrix is presented in Table 2. It was analyzed with Hennig 86 and the resultant trees produced graphically with Treeview (Page, 1996). The results of weighting and unweighting the number of cervical vertebrae gave slightly different results (Figure 15). Unweighted, only a single tree was produced (I = 21, ci = 71, ri = 85; Figure 15A), whereas weighting the number of cervicals in excess of the plesiomorphic

condition of 24 vertebrae resulted in six trees (length = 66, ci = 71, ri = 86). Only a single tree of the six was selected based on the frequency that taxa co-occurred. For example, *Pistosaurus*, Cryptoclididae, Plesiosauridae, *Brancaosaurus*, and *Microcleidus* occurred in the same sequence low in all six trees and was therefore judged to be a stable sequence. On the other hand, *Elasmosaurus* and *Libonectes* co-occurred at the terminal position of two trees, whereas *Thalassomedon* and *Tuarangisaurus* co-occurred in the same position in three trees. Therefore, *Thalassomedon* and *Tuarangisaurus* were selected to occupy this position. In this manner, all of the taxa were allocated a sequential position in the list of names and a tree was selected that matched this sequence. The selected tree was nearly identical to the unweighted tree except for the position of *Muraenosaurus*. The weighted tree (Figure 15B) is preferred because *Muraenosaurus* is placed higher up the tree as an elasmosaurid, rather than below the elasmosaur node. I conclude that neck length is indeed important in the evolution of elasmosaurs, but perhaps less than Welles (1943) would have conceded.

One surprising outcome of the analysis is that the Cryptoclididae consistently came out as the sister taxon to the Plesiosauridae + Elasmosauridae. I conclude that cryptoclidids are more primitive than Brown (1981; 1993) realized. Furthermore, the plesiomorphic state for plesiosaurs in general is to have a posteriorly sloped suspensorium (Carpenter, 1996), a point also illustrated by nearly uncrushed skull of *Leptocleidus* (Andrews, 1922). I therefore believe that the cryptoclidid skull reconstruction by Andrews (1910) is more correct than those by Brown because the suspensorium is sloped posteriorly.

TABLE 2. Data matrix used in the phyletic analysis of the Plesiosauroidea and *Pistosaurus*. See Appendix 2 for characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Pistosaurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plesiosauridae	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Cryptoclididae	1	?	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
<i>Brancaosaurus</i>	1	0	?	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1
<i>Callawayasaurus</i>	1	1	1	1	1	1	1	1	1	?	0	1	1	0	0	?	1	1	1	0
<i>Elasmosaurus</i>	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	0	1	1
<i>Hydralosaurus</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0
<i>Hydrotherosaurus</i>	1	1	1	1	1	1	?	1	1	1	0	1	1	0	0	?	1	1	1	0
<i>Leptocleidus</i>	?	?	1	1	1	1	?	0	0	?	0	?	?	?	0	?	?	0	0	?
<i>Libonectes</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0	1	?
<i>Microcleidus</i>	1	0	?	0	0	1	?	?	0	1	0	1	0	0	0	?	1	0	1	1
<i>Muraenosaurus</i>	1	0	0	0	?	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0
<i>Styxosaurus</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0
<i>Thalassomedon</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0
<i>Tuarangisaurus</i>	1	1	1	1	1	1	1	1	1	1	0	?	1	?	0	0	1	1	?	0

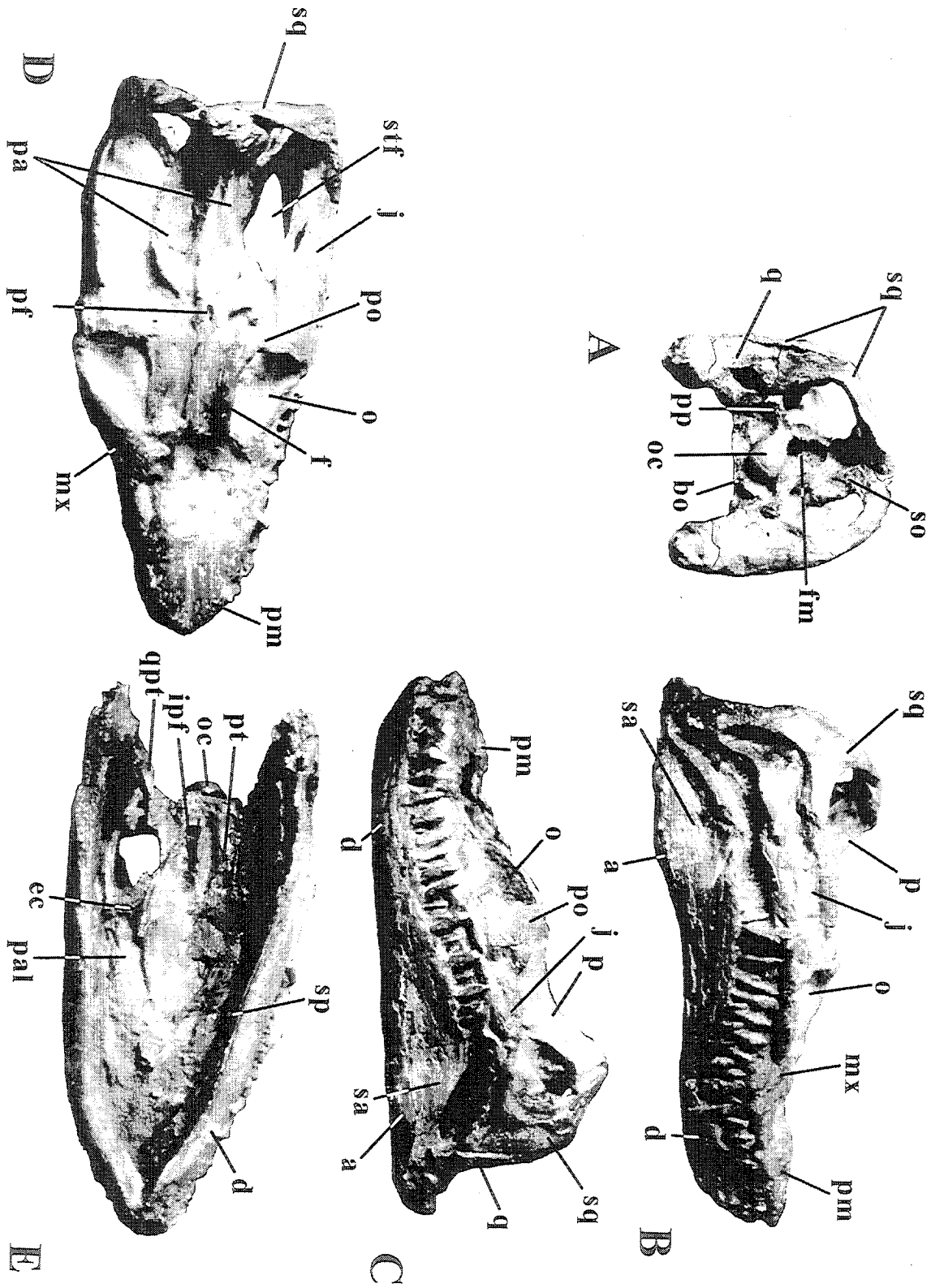


Figure 13. Holotype of *Callawapasaurus columbiensis*, UCMF 38349. Skull in posterior (A), right lateral (B), left lateral (C), dorsal (D), and ventral (E) views. See Figure 7 for abbreviations.

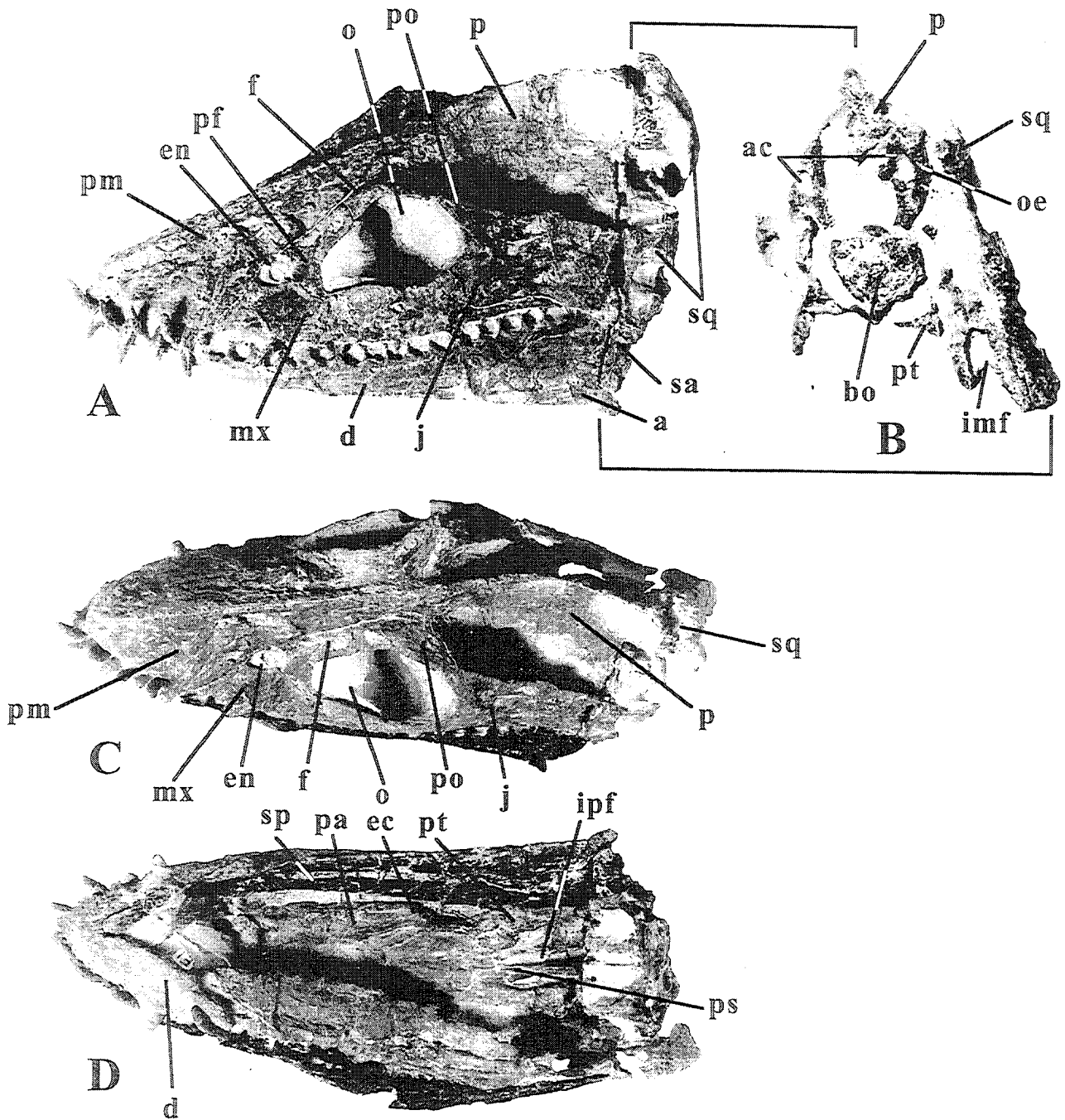


Figure 14. Holotype of *Tuarangosaurus keyesi*, NZGS CD425. Skull in left lateral view (A), anterior view of rear portion of skull (B), dorsal (C) and ventral (views). See Figure 7 for abbreviations. Photographs courtesy of Joan Wiffen

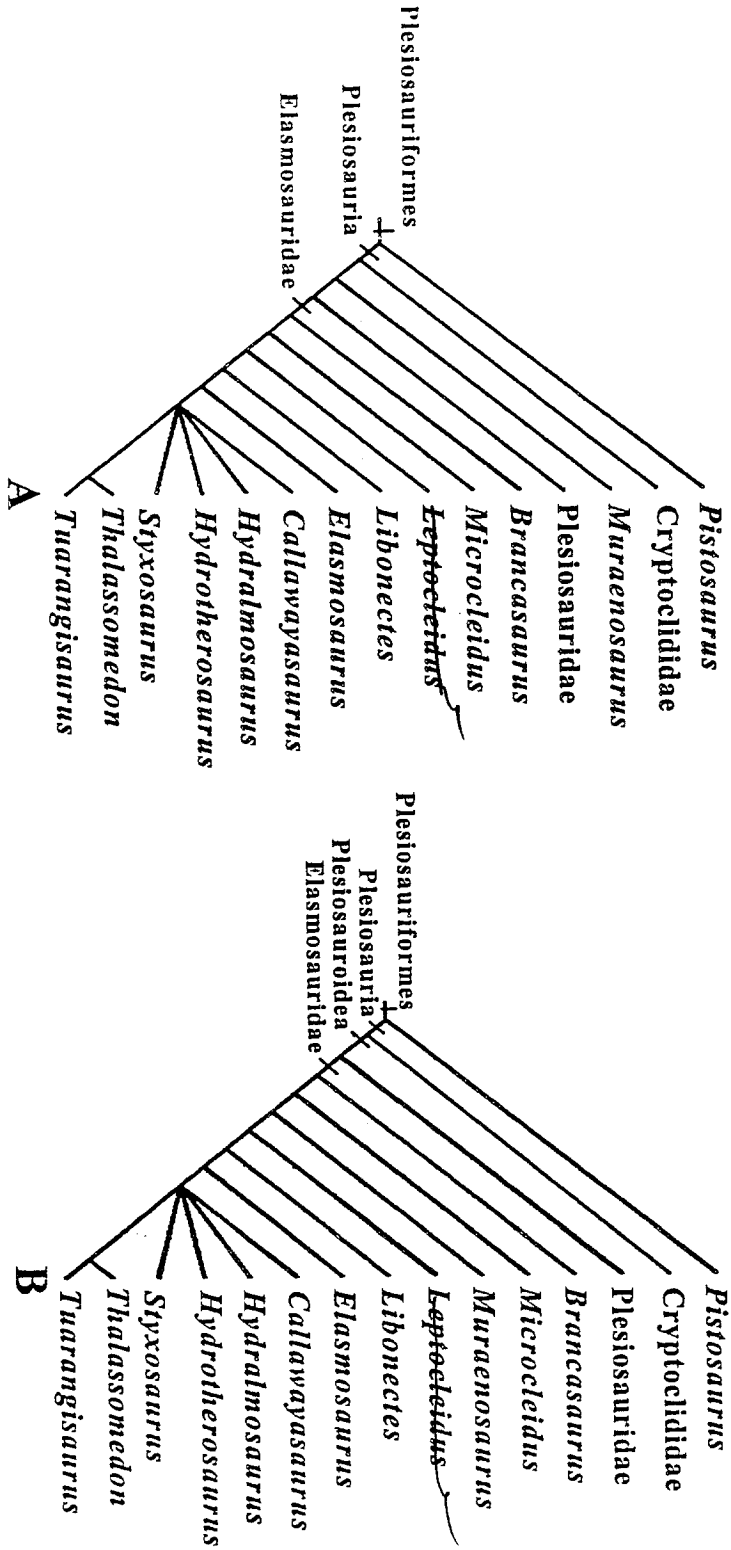


Figure 15. Comparison of two phyletic trees with number of cervical vertebrae unweighted (A) and weighted (B). The biggest difference between them is the placement of *Muravenosaurus*. In A, *Muravenosaurus* is below the node for the *Elasmosauridae*, but in B, is above. For this reason, tree B is preferred implying that neck length is an important character in the evolution of plesiosaurs. *Plesiosauriformes* includes *Plistosaurus* + *Plesiosauria* and may be defined as having: nasals very small or absent, and if present excluded from margin of external nares; external nares small; high occipital arch formed by squamosals; enlarged pectoral and pelvic girdles; coracoids with extensive medial contact; humerus without entepicondylar foramen; ilium with posterodorsally elongated blade (modified from Sues, 19987). The *Plesiosauria* may be defined as: coracoids expanded into large plate; pubis expanded into large plate; ischium expanded into large plate; loss of contact between ilium and pubis; epipodials broader than long; hyperphalangy (modified from Sues, 1987). *Elasmosauridae* may be defined as having: 36 or more cervical vertebrae; anterior mid-cervicals elongated; lateral ridge on cervical vertebrae.

CONCLUSIONS

A review of Upper Cretaceous elasmosaurs from the Western Interior of North America shows that they are morphologically conservative, with few features separating them. The most reliable characteristics appear to be the number of cervical vertebrae, the structure of the atlas-axis complex, and the position of the external nares relative to the maxillary teeth. The presence of a pectoral bar in Jurassic plesiosaurs may be ontogenetic (Brown 1981), but its absence in "adult" specimens of *Hydralmosaurus serpentinus* and *Styxosaurus snowii* equal in size to *Elasmosaurus platyurus* and *Libonectes morgani* suggests that this feature may have some taxonomic utility in elasmosaurs. Valid taxa from the Upper Cretaceous of the Western Interior include *Elasmosaurus platyurus*, *Hydralmosaurus serpentinus*, *Libonectes morgani*, *Styxosaurus snowii*, and *Thalassomedon hanningtoni*.

Finally, I would like to take the opportunity of correcting an error in Carpenter (1996). The genus *Plesiopleurodon* should be in the family Pliosauridae and not Brachauchiidae as the paper implies.

ACKNOWLEDGMENTS

Analysis of the uncrushed elasmosaur skull was made possible by Computer Axial Tomography and X-rays images made by Janet Alband, RT, and Robert Meals, DO (Chairperson) of the Department of Radiology, Osteopathic Medical Center of Philadelphia, and Luther Brady, MD (Chairperson), Joanne Bethold, RTT, and Mary Lansu, BS, of the Radiation Therapy Department, Hahnemann University, Philadelphia. Access to numerous specimens in museums, information and data was made possible by: Phil Bjork (South Dakota School of Mines), John Bolt (Field Museum of Natural History), Gregory Brown (Nebraska State Museum), Charlotte Holten and Gene Gaffney (American Museum of Natural History), Robert Purdy and Nicholas Hotton (National Museum of Natural History), Larry Martin (University of Kansas Museum of Natural History), and John Ostrom and Mary Ann Turner (Yale Peabody Museum). This paper is dedicate to the memory of Dr. Jack Callaway for his work and interest in fossil marine reptiles.

LITERATURE CITED

Almy, K. 1987. Thof's dragon and the letters of Capt. Theophilus H. Turner, M.D., U.S. Army. *Kansas History* 10:170-200.

- Andrews, C. W. 1910. A descriptive catalogue of the marine reptiles of the Oxford. Clay. British Museum (Natural History) Part 1:1-205.
- Andrews, C. W. 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society* 78:285-298.
- Brown, D. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *British Museum (Natural History), Geology Bulletin* 35:253-347.
- Brown, D. S. 1993. A taxonomic reappraisal of the families Elasmosauridae and Cryptoclididae (Reptilia: Plesiosauroidea). *Revue de Paléobiologie, Special Volume* 7:9-16.
- Carpenter, K. 1990. Variation in *Tyrannosaurus rex*. Pp. 141-145 in Carpenter, K., and Currie, P., (eds) *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, New York.
- Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 201:259-287.
- Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. Pp. 191-216 in Callaway, J.M., and Nicholls, E.L. (eds.) *Ancient Marine Reptiles*, Academic Press, San Diego.
- Carroll, R. L. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London* 293:315-383.
- Colbert, E. H. 1959. The Paleozoic Museum in Central Park, or the museum that never was. *Curator* 2:137-150.
- Condra, G. and Reed, E. 1959. The geological section of Nebraska. *Nebraska Geological Survey Bulletin* 14A:1-82.
- Cope, E. D. 1869. Extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society* 14:1-252.
- Cope, E. D. 1875. The Vertebrata of the Cretaceous formations of the West. F.V. Hayden, Report of the United States Geological Survey of the Territories, 2:1-303.
- Cope, E. D. 1877. Report on the geology of the region of the Judith River, Montana, and on the vertebrate fossils obtained on or near the Missouri River. Part 2. Vertebrata from the Niobrara Cretaceous. U.S. Geological and Geographical Survey of the Territories, Hayden Survey, *Bulletin* 3:565-597.

- Cope, E. D. 1894. On the structure of the skull in the plesiosaurian reptile, and two new species from the Upper Cretaceous. *Proceedings of the American Philosophical Society* 33:109-113.
- Fitch, H. 1981. Sexual size differences in reptiles. University of Kansas Museum of Natural History Miscellaneous Publication 70:1-72
- Hoffstetter, R., and Gasc, J.-P. 1969. Vertebrae and ribs of modern reptiles, in Gans, C. (ed.) *Biology of the Reptilia*, 1:201-310.
- ICZN (International Code of Zoological Nomenclature). 1985. University of California Press, Berkeley, CA, 338pp.
- Kuhn, O. 1964. *Fossilium Catalogus, Sauropterygia*. Ysel Press, Deventer, Netherlands 106:1-72.
- Merewether, E. and Cobban, W. 1981. Mid-Cretaceous formations in eastern South Dakota and adjoining areas - stratigraphic, paleontologic, and structural interpretations. *Iowa Geological Survey Guidebook series* 4:43-56.
- Meek, F. and Hayden, F. 1861. Descriptions of new Lower Silurian (Primordial), Jurassic, Cretaceous, and Tertiary fossils collected in Nebraska. *Academy of Natural Sciences of Philadelphia, Proceedings* 13:415-447.
- Page, R. D. 1996. Treeview: an application to display phylogenetic trees on personal computers. *Computer Applications in Biological Sciences* 12:357-358.
(<http://taxonomy.zoology.gla.ac.uk/rod/rod.html>)
- Persson, O. 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Arsskrift* 59:1-59.
- Raath, M. 1990. Morphological variation in small theropods and its meaning in systematics. evidence from *Syntarsus rhodesiensis*. Pp. 91-105 in Carpenter, K., and Currie, P., (eds) *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, New York.
- Rieppel, O. 1997. Part II. Introduction. Pp.107-119 in Callaway, J.M., and Nicholls, E.L. (eds.) *Ancient Marine Reptiles*. Academic Press, San Diego.
- Riggs, E. 1939. A specimen of *Elasmosaurus serpentinus*. *Field Museum of Natural History, Geology Series* 6:385-391.
- Ryder, R. 1988. Dusting off America's First Dinosaur. *American Heritage* 1988, number 3.
- Seeley, H. G. 1874. On *Muraenosaurus Leedsii*, a Plesiosaurian from the Oxford Clay. Part I. *Quarterly Journal of the Geological Society*, 30:197-208
- Shuller, E. 1950. A new elasmosaur from the Eagle Ford Shale of Texas. *Southern Methodist University, Fondren Science Series* 1(2):1-32.
- Smellie, W. 1917. *Apractocleidus teretipes*: a new oxfordian plesiosaur in the Hunterian Museum, Glasgow University. *Royal Society of Edinburgh Transactions* 51:609-629.
- Sollas, W. J. 1881. On a new species of *Plesiosaurus* (*P. Conybeari*) from the Lower Lias of Charmouth; with observations on *P. megacephalus*, Stutchbury, and *P. brachycephalus*, Owen. *Quarterly Journal of the Geological Society of London* 37:440-480.
- Stewart, J. D. 1990. Niobrara Formation vertebrate stratigraphy. Pp. 19-30 in Bennett, C. (ed.) *Niobrara Chalk Excursion Guidebook*. University of Kansas Museum of Natural History.
- Storrs, G. 1981. A review of occurrences of the Plesiosauria (Reptilia: Sauropterygia) in Texas with description of new material. Unpublished MA thesis, University of Texas, 225pp.
- Storrs, G. 1991. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Peabody Museum of Natural History Bulletin* 44:1-151.
- Storrs, G. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*. Pp. 145-190 in Callaway, J. M., and Nicholls, E. L. (eds.) *Ancient Marine Reptiles*, Academic Press, New York.
- Sues, H.-D. 1987. Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). *Zoological Journal of the Linnean Society* 90:109-131,
- Swinton, W. E. 1947. Plesiosaurs in the City Museum, Bristol. *Bristol Naturalist Society, Proceedings* 27:343-360.
- Tarlo, B. 1960. A review of the Upper Jurassic pliosaurs. *British Museum (Natural History), Geology Bulletin* 4(5):145-189.
- Taylor, M. 1992. Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast. *Yorkshire Geological Society Proceedings* 49:49-55.
- Taylor, M. and Cruickshank, A. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London, B* 341:399-418.

- Watson, D. 1924. The elasmosaurid shoulder-girdle and forelimb. Zoological Society of London Proceedings 58:885-917.
- Wegner, T. 1914. *Brancaosaurus brancai* n.g. n. sp., ein Elasmosauridae aus dem Wealden Westfalens. Pp.235-305 in Schoendorf, F. (ed.) Branca Festschrift, Berlin.
- Welles, S. 1943. Elasmosaurid plesiosaurs with a description of new material from California and Colorado. University of California Memoirs 13:125-254.
- Welles, S. 1949. A new elasmosaur from the Eagle Ford Shale of Texas. Fondren Science Series, Southern Methodist University 1:1-28.
- Welles, S. 1952. A review of the North American Cretaceous elasmosaurs. University of California Publications in Geological Sciences 29:47-144.
- Welles, S. 1962. A new species of elasmosaur from the Aptian of Columbia, and a review of the Cretaceous plesiosaurs. University of California Publications in Geological Sciences 46:1-96.
- Welles, S. 1970. The longest neck in the ocean. University of Nebraska News, Museum Notes 43, p. 1-2.
- Welles, S. and Bump, J. 1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. Journal of Paleontology 23:521-535.
- Wiffen, J. and Moislley, W. 1986. Late Cretaceous reptiles (Families Elasmosauridae) from the Mangahouanga Stream, North Island, New Zealand. New Zealand Journal of Geology and Geophysics 29:205-252.
- Williston, S. 1890. A new plesiosaur from the Niobrara Cretaceous of Kansas. Transactions of the Kansas Academy of Science 12:174-178.
- Williston, S. 1903, North American plesiosaurs, part 1. Field Columbian Museum Publication 73, Geological Series 2:1-77.
- Williston, S. 1906, North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. American Journal of Science, 4th ser. 21:221-236.

APPENDIX 1
Plesiosauroidea
Elasmosauridae
Callawayasaurus n.g.
Figure 14

Type Species--*Callawayasaurus columbienesis* (Welles, 1962).

Diagnosis--External nares above maxillary teeth 3-5, over maxillary teeth 6-7 in *S. snowii*, teeth 2 and 3 in *Tuarangosaurus keyesi*, teeth 3 and 4 in *L. morgani*, and tooth 4 in *Thalassomedon hanningtoni*. External nares elongate as in *Hydralmosaurus* and *Libonectes*, circular in *Thalassomedon*. 56 cervicals compared to 37 cervicals in *Brancasaurus*, 46 in *Morenosaurus*, 60 in *Hydrotherosaurus*, 62 in *Thalassomedon* and *Styxosaurus*, 63 in *Hydralmosaurus* and 72 in

Elasmosaurus platyurus. No pectoral or pelvic bar in adults.

Etymology--For Jack Callaway, who in his brief career as a vertebrate paleontologist, did much to improve our understanding of marine reptiles.

Callawayasaurus columbienesis (Welles, 1962)

Holotype--UCMP 38349, nearly complete skeleton with crushed skull.

Type Horizon and Locality--Paja Formation (Upper Aptian), near Villa de Leyva, Province Boyacá, Columbia.

Diagnosis--As for the genus.

APPENDIX 2. Characters used in the data matrix of Table 2.

1. Presence of the nasals in *Pistosaurus* is the primitive condition; its loss unites the Plesiosauria: 0 = present, 1 = absent.
2. The postfrontal is present primitively, but with the posterior expansion of the dorsal process of the premaxilla between the orbits in elasmosaurs, this element is lost: 0 = present, 1 = absent.
3. Primitively, the basicranium is visible in its entirety between the pterygoids. However, in most elasmosaurs the pterygoids have expanded horizontally and part covers under the basicranium: 0 = pterygoids not expanded, 1 = expanded.
4. Primitively, the jugal is excluded from contributing to the rim of the temporal fenestra, in advanced elasmosaurs it does form part of the rim: 0 = excluded, 1 = contacts.
5. The parasphenoid is rounded primitively, but Y-shaped in cross-section in most elasmosaurs. This change is correlated with the horizontal expansion of the pterygoids: 0 = rounded, 1 = Y-shaped.
6. In the non-expanded pterygoid condition, a large gap is present between them. With the formation of the pterygoid plate (#3), a pair of interpterygoid fenestrae are formed with the parasphenoid between them. 0 = single interpterygoid fenestra, 1 = paired interpterygoid fenestrae.
7. In *Pistosaurus*, the vomer-nasal fenestra for the Jacobson's organ is paired. It is apparently lost in the plesiosaurids and cryptoclidids. In elasmosaurs, the paired fenestrae have merged forming an inverted V-shaped fenestra along the sutural contact of the premaxillaries and vomer. 0 = vomer-nasal fenestra absent, 1 = V-shaped vomer-nasal fenestra between premaxillaries and vomer.
8. The dorsal process of the premaxilla is separated from the parietals primitively in the plesiosaurs by the frontals. The derived condition is contact of the premaxilla with the parietals between the orbits. The functional purpose for this condition may be to strengthen the snout, although why this did not occur in the giant-headed plesiosaurus is puzzling. 0 = premaxilla separated from the parietals by the frontals, 1 = premaxilla contacts the parietals.
9. A erect or nearly erect suspensorium formed by the quadrate and squamosal is present in *Pistosaurus*, but became sloped posteriorly in plesiosaurids and cryptoclidids. In elasmosaurs, the suspensorium became secondarily erect again. 0 = suspensorium primarily erect or sloped posteriorly, 1 = secondarily erect.
10. Primitively, the teeth of the premaxilla and anterior portion of the maxilla are nearly uniform in length, but in elasmosaurs the teeth on each side of the premaxillary-maxillary suture are small. 0 = teeth on each side of the premaxillary-maxillary suture uniform in length, 1 = teeth smaller.
11. The number of premaxillary teeth in plesiosaurs is 5 primitively, but is more than five in cryptoclidids. 0 = 5 premaxillary teeth, 1 = more than 5 premaxillary teeth.
12. The primitive number of cervicals for plesiosauriforms is 24. This number increases in the Plesiosauria. 0 = 24 cervical vertebrae, 1 more than 24 cervicals.
13. Advanced elasmosaurs have increased the number of cervicals more than 40 cervicals. 0 = fewer than 40 cervicals, 1 = more than 40 cervicals.
14. Very advanced Cretaceous elasmosaurs have more than 60 cervicals. 0 = fewer than 60 cervicals, 1 = 60 or more cervicals.
15. The most advanced condition in elasmosaurs is to have more than 70 cervicals, seen only in *Elasmosaurus*. 0 = fewer than 70 cervicals, 1 = more than 70 cervicals.
16. Typically, the axis centrum of the plesiosauriforms is about as tall as it is long, but in very advanced elasmosaurs, the centrum is considerably longer than tall. 0 = height and length about equal, 1 = length considerably longer than height.
17. The anterior cervicals have a rounded lateral surface primitively, but a lateral ridge placed horizontally on the centrum in the derived state. 0 = no lateral ridge, 1 = lateral ridge on anterior cervical centra.
18. A pectoral bar is absent in *Pistosaurus* and its absence in adult plesiosaurs is the primitive condition. A pectoral bar does form ontogenetically in some plesiosaurs and this is the derived condition. 0 = no pectoral bar in adults, 1 = pectoral bar in adults.
19. The scapula are separated from each other in the primitive state, as seen in *Pistosaurus*, but contact each other at the mid-line in the derived state. This feature is ontogenetically controlled and is only seen in adults; a pectoral bar is not always present. 0 = scapula separate in adults, 1 = scapula in contact medially in adults.
20. A counterpart of the pectoral bar is the pelvic bar formed by contact of the pubis and ischium along the midline. This feature is ontogenetically controlled and is only seen in some adults. 0 = no pelvic bar in adults, 1 = pelvic bar in adults.