

**REDESCRIPTION OF *ELASMOSAURUS PLATYURUS* COPE 1868
(PLESIOSAURIA: ELASMOSAURIDAE) FROM THE UPPER CRETACEOUS
(LOWER CAMPANIAN) OF KANSAS, U.S.A.**

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ABSTRACT

The type specimen of *Elasmosaurus platyurus* Cope, 1868 from the Upper Cretaceous (lower Campanian) of Kansas, U.S.A. is redescribed. It consists of part of the skull (e. g., both premaxillae, parts of the maxillae, the occipital condyle and parts of the dentaries), the almost complete vertebral column, including the atlas-axis complex, as well as the pectoral and pelvic girdles (although the latter are now lost). The genus *Elasmosaurus* can be defined by two unambiguous autapomorphies, the presence of six premaxillary teeth and the high number of 71 cervical vertebrae. It also exhibits a number of advanced features, which are discussed and compared with other elasmosaurs.

INTRODUCTION

Elasmosaurus platyurus is the first described and nominal genus of the Elasmosauridae, a family of long necked plesiosaurs recorded from the Lower Jurassic to the Upper Cretaceous. In 1867 a military physician Dr. Theophilus H. Turner discovered the first remains of the type specimen, two fragments of vertebrae, in a ravine, approximately 23 km northeast of Fort Wallace in western Kansas. In the same year, Dr. John W. Le Conte brought the specimens to the Academy of Natural Sciences in Philadelphia, where Edward Drinker Cope examined them (Almy, 1987). Cope recognized that they were from a plesiosaur and noticed the importance as being part of a then barely represented group of fossil reptile in the New World. The remaining parts of the skeleton were excavated and brought to Philadelphia with support by the Academy in early 1868. Later Cope more fully described the specimen in a preprint of the final paper. In his first attempt of a reconstruction Cope erroneously placed the head at the end of the tail. After realizing this mistake all copies of the preprint were recalled and were then reprinted with a new reconstruction (Storrs, 1984; for further historic information, also see Almy, 1987, and Davidson, 1997, 2002).

Although *Elasmosaurus platyurus* is the first described member of the Elasmosauridae, a detailed description, including all parts of the type specimen has only been provided by Cope (1869, 1875). Additional studies, mainly on the postcranium, have been undertaken by Welles (1952), Storrs (1999) and

Carpenter (1999). In the present paper the type specimen of *Elasmosaurus platyurus* (ANSP 10081) is redescribed and the diagnostic features are pointed out in order to state the taxonomic position of the genus within the Elasmosauridae.

Institutional abbreviation: ANSP: Academy of Natural Sciences in Philadelphia.

SYSTEMATIC PALAEOLOGY

Order PLESIOSAURIA de Blainville, 1835
Superfamily PLESIOSAUROIDEA Welles, 1943
Family ELASMOSAURIDAE Cope, 1869

ELASMOSAURUS PLATYURUS Cope, 1868

Diagnosis—Premaxillae bear six teeth per side; atlas-axis complex long and low, with distinct sagittal keel on ventral side; total number of cervical vertebrae 71; mid-cervicals anteroposteriorly elongate; feature-complex of 4 sacral vertebrae and prominent midline bar in pectoral and pelvic girdles.

Material—ANSP 10081, incomplete skeleton, comprising both premaxillae, part of the posterior section of the right maxilla, 2 maxillary fragments with teeth, anterior portions of dentaries, three additional jaw fragments, 2 indeterminable cranial fragments, 72 cervical vertebrae, including the atlas-axis complex, 3 pectoral, 6 dorsal, 4 sacral and 18 caudal vertebrae, as well as a number of rib fragments. Pectoral and pelvic girdles originally preserved, but now missing.

Measurements of cranial elements are given in Table 1; those of vertebrae in Table 2.

Locality and Horizon—Near McAllaster, Logan County, Kansas. Sharon Springs Shale Member, Pierre Shale (lower Campanian) (for more information see Storrs, 1999:3-4).

DESCRIPTION

Cranium

Premaxilla—Both premaxillae (Figure 1 A, B) are almost completely preserved and well co-ossified, as no medial suture is visible. They fit well together with the dentary portions, but show clear traces of dorsoventral crushing. Dorsally, along the midline, a low keel is present (Figure 2) that might have been more distinct before the skull was compressed. Anteriorly the tip of the snout is well-rounded and almost semicircular in dorsal view. The ventral sides of the premaxillae are not well preserved. Medially, behind the alveolar part, the vomeronasal fenestrum is visible as a broad triangular depression (Figure 2).

Cope (1868:53) stated that eight teeth are present in each premaxilla. This statement cannot be confirmed. Indicators for tooth positions are concavities in the lingual edges of the alveolar parts (Figure 2). Six of these concavities are present on each side. Comparing the specimen with the premaxillae of other elasmosaurs and considering the fact that a suture to the maxillae is not visible, it can be concluded that the fragment represents the premaxillae only. The premaxillary-maxillary contact would most probably have been immediately behind the last concavity, thus a total number of six teeth per premaxilla is most parsimonious. Only fragments of the second and third tooth are preserved in the right premaxilla, being formed as large fangs. The first premaxillary teeth, of which only cross-sections are present, are clearly smaller than the succeeding ones and are located between the first two teeth of the dentaries. The apex of what appears to be a replacement tooth, is visible in the second alveolus of the left premaxillary. A fragment of the sixth tooth of the right premaxilla is attached to the lower jaw as can be seen when reassembling the jaws.

Maxilla—One fragment (Figure 3A) apparently represents part of the posteriormost section of the right maxillary. Its medial side is formed as a strong dorsolaterally curved wall, while the lateral side is less curved and not as strong. The fragment bears some alveoli of which only four are clearly visible. They are very small, compared with the other tooth-bearing fragments. Among the latter are two (here called fragment B and C) that are lateromedially flattened, bearing one large tooth each (Figure 3B, C). Their general appearance would be unusual for the lower

jaw, thus they are determined as fragments of the maxillary.

Occipital Condyle—The hemispherical occipital condyle is present and still articulates with the atlas centrum (Figure 4A, B), thus no further observations were possible.

Mandible—The present anterior portions of the dentaries are well preserved and still bear parts of the teeth in all alveoli (Fig. 1C, D). Five teeth are present per side, which are all developed as large fangs and appear to be about equal in diameter as indicated by their cross sections. The symphysis is well ossified so that no suture is visible between the rami, and extends to the level of dentary tooth four. Dorsally, in about the posterior half of the symphyseal margin, a prominent triangular shaped bulge is formed. From here, at the point where the rami are separated, two medially situated, elongate, thickened structures are formed that follow the rami posteriorly.

Additional Jaw Fragments—Among the jaw fragments are three other tooth bearing elements that cannot be referred to the maxillary or the dentary with certainty. One of them (here called fragment D, Figure 3D) bears two large alveoli which served strong fang-like teeth as they are usually present in the anterior half of the dentary. The other two (here called fragment E, Figure 3E and fragment F, Figure 3F) have comparatively small alveoli, which indicates that were situated in the posterior half of the jaw.

Additional Cranial Material—Among the numerous indeterminable fragments are two pieces, which probably belong into the cranium. One (here called fragment G, Figure 3G, H) has a robust appearance and bears a pan-like structure that could have served for articulation. On one side, this structure is bordered by a blunt, broad process. Its general appearance is similar to the articular, in which the pan-like structure would be part of the glenoid fossa, however the preservation is too poor to provide an unambiguous determination. Another possible interpretation is that the element represents a fragment of the right squamosal with part of the right articular fused onto its inner surface. Figure 3G would then show the inner surface of the eroded or broken off right quadrate. The blunt process then could be the temporal arch process of the squamosal. The other fragment is curved and has one flat side (here called fragment H, Figure 3I). Again, a clear determination is not possible, because of the poor preservation. Eventually it could have been part of the skull roof (e.g. the frontal).

Vertebral Column

Atlas-axis Complex—The atlas-axis complex is almost completely preserved. Only the cervical ribs and the most posterodorsal section of the neural spine are missing. It is horizontally rectangular in outline in

Premaxilla		Apicobasal length of third tooth as preserved (right)	1.7
Length anteroposteriorly as preserved	10	Diameter of third tooth as preserved (right)	0.8
Greatest diameter at the preserved posterior end	9.6	Apicobasal length of fourth tooth as preserved (right)	2
Apicobasal length of second tooth as preserved (right)	1.3	Diameter of fourth tooth as preserved (right)	0.8
Diameter of second tooth as preserved (right)	1	Apicobasal length of fifth tooth as preserved (left)	1.4
Apicobasal length of third tooth as preserved (right)	2.9	Diameter of fourth tooth as preserved (left)	0.8
Diameter of third tooth as preserved (right)	1.1	Fragment D	
Vomer		Length anteroposteriorly	4.5
Anteroposterior length of attachment surface as preserved	5	Diameter anteroposteriorly of first alveol	1.4
Greatest diameter lateromedially	1.2	Diameter lateromedially of first alveol	0.8
Fragment of right maxillary		Diameter anteroposteriorly of second alveol (incomplete)	1
Length anteroposteriorly	9	Diameter lateromedially of second alveol (incomplete)	1
Diameter anteroposteriorly of best preserved alveol	0.6	Fragment E	
Diameter lateromedially of best preserved alveol	0.6	Length anteroposteriorly	2.5
Fragment B		Apicobasal length of tooth as preserved	1.2
Length anteroposteriorly	2.9	Diameter of tooth	0.5
Greatest height dorsoventrally	3.9	Fragment F	
Apicobasal length of tooth as preserved	4.4	Length anteroposteriorly	2.6
Diameter of tooth as preserved	0.8	Diameter anteroposteriorly of first alveol (incomplete)	0.5
Fragment C		Diameter lateromedially of first alveol (incomplete)	0.6
Length anteroposteriorly	4.5	Diameter anteroposteriorly of second alveol	0.8
Greatest height dorsoventrally	3.3	Diameter lateromedially of first alveol	0.7
Apicobasal length of tooth as preserved	2.6	Fragment G	
Diameter of tooth as preserved	0.7	Greatest length	9.8
Dentary		Greatest diameter	3
Length anteroposteriorly as preserved	11	Length of pan-like structure	3.8
Length of symphysis	7	Greatest width	2.3
Apicobasal length of first tooth as preserved (right)	2	Height of blunt process	1.4
Diameter of first tooth as preserved (right)	0.9	Fragment H	
Apicobasal length of second tooth as preserved (right)	2.1	Greatest length	7.4
Diameter of second tooth as preserved (right)	0.8		

TABLE 1. Measurements (in cm) of the cranial elements of ANSP 10081.

lateral view (Figure 4A-C). Although both centra are well co-ossified, a suture-like structure is visible at the right lateral side. However, this structure might be an artefact, due to lateral pressure onto the centrum. The co-ossification indicates that the specimen was an adult individual.

The neural arches are well preserved on the right side of the complex and are broken off on the left. Sutures between the centra and neural arches are not visible. Interestingly, the neural arches are extraordinarily thin and relatively high. Thus the neural canal has a high triangular outline in posterior view. The ventral section of the neural canal is rather narrow posteriorly, at the axis, where it occupies about half of the breadth of the centrum. It becomes clearly broader anteriorly and is expanded almost over the entire breadth of the centrum of the atlas. Here also the neural arches are slightly more robust than in the axis and the

neural canal is clearly higher. On the preserved right side a moderately large circular foramen is present. It is situated at the base of the neural arches, between the posterior edge of the neural arch of the atlas and the anterior side of the neural arch of the axis.

The neural spine is incompletely preserved, as the posterior half of the axis section is missing. It is very low and posterodorsally oriented at an angle of approximately eight degrees to the horizontal plane.

The centra of the atlas and axis vertebra are about equal in length, each having a quadrate shape in lateral view. The axis centrum shows prominent depressions in about the center of the lateral sides. They are probably enlarged due to the compression onto the centrum, but appear to have been present in the pre-compressed state too.

The articular facet of the atlas is still connected to the occipital condyle and can thus not be observed,

	Length	Width	Height		Length	Width	Height		Length	Width	Height
CV 1+2	5.5 cm	3 cm i.c.	3 cm	CV 37	9.4 cm	6.5 cm	6.2 cm	PV 1	8.5 cm	11.5 cm	9 cm
CV 3	3.7 cm	4.1 cm	2.6 cm	CV 38	10.5 cm	6 cm	7.5 cm	PV 2	8.5 cm	-	-
CV 4	3.9 cm	3.7 cm	2.8 cm	CV 39	10.3 cm	6.5 cm	6.8 cm	PV 3	8.8 cm	-	-
CV 5	3.9 cm	3.8 cm	3 cm	CV 40	10 cm	6 cm	7 cm	DV 1	8.5 cm	12.8 cm	9.5 cm
CV 6	4.3 cm	4.1 cm	3.1 cm	CV 41	10.8 cm	6 cm	7 cm	DV 2	9.5 cm	13 cm	9 cm
CV 7	5 cm	4 cm	3.2 cm	CV 42	10.7 cm	6.4 cm	7.4 cm	DV 3	9 cm	12 cm	10 cm
CV 8	4.7 cm	3.3 cm	3.3 cm	CV 43	11.2 cm	7.7 cm	8.2 cm a.	DV 4	9 cm	11.8 cm	10.5 cm
CV 9	5 cm	4 cm	3.1 cm	CV 44	11 cm	6.9 cm	8 cm	DV 5	8.5 cm	11.5 cm	10.5 cm
CV 10	5.1 cm	4.3 cm	3.1 cm	CV 45	11.3 cm	6.5 cm a.	8 cm a.	DV 6	9 cm	12.5 cm	10.5 cm
CV 11	5.9 cm	4.8 cm	3.5 cm	CV 46	12 cm	6.6 cm a.	8 cm a.	DV 7	-	9.5 i.c.	-
CV 12	5.5 cm	4 cm	3.1 cm	CV 47	11.8 cm	-	-	SAV 1	8 cm	8 cm i.c.	8.5 cm a.
CV 13	5.4 cm	4.1 cm	3.8 cm	CV 48	12 cm	6.2 cm	7.5 cm	SAV 2	8 cm	-	-
CV 14	5.5 cm	4.8 cm	3.7 cm	CV 49	11.5 cm	7 cm	8 cm	SAV 3	8 cm	-	-
CV 15	5.9 cm	5 cm a.	3.7 cm a.	CV 50	-	-	8.5 cm	SAV 4	7.5 cm	-	-
CV 16	5.8 cm	4.9 cm	3.7 cm	CV 51	11 cm	-	-	CAV 1	6.5 cm	-	-
CV 17	6.2 cm	4.6 cm	4.2 cm	CV 52	11.5 cm	-	-	CAV 2	6.5 cm	10.5 cm	8 cm
CV 18	6.4 cm	4.8 cm	4.3 cm	CV 53	-	6.8 cm	8.5 cm	CAV 3	6.5 cm	10.5 cm a.	8 cm a.
CV 19	6.4 cm	5.7 cm	4.3 cm	CV 54	10.5 cm	-	-	CAV 4	6.5 cm	-	-
CV 20	7.3 cm	5.2 cm	4.3 cm	CV 55	11 cm	-	-	CAV 5	6.5 cm	-	-
CV 21	7 cm	6.5 cm	4.2 cm	CV 56	12 cm	-	-	CAV 6	6.5 cm	9.5 cm	7.5 cm
CV 22	7 cm	5.4 cm	4.8 cm	CV 57	11.5 cm	-	-	CAV 7	6.5 cm	8.5 cm	7 cm
CV 23	7.1 cm	5.8 cm	4.7 cm	CV 58	11.5 cm	-	-	CAV 8	6.5 cm	8 cm a.	8.5 cm a.
CV 24	7.7 cm	5.6 cm	5.2 cm	CV 59	11 cm	-	-	CAV 9	6.5 cm	-	-
CV 25	7.8 cm	6.2 cm	4.5 cm	CV 60	11 cm	10 cm	10 cm	CAV 10	6 cm	7.5 cm	7 cm
CV 26	8 cm	5.8 cm	4.7 cm	CV 61	10.5 cm	10 cm i.c.	9.5 cm	CAV 11	6 cm	7 cm a.	7 cm a.
CV 27	8 cm	6 cm	5.2 cm	CV 62	10.5 cm	-	-	CAV 12	6 cm	7.5 cm a.	7 cm a.
CV 28	8 cm	5.6 cm	5.2 cm	CV 63	10.5 cm	10.5 cm	9 cm	CAV 13	6 cm	7.5 cm	-
CV 29	8.5 cm	6 cm	5.3 cm	CV 64	9.5 cm	11.5 cm	10 cm	CAV 14	5.5 cm	7 cm	6.5 cm
CV 30	8.7 cm	6.2 cm	5.7 cm	CV 65	10.5 cm	11 cm	10.5 cm	CAV 15	5 cm	7.5 cm	6.5 cm
CV 31	8.7 cm	6.5 cm	6.2 cm	CV 66	10 cm	-	-	CAV 16	5 cm	6.5 cm a.	6.5 cm a.
CV 32	9.3 cm	6.5 cm	5.4 cm	CV 67	9.5 cm	13 cm	10 cm	CAV 17	5.5 cm	7 cm	6.5 cm
CV 33	10 cm	5.8 cm a.	6 cm a.	CV 68	10 cm	13 cm	10 cm	CAV 18	5 cm	7 cm	6 cm
CV 34	9.8 cm	6.2 cm	5.8 cm	CV 69	10 cm	13 cm	10 cm				
CV 35	9.5 cm	6.2 cm	5.8 cm	CV 70	9 cm	-	-				
CV 36	9.2 cm	6.2 cm	6.4 cm	CV 71	9 cm	12 cm	10 cm				

TABLE 2. Measurements of the vertebrae of ANSP 10081. CV = Cervical vertebrae; PV = pectoral vertebrae; DV = dorsal vertebrae; SV = sacral vertebrae; CAV = caudal vertebrae; a. = as measurable, i.c. = incomplete.

whereas the articulation surface of the axis is clearly visible. It has a broad oval outline, with an excavation for the neural canal in the middle of its dorsal edge, and a small notch at about the same level ventrally. The facet itself is deeply concave and has robust, rounded edges. Only the basal sections of the cervical ribs are visible. At the right lateral side, they occur in the posterior most section of the atlas and are prominently developed in the axis.

The ventral side of the atlas-axis complex shows a distinct medial keel that runs between the anterior edge of the atlas and the posterior edge of the axis. Although only the basal section of this keel is preserved, it can be seen that it is transversally broader at the atlas. Lateral to the keel, the ventral surface is longitudinally depressed. There is only a slight depression present in the atlas, whereas the depression is more prominent in the axis.

Cervical Vertebrae—Including the atlas-axis complex, a total number of 71 cervical vertebrae are present (Figure 4D-K). Of these, only two are incomplete so that the series fits together almost perfectly and can also be reassembled on basis of the original matrix that is still attached to many vertebrae.

Most vertebrae are laterally compressed, with this compression being stronger in the mid-cervical region, than in the anterior or posterior sections. The longitudinal lateral crest is well developed. It is slightly visible in the third cervical, clearly developed from the 6th to the 45th and still visible to the 55th cervical vertebra, thus into the posterior section of the neck. The position of the crest is in the middle of the centrum in the anterior vertebrae and in its dorsal half from vertebra number 19 onwards.

The shape of the centra differs depending on the position in the neck. The third cervical is about as long

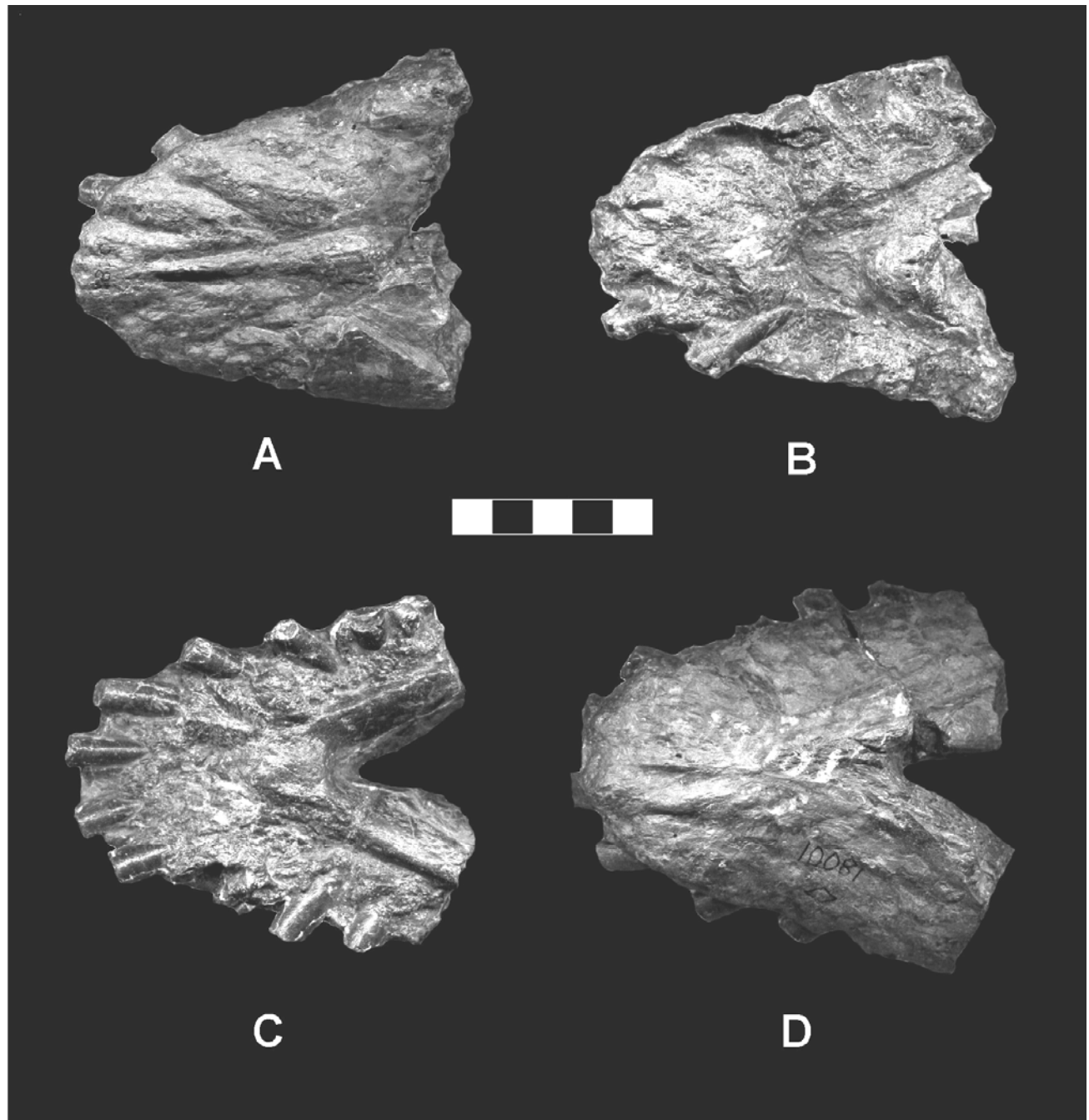


FIGURE 1 *Elasmosaurus platyurus* Cope 1868. **A.** Dorsal view of premaxillae. **B.** Ventral view of premaxillae, with the vomeroventral fenestration visible posteromedially. Anterior portions of dentaries in **C** dorsal and **D.** ventral view. Scale = 5 cm.

as broad. Beginning with the fourth cervical, the centra become longer than broad. The vertebrae are extraordinarily elongate in the mid-cervical region. In the posterior neck, they become again shorter and are rather broad, so that in number 61 the breadth and length are about equal and the posteriormost cervicals are broader than long. The shape of the articulation

facets cannot always be stated accurately, due to the aforementioned compression. In the most anterior centra they are broad oval and moderately deepened. The edges are rounded and thickened and show a clear excavation in the middle of the dorsal and ventral side. In the more posterior section of the anterior neck (e.g. in number 25) the concavity of the ventral edge of the

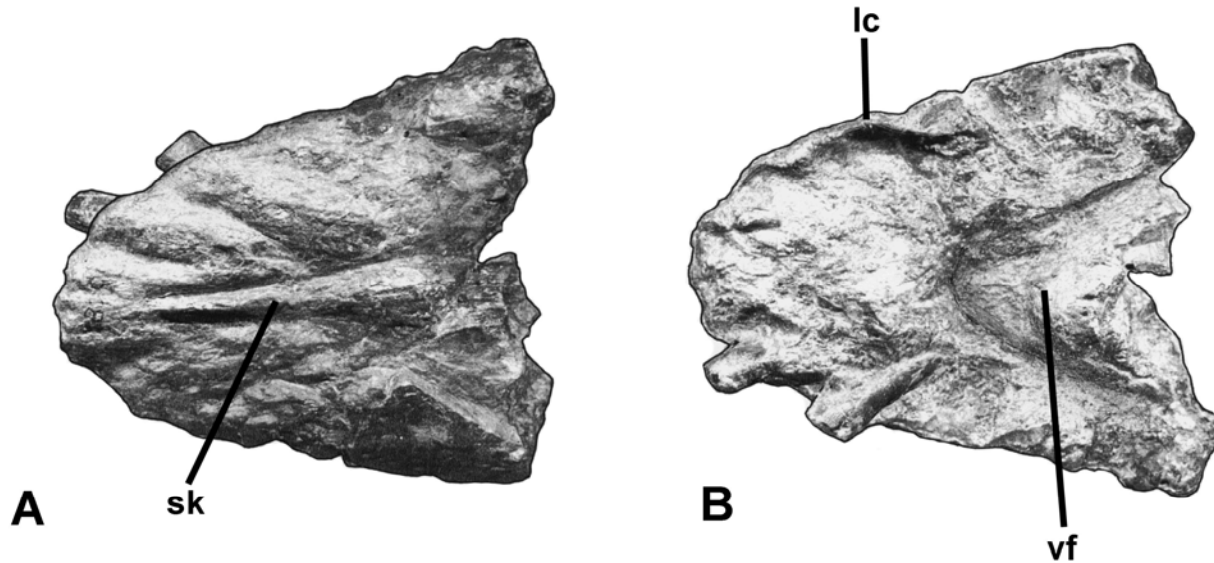


FIGURE 2. *Elasmosaurus platyurus* Cope 1868. Premaxillae in **A.** dorsal and **B.** ventral view. Abbreviations: lc = lingual concavity, indicating tooth position, sk = sagittal keel, vf = vomeronasal fenestrum.

articulation facets becomes more prominent and the shape of the facets is quadrate with rounded edges. Cervicals number 38 – 49 are strongly deformed, whereas numbers 50-60 are still in the matrix so that no statement about their shape can be given. The centrum of cervical number 63 is less compressed. Its articulation facet is also rather quadrate in general shape, but with rounded edges. The facets of the most posterior centra are broad oval in outline.

The neural arches are preserved in most cervicals. Generally they are well fused with the centrum, so that no suture is visible. The neural canal is rather narrow in the anterior cervicals and prominently developed in the most posterior ones. Here it is about as broad as high and almost circular in the last cervical. Its shape cannot be observed in the mid-cervicals, due to crushing of the centrum.

The zygapophyses are present on a number of vertebrae. Pre- and post-zygapophyses are about equal in length. The pre-zygapophyses reach over the level the centrum with their entire length. This can be observed throughout the cervical vertebral column. The post-zygapophyses reach over the level of the centrum with about their posterior half.

The neural spines are completely preserved only in the 19th and 20th cervical vertebra. Here they are rather low, so that its shape in the 20th cervical can be described as almost semicircular in lateral view.

The rib facets are readily visible on all cervicals. They are situated laterally in the ventral section of the vertebra almost throughout the cervical vertebral column and they migrate dorsally only in the last three vertebrae. In the next to last cervical, they are situated in the middle of the lateral side of the centrum, are prominently developed, and high ovals in outline. In the last cervical vertebra they are situated somewhat more dorsally and have a more triangular outline. Here also, a distinct horizontal crest is formed anteriorly at the lower side of the rib facets.

In a number of vertebrae the cervical ribs are still attached to the centra, which are completely preserved only in the anterior cervicals. In the fourth and fifth, they are almost semicircular in lateral view, while in the seventh they are more quadrate. In all cases the cervical ribs are rather straight ventrally directed, although this position could also be a result of the lateral compaction.

The ventral side of the centra is mostly not well preserved. A pair of nutritive foramina is placed in the middle, separated by a short ridge. This ridge becomes more prominent towards posterior in the neck and is thickened in the most posterior cervical vertebrae.

Pectoral Vertebrae—Three pectoral vertebrae are preserved (Figure 5A). They are still in the matrix, so that an anterior view is not possible. In the first pectoral centrum, the rib facets are triangular in outline

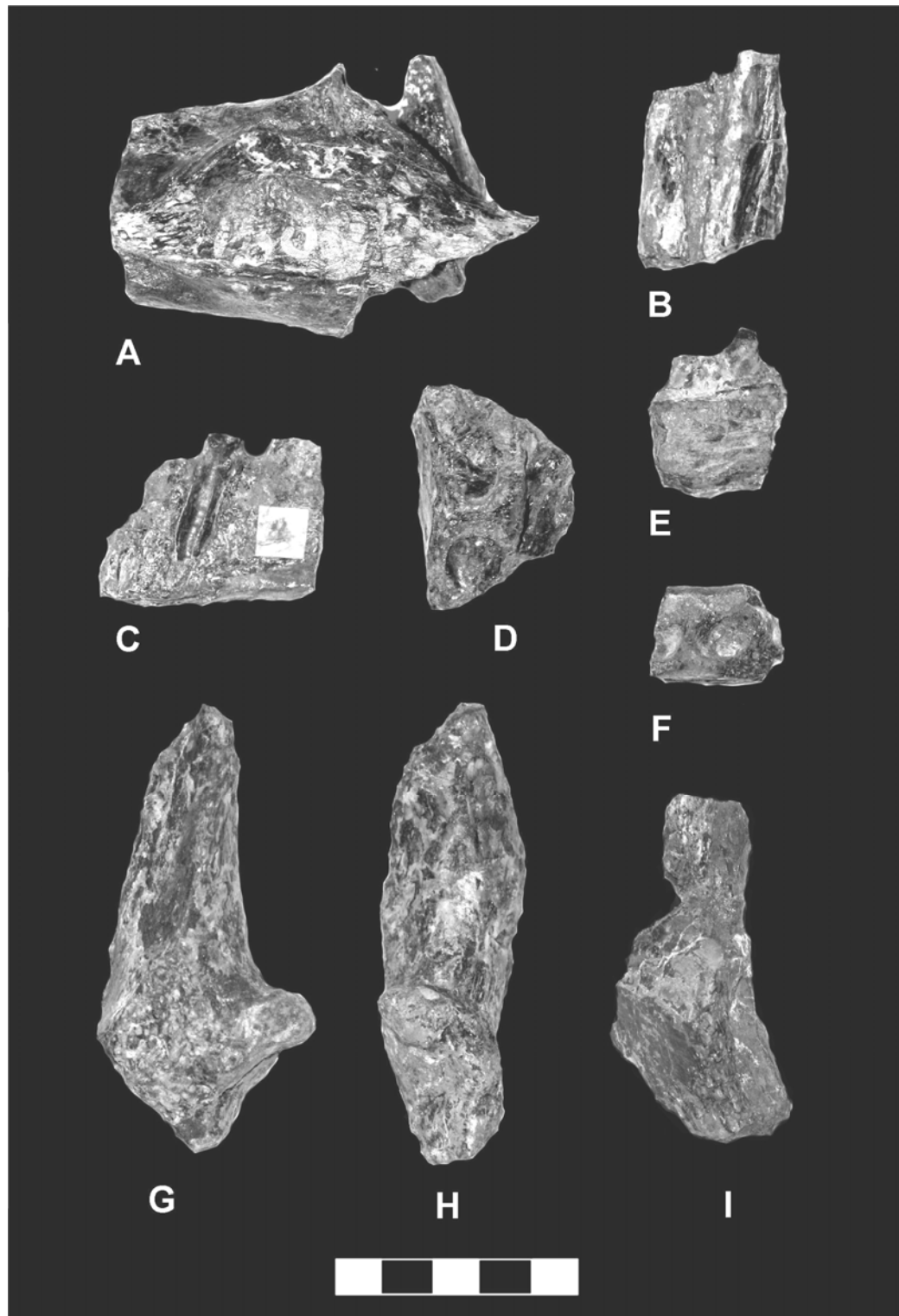


FIGURE 3. *Elasmosaurus platyurus* Cope 1868. Additional cranial elements. **A.** Posteriormost part of the right maxilla. **B.** Fragment B, **C.** Fragment C, toothbearing fragments probably belonging to the maxilla. **D.** Fragment D, possibly part of the anterior dentary. **E.** Fragment E, **F.** Fragment F, toothbearing fragments from the posterior half of the jaw, **G, H.** Undeterminable fragment G in two views, **I.** Undeterminable fragment H. Scale = 5 cm.

and are situated on small lateromedially-directed transverse processes. At their anterodorsal margins, a crest is formed that projects anteromedially and represents the border of the transverse process. Another much smaller crest is developed at the bottom of the rib facets, forming the ventral border of the transverse process. In the second pectoral vertebra, the rib facets are still triangular in cross-section, but are not as elongate ventrally as in the last cervical and first pectoral vertebra. Thus it has a more robust appearance. The dorsal margin of the transverse processes is formed as a plate that is slightly oblique ventrally. The anterior and posterior edges of this plate form a clear ridge. The posterior surface of the transverse process is directed straight vertically, whereas the anterior one is smoothly curved ventromedially. At the ventral portion of the transverse process another, but clearly broader ridge is formed that is slightly curved, ventrally directed, and there fused with the centrum in a broad base. The ventral sides of the centra bear a pair of nutritive foramina in the middle. They are separated by a broad ridge, which is formed as a rounded back that becomes more expanded transversally towards the articulation facets. In the last pectoral vertebra, there is also a broad, but only slightly visible, ridge developed at the intersection of lateral and ventral edges. In the third pectoral vertebra the rib articulation section differs from that of the second one in that it is situated more dorsally. The transverse processes are directed almost straight vertically. A distinct ridge is present at the posterior and ventral side of the processes, but both are not as sharp as in first two pectorals. The rib facets are broad and triangular in shape, with a long, straight dorsal margin and shorter, ventromedially directed anterior and posterior sides. The mentioned ridge at the intersection of the lateral and ventral edge is broader and more distinct than in the next to last pectoral vertebra.

Dorsal Vertebrae—Of the dorsal vertebral column only six vertebrae are present, thus only about 1/3 of the actual number, compared with e.g. *Hydralmosaurus serpentinus* where the number is 19 (Welles, 1952). Cope (1869: 49) thought that 10 dorsals were missing; Welles (1952:54) believed the number was 18. The first and second preserved dorsals belong into the anterior section of the column and may represent positions four and five. The rib facets are situated at the level of the neural canal. The transverse processes, which are completely preserved in the ?fifth vertebra, are more flattened dorsoventrally (although this is probably also effected by the compaction) and slightly oblique posterodorsally. The anterior and posterior sides of the processes bear a distinct ridge along their margins.

The rib facets are situated at a higher level than the neck of the transverse processes and are thus somewhat separated from them. They are broad oval to rectangular in outline. The centrum of the ?fifth dorsal is almost circular; its articulation facets are only very slightly concave. Also the lateral sides of the centrum show a horizontal depression.

The next preserved centrum might represent the seventh or eight dorsal. Only the basal parts of the transverse processes are preserved. As in the ?fifth dorsal they are dorsoventrally narrow. The articulation facets of the centrum are circular and the edges are rather sharp, not well rounded as in the cervicals. Also a longitudinal concavity is present at the lateral sides of the centrum, beneath the transverse processes. The next vertebra is only represented by the centrum. Here the rib facets were situated clearly over the level of the centrum, so that this vertebra might belong into the mid-dorsal section. The last two vertebrae represent another mid-dorsal, as well as large parts of a posterior dorsal vertebra. The mid-dorsal is completely preserved (Figure 5B, C). The shape of its centrum corresponds with that of the previously described ones. The rib facets are situated over the level the centrum. The transverse processes are very elongate. Their dorsal surfaces are slightly horizontally curved from the edge of the neural spine to the rib articulation surface. The later is slightly vertically convex. The ventral margin is more prominently vertically convex. The anterior and posterior edges of the transversal processes bear sharp ridges. The shaft has a broad oval cross-section. The rib facets are situated prominently higher than the shaft. They are slightly oblique posteriorly and are broad oval in outline. The pre-zygapophyses are shorter than those of the cervical and pectoral vertebrae and reach over the level of the centrum only with about the anterior third of their length. The post-zygapophyses are still very prominent and reach over the level of the centrum with about the posterior half of their length. The anterior hiatus is very long, rather deep, and occupies about 60% of the length of the neural spines. It thereby thins out dorsally and thus has an elongated triangular outline. The posterior hiatus is much shorter and only about half as long as the anterior one. Dorsal of the hiatuses, the neural spine becomes extraordinarily thin as can be observed posteriorly. The last vertebra that belongs in the posterior section of the column is only partially present on the left side as the transversal process, the pre-zygapophyses and most of the centrum are missing. The neural canal is circular and surrounded by very thick neural arches. The transverse process is shorter and more robust than in the previously described vertebra. Its basal sections at the neural arches are very elongate anteroposteriorly and are broad ovals in cross section. Laterally, the process, and especially its

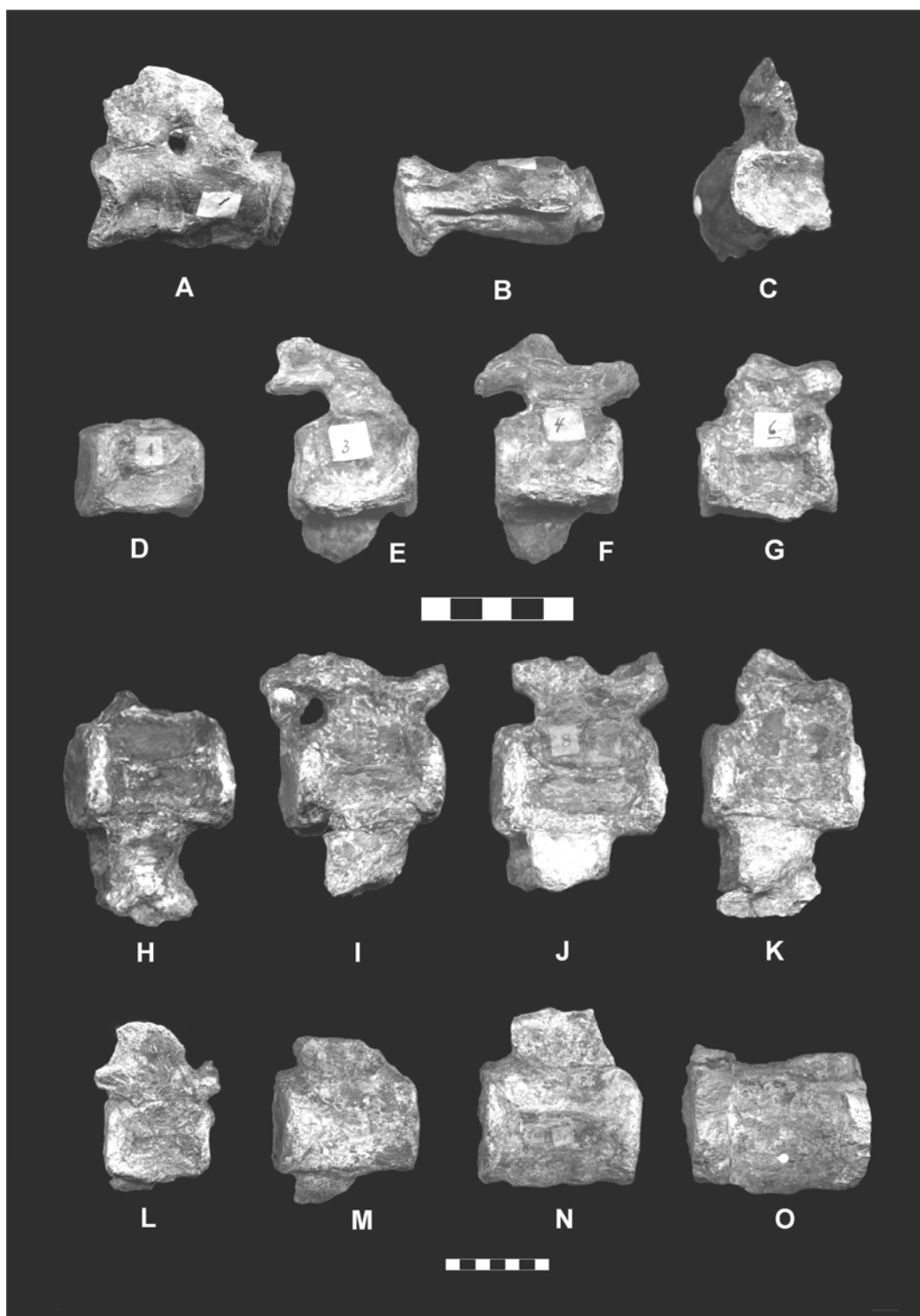


FIGURE 4. *Elasmosaurus platyurus* Cope 1868. Cervical vertebrae. A-C Atlas-axis complex with attached occipital condyle in A. lateral, B. ventral and C. posterior view. D-K Ten anteriormost cervical vertebrae in lateral views. D. cervical vertebra 3, E. cervical vertebra 4, F. cervical vertebra 5, G. cervical vertebra 6, H. cervical vertebra 7, I. cervical vertebra 8, J. cervical vertebra 9, K. cervical vertebra 10. Scale = 5 cm. L-O. Cervical vertebra examples from the anterior-, mid- and posterior cervical region in lateral views (size reduced). L. cervical vertebra 20, M. cervical vertebra 30, N. cervical vertebra 40, O. cervical vertebra 49. Scale = 7 cm.

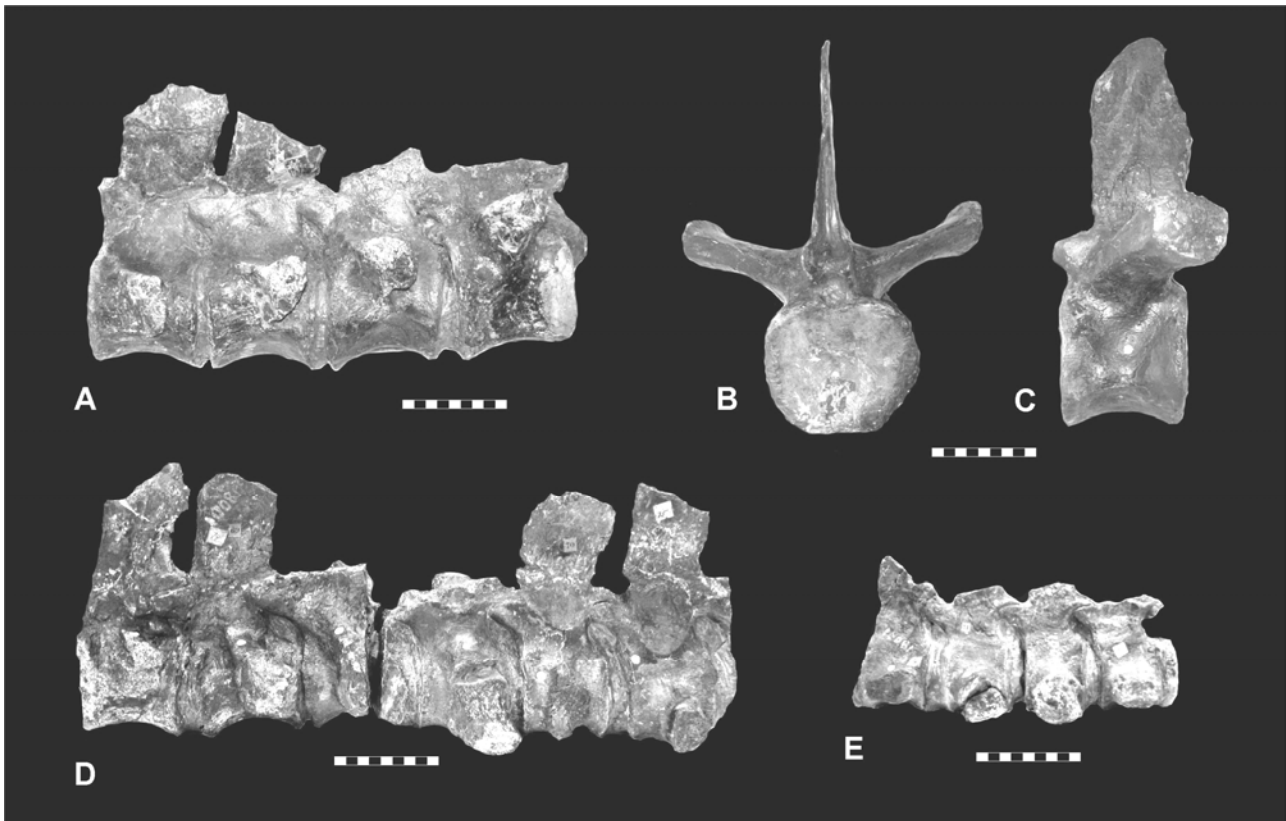


FIGURE 5. *Elasmosaurus platyurus* Cope 1868. A. Last cervical and pectoral vertebrae in lateral view. B. Mid-dorsal vertebra in anterior and C. lateral view. D. Sacral vertebral column associate with the two anterior-most caudal vertebrae in lateral view. E. Posterior caudal vertebrae in lateral view. Scales = 9 cm.

anterior side, curve posteriorly. It thereby becomes a high oval in outline, so that the lateral surface of the anterior side of the process is formed as a high plate. The posterior edge is generally thinner and also forms a distinct ridge in its medial half. The lateral half is expanded dorsoventrally. The rib facet is oval in outline. Of the hiatuses, only the posterior one is visible. It is larger than in the previously described one and occupies about 50% of the neural spine. The latter also has a very thin posterior edge above the hiatus.

Sacral Vertebrae—An articulated series of four sacra is present (Figure 5 D). In all vertebrae the transverse processes are very short. In the first sacral, the rib facets are situated in the posterodorsal section of the centrum and are not as prominent as in the others. They are posteromedially directed and have a somewhat triangular outline, with a concave anterior edge. On the dorsal side, a distinct, but short and rather broad, anterior ridge is formed. In the second sacral vertebra, the rib facets are more prominent than in the first and are dorsoventrally elongated oval in shape. They are situated posterior to the midline of the

centrum, but in its dorsal half and are only slightly posteriorly directed. The anterodorsal ridge is longer than in the first sacral. In the third sacral, the rib facets are also dorsoventrally elongated ovals and are situated at about the same level as in the second one, but are clearly more prominent and about twice as large as in the first sacral centrum. They are slightly posteriorly orientated. The dorsal part of the transverse process is situated at about the same level as the dorsal edge of the neural canal. It is well rounded transversely and forms an anterior edge that is not as distinct as in the second sacral. The rib facets of the fourth sacral are slightly larger than those of the third, and occupy almost the entire lateral margin of the centrum. The dorsal side of the transverse process is well rounded and therefore distinctly separated from the surface of the centrum. The rib facets have an almost straight lateral orientation. Basal fragments of the sacral ribs are attached to the second, third and fourth centrum. The pre-zygapophyses are rather prominent and reach over the level of the centrum for almost their entire length. The post-zygapophyses are still connected to

the pre-zygapophyses so that no clear statement about their length can be given. The neural spines are present at the first and second vertebra, but are incomplete and somewhat compressed laterally so that the shape of the hiatuses cannot be observed. The ventral sides of the centra are well rounded and bear a pair of nutritive foramina that is separated by a broad but low ridge.

Caudal Vertebrae—A series of 18 caudal vertebrae is present, in which the first two are in the same block containing the sacral vertebrae (Figure 5D) and are attached by matrix. The first caudal can clearly be distinguished from the sacrals by the smaller size of the rib facets, which are only about half as large as those of the last sacral, and their position in the ventral half of the centrum. They are almost circular in shape and in the first and second caudal vertebrae also bear a narrow horizontal keel in the middle of their dorsal side. The rib facets are situated in the ventral section of the centra throughout the caudal vertebral column. They become larger and broader oval in shape from the third caudal vertebra onwards. In the 6th-13th vertebra, they are very large and occupy almost the entire lateroventral margin of the centrum. In the 14th to 18th vertebra, the rib facets are still prominent but somewhat smaller compared to the size of the centra (Figure 5E). The edges of the facets are rather sharp in the anterior caudals and become well rounded in the posterior ones. As in the other vertebrae, the pre-zygapophyses reach over the level of the centra for almost their entire length while the post-zygapophyses reach over this level by about half of their length. The neural spines are rather completely preserved in the first, second, third and seventh caudal, but are compressed laterally at their basis. Ventrally, the surfaces for the haemapophyses are first clearly visible in the fifth caudal, although according structures are slightly visible in the third and fourth caudal too, but here no depressions for the articulation are present. The ventral margin of the centra is well rounded in the first, second and third vertebra, rather plain and just slightly concave in the fourth and fifth centrum, and strongly transversally concave from the sixth to the 18th vertebra. It should be noted that Cope (1870) stated that some 30 caudals were missing, however, the usual number of caudal vertebrae in elasmosaurs is around 30 (Welles, 1952).

Pectoral and Pelvic Girdles—Cope (1869, 1875) described and figured large parts of the pectoral and pelvic girdles (Figure 6). These elements could not be located in the collection of the Academy of Natural Sciences in Philadelphia. Williston (1906: 225) had already stated: "Unfortunately, the type specimen of *Elasmosaurus* no longer has the girdles described by Cope. What has become of them is not known". Carpenter (1999: 152) pointed out that the girdles possibly were destroyed while on loan to Waterhouse Hawkins, who, with his assistant, prepared them out of the hard concretion (Cope, 1869: 51). Cope mentioned

to Turner that Hawkins was going to reconstruct *Elasmosaurus* for a planned Paleozoic Park in New York Central Park (Almy, 1987). However, this project came to an end on May 3, 1871 when all of Hawkins work was destroyed by vandals (Colbert and Beneker, 1959). It might well be possible that the missing girdle elements were in Hawkins workshop at that time and would have also been destroyed. Conspicuously, nothing about their loss was mentioned in Cope's 1875 publication.

The illustrations provided by Cope (1869, 1870) are not very detailed, but still give an impression about the shape of the bones. One scapula and the posterior part of another, as well as the anterior portions of both coracoids, had been preserved, whereas the pelvic girdle was complete. Welles (1952: 56-59) redescribed the missing parts on basis of Cope's figures and descriptions and concluded that (1) Cope's clavicae or procoracoida are the scapulae, as has been suggested before by Seeley (1874); (2) the fused scapulae met in the midline with no trace of a median bar; (3) the dorsal processes of the scapulae were very broad and the scapular neck was rather long; (4) the scapulocoracoid suture was probably running to the center of the glenoid; (5) the scapular foramen are too long in Cope's reconstructions and were separated by a pectoral bar; (6) the anteromedial growth of the scapulae probably included the clavicular arch and (7) a pelvic bar was present. Welles (1952: 59) furthermore pointed out that in Cope's reconstruction the greatest width of the pubes is at the front of the acetabulum, whereas in other elasmosaurs the pubes have anterolaterally directed external borders.

All other features, which can be taken from the data provided by Cope (1869, 1870) are synapomorphic for the *Elasmosauridae* and shall therefore not be discussed.

DISCUSSION

Although relatively incomplete, the type specimen of *Elasmosaurus platyrus* is of importance as it represents the first described and nominal member of the *Elasmosauridae* and the only specimen clearly referable to this taxon. In the North American Cretaceous, elasmosaurs are common, but are represented mostly by isolated skeletal elements. A number of genera have been described based upon these remains (see Welles, 1952, 1962). In recent reviews by Carpenter (1999) and Storrs (1999) many taxa have been synonymized so that, besides *Elasmosaurus*, currently ten elasmosaur genera are known from the Cretaceous of North America. These are (in stratigraphic order): *Libonectes* Carpenter (1997, Britton Formation, Turonian), *Thalassomedon* Welles (1943, Graneros Shale and Niobrara Formation, Coniacian-Campanian), *Hydralmosaurus* and *Styxosaurus* both Welles (1943, Niobrara Formation

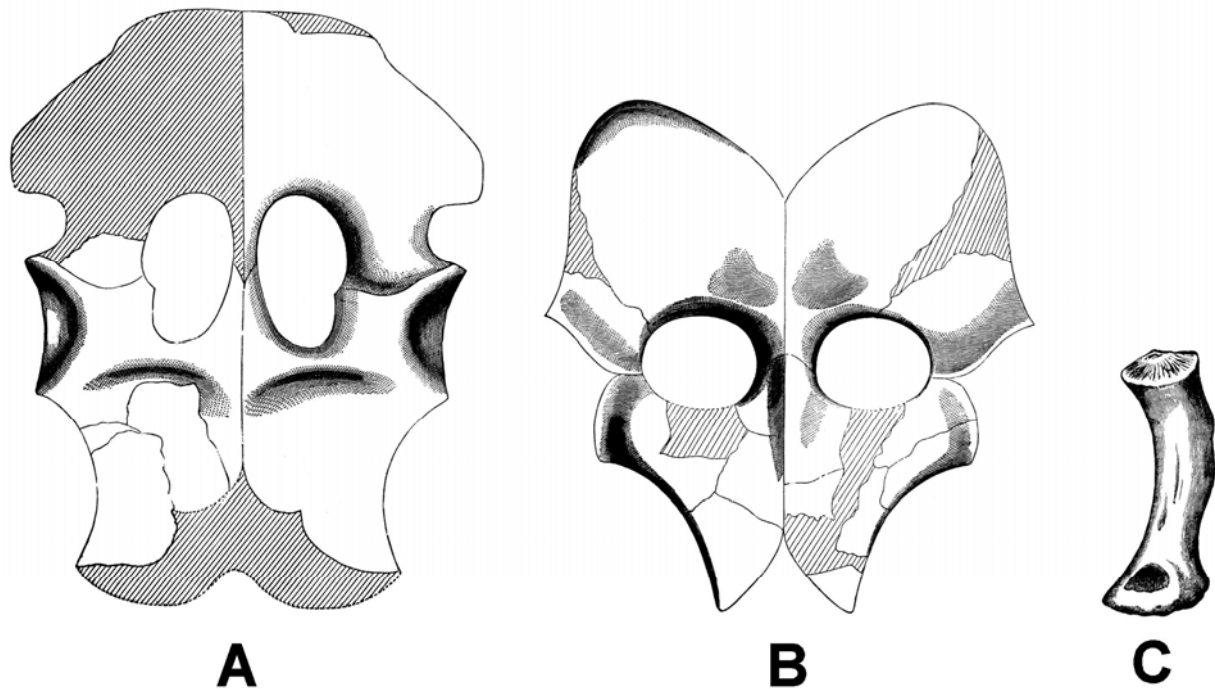


FIGURE 6. *Elasmosaurus platyurus* Cope 1868. Original reconstructions of the pectoral- and pelvic girdles of Cope (from Cope, 1869). A. Pectoral girdle, B. Pelvic girdle, C. Ilium. Not to scale.

and Pierre Shale formations, Campanian), *Terminonatator* Sato (2003, Bearpaw Formation, Campanian), and *Hydrotherosaurus*, Welles (1943), *Morenosaurus*, *Aphrosaurus*, and *Fresnosaurus* all Welles, (1943, Moreno Formation, Maastrichtian). The latter genera *Morenosaurus*, *Aphrosaurus* and *Fresnosaurus* are only based upon postcranial material. In the following, the features of the type material of *Elasmosaurus platyurus* are discussed and compared.

Cranial Remains—The premaxilla bears more than five teeth (for character discussion see Sachs, 2005: character 2). Primitively plesiosauroids and most elasmosaurs have five teeth per premaxilla. Exceptions among the Elasmosauridae are *Terminonatator* (Sato, 2003) with nine teeth and *Aristonectes* 10-13 teeth per premaxilla (Gasparini et al., 2003).

The dentary symphysis extends to a point between the fourth and fifth tooth in the dentary. This condition is also present in *Tuarangisaurus australis* (Sachs, 2005), *Hydrotherosaurus* and *Libonectes* (Carpenter, 1997: fig. 2). For the other elasmosaurid taxa, the information is not provided in the literature.

Cervical Vertebrae—Atlas-axis complex is long and low. In all sauropterygian taxa, except for some members of the Elasmosauridae, the axis centrum is

either shorter than high or about as long as high. The only elasmosaur taxa where the condition present in *Elasmosaurus platyurus* is known are *Styxosaurus* (Welles and Bump 1949; Sachs, 2004) and *Hydralmosaurus* (Cope, 1877). It thus can be considered as an advanced feature (see also Carpenter 1999, character 16; Sachs, 2004).

The number of cervical vertebrae is higher than 60 (for character discussion see Sachs, 2005, character 18). Including the atlas-axis complex, the type specimen of *E. platyurus* (ANSP 10081) has 71 vertebrae in the neck. Various researchers have given different numbers of cervical vertebrae for this specimen. According to Cope (1869, 1875), 68 1/2 cervicals are present, to which he added another 3 1/2 that he mentioned as being lost. Wegner (1914) gives a number of 60-78 cervicals; Welles (1949, 1952), Brown (1981) and Storrs (1999) state 71 cervicals; Carpenter (1997) reported 74 cervicals and then (Carpenter, 1999) revised his count to 72 cervicals; Sachs (2005) mistakenly also stated 72 cervicals; whereas Welles (1943) also stated that there were 74 cervicals. Williston (1906) gave a total of 76 vertebrae for the neck of *Elasmosaurus*. Apparently, some of the

pectoral vertebrae have been included in the higher counts.

More than 60 cervical vertebrae is a very advanced number among the Plesiosauroidea. In the Jurassic elasmosaurid *Occitanosaurus* the number is 43 (Bardet et al., 1999). However the early Cretaceous elasmosaurid *Brancasaurus* has only 37 cervical vertebrae (Wegner, 1914). The number is higher than 60 in *Libonectes* (=62, Carpenter, 1999), *Thalassomedon* (=62, Welles, 1943), *Styxosaurus* (=62, Carpenter, 1999) and *Hydralmosaurus* (=63, Carpenter, 1999). The number of cervicals is unknown in *Aphrosaurus*, *Fresnosaurus* and *Morenosaurus* (Welles, 1943). The only sauropterygian where the number of cervical vertebrae is higher than 70 is *Elasmosaurus platyurus*, accordingly this character is a clear autapomorphy of *Elasmosaurus* and can be considered as an advanced feature.

The anterior cervical vertebrae are long and low (for character discussion see Sachs, 2005: character 17). As with the axis centrum, the shape of the anterior cervical vertebrae is usually either high and short (e.g. in the Pliosauridae, Tarlo, 1960) or about as long as high (e.g. in the Plesiosauridae, Brown, 1981). The centra become longer than high in most elasmosaur taxa, like *Styxosaurus* (Sachs 2004), *Hydralmosaurus* (Cope, 1877), *Libonectes* (Welles, 1949), *Occitanosaurus* (Bardet et al., 1999), *Callawayasaurus* (Welles, 1962), *Terminonatator* (Sato, 2003), *Hydrotherosaurus* (Welles, 1943) and *Tuarangisaurus* (Wiffen and Moisley, 1986; Sachs 2005). The condition is unknown in *Aphrosaurus*, *Fresnosaurus* and *Morenosaurus* (Welles, 1943).

A longitudinal lateral crest is present in the anterior cervical vertebrae. This character has been discussed before by Brown (1981, 1993), Carpenter (1999) and Sachs (2004) and is synapomorphic for the Elasmosauridae.

Pectoral and Dorsal Vertebrae—Three pectorals are known in *Occitanosaurus* (Bardet et al. 1999), *Brancasaurus* (Wegner, 1914), *Styxosaurus* (Welles and Bump, 1949), *Thalassomedon* (Welles, 1943), *Aphrosaurus* (Welles, 1952), and *Hydralmosaurus* (Welles, 1952), thus this number is common among the Elasmosauridae, although there are only two pectorals present in *Callawayasaurus* (Welles 1962), *Morenosaurus* (Welles, 1952), and *Hydrotherosaurus* (Welles, 1943). The number is unknown for *Tuarangisaurus* (Wiffen and Moisley, 1986; Sachs, 2005), *Fresnosaurus* (Welles, 1952) and *Aristonectes* (Gasparini et al., 2003) and is not provided for *Libonectes* (Welles, 1949).

Dorsal vertebrae are not diagnostic at genus level in the Upper Cretaceous elasmosaurs and are thus not useful for comparison.

Sacral and Caudal Vertebrae—The number of sacral vertebrae is four in the type specimen of *Elasmosaurus platyurus*. Among the Elasmosauridae

four sacrals are the usual number as seen in *Occitanosaurus* (Bardet et al., 1999), *Terminonatator* (Sato, 2003), *Styxosaurus* (Sachs, 2004) or *Hydralmosaurus* (Welles, 1952). Only three are present in *Brancasaurus* (Wegner, 1914), *Thalassomedon* (Welles, 1943), *Morenosaurus* (Welles, 1943), and *Hydrotherosaurus* (Welles, 1943). The number is unknown in *Libonectes* (Welles, 1949), *Tuarangisaurus* (Wiffen & Moisley, 1986; Sachs, 2005), *Callawayasaurus* (Welles, 1962) *Aristonectes* (Gasparini et al., 2003), *Aphrosaurus* (Welles, 1943) and *Fresnosaurus* (Welles, 1943).

The tail is relatively complete, consisting of 18 vertebrae, but like the dorsal vertebrae also caudals are not diagnostic among Cretaceous elasmosaurs and can thus not be used for comparisons.

Pectoral and Pelvic Girdle—As mentioned before, the pectoral and pelvic girdles are lost, so that the comparative observations are totally based upon the descriptions and figures of Cope (1869, 1870) and the conclusions and figure of Welles (1952).

In the pectoral girdle the most conspicuous feature is the long pectoral bar. Carpenter (1999) discussed this feature and mentioned that according to Brown (1981) there is an ontogenetic variation of this character (demonstrated with an ontogenetic series of *Cryptoclidus eurymerus* Phillips, 1871), in which the bar is absent in juvenile and present in adult individuals. Carpenter (1999) states that in *Pistosaurus* and in some plesiosaurs, the bar is not developed in adult specimen, thus its absence must be considered as the plesiomorphic condition. Accordingly the presence of the pectoral bar in *Elasmosaurus platyurus* is an advanced feature.

On the scapula, the coracoidal margin appears to be about as long as the glenoidal one. Synapomorphically, the coracoidal margin is longer (usually 1.5 times) than the glenoidal one (Sachs, 2004), although we don't know how exact Cope's (1869) figure is in this respect. Also, the pelvic girdle has a rather unusual shape in Cope's reconstruction. Here the pubes are very prominent and are medially connected over their entire length. Their anterior edge is anterolaterally directed and almost straight, not gradually curved as usual in elasmosaurs. Also, the ischia are connected medially so that along the length of the pelvic girdle a medial pelvic bar is present. The latter is the most conspicuous feature because a bar is usually not present in plesiosaurs. Among the Elasmosauridae, a pelvic bar is known in *Brancasaurus brancai* from the Lower Cretaceous (Berriasian) of Germany and in a specimen from the Upper Cretaceous (Campanian-Maastrichtian) of Patagonia, described by Gasparini & Salgado (2000) as *Elasmosauridae* gen. et sp. indet. Of the latter, other elements also are similar in shape to ANSP 10081. However, on basis of the preserved material, it cannot be judged whether both specimens are congeneric.

RESULTS OF THE DISCUSSION

As shown here, *Elasmosaurus platyurus* comprises two clear autapomorphies; the presence of six teeth per premaxilla and 71 cervical vertebrae. Additionally, it shows one feature-complex that is unique within the Elasmosauridae: four sacral vertebrae + presence of a pelvic bar. *Elasmosaurus* also shows two advanced feature complexes that are also only present in *Styxosaurus* and *Hydralosaurus*: (1) long and low axis centrum + anterior cervical centra long and low. (2) number of cervicals higher than 60 + three pectoral vertebrae. *Elasmosaurus* is more advanced than most elasmosaur taxa as shown by the presence of six premaxillary teeth, a long and low axis centrum, the high number of 71 cervical vertebrae and the development of both a pectoral and a pelvic bar. A close relationship of *Elasmosaurus platyurus* with *Styxosaurus* and *Hydralosaurus* can be concluded on basis of the present material.

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LITERATURE CITED

- Almy, K. 1987. Thof's dragon and the letters of Capt. Theophilus H. Turner, M.D. Army. Kansas History 10: 170-200.
- Bardet, N., P. Godefroit, and J. Sciau. 1999. A new elasmosaurid plesiosaur from the lower Jurassic of southern France. Palaeontology 42:927-952.
- Blainville, H. D. de. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpetologie et d'Amphibiologie. Nouvelle Annales de la Musée de histoire Naturelles de Paris 3:233-296.
- Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. British Museum (Natural History) Bulletin, Geology Series 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. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. Pp. 191-216 in J. M. Callaway and E. L. Nicholls, (eds.), Ancient Marine Reptiles, Academic Press, San Diego.
- Carpenter, K. 1999. Revision of North American elasmosaurs from the Cretaceous of the western interior. Paludicola 2:148-173.
- Colbert, E. and K. Beneker. 1959. The Paleozoic Museum in Central Park, or the museum that never was. Curator 2:137-150.
- Cope, E. D. 1868. Remarks on a new enaliosaurian, *Elasmosaurus platyurus*. Proceedings of the Academy of Natural Sciences of Philadelphia 1868:92-93.
- Cope, E. D. 1869. Synopsis of the Extinct Batrachia Reptilia, and Aves of North America. Part I. Transactions of the American Philosophical Society, New Series 14:1-104.
- Cope, E. D. 1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Part II. Transactions of the American Philosophical Society, New Series 14:105-252.
- Cope, E. D. 1875. The Vertebrata of the Cretaceous formations of the West. Report of the United States Geological Survey of the Territories, pp. 1-303.
- Cope, E. D. 1877. Report on the geology of the region of the Judith River, Montana, and on vertebrate fossils obtained on or near the Missouri River. Bulletin of the United States Geological and Geographical Survey 3:565-597.
- Davidson, J. P. 1997. The bone sharp. The life of Edward Drinker Cope. Academy of Natural Sciences of Philadelphia Special Publications 17:1-237.
- Davidson, J. P. 2002. Bonehead mistakes: The background in scientific literature and illustrations from Edward Drinker Cope's first restoration of *Elasmosaurus platyurus*. Proceedings of the Academy of Natural Sciences of Philadelphia 152:215-240.
- Gasparini Z, and Salgado L. 2000. Elasmosáuridos (Plesiosauria) del Cretácico Tardío del norte de Patagonia. Revista Español de Paleontología 15:13-21.
- Gasparini Z., Bardet N., Martin J., and Fernández M. 2003. The elasmosaurid plesiosaur *Aristonectes cabrera* from the latest Cretaceous of South America and Antarctic. Journal of Vertebrate Paleontology 23:104-115.
- Gray, J.E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annales of the Philosophical Society of London 26:193-217.
- Phillips, J. 1871. Geology of Oxford and the valley of the Thames. 523 pp. Oxford.
- Sachs, S. 2004. Redescription of *Woolungasaurus glendowerensis* (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of Northeast

- Queensland. *Memoirs of the Queensland Museum* 49:215-233.
- Sachs, S. 2005. *Tuarangisaurus australis* sp. nov. (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of northeastern Queensland, with additional notes on the phylogeny of the Elasmosauridae. *Memoirs of the Queensland Museum* 50:429-444.
- Sato, T. 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia: Sauropterygia) from the Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23:89-103.
- Seeley, H. G. 1874. Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society of London* 30:436-449.
- Storrs, G. W. 1984. *Elasmosaurus platyurus* and a page from the Cope-Marsh war. *Discovery* 17:25-27.
- Storrs, G. W. 1999. An examination of Plesiosauria (Diapsida: Sauropterygia) from the Niobrara Chalk (Upper Cretaceous) of central North America. *University of Kansas Paleontological Contributions* 11:1-15.
- Tarlo, L. B. 1960. A review of the Upper Jurassic pliosaurs. *British Museum (Natural History) Bulletin, Geology Series* 4:145-189.
- Wegner, T. 1914. *Brancasaurus brancai* n. g., n. sp., ein Elasmosauride aus dem Wealden Westfalens. Pp. 234-305 in F. Schoendorf (ed.) *Branca Festschrift, Gebrüder Borntraeger, Stuttgart*.
- Welles, S. P. 1943. Elasmosaurid plesiosaurs with a description of the new material from California and Colorado. *University of California Memoirs* 13:125-254.
- Welles, S. P. 1949. A new elasmosaur from the Eagle Ford Shale of Texas. *Fondren Science Series* 1:1-28.
- Welles, S. P. 1952. A review of the North American Cretaceous elasmosaurs. *University of California Publications in Geological Sciences* 29:47-143.
- Welles, S. P. 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* 44:1-96.
- Welles, S. P., and J. Bump. 1949. *Alzadasaurus pambertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. *Journal of Paleontology* 23:521-535.
- Wiffen, J. and W. L. Moisley. 1986. Late Cretaceous reptiles (Families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics* 29:205-252.
- Williston, S. W. 1906. North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. *American Journal of Science Series* 4, 21:221-234.

ERRATA:

p. 92, column 2, “**Materials**” section:

Line 5-6 should read “71 cervical vertebrae including atlas-axis complex”

p. 104, column 2, “**Pectoral and Pelvic Girdle**” section, paragraph 2:

Line 6: *Cryptoclidus* is spelled incorrectly