AN EXAMINATION OF PLESIOSAURIA (DIAPSIDA: SAUROPTERYGIA) FROM THE NIOPRARA CHALK (UPPER CRETACEOUS) OF CENTRAL NORTH AMERICA

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Abstract.—Detailed examination of the holotypes of all described plesiosaurs from the Niobrara Chalk reveals that only three of the nine named species can be retained as valid. Polycotylus latipinnis Cope, 1869 and Dolichorhynchops osborni Williston, 1902 are based on adequate material and can be recognized as distinct species of polycotylid plesiosaur. Of the several elasmosaurian taxa from the Niobrara all save Styxosaurus snowii (Williston, 1890) are specifically nondiagnostic; however, more than one genus may be represented by the existing material. Several holotypes once considered to be of Niobrara origin were actually collected from other units.

INTRODUCTION

Sedimentary rocks of the Niobrara Chalk are an important constituent of the Late Cretaceous epicontinental seaway deposits of the American western interior. Stretching in outcrop from New Mexico to Canada and from Wyoming to Minnesota, they are best exposed and most well known from the Smoky Hill River valley of western Kansas. They form the classic unit indicative of a widespread, warm, stable marine environment in the interior of the North American continent during latest Turonian, Coniacian, Santonian, and early Campanian times (Hattin, 1982; Nicholls and Russell, 1990). Fine-grained, low-energy-regime carbonate rocks of the Smoky Hill Chalk Member (upper Santonian to lower Campanian) of the Niobrara Chalk that were deposited in this seaway are notable for the great range and abundance of marine vertebrates generally well preserved within them. Occasional vertebrate fossils occur also in the other (basal) member of the Niobrara Chalk, the Fort Hays Limestone Member.

Among the fish, turtles, mosasaurs, pterosaurs, birds, and other fossil vertebrates of the Niobrara Chalk, occasionally are found the remains of sauropterygian reptiles of the clade Plesiosauria. The plesiosaurs are secondarily aquatic tetrapods featuring symmetrical, limb-mediated (paraxial) locomotion through two pairs of similarly shaped and sized hyperphalangic flippers (Robinson, 1975; Godfrey, 1984; Storrs, 1993). They also possess a relatively elongate neck and have been known to paleontologists and the public alike for many years. Some of the most spectacular representatives of the Plesiosaursia, the giant elasmosaurs, were first identified from the American western interior (Cope, 1868a) before being recognized anywhere else in the world; and, in fact, Niobrara specimens helped form our initial image of these creatures (Williston, 1890, 1903, 1906, 1914).

At the most general level, however, the taxonomic status of many plesiosaurian taxa remains chaotic, and this particularly applies to the several species that have been described from the Niobrara Chalk. Niobrara specimens are uncommon and are often incomplete and the historical holotypes of such early workers as Cope and Marsh are notoriously so. Most species from the Niobrara Chalk have not been based upon fossils with associated cranial material, the most diagnostic parts of any specimen. This situation is compounded by our continued poor understanding of the range of ontogenetic and individual variation in plesiosaur morphology that is only beginning to be addressed in recent works (Carpenter, 1996, 1997; Storrs and Taylor, 1996; Storrs, 1997). Thus much of the plesiosaur type material from the Niobrara must be considered nondiagnostic at even the generic level. These factors...
demand that a review of Niobrara plesiosaurs be undertaken with a view toward clarifying the taxa represented. This preliminary report examines the described species and their holotypes (Table 1), but a fuller treatment must of necessity be deferred until better material becomes available. Some of the forms included below were once believed to have originated within the Niobrara Chalk, but are now known not to have done so. They are briefly discussed because of previous confusion about their stratigraphic provenance.

Some of the first western interior (Niobrara) plesiosaur specimens to be described and named were those made available to E. D. Cope by his collectors in Kansas. Other significant collections were made for O. C. Marsh by such individuals as S. W. Williston, B. F. Mudge, and H. T. Martin. Indeed, the rush to collect vertebrates from the Kansas chalk beds formed an early part of the competitive rivalry between Cope and Marsh (Schuchert and LeVene, 1940). Williston, as a collector for Marsh, was initially caught in the thick of the conflict but later became virtual dean of the Niobrara through his professorship at the University of Kansas (Shor, 1971; Martin, 1994). One of Cope’s early collectors, C. Sternberg, later provided specimens for Williston, as did H. T. Martin (Rogers, 1991; Martin, 1994). Essentially all of the Niobrara plesiosaur holotypes were thus described by either Cope or Williston in these early years until Welles (1943, 1952, 1962) began his monographic studies of Cretaceous plesiosaurs. Only Carpenter (1996, 1997) has examined any of this material meaningfully since that time, and the complete plesiosaur fauna has not been reviewed significantly. Planned study by Marsh of his material held at Yale (e.g., YPM 1125, 1130, 1640, 1645, and 1646) never came to fruition (Williston, 1906).

A serious deficiency of information exists regarding the biostratigraphic position of plesiosaurs from the Niobrara Chalk. Virtually all of the important plesiosaur material from the Niobrara Chalk comes from the Smoky Hill Chalk Member (Santonian to Campanian). More specific biostratigraphic zonations are usually absent, however, although Stewart (1990) identified most articulated polycotylid remains as having come from the uppermost beds of the Smoky Hill Chalk Member (Zone of Hesperornis). According to Stewart (1990), a few juvenile polycotylid propodials certainly came from the basal beds of the Smoky Hill Chalk Member (Zone of Protosphyraena pernicens). A single holotype, that of *Thalassonomosaurus nobilis*, came from the Fort Hays Limestone Member (Coniacian).


### SYSTEMATIC REVIEW

**DIAPSIDA Osborn, 1903**

**LEPIDOSAUROMORPHA Benton, 1985**

**SAUROPTERY gia Owen, 1860**

**PLESIOSAURIA de Blainville, 1835**

**ELASMOSAIRIDAE Cope, 1869**

**ALZADASAURUS Welles, 1943**

**ALZADASAURUS KANSASENSIS Welles, 1952**


*Ogniodirus ischiadicus* (Williston); Williston and Moodie, 1917, p. 61, referred specimen.

*Thalassiosaurus ischiadicus* (Williston); Welles, 1943, p. 191, referred specimen.


**Holotype.** YPM 1130.

**Accession Number.** 884.

**Field Number.** Saurian 190.

**Stratigraphy.** Smoky Hill Chalk Member, upper Niobrara Chalk (Santonian to Campanian). Carpenter (1990) was the first to assign this specimen to the Smoky Hill Chalk Member, and his determination is confirmed here following examination of the fossil’s matrix.

**Locality.** Wallace County, Kansas, on the specimen label but almost certainly Logan County, Kansas. Bennett (1990) related the history of the 1881 division of Wallace County into two parts, the current Logan County portion having produced virtually all Niobrara Chalk vertebrate fossil remains from Wallace County.

**Collectors.** H. A. Brous and B. F. Mudge, 1876.

**Material.** Sixty-three vertebral centra comprising 28 cervicals, 5 pectorals, 3 dorsals, 5 sacrals, and 22 caudals; associated spine and other vertebral fragments, rib fragments, the nearly complete right rear limb (Fig. 1.1), 6 isolated phalanges, and most of the pelvis. The right pubis is partially reconstructed, and the right ilium is not preserved. The pelvis was thought by Welles (1952) to have been lost but is currently stored in oversized shelving along with the limb but apart from the vertebrae and other bones.

**Remarks.** This specimen represents a relatively small, although mature elasmosaur. The centra and other remains are characteristically elasmosaurian but otherwise unremarkable. The pelvis and limb were figured originally by Williston (1906) as a referred specimen of "Elasmosaurus" *ischiadicus* and later referred by Williston and Moodie (1917) to *Ogniodirus ischiadicus*. The material was then transferred to *Thalassiosaurus ischiadicus* by Welles (1943) as part of the hypodigm of his new genus *Thalassiosaurus*. Later, Welles (1952) considered YPM 1130 to represent a new species of *Alzadasaurus* Welles, 1943, *A. kansasensis* (a
sentiment hinted at by Welles in 1943), and provided a supplemental description of the pelvis and limb. Finally, Welles (1962) expressed doubt about the validity the species *Alzadasaurus kansaensis* and the diagnostic quality of this specimen.

The fossil could possibly be assigned to *Alzadasaurus*, but it is unlikely to be specifically diagnostic. *Alzadasaurus* (also requiring revision) represents a moderately sized elasmosaurid (compared to, e.g., *Elasmosaurus* and *Thalassomedon*) with no longitudinal girdle bars, smoothly convex anterior pubic borders, ischia that are approximately as long as broad with uniformly tapering (almost pointed) distal ends, slender femora with a sharply truncated posterior distal corner, and little or no epipodal foramen in the hind limb. The present specimen broadly corresponds to this diagnosis but should be considered Elasmosauridae, indeterminate. Many of the putative *Alzadasaurus* characters may themselves represent relative immaturity, and it is not impossible that this specimen is an immature individual of *Styxosaurus snowii* (see p. 7, herein). The fragmentary nature of this fossil highlights the taxonomic problems inherent in specimens that lack cranial material. Plesiosaur postcrania are notoriously poor for identification below the family level because, although highly transformed from the terrestrial condition, they are relatively conservative with respect to each other (Storrs and Taylor, 1996; Storrs, 1997). A good deal of ontogenetic variation within taxa also is probable (Andrews, 1910; Watson, 1924; Brown, 1981).

**CIMOLIASAURUS** Leidy, 1851

*CIMOLIASAURUS* SNOWII Williston, 1890

See *Styxosaurus snowii* (Williston, 1890), p. 7 herein.

**DISCOSAURUS** Leidy, 1851

“DISCOSAURUS” CARINATUS Cope, 1868b

See *Elasmosaurus platyurus* Cope, 1868a, below.

**ELASMOSAURUS** Cope, 1868a

“ELASMOSAURUS” MARSHII Williston, 1906

See *Thalassonomosaurus marshii* (Williston, 1906), p. 7 herein.

“ELASMOSAURUS” NOBILIS Williston, 1906

See *Thalassonomosaurus nobilis* (Williston, 1906), p. 9 herein.

**ELASMOSAURUS PLATYURUS** Cope, 1868a

*Elasmosaurus platyurus* Cope, 1868a, p. 92.

*Discosaurus carinatus* Cope, 1868b, p. 68.

*Cimoliasaurus platyurus* (Cope); Zittel, 1890, p. 492.

*Elasmosaurus platyurus* Beard, 1901, p. 267.

*Elasmosaurus platyurus* Lane, 1947, p. 309.

*Holotype.—ANSP 10081 (not 18001 contra Welles, 1952, 1962).*

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**Table 1. Summary of taxonomic status of Niobrara Formation plesiosaurs and others discussed herein.**

The genera *Elasmosaurus* Cope, 1868a and *Hydralmosaurus* Welles, 1943 are presumed to be valid Pierre Shale taxa whose original descriptions are sufficient for generic diagnosis, but their type species *E. platyurus* Cope, 1868a and *H. serpentinus* (Cope, 1877), respectively, require additional characterization (new).

<table>
<thead>
<tr>
<th>Valid Niobrara species</th>
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<tr>
<td>Dolichorychops osborni Williston, 1902</td>
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<tr>
<td>Polycotylus latipinnis Cope, 1869</td>
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<tr>
<td>Styxosaurus snowii (Williston, 1890)</td>
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Other valid species examined

*Elasmosaurus platyurus* Cope, 1868a* [restricted to holotype]
*Hydralmosaurus serpentinus* (Cope, 1877)*

**Synonymies**

*Styxosaurus snowii* (Williston, 1890)

- *Cimoliasaurus snowii* Williston, 1890; *Elasmosaurus snowii* (Williston, 1901)
- *Elasmosaurus platyurus* Cope, 1868a
- *Discosaurus carinatus* Cope, 1868b*
- ?*Styxosaurus sp.*., herein
- *Elasmosaurus marshii* Williston, 1906; *Thalassonomosaurus marshii* (Williston, 1906)
- *Hydralmosaurus serpentinus* (Cope, 1877)
- *Elasmosaurus serpentinus* Cope, 1877)*
- *Polycotylus latipinnis* Cope, 1869
- *Polycotylus dolichopus* Williston, 1906
- *Hydralmosaurus serpentinus* (Cope, 1877)
- *Styxosaurus brownii* Welles, 1952*
- *Dolichorychops osborni* Williston, 1902
- *Trinacromerum osborni* (Williston, 1902)

**Nomina dubia**

*Elasmosauridae indeterminate*

- *Alzadasaurus kansaensis* Welles 1952
- *Elasmosauridae indeterminate* [Elasmosaurus ischiadicus Williston, 1903; *Ogmodirus ischiadicus* Williston, 1903; *Polycotylus ischiadicus* Williston, 1903; *Thalassiosaurus ischiadicus* (Williston, 1903)]
- *Elasmosauridae indeterminate* [Elasmosaurus nobilis Williston, 1906; *Thalassonomosaurus nobilis* (Williston, 1906)]
- *Elasmosauridae indeterminate* [Elasmosaurus sternbergi Williston, 1906]
- ?*Elasmosauridae indeterminate* [Ogmodirus martini Williston and Moodie, 1913]*
- ?*Elasmosauridae indeterminate* [Plesiosaurus gudo Cope, 1872]*
- Plesiosauria indeterminate [Piratosaurus plicatus* Leidy, 1865]*

*Holotype not from the Niobrara Formation, although once considered to be so.*

**Stratigraphy.**—Sharon Springs Shale Member, Pierre Shale (lower Campanian). Cope (1868c) stated (from second-hand information) that the specimen came from below the type occurrence of *Polycotylus latipinnis*. This would make the holotype of *E. platyurus* also from the Niobrara Chalk. Williston (1902, 1903), however, considered this designation erroneous and listed the horizon as “Fort Pierre.” This latter position, in the basal Sharon Springs Shale Member of the Pierre Shale, which immediately and conformably overlies the Smoky Hill Chalk Member, was
confirmed by Welles (1952), Carpenter (1990), and Storrs (personal observation, 1993) as the matrix is a gray shale with abundant selenite crystals. (The holotype of *P. latipinnis* is from a chalky limestone in the undoubted Niobrara, it must therefore in reality have been recovered below, not above, the level of *E. platyurus*.)

**Locality.**—Near McAllaster (probably at McAllaster Butte), Logan County, Kansas, in a ravine 24 km northwest of old Fort Wallace. The ravine debouches into the Smoky by the Henshaw Springs, according to the specimen label.

**Collector.**—Theophilus H. Turner, physician at Fort Wallace, Kansas, circa 1868 (see Almy, 1987). Three original vertebrae were sent to the Academy of Natural Sciences, Philadelphia by Dr. Turner via J. W. LeConte and presented to the Academy in 1868 (LeConte, 1868). The rest of the fossil was collected by Turner at Cope’s behest.

**Material.**—Originally the nearly complete vertebral column consisting of 71 cervical vertebrae, 5 pectorals, 5 dorsals, 6 sacrals, and 16 caudals; also collected were the base (occiput) of the skull, the partial rostrum, and thepectrum and pelvis. Only the vertebrae, rostrum, and occiput remain; the girdles are now lost (Williston, 1906).

**Remarks.**—This specimen is discussed here because of its significance, it being the original basis for the reconstruction of elasmosaurs and because it was first thought to be from the Niobrara Chalk. *Elasmosaurus platyurus* is among

Figure 1. Articulated appendages of Niobrara plesiosaurs in dorsal aspect: 1, right hindlimb of *Alzadasaurus kansasensis* Welles, 1952, holotype, YPM 1130, here referred to Elasmosauridae indet.; 2, left forelimb of *Thalassonomosaurus marshii* (Williston, 1906), holotype, YPM 1645, here referred to ?Styxosaurus sp.; 3, right hindlimb of *Polycotylus latipinnis* Cope, 1869, referred specimen, YPM 1125; scale bars = 15 cm (new).
the largest of all known plesiosaurs and had perhaps the longest neck of any known taxon. If Cope's (1869) interpretation of both the pectoral and pelvic girdles having a median bar is correct, this animal would be virtually unique among known elasmosaur genera. *Libonectes* (*Elasmosaurus* morgani) (Welles, 1949) from the Eagle Ford Shale of Texas has also been described as possessing a full median pectoral bar, but the pectrum in this specimen has also been lost. Carpenter (1997) distinguished *Libonectes* from *Elasmosaurus* on the basis of possible differences in the atlas-axis complex. The pelvis of *Libonectes morgani* is unknown.

Cope (1868b) once considered that the anteriormost cervical of ANSP 10081 represented a separate species, which he designated *Discosaurus carinatus*. As noted by Leidy (1870) and discussed by Welles (1943), the types of *Elasmosaurus platyurus* and *D. carinatus* are from the same individual, and *E. platyurus* has priority. See Welles (1962) and Storrs (1984) for discussions of Cope's handling of this material. It is doubtful that the species can presently be diagnosed from the currently available remains. Cope's (1869) description of the pectrum and pelvis, on the other hand, if accurate, may be sufficient for identification of a distinct genus (i.e., girdles each with a complete longitudinal median bar), as may the extremely elongate neck containing 71 cervical vertebrae. Carpenter (1997) has wisely restricted the name *E. platyurus* to the holotype.

**“ELASMOSAURUS” SERPENTINUS** Cope, 1877

See *Hydralmosaurus serpentinus* (Cope, 1877), below.

**“ELASMOSAURUS” SNOWII** (Williston, 1890)

See *Styxosaurus snowii* (Williston, 1890), p. 7 herein.

**ELASMOSAURUS STERNBERGI** Williston, 1906


*Holotype.—KUVP 1312.*

*Stratigraphy.—Smoky Hill Chalk Member, upper Niobrara Chalk (Santonian).*

*Locality.—Gove County, Kansas.*

*Collector.—C. H. Sternberg, 1895.*

*Material.—Two cervical and one dorsal vertebrae and a neural spine fragment. This is at variance with Williston (1906) and Welles (1952), who said that the vertebrae represented two dorsals.*

*Remarks.—Welles (1952, 1962) believed, on the basis of published dimensions alone, that these vertebrae were probably pliosaurian, perhaps polycotylid. This specimen emphatically is not a pliosaur but rather part of a giant elasmosaur as indicated first by Williston (1906). It is, however, generically indeterminate. Williston (1906) suggested that the fossil required description by virtue of the large size of the individual. As noted by Welles (1943), however, this is not a valid character for definition of a species. Some confusion also has existed regarding what material should be attributed to the type (Welles, 1952). KUVP 1302, which was involved in the numbering confusion, also is an indeterminate elasmosaur but one of smaller dimensions. The current status of this material has been discussed by Schultze et al. (1985). The size of the vertebrae numbered KUVP 1312 are in the range for those of *Thalassomedon* Welles, 1945 (see also Welles, 1952, 1970) and perhaps *Elasmosaurus*. Currently, *Thalassomedon* is known only from the Cenomanian. Welles's (1952) trouble with the *E. sternbergi* holotype illustrates the danger of using vertebral indices for identification. The seemingly short lengths of the centra are due partially to postmortem compression.

**HYDRALMOSAURUS Welles, 1943**

**HYDRALMOSAURUS SERPENTINUS** (Cope, 1877)

*Elasmosaurus serpentinus* Cope, 1877, p. 578.

*Hydralmosaurus serpentinus* (Cope); Welles, 1943, p. 185.

*Holotype.—AMNH 1495.*

*Stratigraphy.—Sharon Springs Shale Member, Pierre Shale (Campanian).* Cope (1877) described the provenance as Cretaceous No. 3 (i.e., Niobrara Chalk), but Welles (1962) pointed out that it is probably Pierre Shale. The matrix is a blue shale with selenite venation, quite unlike Niobrara rocks but identical to matrix associated with known Pierre specimens.

*Locality.—Cedar, Dixon, or Dakota County, Nebraska, on the southwestern side of the Missouri River between Yankton, South Dakota, and Sioux City, Iowa.*

*Collector.—E. D. Cope, 1876.*

*Material.—Most of a skeleton (approximately 58 cervical, 3 pectoral, 19 dorsal, 4 sacral, and 20 caudal vertebral centra) but lacking the skull. The limb girdles are moderately well preserved, although the clavicular arch is absent. Portions of at least two limbs are present. Some of this material currently is stored in oversized shelving.*

*Remarks.—Welles (1943) erected the genus *Hydralmosaurus* to contain the single specimen of *Elasmosaurus serpentinus* Cope, 1877. This fossil was further discussed by Welles (1952, 1962) and may represent a valid elasmosaurian taxon. The prominent posterior expansions of the distal ends of the propodials, particularly the humerus, are noteworthy and seemingly allow diagnosis of this genus. Also significant are the lack of any median longitudinal bar across the limb girdle fenestrae, the short and unexpanded coracoids, the jagged appearance of the anterior pubic border, the relatively long and blunt ilia, and the large epipodial foramen between the radius and ulna. Although pectoral morphology is clearly tied to ontogeny (Andrews, 1910; Watson, 1924; Brown, 1981), the absence of a longitudinal bar in an adult (versus the supposed condition in *Elasmosaurus*), may be diagnostic. *Hydralmosaurus* resembles “*Styxosaurus*” *browni* Welles, 1952 in regard to its very broad humerus and may be closely
allied. In any event, AMNH 1495 is not from the Niobrara Chalk.

**OGMODIRUS** Williston and Moodie, 1913

“**OGMODIRUS**” ISCHIADICUS (Williston, 1903)

See *Thalassiosaurus ischiadicus* (Williston, 1903), p. 7 herein.

**OGMODIRUS MARTINI** Williston and Moodie, 1913

*Ogmodirus martini* Williston and Moodie, 1913, p. 120.


?Elasmosauridae indeterminate; herein.

*Holotype.*—KUVP 441.

*Stratigraphy.*—Greenhorn Limestone (Cenomanian to Turonian). Williston and Moodie (1917) referred the holotype to the Fort Hays Limestone Member, basal Niobrara (Coniacian) or possibly uppermost Benton; however, it is undoubtedly from the lower Turonian or upper Cenomanian Greenhorn Limestone (Schultze et al., 1985).

*Locality.*—Near Aurora, Cloud County, Kansas.

*Collector.*—C. Boyce, 1909.

*Material.*—An incomplete juvenile skeleton consisting of 51 cervical and 18 caudal vertebral centra, various rib and spine fragments, and portions of the limbs and limb girdles. Most of the limb elements noted by Williston and Moodie (1913) and later figured (Williston and Moodie, 1917) are now lost, as are the girdle bones (Schultze et al., 1985).

*Remarks.*—This immature individual represents an animal of seemingly intermediate neck length, but while the relatively short centra (compared with typical elasmosaurs) are reminiscent of *Cimoliasaurus* Leidy, 1851 and *Scaniasaurus* Persson, 1959, they are nondiagnostic. The status of the Cimoliasauridae as a valid family is itself in doubt. The species was named in an abstract (Williston and Moodie, 1913) as *Ogmodirus martini*, but was unjustifiably emended to *O. martini* by Moodie (1916). This error was repeated by Williston and Moodie (1917). Welles (1962) called the species *nomen vanum* because of its youth (see Chorn and Whetstone, 1978, for a discussion of the appropriateness of this term). The taxon cannot be characterized on the basis of the relatively poor type material and is a *nomen dubium*.

**PLESIOSAURUS** De la Beche and Conybeare, 1821

“**PLESIOSAURUS**” GULO Cope, 1872

*Plesiosaurus gulo* Cope, 1872, p. 127.

“*Plesiosaurus*” *gulo* (Cope); Welles, 1952, p. 113.

?Elasmosauridae indeterminate; herein.

*Holotype.*—KUVP 1929.

*Stratigraphy.*—Cretaceous. Reported by Cope (1872) as from the Santonian Niobrara Chalk or Campanian Pierre Shale. Schultze et al. (1985) stated that the holotype is probably from the Lower Cretaceous Kiowa Formation, although they were at a loss to explain the absence of exposures of the Kiowa Formation in Logan County. Williston (1903, p. 7; 1908, p. 736) and Lane (1947, p. 305) listed the specimen as being from the Pierre Shale. Detailed study of the matrix and of its contained calcareous nanofossils may shed light on this dilemma. Nonetheless, the preservation of this skeleton is quite unlike that of typical specimens from the Niobrara Chalk, in particular the Smoky Hill Chalk Member of Logan County, and it can be discounted as having originated there. Only the Pierre Shale is exposed at McAllaster.

*Locality.*—Sheridan (now McAllaster), Logan County, Kansas.

*Collector.*—Joseph Savage of Leavenworth, Kansas.

*Material.*—Eleven cervical, 13 dorsal, and other vertebrae, as well as parts of the limb girdles.

*Remarks.*—As discussed by Schultze et al. (1985), this material cannot be distinguished now from other poorly preserved bones also catalogued as KUVP 1329. All of the material is nevertheless nondiagnostic and certainly does not belong to the Liassic genus *Plesiosaurus* De la Beche and Conybeare, 1821. In many regards, *Plesiosaurus* has become a wastebasket taxon. Many poor specimens from numerous localities around the world have been assigned to it, but few of these represent *Plesiosaurus* proper. The genus should be restricted to *Plesiosaurus dolichodeirus* and *P. guilemiimperatoris*, following recent revision (Storr, 1997).

**POLYCOTYLUS** Cope, 1869

“**POLYCOTYLUS**” ISCHIADICUS Williston, 1903

See *Thalassiosaurus ischiadicus* (Williston, 1903), p. 7.

**STYXOSAURUS** Welles, 1943

**STYXOSAURUS BROWN** Welles, 1952

*Styxosaurus browni* Welles, 1952, p. 69.

*Hydralmosaurus serpentinus* (Cope); herein.

*Holotype.*—AMNH 5835.

*Stratigraphy.*—Sharon Springs Shale Member, Pierre Shale (Campanian). Barnum Brown’s field identification labeled the locality as Niobrara Chalk, but Welles (1962) stated that it was probably in reality the Pierre Shale. Carpenter (1990) agreed with the latter determination, referring the specimen to the Sharon Springs Shale Member. The presence of diagenetically formed selenite crystals, a gray shale matrix, and the general preservation of the fossil all suggest that it is from the Pierre Shale.

*Locality.*—Mule Creek, Niobrara County, Wyoming, 24 km west of Edgemont, South Dakota.

*Collector.*—Barnum Brown, 1904.

*Material.*—A laterally crushed skull, 75 vertebrae, ribs, the fragmented pectoral, one front limb, and numerous quartzite gastroliths of various sizes.

*Remarks.*—This is one of the better specimens of midcontinental North American elasmosaur, in that the skull is present, although crushed. As the fossil is not from
the Niobrara Chalk, little need be said here, although the limb and girdle elements are closely comparable to those of Hydralmosaurus Welles, 1943 with which it is likely to be synonymous. The great posterior expansion of the distal end of the humerus is remarkable. This is relatively larger than the expansion of Hydralmosaurus serpeninus but may be an ontogenetic effect. The Styxosaurus browni is said to be that of a larger individual. Welles (1952, 1962) provided the only discussions of this specimen. It requires further study, some of which is being undertaken by Carpenter (personal communication, 1994).

**STYXOSAURUS SNOWII** (Williston, 1890)

Figure 2.1

Cimoliasaurus (Elasmosaurus?) snowii Williston, 1890, p. 174.
Cimoliasaurus snowii Cope, 1894, p. 109.
Cimoliasaurus snowii (Williston); Williston, 1902, p. 242.
Elasmosaurus snowii (Williston); Williston, 1906, p. 226.
Elasmosaurus snowi Williston, 1907, p. 481.
Styxosaurus snowi (Williston); Welles, 1943, p. 188.

Holotype.—KUP 1301, on exhibit in the University of Kansas Natural History Museum, Lawrence.

Stratigraphy.—Smoky Hill Chalk Member, upper Niobrara Chalk (Santonian to Campanian).

Locality.—Hell Creek, Logan County, Kansas.

Collector.—Judge E. P. West, 1890.

Material.—An excellent, largely uncrushed skull (Fig. 2.1) and 28 to 30 articulated cervical vertebrae.

Diagnosis.—Elasmosaurid with low, thin sagittal crest, subovate supratemporal fenestrae, strongly posteriorly sloping suspensorium; preorbital and postorbital areas of skull subequal in length; external nare greatly retracted; anterior teeth large and interlocking in alternate fashion. Dif-

fars from other midcontinental elasmosaurs by greater retraction of external nare and general skull proportion (relatively shorter preorbital area in Libonectes, Hydralmosaurus, and Thalassomedon).

Remarks.—First described (Williston, 1890) as Cimoliasaurus [sic] (Elasmosaurus?) snowii, the specimen was transferred by Williston (1906) to Elasmosaurus snowii. Welles (1943) created the genus Styxosaurus for this specimen and then abandoned it (Welles, 1962), calling the material insufficient for diagnosis and the name a nomen vanum. The skull was generally well described by Williston (1903), but it is one of the best known for any elasmosaur and is therefore worthy of renewed study in light of recent advances in our understanding of sauropterygian phylo-

gy and cranial anatomy (e.g., Brown, 1981; Sues, 1987; Storrs, 1991, 1997; Storrs and Taylor, 1996; Carpenter, 1997). While the specimen is not directly comparable with many other holotypes, comparison with the skull of Hydralmosaurus serpeninus (which has a shorter preorbital area, among other differences) indicates that it bears no probable relationship to S. browni contra Welles (1952). The excellent quality of the material demands that the taxon be considered valid, although presently only the holotype can be considered to represent Styxosaurus snowii. The possibility that other specimens from the region may be referable to S. snowii should be explored more fully.

**THALASSOSAURUS Welles, 1943**

**THALASSOSAURUS ISCHIADICUS** (Williston, 1903)

_Polyctosaurus ischiadicus_ Williston, 1903, p. 10.

Elasmosaurus ischiadicus (Williston); Williston, 1906, p. 231, type specimen only.

_Ogmodirus ischiadicus_ (Williston); Williston and Moodie, 1917, p. 61, type specimen only.

Thalassosaurus ischiadicus (Williston); Welles, 1943, p. 191, type specimen only.

Elasmosauridae indeterminate; herein.

Holotype.—KUP 434.

Stratigraphy.—Smoky Hill Chalk Member, upper Niobrara Chalk (Santonian to Campanian).

Locality.—Plum Creek, Logan County, Kansas.

Collectors.—B. F. Mudge and S. W. Williston, 1874.

Material.—A young individual represented only by 19 vertebral centra (3 presacras, 4 sacrals, and 12 caudals), the ischia and ilia (pelvic elements now lost), and the proximal end of the right femur.

Remarks.—Originally described (Williston, 1903) as Polyctosaurus ischiadicus, the ischia of this species are clearly elasmosaurian, and the fossil was transferred to Elasmosaurus ischiadicus by Williston (1906). Williston and Moodie (1917) removed the specimen to Ogmodirus ischiadicus on the basis of its presumed status as a structural precursor of Elasmosaurus. This course of action cannot be justified currently. Welles (1943) erected the genus Thalassosaurus for KUP 434 and referred (Welles, 1943, 1952) many other specimens to this poorly defined taxon, but later (Welles, 1962) abandoned the genus and species altogether. This latter course is appropriate, as the fragmentary material is completely nondiagnostic below the familial level.

**THALASSONOMOSAURUS Welles, 1943**

**THALASSONOMOSAURUS MARSHII** (Williston, 1906)

Figure 1.2, 3.1

Elasmosaurus marshall Williston, 1906, fig. 4.
Elasmosaurus marshi Kuhn, 1935, p. 90.
Thalassonosaurus marshii (Williston); Welles, 1943, p. 189.

? Styxosaurus sp.; herein.

Holotype.—YPM 1645.

Accession Numbers.—2062, 2083.

Stratigraphy.—Niobrara Chalk, Yellow Chalk, probably the Smoky Hill Chalk Member (Santonian to Campanian). Yellow Chalk is an archaic lithostratigraphic division of the Smoky Hill Chalk Member that is actually based upon
Figure 2. Skulls and mounted skeleton of Niobrara plesiosaurs; 1, skull and anteriormost cervical vertebrae of *Styxosaurus snowii* (Williston, 1890), holotype, KUVP 1301; 2, mounted postcranial of *Dolichorhynchops osborni* Williston, 1902, holotype, KUVP 1300, mounted skull is a model; 3, skull of *Dolichorhynchops osborni* Williston, 1902, holotype, KUVP 1300; scale bars = 15 cm (new).
degree of weathering and is invalid for stratigraphic purposes (Williston, 1893, 1897; Stewart, 1990).

Locality.—Logan County, Kansas.

Collector.—H. T. Martin, 1889.

Material.—A moderately sized partial skeleton currently consisting of 14 vertebral centra (cervical, pectoral, and dorsal) [Williston (1906) listed 32 or 33 vertebrae, but the difference now cannot be accounted for]; numerous spine, centrum, and rib fragments, the left scapula (Fig. 3.1), numerous tiny girdle fragments, and the largely complete left forelimb (Fig. 1.2), which is now housed in oversized shelving. The type probably also includes 4 additional and certainly elasmosaurian vertebrae labeled Brimosaurus.

Remarks.—Described and figured as ?Elasmosaurus marshii by Williston (1906), this very fragmentary specimen nevertheless possesses a nearly complete scapula and forelimb, which are noteworthy. A broad, median suturing of the ventral plate of the scapula to itsformer twin is evident. This condition was also reported (Cope, 1869; Welles, 1949) for Elasmosaurus and Libonectes, but a prominent, sharp posterior projection of the ventral plate’s midline in YPM 1645 may not have contacted the coracoid to form a pectoral bar as in those genera. The adult nature of the specimen may account for this projection relative to the scapulae of other Niobrara-Pierre fossils. Watson (1924) suggested that the length of the median bar projection in elasmosaur might have been ontogenetically controlled.

The very remarkable, perhaps unique limb with its sigmoidal twist to the humerus, large epipodial foramen, and distinct supernumerary elements, however, clearly distinguish Thalassonomosaurus marshii from Hydralmosaurus. Williston (1906) believed the presumably reconstructed positioning of the limb elements to be largely correct. Welles (1943) recognized the uniqueness of the fossil by creating for it the genus Thalassonomosaurus; however, he reconsidered (Welles, 1962) only to suggest that without knowledge of the limb structure of Elasmosaurus, the fossil should best be identified as ?Elasmosaurus sp. pending discovery of better material. It should be noted, however, that Styxosaurus neither possesses girdle nor limb elements and that assignment of the T. marshii holotype to S. snowii is just as likely, perhaps more so considering that the Styxosaurus holotype is also from the upper Niobrara. If synonymous, S. snowii would have priority. A large forelimb epipodial foramen is known (Welles, 1949) in Libonectes but also in species of certain other taxa (e.g., the putative genus Alzadasaurus).

**THALASSONOMOSAURUS NOBILIS** (Williston, 1906)


*Thalassonomosaurus nobilis* (Williston); Welles, 1943, p. 190. Elasmosauridae indeterminate; herein.

**Holotype.**—YPM 1640.

**Accession Number.**—581.

**Stratigraphy.**—Fort Hays Limestone Member, lower Niobrara Chalk (Coniacian).

**Locality.**—4.8 km west of Jewell City, Jewell County, Kansas.

**Collector.**—B. F. Mudge, 11 May 1874.

**Material.**—A relatively small elasmosaur comprising 27 vertebrae from throughout the column (some complete but most preserved as isolated centra or partial centra) plus associated spine and other vertebral fragments, numerous rib fragments, the right scapula minus the dorsal process, the posterior flange of a coracoid, both ilia, numerous small additional portions of the pectoral and pelvic girdles, and various limb elements (the right femur and parts of the other propodial; epipodials, mesopodials, metapodials, and phalanges).

**Remarks.**—*Elasmosaurus nobilis* Williston, 1906 as originally described was transferred by Welles (1943) to Thalassonomosaurus merely on the basis of the possible presence of a supernumerary epipodial. Welles (1962) considered the material to be nondiagnostic. The taxon is certainly *nomen dubium* because the type material is so fragmentary. It can be considered Elasmosauridae indeterminate yet is somewhat similar to young adult specimens currently assigned to Alzadasaurus. For example, the weathered scapula displays no midline pectoral bar and little median contact with its neighbor, just as in putative Alzadasaurus, and may form part of a growth series for typical elasmosaurs. The holotype (first noted by Williston, 1897) is, however, notable for its apparent recovery from the lowermost (Coniacian) member of the Niobrara Chalk, from which vertebrate fossils are relatively rare. By itself, this fact is insufficient for diagnosis.

**POLYCOTYLIDAE** Williston, 1908

**DOLICHORHYNCHOPS** Williston, 1902

**DOLICHORHYNCHOPS ONSORNI** Williston, 1902

Figure 2.2, 2.3


*Trinacronterum osborni* (Williston); Williston, 1908, p. 715.

**Holotype.**—KUVP 1300.

**Stratigraphy.**—Smoky Hill Chalk Member, upper Niobrara Chalk (Campanian).

**Locality.**—Logan County, Kansas.

**Collector.**—C. H. Sterneberg, 1901.

**Material.**—A nearly complete skeleton mounted at the University of Kansas Natural History Museum (Fig. 2.2). The nearly perfect skull (Fig. 2.3) is maintained separately in the vertebrate paleontology collection of the museum.

**Diagnosis.**—*Dolichorhynchops osborni* Williston, 1902. Polycotylid plesiosaur with elongate head, facial region much attenuated; teeth nearly uniform in size, slender and sharp with prominent distal carinae; prefrontals and postfrontals distinct; parietals extending into a high crest; supraoccipital separated; internal nares small, included between vomer
Figure 3. Postcranial elements of Niobrara plesiosaurs; 1, left scapula of *Thalassonosaurus marshii* (Williston, 1906), holotype, YPM 1645, here referred to *?Stylosaurus* sp., in ventral aspect; 2, left humerus of *Polycotylus dolichopus* Williston, 1906, holotype, YPM 1646, here referred to *Polycotylus latipinnis* Cope, 1869, in ventral aspect; 3, 4, dorsal vertebra of *Polycotylus latipinnis* Cope, 1869, referred specimen, YPM 1125, in left lateral and anterior aspects, respectively; scale bars = 5 cm (new).
and palatine only; palatines broadly separated throughout; large pterygoid vacuity anteriorly; quadrate process of pterygoids short. Distinguished from Trinacromerum by its shorter, rounder supratemporal fenestrae and a vertically oriented suspensorium. Neck slightly longer than head, composed of 19 or 20 vertebrae; all presacras of nearly equal length and moderately concave, centra only slightly higher than long; neural spines short and blunt, uniform in length; clavicles and scapulae free; interclavicle with anterior and posterior emargination, the latter forming part of a large interclavicular fenestra. Anterior border of pubis convex. Ischium elongated but somewhat curved. Sacral end of ilium spatulate. Podial bones and phalanges cylindrical in section. Length approximately 3 meters. [Diagnosis modified from Williston, 1903, and Carpenter, 1996.]

**Remarks.**—Named in 1902, only later was the specimen described fully and figured (Williston, 1903). It is one of the best preserved of all plesiosaurs from the Niobrara Chalk and as such is sufficient to characterize the species. Williston (1902), however, erected a new genus, Dolichorhynchops, for the material. Later (Williston, 1908), he acknowledged the suspected (Williston, 1906, p. 234) synonymy of this genus with Trinacromerum Cragn, 1888 and transferred *D. osbornii* to the senior taxon. Welles (1962), believing that Cragn’s (1888) *Trinacromerum bentonianum* holotype (the genotypic species) was lost and unavailable for diagnosis, returned *T. osbornii* (and all other pycnotylids) to Dolichorhynchops. This is inappropriate and, in fact, the holotype of the type species *Trinacromerum* is now to be found at the United States National Museum in Washington, D.C. (USNM 10945) where most of it was deposited in 1967 by Welles and R. A. Long (personal communication, 1993) following its rediscovery at Colorado College, Colorado Springs, Colorado. Portions of the specimen were already residing at the Smithsonian (USNM). Recently, Carpenter (1989, 1996, 1997) has suggested that Trinacromerum and Dolichorhynchops are distinct and must both be retained. As the most recent study, his decision is accepted here, although some of the characters used for separation require further examination. It is possible that perceived differences in the postorbital region of the skull and suspensorium are related only to preservational or specific variation. The teeth of the two are far more similar to each other (relatively slender) than to Polycotylus, contra Carpenter (1996), and the vertebral counts are nearly, if not, identical. Given the ontogenetic control of limb girdle morphology, apparent differences here are also suspect. However, pending a thorough reexamination of both taxa, Carpenter’s (1996) judgment identifying Trinacromerum and Dolichorhynchops as separate genera is adopted here. As currently constituted, Trinacromerum is known from the Cenomanian and Turonian, while Dolichorhynchops occurs in the Campanian (and probably also the Santonian). Williston’s (1903) thorough description of *D. osbornii* requires no further comment. Of particular interest is Williston’s (1906) suggestion, recently reelaborated by Carpenter (1997), that the short neck of polycotylids is not a plesiomorphic character but one that had occurred independently on several occasions. Carpenter (1997) allies the Polycotylidae with the Elasmosauridae on the basis of palatal and basicranial features, concluding that polycotylids are not pliosaurs in the traditional sense.

**POLYCOTYLUS Cope, 1869**

**POLYCOTYLUS DOLICHOPUS Williston, 1906**

Figure 3.2


Dolichorhynchops sp. Welles, 1962, p. 66.

Polycotylus latipinnis Cope; herein.

**Holotype.**—YPM 1646.

**Accession Number.**—780.

**Field Number.**—Saurian 194.

**Stratigraphy.**—Niobrara Chalk. Member unknown, but most probably Smoky Hill Chalk Member (Santonian to Campanian).

**Locality.**—Wallace County, Kansas. As discussed above, this material is most probably from the present Logan County of Kansas.

**Collectors.**—H. A. Brous and B. F. Mudge, 1875.

**Material.**—One propodial and several small fragments of a limb girdle.

**Remarks.**—Williston (1906) designated the humerus (Fig. 3.2) and some mesopodials and epipodials (these latter two groups now lost) of YPM 1646 as the type of this species but figured the femur of a second individual (YPM 1642) from the Niobrara Chalk of Trego County. As a result of this figure, Welles (1962) considered the latter to be the holotype. Williston (1906) suggested that both individuals were conspecific; however, neither specimen is sufficiently distinct from Polycotylus latipinnis to justify erection of a new species, and *P. dolichopus* must be discarded. The prominent epipodial and supernumerary facets, large distal expansions, and slightly sigmoid nature of the shafts indicate that both propodials belong to *Polycotylus*, and in the absence of other distinguishing features they can be regarded as *Polycotylus latipinnis*.

**POLYCOTYLUS LATIPINNIS Cope, 1869**

Figure 1.3, 3.3, 3.4

Polycotylus latipinnis Cope, 1869, p. 36.

**Holotype.**—USNM 244534 and AMNH 1735.

**Stratigraphy.**—Smoky Hill Chalk Member, upper Niobrara Chalk (Campanian).

**Locality.**—Approximately 8 km west of Fort Wallace, on the plains near the Smoky Hill River, Wallace or (here again, perhaps) Logan County, Kansas. As the holotype of *P. latipinnis* is clearly from the Smoky Hill Chalk Member, it must have come from below, not above, the horizon of Elasmosaurus platyurus, as noted above. Cope (1869) considered that the reverse was the case, but Carpenter (1996) concludes that he mistook the locality as west rather than,
in fact, east of Fort Wallace, putting the locality near the border with Logan County.

**Collector.**—W. E. Webb.

**Material.**—Twenty-one vertebrae (one or perhaps two at the American Museum of Natural History), a partial ilium and other pelvic fragments, and parts of a hind limb (distant end of femur, possible tibia, several tarsals, metatarsals, and phalanges; thirteen of the smaller bones are at the American Museum, including the nine figured by Cope in 1869).

**Diagnosis.**—*Polycotylus latipinnis* Cope, 1869. Polycotylid plesiosaur with extremely short, amphicoelous vertebral centra (approximately half as long as high). Approximately 26 cervical vertebrae with deeply concave articular faces. Dorsal vertebrae with raised, central mammillae on articular faces and relatively pointed, narrow neural spines. Longitudinally ribbed teeth short and squat; dental ribs of equal length. Coracoid with complex, crenulated margin. Anterior border of pubis concave. Ischium very long and narrow; posterior process pointed, relatively longer and less curved than that of *Dolichorhynchops*. Ilium long, slender, and recurved; sacral end sharp. Propodials with slender shafts, expanded distal ends; distinct epipodial and supernumerary facets, more so than in *Dolichorhynchops* or *Trinacromerum*. Epipodial bones much broader than long. Podial bones and phalanges subquadrate (blocky).

**Remarks.**—As with the first elasmosaur it was Cope (1869) who described the first good material of a North American short-necked plesiosaur. This specimen, the holotype of the type species, is very fragmentary and normally would be considered nondiagnostic as, in fact, Welles (1962) regarded it (although Welles, in Welles and Gregg, 1971, accepted its validity). The vertebrae, however, are extremely short, and several of the dorsals possess a raised, central mammilla on each articular face. In both of these characteristics, the vertebrae can be distinguished from those of *Dolichorhynchops* and *Trinacromerum*. It thus appears that this species should be retained as a form of Niobrara *Polycotylus* distinct from *Dolichorhynchops*.

Williston (1906) referred an excellent specimen at Yale (YPM 1125, from the south side of the North Fork of the Smoky Hill River, 22 km east of Fort Wallace, Logan County, Kansas, O. C. Marsh collector, Yale College Scientific Expedition, 1870) to *P. latipinnis*, and this material aids greatly in the characterization of the taxon (Fig. 1.3, 3.3, 3.4). Without a doubt it is generically identical to the type, and no characters exist to suggest that it is specifically distinct. Numerous other partial individuals are known; for example, a limb in the Kansas collection (KUVP 5916) that was figured by Williston (1903) and additional, undescribed material from the Upper Cretaceous of Texas. The pectrum and pelvis of YPM 1125 were illustrated by Williston (1906). Carpenter (1996) accepted the validity of *P. latipinnis* on the basis of Williston’s referral of YPM 1125 and relied upon it for his descriptive review.
not part of a growth series, and a larger form such as *Elasmosaurus* are perhaps questionably represented.

Aside from the type materials discussed herein, other Niobrara plesiosaur specimens can be found in the collections of museums around the country, and some of these are of very high quality. Numerous referred or undescribed fossils of this sort are to be found not only at the institutions listed above but most notably also at the Sternberg Museum of Fort Hays State University in Hays, Kansas. Future study of such specimens will likely aid in the clarification of the composition of the Niobrara plesiosaur fauna as well as the biostratigraphic positions of taxa and aid in understanding the interrelationships of the Plesiosauria as a whole.

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