THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

August 1999 Number 11

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

Glenn W. Storrs

Cincinnati Museum Center, Geier Collections and Research Center, 1720 Gilbert Avenue, Cincinnati, OH 45202, storrsgw@email.uc.edu

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 Plesiosauria, 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 pernicosa*). A single holotype, that of *Thalassonomosaurus nobilis*, came from the Fort Hays Limestone Member (Coniacian).

Abbreviations for repositories cited in systematic review: AMNH, American Museum of Natural History, New York, New York; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; KUVP, University of Kansas Natural History Museum, Lawrence, Kansas; USNM, United States National Museum of Natural History, Washington, D.C.; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

SYSTEMATIC REVIEW

DIAPSIDA Osborn, 1903
LEPIDOSAUROMORPHA Benton, 1985
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
ELASMOSAURIDAE Cope, 1869
ALZADASAURUS Welles, 1943
ALZADASAURUS KANSASENSIS Welles, 1952

Figure 1.1

Elasmosaurus ischiadicus Williston, 1906, p. 231, referred specimen.

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

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

Alzadasaurus kansasensis Welles, 1952, p. 80.

Elasmosauridae indeterminate; herein.

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 *Ogmodirus 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 kansasensis* 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 posterodistal corner, and little or no epipodial 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 platurus Beard, 1901, p. 267.
Elasmosaurus platyuris Lane, 1947, p. 309.

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

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).

Valid Niobrara species
- *Dolichorhynchops osborni* Williston, 1902
- *Polycotylus latipinnis* Cope, 1869
- *Styxosaurus snowii* (Williston, 1890)

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, 1890)]
- *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 browni* Welles, 1952]*
- *Dolichorhynchops osborni* Williston, 1902
  - [*Trinacromerum osborni* (Williston, 1902)]

Nomina dubia
- Elasmosauridae indeterminate
  - [*Alzadasaurus kansasensis* 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 gulo* 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

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).

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 the pectrum 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

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 cervicals 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

Elasmosaurus sternbergi Williston, 1906, p. 232.
"*Elasmosaurus*" *sternbergi* (Williston); Welles, 1952, p. 116.

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, 1943 (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.
Ogmodirus martinii Moodie, 1916, p. 402.
?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 *Scanisaurus* 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. martinii* 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 1329.

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. guilelmiimperatoris*, following recent revision (Storrs, 1997).

POLYCOTYLUS Cope, 1869
"POLYCOTYLUS" ISCHIADICUS Williston, 1903

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

STYXOSAURUS Welles, 1943
STYXOSAURUS BROWNI 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 pectrum, 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 serpentinus* but may be an ontogenetic effect. The *Styxosaurus browni* type is 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

Cimoliosaurus (*Elasmosaurus?*) *snowii* Williston, 1890, p. 174.
Cimoliasaurus snovii 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 snowii (Williston); Welles, 1943, p. 188.

Holotype.—KUVP 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 nares greatly retracted; anterior teeth large and interlocking in alternate fashion. Differs from other midcontinental elasmosaurs by greater retraction of external nares and general skull proportion (relatively shorter preorbital area in *Libonectes*, *Hydralmosaurus*, and *Thalassomedon*).

Remarks.—First described (Williston, 1890) as *Cimoliosaurus* [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 phylogeny 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 serpentinus* (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 referrable to *S. snowii* should be explored more fully.

THALASSIOSAURUS Welles, 1943
THALASSIOSAURUS ISCHIADICUS (Williston, 1903)

Polycotylus 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.
Thalassiosaurus ischiadicus (Williston); Welles, 1943, p. 191, type specimen only.
Elasmosauridae indeterminate; herein.

Holotype.—KUVP 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 presacrals, 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 *Polycotylus 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 *Thalassiosaurus* for KUVP 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(?) *marshii* Williston, 1906, p. 229.
Elasmosaurus marshii Williston, 1906, fig. 4.
Elasmosaurus marschi Pravoslavlev, 1916, p. 333.
Elasmosaurus ? marshi Hay, 1930, p. 118.
Elasmosaurus marshi Kuhn, 1935, p. 90.
Thalassonomosaurus marshii (Williston); Welles, 1943, p. 189.
?*Styxosaurus* sp.; herein.

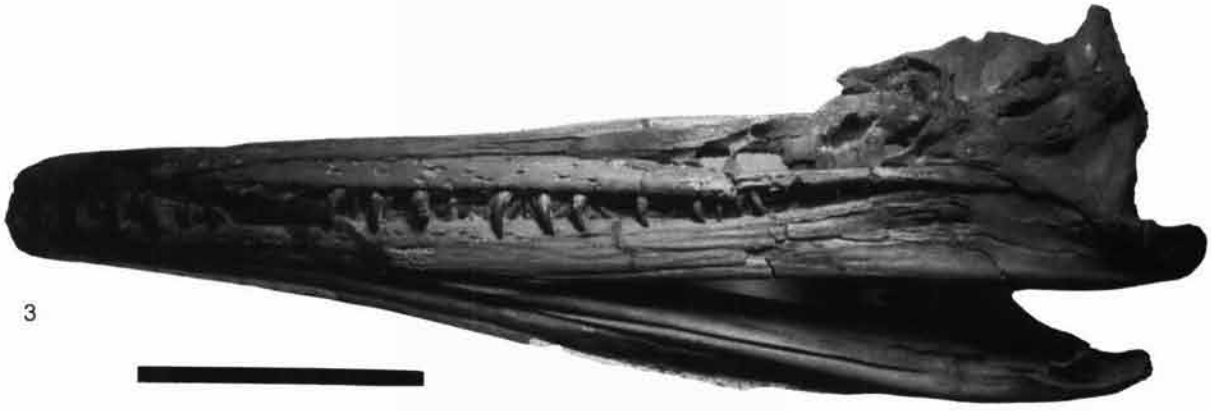
Holotype.—YPM 1645.

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

1

2



3

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 postcrania 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 its former 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 elasmosaurs 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)

Elasmosaurus nobilis Williston, 1906, p. 232.
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 propodials; 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 OSBORNI Williston, 1902

Figure 2.2, 2.3

Dolichorhynchops osborni Williston, 1902, p. 241.
Trinacromerum 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. Sternberg, 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; supraoccipitals separated; internal nares small, included between vomer

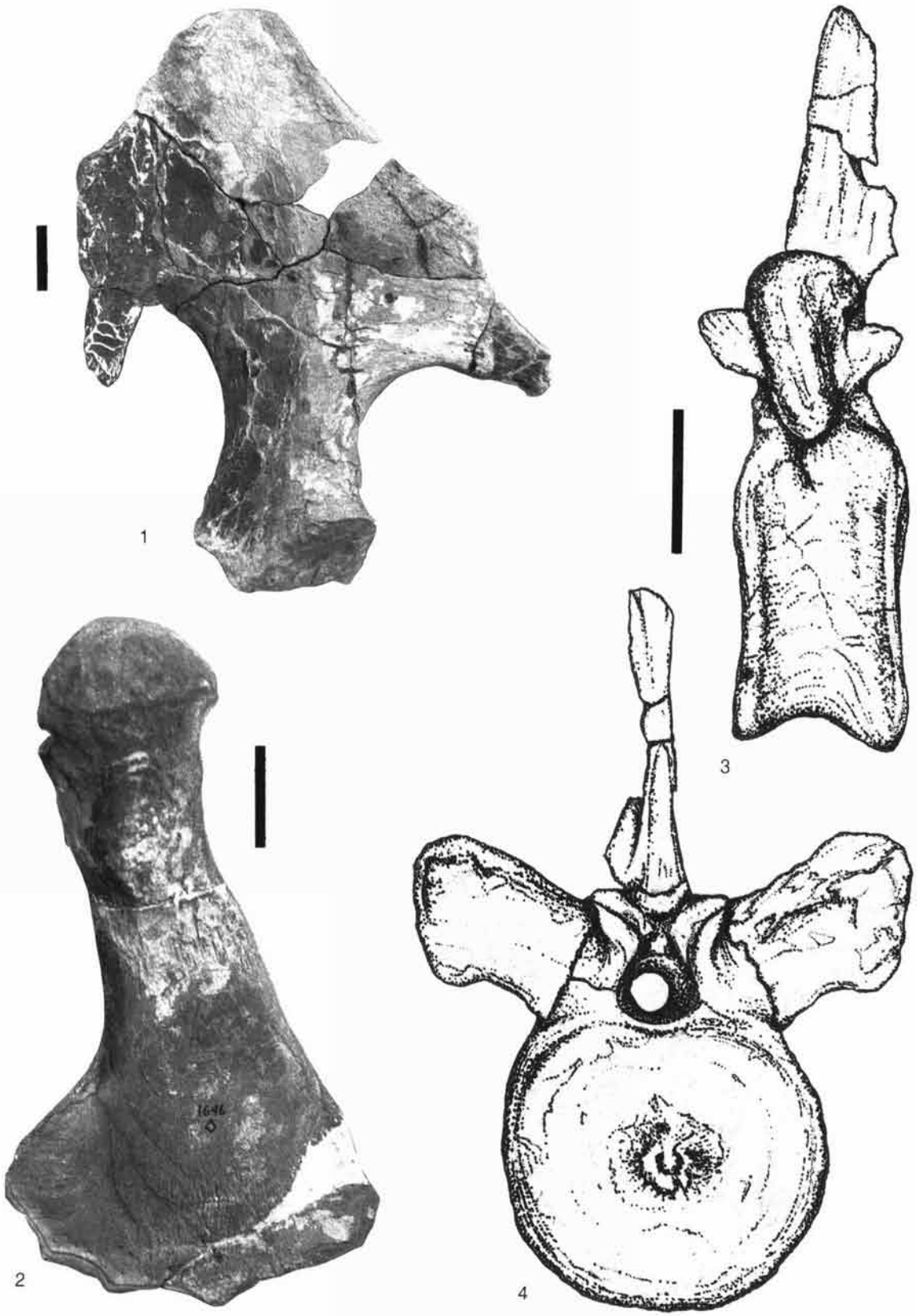


Figure 3. Postcranial elements of Niobrara plesiosaurs; *1,* left scapula of *Thalassonomosaurus marshii* (Williston, 1906), holotype, YPM 1645, here referred to *?Styxosaurus* sp., in ventral aspect; *2,* left humerus of *Polycotylus dolichopus* Williston, 1906, holotype, YPM 1646, here referred to *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 presacrals 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* Cragin, 1888 and transferred *D. osborni* to the senior taxon. Welles (1962), believing that Cragin's (1888) *Trinacromerum bentonianum* holotype (the genotypic species) was lost and unavailable for diagnosis, returned *T. osborni* (and all other polycotylids) 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. osborni* 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

Polycotylus dolichopus Williston, 1906, p. 235.
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 (distal 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 pliosaur 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 polycotylid 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.

TRINACROMERUM Cragin, 1888
"TRINACROMERUM" OSBORNI (Williston, 1902)

See *Dolichorhynchops osborni* Williston, 1902, p. 9 herein.

PLESIOSAURIA indeterminate
PIRATOSAURUS Leidy, 1865
PIRATOSAURUS PLICATUS Leidy, 1865

Piratosaurus plicatus Leidy, 1865, p. 29.
Plesiosauria indeterminate; herein.

Holotype.—USNM 1000.

Stratigraphy.—Cretaceous, formation unknown. Leidy (1865) provided no stratigraphic information on this tooth other than Cretaceous. Williston (1903) suggested that the specimen, from a marine deposit, had probably originated in the Niobrara on the basis of the associated fossils listed by Leidy (1865). This placement is by no means certain, and later Williston (1908) was less definite, echoing Cretaceous.

Locality.—Red River of the North, Manitoba, from drift of Red River Settlement, about 80.5 km south of Selkirk Settlement, in Red River Valley region south of Winnipeg, Manitoba. Williston (1906) had mistakenly referred to the tooth as being from Minnestota.

Collector.—Unknown.

Material.—A single, isolated tooth.

Remarks.—This specimen, considered to be crocodilian by Leidy (1865), is quite probably plesiosaurian, but is certainly no more diagnostic. The name must be regarded as a *nomen dubium*, even though Williston (1906, 1908) suggested possible synonymy with *Polycotylus*.

SUMMARY

Sixteen species of Plesiosauria have been described from the Niobrara Chalk, but only nine of the holotypes now are known to have originated in this formation and of these only three are considered here to be valid taxa. Those taxa that may be retained are the species of the family Polycotylidae *Dolichorhynchops osborni* Williston, 1902, which is founded upon beautiful and well-known material, and *Polycotylus latipinnis* Cope, 1869, which, although incomplete and relatively poorly preserved, has been shown to be distinct. Furthermore, sufficient referred material exists to diagnose the latter species.

Only one of the several confirmed Niobrara species of the family Elasmosauridae is based upon material that is good enough for specific diagnosis. The holotype of *Styxosaurus snowii* is significant because it preserves a complete elasmosaur skull. It is to be stressed again that cranial material exhibits the most important features for the diagnosis of taxa and for the establishment of hypotheses of phylogenetic relationship. All plesiosaurian skulls, either partial or complete, should be regarded as being of special interest, and that of *Styxosaurus* should be redescribed. Other genera (such as *Alzadasaurus*, if truly distinct and

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.

ACKNOWLEDGMENTS

I thank S. Christopher Bennett for organizing a Society for Vertebrate Paleontology symposium on the faunas of the Niobrara Chalk, which provided the stimulus for the preparation of this paper. I am especially grateful to Roger L. Kaesler for bringing this review to a happy conclusion. Kenneth Carpenter, Gregory Liggett, Thomas R. Holtz, Makoto Manabe, and Robert Purdy graciously supplied me with information on relevant comparative specimens. Larry Martin and Desui Miao, and Mark Norell and Charlotte Holton provided access to material at the University of Kansas and the American Museum of Natural History, respectively. Michael and Pam Everhart and Jerome "Pete" Bussen provided invaluable assistance during field work in Logan County and turned relevant plesiosaur specimens over to my care. S. Christopher Bennett, Elizabeth L. Nicholls, the late Samuel P. Welles, and an anonymous referee kindly reviewed the manuscript. This research was supported by the Yale University Peabody Museum of Natural History, the Department of Geology of the University of Bristol, the Leverhulme Trust, the Natural Environment Research Council of the United Kingdom, and Cincinnati Museum Center.

REFERENCES

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

Andrews, C. 1910. A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, Part I. British Museum (Natural History). London. 205 p.

Beard, J. C. 1901. Something about ancient American saurians. Scientific American 85:267.

Bennett, S. C. 1990. Inferring stratigraphic position of fossil vertebrates from the Niobrara Chalk of western Kansas. *In* S. C. Bennett, ed., Niobrara Chalk Excursion Guidebook. Kansas Geological Survey. Lawrence, Kansas. p. 43–72.

Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. Zoological Journal of the Linnean Society 84:97–164.

de Blainville, H. D. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpetologie et d'Amphibiologie. Nouvelles Annales de la Muséum National d'Histoire Naturelle, Paris 3(4):233–296.

Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bulletin of the British Museum (Natural History), Geology Series 35(4):253–347.

Carpenter, K. 1989. *Dolichorhynchops* does not equal *Trinacromerum* (Reptilia: Plesiosauria) (Abstract). Journal of Vertebrate Paleontology 9(suppl. to no. 3):15A.

———. 1990. Upward continuity of the Niobrara fauna with the Pierre Shale fauna. *In* S. C. Bennett, ed., Niobrara Chalk Excursion Guidebook. Kansas Geological Survey. Lawrence, Kansas. p. 73–81.

———. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 201(2):259–287.

———. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. *In* J. M. Callaway and E. L. Nicholls, eds., Ancient Marine Reptiles. Academic Press. San Diego. p. 191–216.

Chorn, J., and K. N. Whetstone. 1978. On the use of the term *nomen vanum* in taxonomy. Journal of Paleontology 52:494.

Cope, E. D. 1868a. [On a new large enaliosaur.] Proceedings of the Academy of Natural Sciences, Philadelphia 20:92–93.

———. 1868b. Notes on fossil reptiles near Fort Wallace. *In* J. L. LeConte, Notes on the Geology of the Survey for the Extension of the Union Pacific Railroad, Eastern Division, from the Smoky Hill River, Kansas, to the Rio Grande. Review Printing House. Philadelphia. p. 68.

———. 1868c. [Remarks on fossil vertebrates]. Proceedings of the Academy of Natural Sciences, Philadelphia 20:313.

———. 1869. Synopsis of the extinct Batrachia and Reptilia of North America, Part 1. Transactions of the American Philosophical Society (new series) 14:1–235.

———. 1872. [On some vertebrates from Sheridan, Kansas]. Proceedings of the Academy of Natural Sciences, Philadelphia 24:127–129.

———. 1877. Report on the geology of the region of the Judith River, Montana, and on the vertebrate fossils obtained on or near the Missouri River. Bulletin of the United States Geological and Geographical Survey of the Territories 3:565–597.

———. 1894. On the structure of the skull in the plesiosaurian Reptilia and on two new species from the Upper Cretaceous. Proceedings of the American Philosophical Society 33:109–113.

Cragin, F. W. 1888. Preliminary description of a new or little known saurian from the Benton of Kansas. American Geologist 2:404–407.

De la Beche, H. T., and W. D. Conybeare. 1821. Notice of the discovery of a new fossil animal, forming a link between the *Ichthyosaurus* and crocodile, together with general remarks on the osteology of the *Ichthyosaurus*. Transactions of the Geological Society of London 5:559–594.

Godfrey, S. J. 1984. Plesiosaur subaqueous locomotion, a reappraisal. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1984(11):661–672.

Hattin, D. E. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. Bulletin of the Kansas Geological Survey 225:1–108.

Hay, O. P. 1930. Second bibliography and catalogue of the fossil Vertebrata of North America. Carnegie Institution of Washington Publication 390(2):1–1074.

Kuhn, O. 1935. Sauropterygia. Fossilium Catalogus I: Animalia, vol. 69. W. Junk. s.-Gravenhage. p. 1–127.

Lane, H. H. 1947. A survey of the fossil vertebrates of Kansas. Part III. The reptiles. Transactions of the Kansas Academy of Science 49(3):289–332.

LeConte, J. L. 1868. Notes on the Geology of the Survey for the Extension of the Union Pacific Railroad, Eastern Division, from the Smoky Hill River, Kansas, to the Rio Grande. Review Printing House. Philadelphia. 76 p.

Leidy, J. 1851. [Description of fossils]. Proceedings of the Academy of Natural Sciences, Philadelphia 5:325–328.

———. 1865. Cretaceous reptiles of the United States. Smithsonian Contributions to Knowledge, Philadelphia 14(192):1–135.

———. 1870. On the *Elasmosaurus platyurus* of Cope. American Journal of Science 49(147):392.

Martin, L. D. 1994. S. W. Williston and the exploration of the Niobrara Chalk. Earth Sciences History 13(2):138–142.

Moodie, R. L. 1916. The structure and growth of the plesiosaurian propodial. Journal of Morphology 27:401–410.

Nicholls, E. L., and A. P. Russell. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: The vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79:149–169.

Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Memoirs of the American Museum of Natural History 1:449–507.

Owen, R. 1860. Palaeontology; or a systematic summary of extinct animals and their geological relations. Adam and Charles Black. Edinburgh. 420 p.

Persson, P. O. 1959. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). Arkiv för Minerologi och Geologi 2(35):431–478.

Pravoslavlev, P. A. 1916. On the problem of the pectoral girdle in the *Elasmosaurus* Cope. Bulletin of the Imperial Academy of St. Petersburg 10(5):327–343.

In Russian.

Robinson, J. A. 1975. The locomotion of plesiosaurs. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 149(3):286–332.

Rogers, K. L. 1991. The Sternberg Fossil Hunters: A Dinosaur Dynasty. Mountain Press. Missoula. 288 p.

Schuchert, C., and C. M. LeVene. 1940. O. C. Marsh, Pioneer in Paleontology. Yale University Press. New Haven. 541 p.

Schultze, H.-P., L. Hunt, J. Chorn, and A. M. Neuner. 1985. Type and figured specimens of fossil vertebrates in the collection of

the University of Kansas Museum of Natural History. Part II. Fossil amphibians and reptiles. University of Kansas Museum of Natural History Miscellaneous Publication 77:1–66.

Shor, E. N. 1971. Fossil and Flies, the Life of a Compleat Scientist, Samuel Wendell Williston (1851–1918). University of Oklahoma Press. Norman. 295 p.

Stewart, J. D. 1990. Niobrara Formation vertebrate stratigraphy. *In* S. C. Bennett, ed., Niobrara Chalk Excursion Guidebook. Kansas Geological Survey. Lawrence, Kansas. p. 19–30.

Storrs, G. W. 1984. *Elasmosaurus platyurus* and a page from the Cope-Marsh war. Discovery 17(2):25–27.

———. 1991. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Bulletin of the Peabody Museum of Natural History 44:1–151.

———. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. American Journal of Science 293-A:63–90.

———. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*. *In* J. M. Callaway and E. L. Nicholls, eds., Ancient Marine Reptiles. Academic Press. San Diego. p. 145–190.

Storrs, G. W., and M. A. Taylor. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. Journal of Vertebrate Paleontology 16(3):403–420.

Sues, H.-D. 1987. The postcranial skeleton of *Pistosaurus* and the interrelationships of the Sauropterygia (Diapsida). Zoological Journal of the Linnean Society 90:109–131.

Watson, D. M. S. 1924. The elasmosaurid shoulder-girdle and fore-limb. Proceedings of the Zoological Society of London 1924:885–917.

Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13:125–254.

———. 1949. A new elasmosaur from the Eagle Ford Shale of Texas. Systematic description. Fondren Science Series 1(1):1–28.

———. 1952. A review of North American Cretaceous elasmosaurs. University of California Publications, Bulletin of the Department of Geological Sciences 29:47–143.

———. 1962. A new species of elasmosaur from the Aptian of Columbia and a review of the Cretaceous plesiosaurs. University of California Publications in Geological Science 44(1):1–89.

———. 1970. The longest neck in the ocean. University of Nebraska State Museum, University of Nebraska News, Museum Notes 50(9):2.

Welles, S. P., and D. R. Gregg. 1971. Late Cretaceous marine reptiles of New Zealand. Records of the Canterbury Museum 9(1):1–111.

Williston, S. W. 1890. A new plesiosaur from the Niobrara Cretaceous of Kansas. Transactions of the Kansas Academy of Science 12:174–178.

———. 1893. The Niobrara Cretaceous of western Kansas. Transactions of the Kansas Academy of Science 13:107–111.

———. 1897. The Kansas Niobrara Cretaceous. Bulletin of the Kansas Geological Survey 2:235–246.

———. 1902. Restoration of *Dolichorhynchops osborni*, a new Cretaceous plesiosaur. Kansas University Science Bulletin 1(9):241–244.

———. 1903. North American plesiosaurs, Part 1. Field Columbian Museum Publications in Geology 2:1–77.

———. 1906. North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. American Journal of Science 4(21):221–236.

———. 1907. The skull of *Brachauchenius*, with observations on the relationships of the plesiosaurs. Proceedings of the United States National Museum 32:477–489.

———. 1908. North American plesiosaurs: *Trinacromerum*. Journal of Geology 16:715–736.

———. 1914. Water Reptiles of the Past and Present. University of Chicago Press. Chicago. 251 p.

———. 1925. The Osteology of the Reptiles. Harvard University Press. Cambridge. 470 p.

Williston, S. W., and R. L. Moodie. 1913. New plesiosaurian genus from the Niobrara Cretaceous of Nebraska [sic] (Abstract). Bulletin of the Geological Society of America 24:120–121.

———. 1917. *Ogmodirus martinii*, a new plesiosaur from the Cretaceous of Kansas. Kansas University Science Bulletin 10:61–73.

Zittel, K. A. 1890. Handbuch der Palãontologie. I. Palãozoologie. R. Oldenbourg. Munich and Leipzig. 900 p.