Bite marks on an elasmosaur (Sauropterygia; Plesiosauria) paddle from the Niobrara Chalk (Upper Cretaceous) as probable evidence of feeding by the lamniform shark, *Cretoxyrhina mantelli*

M.J. Everhart
Sternberg Museum of Natural History
Fort Hays State University, Hays, KS 67601
meverhar@fhsu.edu

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4 figures, 1 table

Abstract

The left front paddle of an unidentified elasmosaurid in the collection of the Fick Fossil and History Museum exhibits two groups of deeply incised grooves across the dorsal and ventral sides of the humerus that suggest a series of bites by the lamniform shark, *Cretoxyrhina mantelli*. The remains were discovered by George F. Sternberg in 1925 in the Smoky Hill Chalk Member of the Niobrara Chalk, Logan County, Kansas, USA. Archival photographs, along with Sternberg's hand written note, document the condition of the specimen when originally collected. The specimen is significant because it preserves the first evidence of probable feeding by *C. mantelli* on an elasmosaurid, and because it represents the rare occurrence of an elasmosaurid in the upper Smoky Hill Chalk of western Kansas.

Contents

Abbreviations

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania
ESU	Emporia State University Johnston Geology Museum, Emporia, Kansas
FFHM	Fick Fossil and History Museum, Oakley, Kansas
FHSM	Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas
KUVP	University of Kansas Museum of Natural History, Lawrence, Kansas
NJSM	New Jersey State Museum, Trenton, New Jersey
SDSMT	Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota
UNSM	United States National Museum, Washington, D.C.
YPM	Yale Peabody Museum, New Haven, Connecticut

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1. Introduction

Long–necked plesiosaurs called elasmosaurids flourished worldwide during the Late Cretaceous, with ten of fourteen taxa known from North America (Gasparini *et al.,* 2003). However, their remains are uncommon occurrences in most Upper Cretaceous marine deposits (Russell, 1988), and they are conspicuous for their relative scarceness in the otherwise fossiliferous Smoky Hill Chalk Member (upper Coniacian – lower Campanian) of the Niobrara Chalk of western Kansas. Whereas the remains of thousands of fish, mosasaurs and pteranodons have been recovered from the chalk since the late 1860s, the number of verified specimens of elasmosaurids from the same formation is less than a dozen (Everhart, 2005). Thus any remains attributable to an elasmosaurid are important to our understanding of the palaeoecology of the Western Interior Sea during that period of time.

Almost all (8 of 10) of the known elasmosaurid specimens were collected between 1874 and 1895 (Williston, 1903, 1906; Lane, 1946; Schultze *et al.,* 1985; Carpenter, 1999; Storrs, 1999). Only two of the specimens were collected after 1895, including the one described herein. The last to be discovered (USNM 11910) was found by G.F. Sternberg in 1927 and donated to the United States National Museum (Smithsonian). All but one are from the Smoky Hill Chalk Member of the Niobrara Chalk. The only specimen (YPM 1640) from the underlying Fort Hays Limestone Member was also one of the first plesiosaurs to be discovered in Kansas. It was collected by B.F. Mudge in 1874 from an exposure in Jewell County and described as "*Elasmosaurus nobilis*" by Williston (1906). All of the other specimens were apparently found in Logan County (table 1).

Specimen	Original name	Collected	Locality	Description of remains
YPM 1640	*Elasmosaurus nobilis* Williston (1906)	1874	Jewell County Fort Hays Limestone	27 vertebrae, portions of both girdles, and limb elements
YPM 1644	*Elasmosaurus snowii* Williston (1906)	1874	Logan County	Vertebrae, portions of both girdles, and limb elements
KUVP 434	*Elasmosaurus ischiadicus* Williston (1903; 1906)	1874	Logan County	19 vertebrae, pelvic girdle, proximal end of left femur
YPM 1130	*Elasmosaurus ischiadicus* Williston (1906)	1876	Wallace County (Logan Co. ?)	63 vertebrae, pectoral girdle, nearly complete limb
YPM 1645	*Elasmosaurus marshii* Williston (1906)	1889	Logan County	33 vertebrae, scapula, limb elements
KUVP 1301	*Elasmosaurus snowii* Williston (1890)	1890	Logan County	Articulated skull, 18 cervical vertebrae – Holotype
KUVP 1302	Elasmosauridae indet. (Undescribed)	1895	Logan County	7 vertebrae, limb fragments
KUVP 1312	*Elasmosaurus sternbergi* Williston (1906)	1895	Logan County	3 dorsal vertebrae (possibly more complete originally)
FFHM 1974.823	Elasmosauridae indet. (described herein)	1925	Logan County	Partial left front limb
USNM 11910	*Styxosaurus snowii* (Undescribed)	1927	Logan County	Many vertebrae and pelvic girdle

Table 1. Elasmosaurid remains collected from the Niobrara Chalk of Kansas, including species names by Williston (1890, 1903, 1906). All specimens are from the Smoky Hill Chalk Member unless otherwise indicated. With the exception of the type of Styxosaurus snowii *(KUVP 1301), most are considered to be Elasmosauridae indeterminate by Storrs (1999), or synonymous with* Styxosaurus snowii *Carpenter (1999).*

Four of the specimens were collected by Mudge and his field party during the summer of 1874. In regard to the locality of record given for YPM 1130, Logan County was a part of Wallace County until the late 1880s (Bennett, 2000). The list also includes the type specimen of "*Elasmosaurus sternbergi*" (KUVP 1312) that was reported by Williston (1906) and Storrs (1999) as being found in Gove County (see the corrected account by Sternberg, 1917: 166). Williston (1890, 1903, 1906) described a total of five new elasmosaurid species from the Niobrara Chalk, but only the first named (*Styxosaurus snowii* Williston, 1890) is currently recognised as valid. Most of the others are considered to be "elasmosauridae indeterminate" by Storrs (1999), or have been synonymised with *S. snowii* by Carpenter (1999).

Much of the difficulty encountered over the years with identifying these remains to species has been due to their fragmentary nature and the consistent lack of good diagnostic material. Unlike the relative wealth of nearly complete specimens of many fish (Everhart, 2005), marine reptiles, including three polycotylid plesiosaurs (Williston, 1903; Bonner, 1964; see also Everhart, 2004a), mosasaurs, (Russell, 1967; Everhart, 2001), pteranodons (Bennett, 1994), and toothed birds (Clarke, 2004) in the Niobrara Chalk, the elasmosaurids that have been collected are almost always fragmentary and disarticulated. The remains generally consist of isolated limbs, girdles, and vertebrae. None of the ten specimens are anywhere near complete and there is only one elasmosaurid skull known from the chalk (KUVP 1301, the type specimen of *Styxosaurus snowii*, discovered by E. P. West in 1890). Their carcasses may have been scattered by predators or simply fallen apart as the result of a 'bloat and float' scenario (Schwimmer, 1997).

In November 1925, G.F. Sternberg found an articulated plesiosaur paddle (interpreted here as the left front limb of an elasmosaurid; Schumacher, pers. comm., 2004) in the upper Smoky Hill Chalk of Logan County, several miles south of the town of Oakley, Kansas. An early black and white photograph (figure 1) in the collection of the Sternberg Museum of Natural History, probably taken by G.F. Sternberg, shows the specimen laid out on a flat surface, dorsal side up, with a 36 in. (0.91 m) ruler included for scale. A hand written note in the photograph reads: "No–2–25 A nearly complete paddle of an extinct reptile (Plesiosaur) which was collected south of Oakley. Note the scars on the larger bone, Humerus. They were left by some reptile. Oakley School." Sternberg's specimen number (No–2–25) may be the collection date (November 2, 1925), however, on the dorsal side of the propodial, another number (SP–NO–16–24) is written in black ink. No explanation was provided for either number.

In a later version of the same photograph curated in the archives of the Sternberg Museum, a typewritten note has been pasted over the legend in the photograph, with a shortened version of the original text: "A nearly complete paddle of an extinct reptile (Plesiosaur) which was collected south of Oakley. One of the Oakley School specimens."

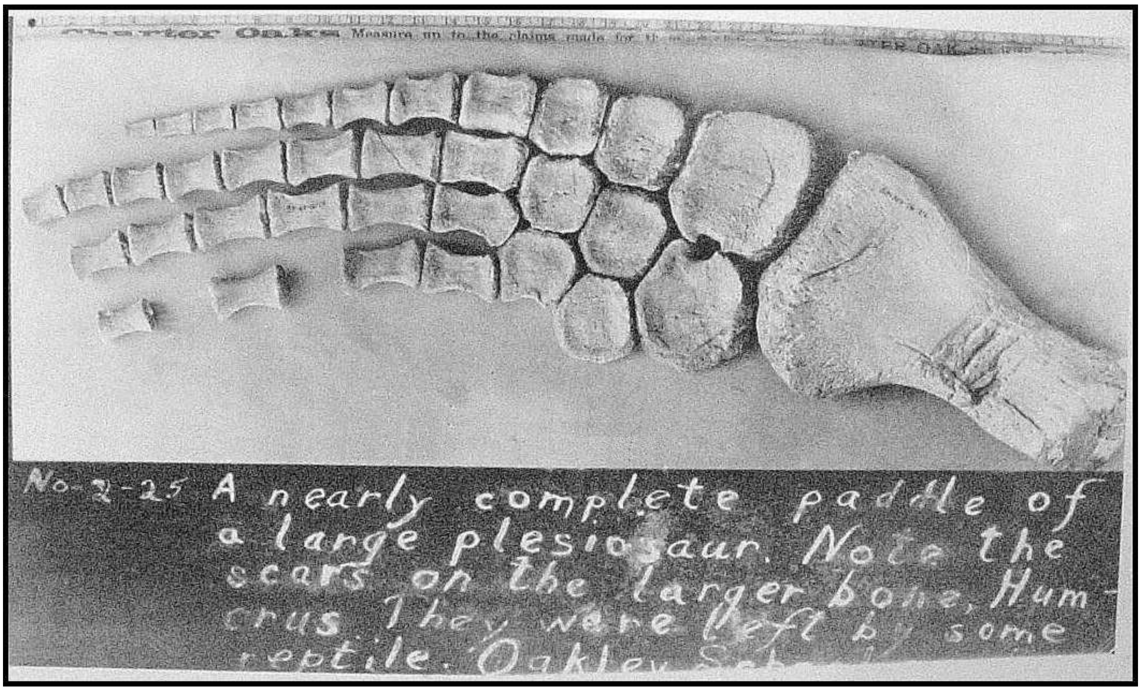

Figure 1. A photograph taken about 1925 by George F. Sternberg of the elasmosaurid paddle (FFHM 1974.823) in dorsal view. Note the yardstick (36 in. /0.91 m) along the top margin. Sternberg's comments are written in white chalk on a blackboard.

The specimen was apparently on exhibit in the Oakley school system until the mid–1970s. In 1974, it was acquired by the Fick Fossil and History Museum, Oakley, Kansas, and curated as FFHM 1974.823. A sign in the exhibit case notes that the following information was provided by G.F. Sternberg (source unknown, but probably from a note accompanying the specimen when it was donated to the Oakley schools): "The bones of Plesiosaurs are by no means common and even so little as a paddle is rarely found. These bones are in a remarkable state of preservation. It is doubtful if another Plesiosaur paddle in which the bones were associated has ever been found in the Kansas chalk beds. Note the scars on the larger bone, (humerus) which was evidently made by one of the large carnivorous Mosasaurs. A rare specimen."

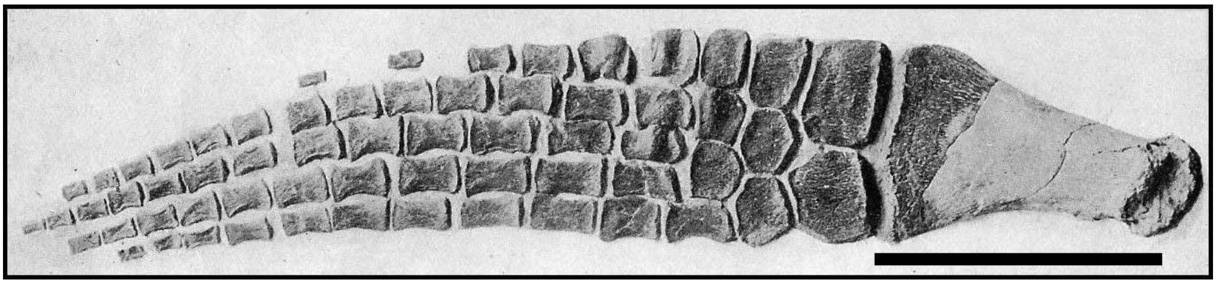

Figure 2. An early photograph of the right rear paddle of YPM 1130 ("Elasmosaurus ischiadicus") in dorsal view published by Williston (1906, pl. II, fig. 1). The image is here reversed for purposes of comparison with FFHM 1974.823. Total length is approximately 1.1 m. Scale bar = 30 cm (scale added from Storrs, 1999).

Possibly unknown to G.F. Sternberg at the time, the fourth elasmosaurid specimen ("*Elasmosaurus ischiadicus*" YPM 1130) collected from the Smoky Hill Chalk included a nearly complete right rear paddle (figure 2). A photograph of that specimen (Williston, 1906, pl. II) compares favourably in size with the bitten specimen described here (FFHM 1974.823). YPM 1130 is probably the most complete of the known elasmosaurid specimens from the chalk, including 63 vertebral centra, most of the pelvis and the complete rear limb (Storrs, 1999). It was collected by Brous and Mudge in 1876 and is considered to be "Elasmosauridae indeterminate" by Storrs (*ibidem*).

The elements of FFHM 1974.823 are also similar to those of the front paddle of a nearly complete *Styxosaurus snowii* (SDSMT 451) from the Pierre Shale of South Dakota (Welles & Bump, 1949: figure 3A). However, the remains are too incomplete for a positive identification and are considered here to be "Elasmosauridae indeterminate."

2. Locality and stratigraphic occurrence

The exact locality where FFHM 1974.823 was discovered is unknown, other than the statement by G.F. Sternberg that it was south of Oakley in Logan County, Kansas. It is likely that it was found in the exposures of upper chalk along the Smoky Hill River and its tributaries where Charles Sternberg and later, his sons, including G.F., had collected many fossils during the previous five decades (Sternberg, 1917). The age of the chalk in this area ranges from middle Santonian through the lower Campanian (Hattin, 1982; Bennett, 2000). All other elasmosaurid remains recovered from the Smoky Hill Chalk appear to have come from this same stratigraphic interval (Carpenter, 1999; Storrs, 1999; Everhart, 2005).

3. Description

The plesiosaur paddle as mounted by G.F. Sternberg, FFHM 1974.823 (figure 3) consists of a complete propodial (humerus), epipodials (radius, ulna), mesopodials (radiale, intermedium, ulnare), and three metapodials (for plesiosaur paddle terminology, see Welles & Bump, 1949). A distinct epipodial foramen is present between the radius and ulna. The proximal–most portions of the first four of the five digits are present (digit V is missing completely). Digits I and II have eight podials each; digit III has six and digit IV apparently has four podials remaining (1, 2, 4, and 6), assuming Sternberg’s interpretation is correct. The remains are sun–bleached, indicating some period of exposure prior to collection. The specimen was mounted by Sternberg by drilling holes in the bones and attaching them to a piece of plywood with small nails. The much larger humerus is attached with a bolt, however, and is readily removable for examination. The total length of the paddle is about 91 cm. From a comparison with a similar–sized, complete hind paddle of another Smoky Hill Chalk elasmosaurid (YPM 1130; figure 2), it is estimated that about 10 % (9 cm) of the length of this paddle is missing. This missing length would include the distal five or six podials in digits II, III and IV.

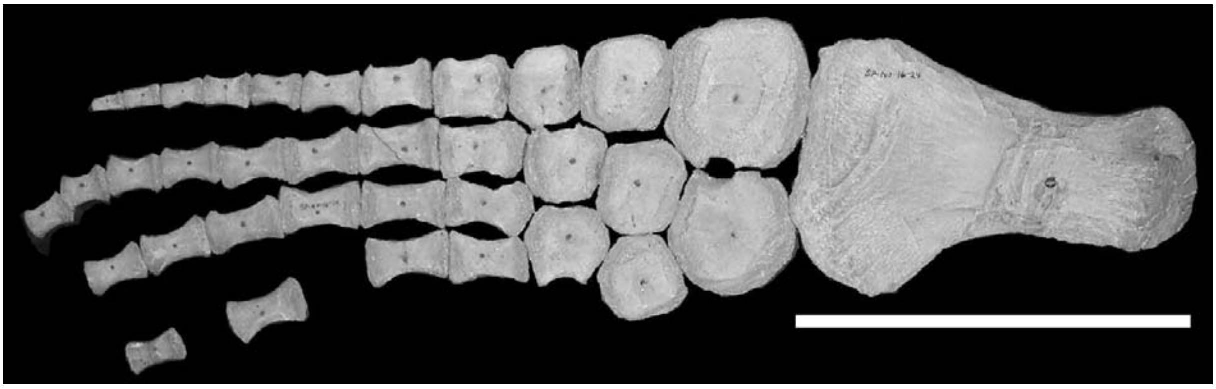

Figure 3. The left front paddle of an unidentified elasmosaurid (FFHM 1974.823) in dorsal view as currently exhibited at the Fick Fossil and History Museum in Oakley, Kansas. Note bite marks on the humerus. Scale bar = 30 cm.

The uncrushed humerus has a slight sigmoid curve, and is 30 cm long and 19 cm wide near the distal end. Four deeply incised, slightly curved grooves, up to 1 cm in width and 0.5 cm in depth are visible across both sides of the distal end of the humerus, generally running from near the centre to the posterodorsal corner. The grooves are roughly triangular in cross–section, and the incised edges have a 'stepped' appearance in some areas, suggesting that they were made by the repeated passage of one or more sharp objects, most likely the teeth of a large lamniform shark. They do not appear to be tool marks or other artifacts of preparation or weathering. These probable bite marks continue to a lesser extent across the upper right portion of the ulna. Total length of the bite marks across the distal humerus and ulna is about 15 cm.

A second group of at least five deep cuts is visible on both sides of the humerus at mid–shaft, also trending slightly downward toward the posterior as viewed on the dorsal side. The humerus is about 10 cm in diameter at mid–shaft and the bite marks extend across most of the dorsal and ventral surfaces. Other than those found on the proximoposterior edge of the ulna, no bite marks were observed on the dorsal side of any of the other bones of the paddle. The ventral side of the other paddle bones could not be examined due to their attachment to the mounting.

The nearly complete remains of an adult, 10 m *Styxosaurus snowii* (minus anteriormost cervical vertebrae and skull) were collected from the Sharon Springs Member (middle Campanian) of the Pierre Shale by the New Jersey State Museum in 1991–1993 (Cicimurri & Everhart, 2001). The left rear paddle of that specimen (NJSM 15435) is intact and completely articulated. It measures 1.7 m compared to an estimated total length of about 1 m for FFHM 1974–823, and suggests that the bitten paddle came from a sub–adult elasmosaurid that was approximately 6 m in length. This is roughly the same length as the largest known specimens of *Cretoxyrhina mantelli*.

4. Discussion

While the remains of elasmosaurids are relatively rare in the Smoky Hill Chalk, direct and indirect evidence of probable feeding activities by the lamniform shark, *Cretoxyrhina mantelli*, on other species is common. *C. mantelli* was the largest shark in the Western Interior Sea, reaching lengths of 6+ m (Shimada, 1997a; Shimada *et al.,* 2004). It had razor–sharp teeth as large as 6.5 cm (FFHM 1972.196; per. obs.), and a bite that was powerful enough to shear through 5 cm diameter mosasaur vertebrae (Everhart, 1999, 2004b). According to Shimada (1997a), this large pelagic shark would have been comparable to the modern great white shark (*Carcharodon carcharias*). Present in the Western Interior Sea from about the middle Cenomanian (Shimada, 1997b), *C. mantelli* had reached its greatest size and abundance by the upper Coniacian (pers. obs.) and then apparently became extinct worldwide during the lower Campanian (Stewart, 1990). *Cretoxyrhina* was an apex predator in the Western Interior Sea and it is likely that it fed on plesiosaurs as well as the more abundant mosasaurs (Everhart, 1999; 2004b), marine turtles (Shimada & Hooks, 2004), and larger fish (Shimada & Everhart, 2004).

C.H. Sternberg (1917) collected the scattered remains of a large *Cretoxyrhina mantelli* (KUVP 247) that included a disarticulated *Xiphactinus audax* as an apparent last meal. Shimada (1997a) documented feeding activity by *C. mantelli* on the remains of teleosts, including the KUVP 247 specimen, mosasaurs and possibly plesiosaurs (KUVP 68979, see also Moodie, 1912). One specimen (FHSM VP–13283) consists of partially digested, but still articulated vertebrae from the lower back of a mosasaur, and includes severed bone, bite marks and embedded fragments of *Cretoxyrhina* teeth (Everhart *et al.,* 1995; Shimada, 1997a). Evidence of predation and/or scavenging by *C. mantelli*, including many examples of partially digested bones, was reported by (Everhart, 1999) on mosasaur remains from the lower Smoky Hill Chalk. The scavenged remains of a mosasaur (FHSM VP–13746) that included bite marks and the embedded tip of a tooth of *C. mantelli*, and bite marks attributable to *Squalicorax falcatus* were described by Everhart (2004b). Tips of three *Cretoxyrhina* teeth embedded in the skull and lower jaws of a large *Tylosaurus* (FHSM VP–13742) are evidence of several bites by a large shark. Everhart & Hamm (2005) reported the discovery of the radius and ulna of a sub–adult nodosaur (FHSM VP–13985) in the Smoky Hill Chalk that may have been scavenged from a floating carcass. The size of the specimen, partially digested appearance and the distinctive, unserrated bite marks on the distal shaft of the radius suggest that the scavenger was probably *C. mantelli*. Shimada & Hooks (2004) noted bite marks and embedded teeth attributable to *C. mantelli* on the remains of a protostegid turtle, and Shimada & Everhart (2004) reported an embedded *C. mantelli* tooth fragment in the vertebral column attached to the severed skull of a teleost fish (*Xiphactinus audax* – ESU 1047).

FFHM 1974.823 exhibits two sets of deep, generally parallel bite marks; the first is across the distal end of the humerus, and the second is located near the mid–shaft of the humerus. Sternberg's contention that they were made by some other marine reptile (*e.g.* mosasaur) appears unlikely when compared to wounds that have been attributed to these marine reptiles. Bell & Martin (1995) reported on the skull of a *Plioplatecarpus* with puncture wounds and fractures attributed to another mosasaur. Schumacher (1993) and Everhart (2002) noted gouges and puncture wounds on the skull of a *Tylosaurus* (FHSM VP–2295) that were mostly likely caused by another mosasaur. None of the bones discovered as stomach contents of a large *Tylosaurus* (Martin & Bjork, 1987), including those of a smaller mosasaur and a marine bird, showed bite marks. Everhart (2004c) described the remains of a polycotylid plesiosaur found as stomach contents of a 9 m *Tylosaurus proriger*, which included two probable humeri. Although the proximal and distal ends of both bones were partially digested by the mosasaur's stomach acids, neither showed evidence of bite marks. The presence of numerous bone fragments, however, indicated that some of the plesiosaur's bones had been fractured in the process of being swallowed by the mosasaur. In her study of the tooth morphology of marine reptiles, Massare (1987) noted that mosasaurs use their teeth for seizing, not dismembering, large marine vertebrates. Everhart (2005) suggested that the teeth, kinetic skull and probable method of feeding by mosasaurs made them unlikely to seek prey larger than they could swallow intact. By Campanian time, the only other predator known from the Western Interior Sea that was large enough to have made the bite marks found on FFHM 1974.823 was the giant lamniform shark, *Cretoxyrhina mantelli*.

Shimada (1997a; pers. comm., 2004) noted that actual 'feeding' by *Cretoxyrhina* on this, or other apparently shark–bitten remains from the Upper Cretaceous cannot be observed, and the damage may therefore have some other explanation. However, in view of the severity of the bite marks on this specimen, and the abundance of other specimens showing similar damage, severed bone, embedded *C. mantelli* teeth fragments, and evidence of partial digestion, feeding appears to be the most likely activity that would produce this damage on a plesiosaur paddle. While the behaviour of this extinct shark can never be observed directly, it is likely that a predator of this size and power would have had feeding strategies similar to those of extant species. Motta & Wilga (2001) noted that most modern species of carcharhinid and lamnid sharks rely primarily on "ram feeding" to acquire and disable prey, and may approach at high rates of speed. Observations made by Gabriotti & De Maddalena (2004) of great white sharks (*Carcharodon carcharias*) feeding on elephant seals in Spencer Gulf, Australia, suggested that while smaller sharks (< 4 m) approached prey cautiously, larger individuals used a more direct approach, probably related to their size and strength. In some cases, they reported that the attack is made at such a velocity that the prey is propelled out of the water by the force of the impact. In their study of sea turtle taphonomy in the Late Cretaceous Pierre Shale, Knell & Bishop (2004) figured a modern loggerhead turtle (*Caretta caretta*) found washed ashore in August, 2001, on St. Simons Island, Georgia, USA. The 1.2 m turtle appeared to have been killed by a single bite of a large shark across the middle of the carapace. The remains were measured and photographed by Adam Mackinnon (George Department of Natural Resources). According to Mackinnon (pers. comm., 2005), the width of the carapace in the vicinity of the bite was about 62.5 cm. Measurements indicate that about 70 cm of the turtle was inside the mouth of the shark when the bite occurred. This is approximately the same distance from the distal tip of the FFHM 1974–823 paddle to lowermost series of bite marks across the humerus.

Scavenging on a variety of marine and terrestrial species by the Late Cretaceous shark genus *Squalicorax* is generally accepted (Mudge, 1877; Schwimmer *et al.,* 1997; Shimada, 1997a; Hanks & Shimada, 2002; Everhart, 2004b) on the basis of readily identifiable (serrated) bite marks left on the bones. Non–fatal bites, mostly by sharks, which caused an infection and where some healing had occurred are seen less often, but are occasionally found in the fossil record. In mosasaurs, such injuries are found most often on the tail (Martin & Rothschild, 1989; Shimada, 1997a; Everhart, 1999) and probably were the result of a "bite–and–spit' (release) attack by a shark (Gabriotti & De Maddalena, 2004). There are no specimens from the Late Cretaceous Western Interior Sea that I am aware of, however, that preserve as severe a series of shark bites as does FFHM 1974.823.

The bite marks occur on both sides of the humerus (figure 4) and are of similar length and depth. Those on the end of the humerus are curved distally while those at the middle of the shaft are slightly curved toward the proximal end. Most of the damage appears to have been done by raking the teeth repeatedly back and forth across the bone. A vigorous 'head–shaking' movement is used by modern sharks to remove chunks of flesh from their prey and, in this case, would have severed the skin, muscles and other tissue on the humerus as the shark attempted to bite through the bone. There is no indication that the teeth were serrated (*i.e.* teeth of *Squalicorax*) and the size of the paddle, and the amount of damage done by the bites would appear to rule out this smaller (2–3 m), less powerful shark.

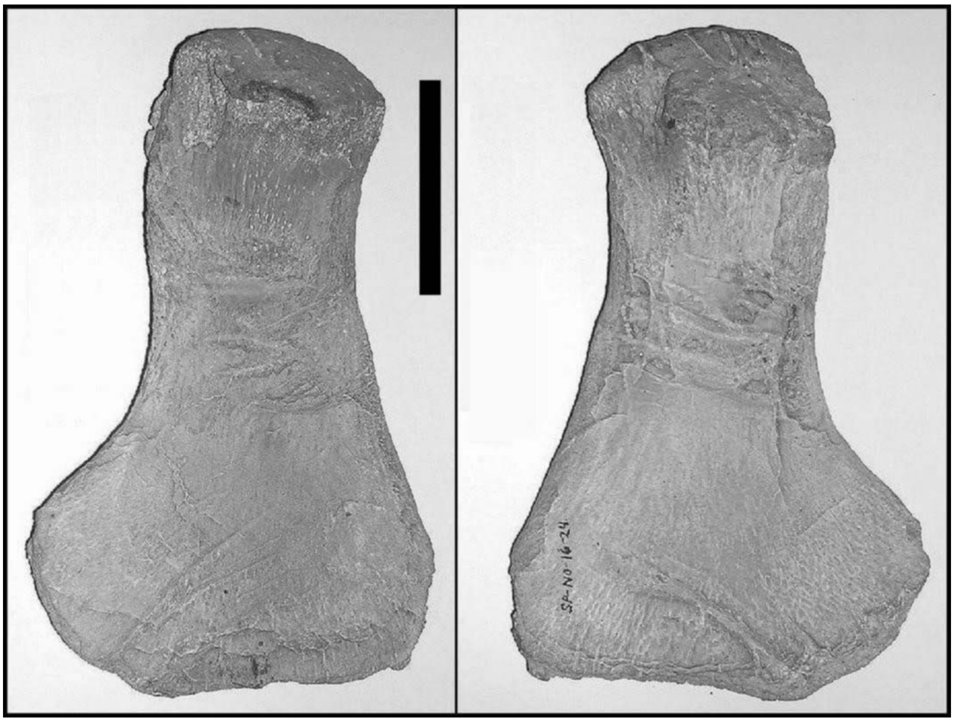

Figure 4. Ventral (left) and dorsal (right) views of the humerus of FFHM 1974-823, showing bite marks on the distal end and on the mid-shaft of the humerus. Scale bar = 10 cm.

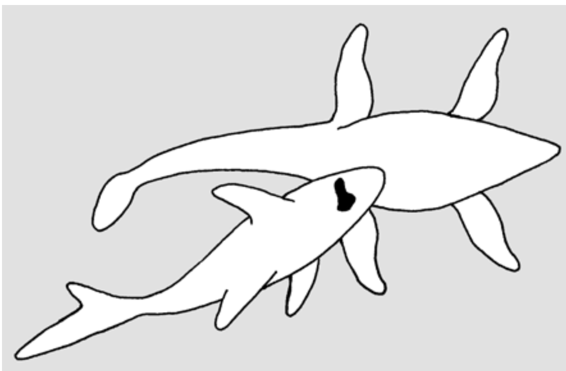

Figure 5. A view from above of the possible orientation of a 5 m shark biting the left front paddle (humerus shown in black) of a sub-adult (6 m) elasmosaurid.

The direction from which the bites occurred is unclear. There is no way of knowing the orientation of the elasmosaurid relative to the shark at the time of the bite(s). If the elasmosaurid was already dead (*i.e.* bloated and floating, or laying on the sea bottom), it is possible that the carcass could have been upside down. For the purpose of this discussion, however, it is assumed that the plesiosaur was upright and level, that the left front paddle was more or less horizontal, and positioned at a near 90 degree angle to the long axis of the body (Sanders *et al.,* 2004). The bite on the distal portion of the humerus appears to have most likely come from the front, at an angle of about 45 degrees to the paddle (figure 5). The jaws of *Cretoxyrhina* have a significant overbite (Shimada, 1997a) and the marks made by the upper teeth would normally be anterior to those made by the lower teeth. In this case, however, the tooth marks on the ventral side of the paddle are placed 1–3 cm further in from the leading edge of the paddle than those on the dorsal surface. This may indicate that the paddle was upside down relative to the shark, or more simply that the shark approached from below horizontal causing the teeth of the lower jaw to impact the paddle at a greater distance from the leading edge. Because the largest teeth in the jaws of *Cretoxyrhina mantelli* are in the front of the mouth (Shimada, 1997c), it is possible that the lack of bite marks on the more distal elements of the limb can be explained by the smaller teeth not cutting deep enough through the skin, muscle and connective tissue to contact the smaller, thinner bones of the paddle.

The bite marks on the mid–shaft are even more difficult to explain if the paddle was still attached to the elasmosaurid. These grooves are almost at right angles to the long axis of the bone and would have almost required the shark to have taken the distal three fourths of the paddle (about 75 cm) in its mouth while attempting to bite through the shaft of the humerus. This is about the same length as the bitten portion of the shell of the loggerhead turtle cited above, and most likely would have been possible for a large (5+ m) *Cretoxyrhina.* Another feasible scenario would be that the paddle had been torn free by the series of bites on the distal end of the humerus, briefly released by the shark, and then bitten from the other end as it sank. However, it would have been difficult to effectively perform the same 'head shaking' and produce the same series of deep grooves on the mid–shaft of the humerus as a result when the paddle was no longer solidly attached to the body of the elasmosaurid.

The most likely scenario appears to be an attack by a very large (5+ m) *Cretoxyrhina mantelli* from the front of the left front limb. The shark bit down on the distal end of the humerus first, cutting several grooves deeply into the bone, then moved upward to the mid–shaft before biting down again. At that point, the paddle may have been torn from the shoulder of the elasmosaurid by the violence of the shark's attack. If not, the shark may have moved further up the limb and made a third bite on or above the shoulder joint. However, no evidence of such a bite was visible on the specimen. Once detached, the limb was apparently dropped by the shark without further damage. The missing distal elements may have been removed by an earlier bite, by scavengers after the limb reached the bottom or by modern weathering or erosion following exposure on the surface. The fact that podials 3 and 5 are missing from digit 4, and that digit 5 is missing entirely may also indicate that the distal and posterior edges of the paddle had weathered out of the chalk first and that some digits were lost.

Although it is likely that this elasmosaurid paddle had been largely de–fleshed by the series of bites that left deep gouges in the surface of the bone, there is no indication that it had been ingested. Once detached from the body of the plesiosaur, and released by the shark, it was probably heavy enough to sink quickly to the bottom where it was preserved in articulation and more or less intact as originally reconstructed by G.F. Sternberg.

5. Conclusion

Whereas elasmosaurids survived and apparently flourished world–wide following a mid–Cretaceous extinction event (Bakker, 1993), there is little or no evidence in the fossil record that they were present in significant numbers in the central portions of the Western Interior Sea during upper Coniacian and lower Santonian time. The remains of polycotylids are also very rare in the Smoky Hill Chalk during that interval of time (Everhart, 2003), suggesting that plesiosaurs in general preferred habitats other than deep waters far from shore. The shark–bitten, left front paddle of an unidentified elasmosaurid (FFHM 1974.823) provides additional data regarding the possible re–entry of elasmosaurids into these waters as the Western Interior Sea diminished in depth and width during the upper Santonian and lower Campanian. This specimen, as well as the incomplete and fragmentary remains of nine other elasmosaurids, suggests a predator–prey relationship between the large lamniform sharks (*Cretoxyrhina mantelli*) and elasmosaurids. Predation on live plesiosaurs and the scavenging of carcasses can be reasonably assumed from the observed behaviour of the similar sized, modern Great White shark (*Carcharodon carcharias*). Although no direct cause and effect is inferred here, the occurrence of nearly complete, articulated elasmosaurid remains is much more common in the Pierre of western Kansas following the extinction of *C. mantelli* during the lower Campanian.

6. Acknowledgements

Janet Bean and Lucille Jennings (Fick Fossil and History Museum) provided access to the specimen and valuable information regarding its history. Larry Martin and Desui Miao (University of Kansas Museum of Natural History) provided access to elasmosaurid material in their care. Bruce Schumacher assisted in the identification of the specimen and reviewed an early draft of the paper. Mike Knell (Montana State University) and Adam Mackinnon (Georgia Department of Natural Resources) provided data regarding a sea turtle bitten by a large shark. Comments by Marie–Céline Buchy, Eric Mulder and Kenshu Shimada greatly improved the quality of an earlier version of this paper.

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