Late Cretaceous interaction between predators and prey. Evidence of feeding by two species of shark on a mosasaur.

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5 figures

Abstract

The fragmentary remains of a mosasaur discovered in the Smoky Hill Chalk Member (Late Coniacian) of the Niobrara Chalk of Gove County, Kansas, U.S.A., preserve a number of injuries consistent with scavenging by two species of lamnid shark. The mosasaur remains (FHSM VP-13746) were identified as *cf. Ectenosaurus clidastoides* and consisted of a continuous series of 21 dorsal vertebrae. No evidence was found of the anterior neck and skull, limbs or caudal vertebrae. A single cervical vertebra was located in front of the first dorsal and one posterior dorsal vertebra had been fractured prior to burial. Although still associated with the vertebral column, most of the ribs were severed or otherwise damaged. No residual of the cartilaginous sternum was found. Deep bite marks on several of the vertebrae, severed ribs and the tip of a large, embedded tooth are interpreted as evidence that the lamniform shark, *Cretoxyrhina mantelli*, had fed on the mosasaur remains. The spacing of the individual tooth marks (3 cm) indicate the bites were from a very large (estimated 5 m) shark. Lesser damage, including serrated bite marks and scrapes indicated that another shark species, *Squalicorax falcatus*, had also been involved. This specimen is important palaeoecologically because it documents a predator-prey relationship between these two species of sharks and mosasaurs, and because it provides further evidence that *Cretoxyrhina* and *Squalicorax* fed on large vertebrates in the Late Cretaceous seas of North America.

Contents

1. Introduction

The Smoky Hill Chalk Member of the Niobrara Chalk (Late Cretaceous) was deposited from Late Coniacian through Early Campanian time in the middle of North America. The age of the chalk coincides with the rise of mosasaurs as an apex predator and documents early stages of their evolution and dispersal in the Western Interior Sea. The chalk is well known for the excellent preservation of marine vertebrates including mosasaurs, plesiosaurs, giant turtles, pteranodons, toothed birds, bony fish and sharks, as well as the remains of one of the largest lamniform sharks of the Late Cretaceous, *Cretoxyrhina mantelli* Agassiz, 1843. The teeth and remains of smaller sharks, including *Squalicorax falcatus* Agassiz 1843, are also well documented.

Evidence of feeding by sharks on a variety of vertebrate species, including mosasaurs, from the Smoky Hill Chalk, as indicated by bite marks, severed bone and embedded teeth, has been recorded for more than 125 years. The serrated teeth of *Squalicorax* left distinctive marks on the bones of many kinds of marine animals. An unusual instance of feeding by two shark species feeding on the carcass of a marine lizard (Squamata; Mosasauridae) is reported here.

Mudge (1877: 287) was the first to report evidence of scavenging on marine reptiles by sharks, noting that "frequently […] the bones of Saurians were found with the marks of the serrate teeth of *Galeocerdo* [*Squalicorax*], which could not have been made unless the bones were still fresh and unhardened." In his discussion of mosasaurs from the Smoky Hill Chalk, Williston (1898: 214) indicated that their bones "[…] frequently bear the impression of teeth of post-mortem origin, and in many cases I have found the teeth of small sharks imbedded in them." Williston & Moodie (1917: 69) reported that the humerus of a juvenile plesiosaur had been "distinctly marked […] by the teeth of some predaceous fish or reptile. […] This is not a rare occurrence among Kansas Cretaceous fossils." An examination of this specimen (KUVP 441) in the University of Kansas Museum of Natural History by the author in 2004 revealed that the tooth marks were made by serrated teeth, most likely those of *S. falcatus*. Schwimmer *et al*. (1997) documented the evidence of *Squalicorax* scavenging on various species of vertebrates on specimens found in museum collections. Their summary of bite marks attributed to this shark (*ibidem:* 77-79) lists more than 30 specimens, including sharks bony fish, turtles, mosasaurs, plesiosaurs and dinosaurs. *Squalicorax* teeth have also been found in association with the remains of other sharks, notably *C. mantelli* (Shimada, 1997; Everhart, pers. observation).

Shimada (1997) documented feeding by *C. mantelli* on the remains of teleosts, mosasaurs and plesiosaurs. One specimen (FHSM VP-13283) consists of five articulated vertebrae from the lower back of a mosasaur included severed bone, bite marks and embedded fragments of *Cretoxyrhina* teeth, and was partially digested (Everhart *et. al*, 1995; Shimada, 1997). Evidence of predation and/or scavenging by *C. mantelli*, including many partially digested bones, was reported by Everhart (1999) on a large number of mosasaur remains from the lower Smoky Hill Chalk. Hamm & Everhart (2001) reported the discovery of the partially digested radius and ulna of a juvenile nodosaur that was apparently removed from a floating carcass by a scavenger. Distinctive bite marks on the distal shaft of the radius indicate that the scavenger was probably a large *Cretoxyrhina*. Shimada *et al*. (2002) noted evidence of feeding by *C. mantelli* on a teleost fish (*Xiphactinus audax* Leidy, 1870) and a protostegid turtle.

In early 1992, an articulated series of dorsal vertebrae and attached ribs from a mosasaur were collected from the lower Smoky Hill Chalk Member (Late Coniacian) of the Niobrara Formation of western Kansas (figure 1). At the time, it was noted that the remains did not include any skull, neck, tail or limb elements and that most of the ribs showed evidence of bite marks. Subsequent preparation indicated severed bone, fractured vertebrae and the bite marks of two species of sharks, *C. mantelli* and *S. falcatus*. In addition, the broken tip of a *Cretoxyrhina* tooth was embedded in one of the vertebra. The mosasaur was identified as *cf. Ectenosaurus clidastoides* Merriam, 1894 (Bell, pers. comm., 1993; Schumacher, pers. comm., 1994) from characteristics of the vertebrae. *Ectenosaurus clidastoides* is a relatively rare mosasaur and is known from only a few specimens, the most complete of which (FHSM VP-401) is also in the Sternberg Museum.

2. Materials

FHSM VP-13746 consists of 21 articulated dorsal vertebrae (approximately 1.6 m in length), one detached cervical vertebra and portions of the ribs of a 5-6 m long mosasaur, collected by the author and curated in the Fort Hays State University, Sternberg Museum of Natural History (FHSM). The posterior cervical vertebra has two deep furrows from an apparent bite and the right side of the vertebral column shows evidence of at least three separate bites by a large shark. The tip of a *C. mantelli* tooth (FHSM VP-13747) is embedded in the right side of the D4 vertebra, near the posterior end. A *S. falcatus* tooth fragment was lying on the partial rib near the left side of vertebra D9. The D14 vertebra was fractured prior to burial and most of the ribs are missing or severed. Serrated bite marks are visible on most of the ribs. During preparation, small (5-6 mm) oysters

(*Pseudoperna congesta* (Conrad, in Nicollet, 1843, p. 169[1])) were noted to be attached to the upper surface of some of the bones.

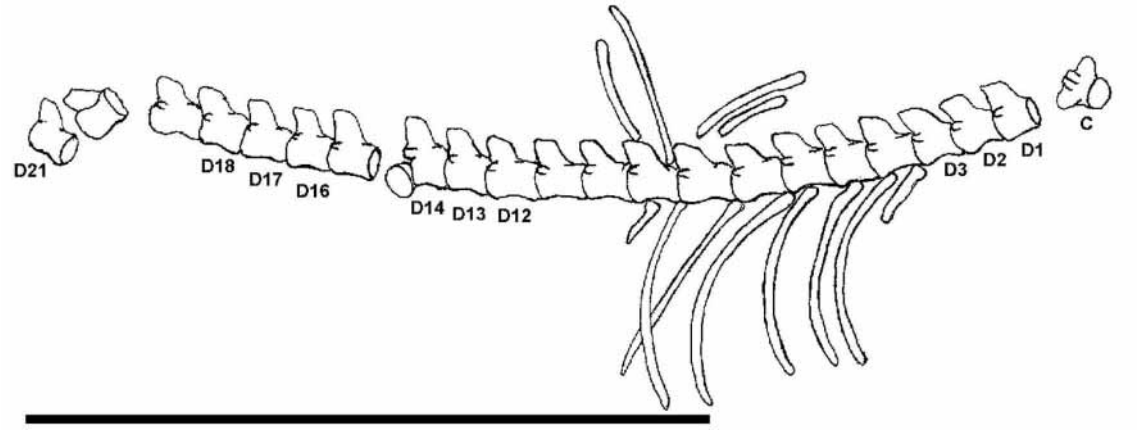

Figure 1. The vertebrae and ribs of a mosasaur (FHSM VP-13746) as found. Anterior is to the right. Scale bar = 1 m. C = Posteriormost cervical vertebra. Dorsal vertebrae numbered from right to left. Drawing by the author.

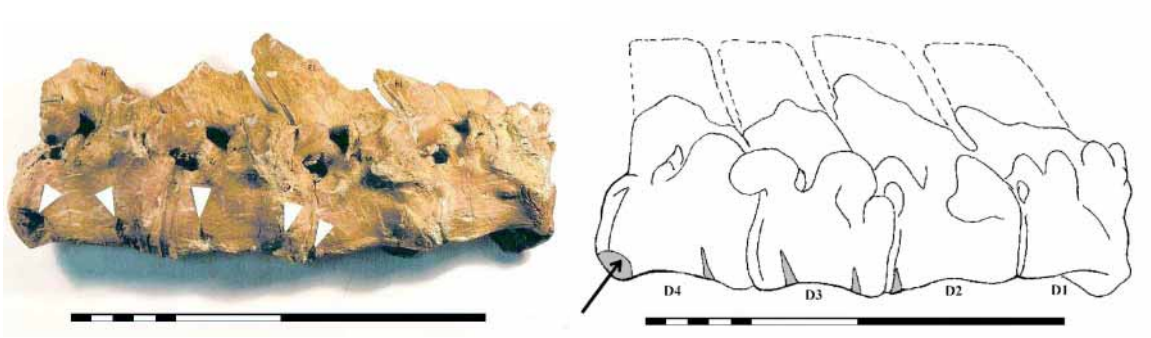

Figure 2 (left). The bite marks on the right side vertebrae D2-D4. Scale bar in cm. Photograph by the author.
Figure 3 (right). Drawing of vertebrae D2-D4. The arrow shows the location of the broken Cretoxyrhina tip (FHSM VP-13747). Gray areas indicate bite marks. Dotted lines indicate missing portions of dorsal processes. Scale bar in cm. Drawing by the author.

Figure 4 (left). Tooth of C. mantelli *in labial and lingual views. Scale bars in mm. Photographs by the author.*
Figure 5 (right). Tooth of S. falcatus *in labial and lingual views. Scale bars in mm. Photographs by the author.*

3. Locality and stratigraphic occurrence

[1] This is confusing but Conrad was not the author of any part of the Nicollet's volume. He simply identified and named specimens brought to him. The exact quote, found as a footnote on the next to the last page (169) in the volume: " * *Conrad's description of the ostrea congesta*: Elongated; upper valve flat; lower valve venticose, irregular; the umbo truncated by a mark of adhesion; resembles a little *gryphea vomer* of Morton."

The remains were found on private property in the Smoky Hill Chalk Member of the Niobrara Chalk in south eastern Gove County, Kansas. The exact location is on file in the records of the Sternberg Museum of Natural History. Stratigraphically, the specimen occurred just above marker unit 5 of Hattin (1982), approximately 38 m above the contact with the Fort Hays Limestone and is Late Coniacian in age.

4. Discussion

The shark-scavenged remains of many vertebrates, especially mosasaurs, are common occurrences in the lower Smoky Hill Chalk (Everhart, 1999, 2003). It is likely that the larger sharks of the Late Cretaceous behaved in a manner similar to modern sharks and would be expected to have fed on the remains of dead animals, or to attack injured, sick or otherwise vulnerable prey.

Cretoxyrhina mantelli was the largest shark known from the Western Interior Sea, reaching lengths of 5.5 m by the Late Coniacian (Shimada, 1997; Corrado *et al*., 2003). This shark was similar in size to a modern Great White and probably had similar feeding habits and behaviour. The robust, triangular teeth of *C. mantelli* have razor sharp cutting edges and are unserrated. The remains of five articulated mosasaur vertebrae mentioned above (FHSM VP- 13283) attest to the sharpness of the teeth and biting power of the jaws of this species (Shimada, 1997). The vertebrae in this specimen are about 5 cm in diameter. Both the anterior and posterior vertebrae in the series are severed, one at right angles to the vertebral column and the other at a 45 degree angle. In the lower chalk (Late Coniacian – Early Santonian), isolated, partial remains of mosasaurs are frequently found, usually partially digested. These mosasaur fragments usually consist of severed skulls, limbs and tails of mosasaurs that could have been removed from a carcass by the single bite of a large shark (Everhart, 1999). *Cretoxyrhina* is found from the Upper Cenomanian through the Santonian and becomes extinct worldwide by the Middle Campanian (Stewart, 1990).

Squalicorax falcatus was a small to medium sized (2-3 m) shark found in the Western Interior Sea from Upper Cenomanian though Santonian time. It is then succeeded by *Squalicorax kaupi* Agassiz, 1843 in the Early Campanian. The serrated teeth marks of *Squalicorax* are found on many vertebrate specimens, from small fish to large sharks to giant mosasaurs, suggesting that they were quite numerous and were opportunistic feeders (Schwimmer *et al*., 1997). These sharks were not able to severe the bones of larger vertebrates, such as mosasaurs, but instead stripped the flesh from the bones, leaving distinctive marks on the bone. In the Western Interior Sea, *S. kaupi* is replaced in the Early to Middle Campanian by a larger species, *Squalicorax pristodontus* Agassiz, 1843. Based on observations of the number of shed teeth of each of these species collected from the chalk, the larger *Cretoxyrhina* were less numerous than the much smaller *Squalicorax* sharks.

FHSM VP 13746 appears to be the remains of a medium sized, older juvenile or young adult mosasaur, probably in the 5-6 m size range. Regardless of the actual fate of the mosasaur, the taphonomy of the specimen indicates a violent dismemberment by one or more large sharks and feeding activity by two species of sharks (Everhart & Everhart, 1998). The remains consist of an articulated series of dorsal vertebrae, associated ribs and one detached cervical vertebra. The dorsal vertebrae are lying on their left side, in a more or less north-south line. They are numbered D1 through D-21, anterior to posterior, and include a nearly complete dorsal series. According to Russell (1967), *Ectenosaurus* has 22 dorsal vertebrae. Vertebra D14, in the lower back of the mosasaur, was fractured completely across prior to being buried. The damage appears to have been caused by twisting of the vertebral column.

In addition to the fractured vertebrae, at least three large bite marks are evident on right side of the remains. Teeth marks on vertebrae D2-D6 indicate a single bite to the right shoulder of the mosasaur which may have removed ribs or limb elements in that area (figure 2 & 3). The bite also left the tip of a tooth embedded in the posterior right side of vertebra D4. The marks made by the shark's teeth are an average of 3 cm apart, consistent with the spacing of teeth of a large (5 m) *C. mantelli*. A second bite is indicated across the right, lower side of vertebrae D12-D14. The D14 vertebra is fractured just in front of the condyle and is displaced slightly from the cotyle of vertebra D15. Evidence of a third bite is indicated across the right side of vertebrae D16-D18. The tops of the dorsal processes appear to have been partially bitten off all of the vertebrae, but no identifiable bite marks were found on the remaining bone.

The single cervical vertebra is posteriormost of seven vertebrae in the mosasaurs neck. It is turned at nearly right angles to the rest of the vertebral column, separated by a distance of about 8 cm, and unlike all the other vertebrae, was sitting upright. Two long gouges on the left side of the vertebra appear to be deep bite marks caused by teeth equivalent in size (5 cm) to those of a large *C. mantelli* (*cf.* figure 4). The position of this vertebra and its damaged condition appear to be the result of a twisting bite by a large shark that severed the anterior neck, and possibly the skull, from the mosasaur carcass.

The remains of four ribs from the right side of the body were displaced and lying above the vertebral column. All but one had been severed within 15 cm of the head of the rib. The ribs remaining on the left side of the body appear to be arrayed in their normal order but were not necessarily still attached to the vertebral

column. Six of the eight remaining ribs are reasonably complete and minimally damaged. However, these six ribs occur within the space of five vertebrae (D4-D8). This probably indicates that at least a portion of the rib cage had been torn loose from the vertebral column and displaced. The ribs ahead and behind these six complete ribs had been severed to within about 10 cm of the rib head. Serrated bite marks attributable to *S. falcatus* (*cf.* figure 5) are found only on the ribs. A small fragment of a *S. falcatus* tooth was lying near the proximal end of the severed rib attached to the left side of the D9 vertebra.

The taphonomy of this specimen suggests that a sick, injured or dead mosasaur was fed upon by one or more large *C. mantelli* sharks. A series of bone shearing bites removed the head, most of the neck, all limbs and limb girdles, the tail and most of the rib cage, gutted the carcass and left only the dorsal vertebrae with a few attached ribs. A single cervical vertebra remained attached to the carcass by muscles or other connective tissue, and the lower back was fractured. At some point, the remains were fed upon by smaller *S. falcatus* sharks that left the marks of their serrated teeth on many of the remaining bones. Eventually the remains reached the sea bottom where the bones remained exposed long enough for small oysters (*P. congesta*) to become attached.

5. Conclusion

The partial remains of a relatively rare mosasaur found in the lower Smoky Hill Chalk documents feeding activities by two species of Late Cretaceous sharks; *C. mantelli* and *S. falcatus*. Whether this specimen represents an attack on a living mosasaur, or scavenging of a carcass cannot be determined from the information available. It does, however, provide evidence that these three species were contemporaneous**,** that *Cretoxyrhina* and *Squalicorax* fed on large vertebrates, and further documents the palaeoecology of the Western Interior Sea during Late Coniacian time.

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