



Mosasaur predation on a nautiloid from the Maastrichtian Pierre Shale, Central Colorado, Western Interior Basin, United States

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Mosasurs were common predators on the ammonites that inhabited the upper water column of the Late Cretaceous Western Interior epicontinental seaway of North America. Mosasurs developed predictable behaviour patterns for feeding on ammonite prey. There are no previous reports of mosasaur predation on the much less common Cretaceous nautiloids, possibly because of the prey's predominantly deep, epibenthic habitat, as deduced from modern *Nautilus* life habits. A single specimen of the highly inflated nautiloid, *Eutrephoceras dekayi* (Conrad), prey to a small adult mosasaur, likely *Platycarpus*, *Prognathodon* or *Mosasaurus*, is reported herein from the Pierre Shale of Colorado in the Early Maastrichtian biozone of *Baculitesgrandis* transitional to the biozone of *B. clinolobatus*. The nautiloid was killed in the same manner as described previously for discoid ammonites (*Placenticerus*, *Sphenodiscus*) from coeval strata in the USA and Canada. □ *Cretaceous, mosasaur, nautiloid, Pierre Shale, predation.*

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It has long been assumed that Mesozoic marine reptiles fed primarily or exclusively on fish, squid and, rarely, other reptiles. These observations are based on stomach contents in adult specimens mainly preserved in Jurassic Lagerstätten (e.g. the Posidonienschiefer of Germany; i.e. Hauff 1921; Kauffman 1978, 1981). Functional morphological observations from Triassic and Jurassic marine reptiles indicate they lacked adequate jaw articulation capable of crushing large prey and/or hard objects such as shelled cephalopods. Small ammonites were probably swallowed whole for food by some pre-Cretaceous marine reptiles, as evidenced by the occurrence of numerous Lower Jurassic *Amaltheus* in the stomach contents of marine reptiles (Frentzen 1936; Chamberlain 1987). Cretaceous mosasurs, however, developed more strongly articulated jaws and long recurved stabbing teeth capable of grasping and wounding/killing large prey which was then ripped out of the shell and commonly swallowed whole. The mosasaurine clade also developed blunt-toothed forms (i.e. *Globidens*) capable of crushing large shells of swimming and benthic molluscs.

Mosasurs apparently expanded their feeding behaviour from a primary diet of fish, to a secondary diet of ammonites and squids, and then to a tertiary diet of nautiloids while still keeping the first

two diets in place. Mosasurs enlarged on the secondary diet of ammonoid cephalopods at the same time they were diversifying. The nautiloid diet must have been a difficult one, and rarely tried because of the width of the nautiloid shell and the depth of diving, which normally ranged deeper than the mosasurs'. This was coupled with the difficulty in penetration of the robust shell brought on by its natural resistance to crushing. Nautiloids did make brief forays to the surface for breeding, and/or impending death by predation.

Kauffman & Kesling (1960) first documented a successful mosasaur (*Platycarpus* or *Prognathodon*) predation on a Campanian ammonite, *Placenticerus* sp. cf. *P. whitfieldi*, from the Pierre Shale of South Dakota. This discoid ammonite was a relatively rapid swimmer, probably a predator that primarily inhabited the upper water column of Cretaceous seas (based on broad facies distribution and functional design; Ward 1980; Chamberlain 1987). In tracing the sequencing of 16 discrete bite marks on the ammonite, Kauffman & Kesling (1960) concluded that the mosasaur intentionally attacked the ammonite from its blind side (dorsally to dorsoposteriorly, in swimming position), and penetrated the conch behind the living chamber. Through a series of subsequent bites from the dorso-posterior sides,

the mosasaur destroyed completely the buoyancy system of the ammonite and its ability to escape. The injured ammonite was then positioned in the mosasaur's mouth until the living chamber was crushed and the cephalopod animal was ripped from its shell. Kauffman & Kesling (1960) concluded that the attack reflected a well-established trophic behaviour pattern of mosasaurs on ammonites.

More than 100 *Placenticer*s, *Sphenodiscus* and much less commonly *Baculites* have been located in various museums and university collections in both Canada and the USA which show mosasaur and, rarely, giant fish predation marks (Kauffman 1990). Kauffman (1990) summarized these findings and observations on the temporal and ecological patterns of predation by marine reptiles on Cretaceous ammonites in the Western Interior Basin. He concluded that:

- 1 Mosasaurs commonly fed on ammonites, although it was probably not their main food source.
- 2 The great majority of mosasaur attacks on ammonites followed the same predatory behaviour pattern as first described, but with greater efficiency: an initial attack from the blind spot, i.e. the top or rear (anterodorsal to posterodorsal) of the animal. The initial bite or set of bites was designed to puncture the flotation chambers of the ammonite and destroy its buoyancy control and ability to escape. After repositioning the shell involving both the marginal and pterygoid teeth, a final set of bites across the living chamber effectively wounded or killed the animal, and tore it out of the shell for consumption.
- 3 The great majority of prey ammonites were inhabitants of the upper water column, mainly rapid swimmers with smooth discoid shells (e.g. *Placenticer*s and *Sphenodiscus*). Prey ammonites also include geographically widespread, probably plankton-feeding, pelagic floaters and slow swimmers like *Baculites* (Kauffman 1990; Cobban 1993; Kauffman *et al.* 1993). The only bite marks found to date on ammonite morphs thought to inhabit deeper water and the benthic zones were those of shell-crushing fish (e.g. *Ptychodus*) and/or blunt-toothed, bottom feeding mosasaurs (e.g. *Globidens*, sub-family Mosasaurinae) (Kauffman 1990).
- 4 Documented mosasaur predation is mainly known from the Western Interior Basin of North America, and predated specimens, as well as the diversity of prey, increased through time to a peak in the Campanian and Early Maastrichtian. This peak is coeval with the greatest diversification of Cretaceous mosasaurs, suggesting predator-prey co-evolution (Kauffman 1990). Both mosasaur diversity and the

number and diversity of prey ammonites decreased drastically through the Late Maastrichtian.

The depth of ammonite diving is not known precisely, but we have a general idea (Westermann 1988) based on facies mapping versus the spread of ammonites. Those ammonites with the widest distribution, encompassing virtually all marine facies, probably lived at the shallowest depths. This was also the domain of *Placenticer*s, *Sphenodiscus* and other streamlined forms that were predators in the upper water column. Similar distributions are shown by *Baculites* and *Sciponoceras*, although these were rarely prey. At a slightly deeper level were the heavily ornamented genera, such as *Prionocyclus*, *Acanthoceras*, and *Euomphaloceras*, etc. These fossils are limited to silty clay to clay shale, calcareous clay shale, limestone and chalk, and show a low incidence of mosasaur attacks. The deepest zone is made up of the aberrant heteromorphs *Didymoceras*, *Exiteloceras*, *Solenoceras*, etc., and the smooth-sided, inflated ammonites which spent a lot of time resting or dwelling on the bottom.

By analogy, the smooth-sided, inflated Nautiloidea (i.e. *Eutrephoceras dekayi*; Figs 1–3, the actual specimen and our interpretive drawings of the fossil Nautiloidea and the mosasaur attack mode) would be a moderately deep-water genus (as deduced from the modern counterpart, *Nautilus*), and relatively speaking, out of harms way of the mosasaur. However, this is an incorrect interpretation because nautilids ranged throughout the water column, as evidenced by their widespread occurrence in tidal sands and deeper water shales and carbonates (c. 60–1000 m, Western Interior maximum water depths), where they spent most of the time. Different species of 'Nautilus' are found sub-equally from their normal deep-water habitat to the surface for breeding and back again, often making the trip several times a year. They are not depth zoned, as were the ammonites. This is reflected in shell structure, with more compact stacking of crystallites in the nautiloid versus less compact in the ammonites.

Nautiloids, mainly species of *Eutrephoceras*, are much rarer than ammonites in the Western Interior Cretaceous Basin, possibly due to competitive exclusion from many habitats. However, nautiloids presented the same potential trophic resource to Late Cretaceous mosasaurs as did ammonites, but may have escaped the same level of predation. Modern and probably ancient inflated nautiloid species (e.g. *Nautilus pompilius* or *N. macromphalus* compared with the Cretaceous *Eutrephoceras dekayi*) are deeper water epibenthic cephalopods which may have fed upon benthic to epibenthic arthropods (Ward *et al.*

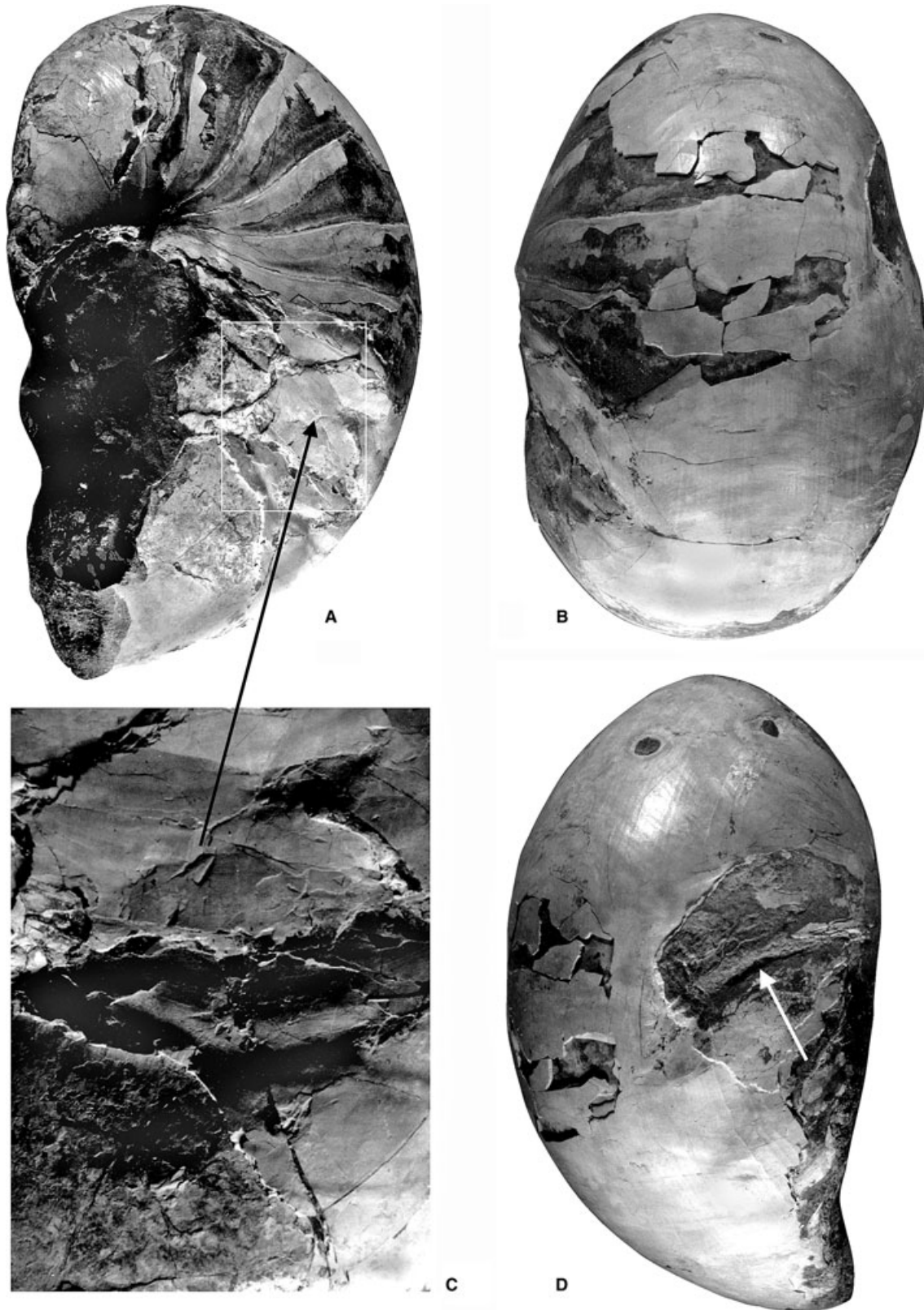


Fig. 1. Right-lateral (A), posterior (B) and left-lateral (D) views, in the life position of the nautiloid ($\times 0.5$), showing distribution of the marginal teeth ('stabbing') and pterygoid crushing teeth near the back of the jaw. (A, D) Bites on opposite sides of the nautiloid shell involving both the marginal and the pterygoid teeth (the latter can be best seen in D). (B) Ventral view showing marginal teeth on lower flanks of the nautiloid. (C) Close-up of the left flank of the nautiloid ($\times 2.5$) shown in A; arrow links the same places on A and C. White arrows on D point to the best example of pterygoid teeth on the prey nautiloid, convex towards the front of the jaw.

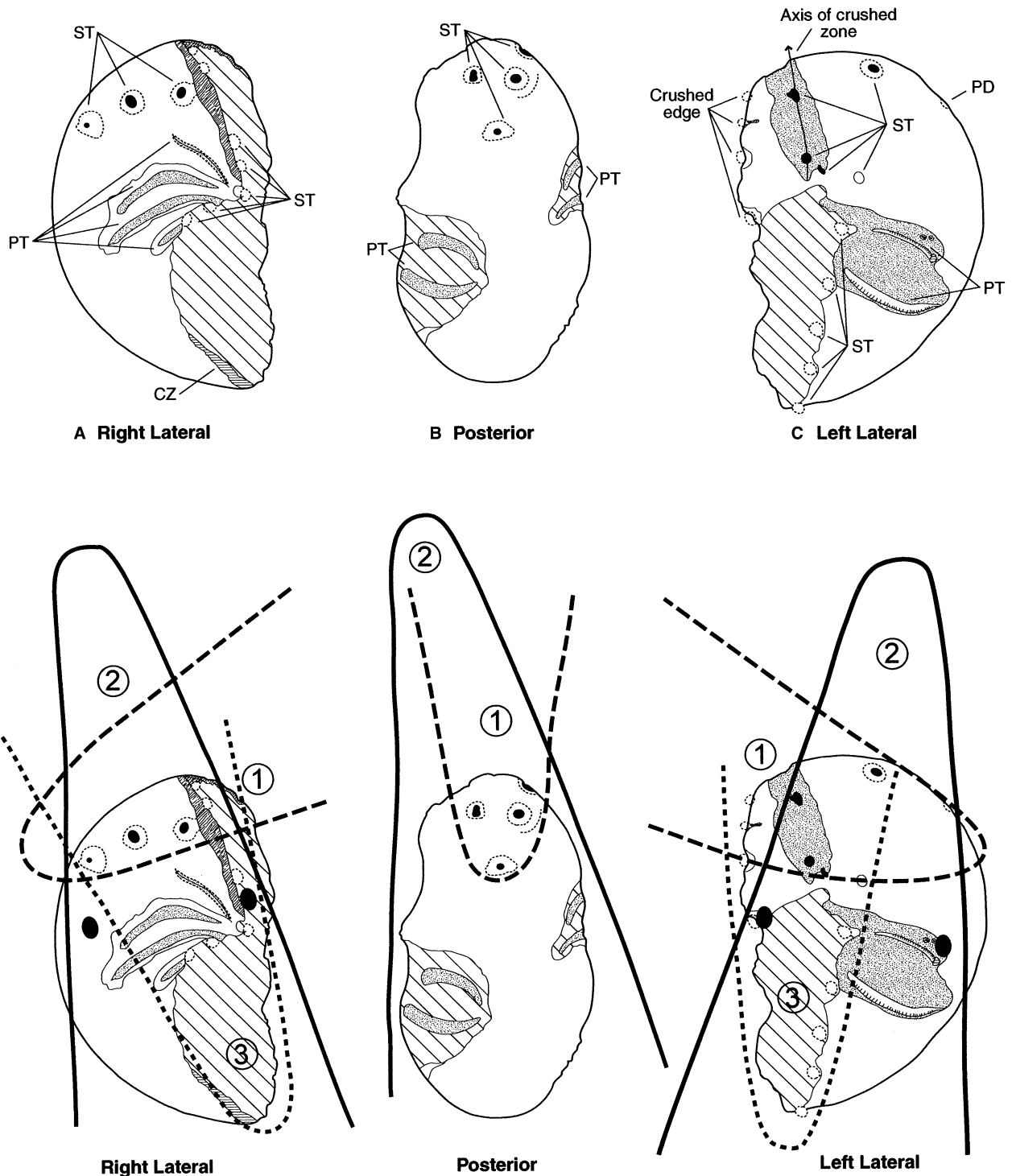


Fig. 2. (A) Right-lateral; (B) posterior and (C) left-lateral views of specimen ($\times 0.3$) of the nautiloid *Eutrephoceras dekeyi* (Conrad) in life position attacked by *Mosasaurus* sp., *Platycarpus* sp. or *Prognathodon* sp. These show marks left by marginal or 'stabbing' teeth, pterygoid teeth and crushed edge. Many marks left by marginal teeth consist of a black hole (tooth penetration) surrounded by a small series of dots (edge of crushed zone representing the expanded base of the tooth). Lower row of images (right-lateral, posterior and left-lateral views) of the same nautiloid showing our interpretation of the mosasaur head during the first, second and third bites, some of which are multiple bites.

1997). Being relatively slow swimmers (Ward *et al.* 1997 record escape speeds under stress of only 0.25 m/s maximum for *N. pompilius*), nautiloids

would have been easy prey to fast-swimming reptiles and large fish (i.e. *Xiphactinus* spp.) in the Cretaceous.

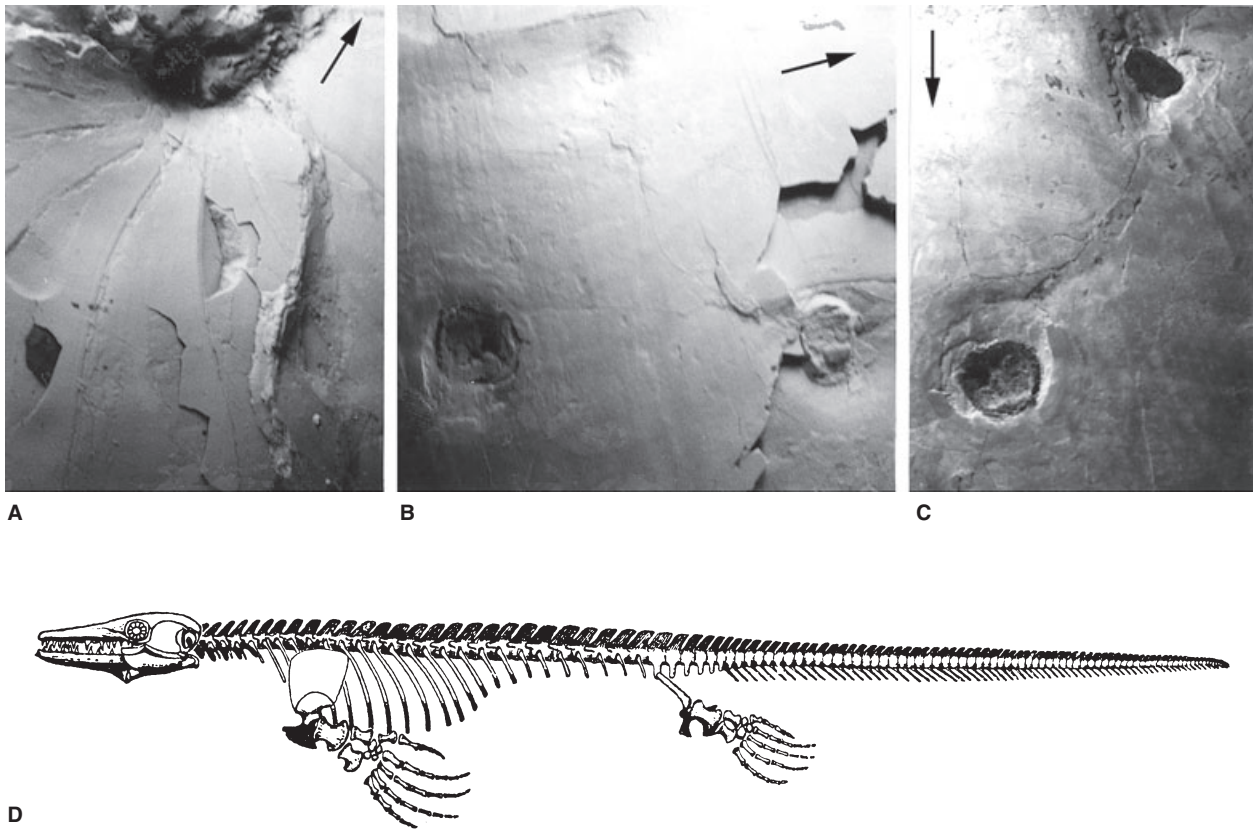


Fig. 3. Close-ups ($\times 1.0$). (A) Pair of dents made by the pterygoid teeth near the back of the mosasaur jaw (see Fig. 2 for better examples). Aperture towards the northeast, as evidenced by the septa. (B) Impressions left by the marginal teeth. Aperture towards the west-southwest, as evidenced by the fine growth lines. (C) Two marginal teeth impressions; aperture towards the bottom (ventral) as evidenced by the fine growth lines which are concave in that direction. All three of the bite marks are on the same specimen of the nautiloid, *Eutrephoceras dekayi* (Conrad). (D) Schematic representation of the mosasaur which most likely attacked the nautiloid, as determined from the relatively wide spacing of the tooth marks: *Platycarpus*, *Prognathodon* or *Mosasaurus* (4 m long, as shown).

To date, there have been no reports of mosasaur predation on Cretaceous nautiloids from the Western Interior Basin, Gulf Coast, or the Caribbean (but see Kauffman 2004; on a single specimen from the Pacific Coast). This study describes the first known occurrence of mosasaur predation on a Late Cretaceous nautiloid from the Western Interior Basin, and confirms that the predatory behaviour developed by mosasaurs for ammonites was also partially effective for more inflated nautiloids. The prey nautiloid specimen, discovered in 1982 by J.K. Sawdo, allows attribution to a limited pool of mosasaur genera based on the size and spacing of the marginal teeth, curvature and spacing of the pterygoid teeth and the jaw angle, utilizing the guidelines developed by Kauffman & Kesling (1960) for identifying mosasaur predators (*Mosasaurus* or *Platycarpus*). In addition, mosasaur predatory bite marks on the Cretaceous nautiloid provide sufficient data to document the probable genera and the sequence of events during the successful attack.

The nautiloid comes from the upper shale member of the Pierre Shale at a locality 6 km south of the

south edge of Boulder, in northern Jefferson County, Colorado, 100 m west of Colorado State Highway 93, within a shale cut marking an old access road into a Pierre Shale pit, now quarried by the Western Aggregates Company for light aggregate.

Description and interpretation of the specimen

The prey specimen is a typical adult *Eutrephoceras dekayi* (Conrad) measuring 21.5 cm in maximum diameter and 14 cm in maximum width, as measured across the preserved remnant of the living chamber. The living chamber, partially missing, is at least 10.5 cm long. Twelve septa and associated chambers are visible within the last volution, and we have numbered these 1–12 beginning just behind the living chamber. The inner whorls are not visible. Aragonitic shell material is on the ventrolateral flank, and discrete pieces occur where punctured or torn by bite marks of the mosasaur. Maximum preserved

thickness of this shell layer is 1.5 mm. The shell material around the crushed margin of the living chamber and part of the chambered conch are bent inward and preserved as if some mantle tissue remained attached after the predation event to hold these broken shell fragments in place. This is a common pattern in the living chamber of predated ammonites, including the first specimen described by Kauffman & Kesling (1960). An initial set of bite marks with the front of the jaw and engaging the marginal ('stabbing') teeth came from the blind side (anterodorsally to posterodorsally). The bite broke through the gas-filled chambers of the conch, damaged the nautiloid's buoyancy control system and hindered evasive action (Fig. 2). The shell was then positioned in the back of the mosasaur's mouth, as evidenced by marginal teeth plus pterygoid teeth impressions. Finally, the marginal teeth went across the entire shell (the outer portion of the living chamber), and presumably ripped the animal out of the shell for consumption. The great inflation of the nautiloid shell, compared with commonly predated discoid ammonites, and the nature of the successful bite marks, strongly suggest that the jaws of predatory mosasaurs were capable of unusually wide gape during feeding. Cretaceous nautiloid shell walls responded similarly to those of ammonites during reptilian predation, but they were more brittle and tough, reflecting a different arrangement of crystallites.

The mosasaur predation is apparent because: (1) the marginal teeth leave perforations through the shell (all layers), the mantle, the mantle cavity and the soft parts, considering the comparative length of the mosasaur teeth and the nautiloids probable hard and soft parts; (2) the crushed zone around the perforations, where the teeth are driven into their expanded bases, consists of fragmented shell material 1–5 mm wide, held in place by the mantle and possible periostracum of the nautiloid; (3) the pterygoid teeth, in the back of the jaw, have been used in the arrangement of the nautiloid between the jaws; and (4) the angle described by the mosasaur jaw segments suggests a narrow arc with the teeth, a feature known only in mosasaurs among marine reptiles (Figs 1–3).

The *Eutrephoceras dekayi* specimen is preserved in a sideritic limestone concretion within silty, dark olive grey, clay shale representing the middle high-stand system tract of the Bearpaw Marine Cyclothem. It is associated with the zonal index ammonite, *Baculites grandis* transitional to *B. clinolobatus*, which indicates an Early Maastrichtian age, about 68.5 Ma (Obradovich & Cobban 1975; corrected for modern decay constants, Obradovich 1992).

Comparison of limpet excavations with mosasaur bite marks

The limpet theory for 'bite marks' has been recently published by Kase *et al.* (1994, 1995, 1998) and by Seilacher (1998). General abiotic and/or biotic deformation of mollusc shells (recent and fossil) are reviewed by Zuschin *et al.* (2003). Limpets make rather large, shallow indentations in shells, rarely penetrating. They do so by crawling in circles, allowing the radular teeth to create a broad circular trough approximately 2.5–3.5 cm in diameter. The microscopic radular marks serve to anchor the foot firmly. Modern studies indicate that firm anchorage makes it very hard to detach the snail foot; usually some kind of small pry bar is used to detach limpets from a substrate. This is especially true in their 'home', near the centre of the depression.

Mosasaurs, on the other hand, normally pierce the shell, commonly to the extent that the tooth bases are impressed into the shell. This leaves a narrow zone of fractured shell behind, held in place by the mantle tissue and in some cases by the thin periostracum of the prey species; this is much different than the limpet depression. The mosasaur penetrates, leaving behind a narrow zone of crushed shell, much smaller than a limpet depression that has circular radular marks and enters at a much lower angle. The mosasaur has a near-vertical insertion angle, normally 70–90° penetration with a 1–3 mm crushed zone. The limpet slope is about 10–30°, normally without a hole, or with rare penetrations about 2.5 cm, which are elongate in the direction of entry.

The mosasaur origin for Cretaceous bite marks has been supported by Kauffman (1990, 2004), Kauffman & Kesling (1960), Tsujita & Westermann (2001), Westermann (1988, 1996), Westermann & Hewitt (1995) and Davis *et al.* (1999). Stewart & Carpenter (1990) review predation by vertebrates and mention Kauffman & Kesling's (1960) study on mosasaurs, and seem to agree with the conclusions. Martin & Bjork (1987) have done a comparative study on gastric residues of various marine reptiles. Massare (1987, 1988) studied swimming capabilities, both morphology and prey preference, and implied that mosasaur predation upon nautiloids was possible, but through 'ambush' rather than speed that exceeded that of the prey species. To quote Massare (1987), '...although the stomach contents of the mosasaurs suggest that some of these predators were capable of eating just about anything they encountered.' So why not an occasional nautiloid?

Conclusion

This is the first mosasaur attack on a nautiloid recorded from the Western Interior Basin. The attack probably occurred near the surface during a breeding period. The mosasaur had a special hinge feature capable of gaping two or more times the commonly preyed upon ammonites, so it was able to accommodate the nautiloid by killing and then presumably swallowing it whole.

The Late Cretaceous saw the origin of the Mosasaurinae as a separate sub-family. The diversification of mosasaurid genera took place in the middle Late Cretaceous, and by the Campanian – Early Maastrichtian, the Mosasauridae reached a peak in diversification. This was also a time of ammonite diversification among the large, laterally nearly flat, involute streamlined genera like *Placentoceras*, *Sphenodiscus*, etc., which became a secondary food source of mosasaurs. Nautiloids probably ranked number three or four as prey items, mainly because of their preference for deep water. Mosasaurs, however, had unusually wide gaping jaws, and the problem of getting the nautiloid in the mouth may have been resolved without too much difficulty. Is this an example of predator–prey co-evolution? This study bears witness to this behaviour pattern.

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