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Ventral bite marks in Mesozoic ammonoids

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ABSTRACT

Reports on the predators of ammonoids are rare, although ammonoids were abundant and diverse invertebrates in many Paleozoic and Mesozoic marine ecosystems. Most previous work on lethal ammonoid predation has focused on (sub)circular tooth marks which resulted from fish and mosasaur attacks. In the present study we discuss a relatively common type of bite mark in ammonoid shells, the 'ventral bite mark'. This typically occurs in a restricted position on the ventral side of the outer body chamber whorl and does not affect either the aperture or the phragmocone. Ammonoid specimens revealing ventral bite marks used in this study were collected from a wide range of strata which range in age from the Lower Jurassic to the uppermost Cretaceous (close to the Cretaceous–Paleogene boundary). These ventral bite marks are absent in the Paleozoic collections studied. The vast majority of ventral bite marks are situated at the end of the body chamber, close to the phragmocone. This is interpreted as the result of predatory attacks on the back or blind side of ammonoids in their living position. The predators aimed for the vital parts and muscle attachments to obtain the edible soft tissues. The agents for most of the ventral bite marks to ammonoids are probably coleoid cephalopods (especially teuthoids) and predatory fishes to a lesser extent.

1. Introduction

1.1. Predation on cephalopods

Predation on shelled cephalopods can be divided into two categories: sublethal and lethal. Sublethal predation, abundantly studied, is unsuccessful predation in which the shell could regenerate (Hengsbach, 1996; Keupp, 2006), because it was in direct contact with the carbonate-producing mantle. There is no evidence to suggest that injuries of the phragmocone could be repaired (Bond and Saunders, 1989). Lethal injuries can be divided into lateral, ventral and other types of damage.

1.2. Lateral damage

Lateral predatory damage on ammonoid shells were caused by Late Cretaceous mosasaurs, Carboniferous sharks, and possibly Late Cretaceous swimming crabs. The most widely known example of lateral damage in ammonoids was documented by Kauffman and Kesling (1960), who ascribed circular holes on both sides of the shell of a Cretaceous ammonoid *Placenticeras* from South Dakota (USA) to platecarpine mosasaur predation. Kase et al. (1994, 1995) raised doubts, and pointed that, when punched through, limpet home scars were preserved as similar shaped holes and could be misidentified as mosasaur tooth marks. Tsujita and Westermann (2001) eventually concluded that either hypothesis might be valid, as based on a study of 150 specimens of Late Cretaceous *Placenticeras* from the Bearpaw Formation of Alberta, Canada, noting that the vast majority of holes must have been produced by mosasaurs, on account of their size, the position relative to one another and of the low abundance of gastropods.

Sharks are important predators of shelled cephalopods as well. Most reports are based on bitten, Carboniferous ammonoids. For example, Mapes and Hansen (1984) reported three circular punctures and one indentation in a coiled cephalopod shell from the Carboniferous Kendrick Shale of Floyd County, Kentucky (USA), possibly the result of three tooth cusps on a file of single teeth in the lower jaw of a large symmoriid shark. Mapes and Chaffin (2003) performed a study on coiled nautiloids and ammonites from the Upper Carboniferous of the Finis Shale Member of the Graham Formation in Texas. A part of the damaged cephalopod shells possessed circular to subcircular holes, which were ascribed to sharks and other fish that attacked from behind and below.

Radwański (1996) studied specimens of the latest Maastrichtian ammonoid *Hoploscaphites constrictus* from central Poland, which displayed subcircular damages on both lateral sides. According to Fraaye (1996), such marks were possibly made by swimming crabs, attacking the living ammonoid from behind, out of reach of the tentacles, and aiming for the vulnerable internal muscle attachment by their strong and pointed chelae.

1.3. Ventral damage

Currently, evidence on ventral predation is very scarce. The existence of bite marks on the ventral side of ammonoids from the

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Toarcian Posidonia Shale of Dotternhausen, southern Germany, was first documented by Taverne (2000). His study was based on four hundred, randomly selected specimens of the common genera *Dactylioceras*, *Hildoceras* and *Harpoceras*. Schweigert (1997) stated that many Late Jurassic ammonoids from near Salmendingen (Germany) also possessed bite marks at the end of the body chamber, and he suggested that the attacker came from behind. There are numerous photographs in the literature that show bite marks as well (e.g., Lehmann, 1976: Figs. 51, 97; Keupp, 2000: Fig. on p. 79; Landman and Cobban, 2003: Figs. 10B, 17A; Machalski, 2005: Figs. 10A, 25C; and Landman et al., 2007: Fig. 41I).

1.4. Other types of damage

Other evidence of lethal predation on ammonoids include stomach content, feces and shell accumulations. Sato and Tanabe (1998) made a good case for plesiosaur predation, on the basis of the stomach content of a Late Cenomanian plesiosaur from Japan, while Massare (1987) had earlier noted scaphitid ammonoids in the stomach of Late Cretaceous plesiosaurs. Jäger and Fraaye (1997) studied the food remains within numerous adult *Harpoceras falciferum*, and showed several specimens to contain small aptychi from the same species, suggesting cannibalism was quite common within this ammonoid group.

Late Cretaceous fish feces from Kansas (USA) contained a juvenile ammonoid, probably a scaphitid (Stewart and Carpenter, 1999). Portions of ammonoid shells also occur in fish feces from the Solnhofen Limestone in Germany (Schindewolf, 1958). Mehl (1978b) examined a coprolite, possibly from the bony fish *Lepidotes*, from the Late Jurassic Solnhofen Plattenkalk that contained ammonoid aptychi. Mapes (1987) described mandible clusters of ammonoids in coprolites in phosphate concretions from the Carboniferous.

Many accumulations of fragmentary ammonoid shells occur in Lower and Upper Jurassic sediments in southern Germany (Mehl, 1978a). He interpreted these as teuthoid meal remains.

The occurrence of numerous smaller ammonoids surrounding collapsed larger nautiloid chambers in the Carboniferous (Mississippian) of northern Arkansas (USA) was reported by Zangerl et al. (1969) and Quinn (1977). These authors concluded that the ammonoids must have been part of the stomach contents of the nautiloids. Mapes and Dalton (2002) concurred.

1.5. Goal

To summarize, only a few predators of ammonoids have been identified, especially concerning non-regenerated shells. Vermeij (1987) stated that reviews of ammonoid shell architecture and traces of predation on cephalopods were critically needed for the Paleozoic and Mesozoic. This report focuses on relatively common ventral damage on ammonoid shells that was lethal.

2. Materials and methods

2.1. Materials

The main collections used in this study are housed in the following museums in the Netherlands; Nationaal Natuurhistorisch Museum 'Naturalis', Leiden (RGM numbers); Natuurhistorisch Museum Maastricht (JJ number); Oertijdmuseum De Groene Poort, Boxtel (MAB numbers); and the Geologisch–Paläontologisch Institut der Universität Münster, Germany. Many ammonoid specimens in these collections were not suitable for the study of ventral damage since they show only the inner whorls of ammonoid shells. All of the examined Cretaceous and Jurassic collections contained specimens with ventral damage. Table 1 summarizes the material used.

2.2. Methods

The selected ammonoids showed ventral damage extending to both lateral sides. Also, only specimens with visible damage on the outer whorl were selected. The damage was not connected to the aperture. When only one of the two sides of a specimen was visible, it was assumed that the other side also possessed the damage. This assumption was judged to be valid since only a few of the ammonoids with both sides exposed, showed damage that was only present on the venter and on one side. All ventrally damaged ammonoids lack broken shell pieces in the surrounding sediment next to or at the position of damage. Other, similar types of damage were extremely rare.

The ventrally damaged ammonoids were studied quantitatively, using the 'Angular Approach method'. This method is part of the 'Within-element method', a method to test for non-randomness in the spatial distribution of damages on a particular type of skeletal element (Kowalewski, 2002). The Angular Approach method was used to

Table 1
The table shows the age, museum, collecting site and country, stratigraphic position, and overall sample size available for this research.

System and series	Museum	Age	Country of origin	Location(s)	(Bio)Stratigraphical origin	Amount	Collecting method	Found in-situ?
Upper Cretaceous	Natuurhistorisch Museum, Maastricht	Maastrichtian	NE Belgium and SE Netherlands	ENCI, Geulhem (NL) & CBR, CPL, Vroenhoven (BEL)		300	Aselective	Y
Lower Cretaceous	Naturalis, Leiden	Hauterivian–Valanginian	SE France	Aulan/Angles/Rottier/La Charce/Buis les Baronnies		200	Aselective	Y
Lower Cretaceous	Naturalis, Leiden	Tithonian–Aptian	SE Spain	Region Murcia, west of Caravaca	Miravetes Formation	8,000	Aselective	Y
Upper Jurassic	Oertijdmuseum 'De Groene Poort', Boxtel	Oxfordian and Kimmeridgian	SW Germany	Plettenberg and Geisingen	Malm β and γ 2	50	Selective[a]	Y
Middle Jurassic	Naturalis, Leiden	Callovian	W France	Pamproux		200	Selective[a]	Y
Middle Jurassic	Naturalis, Leiden	Bathonian–Callovian	Indonesia	New Guinea (Irian Jaya), Kemabu Valley		500	Aselective	N[b]
Lower Jurassic	Oertijdmuseum 'De Groene Poort', Boxtel	Toarcian	SW Germany	Dotternhausen	Posidonia Shale	243	Selective[a]	Y
Triassic	Naturalis, Leiden	Ladinian, Olenekian	Norway	Spitsbergen, Kapp Lee Edgeöya	Sticky Keep Formation	1000	Aselective	Y
Mainly Devonian	Naturalis, Leiden; Geologisch–Paläontologisch Institut der Universität Münster	Mainly Frasnian and Famennian	Mainly Morocco and Australia	Various		15,230	Aselective	Y

[a] The collecting method is either selective or aselective. Selective means that not every ammonoid specimen found was present in the collection. Aselective means that every ammonoid specimen was collected and thus present in the collection. The ammonoids from Pamproux were bought by Naturalis, Leiden and were nearly all pristine which likely implies that most incomplete specimens were not part of the deal; ammonoids with ventral damage from Dotternhausen were selected in the quarry; ammonoids from Geisingen/Plettenberg were selectively collected as well.

[b] Ammonoids were probably found in pebbles derived from more or less broken concretions in the Iwaboe river (Westermann and Getty, 1970).