Ammonites are among some of the best fossils to collect. They are relatively easy to find, for example, in the Lower Jurassic Posidonia Shale in Germany and the Jurassic sediments of Dorset in the south of England. The larger, well-preserved ones will always be sought after and, if of sufficiently high quality, may even be displayed in museum exhibitions. However, while these nicely-preserved, complete ammonites are ideal for identifying species, they often do not say much about the life history and, more specifically, the death of the ammonite itself. On the other hand, studying the sub-lethal or lethal damage to the fossil shell certainly does.

This article is about a relatively newly discovered type of bite mark. It is found on Jurassic and Cretaceous ammonites, might have occurred worldwide, is easy to recognise and is also fairly common.

Ventral damage to ammonites cannot be found in every collection, as based on my study of about 35,000 ammonites spread over many such collections. However, Cretaceous and Jurassic collections do display this sort of damage (Figs. 1 and 2). I found it in Maastrichtian ammonites from the Netherlands and Belgium, notably in the species, *Hoploscaphites constrictus*. I also discovered that the Lower Cretaceous of southeast Spain (Miravetes Formation), in a collection I examined, yielded many ammonites with ventral damage, for example, in the genera, *Barremites* and *Pseudothurmannia*. In total, 17.1% of the ammonites in that collection were ventrally damaged. In addition, I found similar damage in Lower Cretaceous ammonites from Colombia, South America. Cretaceous ammonites from southeast France also showed ventral damage - 17.9% of the collection I looked at. I also found similar ventral damage in Upper Jurassic ammonites from southwest Germany (Plettenberg and Geisingen), in the Middle Jurassic ammonite *Irianiates moermanni* from Indonesia, and Middle Jurassic ammonites from Pamproux, France. Lower Jurassic collections from Dotternhausen, which have two-dimensionally preserved ammonites, are no different. As mentioned by Taverne (2000), the genera, *Dactylioceras*, *Hildoceras* and *Harpoceras*, show abundant ventral damage. Later on, our team discovered that *Lytoceras* specimens also exhibit this sort of damage.

When I was browsing through the ammonite collections of several Dutch museums (including, Naturalis and Oertijdsmuseum De Groene Poort) and the Geologisch-Paläontologisch Institut der Universität Münster in Germany, it became apparent to me that there were many specimens with damage to the outer whorl, on the back side of an ammonite (the ventral side) in its living position. This damage was not only visible on the ventral side, but could also be seen on both lateral sides, if preservation permitted. When viewed from the lateral side, the damage has different shapes, including triangular, sub-circular, rectangular and irregular. These appear to be related to the degree of ornamentation of the ammonite shell - the stronger the ribs, the more rectangular the damage becomes laterally.

**Fig. 1. Four Cretaceous ammonites with ventral damage: A. Upper Cretaceous (Maastrichtian) *Hoploscaphites constrictus* from Belgium; B. Lower Cretaceous (Valanginian–Hauterivian) *Taschenites sp.* from southeast France; C. Lower Cretaceous (Valanginian) *Thurmanniceras lory* from southeast Spain and D. Lower Cretaceous (Barremian) *Barremites vocontius* from southeast Spain. Scale bars are 1cm. After Klompmaker et al. (2009).**
Fig. 2. Six Jurassic ammonites showing ventral damage: A. Upper Jurassic (Oxfordian) *Orthosphinctes cf. tiziani* from southwest Germany; B. Middle Jurassic ammonite from Pamproux, France; C. Middle Jurassic *Irianites moermanni* from Indonesia; D. Lower Jurassic (Toarcian) *Dactylioceras commune* from southwest Germany; E. Lower Jurassic (Toarcian) *Hildoceras* sp. from SW Germany and F. Triassic ammonite from Spitsbergen (Norway). Scale bars are 1cm. After Klompmaker et al. (2009).
damage. The percentage of ventral damage in ammonites in some layers of the Posidonia Shale in Dotternhausen is quite high, with up to 50% of specimens showing evidence of such injuries. Lower Jurassic ammonites also exhibit ventral damage, notably in specimens of *Dactylioceras* from Dorset studied mainly by Natascha Waljaard, as well as some Pliensbachian ammonites from Germany (Fig. 3).

The position of the ventral damage is remarkably uniform across collections. The position of this damage was measured by two methods, which are explained in Figure 4. The greater majority of the damage can be found at about 180° from the aperture. Additional analysis of the large collections of the Lower Cretaceous of Spain and Lower Jurassic of southwest Germany clearly shows that most damage is located at the end of the living chamber, close to the last septum. Apparently, this was a favourite position to break.

The Triassic yielded mixed results. Rather vague, sub-circular damage was found in Triassic ammonites from Spitsbergen (Fig. 2F). However, the ceratite ammonite did not yield similar ventral damage. Compared to the Mesozoic, the Palaeozoic is a completely different story. Browsing through the Palaeozoic ammonite collection of Naturalis, it struck me that ventral damage was virtually absent in about 1,400 specimens. To confirm this, I studied about 13,000 Devonian ammonites from Morocco and Australia. The conclusion was the same - ventral damage of this sort was extremely rare. But why?

### Ventral bite marks

The reason for the difference between Mesozoic and Palaeozoic ammonites lies in the cause of the ventral damage, which is discussed below. Physical causes of damage to ammonite shells (such as collision while floating or damage while rolling) can be excluded, because they would be expected to show up in comparable numbers in both Palaeozoic and Mesozoic ammonite collections. Moreover, such physical damage is expected to be more random and not always at the same location at the end of the living chamber. To the extent that it does appear in the same place, these kinds of physical processes primarily tend to generate damage at the aperture. Implosion, another rare physical cause of damage to the shell, causes sub-circular damage to the phragmocone or shatters the shell completely.

Damage by biological agents includes that inflicted by infaunal/boring organisms, caused by the scavenging of the dead animal while it lay on the seafloor, and predation. The first and second are expected to produce random damage, and the second should usually result in damage only on one lateral side and fossil shell pieces found close to the fossilised shell. This is not the case with ventrally damaged ammonites. However, predation in the water column can cause damage to the same part of the shell, cause the bitten-off shell pieces to float away and give rise to damage to the ventral side that can also be easily seen on the lateral side. Therefore, ventral damage must have been caused by predation and, hence, should be referred to as ‘ventral bite marks’.

The location of the bite suggests that the predator came from behind, attacking the ammonite in its living position on its blind side. This led to the swimming ability of the ammonite being severely impaired, as the ventral muscle was (presumably) often damaged. Moreover, once the shell was locally crushed, the edible tissue was easily accessible. It also appears that this method of attack was very successful, as I have only found a few regenerated examples from such damage.

### What did it?

So what kind of predator do we need to cause these bite marks? Clearly, we require one that first became common during the Early Jurassic or a little earlier, to explain the huge difference in the number of examples of ventral damage between the Jurassic/Cretaceous and Triassic/Palaeozoic. We also need a predator that is able to break the shell with its beak at the same, confined position at the end of the living chamber, and it should be agile and free-swimming.

Reptiles, such as mosasaurs, turtles, marine crocodiles, ichthyosaurs and plesiosaurs, can be excluded, as they were generally too large to produce a confined bite mark. Rather, they would have completely crushed the shell. Crustaceans cannot have been the predator either. They do not live in the water column and are, for example, very rare in the Lower Jurassic of southwest Germany, the ideal place to find ventral bite marks on ammonites.

Predatory fishes, other than large sharks, are possible culprits for ventral damage (although, so far, they have been reported mainly to attack the aperture). Such fishes are free-swimming, and have a jaw that can open to catch and break the ammonite shell. Teleost fishes are particularly likely to be responsible, because they appeared in the Late Triassic and evolved from there.

Notwithstanding this, I believe that most ventral bite marks must have
been inflicted by cephalopods, but not by ammonites or nautiloids. The latter are relatively scarce in the Mesozoic, so they cannot have produced the vast number of bite marks. In addition, the beaks of the former were mostly not able to open wide enough, and were not suitable for biting and cutting. Belemnites might have been one of the culprits, as they were especially abundant in the Jurassic and Cretaceous. Despite the fact that they had hooks instead of suckers (which might have hampered them when grabbing ammonite shells), at least some of their beaks appear to have been suitable for biting through ammonite shells.

However, I believe that the major culprits are coleoids (Fig. 5), because of their relatively sharp, triangular beaks and their suckers, which would have aided them in grabbing the ammonite shell. Today, coleoids (such as squid and octopuses) are fast-swimming, specialised predators, able to catch and manipulate their prey and, most probably, so were their fossil counterparts. Coleoid diversity was highest after the Triassic-Jurassic boundary, when many new forms appeared, and remained high until the K-T (now known as the K-Pg) boundary, when many groups became extinct. Therefore, I believe that coleoid cephalopods probably caused most of the ventral bite marks (Fig. 6); other culprits were predatory fishes and belemnites.

Research dealing with predation on ammonites shells is scarce. Studies that have been published are largely based on a low number of specimens from a restricted geographical area and/or time span. Examples of predation have included rows of circular holes on Late Cretaceous ammonites attributed to mosasaurs, holes in phragmocones of Carboniferous ammonites from North America, caused by sharks, and lateral holes on Late Cretaceous ammonites from Poland, caused by swimming crabs. Therefore, the ventral bite mark is an important addition to the growing evidence of predation on ammonites. Given the collections studied, it is likely that this type of predation was a large-scale, possibly worldwide phenomenon. In addition, the behaviour spans a long period of geological time. My suspicion that ventral bite marks are likely to be present in many more Jurassic and Cretaceous collections all over the world seems to have been confirmed by recent publications. The article in *Palaeogeography, Palaeoclimatology, and Palaeoecology* that we published as a result of the research discussed above was picked up by a team led by Neil Landman (USA). As a result, they featured quite a few images of ventrally bitten specimens in their work on North American scaphites published in *Bulletin of the American Museum of National History*. In addition, very recently, Chris Andrew and colleagues published an article on ventrally damaged ammonites from the Lower Jurassic of Lyme Regis (Dorset) in *Proceedings of the Yorkshire Geological Society* (see also the BBC News article at: http://news.bbc.co.uk/local/dorset/hi/people_and_places/nature/newsid_9225000/9225848.stm). They named a new ichnogenus and ichnospecies after this ventral bite mark. Quite possibly, there are further studies on this ventral bite currently being undertaken.

**About the author**

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**Further reading**
