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Ichnology of Late Cretaceous echinoids from the Maastrichtian Type area (The Netherlands, Belgium) – 4. Shark *versus* echinoid: failed predation on the holasteroid *Hemipneustes*

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Abstract

Hemipneustes striatoradiatus (Leske) is a medium- to large-sized (up to *c*. 115 mm in length) holasteroid sea urchin that is locally common in the upper Maastrichtian (Upper Cretaceous) of the type area of that stage in the south-east Netherlands and contiguous Belgium. Tests of this species were bored both *in vivo* and *post-mortem*, and encrusted *post-mortem*, but evidence of predation by vertebrates in the form of tooth marks is surprisingly rare. A peculiar specimen from the upper Nekum Member (Maastricht Formation) preserves two clusters of parallel grooves in trapezoid groups, and on opposite sides of the test. These are interpreted as evidence of failed predation, namely the bite marks of a marine carnivore with a fairly large mouth and closely spaced teeth with a pointed, conical cusp and, possibly, smaller cusplets. The most probable culprit was a non-durophagous shark such as a representative of the families Scyliorhinidae Gill or Squalidae Bonaparte, but certain types of teleost fish (aspidorhynchids, saurodontids or ichthyotringids) cannot be ruled out either.

Key words: Hemipneustidae, Maastricht Formation, Nekum Member, dentition, taphonomy, benthic islands

Introduction

In the type area of the Maastrichtian Stage (Upper Cretaceous), the region that is now the southernmost Netherlands and adjacent Belgium, the echinoid *Hemipneustes striatoradiatus* (Leske, 1778) is a common constituent of benthic assemblages in the upper Maastrichtian (Jagt, 2000) and may be regarded as an ichnological ‘laboratory animal’. Tests of this conspicuous and much-sought-after species of sea urchin were infested in life, showing growth responses, by various organisms known only from their traces. The most confidently recognised examples of these are in specimens of *H. striatoradiatus* that are infested by a round pit with a central boss, presumably a domicile, and named *Oichnus excavatus* Donovan and Jagt, 2002. Apparently, the pit producer attacked only living echinoids, which responded by producing an interior stereom swelling within the test (Donovan and Jagt, 2002, fig. 5). *Post-mortem*, tests of *H. striatoradiatus* and other similar-sized holasteroids (such as the genus *Echinocorys* Leske, 1778) made large, solid and persistent benthic islands that provided hard, calcareous substrates which were elevated for some time above the seafloor. These were colonised by a range of cementing and boring invertebrates, including crinoids, foraminifera, sponges, bryozoans, sabellid and serpulid polychaetes and other ‘worms’, acrothoracican barnacles, inarticulate brachiopods and a range of molluscs (Jagt et al., 2012, 2018a; Donovan and Jagt, 2013, 2014, 2018, 2020; Donovan et al., 2018).

While, for example, locally common examples of *O. excavatus* provide excellent evidence for infestation of live *H. striatoradiatus* by another invertebrate, albeit indeterminate (perhaps gastropod or copepod?), some organism-organism interactions are too fast to permit a preserved response by the echinoid. Failed predation by vertebrates (fishes) or invertebrates (crabs, lobsters and cephalopods) may produce healed wounds in holasteroid echinoids (see: for example, Donovan et al., 2008); but what if failed predation leads to subsequent death? A distinctive specimen, described below, may be evidence of such an interaction.

Locality, material and methods

The present test, registered in the collections of the Natuurhistorisch Museum Maastricht, the Netherlands (prefix NHMM) as NHMM 1998 013, was found in a lot of some 100 specimens that were bought from workers at the former Nekami quarry (now ‘t Rooth, Bemelen, about 5.5 km east of Maastricht, the Netherlands; Fig. 1) in the mid-1970s. The idea was that all attendees of the joint meeting in 1978 of the Palaeontological Association (United Kingdom) and the Paläontologische Gesellschaft (Germany) would be presented a test of this echinoid for memory. The remaining lot remained at the museum, but were never labelled nor numbered.

At this particular quarry, and up to the early 1980s, limestone excavated was first dumped on conveyor belts and sieving tables by quarry workers, who picked out these echinoids (and many other fossils; see Mulder et al., 2016) for some additional cash on top of their wages. The level with numerous adult tests of *Hemipneustes striatoradiatus* is situated within the upper metres of the Nekum Member (Maastricht Formation), below the Kanne Horizon (upper Maastrichtian, *c.* 66.3 Ma; see Keutgen, 2018). This level was excavated on a large scale in the 1970s and 1980s (compare Felder et al., 1978a, b).

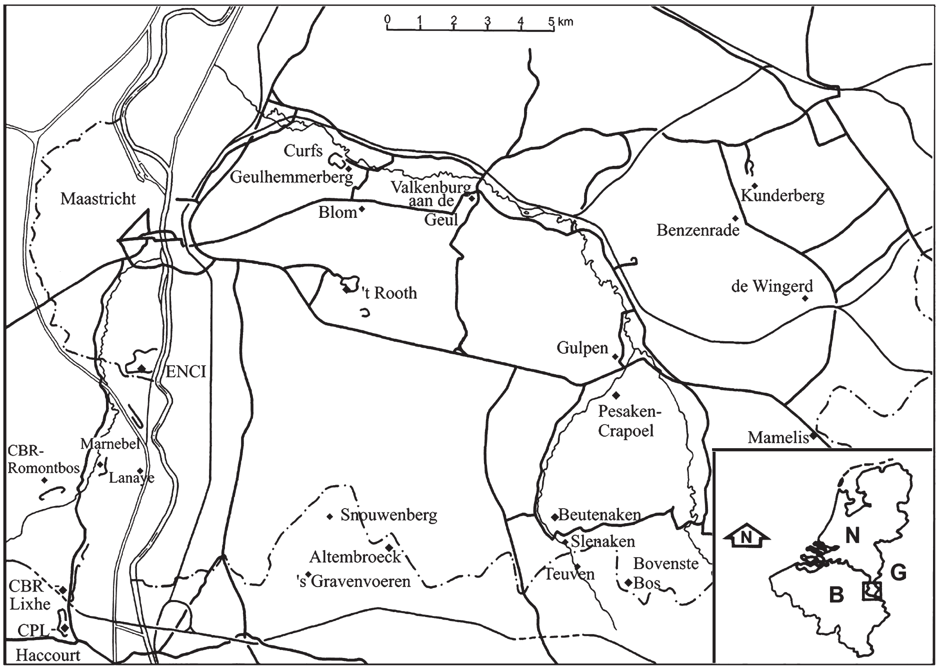

Fig. 1. Map of southern Limburg, the Netherlands, and contiguous areas in north-east Belgium (Voerstreek, provinces of Limburg and Liège) and western Germany (Aachen area), showing the most important localities ([temporary] outcrops and quarries) in the type area of the Maastrichtian Stage (modified after Jagt and Jagt-Yazykova, 2012, fig. 1). Specimen NHMM 1998 013 is from the ‘t Rooth [formerly Nekami] quarry at Bemelen. The inset map of northern Europe (B = Belgium; G = Germany; N = Netherlands) shows the position of the main map (box).

The specimen was first painted with red food colouring. Once dry, this was coated with a uniform layer of ammonium chloride and photographed with a Canon G11 digital camera in natural light (Fig. 2). Descriptive terminology used herein follows Melville and Durham (1966), Durham and Wagner (1966), Smith (1984), Smith and Kroh (2011), and Donovan et al. (2014).

Description

The present test, NHMM 1998 013, is an incomplete specimen of *Hemipneustes striatoradiatus*. The test is broken in three places: posteriorly in the region of the periproct (interambulacrum 5; not illustrated); left laterally (ambulacrum IV – interambulacrum 3; Fig. 2A, B) and just posterior of the apical system (interambulacrum 1 – ambulacrum I – interambulacrum 5 – ambulacrum V; Fig. 2A, C). Test length, width and height are 87.1 mm (but incomplete), 80.4 mm and 63.8 mm (highest anterior of apical system), respectively. Reference is made to Donovan et al. (2014, fig. 2A) for a diagram explaining the numbering of the ambulacra and interambulacra in *H. striatoradiatus*.

The test reveals two clusters of parallel grooves arranged as rounded trapezoid groupings; these are here informally referred to as Clusters 1 and 2. Cluster 1 (Fig. 2A lower right, C) has one of the areas of breakage within it; the grooves span interambulacrum 1 – ambulacrum I – interambulacrum 5 – ambulacrum V; there are 12 grooves in total. Grooves are parallel sided and parallel for most of their length, tapering towards the ambitus, but are bifid adapically; longest towards the centre of the group and with a broad U-shaped section.

Cluster 2 (Fig. 2A upper left, B) consists of *c*. 15 grooves. The imprecision in the number of grooves is due to short grooves on the right of Figure 2B, in which those on the upper half are slightly offset from those on the lower half of the structure. Overall, the features shown by these grooves are similar to those of Cluster 1, although bifid terminations also occur towards the ambitus. The two clusters are, essentially, on opposite sides of the test and with the grooves of each having similar orientations.

Discussion

> "Obtaining unequivocal evidence of predation in the fossil record is notoriously difficult (Vermeij, 1987) and usually can be done only in instances where some distinctive evidence of the predator is left on the hardparts of the prey, such as the toothmarks of a shark on a bone …" (Donovan, 1991, p. 246).

We consider NHMM 1998 013 to provide unequivocal evidence of failed predation of a large-jawed vertebrate with close-set and pointed teeth on *Hemipneustes striatoradiatus*. The two lozenge-shaped clusters of parallel grooves in different parts of the test (Fig. 2) are best interpreted as scratch marks made by the pointed cusps of lower and upper jaw dentition, scraping across the test as a predator attempted to grab, handle, pierce or crush the echinoid. The grooves have the same orientation in both clusters, indicating that they are most likely the spoor of the same attack (and attacker). That the test survived shows that not only was the attack unsuccessful, but also it was not repeated. The latter may be most easily explained by the predator having multiple potential prey organisms from which to choose; *H. striatoradiatus* was likely gregarious. This attack failed, but perhaps the next was successful.

What was the predator? The largest predatory vertebrates in the Maastrichtian seas, with a gape wide enough to bite a test of *Hemipneustes*, were mosasaurs, plesiosaurs, crocodiles, sharks and rays, and teleost fish. Mosasaur tooth crowns were either low, compressed and bulbous (for crushing, by durophagous species) or conical and slightly recurved, with or without carinae, and adapted for tearing, piercing and slicing (Massare, 1987; Neumann and Hampe, 2018; Milàn and Jagt, 2019). The latter produced trace fossils that are identifiable as punctures, although debate has clouded these identifications over the past decades (see: for example, Kauffman and Kesling, 1960; Saul, 1976; Kauffman, 1990, 2004; Kase et al., 1998; Seilacher, 1998; Machalski, 1999; Tsujita and Westermann, 2001; Kauffman and Sawdo, 2013; Oduzne and Mapes, 2013; Gale et al., 2017). However, other types of bite marks must have been possible, inflicted by juvenile individuals of the larger species or adults of smaller mosasaur taxa, such as plioplatecarpines. Experiments with modern-day varanid lizards could prove useful in this respect (see D'Amore and Blumenschine, 2009, 2012).

Elasmosaurid plesiosaurs (Mulder et al., 2000; Schulp et al., 2017; Miedema et al., 2019), with comparatively slender and slightly recurved teeth, were primarily piscivorous and teeth would have been too far apart in the jaws to create such traces on an echinoid test. The same goes for the equally rare crocodylian taxa (Mulder et al., 2016).

Rather, the more likely culprit, with a fairly large mouth and batteries of close-set, pointed teeth, was a small- to medium-sized shark. Fishes are major predators of echinoids, although Kowalewski and Nebelsick (2003, pp. 285–286) did not specifically identify sharks as making a significant impact. Various families of shark and ray are widely distributed in the Maastrichtian of the type area of that stage (Herman, 1977; Halter, 1990, 1995; Bastiaansen, 2004–2018; Jagt et al., 2018b; www.somniosus.be). Only a minority of these, and first and foremost, the anacoracid

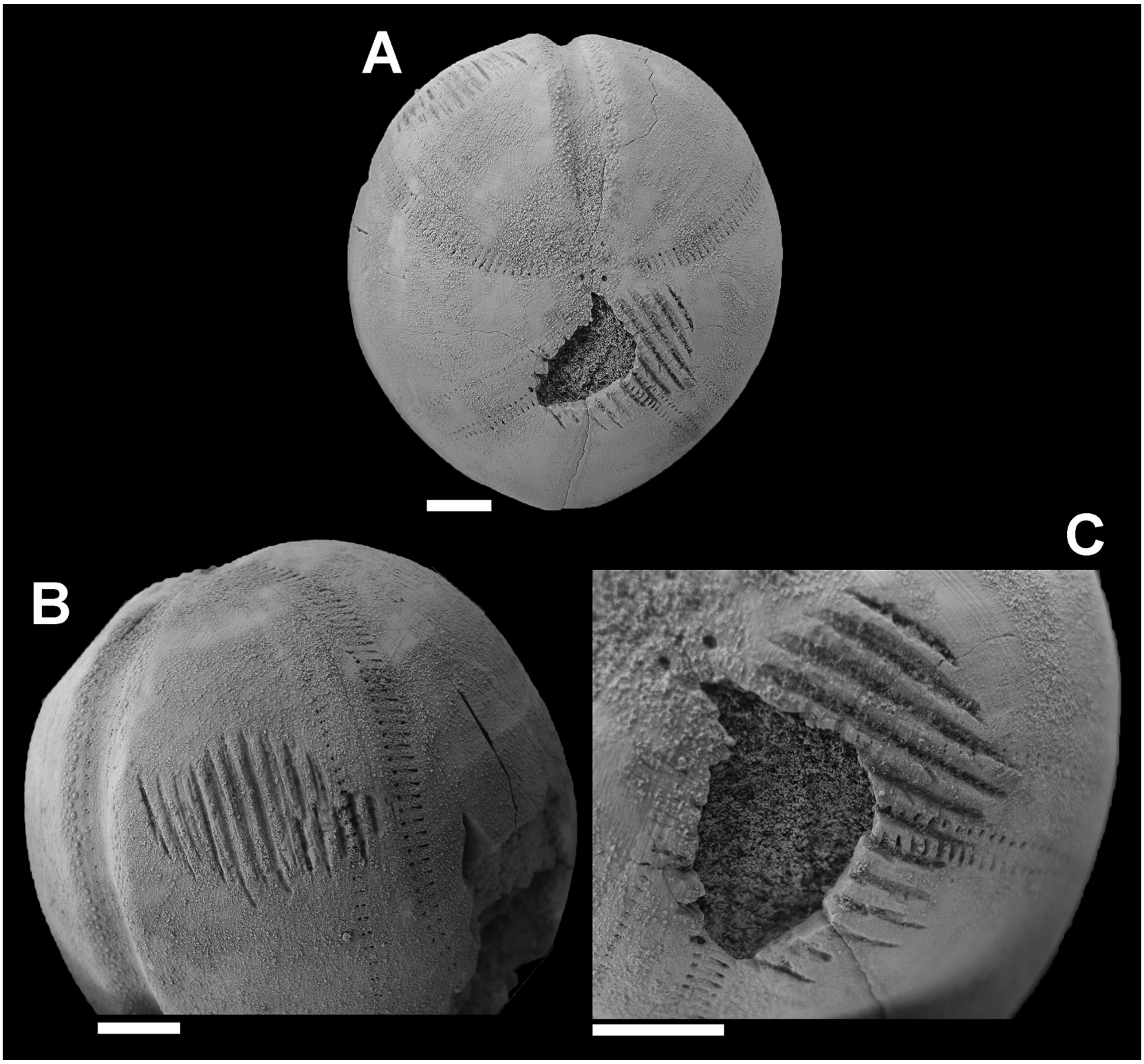

Fig. 2. The late Maastrichtian (Late Cretaceous) holasteroid echinoid *Hemipneustes striatoradiatus* (Leske, 1778), NHMM 1998 013, from the upper Nekum Member, Maastricht Formation at the 't Rooth quarry, Bemelen. **A**, Apical view, showing breakage posterior of apical system, Cluster 1 (lower right) and Cluster 2 (upper left) of parallel grooves. **B**, Cluster 2 of parallel grooves on surface. **C**, Cluster 1 of parallel grooves on surface, with later breakage. Echinoid coated with ammonium chloride. All scale bars represent 10 mm.

Squalicorax pristodontus (Agassiz, 1843), has large serrated teeth. Serration is a common feature of several lineages amongst sharks; these cutting-type teeth are particularly adapted for slicing through soft tissues (Moyer and Bemis, 2017). Further, sharks with serrated teeth are amongst the largest apex predators in modern ecosystems (Becker and Chamberlain, 2012). The same holds true for the Late Cretaceous, where the larger anacoracid sharks occupied such a position, with numerous examples of chipped or broken teeth and bite marks on skeletal elements of vertebrates (Schwimmer et al., 1997; Becker and Chamberlain, 2012) having been recorded. In the Maastrichtian type area, smaller- to medium-sized sharks were also common, in particular members of the families Squalidae Bonaparte, 1834, and Scyliorhinidae Gill, 1862, abounding (Herman, 1977; Halter, 1990, 1995). Bite marks on skeletal elements of certain marine vertebrates of Mesozoic and Cenozoic age have been ascribed to squalid (or squaloid) sharks (see: for instance, Welton and Farish, 1993; Bigelow, 1994; Bardet et al., 1998; Underwood et al., 2016). Scyliorhinids include forms with a dentition that could be envisaged to have produced such scratches on an echinoid test, with a conical, pointed cusp and smaller cusplets on either side of the cusp. Such cusplets may have been responsible for the shallower scratches directly adjacent to the deeper ones (Fig. 2B, C). It is suggested that such a shark, attacking a *Hemipneustes*, may have made a mistake, grasping a thick, calcite test lacking a thick layer of soft tissues.

As far as bony fish are concerned, certain aspidorhynchids, saurodontids or ichthyotringids in the Maastrichtian type area (compare Friedman, 2012; Jagt et al., 2014) cannot be ruled out either, although their upper and lower jaws may have been too acutely pointed to have left such close-set marks on a bulbous surface such as an echinoid test. Perhaps only an oblique, lateral attack, using the median portion of the lower and upper jaws could have resulted in such scratches, similar to what was described by Godfrey and Palmer (2015).

Was shark predation on *H. striatoradiatus* a common occurrence? It seems improbable, but it obviously did happen from time to time. An exercise in taphonomic contemplation teaches us the following: there are two obvious end-members perceptible in the fossil record of *H. striatoradiatus*. Firstly, there are complete tests, perfectly preserved, that yield no evidence of interactions with any other organism; secondly, there are unidentifiable fragments of test which may have been produced by a range of pathways – such as predation, disease (including parasitism), environmental stress, storms or old age (Donovan, 1991) – or broken by post-mortem processes or a mixture of these. Identifiable failed predation obviously lies somewhere between these extremes. Such evidence will be rare, because even when it occurs, fragmentation may happen subsequently; it is likely easy to recognise if complete (Fig. 2), but difficult to interpret. Further, failed predation probably weakens the test (note breakage in Cluster 1; Fig. 2A, C), favouring its eventual fragmentation as is the case in the analogous example of bored shells (Roy et al., 1994).

There is no undoubted tuberculation within the grooves of Clusters 1 and 2. It is a well-known attribute of echinoids that damage can be healed and tuberculation restored on test surfaces. The grooves on this specimen do not show indisputable tubercles in the bottoms of the grooves. The large hole is of a later date, and may even have originated when the test was on the conveyor belt at the quarry. In any case, the single bite of what looks to have been a shark probably did not result in the echinoid being eaten, but the lack of regeneration may be evidence of death shortly afterwards.

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