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Ichnology of Late Cretaceous echinoids from the Maastrichtian type area (The Netherlands, Belgium) - 1. A healed puncture wound in *Hemipneustes striatoradiatus* (Leske)

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Abstract

A test of the holasteroid echinoid *Hemipneustes striatoradiatus* (Leske) from the upper Maastrichtian (Upper Cretaceous) of quarry ‘t Rooth (Bemelen, southern Limburg, The Netherlands) is perforated by a pit on the mid-line of the adoral surface. This structure is large (maximum width 13.5 mm, depth 5.8 mm), rounded pentagonal in outline, bilaterally symmetrical and irregularly conical with a flat base. It may be an invertebrate trace fossil, although not the boring *Oichnus* Bromley or an embedment structure, or it may represent a healed puncture wound produced after a failed predatory attack by a marine vertebrate such as a bony fish or a mosasaur. If the latter, the shape of the pit may have been modified by the echinoid healing the wound; alternately, the tooth that caused the wound may have been truncated.

Key words: Ichnology, *Hemipneustes*, predation, Upper Cretaceous, Maastrichtian, The Netherlands.

Introduction

The holasteroid echinoid *Hemipneustes striatoradiatus* (Leske, 1778) is a large, locally common and striking element of the invertebrate macrofauna of the type Maastrichtian (Upper Cretaceous) of the provinces of Limburg and Liège, The Netherlands and Belgium. Live and dead tests of this taxon provided hard substrates for infestation by diverse encrusting and pit-forming organisms, such as the prominent embedment structure *Oichnus excavatus* Donovan and Jagt, 2002 (also see Donovan and Jagt, 2004, 2005), which may occur as multiple pits over the aboral surface of an individual. Other evidence of biotic interactions provided by *H. striatoradiatus* substrates includes other borings, encrustation by bivalves, bryozoans and worms, and marks of predation, most notably healed wounds (Donovan, Jagt and Neumann, research in progress). The unusual specimen discussed herein is distinctive, but it is uncertain if it represents a large invertebrate trace or an example of a deep puncture made by a predatory marine vertebrate and subsequently repaired by the echinoid. The pit has an unusual morphology, unlike any other trace fossil found in these common echinoids.

The specimen discussed herein is deposited in the Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands (NHMM).

Material and methods

In the type area of the Maastrichtian Stage, *Hemipneustes striatoradiatus* ranges from the middle Lanaye Member (Gulpen Formation) to just below the Vroenhoven Horizon in subunit IVf-7 of the Meerssen Member (Maastricht Formation) (Jagt, 2000, p. 283). This part of the upper Maastrichtian represents the *Belemnitella junior* and *Belemnella* (*Neobelemnella*) *kazimiroviensis* belemnite zones (Felder and Bosch, 2000, pp. 88–92). *Hemipneustes striatoradiatus* is among the most common echinoid species in this area (Jagt, 2000, p. 281).

The specimen discussed herein, NHMM 2007035, comes from the upper 2 m of the Nekum Member (Maastricht Formation), as exposed at the quarry ‘t Rooth (Bemelen, southern Limburg, The Netherlands) and is one of hundreds of tests of this species from this locality in the collections of the Natuurhistorisch Museum Maastricht, but is the only one to have been infested in this manner. Indeed, a survey of some hundreds of tests of this species in various collections by Jagt (2000, p. 281) failed to reveal any similar structures.

Description

The test of *Hemipneustes striatoradiatus* is well preserved apart from a few cracks of probable post-depositional origin (both following sutures and cross-cutting plates), the pit on the adoral surface that is the subject of this description (Fig. 1), and two small, faint, teardrop-shaped depressions on the aboral surface. One of the latter is close to the apical system on the anterior column of pores of ambulacrum V, whereas the second is at about mid-height of the test on the anterior column of plates in interambulacrum 4 (see Melville and Durham, 1966, figs 163, 171, for explanation of relevant morphological terms of echinoids). The test is 103.8 mm long, 86.2 mm wide and 67.6 mm high. The pit on the adoral surface lies on the midline, towards the posterior of the plastron and with the centre about 65.9 mm from the anterior margin. There is no indication of any other ancient surface abrasion or puncture.

The deep pit on the adoral surface is rounded pentagonal in outline, elongated coincident with the antero-posterior axis of the echinoid and approximately bilaterally symmetrical perpendicular to this axis (Fig. 1A). The pit has a sunken rim surrounding a more circular, deeper part of the pit. This deeper part slopes down more gently on the left side of the adoral surface, in the view in Figure 1A (=right side of the echinoid), than the steep right side; the latter is further distinguished by two deeper depressions on either side of the plane of symmetry. The base is approximately flat. This base and the sides of the depression bear primary and secondary tubercles. Maximum width of the pit is 13.5 mm, minimum width is 12.6 mm and depth is 5.8 mm.

Discussion

The size, position and morphology of the adoral pit are all unusual (Fig. 1). The pit is lined with test that bears tubercles, demonstrating that whatever sort of infestation it represents, it was not lethal, because the echinoid was able to repair itself subsequently. The pit is large, close in size to the trace fossil *Oichnus* Bromley, 1981, particularly *O. excavatus*, but it is bilaterally and not radially symmetrical, lacks concave walls and a central boss, and is situated on the 'wrong' part of the test; with

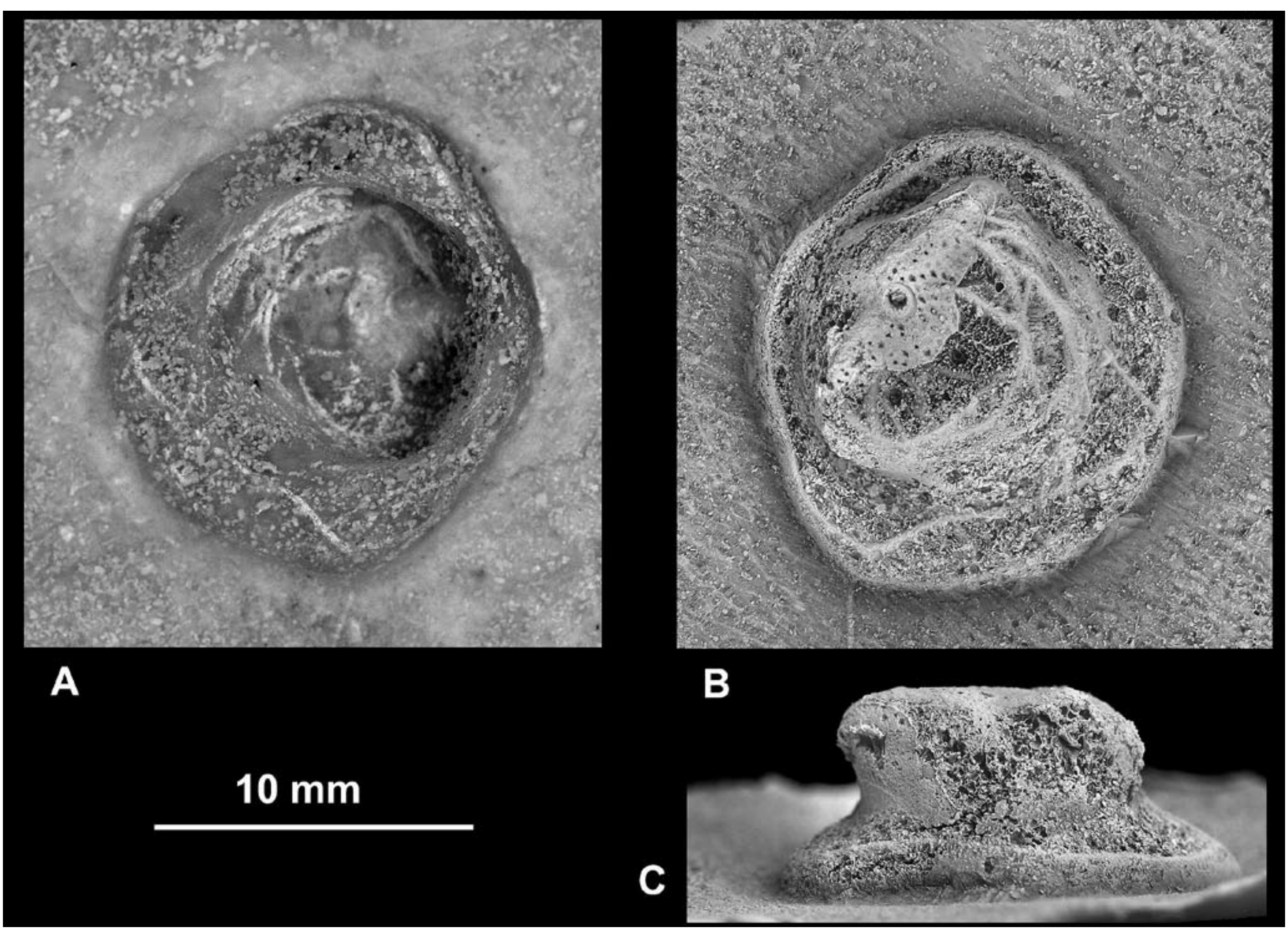

Fig. 1. Puncture hole in *Hemipneustes striatoradiatus* (Leske), NHMM 2007035. A, Hole in the oral surface, in the mid-line and just posterior of centre; the plane of symmetry of the wound is orientated left-to-right at about mid-height of the figure. Anterior of echinoid towards top of figure. B, C, Latex cast. B, Latex cast of pit in plan view, anterior towards top of page. Note the larger and smaller hollows, particularly apparent to the upper left, representing external moulds of primary (large) and secondary tubercles (small). C, Lateral view from the upper left in (B).

only rare exceptions, *O. excavatus* is found on the aboral surface and such a well-developed specimen is unknown from such a central position on the adoral surface. NHMM 2007035 is also more deeply impressed than an attachment scar of, for example, a benthic foraminiferan (Neumann and Wisshak, 2006). Intuitively, the position of the pit seems to be in a poor position for a large, filter-feeding, invertebrate infesting organism that was 'hitching a ride' on a live, furrowing, epifaunal echinoid (compare with ethology of producer of *O. excavatus*, as discussed by Donovan and Jagt, 2002, 2004, 2005). However, some borers appear to have thrived in analogous situations on another Maastrichtian echinoid from northern Germany (Wisshak and Neumann, 2006), although the borings of *Caulostrepsis* described therein are very different in morphology from the present example.

The trace described herein is a deep indentation on an area of the test that commonly was not available for infestation by invertebrates during the life of the echinoid. The bilateral symmetry of the pit is notable; invertebrates that form large pits in calcareous substrates tend to produce structures with radial symmetry or irregular rounded pits (e.g., parasitic eulimid gastropods; Warén and Moolenbeek, 1989). The position and morphology of this trace lead us to make the tentative suggestion that it may be vertebrate in origin, rather than invertebrate, and possibly represents a scar of a sub-lethal predatory attack; the wound healed subsequent to the attack, but evidence was preserved as a pit. This is supported by it being of comparable diameter to other traces deduced to have been produced by vertebrates in the same species (Donovan, Jagt and Neumann, research in progress).

Mulder (2003, p. 165) provided a list of the palaeoherpetofauna of the type Maastrichtian, including mosasaurs (six species), elasmosaurid plesiosaurs, turtles (three species), a crocodile and dinosaurs (members of at least three groups based on fragmentary specimens and presumably derived from nekroplankton). To these need to be added various fishes (Lambers, 1998; Reynders, 1998). The pit could have been made by a vertebrate with rounded, well-separated teeth, because this is the only penetrative wound in the test; the distance from the circumference of the perforation to the closest parts of the ambitus is about 30 mm. The tooth may have been pointed or blunt, evidence for the former being disguised by the base to the pit secreted to the echinoid. The two, teardrop-shaped indentations on the aboral surface may have been produced by two teeth of the other jaw failing to gain purchase and slipping across the surface. Based on these observations and deductions, the most probable culprits were a mosasaur or a bony fish; the tooth was conical, but may have been truncated, perhaps due to an earlier breakage.

Mosasaur predation on shelly invertebrates was apparently rare, but well known (Kauffman and Kesling, 1960; Saul, 1979; Kauffman, 1990). Jagt (2005, fig. 1) recognised five species of mosasaur in the Nekum Member, including durophagous *Carinodens belgicus*, which was capable of crushing a small echinoid (Schulp, 2005, fig. 8). Without implying that it was the predator, which remains unknown, the teeth of *C. belgicus* are the right order of magnitude to have inflicted this wound, but are too close together not to have made more than one penetration (compare with Kauffman and Kesling, 1960), unless some teeth had been lost. Larger mosasaurs with larger teeth would most likely have been able to crush the test.

In conclusion, the origin of this trace fossil is uncertain. Although broadly similar to certain structures made by invertebrate borers and encrusters, its origin is uncertain. It may be that this specimen demonstrates an example of failed predation. The predator was able to puncture the test, but failed to crush it. Possible reasons for this failure include disturbance during feeding, or the test being distasteful or too big for the predator to manipulate. Based on morphology of the pit and, thus, tooth morphology (Fig. 1), the predator was most probably a bony fish or a small mosasaur. But we emphasise that such an interpretation is speculative. We are unaware of other specimens of punctured *H. striatoradiatus* of similar morphology from this horizon.

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