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REGULAR RESEARCH ARTICLE

Big oyster, robust echinoid: an unusual association from the Maastrichtian type area (province of Limburg, southern Netherlands)

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Abstract

Large, denuded tests of holasteroid echinoids were robust benthic islands in the Late Cretaceous seas of northwest Europe. A test of *Hemipneustes striatoradiatus* (Leske) from the Nekum Member (Maastricht Formation; upper Maastrichtian) of southern Limburg, the Netherlands, is encrusted by a large oyster, *Pycnodonte* (*Phygraea*) *vesiculare* (Lamarck). This specimen is a palaeoecological conundrum, at least in part. No other members of the same oyster spatfall attached to this test and survived. Indeed, only two other, much smaller bivalve shells, assignable to the same species, attached either then or somewhat later. The oyster, although large, could have grown to this size in a single season. The larval oyster cemented high on the test and this would have been advantageous initially, the young shell being elevated above sediment-laden bottom waters. However, as the oyster grew, the incurrent margin of the commissure would have grown closer to the sediment surface. Thus, the quality of the incurrent water probably deteriorated with time.

Keywords Late Cretaceous · *Pycnodonte* · *Hemipneustes* · Taphonomy · Palaeoecology

Introduction

Large holasteroid echinoids, such as the genera *Echinocorys* Leske, 1778, *Cardiaster* Forbes, 1850, and *Hemipneustes* Agassiz, 1836, in the Upper Cretaceous of northern Europe were important both in life, as common components of the vagile benthos (Schmid 1949; Nestler 1965; Jagt 2000; Smith and Wright 2002, 2003) and post-mortem, where they formed benthic 'islands' that were important substrates for a range of encrusting and boring organisms (compare Nebelsick et al. 1997; Belaústegui et al. 2013, 2017). Associations on holasteroid tests may be monospecific or nearly so, such as dense accumulations of pits assigned to *Oichnus* Bromley, 1981 (see, for example, Donovan and Jagt 2002; Hammond and Donovan 2017; Donovan et al. 2018), or include two or more distinct taxa (see, for example, Jagt et al. 2012). Rarely does a test bear a solitary encruster or boring; commonly, there may be tens of individuals, small in size, closely associated and often in a regular pattern ('Inkrustationszentrum' of Schmid 1949). Further, in life, these were undoubtedly supplemented by unmineralized invertebrate taxa, and possibly algae and fungi, which have left no recognizable fossil record.

So, the subject of the present communication is an unusual specimen in more ways than one. It is a large holasteroid encrusted by a single oyster that attained large size. The oyster is cemented in an elevated position and in an orientation which invites interpretation. In short, this specimen is considered to be an instructive example that allows us to gaze, albeit dimly, into one small corner of the benthic environment of the Late Cretaceous sea.

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Locality and horizon

The specimen is part of the Brock-Meessen Collection at the Natuurhistorisch Museum Maastricht, the Netherlands (Jagt 2011) and bears the registration number NHMM BM MK.151. It was collected, possibly, when the conveyor belt was still in operation (see Mulder et al. 2016), from quarry ‘t Rooth (formerly Nekami) at Bemelen, southern Limburg (Felder and Bosch 2000, pp. 85–86, 106, figs. 3.42, 4.4; Fig. 1 herein), originating from the upper third of the Nekum Member (Felder and Bosch 2000, fig. 3.48) of the Maastricht Formation, Consequently, it is of late Maastrichtian age (Jagt 1999a, pp. 29–30; Jagt and Jagt-Yazykova 2012, p. 17, table 1).

Description

NHMM BM MK.151 is a test of the large holasteroid echinoid *Hemipneustes striatoradiatus* (Leske, 1778), measuring about 88.7 mm in length, 82.7 mm in width and 63.5 mm in height. The test has a broad, flat oral surface; a high anterior region with the apical system anterior of centre and the highest point of the test more anterior still. The more posterior test slopes posteriorly; the anterior test is steep (Fig. 2c, d). The test is cracked on both the oral and apical surfaces (Fig. 2) and was undoubtedly dead on the seafloor—a benthic island (compare Nestler 1965; Nebelsick et al. 1997; Belaústegui et al. 2013)—at the time of encrustation (Donovan 1991).

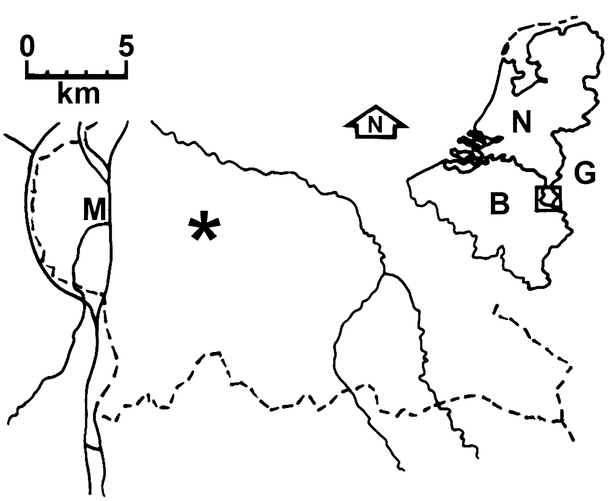

Fig. 1 Outline map of study area (redrawn and simplified after Jagt 1999b, fig. 1). Key: dashed lines = political boundaries; solid lines = rivers and canals; M = city of Maastricht; asterisk = quarry ‘t Rooth, Bemelen. For more detailed locality maps of this region, see Jagt and Jagt-Yazykova (2012, fig. 1) and, particularly, Felder and Bosch (2000, fig. 3.42). The inset map of the Netherlands (N), Belgium (B) and Germany (G) shows the approximate position of the main map (box)

Cemented to the echinoid test on the apical system, and with its dorsal margin oriented almost perpendicular to the long axis of the echinoid (Fig. 2a), is the attached valve of the pycnodonteine oyster *Pycnodonte* (*Phygraea*) *vesiculare* (Lamarck, 1806) (Stenzel 1971; Cleevely and Morris 2002, p. 147, pl. 24, figs. 8–10; Fig. 2 herein). This is a particularly large specimen for an endoskeletozoan (sensu Taylor and Wilson 2002; it is convenient to here recall that the echinoid test is an endoskeleton) from these deposits, about 57 × 54 mm. The ligament pit is triangular and flanked by a triangular dentition on each side (edentulous denticulate dentition; Skelton 1985, table 6.4.1), and a solitary, moderately large adductor muscle scar within the pallial line. The commissure is curved and raised up above the surface of the echinoid test (Fig. 2a, d).

Other endoskeletozoans are small to minute and some may have been lost by cleaning after collection. The largest of these are seen in the shallow depression of the anterior ambulacrum (amb III) of the echinoid, near the apex of the test; these are two incomplete cemented valves of conspecific oysters that are presumed to represent either failed members of the same spat fall as the large oyster or part of a later spat fall than its larger neighbour (Fig. 2a). Small benthic foraminifera (*Planorbinella* sp.; compare Hofker 1966) are dotted over the test. A number of pore pairs of mainly the three anterior ambulacra have been altered to single, lensoid pores, by boring barnacles (*Rogerella* isp.; Donovan and Jagt 2013; Donovan et al. 2016).

Remarks

What makes a single specimen of a common Late Cretaceous species of irregular echinoid encrusted by a common bivalve worthy of comment? We consider that there are at least four points that make this specimen worthy of special attention.

1. *Only one successful encrusting oyster* This specimen is an unusual and rare biotic association in the type Maastrichtian (J. W. M. J. and S. K. D., pers. obs.). There is a large, cemented oyster valve on this echinoid and little else. Extant and fossil oysters are commonly, albeit not invariably, gregarious (e.g., Yonge 1960; Stenzel 1971; Littlewood and Donovan 1988), settlement behaviour of larvae being controlled by factors such as high light intensities, food concentrations (Bayne 1969) and chemical cues (Veitch and Hidu 1971; Turner et al. 1994; Vasquez et al. 2013). Although ostreid and gryphaeid oysters are locally common in the Nekum Member, “The upper part of the member (Felder and Bosch 2000, Fig. 3.48) comprises porous, fine-grained carbonate sands, with undulating erosion surfaces” (Jagt and Jagt-Yazykova

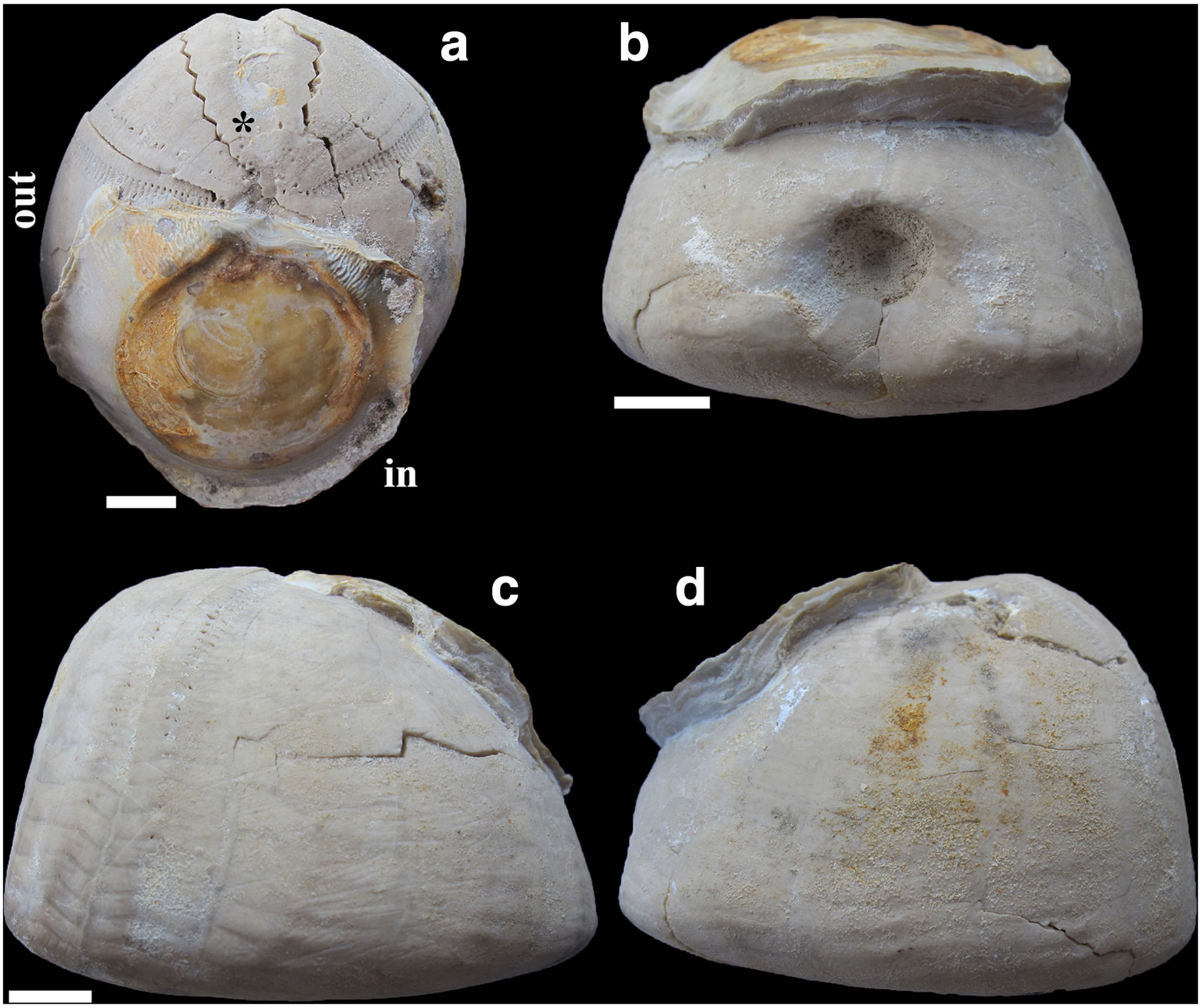

Fig. 2 NHMM BM MK.151, *Hemipneustes striatoradiatus* (Leske, 1778) encrusted by the left (= attached) valve of *Pycnodonte* (*Phygraea*) *vesiculare* (Lamarck, 1806), from the Nekum Member (Maastricht Formation) of quarry 't Rooth, Bemelen (southern Limburg, the Netherlands). **a** Apical view, anterior towards top of page. *Pycnodonte* (*Ph.*) *vesiculare* attached to posterior of apical system and much of the posterior test. The long, straight dorsal margin is arrayed sub-perpendicular to the long axis of the echinoid. For numbering of *Hemipneustes* ambulacra and interambulacra, see Donovan et al. (2014, fig. 2a). A small black asterisk marks to positions of the (pale coloured) small oysters in the anterior ambulacrum. 'In' and 'out' mark the approximate incurrent and outcurrent positions of the oyster. (**b**) Posterior view showing how *Pycnodonte* (*Ph.*) *vesiculare* extended to just above the periproct. (**c**, **d**) Left and right lateral views, respectively, showing *Pycnodonte* (*Ph.*) *vesiculare* extending across the posterior test. Stated orientations refer to the echinoid test. All scale bars represent 10 mm

2012, p. 17), suggesting shallow-water deposition, but possibly in a turbid environment. Chemical cues may have been rapidly dispersed in an energetic environment hostile to larval oysters.

Another contributing factor may have been that high current energy frequently reoriented or overturned exposed echinoid tests. For the oyster to grow to large size, this echinoid may have been unusually stable. This would be analogous to dead tests of Recent *Clypeaster rosaceus* (Linnaeus, 1758) in the tropical western Atlantic, a large echinoid commonly found in life position, and abundantly encrusted and bored by invertebrates (S.K.D., pers. obs.).

2. *The oyster is large* Presumably this indicates a long residence time on the dead test. However, growth rates of one extant oyster as an example, *Crassostrea rhizophorae* (Guilding, 1828), the West Indian mangrove oyster, vary between 0.1 and 0.5 mm day^{-1} (reviewed by Littlewood and Donovan 1988, p. 1023). That is, the individual of *P.* (*Ph.*) *vesiculare* on NHMM BM MK.151 could conceivably represent

growth during only one season. Other *P.* (*Ph.*) *vesiculare* in these deposits may attain a comparable size.

3. *The oyster cemented high on the echinoid test* "Later crawling movements [of oyster larvae] have been described as upwards … any movement away from possible accumulation of mud could be of value" (Yonge 1960, p. 69). Thus, it is likely that *P.* (*Ph.*) *vesiculare* selected this elevated position. However, as it grew, the commissure of the shell would have moved down the shell side towards the sediment surface, assuming the empty echinoid test remained on the seafloor in life position. This seems likely, as the only other bivalve encrusters (Fig. 2a, anterior of apical system) attained even higher positions, just anterior to the highest point on the text. Further, *Rogerella* isp. and benthic foraminifera are commoner on the upper half of the test (Donovan et al. 2016). These distributions all support an interpretation of the echinoid test resting on its flat and stable oral surface.
4. *Was the orientation of the echinoid test favourable to feeding currents?* Here we must venture further into the realm of informed speculation. By comparison with feeding currents in a typical extant oyster, *Ostrea edulis* Linnaeus, 1758 (Yonge 1960, fig. 9), incurrents would have been drawn into the shell from to the right of the echinoid's periproct (Fig. 2b) and expelled parallel to the left anterior petal (ambulacrum IV) (Fig. 2a). As the oyster grew down the posterior test surface of the echinoid, its incurrent water would have come from progressively closer to the sediment surface; that is, incurrent water would have become more sediment laden. The oyster would have benefitted more from having an orientation, for example, rotated through 180°, whereby the shell would have grown onto higher elevations and perhaps become elevated above the shell.

Indeed, why the attached valve is so completely in contact with the echinoid test is uncertain, although comparable conspecific examples are known on tests of *Echinocorys* of the *limburgica* and *conoidea* groups from the Vijlen and Lixhe 1 members, respectively, in the Haccourt-Lixhe area (J. W. M. Jagt, pers. obs.). Cleevely and Morris (2002, p. 147) noted that this species was "Usually with small-medium attachment area …", whereas this valve has 100% attachment. The reason for such a large attachment area in this example remains uncertain, but it may be related to a particularly energetic current regime.

In conclusion, the palaeoautecology of a specimen of the large oyster, *P.* (*Phygraea*) *vesiculare*, poses as many questions as it answers. The oyster encrusted a benthic island, namely a dead holasteroid echinoid, *H. striatoradiatus*, but no other members of the same spat fall successfully attached to this test. Indeed, only two other, much smaller conspecific shells attached either then or somewhat later. Although the oyster is large, it may have attained this size in a single season. The larval oyster cemented high on the test, which may have been initially advantageous, but, as it grew, the incurrent margin of the commissure became progressively closer to the sediment surface. That is, as it grew larger, the quality of the incurrent water probably deteriorated as the sediment content of the water increased.

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