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Strange taphonomy: Late Cretaceous *Echinocorys* Leske (Echinoidea) as a hard substrate in a modern shallow marine environment

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Abstract The holasteroid *Echinocorys* is a common, robust echinoid in the Upper Cretaceous–Danian Chalks and limestones of northern Europe. It formed hard substrates that were infested by a variety of encrusters and borers during its life and after death. *Echinocorys* is also a durable fossil. Tests occur as clasts on the beach at Overstrand, and between Overstrand and Cromer, north Norfolk, eastern England. Reworking from (mainly) coastal sections has reintroduced Chalk *Echinocorys* into the benthic environment over 70 million years after its death and inhumation, with rare specimens washing up on the beach at these localities. Unsilicified *Echinocorys* tests form a taphonomic series. The oral surface is the stable resting surface which is commonly not bored unless the exposed Chalk infill is strongly infested by *Entobia* isp. Clean, unbored tests grade through specimens where the test calcite is perforated by *Entobia* isp. to remnants where most of the apical surface of the echinoid has been lost by boring, and the Chalk infill is perforated by *Caulostrepsis* cf. *taeniola* Clarke, *Entobia* isp. and rare *Gastrochaenolites* isp. In contrast, flint steinkerns and external moulds are not bored. Four principal lines of evidence are used to determine the time of occurrence of these borings: (1) comparison with common Chalk borings known from *Echinocorys*; (2) tests are invariably infilled with well-lithified Chalk, but (with one exception) borings preserve no evidence of prior infilling; (3) the suite of borings are typical of modern lithoclasts on the beach; and (4) flint echinoids preserve no evidence of modern borings. Lack of Cretaceous encrusting organisms is further evidence that suggests most borings may be modern. There is only a limited indication of a mix of modern and ancient (*Oichnus* isp., indeterminate U-shaped boring) borings as has been noted previously in a belemnite from Overstrand.

Keywords Biostratinomy · Reworked fossils · Holasteroids · Beachcombing · Ichnology · Borings

Introduction

The holasteroid echinoid *Echinocorys* Leske is a common, robust, long-ranging form of conservative morphology in the Upper Cretaceous and Danian chalk and related limestone deposits of northern Europe (Jagt 2000; Smith and Wright 2003). The large and robust tests of this irregular echinoid formed hard substrates that were infested by a variety of encrusting and boring invertebrates both when the organism was alive and, more commonly, after death (for example, Joysey 1959; Voigt and Soule 1973; Donovan and Jagt 2005; Neumann and Wisshak 2006, 2009; Wisshak and Neumann 2006; Jagt et al. 2007; Donovan et al. 2010b). It thus formed a natural taphonomic experiment in the Late Cretaceous and across the Cretaceous–Paleogene boundary that has yet to be fully exploited by palaeontologists.

The tests of *Echinocorys* were robust in both life and death, and can be durable as fossils. For example, they occur as common clasts on the beach at Margate, Kent (England), where they are derived from the *Echinocorys*

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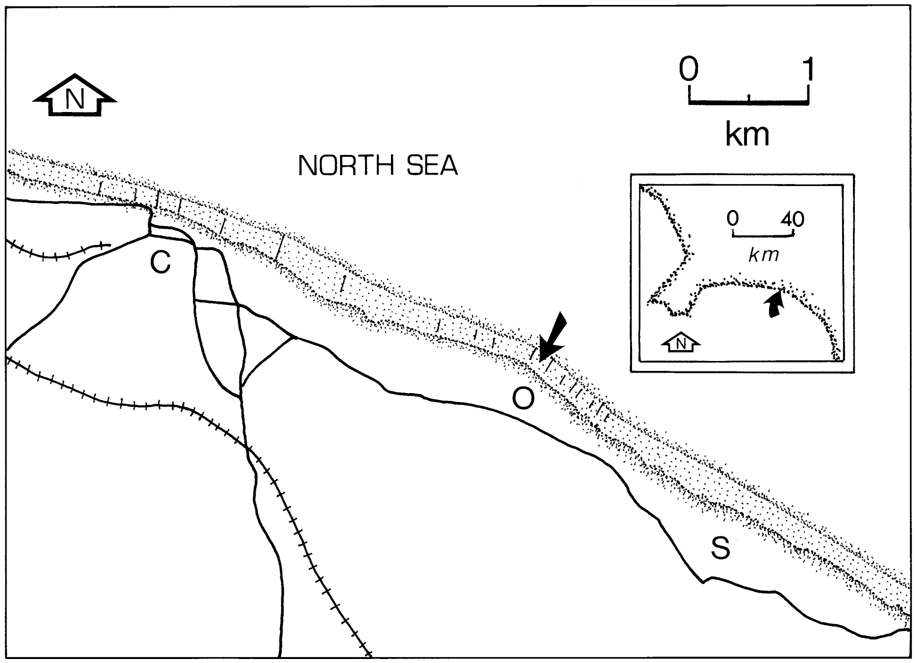

Fig. 1 Outline map of the north coast of Norfolk between Cromer (C), Overstrand (O) and Sidestrand (S) (after Donovan 2010, fig. 1). The dark arrow indicates the point of beach access used by S. K. D.; specimens were collected to the limits of the groynes to the southeast and towards Cromer in the northwest. The stippled area is between the low water mark and cliff top; it includes both the beach (groynes are indicated) and slope of the cliffs. Principal roads are shown as solid lines; railways are shown as trellised lines. The inset map, with a stippled coastline, shows part of the east coast of England, with Lincolnshire (left), the Wash (towards bottom left) and Norfolk (centre and right). The area of the main map is arrowed

band exposed in the Chalk cliffs (Rowe 1900). Reworking from coastal and, less likely, shallow marine sections reintroduces Chalk *Echinocorys* into the benthic environment over 70 million years after its death and inhumation. These borings are unlikely to have been formed while the tests were still entombed in Chalk because most or all of them were most probably liberated from cliffs by coastal erosion. Like "… erratics [they] are seldom seen in cliff section, but may be observed on the beach… the accumulation probably of centuries of coastal erosion" (Harmer 1910, p. 4). Herein, we consider *Echinocorys* as a reworked fossil in the modern environment, and interpret the evidence provided by the borings in its test and Chalk infill.

A brief comment on systematics of *Echinocorys* in the Upper Cretaceous of northern Europe is relevant. Jagt (2000, pp. 269–274) recognised nine groups of *Echinocorys* taxa, albeit based on well preserved specimens. The battered and bored tests described below do not warrant such detailed systematic treatment. We have therefore followed Smith and Wright (2003) in 'lumping' all specimens in *Echinocorys* ex gr. *scutata* Leske 1778, a step warranted by the assurance that encrusting and boring organisms would not have differentiated between particular species as substrates over 70 million years after the echinoid had died.

The terminology of the echinoid endoskeleton used herein follows Melville and Durham (1966) and Durham and Wagner (1966); descriptive ichnology follows the terminology of Häntzschel (1975). Our philosophy of open nomenclature follows Bengtson (1988). The material described and illustrated herein is deposited in the Netherlands Centre for Biodiversity—Naturalis, Leiden (NNM RGM, formerly the Nationaal Natuurhistorisch Museum, incorporating the Rijksmuseum voor Geologie en Mineralogie, now part of the Netherlands Centre for Biodiversity). Specimens in Figs. 2 and 3 were painted with black food colouring and coated with ammonium chloride for photography; those in Fig. 4 were coated with ammonium chloride only.

Locality and horizon

The specimens described herein were collected by the senior author and his family on the beach at Overstrand, and between Overstrand and Cromer, north Norfolk, eastern England, approximately NGR TH 249 410, during late July 2009 (Fig. 1). The beach at Overstrand, although dominantly sandy, has numerous pebbles and cobbles, the majority of which are locally derived from the Upper Cretaceous, including those of flint and, less commonly, chalk (for example, Donovan and Lewis 2010). Other, rarer erratics include some of igneous origin and Derbyshire screwstones (Harmer 1910; Moorlock et al. 2002; Donovan 2010).

It is probable that chalk and flint cobbles described from the the beach at Overstrand are local in origin. The Chalk of north Norfolk ranges in age from the Cenomanian to the Early Maastrichtian (Burke et al. 2010, Fig. 1); the latter is

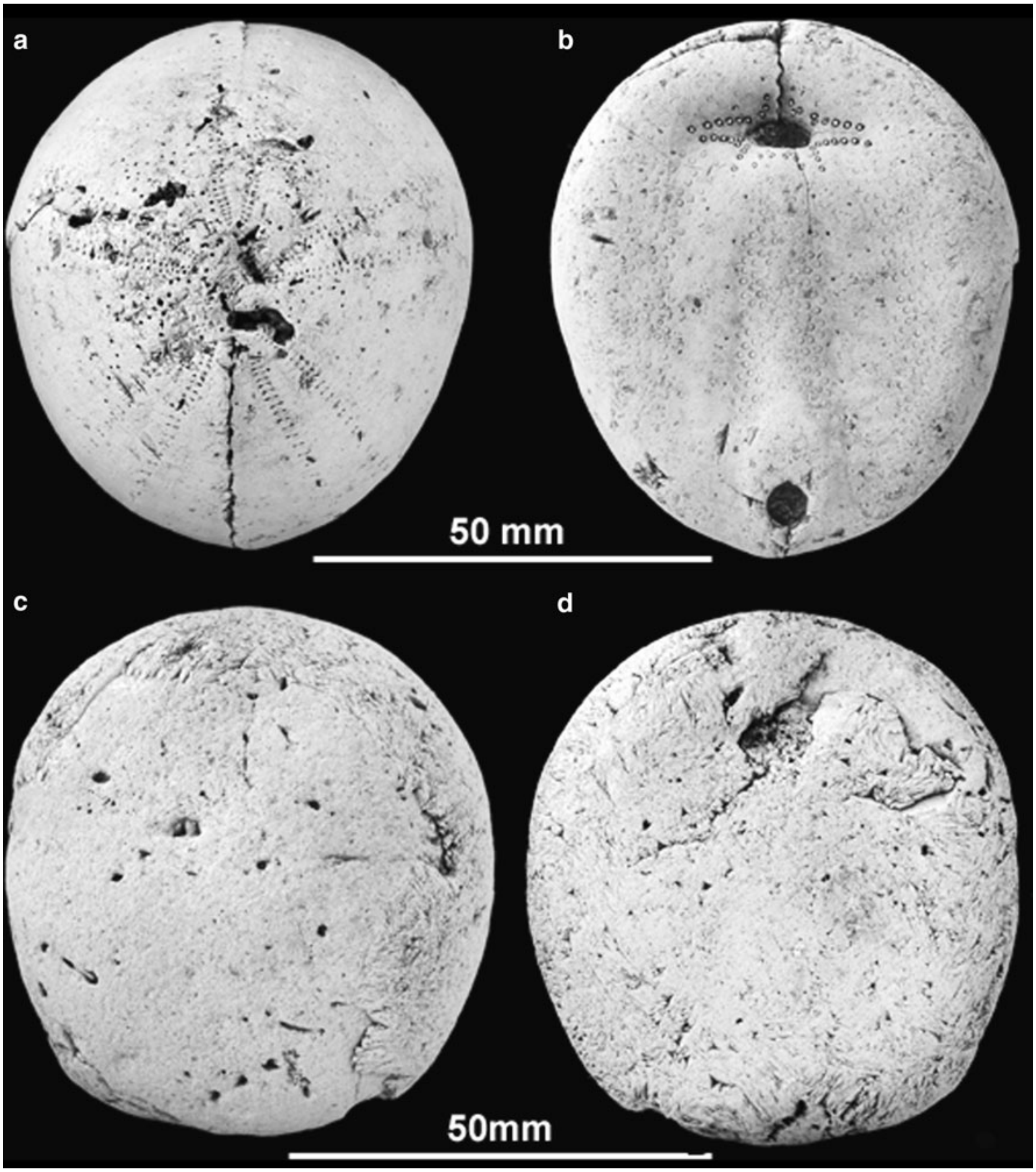

Fig. 2 *Echinocorys* ex gr. *scutata* Leske 1778, preserving calcitic test in Chalk. **a**, **b** NNM RGM 617 801. Specimen collected by Hannah Donovan. **a** Apical surface of most complete test showing minor damage due to physical abrasion and bioerosion. **b** Oral surface. **c**, **d** NNM RGM 617 802. **c** Apical surface with calcite of test largely abraded away, presumably mainly by physical processes. **d** Oral surface

unusually young for the English Cretaceous succession (Chatwin 1961, p. 35; Peake and Hancock 1961; Rawson et al. 1978, pp. 30, 52; Moorlock et al. 2002, pp. 3–5). The specimens are Late Cretaceous in age and older than the Late Maastrichtian (*circa* 70 million years old or more). Rafts of Chalk thrusted by glacial ice during the Pleistocene are similarly Campanian–Maastrichtian in age as based on both micro- and macro-fossil evidence (Burke et al. 2010, pp. 621–623).

Description

Tests preserved in calcite (Figs. 2, 3)

Eight tests, NNM RGM 617 801-617 808, that vary from specimens showing little more than surface abrasion to those that have been extensively altered by bio- and physical erosion. The illustrations are arranged to show this taphonomic gradient.

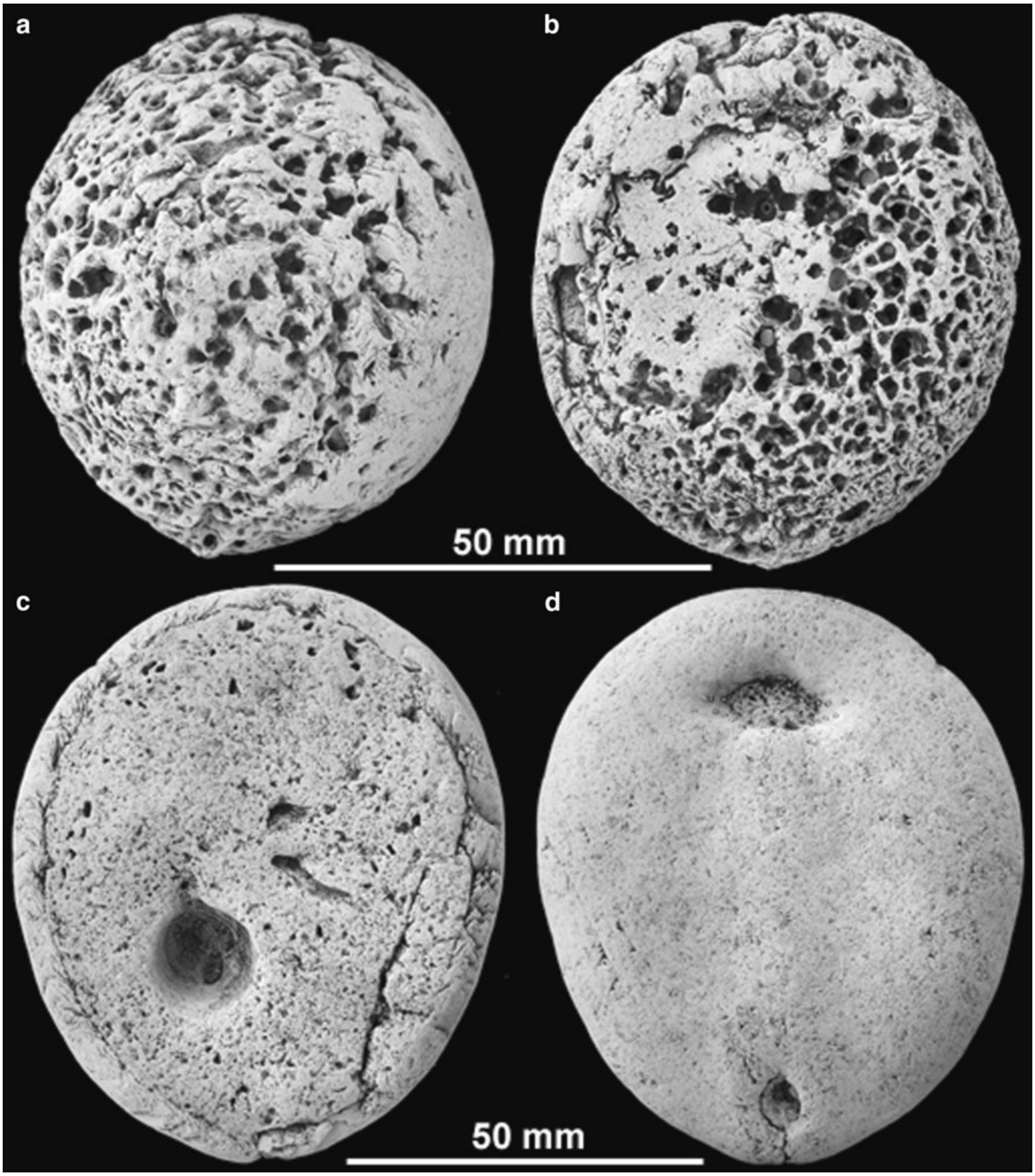

Fig. 3 *Echinocorys* ex gr. *scutata* Leske 1778, preserving calcitic test in Chalk. **a**, **b** NNM RGM 617 803, specimen densely infested with *Entobia* isp. Specimen collected by Pelham Donovan. **a** Apical surface. **b** Oral surface. **c**, **d** NNM RGM 617 804. **c** Apical surface, albeit largely abraded away. The thick test can be seen at the perimeter. The Chalk infill includes some borings, most prominently an incomplete *Gastrochaenolites* isp. **d** Oral surface, which has suffered much less than the apical surface (compare with Fig. 2b)

NNM RGM 617 801 is the most complete test (Fig. 2a, b). Primary tuberculation is moderately well preserved on the oral surface, with some secondary tubercles apparent in the depressed area surrounding the peristome. The apical surface is smooth and worn free of tubercles. Some plate sutures have opened up and there are cracks that cross plates (Fig. 2a, posterior and left, respectively). There are no encrusting organisms and irregular holes are probably produced by physical impacts (Fig. 2a, close to apex). There are numerous small, circular pits close to the apex of the sort referred to as putative *Oichnus* isp. by Donovan et al. (2010b, p. 52).

Other specimens have either had part of the test removed by physical erosion or breakage, more or less assisted by weakening produced by borings, particularly *Entobia* isp. NNM RGM 617 802 has a complete oral surface which has lost surface detail (Fig. 2d). Apically the calcite of the test has been breached and eroded away, particularly in the left anterior region where the Chalk infill is exposed down to the ambitus. Some test is preserved anteriorly and on the right lateral side of the apical surface (Fig. 2c); the junction with the Chalk infill is chamferred, suggesting physical abrasion. Puncture marks in, particularly, the Chalk are irregular and no undoubted bioerosional structures are identifiable. In this and other specimens described below, remnants of the test are essentially continuous between oral and apical surfaces.

NNM RGM 617 805 has some similarities to the previous specimen, the test being worn thin on the right side of the apical surface, but exposed on the left. However, in this Chalk infill and, to a lesser extent, the test of the oral surface the specimen is infested by *Entobia* isp. Posteriorly, the Chalk exposes numerous small *Caulostrepsis* isp. borings.

NNM RGM 617 806 repeats this pattern of exposure of the Chalk infill with a more completely preserved oral surface and Chalk infill large exposed apically. The test and Chalk are intensely bored on the left apical surface by *Entobia* isp., with some apertures puncturing the test of the oral surface. The internal chambers of *Entobia* isp. are well exposed in the Chalk. Slender, gently curved borings on this surface are juvenile parts of the *Entobia* network. More *Entobia* chambers, less well preserved, are apparent in the right lateral position. Modern serpulid worm tubes encrust the oral surface of NNM RGM 617 806 adjacent to the peristome and are best preserved in the depression surrounding this region. The anterior part of the oral surface has been depressed mechanically, leading to preservation of both primary and secondary tubercles adjacent to the serpulids. Chalk exposed anterior to the peristome includes small, slot-like openings of the borings of *Caulostrepsis* isp.; similar borings are found above the *Entobia* on the right posterior apical surface. Below this same *Entobia* infestation are *Caulostrepsis* isp. close to *C. taeniola* Clarke 1908, as illustrated by Bromley and d'Alessandro (1983, pl. 21, fig. 2).

A small specimen, NNM RGM 617 808, preserves a disharmonious combination of features. The oral surface is near-complete and preserves most of the primary tubercles, with secondary tubercles apparent adjacent to the sunken peristome. Yet most of the supra-ambital test is lost and the highest remnant on the apical surface only extends for 14.4 mm above the ambitus. Nevertheless, the specimen is 40.1 mm high because much of the Chalk infill is preserved. Small borings are not uncommon, but only *Caulostrepsis* isp. is identifiable.

Some specimens are particularly heavily infested by *Entobia*. NNM RGM 617 803 (Fig. 3a, b) preserves some test on the right side of the specimen as illustrated, although its true orientation is indeterminate (primary tubercles are rarely preserved at the front of the oral surface as oriented, which may indicate the position of the sunken peristome). The rest of the specimen is a Chalk internal mould with a dense *Entobia* isp. infestation. The residual test is weakly bored, mostly on the oral surface. NNM RGM 617 807 retains more of the test, including most of the oral surface, but the apex is planed off. Where the Chalk infill is exposed it is densely infested by *Entobia* isp. and *Caulostrepsis* isp. *Caulostrepsis* occurs posteriorly, on the planed apical surface and in the left lateral test of the apical surface; *Entobia* infestation is dense on the right side of the apical surface, both test and infill, and the test of the oral surface is perforated by numerous apertures, mainly on the same side. Other perforations of the test appear to be common mechanical damage, in part controlled by plate sutures and the distribution of borings. Primary and secondary tubercles are preserved in the depression adjacent to the peristome.

The final recognisable state of test breakage is in specimens where it is reduced to the oral surface and little else. NNM RGM 617 804 has an entire oral surface, worn smooth, although primary and secondary tubercles are still apparent around the depressed peristome (Fig. 3d). The apical surface is largely planed away (Fig. 3c); the greatest preserved height is 29.0 mm, although it may originally have been 60–70 mm high. The Chalk infill has some rare *Caulostrepsis* isp. apertures and other indeterminate borings or mechanical damage. The prominent, circular depression is the distal termination of a *Gastrochaenolites* isp. that must have penetrated the infill when it was more complete, but has otherwise been lost with the planing off of the apex. No borings penetrate the test.

Tests preserved in flint (Fig. 4)

Four tests are preserved in flint, NNM RGM 617 809-617 812. Although all show at least some physical damage, none preserves definite evidence of modern biological interactions such as encrustation or boring. NNM RGM 617 809 is the most complete specimen preserved in flint, a *steinkern* with a large conchoidal fracture anteriorly (best seen in oral view; Fig. 4b) and some of the calcite test remaining although eroded through in places. More or less elongate structures in the calcite test, but not penetrating the *steinkern*, are concentrated on the apical surface (Fig. 4a) and are most probably the result of physical abrasion, not showing the geometry of any bored tests preserved in Chalk. A U-shaped groove just posterior to the peristome (Fig. 4b) is infilled with limonite, as is the periproct, and is possibly part of an ancient, albeit indeterminate boring, although its origin is equivocal. NNM RGM 617 812 preserves a less complete test in a flint

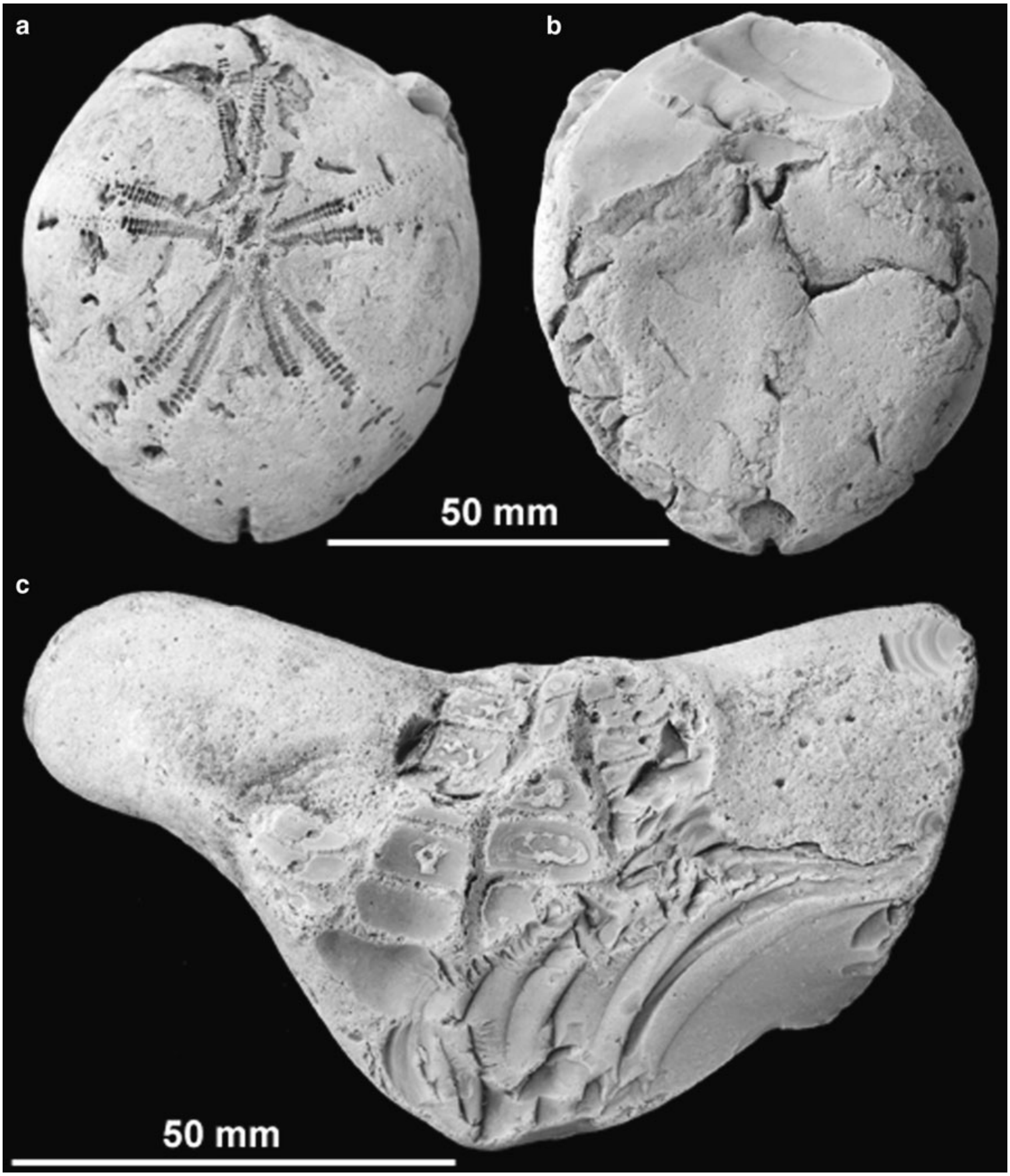

Fig. 4 *Echinocorys* ex gr. *scutata* Leske 1778, preserving tests in flint. **a**, **b** NNM RGM 617 809, steinkern, not bored, but showing signs of physical abrasion. **a** Apical surface. **b** Oral surface; note particularly anterior conchoidal fracturing. **c** NNM RGM 617 810, external mould of plate columns on a flint cobble; conchoidal fractures in the lower right and upper right, adjacent to the broken ends of this reworked nodule

nodule. The *steinkern* lacks part of the apical surface, the calcite test is less well preserved than the figured specimen and there is no evidence for biological infestation.

Two specimens are very incomplete. NNM RGM 617 810 (Fig. 4c) is an external mould of parts of four plate columns in a flint cobble. As illustrated, the apex is towards the top of the page. The two centre plate columns are part of an interambulacrum, flanked on either side by single plate columns derived from contiguous ambulacra and each preserving single central pits that are poorly preserved pore pairs. Some small and discontinuous calcite fragments shaped by dissolution adhere to the surface of some plates. There is no evidence of boring and encrustation. NNM RGM 617 811 is a triangular, reworked flint nodule preserving a test fragment seen in internal view, retaining parts of two interambulacra and two ambulacra, and the apical system. This test has not been punctured by any borings; the external surface is not seen.

Discussion

Studying the modern taphonomy of a reworked holasteroid taxon may appear eccentric. However, there are two reasons why the specimens described above are worthy of detailed analysis. They provide a relatively large data set for the senior author's ongoing research programme into the determination of the timing of infestation of borers in reworked fossils (Donovan and Lewis 2010; Donovan et al. 2010a). Further, the unsilicified tests provide a taphonomic series from specimens that, at most, bear only superficial physical abrasion (Fig. 2a, b) to those that have been largely destroyed by bio- and physical erosion (Fig. 3).

It is assumed that the tests discussed above were not markedly bored nor encrusted prior to their recent disinterment. But how can the Late Cretaceous encrustation and boring activities on an *Echinocorys* test be separated from those that occurred after modern reworking? This question relates to the more general problem of how to determine the timing of boring infestation of any reworked fossil (Donovan et al. 2010a). None of the *Echinocorys* tests discussed herein bears any ancient encrusting organisms, but, if there were, it should be possible to differentiate Upper Cretaceous from extant taxa. For example, craniid brachiopods infested dead tests in the Late Cretaceous (Donovan et al. 2011); their occurrence on a reworked *Echinocorys* in the shallow coastal waters of the North Sea would be unlikely unless they were fossils. Similarly, different suites of ichnotaxa may be more typical of the two time periods; for example, the brachiopod pedicle trace *Podichnus* ispp. would be more likely to be Late Cretaceous than Recent.

As an attachment scar *Podichnus* caused minimal bioerosive damage, whereas the modern borers identified herein are destroyers of hard substrates. The latter are found in specimens with a uniformity of infestation that suggests that ancient and modern borings are not mixed except in the instances determined below. Four principal lines of evidence were used to determine the timings of occurrences of the borings in these tests.

Comparison with common Chalk borings known from *Echinocorys*

The only borings that are similar in morphology and position to ichnofossils known to have commonly infested *Echinocorys* in the Cretaceous are the small, pit-like *Oichnus* isp. found apically on the most complete test, NNM RGM 617 801 (Fig. 2a) (compare with Donovan et al. 2010b; see also Müller 1969; Bromley 1981). The infilled, U-shaped boring (Fig. 4b) is also undoubtedly ancient (see below). The weight of evidence favours all other borings to be modern.

Infilled borings

This criterion proved efficacious in differentiating between Late Cretaceous and modern *Entobia* in a belemnite from Overstrand (Donovan and Lewis 2010). Echinoid tests are invariably filled by Chalk or flint *steinkerns*. But, in contrast, only one boring preserves an infill and none of the others retains any suggestion of such a lithological structure. The exception comes from the most complete test with a flint *steinkern* (NNM RGM 617 809; Fig. 4b), in which a U-shaped boring is infilled with limonite. This boring is regarded as Late Cretaceous.

Comparison with modern lithoclasts from the same beach

Although a comparative suite of specimens has not been collected, the match is exact. *Entobia* (Donovan and Lewis 2010, Fig. 1), *Caulostrepsis* and *Gastrochaenolites* all occur as modern borings in water-worn Chalk clasts on the beach at Overstrand. Their morphology and preservation are similar to those of specimens found in *Echinocorys* tests and Chalk infills.

Lack of borings in flint *steinkerns*

If borings into tests had occurred on the Late Cretaceous sea floor, then subsequent silicification would have preserved such structures rather better than Chalk. Although the sample is small, only two flint *steinkerns* (e.g., Fig. 4a, b), neither preserves any evidence of preserved ancient borings. In contrast, of seven specimens infilled by Chalk and with breached tests, only one (Fig. 2c) does not preserve identifiable borings. The other six specimens all preserve one to three bioerosive ichnofossils (e.g., Fig. 3a, c). Thus, flint *steinkerns* do not contradict other evidence that most borings are modern.

We conclude that two rare ichnofossils are relics from the Campanian–Maastrichtian, whereas three ichnotaxa are modern, two of which are represented by numerous specimens in multiple tests (Table 1). We emphasise that patterns of borings described in infested tests may be incomplete, having been modified by subsequent physical abrasion, which would have removed the weakened Chalk and test preferentially. This may have reduced the diversity of borings therein.

Table 1 Summary of borings in *Echinocorys* tests collected from the beach at Overstrand, north Norfolk, England

Campanian–Maastrichtian	Recent
Oichnus isp. (r)	*Caulostrepsis* cf. *taeniola* Clarke (C)
U-shaped boring (R)	*Entobia* isp. (C)
	Gastrochaenolites isp. (R)

R known from one specimen only, *r* known from multiple specimens on one test only, *C* known from multiple specimens on two or more tests

Considering the ichnology of reworked fossils in general, this and related studies suggest that there are a number of attributes that can be examined to determine the timing of infestation by boring organisms. However, not all will be determinable or relevant in every instance. For example, in the bored cobble described by Donovan and Lewis (2010), Late Cretaceous *Entobia* were separated from those of modern origin by the former being filled by lithified Chalk and the latter lacking any infill. Reworked *Kuphus* tubes from the Miocene of Jamaica are infilled by lithified limestone; Pleistocene borings in them are not infilled (Donovan 2010). The timing of boring was further indicated by prior knowledge that unreworked *Kuphus* tubes in the Oligo-Miocene of the island are not known to be bored. It was also significant that the infested tubes in the Pleistocene deposit are preserved with other clasts that preserve a similar suite of borings to the reworked fossils. All of these deductions were further utilised in the examination of bored and reworked *Echinocorys* herein.

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