Cutting through sponge and time – a new record of *Koptichnus rasmussenae* (trace fossil) from the Kerteminde Marl (middle Paleocene), Denmark

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A new trace fossil, *Koptichnus rasmussenae*, was recently reported from the Cretaceous of Denmark. This burrow is thickly lined with cuboids that the tracemaker cut from siliceous sponges. A newly discovered specimen from the lower Selandian Kerteminde Marl, found in a loose boulder in the Gundstrup gravel pit (Fyn, Denmark), extends the stratigraphical range of this ichnotaxon from the previously known Coniacian to the middle Paleocene and demonstrates that this distinct behaviour of harvesting and shaping building material survived the K-Pg extinction event.

Keywords: domichnia, armoured burrow, sponge, Selandian, K-Pg extinction event.

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The trace fossil *Koptichnus rasmussenae* was recently described by Vallon *et al*. (2020). It is an armoured burrow system (Buatois *et al*. 2017) similar to *Ophiomorpha* Lundgren, 1891, but using cuboids (cubelike polyhedra) of siliceous sponges instead of sediment nodules as lining material. These building blocks are characterised by having a fairly uniform size and shape and they are interpreted as being cut from sponges by an arthropod tracemaker (Vallon *et al*. 2020).

Previous records of this peculiar trace fossil from Denmark include the Coniacian (Arnager Limestone; Bornholm) and Maastrichtian chalk localities at Stevns Klint (Sjælland) and northern Jylland (Fig. 1; Vallon *et al*. 2020). Although the newly recovered specimen derives from ice-rafted loose material in a gravel pit, the specimen can be assigned with certainty to the Kerteminde Marl by lithological comparison. Micropalaeontological analyses of lithologically similar blocks from the same locality have proved that they represent the Kerteminde Marl (Schnetler & Nielsen 2018).

Geological setting

The Gundstrup gravel pit is located about 20 km north of Odense on Fyn (Fig. 1). There, glacially transported boulders represent the Kerteminde Marl, which crops out in the northern and eastern parts of Fyn (Gry 1935, Schnetler & Nielsen 2018). The boulders, therefore, are expected to have been transported less than 50 km (Schnetler & Nielsen 2018; see also Fig. 1). The Kerteminde Marl was deposited during the lowermost Selandian, immediately above the Danian–Selandian transition, and has a similar if not identical age as the Lellinge Greensand Formation of Sjælland (Schnetler & Nielsen 2018).

The Kerteminde Marl is predominantly a monotonous, light grey silty marl, in places with slightly silicified layers. It may contain pyrite (Gry 1935) and has been homogenised by intensive bioturbation (Heilmann-Clausen 1995), probably by meiofauna. Body fossils are diverse and common at the Gundstrup locality (Foraminifera, Porifera, Annelida,

Decapoda, Cirripedia, Bryozoa, Brachiopoda, Echinodermata, and Vertebrata including 'ganoid fishes', Elasmobranchii, Cheloniidae, and Aves). Only a few groups (e.g. molluscs: Schnetler & Nielsen 2018 and some vertebrates, e.g. Myrvold *et al*. 2018) have been treated systematically. Trace fossils have so far only been briefly mentioned in other studies (e.g. *Teredolites* by Schnetler & Nielsen 2018; *Lepidenteron* by Schwarzhans *et al*. 2021).

In the palaeoenvironmental interpretation of Clemmensen & Thomsen (2005), the Kerteminde Marl was deposited under fully marine conditions at a water depth between 100 and 150 m (see also King 1994, 2016, who inferred an outer to middle neritic setting). Compared to those of other localities, the silicified boulders from Gundstrup are of coarser sediment than the typical Kerteminde Marl and have a higher content of benthic fossils (Heilmann-Clausen & Surlyk 2017, p. 195). A relatively high sedimentation rate is indicated by reworking of Cretaceous chalk sediments from the uplifted Tornquist–Sorgenfrei Zone (Fig. 1; Heilmann-Clausen & Surlyk 2017). Slight silicification of the sediment (Gry 1935; Heilmann-Clausen 1995) might have its origin in the occurrence and dissolution of abundant siliceous sponges (Fig. 3; see also Gry 1935). According to Clemmensen & Thomsen (2005), the bottom water was well ventilated at least in more arenaceous and glauconitic strata of the Kerteminde Marl (Gry 1935, p. 77), but planktonic production was low, resulting in a reduction of benthic food supply to the depositional environment of the Kerteminde Marl. The seafloor was probably influenced by weak water currents, as deduced from small, patchy accumulations of molluscs, together with driftwood containing *Teredolites* isp. (Schnetler & Nielsen 2018). The other trace fossils, however, are deeper-tier structures that imply oxygen-depleted sediments – as is usual below the redox potential discontinuity within a soft substrate. Oxygen depletion below this discontinuity is also suggested by micropyrite (cf. Gry 1935; Wilkins & Barnes 1997).

Fig. 1. Map of Denmark and adjacent countries with major tectonic units. The locality of the Gundstrup gravel pit (star) is shown within the outcrop of Selandian sediments. Previously documented localities from the Cretaceous are indicated with arrows. Modified from Schnetler & Nielsen (2018) and Schwarzhans *et al*. (2021) with additional data from Brandes *et al*. (2018) and Vallon *et al*. (2020).

Description of the specimen

The specimen (Fig. 2) was collected and donated by Mette Hofstedt and Peter Mortensen in 2019. It is preserved in full relief, split longitudinally into two slabs. As in the specimens from the Cretaceous Arnager Limestone (Vallon *et al*. 2020), the sponge spicules have completely dissolved and only their moulds are preserved. These moulds have a light orange stain from metal oxides.

The two halves of the rock sample (Fig. 2A) have approximately the shape of a triangular prism. The slightly larger piece has edge lengths of about 10 cm each and contains the burrow itself. The burrow is flattened and individual cuboids of the lining material are somewhat weathered. The preserved burrow stretch is fairly rectilinear and unbranched. It is about 73 mm long and about 12 mm wide. Individual cuboids are about 3–4 mm in edge length.

The slightly smaller other half of the rock sample (Fig. 2B) contains the outermost area of the lining and shows well-preserved moulds of bundles of monaxone sponge needles (Fig. 2C). According to Dorte Janussen (written communication, 2021), the spicules appear to be rather similar and potentially derive from the same sponge genus. The monaxones appear to be root tuft spicules, probably belonging to the order Lyssacinosida, perhaps to the modern family Rossellidae.

The surrounding sediment is slightly silicified and contains an abundance of small bioclasts, most of them indeterminable. Amongst the identifiable bioclasts are mollusc and echinoderm fragments and an abundance of isolated sponge spicule moulds (Fig. 3).

Both halves of the specimen are housed in the collection of the National Museum of Natural History of Denmark, Copenhagen: MGUH 34070.

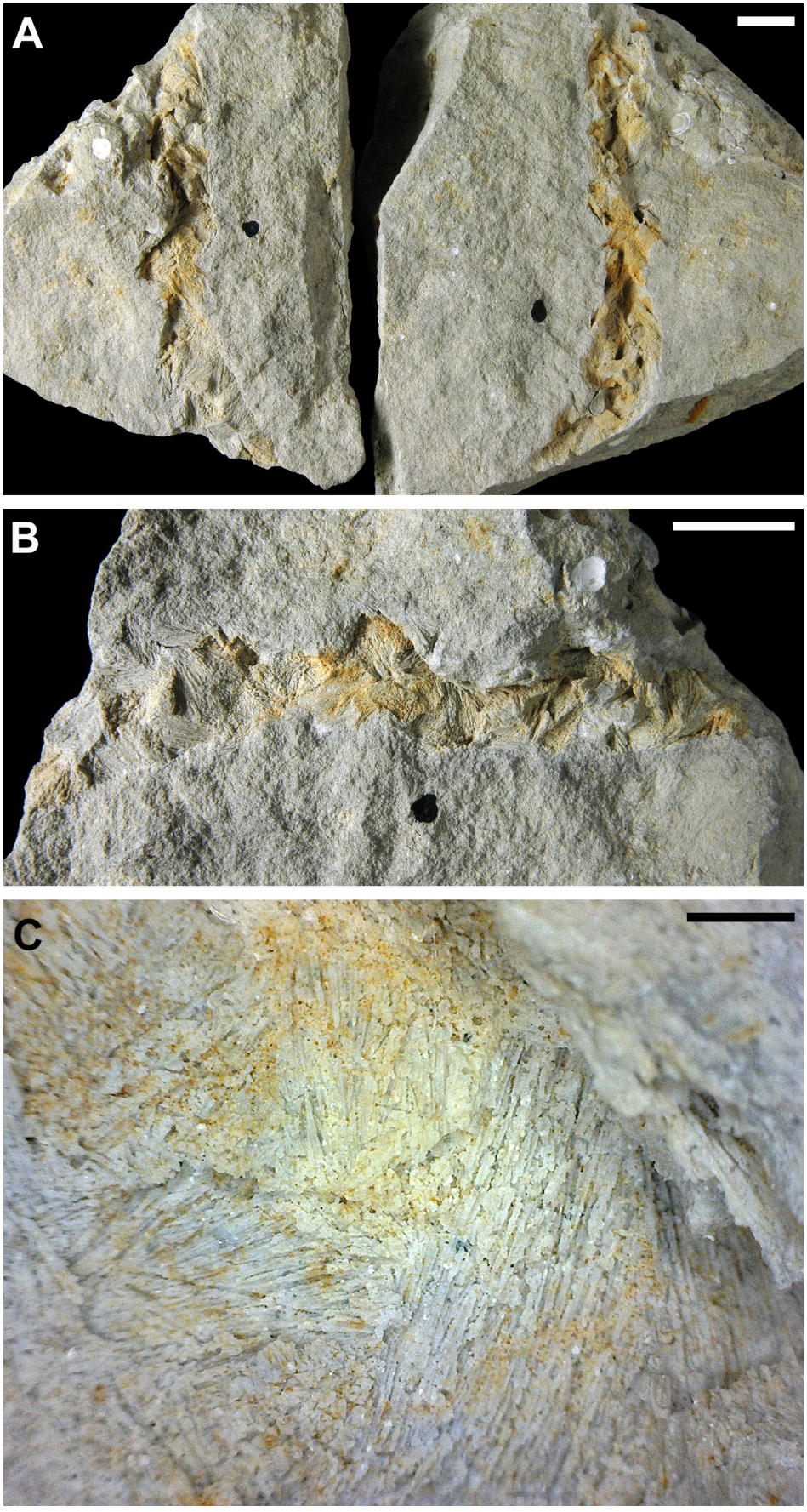

Fig. 2. *Koptichnus rasmussenae* (MGUH 34070) from the Gundstrup gravel pit. Scale bar: 10 mm. **A:** Overview of the two halves of the specimen. **B:** Smaller half. **C:** Detail of B. Imprints of monaxone spicular bundles cut into cuboids as building material for the burrow's lining.

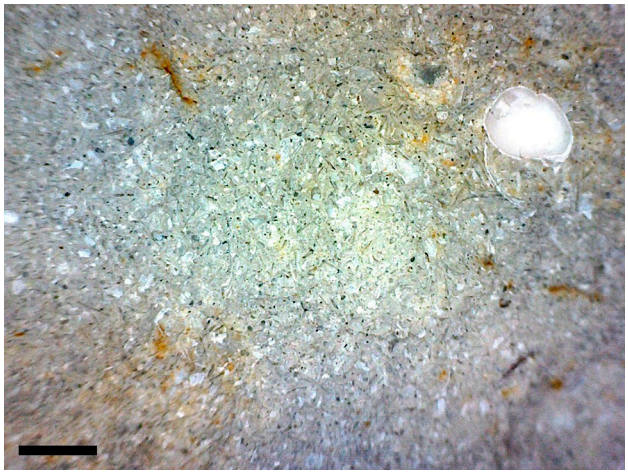

Fig. 3. Detail of the surrounding sediment with numerous cross-cuts of unoriented sponge spicules and other bioclasts. Scale bar: 1 mm.

Interpretation

Vallon *et al.* (2020) inferred that *Koptichnus* is a shallow-tier trace fossil and that its thick lining was constructed to prevent collapse within soft chalk sediments. It particularly occurs close to small sponge accumulations or patch reefs. These not only provided the tracemakers with building material for the trace's lining, but also aided preservation of the burrows. At the previously described Cretaceous locations where *Koptichnus* occurs (Vallon *et al.* 2020), most other burrows lack such thick linings, suggesting that they were constructed in subsequently firmer substrates in the lower tier (Bromley & Ekdale 1984a; Ekdale & Bromley 1991). The preserved fauna, however, shows adaptations to softgrounds (e.g. cf. Heinberg 2012; Hansen & Surlyk 2014).

This apparent contradiction has its origin in continuous sedimentation. Most burrows from these locations were constructed in deep tiers below the seafloor, where the sediment was much firmer than in shallower tiers. With continuous sedimentation, the tracemakers and their burrows gradually moved upward. Under normal circumstances, bioturbation by these deep-tier burrowers erases the record of previous shallow-tier tracemakers (e.g. Howard 1978; Bromley 1996). However, the tiny sponge reefs were evidently impenetrable to these deep-tier burrowers and therefore acted, first, as shields against colonisation by deep-tier burrowers, and later as protection for shallow-tier traces that were made immediately below the sponge thickets.

The trace and body fossils occurring in the Kerteminde Marl indicate a very similar condition on the Paleocene seafloor with softgrounds at the sediment-water interface grading into firmgrounds at some distance below the seafloor characterised by deep-tier trace fossils. The abundance of sponge spicules in the host sediment surrounding the new *Koptichnus* specimen points to a close proximity of sponges. These needles seem not to have been fused and therefore probably belong to the order Lyssacinosida. Most sponges associated with the previously described *Koptichnus rasmussenae* at Arnager (Vallon *et al.* 2020) also belong to the Lyssacinosida (e.g. Brückner 2006).

No systematic treatment of the Kerteminde Marl trace fossils is yet available, but in our own brief observations, the assemblage includes common *Chondrites* ispp., *Zoophycos* ispp. and very abundant *Lepidenteron mortenseni* (see also Schwarzhans *et al.* 2021). These deep-tier ichnotaxa generally are present below the redox potential discontinuity (e.g. Bromley & Ekdale 1984b; Ekdale & Mason 1988; Savrda 2007 and references therein). Typical trace-fossil taxa from upper tiers (except *Koptichnus*) have either been erased, eroded by glacial transport or have never been established. Together with *Koptichnus,* however, this association places the Kerteminde Marl in a transitional zone between the Seilacherian *Cruziana* and *Zoophycos* ichnofacies.

Seilacher (1964, 1967) recognised that certain trace fossils occur more frequently in specific environments because they express an assertive response (ethology) of their tracemakers to these particular environmental conditions (e.g. Buatois & Mángano 2011; MacEachern *et al.* 2012). The *Cruziana* ichnofacies is dominated by horizontal trace fossils, and inclined and vertical burrows occur subordinately. Its typical ethological trace-fossil groups belong to repichnia, fodinichnia, cubichnia, domichnia and pascichnia with a dominance of deposit- and detritus-feeding strategies. Most traces are produced by mobile organisms, but sedentary burrow-dwellers are present as well. The *Cruziana* ichnofacies is characterised by high ichnodiversity and abundance of trace fossils (Buatois & Mángano 2011). Only deep-tier trace fossils have been recovered so far in the Kerteminde Marl boulders from Gundstrup. Common ichnotaxa therefore belong to the fodinichnia and domichnia: e.g. *Rhizocorallium commune* and *Thalassinoides paradoxicus*? together with fanlike feeding burrows. The *Cruziana* ichnofacies is typically associated with medium-energy, sandy to silty substrates which can be found in shelf settings (Bromley 1996).

Originally, the *Zoophycos* ichnofacies was defined as dominated by deep-tier fodinichnia, ranging from relatively simple forms to rather complex structures having a spreite. Many of these deep-tier structures have been reinterpreted and are now regarded as

belonging to the recently introduced ethological category sequestrichnia (Uchman & Wetzel 2016, 2017; Uchman & Rattazzi 2017; Jurkowska *et al.* 2018; Rodríguez-Tovar *et al.* 2019; Uchman *et al.* 2019, 2020). This category comprises storage behaviour that is predominantly applied by tracemakers in deep-sea settings, where food availability fluctuates seasonally or episodically. In times of food abundance, the tracemakers store it within the deeper tiers, an activity that can be referred to as *stowing*, after Schäfer (1972); the tracemakers are then *stowers*. Here, the organic matter is preserved in poorly oxygenated sediments out of the reach of shallow-dwelling deposit feeders (Uchman & Wetzel 2016, 2017; for shallower environments see also Bromley 1996, pp. 100–101, fig. 4.25; Seilacher 2007, p. 54, pl. 18). Subordinately to sequestrichnia, pascichnia may also be present. The *Zoophycos* ichnofacies typically is dominated by deposit feeders and characterised by a low ichnodiversity with a high trace-fossil abundance (Buatois & Mángano 2011). In light of recent discoveries, stowing traces (sequestrichnia) should be added to the list (cf. Uchman & Wetzel 2016). Typical ichnotaxa of the *Zoophycos* ichnofacies that occur in the Kerteminde Marl are *Zoophycos* and *Chondrites*. This ichnofacies is characteristic of low-energy environments with muddy substrates in slope to abyssal settings (e.g. Bromley 1996).

Because elements of both Seilacherian ichnofacies are present, the Kerteminde Marl was likely deposited in the transitional zone between the *Cruziana* and *Zoophycos* ichnofacies. The trace-fossil content further supports previous palaeoenvironmental interpretations for the Kerteminde Marl as being deposited under fully marine conditions at water depths between 100 and 150 m (Clemmensen & Thomsen 2005; King 1994, 2016). Clemmensen & Thomsen (2005) inferred well ventilated bottom waters. Although the ichnocoenosis at hand was adapted to oxygen-depleted conditions, there is no contradiction. Most observed ichnotaxa derive from deeper tiers where oxygen availability was reduced (e.g. Bromley 1996).

Many shallow-tier tracemakers need to strengthen their burrows within the relatively soft sediment in order to prevent collapsing (e.g. Bromley 1996; Vallon *et al.* 2020). The use of bioclasts in such linings is rather uncommon compared to mucus-bound sediment because the tracemakers need to expend much time to collect, shape and assemble suitable material (Vallon *et al.* 2020). In *Koptichnus*, the collection and shaping of cuboids cut from hexactinellid sponges is unique (Vallon *et al.* 2020). Therefore, the range extension of *Koptichnus* across the K-Pg boundary suggests the persistence not only of an unusual behavior, but also of its makers, through the end-Cretaceous mass extinction. This is consistent with the hypothesis that animals living in deep burrows were relatively well protected during this event (Robertson *et al.* 2004; Labandeira *et al.* 2016; Martin 2017).

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