TRACE FOSSILS FROM THE EOCENE LILLEBÆLT CLAY FORMATION, RØSNÆS PENINSULA, DENMARK

Jan Kresten NIELSEN[1], Jesper MILÀN[2,3] & Daniel MESFUN[4]

[1] *VNG Norge, Filipstad Brygge 1, NO-0252 Oslo, Norway; e-mail taphofacies@hotmail.com*
[2] *Geomuseum Faxe / Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark*
[3] *Natural History Museum of Denmark, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark*
[4] *GXU - Gladsaxe 10. Klasse og Ungdomsskole, Gladsaxevej 198, DK-2860 Søborg, Denmark*

Abstract: A cliff exposure of the Eocene Lillebælt Clay Formation, on the Røsnæs peninsula of Zealand, Denmark, has yielded a diverse trace-fossil assemblage. The trace fossils are described formally for the first time and assigned to *Phymatoderma melvillensis*, unnamed clusters of small burrows, *Ophiomorpha nodosa*, *Spongeliomorpha* isp., *Dreginozoum beckumensis*, *Bichordites* isp., *Chondrites* isp., *Atollites zitteli*? and ?*Rhizocorallium* isp. The preservation of the trace fossils is strongly related to early diagenetic enhancement. The trace-fossil assemblage is dominated by a combination of dwelling and feeding burrows. The bioturbation took place in very clean clay of a shelf setting far offshore. The trace-fossil assemblage is indicative of the distal Cruziana ichnofacies.

Key words: Ichnotaxonomy, bioturbation, ethology, ichnofacies.

INTRODUCTION

The Røsnæs peninsula in western Zealand, Denmark, is geologically a classical area, which has been the subject of several investigations during the last century (Fig. 1). The glacio-tectonical complexity and ice-movement directions evident in northwestern Zealand have been thoroughly discussed and reviewed by Andersen (1964), Berthelsen (1971, 1975), Petersen (1973b), Houmark-Nielsen (1981, 1987) and others. Also, field excursions have taken place frequently in this area (e.g., Petersen, 1970). The peninsula comprises strata from the Ølst Formation, Røsnæs Clay Formation, Lillebælt Clay Formation and Quaternary deposits. It is the type area for the Røsnæs Clay Formation. Petersen (1969) found trace fossils at the +103 ash layer of the Paleocene Ølst Formation, close to the overlying Eocene Røsnæs Clay Formation. He briefly subdivided the trace fossils into morphological groups. No other ichnological studies have been carried out on the Røsnæs peninsula. The localities in inland quarries examined by Petersen (1969) are today totally overgrown and inaccessible. A few accessible outcrops are found in the coastal cliffs. A preliminary subdivision of the trace fossils into morphological groups was done by Nielsen and Milàn (2014). The aim of this study is to formally describe the trace-fossil assemblage of the Lillebælt Clay Formation on the Røsnæs peninsula (Figs 1–3), and to present the view that the animal behaviour reflected in the trace fossils sheds light on the depositional conditions.

GEOLOGICAL SETTING

A major transgression, the Ypresian transgression, took place in northwestern Europe after the earliest Eocene (e.g., Rasmussen *et al.*, 2008). The Eocene strata of Denmark comprise mainly very fine-grained deposits of the Røsnæs Clay, Lillebælt Clay and Søvind Marl formations. These accumulated in a deeper marine environment, far from the palaeocoastline in North Germany, South Sweden and South Norway (Gravesen, 1998). The Eocene accumulations are up to 200 m thick in western Denmark. Owing to Neogene uplift and Quaternary glaciations, the accumulations were eroded near the Fennoscandian Shield (Rasmussen *et al.*, 2008).

The Lillebælt Clay Formation was formed during late Ypresian to early Lutetian (Schnetler and Heilmann-Clausen, 2011). It consists mostly of greyish to greenish, non-calcareous clay (Heilmann-Clausen *et al.*, 1985). The clay is of hemipelagic origin. Molluscs from the northern Lillebælt area between Funen and Jutland indicate water depths from lower sublittoral to upper bathyal, equal to about 100–300 m (Schnetler and Heilmann-Clausen, 2011). Fossils of marine crabs, squillae, pteropods and fishes have been found at various localities (Collins and Jakobsen, 2003; Janssen *et al.*, 2007; Schwarzhans, 2007; Bonde *et al.*, 2008). The Lillebælt Clay Formation is widepread in the Danish area of Eocene deposits, except in northern Jutland. The formation is laterally equivalent to a part of the Horda Formation in the
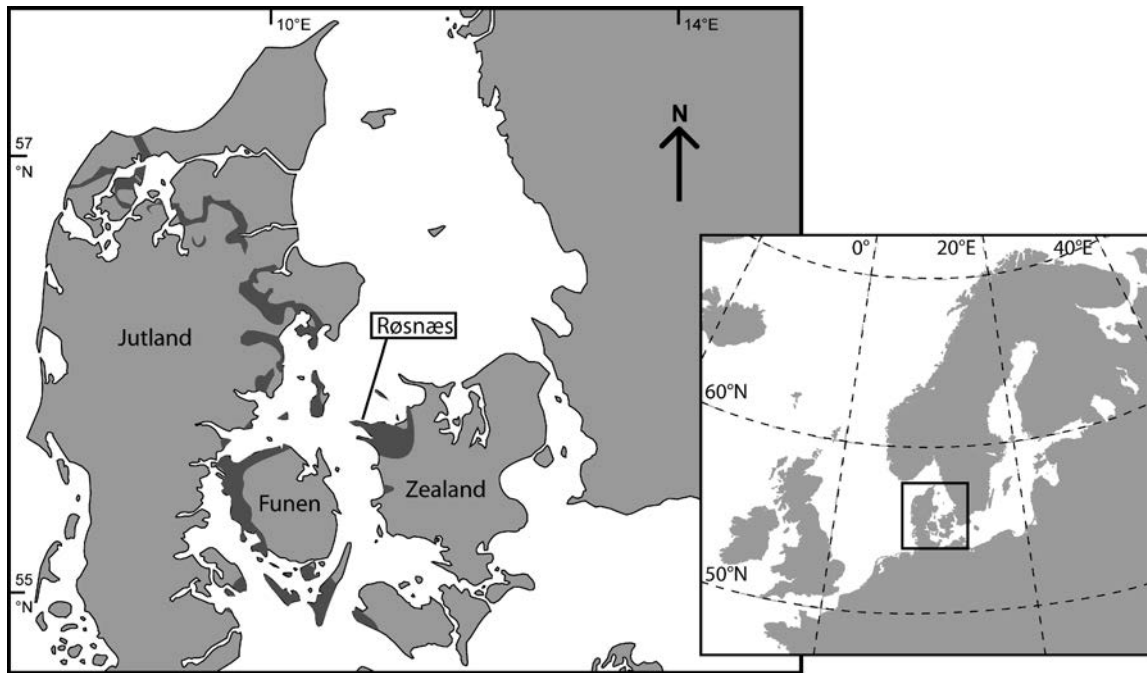
Fig. 1. Location of investigated sea cliff with the Lillebælt Clay Formation in the Røsnæs peninsula, Denmark. The Eocene at the pre-Quaternary surface is indicated by dark grey shading (after Sorgenfrei, 1939; Gravesen, 1998).

North Sea Central Trough (Michelsen, 1994; Schiøler *et al.*, 2007; Rasmussen *et al.*, 2008). The Røsnæs peninsula in the western part of Zealand contains glacio-tectonically disturbed intervals of the Paleocene Ølst Formation as well as the Eocene Røsnæs Clay and Lillebælt Clay formations (see Petersen, 1973a, b, 1978; Berthelsen, 1975; Heilmann-Clausen *et al.*, 1985). The lithological units R5 and R6 of the Røsnæs Clay Formation are overlain by the Lillebælt Clay Formation. The latter is represented by the lithological units L1, L2, L3 and L4 in coastal sea cliffs and clay pits present on the Røsnæs peninsula (Heilmann-Clausen *et al.*, 1985). The present authors investigated a sea cliff located on the southwestern coast of the peninsula (Figs 1–3). The sea cliff is about 520–575 m north-northwest of the road Charlesvej. It is about 15 m high and 55 m in total length. Unit L4 is present in the north-northwestern 25 m part of the cliff (WGS84: 55°43 18 N, 10°59 50 E). The lower part of unit L4 comprises greenish to bluish clay. The upper part consists of greenish clay with brownish clay beds and carbonate concretions. The middle part of the cliff is covered by 25 m of scree deposits. Unit L3 occurs in the south-southeastern 5 m of the cliff (55°43 17 N, 10°59 51 E). This unit comprises red-brown clay, where carbonate concretions are rare near its middle. At this location, unit L2 is partly present and is characterised by grey-green clay with numerous thin lenses of black clay.

According to Schnetler and Heilmann-Clausen (2011), a distinct horizon is present within or at the base of unit L3. The horizon, which is bioturbated and cemented, exists in all Danish onshore occurrences of this unit. The horizon is most likely a condensed section, the age equivalent of the maximum flooding surface at the Ypresian-Lutetian Global Stratotype Section and Point (Schnetler and Heilmann-Clausen, 2011). Concretions occur discontinuously approx-

imately in the middle of unit L3 in the sea cliff. These might indicate the Ypresian-Lutetian boundary.

The units of the Lillebælt Clay Formation are folded in a complex way and are characterised by densely occurring fractures that lower the preservation potential and visibility of trace fossils within the sea cliff. This complexity is related to glacio-tectonic compression as well as late glacial to postglacial landslide events (Berthelsen, 1975, p. 13–14).

MATERIAL AND METHODS

The Lillebælt Clay Formation is poorly exposed in the sea cliff investigated. The cliff is partly covered by vegetation and difficult to access during periods of rainy weather. Observation of trace fossils *in situ* is therefore challenging in the field. Specimens, partially or entirely preserved as ironstone concretions (see Huggett, 1993; Gravesen, 1995), were hand-picked from the outcrop itself and the scree deposits. Some specimens were cross-sectioned and polished by using an ordinary drilling machine equipped with diamond cutting and polishing discs. The specimens were classified systematically, following the ichnotaxobase guidelines by Bertling *et al.* (2006). All the specimens are lodged in the collections of Østsjællands Museum as unnumbered items.

RESULTS

Systematical ichnology

Ichnogenus *Phymatoderma* Brongniart, 1849

Phymatoderma melvillensis Uchman and Gaździcki, 2010
Figs 4, 5

Material: 45 specimens (unit L4, outcrop scree).
Description: All specimens are preserved in full relief, derived
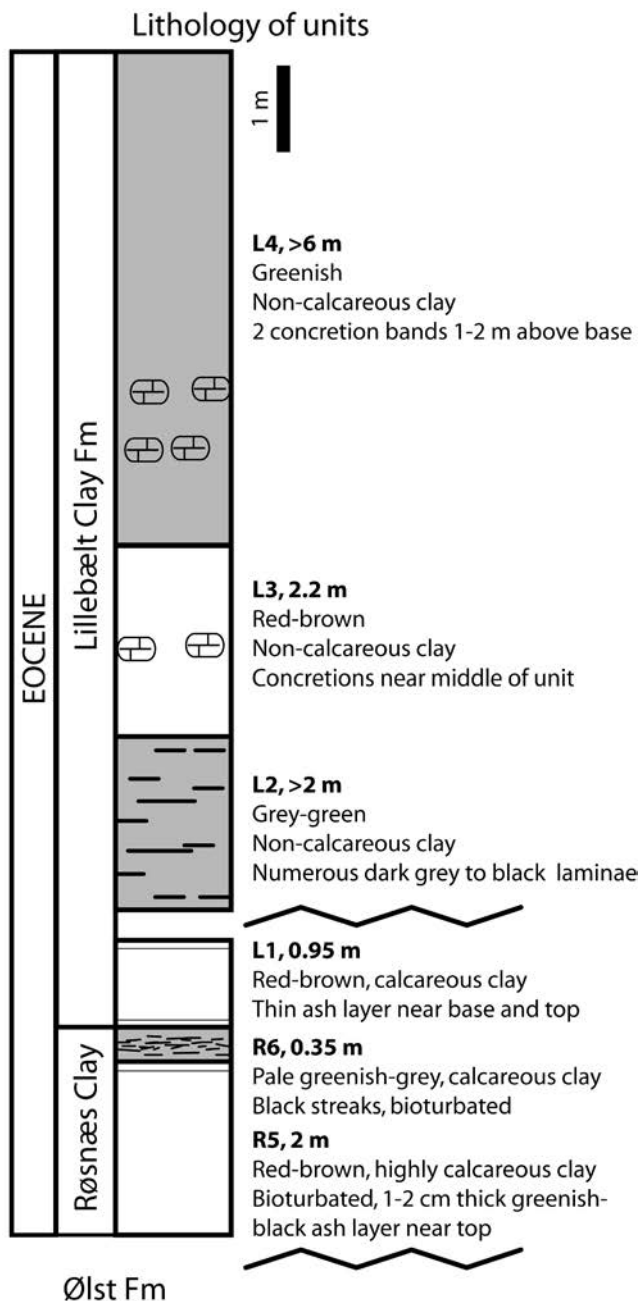
Lithology of units

Fig. 2. Stratigraphical overview and lithology of units in the Lillebælt Clay Formation, Røsnæs peninsula. Modified from Heilmann-Clausen *et al.* (1985, fig. 11).

Fig. 3. Cliff exposures of the Lillebælt Clay Formation. **A.** Lithological unit L4. **B.** Units L3 and L2.

from burrow systems with irregularly bifurcation. The angle of bifurcation is acute, typically less than 45°. The burrow diameter is 13.4–18.6 mm. Individual specimens are fairly constant in diameter. Branching is irregular, typically as first-order side branches from the main burrow. Branches have round or tapered ends. Specimens preserved *in situ* are preferentially oriented horizontally to slightly obliquely. The burrow fill, which is dark grey to black, contains pellets that are oval to circular in cross-section. The length and width of the pellets are 2.0–3.1 and 1.0–1.8 mm, respectively. The pellets are visually most distinct on the burrow margin, which they tend to parallel. Internally the pellets appear to be randomly distributed.

Remarks: These fossilised burrows are most common in the outcrop of the Lillebælt Clay Formation investigated. Because of
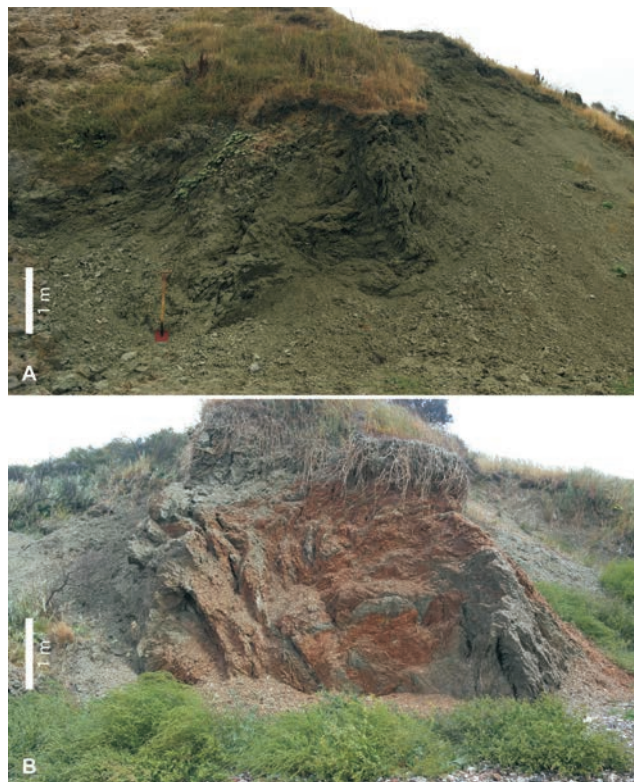
compaction, their original orientation may have been more vertical. The burrows are preserved as ironstone concretions. As indicated by a bright yellowish colour, the infilling of the burrows can locally contain weathered pyrite. The occurrence of pyrite in the Lillebælt Clay Formation was also recognised by Huggett (1993) and Gravesen (1995). Pyritisation possibly occurred in the mucus lining, secreted by the tracemaker; Simpson (1957) tentatively suggested this for *Chondrites*.

Similar trace fossils are illustrated unnamed by Gravesen (1995, p. 18), preserved as clay-ironstone concretions from Trelde Næs in eastern Jutland. His illustration confirms the irregular branching pattern and pellet distribution. Fu (1991) provided a description and comprehensive synonym list for *Phymatoderma granulata* (von Schlotheim, 1822), which is branching in a *Chondrites*-like manner, with feathering appearance of probes (Fu 1991; Seilacher 2007; see von Schlotheim, 1822, pl. 5, fig. 1). *Phymatoderma melvillensis* Uchman and Gaździcki, 2010 is distinguished by a local meniscate structure with pellets and its branching pattern. The menisci are weak in appearance and can be absent in some specimens (Uchman and Gaździcki, 2010). A similar branching pattern occurs in the specimens from the Røsnæs peninsula. Uchman and Gaździcki (2010) also discussed the differentiation from other ichnotaxa. More recently, García-Ramos *et al.* (2014) defined the ichnogenus *Tubotomaculum* García-Ramos *et al.* for horizontal, spindle-shaped burrows, displaying teichinoid spreite and ellipsoidal pellets. Even though the pellets are similar in shape, *Tubotomaculum* differs from *P. granulata* and *P. melvillensis* in burrow outline and the lack of bifurcation.

Cluster of small burrows
Fig. 5

Material: 6 specimens (unit L4, outcrop scree).
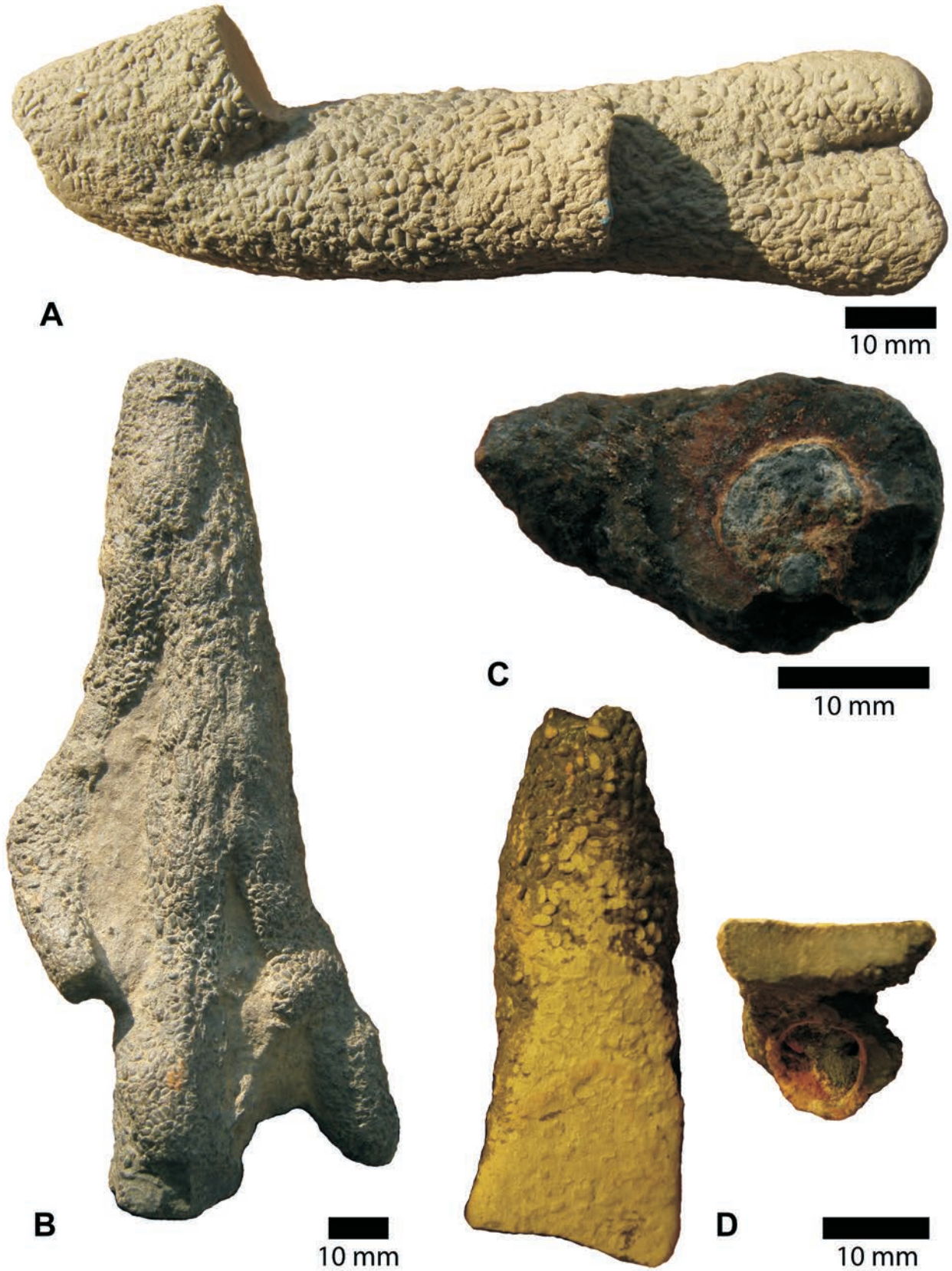**Description:** This structure is a bulbous to elongate lump, charac-

Fig. 4. *Phymatoderma melvillensis* from the Lillebælt Clay Formation. **A, B.** Side views. **C.** Cross-section with diagenetic zonation. Thin yellowish zone is probably weathered pyrite. **D.** Diagenetic enhancement of lower part of pelletal burrow fill, the upper part is absent. Upper view and cross-section.

terised by an irregular outline. The lump is an elongate feature around a branch of *Phymatoderma melvillensis*, or it is present as a sub-spherical feature at the margin of such a branch. The lump comprises a complexity of small burrows. These burrows are cylindrical in outline and they are irregular in curvature and orientation and bifurcate at acute angles. The burrow diameter is about 3.0–4.5 mm. The burrow fill is structureless and dark grey to black, while the matrix between the small burrows is light grey.

Remarks: Modern, analogous structures were described by Bromley and Frey (1974) and Frey and Howard (1975) as terminal chambers, from which minute burrows extend. Frey and Howard (1975) interpreted the burrows as possibly excavated by young post-larvae of the decapod crustacean *Upogebia affinis* (Say). The chambers may have contained organic matter utilised by the juveniles. Also, Forbes (1973) described how juveniles of another burrowing crustacean *Callichirus kraussi* (Stebbing) metamorphose to the post-larval stage inside the parent burrow. Afterwards, they dig into the burrow wall (Forbes, 1973). This is a probable mode of origin for the clusters from the Lillebælt Clay Formation. Also, they could have emerged as actual hatching structures made by the offspring. For instance, D'Alessandro and Bromley (1995) characterised Pleistocene *Spongeliomorpha sicula* D'Alessandro and Bromley as having two types of ovoid chambers, (A) subspherical structures at and below horizontal maze burrow system and (B) vertically elongated structures rising above the maze. The chambers were probably made by crustaceans for microbial gardening (agrichnion), or breeding (D'Alessandro and Bromley, 1995).

The clusters could otherwise be a result of the activities of secondary tracemakers that explored the burrow fill for organic material, as a commensal interrelationship. However, the clusters are not associated with any kinds of trace fossils other than *P. melvillensis*. Also, the clusters may occur rather marginally to the burrow fill of *P. melvillensis*.

Crowded tangles of tortuously branched tubes occur in the Jurassic Sorthat Formation (Bromley and Uchman, 2003). The tangles, *Bornichnus tortuosus* Bromley and Uchman, are ovoid and a few centimetres in size. A distinct wall lining distinguishes them from the clusters in the Lillebælt Clay Formation.

Ichnogenus *Ophiomorpha* Lundgren, 1891

Ophiomorpha nodosa Lundgren, 1891
Fig. 6A, B

Material: 1 specimen (outcrop scree).

Description: The ichnotaxon is represented by a single burrow segment that is distinctly lined with pellets of agglutinated muddy sediment. The pellets are globular in outline and about 4 mm across. The pellets appear as numerous protuberances (knobby) in the outer surface of the wall lining. The wall lining is smooth on the inside. There is no burrow fill inside. Bifurcations have not been recognised in the present specimens.

Remarks: The recognition of *O. nodosa* in the present material is based on the prominent wall lining and the cylindrical circumference of the burrow, which are diagnostic characters for the ichnotaxon. Branching of the burrows is also included in the diagnosis of *Ophiomorpha* (e.g., Fürsich, 1973, 1974; Bromley and Frey, 1974; Nielsen *et al.*, 1996 and references therein); however, it is not present in the specimen studied. The material by Lundgren (1891; see Andersson, 1981) is unbranched, except for one specimen. The authors therefore assign the specimen with confidence to *O. nodosa*.

The scarcity of specimens is probably related to the general lack of a need for burrow reinforcement in the clay-rich succession. The pellets were formed during sediment sorting by the tracemaker, using its mouth parts. Generally, the wall lining of *O. no-*
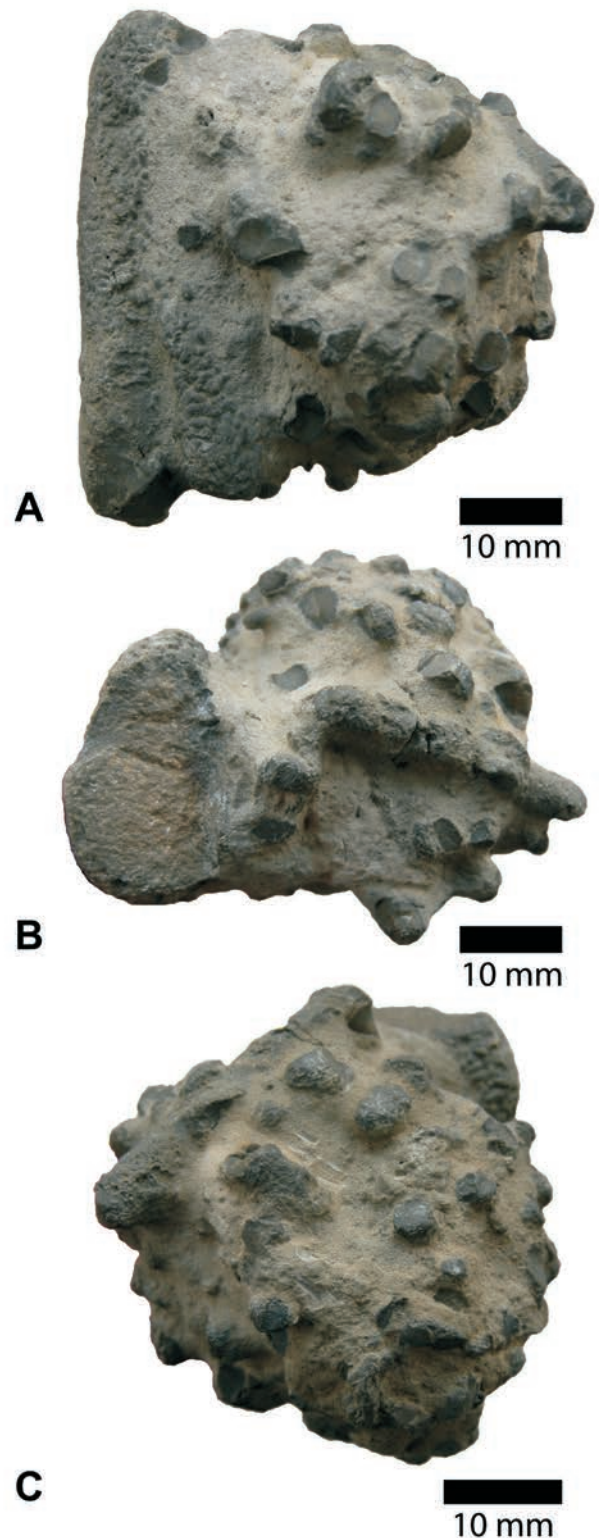

Fig. 5. Trace fossils from the Lillebælt Clay Formation. **A.** Spherical cluster of irregular smaller burrows associated with *Phymatoderma melvillensis*, side view. **B.** Upper view. **C.** Lower view.

dosa tends to be preserved as a concretionary halo, where the interior and surrounding sediment is less consolidated (Seilacher, 2007, p. 54). The present specimen shows a similar way of preservation.
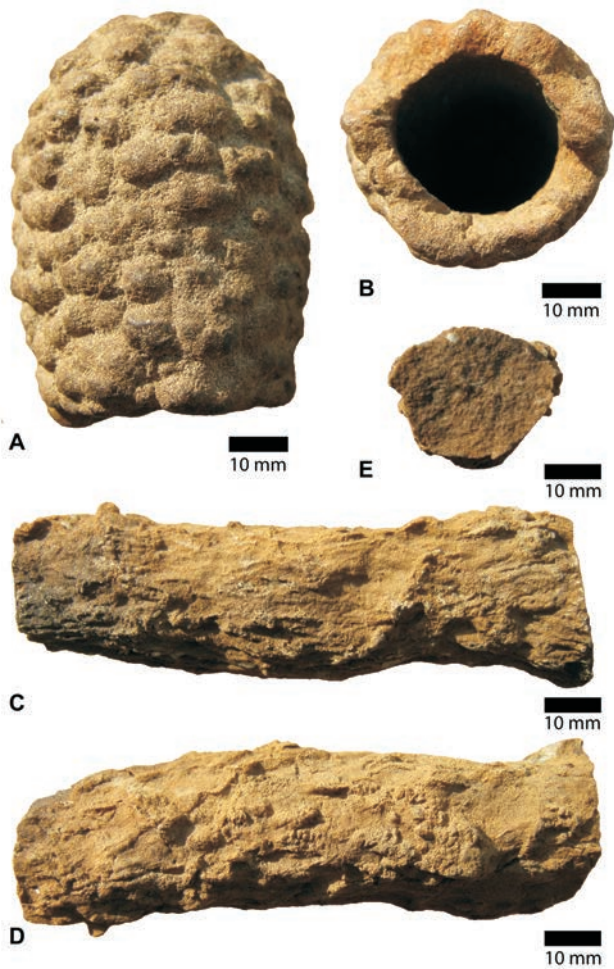
Fig. 6. Some crustacean trace fossils from the Lillebælt Clay Formation. **A.** *Ophiomorpha nodosa*, side view of terminal end. **B.** Cross-section. **C.** *Spongeliomorpha* isp., lower view. **D.** Upper view. **E.** Cross-section.

Ichnogenus *Spongeliomorpha* Saporta, 1887

Spongeliomorpha isp.
Fig. 6C–E

Material: 5 specimens (units L4 and L3, outcrop scree).
Description: A cylindrical burrow system with a smooth to striated, unlined burrow margin. The striation is present as ridges oriented longitudinal to oblique with respect to the main axis of the burrow. The burrow fill is structureless. The burrow is oval in cross-section, about 25–35 mm wide. The dimensions are fairly uniform in individual burrows. The burrows are linear to curved in outline. Burrows found *in situ* are all horizontally oriented.
Remarks: The specimens are oval in vertical cross-section, because of the original burrowing dimensions or partial compaction. The latter would be in contrast to the indication of stiff mud by the striations, which are interpreted as scratches made by the tracemaker (bioglyphs). The substrate was sufficiently firm for wall reinforcement not to be required. The bioglyphs are commonly indicative of a muddy firmground (e.g., Seilacher, 2007; Gibert and Ekdale, 2010). *Spongeliomorpha* can clearly be differentiated from *Thalassinoides* by its bioglyphs (Gibert and Ekdale, 2010).

The systematic validation of *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides* at ichnogeneric level has been extensively dis-

cussed by Fürsich (1973, 1974), Bromley and Frey (1974), Frey *et al.* (1978), Schlirf (2000), Melchor *et al.* (2010) and others. Wall structures, such as lining and striation, are considered as valid taxobases, among others, for ichnogeneric distinction (e.g., Melchor *et al.*, 2010). The specimens described herein are assigned to an unspecified ichnotaxon of *Spongeliomorpha* isp. and do not show a repetitive pattern of bioglyphs. Its irregularity indicates that the purpose of the burrows was dwelling; deposit feeding is not evident. A similar interpretation was reached by Gibert and Robles (2005) for Miocene *S. sudolica* (Zaręczny) in the Vallès-Penedès Basin, Spain.

Ichnogenus *Dreginozoum* Marck, 1894

Dreginozoum beckumensis (Marck, 1858)
Fig. 7A–C

Material: 4 specimens (unit L4, outcrop scree).
Description: Subhorizontal, unbranched burrows, characterised by a median string about 1–2 mm wide. Biserially arranged lobes are placed laterally along the string. The lobes are like coffee beans in outline, up to about 16 mm laterally out from the string. They are up to about 11 mm, measured parallel to the string. Overall burrow width is up to 33 mm.
Remarks: Häntzschel (1964) tentatively compared *Dreginozoum* with egg capsules of marine prosobranch gastropods; *Dreginozoum* was considered as unrecognisable (Häntzschel, 1975). Specimens from the Lower Eocene of Germany were stated by Reich and Klafack (2002) to be fossilised egg capsules, but the taphonomical process was not clarified to justify the three-dimensional preservation of soft tissue during decay and compaction. They rejected an interpretation as trace fossils. In contrast, Kappel (2002) comprehensively argued *Dreginozoum* to be a monospecific ichnogenus on the basis of specimens found at bedding interfaces. The lobes, which resembled coffee beans in outline, contained backfill structures related to active grain sorting (Kappel, 2002). The process of backfilling was supported by Seilacher (2007), who considered *Dreginozoum* as the hypichnial preservation of nereitid traces on sole surfaces.

Ichnogenus *Bichordites* Plaziat and Mahmoudi, 1988

Bichordites isp.
Fig. 7D

Material: 3 specimens (unit L4, outcrop scree).
Description: Horizontal, unbranched burrows, which are tubular in outline and slightly oval in cross-section. The width is up to 27 mm. The burrow shows a meniscate backfill that is partially cemented. Individual menisci are slightly crescent and about 6 mm thick. The menisci are penetrated by a weakly developed string. The string is located a little below the centre of the burrow. Preserved in full relief. The substrate around the string is commonly more heavily mineralised, forming a preservational core.
Remarks: The partial cementation of the backfill menisci may be due to biogenic grain sorting; however, the sediment consists of very clean clay. It is more likely that differential mucus secretion by the tracemaker enhanced the possibility for diagenesis. Bromley and Asgaard (1975) described a similar cementation pattern as dependent upon mucus distribution in Pleistocene specimens from Greece. They thoroughly described and interpreted these backfill structures and the burrowing ability of spatangoid echinoids found *in situ*. The echinoids were deposit-feeders and formed the backfill by packing sediment and faecal material into menisci and a drain behind themselves (Bromley and Asgaard, 1975). The drain is in the present case preserved as a thin string.

The ichnogenus *Bichordites* and its type ichnospecies *B. monastiriensis* were originally coined by Plaziat and Mahmoudi (1988) for the heart-shaped burrow core around a drain. The diagnosis was emended by Uchman (1995) to consider the surrounding meniscate backfill. Later, Demircan and Uchman (2012) modified the diagnosis for *Bichordites* to include the structurally more complex *B. kuzunensis*. The specimens from the Lillebælt Clay Formation resemble *B. monastiriensis*. Because the specimens tend to lack the marginal rim of the menisci, they are assigned to *Bichordites* isp. A specimen from the same formation at Trelde Næs (Jutland) was under the term "hunde-høm-høm", illustrated by Gravesen (1995, p. 18, fig. B). Similar trace fossils are also known as echinoid burrows from the Miocene Hagenør-Børup succession at Lillebælt, probably the Vejle Fjord Formation (Radwański *et al.*, 1975). The margin of the Miocene North Sea had periods of open and restricted conditions with high and low hydrodynamic energy, respectively (Radwański *et al.*, 1975).

Ichnogenus *Chondrites* von Sternberg, 1833

Chondrites isp.
Fig. 7E

Material: 3 specimens (unit L4).
Description: Tunnel system ramifying regularly downward to laterally. The angle of branching is commonly acute. The branches are about 2.5–3.3 mm wide and tend to be slightly curved. They are oval in cross-section, rarely circular, and clustered into groups. The structureless fill is faintly lighter than the rest of the beige concretion. The fill appears to be more densely cemented.
Remarks: A comprehensive revision of the ichnogenus *Chondrites* was done by Fu (1991). Besides the mode of branching, Uchman *et al.* (2012) emphasized the relative ratio between the width of the burrow system and the width of the tunnels. The ratio was considered important for distinguishing various ichnospecies. Within the Lillebælt Clay Formation, the width of the tunnels preliminarily suggests *Chondrites targionii* (Brongniart). The concretionary preservation of the burrow systems makes an evaluation of the complete system size difficult. They are therefore determined to unspecified ichnospecific level.

Tracemakers of *Chondrites* have commonly been interpreted as endobenthic deposit-feeders (e.g., Simpson, 1957; Osgood, 1970; Bromley and Ekdale, 1984). It is known that *Chondrites* typically is produced in a relatively deep tier within the anaerobic zone (Bromley and Ekdale, 1984). The bottom water was possibly poorly oxygenated. The tracemaker could have benefited from chemosymbiosis, based on hydrogen sulphide and methane (Seilacher, 1990; Fu, 1991). Alternatively, the tracemaker fed from the surface sediment and by its excretory behaviour filled the burrow system (Kotake, 1992). Because a pelletal texture is absent, this explanation is less likely in this case.

Ichnogenus *Atollites* Maas, 1902

Atollites zitteli? Maas, 1902
Fig. 8A

Material: 1 specimen (outcrop scree).
Description: Circular structure which is about 75 mm in diameter. The thickness is 15 mm. There is a 2-mm-wide depression in the centre. The surface area around the center is structureless. The area is about 40 mm in diameter. The rim is 18 mm wide and particularly detailed on one side. It contains about 22 radial lobes. Each lobe is about 7 mm wide. The outermost part of the rim tends to be swollen in thickness.
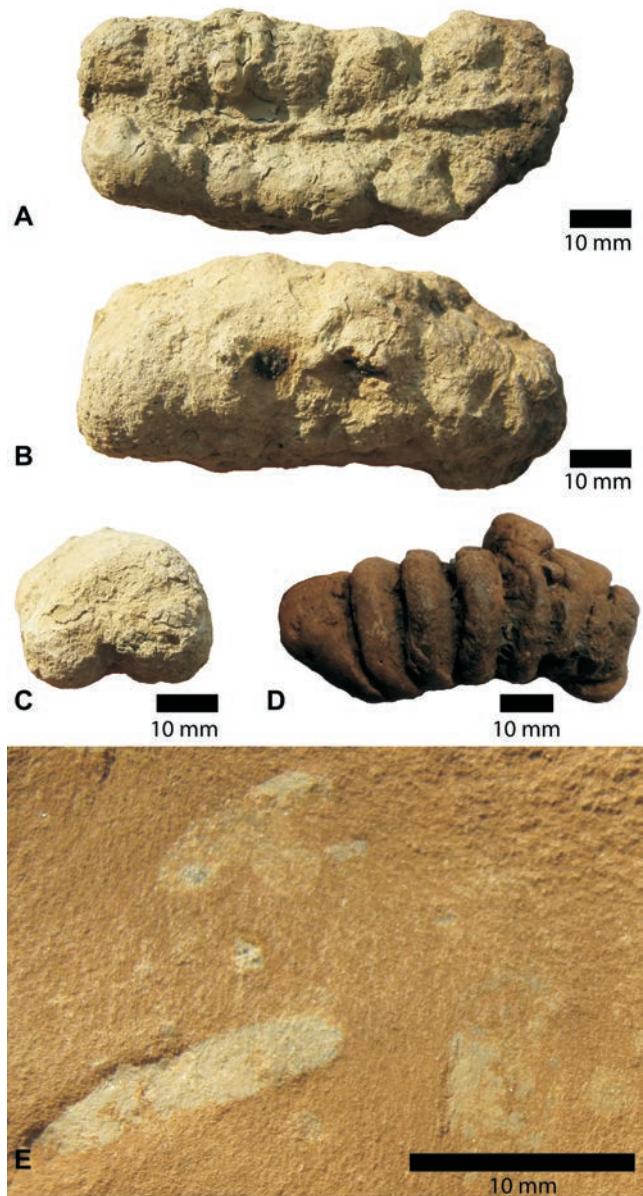**Remarks:** Only one specimen was obtained from a scree surface.

Fig. 7. Trace fossils from the Lillebælt Clay Formation. **A.** *Dreginozoum beckumensis*, upper view. **B.** Lower view. **C.** Cross-section. **D.** *Bichordites* isp., meniscate backfill, side view. **E.** *Chondrites* isp., cross-section.

It is ethologically categorised as a fodinichnion. The tracemaker is interpreted to have mined the subsurface for nutrients in a radial pattern out from a central shaft. A similar interpretation was made by Durkin (1968) for a similar structure with a cylindrical tube, surrounded by radial overlapping lobes. That structure belongs to *Gyrophyllites* Glocker that was diagnosed by Strzeboński and Uchman (2015; see Fu, 1991, Uchman, 1998) as including radial burrows with subhorizontal, swollen leaf-like lobes that radiate from a vertical shaft at one or more levels. Because the Røsnæs specimen is characterised by a structureless central area and enlargements at the rim, it merely resembles *Atollites* Maas.

A three-dimensional reconstruction of *Atollites italicum* Serpagli indicates that the central circular area represents a vertical, axial shaft, compacted during burial (Serpagli, 2005). There are about 30–35 cylinders radiating laterally from the shaft. Each cylinder ends distally in a club. *Atollites minor* Maas and *A. zitteli*

Maas are similarly characterised by a central circular area (Maas, 1902). Cylinders are radiating from this area; each cylinder ends distally in a club. *Atollites minor* and *A. zitteli* differ from *A. italicum* by equally sized clubs in a certain specimen (Serpagli, 2005). The overall size difference between *A. minor* and *A. zitteli* was emphasized by Maas (1902). Considering them as trace fossils, size is an invalid ichnotaxobase (e.g., Bertling *et al.*, 2006). Apparently, *A. minor* has internally structured clubs, possibly backfilled, whereas those of *A. zitteli* are structureless (see Maas, 1902, pl. 23, figs 5, 6). The specimen of the authors resembles the latter. Because the diagnostic cylinders are unobservable, probably owing to poor preservation, the specimen is left in open nomenclature, *Atollites zitteli*?.

Ichnogenus *Rhizocorallium* Zenker, 1836

?*Rhizocorallium* isp.
Fig. 8B–D

Material: 4 specimens (outcrop scree).
Description: Spreite structures of sub-parallel, curved laminae. Dimensions of individual lobes are variable. Preserved in full relief.
Remarks: Only a few spreite structures, which are in a poor state of preservation, have been found at the cliff exposures investigated. They appear to have derived from larger burrow systems. For example, the coil shown in Figure 8D is most likely to be from *Zoophycos* Massalongo. Uchman (1998) described *Zoophycos* as spreite arranged in a helicoidal spiral and with a central, vertical or marginal tunnel. The other specimens from the Lillebælt Clay Formation may belong to *Rhizocorallium* Zenker, following the emended diagnosis by Knaust (2013). Both *Zoophycos* and *Rhizocorallium* are known to occur in the Lillebælt Clay Formation (Gravesen, 1995). The spreite structures were formed by endobenthos that moved laterally back and forth to mine the substrate for food (fodinichnia). Other interpretations may be suggested (Uchman, 1998, for review); however, the condition of the material does not allow a further assessment.

DISCUSSION

Pelletal texture

Phymatoderma melvillensis from the Lillebælt Clay Formation is characterised by a pelletal texture in the burrow fill (Fig. 4). This kind of burrow was made in the clayey substrate with a consistency like softground. There are no bioglyphs that could indicate a firmer substrate. There are two ways the burrows may have been filled with pellets. It appears most likely that they originated as faecal pellets made by the tracemaker, which was a crustacean according to Gravesen (1995). A pelletal burrow fill commonly was related to subsurface deposit feeding (Fu, 1991), surface deposit feeding followed by subsurface stowage for later food utilisation (Miller and Vokes, 1998; Uchman and Gaździcki, 2010), or surface deposit feeding adapted for effective nutrient absorption and subsurface excretion (Izumi, 2012). An alternative explanation is that the pellets hydrodynamically acted as large grains that were transported into open burrows. This would have required deeper marine currents, far from the coastline. The authors consider this to be less likely. Similar pellets were not observed in the uncemented sediment surrounding the trace fossils; a pelletal texture could have been homogenised by compaction (Friis, 1995).

Because the fossilised burrows are mainly circular in cross-section, they must have been cemented soon after they were abandoned by the tracemakers. The cementation prevented compaction. Diagenetic enhancement of the burrows can be related to the pelletal texture that facilitated as a conductor for fluid irrigation (see Seilacher, 1951). In addition, the burrows may have become cemented because of mucus secreted from the tracemakers. The mucus could have facilitated the cementation. It is well known that mucus can cause differential preservation of bioturbation structures (e.g., Bromley and Asgaard, 1975). The outcrop quality and the clay-dominant succession do not allow an assessment of the original depth of burrowing. Only the lowest parts of *P. melvillensis* may have been preserved by diagenesis (see Izumi, 2012, fig. 5; Fig. 4D). Generally, Fu (1991) stated that *P. granulata* could have formed up to 50 cm into the seafloor; with post-compaction preservation of 15 cm. Miller and Vokes (1998) recognised *Phymatoderma* as a shallow-tier trace fossil, with less than 10 cm preserved post-compaction.

Depositional conditions

The sediment of the Lillebælt Clay Formation is very clean clay and barren with respect to the remains of terrestrial plants. The lithological units have a regional continuity (Heilmann-Clausen *et al.*, 1985) that makes an embayment setting unlikely. This indicates that deposition occurred under very low levels of hydrodynamic energy, far from the shore. An absence of colonisation surfaces indicates continuous sedimentation. Intervals of structureless clay indicate stagnant bottom conditions with oxygen deficiency. Alternatively extensive compaction may have erased biogenic sedimentary structures, including pelletal texture (see Friis, 1995). At least periodically, the sea floor became colonised by tracemakers that made the burrow systems elaborated. The occurrence of recognisable burrows may reflect the duration of colonisation windows and may be related to differential preservation potential, dependent upon the chemical threshold for diagenetic enhancement. An oxygenated water column above the sea bottom was a prerequisite for sustaining macrobenthic life forms. Irrigation of their burrows may locally have affected the position of the redox potential boundary within the substrate (e.g., Seilacher, 1951, fig. 3; Bromley, 1996). Heilmann-Clausen *et al.* (1985) stated that oxygen overall was more restricted in the bottom water than during the deposition of the underlying Røsnæs Clay Formation. There were brief incursions of oxygen.

As observed in the Lillebælt Clay Formation, *Ophiomorpha nodosa*, *Spongeliomorpha* isp. and *Phymatoderma melvillensis* are characterised by wall lined margin, scratched margin and smooth margin, respectively. The single specimen of *O. nodosa* is from outcrop scree and cannot be linked to a particular lithological unit. *Spongeliomorpha* isp. and *P. melvillensis* may occur together in intervals of the clay-dominated succession that are uniform in grain size and sorting. It is most likely that the substrate consistency changed from softground to firmground as the substrate became firmer over time. Increasing burial depth resulted in dewatering and initial compaction of the substrate, while the
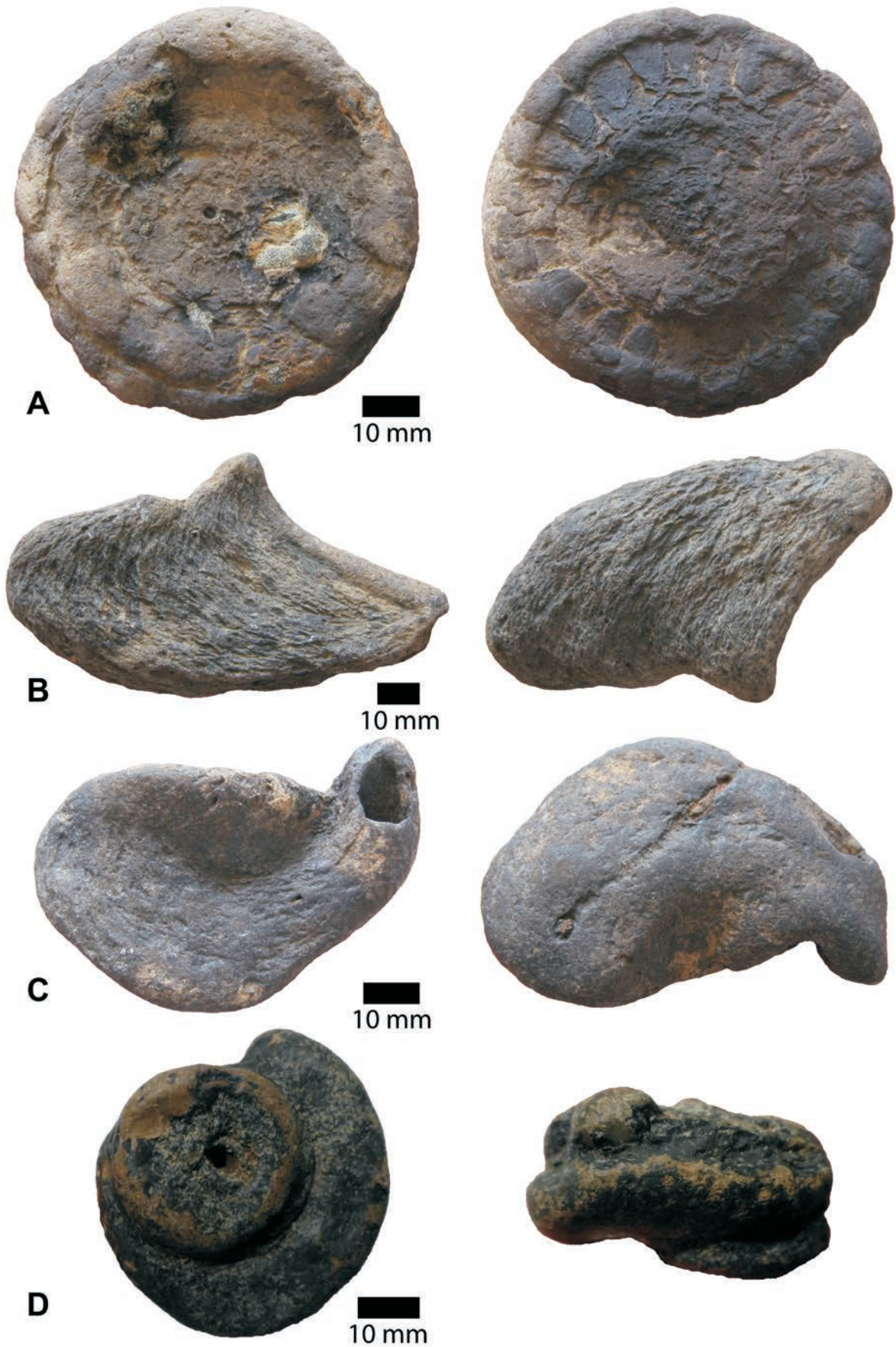
Fig. 8. Other trace fossils from the Lillebælt Clay Formation. **A.** *Atollites zitteli*?, apparently upper and lower views. **B.** ?*Rhizoco-rallium* isp., single lobe. **C.** ?*Rhizocorallium* isp., abraded on the modern shore. **D.** Indet. isp., a central coil of a larger burrow system.

colonisation window was open. The transition from soft-ground to firmground can reflect a development within the transition layer, before it became a historical layer (see Ekdale *et al.*, 1984). This would explain the differences in burrowing behaviour by the tracemakers. It is noteworthy that the substrate was dominated by clay and, thus, the sea bottom could be expected to have been a soupground in the superficial layer. Because of the pelletal texture, however, its consistency might have been firmer.

The concept of archetypical ichnofacies was founded by Seilacher (1964, 1967). The marine ichnofacies reflect behaviour controlled to some extent by substrate consistency (e.g., Ekdale, 1985; Bromley, 1990). Those formed in softground are the Psilonichnus, Skolithos, Cruziana, Zoophycos and Nereites ichnofacies. The sea cliff on Røsnæs peninsula has yielded trace fossils, most of which can be interpreted as fodinichnia that served as a combination of dwelling and feeding locations. *Phymatoderma melvillensis* is the most abundant fodinichnion. *Ophiomorpha nodosa* and *Spongeliomorpha* isp. appear to have had the sole purpose of dwelling and can be classified as domichnia. The presence of *Spongeliomorpha* isp. is indicative of burrowing in stiff mud (e.g., Seilacher, 2007, plate 18); it is not necessarily evidence of an exposed firmground, but of a firm substrate at a deep tier. The trace-fossil assemblage also includes pascichnial structures formed by vagile deposit feeders, exploiting the substrate. *Bichordites* isp. and *Dreginozoum beckumensis* are examples.

Overall, the lithology reflects predictable conditions, typical of the Zoophycos ichnofacies (see Seilacher, 1967, 2007; Pemberton *et al.*, 1992a, b). The depositional setting was clay-dominated and characterised by low hydrodynamic energy, without any evidence of storm events. The bioturbation took place in a shelf setting, located far offshore from sedimentary sources. The present assemblage mainly comprises trace fossils of mid tiers. The Zoophycos ichnofacies is normally characterised by a low diversity of fodinichnia, formed in both mid and deeper tiers. As further stated by Bromley (1990, p. 241), the deeper tiers may be absent. The possible periods of oxygen deficiency, substrate consistency and the differential preservation by diagenetic processes can explain the lack of deeper-tier trace fossils. Oxygen deficiency may be a major control on Zoophycos ichnofacies, associated with organic matter and calm hydrodynamic conditions (Frey and Seilacher, 1980). However, the trace-fossil assemblage of the Lillebælt Clay Formation does not represent a typical Zoophycos ichnofacies. The diversity is moderate and trace fossils, such as *Bichordites* isp., *Spongeliomorpha* isp. and ?*Rhizocorallium* isp., are ethologically more representative of the Cruziana ichnofacies. Trace fossils of varying orientation are a characteristic feature of the Cruziana ichnofacies, which generally shows high diversity and abundance of mostly fodinichnia and pascichnia, formed by vagile deposit feeders (Pemberton *et al.*, 1992a, b). The idealized shoreface model of Pemberton *et al.* (1992b; see also MacEachern and Pemberton, 1992; Gingras *et al.*, 1998) indicates that the Cruziana ichnofacies may occur from the lower shoreface, across the offshore transition and upper offshore, to the lower offshore. These depositional environments are periodically affected by

tempestitic deposition, located above the storm-weather wave base (e.g., MacEachern and Burton, 2000; Seilacher, 2007). The Carboniferous offshore deposits of the Morrow Sandstone in Kansas show a low diversity of diminutive trace fossils of distal Cruziana ichnofacies, reflecting a stable deposit-feeder community (Buatois *et al.*, 2002). Instead of reflecting an impoverished fauna, traces of deeper tiers may have obliterated those of shallower tiers (Buatois *et al.*, 2002; see Bromley, 1990). The Cretaceous Westgate Formation in Alberta contains silt-poor mudstones with a low-abundance, distal Cruziana ichnofacies and is recognised as a shelf deposit (MacEachern and Burton, 2000). These show a general lack of lithological contrast between the trace fossils and the surrounding sediment. Originally the mudstones were probably thoroughly bioturbated; however, burial, dewatering and compaction may have removed most traces (MacEachern and Burton, 2000). The Lillebælt Clay Formation bears similarities to the cases mentioned above and the authors therefore argue for a distal Cruziana ichnofacies.

CONCLUSIONS

Even though the outcrop quality is poor, 9 ichnotaxa have been identified from the cliff exposure of the Lillebælt Clay Formation. The trace-fossil assemblage is representative of the distal Cruziana ichnofacies. The depositional setting was in a siliciclastic shelf environment with slow background sedimentation. The formation is largely structureless clay, in which trace fossils are preserved locally as diagenetic concretions. Compaction of the uncemented clay might have erased other traces and the pelletal texture. However, the clay originally could have been unbioturbated, which would clearly indicate stagnant bottom conditions with an oxygen deficiency. At least periodically, the oxygen level was sufficiently high to sustain endobenthic tracemakers.

REFERENCES

Andersen, S. A., 1964. Grusgravene i bakkerne ved Kalundborg. *Meddelelser fra Dansk Geologisk Forening*, 15: 359–367. [In Danish.]

Andersson, K. A., 1981. Bernhard Lundgren's (1891) description of *Ophiomorpha*. *Geologiska Föreningen i Stockholm Förhandlingar*, 103: 105–107.

Berthelsen, A., 1971. Fotogeologiske og feltgeologiske undersøgelser i NV-Sjælland. *Dansk Geologisk Forening, Årsskrift,* 1970: 64–69. [In Danish.]

Berthelsen, A., 1975. Geologi på Røsnæs. *Varv, Ekskursionsfører*, 3: 1–78. [In Danish.]

Bertling, M., Braddy, S., Bromley, R. G., Demathieu, G. D., Genise, J., Mikuláš, R., Nielsen, J. K., Nielsen, K. S. S., Rindsberg, A., Schlirf, M. & Uchman, A., 2006. Names for trace fossils: a uniform approach to concepts and procedures. *Lethaia*, 39: 265–286.

Bonde, N., Andersen, S., Hald, N. & Jakobsen, S. L., 2008. *Danekræ – Danmarks Bedste Fossiler*. Gyldendal, København, 224 pp. [In Danish.]

Bromley, R. G., 1990. *Trace Fossils: Biology and Taphonomy*. Unwin Hyman, London, 280 pp.

Bromley, R. G., 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Chapman & Hall, London, 361 pp.

Bromley, R. G. & Asgaard, U., 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bulletin of the Geological Society of Denmark*, 24: 261–281.

Bromley, R. G. & Ekdale, A. A., 1984. *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science*, 224: 872–874.

Bromley, R. G. & Frey, R. W., 1974. Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. *Bulletin of the Geological Society of Denmark*, 23: 311–335.

Bromley, R. G. & Uchman, A. 2003. Trace fossils from the Lower and Middle Jurassic marginal marine deposits of the Sorthat Formation, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark*, 52: 185–208.

Brongniart, A. T., 1849. Tableau des Genres de Végétaux Fossils Considérés sous le Point de Vue de leur Classification Botanique et de leur Distribution Géologique. In: d'Orbigny, A. C. V. D. (ed.), *Dictionnaire Universel d'Histoire Naturelle*, 13. Imprimerie de L. Martinet, Paris, pp. 1–127 [Extrait 52–176].

Buatois, L. A., Mángano, M. G., Alissa, A. & Carr, T. R., 2002. Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal- to open-marine reservoir, Morrow Sandstone, subsurface of southwest Kansas, USA. *Sedimentary Geology*, 152: 99–132.

Collins, J. S. H. & Jakobsen, S. L., 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum*, 30: 63–96.

D'Alessandro, A. & Bromley, R. G., 1995. A new ichnospecies of *Spongeliomorpha* from the Pleistocene of Sicily. *Journal of Paleontology*, 69: 393–398.

Demircan, H. & Uchman, A., 2012. The miniature echinoid trace fossil *Bichordites kuzunensis* isp. nov. from early Oligocene prodelta sediments of the Mezardere Formation, Gökçeada Island, NW Turkey. *Acta Geologica Polonica*, 62: 205–215.

Durkin, M. K., 1968. Notes on the trace fossils at Bean, Kent. *Proceedings of the Geologists' Association*, 79: 215–218.

Ekdale, A. A., 1985. Paleoecology of the marine benthos. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 50: 63–81.

Ekdale, A. A., Muller, L. N. & Novak, M. T., 1984. Quantitative ichnology of modern pelagic deposits in the abyssal Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 45: 189–223.

Forbes, A. T., 1973. An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). *Marine Biology*, 22: 361–365.

Frey, R. W. & Howard, J. D., 1975. Endobenthic adaptations of juvenile thalassinidean shrimp. *Bulletin of the Geological Society of Denmark*, 24: 283–297.

Frey, R. W., Howard, J. D. & Pryor, W. A., 1978. *Ophiomorpha*: Its morphologic, taxonomic, and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23: 199–229.

Frey, R. W. & Seilacher, A., 1980. Uniformity in marine invertebrate ichnology. *Lethaia*, 13: 183–207.

Friis, H., 1995. The role of faecal pellets in deposition of marine muddy sediments – examples from the Danish Tertiary. *Bulletin of the Geological Society of Denmark*, 42: 68–73.

Fu, S., 1991. Funktion, Verhalten und Einteilung fucoider und lophocteniider Lebensspuren. *Courier Forschungsinstitut Senckenberg*, 135: 1–79.

Fürsich, F. T., 1973. A revision of the trace fossils *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1973: 719–735.

Fürsich, F. T., 1974. Corallian (Upper Jurassic) trace fossils from England and Normandy. *Stuttgarter Beiträge zur Naturkunde, Serie B*, 13: 1–52.

García-Ramos, J. C., Mángano, M. G., Piñuela, L., Buatois, L. A. & Rodríguez-Tovar, F. J., 2014. The ichnogenus *Tubotomaculum*: an enigmatic pellet-filled structure from Upper Cretaceous to Miocene deep-marine deposits of southern Spain. *Journal of Paleontology*, 88: 1189–1198.

Gibert, J. M., de & Ekdale, A. A., 2010. Paleobiology of the crustacean trace fossil *Spongeliomorpha iberica* in the Miocene of southeastern Spain. *Acta Palaeontologica Polonica*, 55: 733–740.

Gibert, J. M., de & Robles, J. M., 2005. Firmground ichnofacies recording high-frequency marine flooding events (Langhian transgression, Vallčs-Penedčs Basin, Spain). *Geologica Acta*, 3: 295–305.

Gingras, M. K., MacEachern, J. A. & Pemberton, S. G., 1998. A comparative analysis of the ichnology of wave- and river-dominated allomembers of the Upper Cretaceous Dunvegan Formation. *Bulletin of Canadian Petroleum Geology*, 46: 51–73.

Gravesen, P., 1995. *Tertiærtidens Lag i Danmark*. Midtsønderjyllands Museum, Gram Slot, 32 pp. [In Danish.]

Gravesen, P., 1998. Danske Forsteninger fra Tertiærtiden. *Natur og Museum*, 2: 1–35. [In Danish]

Häntzschel, W., 1964. Spurenfossilien und Problematika im Campan von Beckum (Westf.). *Fortschritte in der Geologie von Rheinland und Westfalen*, 7: 295–308.

Häntzschel, W., 1975. Trace fossils and problematica. In: Teichert, C. (ed.), *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement I, Trace Fossils and Problematica*. The Geological Society of America and the University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. W1–W269.

Heilmann-Clausen, C., Nielsen, O. B. & Gersner, F., 1985. Lithostratigraphy and depositional environments in the Upper Paleocene and Eocene of Denmark. *Bulletin of the Geological Society of Denmark*, 33: 287–323.

Houmark-Nielsen, M., 1981. Glacialstratigrafi i Danmark øst for Hovedopholdslinien. *Dansk Geologisk Forening, Årsskrift*, 1980: 61–76. [In Danish.]

Houmark-Nielsen, M., 1987. Pleistocene stratigraphy and glacial history of the central part of Denmark. *Bulletin of the Geological Society of Denmark*, 36: 1–189.

Huggett, J., 1993. Petrology and diagenesis of Palaeogene clays from Ølst and Ålbækhoved, Denmark. *Bulletin of the Geological Society of Denmark*, 40: 256–271.

Izumi, K., 2012. Formation process of the trace fossil *Phymatoderma granulata* in the Lower Jurassic black shale (Posidonia Shale, southern Germany) and its paleoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 353–355: 116–122.

Janssen, A. W., Schnetler, K. I. & Heilmann-Clausen, C., 2007. Notes on the systematics, morphology and biostratigraphy of

fossil holoplanktonic Mollusca, 19. Pteropods (Gastropoda, Euthecosomata) from the Eocene Lillebælt Clay Formation (Denmark, Jylland). *Basteria*, 71: 157–168.

Kappel, J., 2002. *Ichnofossilien im Campanium des südöstlichen Münsterlandes*. Doctoral Thesis, Mathematisch-Naturwissenschaftlichen Fakultät der Westfälischen Wilhelms-Universität Münster, 236 pp. http://d-nb.info/968349412/34 [28.01.2015].

Knaust, D., 2013. The ichnogenus *Rhizocorallium*: Classification, trace makers, palaeoenvironments and evolution. *Earth-Science Reviews*, 126: 1–47.

Kotake, N., 1992. Deep-sea echiurans: possible producers of *Zoophycos*. *Lethaia*, 25: 311–316.

Lundgren, B, 1891. Studier öfver fossilförande lösa block. *Geologiska Föreningens i Stockholm Förhandlingar*, 13: 111–121. [In Swidish.]

MacEachern, J. A. & Burton, J. A., 2000. Firmground *Zoophycos* in the Lower Cretaceous Viking Formation, Alberta: A distal expression of the *Glossifungites* ichnofacies. *Palaios*, 15: 387–398.

MacEachern, J. A. & Pemberton, S. G., 1992. Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America. In: Pemberton, S. G. (ed.), *Applications of Ichnology of Petroleum Exploration. A Core Workshop. Society of Economic Paleontologists and Mineralogists*, *Core Workshop*, 17: 57–84.

Maas, O., 1902. Ueber Medusen aus dem Solenhofer Schiefer und der unteren Kreide der Karpathen. *Palaeontographica*, 48: 297–322.

Marck, W., von der, 1858. Ueber einige Wirbelthiere, Kruster und Cephalopoden der Westfälischen Kreide. *Zeitschrift der Deutschen geologischen Gesellschaft*, 10: 231–271.

Marck, W., von der, 1894. *Dreginozoum nereitiforme*, ein vergessenes Fossil der oberen Kreide Westfalens von Dolberg bei Hamm. *Verhandlungen des Naturhistorischen Vereins der preußischen Rheinlande und Westphalens*, 51: 1–9.

Melchor, R. N., Bromley, R. G. & Bedatou, E., 2010. *Spongeliomorpha* in nonmarine settings: an ichnotaxonomic approach. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 100 (for 2009): 1–8.

Michelsen, O., 1994. Stratigraphic correlation of the Danish onshore and offshore Tertiary successions based on sequence stratigraphy. *Bulletin of the Geological Society of Denmark*, 41: 145–161.

Miller, W., III & Vokes, E. H., 1998. Large *Phymatoderma* in Pliocene slope deposits, northwestern Ecuador: Associated ichnofauna, fabrication, and behavioral ecology. *Ichnos*, 6: 23–45.

Nielsen, J. K., Hansen, K. S. & Simonsen, L., 1996. Sedimentology and ichnology of the Robbedale Formation (Lower Cretaceous), Bornholm, Denmark. *Bulletin of the Geological Society of Denmark*, 43: 115–131.

Nielsen, J. K. & Milàn, J., 2014. Trace fossils from the Eocene Lillebælt Clay Formation, Røsnæs (Denmark). In: Milàn, J. & Vallon, L. H. (eds), *One Ichnology, Symposium in honour of Richard G. Bromley and Ulla Asgaard, Eigilsholm, 14.–16. May 2014*. Eigilsholm, p. 21. http://www.ichnopolis.dk/Abstracts.pdf

Osgood, R. G. Jr., 1970. Trace fossils of the Cincinnati area. *Palaeontographica Americana*, 6: 277–444.

Pemberton, S. G., Frey, R. W., Ranger, M. J. & MacEachern, J., 1992a. The conceptual framework of ichnology. In: Pemberton, S. G. (ed.), *Applications of Ichnology of Petroleum Exploration. A Core Workshop. Society of Economic Paleontologists and Mineralogists*, *Core Workshop*, 17: 1–32.

Pemberton, S. G., MacEachern, J. A. & Frey, R. W., 1992b. Trace fossil facies models: environmental and allostratigraphic significance. In: Walker, R. G. & James, N. P. (eds), *Facies Models: A Response to Sea-Level Changes*. Geological Association of Canada, St. John's Newfoundland, pp. 47–72.

Petersen, K. S., 1969. Fossiler og hærdnede spor af liv i eocænt ler fra Røsnæs. *Meddelelser fra Dansk geologisk Forening*, 19: 139–141. [In Danish.]

Petersen, K. S., 1970. Ekskursion til Nordvestsjælland og Røsnæs. *Dansk Geologisk Forening, Årsskrift*, 1969: 71–75. [In Danish.]

Petersen, K. S., 1973a. Some features in clay with tuff-beds from Lower Eocene on Røsnæs, Danmark. *Danmarks Geologiske Undersøgelse, Årbog*, 1972: 69–78.

Petersen, K. S., 1973b. Tills in dislocated drift deposits on the Røsnæs peninsula, northwestern Sjaelland, Denmark. *Bulletin of the Geological Institution of the University of Upsala, New Series*, 5: 41–49.

Petersen, K. S., 1978. Anwendung glaziotektonischer Untersuchungen bei der geologischen Kartierung in Dänemark. *Eiszeitalter und Gegenwart*, 28: 126–132.

Plaziat, J.-C. & Mahmoudi, M., 1988. Trace fossils attributed to burrowing echinoids: A revision including new ichnogenus and ichnospecies. *Geobios*, 21: 209–233.

Radwański, A., Friis, H. & Larsen, G., 1975. The Miocene Hagenør-Børup sequence at Lillebælt (Denmark): its biogenic structures and depositional environment. *Bulletin of the Geological Society of Denmark*, 24: 229–260.

Rasmussen, E. S., Heilmann-Clausen, C., Waagstein, R. & Eidvin, T., 2008. The Tertiary of Norden. *Episodes*, 31: 1–7.

Reich, M. & Klafack, R., 2002. *Dreginozoum* (Gastropoda, Laichkapseln) aus dem Unter-Eozän Mecklenburgs und Pommerns. *Geschiebekunde Aktuell*, 18: 56–60.

Saporta, G. de, 1887. Nouveaux documents relatifs aux organismes problématiques des anciennes mers. *Bulletin de la Société Géologique de France, Series 3*, 15: 286–302.

Schiøler, P., Andsbjerg, J. Clausen, O. R., Dam, G., Dybkjær, K., Hamberg, L., Heilmann-Clausen, C., Johannesen, E. P., Kristensen, L. E., Prince, I. & Rasmussen, J. A., 2007. Lithostratigraphy of the Palaeogene – lower Neogene siliciclastic sediments in the Danish sector of the North Sea. *Geological Survey of Denmark and Greenland Bulletin*, 12: 1–77.

Schlirf, M., 2000. Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica*, 34: 145–213.

Schlotheim, E. F., von, 1822. *Nachträge zur Petrefactenkunde*. Becker'schen Buchhandlung, Gotha, 100 pp.

Schnetler, K. I. & Heilmann-Clausen, C., 2011. The molluscan fauna of the Eocene Lillebælt Clay, Denmark. *Cainozoic Research*, 8: 41–99.

Schwarzhans, W., 2007. Otoliths from casts from the Eocene Lillebælt Clay Formation of Trelde Næs near Fredericia (Denmark), with remarks on the diet of stomatopods. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 246: 69–81.

Seilacher, A., 1951. Der Röhrenbau von *Lanice conchilega* (Polychaeta). Ein Beitrag zur Deutung fossiler Lebensspuren. *Senckenbergiana*, 32: 267–280.

Seilacher, A., 1964. Biogenic sedimentary structures. In: Imbrie, J. & Newell, N. (eds), *Approaches to Paleoecology*. Wiley, London, pp. 296–316.

Seilacher, A., 1967. Bathymetry of trace fossils. *Marine Geology*, 5: 413–428.

Seilacher, A., 1990. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, 3: 289–311.

Seilacher, A., 2007. *Trace Fossil Analysis*. Springer, Berlin, 226 pp.

Serpagli, E., 2005. First record of the ichnofossil *Atollites* from the Late Cretaceous of the northern Apennines, Italy. *Acta Palaeontologica Polonica*, 50: 403–408.

Simpson, S., 1957. On the trace-fossil *Chondrites*. *The Quarterly Journal of the Geological Society of London*, 107: 475–499.

Sorgenfrei, T., 1939. Et geologisk kort over Danmarks prækvartære undergrund. *Meddelelser fra Dansk Geologisk Forening*, 9: 387–412. [In Danish.]

Sternberg, K. M. von, 1833. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*. Johann Spurny, Prague, 2 [parts 5–6]: 1–80.

Strzeboński, P. & Uchman, A., 2015. The trace fossil *Gyrophyllites* in deep-sea siliciclastic deposits of the Istebna Formation (Upper Cretaceous–Palaeocene) of the Carpathians: An example of biologically controlled distribution. *Palaeogeography, Palaeoecology, Palaeoclimatology*, 426: 260–274.

Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria*, 15: 1–115.

Uchman, A., 1998. Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae*, 68: 105–218.

Uchman, A., Caruso, C. & Sonnino, M., 2012. Taxonomic review of *Chondrites affinis* (Sternberg, 1833) from Cretaceous-Neogene offshore-deep-sea Tethyan sediments and recommendation for its further use. *Rivista Italiana di Paleontologia e Stratigrafia*, 118: 313–324.

Uchman, A. & Gaździcki, A., 2010. *Phymatoderma melvillensis* isp. nov. and other trace fossils from the Cape Melville Formation (Lower Miocene) of King George Island, Antarctica. *Polish Polar Research*, 31: 83–99.

Zenker, J. C., 1836. *Historisch-topographisches Taschenbuch von Jena und seiner Umgebung*. Friedrich Frommann, Jena, 338 pp.