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Article *in* Proceedings of the Yorkshire Geological Society · December 2013

DOI: 10.1144/pygs2013-336

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PROCEEDINGS OF THE YORKSHIRE GEOLOGICAL SOCIETY, VOL. 59, PART 4, PP. 227–245, 2013

Endolithic biota of belemnites from the Early Cretaceous Speeton Clay Formation of North Yorkshire, UK

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SUMMARY: The Berriasian–Albian Speeton Clay Formation is renowned for its rich and diverse belemnite fauna. Borings occur in a considerable proportion of the belemnite guards that can be found in the type locality south of Filey, but have never been described. This preliminary survey of the endolithic biota colonizing Speeton belemnites reveals the presence of at least 15 ichnotaxa, including traces made by grazing echinoids (*Gnathichnus pentax*), brachiopod pedicles (*Podichnus centrifugalis*), and a variety of macro- and microendoliths. The commonest macroendolith borings belong to two ichnospecies of *Trypanites* and were probably excavated by polychaete worms. Examples of borings made by other suspension feeding animals, including bivalves (*Gastrochaenolites lapidicus*), acrothoracican barnacles (*Rogerella mathieui*) and sponges (*Entobia*), are less abundant. Among the microendoliths, *Orthogonum* ispp. and *Saccomorpha clava*, both of which are very common, were probably made by fungi, whereas *Semidendrina pulchra* is thought to be the trace of a boring foraminifer. The tentative identification of the microboring *Rhopalia catenata*, which is made by autotrophic chlorophyte algae, suggests that at least some of the Speeton Clay Formation was deposited within the photic zone. Endoliths in the Speeton belemnite guards have future potential for developing a better understanding of the changing environments on the seabed during the long period of deposition of the Speeton Clay.

Belemnites are ubiquitous fossils in the slumped cliffs of Speeton Clay exposed south of Reighton Gap on the Yorkshire Coast. Indeed, Lamplugh (1889) based his subdivision of the Speeton Clay largely on the characteristic belemnite species present through the *c.* 100 m thickness of this Berriasian–Albian formation. The chambered, aragonite phragmocones of the Speeton belemnites are seldom collected. Instead, most specimens are represented only by their bullet-shaped, resistant calcite guards, as is often the case elsewhere in the Jurassic and Cretaceous. In the coastal exposure of the Speeton Clay, these guards may be heavily surface weathered and corroded, perhaps diverting attention away from the presence of numerous borings made by organisms that colonized the belemnite guards when they were resting on the Cretaceous sea-bed. The density and variety of such borings only becomes fully evident when they are cast by resin impregnation and the guards are dissolved in acid to expose the casts. Very few papers have remarked on the presence of borings in Speeton belemnites. An exception is Mitchell's (1992) study of the belemnites across the Hauterivian–Barremian boundary in the Speeton Clay, in which belemnites bored particularly by sponges in the dark glauconitic clay facies, especially C2D, were noted.

The aims of this paper are to provide a preliminary description of the ichnotaxonomic diversity of borings in belemnites from the Speeton Clay Formation, and to explore the potential information they can reveal about palaeoenvironments on the sea-bed during deposition of this Early Cretaceous mudrock sequence. Particular emphasis is placed on illustrating the range of borings encountered in order that this paper can function as an identification guide for any future work on this hitherto overlooked part of the Speeton Clay biota.

1. GEOLOGICAL SETTING

The Speeton Clay Formation (see Rawson 1992) is *c.* 100 m thick at its type locality in Filey Bay on the Yorkshire coast (Fig. 1). This coastal outcrop of the formation is located slightly north of the Market Weighton High, which controlled sedimentation for much of Mesozoic time in the Yorkshire Basin. Deposited through much of the Early Cretaceous, the Speeton Clay rests unconformably on the Late Jurassic Kimmeridge Clay and is overlain by the Late Albian Hunstanton Formation (Red Chalk). At the base of the Speeton Clay is a bed of phosphatic nodules, the so-called Coprolite Bed, indicative of condensation and non-sequence. Higher levels of the formation also give evidence of depositional breaks in the form of phosphate nodules and concentrations of glauconite.

Belemnites were important in the original subdivision of the Speeton Clay by Lamplugh (1889), although the 'beds' he recognized are lithostratigraphical units. Lamplugh's subdivisions begin with the D beds at the base and pass upwards through the C beds, B beds and into the A beds at the top, that is, they are lettered in the reverse of the conventional sequence. The D beds range in age from Late Ryazanian (=Late Berriasian) to Early Hauterivian. They comprise variously glauconitic, pyritic and selenitic clays (Neale & Catt 1994), and contain the large belemnite *Acroteuthis*. At the top is the condensed Compound Nodular Bed. The C Beds above range from Early Hauterivian to Early Barremian in age, and yield the torpedo-shaped *Hibolites jaculoides*, among others species of belemnites. Characterized by the belemnite *Oxyteuthis*, the B Beds are mostly Barremian in age with the top parts deposited in the earliest Aptian. Finally, the A beds of Early Aptian to Late Albian age contain guards of the small belemnite *Neohibolites*.

Danford (1906) published a more complete summary of the distributions and relative abundances of the numerous belemnite species found in the Speeton Clay, accompanied by useful illustrations of the morphology of their guards. Subsequently, Swinnerton (1937, 1948, 1952) comprehensively described these species as part of his monograph of British Lower Cretaceous belemnites.

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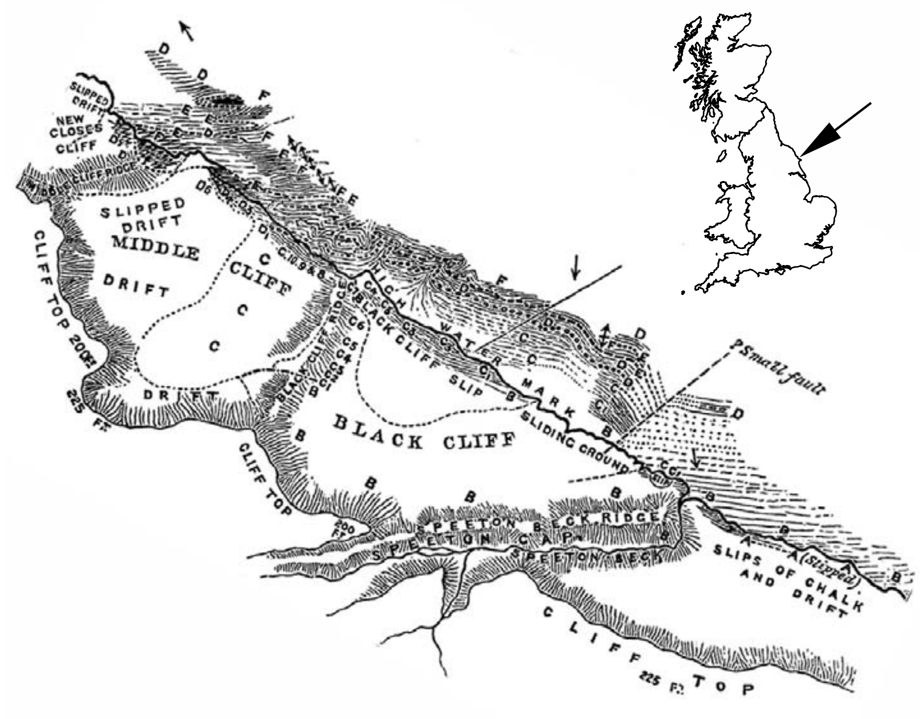

Stage	Zone	Lithostratigraphy	
Albian	*dispar*	Hunstanton Fm.	
	inflatum	Speeton Clay Fm.	A Beds (9 m)
	lautus		
	loricatus		
	dentatus		
	mammillatum		
	tardefurcata		
Aptian	*jacobi*		
	nutfieldensis		
	martinioides		
	bowerbanki		
	dehayesi		
	forbesi		
	fissicostatus		B Beds (40 m)
Barremian	*bidentatum*		
	stolleyi		
	innexum		
	denckmanni		
	elegans		
	fissicostatum		
	rarocinctum		
	variabilis		
Hauterivian	*marginatus*		C Beds (39 m)
	gottschei		
	speetonensis		
	inversum		
	regale		
	noricum		D Beds (14 m)
	amblygonium		
Valanginian	gap		
	Dichotomites		
	Polyptychites		
	Paratollia		
Ryazanian	*albidum*		
	stenomphalus		

Fig. 1. Lamplugh's (1889) map of the cliffs at Speeton, Yorkshire (left); inset of Great Britain marks the location of Speeton with an arrow. The Early Cretaceous stratigraphy of Speeton (right) is modified after Rawson (1992, table 12.2).

2. MATERIAL AND METHODS

The material used in this pilot study was collected by field parties from the Natural History Museum, London (NHMUK), during two visits to Speeton, in October 2009 and March 2011. Because of the poor state of the exposures at the time, it was not possible to ascertain the stratigraphical provenance of most of the belemnite guards picked from the surface of the slumped cliffs. All reasonably preserved guards (several hundred) were collected and taken to the laboratory for cleaning. After discarding heavily weathered or corroded specimens, the cleaned guards were sorted into bored and non-bored categories. Initial examination of the bored guards, which constituted the majority of specimens, was undertaken using a binocular microscope. Specimens exemplifying the range of borings and bioerosional structures visible were selected for detailed study using SEM, for which a LEO 1455-VP scanning electron microscope at the NHMUK was employed. This instrument has the capability of accommodating large, uncoated specimens, operating at low vacuum and using back-scattered electrons (BSE) for image generation. Unlike more conventional secondary electron images, BSE images do not have bright object borders and are more natural in appearance (Taylor & Jones 1996). BSE image intensities are in part dependent on chemical composition, with areas of higher atomic weight (notably pyrite) appearing brighter. This is evident, for example, in the pyrite-filled boring depicted in Figure 15A exposed by the fracturing of a guard.

Twelve belemnites were chosen for resin casting of the borings, a standard technique in the study of endoliths, especially those of small size (e.g. Golubic *et al.* 1975). These guards were cleaned ultrasonically to remove as much sediment as possible from within the borings. Impregnation with Specifix 20 (Strues) epoxy resin overnight under a pressure of 2 bars filled the borings to produce the casts required. After the resin had hardened, the blocks containing the belemnites were cut with a rock-saw, roughly bisecting the embedded belemnites along their lengths. Each half was soaked in domestic acetic acid to dissolve the calcite guard of the belemnite. Beakers containing the blocks were periodically agitated and the acetic acid was replenished when dissolution slowed. Typically, the guards had dissolved completely within a week. The resin blocks were then rinsed and dried, ready for SEM using the same technique as for surface study. Complete casting of all of the borings was not possible because of residual fine-grained sediment within them. Some borings were found to be infilled partly with pyrite, in which case a composite cast of resin and pyrite was obtained (e.g. Fig. 16B).

Figured material has been registered into the trace fossil collection of the NHMUK (prefaced NHMUK PX). Numbers in round brackets after the registration numbers are used when more than one ichnotaxon is present in the same belemnite guard. Unless otherwise indicated by information in square brackets, all specimens come from undifferentiated Speeton Clay Formation in the cliffs between Reighton Gap and Speeton Beck, North Yorkshire.

3. ICHNOTAXONOMY

Rather than trying to order the ichnogenera according to either inferred biological affinities or behavioural characteristics, we deal with the ichnogenera strictly in alphabetical order. Descriptions refer specifically to examples in belemnites from the Speeton Clay Formation, and are not intended to summarize all characteristics of the ichnotaxa across their entire ranges in time and space. In view of the higher degree of subjectivity in identifying ichnotaxa than body fossils, we have deferred from compiling synonymies and instead have cited key references, when appropriate.

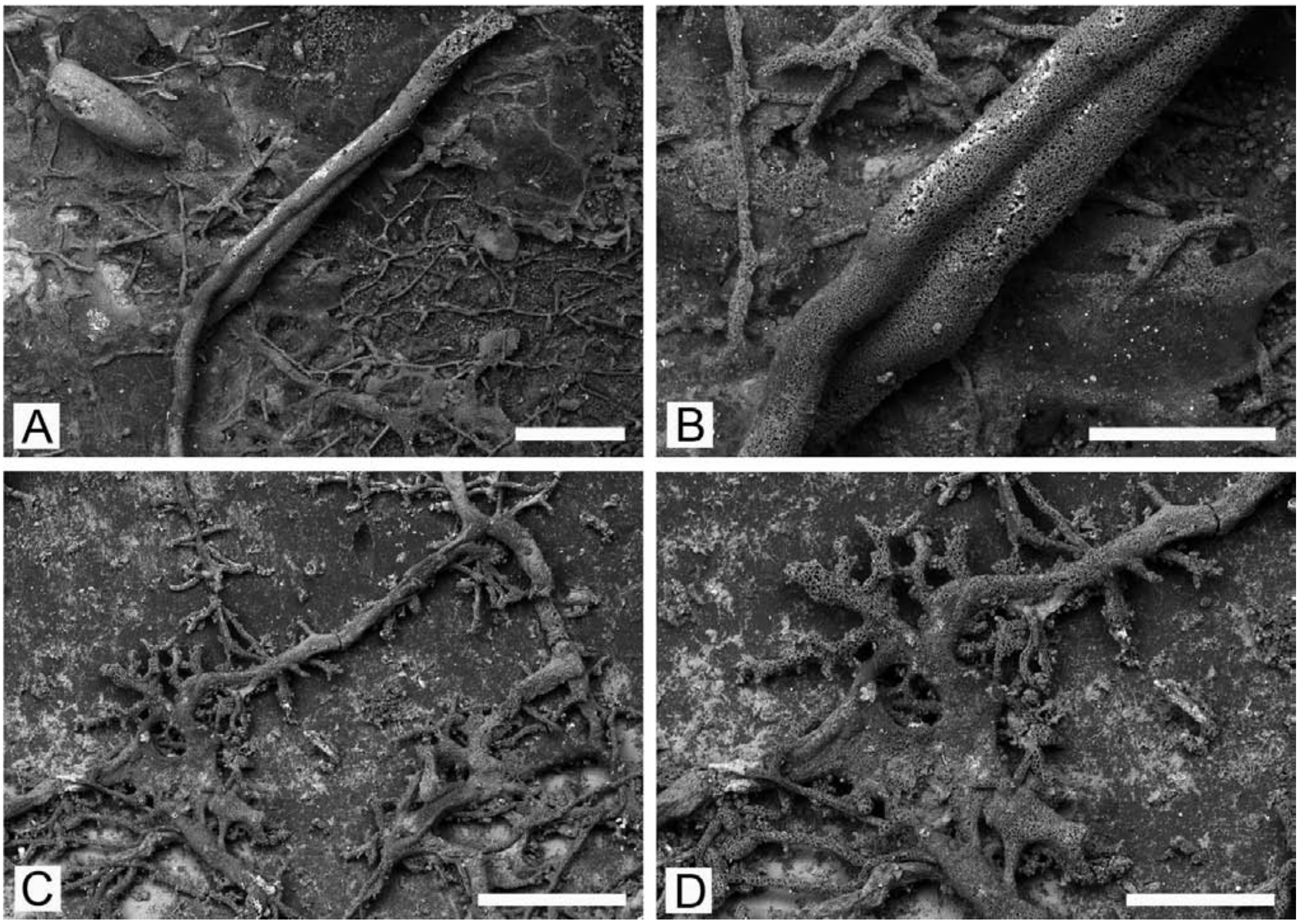

Fig. 2. Resin casts of boring ichnofossils in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**, **B**) *Caulostrepsis*? isp. cf. *C. cretacea* (Voigt 1971), TF 274(1); (**A**), vermiform boring (centre) along with an individual of *Rogerella mathieui* (top left) and fine branches of *Orthogonum tubulare* (best seen in the lower right), scale bar 1mm; (**B**) detail showing twisted axial depression, scale bar 500 μm. (**C**, **D**) *Entobia* sp., TF 275(1); (**C**) primary canals connecting poorly defined galleries (e.g. bottom left), scale bar 1 mm; (**D**) detail of a gallery with small lateral canals, scale bar 500 μm.

Ichnogenus **CAULOSTREPSIS** Clarke 1908

Type species. Caulostrepsis taeniola Clarke 1908. See Bromley & D'Alessandro (1983) for a revision of this ichnogenus, which has a Devonian–Recent range (Bromley 2004, p. 460).

Remarks. Caulostrepsis is used for U-shaped 'worm' borings in which a vane connects the two limbs of the 'U'. The trace is produced by polychaete worms, usually Spionidae ('polydorids') (Bromley 2004). A seemingly two-limbed boring from the Speeton Clay is assigned to *Caulostrepsis* very tentatively because its U-shaped morphology cannot be confirmed as the end of the boring is missing.

***Caulostrepsis*? isp. cf. *C. cretacea* (Voigt 1971)** (Fig. 2A, B)

Material. TF 274(1).

Description. Slightly twisted, incomplete vermiform boring excavated subparallel to the surface of the substrate. A depression runs along one side of the boring, probably matched by one on the opposite side (which is not visible), giving the boring a dumbbell shape in cross section. Preserved length exceeds 5 mm, width is 0.3–0.4 mm.

Remarks. This Speeton boring, preserved as a resin cast, has a slightly twisted shape with an axial depression running the length of the visible side, giving it a strong resemblance to a boring from the Santonian called *Dodecaceria* (?) sp. by Voigt (1970, fig. 6.2). However, the genus *Dodecaceria* is not a trace fossil, but an extant cirratulid polychaete.

There are clear similarities between the Speeton boring and modern *Polydora ciliata* borings figured by Bromley (1970, fig. 4i). The closest match among species of *Caulostrepsis* is with *C. cretacea* (Voigt, 1971) as illustrated, for example, by Rodrigues *et al.* (2008, fig. 6B). Unlike the type species of *Caulostrepsis*, the two limbs of this U-shaped boring remain close together throughout most of their length, as must be the case for the Speeton boring if it is indeed U-shaped (see above).

Ichnogenus **ENTOBIA** Bronn 1837

Type species. Entobia cretacea Portlock 1843. See Bromley & D'Alessandro (1984) for a comprehensive revision of *Entobia* and its constituent ichnospecies.

Remarks. Ranging from Jurassic to Recent (Bromley 2004, p. 459), and possibly back to the Devonian (Tapanila 2006), this clionoid sponge boring is common in calcareous substrates of Cretaceous age.

***Entobia* sp.** (Fig. 2C, D)

Material. TF 275(1) [C Beds, C1–C6].

Description. Branching boring of irregular morphology, spreading in a plane subparallel to the surface of the belemnite substrate;

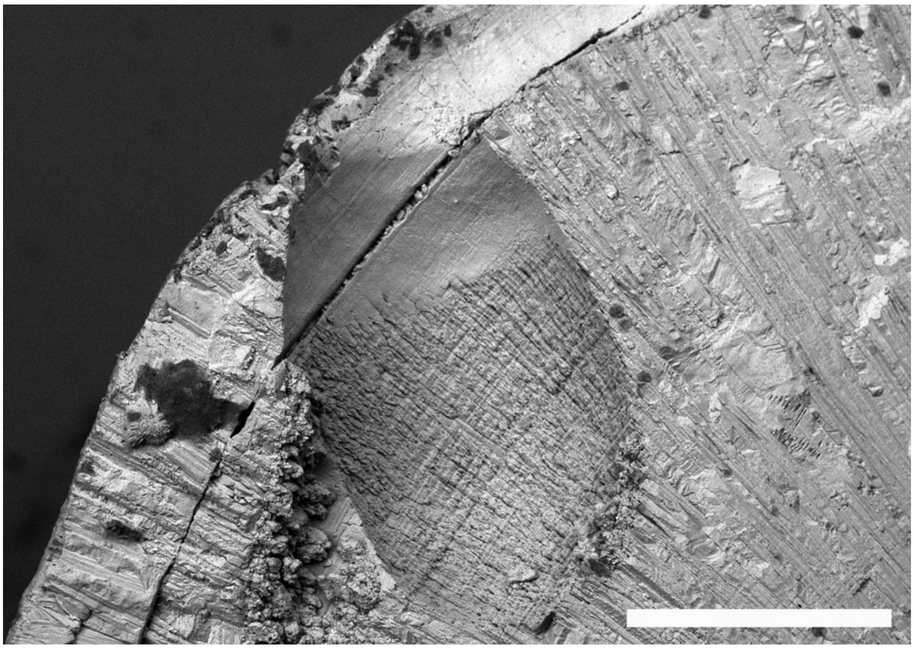

Fig. 3. Bivalve boring *Gastrochaenolites lapidicus* Kelly & Bromley 1984, visible in a fractured belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 276(1). Scale bar 500 μm.

primary canals cylindrical, long, relatively straight, bifurcating, linking galleries and with occasional short and narrow lateral canals; galleries broad, sinuous, flattened, giving rise to a dendritic and reticulate (anastomosing) system of small lateral canals; primary canal width 0.10 mm, galleries 0.20 mm wide, lateral canals as little as 0.06 mm wide.

Remarks. Both in overall morphology and the small size of the chambers, the Speeton boring is most similar to *E. laquea* Bromley & D'Alessandro 1984, among the ichnospecies of *Entobia* described by Bromley & D'Alessandro (1984). As the resin-cast specimen shows only the underside of the boring, no information is available about the apertures that are presumed to open in rows on the surface of the bored belemnite.

Ichnogenus **GASTROCHAENOLITES** Leymerie 1842

Type species. Gastrochaenolites lapidicus Kelly & Bromley 1984; the holotype was described from the Upper Jurassic (Volgian) of Lincolnshire. The genus has been recorded from Ordovician–Recent deposits globally (Bromley 2004, fig. 1).

Remarks. Gastrochaenolites is one of the commonest macroborings found in ancient hard substrates. In the older literature they are commonly referred to as 'lithophagid borings'. However, lithophagids are just one of several groups of mostly bivalve molluscs able to produce these club-shaped traces, including gastrochaenids and pholadids.

***Gastrochaenolites lapidicus* Kelly & Bromley 1984** (Fig. 3)

Material. TF 276(1).

Description. Clavate boring with a subcircular cross section, generally oriented at a high angle to the surface of the substrate; neck region well-delineated from the main chamber of the boring which is larger, round-bottomed and attains a maximum width at approximately mid-length. The best example from Speeton has a total length of 1.26 mm, neck length 0.30 mm, maximum width 0.60 mm, and neck width 0.34 mm. The inner part of the boring preserves a clear xenoglyph of the lamellae and radial fabric of the belemnite guard.

Remarks. Although uncommon in the Speeton Clay belemnites studied here, a few small examples of *Gastrochaenolites lapidicus* have been found resembling those described recently, for example, by Donovan (2013) and Donovan & Jagt (2013). They are more likely to be noticed than most other borings, especially in cases where breakage of the guard is promoted by the boring.

Ichnogenus **GNATHICHNUS** Bromley 1975

Type species. Gnathichnus pentax Bromley 1975, the holotype was described from the Pleistocene of Rhodes. Bromley recorded the range of the genus as Early Jurassic–Recent, but examples of *Gnathichnus* are also known from the Triassic (Fürsich & Wendt 1977; Gibert *et al.* 2007).

Remarks. This trace fossil is typically produced in marine settings by regular echinoids that graze encrusting and boring organisms on hard substrates. The teeth of these echinoids gouge furrows. Grazing echinoids can be powerful agents of bioerosion in modern communities (Bromley 1975), to the extent of being the main producers of so-called intertidal notches along tropical coastlines. In ideal circumstances on flat substrates, each bite leaves a pentaradiate trace of five gouge marks. However, this simple pattern can become obscured when several bites are superimposed (e.g. Radley 2006, fig. 4), or if the substrate has a curved surface and not all five teeth make contact.

***Gnathichnus pentax* Bromley 1975** (Fig. 4)

Material. TF 277.

Description. Pattern of shallow grooves, oriented in various directions, most clearly seen under low-angled light; individual grooves are to 0.5 mm long and about 0.02–0.04 mm wide.

Remarks. While lacking a clearly pentaradiate morphology, the single studied example of this trace from the Speeton Clay leaves no doubt as to its identity. The strong curvature of the grazed belemnite guards biased against the formation of *Gnathichnus pentax* with perfect pentaradial symmetry. Echinoids have seldom been recorded from the Speeton Clay, although Mitchell (1992, p. 129) did note the presence of

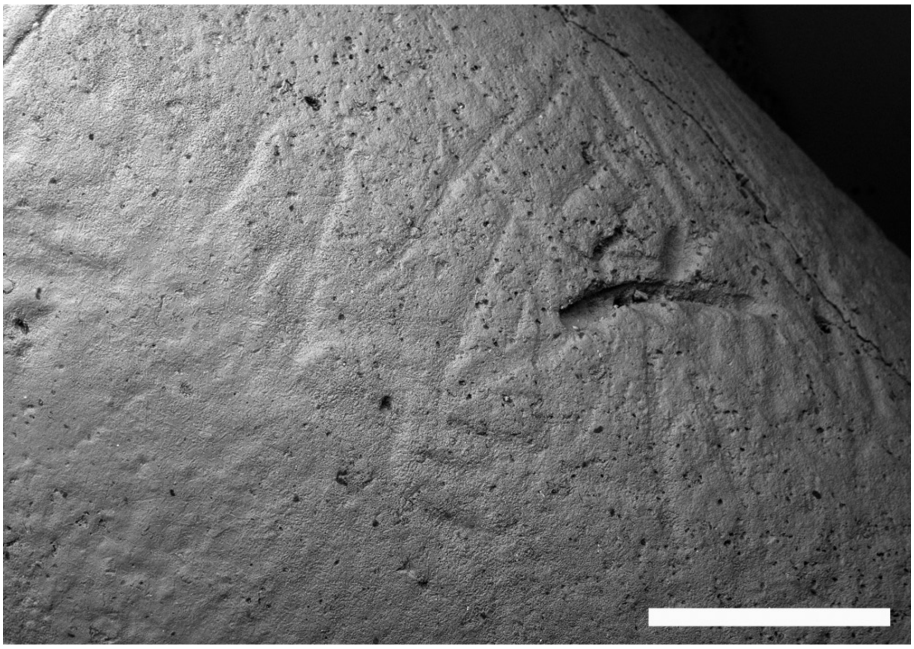

Fig. 4. Echinoid grazing trace *Gnathichnus pentax* Bromley 1975, on the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 277. Scale bar 1 mm.

numerous pyritized echinoids in the upper parts of C3. The occurrence of *G. pentax* has the potential to indicate the presence of regular echinoids even where body fossils are not preserved. Although grazing echinoids were powerful agents of bioerosion in some parts of the Mesozoic (Radley 2010), this was not the case for the Speeton Clay.

Ichnogenus **MAEANDROPOLYDORA** Voigt 1965

Type species. Maeandropolydora decipiens Voigt 1965, first described from the Upper Cretaceous.

Remarks. Revised by Bromley & D'Alessandro (1983), this ichnogenus of worm borings is characterized by having long cylindrical galleries running through the substrate sinuously or in irregular contortions, with two or more apertures. Dichotomous branching may occur. Although *Maeandropolydora* has usually been applied to cylindrical borings, with examples preserved in the form of grooves being due to the loss of half of the original bored substrate (Bromley & D'Alessandro 1983, p. 293), it has also been used by some authors (Bianucci *et al.* 2006) for primarily grooved traces. We here very tentatively assign branched, meandering grooves visible on the external surfaces of some Speeton belemnites to *Maeandropolydora* while acknowledging that further study may necessitate reassignment, possibly to a new ichnogenus. Ranging back at least to the Triassic (Bromley 2004, p. 461), *Maeandropolydora* is believed to be produced by polychaetes (e.g. Parras & Casadio 2006).

***Maeandropolydora* ispp.** (Fig. 5)

Material. TF 278, 279.

Description. Meandering grooves with bifurcations and occasional short lateral extensions, forming a tracery extending across large parts of the surfaces of some belemnites; groove width variable, ranging from about 0.03–0.07 mm.

Ichnogenus **ORTHOGONUM** Radtke 1991

Type species. Orthogonum tubulare Radtke 1991. Originally described from the Palaeogene of Europe, *Orthogonum* ranges from Upper Ordovician–Recent (Vogel & Brett 2009).

Remarks. As pointed out by Bromley (2004, p. 458), this ichnogenus encompasses a heterogeneous set of traces with right-angled branching. Trace-producers of *Orthogonum* living today include heterotrophic fungi and red algae.

***Orthogonum tubulare* Radtke 1991** (Figs 6, 7)

Material. TF 274(3) [C Beds, C1–C6], 275(3) 280, 281(1), 282(1), 283(1) [C Beds, C1–C6], 297 (1), 298 (1).

Description. Network parallel to the surface of the belemnite guard formed of a ramifying system of narrow tunnels branching more or less at right angles. Tunnels are about 15 µm in width and very occasionally appear to bear short filaments less than 1 µm in width on their sides (Fig. 7F). Bulbous swellings developed sporadically, exceptionally up to 50 µm in width, generally forming short side branches (Fig. 7C, F).

Remarks. This is one of the commonest borings in the belemnite guards from the Speeton Clay. Although resin casting is usually required to appreciate the morphology fully, examples of *Orthogonum tubulare* can also be distinguished on the exteriors of guards as delicate traceries with an orthogonal branching pattern (Fig. 6). Bulbous swellings represent sporangia (Fig. 7C, F). Some examples of *O. tubulare* seen in artificial casts grew around the margins of the much larger ichnogenus *Rogerella* (Fig. 11D, E). Shelf-like prolongations of some *O. tubulare* tunnels along laminae in the belemnite guards produced a particular kind of 'halo boring' (see below), modifying the normal morphology of this microendolith (Fig. 7E).

***Orthogonum* isp. cf. *O. fusiferum* Radtke 1991** (Fig. 8)

Material. TF284(1) [C Beds].

Description. Gently curved, seldom branching, boudinaged tunnel that expands and contracts in width along its length from about 20 to 50 µm; larger swellings (up to 150 µm) developed at bends or branching points.

Remarks. A narrow, rarely branching microboring that expands and contracts along its length can be compared to *Orthogonum fusiferum*, even though the swellings are less sharply defined in the Speeton ichnospecies than in at least some other material

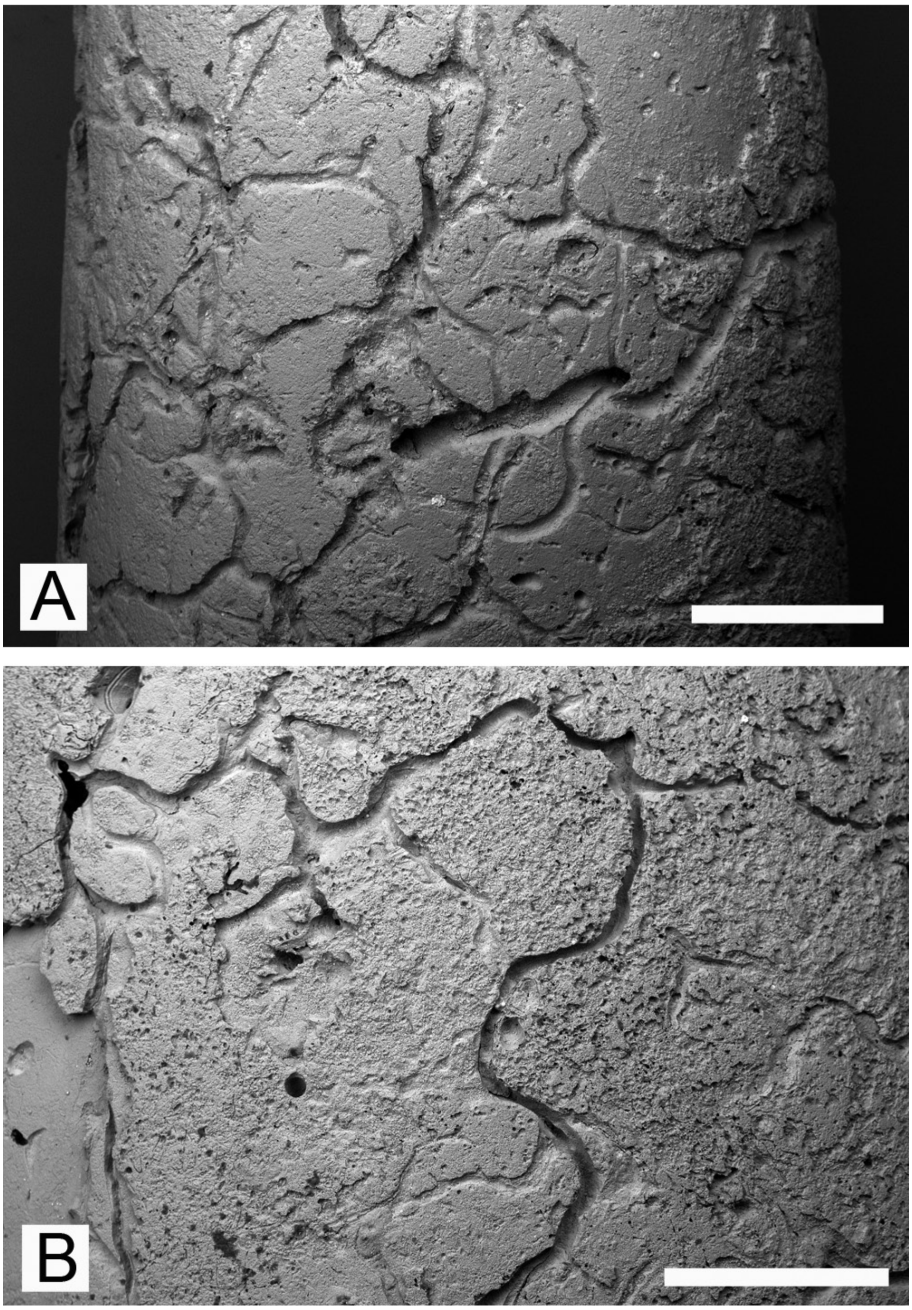

Fig. 5. *Maeandropolydora*? isp. on the surfaces of belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**) TF 278. (**B**) TF 279. Scale bars 1 mm.

assigned to *O. fusiferum* (e.g. Golubic *et al.* 2005, fig. 1b; Vogel & Brett 2009, fig. 20).

Ichnogenus **PODICHNUS** Bromley & Surlyk 1973

Type species. *Podichnus centrifugalis* Bromley & Surlyk 1973, originally described from the Upper Cretaceous (Campanian) Chalk of Norwich, but since recorded from Ordovician–Recent deposits globally (Bromley 2004, p. 464; Vogel & Brett 2009).

***Podichnus centrifugalis* Bromley & Surlyk 1973** (Fig. 9)

Material. TF 285 [C Beds], 286(1).

Description. Clusters of approximately 65 shallow pits in a circular to slightly elliptical grouping of 0.9–1.0 mm in overall diameter. Each pit has a strongly bevelled edge, is subcircular in outline shape and measures up to 83 μm in diameter, pit diameter being characteristically larger on the edge of the grouping than in the centre where their diameter may be as little as 30 μm. The distance between pits is roughly equal to their diameter.

Remarks. As shown by Bromley & Surlyk (1973) in their original description, *Podichnus centrifugalis* is the trace left by pedically attached brachiopods, each pit representing where one of the filaments (or rootlets) of the pedicle etched into the substrate. Brachiopods, with the exception of infaunal lingulids, are not a well-known element of the Speeton biota, although the presence of terebratulids has been noted in the Speeton Clay (e.g. Harper *et al.* 2005, p. 220).

Ichnogenus **RHOPALIA** Radtke 1991

Type species. Rhopalia catenata Radtke 1991. Originally described from the Eocene, this ichnogenus is now known to range down to the Carboniferous (Wisshak *et al.* 2008).

Fig. 6. Photograph of the fungal boring *Orthogonum tubulare* Radtke 1991, visible immediately beneath the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire; TF 280. Scale bar 1 mm.

Remarks. Radtke & Golubic (2005, p. 125) published a revised diagnosis in English of the type species of this ichnogenus: "A system of straight branched tunnels extending parallel to the substrate surface (shell) from a single point of origin, with spherical to clavately or ellipsoidal swellings located at branch points or terminally and linked with the substrate surface with thin rhizoidal connections." More than one tracemaker may be responsible, including the septate chlorophyte algae *Phaeophila* (Radtke & Golubic 2005) and *Eugomontia* (Golubic & Radtke 2008).

***Rhopalia* isp. ?*R. catenata* Radtke 1991** (Fig. 10)

Material. TF 287.

Description. System of borings in the form of narrow bifurcating branches radiating from a central origin. The borings are apparently located immediately beneath the substrate surface and grew parallel to it. Branches are divisible into club-shaped units, wider and deeper at their distal ends further away from the centre of the system. The length of individual units is 80–90 µm, with a minimum width (proximal) of 4 µm and a maximum width (distal) of up to 20 µm.

Remarks. Several individuals of this ichnospecies have been observed on the abraded exterior of a single belemnite guard. The boring has not been cast, which in part accounts for its questionable identification as the expected thin rhizoidal connections to the exterior cannot be observed.

Compared with the holotype of *R. catenata* (see Radtke 1991, pl. 9, figs 1–2), the swellings along the branches of the Speeton microboring are more asymmetrical, the units having a pyriform shape rather than the more beaded appearance seen in the cast of the holotype. However, Wisshak *et al.* (2008, p. 37) noted the variability of this ichnospecies and the Carboniferous specimens illustrated by them lack the beading apparent in the holotype.

Ichnogenus **ROGERELLA** Saint-Seine 1951

Type species. Rogerella lecointrei Saint-Seine 1951, Cretaceous of Marne, France. The oldest record of this extant ichnogenus is from the Late Ordovician (Vogel & Brett 2009).

Remarks. Tomlinson (1969) and Lambers & Boekschoten (1986) have provided useful reviews of boring acrothoracican barnacles and the trace fossils produced by them, which are usually referred to the ichnogenus *Rogerella*.

***Rogerella mathieui* Saint-Seine 1955** (Fig. 11)

Material. TF 274(2), 282(2), 288, 289(1).

Description. Boat-like or 'short sock'-shaped borings, oriented perpendicularly to the substrate; elongate, with one end sloping more shallowly than the other; opening on the substrate surface smaller than the maximum cross-sectional size of the boring, teardrop-shaped with one end pointed and the other rounded, 0.4–1.2 mm long by 0.15–0.25 mm wide; chamber measuring 1.1–1.7 mm long by about 0.4 mm wide and 0.8 mm deep.

Remarks. The palaeoecology of acrothoracican barnacle borings was summarized by Seilacher (1968, 1969). Some examples that he described, penetrating Late Jurassic and Early Cretaceous belemnites belonging to the genera *Hibolites, Neohibolites* and *Duvalia*, were found to be distributed over the entire surface of the guard and oriented in parallel to one another and the long axis of the guard. This led Seilacher (1968) to conclude that the barnacles infested living belemnites swimming above the sea-bed that had a reduced coverage of soft tissue on the guard in the adult stage. However, this hypothesis has not won much support. None of the Speeton examples show circumferential distribution patterns or parallel orientations and there is no evidence for a life association between the barnacles and belemnites.

Lukeneder (1999) also described Early Cretaceous belemnites containing *Rogerella* from Austria. Compared to the Speeton Clay examples, the Austrian borings appear to be present in greater densities on the belemnite guards; the group of closely spaced *Rogerella* on the Speeton belemnite shown in Figure 11A is notable for being unusual.

Ichnogenus **SACCOMORPHA** Radtke 1991

Type species. Saccomorpha clava Radtke 1991. Originally described form the Palaeogene of Europe, this ichnogenus ranges from Upper Ordovician–Recent (Vogel & Brett 2009).

Remarks. Tiny club-shaped borings, interconnected by very thin filamentous tunnels in at least some examples, were placed by Radtke (1991) in her new ichnogenus *Saccomorpha*. The clubs

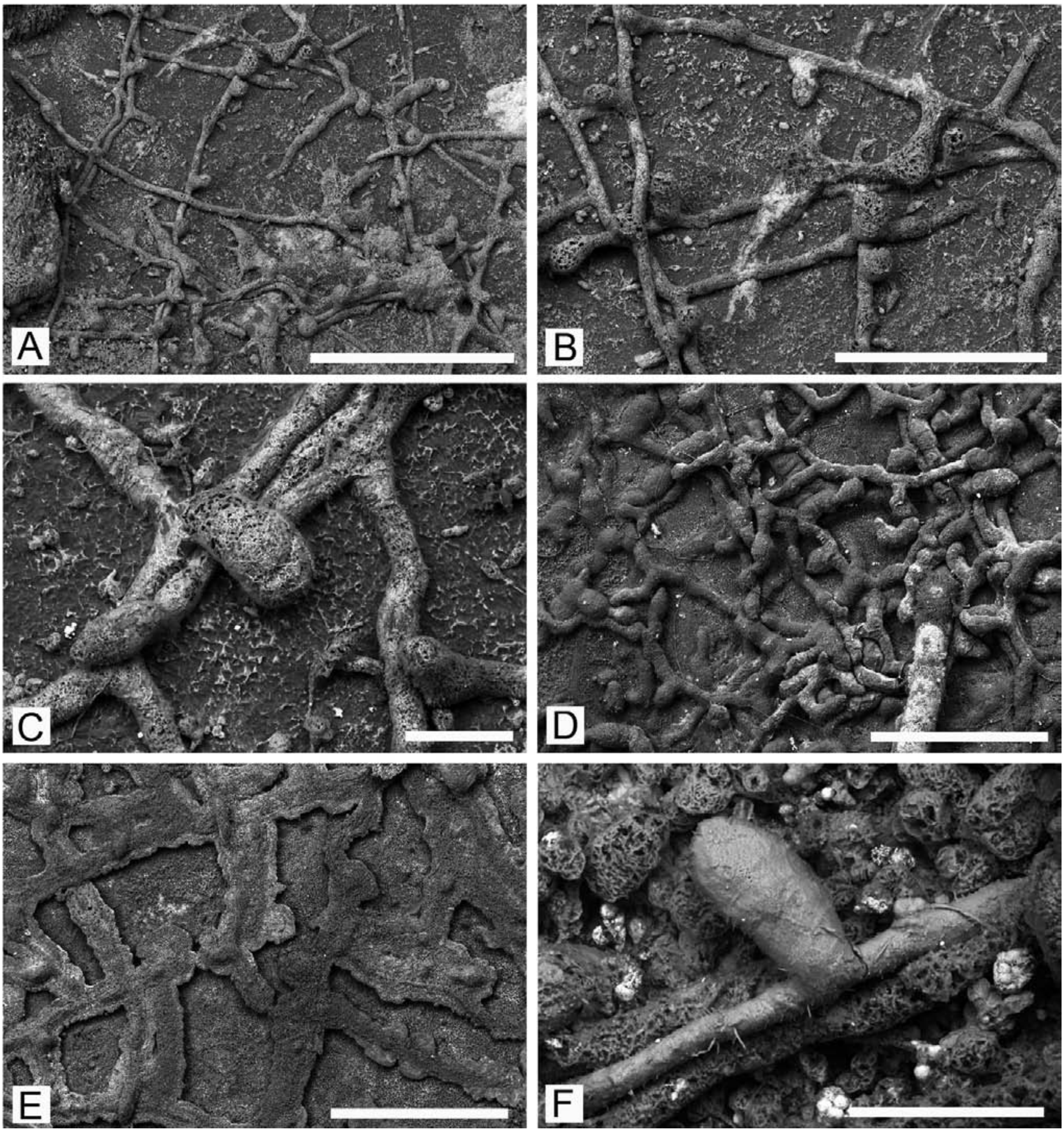

Fig. 7. Resin casts of the fungal boring *Orthogonum tubulare* Radtke 1991, in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**–**C**) TF 281(1); (**A**) rectilinear network of branches, scale bar 1mm; (**B**) detail of branches and bulbous swellings, scale bar 500 µm; (**C**) bulbous swelling (fruiting body), scale bar 100 µm. (**D**–**E**) TF 282(1); (**D**) mass of branches and swellings, scale bar 500 µm; (**E**) branches enlarge by shelf-like haloes resulting from etching along laminae in the belemnite guard, scale bar 500 µm. (**F**) TF 283(1), branch and swelling, the former with short filaments, scale bar 100 µm.

are sporangial swellings of endolithic fungae, especially *Dodgella*, with the filaments linking them being the hyphae (e.g. Golubic *et al.* 2005).

Saccomorpha clava **Radtke 1991** (Fig. 12)

Material. TF 283(2) [C Beds, C1–C6], 289(2) [C Beds, C1–C6], 281(2), 297(2).

Description. Simple, club- or flask-shaped borings of minute size, about 20 µm in diameter. Most are oriented approximately perpendicular to the substrate surface; they are often clustered and some have associated, very narrow, thread-like tunnels of 2–3 µm width.

Remarks. This ichnofossil has been observed only in resin-cast material; its small size would undoubtedly make it difficult to distinguish on the surfaces of belemnite guards. It often co-occurs with *Orthogonum tubulare*.

Ichnogenus **SEMIDENDRINA** Bromley, Wisshak, Glaub & Botquelen 2007

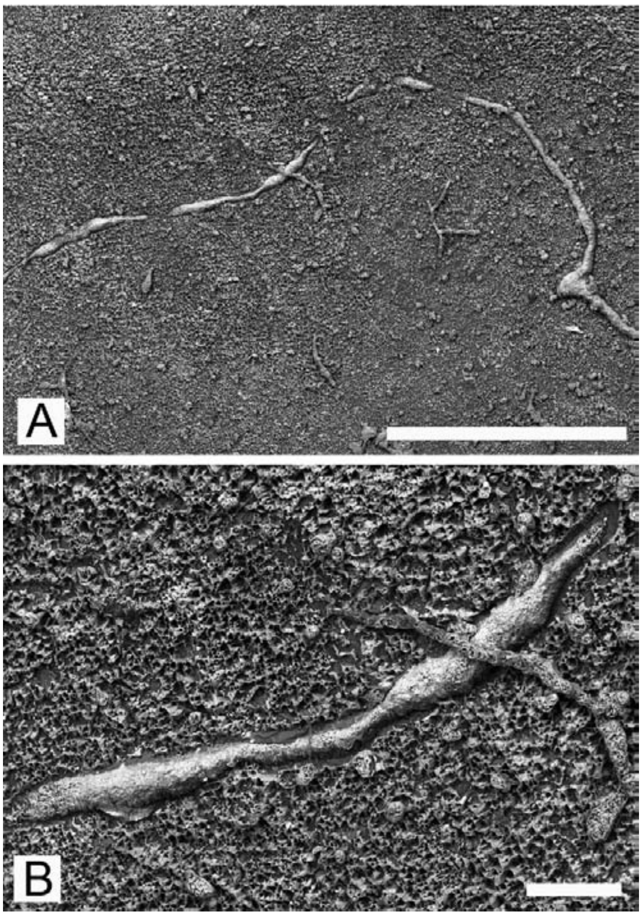

Fig. 8. Resin casts of *Orthogonum* cf. *fusiferum* Radtke 1991, in a belemnite guard from the C Beds, Speeton Clay Formation of Speeton, Yorkshire, TF 284(1). (**A**) general view of part of a gracile boring with swelling on the right, scale bar 1 mm. (**B**) detail of boudinaged branch, scale bar 100 µm.

Type species. Semidendrina pulchra Bromley, Wisshak, Glaub & Botquelen 2007, Jurassic (Oxfordian), Villers-sur-Mer, France.

Remarks. Small dendritic or rosette-like borings are a common component of endolithic biotas and have been found in calcareous substrates as far back as the Ordovician. Bromley *et al.* (2007) introduced the ichnofamily Dendrinidae to encompass such traces, including eight genera of which their new genus *Semidendrina* was characterized by its fan-shaped plexus of branching galleries issuing from one side of a large main chamber.

It is generally considered that foraminifera are the producers of dendritic borings such as *Semidendrina*. Indeed, Cherchi & Schroeder (1991) discovered tests of foraminifera within borings subsequently identified by Bromley *et al.* (2007) as *Semidendrina pulchra*. A putative foraminiferan, *Globodendrina monile*, described by Plewes *et al.* (1993) from the Oxford and Kimmeridge clays, is a body fossil that includes a *Semidendrina* boring beneath an agglutinated collar around the aperture. Nevertheless, Bromley *et al.* (2007) failed to find any examples of foraminiferan tests within the extensive material of *S. pulchra* that they studied and consequently questioned the identity of the *Semidendrina* tracemaker.

Semidendrina pulchra Bromley, Wisshak, Glaub & Botquelen 2007 (Fig. 13)

Material. TF 284(2) (C Beds), 290, 291, 292(1) (C Beds, C1–C6), 298(2).

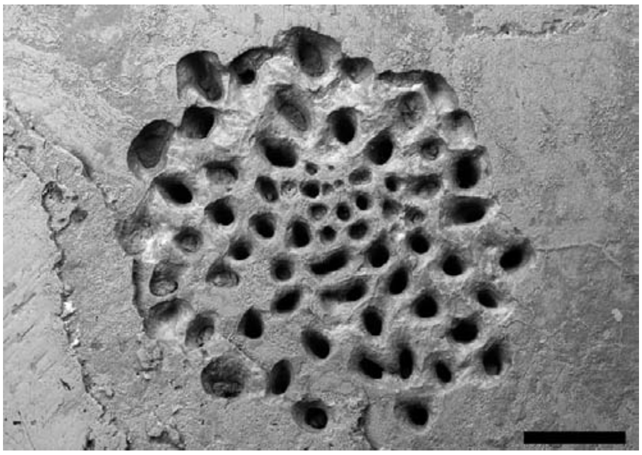

Fig. 9. Brachiopod pedicle trace *Podichnus centrifugalis* Bromley & Surlyk 1973, on the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 285. Scale bar 500 µm.

Description. Small, shallow boring consisting of a main chamber giving rise to a fan-like system of branching galleries on one side. The main chamber is oriented perpendicularly to the surface of the substrate and opens in a subcircular aperture on the surface. In the Speeton examples, the main chamber is about 50–110 µm in diameter and appears to have a rounded base. The fan of galleries is oriented parallel to and just beneath the surface of the belemnite, covering an area of 635–730 µm by 200–345 µm. A short tunnel connects the main chamber to the galleries, which bifurcate irregularly and become narrower towards their ends.

Remarks. Aggregations of *Semidendrina pulchra* are evident on some of the Speeton belemnites (Fig. 13A). Adjacent borings can be very closely spaced, with intergrowing gallery systems. The orientation of the borings (i.e., which side of the main chamber they originate) varies between individuals in these clusters. Examples of resin-cast borings may contain a considerable amount of pyrite, with framboids occasionally almost completely infilling the galleries but lacking in the main chamber (Fig. 13D).

Ichnogenus **SULCICHNUS** Martinell & Domènech 2009

Type species. Sulcichnus maeandriformis Martinell & Domènech 2009. Late Miocene–Recent.

Remarks. This ichnogenus was introduced by Martinell & Domènech (2009) for long bioerosional grooves running along the substrate surface in a sinuous or contorted pattern. The three ichnospecies described by these authors were all found on corallites of fossil scleractinian corals and were probably produced by symbiotic eunicid polychaete worms etching into the skeletons of their hosts. *Sulcichnus* is applied here for bioerosional grooves found in Speeton belemnites with some reservation in view of the contrast in substrates (belemnites vs. corals) and geological age (Cretaceous vs. Neogene). Furthermore, the Speeton trace fossil is straighter than those described by Martinell & Domènech (2009) and smaller in width.

***Sulcichnus*? isp.** (Fig. 14)

Material. TF 286(2).

Description. Unbranched groove of semicircular cross-section, curving slightly; preserved length 5 mm, width about 0.2 mm,

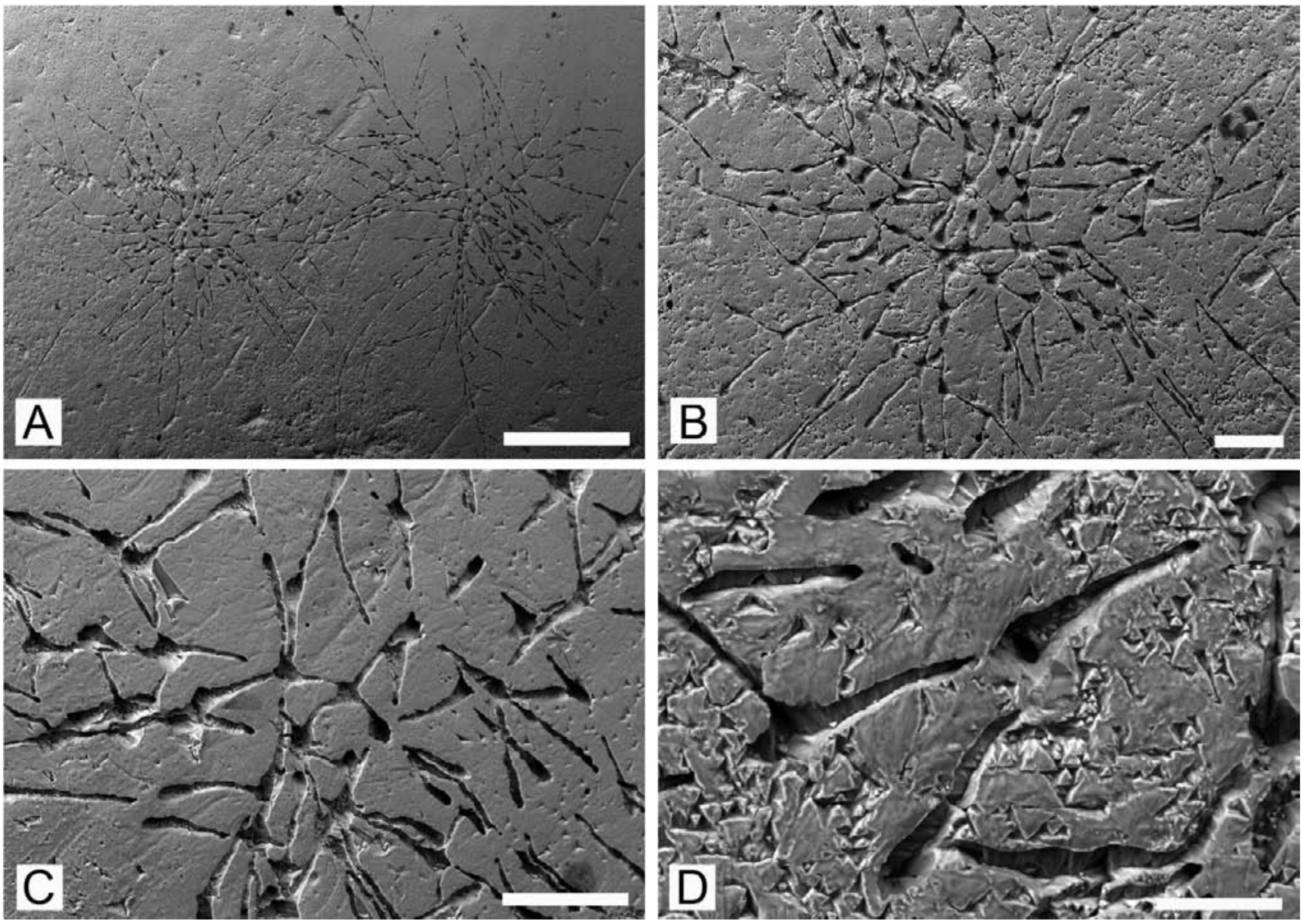

Fig. 10. *Rhopalia* isp. ?*R. catenata* Radtke 1991, interpreted as the trace of a green alga, exposed on the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 287. (**A**) two adjacent examples, scale bar 500 µm. (**B**) branches composed of club-shaped units, scale bar 100 µm. (**C**), detail of branches, scale bar 100 µm. (**D**) club-shaped units at branch bifurcation, scale bar 50 µm.

varying slightly along the length of the boring; presumed proximal end missing, distal end rounded.

Remarks. Although this trace somewhat resembles a bisected *Trypanites* boring, it is evidently a groove with a semicircular cross-section rather than a cylindrical boring with an originally circular cross-section that has been exposed by loss of the upper layers of the substrate. It is possible that during life the tracemaker constructed an unfossilized roof to make a tubular dwelling, as in some spionid worms. For example, the spionid responsible for the groove-like ichnogenus *Helicotaphrichnus*, which occurs in gastropod shells tenanted by hermit crabs, secretes a roof of agglutinated sediment particles (Kern *et al.* 1974; Darrell & Taylor 1989). Alternatively, the tracemaker may simply have occupied a mucus tube, as is the case for the modern *Sulcichnus*-producing worms illustrated by Martinell & Domènech (2009, fig. 5).

Ichnogenus **TRYPANITES** Mägdefrau, 1932

Type species. Trypanites weisei Mägdefrau, 1932, originally described from the Muschelkalk (Triassic) of Germany.

Remarks. An extremely common boring, *Trypanites* was revised by Bromley (1972) and diagnosed as follows (p. 95): “Simple, unbranched borings in hard substrate with a single opening to the surface”. The ichnogenus ranges from Cambrian–Recent (Bromley 2004, p. 461).

There appear to be two ichnospecies of *Trypanites* present in the Speeton belemnites, differing in size, including diameter, and straightness. The larger diameter (0.35–0.40 mm) boring is straighter and best matches the type species *T. weisei*, whereas the smaller diameter (0.10–0.20 mm) boring, which is commoner, is often curved and can be placed in *T. solitarius* (Hagenow 1840). Both Speeton ichnospecies have somewhat swollen ends, but are insufficiently dilated to favour transfer to an alternative ichnogenus, *Palaeosabella* (see Wilson 2007, fig. 20.3).

Trypanites weisei **Mägdefrau 1932** (Fig. 15)

Material. TF 275(2) [C Beds, C1–C6], 293.

Description. Cylindrical boring, straight; longest complete example measuring 10.2 mm; diameter of boring 0.35–0.40 mm, increasing slightly towards the rounded end; typically entering the belemnite at a low angle (<45°); laminae of the belemnite may be reproduced as xenoglyphs on the walls of the boring.

Remarks. Two differences exist between these borings and *T. weisei* as redescribed by Bromley (1972), which is oriented vertically with respect to the substrate surface and is roughly twice the diameter of the Speeton borings. Pickerill *et al.* (2002) also noted that *T. weisei* is consistently perpendicular to its substrate, thereby raising some doubts about the correct identification of the Speeton boring.

Trypanites solitarius (**Hagenow 1840**) (Fig. 16)

Material. TF 276(2), TF 282(3), 292(2) [C Beds, C1–C6], 294.

Description. Cylindrical boring, usually slightly curved, with flexures typically occurring at laminae in the belemnite substrate;

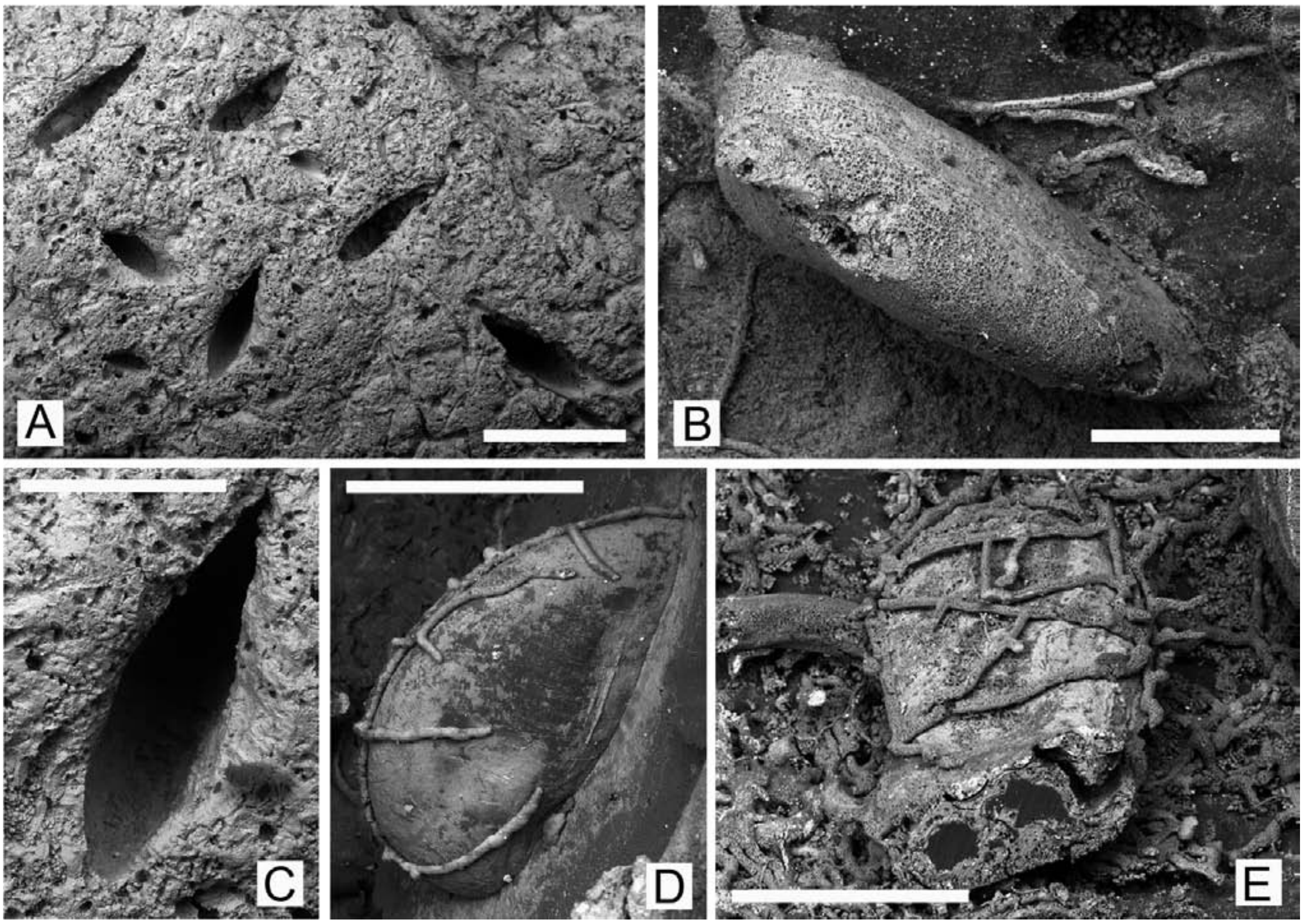

Fig. 11. *Rogerella mathieui* Saint-Seine 1955, an acrothoracican barnacle boring, in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**, **C**) TF 288; (**A**) group of openings on the guard surface, scale bar 1 mm; (**C**) elongate teardrop-shaped opening, scale bar 500 µm. (**B**) resin cast of boring, TF 274(2), scale bar 500 µm. (**D**) profile of resin cast of boring boring surrounded by *Orthogonum tubulare*, TF 282(2), scale bar 1 mm. (**E**) oblique view of resin cast of boring also surrounded by *O. tubulare*, TF 289, scale bar 1 mm.

longest complete example measuring 2.2 mm; diameter of boring 0.10–0.20 mm, increasing slightly towards the rounded end; entering belemnite substrate at varying angles, from acute to perpendicular.

Remarks. Trypanites solitarius was first used for borings in Upper Cretaceous belemnites, but has since been recorded from other substrates (Bromley 1972). The curved shape of the boring is characteristic. Examples from Speeton are substantially smaller than those cited in Bromley's revised diagnosis of the ichnospecies, measuring one-fifth to one-tenth of the diameter. Indeed in diameter, overall shape and orientation with respect to the surface of the substrate, they resemble borings figured by Radtke (1991, pl. 4, fig. 2) as *Caulostrepsis cretacea* (Voigt), but are likely not that species as they lack evidence of being two-limbed (cf. Fig. 2A, B).

Multiple examples of this small species of *Trypanites* may penetrate the same belemnite guard and can be quite closely spaced (Fig. 16C). One or a few ring-like halo structures (Fig. 16D, E) may be evident around the cylindrical casts of *T. solitarius*, formed by dissolution of belemnite laminae centred on the boring.

Un-named euendolith (Fig. 17)

Material. TF 286(3).

Remarks. Tiny borings, less than 1 µm in diameter, became evident during SEM study of one of the belemnite guards. These borings form clusters of straight, radiating, filament-like tunnels, ranging from perpendicular to subparallel to the substrate surface. The minute size of the borings suggests their formation by a bacterial group. Indeed, they resemble the boring *Eurigonum nodosum* Schmidt made by the cyanobacterium *Mastigoleus testarum* Lagerhein as illustrated by Cherchi *et al.* (2012). In the absence of casts, we defer a more precise identification of this trace fossil.

4. PALAEOECOLOGY AND PALAEOENVIRONMENTS

4.1. Trophic groups

Four major trophic groups are responsible for the borings found in the belemnite guards from the Speeton Clay Formation: (1) suspension feeding animals; (2) grazing animals; (3) decomposers; and (4) autotrophs.

The suspension feeders used the guards as protective domiciles from which to feed on particles in the water column. However, in the case of *Podichnus*, the anchorage trace of a brachiopod pedicle, the guard provided no protection for the suspension-feeding animal above. The other suspension feeding ichnogenera at Speeton (with their likely producers in brackets) are: *Caulostrepsis* (polychaete), *Entobia* (sponge), *Gastrochaenolites* (bivalve), *Maeandropolydora* (polychaete), *Rogerella* (barnacle), *Semidendrina* (foraminiferan), *Sulchichnus* (polychaete) and *Trypanites* (polychaete). All of these animals required regular access to the exterior for feeding. With the

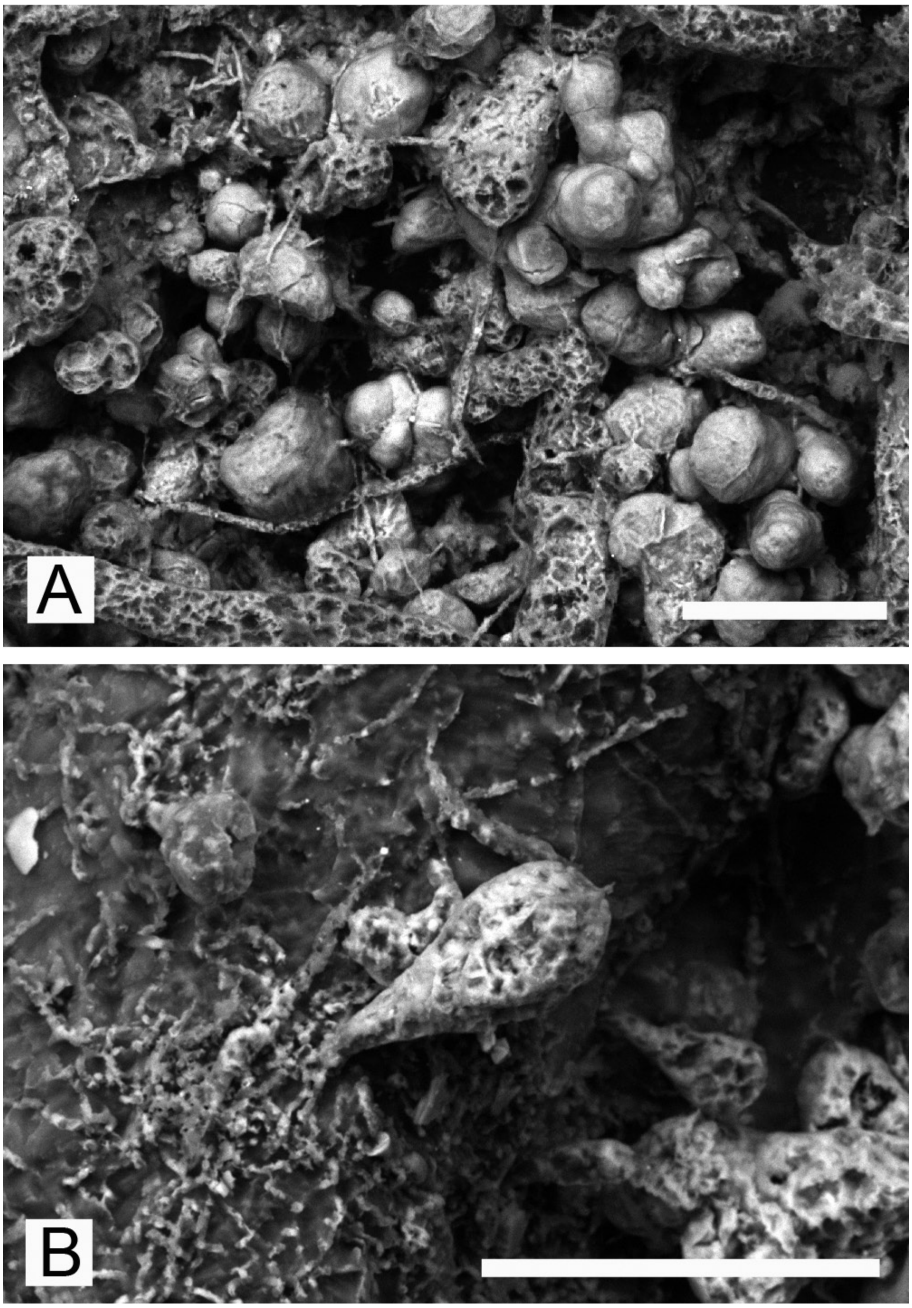

Fig. 12. Resin casts of *Saccomorpha clava* Radtke 1991, made by fungi in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**) cluster of flask-shaped borings, TF 289(2). (**B**) flask-shaped boring in profile, TF 281(2). Scale bars 50 μm.

exception of the tracemaker of the large *Trypanites weisei*, none bored deeply into the belemnite guards and instead are concentrated close to the surface.

Only one grazing trace, *Gnathichnus*, was recognized on the Speeton belemnites. This ichnogenus comprises the gouge-like scrapings made by the teeth of regular echinoids that fed on the animals and plants living either on the surface of the substrate or boring shallowly into it.

Two ichnogenera of endoliths present at Speeton, *Orthogonum* and *Saccomorpha*, were probably made by fungi, which are decomposers. They are among the most common ichnogenera detected in the Speeton belemnites, sometimes growing around the larger borings such as *Trypanites* and *Rogerella* (Fig. 11D, E). Like the majority of the borings made by suspension feeding animals, these endolithic fungi bored close to the surface of the belemnite guards. The implication is that they were subsisting on organic matter derived either from the other shallow boring organisms or the exterior. If these fungi had utilized inter- or intracrystalline organic matter remaining within the belemnite guards, they would be expected to have penetrated deeper into the guards. In this respect, the Speeton belemnites differ from some Late Jurassic bored belemnites recently described by Reolid & Benito (2012) in which endoliths penetrate deeply into the guards.

Apart from a possible cyanobacterial boring (Fig. 17), only one ichnogenus made by an autotroph, *Rhopalia* (Fig. 10), has been provisionally identified in the Speeton belemnite guards. *Rhopalia* was probably made by a chlorophyte alga.

4.2. Bioerosion and halo structures

Boring organisms contribute to the destruction of hard substrates through bioerosion (e.g. Wilson 2007). For example, Underwood

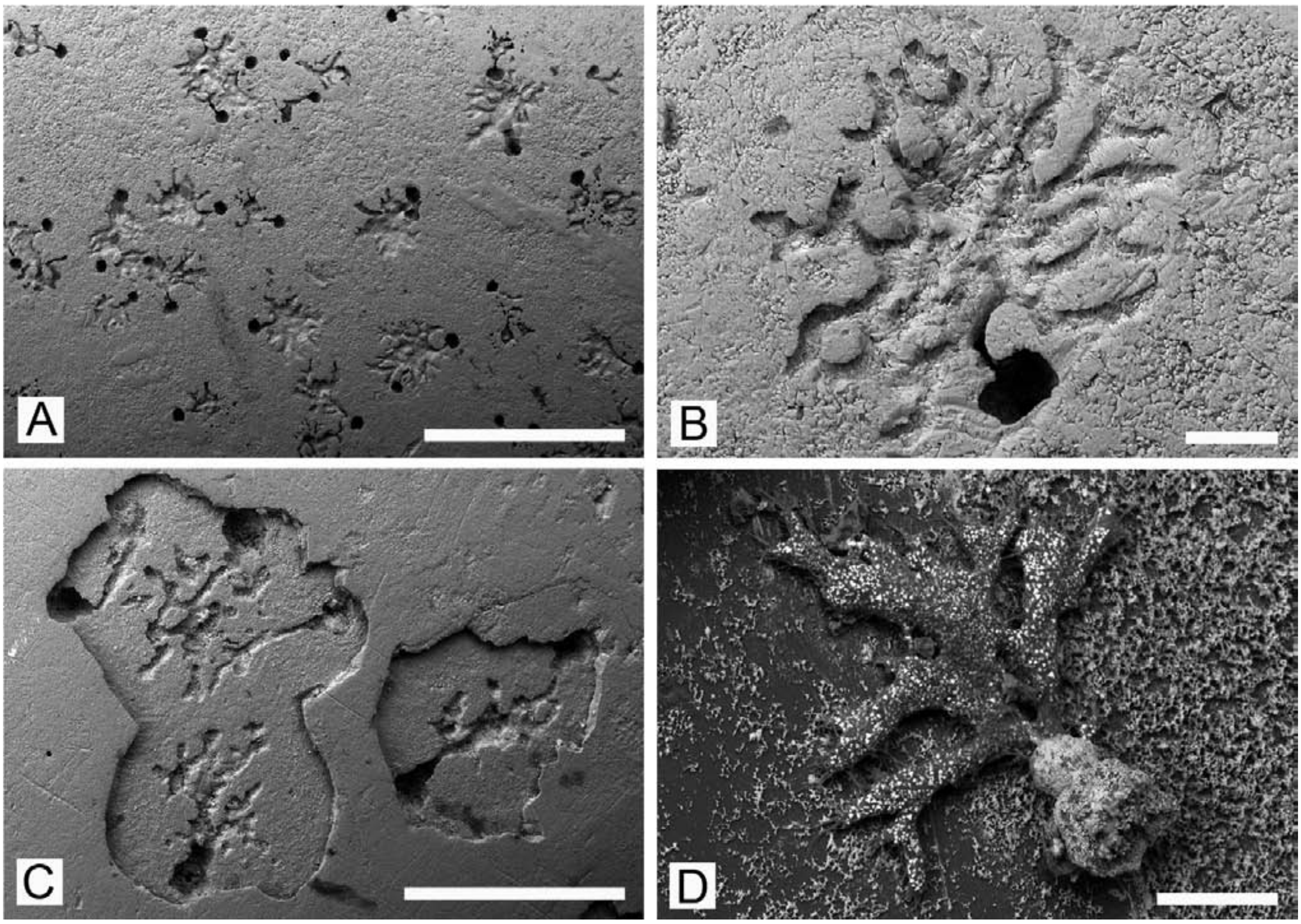

Fig. 13. *Semidendrina pulchra* Bromley, Wisshak, Glaub & Botquelen 2007, a probable foraminiferan boring, in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A, B**) TF 290; (**A**) group of individuals, scale bar 1 mm; (**B**) single individual showing main chamber (lower right) and dendritic pattern of branching galleries, scale bar 100 µm. (**C**) several individuals exposed by exfoliation of laminae from a belemnite guard, TF 291, scale bar 500 µm. (**D**) resin cast of an individual boring with sediment-filled main chamber (lower right) and dendritic branches filled partly by resin and partly by pyrite (bright spots), TF 292(1), scale bar 100 µm.

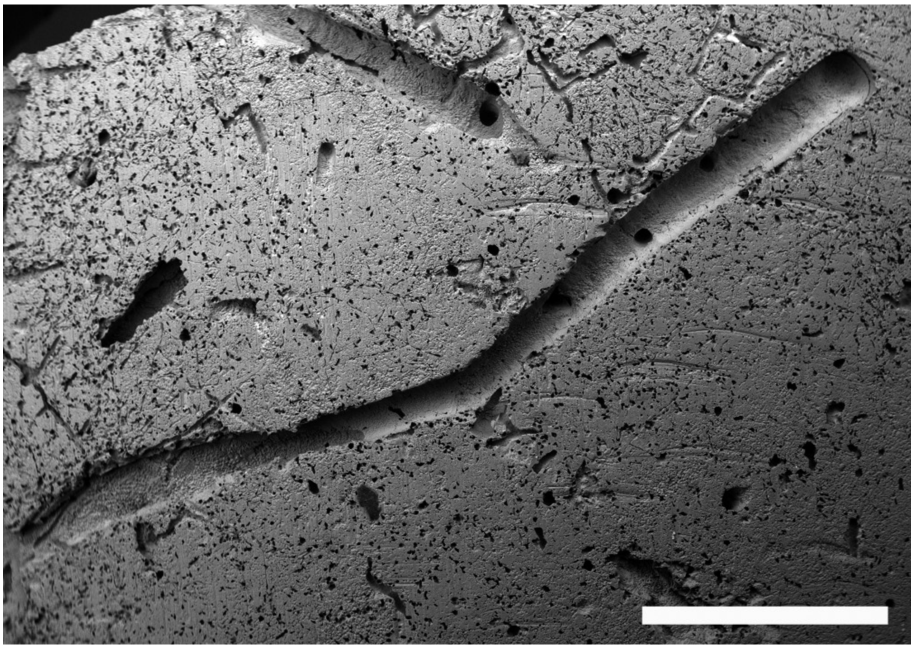

Fig. 14. Groove-like trace *Sulcichnus*? isp. on the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 286(2), scale bar 1 mm.

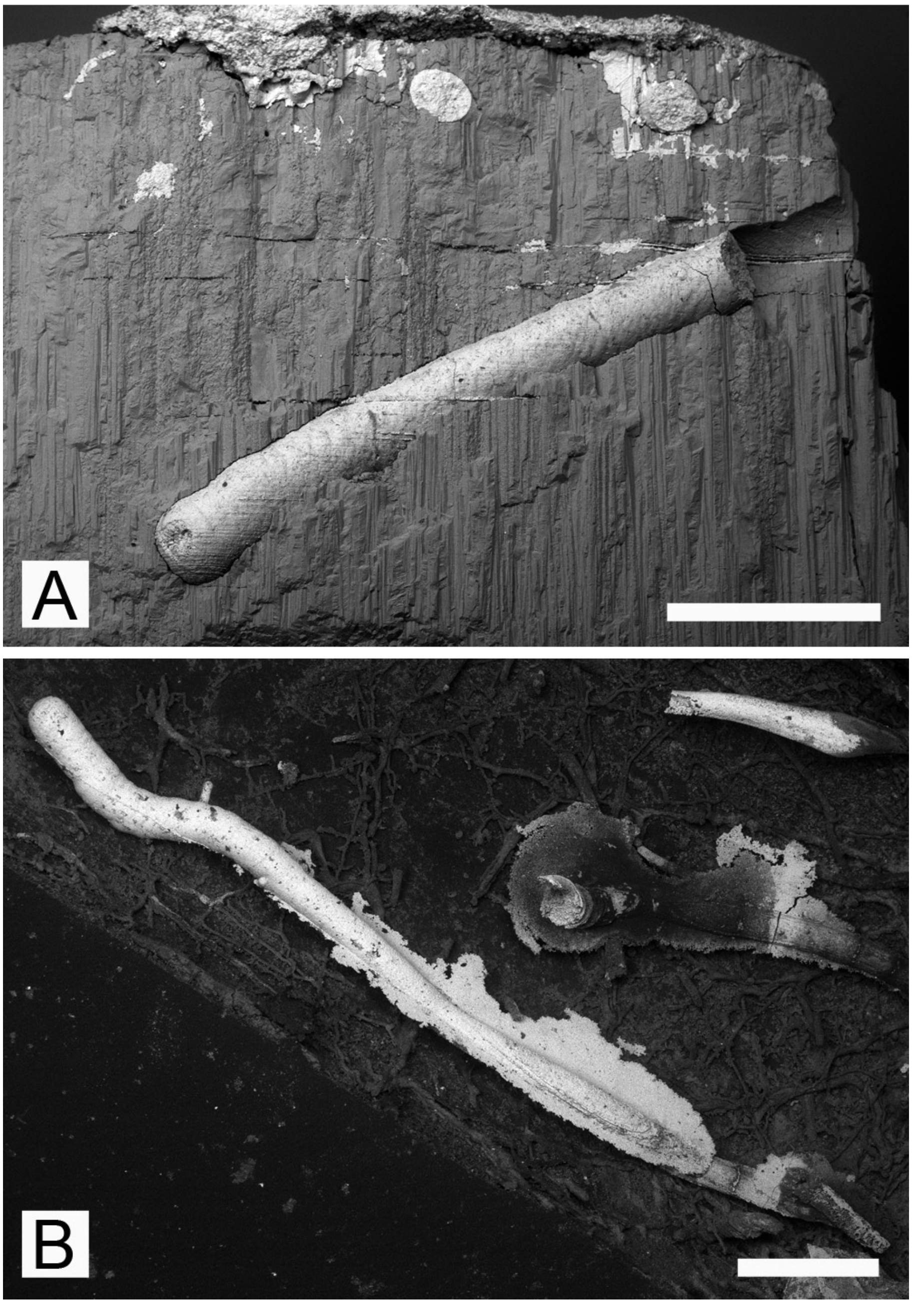

Fig. 15. *Trypanites weisei* Mägdefrau 1932, in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**) fractured guard exposing boring infilled by pyrite, TF 293, scale bar 1 mm. (**B**) resin cast with worm boring mostly infilled by pyrite; note, shelf-like prolongation of the pyrite (halo) which evidently extended into lamellae of the guard (exterior of belemnite is bottom left), TF 275(2), scale bar 1 mm.

et al. (1999) considered that microboring of fish teeth from the Speeton Clay and other Cretaceous formations could lead to taphonomic loss of these vertebrate fossils. Not only does bioerosion cause substrate deterioration, but it also generates sediment, usually in the form of micrite when calcareous substrates are attacked. Different levels of bioerosion are apparent in the belemnite guards from the Speeton Clay (Fig. 18). Dense microboring close to the surface of the guards (Fig. 19) promoted exfoliation of the outer layers of the guards. Exposure of formerly subsurface borings on the outer surfaces of the guards (e.g. Fig. 13C) is a consequence of such exfoliation. Grazing on the shallow endoliths by echinoids (and possibly other organisms) is another source of bioerosion of the Speeton belemnites (Fig. 4). Occasional larger borings may also have led to weakening and eventual breakage of guards, although this phenomenon seems not to be widespread among Speeton Clay belemnites.

Structures here termed 'haloes' are a notable feature of the Speeton belemnite guards. Haloes are pale, almost circular patches on the surface of the belemnite guard centred on a boring (Fig. 20). Some halo structures have concentric bands of different tone. Despite being very conspicuous when guards are studied with a hand lens or optical microscope, the same haloes are invisible under SEM. This shows that the haloes are subsurface rather than surface features. Resin casting confirms their subsurface locations and shows the haloes to be thin, planar extensions of the borings along laminae in the belemnite guards. Often only one halo is developed as a collar-like structure around each boring (Fig. 16E), but two or more may be present in successive laminae of the guard (Fig. 16D). Borings oriented parallel to the belemnite laminae have haloes in the form of flanges running along the length of the boring (Fig. 15B). In the case of the branching trace fossil *Orthogonum tubulare*, the halo forms a shelf-like structure extending outwards from the sides of the branches (Fig. 7E).

Understanding the origin of haloes necessitates consideration of the structure and mineralogy of the belemnite guard. These biomineralized structures are composed of low-magnesium calcite, which

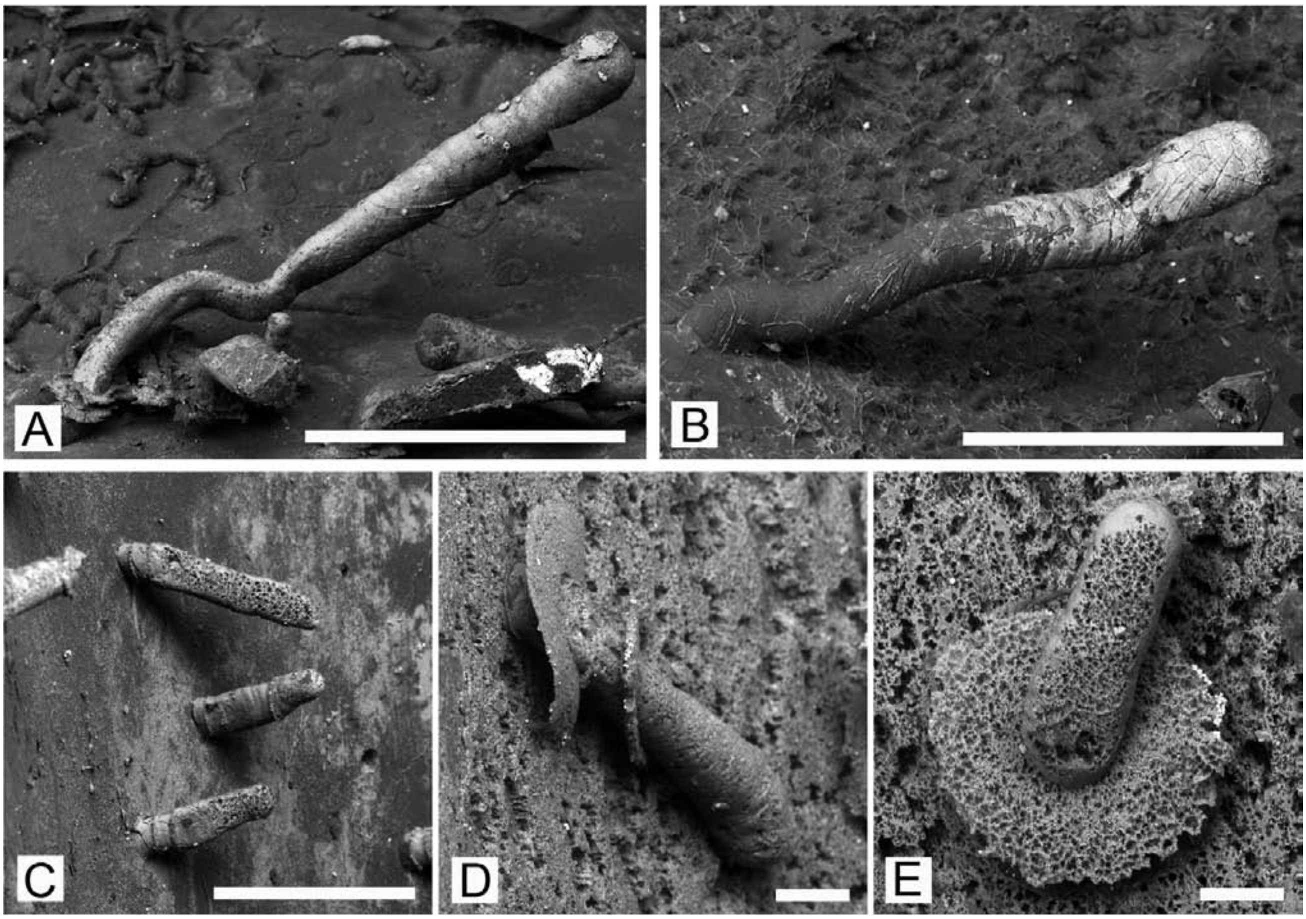

Fig. 16. Resin casts of *Trypanites solitarius* (Hagenow 1840) in belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**) long, slightly curved boring at a low angle to the surface of the substrate, TF 282(3), scale bar 1 mm. (**B**) another low-angled boring cast by pyrite near the rounded end, TF 294, scale bar 1 mm. (**C–E**) TF 292(2); (**C**) three borings penetrating the guard almost perpendicularly, scale bar 500 μm; (**D**) boring with two collar-like halos, scale bar 100 μm; (**E**) boring with collar-like halo, scale bar 100 μm.

is generally regarded as representing their primary mineralogy, notwithstanding evidence for aragonitic guards in *Goniocamax* from the Turonian (Dauphin *et al.* 2007). In the most comprehensive study of belemnite guard structure, Saelen (1989) described the dominant radial crystalline fabric, which is oriented perpendicularly to the surface of the guard and may be either original or diagenetic in origin (see O'Neill *et al.* 2003). The radial structures are intersected by concentric growth bands, comprising alternations of organic-rich and organic-poor laminae, the latter typically thicker. Halo structures observed around the Speeton borings appear to penetrate the thin organic-rich laminae of the guards and represent localized dissolution of these layers. The timing of this dissolution is uncertain. One possibility is that it occurred concurrently with boring, by 'leakage' of the demineralizing fluids produced by the endoliths laterally along organic-rich laminae. A second is that the haloes were formed during diagenesis, with the empty borings acting as conduits along which pore waters could attack the organic-rich laminae of the belemnite guard. Further research is needed to discriminate between these two options. Should the first hypothesis be correct, the haloes are primary structures, i.e. they are parts of the borings themselves. If so, the combined boring and halo arguably qualify for new ichnotaxon names.

4.3. Palaeobathymetry

Microendoliths have attracted considerable interest because of their potential as palaeobathymetrical indicators (Vogel *et al.* 1995, 1999; Glaub *et al.* 2007; Perry & Macdonald 2002). Light is the most important single determinant of microendolith distribution. Different communities of microendoliths therefore characterize different depths, with shallow-water communities that inhabit the photic zone containing autotrophs as well as heterotrophs, whereas communites from deeper water lack autotrophs and consist only of heterotrophs.

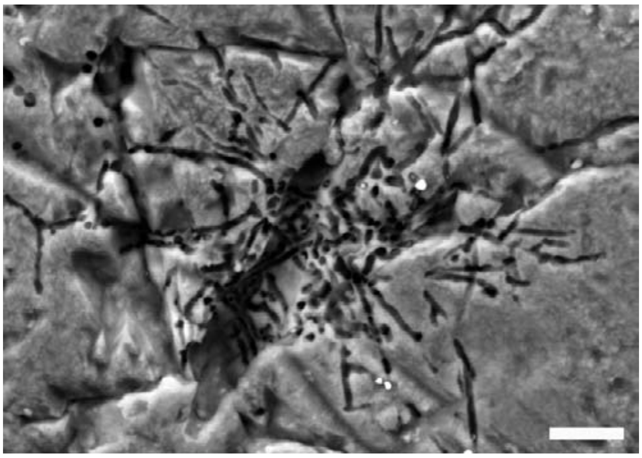

Fig. 17. Un-named euendolith (?cyanobacterial) on the surface of a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 286(3), scale bar 10 μm.

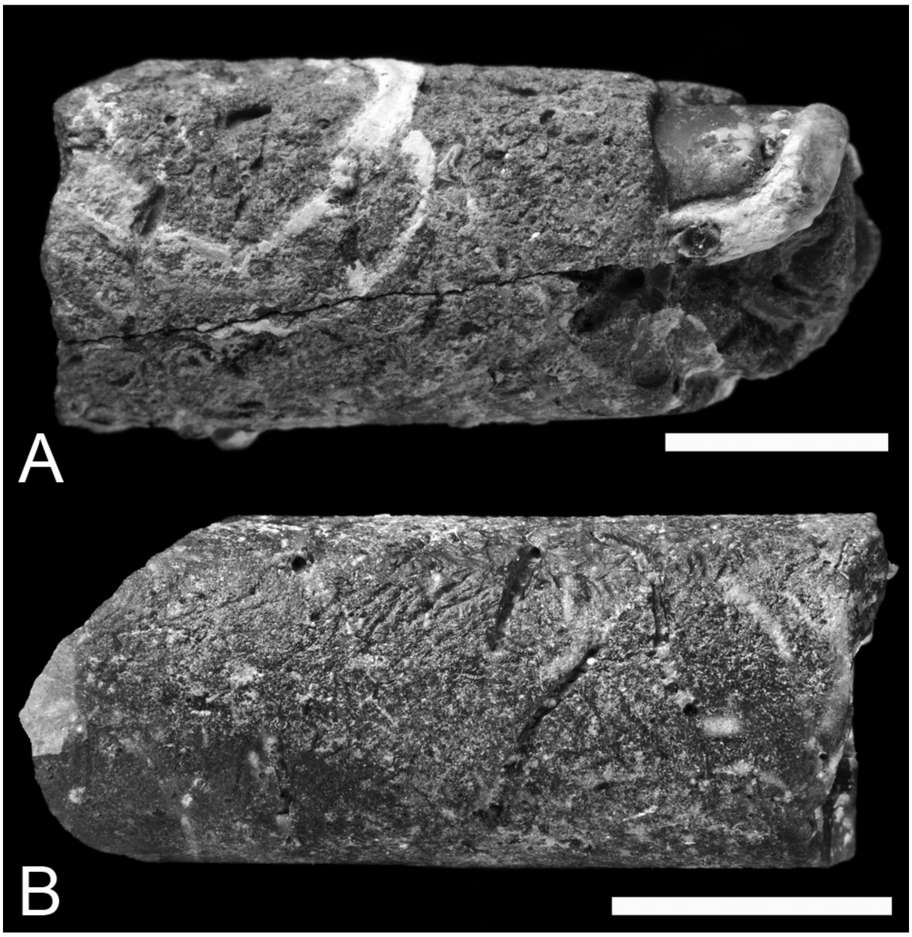

Fig. 18. Broken, bioeroded belemnite guards from the Speeton Clay Formation of Speeton, Yorkshire. (**A**) guard fragment with old borings overgrown by a serpulid worm (right), TF 294. (**B**) biocorroded guard fragment, TF 295. Scale bars 5 mm.

The microendoliths described here from Speeton Clay belemnites are dominantly heterotrophs, suggesting that most of the belemnite guards were deposited beneath the photic zone. However, the occurrence of the probable green algal boring *Rhopalia* in a few belemnite guards points to shallower water deposition within the photic zone for these examples at least, unless boring occurred while the belemnites were floating in the photic zone, which seems unlikely.

5. CONCLUSIONS

Jurassic and Cretaceous belemnite guards were commonly bored after death of the cephalopods and decay of the soft tissue investment (e.g. Pugaczewska 1965; Hölder 1972; Hillmer & Schulz 1973; Ghare 1982; Lambers & Boekschoten 1986; Lukeneder 1999; Reolid & Benito 2012). Boring taxa are far more numerous than are encrusting taxa on the Speeton belemnites; the latter, which await description, tend to be poorly preserved and consist mainly of foraminifers belonging to at least two genera, along with rarer serpulid worms (Fig. 18A), anomiid bivalves and bryozoans. The experience of one of us (PDT) with Mesozoic sclerobionts suggests that this pattern of endolith dominance is not unique to the Speeton Clay, but may characterize the majority of sclerobiont communities associated with belemnite guards.

The diverse endobionts recorded here in belemnite guards from the Speeton Clay Formation include most of the ichnotaxa typical of Mesozoic hard substrates. However, there are two notable absentees. *Talpina*, a ramifying boring attributed to a *Phoronis ovalis*-like phoronid worm (see Voigt 1975), is relatively common in the Jurassic and Cretaceous, but has not been found in the Speeton belemnites. Also common elsewhere in the Mesozoic, but not detected at Speeton, are borings made by ctenostome bryozoans (Pohowsky 1978). Phoronids and bryozoans are both lophophorate suspension feeders that may have been deterred by turbid bottom conditions and heavy concentrations of particulate sediment.

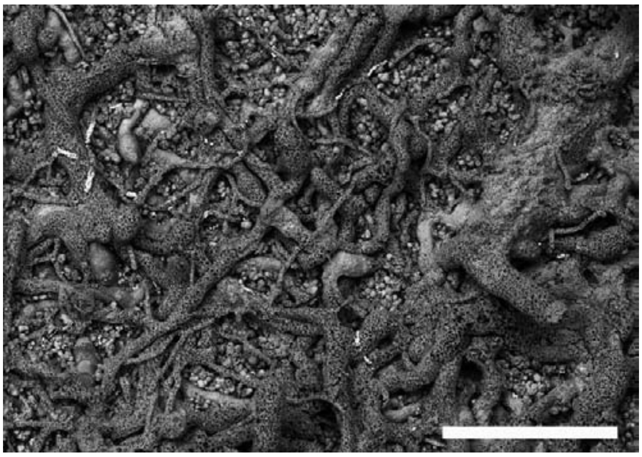

Fig. 19. Resin casts of dense microborings in a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 289.

The excellent preservation of the Speeton Clay belemnite guards and their endoliths provides ample opportunities for future more detailed investigations. For example, spatial relationships between different ichnotaxa of endoliths permit the order in

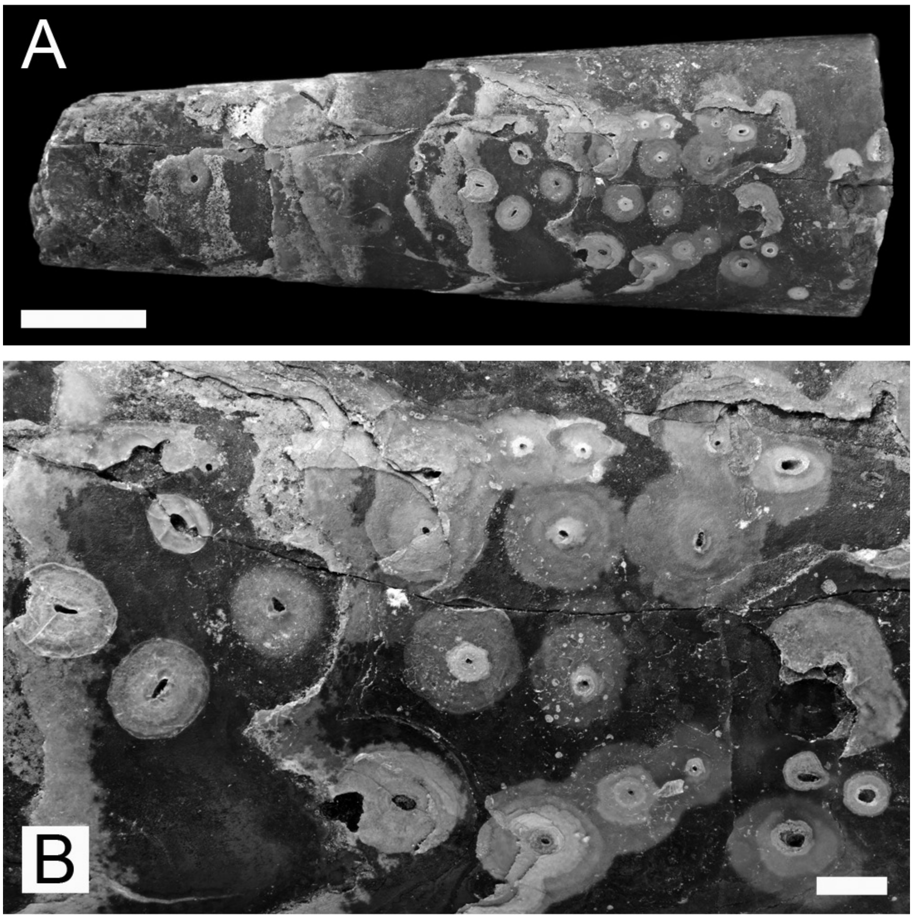

Fig. 20. Halo structures visible around borings on a belemnite guard from the Speeton Clay Formation of Speeton, Yorkshire, TF 296. (**A**) haloes in a partly exfoliated guard, scale bar 5 mm. (**B**) detail showing haloes with concentric rings of different tone, scale bar 1 mm.

which they colonized individual guards and hence ecological succession to be inferred. Late-stage borings either crosscut earlier borings, or follow their outlines, as is the case of the *Orthogonum* growing around the margins of *Rogerella* (Fig. 11D, E). Because each belemnite guard provides a replicate substrate island (see Taylor & Wilson 2003), the degree to which the succession of endoliths is predictable could be investigated. Also worthy of study are: associations between particular ichnotaxa; the spatial patterning of borings around individual guards and its relevance to the stability of guards on the sea-bed; and whether the identity of the host belemnite has any effect on the endoliths present.

Further research is needed to ascertain the stratigraphical distributions of the endoliths. This would best be done through bed-by-bed collecting of the seldom-available foreshore exposures of the Speeton Clay. Any variations detected in the distributions of these geologically long-ranging ichnotaxa will reflect fluctuations in palaeoenvironmental parameters (e.g. depth, illumination, turbidity) rather than evolutionary changes during the *c.* 40 ma duration of discontinuous deposition of the Speeton Clay Formation. The potential use of microendoliths in palaeoenvironmental analysis has been previously demonstrated (summarized by Glaub *et al.* 2007), and they may be of particular value in mudrock sequences where informative sedimentary structures can be less evident.

Acknowledgements. We are especially grateful to Peter Rawson and John Hudson for guiding a field party from the NHMUK to Speeton during October 2009, and to the following members of this and a subsequent party in March 2011 for helping with the collection of belemnites: Emanuela Di Martino, Tim Ewin, Luanne Faulkner, Sue Greene, Hilary Ketchum, Claire Mellish, Rory Milne, Noel and Solene Morris, Martin Munt, Lindsey Percival, Lil Stevens and Jeremy Young. Tony Wighton embedded belemnites for the purpose of casting the borings. We benefitted greatly from discussions with Gudrun Radtke, Mark Wilson and Tim Palmer.

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Revised manuscript received: 14th August 2013
Scientific editing by Steven Donovan