

Engineering the Cambrian explosion: the earliest bioturbators as ecosystem engineers

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Abstract: By applying modern biological criteria to trace fossil types and assessing burrow morphology, complexity, depth, potential burrow function and the likelihood of bioirrigation, we assign ecosystem engineering impact (EEI) values to the key ichnotaxa in the lowermost Cambrian (Fortunian). Surface traces such as *Monomorphichnus* have minimal impact on sediment properties and have very low EEI values; quasi-infaunal traces of organisms that were surficial modifiers or bioturbators, such as *Planolites*, have moderate EEI values; and deeper infaunal, gallery bioturbative or upward-conveying/downward-conveying traces, such as *Teichichnus* and *Gyrolithes*, have the highest EEI values. The key Cambrian ichnotaxon *Treptichnus pedum* has a moderate to high EEI value, depending on its functional interpretation. Most of the major functional groups of modern bioturbators are found to have evolved during the earliest Cambrian, including burrow types that are highly likely to have been bioirrigated. In fine-grained (or microbially bound) sedimentary environments, trace-makers of bioirrigated burrows would have had a particularly significant impact, generating advective fluid flow within the sediment for the first time, in marked contrast with the otherwise diffusive porewater systems of the Proterozoic. This innovation is likely to have created significant ecospace and engineered fundamentally new infaunal environments for macrobiotic and microbiotic organisms alike.



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The development of infaunal bioturbation is one of the key Phanerozoic innovations and its first appearance is used to define the Ediacaran–Cambrian boundary (Brasier *et al.* 1994). The evolution of burrowing, and especially bioirrigation, by macrobiotic organisms is a key aspect of the ecological changes seen at the base of the Cambrian. It is likely to have been a fundamental evolutionary stimulus, since the seafloor and its nutrient flux underwent fundamental changes from the mat-ground-dominated Proterozoic – which had only meiofaunal bioturbation/mixing – to the Phanerozoic style of infaunal bioturbation (Brasier & McIlroy 1998; McIlroy & Logan 1999; Mazurek 2013; Tarhan *et al.* 2015). In this study, we apply functional bioturbation analysis (cf. Solan & Wigham 2005; Bambach *et al.* 2007) to this turning point in Earth history, which will allow the assessment of the relative importance of different trace fossil types as ecosystem engineers.

Bioturbators as ecosystem engineers in modern ecosystems

Ecosystem engineering is the construction, modification and maintenance of environments by organisms, which may be classified as being either autogenic or allogenic ecosystem engineers (Jones *et al.* 1994). All ecosystem engineers modify the flow of resources within their environment. Autogenic ecosystem engineers, such as reef-building corals, provide a physical structure for other taxa to utilize (Jones *et al.* 1994; Wood 2016). Allogenic ecosystem engineers create new habitats and resource flows by redistributing materials from their environment, such as dam-building beavers (Pollock *et al.* 1995) and mound-forming termites (Dangerfield *et al.* 1998), but also those bioturbating organisms that significantly affect the distribution of both particles and solutes. The structures created by ecosystem engineers commonly

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persist long after the engineer has either died or relocated (Jones *et al.* 1997).

In marine environments, the key form of allo-genic ecosystem engineering is bioturbation, in which burrowing organisms create and modify sedi-mentary environments. The impact of bioturbation on benthic ecosystems is broadly two-fold, leading to: (1) the creation of new habitats through the mod-ification of the two-dimensional sediment–water interface into a three-dimensional complex (McIlroy & Logan 1999), which additionally varies through time (e.g. Solan & Kennedy 2002); and (2) the physical redistribution of nutrients and par-ticulate matter (Aller 1982; McIlroy & Logan 1999; Michaud *et al.* 2005, 2006). Bioturbation brings about several key physicochemical changes to the sediment, including: alteration of the pore-water chemistry (Aller 1982); increasing the depth of the redox potential discontinuity below the sedi-ment–water interface from its Proterozoic position close to the sediment–water interface (McIlroy & Logan 1999); increased water content (Rhoads 1970); and modifications to the topography and roughness of the sediment–water interface (Orvain 2005). Marine bioturbation is therefore one of the most important forms of allo-genic ecosystem engineering (Levinton 1995). All bioturbating organisms are ecosystem engineers to some extent, particularly when taken in the context of the ichno-logical expression of the Cambrian explosion (McIlroy & Brasier 2016), when there was a fundamental change from small, essentially interface, burrows to deeper, more pervasive burrowing. It is clear that different types of bioturbation have different effects on microbial processes and nutrient fluxes within the sediment and therefore on benthic eco-systems (McIlroy & Logan 1999; McIlroy & Brasier 2016). The impact of a burrowing taxon is greatest where its bioturbation produces conditions that contrast most significantly with the pre-existing environment, such as particle and solute redistribution, particularly through bioirrigation (Mermillod-Blondin & Rosenberg 2006). The basal Cambrian expansion of infaunal bioturbation was one of the most profound changes of environment caused by organisms in the history of life on Earth and this ichnological diversification is used to help define the base of the Phanerozoic (McIlroy & Brasier 2016; Geyer & Landing 2016).

Marine bioturbating organisms can be sub- divided into seven different functional groups: (1) epifaunal bioturbators; (2) surficial modifiers; (3) biodiffusive bioturbators; (4) regenerators; (5) upward conveyors; (6) downward conveyors; and (7) gallery biodiffusors (Francois *et al.* 1997, 2002; Solan & Wigham 2005). In terms of their impact on sedimentary ecosystems, the seven func- tional groups are characterized as follows.

- (1) Epifaunal bioturbators, i.e. mobile organisms that live on the substrate and do not penetrate the sediment–water interface to any signifi- cant degree (e.g. pagurid arthropods), pro- ducing structures such as locomotion trails (cf. the trace fossil *Rusophycus*). As such, their ecological impact on modern sedi- mentary environments is minimal.
- (2) Surficial modifiers, i.e. taxa that live in the uppermost layers of sediment, typically at depths of no more than 2 cm (e.g. modern cly- peasteroid echinoderms; cf. Cambrian traces such as *Gordia* isp.). They have a low impact on sedimentary ecosystems because their activities are restricted to short distance par- ticle redistribution at, or at very shallow depths beneath, the sediment–water interface (Solan & Wigham 2005). Rather than engineering new ecosystems, the behaviour of some sur- ficial modifiers may actually lead to the exclu- sion of other, potentially more significant, ecosystem engineers through predation on larval forms and sediment disturbance that precludes larval settling (DeWitt & Levinton 1985; Snelgrove 1999), although the dis- aggregation of surficial microbial mats may introduce mucus into the sediment, which significantly affects microbial productivity (McIlroy & Logan 1999).
- (3) Biodiffusive bioturbators, such as venerid bivalves (comparable Cambrian trace fossils being *Psammichnites* or *Plagiogmus*; McIlroy & Heys 1987), move particles short distances over greater depths within the mixed layer, introducing oxygenated water and particulate organic matter into the mixed layer of the sedi- ment (Francois *et al.* 1997). As such, they are more significant ecosystem engineers than surficial modifiers.
- (4) Regenerators are taxa such as fiddler crabs that excavate semi-permanent burrows in the sediment, the removed sediment being trans- ported back to the sediment–water interface, and can therefore be responsible for relatively large particle fluxes and the generation of sig- nificant amounts of new ecospace, which is essentially a vertical extension of the sedi- ment–water interface (cf. the trace fossils *Gyrolithes* and *Skolithos*).
- (5) Upward conveyors are organisms that occupy vertical burrows in a head-down orientation, transferring sediment actively or passively toward the surface, often by deposit feeding at depth (e.g. arenicolid polychaetes). Larger organisms in deeper burrows can transport significant volumes of buried sediment (*Trep- tichnus* is a possible trace fossil analogue to modern upward conveyors).

ECOSYSTEM ENGINEERING IN THE CAMBRIAN

- (6) Downward conveyors (e.g. capitellid polychaetes) also live in vertical burrows, but with their head at or close to the surface, and move sediment down into the subsurface, either by ingestion and excretion, or by passive movement under gravity within the burrow. Some taxa may exhibit both upward- and downward-conveying behaviour at different times. Downward conveyors can transfer nutrients to depths of many centimetres, creating sedimentary habitats that would otherwise not exist deep within the sediment (e.g. Herringshaw *et al.* 2010; Kristensen *et al.* 2012; trace fossil examples include *Halopoa*, *Asterosoma* and similar mud-packed taxa).
- (7) Gallery biotransporters, exemplified by nereidid polychaetes (Francois *et al.* 2002), build complex burrow systems within the sediment, with galleries connected to the sediment–water interface by one or more openings. Essentially, this behaviour combines short distance biotransportive particle transport around the burrow walls with the rapid, larger scale flow of nutrients and sediment throughout the burrow network. Intense burrowing and bioirrigating activity within such galleries means that the trace-makers can potentially engineer significant volumes of new ecospace (*Multina* is a common Cambrian trace fossil exhibiting this type of behaviour).

The most effective ecosystem engineers are those bioturbators that move substantial quantities of particulate material through large and/or deep burrow systems (i.e. upward and downward conveyors and gallery biotransporters; Fig. 1). Taxa that utilize one or more of these bioturbation modes over

considerable periods of time, such as polychaete annelids and thalassinid crustaceans (Fig. 1; Mermillod-Blondin & Rosenberg 2006; Herringshaw *et al.* 2010; Hale *et al.* 2014), can have significant impacts on the benthic environment, creating ecospace, altering the topography of the sediment–water interface and enhancing the sedimentary flux of nutrients (e.g. Reise 1981; McIlroy & Logan 1999; D’Andrea & DeWitt 2009; Herringshaw *et al.* 2010; Herringshaw & McIlroy 2013).

In addition to bioturbation type, the impact of a burrowing organism on the sedimentary environment is greatly increased if it bioirrigates its burrow. Bioirrigation is used by most macroscopic burrowing organisms to oxygenate the burrow system and create currents that eject metabolites and faecal material from the burrow (Kristensen & Kostka 2005). The net effect of bioirrigation is to elevate nutrient levels and microbial productivity in and around the burrow; it can also change the permeability and grain size profiles of the substrate (Herringshaw & McIlroy 2013). It has the greatest ecological impact in low permeability substrates where the bioirrigated burrows create advective flow pathways in otherwise diffusive porewater systems (Mermillod-Blondin & Rosenberg 2006).

Ichnology of the Ediacaran–Cambrian transition

Surface traces from the Conception Group (565 Ma) of Newfoundland are the first reliable evidence for macrofaunal animal locomotion (Liu *et al.* 2010a, b, 2014). Simple surficial grazing and feeding trails (e.g. *Helminthorhapha* and *Archaeonassa*) and

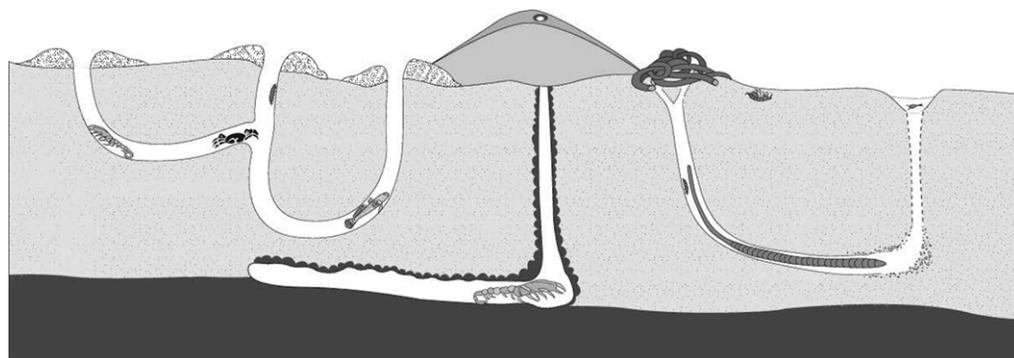


Fig. 1. Bioturbators as ecosystem engineers. Composite image showing how bioirrigating, gallery-network-building infaunal organisms such as thalassinid crustaceans (left) and polychaete annelids (right) modify the seafloor topography, sedimentary distribution and particle flux, and create habitats for other organisms. Figure shows (from left to right): unlined *Thalassinoides*-type crustacean burrow network (after MacGinitie & MacGinitie 1949); mud-pellet-lined *Ophiomorpha*-type crustacean burrow network (after Leaman *et al.* 2015); and unlined *Arenicolites*-like annelid burrow with feeding pit and faecal mound (after Reise 2002).

slightly more penetrative horizontal burrows (e.g. *Planolites*) become abundant in the late Ediacaran (e.g. Jensen 2003; McIlroy & Brasier 2016). The most common Ediacaran trace fossils are tiny horizontal traces, often attributed to burrowing within microbial mats, and commonly termed ‘undermat miners’ (Seilacher 1999), although this is something of a misnomer as many such trace fossils show no evidence of systematic mining behaviour and their mode of feeding is not based on any objective evidence.

Eustatic sea-level rise in the late Ediacaran and early Cambrian led to an increase in the surface area occupied by shallow marine environments (e.g. Brasier 1992; Peters & Gaines 2012). This transgression also led to decreased sediment flux to the continental shelf, resulting in an increase in the ratio of organic to inorganic material in shelf sediments (McIlroy & Logan 1999). The build-up of organic nutrient reserves beneath the sediment–water interface has been proposed as a major trigger for the development of bioturbation across this interval (McIlroy & Logan 1999). It has been noted that trace fossils appear in a broadly consistent order in Ediacaran–Cambrian successions (Gehling *et al.* 2001; McIlroy & Brasier 2016). This rapid increase in both bioturbation intensity and depth of bioturbation across the Ediacaran–Cambrian transition is sometimes known as the ‘agronomic’ or ‘substrate revolution’ (Seilacher & Pflüger 1994; Bottjer *et al.* 2000). The increase in depth of bioturbation coupled with the widespread expansion of the palaeobathymetric range of exploited ecospace (from shallow- to deeper-marine environments), represents the first example of large-scale manipulation of the sedimentary environment by macroscopic animals (e.g. Marenco & Bottjer 2008; Dufour & McIlroy 2016).

In the siliciclastic successions of the Ediacaran–Cambrian, three ichnozones have been recognized: the *Harlaniella podolica* Zone (latest Ediacaran); the earliest Cambrian (Terreneuvian) *Treptichnus* (*Phycodes*) *pedum* Zone; and the overlying *Rusophycus avalonensis* Zone (Fig. 2; Narbonne *et al.* 1987; after Crimes 1987). The low ichnodiversity *H. podolica* Zone has only recorded shallow tier, simple, unbranched, horizontal trace fossils, most commonly the shallow tier trace fossil *Planolites* (Narbonne *et al.* 1987; Droser *et al.* 2002). The appearance of penetrative burrows, diagnostically *T. pedum*, but also trace fossils of the *T. pedum* ichnozone – including *Skolithos*, *Arenicolites* and *Gyrolithes* – marks the base of the *T. pedum* Zone (see Gehling *et al.* 2001; Jensen & Runnegar 2005; Geyer & Landing 2016; McIlroy & Brasier 2016), while the *R. avalonensis* ichnozone contains the first unequivocal arthropod trace fossils (*Rusophycus* and *Cruziana*), as well as the graphoglyptid

trace fossil *Squamodictyon* (Crimes & Anderson 1985; Narbonne *et al.* 1987).

Despite the increase in ichnodiversity in the Cambrian portion of the Chapel Island Formation, both the intensity of bioturbation and trace fossil size are generally low throughout the succession (McIlroy & Logan 1999). Most trace fossils are of small diameter and there is a lack of burrows deeper than a few centimetres, even in sedimentary facies where deeper bioturbation might be expected (Crimes & Anderson 1985). The *H. podolica* Zone has an ichnofabric index (ii) of 0–2 at the lamina scale and burrow depths and diameters <10 mm (Fig. 2). The *T. pedum* ichnozone has a maximum burrow diameter of 30 mm (typically *c.* 10 mm), a maximum tiering depth of 20 mm and a typical ii of 2 (Fig. 2; McIlroy & Logan 1999). In the *R. avalonensis* ichnozone, the maximum burrow depth recorded is 70 mm, but is typically 20–30 mm; the maximum burrow diameter is 30 mm (typically *c.* 10 mm) and the ii value is generally 2, only occasionally rising to 3 or 4 at the bed scale (Fig. 2; McIlroy & Logan 1999). Recent work by Tarhan *et al.* (2015) argues that low levels and depths of bioturbation persisted in siliciclastic marine environments from the Early Cambrian to the Silurian, although the intensity of bioturbation is clearly a function of the relative rates of bioturbation *v.* sedimentation (McIlroy 2004, 2008). The same researchers recognized the evolution of many infaunal behavioural types in the Early Cambrian, but suggest that major sediment mixing by ‘bulldozing’ infauna did not evolve until the mid–late Palaeozoic (Tarhan *et al.* 2015).

Methodology

This work documents the distribution of trace fossils through the late Neoproterozoic to pre-trilobitic Lower Cambrian (Terreneuvian) Chapel Island Formation of Fortune Head, SE Newfoundland (Crimes & Anderson 1985; Narbonne *et al.* 1987). This stratigraphically continuous, ichnologically rich section (Fig. 2) is the Global Stratotype Section and Point (GSSP) for the Precambrian (Ediacaran)–Cambrian boundary, with the boundary itself being defined on the appearance of the trace fossil *T. (Phycodes) pedum* at the boundary between the *H. podolica* Zone and the *T. pedum* ichnozone (Brasier *et al.* 1994; Landing 1994; Geyer & Landing 2016; McIlroy & Brasier 2016). As the stratotype succession was deposited exclusively in a shelf setting, it is possible to examine evolutionary changes in trace fossil assemblages without the biases imparted by facies and palaeoenvironmental shifts (Landing *et al.* 1988). For these reasons, the Chapel Island Formation also represents an

ECOSYSTEM ENGINEERING IN THE CAMBRIAN

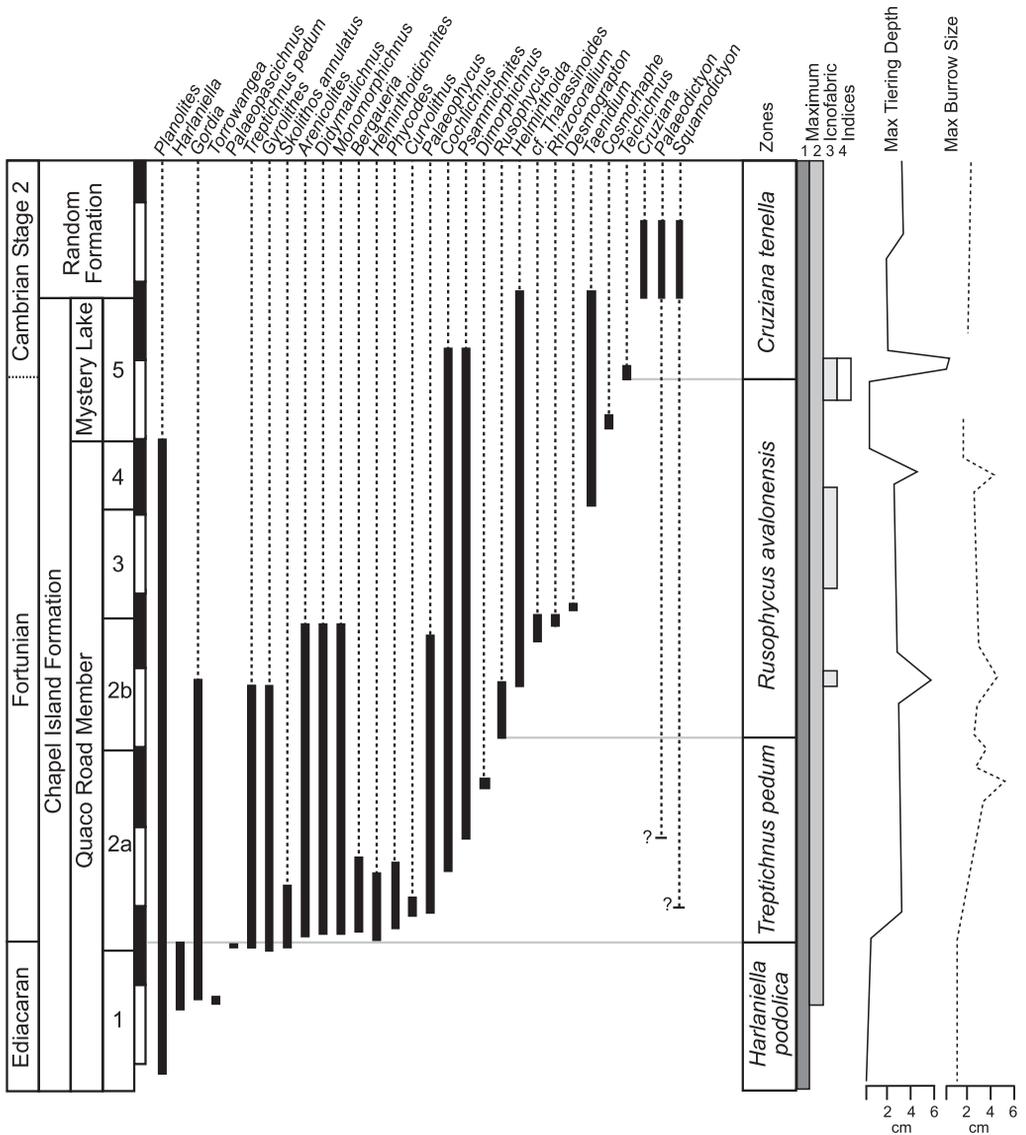


Fig. 2. Stratigraphy and ichnology of the Ediacaran–Cambrian strata of Fortune Head, Newfoundland, Canada (after Crimes 1987; Narbonne *et al.* 1987; McIlroy & Logan 1999; Geyer & Landing 2016).

ideal case study to examine the role of ecosystem engineers during the Ediacaran–Cambrian transition.

We examined 11 of the key Ediacaran–Cambrian ichnotaxa from the Chapel Island Formation: *Planolites*, *Gordia*, *Treptichnus*, *Monomorphichnus*, *Skolithos*, *Palaeophycus*, *Psammichnus*, *Helminthoidichnus*, *Teichichnus*, *cf. Thalassinoides* and *Gyrolithes* (Table 1; Figs 3 & 4). To assess the potential impact of the trace-makers as ecosystem engineers, we assessed each ichnotaxon based

on three criteria: the infaunal ecospace created by the ichnotaxon; burrow function(s); and the likelihood of bioirrigation behaviour. To code for the ecospace created, we assigned a numerical value to the depth of the trace or burrow (methodology modified from Bambach *et al.* 2007): (1) surface traces; (2) semi-infaunal traces (shallowly penetrative structures in which the trace-maker was partly infaunal and partly exposed to the water column); (3) shallow infaunal (<5 cm deep) burrows; and (4) deep infaunal (>5 cm deep) burrows.

Table 1. Ecosystem engineering impact (EEI) values for key trace fossils from the Chapel Island Formation, Fortune Head, Newfoundland, Canada

Ichnogenus	(a) Depth*	(b) Functional group [†]	(c) Bioirrigation [‡]	(d) EEI value [§]
<i>Planolites</i>	1–3	2–3	2	5–8
<i>Gordia</i>	1–2	2	1	4–5
<i>Helminthoidichnites</i>	1	1–2	1	3–4
<i>Monomorphichnus</i>	1	1	1	3
<i>Psammichnites</i>	1–2	1–2	1	3–5
<i>Palaeophycus</i>	1–2	2–3	2	5–7
<i>Skolithos</i>	2–3	3	2	6–7
<i>Treptichnus</i>	3	2–6	2–3	7–12
<i>Gyrolithes</i>	3	2–6	2–3	7–12
<i>Teichichnus</i>	3–4	3–5	2	8–11
? <i>Thalassinoides</i>	3	3–5	3	10–12

*After Bambach *et al.* (2007): 1, surficial; 2, semi-infaunal; 3, shallow infaunal (<5 cm); 4, deep infaunal (>5 cm).

[†]After Solan & Wigham (2005): 1, epifaunal locomotion; 2, surficial modification; 3, biodiffusion; 4, regeneration; 5, downward-/upward-conveying; 6, gallery biodiffusion.

[‡]Likelihood burrow/trace was bioirrigated: 1, highly improbable; 2, possible; 3, probable.

[§]EEI calculated as a range based on the addition of minimum–maximum values for columns a, b and c.

The likely behaviour of the trace-maker and the functional/ethological group or groups to which the trace-maker could have belonged were then assigned (method of Solan *et al.* 2004; Solan & Wigham 2005; after Francois *et al.* 1997, 2002). Using this functional group classification, the inferred relative sedimentary particle and nutrient fluxes associated with each ichnotaxon could be assigned, with increasing values indicating increasing impact on particle transport and nutrient flux. The functional groups were assigned as follows: (1) epifaunal locomotion; (2) surficial modification; (3) biodiffusion; (4) regeneration; (5) downward- and/or upward-conveying; and (6) gallery biodiffusion. Where a number of functions were considered to be likely for an ichnotaxon, more than one value was assigned to the same taxon.

The likelihood that a trace was bioirrigated was given one of three values: (1) highly improbable (surficial locomotion or grazing traces for which irrigation is unlikely to have been necessary); (2) possible (shallow, simple burrows, possible dwelling structures, which might have required at least short-term irrigation); or (3) probable (deeper and/or more complex burrow systems, probably dwelling structures, in which irrigation is likely to have been required for longer term occupation).

By then combining the ecospace, functional group and bioirrigation values, the relative ecosystem engineering impact (EEI) of each ichnotaxon can be estimated. A non-bioirrigated surface locomotion trail therefore has an EEI of 3 (1 + 1 + 1), whereas a deep infaunal network with gallery biodiffusion and bioirrigation has an EEI of 12 (3 + 6 + 3). For most ichnotaxa, where more than one function is possible, a range of EEI values

was obtained. It should be noted that the value of the EEI obtained for a taxon does not imply position on a linear scale of impact, but is a means of classifying the impact of an organism on its environment.

Results

The results of the EEI analysis of key Ediacaran–Cambrian ichnotaxa are summarized in Table 1. In the *H. podolica* ichnozone, all ichnogenera present – e.g. *Planolites*, *Harlaniella*, *Gordia* and *Torrowangea* – are bedding-parallel, shallow tier trace fossils with little vertical penetration of the sediment (cf. Marengo & Bottjer 2008). The biological affinity of *Palaeopascichnus* is currently unclear (e.g. Dong *et al.* 2008; Antcliffe *et al.* 2011), but it is unlikely to be a trace fossil and is therefore not considered here. *Planolites* and *Gordia* (along with *Harlaniella* and *Torrowangea*) are interpreted to represent biodiffusive bioturbation. Both *Planolites* and *Gordia* are essentially surficial traces, although Droser *et al.* (2002) interpret *Planolites* as having been shallowly penetrative, in which case *Planolites* trace-makers could also have been biodiffusers. *Gordia* most probably represents only surficial modification and it is therefore improbable that *Gordia* burrows were bioirrigated, but possible that *Planolites* traces were. As such, *Gordia* is given a maximum EEI value of 5 and *Planolites* a maximum EEI value of 8 (Table 1). The first occurrence of burrows such as *Gordia* and *Planolites* increased the surface area of the sediment–water interface (McIlroy & Logan 1999) and initiated the development of a sediment mixed layer (Savrdra & Bottjer 1989; Bromley 1996; Droser *et al.* 2002, 2004; Tarhan

ECOSYSTEM ENGINEERING IN THE CAMBRIAN

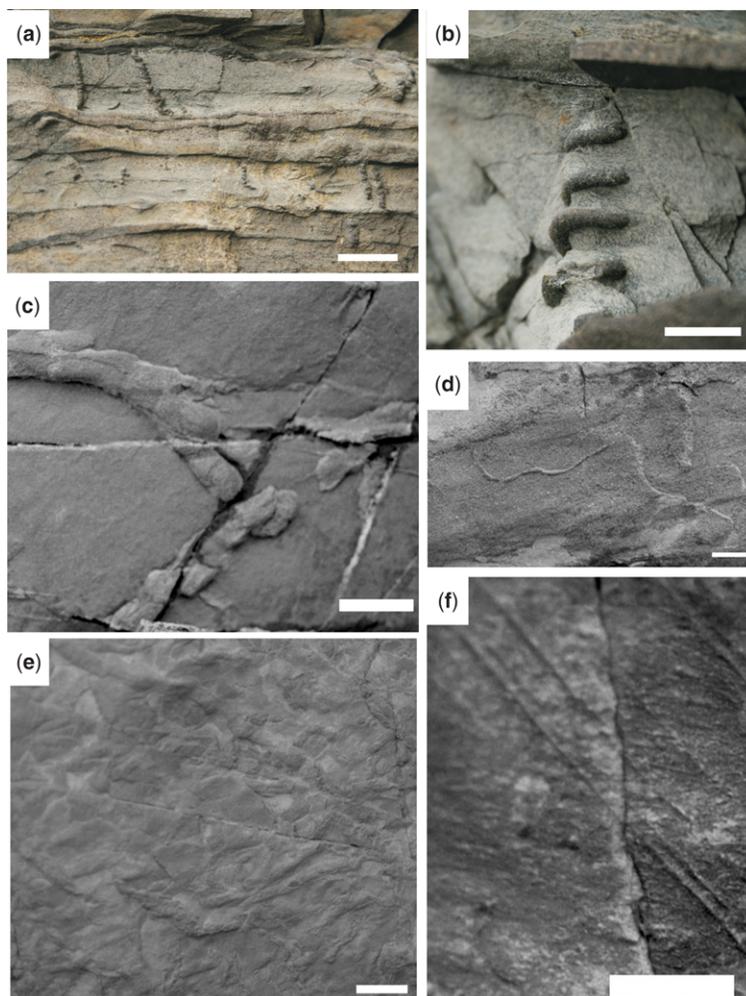


Fig. 3. Trace fossils from the Ediacaran–Cambrian successions of Fortune Head and Grand Bank, Newfoundland, Canada: (a) *Skolithos annulatus*; (b) *Gyrolithes polonicus*; (c) *Treptichnus pedum*; (d) *Helminthoidichnites* isp.; (e) *Planolites* isp.; and (f) *Monomorphichnus* isp. All scale bars 1 cm.

et al. 2015). The new ecospace produced by the trace-makers would have been relatively limited and only a small net increase in endobenthic nutrient flux is to be expected, although, compared with the completely unbioturbated stratigraphic levels of the Proterozoic, this is likely to be relatively significant (McIlroy & Logan 1999).

In the succeeding *T. pedum* ichnozone (Fig. 2), a greater diversity of ichnotaxa and behaviours is encountered. Not only do horizontal trace fossils become more morphologically diverse, with the appearance of ichnotaxa such as *Helminthoidichnites* and *Psammichnites* (used in preference to *Taphrhelminthopsis* and *Archeonassa*, cf. Jensen 2003; Jensen & Palacios 2016), and the arthropod

scratch marks of *Monomorphichnus* (Fig. 3f; Table 1), but vertical burrows, such as *Skolithos*, also appeared for the first time. The dwelling trace *Skolithos* did not create significant volumes of ecospace and any bioturbation associated with these burrows is likely to have been essentially biodiffusive. Nonetheless, the depth and abundance of *Skolithos* burrows in some Early Cambrian successions – often forming ‘pipe rock’ ichnofabrics (McIlroy & Garton 2004, 2010) – indicates a fundamental change in infaunal habitats. A greater diversity of functional groups and the increased generation of ecospace is implied for the *T. pedum* ichnozone owing to the occurrence of more three-dimensional ichnogenera, most notably the branching, penetrative trace fossils

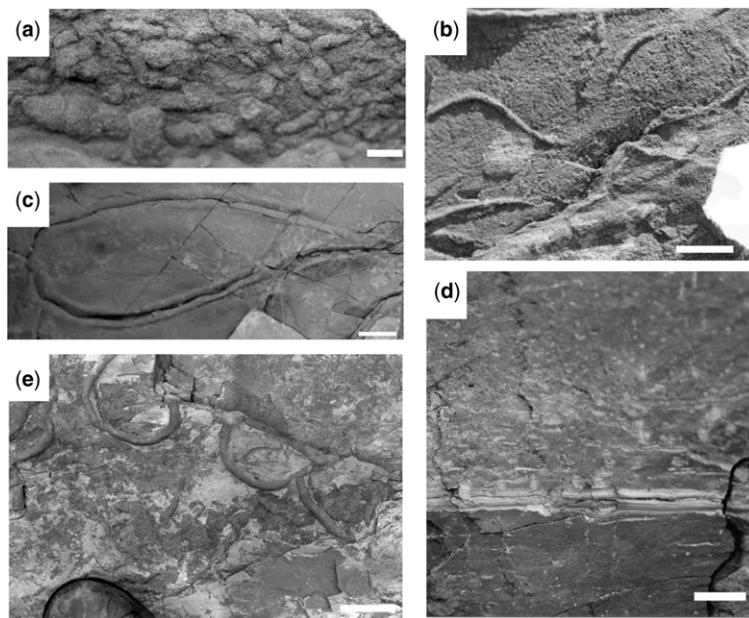


Fig. 4. Trace fossils from the Ediacaran–Cambrian successions of Fortune Head and Grand Bank, Newfoundland, Canada: (a) *Palaeophycus* isp.; (b) *Gordia* isp.; (c) *?Psammichnites* isp.; (d) *Teichichnus* isp.; and (e) *?Thalassinoides* isp. Scale bars in parts (a), (b) and (d) 1 cm and in parts (c) and (e) 5 cm.

Treptichnus and *Gyrolithes*, but also *Arenicolites*, which indicate the increasing behavioural complexity of infaunal organisms (Narbonne *et al.* 1987 and herein). The diagnostic trace fossil *Treptichnus* is widely taken as the first burrow that shows probable shallow tier gallery diffusion, although it has also been interpreted as the probing burrow of a carnivorous priapulid (Dzik 2005; Vannier *et al.* 2010). As such, its EEI value has a range of 7–12.

Although many new horizontal trace fossils appear in the *Rusophycus avalonensis* Zone, such as the geometrical graphoglyptid trace fossil *Squamodictyon* – which is considered to represent shallow gallery diffusion – along with additional vertical burrows, the functional groups of trace-makers in this interval appear to have been essentially the same as those of the *T. pedum* Zone. The most significant first appearance datums are those of *Teichichnus*, and possibly *Diplocraterion*, which allow the inference of the evolution of vertical and horizontal biodiffusion, upward- and downward-conveying and regeneration (Table 1; McIlroy & Logan 1999). *Teichichnus* has its first reliable occurrence at around the base of Cambrian Stage 2 (Landing *et al.* 1988; McIlroy & Brasier 2016), but purported *Diplocraterion* (Narbonne *et al.* 1987), which can be difficult to distinguish from cross-sections of *Teichichnus*, could not be confirmed in this study.

Discussion

Although the diagnostically Lower Cambrian ichnotaxon *T. pedum* has a relatively wide range of potential EEI values, depending on the interpretation of the behaviour of the trace-maker (Table 1), it might not have been the trace fossil with the highest ecosystem impact. Ichnotaxa such as *Teichichnus* have a narrower range of EEI values and their trace-makers can be interpreted more confidently as higher impact ecosystem engineers. Nonetheless, the effects of *Treptichnus* and similar trace fossils on the Cambrian seafloor should be seen in the context of change relative to the minimal ecosystem engineering potential of the latest Ediacaran trace fossil assemblages. When viewed in this manner, it is clear that *T. pedum* and similar trace fossils are likely to have had a profound effect on the marine ecosystem. Our assessment of the ichnology of the Chapel Island Formation suggests that most, if not all, of the major functional groups of modern bioturbators appear to have evolved by the base of Cambrian Stage 2 in the Global Stratotype Section – that is, within the first 12 million years of the Phanerozoic (corroborated by findings from northern Norway by McIlroy & Brasier 2016).

It is well known that matground facies persisted locally in marine environments into the Silurian (e.g. Tarhan *et al.* 2015), but they did so in

ECOSYSTEM ENGINEERING IN THE CAMBRIAN

increasingly restricted, commonly nutrient-starved sedimentary environments (Harazim *et al.* 2013; McMahon *et al.* 2016). This marginalization of the matground ecosystem to environments with ecologically harsh conditions, such as brackish and freshwater facies, reflects the effects of the Cambrian-style ecosystem engineering bioturbators that gradually shaped the marine realm toward its modern state.

As with any ichnological study that requires the functional interpretation of trace fossils, there is always some ambiguity as to the life activity of the trace-maker, indeed many modern burrows can reflect a diverse range of behaviours that can change due to ontogenetic or palaeoenvironmental controls as well as ecosystem engineering (Herringshaw *et al.* 2010). The accuracy/importance of the functional groups assigned to the ichnotaxa has significant potential bearing on their EEI value. We addressed this issue by assigning a potential range of ecosystem impacts to some trace fossils, which affects the EEI value (i.e. their inferred significance as ecosystem engineers). The magnitude of the impact that a burrowing organism has on its environment should be considered in the context of its stratigraphic level and whether the sedimentary environment it occurred in was diffusion- or advection-dominated.

Ecosystem engineering of fine-grained Cambrian sediments

Bioirrigating organisms that construct networks or galleries in fine-grained sediments (mud and silt) create a greater contrast to natural sedimentary flow conditions than those that burrow in sands (cf. Mermillod-Blondin & Rosenberg 2006; Meysman *et al.* 2006). The shallow, narrow, vertical tube *Skolithos* (Fig. 3a) and the similar, but spiralling, *Gyrolithes* (Fig. 3b), first encountered in the *T. pedum* ichnozone of the Early Cambrian (Fig. 2), are blind-ended subvertical burrows, whose trace-makers may well have bioirrigated their burrows. The evolution of such behaviour would have had a particularly profound impact on infaunal ecosystems, particularly in terms of microbial and meiofaunal activity in the near-burrow zone (cf. Reise 1981; McIlroy & Logan 1999). As such, morphologically comparable ichnotaxa found in early Phanerozoic mudstones and siltstones, which would have been diffusive sedimentary environments, are of greater significance than those found in sandstones, which are likely to have been advective.

Ecosystem engineering in coarse-grained Cambrian sediments

In coarser grained Lower Cambrian successions, from about the base of Cambrian Stage 3, the

vertical tubular trace fossil *Skolithos* is commonly found in composite ichnofabrics, sometimes in very high densities (up to 7500 burrows/m², Davies *et al.* 2009) that may have been due to very dense assemblages of organisms in the typical 'pipe rock' biotope (McIlroy & Garton 2004, 2010). High densities of burrowing organisms may have increased the sedimentary impacts of such simple burrows (cf. Miron *et al.* 1992; Volkenborn & Reise 2006; Herringshaw *et al.* 2010), but their potential for ecosystem engineering is likely to have been low because the sandy sediments in which they formed would already have had advective flow through them. The impact of *Skolithos* on sediments and nutrients is likely to have been restricted to upward-conveying, arguably during burrow excavation only, with associated bioturbation and possibly downward-conveying during the period that the burrow was inhabited. The amensalism that might have resulted from dense assemblages of vertical burrow dwellers that is evident in the low diversity of pipe rock facies is difficult to prove owing to the palimpsesting of assemblages (McIlroy & Garton 2010).

Comparison of ichnological trends with other Lower Cambrian successions

The trends indicated by the ichnological data from the Chapel Island Formation are augmented by contemporaneous successions bearing trace fossils elsewhere. In western Mongolia, the Ediacaran–Cambrian transition is preserved in a mixed carbonate–siliciclastic succession with a trace fossil fauna showing similar patterns to those observed in Newfoundland (Goldring & Jensen 1996). Questionable short vertical and horizontal burrows are described from the latest Ediacaran Tsagaan Oloom Formation (Goldring & Jensen 1996; Khomevsky & Gibsher 1996; Brasier *et al.* 1997), while the ichnogenera *Didymaulichnus*, *Helminthoidichnites* and *Planolites* were described from the earliest Cambrian Bayan Gol Formation. These simple, bedding-parallel ichnotaxa are morphologically and behaviourally comparable with those of the *H. podolica* assemblage Zone of Newfoundland. The overlying unit of the Bayan Gol Formation contains these taxa, as well as *Cochlichnus*, *Homosiroidea* (probably a taphomorph of *T. pedum*), *Palaeophycus*, *Phycodes* (?*Trichophycus*) and *Treptichnus*. As with the trace fossil assemblage of the *T. pedum* assemblage Zone of Newfoundland (Fig. 2; Geyer & Landing 2016), the upper unit includes increasingly complex burrow morphologies. Trace fossils in the Mongolian successions therefore show progressively greater vertical depths of burrow penetration, and an increasing abundance of burrows that are inferred to have been created for

shallow gallery diffusion, through the Lower Cambrian succession.

The Ediacaran–Cambrian succession of lower shoreface–offshore transition zone sediments in western Canada also show comparable ichnological patterns to those of the Chapel Island Formation (MacNaughton & Narbonne 1999; Carbone & Narbonne 2014), which might be elucidated further from this type of ecological assessment. In a review of Proterozoic–Cambrian ichnology, Jensen (2003) described the increase in morphological and behavioural complexity across the Ediacaran–Cambrian boundary, noting trends that are very similar to the specific patterns described herein from the GSSP. This stratigraphic trend toward both increasing diversity and behavioural complexity is consistently found in Ediacaran to Lower Cambrian siliciclastic sediments around the world (Gehling *et al.* 2001; Geyer & Landing 2016; McIlroy & Brasier 2016). Some Ediacaran to Cambrian sections have been considered to have Cambrian-type trace fossils slightly below the Cambrian boundary and overlapping with the Ediacaran biota (e.g. Jensen & Runnegar 2005; Darroch *et al.* 2015). The precise level at which trace fossils of Cambrian aspect appear is significant for global correlations, but it is perhaps to be expected that the event was somewhat diachronous. This does not detract from the fact that this emerging biota fundamentally changed the marine realm and that its development occurred globally within a geologically short interval of time.

In comparison with later Phanerozoic successions, one of the distinctive aspects of the Lower Cambrian is that most burrows were small and did not penetrate deeply into the sediment. Even though vertical bioturbation evolved in the late Ediacaran, it was not until the Cambro-Ordovician that significantly larger, deeper gallery networks such as *Thalassinoides* became prevalent (Sheehan & Schiefelbein 1984; Myrow 1995). The stratigraphically lowest *Thalassinoides s.s.* are known from the Cambrian Stage 3 of Finnmark, Norway (McIlroy & Brasier 2016), but are – much like the ?*Thalassinoides* figured herein (Fig. 4e) – comparatively shallow tier relative to later Palaeozoic and younger examples (Myrow 1995).

Conclusion

In terms of the ecospace they created, the likely nutrient flux they generated and the probability that they bioirrigated the burrow systems, the trace-makers of *Treptichnus* would have been high-impact Early Cambrian ecosystem engineers. This is especially true when taken in the context of the probable ecological impact of Ediacaran trace

fossils, which is likely to have been low. *T. pedum* is therefore unquestionably an important ichnotaxon for stratigraphic purposes because its first occurrence represents a major change in the seafloor ecosystems relative to those of the Ediacaran, but it is not the Early Cambrian trace fossil that is likely to have had the greatest EEI value.

The trace-makers of the diagnostically Cambrian deeper penetrative trace fossils *Gyrolithes* and the deposit-feeding burrow *Teichichnus* were potentially more significant ecosystem engineers than *T. pedum*. By comparison with modern burrows similar to these ichnotaxa (e.g. Dworschak & Rodrigues 1997; Gingras *et al.* 1999), we consider that both *Gyrolithes* and *Teichichnus* are likely to have been multifunctional, with the trace-maker occupying the same position for significant periods of time while bioirrigating the sediment. The spreiten burrow *Teichichnus* may have been particularly high impact because it is associated with the highest ichnofabric indices and deepest tiering in Early Cambrian successions (McIlroy & Logan 1999). The presence of spreiten in *Teichichnus* indicates bulk sediment processing behaviour during a relatively protracted period of burrow occupation. The trace-maker is likely to have bioirrigated the sediment – suggesting that the *Teichichnus* trace-maker was an engineer of new ecospace that caused significant biogenic particle flux. Its occurrence at about the base of Cambrian Stage 2, and its abundance in siliciclastic deposits of Cambrian age (Landing *et al.* 1988; McIlroy & Brasier 2016), make it a potentially useful marker for Cambrian Stage 2 in facies without small shelly fossils.

The trace fossil assemblage that marks the base of the Cambrian in the GSSP is herein demonstrated to result from the actions of animals that interacted with the seafloor much more significantly than their Ediacaran counterparts. Nonetheless, there are aspects of the sedimentary facies that need to be isolated from those of stratigraphy and evolution. It appears that, close to the boundary level, the first pervasive bioturbators evolved, with composite ichnofabrics of cf. *Gyrolithes* being common in the offshore facies and shallow tier *Treptichnus*-dominated assemblages occurring in association with fair weather mudstones in high-energy, lower shoreface facies, both in the GSSP (herein) and in Norway (McIlroy & Brasier 2016). The changes in microbial nutrient cycling that are likely to have accompanied the first bioturbators (McIlroy & Logan 1999) provide evidence to suggest that complex animals did indeed engineer the Cambrian explosion, irrevocably changing the biogeochemistry of sediments, porewaters and oceans alike (Brasier & McIlroy 1998; McIlroy & Logan 1999; Canfield & Farquhar 2009). Our work further refines that conclusion and identifies the basal

ECOSYSTEM ENGINEERING IN THE CAMBRIAN

Cambrian ichnogenera/ecosystem engineers that are likely to have had the most impact at this time.

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L. G. HERRINGSHAW *ET AL.*

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