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Review

Were the first trace fossils really burrows or could they have been made by sediment-displacive chemosymbiotic organisms?

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Abstract: This review asks some hard questions about what the enigmatic graphoglyptid trace fossils are, documents some of their early fossil record from the Ediacaran-Cambrian transition and explores the idea that they may not have been fossils at all. Most researchers have considered the Graphoglyptida to have had a microbial-farming mode of life similar to that proposed for the fractal Ediacaran Rangeomorpha. This begs the question "What are the Graphoglyptida if not the Rangeomorpha persevering" and if so then "What if…?". This provocative idea has at its roots some fundamental questions about how to distinguish burrows sensu-stricto from the external molds of endobenthic sediment displacive organisms.

Keywords: Ichnology; Ediacaran; Cambrian; Rangeomorpha; Graphoglyptida; Endobenthos

1. Introduction

The importance of the first colonization of the sedimentary realm by infaunal organisms has been at the heart of discussions around the evolution of complex animal life and the beginning of the Cambrian Explosion of animal life (Crimes & Anderson 1987; McIlroy & Logan 1999; McIlroy & Brasier 2017; Buatois 2018). The base of the Cambrian period (and end of the Ediacaran) is defined by the first occurrence of trace fossils belonging to the *Treptichnus pedum* Assemblage Zone (Brasier *et al*. 1992; Geyer & Landing 2017) at a point in rock in Fortune Head in Newfoundland, Canada approx. 540Ma). The precept behind this decision was the recognition that burrowing is an easily preservable—fundamentally animalian—trait either in the form of fossil burrows or burrowing fabrics (e.g. Crimes & Anderson 1987; McIlroy 2004).

It has become increasingly clear in recent years that complex animals evolved well before the base of the Cambrian. Indeed, recent studies consider two of the major Ediacaran clades (the Arboreomorpha and Rangeomorpha) as members of total group Eumetazoa (Dunn *et al*. 2021). Evidence for the existence of Ediacaran animals includes: preserved cnidarian muscles (*Haootia*; Liu *et al*. 2014, 2015) and surface locomotion trails (Liu *et al*. 2010) both from around 565Ma; the mollusk-like grazing trace (*Kimberichnus*; Ivantsov 2009) c. 550Ma; serial impressions of placozoan-type feeding (*Dickinsonia, Epibaion*; Ivantsov & Malakhovskaya 2002; Sperling & Vinther 2010) c. 550Ma; as well as bilaterian burrows (Parry *et al*. 2017) and ?annelid trails close to the basal Cambrian (Chen *et al*. 2018) both c. 542Ma. Debates around whether the Cambrian explosion of complex animal life had a short or long Ediacaran fuse (Brasier 2000; Zhu *et al*. 2017) have thus mostly converged on a consensus that there was a long Ediacaran pre-history to the Cambrian biotas. The issue of how and why complex animal life diverged so markedly during the Ediacaran-Cambrian transition is still a source of debate (Brasier 1979; Runnegar 1982; Seilacher 1997; Dzik 2005; Xiao & Laflamme 2009; Erwin & Tweedt 2012; Droser *et al*. 2017; Wood & Erwin 2017; Wood *et al*. 2019).

Perhaps the most interesting questions around Ediacaran palaeobiology relate to first and last occurrences of taxa (e.g. Narbonne & Gehling 2003; Liu *et al*. 2011; Liu *et al*. 2014;

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Matthews *et al*. 2020), but also the biotic transition from the Ediacaran into the Cambrian (Droser *et al*. 2017). With almost all first order evolutionary innovations (e.g. biomineralization, terrestrialization etc.) there is a period of time with equivocal evidence for the event prior to its universally accepted advent. This is likely usually due to localized innovation that is difficult to characterize, followed by rapid radiation/dispersal (e.g. Budd & Jensen 2017). The record of the end of the Ediacaran and the Cambrian explosion of animal life include examples of Ediacaran survivors in Cambrian rocks (e.g. *Swarpuntia* Jensen *et al*. 1998; Hagadorn & Waggoner 2000), and also evidence of putative Cambrian type trace fossils below the recognized Ediacaran Cambrian boundary (Gehling *et al*. 2001; Högström *et al*. 2013; Jensen *et al*. 2019; Jensen *et al*. 2000). It is to this latter transition, from the matground dominated Ediacaran to the macroscopically bioturbated Cambrian (McIlroy & Logan 1999; Seilacher *et al*. 2005), that our attention is drawn herein.

2. Microbially dominated seafloors at the dawn of animal life

Matgrounds were common in late Proterozoic marine ecosystems, forming wherever there was a sufficiently low rate of sedimentation to allow organic matter to settle onto sediment surfaces. In the absence of surficial detritus-feeders and conveyor activity by bioturbators, the development of matgrounds developed largely unchecked for the majority of the Proterozoic history of microbial life (Walter 1977). The microbial consortia that made up Proterozoic and lowermost Palaeozoic matgrounds, the physical integrity of matgrounds, and their shear strength remain effectively unknown. It is presumed that in shallow water depositional settings there was a strong photosynthetic component and that matgrounds were dominantly algal in nature (e.g. Gehling 1999), but in deep marine settings the matgrounds likely also had a range of sulphur-oxidizing bacteria close to the sediment-water interface (McIlroy *et al.* 2005; Menon *et al.* 2017). Modern matgrounds are loci of large amounts of microbial biomass and microbial DOM production (Prieto-Barajas *et al.* 2018). In fine-grained sediments, the matground microbiota occludes pore throats with filaments, resulting in porewater dysoxia or even anoxia very close to the sediment-water interface (Lawrence *et al.* 1994). The fine-grained sediment below the (macro)fossiliferous Ediacaran matgrounds of Avalonia was most commonly pelagite or hemipelagite, probably with relatively high amounts of porewater (Brasier *et al*. 2013; Harazim *et al.* 2013). The smothering of these matground surfaces by the growth of reclining organisms or fallen erect organisms commonly caused the preservation of negative impressions of even the delicate fronds of Ediacaran organisms (McIlroy *et al*. 2009; **Fig. 1a**).

One of the most distinctive aspects of the earliest Ediacaran soft-bodied macrobiotas is that—with few rare exceptions—they were immotile, and in many cases grew to very large sizes on matgrounds (Narbonne & Gehling 2003; Liu *et al*. 2016; Taylor *et al*. 2021; **Fig. 1b**). Being immotile on a porous organic-rich seafloor potentially results in serious biogeochemical challenges in the form of hydrogen sulfide buildup below the body tissues (Ortega *et al*. 2008; Dufour & McIlroy 2017a, b). If hydrogen sulfide accumulates unchecked next to the epithelium of an immotile recliner it would likely cause cell-death, meaning that soft-bodied Ediacaran organisms must have been able to modify the organism-substrate interface in a manner that detoxified, or otherwise mitigated, sulfide toxicity (McIlroy *et al*. 2021). Other strategies that animals employ to allow growth on sulfidic porewater substrates involve creation of an inert barrier between the sediment and the organism such as the holdfasts of Crinoids (Seilacher & MacClintock 2005), the basipinacocytes of sponges (Dufour & McIlroy 2017b), or the mucous burrow linings of burrowers that make permanent dwellings (e.g. cerianthid anemones, Frey 1970; Bromley 1996). The most common way for modern soft-bodied organisms to avoid sulfide toxicity is to either move on a regular basis (e.g. the placozoan *Trichoplax* initiates movement in response to sulfide concentrations (Loenarz *et al.* 2011) or to detoxify this hydrogen sulfide by pumping oxygen to the sediment interface, causing oxidation of sulfide to thiosulphate (cf. Dufour & Felbeck 2003; Dufour & McIlroy 2017a; **Fig. 1c**). There are many common ecto- and endo-symbioses between sulfur oxidizing bacteria and animals, particularly on high surface area, oxygen-rich, epithelia such as gills (Dufour 2005; Dubilier *et al*. 2008).

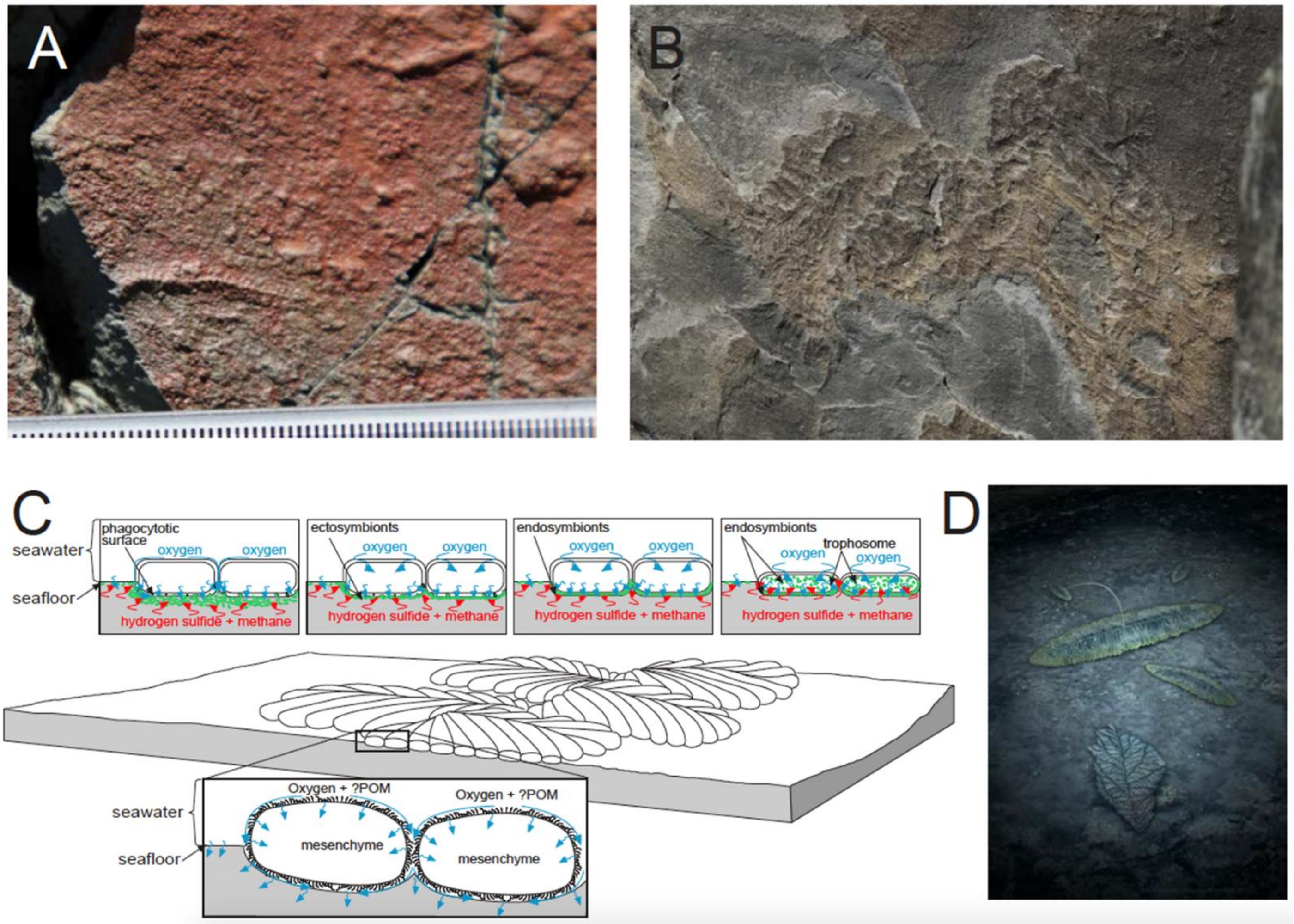

Figure 1. A) Long, narrow Ediacaran frond from Mistaken Point Ecological reserve, NL (scale bar in mm); B) Large reclining rangeomorph Ediacaran frond. aff. *Bradgatia* sp. from the MUN surface, Catalina Dome, NL; C) Diagrammatic reconstruction of a generic reclining rangeomorph detailing the ways that it might have interacted with the substrate. The lower surface is irrigated with seawater by ciliary action and diffusion. The supply of oxygen to the lower surface is considered to have increased microbial productivity. The top row of images show possible feeding modes with green circles showing the distribution of chemolithoautotrophic symbionts and arrows show diffusion of solutes. Furthest left is phagotrophy, next is ectosymbiosis, then endosymbiosis and furthest right is endosymbiosis with a trophosome (requiring diffusion of sulfide/methane into a thin organism) POM = Particulate Organic Matter. All of these methods of gaining nutrition would work for endobenthic graphoglyptids; D) reconstruction of the Ediacaran seafloor of Mistaken Point Formation.

The earliest examples of Ediacaran fossils include the epibenthic Rangeomorpha, some of which had fractal-like lower surfaces and lived reclined on the seafloor (Hawco *et al*. 2020; McIlroy *et al*. 2020, 2021; **Fig. 1d**). Some rangeomorphs actively displaced sediment during growth such that they grew slightly below the ambient sediment-water interface (Droser *et al*. 2014) and as such were likely adapted to exploit sedimentary biogeochemical gradients, especially the very large reclining organisms (e.g. *Bradgatia* (see Liu *et al*. 2016) and *Gigarimaneta* (Taylor *et al*. 2021)). Fractal-like morphologies in reclining organisms are most consistent with sedimentary nutrient exploitation via symbioses with lithoautotrophic bacteria, based around the metabolism of methane, hydrogen, and hydrogen sulfide in particular. In these symbioses, the rangeomorph probably provided oxygen to and gained nutriment from the symbionts that it hosted. It is most likely in these simple organisms that there was a mixture of symbiosis and phagocytosis on the lower surface of the organism, in the microbial productivity hotspot generated by the localized enhanced near-organism oxic zone (Dufour & McIlroy 2017a; **Fig. 1c**).

Due to the low rate of diffusion of oxygen into the sediment porewater systems that underlay the ubiquitous Ediacaran seafloor matgrounds, the redox profile of Ediacaran sediments is likely to have been significantly condensed (Aller 1978, 1982, 1984, 1994;

McIlroy & Logan 1999). As a result, very little of the particulate and dissolved organic matter in such sub-mat settings will have been subject to aerobic respiration (the greatest energy yield per unit of organic carbon metabolized, e.g. White 1983; Konhauser 2007), leading to a predominance of sulfate reduction and methanogenesis. However, should a reclining organism grow atop an established matground and pump oxygenated seawater to its lower surface, this would stimulate productivity of chemolithoautotrophic bacteria such as sulfur oxidizers (which could utilize reductants diffusing from the sub-mat sediment profile, e.g. HS^-, $NH_4{}^+$, Fe (II); Blackburn & Blackburn 1993) as well as methanotrophs (e.g. Petersen & Dubilier 2009). Such stimulation of microbial productivity is likely to have constituted the basis for simple ectosymbiosis/phagotrophic nutrition for reclining macro-organisms (McIlroy *et al.* 2020).

3. The slow death of the Ediacaran-type matground biotope

From their acme in the Proterozoic, matgrounds like stromatolites slowly declined, becoming increasingly marginalized in the lowermost Paleozoic (Walter & Heys 1985). Paleozoic matground facies became increasingly associated with environments that were somewhat hostile to burrowing animals such as low TOC mud-belts in front of deltas (Harazim *et al*. 2013; Harazim & McIlroy 2015), whereas in the lowermost Cambrian matgrounds were common in normal marine settings such as the lower shoreface (McIlroy & Logan 1999). Evidence for matground facies in siliciclastic settings is commonly in the form of Microbially Induced Sedimentary Structures (MISS) such as lineated bedding planes of *Arumberia*, wrinkled surfaces such as *Kinneya* and elephant-skin textures (McIlroy & Walter 1997; Pflüger 1999; McIlroy *et al.* 2005; Noffke 2000; Noffke *et al*. 2002; McMahon *et al*. 2021). These same textures commonly recur after mass extinction events until biotic recovery re-establishes ecosystem services in the benthic realm, including the all-important ecosystem engineering burrowing endobenthos (e.g. Sheehan & Harris 2004; Herringshaw *et al*. 2010; Herringshaw & McIlroy 2013; Mata & Bottjer 2009; Feng 2021).

The stresses on the matground biotope that dominated hiatal marine seafloors of the Proterozoic largely result from the effects of bioturbation, which seemingly started in the Ediacaran with the evolution of bilaterian burrowers (Parry *et al*. 2017) along with the grazing activity of metazoans (e.g. Ivantsov 2009; Seilacher & Hagadorn 2010; Chen *et al*. 2018). This matground stress likely escalated with the evolution of larger bulk-sediment deposit feeders around the base of Cambrian Stage 2 (Herringshaw *et al*. 2017), becoming better established as bioturbators increasingly sought out surficial and buried organic rich substrates through the lower Palaeozoic (**Fig. 2a** Bell Island). Modern levels of bioturbation and distribution would likely have developed very quickly.

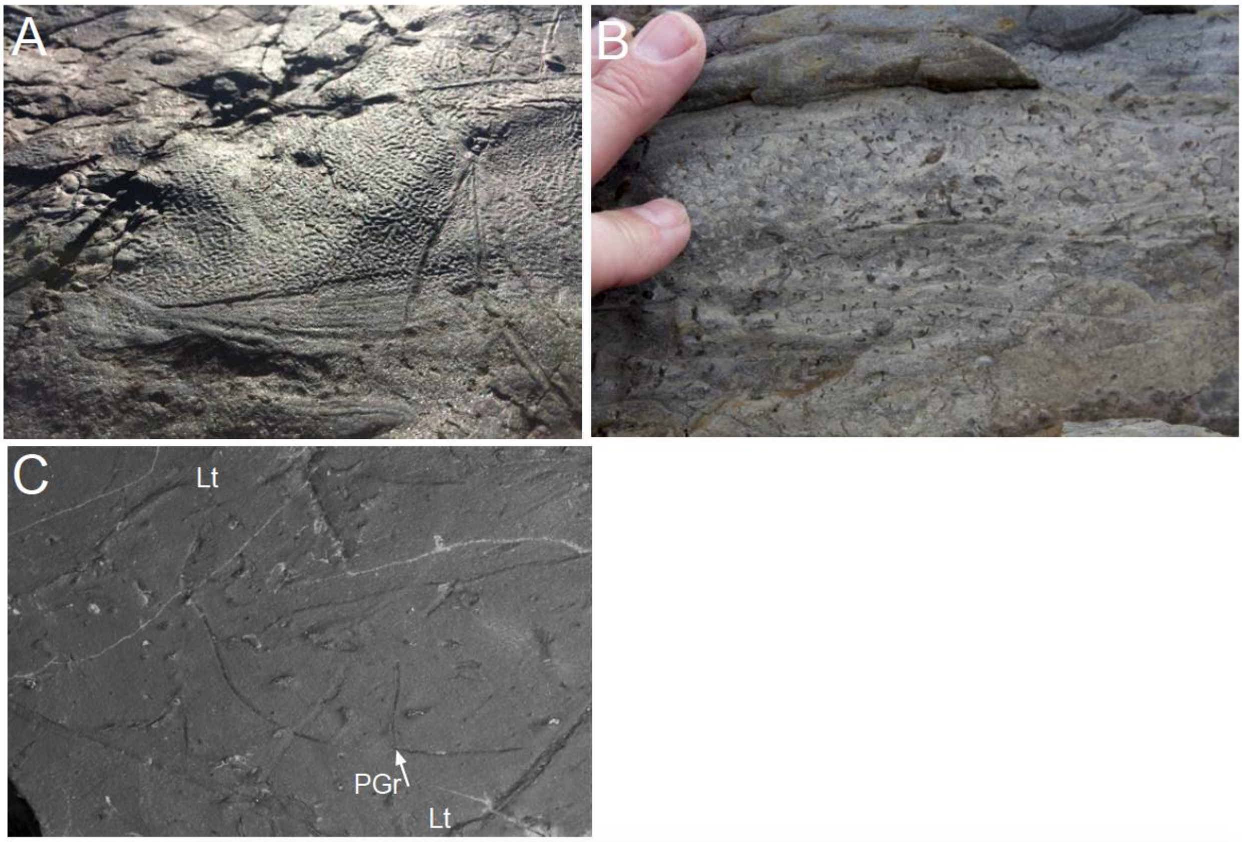

Figure 2. A) Microbial matground surface with wrinkled texture and abundant sediment mining trace fossils from the Ordovician of Bell Island, NL. Field of view c. 30cm; B) typical ichnofabric from the lower Fortunian of Fortune Head showing abundant curved, spiralling and branching pyritized burrows; C) bedding plane view of *Lamonte trevallis* burrows (Lt) and pyritized graphoglyptid burrows with T junction arrowed (field of view 15cm).

The presence of shallow burrows co-existing with elements of the soft bodied Ediacaran biota, while not entirely unexpected, does need to be considered with an open mind to alternative hypotheses. The morphologies of late Ediacaran burrows are commonly simple and narrow (**Fig 2b**). The most abundant trace in this period is the simple tubular burrow *Lamonte trevallis* (Meyer et al. 2014; **Fig. 2c**), which is interpreted as a member of an ichnoguild of under-mat miners (Seilacher 1999). Other regularly serial or branched burrows are commonly attributed to the treptichnid genera *Treptichnus* and *Streptichnus* (Jensen & Runnegar 2005; Högström *et al*. 2013; Jensen *et al.* 2020). The importance of identifying *Treptichnus* alongside elements of the Ediacaran biota stems from the fact that the *Treptichnus pedum* (originally *Phycodes pedum* Seilacher 1966) ichnoassemblage zone is diagnostic of the base of the Cambrian, thereby creating an apparent stratigraphic conundrum, though in the present author's opinion, none of the purported Ediacaran *Treptichnus* closely resemble *T. pedum*. Which begs the question, to me at least, if they are not *Treptichnus* s.s. then what are they?

4. The early putative burrowers of the Ediacaran-Cambrian Transition

It is a seldom appreciated precept of ichnological (trace-fossil) studies that burrows do not generally betray the taxonomic affinities of the burrowing organism (Baucon *et al.* 2012), nor do they always represent a single life activity in most cases (e.g. Bromley 1996). A simple vertical burrow in a sand, for example, works just as well as a den for a predator or mucous net feeder as it does for a head-down deposit feeder (e.g. Herringshaw & McIlroy 2013). While most biologists would accept that as a truism, many palaeo-ichnologists are surprisingly content with making broad-brush assumptions of behaviour based on burrow morphology (McIlroy 2008).

The majority of the earliest fossil burrows do not show good evidence for deposit feeding activity, but rather are passively sediment-filled, diagenetic mineral-filled, or collapsed (**refs**; Herringshaw *et al.* 2017). In the type section for the Ediacaran-Cambrian boundary in southeastern Newfoundland, Canada, the open, passive filled burrows *Treptichnus* and *Gyrolithes,* dominate the ichnology of the Fortunian-aged *Treptichnus pedum* assemblage ichnozone (Crimes & Anderson 1985; McIlroy & Logan 1999; Herringshaw *et al.* 2017; Laing *et al.* 2018; **Fig. 3**). In the Fortunian stage of the lower Cambrian there are also abundant surface traces including arthropod burrows and surficial grazers/bulldozers (Crimes & Anderson 1985; Narbonne *et al*. 1987), but it is not until slightly higher in the lower Cambrian (Cambrian Stage 2) that there is unequivocal evidence of bulk sediment deposit feeding activity (Herringshaw *et al*. 2017; McIlroy & Brasier 2017).

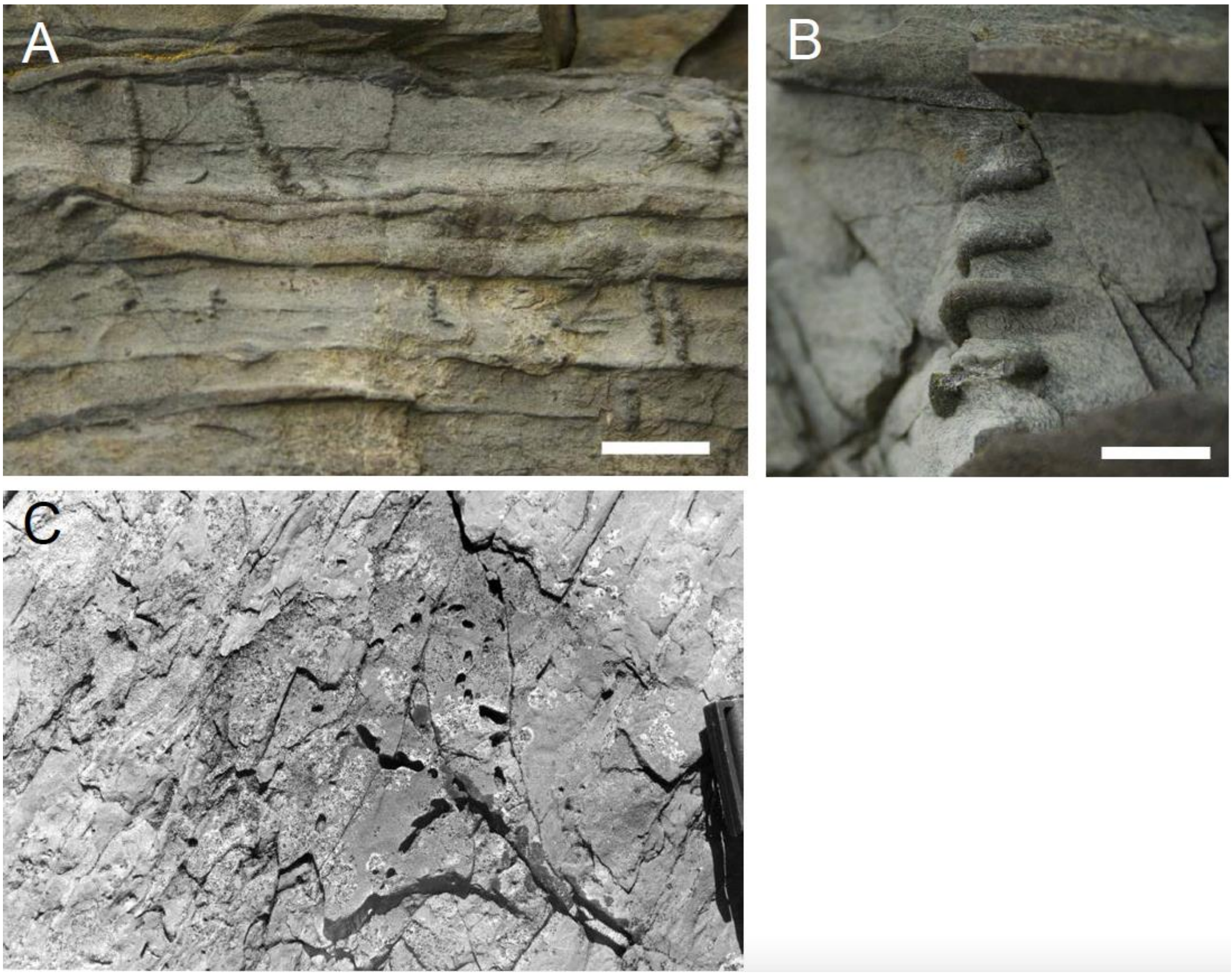

Figure 3. Tubular open "burrows" from the Fortunian of Fortune Head NL showing spiralling morphologies of: A) *Gyrolithes gyratus*; and B) *G. scintillus* with pyrite rich silty sandstone fill. C) shows the bedding plane view of a monopodially branching *Treptichnus pedum* in which the pyritic fill has weathered away showing the mold of the burrow, the space that would have been occupied in life. Whether these structures were burrows sensu stricto or casts of the exterior of spiralling or branching organisms remains to be determined.

The ichnogenus *Treptichnus* (*sensu stricto*) was created for fossilized burrows (Miller 1889) and has subsequently been applied to a range of marine trace fossils from deep marine turbidite successions throughout the Phanerozoic, as well as shallow marine trace fossils of the Palaeozoic and burrows of modern insect larvae (Muñiz-Guinea *et al.* 2014). The generic diagnoses of the similarly branching burrows of *Trichophycus* and *Phycodes* include the formation of spreite by serial bulk sediment deposit feeding and direct evidence of movement in the form of bioglyphs; fecal pellets are known from Cambrian Stage 2 (Jensen 1997; Orłowski & Żylińska 1996; **Fig. 4).** Both *Trichophycus* and *Phycodes* have *Treptichnus*-like biserial and uniserial branching, which is almost certainly an example of convergent behavioural evolution for effective sediment exploration and exploitation using sympodial/feather stitch branching (Babcock *et al.* 2014; McIlroy & Brasier 2017; Buatois 2018).

Figure 4. Segments of *Trichophycus* ispp. from the lower Cambrian Arumbera Sandstone of central Australia showing the stacked spreite (A) and scratch marks (B) that distinguish the genus from *Treptichnus*. Field of view A is 3cm, B is 6cm.

While the ichnotaxonomic minutiae have been explored in detail, the question that seems not to have been asked is: what evidence do we have for the behaviour represented by the lowermost Cambrian marine treptichnids? We know that organisms have been able to exploit sub-seafloor settings by sediment displacive growth since the Ediacaran (Droser *et al.* 2014), so the question remains ”Do we even know if the earliest endogenic structures were trace fossils *sensu stricto* and not just external molds of the first sediment displacive endobenthos?” I would posit that we do not.

If we are to open ourselves to the possibility of sediment displacive growth (*sensu* Droser *et al.* 2014) persisting beyond the Ediacaran, then there are a wide range of lower Cambrian burrow-like structures that are always passively filled with sediment or collapse (i.e. not backfilled by the trace maker) that could be reinvestigated. In this case rather than being burrows we could think of them as external molds.

Note that this is not the same as the approach to *Treptichnus pedum* by Dzik (2005) who conflated biotaxa and ichnotaxa (creating a priapulid genus *Manycodes*), even though the two do not complete under the ICZN. *Manycodes* has not been accepted as being synonymous with *Treptichnus*, though the Scalidophora are considered a likely trace-makers of *Treptichnus*- and *Trichophycus*-like burrows both modern and ancient (Kesidis *et al.* 2019).

5. What are the Graphoglyptida if not the Rangeomorpha persevering?

One of the remarkable things about the “trace fossil” record of the shallow marine matground-rich facies of the lowermost Cambrian is that there are numerous narrow, geometric graphoglyptids (*sensu* Fuchs 1895; Seilacher 1977). Graphoglyptids are primarily known from deep marine depositional settings (Seilacher 1962; Miller 1991; Uchman 2004; though see Fürsich *et al.* 2007; Olivero *et al.* 2010) from the Ordovician onwards and having a major radiation in the Cretaceous (Uchman 2004), perhaps coincident with the expansion of deciduous trees. The affinities of the Graphoglyptida are contentious, and even though some examples are known from modern seafloors, no trace-maker has yet been identified (Rona *et al.* 2009).

Recent work has divided the Graphoglyptida into three topological groups (Fan *et al.* 2018): 1) “line graphoglyptids” (mostly meanders and spirals) which are common in the

Fortunian lower Cambrian worldwide (**Fig. 5a, b**); 2) "tree-form (mainly sympodially-branching) graphoglyptids" (including *Treptichnus*; Uchman *et al.* 1998) which are locally common in lower shoreface settings (**Fig. 5c, d**); and 3) "net-type graphoglyptids" that are generally rare except in tempestite and prodelta turbidite deposits (e.g. Crimes & Anderson 1985; McIlroy *et al*. 1997; McIlroy & Brasier 2017; **Fig. 5e, f**).

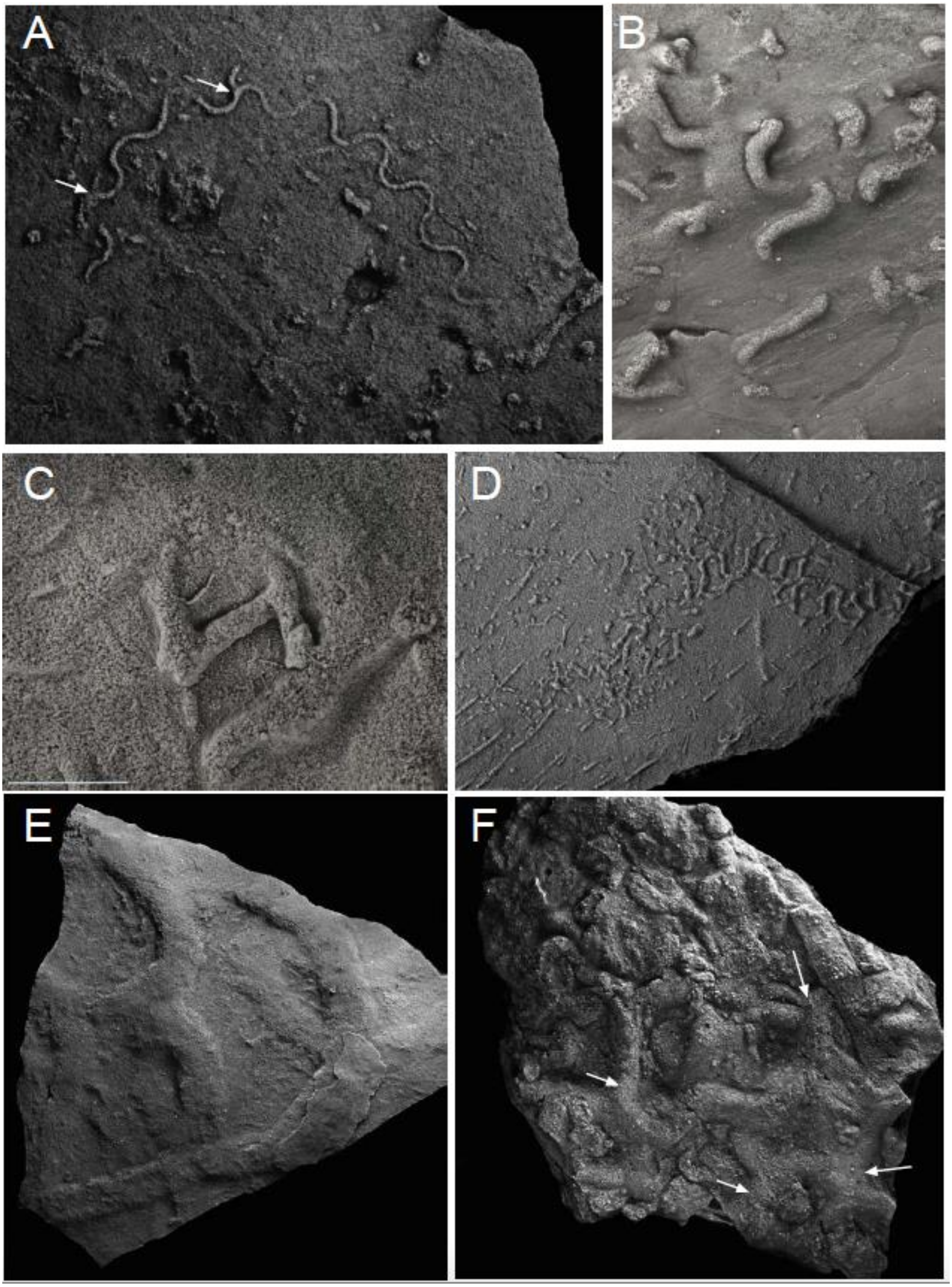

Figure 5. Graphoglyptid morphologies: A, B are line graphoglyptids (A *Helminthoida* though note the branching from the Cambrian Arumbera Sandstone Australia; B is *Helicolithus* from the latest Ediacaran of Tanafjord, Norway); C-D are branching graphoglyptids. (B is *Belorhaphe* from the late Ediacaran of Tanafjord, Norway, D is cf. *Paleomeandron* from the Cambrian Arumbera Sandstone); E-F are net graphoglyptids (E is *Squamodictyon* from the Arumbera Sandstone, Australia and F is *Paleodictyon* also from the Arumbera Sandstone).

Most authors have considered the mode of life of the graphoglyptid-making organisms to include a combination of: 1) intensive [near]surficial bulk-sediment detritus feeding in meanders and spirals (Seilacher 1977; Fan *et al*. 2018); and 2) the creation of open sub-surface branching burrows and networks that were maintained for the purpose of "farming" microbes on the burrow wall (Seilacher 1977).

5.1. The early Vermiform/Line Graphoglyptids

In the Cambrian, hiatal matground facies prior to the onset of deep deposit feeding activity is likely to have been associated with surficially-concentrated nutrients similar to the distribution of food on the deep basin floors exploited by modern systematic (meandering/spiraling) deposit feeders (e.g. Ekdale 1980). The similar trace fossil assemblage is perhaps to be expected.

That the surficial matground biotope was host to some of the earliest Ediacaran endogenic structures (e.g. *Lamonte trevallis*) is to be expected (Gingras *et al*. 2011). The ability of the organisms to penetrate matground textures is a most surprising and fundamental innovation, potentially opening up the sub-matground porewater systems to a second phase of microbial oxidation of buried organic matter. Since backfill is yet to be demonstrated in this under-mat-miner guild, it should also be considered that the open tubular structures with their high surface area to volume ratio might have been suitable for cilial bioirrigation by a very simple immotile animal living in the sediment. Such a mode of life would be particularly effective if the *Lamonte*-making organism had symbionts as did some of the rangeomorphs.

Other similar, open, unbranched features described as burrows are common in the latest Ediacaran and lower Cambrian. Several distinctive spiraled/sinuous taxa of uniform diameter without backfill are known from within meters of the Ediacaran-Cambrian boundary, including the vertically spiraled *Gyrolithes scintillus* and *G. gyrates* (**Fig. 3**) and horizontally spiraled *Helicolithus* (Banks 1970; Herringshaw *et al*. 2017; McIlroy & Brasier 2017; Laing *et al*. 2018; **Fig. 5a**), *Streptichnus* (Jensen & Runnegar 2005), and some ?*Treptichnus* (Jensen *et al*. 2020). All of these taxa are considered to have been maintained such that they were constantly open to seawater and are commonly partly pyritized. That the burrows are commonly pyritized is suggestive of the presence of sulfur oxidizing bacteria that would be predicted by the ciliary irrigating mode of life of the symbiotic/phagocytotic Rangeomorpha proposed by Dufour & McIlroy (2017a).

Previous work has noted the potential for bacterial farming in *Gyrolithes* (Laing *et al.* 2018), presumably via bioirrigation (Herringshaw *et al*. 2010), but did not consider a rangeomorph-like chemosymbiotic mode of life. The bacterial farming mode of life seems to rely on some form of burrow wall grazing for which there is to date no convincing evidence. Younger occurrences of *Gyrolithes* are commonly attributed to conventional dwelling or deposit feeding burrows of bilaterian taxa from various "worms", arthropods and even vertebrates (e.g. Laing *et al.* 2018). Modern *Helicolithus*-like burrows are known to be formed in sulfidic marine sediments by the deposit feeding enteropneust *Saccoglossus* (Gingras *et al*. 2010).

If the paradigm for a rangeomorph-like symbiotic lifestyle (McIlroy *et al*. 2021) can be extended to unbranched, high surface area-volume ratio burrows without evidence of burrowing action/feeding, then the atypical nature of the earliest trace-fossil biotas and their overlap with the Ediacaran biotas might be explainable.

5.2. The Tree-like Graphoglyptids of the E-C boundary

Recognition of the tree-like graphoglyptids in bedding plane expression is commonly facilitated by the presence of sharp, commonly high angle branches—even 90º branching.

That in itself is unremarkable (e.g. Frey & Bromley 1985), but to have 90º branching without corner rounding (see *Treptichnus* in Baucon *et al.* 2014, their fig. 6) is unusual/unknown in burrows that are constantly patrolled by the trace-maker. A large number of trace fossils fall into this category; many of them are very beautiful, consisting of high angle branching in complex shapes, often forming meanders and almost never self-crossing. Most Phanerozoic examples of the tree-like graphoglyptids have very long chains of self-similar elements in a single meandering burrow (e.g. Uchman 2004). Cambrian examples attributed to the same ichnotaxa tend to be short and slightly atypically irregular (McIlroy & Brasier 2017; **Fig. 5c, d**).

In the farming model for graphoglyptid palaeobiology (Seilacher 1977), the endobenthic organism is inferred to have either actively or passively irrigated the burrow, thereby providing a large surface area supplied with oxygenated seawater upon which a microbiota could be cultured.

The most common tree-like, branching open burrow in the Cambrian is *Treptichnus pedum*, which may have alternated between biserial and uniserial sympodial branching. The feather-stitch biserial branching produces effectively straight burrows, with terminal openings at the end of each blind ended branch (**Fig. 6a**). The length of branches and their angle can vary considerably, affecting spacing between branching (**Fig. 6b**). The same burrows can curve by undergoing uniserial sympodial branching (**Fig. 6c**) while avoiding self-crossing, perhaps in response of physico-chemical seafloor gradients.

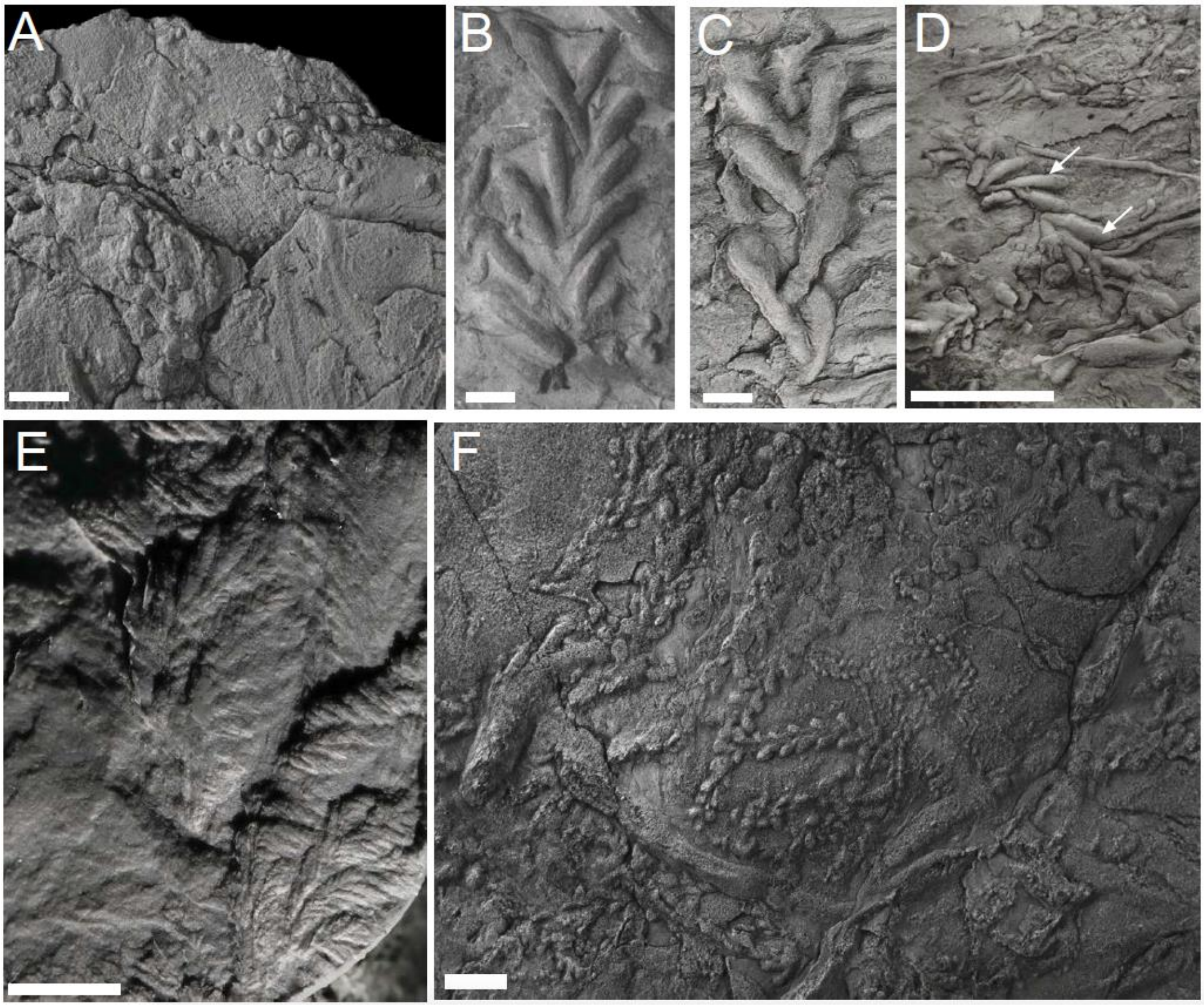

Figure 6. A-D *Treptichnus pedum* showing a range of branching types. All preserved as open burrow fills from the Fortunian of Tanafjord, Norway. D shows both uniserial and biserial monopodial branching. E is a small portion of aff. *Bradgatia* showing *Treptichnus* like branching. F *Treptichnus lublinensis* showing meandering habit and very rangeomorph-like branching. Scale bars 1cm except D, which is 5cm.

The epibenthic rangeomorph *Bradgatia* undergoes similar branching in search of nutrients (**Fig. 6d**) and likely had an oxygen-capturing upper surface and a ciliated lower surface providing fresh supplies of seawater to its episymbionts. The other species of *Treptichnus* that is only known from the lower Cambrian is the very shallow tier rangeomorph-like *Treptichnus lublinensis*, which would not look out of place in some of the iconic deep marine Ediacaran biotas (McIlroy *et al*. 2021; **Fig. 6e**). Additionally, zig-zagged open burrows attributed to *Belorhaphe* sp. (**Fig. 5c**) from the latest Ediacaran of Norway (McIlroy & Brasier 2017) are much like *Treptichus* except for the branching position and small size. This not to say that the treptichnids and forms like *Belorhaphe* were indeed rangeomorphs per-se, just that they may have had a rather rangeomorph-like mode of life and growth (albeit endobenthically rather than epibenthically) and were not necessarily deposit feeders as is commonly stated but may have had a sediment-displacive mode of life. As we strive to understand these purported trace fossils, we need to bear in mind the possibility that they could be external molds rather than burrows.

5.3. The Net-like Graphoglyptida

The net-like Graphoglyptida are some of the most complex burrow systems in marine depositional settings. If they were to be created by burrowing, their excavation would require complex "programming" (Seilacher 1977) to evolve at or before the Ediacaran-Cambrian boundary since the net-like graphoglyptids are known from the latest Ediacaran (described as *Multina* or *Olenichnus*; Fedonkin 1985; Parry *et al*. 2017; McIlroy & Brasier 2017; **Fig. 7**).

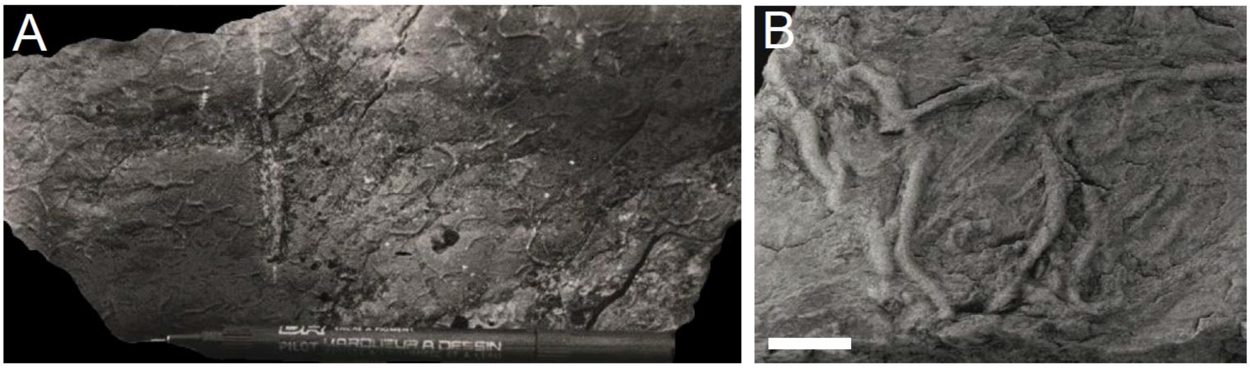

Figure 7. Net-type graphoglyptids from the Ediacaran (A) *Multina* and Fortunian (B) *Paleodictyon* of Tanafjord. Some of the supposedly most complicated marine trace fossils amidst the earliest record of endobenthic activity. Scale bar 1cm.

Modern soft-sediment cores have occasionally recovered shallow-tier polygonal xenophyophore-like protistan organisms (Swinbanks 1982) comparable to partial *Palaeodictyon*. At the same time, however, it is possible for simple organisms such as nematodes and foraminifera to make multi-tiered network burrows comparable to *Multina* sp. (Severin *et al*. 1982; Balinski *et al*. 2013). Some of the network-like morphology of *Multina* and *Olenichnus* have sharp (unrounded) angles at the branching points of the Graphoglyptida. That lack of corner rounding is common to all *Palaeodictyon* and, for this author at least, is very suggestive of branched growth evincing preservation of external molds of an organism rather than being a constantly patrolled burrow. Corner rounding is common in all long trace makers, e.g. worms and some arthropods. Some authors have argued that sharp corners could be maintained in networks if burrowed by a trace-maker that is about as long as the burrow is wide (Fan *et al.* 2018).

6. Conclusion or "What if….?"

The ideas outlined above constitute testable hypotheses that admittedly ask very difficult questions of the rock specimens we have to work with, but should not be discarded in preference for conventional interpretations without careful consideration.

The questions around the demise of the Ediacaran biotas and the diversification of animals in the lower Cambrian are first order palaeontological questions. Whether the graphoglyptids function as microbe farms that were patrolled, irrigated and browsed upon by a short-bodied active burrower; or whether they are the external molds of a simple pre-placozoan-grade rangeomorph-like organism that grew in or through the sediment is also key.

If we could know unequivocally what the enigmatic open burrow-like structures in the lowermost Cambrian are, we might become a step closer to understanding either the persistence or otherwise of the chemosymbiotic Rangeomorpha, or better appreciate the palaeobiology of the earliest burrows. Either way, it is considered here that they might make a poor choice for delineating the base of the Phanerozoic. The abundant traces of arthropods might be preferable for their lack of ambiguity if nothing else.

The fossil record of the dawn of animal life is full of hints and contradictory evidence, provincialism and incomplete datasets. The questions around the affinities of the Ediacaran biota and the appropriate choice of marker for the Ediacaran boundary are still far from resolved. There is much yet to do, and the hypotheses generated by asking the awkward question ‘What if…?’ are more likely to provide novel answers than not asking.

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