Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway

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Abstract: The Ediacaran to Cambrian transition of the Digermul Peninsula consists of an ichnologically rich, thick, conformable, shallow marine siliciclastic succession that crosses the Neoproterozoic–Cambrian boundary. The Tanafjord section has been independently dated by published palynological and new body fossil discoveries. As is also observed at the current Global Stratotype Section and Point (GSSP) for the Ediacaran–Cambrian boundary at Fortune Head in Newfoundland, Canada, there is a marked increase in burrow size and inferred behavioural diversity around the inferred boundary level at a surface without a significant hiatus. The diversity of this trace fossil assemblage presents an opportunity to compare the ichnological first appearance datums between the GSSP and another sedimentologically similar, but palaeogeographically remote, succession. We found that the first appearance datums of taxa in Finnmark broadly support the definition and stratigraphic extents of the Harlaniella podolica, Treptichnus pedum, Rusophycus avalonensis and Cruziana tenella zones. Our work shows that there is a marked increase in ichnodiversity in the lowermost Fortunian, mostly in the form of shallow tier traces. The main post-Fortunian ichnological innovation is the evolution of bulk sediment deposit feeding that is first evidenced by spreiten burrows at around the base of Cambrian Stage 2 in both the GSSP and in the Tanafjord section.

Supplementary material: Additional images of trace fossils from the studied section are available at https://doi.org/10.6084/m9.figshare.c.3462561

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The ichnology of the Neoproterozoic–Cambrian transition has been the focus of much interest since the decision to place the Global Stratotype Section and Point (GSSP) for the Ediacaran–Cambrian Boundary Stratotype at the base of the Treptichnus (Phycodes) pedum Zone at a point in rock at Fortune Head in southeastern Newfoundland (Brasier et al. 1994), above the uppermost Ediacaran Harlaniella podolica Zone (Narbonne et al. 1987). However, this has recently been called into question as a useful tool for international correlation (Babcock et al. 2014). The marked similarities between the stratigraphic succession of the Digermul Peninsula, Norway (Fig. 1) and the GSSP may be able to inform our understanding of ichnological diversification through the Neoproterozoic–Cambrian transition. A better appreciation of the rate of behavioural explosion at the base of the Cambrian also informs the use trace fossils both in the stratigraphic correlation of the Lower Cambrian and in elucidating the behavioural record of the Cambrian explosion (Budd & Jensen 2000).

The succession of trace fossils in the Chapel Island Formation of southeastern Newfoundland has been of key importance in the discussion of trace fossils through the Ediacaran to Cambrian (Crimes & Anderson 1985; Narbonne et al. 1987; Fig. 2). This study aimed to independently test the current ichnostratigraphic understanding (Crimes 1987, 1992, 1994; Narbonne et al. 1987; Fig. 2). This study aimed to independently test the current ichnostratigraphic understanding (Crimes 1987, 1992, 1994; Narbonne et al. 1987; MacNaughton & Narbonne 1999) against a similarly well exposed, stratigraphically continuous Neoproterozoic–Cambrian succession in Finnmark, northern Norway. It should be noted that the simple use of a T. pedum first appearance datum (FAD) to define the base of the Cambrian GSSP at Fortune Head is limited by the fact that FADs always underestimate the lowest occurrence of fossil remains in a section.

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The *T. pedum* Zone is an assemblage zone containing the FADs of many ichnotaxa and the boundary is also defined by both the highest occurrence of the (diagnostically Ediacaran) *H. podolica* Assemblage Zone (Landing *et al.* 2013; Geyer & Landing, this volume, in press).

**Sequence stratigraphic correlation**

The lithostratigraphy of the Neoproterozoic–Cambrian Vestertana Group in Finnmark was established by the Oxford Group of Harold Reading (Reading 1965; Banks 1970, 1973; Banks *et al.* 1971) and updated by Siedlecka *et al.* (2006). The thick silicilastic sedimentary succession of the Digermul Peninsula (Fig. 1) was deposited in a foreland basin on the margin of Baltica (Roberts & Siedlecka 2002; Nielsen & Schovsbo 2011). The lowermost age constraint on the Ediacaran–Cambrian transition in the succession is provided by the correlation of the glaciogenic Mortenses Formation (Rice *et al.* 2011) with the unpublished c. 580 Ma date widely used for the Gaskiers Formation of southeastern Newfoundland. The inference that the base of the Cambrian may lie low in the Ståhpogieddi Formation (base of the Innerelva Member) – based on Scandinavia-wide sequence stratigraphic synthesis (Nielsen & Schovsbo 2011) – does not adequately account for the rapid rate of accommodation generated during the Ediacaran–Cambrian interval of the Digermul region. Relative sea-level changes in a foreland basin setting such as that in which the Vestertana Group was deposited are much more likely to be driven by local basin-scale tectonics than by eustatic sea-level events that can be correlated on a regional scale (Beaumont 1981). Although the concept of a globally synchronous Cambrian transgression is appealing because of the common presence of a transgressive surface below Cambrian deposits in many cratonic regions (e.g. the ‘Great Unconformity’ of Peters & Gaines 2012),
transgressive surfaces are—by their very nature—highly diachronous and of little use in chronostratigraphy (Posamentier & Allen 1999). Sequence stratigraphers generally prefer to correlate sequence boundaries and maximum flooding surfaces rather than the transgressive surface of erosion (e.g. Galloway 1989). We also note that there is c. 2500 m of stratigraphy between the Gaskiers Formation and the GSSP in southeastern Newfoundland (Dalrymple et al. 2006), which suggests that there is a sizeable stratigraphic hiatus somewhere in the Digermul succession. The most likely point in the succession for such a large hiatus is the sequence boundary at the base of the fluvial Lillevannet Member of the Stáhpogieddi Formation and/or at the transgressive surface at the base of the Innerelva Member (Fig. 1).

**Stratigraphic palaeontology**

The assemblage of Ediacaran body fossils reported from the Innerelva Member of the Stáhpogieddi Formation (Farmer et al. 1992; Högström et al. 2013) is typical of the depauperate assemblages characteristic of the latest Ediacaran (Kotlin) of the Acado-Baltic and Siberian regions (e.g. Brasier 1992; Gehling et al. 2000; Mapstone & McIlroy 2006; Liu et al. 2013; Menon et al. 2013). We do, however, note that there are marked similarities between the low relief circular impressions that have been interpreted as discoidal fossils and the circular pseudofossils attributed to fluid escape in association with fossil matgrounds in the Ediacaran Longmyndian Supergroup in the UK (Menon et al. 2016). Purported soft-bodied Ediacara-type fossils
have also been reported from the Cambrian Lower Breidvika Member and the Lower Duolbasgaissa Member (Crimes & McIlroy 1999; Fig. 2).

Palynological data adequately constrain the age of the last parasequences of the Manndraperelva Member as Cambrian in age, given the presence of Granomarginata prima, Ceratophyton sp., Cochliata sp., and Eoschizotrix composita (Högström et al. 2013). The same authors also documented an Asteridium–Comasphaeridium Zone acritarch assemblage that included leiosphaerid acritarchs and cf. Polygonium varium at the same stratigraphic level as the previously reported assemblage of the giant foram Platysolenites antiquissimus and P. cooperi (Crimes & McIlroy 1999; McIlroy et al. 2001; Fig. 1). Other organic-walled fossils present at the base of the Lower Breidvika Member include Sabellidites cambriensis and undetermined vendo-taenids (Farmer et al. 1992; Fig. 1), which are at a comparable stratigraphic level to their range in the GSSP (Fig. 2).

Stratigraphic constraints on the upper part of the Digermul section include the presence of Holmia Zone trilobites in the Upper Duolbasgaissa Member (Nicholaisen & Henningsmoen 1987). The Lower Cambrian strata below the Holmia kjerulf Zone include a pyritized Ladatheca assemblage containing only Ladatheca cylindrica and S. cambriensis, which is found in the basal 100 m of the Lower Breidvika Formation, an overlying ‘Platysolenites assemblage’ containing P. antiquissimus, P. cooperi and L. cylindrica that encompasses the upper 100 m of the Lower Breidvika Formation and the basal 30 m of the Upper Breidvika Formation (cf. the L. cylindrica Zone of Narbonne et al. 1987; Fig. 2). The only stratigraphic constraint on the Lower Duolbasgaissa Member is the presence of Volborthella tenuis reported herein (Figs 2 & 3), which is taken to mark a point at around the base of Cambrian Stage 3.

The Neoproterozoic–Cambrian boundary level in this succession lies between the highest stratigraphic occurrence of the problematicum H. podolica and the lowest occurrence of the trace fossil Treptichnus (Phycodes) pedum as in the stratotype section (cf. Brasier et al. 1994; Fig. 2). Correlation of these biozones with the GSSP strata in Newfoundland is unequivocal and provides a framework

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**Fig. 3.** Body fossils from the Ediacaran–Cambrian of the Digermul Peninsula. (a) Sabellidites cambriensis, an organic-walled tubular macrofossil from the Lower Breidvika Member used as a regional zonal index. (b) Ladatheca cylindrica, pyritized narrow conical small shelly fossil from the Lower Breidvika Member, with calcitic cavity fill, used as a zonal index in Avalonia for the Fortunian. (c) In situ Ladatheca cylindrica from the Lower Breidvika Member. (d) Assemblage of the zone fossil Volborthella tenuis from the Lower Duolbasgaissa Member. (e) Petrographic thin section through an isolated specimen of V. tenuis. (f) Conical tentaculid-like problematicum with external ornament of annular constrictions. All scale bars 1 cm.
for the stratigraphic discussion of the ichnology of the Digermul Peninsula.

**Sedimentology**

The sedimentological interpretations presented in this paper are based on a field season of detailed sedimentological logging that encompassed the whole succession above the glaciogenic Mortenses Formation to the upper part of the Upper Duolbasgaissa Formation (Fig. 2).

The Innerelva Member overlies the braided fluvial deposits of the Lillevannet Member, which is in sharp erosional unconformity with the Mortenses Formation. The lowermost portion of the Innerelva Member is composed of an upwards-fining cycle similar to that which characterizes rapid relative sea-level rise in a sediment-starved depositional system. The overlying stratigraphy suggests three cycles of weak progradation and includes thin intervals rich in turbidite- or tempestite-like current-rippled sandstones with tool-marked bases interbedded with thick silty mudstones (Fig. 2).

The Manndraperelva Member is composed of three parasequences characterized by green- and red-coloured siltstones and mudstones with minor event-bed sandstones that show a net upwards increase in grain size from very fine- to medium-grained sandstones. There is a decrease in the proportion of siltstone and mudstone beds as the sandstones increase in thickness towards the top of each cycle (Fig. 2). The sandstones are typical event-bed sandstones with weakly erosive, tool-marked bases and wave- or current-rippled tops. The ichnological assemblage of this unit (Figs 2 & 4) attests to its marine nature and the event-bed sedimentation is most consistent with deposition in a wave-dominated delta or shoreface; the red coloration of the succession is normal for marine rocks of this age (Callow et al. 2013). This parasequence set shows a net decrease in grain size (Fig. 2), reflecting an increase in the rate of generation of accommodation space relative to the sediment supply through the Manndraperelva Member.

The Breidvika Formation consists of two progradational parasequence sets separated by a prominent, low-order flooding surface that divides the Lower and Upper Breidvika members (Fig. 2). The five parasequences of the Lower Breidvika Member show a net upwards-coarsening trend. The sedimentary facies are dominantly green- to grey-coloured silty mudstones interbedded with tempestite-type event-bed sandstones with tool-marked soles, which may be rich in interface trace fossils, and show current- and wave-generated ripple cross-lamination with minor hummocky cross-stratification at the tops of parasequences. The facies thus represents progradational packages of

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**Fig. 4.** Fossils from the Ediacaran Manndraperelva Member of the Stáhpogieddi Formation. (a) The zone fossil *Harlaniella podolica*. (b) *Palaeopascichnus delicatus* on the upper surface of a sandy siltstone. (c) The corkscrew-like trace fossil *Helicolithus* on the sole of a fine-grained sandstone. (d) *Belorhaphe*, a zig-zagged trace fossil on the sole of a fine grained sandstone. (e) Whole specimen view of (b) showing the transitions from narrow *Palaeopascichnus* to broad sausage-shaped *Yelovichnus*. Scale bars in (a–d) 1 cm and in (e) 2 cm.
siliciclastic sedimentation in nearshore shelf to offshore transition zone settings and, rarely, the lower shoreface. The Upper Breidvika Member is rich in highly bioturbated green sandy siltstones interbedded with rare sandstone beds. The succession coarsens upwards into highly bioturbated purple- to red-coloured, silty, medium-grained sandstones with ripple cross-lamination and trough cross-bedding. The absence of hummocky cross-stratification suggests deposition in a prodeltaic depositional environment in which the riverine output largely masks basal wave and tidal processes. Parasequence-scale organization of the stratigraphic succession cannot be confidently determined due, in a large part, to the intense bioturbation, which suggests a consistently low rate of sedimentation.

The Duolbasgaissa Formation consists of two members that are both rich in quartzitic beds, although the Lower Duolbasgaissa Member is richer in mudstone–sandstone heterolithic units than the Upper Duolbasgaissa Member. The Lower Duolbasgaissa Member consists of a net upwards-fining succession of silty sandstones in upwards-coarsening cycles of heterolithic facies (Fig. 2). The heteroliths consist of ripple cross-laminated sandstones and siltstones with rare fossiliferous laminae composed of the agglutinated problematicum V. tenus (Fig. 3). The silty heterolithic sandstones are interbedded with rare thick beds of quartzite containing trough cross-bedding at the top of thin progradational cycles. The depositional setting of the Lower Duolbasgaissa Member is tentatively interpreted as being peritidal or a delta front with strong wave and riverine influences. The Upper Duolbasgaissa Member is a thick succession of medium- to coarse-grained quartzites with rare silty intervals. This interval requires additional sedimentological study, but is comparable with the Cambrian quartzites common around Laurentia and Gondwana in being composed of a mixture of thick compound cross-bedded units up to 3 m in thickness associated with thinner trough cross-bedded units (cf. Baldwin 1977). This highly quartzose facies is generally considered to be a non-uniformitarian depositional environment associated with extensive coastal sand-dominated systems. The marine nature of the succession is demonstrated by its marine biota (Nicholaisen & Henningsmoen 1987), the abundant trilobite trace fossils described herein, but, interestingly, the typical pipe rock biotite (see McIlroy & Garton 2009) is lacking.

Stratigraphic ichnology

Given the palaeoenvironmental similarities between the Ediacaran–Cambrian succession of the Digermul Peninsula and the GSSP – and also the fact that both sections show no significant stratigraphic hiatus – it is important to compare the ichnology of the two sections to consider which aspects of the ichnology have real potential for correlation. Our ichnological observations build on those of Banks (1970, 1973). All material is housed in the Oxford University Museum.

Innerelva Member

The short hypichnial sand-filled knobs from this member that have previously been attributed to Skolithos and Arenicolites (Banks 1970; Crimes 1987) have been reinterpreted as fluid escape structures (Farmer et al. 1992; Callow et al. 2011). Such forms have also, until recently, been compared with Beltanelliformis minutae (McIlroy et al. 2005), which has similarly been reinterpreted as fluid escape features associated with the perforation of microbial matgrounds (cf. Menon et al. 2016).

Manndraperelva Member

Recent claims for Treptichnus from the second para-sequence of the Manndraperelva Member (Högström et al. 2013) require careful validation as a result of the potential implications for the use of the ichnogenus as a stratigraphic marker (Baccock et al. 2014). Although we recognize that it is not the ichnogenus Treptichnus but the ichnospecies T. pedum that actually defines the boundary, the fundamental behavioural type used in the rationale for assigning the base of the Cambrian to the base of the T. pedum Zone is that of the trace-maker of T. pedum itself.

Although the trace fossils from this member do have comparatively straight Treptichnus-like segments (Högström et al. 2013), it is not clear whether the burrows cross-cut the bedding planes, in which case they might be considered as Planolites, or whether they are the result of branches that all arise from the underlying mudstone, in which case their assignment to Treptichnus would be validated. The only means by which this can be achieved is through careful sectioning or serial grinding (cf. Bednarz et al. 2015). The onus is on researchers to prove a more complex bedding plane pattern than could be created by a simple tubular trace fossil such as Planolites. To us, such a claim requires more work and we prefer not to accept the presence of Treptichnus from the middle part of the Manndraperelva Member at present.

The Manndraperelva Member contains a number of simple trace fossils and related problematica that are characteristic of the H. podolica Zone. Linear, late Ediacaran, structures that were described as trace fossils appear to be composed of roughly
tubular to spherical, sand-lined agglutinated chambers comparable with those of large protists (Zhuravlev 1993; Seilacher et al. 2003; Antcliffe et al. 2011). Of these, *Palaeopascichnus delicatus, Yelovichnus gracilis, Intrites punctatus* and *H. podolica* are all present in the second parasequence of the Manndraperelva Member (Fig. 4a, b, c). Simple trace fossils of very shallow tier or epibenthic organisms are also common in the second and third parasequences, including: possible *Monomorphichnus* (or similar tool marks), *Planolites, Gordia, Helminthoidichnites, Cochlichnus, Helicolithus, Belorhaphes* and rare *Curvolithus* in the third parasequence (Fig. 4c, d).

The clear presence of *P. delicatus* that transitions into *Y. gracilis, I. punctatus* and *H. podolica* in the middle Manndraperelva Member demonstrates the presence of the *H. podolica Zone*. Reports of elements of the *T. pedum* Zone stratigraphically overlapping with the *H. podolica Zone* are consistent with similar reports from other boundary sections (Brasier et al. 1994). The third parasequence of the Manndraperelva Member contains large obvious trace fossils of the *T. pedum Zone* and the oldest known *Treptichnus*-type burrows (if confirmed) would appear to consistently define a very narrow stratigraphic interval close to the level chosen for the GSSP (Brasier et al. 1994). The third parasequence of the Manndraperelva Member contains large obvious trace fossils of the *T. pedum Zone* including *T. pedum* and *Curvolithus* isp. (Banks 1970; Högström et al. 2013; Fig. 5a–c).

**Lower Breidvik Member**

The bulk of the first occurrence datums in the succession come from the Lower Breidvik Member. This is in line with our understanding of animal evolution at this time, namely the Cambrian explosion of complex animal life (Narbonne et al. 1987; Crimes 1992; Gehling et al. 2001). The most common of these are shallow, small *Skolithos*, the spiral **Gyrolithes polonicus, Arenicollites** (usually recognized by paired openings on bedding planes) and cf. *Monocraterion tentaculum*. The Lower Breidvik Member has all of these taxa close to the inferred boundary level (Fig. 6a–d). The implication that these traces represent the activities of suspension-feeding organisms is generally overstated, as many activities can be undertaken from within a simple tubular burrow of this nature (Herringshaw et al. 2010). Such an interpretation is an extrapolation of behaviour from the very different burrows of *Skolithos* (Seilacher 1967) that form a Cambrian non-actualistic ecosystem termed the pipe rock biotope (McIlroy & Garton 2009). What is clear, however, is that small organisms at around the Ediacaran–Cambrian boundary first developed the capability to burrow below the mixed layer of the sediment and/or surficial matgrounds and created semi-permanent burrows. This burrowing activity required organisms to be able to cope with elevated sulphide concentrations in pore waters and, as such, probably required some combination of bioirrigation, a mucous lining of the burrow walls and thiotrophic chemosymbionts that converted hydrogen sulphide to thiosulphate, thus producing food for the host (cf. Dubilier et al. 2008; Dufour & McIlroy 2016).

Loosely included in this trophic grouping are the trace makers of *Bergaueria* (e.g. *B. major*, Fig. 6e–g) that are probably congeneric with some of the latest Ediacaran plug-shaped fossils given the probable presence of rare motile benthic cnidarians in the mid-Ediacaran of Avalonia (Liu et al. 2010a, b, 2014). Their mode of life could be considered to be a modified version of an epibenthic lifestyle and they were probably protected from sulphidic pore waters by thick mucous linings as in modern...
burrowing cnidarians (e.g. Bromley 1990; cf. Dufour & McIlroy 2016).

The typical trace fossils of the Ediacaran–Cambrian boundary belong to the Treptichnus group of trace fossils such as *T. pedum, T. lublinensis*, tri-lobed *Treptichnus triplex* (Fig. 7a–d) and a biserial form of *Phycodes* (Fig. 7e). The trace fossils are always preserved in mudstones and as sandstone casts in positive hyporelief or full relief (Jensen et al. 2005). The burrow-fill is passive, indicating that these structures were maintained as open burrows by the trace-maker. As such, the trace-maker,
like that of the deeper subvertical burrows discussed earlier, is likely to have experienced life in potentially toxic sulphidic pore waters. The creation of shallow burrows is advantageous in that the close proximity of the burrow to oxygenated seawater means that maintaining higher levels of oxygenation is easier, perhaps enabling the culture of sulphur-oxidizing and/or methanotrophic microbiota on the burrow walls (i.e., farming behaviour). Such a mode of life is more likely to be undertaken by metazoan bilaterian animals and provides a good potential marker for the ecological and trophic diversification expected at the Ediacaran–Cambrian boundary (McIlroy & Logan 1999). Synonyms of *Treptichnus* and *Phycodes* that artificially inflate the ichnogeneric diversity of some Cambrian sections include *Saerichnites*, *Hormosiroidea* and *Neonereites*.

One of the marked differences between Ediacaran and Cambrian strata is the size and abundance of surface burrows produced by vagile near-surface deposit feeders in the Cambrian. Many of the typically Cambrian forms such as *Archaeonassa* (often historically reported as *Taphrhelminthopsis* and *Nereites*), *Psammichnites*, *Plagiogmus*, *Parataenidium*, *Didymaulichnus* and *Helminthoidichnites* clearly represent surficial or near-surface grazing activity (Fig. 8a, b). Organisms evolved the capacity to locomote in the Ediacaran (Liu et al. 2010a, b, 2014) and diversified in the latest Ediacaran (Jensen et al. 2005; Liu & McIlroy 2015), but the ichnogeneric diversity and size of the surface trails only
increases markedly in rocks of Fortunian age (McIlroy & Logan 1999; Fig. 2).

The Fortunian Lower Breidvika Member additionally includes the stratigraphically lowest examples of authentically arthropodan surficial scratch marks *Monomorphichnus* ispp. and *Dimorphichnus* (Fig. 8c, d), the bi-lobed arthropod excavation *Rusophycus* (Fig. 8e–g), as well as unusual tri-lobed burrows with biserial transverse scratch marks comparable with *Cruziana* (Fig. 8h; cf. Torell 1868, pl. 3, fig. 4). The low stratigraphic occurrence of these taxa either suggests significant overlap of the *T. pedum* and *Rusophycus avalonensis* zones of (Narbonne et al. 1987) or that the *T. pedum* interval is stratigraphically very narrow. The Lower Breidvika Formation *Cruziana* might also suggest overlap with the Cambrian Stage 2 equivalent *Cruziana tenella* Zone (MacNaughton & Narbonne 1999), although *Plagiogmus arcuatus* which is considered typical of *C. tenella* Zone, does indeed seem to define a narrow interval around the boundary between Cambrian Stages 2 and 3 (McIlroy & Heys 1999). Other arthropod trace fossils in the Lower Breidvika Member include arthropod scratching traces that cross-cut vermiform burrows, possibly evincing predatory activity (cf. Jensen 1990; Fig. 8e–f).

This high behavioural and ichnogenic diversity stratigraphically close to the base of the Cambrian demonstrates a remarkably sudden occurrence of diverse ichnological assemblages composed of large trace fossils comparable with that seen at the GSSP in Newfoundland. As there is no evidence for a significant hiatus in the Lower Breidvika Member, we are confident that there is a rapid evolutionary event at around the Precambrian–Cambrian boundary, as currently defined, which has a distinctive ichnological expression and significant potential for international correlation. The likely cause of this ichnological diversification was the
explosive radiation of complex animal life known as the Cambrian explosion and the associated palaeoenvironmental feedback loops involving the sedimentary effects of burrowing and its stimulation of microbial productivity as the fuel for the Cambrian explosion itself (McIlroy & Logan 1999).

**Upper Breidvika Member**

The intense bioturbation that characterizes much of the Upper Breidvika Member is the last remaining significant ichnological innovation in the Cambrian. Systematic bulk sediment deposit feeding, as evidenced by the presence of spreiten burrows, is not

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**Fig. 8.** Hypichnial burrows from the Lower Breidvika Member including *Parataenidium* (a, b) with a tri-lobed *Curvolithus*-like lower surface. (c) *Monomorphichnus bilinearis* (top) and *Dimorphichnus* (bottom right) associated with vermiform *Helminthoidichnites*. (d) Long *Monomorphichnus lineatus* scratch marks. (e, f) *Rusophycus avalonensis* centred on *Planolites* burrows in possible predatory associations. (g) Typical *R. avalonensis*. (h) Unusual *Cruziana* with paired laterally directed scratches, but associated with a tri-lobed *Curvolithus*-like form. All scale bars 1 cm.
known from strata reliably characterized as being Fortunian in age, but is common in Cambrian Stage 2 (McIlroy & Logan 1999). There is a marked increase in the average size of the trace fossils attributed to infaunal organisms at this stratigraphic level in siliciclastic successions (McIlroy & Logan 1999), which seems to be delayed in carbonate-rich successions (Droser & Bottjer 1988) and may have a climatic or latitudinal control (Mochizuki et al. 2014). We note that there is a significant marine flooding surface at the base of the Upper Breidvika Member that probably resulted in low rates of sedimentation, which enhances the development of intense ichnofabrics (McIlroy 2004, 2008). As such, offshore facies are not seen at lower stratigraphic levels in the studied section and we cannot be sure that the evolution of large deposit-feeding organisms did not occur earlier, but is only seen at this level because of a facies shift (McIlroy & Logan 1999). The combination of large bioturbators and low rates of sedimentation produces intense bioturbation that typically results in the destruction of 70–100% of the sedimentary laminae in this member.

The ichnodiversity of the Upper Breidvika Member is low and mostly includes the trace fossils of bulk sediment deposit feeders such as *Teichichnus, Rhizocorallium* and possible *Zoophycos* (Fig. 9a–d). No reliable spreiten burrow is known from older strata in the section, although claims of Ediacaran spreiten burrows have been posited (MacDonald et al. 2014). The only other FAD is for reliable mud-lined burrows of *Palaeophycus tubularis*, which is also the first record of constructional burrow linings in the succession (Fig. 9e). Such burrow linings are commonly formed around semi-permanent burrows either for protection from toxic pore waters or endobenthic predators/parasites, or for stability (cf. Evans & McIlroy 2016b). This member also includes a highly distinctive problematicum, which consists of an oblique burrow with numerous short ventral projections of unknown affinity (Fig. 9f).

**Lower Duolbasgaissa Member**

The Lower Duolbasgaissa Member is remarkable for the first occurrence of large shallow to mid-tier
burrows of endobenthic arthropods, including striated *Thalassinoides* and a radial form of *Trichophractus* (Fig. 10a, b). This occurs in addition to high abundances of large *Teichichnus stellatus* and *Asterichnus* (Fig. 10c, e). Prior to this stratigraphic level the burrows produced by infaunal organisms are comparatively small and most would conventionally be considered as the burrows of worm-like organisms. This invasion of the endobenthic realm by large arthropods is significant in that many arthropods are predatory, and those that live in permanent burrows are usually highly efficient bioirrigators and ecosystem engineers (Herringshaw et al. 2010; Herringshaw & McIlroy 2013). The strata with *Thalassinoides* also contain thin shell beds of the problematic agglutinated fossil *V. tenuis*, a marker for the *Schmidtiellus mickwitzi* Zone in the Baltic scheme, roughly equivalent to the base of Cambrian Stage 3. This stratigraphic interpretation is confirmed by the abundance of *P. arcuatus* (Fig. 10d; McIlroy & Heys 1999), which is a marker fossil for the *C. tenella* Zone (MacNaughton & Narbonne 1999). The trace fossil assemblage of this member is also remarkable for the presence of an exceptionally large example of *Diplichnites*, which may be taken to suggest that there were arthropods in the ecosystem of the order of 50 cm in width (Fig. 10f).

**Upper Duolbasgaissa Member**

The quartzites of the Upper Duolbasgaissa Member are generally non-fossiliferous apart from the occurrence of *Syringomorpha nilssoni* in the second quartzite and in the silty heterolithic intervals between the thick quartzites from which *Cruziana* spp., *Rusophycus* spp. and a single trace fossil resembling *Phoebichnus* (cf. Evans & McIlroy 2016a) is recorded. Some rare examples of *Rusophycus* in this facies cross-cut horizontal burrows of *Trichophycus venosus* in a manner considered by some to reflect predatory behaviour (cf. Jensen 1990; Selly et al. 2016), along with a range of body fossils including trilobites and hyolithids (Nicholaisen & Henningsmoen 1987).

**Stratigraphic ichnology of the Ediacaran–Cambrian transition**

The Neoproterozoic–Cambrian boundary is an excellent candidate for using an ichnostratigraphic approach because many animal groups evolved during the Cambrian explosion of complex animal life (e.g. Erwin 2007; Budd & Jackson 2016). This biological radiation is likely to have been paralleled by an adaptive radiation of behavioural types within

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**Fig. 10.** Trace fossils of the Lower Duolbasgaissa Member. (a) *Thalassinoides* with long scratches on burrow floor (scale 5 cm). (b) Radial species of *Trichophycus* with longitudinal scratches and rare radial scratches (scale 5 cm). (c) *Teichichnus stellatus* with typical radiating form (scale 5 cm). (d) *Plagiogmus arcuatus* typical of the *Cruziana tenella* Zone (scale 2 cm). (e) Intense bioturbation by *Asterichnus* (scale 5 cm). (f) Enormous *Diplichnites* (see hammer handle bottom right for scale) produced by a large arthropod-like organism.
the newly evolved clades into the vacant ecospace (Seilacher 1956; McIlroy & Logan 1999).

The first attempts to define the base of the Cambrian on ichnological grounds emphasized the presence of trace fossils attributed to trilobites that occur below the first occurrence of trilobite body fossils (Bergström 1970; Daily 1972; Alpert 1977). The description of trace fossils from the current GSSP in southeastern Newfoundland (Crimes & Anderson 1985; Narbonne et al. 1987) focused attention on assessing the utility of ichnology in defining the Neoproterozoic–Cambrian boundary on a global scale (Geyer & Landing, this volume, in press). The ensuing data and global compilation of FADs led to the proposal of a four-fold ichnological subdivision of the Neoproterozoic to Lower Cambrian interval (Crimes 1987, 1992, 1994). These compilations infer a slowly increasing ichnodiversity through the Lower Cambrian, but suffer from unresolved issues of stratigraphic correlation, facies bias and palaeogeography that are generally too complex and non-transparent to be reliable.

The choice of ‘Phycodes pedum’ to mark the boundary level sparked a sudden interest in the ichnotaxonomy of this taxon that has since variously been considered to belong to the following ichnotaxa: Phycodes (Seilacher 1955); Treptichnus (Jensen & Grant 1998); Trichophycus (Geyer & Uchman 1995); and Manykodes (Dzik 2005). The most recent works use T. (Phycodes) pedum. We also consider than many researchers in the 1980s and 1990s in particular used a liberal taxonomic approach when describing the ichnology of Ediacaran–Cambrian successions that has, in some cases, artificially increased ichnodiversity by publishing taphomorphs of the same taxon under a number of genera, which unnecessarily inflates the apparent suddenness of the ichnological expression of the Cambrian explosion (cf. Mángano & Buatois 2014). We emphasize that ichnological diversity cannot be equated to biological diversity, but that the evolution of fundamentally new behaviours is of evolutionary and stratigraphic importance (see Dufour & McIlroy 2016).

**Ediacaran–Cambrian ichnological zones**

By combining the first and last occurrence data of trace fossils collected during our study of both the GSSP (Narbonne et al. 1987 updated by our own field investigations) and this study, it can be seen that the vast majority of the ichnotaxa considered to be stratigraphically important in the Lower Cambrian have their first occurrence in strata of Fortunian age. It is considered that there was a real ichnological event at about this point in the rock chosen as the boundary level in the GSSP (Brasier et al. 1994). This marks a sudden increase in ichnogeneric diversity, burrow diameter and the first occurrence of abundant shallow tier open burrows, graphoglyptids and surface trails. This is in contrast with the low diversity of the underlying H. podolica Zone, which is typified by small burrows of simple construction from about 560 Ma onwards (Liu et al. 2010a, b; Liu & McIlroy 2015), along with bead-like forms similar to protists (Antcliff et al. 2011). In addition, there is a consistent stratigraphic level around the base of Cambrian Stage 2, in Baltica and Avalonia that is characterized by a rapid increase in relative sea-level and the first mid-tier spreiten burrows of deposit-feeding organisms, especially Teichichnus. Note that the occurrence of *Teichichnus* in the Fortunian of Newfoundland is not supported here and that the documented occurrences of *Diplocraterion* are reinterpreted as cross-sections of *Teichichnus*. This evolution of bulk sediment deposit-feeding organisms, as reflected in the presence of spreiten-bearing trace fossils, has some potential for wide recognition and, because it effected a change in the carbon cycle, it may even have an effect on the carbon isotope record of this interval (Brasier & McIlroy 1998).

**Conclusion**

The Ediacaran–Cambrian succession of the Diggerm Peninsula in Finnmark has provided an opportunity to calibrate the rate of ichnological innovation during the Cambrian explosion of complex animal life. The absence of a significant hiatus throughout the thick stratigraphic interval spanning the boundary level means that direct comparisons can be made with the stratotype section for the Ediacaran–Cambrian boundary in southeastern Newfoundland.

Evidence from Finnmark and Newfoundland appear to indicate that the Lower Cambrian trace fossil radiation may have been much more rapid than has hitherto been recognized.

Key stratigraphic boundaries through the Ediacaran–Cambrian are recognized by the boundary between the *H. podolica* and *T. pedum* zones, as well as the *P. antiquissimus* and *S. mickwitzii* zones and through the new discovery of the biostratigraphically significant problematic fossil *Volborthella* (Fig. 3).

Elements of the Lower Cambrian *R. avalonisensis* Zone (Narbonne et al. 1987) occur as low as the top of the first Cambrian parasequence in the Tanafjord section, confirming that the *T. pedum* Zone is consistently a very narrow stratigraphic interval (Narbonne et al. 1987; MacNaughton & Narbonne 1999). The basis of the overlying *C. tenella* Zone (MacNaughton & Narbonne 1999) is in need of further exploration because *Cruziana* is now known
from the Fortunian of Finnmark, but *P. arcuatus* generally has its first occurrence datum in Cambrian Stage 2 and its last occurrence datum in the lower part of Cambrian Stage 3.

In terms of ichnodiversity at the ichnogeneric level, there appears to have been a rapid evolution during the Fortunian (Fig. 2), especially in the form of shallow tier open sand-filled burrows and surficial traces, but it is not until a prominent marine flooding surface at around the base of Cambrian Stage 2 that bulk sediment deposit feeders evolve, especially *Teichichnus* (Fig. 2) and other deposit-feeding spreiten burrows (cf. Leaman & McIlroy in press). This bioturbational event roughly equates to the informal ‘*Teichichnus Zone*’ (Landing et al. 1989).

Although much remains to be done to trace the evolution of different body plans that enable us to recognize an ichnological trend through the evolution of the major clades, some progress has been made (Liu et al. 2010a, b; Liu & McIlroy 2015). If we are to truly understand the early evolution of the endobenthos and their impacts on sedimentary nutrient cycling through the Cambrian explosion (Brasier & McIlroy 1998; McIlroy & Logan 1999), it is vital that we realistically interpret the behaviours responsible for the trace fossils that are so common at this key moment in Earth history.

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