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A protracted Ediacaran–Cambrian transition: an ichnologic ecospace analysis of the Fortunian in Newfoundland, Canada

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Abstract

The transition between the seemingly disparate Ediacaran and Cambrian faunas is both enigmatic and body-fossil poor. The Chapel Island Formation on the Burin Peninsula, Newfoundland, Canada, contains a rich diversity of ichnofossils, providing new insight into the nature of the Ediacaran–Cambrian transition and early Fortunian ecosystems. Five ichnoguilds are recognized within the *Treptichnus pedum* zone. Ichnologic data are analysed from an ecospace perspective, revealing a more protracted transition between Ediacaran and Cambrian ecosystems. Our analysis documents the appearance of limbs, vertical burrows and uncontroversial equilibrium structures, as well as the retention of 'other' feeding styles, such as microbial grazing and chemosynthesis.

1. Introduction

The appearance of the complex, mineralized Cambrian fauna has fascinated scientists for decades. There exists a general consensus that the Ediacara biota marks the advent of metazoans (Fedonkin & Waggoner, 1997; Bobrovskiy *et al.* 2018; Dunn *et al.* 2018), though their specific phylogeny remains controversial (Bonner, 1998; Budd, 2008; Dececchi *et al.* 2017). The Cambrian fauna, however, is more easily assigned to various phylogenetic ranks (Conway Morris, 1979; Erwin *et al.* 1997; Davidson & Erwin, 2006; Chen, 2009; Budd & Jackson, 2016). With few similarities in constructional morphologies, the relationship between the Ediacaran and Cambrian biotas remains enigmatic (Droser & Gehling, 2015). This has led many researchers to question what caused this faunal turnover, commonly referred to as the 'trigger' to the 'Cambrian Explosion'. The proposed hypotheses are numerous (for reviews see Conway Morris, 2000; Marshall, 2006; Zhang *et al.* 2014; Darroch *et al.* 2018; Sperling & Stockey, 2018) and are broadly categorized into genetic, ecological and environmental causes (Erwin, 2015). There is a growing consensus that bioturbation may have played a key role in this evolutionary event (e.g. Mángano & Buatois, 2014; Hantsoo *et al.* 2018; Kaufman, 2018; Lenton & Daines, 2018). During the Ediacaran–Cambrian transition and early Cambrian Period there exists a marked infaunalization, and a switch from an Ediacaran-style matground ecology to a Cambrian-style mixground ecology (Seilacher, 1999; Mángano & Buatois, 2017; Gougeon *et al.* 2018). Whether bioturbation is a cause or consequence of the Cambrian explosion ultimately depends on the drivers of infaunalization. In turn, the elucidation of these drivers will assist in understanding the selective pressures at this time in Earth's evolution.

Using primarily body-fossil data, supplemented by ichnologic data, palaeontologists have previously conducted ecospace analyses for the Ediacaran and Cambrian periods (Bambach *et al.* 2007; Bush & Bambach, 2011; Bush *et al.* 2011; Laflamme *et al.* 2013; Knope *et al.* 2015). In these analyses a few trends are evident. A large amount of ecospace remains unoccupied in the Ediacaran, which is in stark contrast to Cambrian ecospace occupation. First, the advent of diverse groups of swimming and floating animals in the Cambrian Period marks an expansion into the pelagic realm that, with the lone possible exception of jellyfish, was largely unexplored in Ediacaran seas (Gold, 2018). Additionally, Cambrian bioturbators begin to exploit the deep-infaunal realm. Finally, the osmotrophic or 'other' feeding styles of the Ediacaran Period become rare, replaced by predation, deposit-feeding and suspension-feeding (but see Rahman *et al.* 2015; Darroch *et al.* 2017).

Due to the paucity of the body-fossil record in the Fortunian Stage, the illumination of the transition between these seemingly disparate faunas inevitably will rely on trace-fossil data. While body fossils are excellent sources to help reconstruct phylogeny, their utility to reveal behavioural information is more limited. For this, researchers must turn to ichnology, which provides an independent line of evidence to track not only the appearance of new body plans, but also the establishment of a Phanerozoic benthic ecosystem.

The lowermost Cambrian boundary section at Fortune Head, Newfoundland, Canada, as well as equivalent strata at Grand Bank Head, provides a reasonably continuous 1 km thick record through the late Ediacaran and early Cambrian periods (Myrow & Hiscott, 1993). This is recorded by the five informal members of the Chapel Island Formation (CIF). Member 1 and the first 2.4 m of member 2 are Ediacaran in age, while the Fortunian Stage is documented by the remainder of member 2 and the whole of member 3. The remaining members 4 and 5 are Cambrian Stage 2 in age (Landing, 1989). The CIF contains remnants of the Ediacaran matground ecology in Fortunian strata (Buatois *et al.* 2014) and only becomes truly Cambrian in aspect with the onset of the mixed sediment layer in the lower Cambrian Stage 2 (Gougeon *et al.* 2018). The appearance of penetrative bioturbation at the section is evidenced by the *Treptichnus pedum* Ichnofossil Assemblage Zone (IAZ). This zone is delineated by the probing sub-horizontal index fossil *Treptichnus pedum*, demarcating the beginning of the Cambrian Period (Narbonne *et al.* 1987; Landing, 1994; Buatois, 2018). While it is generally accepted that the ichnofauna of the *Treptichnus pedum* IAZ represents a higher-diversity benthos with novel feeding strategies (Narbonne *et al.* 1987; Buatois *et al.* 2014; Herringshaw *et al.* 2017), few systematic analyses of this ichnofauna exist (Crimes & Anderson, 1985).

2. Concepts and methods

The palaeoecological concept of ecospace describes the ecological space (i.e. mode of life) that an organism occupies or may theoretically occupy (Bambach *et al.* 2007). The time-averaged nature of the fossil record, and other taphonomic loss of information, cause discernible ecological parameters to be limited. Instead, palaeontologists rely heavily on functional morphology to glean insights on the lifestyles of ancient organisms (Bambach *et al.* 2007).

The guild concept, originally introduced by Root (1967) and subsequently adopted for palaeobiology by Bambach (1983), draws on this, and is a framework for classifying fossil taxa and the niches they occupy by using discernible ecological parameters. Bromley (1990; 1996) modified the Bambachian guild concept to better suit ichnological data and proposed the ichnoguild concept

The life habits of organisms were subsequently categorized into theoretical modes of life based on three ecologic parameters that can be reasonably defined with fossil data: tiering, motility and feeding (Bambach *et al.* 2007; Bush *et al.* 2007). Each parameter was divided into six subcategories, and used to construct a 6 by 6 by 6 matrix. Each axis within the matrix represents an ecological property. The subcategories are represented by rows and columns of cubes, and modes of life by individual cubes. This framework was adapted solely for ichnological data by Minter *et al.* (2016*a*) and has been useful in examining behavioural innovations and the role of bioturbation through time (Minter *et al.* 2016*b*, 2017). However, two disparate schemes for body fossils and ichnofossils may inhibit collaboration between the two bodies of evidence. In turn, both the original ecospace occupation framework of Bush *et al.* 2007 and the ecospace analysis of Bambach *et al.* (2007) took ichnofossils into account in an effort to include this pivotal body of evidence. Herein, a slightly modified version of the ecospace occupation framework of Bush *et al.* 2007 is employed (Fig. 1).

In order to achieve a greater resolution of ecological changes, particularly as it pertains to ichnofossils, some tiering ecologic subcategories have been subdivided herein, as per Minter *et al.* (2016*a*). For example, a classification of 'shallow infaunal' as living in the top 5 cm of sediment is broad, and may dilute evolutionary signals. In this case, all modes-of-life cubes for that subcategory were divided in half, to represent two subdivisions of the 'shallow infaunal tier' subcategory. These divided subcategories rows are represented in Figure 1 as half-cubes. When Ediacaran body fossils with a generalized tiering depth or height (e.g. a body fossil broadly occupying '5-shallow infaunal') were combined into this new subdivided ecospace framework, both halves (e.g. both '5a- very shallow' and '5b- shallow') of the original mode-of-life cube were occupied. Likewise, in cases where ichnological affinity was uncertain (in this case, usually within the feeding parameter) all possible modes of life were occupied in semi-transparent colour. In this manner all possible modes of life are shown, with uncertainty demonstrated through the use of semi-transparent boxes.

Ichnologic data were collected from member 2 of the CIF, located at Fortune Head and Grand Bank Head, Newfoundland. Stratigraphic sections were measured, and ichnofossil occurrences documented and photographed when possible.

3. Ichnoguild analysis

3.a. *Bergaueria* ichnoguild

The *Bergaueria* ichnoguild consists of *Bergaueria* isp., *Bergaueria perata* and *Conichnus conicus*. All three are plug-shaped burrows, likely produced by sea anemones (Alpert, 1973; Pemberton *et al.* 1988), and therefore these ichnotaxa are interpreted as reflecting the work of predators. *Bergaueria perata*, *Bergaueria* isp. and *Conichnus conicus* are very shallow, semi-infaunal burrows, and *Bergaueria* isp. demonstrates burrow adjustment with sedimentation (Fig. 2p, q). In turn, the producer actively wedged within the sediment, and in the case of *Bergaueria* isp. demonstrated motility with sedimentation. Therefore, they are classified as attached, facultative motile, semi-infaunal burrowers which likely fed through predation.

3.b. *Dimorphichnus* ichnoguild

The *Dimorphichnus* ichnoguild consists of *Dimorphichnus* cf. *obliquus*, *Monomorphichnus* isp. A, *Monomorphichnus* isp. B and *Monomorphichnus* isp. C (Fig. 2r, n, m, l, respectively), all representing animals with articulated appendages able to produce 'scratch marks' (i.e. striae). They are all the result of fast fully motile arthropods walking on, or scratching, a sediment surface and as such occupied the surficial tier (Seilacher, 1955; Crimes, 1970; Fillion & Pickerill, 1990). The feeding habits of these primitive arthropods are still a debated topic among researchers. *Dimorphichnus* is generally regarded as a 'grazing' trace (Seilacher, 1955, 1990); however, it is not clear whether or not this organism grazed on microbial mats, fed on organic detritus, or preyed on meiofauna or small macrofauna. In fact, there is growing evidence that small epibenthic organisms may have constituted a significant part of the diet of many Cambrian arthropods (Vannier, 2012; Zacai *et al.* 2016). Minter *et al.* (2012) interpreted large, arthropod trackways attributed to a Tegopeltid arthropod as recording predation on meiofauna and small macrobenthic elements. As a result, all three possible feeding modes of life are shown as occupied in Figure 1. Therefore, they are classified as fast freely motile, surficial organisms, with a variety of feeding styles.

3.c. *Gyrolithes* ichnoguild

The *Gyrolithes* ichnoguild consists of *Gyrolithes gyratus*, *Gyrolithes scintillus* and *Trichichnus* cf. *simplex* (Fig. 2h, i, o, respectively).

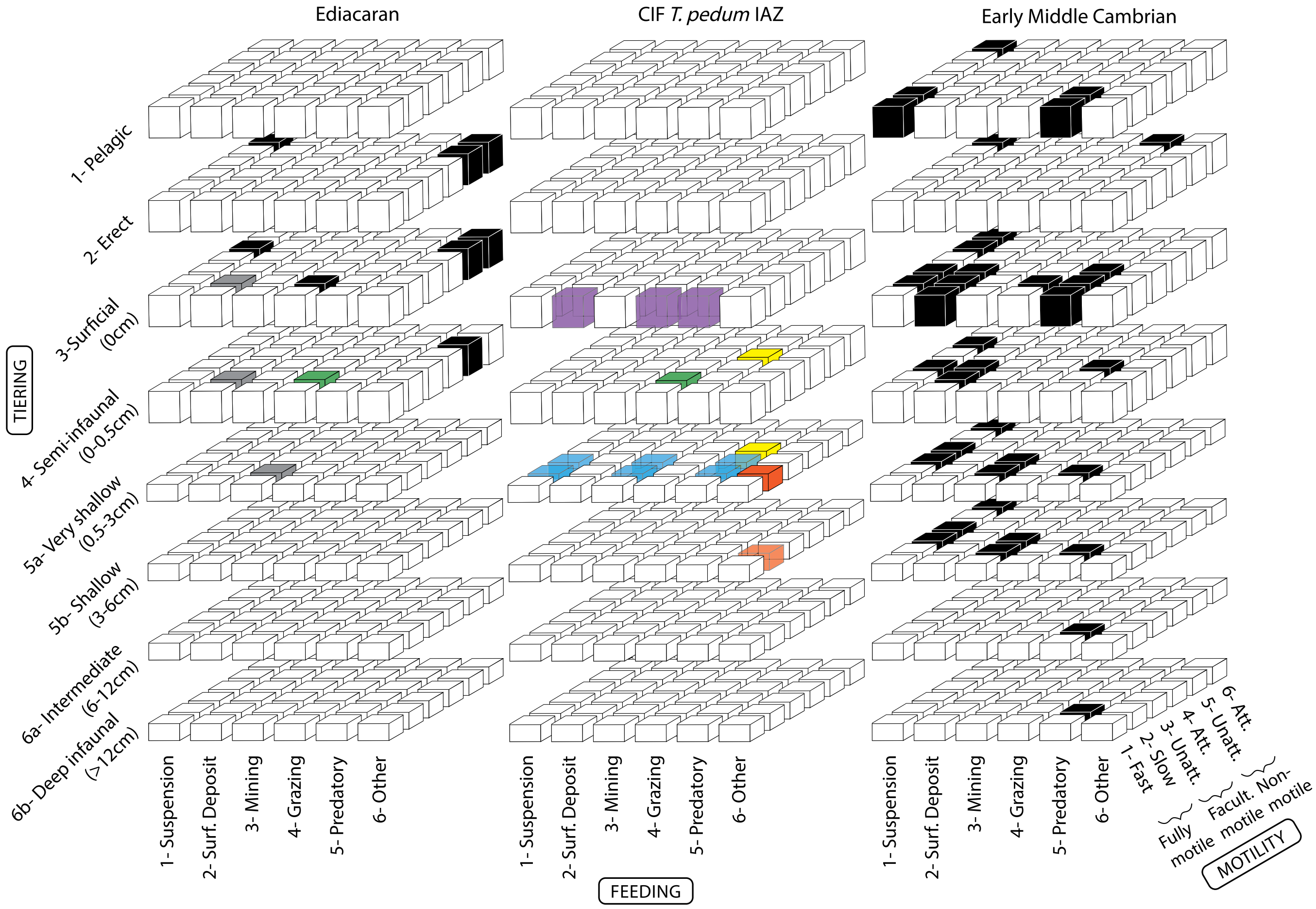

Fig. 1. (Colour online) Ecospace analysis for the Ediacaran Period to early-middle Cambrian. Black boxes represent modes of life occupied by body fossils globally, and grey boxes represent modes of life occupied by trace fossils globally (data from Laflamme *et al.* 2013). Coloured boxes represent modes of life occupied by CIF *T. pedum* IAZ ichnoguilds (IG). Green = *Helminthoidichnites* IG. Blue = *Treptichnus* IG. Yellow = *Bergaueria* IG. Orange = *Gyrolithes* IG. Purple = *Dimorphichnus* IG. Transparent boxes indicate modes of life with several possible tiers, feeding styles or motility levels.

These are all vertical burrows, attaining a maximum depth of 3 cm, representing very shallow tier burrowers. They were probably originally deeper however, as all burrows have been truncated by erosion. The *Gyrolithes* ichnospecies were likely constructed by a vermiform organism (Laing *et al.* 2018), while *Trichichnus* has been hypothesized as formed by large bacterial colonies (Kędzierski *et al.* 2015; although see McBride & Picard, 1991 and Gingras & Pickerill, 2002 for alternative possible producers). They are both slow, fully motile organisms. The *Trichichnus* producer is suspected to have relied on chemosynthesis, while *Gyrolithes scintillus* and *G. gyratus* likely fed through microbial gardening. Therefore, they are classified as slow fully motile organisms, occupying the very shallow tier, with ‘other’ feeding styles.

3.d. *Helminthoidichnites* ichnoguild

The *Helminthoidichnites* ichnoguild consists of *Archaeonassa fossulata*, *Cochlichnus anguineus*, *Gordia* isp., *Helminthoidichnites tenuis* and *Helminthopsis tenuis* (Fig. 2a, e, c, d, b respectively). These are all simple, horizontal trails, occupying the uppermost 0.5 cm of sediment (semi-infaunal). Their common association with microbially induced sedimentary structures suggests they all fed on microbial mats, implying a grazing feeding style (Buatois & Mángano, 2003; Buatois *et al.* 2014; Carbone & Narbonne, 2014). While *Helminthoidichnites* has been suggested as recording opportunistic scavenging of Ediacaran organisms in Australia (Gehling & Droser, 2018), this behaviour has not been documented in the CIF specimens. Consequently, these ichnofossils are essentially interpreted as pascichnial trails, combining feeding and locomotion, and as a result were likely slow fully motile semi-infaunal, grazers.

3.e. *Treptichnus* ichnoguild

The *Treptichnus* ichnoguild consists of *Palaeophycus* isp., *Palaeophycus tubularis*, *Treptichnus coronatum* (Fig. 2g, f, j respectively), *Treptichnus* isp. and *Treptichnus pedum* (Fig. 2k). These sub-horizontal to horizontal burrows penetrated 0.5–3 cm into the substrate, occupying a very shallow tier. As vermiform burrowers of a possible priapulid-like scalidophoran affinity (Kesidis *et al.* 2019), that likely seldom left their burrows, they are classified as either slow fully motile or facultative motile. The feeding mechanism of these tracemakers is difficult to discern, and it would be premature to create multiple ichnoguilds given this uncertainty. *Palaeophycus* may be the burrow of a passive predator or suspension feeder (Pemberton & Frey, 1982). *Treptichnus* is often hypothesized to be the result of passive predation (Vannier *et al.* 2010) or undermat mining (Seilacher *et al.* 2005). As a result, only one ichnoguild is currently proposed; however, this may need to be subdivided when more information on the lifestyle of the burrowers is

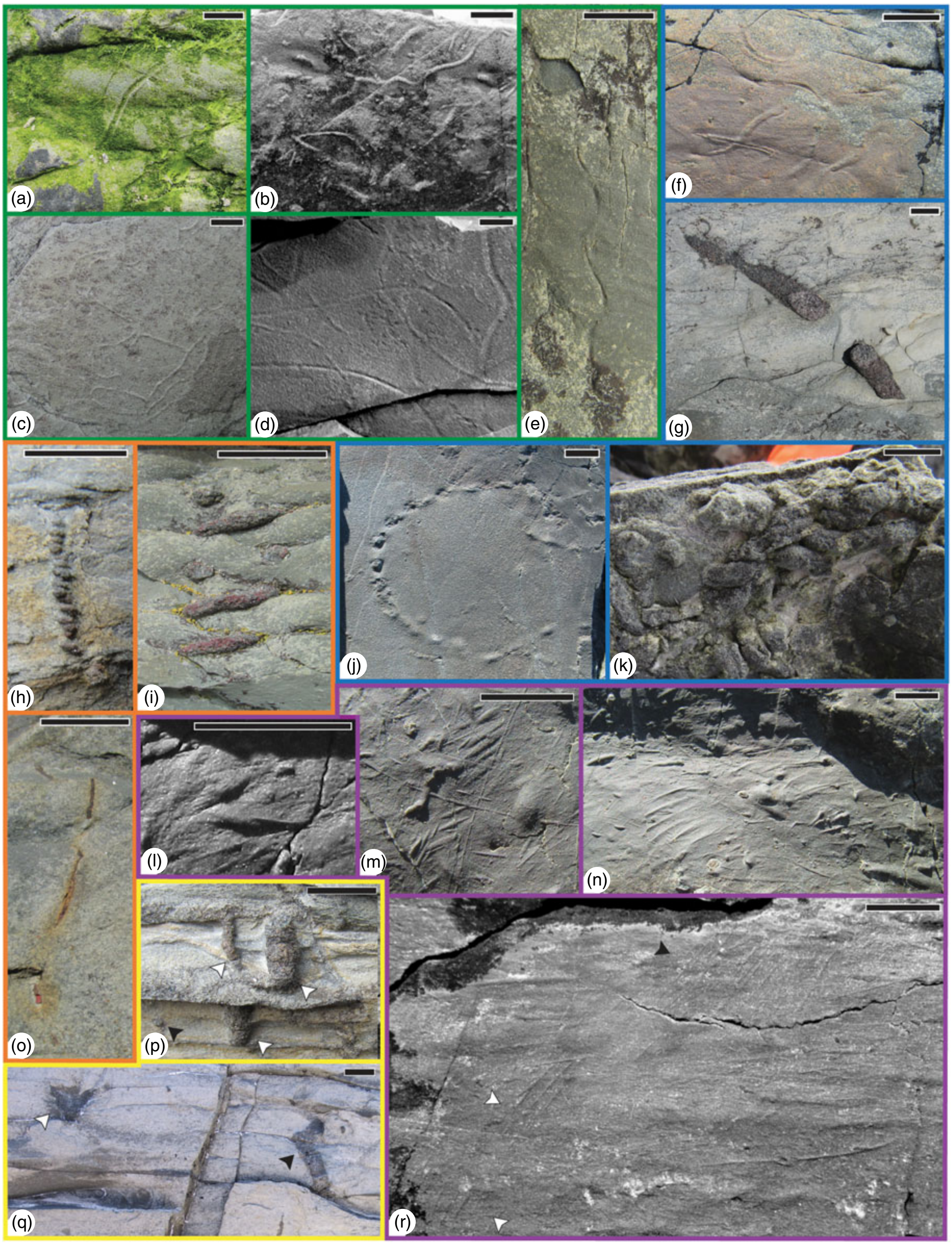

Fig. 2. (Colour online) Ichnotaxa from member 1 and the *T. pedum* IAZ of member 2 of the Chapel Island Formation. All scale bars are 1 cm. (a) *Archaeonassa fossulata*, preserved in epirelief (FH 2.6 m). (b) *Helminthopsis tenuis*, preserved in positive hyporelief (FH 87 m). (c) *Gordia* isp., preserved in positive hyporelief (FH 142 m). (d) *Helminthoidichnites tenuis*, preserved in positive and negative hyporelief. (e) *Cochlichnus anguineus*, preserved in negative epirelief (FH 12 m). (f) *Palaeophycus tubularis*, preserved in negative epirelief and full relief (FH 20.9 m). (g) *Palaeophycus* isp. preserved in full relief (FH 69 m). (h) *Gyrolithes gyratus*, preserved in full relief (FH 14.8 m). (i) *Gyrolithes scintillus*, preserved in full relief (FH 7.7 m). (j) *Treptichnus coronatus*, preserved in positive hyporelief (GBH6 12 m). (k) *Treptichnus pedum*, preserved in positive hyporelief (FH 1.35 m). (l) *Monomorphichnus* isp. C preserved in positive hyporelief (GBH6 11.1 m). (m) *Monomorphichnus* isp. B preserved in positive hyporelief (GBH6 11.1 m). (n) *Monomorphichnus* isp. A preserved in positive hyporelief (GBH6 11.1 m). (o) *Trichichnus* cf. *simplex* preserved in full relief (FH 29 m). (p) White arrows: *Bergaueria* isp. Black arrow: *Bergaueria perata*. Both preserved in full relief (FH 4.5 m). (q) White arrow: *Conichnus conicus*. Black arrow: *Bergaueria* isp. Both preserved in full relief (FH 87 m). (r) *Dimorphichnus* cf. *obliquus*, preserved in positive hyporelief. White arrows denote pushers, while black arrows denote rakers (GBH6 12 m). Box outline corresponds with the ichnotaxon's ichnoguild. Green boxes (a, b, c, d and e) are the *Helminthoidichnites* ichnoguild. Blue boxes (f, g, j and k) are the *Treptichnus* ichnoguild. Orange boxes (h, i and o) are the *Gyrolithes* ichnoguild. Purple boxes (l, m, n and r) are the *Dimorphichnus* ichnoguild. Yellow boxes (p and q) are the *Bergaueria* ichnoguild. FH = Fortune Head, GBH6 = Grand Bank Head site 6 (47.108, −55.770).

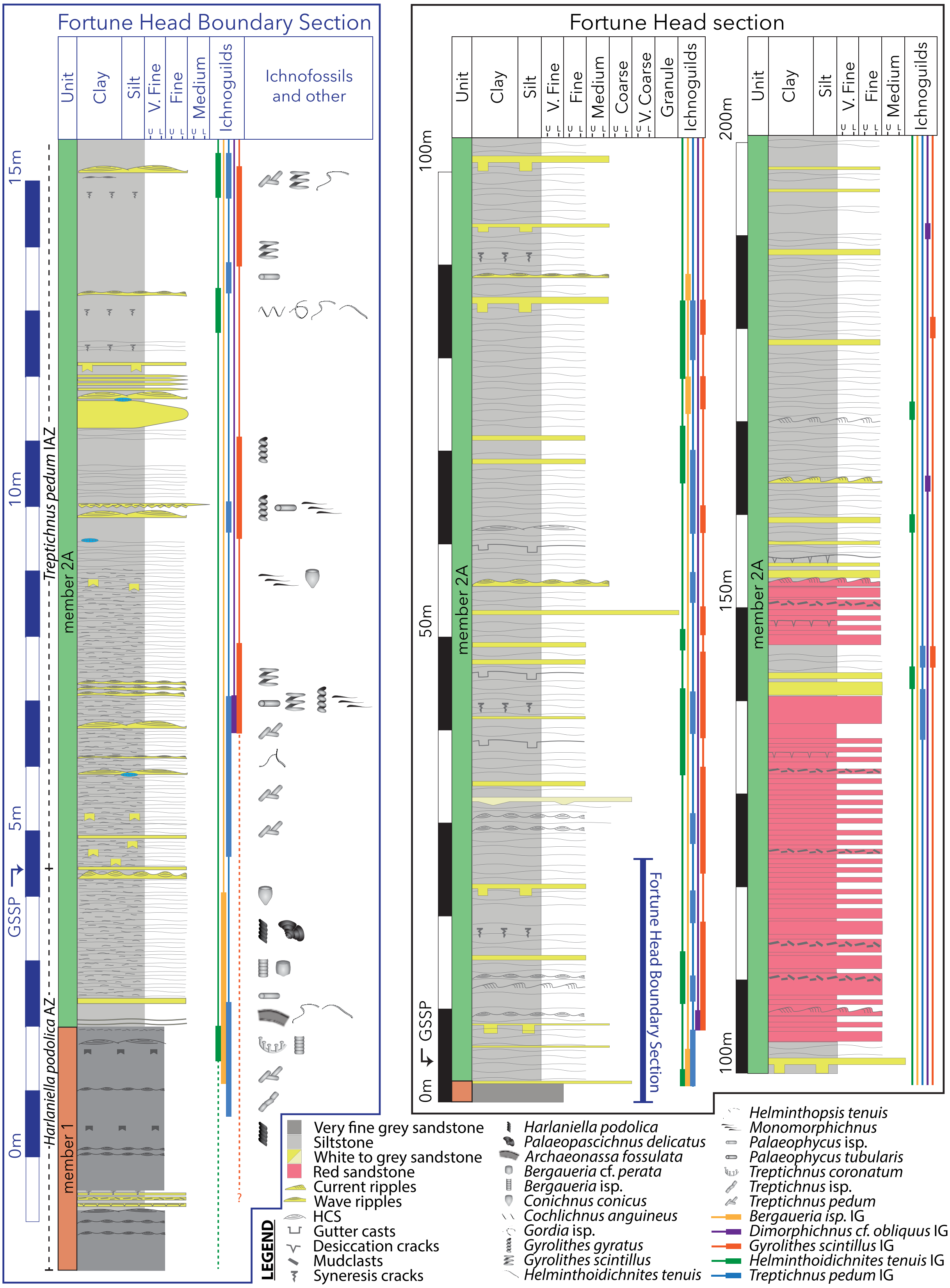

Fig. 3. (Colour online) Stratigraphic sections of the Chapel Island Formation at Fortune Head, Newfoundland. The rightmost two sections (surrounded by a black box) document the sedimentology and ichnoguild appearances of the last 4 m of member 1 and the *T. pedum* IAZ of member 2. In this section, the region indicated by a blue bar corresponds to the leftmost section (surrounded by the blue box). This section encompasses the Ediacaran–Cambrian boundary, and documents the sedimentology, ichnoguilds and ichnofauna therein.

made available. Therefore, they are classified as slow fully motile or facultative motile, very shallow tier burrowers, with a variety of feeding styles (suspension feeding, undermat mining and predation).

4. Discussion

By plotting these ichnoguilds in a stratigraphic (Fig. 3) and ecospace framework (Fig. 1), a few initial trends can be noted. The *Helminthoidichnites* ichnoguild is documented within the Ediacaran Period (Crimes & Anderson, 1985; Narbonne *et al.* 1987; Landing *et al.* 1988). The *Treptichnus* and *Bergaueria* ichnoguilds appear just below the Ediacaran–Cambrian boundary, documenting a deeper tier than the stratigraphically older *Helminthoidichnites* ichnoguild, accompanied by a possible *Gyrolithes* (Gehling *et al.* 2001). Additionally, *Treptichnus* as well as *Bergaueria* isp. document more sophisticated methods of interacting with the substrate. *Treptichnus pedum* and *T. coronatum* are the earliest penetrative burrows, while *Begaueria* isp. may represent the first uncontroversial equilibrium structure. The deeper agrichnial and chemichnial ichnofossils (*Gyrolithes* ichnoguild) appear in large numbers slightly above (~3 m) the Ediacaran–Cambrian boundary accompanied by ichnofossils indicative of fast, freely motile organisms (*Dimorphichnus* ichnoguild). These represent the first true vertical burrows as well as the first evidence of limbs recorded in this section and globally.

The interval documented by the *T. pedum* IAZ is notoriously body-fossil poor, and ecospace analyses have been restricted to the Ediacaran and early-middle Cambrian (Bambach *et al.* 2007; Laflamme *et al.* 2013). Fortunian ichnofossils therefore provide an important window between these two disparate faunas. The CIF trace fossils offer a local view into this critical time period. When contrasted with the modes of life hypothesized for Ediacaran fauna and early-middle Cambrian fauna (Fig. 1), a few initial trends can be detected. First, a transition in feeding styles can be seen. Hypothesized feeding styles for Ediacaran forms range from mat grazing (Buatois *et al.* 2014; Gehling *et al.* 2014), mat digesting (Sperling & Vinther, 2010), osmothrophy (Laflamme *et al.* 2009) and chemosynthesis (Burzynski *et al.* 2017) (for a review see Droser & Gehling, 2015). While the Ediacaran fauna is dominated by ‘other’ and grazing feeding styles, early-middle Cambrian feeding types are similar to those recorded in modern benthic ecosystems, notably predation and deposit-feeding. Interestingly, the CIF ichnofauna documents a transition between the two. The *Gyrolithes* and *Helminthoidichnites* ichnoguilds show affinities with Ediacaran-like feeding-styles, such as chemosynthesis and mat grazing. However, the Cambrian-like predatory and deposit-feeding modes of life are documented by the three remaining ichnoguilds (*Bergaueria*, *Dimorphichnus* and *Treptichnus* ichnoguilds).

Second, burrowers (slow fully motile organisms) begin to explore deeper tiers than previously documented. Ediacaran tiering was restricted to benthic organisms attached to the sea-floor with no definitely pelagic or nektonic organisms (Clapham & Narbonne, 2002; Laflamme *et al.* 2013; Gold, 2018). Documented burrowers existed in the latest Ediacaran Period, although they were restricted to the shallow infaunal realm and there is no discernible infaunal tiering (Jensen *et al.* 2000, 2005, 2006; Jensen & Runnegar, 2005; Laflamme *et al.* 2013; Buatois & Mángano, 2016; Buatois *et al.* 2016, 2018). In the Fortunian of the CIF however, true vertical burrows represented by the *Gyrolithes* ichnoguild (*Gyrolithes gyratus*, *G. scintillus* and *Trichichnus* cf. *simplex*) attained a depth of at least 3 cm (Laing *et al.* 2018). In turn, subhorizontal burrows (*Treptichnus* and *Palaeophycus*) as well as sea anemone resting burrows (*Begaueria* isp.) occupied a greater proportion of the shallow infaunal tier than in the Ediacaran. While not well developed, the *Gyrolithes*, *Treptichnus*, *Bergaueria* and *Helminthoidichnites* ichnoguilds together demonstrate an infaunal tiering structure which was non-existent in the Ediacaran.

Finally, motile modes of life became more common. Arthropod striae of the *Dimorphichnus* ichnoguild mark the appearance of fast freely motile organisms. This evidences the appearance of limbed organisms and likely reflects the diversification and ecological success of the arthropod body plan. In turn, the burrow *Bergaueria* isp. demonstrates an ability to adjust with sedimentation, and may be the first equilibrium burrow recorded.

5. Conclusions

The Fortunian ichnofauna within the *Treptichnus pedum* IAZ at the basal Cambrian GSSP (Global Boundary Stratotype Section and Point) documents a wide variety of innovations characteristic of the Cambrian. Within 3 m of the basal Cambrian boundary, the ichnofossils document: (1) early penetrative burrows, first with the *Treptichnus* ichnoguild, then with the deeper *Gyrolithes* ichnoguild, (2) fast freely motile (limbed) organisms, with the *Dimorphichnus* ichnoguild, (3) uncontroversial equilibrium structures, with *Bergaueria* isp., and (4) the appearance of possible predators, with the *Bergaueria*, *Dimorphichnus* and *Treptichnus* ichnoguilds. In addition to these innovations, the ichnofossils document ecologic strategies characteristic of the Ediacaran, such as (5) chemosynthetic or ‘other’ feeding styles with the *Gyrolithes* ichnoguild and (6) grazing feeding styles, with the *Helminthoidichnites* ichnoguild. The CIF demonstrates that the ichnofauna right above the boundary in Newfoundland employed strategies which mirrored their transitioning ecosystems, utilizing both Ediacaran strategies and Cambrian strategies to survive.

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