

**REDEFINING THE *TREPTICHNUS PEDUM* ZONE AT THE GLOBAL
BOUNDARY STRATOTYPE SECTION AND POINT (GSSP): A
CRITICAL REASSESSMENT OF THE EDIACARAN-CAMBRIAN
BOUNDARY.**

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By
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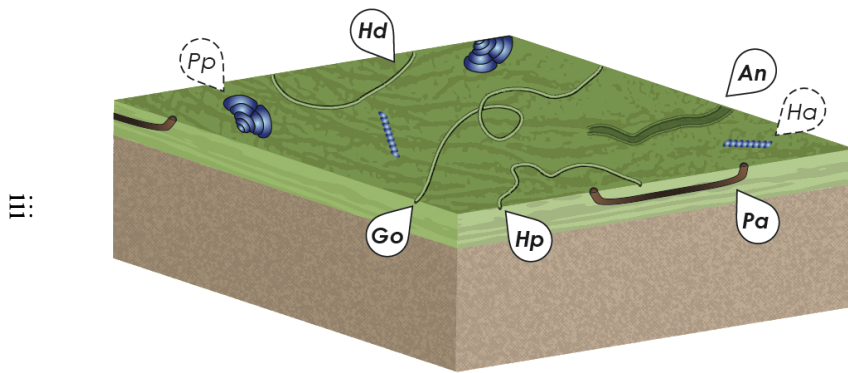
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Abstract

The Cambrian explosion bisects the history of life, separating relatively simple pre-Cambrian life from a complex and diverse Cambrian fauna. Due to the paucity of the body-fossil record, trace fossils often offer the only available insight into these evolutionary milestones, representing a continuous record through the late Ediacaran-early Cambrian. The Chapel Island Formation (CIF) of the Burin Peninsula, Newfoundland, provides an exceptional record of these innovations. Currently, the Global Boundary Stratotype Section and Point (GSSP) for the basal Cambrian boundary is located 2.4 m above the base of member 2 of the CIF, delineated by the lowest observed appearance of the *Treptichnus pedum* Ichnofossil Assemblage Zone (IAZ). Currently, researchers are facing difficulties when attempting to correlate with a few sections worldwide, and a formal revision of the boundary has been proposed. We hypothesize that a revision of the ichnotaxonomy of the GSSP with an emphasis on trace fossil functional morphology may better illustrate evolutionary innovations at the Ediacaran-Cambrian boundary. In turn, this revised ichnotaxonomy may provide further support for the position of the Ediacaran-Cambrian GSSP. Through a bed-by-bed study, the ichnotaxonomy of the *T. pedum* IAZ was revised, and a stratigraphic section was measured. Twenty ichnospecies comprising thirteen ichnogenera were observed (Figure 0.1). The ichnospecies were grouped into five ichnoguilds, which were used to conduct an ecospace analysis of the section. The ichnofauna revealed a more gradual appearance of ichnofossil diversity at the boundary, and a more protracted transition between Ediacaran and Cambrian ecosystems than previously envisioned. The *T. pedum* IAZ in the CIF marks the appearance of novel methods of interacting with the substrate as documented by sub-horizontal branching burrows (treptichnids), equilibrium structures (*Bergaueria* isp.), and complex vertical burrows (*Gyrolithes scintillus*). Additionally, it marks the evolution of novel body plans, as revealed by the presence of arthropod scratch marks (*Dimorphichnus* cf. *obliquus*). However, remnants of Ediacaran matground ecology are also present. Farming feeding styles are utilized by the *Gyrolithes scintillus* ichnoguild, and mat grazing remains a common feeding style. These ichnotaxa provide valuable insight into the very beginnings of vertical, penetrative burrowing. They further illuminate the depth and rate at which this new lifestyle evolved, and shed light on the evolution of three-dimensional burrowing.

Harlaniella podolica IAZ



Treptichnus pedum IAZ

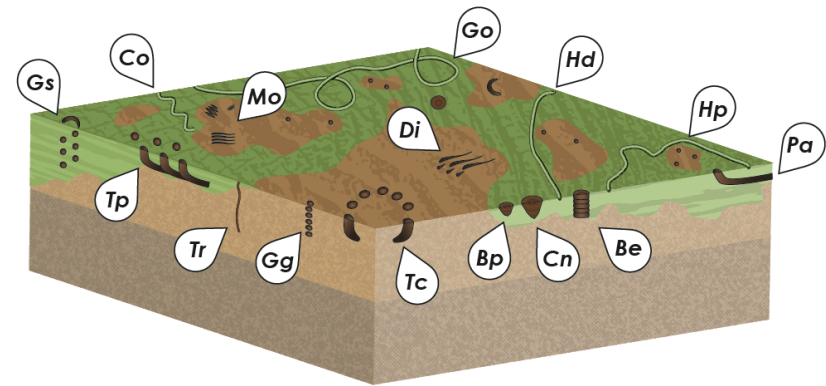


Figure 0.1 Block diagrams of the ichnofauna observed within the *Harlaniella podolica* IAZ and the *Treptichnus pedum* IAZ, as documented within the CIF at Fortune Head. Ichnofossils: *Archaeonassa fossulata* (An), *Bergaueria* isp. (Be), *Bergaueria perata* (Bp), *Conichnus conicus* (Cn), *Cochlichnus anguineus* (Co), *Dimorphichnus* cf. *obliquus* (Di), *Gyrolithes gyratus* (Gg), *Gordia* isp. (Go), *Gyrolithes scintillus* (Gs), *Helminthoidichnites tenuis* (Hd), *Helminthopsis tenuis* (Hp), *Monomorphichnus* (isp. A, isp. B, isp. C) (Mo), *Palaeophycus* (isp. and *tubularis*) (Pa), *Treptichnus coronatum* (Tc), *Treptichnus pedum* (Tp), *Trichichnus* cf. *simplex* (Tr). Body fossils (in blue): *Harlaniella podolica* (Ha), *Palaeopascichnus delicatus* (Pp).

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Dedication

To my family, whose support and enthusiasm is everlasting.

Specifically:

Mom—for pushing me to be the best expression of myself, always.

Dad—for sharing your love of the natural world.

Brendon and Robyn— for your unwavering belief in me.

Grandad and Allison— for your uninhibited encouragement.

To Kimberley and Steph—for always being close by, despite being miles apart.

To Luc.

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List of Abbreviations

CIF	Chapel Island Formation
FH	Fortune Head
GBH	Grand Bank Head
GC facies.....	Gutter Cast Facies
GSSP	Global boundary Stratotype Section and Point
IAZ	Ichnofossil Assemblage Zone
IG	Ichnoguild
ISES	International Subcommittee on Ediacaran Stratigraphy
LDC.....	Little Danzig Cove
SCS	Subcommittee on Cambrian Stratigraphy
SIS-D facies	Siltstone-Dominated Facies
SS-D facies.....	Sandstone-Dominated Facies
MISS	Microbially induced sedimentary structur

CHAPTER 1

1. Introduction

The Proterozoic-Phanerozoic transition is arguably the most profound time of evolutionary change in Earth's History. It bisects the history of life between an enigmatic Precambrian biota and the appearance of shells and brains with the Cambrian fauna. It is therefore imperative that the geological evidence upon which the Precambrian-Cambrian boundary is placed reflects these significant evolutionary innovations. The onset of penetrative bioturbation has long been considered a pivotal component of the rapid animal diversification characteristic of the early Cambrian (Seilacher, 1999). The Ediacaran-Cambrian Chapel Island Formation (CIF) located on the Burin Peninsula, Newfoundland provides an excellent record of these innovations (Crimes and Anderson, 1985; Narbonne et al., 1987; Crimes, 1992; Landing, 1994; Gehling et al., 2001; Droser et al., 2002; Buatois et al., 2014). Of particular use are the thickness and repetitive nature of facies in the CIF. In 1992 the International Commission on Stratigraphy (ICS) chose the first penetrative branching burrows as a reliable criterion to delineate the basal Cambrian boundary (Brasier et al., 1994). This is represented by the *Treptichnus pedum* Ichnofossil Assemblage Zone (IAZ), whose lowermost limit was placed at the lowest observed occurrence (First Appearance Datum) of *Treptichnus pedum* at the time of ratification (Landing, 1994). This decision was based on ichnological studies conducted in the late 1980's (Crimes and Anderson, 1985; Narbonne et al., 1987; Landing et al., 1988). While there has been a resurgence of interest in the lowermost Cambrian boundary section (Gehling et al., 2001; Droser et al., 2002; Buatois et al., 2014; Herringshaw et al., 2017) and the placement of the Global Boundary Stratotype Section and Point (GSSP) itself (Landing et al., 2013; Babcock et al., 2014; Geyer and Landing 2016; Buatois, 2018), the ichnotaxonomic determinations of the trace fossils present in this section have remained relatively untouched. Recently, researchers have encountered difficulties when attempting to correlate the GSSP with a few boundary sections worldwide. As such, the placement of the GSSP along with the IAZ upon which it is based have received scrutiny, and a revision of the boundary has been formally proposed (Babcock et al., 2014).

1.1. Conceptual background, Hypotheses and Objectives

The *T. pedum* IAZ is currently placed 2.4 m above the base of member 2 in the Chapel Island Formation in Fortune Head, Newfoundland (Landing, 1994). At the time of ratification, the IAZ was described as consisting of *Treptichnus pedum*, *Skolithos annulatus*, *Arenicolites* isp., *Monomorphichnus* isp., *Conichnus conicus*, *Helminthopsis tenuis*, *Phycodes* isp., *Gyrolithes* isp., and *Curvolithus* isp. (Narbonne et al., 1987; Landing et al., 1988). Since ratification, the FAD of *Treptichnus pedum* has proven useful for lowermost Cambrian correlation in Namibia (Wilson et al., 2012; Buatois et al., 2013), southern and central Australia (Baghiyan-Yazd, 1998; Jensen et al., 1998; Droser et al., 1999), western United States (Jensen et al., 2002; Smith et al. 2016), central England (McIlroy and Horák, 2006), and northwestern Canada (MacNaughton and Narbonne, 1999; Carbone and Narbonne, 2014), among other sections.

However, some researchers are currently facing problems when attempting to correlate the GSSP horizon, particularly as it pertains to the carbonate-dominated sections in Gondwana and Siberia (Babcock et al., 2014). As a result, the placement of the GSSP has recently resurfaced as a topic of interest (Gehling et al. 2001; Droser et al. 2002; Babcock et al. 2014). In 2013, the International Subcommittee on Ediacaran Stratigraphy (ISES) organized a Working Group on the Terreneuvian Series and Fortunian Stage. Their purpose is to investigate concerns and to consider the possibility of adjusting or redefining the GSSP (Babcock et al., 2014).

A revision of the *T. pedum* IAZ may assist in broadening the constraints of the GSSP and improve the ability to use these ichnotaxa in global correlations. In addition to a taxonomic revision, re-examination of the interval containing the Ediacaran-Cambrian boundary and lowermost Fortunian strata with an emphasis on novel behavioural strategies is critical. Ichnofossils are a direct result of organism behaviour, anatomy, and mode of life. Increased ichnofossil complexity can thus be reasonably used as a proxy for increased behavioural and anatomical complexity. Likewise, the appearance of novel ethologic categories implies novel modes of life. The appearance of ichnofossils evidencing increased substrate penetration, as well as novel ethologic categories, such as *Domichnia*, *Fodichnia*, and *Repichnia*, thus represents true evolutionary innovations. Further, the first possible coelomate bilaterian was likely macroscopic with a benthic lifestyle (Valentine, 1994; Budd and Jensen, 2000; Collins and Valentine, 2001; Budd and Jensen, 2017). There is a growing consensus that the first bilaterians may have produced traces and that there is evidence of bilaterian ichnofossils in Ediacaran strata (Budd and

Jensen, 2000; Mángano and Buatois, 2014; Buatois and Mángano, 2016; Budd and Jensen, 2017).

The following hypotheses will be evaluated:

- (1) Will a reassessment of the ichnotaxonomy of the GSSP section provide further support for the position of the Ediacaran-Cambrian boundary?
- (2) Does a detailed revision of the *Treptichnus pedum* Ichnofossil Assemblage Zone with an emphasis on trace-fossil functional morphology better illustrate evolutionary innovations across the Ediacaran-Cambrian boundary (i.e., major metazoan radiation = Cambrian explosion)?

Through this project we aim to:

- (1) Provide a revision of the ichnology at the Ediacaran-Cambrian GSSP.
- (2) Evaluate the appearance of evolutionary innovations at the Ediacaran-Cambrian GSSP.
- (3) Redefine the *Treptichnus pedum* Ichnofossil Assemblage Zone based on a re-evaluation of the ichnologic content of the GSSP.

1.2. A review of Ichnology

Ichnology, the study of trace fossils, is a unique blend of paleontology and sedimentology (Pemberton et al., 1992). This field comprises the study of sedimentary structures (traces) produced by organisms. This encompasses all features of bioturbation (trails, tracks, and burrows), bioerosion (borings), and biodeposition (e.g., fecal pellets) (Bromley, 1990; 1996; Buatois and Mángano, 2011). After the discovery of the first fossil footprints by Dr. Duncan in 1828 (Duncan, 1828, Pemberton and Gingras, 2003), the study of vertebrate ichnology gained brief popularity (Figure 1.1). Invertebrate trace fossils, however, were commonly misclassified as fossil algae (“fucoids”) (Osgood, 1975a). Once it was determined that these fossils were in fact ichnofossils by Nathorst in 1881, interest in the study waned (Figure 1.1) (Osgood, 1975a), although some systematic studies from this time do exist (Richter, 1927; 1931; 1941). This was in large part due to the fact that it is often difficult to assign a specific tracemaker to an ichnotaxon. This is owing to a few key principles in ichnology (Frey, 1975; Bromley, 1981;

1990; 1996; Ekdale et al., 1984; Pickerill, 1994; Pickerill and Narbonne, 1995; Bertling et al., 2006; Buatois and Mángano, 2011):

- (1) A single organism may produce multiple ichnotaxon
- (2) A single ichnotaxon may be produced by multiple organisms
- (3) Multiple organisms may produce a single structure

Eventually classification and cataloging of ichnofossils grew (Seilacher, 1953; Häntzschel, 1962; 1965), yet interest in the study remained limited (Figure 1.1). In 1967, Dolf Seilacher showed that rather than provide information on a tracemaker, trace fossils uniquely record the behaviour of ancient organisms (Seilacher, 1967). He demonstrated that they provide a rare opportunity to observe organism behaviour through time, which led to a “renaissance” (resurgence) of the field throughout the late 1900’s (Figure 1.1). This resurgence was followed by a focus by the scientific community to provide a classification framework and taxonomical structure for biogenic sedimentary structures (for a review see: Buatois and Mángano, 2011, section 1.1).

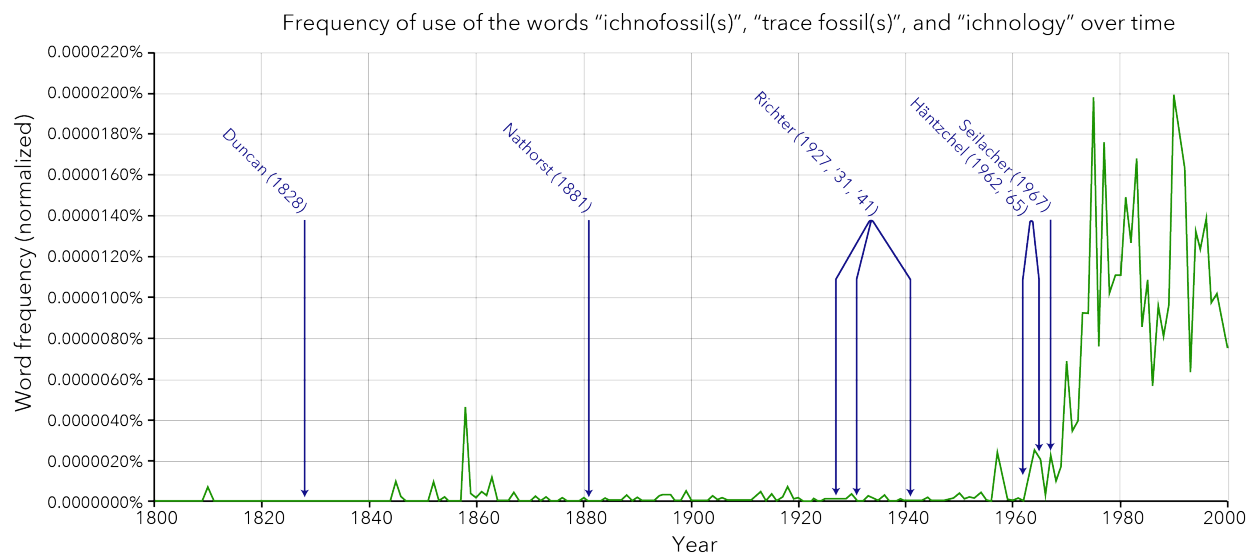


Figure 1.1 Graph of the usage frequency of the words “ichnofossil(s)”, “ichnology”, and “trace fossil(s)” over time. Usage frequency was calculated by dividing the number of times a word was used in a specific year by the number of words in the database (Google Books) for that year. Graph created using Google ngram viewer; for more information see Michel et al. (2011).

1.2.1. Seilacher's (1964) and Martinsson's (1970) preservational categories

One such classification framework deals with the stratinomy (preservation, excluding alteration) of ichnofossils (for reviews see Hallam, 1975; Frey and Pemberton, 1985; Buatois and Mángano 2011 section 1.3.1). Two schemes are currently used today (Seilacher, 1964; Martinsson, 1970), and deal with the relationship between the trace fossil and its casting medium (Figure 1.2). If an ichnofossil is preserved at the top of a stratum, it is described as being preserved in 'epirelief' (Seilacher, 1964) or as 'epichnia' (Martinsson, 1970). An ichnofossil preserved at the base of a stratum is referred to as preserved in 'hyporelief' (Seilacher, 1964) or as 'hypichnia' (Martinsson, 1970). Those ichnofossils preserved within a stratum are described as preserved in 'full relief' (Seilacher, 1964), or separated into 'endichnia' if preserved within the casting medium and 'exichnia' if preserved outside of it (Martinsson, 1970). For Seilacher's (1964) 'epirelief' and 'hyporelief' structures, the terms positive (concave) and negative (convex) are employed to describe trace fossil relief.

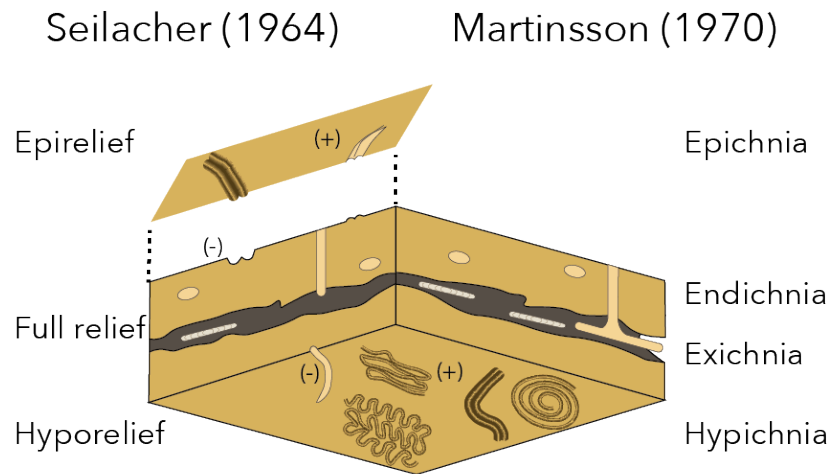


Figure 1.2 Block diagram illustrating Seilacher's (1964) and Martinsson's (1970) stratinomic classification terms (modified from Buatois and Mángano, 2011).

1.2.2. Ichnotaxonomy

Since ichnotaxa cannot be tied to single producers, it is impossible to place them within the classical biotaxonomic scheme. As a result, ichnologists work within a unique taxonomic scheme while still following ICZN rules. Where phylogeny is the governing principle in the biotaxonomic scheme, behaviour is the governing principle in ichnotaxonomy (Bromley, 1990; 1996). While the interpretation of a tracemakers behaviour may be revised (e.g; *Cruziana* as an

internal burrow (Seilacher, 1955b, 1970, 1982; Goldring, 1985) rather than a surface trail (Baldwin, 1977)), the morphology of the ichnotaxon does not. Ichnologists employ the morphology of a trace fossil as a reflection of the producer's behavior in order to classify the structure. They use several distinctive yet variable morphological features, called ichnotaxobases, to guide classification (Bromley, 1990, 1996; Buatois and Mángano, 2011). The variability in an ichnotaxobase reflects behavioural variability, and as a result indirectly links ichnotaxonomic classification with fossil behaviour. Currently, five ichnotaxobases are accepted: (1) general form (2) wall (3) branching (4) fill (5) spreite (Bromley, 1990, 1996). They are concisely explained in Buatois and Mángano (2011, section 2.3). Size, producer, type of passive fill, substrate consistency, geological age, geographic location, facies environment, and preservational aspects are not accepted as useful ichnotaxobases (Magwood, 1992; Pickerill, 1994; Bertling et al., 2006; Buatois and Mángano, 2011).

General form of a trace fossil is the highest ranking ichnotaxobase (Pickerill, 1994). This includes configuration (e.g., straight, winding, meandering, tube, helical, U-shaped, J-shaped, network, boxwork, and sinusoidal), orientation (e.g., vertical, sub-vertical, horizontal, sub-horizontal, and inclined), and placement with respect to stratification (e.g., positive or negative epirelief, positive or negative hyporelief, and full relief). The presence or absence of a wall and features of the burrow boundary are also considered a valid and high rank ichnotaxobase. Bromley (1990, 1996) noted seven main types of burrow boundary that are commonly recognized: unlined walls, dust films, constructional linings, zoned fills, wall compaction, diagenetic haloes, and wall ornaments. Similarly, the presence or absence of branching in an ichnotaxon is considered distinctive, with three main types of branching recognized: secondary successive, primary successive, and simultaneous (Bromely and Frey, 1974; D'Alessandro and Bromley, 1987; Bromley, 1990, 1996). "False branching" occurs when burrow overlap or overcrossings are mistaken for branching, is common, but does not constitute a valid ichnotaxobase (Buatois and Mángano, 2011). The nature of the fill of an ichnotaxon is an important ichnotaxobase, as it clearly relays information regarding trophic type. Passive fill is due to material infilling the burrow gravitationally and is typically structureless, although laminated and draught-fill canals exist as well (Seilacher 1968; Bromley, 1990, 1996; Goldring, 1996; Buatois et al., 2002). Active fill occurs when the infilling material was actively manipulated by the tracemaker, and can be either massive, meniscate (also known as "backfill")

or concentric. This is different from spreite, which is an ichnotaxobase in its own right. Spreite, the thin laminations produced as a result of successive repositioning of the burrow, is produced either as a response to erosion/sedimentation at the water-sediment interface or as a method of strip-mining for food resources.

The variability within an ichnotaxobase should reflect the ethology of the producer (Buatois and Mángano, 2011). By doing so, the ichnotaxonomy of a burrow is tied to the functional morphology, and by extension the ethology, of a burrow (Bromley, 1996). Nevertheless, it is crucial that ichnotaxonomic classification and ethological classification remain separate. Single ichnotaxa often have multiple functions (e.g., *Gyrolithes* as a dwelling, feeding, and farming burrow; see section 4.1.9), meanwhile a single ethology can show a wide morphologic diversity (Vallon et al., 2016).

1.2.3. Ethology

The concept of ethological categories was pioneered by Seilacher (1953). He proposed five basic ethologies: cubichnia (resting traces), repichnia (locomotion traces), pascichnia (grazing traces), fodinichnia (feeding traces), and domicichnia (dwelling traces). Since this time, at least 34 new ethologies have been proposed (Vallon et al., 2016). It is well agreed upon that the number of ethological categories should remain small (Frey and Pemberton, 1985; Buatois and Mángano, 2011; Vallon et al., 2016) and summaries of current categories have been produced at fairly regular intervals (Frey and Pemberton, 1984, 1985; Ekdale, 1984; Bromley, 1990, 1996; Vallon et al., 2016). The most recent summary of the status of current ethological categories (Table 1.1) was conducted by Vallon et al. (2016), who created an updated ethological scheme (Figure 1.3 and Table 1.1).

Only the ethological categories agrichnia, chemichnia, cubichnia, domicichnia, fodinichnia, pascichnia, and repichnia are represented in this study. A summary of common characteristics for these ethologies be seen in table 1.2. Other factors can influence ethological determinations as well, such as environmental conditions at the time of trace fossil emplacement. Thus, while general trends exist between ichnofossil morphology and ethological categories, behavioural interpretations must be conducted on a case-by-case basis.

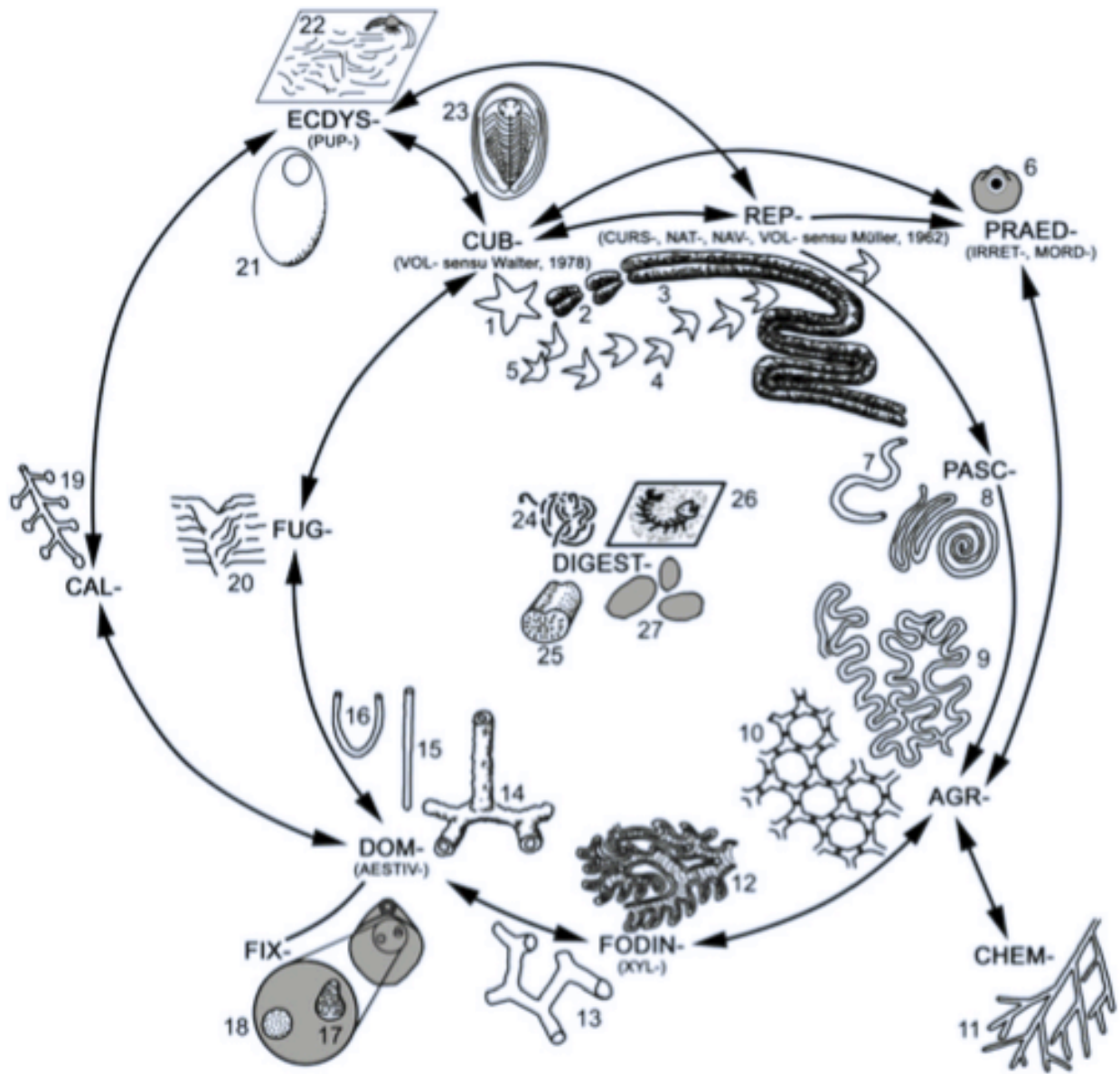


Figure 1.3 A summary of ethological categories and sub-categories as determined by Vallon et al. (2016). Ethology names are abbreviated (lacking the suffix *-ichnia*), and subcategories are indicated with brackets (Vallon et al., 2016).

Table 1.1 Status of all proposed ethological categories.

ETHOLOGICAL CATEGORIES	AUTHORS	BEHAVIOUR	GOOGLE SCHOLAR “HITS” (01/02/18)	CURRENT STATUS
GENERALLY ACCEPTED				
DOMICHNIA	Seilacher (1953)	dwelling	1170	Original categories (Seilacher, 1953); generally accepted (Bromley, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
FODINICHNIA	Seilacher (1953)	feeding + dwelling	914	
PASCICHNIA	Seilacher (1953)	feeding + locomotion	707	
REPICHNIA	Seilacher (1953)	directed locomotion	634	
CUBICHNIA	Seilacher (1953)	temporary immobility (resting)	594	
FUGICHNIA	Frey (1973)	sudden escape	496	Generally accepted category (Bromley, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
AGRICHNIA	Ekdale et al. (1984)	trapping/gardening + dwelling	245	Generally accepted category (Bromley, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
PRAEDICHNIA	Ekdale (1985)	predation	221	Generally accepted category (Bromley, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
CALICHNIA	Genise and Bown (1994)	breeding	86	Generally accepted category (Bromley, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
FIXICHNIA	De Gibert et al. (2004)	anchoring	76	Generally accepted category (Buatois and Mángano, 2011; Vallon et al., 2016)
SUBCATEGORIES				
NAVICHNIA	Gingras et al. (2007)	swimming (in a soupground)	61	Subcategory of repichnia (Vallon et al., 2016)
CURSICHNIA	Müller and Gründel (1962)	locomotion with appendages	24	Subcategory of repichnia (Bromley, 1990, 1996; Buatois and Mángano, 2011; Vallon et al., 2016)
NATICHNIA	Müller and Gründel (1962)	swimming (near sediment surface)	27	Subcategory of repichnia (Bromley, 1990, 1996; Buatois and Mángano, 2011).
VOLICHNIA	Müller and Gründel (1962)	landing/take-off traces	24	Subcategory of repichnia and cubichnia (Buatois and Mángano 2011, Vallon et al., 2016)
TAPHICHNIA	Pemberton et al. (1992)	unsuccessful attempts to escape burial	15	Reassigned to fugichnia (Bromley, 1996; de Gibert et al., 2004; Buatois and Mángano 2011; Vallon et al., 2016)
XYLICHNIA	Genise (1995)	wood feeding borings	17	Subcategory of fodichnia (Genise, 1995; Vallon et al., 2016)
MORDICHNIA	?	predation marks on hard substrates	14	Subcategory of praedichnia (Vallon et al., 2016)
IRRETICHNIA	Lehane and Ekdale (2013)	trapping	4	Subcategory of praedichnia (Vallon et al., 2016)

AESTIVICHNIA	Verde et al. (2007)	aestivation (dormancy/ hibernation)	3	Subcategory of domichnia (Verde et al., 2007; Buatois and Mángano, 2011; Vallon et al., 2016)
RECENTLY PROPOSED, REASSIGNED, OR REVISITED				
EQUILIBRICHNIA	Frey and Pemberton (1985)	gradual adjustment	168	Generally accepted (Buatois and Mángano, 2011) Reassigned to domichnia and fodinichnia (Vallon et al., 2016)
CHEMICHNIA	Bromley (1996)	chemisymbiosis	75	Generally accepted category (Bromley, 1996; Vallon et al., 2016) Reassigned to agrichnia (de Gibert et al., 2004)
MORTICHNIA	Seilacher (2007)	death traces	54	Generally accepted (Buatois and Mángano, 2011). Reassigned to Repichnia, praedichnia and ecdysichnia (Vallon et al., 2016)
PUPICHNIA	Genise et al. (2007)	pupation	64	Generally accepted (Buatois and Mángano, 2011). Subcategory of ecdysichnia (Vallon et al., 2016)
IMPEDICHNIA	Tapanila (2005)	bioclaustration structures	19	Generally accepted (Buatois and Mángano, 2011). Body fossils; recommended term <i>impeditaxa</i> (Vallon et al., 2016)
DIGESTICHNIA	Vallon (2012), Vialov (1972)	digestion processes	12	Recently revived category (Vallon et al., 2016)
QUIETICHNIA	Müller and Gründel (1962)	Resting traces	2	Supercategory proposed for domichnia + cubichnia; not in current use (Vallon et al., 2016)
ECDYSICHNIA	Vallon et al. (2016)	molting traces	6	Recently proposed category (Vallon et al., 2016)
REASSIGNED				
AEDIFICICHNIA	Bown and Ratcliffe (1988)	above-ground structures	22	Reassigned to calichnia (Genise and Bown, 1994a; Buatois and Mángano, 2011) and/or domichnia (Vallon et al., 2016)
POLYCHRESICHNIA	Hasiotis (2003)	social insect structures	18	Reassigned to calichnia and domichnia (Buatois and Mángano 2011, Vallon et al., 2016)
SPHENOICHNIA	Mikuláš (1999)	plant root penetration traces	14	Attributed to plants (Vallon et al., 2016)
CORROSICHNIA	Mikuláš (1999)	plant corrosion traces	16	Attributed to plants (Vallon et al., 2016)
MOVICHNIA	Müller and Gründel (1962)	moving traces	12	Equivalent to repichnia (Müller and Gründel 1962, Vallon et al., 2016)
CIBICHNIA	Müller and Gründel (1962)	feeding traces	10	Equivalent to fodinichnia (Vallon et al., 2016)
CECIDOICHNIA	Mikuláš (1999)	plant reaction tissues	7	Attributed to plants, considered as body fossils (Bertling et al., 2006); recommended term <i>cecidotaxa</i> (Vallon et al., 2016)

Table 1.2 Common features of the ethologies mentioned in this dissertation.

ETHOLOGY (behaviour)	COMMON ICHNOTAXOBASE EXPRESSION						
	Morphology	FORM orientation	stratiform	WALL	BRANCHING	FILL	SPREITE
AGRICHNIA (farming = dwelling + feeding)	Complex (branched meanders, spirals, or nets)	horizontal	(+) hyporelief	none	simultaneous branching common	passive	rare
CHEMICHNIA (chemo-symbiotic feeding)	Deep burrows (simple, or a causative tube and multiple branches)	vertical and horizontal	full relief	none	primary and secondary successive common	active	rare
CUBICHNIA (resting)	Reflect latero-ventral anatomy of producer	horizontal	(+) hyporelief, (-) epirelief	no wall/lining	unbranched	passive	none
DOMICHNIA (dwelling)	Variable (straight, U- shaped, branched systems, plug shaped)	vertical to oblique, some horizontal	full relief	wall and linings common	simultaneous branching common	passive	none
FODINICHNIA (feeding = dwelling + feeding)	Variable complexity of burrows (i.e., simple, branched systems, radial, or U-shaped)	Variable (horizontal, inclined, or vertical)	full relief	no wall/lining	primary and secondary successive common	active	common
PASCICHNIA (grazing = locomotion + feeding)	Trails (i.e., simple, curved, circular, or meandering	horizontal	(+) hyporelief, (-) epirelief	no wall/lining	unbranched	passive	none
REPICHNIA (locomotion)	Trackways, trails (i.e., simple, bilobate, or chevronate)	horizontal	(+) hyporelief, (-) epirelief	no wall/lining	unbranched	passive	none

1.3. A review of the Ediacaran-Cambrian transition

The appearance of the complex, mineralized Cambrian fauna has fascinated scientists for decades. This pivotal time in Earth's evolution was seemingly devoid of a fossil record, and famously led Darwin to propose it as a missing link in his theory of evolution (Darwin, 1859). With the discovery of localities with an Ediacaran biota, such as Mistaken Point (Anderson and Misra, 1968), and the Ediacaran Hills (Sprigg, 1947), it is clear that the fossil record is not nearly as barren as it once appeared. In turn, the discovery of exceptional Cambrian Burgess Shale-type Lagerstätten, such as Burgess Shale (Whittington, 1971, Coway Morris 1986), Chengjiang (Hou et al., 1989), and Sirius Passet (Conway Morris et al., 1987) has led to a greater understanding of the Cambrian fauna. Nevertheless, the relationship between these two biotas remains enigmatic. There exists a general consensus that the Ediacaran biota marks the advent of multicellular organisms (Bonner, 1998; Budd, 2008). However, their specific phylogeny remains hotly contested. Some Ediacaran forms have been proposed as stem-group metazoans (i.e., *Kimberella*), some as large rhizopod protists (Seilacher et al., 2003), and others as housing chemosynthetic bacteria (Burzynski et al., 2017) (for a review, see Droser and Ghelring, 2015). The Cambrian fauna, however, is more easily assigned to various phylogenetic ranks (Conway-Morris, 1979; Erwin et al., 1997; Davidson and Erwin, 2006; Chen, 2009). With few similarities in constructional morphologies, the relationship between the Ediacaran and Cambrian biotas remains enigmatic (Droser and Ghelring, 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 review see Conway Morris, 2000; Marshall, 2006; Zhang et al., 2014) and are broadly categorized into genetic, ecological, and environmental causes (Erwin, 2015).

Bioturbation often plays a key role in environmentally caused hypotheses. During the Ediacaran-Cambrian transition and early Cambrian there exists a marked infaunalization, and a switch from an Ediacaran-style matground ecology to a Cambrian-style mixground ecology. This event has been subdivided into the three “Revolutions”, the “Cambrian Information Revolution” (Plotnick et al., 2010; Carbone and Narbonne, 2014), the “Agronomic Revolution” (Seilacher and Pflüger, 1994), and the “Cambrian Substrate Revolution” (Bottjer et al., 2000). The first revolution, the Cambrian Information Revolution, likely occurred in the Fortunian, as environments and food sources became increasingly heterogeneous (Plotnick et al., 2010;

Mángano and Buatois, 2017). It is posited that a coevolution occurred between heterogeneity (i.e., information) in marine environments and the development of sensory organs, capable of processing this new information (Plotnick et al., 2010; Mángano and Buatois, 2017). The Agronomic Revolution refers to the re-structuring of benthic communities, surrounding the onset of bioturbated substrates (Seilacher and Pflüger, 1994; Mángano and Buatois, 2017). This revolution is documented in the transition from Ediacaran matground communities to Cambrian mixground communities. This transition triggered the Cambrian Substrate Revolution (Bottjer et al., 2000) which deals with the impact of bioturbated substrates, as well as the evolution of hardground communities. It has been suggested that this transition (the Cambrian Substrate Revolution) may have prompted the Cambrian explosion as benthic metazoans would have needed to evolve to this new substrate (Thayer, 1979; Bottjer et al., 2000; Meysman et al., 2006). However, it has also been suggested that the Agronomic Revolution was a consequence of increased predation, and signifies organisms seeking refuge (Seilacher, 2007). Whether bioturbation is a cause or consequence of the Cambrian explosion ultimately relies 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. While body-fossils are excellent sources to help reconstruct the phylogeny, they relay very little in terms of behaviour. 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.

1.4. Controversies surrounding the Ediacaran-Cambrian GSSP

With fascinating discoveries coming from Ediacaran localities (Sprigg, 1947; Anderson and Misra, 1968), and even more prolific discoveries in Cambrian localities (Conway-Morris, 1979; Conway Morris, 1987; Hou et al., 1989), scientists needed a way to correlate their sections worldwide. Two proposals at the 21st International Geological Congress in 1960 (Sørensen, 2007) prompted the creation of a Subcommittee on Cambrian Stratigraphy (SCS) in 1961 (Shergold and Geyer, 2003). One task of this commission was to define a Precambrian-Cambrian boundary in order to aid global correlation for this pivotal time. In 1972, a working group on the Precambrian-Cambrian boundary was created.

GSSP's are the designated type section of the base (beginning) of a stratigraphic stage, marked in the section by the best possible marker events (Cowie et al., 1986). These events may

be biostratigraphic, chronometric, magnetic, geochemical, climatic or otherwise in nature (Figure 1.4) and ideally defined by several overlapping events. In turn, potential GSSP's must meet additional requirements, such as exposure over an adequate thickness with continuous sedimentation, as well as an absence of synsedimentary, tectonic, metamorphic or diagenetic events (Remane et al., 1996). Biostratigraphic event markers, the most commonly employed markers (Figure 1.4), are placed at the first or last appearance of an index fossil or index fossil zone.

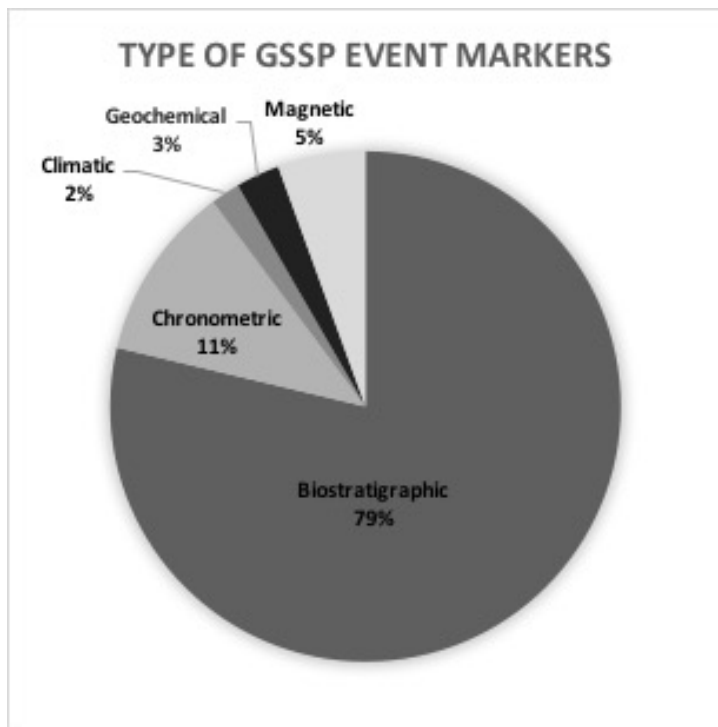


Figure 1.4. Types of GSSP event markers, data from the International Commission on Stratigraphy online repository (International Commission on Stratigraphy, 2018).

An index fossil must meet five general requirements: (1) have rapid rates of evolution, (2) found in a wide range of environments, (3) be abundant, (4) be easily identifiable, and (5) be readily preserved. In some cases, several biostratigraphic events can be used, such as the lowermost Maastrichtian boundary where the first and last appearances of twelve biohorizons are used to delineate the boundary (Odin and Lamaurelle, 2001).

The transition between the Ediacaran and Cambrian faunas is remarkably poor in body fossils. The body fossils that are preserved, the small calcified Small Shelly Fauna (SSF), are strongly provincial and are almost entirely restricted to carbonate lithologies (Bengston, 1988). Ichnofossils, in contrast, show continuous preservation from the Ediacaran to Cambrian, and are

demonstrably less facies controlled than SSF's (Mángano and Buatois, 2014). After nearly two decades of research and deliberation, the committee selected the section located at Fortune Head, Newfoundland, Canada (Figure 1.5) as the Ediacaran-Cambrian GSSP in 1992 (Narbonne et al., 1987; Landing, 1994). This was, and remains, the only boundary defined by the first observed appearance of an ichnofossil.

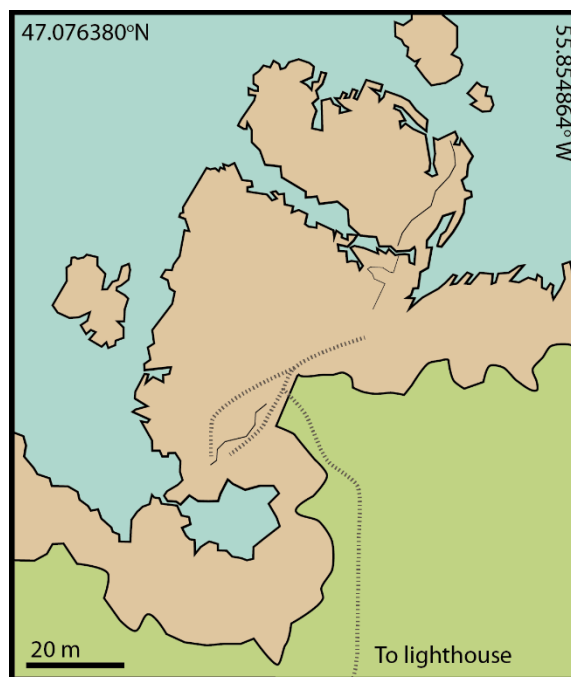


Figure 1.5 Map of the Ediacaran-Cambrian Boundary outcrop. Legend can be seen in Figure. 1.6.

Criticism of the GSSP placement deals with the usage of an ichnotaxon for such an important biostratigraphical purpose. Four points of contention have been outlined and were summarized by Buatois (2018). First, the ichnotaxonomic status of *T. pedum* causes confusion amongst non-ichnologists. Originally classified as *Phycodes pedum* (Seilacher, 1955a), the ichnofossil has subsequently been re-assigned to (in decreasing order of general acceptance by the scientific community): *Treptichnus* (Jensen, 1997), *Trichophycus* (Geyer and Uchman, 1995), and *Manykodes* (Dzik, 2005). Second, it has been suggested that *T. pedum* does not adequately represent the evolutionary innovations characteristic of the “Cambrian Explosion” as it is not a true vertical burrow, but rather a horizontal burrow with inclined branches or “probes” (Babcock et al., 2014). Thirdly, concerns have been raised about possible facies control of *T. pedum*. This stems from the fact that ichnofossils are facies controlled (Seilacher, 2007; Babcock et al., 2014; Laing et al., 2016; Buatois, 2018). While this is true for ichnoassemblages or

ichnofacies in general, individual ichnotaxa often occur in a wide range of environments (Buatois, 2018). In fact, a broad environmental tolerance, ranging from the offshore to intertidal zones, for *T. pedum* has been demonstrated (Buatois et al., 2013). Additionally, Fortune Head facies and ecologies both below and above the first appearance of *T. pedum* are identical (Buatois et al., 2014). As such, false first appearances of *T. pedum* due to facies control have been eliminated by some authors (Landing et al., 2013). Regardless, its suitability as an index fossil is still questioned by some, who cited the diachronic appearance of this ichnospecies in the fossil record as evidence of facies control. Unaddressed in this is the well-known provincialism seen in earliest Cambrian body fossils, which could also account for the diachronous appearance of some ichnofossils (Landing et al., 2013). Finally, early and delayed appearances of *T. pedum* in some sections have led to questions surrounding the stratigraphic distribution of the index fossil (Babcock et al., 2014).

However, the appearance of *T. pedum* is not the only correlatable event at Fortune Head. Aside from contemporaneous first appearances of a variety of ichnofossils, the Ediacaran fossils *Harlaniella podolica* and *Palaeopascichnus delicatus* make their last appearance within 2 m of the golden spike (Narbonne et al., 1987). In turn, the Fortune Head section was chosen for its exceptional thickness with continuous sedimentation, and limited synsedimentary and tectonic disturbances (Landing, 1994).

1.5. Study Area

The outcrops are located on the southwestern tip of the Burin Peninsula, Newfoundland. The Ediacaran-Cambrian boundary is located within the Fortune Head Ecological Reserve (FHER), 1.5 km west of Fortune, Newfoundland on the Burin Peninsula (Figure 1.6) and is protected by the Newfoundland and Labrador government, under Parks and Natural Areas. This strata documents 415 m of reasonably continuous sedimentation during the latest Ediacaran and earliest Fortunian (Narbonne et al., 1987). The section encompasses the last 10 m of member 1 and all of members 2A and 2B of the Chapel Island Formation (CIF). A continuous section of member 1 was measured 7 km to the northeast, at Grand Bank Head, and the remaining members (members 3, 4, and 5) of the CIF have been measured 15 km to the southwest at Little Danzig Cove. Combined, these localities document a 1 km thick continuous succession of the CIF. Only the Fortune Head and Grand Bank Head sections document the *Treptichnus pedum* Ichnofossil Assemblage Zone, and were therefore the focus of this study.

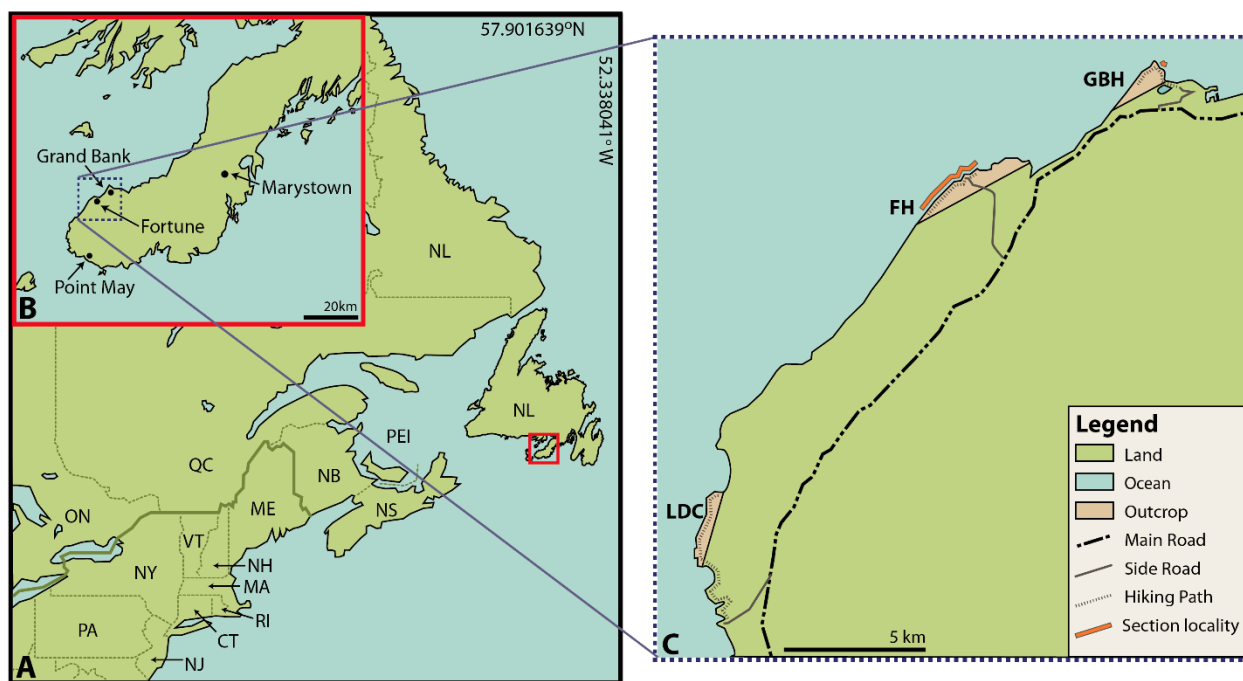


Figure 1.6 Map of the study area. (A) Map of the northeastern coast of North America. NL= Newfoundland. Red box outlines the Burin Peninsula, seen in B. (B) Map of the Burin Peninsula. Blue dashed box outlines the study area, seen in C. (C) Map of the northwestern tip of the Burin Peninsula, showing Chapel Island Formation outcrop locations. The *Treptichnus pedum* IAZ is preserved at Fortune Head (FH) and Grand Bank Head (GBH), younger strata can be found at Little Danzic Cove (LDC).

1.6. Research Methods

1.6.1. Measurement of stratigraphic sections and gathering of trace-fossil data

A 120 cm Jacobs staff was created with 10 cm increments marked. By laying the staff perpendicular to the bedding plane, bed thicknesses were measured and recorded on a cm-scale, along with grain size, sedimentary structures, bedding contacts, and faults. Removable stratigraphic height markers were placed roughly every 2 m. Photographs were taken at regular intervals to demonstrate typical sedimentary features. Marker beds were traced along the three sections, and noted in the stratigraphic logs. Then a thorough search for ichnofossils was conducted. When an ichnofossil or physical sedimentary structure was encountered, their stratigraphic position was measured from the closest marker and logged. Whenever possible, photographs were taken with stratigraphic height marked.

Adobe Illustrator© was used for drawing the stratigraphic sections. Marker beds identified in the field were used for correlation. Special permission was granted by the Fortune Head Ecological Reserve for sampling. Sampling was done twice under the supervision of Richard Thomas from the Government of Newfoundland and Labrador under the provisions that sampling be discrete and kept to a minimum. Any sampling of *Treptichnus pedum* was prohibited and only five samples were taken from the GSSP section. These were taken back to the University of Saskatchewan and made into polished sections by Romain Gougeon, a PhD candidate.

1.6.2. Ichnotaxonomy

Using field observations and photographs, ichnotaxobases were identified and recorded; this characterization of structures allowed either a preliminary ichnotaxonomic classification or narrowing to a few potential names. A thorough literature research collating with observational data followed to test ichnotaxonomic assessments. Several resources were used to aid in this (Seilacher 2007; Buatois and Mángano 2011; Knaust and Bromley 2013, 83–94), as well as primary sources in the literature where the different ichnotaxa have been defined and relevant ichnotaxonomic reviews. Photographs of key ichnotaxa (*G. scintillus*, *G. gyratus*, *Monomorphichnus* isp., and *Treptichnus*) were traced in Illustrator. Dimensions (thickness, width, burrow depth) and ichnotaxobases (form, wall/lining, branching, fill, spreite) were recorded for every sample, when possible.

1.7. Thesis structure

This is a paper-based thesis. Chapter 1 provides an overview of the thesis. It outlines the purpose and objectives and reviews pertinent core concepts, in order to frame the contribution of this research work. It also outlines the organization of the thesis. Chapter 2 offers a background of the geology and previous ichnotaxonomic work of the region. Chapter 3 examines the stratigraphy and ichnology at the section, and provides a detailed and up-to-date characterization of the *Treptichnus pedum* Assemblage Zone in Fortune Head. Chapter 4 documents a new ichnospecies of *Gyrolithes* from the *Treptichnus pedum* Assemblage Zone, discusses its ichnotaxobases, ethology, and potential tracemakers, and hypothesizes on selective pressures underlying the onset of infaunalization. Finally, Chapter 5 summarizes the research findings and presents conclusions.

CHAPTER 2

2. Geological Background

The rocks spanning the Ediacaran-Cambrian boundary in Newfoundland were formed in an extensional or transtentional basin (Smith and Hiscott, 1984). Fault-bounded Cambrian depocenters were formed (Landing, 2004), creating the accommodation potential necessary for the Rencontre, Chapel Island and Random formations to be preserved (Figure 2.1).

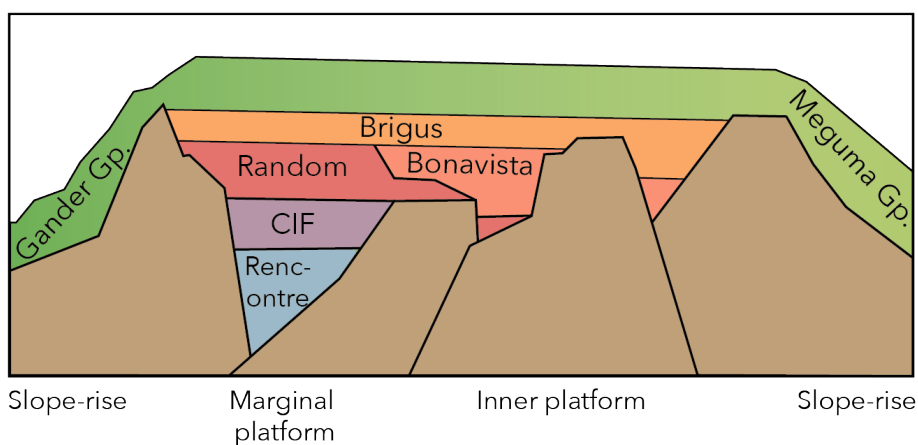


Figure 2.1 Deposition of Avalonian sediments during the late Proterozoic to early Phanerozoic (modified from Landing, 2004).

The sedimentary infill of the Avalon depocenters of interest here have been subdivided into three formations, from base to top; the Rencontre Formation, the Chapel Island Formation, and the Random Formation (Figure 2.2). The Rencontre Formation encompasses alluvial, fluvial, and marginal-marine facies, recording active tectonics during rift stage. The Chapel Island Formation is broadly interpreted as recording sedimentation in a wave-dominated delta (Myrow, 1987). It is interpreted as a transitional stage from active tectonism to more stable tectonic conditions. This was followed by tectonically stable conditions, characterized by intertidal to subtidal deposits of the Random Formation (Anderson, 1981; Hiscott, 1982; Smith and Hiscott, 1984).

Initially, a global Cambrian transgression represented by the transition from the Rencontre to the Chapel Island formations was proposed (Anderson, 1981). Myrow (1993)

argued that tectonics and sedimentation rate may have played a larger role, but did note that the regional onlap of the Random Formation is more indicative of eustatic sea level rise. The three formations taper eastward into an unconformity. They overlie the volcanic Marystown Group, whose uppermost formation (the Mooring Cove Formation) has been U-Pb dated to 552 ± 3 Ma (Tucker and McKerrow, 1995, Ferguson, 2017).

2.1. Chapel Island Formation

The Chapel Island Formation, defined by Hutchinson (1962), is formally divided into the Quaco Road Member and the Mystery Lake Member in New Brunswick (Landing, 1996). These members present differently in Newfoundland, and an informal five-fold subdivision of the CIF is more widely used there (Bengston and Fletcher, 1983). Informal members 1-4 (equivalent to the Quaco Road Member) are a reasonably continuous, nearly kilometer-thick succession of fine-grained siliciclastics, with a disconformity high in member 4. This is overlain by member 5 (equivalent to the Mystery Lake Member). These members are interpreted to have been deposited in a wide variety of shallow-marine environments, ranging from peritidal to shelf (Myrow and Hiscott, 1993). Time-equivalent rocks can be found in Nova Scotia, New Brunswick, Massachusetts, and the British Caledonides (Myrow and Hiscott, 1993). The most in-depth sedimentary study on the Chapel Island Formation was conducted as part of Paul Myrow's PhD thesis (Myrow, 1987; see also Myrow and Hiscott 1991, 1993; Myrow 1995). The GSSP is located within member 2, 2.4 m above the top of member 1. Therefore, only members 1 and 2 are discussed in detail here.

2.1.1. Member 1

Member 1 consists of gray, fine- to very fine-grained sandstone and siltstone which contain flaser, wavy, and lenticular bedding; shrinkage cracks; channel-fill sandbodies; and episodic sediment failure structures (Myrow, 1987). Phosphate and pyrite nodules occur locally. Due to a lack of typically abundant and diagnostic tidal features (e.g., herringbone cross stratification, reactivation surfaces, tidal bundles, and meter-scale fining upwards cycles), as well as a lack of wave-generated structures, it was determined that member 1 was deposited in a low energy microtidal to mesotidal coastline, besides a low relief, mixed sand/mud coastal plain (Myrow and Hiscott, 1993). Recurrent thick, sandstone beds indicate channel and storm deposits, and the presence of pyrite and phosphate imply dysaerobic conditions in the bottom waters.

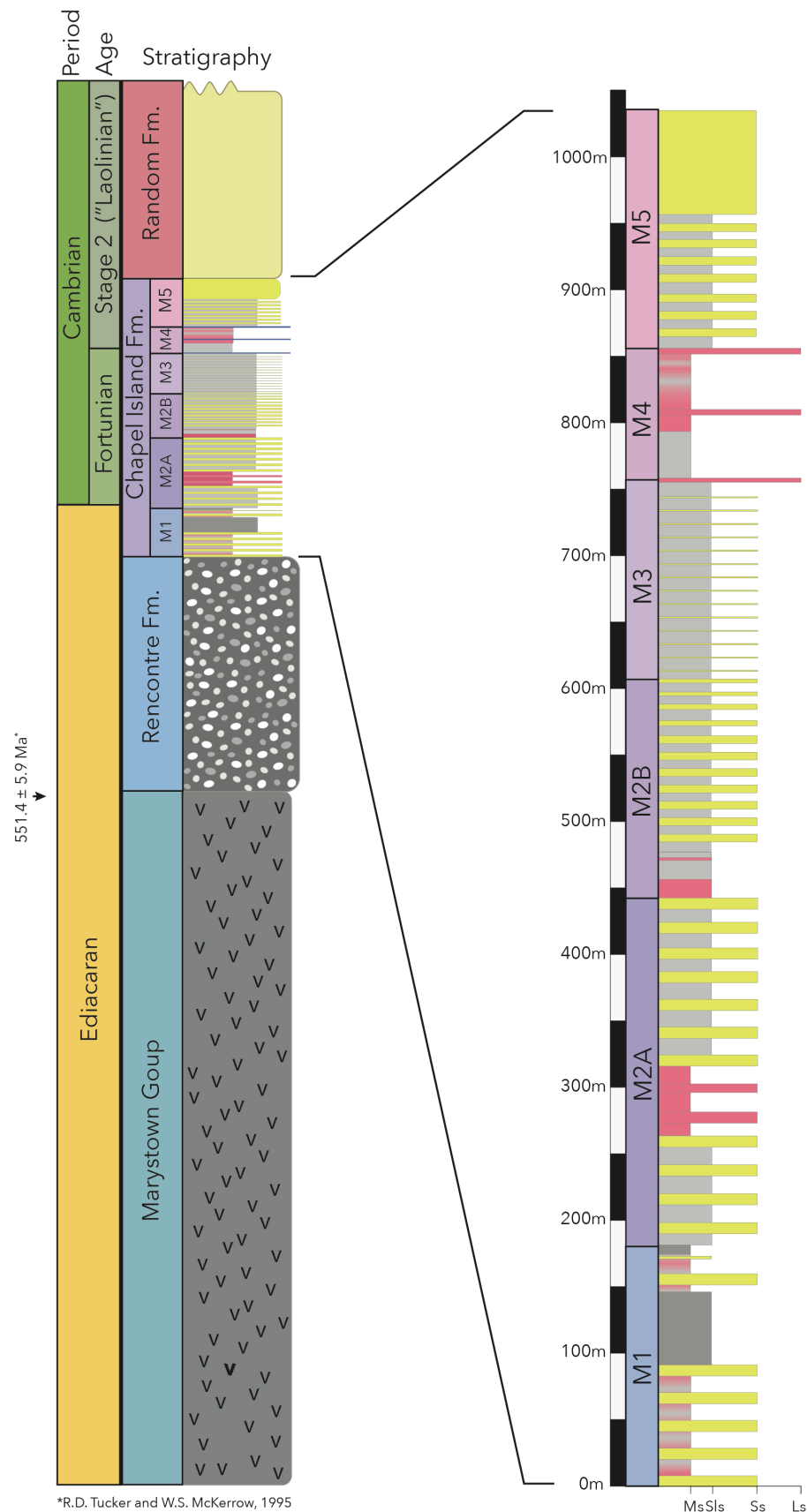


Figure 2.2 Left: A generalized section of the Ediacaran-Cambrian stratigraphy of the Burin Peninsula, NL, showing the Marystown volcanics, followed the sedimentary Rencontre, Chapel Island, and Random formations. Right: A generalized stratigraphic section of the Chapel Island Formation. Legend in figure 3.1.

2.1.2. Member 2

Myrow and Hiscott (1991) have subdivided the 430 m thick member 2 into three lithofacies, namely unifite beds, raft-bearing beds, and slides. Unifite beds are siltstone and silty mudstone, graded to non-graded beds characteristically devoid of structure, and are interpreted to have been formed by single liquefaction and turbulence events. Raft-bearing beds are similar to unifite beds, except they contain clasts similar to the overlying and underlying layers, and they are interpreted to be a type of debris-flow. Slide deposits are a buckling of layers, and are interpreted as reflecting large storm-induced stresses (Myrow and Hiscott, 1991). Thick unifite beds and gutter casts characterize the Gutter Cast Facies, consisting of thin laminae to very thinly bedded fine-grained sandstone and siltstone with abundant wave ripples, synaeresis cracks, gutter casts, and pot casts common. The Siltstone-Dominated Facies consists of laminae to thin beds of fine-grained sandstone and siltstone with pebble lags, flat-pebble conglomerates, uncommon gutter casts, and wave ripples. Raft-bearing beds, unifites, and rare slides are present. The Sandstone-Dominated Facies is characterized by thinly laminated to medium-bedded, fine- to very fine-grained sandstone and siltstone with abundant (generally starved) hummocky cross-stratification, with raft-bearing beds and slides (Myrow and Hiscott, 1991). Additionally, a 33 m thick, red, upward-fining sandstone unit in the bottom half of member 2 shows parallel-lamination and trough cross-stratified beds with channel-like geometries (Myrow, 1987).

The siltstone units were likely firm at the time of burrow excavation, as shown by the lack of wall or lining in all burrows seen, the degree to which delicate imprints are preserved, and the preservation style of burrows (Droser et al., 2002; Jensen et al., 2005; Buatois et al., 2014; Tarhan and Droser, 2014). Substrate consistency is likely due to stabilization of grains, caused by pervasive microbial mats (Buatois et al., 2014) combined with a lack of bioturbation and sediment mixing (Droser et al., 2002; Buatois et al., 2014). Member 2 was deposited in a deltaic setting in shallow subtidal and inner shelf environments, heavily influenced by storms and waves (Myrow, 1987; Myrow and Hiscott, 1991; Myrow and Hiscott, 1993). This interpretation is supported by several lines of evidence. Member 2 lies stratigraphically above the alluvial, fluvial, and marginal marine deposits of the Rencontre Formation, and below the mid-shelf deposits of member 3. Member 2 has been subdivided into three facies: A Gutter Cast Facies (GC facies), Siltstone-Dominated Facies (SIS-D facies), and Sandstone-Dominated Facies (SS-D facies). Their depositional environments have been interpreted as nearshore, subtidal, and



Figure 2.3 Sedimentologic features of the *T. pedum* IAZ. A is from member 1, B-H are from member 2 (A) Mudclasts, viewed in cross-section. (B) Gutter cast, preferentially carbonate cemented, viewed in cross-section. (C) Gutter cast, preferentially carbonate cemented, and inclined bedding. Viewed in cross-section. (D) Pot hole cast, viewed from the top of a bed. (E) Synaeresis crack, viewed in cross-section. (F) Mudcracks, viewed on the top of a bed. (G) Wave ripples, viewed on the top of a bed. (H) Hummocky cross-stratification.

middle shelf respectively (Myrow, 1987; Myrow and Hiscott, 1993). The Gutter Cast Facies is confined to the lowest 100 m of member 2, and the Sandstone-Dominated Facies is most abundant in the upper part of member 2, particularly near the transition with member 3. Myrow and Hiscott (1993) interpreted this as reflecting an overall deepening in the formation; however, this is inconsistent with a deltaic environment and their interpretation needs to be revised. The 33 m thick red sandstone bed abruptly appears (Sh facies), and has been interpreted as marginal-marine deposits just upstream from a distributary mouth, although this interpretation may need revision as well. Additionally, the exceptional thickness of the mudstone-dominated section, as well as the prevalence of gravity flows indicates high rates of sedimentation and accumulation (Myrow, 1987; Myrow and Hiscott, 1991).

2.1.3. Members 3 through 5

Member 3 consists of 150 m of laminated carbonate-concretion-bearing siltstone, with the upper 15-20 m showing intense burrowing. It was likely deposited in a more distal shelf environment, below storm wave base (Myrow, 1987; Myrow and Hiscott, 1993). The overlying member 4 is a mudstone with red bioturbated sections, partly burrowed green sections, and gray, pyritiferous sections. It is punctuated by three limestone beds, each bed increasing in thickness and small shelly content stratigraphically upwards (Myrow, 1987). Member 4 was interpreted to have formed in a low-energy, muddy shelf in an oxygen-stratified basin. Limestone deposition was restricted to the peritidal zone, gray mudstone to deeper, dysaerobic shelf areas, and green and red mudstone in shallow subtidal under moderate to high oxygen levels respectively (Myrow and Hiscott, 1993). Finally, the 178 m thick member 5 consists of two intervals. The lower interval comprises thin to medium bedded sandy siltstone facies, possibly formed by turbidity currents. The upper half is a fine, red micaceous sandstone facies, likely formed between storm wave base and fair weather wave base in a wave-dominated setting (i.e., offshore) (Myrow and Hiscott, 1993).

2.2. Previous Ichnological Work

The first comprehensive study of the Chapel Island Formation ichnofauna was conducted by Crimes and Anderson (1985), who documented the ichnofauna in all members of the Chapel Island Formation and in the overlying Random Formation. This study was supplemented by additional work on the Ediacaran-Cambrian boundary horizon specifically, as part of the 1987 stratotype proposal put forward by Narbonne et al. (1987). In this proposal, the *Treptichnus*

(*Phycodes*) *pedum* IAZ was erected (Figure 2.4). A trip to the Burin Peninsula was organized during the Geological Association of Canada's Annual Meeting in 1988, which took place in St. John's (Landing et al., 1988). In the guidebook for this trip, *Gyrolithes?* isp. was added to the *T. pedum* IAZ along with an additional occurrence of *T. pedum* (Figure 2.4) (Landing et al., 1988). Since then, the *T. pedum* IAZ has remained unchanged, save for the general re-classification of *Phycodes pedum* to *Treptichnus pedum* (Jensen, 1997) or less likely *Trichophycus pedum* (Geyer and Uchman, 1995). The Chapel Island Formation was later examined for tiering and ichnofabric changes, but no further refinements in trace-fossil classifications have been produced (McIlroy and Logan, 1999).

The section regained international interest again during the 2001 Geological Association of Canada's Annual Meeting. Gehling and workers (2001) discovered *T. pedum* below the Ediacaran-Cambrian boundary limit, sparking debate on the utility of the GSSP. However, this discovery is accounted for in the range offset of the ichnospecies. This phenomenon is recognized in GSSPs throughout the geological time scale (Landing et al., 2013; Buatois, 2018). Research concerning ichnofabrics at the section revealed the firm nature of the sediments and documented the common "floating style" preservation at the locality (Droser et al., 2002), also known as concealed bed junction preservation (Hallam, 1975). The exceptional preservation at this locality was highlighted subsequently, when it was suggested that the matground ecology characteristic of the Ediacaran persisted into this earliest Fortunian section (Buatois et al., 2014). In this study, the arthropod locomotion trace fossil *Allocotichnus* was described, along with various microbially induced sedimentary structures (MISS). The concept of bioturbators as ecosystem engineers was also explored for this section (Herringshaw et al., 2017). Finally, the International Symposium on the Ediacaran-Cambrian Transition (ISECT) led a field trip to the locality in June of 2017, and an updated field guide was produced (Landing et al., 2017). This guide book included an updated ichnotaxonomy of the section, reflecting the work done in this master's thesis.

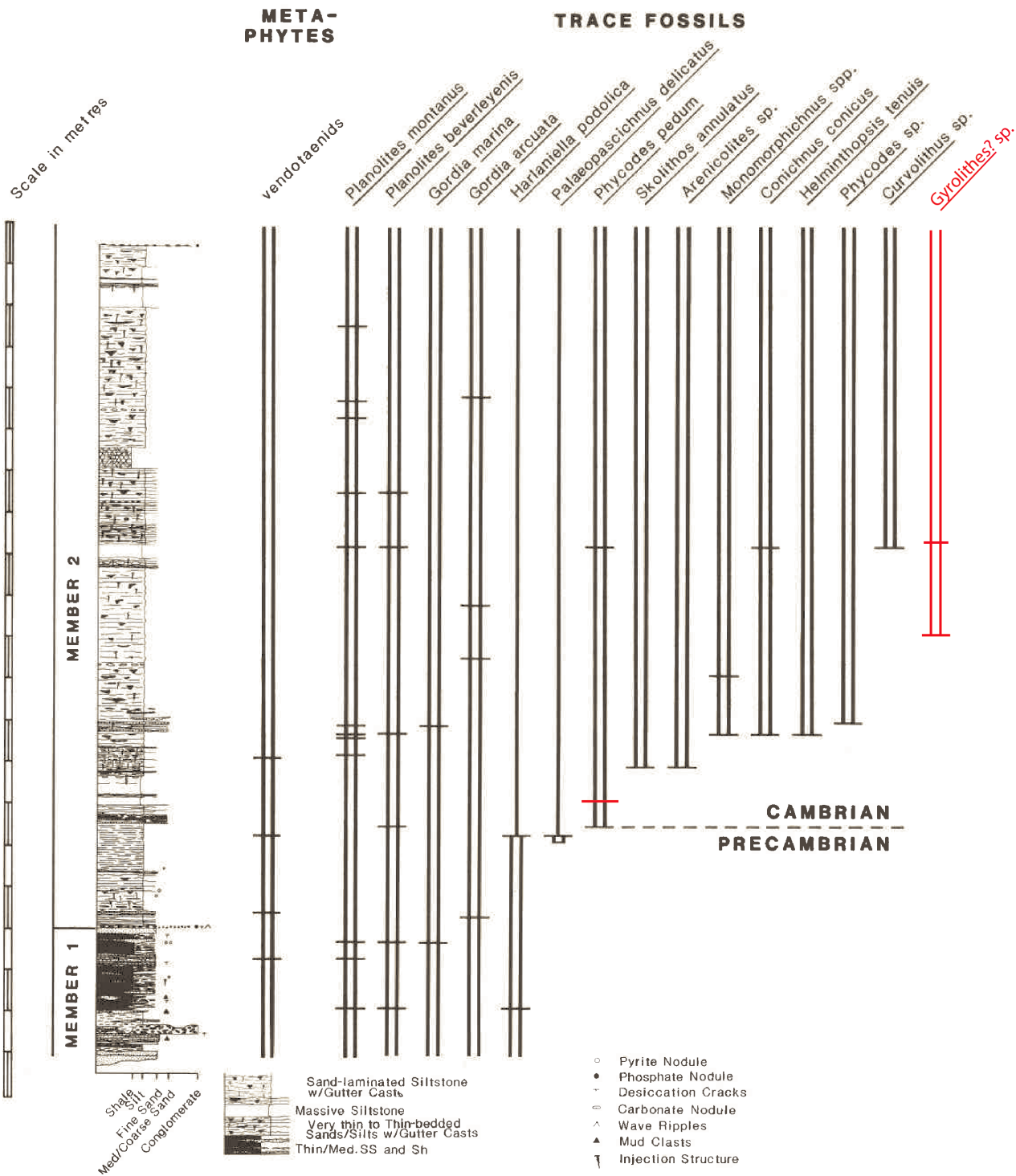


Figure 2.4 Original ichnologic section of the Ediacaran-Cambrian boundary. Determinations added in 1988 are shown in red (after Narbonne et al., 1987 and Landing et al., 1988).

Table 2.1 Summary of ichnotaxonomic studies conducted on the Chapel Island Formation

ARCHITECTURAL DESIGN	ICHNOGENERA	<i>H. PODOLICA</i> IAZ						<i>T. PEDUM</i> IAZ					
		Crimes and Anderson, 1985	Narbonne et al., 1987	Landing et al., 1988	Gehling et al., 2001	Herringshaw et al., 2017	% of reports	Crimes and Anderson, 1985	Narbonne et al., 1987	Landing et al., 1988	Gehling et al., 2001	Herringshaw et al., 2017	% of reports
B.F	<i>Harlaniella podolica</i> *	•	•	•	•	•	100						0
B.F	<i>Palaeopascichnus delicatus</i> *		•	•	•	•	80						0
HS	<i>Gordia arcuata</i>	•	•	•			60	•	•	•		•	40
HS	<i>Gordia marina</i>	•	•	•			60	•	•	•		•	40
HA	<i>Planolites beverleyensis</i>		•	•		•	60	•	•	•		•	60
HA	<i>Planolites montanus</i>		•	•	•	•	60	•	•	•	•	•	80
HS	<i>Buthotrephis</i> isp.	•					20	•					20
HA	<i>Torrowangea</i> isp.					•	20						0
HB	<i>Treptichnus</i> isp.				•		20						0
ICHNODIVERSITY		4	5	5	4	4							
ICHNODISPARIETY		2	3	3	3	2							
SM	<i>Monomorphichnus</i> isp.							•	•	•	•	•	80
VS	<i>Skolithos annulatus</i>							•	•	•	•	•	80
VU	<i>Arenicolites</i> isp.							•	•			•	60
PS	<i>Conichnus conicus</i>							•	•	•			60
TF	<i>Curvolithus</i> isp.							•	•			•	60
VH	<i>Gyrolithes?</i> isp.								•	•	•	•	60
HS	<i>Helminthopsis tenuis</i>							•	•	•			60
HB	<i>Treptichnus pedum</i>							•	•	•	•	•	60
PS	<i>Bergaueria</i> isp.											•	20
HS	<i>Cochlichnus</i> isp.											•	20
BT	<i>Didymaulichnus</i> isp.											•	20
SM	<i>Dimorphichnus</i> isp.											•	20
HS	<i>Helminthoidichnites</i> isp.											•	20
HP	<i>Palaeophycus</i> isp.											•	20
HB	<i>Phycodes</i> isp.											•	20
CA	<i>Psammichnites</i> isp.											•	20
ICHNODIVERSITY			9	10	7	16							
ICHNODISPARIETY			8	9	7	12							

Table 2.2 Summary of architectural designs reported from the Chapel Island Formation (including this thesis).

Code	Architectural design (after Buatois et al., 2017)	Ichnogenera
B.F	Ediacaran body fossils	<i>Harlaniella podolica</i> , <i>Palaeopascichnus delicatus</i>
BT	Bilobate trails and paired grooves	<i>Didymaulichnus</i>
CA	Complex actively filled (meniscate/pelletoidal) horizontal burrows	<i>Psammichnites</i>
HA	Simple actively filled (massive) horizontal to oblique burrows	<i>Torrowangea</i> , <i>Planolites</i>
HB	Horizontal burrows with horizontal to vertical branches	<i>Treptichnus</i> , <i>Phycodes</i>
HP	Passively filled horizontal to oblique burrows	<i>Palaeophycus</i>
HS	Simple horizontal trails	<i>Cochlichnus</i> , <i>Gordia</i> , <i>Helminthopsis</i> , <i>Helminthoidichnites</i>
PS	Plug-shaped burrows	<i>Bergaueria</i> , <i>Conichnus</i>
SM	Trackways and scratch marks	<i>Dimorphichnus</i> , <i>Monomorphichnus</i>
TF	Trilobate flattened trails	<i>Curvolithus</i>
VD	Burrows with shaft or bunch with downward radiating probes	<i>Trichichnus</i>
VH	Vertical helical burrows	<i>Gyrolithes</i>
VS	Vertical simple burrows	<i>Skolithos</i>
VU	Vertical U- and Y- shaped burrows	<i>Arenicolites</i>

CHAPTER 3

3. Ichnology of the *Treptichnus pedum* Zone at the Ediacaran-Cambrian GSSP

One complete stratigraphic section of the *T. pedum* IAZ at Fortune Head was measured (Figure 3.2), as well as one section from Grand Bank Head (Figure 3.3). Due to the presence of *Trichichnus*, as well as a distinctive white medium to very coarse sandstone, it is hypothesized that the base of the Grand Bank Head section is equivalent to roughly 22 m in the Fortune Head section. A smaller-scale section is included for Ediacaran-Cambrian boundary, in order to achieve a greater resolution at this critical interval (Figure 3.3).

In total twenty ichnospecies were documented, belonging to thirteen ichnogenera: *Archaeonassa fossulata*, *Bergaueria* isp., *Bergaueria perata*, *Cochlichnus anguineus*, *Conichnus conicus*, *Dimorphichnus* cf. *obliquus*, *Gordia* isp., *Gyrolithes gyratus*, *Gyrolithes scintillus*, *Helminthoidichnites tenuis*, *Helminthopsis tenuis*, *Monomorphichnus* isp. A, *Monomorphichnus* isp. B, *Monomorphichnus* isp. C, *Palaeophycus* isp., *Palaeophycus tubularis*, *Treptichnus coronatum*, *Treptichnus* isp., *Treptichnus pedum*, and *Trichichnus* cf. *simplex*. These document seven categories of architectural design: simple horizontal burrows, plug-shaped burrows, passively filled horizontal to oblique burrows, horizontal burrows with horizontal to vertical branches, vertical helical burrows, and trackways and scratch marks (Table 3.1). In total this equates to an ichnodiversity of thirteen, and an ichnodisparity of seven.

Ichnogenera previously reported from the *T. pedum* IAZ which were confirmed by this study include: *Cochlichnus*, *Conichnus*, *Bergaueria*, *Dimorphichnus*, *Gordia*, *Gyrolithes*, *Helminthoidichnites*, *Monomorphichnus*, *Palaeophycus*, and *Treptichnus*. Various ichnotaxa were re-assigned. *Skolithos annulatus* has been reassigned to *Gyrolithes gyratus*, due to the helical nature of the burrow. It is suspected that due to the difference in infill and host rock lithology, many *Palaeophycus* were misclassified as *Planolites*. While *Arenicolites* is commonly reported from the section, no cross-section showing the distinctive U-shape of this ichnogenera has been documented in the literature or observed during the course of our study.

Uncontroversial specimens of *Curvolithus*, *Didymaulichnus*, *Phycodes*, or *Psammichnites* were not found within the *T. pedum* IAZ. While *Archaeonassa*, *Helminthoidichnites*, and *Helminthopsis* were recorded within *T. pedum* IAZ strata at Fortune Head, they are also found within the underlying Ediacaran *Harlaniella podolica* IAZ strata and are therefore not constituents of the *T. pedum* IAZ.

Table 3.1 Ichnotaxa recorded within the *T. pedum* IAZ at Fortune Head.

ICHNOGENERA	ICHNOSPECIES
Simple horizontal burrows (HS)	
<i>Archaeonassa</i>	<i>fossulata</i>
<i>Cochlichnus</i>	<i>anguineus</i>
<i>Gordia</i>	isp.
<i>Helminthoidichnites</i>	<i>tenuis</i>
<i>Helminthopsis</i>	<i>tenuis</i>
Plug-shaped burrows (PS)	
<i>Bergaueria</i>	isp.
	<i>perata</i>
<i>Conichnus</i>	<i>conicus</i>
Passively filled horizontal to oblique burrows (HP)	
<i>Palaeophycus</i>	isp.
	<i>tubularis</i>
Horizontal burrows with horizontal to vertical branches (HB)	
<i>Treptichnus</i>	<i>coronatum</i>
	isp.
	<i>pedum</i>
Vertical helical burrows (VH)	
<i>Gyrolithes</i>	<i>gyratus</i>
	<i>scintillus</i>
Trackways and scratch marks (SM)	
<i>Dimorphichnus</i>	cf. <i>obliquus</i>
<i>Monomorphichnus</i>	isp. a
	isp. b
	isp. c
Burrows with shaft or bunch with downward radiating probes (VD)	
<i>Trichichnus</i>	cf. <i>simplex</i>

Ichnotaxonomic determinations were refined, and a few new ichnotaxa were added. The deep chemichnial burrow *Trichichnus* cf. *simplex* was observed, appearing for the first time roughly 10 m above the boundary. A plug-shaped equilibrium vertical burrow, *Bergaueria* isp., is described for the first time, as well as a firmground ichnospecies of *Palaeophycus*. Two ichnospecies of *Gyrolithes* are documented a few meters after the Ediacaran-Cambrian boundary level and the range of *Treptichnus coronatum* has been extended to the lowermost Cambrian in this section. Several specimens of arthropod scratch marks were observed, including *Dimorphichnus* cf. *obliquus* and *Monomorphichnus* isp. C.

Shallow-tier ichnofossils (such as scratch marks and grazing trails) are less likely to be preserved, due to their propensity to be eroded. This phenomenon likely accounts for the dominance of deeper-tier ichnofossils, such as *Gyrolithes*, *Treptichnus*, and *Trichichnus*. In turn, outcrop exposure affects the likelihood of observing certain ichnotaxa. For example, Grand Bank Head has a more prolific exposure of bed bases. As a result, hypichnial ichnotaxa such as *Dimorphichnus*, *Monomorphichnus* and *Treptichnus*, are more likely to be observed at this section. In sections where more cross-sections are exposed, *Gyrolithes* and *Trichichnus* are more likely to be observed. Interestingly, within the GC, SIS-D, and SS-D facies, little to no correlations between facies and ichnotaxa can be observed at this time. In turn, *Treptichnus pedum*, *Palaeophycus* isp., and *Palaeophycus tubularis* are the least facies-controlled ichnotaxa, appearing within member 1 and the Sh facies of member 2a.

Stratigraphic section legend
















































Ichnofauna		
 <i>Archaeonassa fossulata</i>	 <i>Gyrolithes scintillus</i>	 <i>Palaeophycus tubularis</i>
 <i>Bergaueria cf. perata</i>	 <i>Helminthoidichnites tenuis</i>	 <i>Rusophycus avalonensis</i>
 <i>Bergaueria isp.</i>	 <i>Helminthopsis tenuis</i>	 <i>Treptichnus coronatum</i>
 <i>Conichnus conicus</i>	 <i>Monomorphichnus</i>	 <i>Treptichnus isp.</i>
 <i>Cochlichnus anguineus</i>	 <i>Monomorphichnus isp. A</i>	 <i>Treptichnus pedum</i>
 <i>Dimorphichnus cf. obliquus</i>	 <i>Monomorphichnus isp. B</i>	 <i>Trichichnus cf. simplex</i>
 <i>Gordia isp.</i>	 <i>Monomorphichnus isp. C</i>	 Wide, tightly beaded burrow
 <i>Gyrolithes gyratus</i>	 <i>Palaeophycus isp.</i>	 Thin ?branching meandering burrow
Ichnoguilds (IG)		
 <i>Bergaueria isp. IG</i>	 <i>Gyrolithes scintillus IG</i>	 <i>Treptichnus pedum IG</i>
 <i>Dimorphichnus cf. obliquus IG</i>	 <i>Helminthoidichnites tenuis IG</i>	
Stratigraphy and body fossils		
 Very fine grey sandstone	 Current ripples	 Tubular fossil
 Siltstone	 Wave ripples	 Algae?
 White to grey sandstone	 HCS	 <i>Harlaniella podolica</i>
 Red sandstone	 Gutter cast	 <i>Palaeopascichnus delicatus</i>
 Rencontre Fm.	 Desiccation crack	 Scratch circle
 Marystown Fm. volcanics	 Mudclast	
	 Syneresis crack	

Figure 3.1 Legend for the stratigraphic sections seen in figures 2.2, 3.2 and 3.3.

Fortune Head section

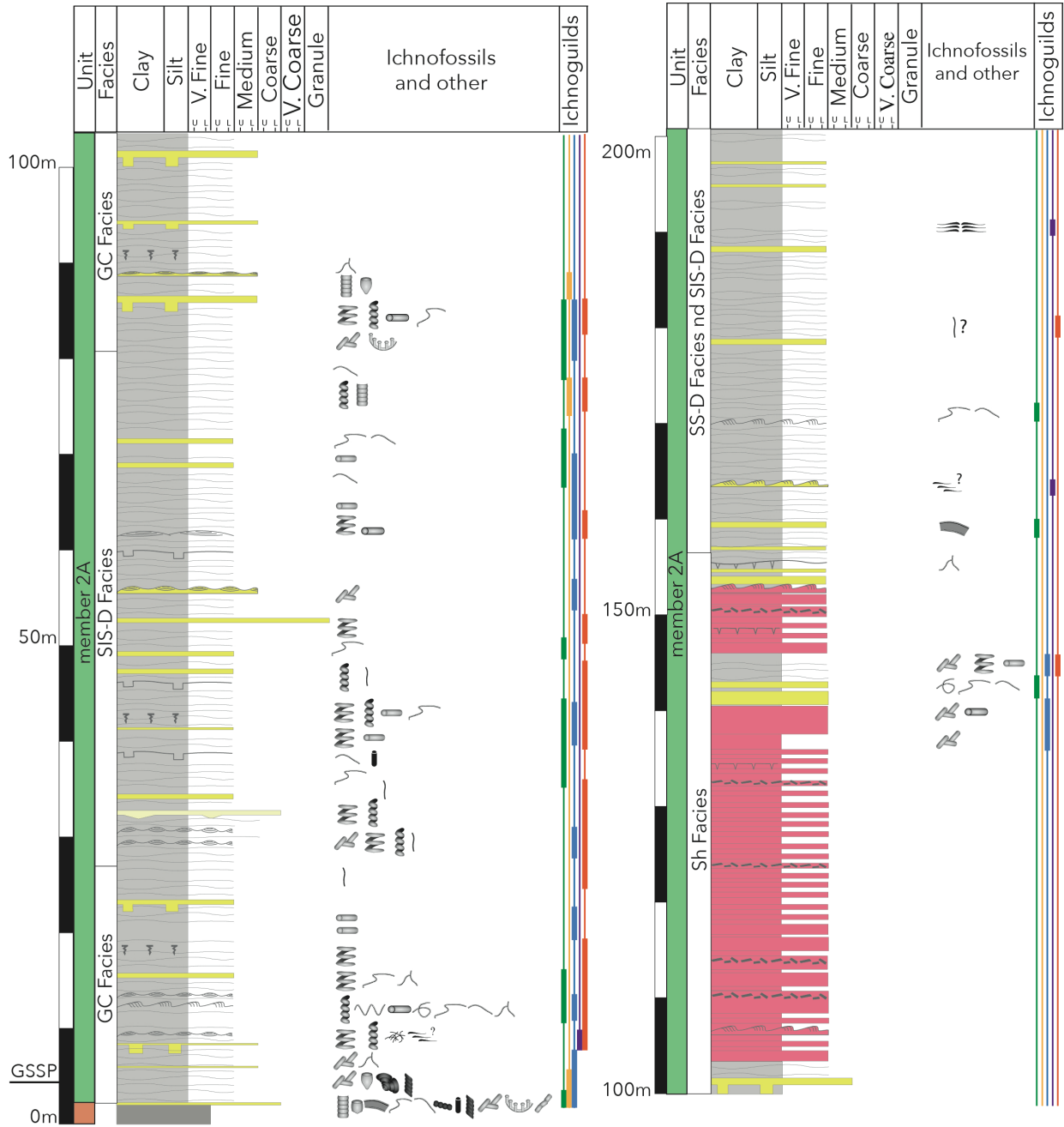


Figure 3.2 Stratigraphic section of the *T. pedum* IAZ (first 200m of member 2 of the CIF) at Fortune Head, with ichnologic and ichnoguild data. For a legend see Figure 3.1. Sedimentology from Myrow, 1987.

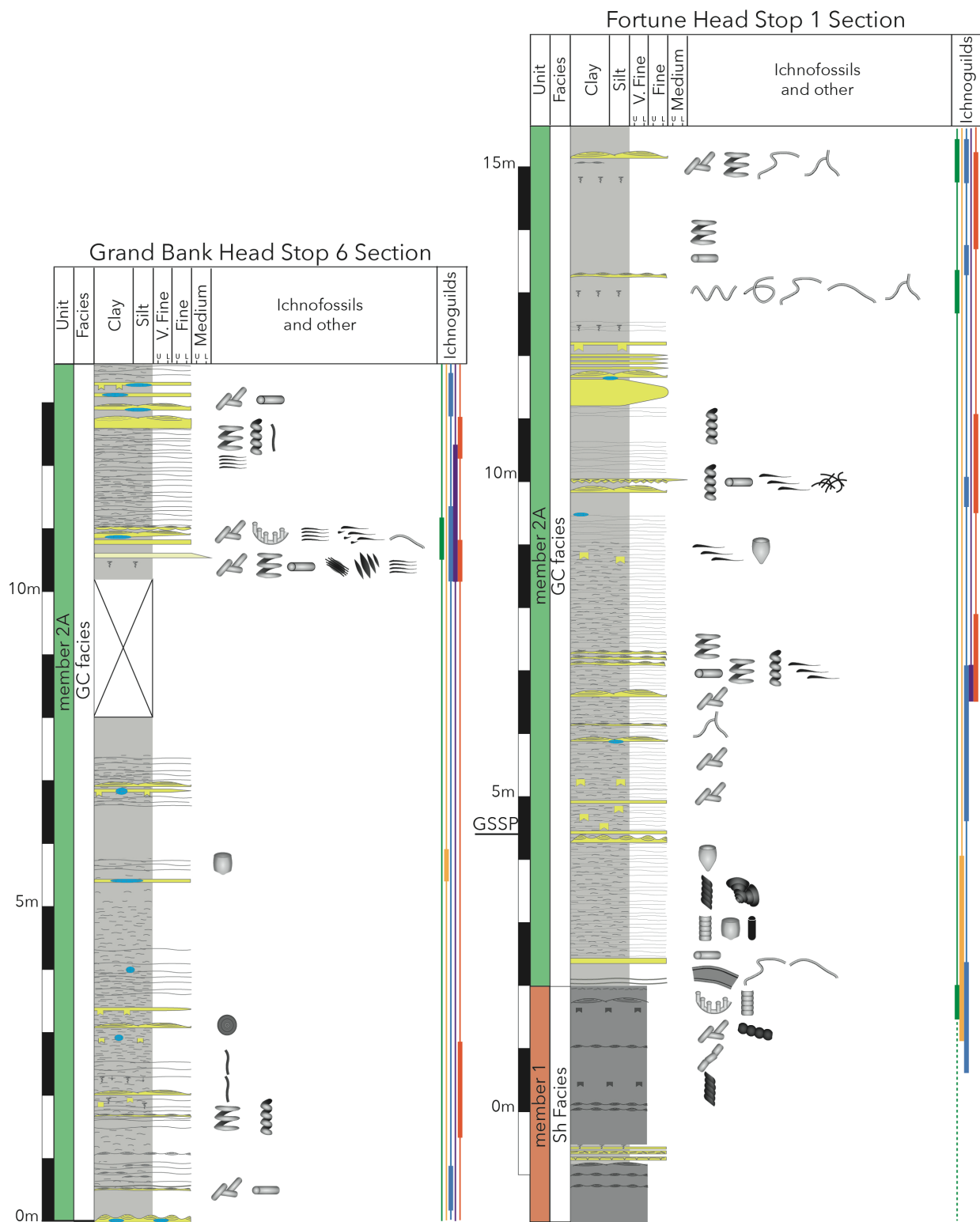


Figure 3.3 Stratigraphic sections of Grand Bank Head stop 6 and Fortune Head stop 1. Legend in Figure 3.1

3.1. Systematic Ichnology

Ichnogenus *Archaeonassa* Fenton and Fenton, 1937

Archaeonassa is commonly reported as epireliefs composed of two convex parallel lateral levees separated by a flat, convex, or concave central zone. The levees and the central zone may be either smooth or variably ornamented (after Buckman, 1997). While present in the latest Ediacaran, documented *Archaeonassa* occurrences increase at the beginning of the Cambrian, and are present globally (Figure 3.4).

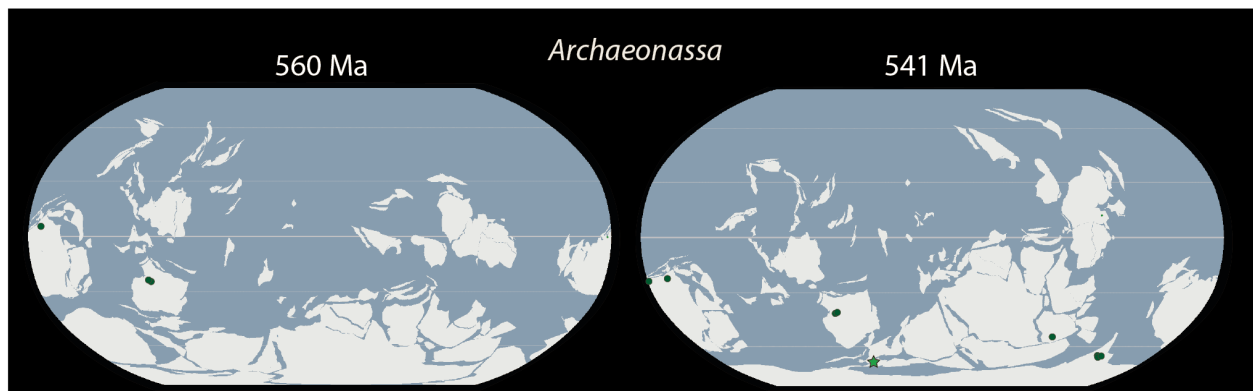


Figure 3.4 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Archaeonassa* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For data used in these reconstructions, see Appendix A

***Archaeonassa fossulata* Fenton and Fenton, 1937**

Figure 3.28 A

Material

Approximately 10 specimens identified and photographed in the field (FH 2.6 m and 159.9 m).

Diagnosis

As for the ichnogenus.

Description

Smooth, shallow furrows, 0.75-1 mm wide, preserved in epirelief on very fine-grained sandstone. Ridge is 0.75-1 mm wide. Course very slightly meandering with no loops or overcrossings. Commonly observed associated with microbially induced sedimentary structures (MISS).

Remarks

The presence of levees distinguishes this horizontal trail from *Helminthoidichnites* and *Helminthopsis*. Only one type ichnospecies of *Archaeonassa* has been erected, *Archaeonassa fossulata*. Other ichnospecies of *Archaeonassa* have been identified, but none formally named (Rodriguez-Tovar et al., 2014). These are in places distinguished by the presence of loops, which the Chapel Island Formation ichnospecies lack. Potential tracemaker of *Archaeonassa* include gastropods and arthropods, but worms cannot be excluded (Buckman, 1994; Yochelson and Fedonkin, 1997). *Archaeonassa fossulata* likely represents the trail of a microbial mat grazer (Mángano and Buatois, 2003). The simple, horizontal morphology with an absence of resting traces suggests continuous movement. The slightly meandering course would be an inefficient mode of locomotion, suggesting an additional purpose for the trail. Prevalent MISS on or near the trace fossil-bearing bed indicates the presence of a rich microbial-mat food source, further supporting the idea that this trail likely records grazing activities (Pascichnia) (Buatois and Mángano, 2004; 2012).

Ichnogenus *Bergaueria* Prantl, 1945

Bergaueria is a smooth cylindrical to hemispherical, vertical burrow with a rounded base and a circular to elliptical cross-section. The base may or may not possess a shallow, central depression and radial ridges, and the fillings are structureless (after Pemberton et al., 1988). These burrows are commonly perceived as burrows of actinarian anenomes, due to their radially symmetrical nature (Alpert, 1973). Known from the late Ediacaran, *Bergaueria* became more common at the lowermost Cambrian boundary, with most specimens around Baltica and Avalonia (Figure 3.5).

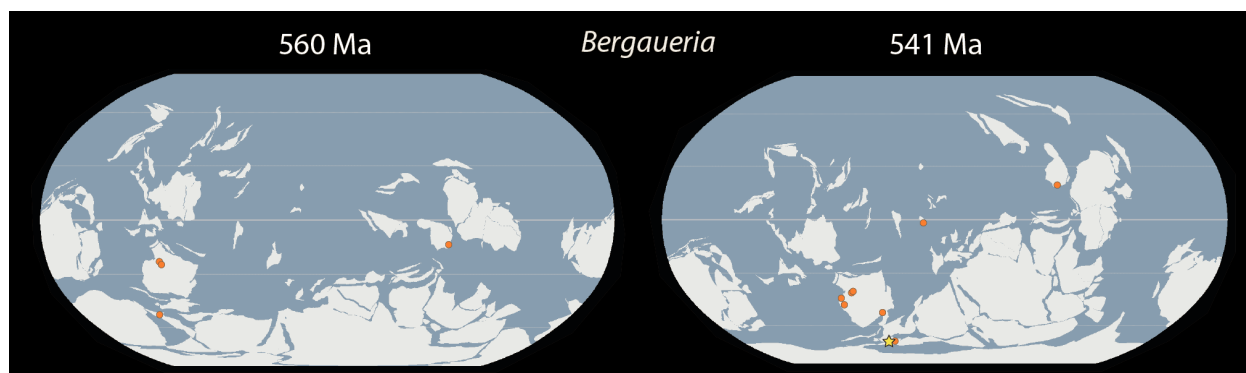


Figure 3.5 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Bergaueria* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For data used in these reconstructions, see Appendix A

Bergaueria isp.

Figures 3.6 A, 3.8 C

Material

Thirteen photographed specimens (FH 3.2 m, 76.3 m, 87 m).

Description

Endichnial, vertical to sub-vertical plug-shaped burrows with subtle constrictions. Burrows is 1-5 mm wide and 2-26 mm long, with an average length to width ratio of 3.7 (range: 1.7-5.2). No backfill visible, burrow fill consists of very fine-grained sand, in places preserved in “floating” preservation-style. Burrows are observed crossing thin (<1 mm) very fine-grained sandstone beds, and are commonly found topped by thicker (>2 mm) very fine-grained sandstone beds.

Table 3.2 Diameter and heights (in mm) of *Bergaueria* isp. specimens found in the *T. pedum* IAZ on the Burin Peninsula, Newfoundland.

	Diameter (mm)	Height (mm)	D/H
BERGAUERIA ISP.	1	5	0.20
	1	2	0.50
	4	9	0.44
	1.5	6.5	0.23
	3	5	0.60
	5	26	0.19

Remarks

The plug-shaped nature of this burrow imparts resemblance to the anemone resting trace *Bergaueria*. Indeed, the range of this burrows diameter to height ratio falls within observed ratios in *Bergaueria*, skewed towards smaller values (Figure 3.7). The constrictions and length imply vertical movement of the burrow, which is best observed in the bottom half of figure. 3.6 A. It is possible to reconstruct the history of these two burrows (Figure 3.6 B). A specimen of *Bergaueria perata* which shows no vertical burrow re-adjustment can be seen in the bottom left. Adjacent to this burrow is a larger *Bergaueria* isp., with one vertical re-adjustment of the burrow preserved (Figure 3.6 A). Both tracemakers colonized the same surface, denoted by a thin very fine-grained sandstone bed (Figure 3.6 B1). The smaller *Bergaueria perata* organism was unable to respond to the subsequent sedimentation event, or was plucked out of their burrow during the event (Figure 3.6 B2). The larger *Bergaueria* isp. organism readjusted their burrow, as evidenced

by the constrictions coincident with the last colonization surface (Figure 3.6 B3). When a larger, higher velocity sedimentation event deposited the overlying thicker, very fine-grained sandstone bed, the larger *Bergaueria* isp. organism likely died, or was plucked from their burrow (Figure 3.6 B4). Eventually, the surface was recolonized by two more *Bergaueria* isp. producers.

Lateral displacement has been observed in *Bergaueria sueta* (Seilacher, 1990; Hofmann et al., 2012; Mángano et al., 2013); however, the displacement is horizontal and much more limited than in *Bergaueria* isp. While *Kulindrichnus* shares a similar diameter to height ratio, it is distinctly shell-filled, phosphatically-lined, and does not display the constrictions found in *Bergaueria* isp. A fossil of a similar shape and with constrictions present was described by Tada (1966), but is much larger than the specimens described herein. Plug-shaped equilibrium structures are figured by Buck and Goldring (2003, Figure 13A) and Menon et al. (2013). These likely appear different to the plug-shaped equilibrium structures described herein, due to differences in sediment consolidation. Additionally, equilibrium behaviour has been interpreted for *Conichnus* (Bromely, 1996; Savdra, 2003). The constrictions in the burrow imply punctuated upward vertical movement. One likely cause would be burrow re-location with sedimentation, suggesting an equilibrichnia ethology for the burrow. The rounded basal morphology of *Bergaueria* isp. suggests a radially symmetrical producer, and it has been argued that these type of burrows were created by actinarian anenomes (Alpert, 1973). As a result, the burrowers were likely predators. The vertical to sub-horizontal orientation of the burrow and lack of active fill imply that this was primarily a dwelling or resting burrow

Some ichnospecies of *Bergaueria* are likely resting burrows (e.g., *Bergaueria sueta*, Seilacher, 1990; Hoffman et al., 2012; Mángano et al., 2013), and it has been suggested that Cubichnia and Domichnia variants of *Bergaueria* may be distinguished by the absence or presence of a burrow lining, respectively. While *Bergaueria* isp. from the CIF lacks a lining, excavation within a firmground (Droser et al., 2002) likely made additional stabilization features (such as a lining) unnecessary. In turn, it would require considerable effort to excavate a burrow in this firm substrate, effort that was likely not expended simply for resting.

Documented “*Skolithos annulatus*” (now *G. gyratus*, see Laing et al., 2018) from below the GSSP are wider and shorter than *G. gyratus* (Gehling et al., 2001) and are likely instead *Bergaueria* isp.

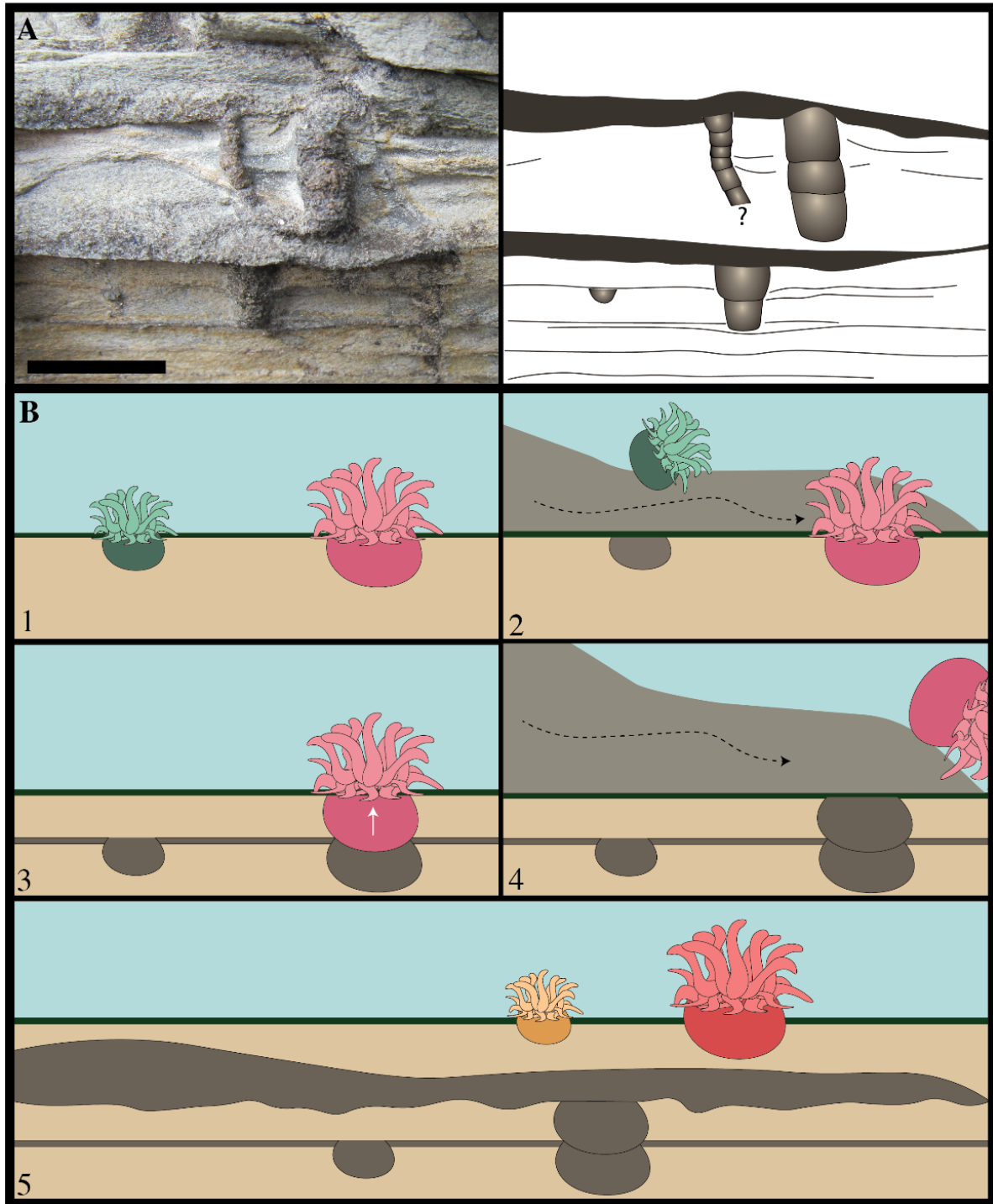


Figure 3.6 (A) Left: field photograph of three *Bergaueria* isp. specimens and one *Bergaueria* (bottom left). Scale bar = 1 cm, stratigraphic height = 3.6 m. Right: Schematic of the field photograph. Sand beds denoted by a darker grey. **(B)** Schematic interpretation of the sequence of events preserved in the bottom half of the field photograph. **1.** Colonization by two *Bergaueria* organisms. **2.** Sedimentation event plucks or smothers the smaller organism (cyan). **3.** The larger *Bergaueria* organism (pink) adjusts their burrow. **4.** A higher velocity sedimentation event plucks or smothers the larger organism (pink). **5.** Recolonization of the surface.

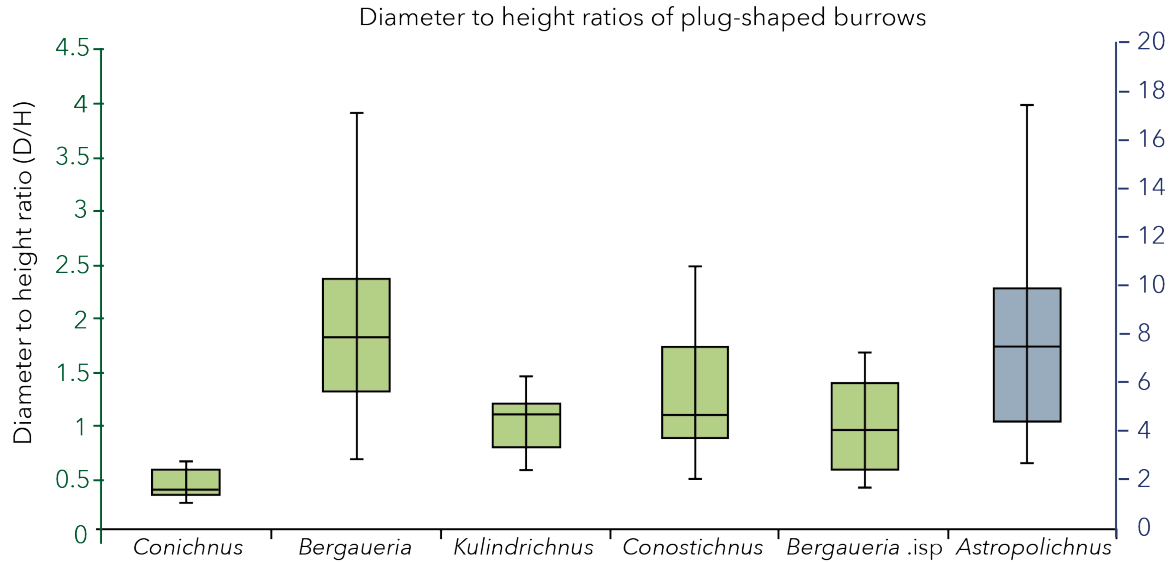


Figure 3.7 A box plot showing the diameter to height ratios of various plug-shaped burrows. Ratios for *Conichnus*, *Bergaueria*, *Kulindrichnus*, *Conostichnus* and *Astropolichnus* taken from Pemberton et al. (1988). Ratios for *Bergaueria* are from this dissertation, and can be seen in Table 3.2. The values for *Astropolichnus* are expressed on the blue axis (right-most y-axis), and the remaining values are on the green axis (left-most y-axis).

***Bergaueria perata* (Prantl, 1945)**

Figure 3.6 A

Material

Five specimens observed and photographed in the field.

Diagnosis

Bergaueria with smooth, unornamented walls and a flat to rounded base that may have faint radial ridges; one or more central depressions; concentric circular impressions (after Pemberton et al., 1988).

Description

Smooth, rounded, unornamented vertical burrows, 1-10 mm wide, 1-8 mm in height, preserved in full relief with no wall or lining present. Infilled with very fine-grained sandstone.

Remarks

The rounded basal morphology of these burrows distinguish them from *Conichnus*, and may suggest construction by an actinarian anemone (Alpert, 1973). Prominent radial ridges, a diagnostic feature of *Conostichnus*, are not present. The lack of lateral constrictions prevents classification as *Bergaueria* isp. These specimens lack a thick lining, distinguishing them from *B. langi*. *Bergaueria* has been interpreted as either dwelling or resting structures, depending on the

presence of a lining (Pemberton et al., 1988). The CIF *Bergaueria perata* are likely domichnial burrows. Lining is common in softground dwelling burrows, as it provides burrow stability. However, these specimens were emplaced in a firmground, and a lining would be unnecessary. In turn, more effort would be required for excavation in a firmground environment, making a resting ethology unlikely. In turn, the specimens are smaller in both diameter and height than average *Bergaueria*'s whose average diameter and height are 29 mm and 18 mm respectively (Pemberton et al., 1988). Care must be taken when identifying *Bergaueria perata* in the CIF, especially within the gutter-cast facies (Myrow, 1987; 1992), as many pot-casts may resemble the rounded morphology distinctive of *Bergaueria* (Figure 3.8 A and B).

Bergaueria perata and *Bergaueria* isp. are likely produced by the same organism, with *Bergaueria perata* being present on only one colonization surface (Figure 3.6 B). With the high sedimentation rates in the CIF (Myrow and Hiscott, 1991; 1993), these organisms likely had to react to multiple sedimentation events in their lifetimes. As a result, the probability of a *Bergaueria* organism only colonizing one surface was likely low, and may explain the rarity of these specimens at this locale.

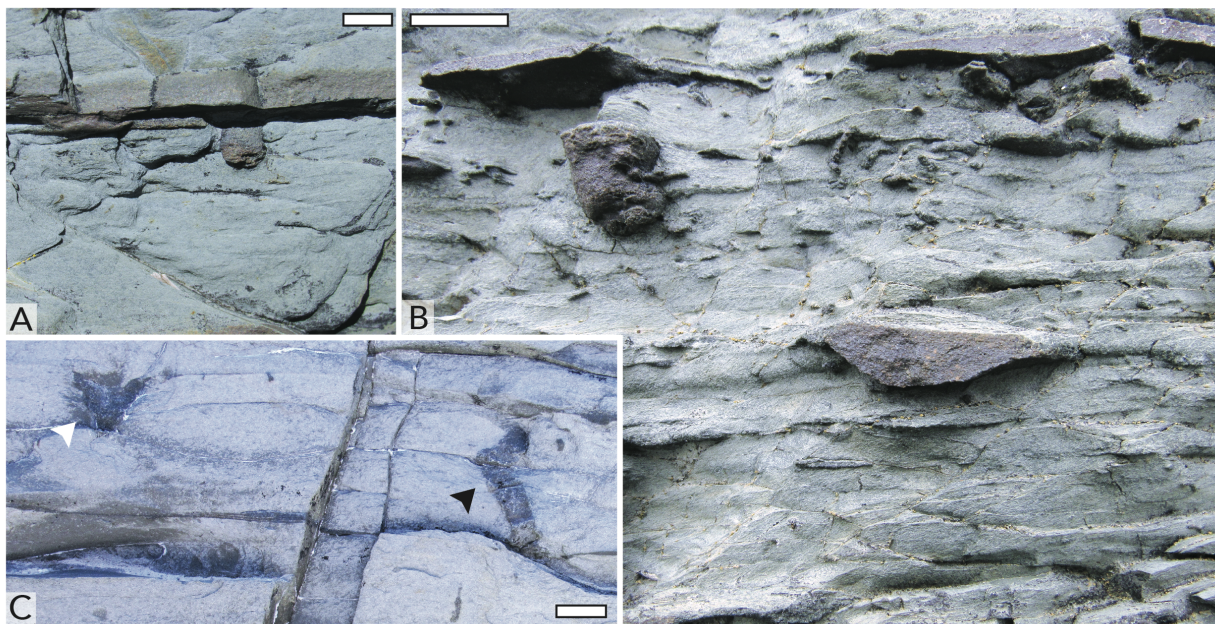


Figure 3.8 (A-B) Pot and gutter casts in the gutter cast facies of Myrow (1987), viewed in cross-section. Pot casts may resemble *Bergaueria*. **(C)** *Conichnus conicus* (white arrow) and *Bergaueria* isp. (black arrow) preserved in “floating” style full relief, viewed in cross-section. Scale bars are 1 cm.

Ichnogenus *Cochlichnus* Hitchcock, 1858

Cochlichnus is described as regular, sinusoidal, horizontal trails and burrows resembling a sine curve (after Fillion and Pickerill, 1990, modified from: Hitchcock 1858; Häntzschel 1975). Although a few specimens have been recorded from the late Ediacaran, available evidence is inconclusive. By the lowermost Cambrian, however, *Cochlichnus* has a global distribution (Figure 3.9).

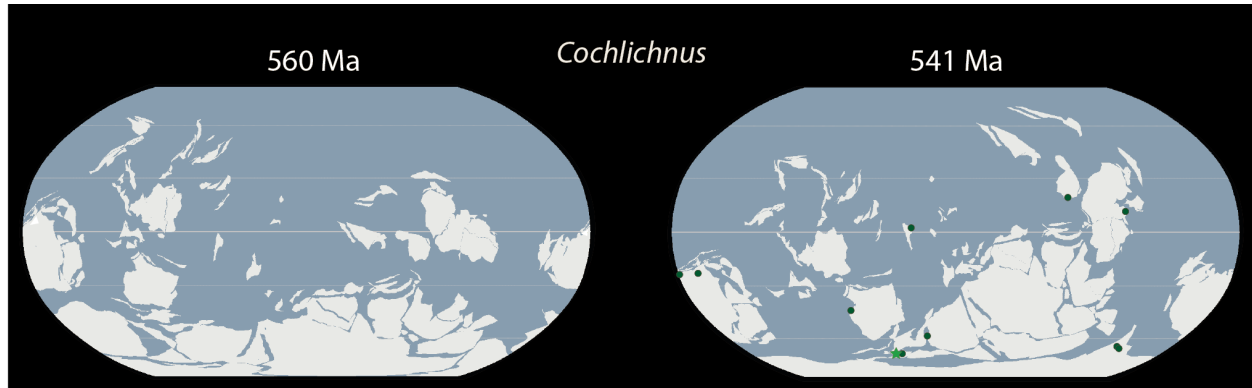


Figure 3.9 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Cochlichnus* is absent from 560 Ma strata, however, all documented *Cochlichnus* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

***Cochlichnus anguineus* Hitchcock, 1858**

Figure 3.28 D

Material

Roughly 20 field identifications (FH 12.5 m).

Diagnosis

Simple, smooth, horizontally undulating trails. Slight vertical undulations can be present as well. The first-order path is either straight or slightly curved. Horizontal wave length may change along the path and is markedly larger than the wave amplitude (after Gámez Vintaned et al., 2006).

Description

Sinusoidal, unbranching, smooth trails following a gently curving second-order path. Commonly preserved in concave epirelief. Two and a half wavelengths preserved (16.2 mm, 16.7 mm). The trail is 0.5-0.6 mm wide, with an amplitude of 4.4-4.5 mm.

Remarks

The perfectly sinusoidal first-order path of the specimen distinguishes *Cochlichnus* from *Helminthopsis* and *Helminthoidichnites*. The regular sinusoidal 1st order path in *Cochlichnus* distinguishes it from *Cosmorhapse*. *Cochlichnus kochi* displays regular second-order meanders, which *C. anguineus* lacks. The perfect regularity of the sinusoidal first-order pattern of *Cochlichnus* has led some authors to suggest it is a result of the mode of locomotion of the producer (Moussa, 1970), rather than representing a complex feeding pattern. Commonly found associated with MISS structures (Buatois et al., 2014), the CIF specimens are likely pascichnial trace fossils.

Ichnogenus *Conichnus* Männil, 1966

Conichnus is a conical or acuminate sub-cylindrical structures oriented perpendicular to bedding with either a rounded base or a distinct, papilla-like protuberance. The burrow fill does not show medusoid symmetry, but may be patterned (after Pemberton et al., 1988). *Conichnus* first appears at the Ediacaran-Cambrian boundary, with only a few documented occurrences (Figure 3.10)

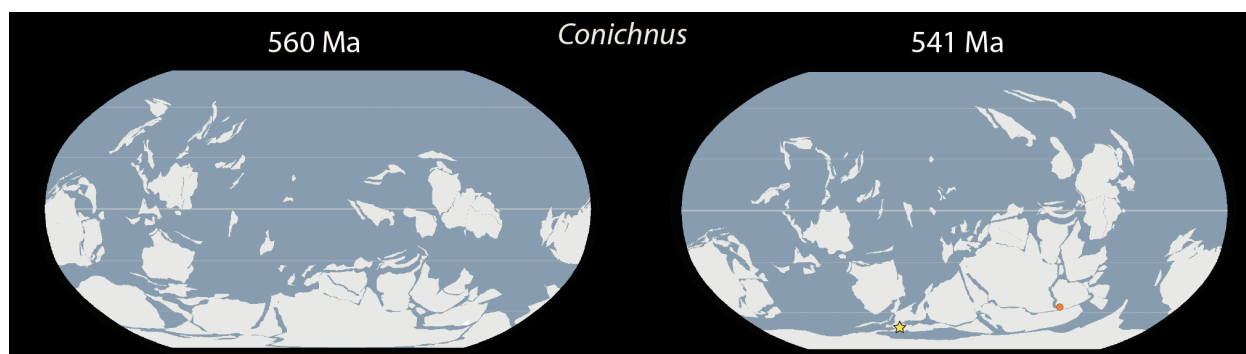


Figure 3.10 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Conichnus* is absent from 560 Ma strata, however, all documented *Conichnus* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

***Conichnus conicus* (Männil, 1966)**

Figure 3.8 C

Material

Two specimens identified in the field (FH 6.9 m, 87 m).

Diagnosis

Indistinctly to thinly lined *Conichnus* tapering to a smooth, rounded, but distinct basal apex (after Pemberton et al., 1988).

Description

Vertical, unornamented, unlined, conical burrows, 10-15 mm deep, preserved in full relief. Infilled with structureless very fine-grained sandstone, found either in “floating” style preservation, or on the base of thin sandstone. Base is rounded, 1-3 mm wide. Top is cusped, 13-15 mm wide.

Remarks

The conical burrow *Amphorichnus* has been synonymized with *Conichnus* (Frey and Howard, 1981; Pemberton et al., 1988). Most specimens of *Conichnus* are found as isolated burrows. Occasional interpenetration or vertical-lateral successions has been observed, suggesting the organism was capable of keeping pace with sedimentation (Frey and Howard, 1981). The distinct conical morphology of this burrow distinguishes it from *Bergaueria*. It lacks the transverse constrictions and longitudinal ridges observed in *Conostichnus*. *Conichnus papillatus* Männil, 1966 has a distant basal protuberance, which the CIF specimens lack. The vertical orientation, simple morphology, and lack of active infill imply this burrow was primarily a dwelling burrow (Frey and Howard, 1981; Pemberton et al., 1988). It has been suggested that the lack of medusoid structure in *Conichnus* may reflect a slightly different behaviour or feeding strategy than *Bergaueria* (Frey and Howard, 1981). No vertical movement has been observed in CIF *Conichnus*.

Ichnogenus *Dimorphichnus* Seilacher 1955b

Dimorphichnus is comprised of asymmetrical trackways with two different types of impressions: thin, straight, or sigmoidal ones, and blunt ones; both types arranged in series oblique to the direction of movement (Fillion and Pickerill, 1990, modified from Seilacher, 1955b). The genera *Dimorphichnus* is restricted to the Cambrian, with only a few documented appearances at the lowermost boundary (Figure 3.11).

Discussion

Structures interpreted as arthropod scratch marks have been assigned to the ichnogenera *Dimorphichnus* (Seilacher, 1955b) and *Monomorphichnus* (Crimes, 1970). Both ichnogenera possess at least one set of straight to sigmoidal scratch marks, either grouped in pairs or singular.

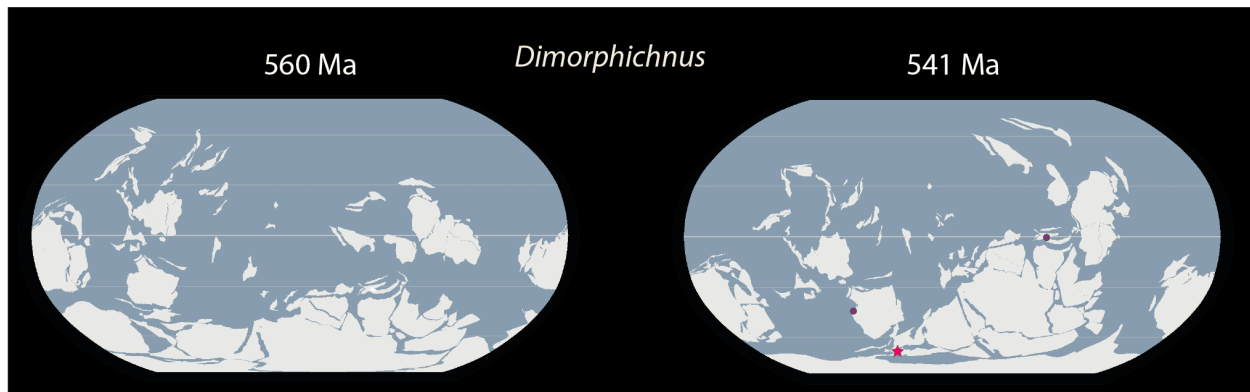


Figure 3.11 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Dimorphichnus* is absent from 560 Ma strata, however, all documented *Dimorphichnus* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A

These sets are commonly called ‘raking marks’ due to their interpretation as the result of a trilobite raking the seafloor with one side of legs (Seilacher, 1955b). A second set of scratch marks are present in *Dimorphichnus*, called ‘pusher marks’, and are interpreted as the result of one side of legs anchoring the trilobite (Seilacher, 1955b). *Monomorphichnus* lacks this secondary set of scratch marks.

The difference between ichnogenera (the presence or absence of pusher marks) has been attributed to undertrack preservation (i.e. preservation on different planes), with *Monomorphichnus* being the deep undertrack of *Dimorphichnus* (Seilacher 1985, 1990). However, Jensen (1997) noted that most raker marks are reported shallower than pusher marks. This would suggest that an undertrack of *Dimorphichnus* would only have the pusher marks preserved and lack the raker marks. Goldring and Seilacher (1971) suggested that the pusher marks are spread out, acting as snow shoes, and are thus shallower than the raker marks.

Additionally, it has been suggested by Seilacher (1985, 1990), and subsequently contested by Fillion and Pickerill (1990) that the type specimen of *Monomorphichnus* has faint elongate pusher marks preserved, as well as partially superimposed raking marks. Jensen (1997) notes that the illustration of the holotype (Crimes 1970, PL12C) shows overlapping between the laterally repeated sets, with another set at an angle. If these are genetically related or there are pusher marks preserved, then the holotype is of *Dimorphichnus*-type, making *Monomorphichnus* a junior synonym of *Dimorphichnus*. Regardless, there are likely still specimens attributed to *Monomorphichnus* that cannot be placed in *Dimorphichnus* (Mángano and Buatois, 2003). In turn, “true” *Monomorphichnus* likely represents a different behavioural strategy, due to the

absence of pusher marks. It has been posited that *Monomorphichnus* is a swimming trace (Crimes, 1970) or a trilobite caught in the current (Osgood, 1975b). Jensen (1997) remarked that the possible behavioural differences between *Monomorphichnus* and *Dimorphichnus* warrants continued distinction between the ichnogenera. This has led multiple authors to retain both *Monomorphichnus* and *Dimorphichnus* and in cases of uncertainty to label the traces as ‘arthropod scratch marks’ (Feng et al., 2017; Jago and Greenhouse, 2014; Tiwari et al., 2013; Hofmann et al., 2012; Kumar and Pandey, 2008; Such et al., 2007; Mángano and Buatois, 2003; Jensen, 1997; McMenamin, 1984). In turn, *Monomorphichnus* is a term deeply entrenched in the literature (Figure 3.12). While a new type ichnospecies may need to be designated, the ichnogenus *Monomorphichnus* may be retained to avoid confusion (per ICZN guidelines, section 70.3) (Welter-Schultes, 2012, p. 111). As a result, *Monomorphichnus* is herein retained to describe unpaired groups of scratch marks, until a re-examination of the type material is conducted.

To complicate matters further, deep undertracks of *Cruziana* and *Rusophycus* can easily be mistaken for *Monomorphichnus* (Mángano et al., 1996; Mángano and Buatois 2003). Some specimens of *Dimorphichnus* may in fact be misclassified *Diplichnites*, as they do not demonstrate a clear distinction between “pusher” and “raker” marks, other than being oriented oblique to the direction of movement (e.g., Kumar and Pandey, 2008).

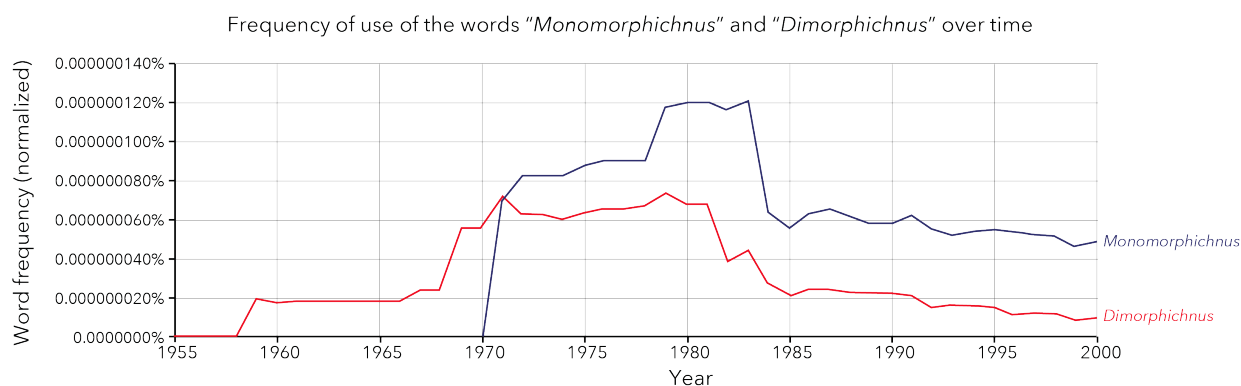


Figure 3.12 Graph of the usage frequency of the words “*Monomorphichnus*” and “*Dimorphichnus*” over time. Usage frequency was calculated by dividing the number of times a word was used in a specific year by the number of words in the database (Google Books) for that year. Graph created using Google ngram viewer; for more information see Michel et al. (2011).

***Dimorphichnus* cf. *obliquus* Seilacher 1955b**

Figure 3.29

Material

Two slabs in the field (GBH6 10.5 m, 11 m), containing at least nine specimens.

Diagnosis

Asymmetrical trackways with two different types of imprints; thin straight or sigmoidal scratch marks and blunt imprints; both types arranged in series oblique to direction of movement (Fillion and Pickerill, 1990, modified after Seilacher, 1955b).

Description

Asymmetrical trackways with two different types of imprint sets, slightly offset or overlapping, oriented in the same direction. One set is comprised of a series of 6-8 thin (0.1-0.2 mm, avg. 0.14 mm) straight to sigmoidal long (7-10.8 mm, avg. 9.6 mm) scratch marks. The other set is comprised of 1 to 4 thick (0.1-0.3 mm, avg. 0.2 mm), shorter (2.2-10.9 mm, avg. 5.8 mm), straight scratch marks (Table 3.3). Preserved in positive hyporelief on variably fluted and bioturbated very fine-grained sandstone beds.

Remarks

While the material is fragmentary and no continuous tracks are easily recognized, two morphologies can be distinguished. The first set is the straight to sigmoidal long scratch marks, herein interpreted as the “raker” marks. The second set is the straight, think, shorter scratch marks, herein interpreted as the “pusher” marks. The original diagnosis of *D. obliquus* included a stipulation that the raking scratch marks must be sigmoidal (Seilacher, 1955b). However, the pattern of the raking marks likely records the action of the current, rather than the producer, and is considered non-diagnostic (Fillion and Pickerill, 1990). This specimen is similar to Crimes (1970) *Dimorphichus* isp. from Locality 5 which has blunt pusher marks and elongate non-sigmoidal raker marks (Crimes, 1970, Figure 4, p. 56). Additionally, he noted the resemblance between his specimen and *D. obliquus*, and interpreted the trackway as produced by a trilobite moving obliquely under current influence. For a discussion on possible tool mark affinities of *D. cf. obliquus*, see the remarks of *Monomorphichnus* isp. B.

Table 3.3 Dimensions of three specimens of *D. cf. obliquus*.

<i>Dimorphichnus cf. obliquus</i>					
Specimen ID	Impression ID	Number of impressions per specimen	Impression width (mm)	Impression length (mm)	Separation between impressions (mm)
Raker marks					
8.1	8.1a	8	0.1	7	
	8.1b	8	0.2	10.5	0.8
	8.1c	8	0.2	10.8	0.6
	8.1d	8	ind.	ind.	
	8.1e	8	ind.	ind.	
	8.1f	8	ind.	ind.	
	8.1g	8	0.1	10	0.5
	8.1h	8	0.1	9.8	8.9
		Average:	0.14	9.62	2.7
Pusher marks					
8	8.1	1	0.3	4.7	
8.6	8.6a	3	0.2	7.1	1.4
	8.6b	3	0.2	8.6	1.3
	8.6c	3	0.2	5.1	
8.8	8.8a	4	0.1	2.2	0.8
	8.8b	4	0.2	3.5	0.9
	8.8c	4	0.2	4	2.6
	8.8d	4	0.2	10.9	
		Average:	0.2	5.76	1.4

Following the directional clues outlined by Seilacher (1955b; 1990; 2007), it is possible to discern tentative trackway directions for some the CIF material. For the uppermost two sets of the green trackway (Figure 3.29 A), the organism moved from the top right corner towards the bottom left. This is evidenced by the slight tapering seen in the pusher marks (Figure 3.29 C), as well as the strike of the rakers. The marching direction is unable to be determined. If the bottommost green set is related, the organism then switched direction, moving towards the bottom right corner.

Ichnogenus *Gordia* Emmons, 1844

Gordia is a predominately horizontal, unbranched, winding, or irregularly meandering trace fossil, that tend to form loops (after Uchman, 1998, modified from Pickerill and Peel, 1991 and Fillion and Pickerill, 1990). In contrast to *Helminthoidichnites*, *Gordia* demonstrate nonrandom behaviour (Hofmann, 1990). This trace fossil first occurs in the Ediacaran, with a global distribution. At the lowermost Cambrian boundary the number of occurrences increases significantly (Figure 3.13).

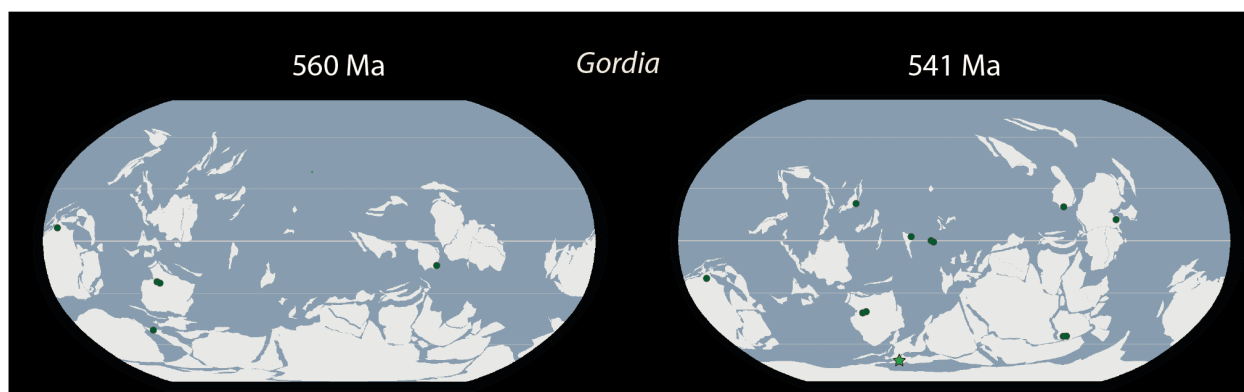


Figure 3.13 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Gordia* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A

***Gordia* isp.**

Material

Two specimens in the field (FH 12.5 m, 142 m) plus roughly 25 specimens identified in the field.

Description

Horizontal, smooth, trails preserved in convex or concave epirelief, showing occasional overcrossing and loops. Trail is 0.50-0.75 mm wide.

Remarks

These trails with occasional overcrossing closely match the description of *Gordia* isp. of Fillion and Pickerill (1990). These differ from *Gordia marina* Emmons, since they do not have fully developed level crossing. The lack of annulations prevents classification as *G. nodosa*. The lack of apical arcuate bends differentiates this ichnospecies from *G. arcuata*. *Gordia* is commonly viewed as a pascichnial trace, due to its simple horizontal morphology and lack of active infill. As a result, the CIF likely represent a grazing behaviour that was of similar complexity to that of *Helminthoidichnites* or *Helminthopsis*.

Ichnogenus *Gyrolithes* de Saporta, 1884

Gyrolithids are spiraled burrows, whose helix is essentially vertical with rare branchings. Their coils are not in contact, and can dextral, sinistral, or reversing (after Uchman and Hanken, 2013, modified from Bromley and Frey, 1974). They are restricted to the Cambrian, with their first occurrence a few meters above the Ediacaran-Cambrian boundary. Interestingly, they show a strong provincialism, and are restricted to Baltica and Avalonia (Figure 3.14).

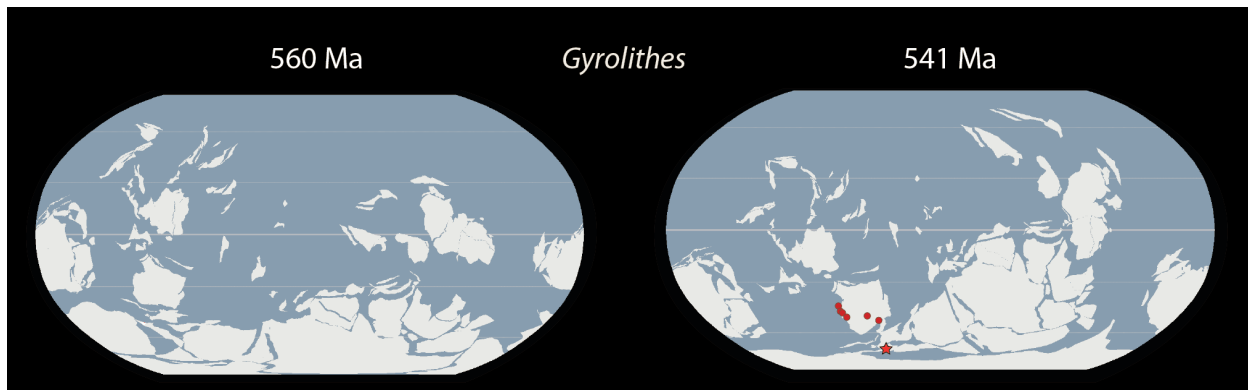


Figure 3.14 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Gyrolithes* is absent from 560 Ma strata, however, all documented *Gyrolithes* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A

Discussion

Vertical spiral burrows, termed “*Gyrolithen*” by Debey (1849), were classified under the ichnogenus *Gyrolithes* by de Saporta in 1884. Over time several ichnospecies were erected, likely due to a lack of clarification regarding *Gyrolithes* ichnotaxobases. Uchman and Hanken (2013) revisited the ichnogenus, and reduced the number of valid ichnospecies from 18 to 13. During their revision, they re-examined *Gyrolithes* ichnotaxobases, which was further expanded upon by De Renzi et al. (2017) and Laing et al. (2018). Kim et al. (2005) reassigned *Skolithos gyratus* Hofmann to the ichnogenus *Gyrolithes*, and Laing et al. (2018) erected the ichnospecies *G. scintillus*, expanding the number of valid ichnospecies to 15.

***Gyrolithes gyratus* (Hofmann), 1979**

Figure 3.28 B, C, E

Material

Seven photographed field specimens (FH 7.7 m, 10.7 m, 40 m) plus roughly 20 specimens identified in the field.

Description

Unlined, smooth, narrow-form, tightly coiled *Gyrolithes*. Specimens are unbranched, passively infilled, circular helical burrows. They are oriented vertical to the bedding plane, and consist of coils which are variably in contact. Burrows are circular in cross-section, with radii ranging from 0.2–0.38 mm, with an average radius of 0.27 mm. Whorl radius is 0.25–0.4 mm with an average

length of 0.34. Height between whorls is 0.5 and 1 mm, with an average height of 0.82 mm. Burrows have between 5 and 15 whorls, with an average of 10 whorls. Overall burrow depth is 4-14.9 mm, with an average depth of 8.7 mm. Burrow radius was measured along both the x- and y- axis when possible. Assuming an original circular cross-section, the difference between the y-axis and x-axis burrow radius can be attributed to compression, and an average compression ratio of 33% was calculated.

Remarks

These burrows were previously classified as *Skolithos annulatus* Howell; however, a re-evaluation of these specimens demonstrated that they are in fact *Gyrolithes* with an exceptionally narrow form and tight coils (Laing et al., 2018). These burrows are interpreted as agrichnial burrows, where the helical morphology served as a sediment anchor and increased surface area for bacterial gardening. For a full review see Chapter 4.

***Gyrolithes scintillus* Laing et al, 2018**

Figure 3.28 G, H, 3.30 A

Material

Twenty-four photographed field specimens (FH 7.1 m, 8.1 m, 14.8 m, 15 m, 15.2 m, 17.6 m, 29 m, 33 m, 42 m, 52 m, 69 m, and 146 m) plus numerous specimens identified in the field.

Description

Unlined, smooth, wide-form, variably coiled *Gyrolithes* oriented vertical to oblique to bedding. Endichnial, unbranched burrows, infilled by very fine-grained sand. Coils not in contact. Burrows are circular in cross-section, and range between 0.25-1 mm in width. Whorl radius, measured from the middle of the burrow, ranged from 0.70-4.65 mm. Height between whorls ranges between 1.4-8 mm. Elongated bottom compartments are locally present.

Remarks

These burrows were previously classified as *G. isp.* or *G. polonicus* Fedonkin (Landing et al., 1988; Tarhan and Droser, 2014; Mángano and Buatois, 2016; Herringshaw et al., 2017). However, *G. polonicus* only has one to two closely spaced coils, and commonly displays striations. As a result, these burrows were classified as *Gyrolithes scintillus* isp. nov. Laing et al., 2018. These burrows are interpreted to be agrichnial burrows, similar to *G. gyratus*. For an in-depth discussion see Chapter 4.

Ichnogenus *Helminthoidichnites* Fitch, 1850

Simple, unbranched, horizontal trails or burrows which are straight, curved, or more rarely circular and commonly overlap among specimens but no self-overcross are classified as *Helminthoidichnites* (after Buatois et al., 1998). This simple trace fossil is present globally in the latest Ediacaran, and becomes more common after the Ediacaran-Cambrian boundary (Figure 3.15).

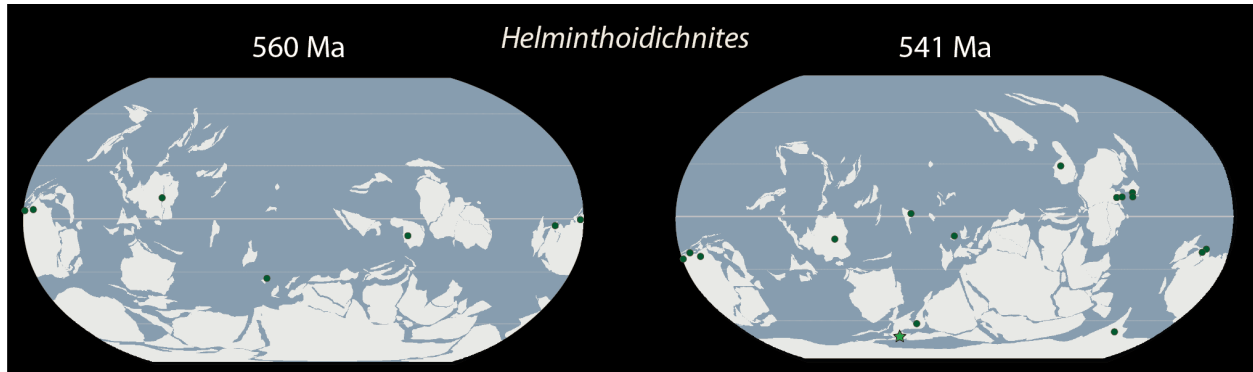


Figure 3.15 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Helminthoidichnites* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

***Helminthoidichnites tenuis* Fitch, 1850**

Figure 3.30 B

Material

Numerous specimens identified in the field.

Diagnosis

Horizontal, small, thin, unbranched, simple, straight or curved burrows that commonly display overlap among specimens, but lack self-overcrossing (modified from Buatois et al., 1998).

Description

Horizontal, smooth, unbranched, gently curving trails or burrows, preserved in convex or concave hyporelief or epirelief. Diameter is 1-3 mm, with several sizes of trails commonly seen on one slab, commonly overlapping one another.

Remarks

Helminthoidichnites is distinguished from *Helminthopsis* by its lack of meanders (Buatois et al., 1998). The newly erected *H. multiaqueatus* Pokorný differs from *H. tenuis* by the dominance of

circular to curved trails, and is more densely arranged (Pokorný et al., 2017). *Helminthoidichnites* is regarded as a grazing trace, likely produced by arthropods or vermiform animals, and is common in Ediacaran and Cambrian strata (Hofmann and Mountjoy, 2010; Carbone and Narbonne, 2014). This is supported in this section by its common association with microbial mat sedimentary structures (Buatois et al., 2014).

Ichnogenus *Helminthopsis* Heer, 1877

Helminthopsis is described as simple, horizontal, unbranched burrows or trails, with curves, windings, or irregular open meanders (after Wetzel and Bromley, 1996). While present globally during the Ediacaran, the ichnogenera became much more common after the Ediacaran-Cambrian boundary (Figure 3.16).

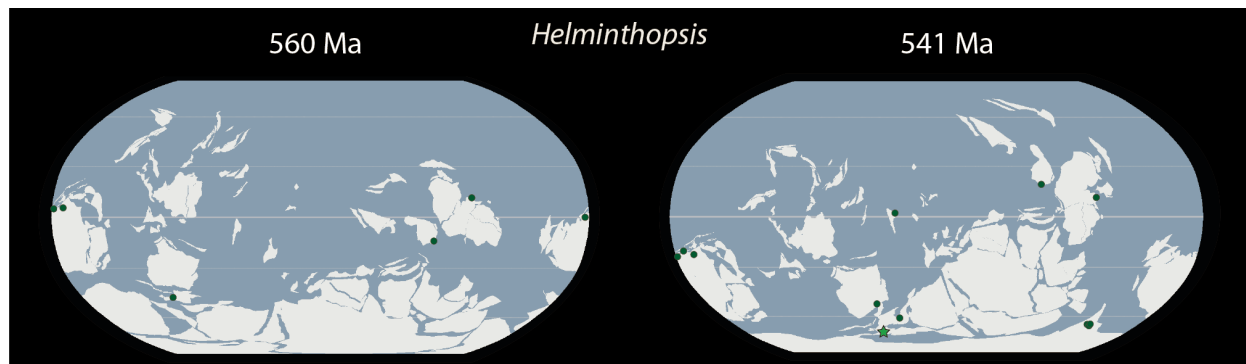


Figure 3.16 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Helminthopsis* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

Remarks

Helminthopsis differs from *Gordia* by its distinct meanders yet minimal overcrossings. During the mid 1990's, two different approaches to the ichnotaxonomy of *Helminthopsis* were proposed. Han and Pickerill (1995) re-analyzed this ichnogenus and suggested three valid ichnospecies: *H. abeli*, *H. granulata*, and *H. hieroglyphica*. They argued that the differing fill in *H. granulata* distinguished it as an ichnospecies. Based on a mathematical analysis, they suggested that *H. tenuis* and *H. abeli* can be synonymized, with the latter having priority. However, Wetzel and Bromley (1996) argued that the type specimen of *H. tenuis* Książkiewicz (1968) lacked horseshoe-like turns, and as such had a different morphology from *H. abeli*, which possesses

horseshoe-like turns. Additionally, they argued that if fill is to be considered a pertinent ichnotaxobase, then *H. granulata* should be reassigned to the ichnogenus *Alcyonidiopsis*. As a result, Wetzel and Bromley (1996) suggested three valid ichnospecies of *Helminthopsis*: *H. abeli*, *H. tenuis*, and *H. hieroglyphica*. In a response, Pickerill et al. (1998) argued that while Książkiewicz's (1968) type specimen of *H. tenuis* lacks horseshoe-like turns, additional specimens from the type locality assigned to *H. tenuis* possess horseshoe-like turns (Książkiewicz, 1977), demonstrating the author's original intentions. In a subsequent reply, Wetzel et al. (1998) showed errors in the statistical treatment employed by Han and Pickerill (1995), demonstrating that synonymizing of *H. abeli* and *H. tenuis* on this basis was incorrect.

***Helminthopsis tenuis* Książkiewicz, 1968**

Figure 3.28 F, 3.30 C

Material

Roughly 30 specimens identified in the field.

Description

Smooth, horizontal, burrows or trails, 1-3 mm wide, with irregular, U-shaped windings. Preserved in convex or concave epirelief or hyporelief on both very fine sandstone and siltstone beds.

Remarks

Helminthopsis tenuis is differentiated from *H. abeli* by the absence of horseshoe-like turns (Wetzel and Bromley, 1996; Wetzel et al., 1998). *Cosmorhapse* possesses regularly winding-meanders, whilst the meanders in *Helminthopsis* are irregular. *Helminthopsis* is commonly regarded as a grazing trace, and is common in Ediacaran and Cambrian strata (Carbone & Narbonne, 2014; Mángano and Buatois 2016). This is supported in this section by its common association with microbially induced sedimentary structures (Buatois et al., 2014).

Ichnogenus *Monomorphichnus* Crimes 1970

Monomorphichnus is described as a series of straight or slightly sigmoidal, parallel or intersecting striae, isolated or grouped in sets, in places repeated laterally and typically preserved in convex hyporelief (Fillion and Pickerill, 1990, modified from Crimes, 1970). Both *M. isp. A*, *M. isp. B*, and *D. cf. obliquus* are found clustered, evenly spaced, and deeply impressed. Skim

marks, and to a lesser extent prod marks and drag marks, have a similar morphology to individual grooves in *M. isp. B*, *M. isp. A*, and *D. cf. obliquus*. However, the probability of having several identical tool marks, spaced evenly apart, is essentially zero. This points to a biologic origin for the impressions. In the absence of large skeletal organisms, possible tools are restricted to tubes and vendotaenids (Landing et al., 1989). Jensen et al. (2002) documented tools (“Kullingia”) created by a tubular organism at this locality; however, these are not ornamented enough to create the deep isolated grooves observed in *M. isp. B*, *M. isp. A*, or *D. cf. obliquus*. In turn, all three ichnospecies are found in various directions on the same bedding surface, essentially eliminating a tool mark origin for these impressions. The genus is restricted to the Phanerozoic with a global distribution at the beginning of the Cambrian (Figure 3.17)

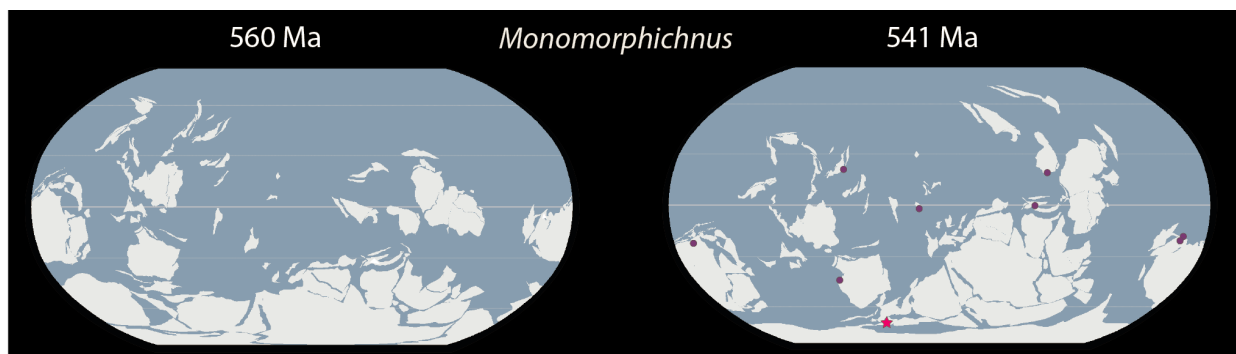


Figure 3.17 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Monomorphichnus* is absent from 560 Ma strata, however, all documented *Monomorphichnus* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

Monomorphichnus isp. A

Figure 3.32 1-3

Material

Four specimens on one slab (Slab B, GBH6, 10.5 m) in the field, photographed and measured (Table 3.4), plus an additional 5 field identifications (FH 7 m, 10 m, 165 m).

Description

Series of six to nine thin (0.1-0.4 mm, avg. 0.3 mm), moderately long (1.7-10.5 mm, avg. 6.25 mm), evenly spaced, arcuate striations, occasionally paired, preserved in positive hyporelief on very fine grained sandstone beds. Paired striations are slightly thinner (0.1-0.3 mm) than those that are single (0.2-0.4 mm).

Table 3.4 Dimensions of three sets of *M. isp. A*.

<i>Monomorphichnus isp. A</i>					
Specimen ID	Impression ID	Number of impressions in specimen	Impression width (mm)	Impression length (mm)	Separation between impressions (mm)
6.1	6.1a2	6	0.3	8.3	1.6
	6.1a1	6	0.1	2	
	6.1b	6	0.4	8.2	1.6
	6.1c	6	0.3	9.9	1.4
	6.1d	6	0.3	7.3	1.4
	6.1e	6	0.3	4.9	1.8
	6.1f	6	0.3	4.9	
6.2	6.2a1	3	0.1	8.2	4.2
	6.2a2	3	0.2	8.5	
	6.2b1	3	0.2	6.7	6.9
	6.2b2	3	0.3	10.5	
	6.2c	3	0.4	9.5	
6.3	6.3a	5	0.3	1.9	1.3
	6.3b	5	0.3	4.2	0.6
	6.3c	5	0.2	6.6	1
	6.3d1	5	0.2	7.2	1.2
	6.3d2	5	0.2	1.7	
	6.3e	5	0.2	2	
Average:			0.26	6.25	2.09

Remarks

The absence of pusher marks inhibits classification as *Dimorphichnus*; however, these relatively elongated scratch sets also resemble the rakers of *Dimorphichnus*, so the possibility of undertrack fallout cannot be totally discarded. For a taxonomic discussion on *Monomorphichnus* and *Dimorphichnus*, see the remarks of *Dimorphichnus*. The presence of straight, deep, equal length scratches in *Monomorphichnus isp. A* clearly differs from *M. multilineatus*, *M. semilineatus* and *M. intersectus*. Based on the limited number of specimens and the fact that many are isolated sets, it is challenging to provide an ethologic interpretation for *Monomorphichnus isp. A*. *Monomorphichnus* has been previously interpreted as a swimming trace (Crimes, 1970), or as a trilobite caught in the current (Osgood, 1975b). Specimens of *Monomorphichnus isp. A* in the CIF are oriented in a wide variety of directions, including perpendicular and oblique to the current direction. It is therefore unlikely that this ichnospecies was the result of an arthropod caught in the current. If this specimen is of *Dimorphichnus*-type, with the pusher marks obscured due to undertrack fallout, then a grazing ethology may be more

applicable (Seilacher, 1955b). For a discussion on a tool-origin for *Monomorphichnus* isp. A see the remarks of *Monomorphichnus* isp. B.

***Monomorphichnus* isp. B**

Figure 3.32 6

Material

Seven specimens on one slab in the field (Slab B, GBH6, 10.5 m) examined and measured by photograph (Table 3.5).

Description

Groups of three to four parallel, short (0.8-6.0 mm, avg. 2.8 mm), wide (0.15-0.9 mm, avg. 0.4 mm), oval-shaped grooves preserved in positive hyporelief on very fine-grained sandstone. Impressions are deepest and widest towards the middle and shallower and thinner near the ends, and are close and evenly spaced apart (0.2-0.9 mm, avg. 0.4 mm). In some specimens the innermost grooves are thicker and longer than the outermost grooves (e.g., specimen 3.1). In others, only one side of the outermost grooves are thicker and longer than the rest of the grooves (e.g., specimens 2.1, 2.3, 3.2, 4.1, 4.2).

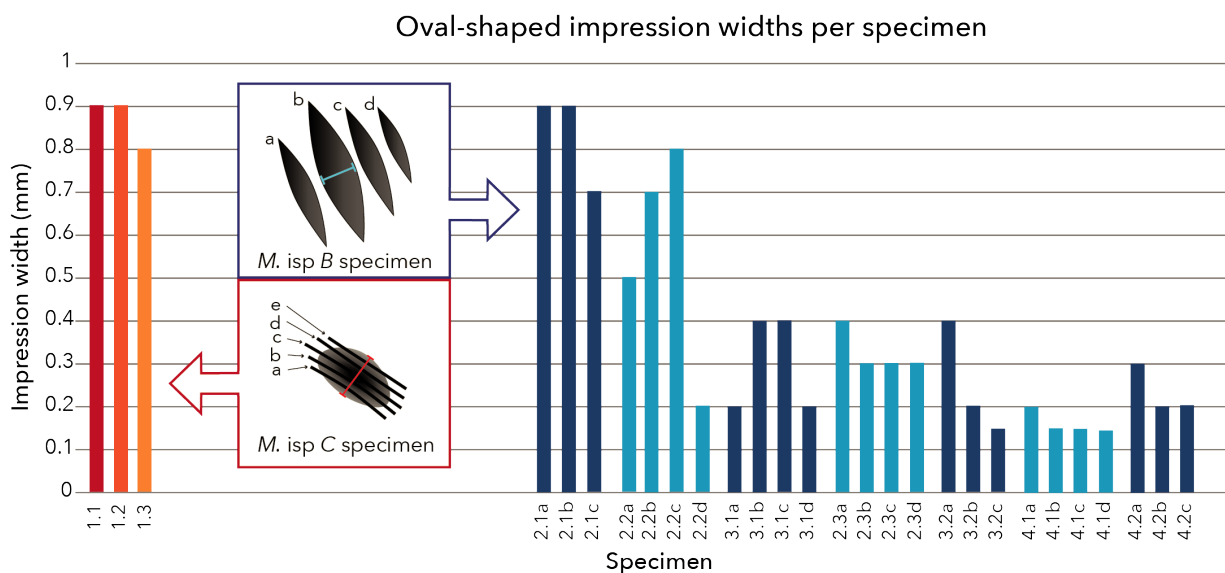


Figure 3.18 Widths of individual oval-shaped impressions per specimen of *M. isp. B*. (blue bars) with the width of the oval-shaped impression in *M. isp. C*. specimens (red and orange bars).

Remarks

One specimen of *M. isp. B* is located below a single *M. isp. C*, and both specimens are oriented in a similar direction, oblique to the current. The oval-shaped groove which encompasses the more delicate scratch marks of *M. isp. C*, has a similar size to the grooves in some specimens of *M. isp. B* (Figure 3.18). Given this close relationship in morphology and size, it is likely that the two ichnospecies are related, and perhaps were created by the same organism. While undertrack fallout is a common phenomenon in arthropod trackways (Seilacher, 1990), it is unlikely that *M. isp. B* is an undertrack preservation of *M. isp. C*, due to the frequency of isolated *M. isp. C* specimens. Affinities between *M. isp. B* and *M. isp. C* will be further discussed in the remarks of *M. isp. C*.

The absence of an association with longer, thinner, scratch marks that could be identified as rakers inhibits classification as *Dimorphichnus*, although this may be due to undertrack fallout. The width comparative to the length of these specimens distinguishes them from the thinner and longer *M. linearis*, *M. bilinearis*, *M. biserialis*, and *M. semilineatus*. A few specimens of *M. isp. B* share characteristics with *M. multilineatus*, where some specimens have deeper innermost grooves (e.g, specimen 2.2 and 3.1). Although, most specimens of *M. isp. B* show only one deeper groove, and therefore as a whole they do not match the diagnosis of *M. multilineatus*. The lack of intersecting striations distinguished *M. multilineatus* from *M. intersectus*.

Monomorphichnus isp. C

Figure 3.19, 3.32 4

Material

Seven specimens on one slab in the field (GBH6, slab B, 10.5 m), photographed. Four specimens were measured.

Description

Small, short, delicate sets of impressions. Sets of four to six parallel short (3-4.3 mm, avg. 3.9 mm), sub-equal, thin (0.1 mm), mostly evenly spaced (0.1 mm, a single striation 0.3 mm apart) striations. These are located on, and extend past for a few tenths of a millimeter, highly convex,

Table 3.5 Dimensions of seven sets of *M. isp. B* specimens.

<i>Monomorphichnus isp. B</i>					
Specimen ID	Impression ID	Number of impressions in specimen	Impression width (mm)	Impression length (mm)	Separation between impressions (mm)
2.1	2.1a	3	0.9	5.7	0.2
	2.1b	3	0.9	6	0.6
	2.1c	3	0.7	2.8	
2.2	2.2a	4	0.5	3.6	0.7
	2.2b	4	0.7	4.3	0.9
	2.2c	4	0.8	4.4	0.2
	2.2d	4	0.2	2.6	
2.2	2.3a	4	0.4	2.7	0.3
	2.3b	4	0.3	4.2	0.3
	2.3c	4	0.3	5.8	0.3
	2.3d	4	0.3	1.4	
3.1	3.1a	4	0.2	3.2	0.3
	3.1b	4	0.4	1.9	0.3
	3.1c	4	0.4	1.7	0.2
	3.1d	4	0.2	1.3	
3.2	3.2a	3	0.4	4.3	0.2
	3.2b	3	0.2	3.3	0.4
	3.2c	3	0.15	1	
4.1	4.1a	4	0.2	1	0.4
	4.1b	4	0.15	2.5	0.35
	4.1c	4	0.15	1.2	0.45
	4.1d	4	0.15	1.3	
4.2	4.2a	3	0.3	2.4	0.3
	4.2b	3	0.2	0.8	0.2
	4.2c	3	0.2	2.2	
Average:			0.37	2.86	0.37

oval-shaped impressions. Oval-shaped impressions are short (1.6 -3.5 mm, avg. 2.6 mm) and wide (0.8-0.9 mm, avg. 0.87 mm). Preserved in positive hyporelief on very fine-grained sandstone beds. Specimens are mostly isolated and do not form any clear trackway yet are often found close to other arthropod scratch marks, commonly oriented in a similar direction. In one instance they are found next to *M. isp. B*, while in another they are found related to long unidentifiable arthropod scratch marks. For a complete discussion on the affinity of *M. isp. B* see Section 3.3.6.

Remarks

A biologic origin is suggested by the even spacing between the striae. The pseudofossil *Eophyton* (Savazzi, 2015), a sail-assisted drag mark (Frey and Dashtgard, 2012), is superficially similar to *M. isp. C*, but has uneven spacings between striae which do not extend past the elongate larger groove as in *M. isp. C* (Figure 3.36, B). In turn, *M. isp. C* is substantially shorter than skim marks, and does not demonstrate the strong asymmetry seen in prod marks (Figures 3.19, 3.36 F, G).

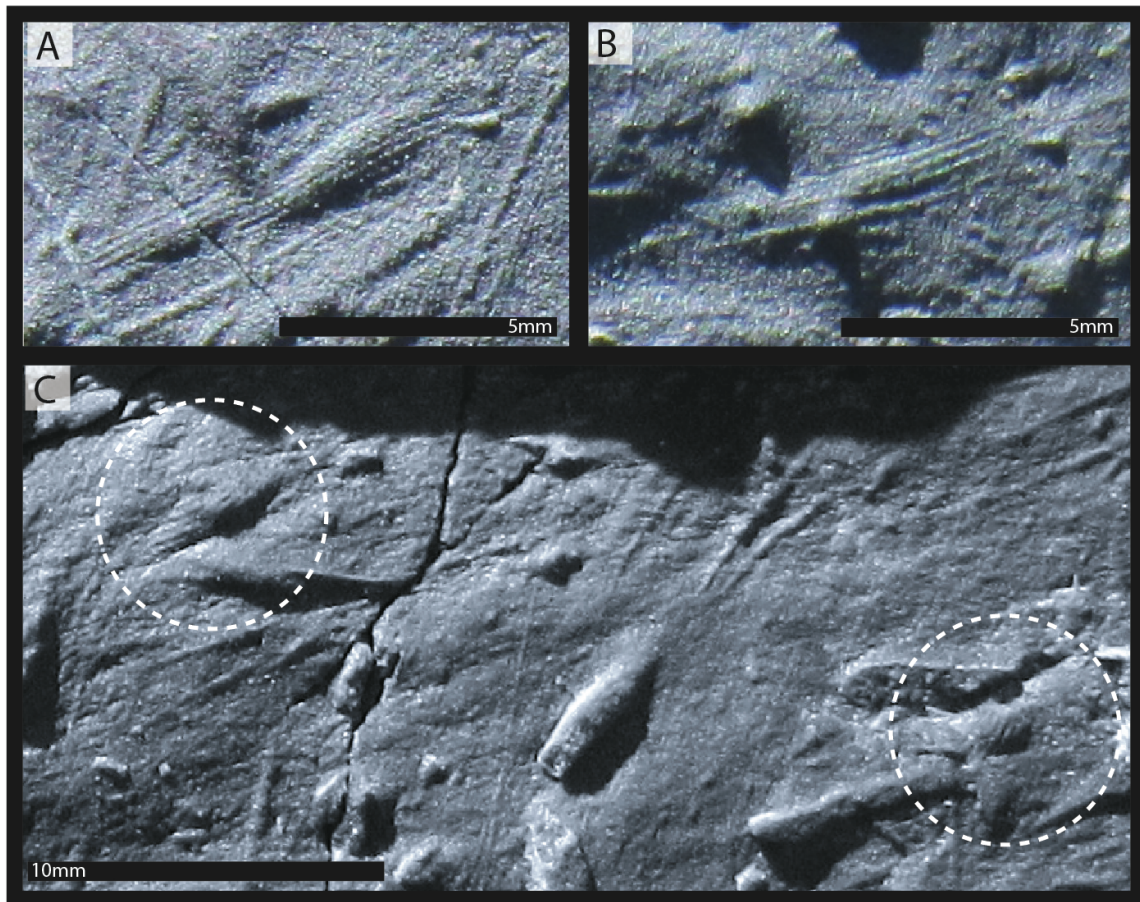


Figure 3.19 *Monomorphichnus. isp. C*. (A) Two specimens of *M. isp. C* (detail of Figure 3.33 6, upper right) (B) A specimen of *M. isp. C*, notice evenly separated central impressions and more separated distal impression. (C) Isolated specimens in slab with diverse orientations do not seem to form a trackway. Notice two specimens cross-cutting each other (upper left) (detail of Figure 3.33 4.)

As a result, *M. isp. C* was probably produced by an organism, and is the result of actual behaviour, rather than the transportation of a deceased or current-swept organism. This is revealed by two features of the ichnofossil. First, *M. isp. C* is found in a variety of directions,

eliminating current as a mode of transportation (Figure 3.19, 3.32, 3.33). When found aligned to the direction of current, *M. isp. C* is more elongate (Figure 3.19, A, B). Yet when found oblique or perpendicular to the current, *M. isp. C* is shorter (Figure 3.19 C-E). Second, the presence of two superimposed specimens at slightly different angles (Figure 3.19, C) demonstrates an intentional digging into the substrate. Therefore, *Monomorphichnus isp. C* was produced by a limbed organism, most likely a primitive arthropod. This ichnofossil may have been created by the endopodite, however it is more likely formed by an exopodite or another ornamented body part such as a telson. For a complete discussion on the affinity of *M. isp. C* see Section 3.3.6.

Table 3.6 Dimensions of four specimens of *M. isp. C*.

<i>Monomorphichnus isp. C</i>						
Specimen ID	Number of impressions in specimen	Impression width (mm)	Impression length (mm)	Separation between impressions (mm)	Oval-shaped impression	
					Width (mm)	Length (mm)
1.1	4	0.1	3	0.1	0.9	1.6
1.2	5, 6?	0.1	4.3	0.1	0.9	3.5
1.3a	6	0.1	4.5	0.1	0.8	2.7
1.3b	6	0.15	0.3	0.3		
	AVG	0.11	3.93	0.10	0.87	2.60

***Ichnogenus Palaeophycus* Hall, 1847**

Branched or unbranched burrows with smooth, ornamented, or lined walls with an essentially circular cross-section and passive infill are classified as *Palaeophycus*. This genera was present during the latest Ediacaran, and became much more common with the onset of the Cambrian (Figure 3.20)

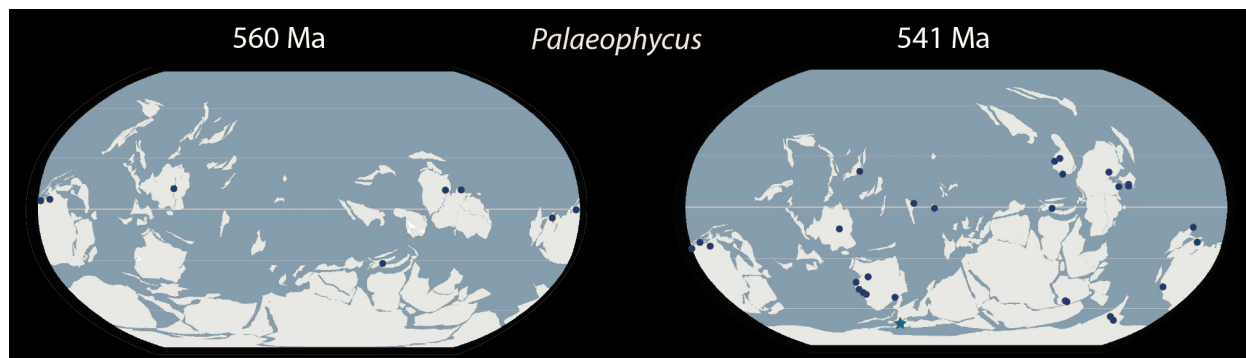


Figure 3.20 Palaeogeographic reconstructions at 560 Ma and 541 Ma. Documented *Palaeophycus* localities with probable age ranges which include either 560 Ma or 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

Palaeophycus isp.

Figure 3.30 F

Material

Approximately 50 specimens identified in the field.

Description

Small, horizontal, burrows preserved in full relief within siltstone beds. Circular to sub-circular in cross-section, infilled with very fine-grained sandstone. Burrow width is 1-10 mm.

Remarks

These burrows have previously been classified as *Planolites* (Narbonne et al., 1987; Gehling et al., 2001). While these burrows are small in diameter (1-2 mm) they show distinct characteristics of *Palaeophycus*. Pivotal to this distinction is the characteristic active infill and unlined burrow walls present in *Planolites* versus the passive infill and ghost-lined burrow walls in *Palaeophycus* (Pemberton and Frey, 1982). While the infill in the Fortune Head burrows does differ from the siltstone host rock, it is identical to the very fine-grained sandstone in the section, and there is no evidence of *Planolites* characteristic active infill. These burrows were excavated in a muddy firmground environment and were then passively infilled by overlying sand (Droser et al., 2002; Jensen et al., 2005). Due to the substrate stability, a burrow lining was not needed. Since substrate stability is not viewed as a valid ichnotaxobase (Bromley, 1990), these burrows are classified as *Palaeophycus*. They differ from *P. striatus* Hall and *P. sulcatus* Miller and Dyer by their lack of striae, despite optimal conditions for their preservation. The burrows differentiate from *P. tubularis* and *P. heberti* de Saporta due to the lack of a lining. *Thalassinoides* has a characteristic branching, which *Palaeophycus* lacks. *Palaeophycus* is commonly regarded as a dwelling burrow of either a passive predator or filter feeder.

***Palaeophycus tubularis* Hall, 1847**

Plate 3.21, D-E, G

Material

Numerous specimens identified in the field.

Description

Small, horizontal, burrows with a ghost lining, preserved in full relief in very fine sandstone beds. Circular to sub-circular in cross-section, infilled with very-fine sandstone. Burrow collapse is common. Burrow width is 0.5-1 mm.

Remarks

These burrows differ from *Palaeophycus* isp. by the presence of a thin lining. They are commonly found within sandstone beds, rather than within the siltstone units. The lack of striations found in the burrows differentiate them from *P. striatus* and *P. sulcatus*, and the presence of a thin rather than thick burrow wall distinguishes these specimens from *P. heberti*. *Palaeophycus* is commonly regarded as a dwelling burrow of either a passive predator or filter feeder.

Ichnogenus *Treptichnus* Miller, 1889

Treptichnus is described as simple or zig-zag, straight or curved segments associated with vertical or oblique tubes comprising a three-dimensional burrow system. Joined points of segments exhibit small pits or short twig-like projections (after Buatois and Mángano, 1993). A few treptichnids appeared in the Ediacaran, the most credible of which have maximum age constraints of at most 551 Ma. The two treptichnids present at 560 Ma have wide age constraints (635 Ma to 529 Ma and 521 Ma), and it is difficult to refine the age of the ichnofossils further. However, at the beginning of the Cambrian the number and distribution of treptichnids increases (Figure 3.21).

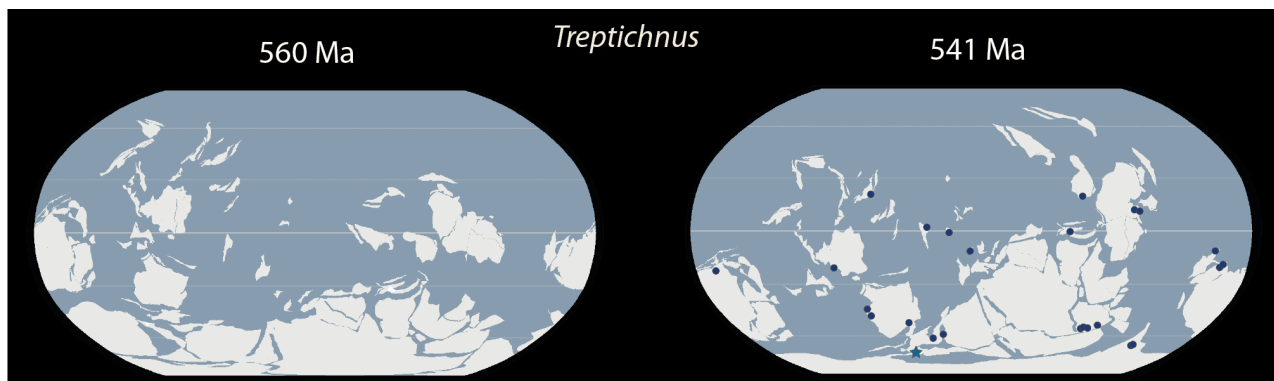


Figure 3.21 Palaeogeographic reconstructions at 560 Ma and 541 Ma. *Treptichnus* is absent from 560 Ma strata, however, all documented *Treptichnus* localities with probable age ranges which include 541 Ma are marked. Star denotes specimens recorded in this study. For the data used in these reconstructions, see Appendix A.

Due to the three-dimensional nature of *Treptichnus*, multiple expressions of this ichnotaxon exist. This phenomenon was illustrated by Maples and Archer (1987), who demonstrated that *Plangtichnus* was simply the expression of *Treptichnus bifurcus* through its middle plane. This was expanded upon by Buatois and Mángano (1993), who reconstructed *Treptichnus pollardi* in a similar fashion. These authors recognized that the difference between *Plangtichnus* and *Treptichnus* is simply the plane through which the ichnofossil is preserved, and suggested that the two genera be regarded as synonyms. When the three-dimensional morphology cannot be reconstructed (i.e., when the middle level is not found), the ichnofossil can be classified to the ichnogenus level, as *Treptichnus* isp. This concept was further expanded upon by Jensen et al. (2000), where they lowered the plane of intersection and demonstrated another preservation style of *Treptichnus*. The variety of preservational styles thus has likely led to a proliferation of ichnotaxon.

For example, the upper plane of a treptichnid has commonly been classified as *Saerichnites* or *Bicavichnites* (Figure 3.22) (Seilacher et al., 2005). With only this expression, it is impossible to decipher the overall three-dimensional morphology of the specimen. In this situation the upper plane of a variety of ichnotaxa may produce *Saerichnites*, such as *Arenicolites*, *Hormosiroidea*, *Treptichnus*, or *Skolithos* (Figure 3.22). This phenomenon underscores the need to carefully examine an outcrop for multiple expressions. Additionally, possible three-dimensional morphologies of an ichnotaxon must be carefully examined before classification can be attempted.

***Treptichnus coronatum* (Crimes and Anderson, 1985)**

Figure 3.31 A

Material

Four photographed specimens, plus roughly 10 field identifications (FH 2.1 m, 81.50 m; GBH 11 m).

Description

Burrow trajectory forms a complete circle, smooth, unlined, and parallel to bedding. Vertical branches extend from the main circular burrow, evenly spaced. Burrow width is 1-3 mm with

branches spaced between 5-97 mm apart (measured from middle of branches). Preserved as positive hyporeliefs, or as endichnial structures infilled with very fine sandstone.

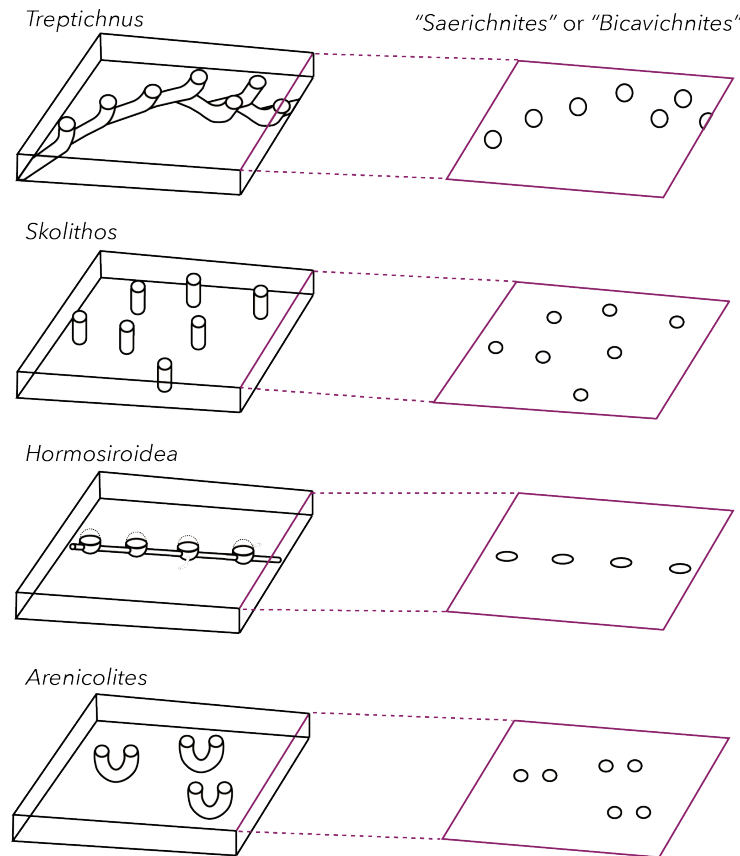


Figure 3.22 Schematic illustrating possible 3D morphologies which may produce “*Saerichnites*” or “*Bicavichnites*”.

Remarks

T. coronatum is distinguished from *T. pedum* due to its overall circular shape, with no burrow segments leading to or from the burrow. *T. coronatum* and the graphoglyptid *Lorenzina* show similarities, in that they both have a main circular burrow with vertical branches, and it has been suggested that *T. coronatum* is a primitive *Lorenzina* (Uchman, 1998). As mentioned in the remarks for *T. pedum*, it is possible that a loop of *T. pedum* may be mistaken for *T. coronatum*. A revision of *T. coronatum* is warranted, to determine if its construction is similar or different than that of *T. pedum*. A closed circular burrow with vertical protuberances would not function well as a feeding burrow. This morphology would however serve well as a graphoglyptids-style burrow as proposed by Uchman (1998), or as the dwelling burrow of a passive predator (Vannier et al., 2010).

Treptichnus isp.
Figure 3.30 H, 3.35 B

Material

One specimen photographed and measured, plus roughly 5 field identifications.

Description

Burrow consisting of smooth, unlined, curved segments massively infilled with very fine sandstone. The segments join each other longitudinally. Segments are irregular, ranging from 1-3 mm in length, and 1-2 mm in width. Burrow trajectory is straight to slightly meandering, no loops are observed. Preserved as positive hyporeliefs on very fine sandstone beds.

Remarks

Treptichnus isp. has been previously documented at Fortune Head, and is distinguished from *Treptichnus pedum* due to its lack of angled protuberances.

***Treptichnus pedum* (Seilacher, 1955a)**

Figure 3.23, 3.31 B, C, E

Material

Eight photographed specimens (FH 1.35 m, 2.4 m, 55.50 m, 81.50 m, 136.0 m, 136.5 m, 139.8 m, 145.0 m), plus approximately 30 field identifications.

Description

Burrow consisting of smooth, unlined, curved segments. The segments either join each other either at low angles or longitudinally, forming short projections. Burrow trajectory forms arcuate bends or follow a straight to slightly sinuous course. Arcuate bends may create loops.

Burrow is 2-5 mm wide, with segment length between 6-11 mm. Preserved as positive hyporeliefs or as full-relief infilled with very fine sandstone, or as negative epireliefs.

Remarks

Previously described as *Phycodes pedum* (Crimes and Anderson, 1985, Narbonne et al., 1987), this ichnotaxon defines the beginning of the Cambrian and the *T. pedum* Ichnofossil Assemblage Zone. Jensen (1997) reassigned *Phycodes pedum* to *Treptichnus pedum*, noting the distinctive treptichnid-style construction through the addition of segments. Interestingly,

Treptichnus pedum appears in the Sh facies (Myrow, 1987), as well as member 1, demonstrating an wide environmental tolerance.

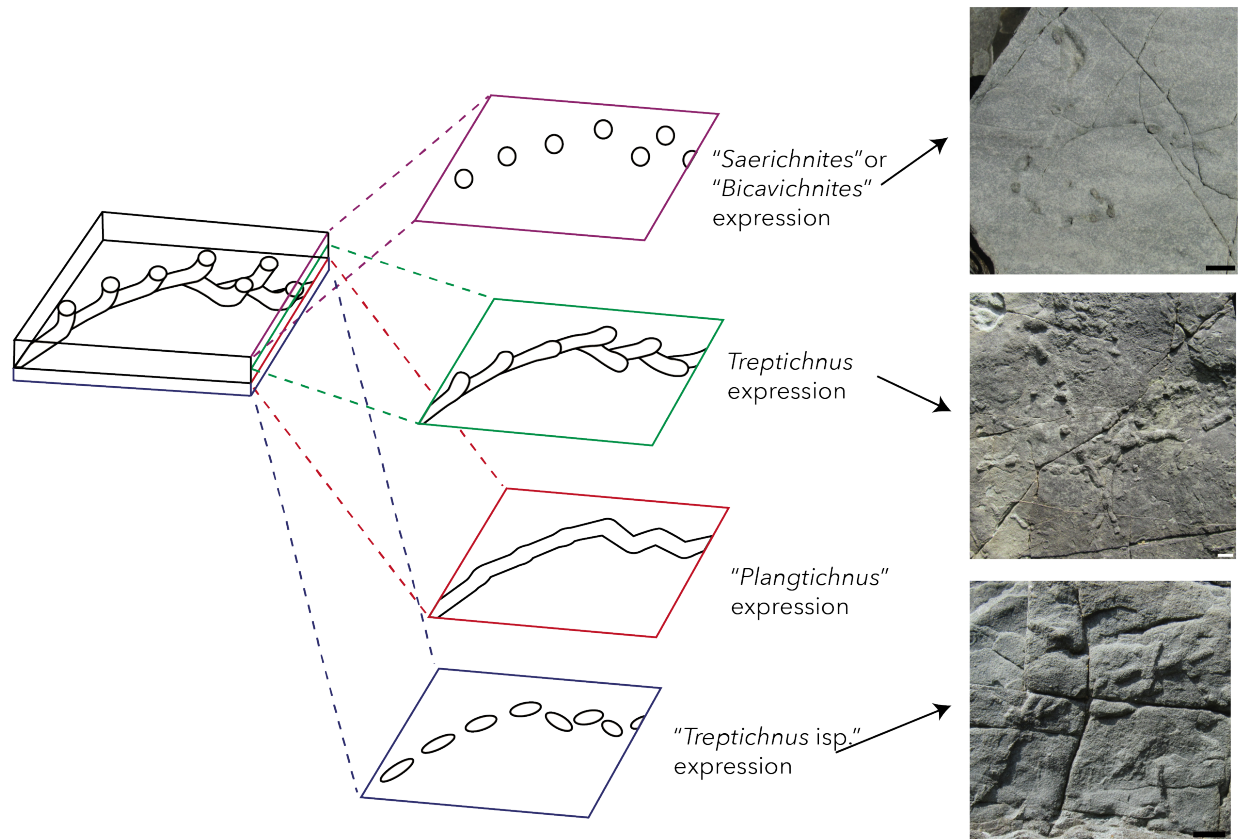


Figure 3.23 Possible three-dimensional expression of *Treptichnus pedum*, with field photographs from the *T. pedum* IAZ of the CIF. The hypothetical “*Plangtichnus*” expression was not documented in the CIF. All scale bars are 1cm.

Due to the alternation of very fine-grained sandstone and siltstone at Fortune Head, multiple expressions of *T. pedum* can be found (Figure 3.23). The upper plane preservation of *Treptichnus* in the early Cambrian has occasionally been classified as *Hormosiroidea*, such as *Hormosiroidea canadensis* Crimes and Anderson. This ichnospecies has since been synonymized with *Ctenopholeus kutcheri* Seilacher and Hemleben (Fürsich et al, 2006). *Hormosiroidea* is characterized by subspherical bodies connected by a horizontal “string” (Uchman 1998), rather than by the addition of curved segments as *Treptichnus*. Jensen (1997) argued that what is

commonly referred to as *Hormosiroidea* isp., is in fact treptichnid whose segments are added in succession, rather than at an angle (Figure 3.24). Prior to the re-evaluation of *Hormosiroidea* by Uchman (1998), this misclassification was common. In turn, heart-shaped bodies connected by a horizontal tube, now classified as *Halimedes*, have formerly been classified as *Hormosiroidea* (Figure 3.24) (Uchman, 1998; Gaillard and Olivero, 2009). As a result, previous reports of *Hormosiroidea* must be carefully re-examined. Arcuate bends in *T. pedum* may form loops, which may strongly resemble *T. coronatum* Crimes and Anderson. However, *T. pedum* has burrows leading to or from the loop, whereas *T. coronatum* does not. It is possible that documented *T. coronatum*'s are simply portions of a greater *T. pedum*. Crimes and Anderson (1985) argued that the irregularity of arcuate bends in *T. pedum* in comparison to *T. coronatum*, as well as the difference in angle of projection of the segments from the main burrow can be used to distinguish between *T. pedum* and *T. coronatum*. There is a general consensus that *T. pedum* is a feeding trace. The original interpretation of *T. pedum* (then *Phycodes pedum*) was as a deposit feeder (Seilacher 1955a); however, backfilling and other active-fill structures have yet to be observed within *T. pedum*. Seilacher (2007) noted that this ichnotaxon is restricted to thin sand beds, and never penetrates into underlying mud layers. This author suggested that this feature is evidence that the tracemaker was a more sophisticated undermat miner (Seilacher, 2007). The passive infill commonly seen in *T. pedum* may suggest a dwelling ethology, as proposed by Jensen (1997) and Vannier et al., (2010). In this scenario, the organism lives in the burrow and feeds from detritus (Jensen, 1997) or epibenthic animals (Vannier et al., 2010) on the surface of the sea floor. Regardless of the specific mechanism, it is evident that

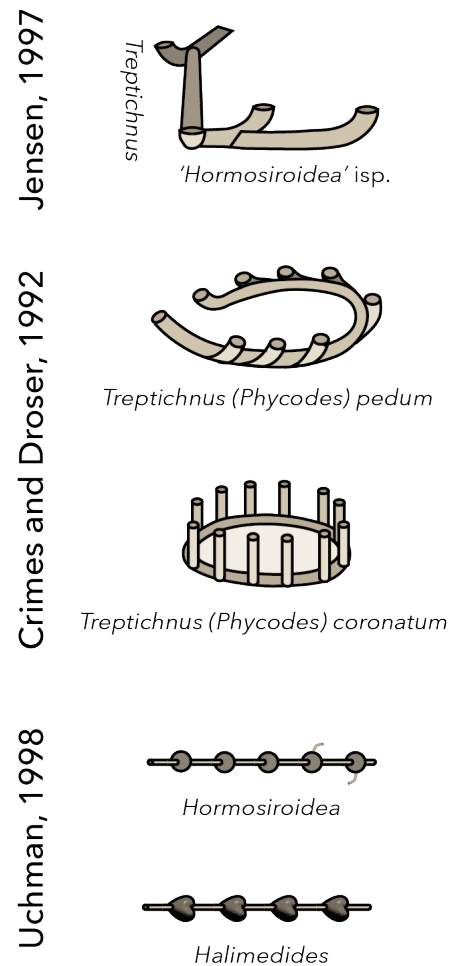


Figure 3.24 Various three-dimensional interpretations of *Treptichnus*, *Hormosiroidea*, and *Halimedes*. Illustrations modified from Crimes and Droser (1992), Jensen (1997), and Uchman (1998).

Treptichnus pedum represents a sophisticated mode of feeding for this time in Earth history (Buatois, 2018).

Ichnogenus *Trichichnus* Frey, 1970

***Trichichnus* cf. *simplex* Fillion and Pickerill, 1990**

Figure 3.26, 3.31 D, F

Material

Approximately 25 specimens photographed in the field.

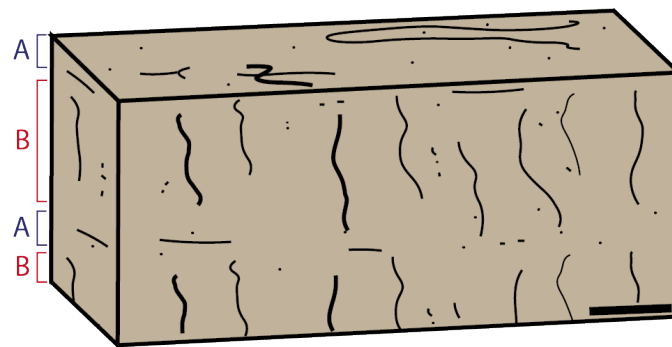
Description

Unbranched, unlined, 0.3-0.5 mm wide, cylindrical burrows, forming a mostly vertical burrow system. Preserved as endichnial structures with a distinctive iron-oxide fill. Burrow system is dominated by a mostly vertical portion with straight to sinuous burrows reaching depths of up to 31 mm (Figures 3.25 and 3.26, part B), with rare horizontal portions with sinuous, occasionally crossing sections (Figures 3.25 and 3.26, part A).

Remarks

Trichichnus simplex Fillion and Pickerill differs from *Trichichnus linearis* by the absence of a lining. Whether or not this lining is a diagenetic (Uchman, 1995, 1998) or not remains to be determined. Unlined *Trichichnus* with rare horizontal portions has been documented in the type specimen in the Upper Cretaceous of Kansas (Frey, 1970) and in the Miocene of Italy (McBride and Picard, 1991), however no known Cambrian occurrences exist. Foraminifera have been observed creating burrows of a similar thickness to *Trichichnus*, as they escape from silty sediment (Severin, 1982), although these burrows are more sinuous than *Trichichnus*. 3-D microCT scanner images reveals an overall structure of *Trichichnus* which is more consistent with a colony of large sulfur bacteria. This, combined with its prevalence in dysoxic environments, has led some researchers to suggest a chemichnial ethology for *Trichichnus* (Kędzierski et al., 2015). In this model, the tracemaker of *Trichichnus* takes advantage of a redox gradient between the sediment and seawater. In the oxidizing zone, nitrate respiration and carbon fixation occur while in the reducing zone, sulphate reduction occurs. Filamentous bacteria facilitate electron transport between the two zones, forming a symbiotic relationship with the larger sulfur bacteria. Over time framboidal pyrite or greigite naturally precipitate within the burrow and, assisted by bacteria pili and biofilms, form a conductive filament in the deeper

portions of the burrow system. This serves as a bioelectric wire, transporting electrons derived from the reducing zone upwards, to be utilized by the large sulfur bacteria (Kędzierski et al., 2015). It is generally accepted that the sediments in Cambrian oceans were oxygen stratified (Seilacher, 1999; Callow and Brasier, 2009; Boyle et al., 2014; Mángano and Buatois, 2014), although there is discussion on the specific amount of dissolved oxygen (Sperling et al., 2013). This gradient would provide an optimal environment for a chemosynthetic organism such as sulphate reducing bacteria.



Trichichnus cf. simplex

Figure 3.25 A schematic reconstruction of *Trichichnus cf. simplex* in the CIF. Two successions of *Trichichnus cf. simplex* are shown. (A) horizontal mesh-like section of the burrow system (B) vertical section of the burrow system. Scale bar is 1cm.

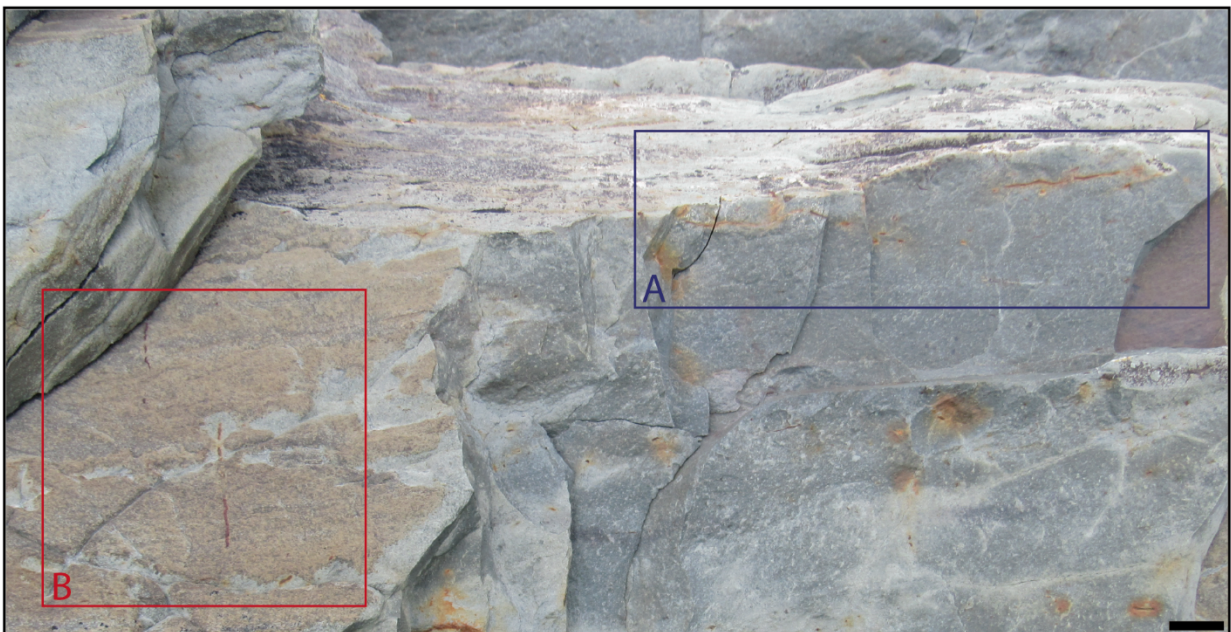


Figure 3.26 Field photograph of *Trichichnus* cf. *simplex* with both horizontal burrows (A) and vertical burrows (B).

3.2. Other ichnofossils and body fossils

Tubular organism

Figure 3.27

Material

Two specimens (FH ~4 m and 37 m), photographed and measured.

Description

Vertical, annulated, cylindrical tube. Width ranges from 0.5-1.5 mm, depth ranges from 5-6 mm. Annulations are 0.3-0.7 mm wide.

Remarks

One specimen (Figure 3.27 A) seems to become thinner with depth, and has more regular constrictions. However, the other specimen (Figure 3.27 B) maintains a similar width with depth, with constrictions which are more irregular and seem to “buckle” (like a corrugated tube being compressed). These specimens are somewhat similar to poor preservations of *Gyrolithes gyratus*, however they are differentiated by their construction out of a solid material and lack of a helical morphology.

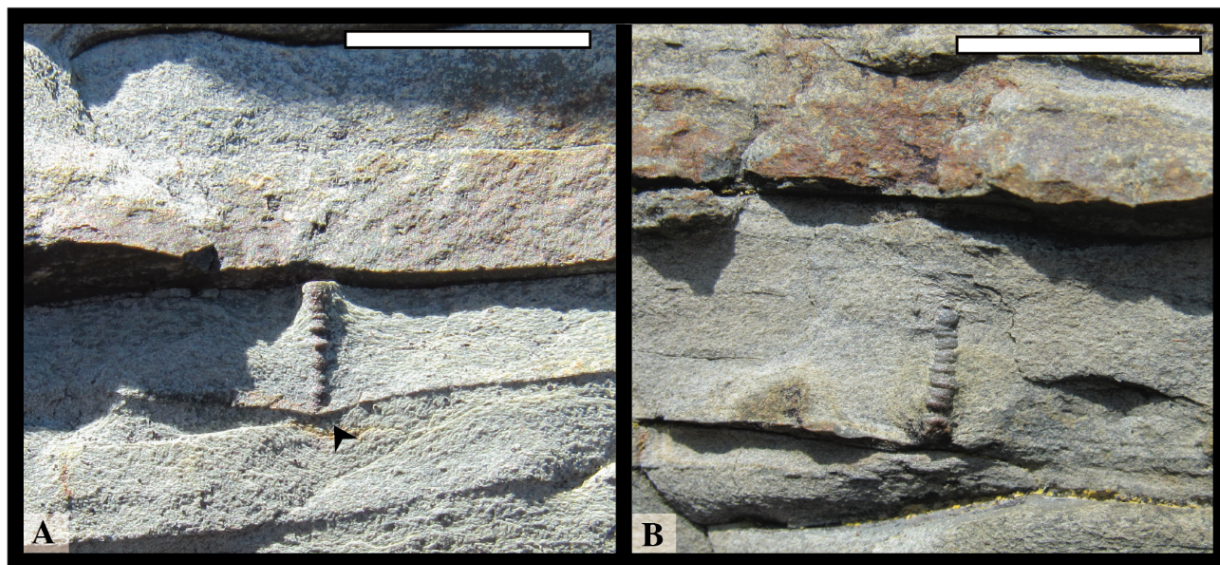


Figure 3.27 Unidentified tubes from the CIF. All scale bars 1cm. (A) A slightly cone-shaped tube, with regular annulations. Note the deformation of the underlying sand layer, implying the tube was lithified at the time of sediment compaction (black arrow). (B) A cylindrical tube, with irregular annulations.

Algae
Figure 3.35 D

Material

One specimen photographed in the field (FH ?10 m).

Description

Thin (0.2-05 mm), non-continuous, dark grey curving cylindrical sheaths. Located on the top of a very fine sandstone bed.

Remarks

Vendotaenids (specifically *Tyrasotaenia*) are commonly found within the *T. pedum* IAZ at the CIF (Landing et al., 1988).

Wide, tightly beaded burrow

Figure 3.35 C

Material

One specimen, photographed and measured (FH 1.45).

Description

A thick (2-2.5 mm) burrow with distinct sub-rounded segments, each 1.5-2 mm long infilled with very fine sandstone. Preserved in positive hyporelief on the base of a very fine-grained sandstone bed.

Remarks

Towards the top of figure 3.35 C, the burrow seems to curve upwards, bearing resemblance to a treptichnid. However, the specimen does not appear to be constructed by the addition of U-shaped segments, and the segments have a considerably smaller length to width ratio than in a treptichnid. Instead, the burrow was likely created by the addition of ball-shaped segments. *Planolites annularis* is less regular, and is characterized by ring-like annulations, rather than rounded expansions.

Thin ?branching meandering burrow

Figure 3.35 E, F

Material

Seven samples photographed and measured in the field (FH, 6 m, 12 m, 15.10 m, 86.90 m, 154 m) plus roughly 5 field identifications.

Description

Thin (0.5-0.75 mm wide) slightly meandering, circular in cross-section, burrows. Found in relatively high density on bedding planes. Turns 2 to 8 mm wide. Burrows occasionally interpenetrate each other, and it is difficult to discern if they are cross-cutting each other or are secondary successive branches. Meander loops are sometimes horse-shoe shaped. Other meander loops bend sharply (~90°) at the apex of the curve, and then change convexity, forming a shape similar to the bottom half of the lowercase Greek letter lambda (λ). Preserved in positive hyporelief as well as positive and negative epirelief.

Remarks

Specimens resemble *Helminthopsis* most closely, and it is possible that they are simply *Helminthopsis* which has been cross-cut by a similar horizontal simple burrow. However, burrows often terminate when intersected by another burrow, and display a strong tendency to avoid each other. As such, it is hypothesized that they may in fact have a network-like morphology, most similar to *Multina*.

Figure 3.28

(A) *Archaeonassa fossulata* preserved in negative epirelief (FH 2.6m) (B, C, E). *Gyrolithes gyratus* preserved in full relief, viewed in cross-section (B: FH 44.5m; C, E: ?6m). (D) *Cochlichnus anguineus* preserved in negative epirelief (FH 12m). (F) *Helminthopsis tenuis* preserved in negative epirelief (FH 142.0m). (G) *Gyrolithes scintillus* preserved in full relief, viewed in cross-section (FH 14.8m). (H) *Gyrolithes scintillus* preserved in full relief, viewed on the top of a bed. (FH 52m). All scale bars are 1cm.

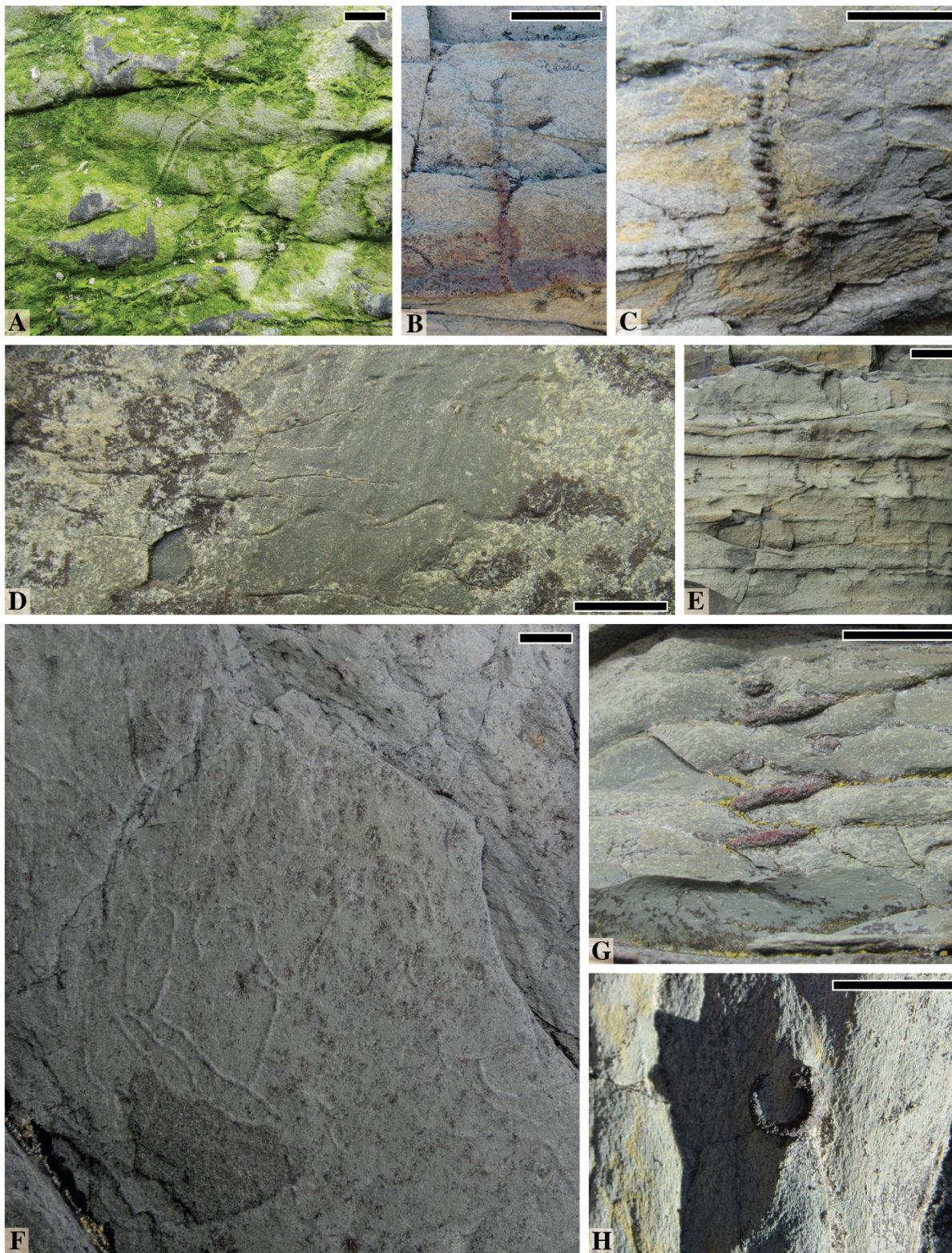


Figure 3.28 Caption on previous page.

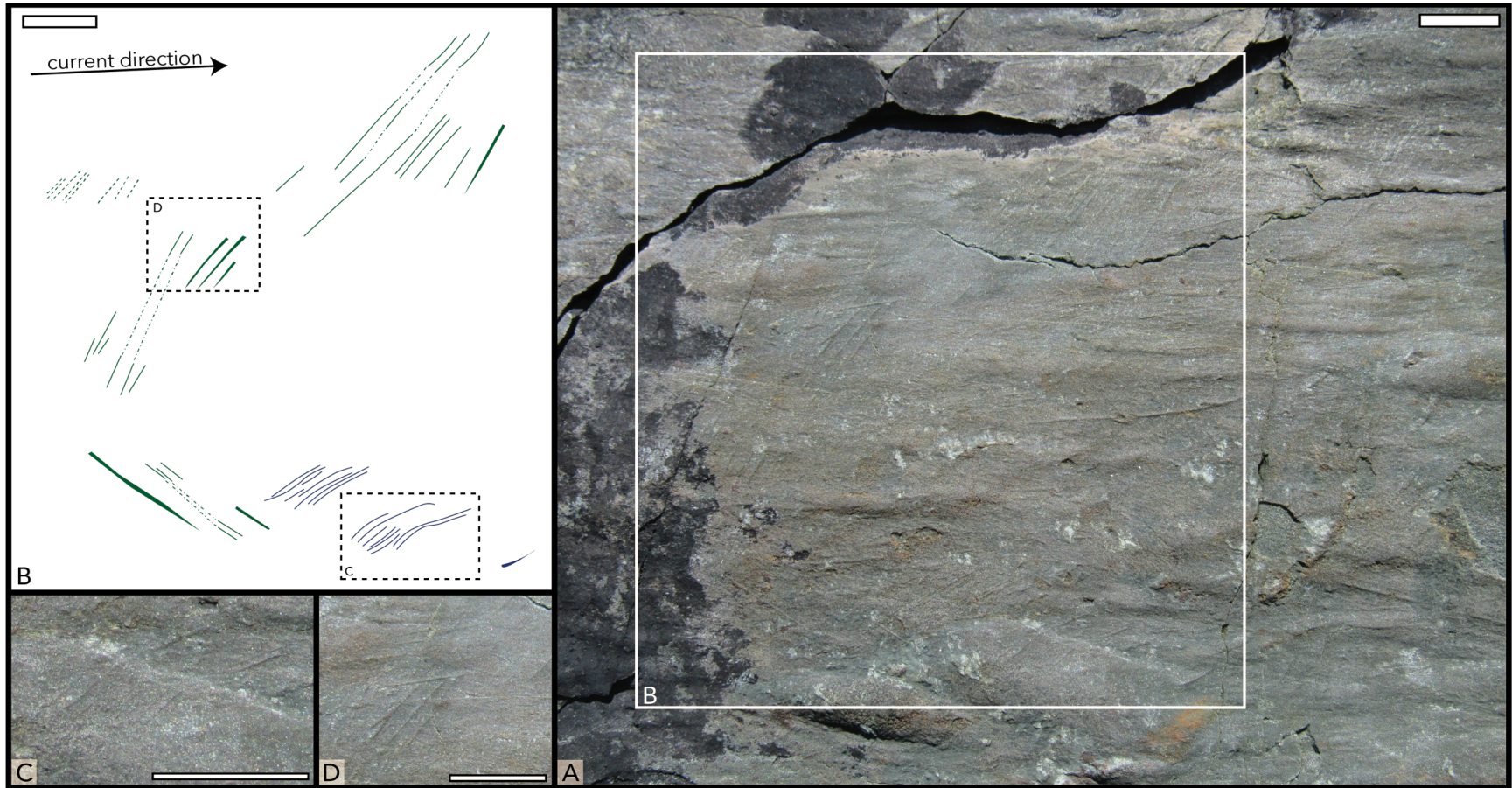


Figure 3.29 Slab A, showing several *Dimorphichnus* cf. *obliquus* at Grand Bank Head (GBH6, 11m). All scale bars are 1cm. **(A)** The trackways viewed in A, preserved in positive hyporelief on a very fine-grained fluted sandstone bed. **(B)** Schematic reconstruction of area highlighted in A. potentially related sets (i.e. conforming a trackway) are shown in the same color. Some directionality of the trackway can be inferred (see remarks of *D. cf. obliquus*). Current direction is inferred from observed flute casts. **(C)** One set of slightly sigmoidal raker marks **(D)** One set of blunt, straight, pusher marks. This set is crosscut by another probable set of pusher marks, oriented parallel to current. A conservative approach was taken, and any marks parallel to current were excluded, in the unlikely case that they were tool marks.

Figure 3.30

(A) *Gyrolithes scintillus* preserved in full relief, viewed in cross-section (GBH). (B) *Helminthoidichnites tenuis* preserved in negative hyporelief (C) *Helminthopsis tenuis* preserved in positive hyporelief (FH 82.0m) (D) *Palaeophycus tubularis* preserved in positive hyporelief (FH 83m). (E) *Palaeophycus tubularis* preserved in positive epirelief, viewed from the top of a bed. (FH 20.9m). (F) *Palaeophycus* isp. preserved in full relief, viewed in cross-section. (G) *Palaeophycus tubularis* preserved in positive epirelief, viewed from the top of a bed. (H) *Treptichnus* isp. preserved in positive hyporelief (FH ?1m). All scale bars are 1cm.

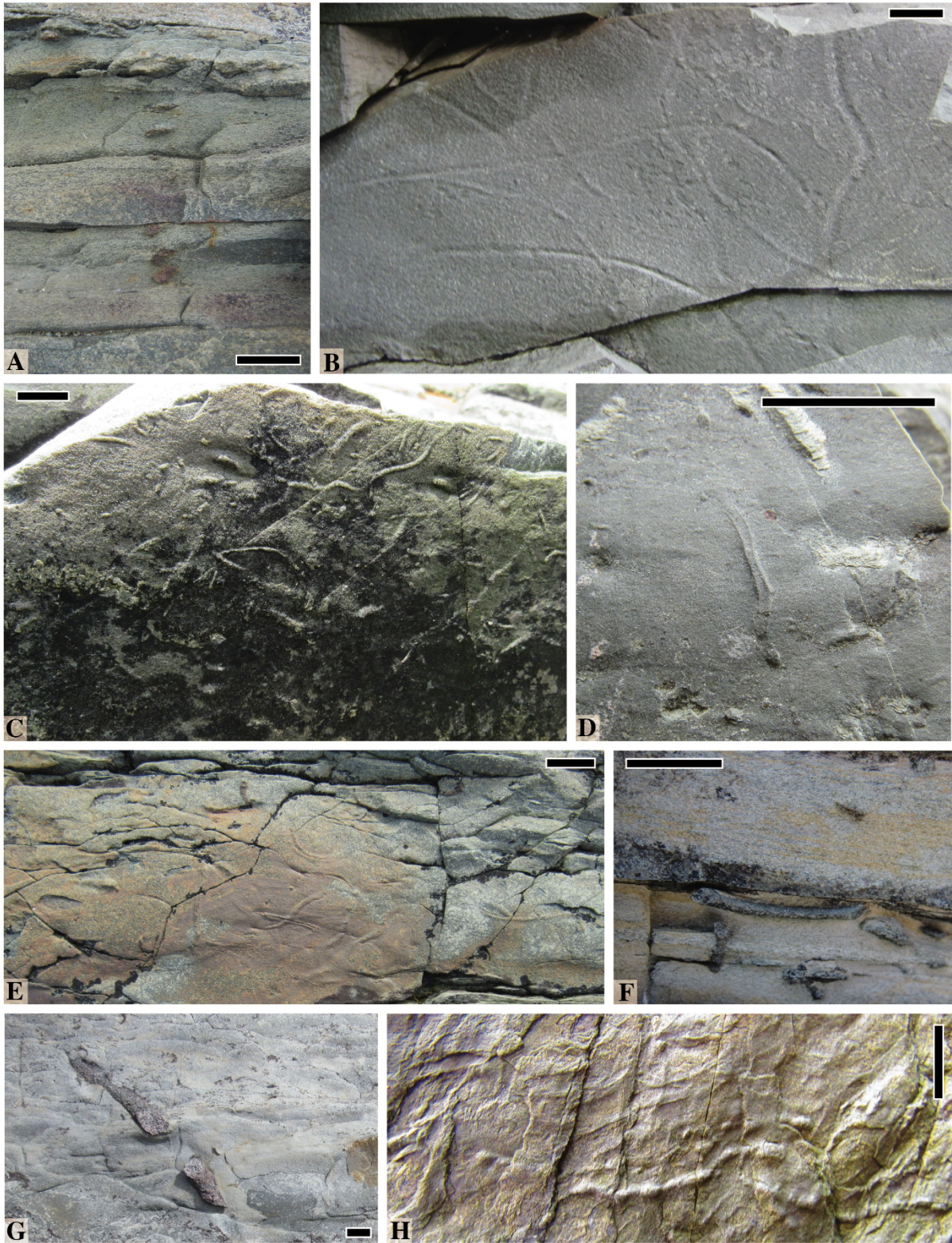


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Figure 3.31

(A) *Treptichnus coronatum* preserved in full relief, viewed on the base of a bed. (GBH). (B) *Treptichnus pedum* preserved in full relief, viewed on the top of a bed. (FH 55.5m). (C, E) *Treptichnus pedum* preserved in positive hyporelief (C: FH 1.35m). (D, F) *Trichichnus* isp. preserved in full relief, viewed in cross-section (D: FH 25m; F: GBH). All scale bars are 1cm.

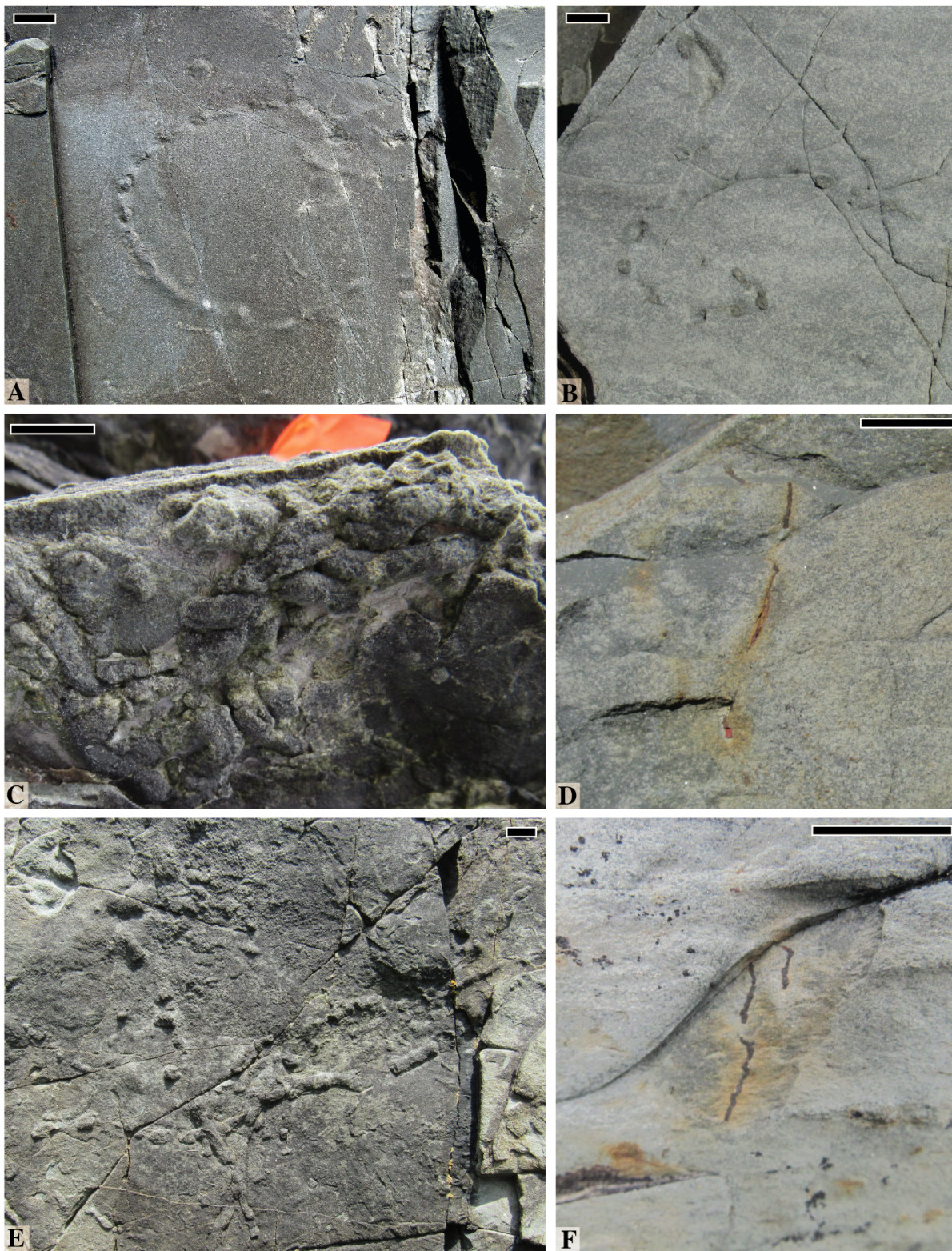


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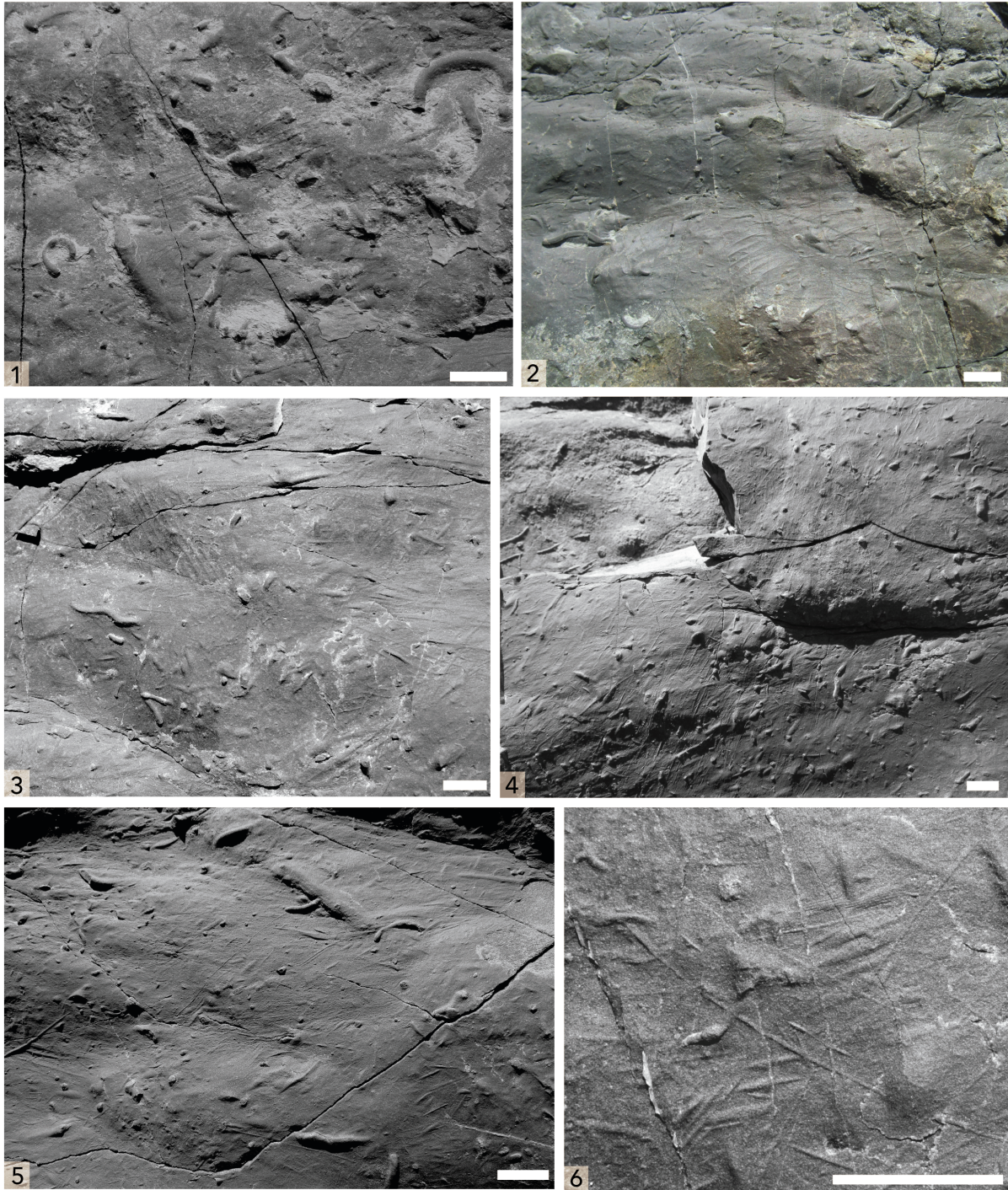


Figure 3.32 Close up photographs of sections on Slab B at GHB 6 (10.5m) outlined in figure 3.33. All specimens preserved in positive hyporelief on the base of a very-fine sandstone bed. All scale bars are 1 cm. **(1)** *Monomorphichnus*. isp A. **(2)** *M* isp. A. **(3)** *M* isp. A. **(4)** Arthropod scratch marks oriented roughly perpendicular to current, with various *M*. isp. C specimens. **(5)** Various arthropod scratch marks. **(6)** 3 specimens of *M*. isp. B., along with two specimens of *M*. isp. C. towards the top of the photo.

Figure 3.33

Slab B at Grand Bank Head 6 (10.5m), the base of a very fine sandstone bed, some flutes visible. Boxes outline photos in figure 3.32 Scale bar is 6 cm long.

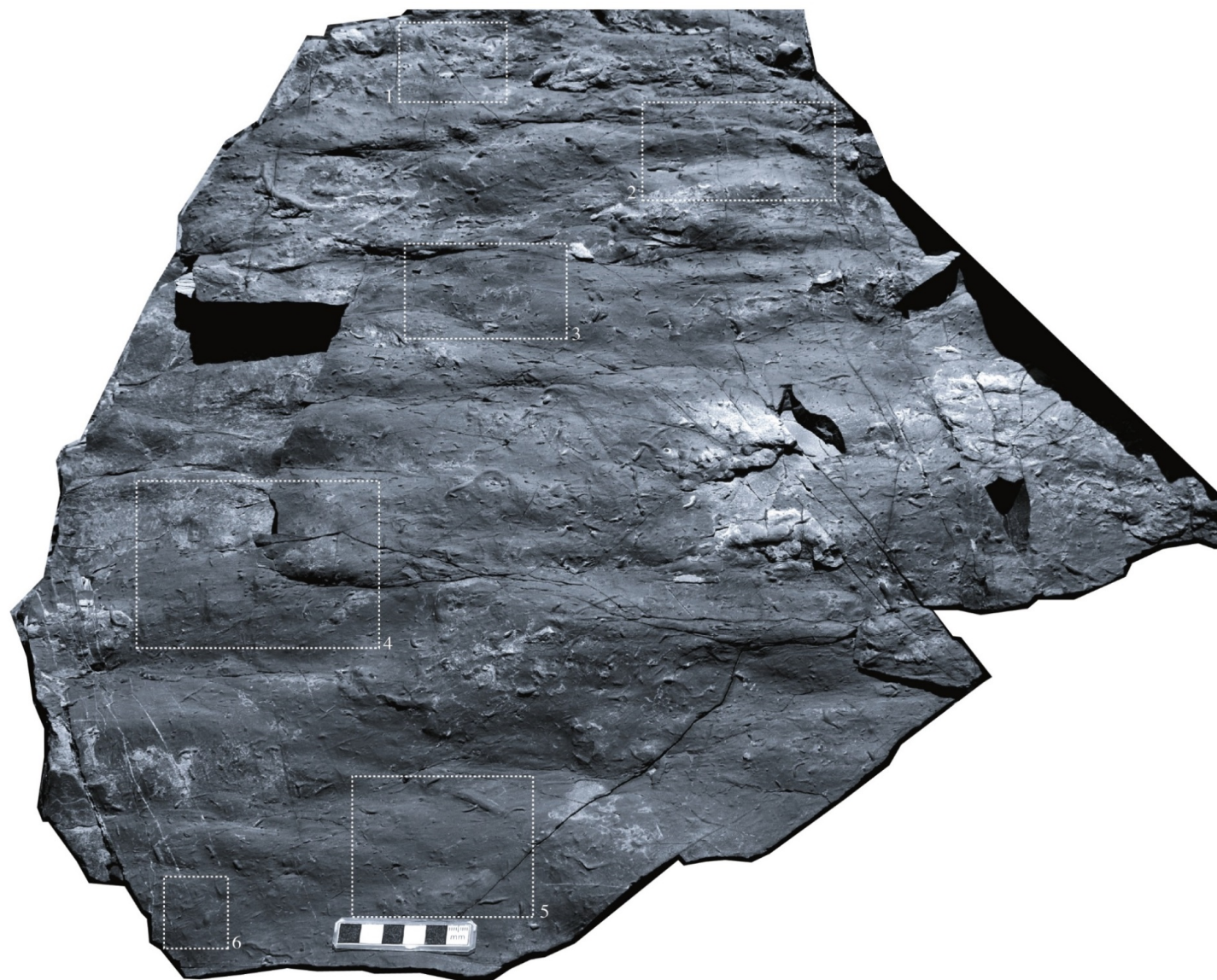


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Figure 3.34

Tracing of arthropod scratch marks in slab B., seen in Figure 3.33. Boxes correspond to photographs in Figure 3.32.
Arrows next to outlined sections illustrate the direction of the arthropod scratch marks

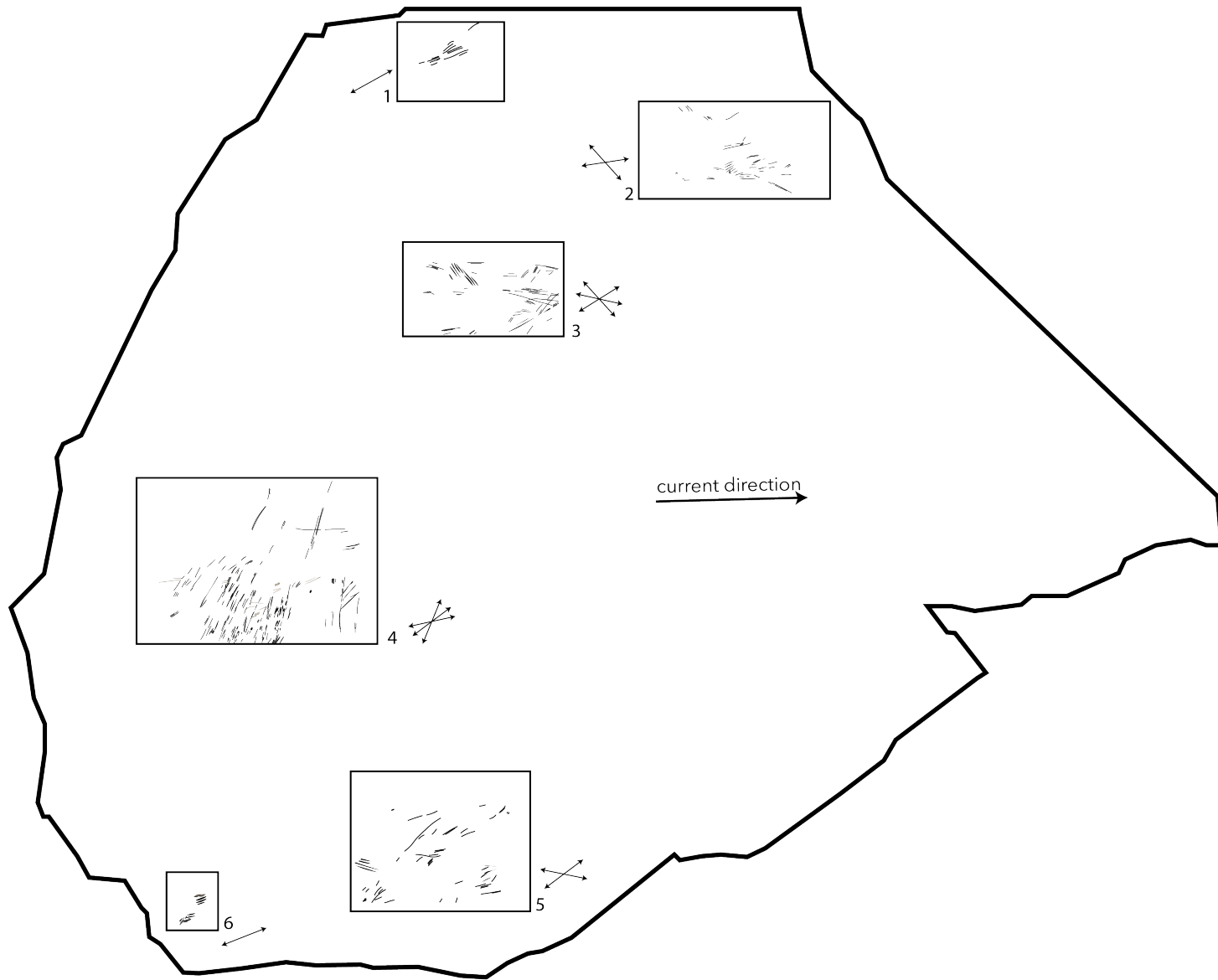


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Figure 3.35

(A) Unidentified beaded burrow preserved in positive and negative epirelief (FH 94 m). (B) *Treptichnus* isp. preserved in negative epirelief (FH 74 m). (C) Wide tightly beaded burrow preserved positive hyporelief (FH 1.45 m). (D) Possible algae preserved in the top of a bed (FH 710 m). (E, F) Thin ?branching meandering burrow preserved in positive hyporelief (FH 15.10 m).



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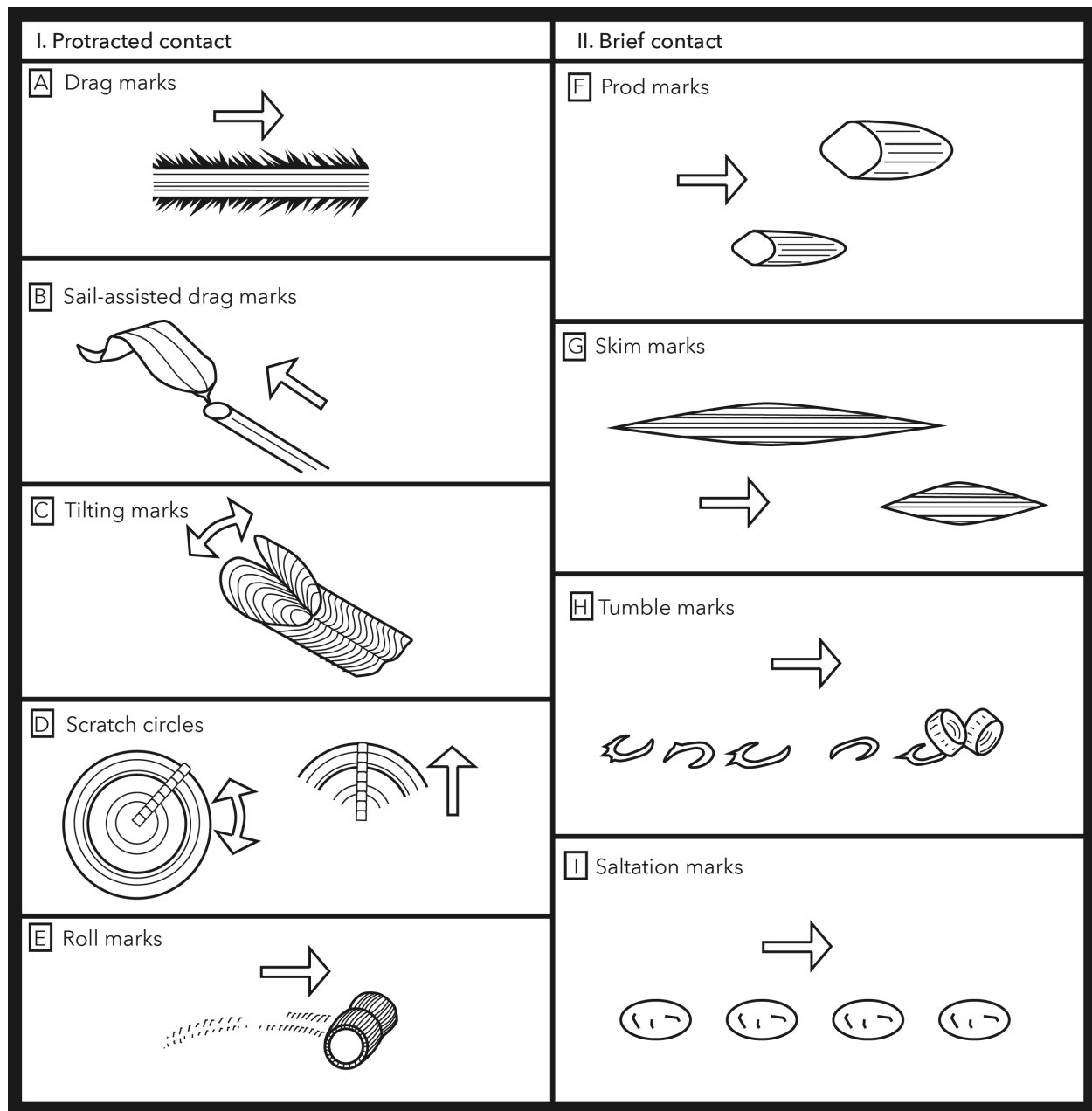


Figure 3.36 A revised classification of took marks in terms of kinetics. Classification revised from Allen (1982, Figure 13-2). **A)** Drag marks (after Allen, 1982). **B)** Sail-assisted drag marks (after Frey and Dashtgard, 2012). **C)** Tilting marks (after Wetzel, 2013). **D)** Scratch marks Left: complete scratch circle (after Jensen et al., 2002) Right: A flag scratch circle, showing current direction (after Uchman and Rattazzi, 2013). **E)** Roll marks (after Seilacher, 2007) **F)** Prod marks (after Allen, 1982). **G)** Skim marks (after Allen, 1982). **H)** Tumble marks (after Seilacher, 2007). **I)** Saltation marks (after Allen, 1982).

Table 3.7 Tool marks created by an organic tool, with their associated cast types and potential pseudofossil or fossil misinterpretations.

Pseudofossil	Tool	Type of casts	Source
	Nautiloids	Saltation, prod, and roll casts.	Kelling and Whitaker, 1970
	Graptolites	Drag marks and prod casts.	Trewin, 1979
	Algae	Drag marks	Haines, 1997
<i>“Kullingia”</i> <i>“Laevicyclus”</i> Medusoids	Anchored tubular organism (sabelliditid?)	Scratch circle (drag marks)	Jensen et al., 2002
	Plant leaves and stems	Wind-generated tool marks (drag marks)	Jones, 2006
<i>“Undichnia”</i> , <i>“Protichnites”</i> , <i>“Koupichnium”</i>	Seaweed-assisted gravel	Sail-assisted tool marks (drag marks)	Frey and Dashtgard, 2012
	Foramnifera	Drag marks (flag scratch circles)	Uchman and Rattazzi, 2013
Various trace fossils	Varies, from jellyfish to wood	Tilting marks	Wetzel, 2013
<i>“Eophyton”</i> Burrows	Unknown—sail attached to a smaller circular structure	Drag (sail-assisted tool) marks	Savazzi, 2015
	Tabulate corals or crinoid stems	Drag marks	Vinn and Toom, 2016
Medusoids	Seaweed	Scratch circles (drag marks)	Seilacher, 2007
Fish trace fossils	Ammonite shells	Roll to tumble marks	Seilacher, 2007
<i>“Paleodictyon”</i>	Tabulate corals	Roll marks	Seilacher, 2007
<i>“Oklahomaichnus”</i>	Fish vertebrae	Tumble marks	Lucas and Lerner 2001; Seilacher, 2007
<i>“Ichnispica”</i>	Cattail stems	Roll marks	Seilacher, 2007
<i>“Chloephytus”</i>	Seaweed	Drag marks	Seilacher, 2007

3.3. Ecospace analysis

Ecospace, as it pertains to paleoecology, describes the ecological space (i.e., mode of life) that an organism occupies (for a review of the term “ecospace” in modern ecology see Brunbjerg et al., 2017). Due to the time-averaging nature of the fossil record, the ecological parameters that paleontologists can discern are limited. Instead, paleontologists rely heavily on functional morphology to glean insights on the lifestyles of ancient organisms (Bambach et al., 2007). The guild concept (Bambach, 1983) draws on this, and is a framework for classifying fossil taxa using discernable ecological parameters. Bush et al. (2007) refined this method, and noted that three ecologic properties can be somewhat reliably determined with fossil data: tiering, motility, and feeding. They argued that these three properties defined one ecospace, and could be used to systematically analyze changes in ecospace utilization through time. As a result, they constructed a 6 by 6 by 6 matrix to represent all possible ecospace, with each ecological property representing an axis (Figure 3.37).

Bromley (1990) modified the bambachian guilds to better suit ichnological data, and categorized ecological complexity by a ichnofossils bauplan (equivalent to motility in Bush et al. 2007), food source, and tier. In turn, Minter et al. (2016a) created an adapted framework for ecospace occupation, specifically for ichnologists. This framework is useful for examining ichnofossil ecospace occupation through time, as demonstrated in his work on continental ichnofossils (Minter et al., 2016b, 2017). However, two disparate schemes for body fossils and ichnofossils inhibits collaboration between the two bodies of evidence. In turn, both Bush’s et al. (2007) original ecospace occupation framework and Bambach’s et al. (2007) ecospace analysis emphasized ichnofossils, in an effort to include this pivotal body of evidence. Herein, a slightly modified version of Bush’s et al. (2007) ecospace occupation framework is employed.

In order to achieve a greater resolution of ecological changes, especially as it pertains to ichnofossils, some ecologic categories were subdivided, as per Minter’s et al. (2016a) scheme. 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, the ecospace “cube” was divided in half, to represent two subdivisions of the “shallow infaunal tier” (Figure 3.37). In this way, ichnofossil and body fossil data may be combined into a single ecospace occupation framework.

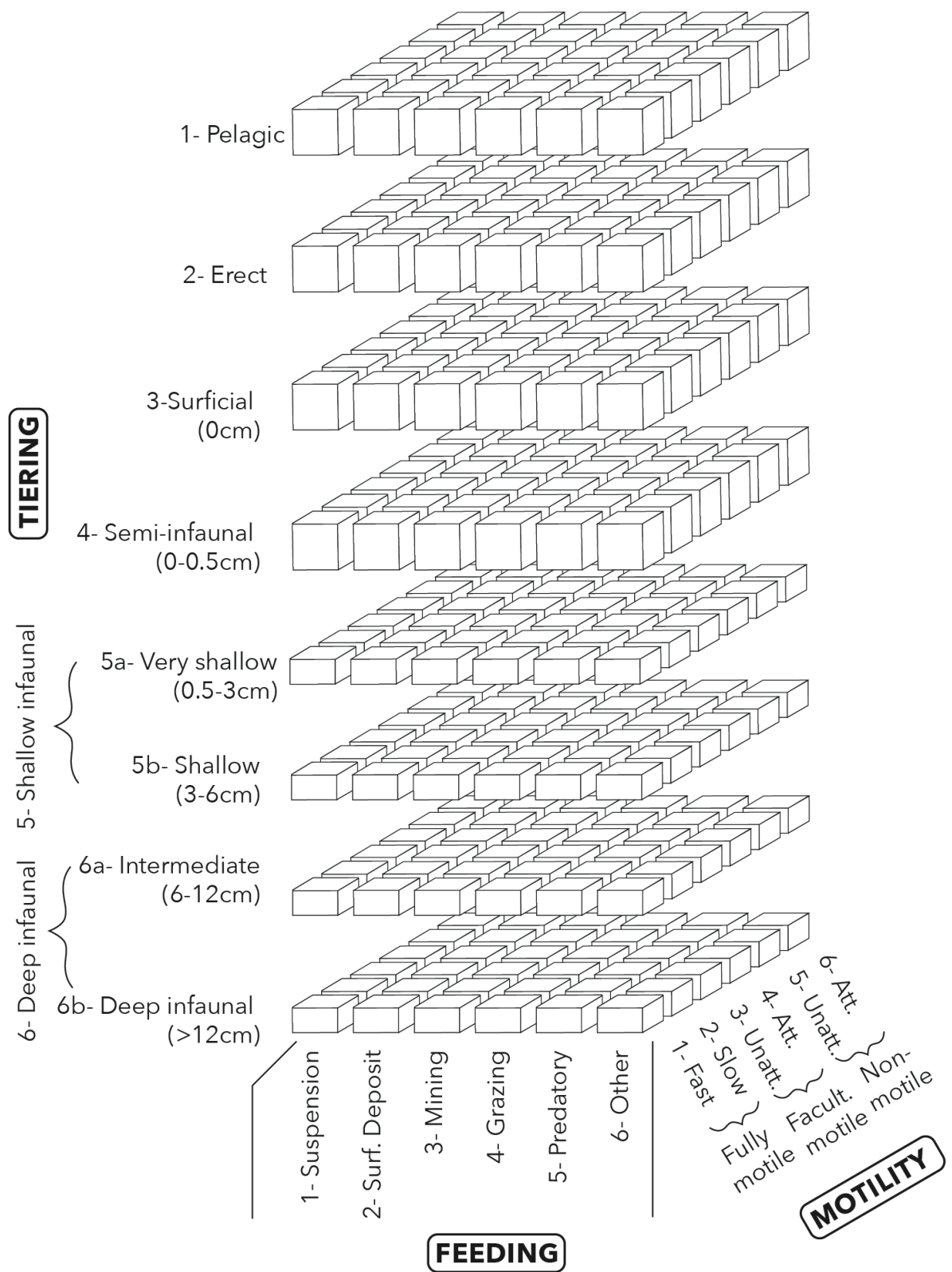












Figure 3.37 Modified ecospace occupation framework, wherein some ecospace sections have been subdivided to better encompass ichnologic data (modified from Bush et al., 2007 with subdivisions from Minter et al. 2016).

Table 3.8 Ecospace and ichnoguild analysis of the Chapel Island Formation *Treptichnus pedum* Ichnofossil Assemblage Zone ichnofossils.

Ichnospecies	Ecospace parameter		
	Tiering	Feeding	Motility
 <i>Bergaueria</i> isp. ichnoguild 			
<i>Bergaueria</i> isp.	4,5a	5	4
<i>Bergaueria perata</i>	4,5a	5	4
<i>Conichnus conicus</i>	4,5a	5	4
 <i>Dimorphichnus</i> cf. <i>obliquus</i> ichnoguild 			
<i>Dimorphichnus</i> cf. <i>obliquus</i>	3	2,4,5	1
<i>Monomorphichnus</i> isp. A	3	2,4,5	1
<i>Monomorphichnus</i> isp. B	3	2,4,5	1
<i>Monomorphichnus</i> isp. C	3	2,4,5	1
 <i>Gyrolithes scintillus</i> ichnoguild 			
<i>Gyrolithes gyratus</i>	5a	6	2
<i>Gyrolithes scintillus</i>	5a	6	2
<i>Trichichnus</i> cf. <i>simplex</i>	5a	6	2
 <i>Helminthoidichnites tenuis</i> ichnoguild 			
<i>Archaeonassa fossulata</i>	4	4	2
<i>Cochlichnus anguineus</i>	4	4	2
<i>Gordia</i> isp.	4	4	2
<i>Helminthoidichnites tenuis</i>	4	4	2
<i>Helminthopsis tenuis</i>	4	4	2
 <i>Treptichnus pedum</i> ichnoguild 			
<i>Palaeophycus</i> isp.	5a	1,5	2
<i>Palaeophycus tubularis</i>	5a	1,5	2
<i>Treptichnus coronatum</i>	5a	2,5,6	2
<i>Treptichnus</i> isp.	5a	2,3,5	2
<i>Treptichnus pedum</i>	5a	2,3,5	2

In cases of uncertain affinities, Bambach et al. (2007) applied a conservative approach and assigned all possible ecospace cubes. Similarly, this can be applied for the new subdivisions. For instance, when combining “5- shallow infaunal” Ediacaran body fossils within the new subdivided ecospace occupation framework herein, it is more conservative to occupy both the “5a- very shallow” and the “5b- shallow” ecospace “cubes”. Likewise, in cases of uncertain ichnofossil affinities (in this case, usually within the feeding parameter), multiple ecospace cubes were occupied. Five ichnoguilds were recognized within the *T. pedum* IAZ (Table 3.8). These ichnoguilds are colour-coded and plotted in a stratigraphic framework (Figures 3.2 and 3.3).

3.3.1. *Bergaueria* isp. ichnoguild

The *Bergaueria* isp. ichnoguild consists of *Bergaueria* isp., *Bergaueria perata*, and *Conichnus conicus*. All three are plug-shaped, probable anemone burrows (Alpert, 1973). As a result, it is hypothesized that they fed through predation. In turn, while *Bergaueria perata* and

Conichnus conicus are very shallow, semi-infaunal burrows, *Bergaueria* isp. demonstrates burrow adjustment with sedimentation (Figure 3.6), and can attain depths of 26 mm. As a result, this ichnoguild occupied both the semi-infaunal tier as well as the very shallow infaunal tier. In turn, the tracemaker actively anchored itself within the sediment, and in the case of *Bergaueria* isp. demonstrated motility with sedimentation. Therefore, they are classified as attached, facultative motile burrowers.

3.3.2. *Dimorphichnus* cf. *obliquus* ichnoguild

The *Dimorphichnus* cf. *obliquus* ichnoguild consists of *Dimorphichnus* cf. *obliquus*, *Monomorphichnus* isp. A, *Monomorphichnus* isp. B, and *Monomorphichnus* isp. C. Broadly, these ichnofossils may be categorized as arthropod scratch marks. They are all the result of an arthropod walking on, or scratching, a sediment surface and as such occupied the surficial tier. This also demonstrates that they were fast fully motile organisms. The feeding habits of these primitive arthropods is still a debated topic among researchers. *Dimorphichnus* is generally regarded as a “grazing” track, however it is not clear whether or not this organism grazed on microbial mats, meiofauna, or detritus (see remarks of *D. cf. obliquus*). As a result, all three possible feeding ecospace were shown as occupied in Figure 3.38.

3.3.3. *Gyrolithes scintillus* ichnoguild

The *Gyrolithes scintillus* ichnoguild consists of *Gyrolithes gyratus*, *Gyrolithes scintillus*, and *Trichichnus* cf. *simplex*. These were all vertical burrows, attaining a maximum depth of 29 mm, classifying them as very shallow tier burrowers. They were likely originally deeper however, as all samples have been truncated by erosion. The gyrolithids were likely constructed by a vermiform organism (Laing et al., 2018), while *Trichichnus* was formed by large bacteria colonies (Kędzierski et al., 2015). They are both slow, fully motile organisms. *Trichichnus* is suspected to have fed through chemosynthesis, while *Gyrolithes scintillus* and *G. gyratus* likely fed through microbial gardening.

3.3.4. *Helminthoidichnites tenuis* ichnoguild

The *Helminthoidichnites tenuis* ichnoguild consists of *Archaeonassa fossulata*, *Cochlichnus anguineus*, *Gordia* isp., *Helminthoidichnites tenuis*, and *Helminthopsis tenuis*. These were all simple, horizontal burrows or trails, occupying the uppermost 0.5 cm of sediment (semi-infaunal). These ichnofossils are all viewed as pascichnial trails or burrows, combining

feeding and locomotion, and as a result were likely slow fully motile. In turn, their common association with MISS suggest they all fed on microbial mats, classifying them as grazers.

3.3.5. *Treptichnus pedum* ichnoguild

The *Treptichnus pedum* ichnoguild consists of *Palaeophycus* isp., *Palaeophycus tubularis*, *Treptichnus coronatum*, *Treptichnus* isp., and *Treptichnus pedum*. These sub-horizontal to horizontal burrows penetrated deeper than 0.5 cm (but less than 3 cm) into the substrate, and as a result constituted the very shallow tier. As burrowers of a probable vermiform affinity, they are classified as slow fully motile. The feeding mechanism of these tracemakers is difficult to discern, and it would be premature to create multiple ichnoguilds due to this uncertainty. As a result, only one ichnoguild is currently proposed; however, this may need to be subdivided when more information of the life style of the burrowers is made available.

By plotting these ichnoguilds in a stratigraphic (Figure 3.2 and 3.3) and ecospace (Figure 3.38) framework, a few initial trends can be observed. The *Helminthoidichnites tenuis* ichnoguild is documented within the *Harlaniella podolica* IAZ (Crimes and Anderson, 1985; Narbonne et al., 1987; Landing et al., 1988), and extends further backward into the Ediacaran worldwide. The *Treptichnus pedum* and *Bergaueria* isp. ichnoguilds appear just below the Ediacaran-Cambrian boundary, documenting a deeper tier than the stratigraphically older *Helminthoidichnites tenuis* ichnoguild. Additionally, the treptichnids as well as *Bergaueria* isp. document more sophisticated methods of interacting with the substrate. *T. pedum* and *T. coronatum* are the earliest penetrative burrows, while *Bergaueria* isp. may represent the first equilibrium structure. Finally, the deeper agrichnial and chemichnial ichnofossils (*Gyrolithes scintillus* ichnoguild), as well as those indicative of fast freely motile organisms (*Dimorphichnus* cf. *obliquus* ichnoguild), occur slightly after the Ediacaran-Cambrian boundary. These represent the first true vertical burrows as well as the first evidence of limbs recorded in this section, perhaps 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., 2012). The CIF ichnofossils therefore provide an important window between these two disparate faunas. When contrasted with the modes of life hypothesized for Ediacaran fauna and early-middle Cambrian fauna (Figure 3.38), a few initial trends can be observed. First,

a transition in feeding styles can be seen. 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. Interestingly, the CIF ichnofauna document a transition between the two. The *Gyrolithes scintillus* and *H. tenuis* ichnoguilds document more Ediacaran-like feeding-styles, such as chemosynthesis and mat grazing. However, the more Cambrian-like predatory and deposit-feeding modes of life are documented by the three remaining ichnoguilds (*B. isp.*, *D. cf. obliquus*, and *T. pedum*). Second, burrowers (slow fully motile organisms) begin to explore deeper tiers than previously documented. Finally, motile modes of life became more common, with the first appearance of fast freely mobile organisms. This likely reflects an evolution of body plans.

3.3.6. Early arthropods and CIF scratch marks

Limbed organisms capable of producing ichnofossils such as *Dimorphichnus* or *Monomorphichnus* had most likely evolved by the lowermost Fortunian (Waloszek et al., 2005; Budd and Telford, 2009). Whether or not these were trilobites remains to be determined; however, it is likely they were arthropods (sensu stricto), more likely euarthropods (Budd and Telford, 2009). It has been hypothesized that primitive arthropods had biramous limbs similar to extant arthropod appendages (Hughes 2003; 2007). These primitive limbs consisted of two rami, an endopodite and exopodite, connected to the body by the basipod (Watling and Thiel, 2012). The endopodite (also known as telopodite) is generally regarded as the walking limb of arthropods, and consisted of a segmented rod-like, lightly sclerotized leg, attached to the inside of the basipod. This limb produces the majority of arthropod scratch mark ichnogenera in the trace fossil record, such as *Diplichnites* and *Dimorphichnus*. *Dimorphichnus cf. obliquus* and *Monomorphichnus isp.* A from the CIF were likely created by primitive arthropod endopodites. The exopodite (also known as epipodite, exite, or “gill branch”) is sometimes thought to be used for respiration (Waloszek et al., 2005), however more recent research supports a non-respiration purpose (Liu et al, 2007; Suzuki and Bergström, 2008). The primitive exopod is a paddle-shaped ramus attached to the outside edge of the basipod, with spines evolving in Euarthropoda. While exopodites have been historically viewed as gills, due to their high surface area, they were in fact

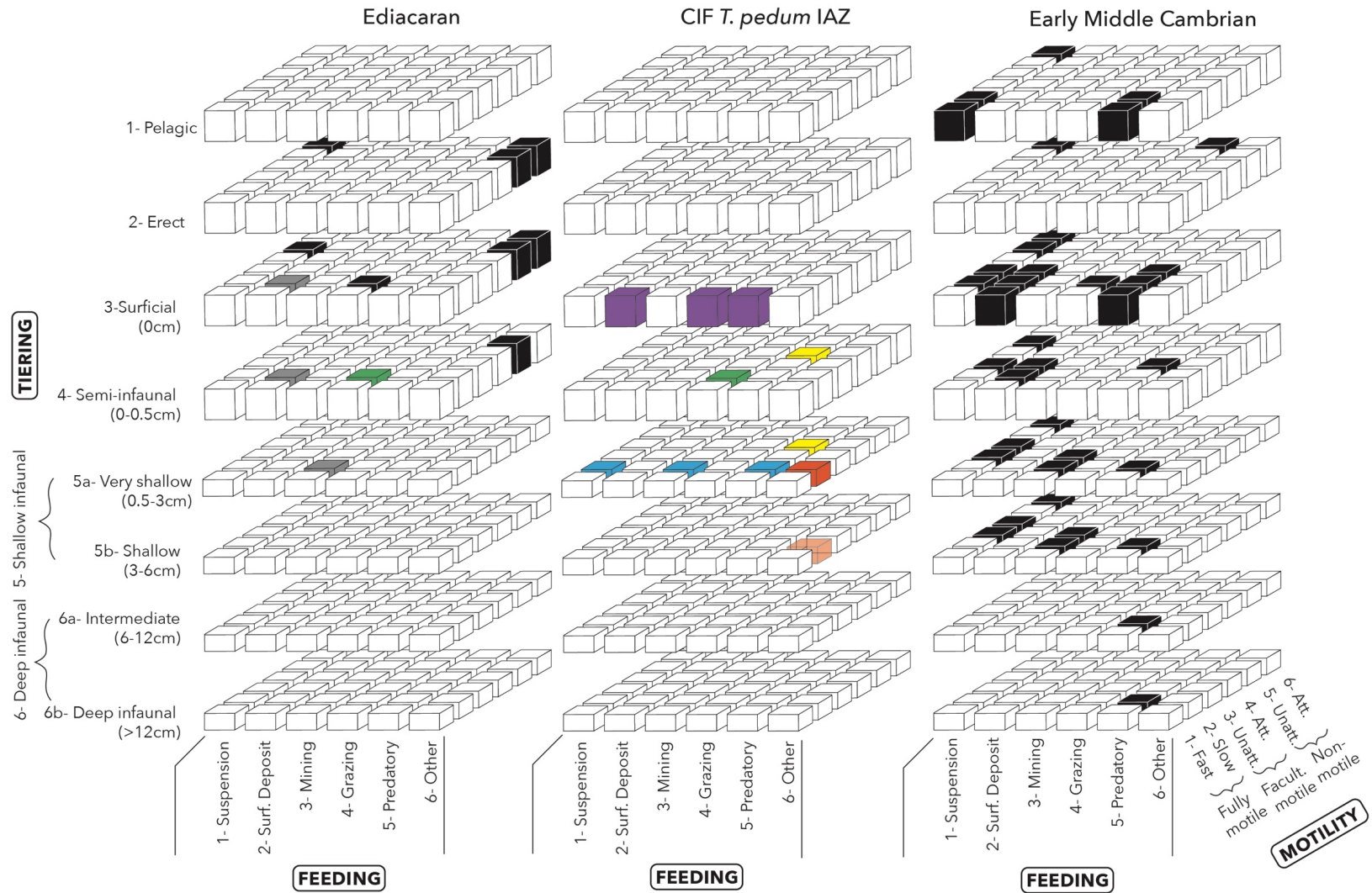


Figure 3.38 Ecospace analysis for the Ediacaran to early- middle Cambrian. Black boxes represent ecospace occupied by body fossils, globally and grey boxes represent ecospace occupied by trace fossils (data from Laflamme et al., 2013). Coloured boxes represent ecospace occupied by CIF *T. pedum* IAZ ichnoguilds, colour scheme found in Table 3.8.

more robust (Bergström, 1969; 1972; Seilacher 1970) and may have been used for swimming (Waloszek et al., 2005; Stein, 2010) or burrowing (Seilacher, 1970, Bergström, 1976).

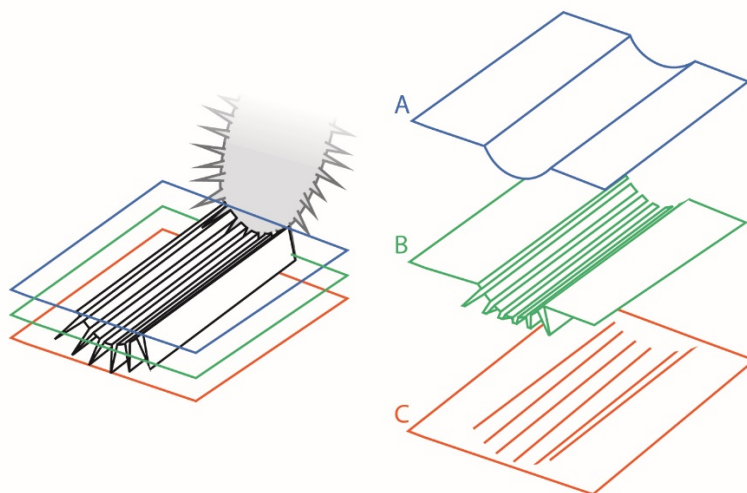


Figure 3.39 Possible three-dimensional expressions of a groove created by a spinose paddle shaped tool. **(A)** Uppermost expression, ressembling *M. isp. B.* **(B)** Middle expression, ressembling *M. isp. C.* **(C)** Lowermost expression.

The spiny flap-shaped exopod would be therefore capable of producing an impression similar to *M. isp. C.* All primitive arthropods had multiple biramous limbs, each which would possess a similar exopod (Watling and Thiel, 2012). Therefore, their scratch marks would likely be preserved in sets. One specimen of *M. isp. C* is found in close proximity with *M. isp. B*, oriented in a similar direction (Figure 3.32, 6). *Monomorphichnus isp. B* does not possess the fine striations found in *M. isp. C*, however the oval-shaped impression of *M. isp. C* is of similar dimensions as *M. isp. B* (Figure 3.18). One possible explanation is that *M. isp. C* is a deeper preservation of *M. isp. B*, where *M. isp. C* preserves the impression of the exopodal spines, and *M. isp. B* preserves the overall flap shape. However, it is unlikely that in a set of limbs only one exopod would be deeper impressed. In turn, the specimen of *M. isp. C* associated with *M. isp. B* is oriented slightly oblique to the *M. isp. B* set. An exopodal flap explanation for *M. isp. C* also does not explain the frequency of isolated specimens found.

Some stem-group euarthropods (Briggs and Collins, 1999) also possessed a spiny, flap or V-shaped telson. It has been hypothesized that this telson may have been used to ‘steer’ a swimming arthropod (Briggs, & Whittington, 1985). The telson would dig into the sediment, acting as a rudder, aiding to direct or balance the organism. In other arthropods, the telson is used

to right an overturned organism (Lin et al, 2009). Given the frequent isolated specimens, a telson imprint is a more likely cause of *M. isp. C*. This hypothesis aligns well with the observation that when *M. isp. C* is more oblique to flow, the impression is shorter. More effort (i.e., a shorter, deeper prod with the telson) would be needed to maintain a swimming course oblique to the current. When swimming with the current, the organism would only need to lightly graze the ground to maintain its balance and course.

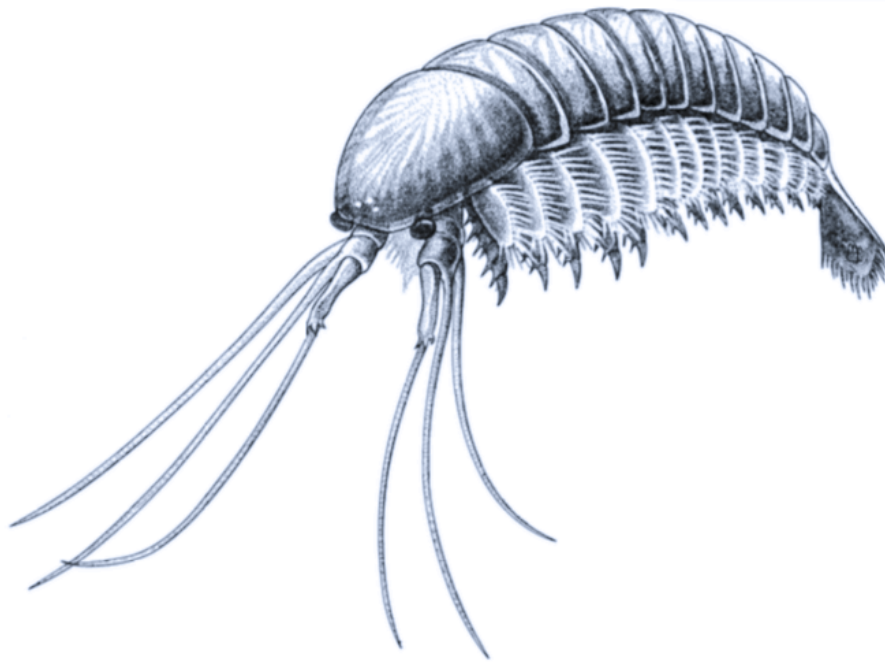


Figure 3.40 Reconstruction of the Leanchoilid *Alalcomenaeus cambricus* (from: Briggs and Collins, 1999, Figure 13)

Several *M. isp. C* specimens are found oriented parallel to elongate arthropod scratch marks but oblique to the dominant current direction (Figures 3.19 and 3.32 4). If these two scratch marks are related, these marks suggest an euarthropod with a spiny telson swimming over the surface. The elongate marks would be similar in genesis to *M. biserialis* (see Mikuláš, 1995 fig. 2), where the euarthropod is swimming parallel to the scratch marks, with similarly oriented telson “rudder” marks preserved. Likely, this would reflect a grazing behaviour.

Due to the absence of arthropod body fossils from the lowermost Fortunian, it is difficult to assign a specific arthropod tracemaker for the CIF scratch marks. However, if *M. isp. C* was formed by an exopodite, then this signifies the presence an ornamented exopodite, a distinctive feature of euarthropods (Watling and Thiel, 2012). Possible stem-group euarthropods

(Leancoilids) have been discovered and described in detail from the Chengjiang and Burgess-Shale lagerstätten (Briggs and Collins, 1999; García-Bellido and Collins, 2007; Liu et al., 2007). Most authors hypothesize that the leancoilids were nektobenthonic, since the endopodites are angled inwards and would be poor walking legs (Briggs & Whittington, 1985; Haug et al., 2012). In turn, thin-section analysis of a phosphatized three-dimensional axial structure in *Leancoilia* revealed the presence of midgut glands (Butterfield, 2002). These are common storage feature in predators, and it is therefore likely that these primitive arthropods were predators. However, a deposit feeding and scavenging lifestyle cannot be excluded (Briggs and Whittington, 1985). A reconstruction of the leancoilid *Alalcomenaeus cambricus* shows spiny inward-projecting endopods (Figure 3.40), suggesting that they were better-suited for capturing and dissecting prey, then for walking (Briggs & Whittington, 1985; Briggs and Collins, 1999).

Chapter 4

4. *Gyrolithes* from the Ediacaran-Cambrian boundary section in Fortune Head, Newfoundland, Canada: Exploring the onset of complex burrowing

Laing, B.A., Buatois, L.A., Mángano, M.G., Narbonne, G.M., Gougeon, R.C. 2018. *Gyrolithes* from the Ediacaran-Cambrian boundary section in Fortune Head, Newfoundland, Canada: Exploring the onset of complex burrowing. *Palaeogeography, Palaeoclimatology, Palaeoecology*. doi: 10.1016/j.palaeo.2018.01.010

4.1. Abstract

The beginning of the Cambrian explosion is characterized by the onset of infaunalization and the appearance of systematic patterns of burrowing. The trace fossil *Gyrolithes* is common in the Ediacaran-Cambrian Global Stratotype Section and Point, where it shows a higher diversity and burrow depth than previously reported from any Cambrian spiral vertical burrows. Two ichnospecies are present: *G. scintillus* isp. nov. exhibits a small burrow radius to whorl radius ratio, whereas *G. gyratus* (Hofmann) exhibits an exceptionally large ratio that formerly led to its identification as an aberrant ichnospecies of *Skolithos*. The helical morphology of these Cambrian *Gyrolithes* is interpreted as having served two purposes: as an anchor a relatively high-energy environment, and as an optimal shape for maximizing surface area for bacterial gardening. These shallow-marine gardening burrows share a similar feeding strategy as graphoglyptids and suggests that shallow early Cambrian sediments may have been relatively poor in organics and thus further support the model for onshore-offshore migration of gardening burrows.

4.2. Introduction

The onset of penetrative bioturbation has long been considered part of the rapid animal diversification characteristic of the early Cambrian. In 1992 the International Commission on Stratigraphy (ICS) chose the first penetrative branching burrows as a reliable criterion to place the basal Cambrian boundary upon. This is represented by the *Treptichnus pedum* Ichnofossil Assemblage Zone (IAZ), whose lowermost limit was placed at the lowest observed occurrence (First Appearance Datum) of *Treptichnus pedum* at the time of ratification (Landing, 1994). Included in the *T. pedum* IAZ is the helical burrow *Gyrolithes* de Saporta, 1884 (Narbonne et al., 1987; Landing, 1994; Laing et al., 2016). This IAZ was based upon the zonation of ichnofossils within the Chapel Island Formation at Fortune Head, Newfoundland. *Gyrolithes* isp. (Narbonne et al., 1987) or *Gyrolithes polonicus* Fedonkin, 1981 (Gehling et al., 2001; Herringshaw et al., 2017) have previously been documented at this section. Because of its importance as a biostratigraphic indicator, most attention in trace fossil studies of the Ediacaran-Cambrian transition has focused on *Treptichnus pedum* (e.g., Vannier et al., 2010; Buatois et al., 2013; Buatois, 2017), with *Gyrolithes* remaining poorly explored. This is somewhat unfortunate because *Gyrolithes* is undoubtedly an archetypical representative of the infaunalization associated with the Cambrian explosion. In fact, this ichnotaxon can be regarded as the earliest vertical burrow recorded to date.

Although Cambrian occurrences are still poorly understood, the common occurrence of the helical ichnofossil *Gyrolithes* throughout the Phanerozoic has led to much research regarding its potential tracemakers (Dworschak and Rodrigues, 1997), paleoenvironmental significance (Gernant, 1972; Netto et al., 2007), and intergradations with other ichnotaxa (Bromley and Frey, 1974; Mayoral and Muñiz, 1995, 1998). At present, only one *Gyrolithes* ichnospecies has been identified with certainty prior to the Permian —the relatively small (2 to 15 mm wide) Cambrian *G. polonicus*, consisting of one to two tightly spaced whorls.

The aims of this paper are to: (1) describe and analyze in detail these earliest Cambrian occurrences of *Gyrolithes*, (2) clarify their ichnotaxonomic status, and (3) discuss their significance with respect to the evolution of burrowing during the Cambrian explosion.

4.3. Geologic and stratigraphic setting

Sedimentary units spanning the Ediacaran-Cambrian boundary on the Burin Peninsula of Newfoundland, Nova Scotia, and New Brunswick (Figure 4.1 A) were deposited within a transtensional regime, infilling a horst and graben basins (Landing, 1996, 2004). The conglomerates and sandstones of the Rencontre Formation were deposited first, recording sedimentation in a fluvial and marginal marine environment (Smith and Hiscott, 1984). The Rencontre Formation is overlain by the Chapel Island Formation (CIF). The Chapel Island Formation was defined by Hutchinson (1962) and subdivided into five informal members by Bengtson and Fletcher (1983) that have been widely used by subsequent workers describing the geology and paleontology of the Burin Peninsula. Members 1-4 are a continuous, nearly kilometer-thick succession of fine siliciclastics collectively equivalent to the formally defined Quaco Road Member in New Brunswick (Landing, 1996) and are disconformably overlain by member 5 which is equivalent to the Mystery Lake Member in New Brunswick (Landing, 1996). These members, are interpreted to have been deposited in a wide variety of shallow-marine environments, ranging from peritidal to shelf (Myrow and Hiscott, 1993). The overlying sandstones of the Random Formation records deposition dominantly in nearshore settings (Hiscott, 1982; Landing et al., 1988).

The outcrops are located within the Fortune Head Ecological Reserve (FHER), 1.5 km west of Fortune, Newfoundland on the Burin Peninsula (Figure 4.1) and are protected by the Newfoundland and Labrador government, under Parks and Natural Areas. They document 415 m of reasonably continuous sedimentation during the latest Ediacaran and earliest Fortunian (Narbonne et al., 1987). The section encompasses the last 10 m of member 1 and all of members 2A and 2B of the Chapel Island Formation (CIF). A continuous section of member 1 was measured 7 km to the northeast, at Grand Bank Head, and the remaining members (members 3, 4, and 5) of the CIF have been measured 15 km to the southwest at Little Danzig Cove. Combined, these localities document a 1 km thick continuous succession of the CIF.

Member 2 is interpreted to have been deposited within a storm-dominated shallow-marine setting at times displaying deltaic influence (Myrow, 1987; Myrow and Hiscott, 1993; Buatois et al., 2014). Fine-grained gravity-flow deposits occur locally (Myrow and Hiscott, 1991). Overall, member 2 deposits are heterolithic, with massive siltstone punctuated by very fine- to fine-grained sandstone beds. Wave-ripple cross-lamination, hummocky cross-

stratification, gutter and pot casts, and carbonate concretions occur in the sandstone (Myrow, 1987).

The siltstone units were likely firm at the time of burrow excavation, as shown by the lack of wall or lining in all burrows seen, the degree to which delicate imprints are preserved, and the preservation style of burrows (Droser et al., 2002; Jensen et al., 2005; Buatois et al., 2014; Tarhan and Droser, 2014). Substrate consistency is likely due to stabilization of grains, caused by pervasive microbial mats (Buatois et al., 2014) combined with a lack of bioturbation and sediment mixing (Droser et al., 2002; Buatois et al., 2014).

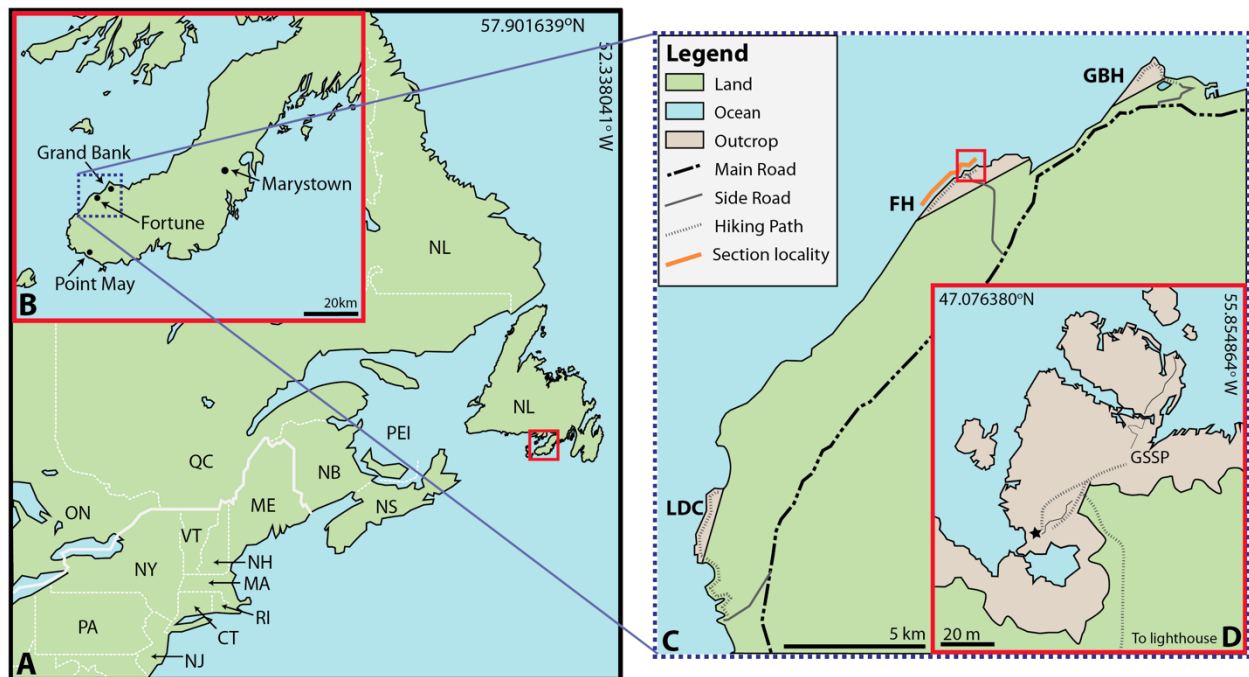


Figure 4.1 (A) Map of eastern Canada and the United states. The red box denotes the Burin Peninsula, shown in map B. (B) Map of the Burin Peninsula, Newfoundland. The blue dashed box is highlighting the field locality, on the northwestern corner of the Peninsula, shown in map C. (C) Map of outcrop localities on the Burin Peninsula. LDC= Little Danzig Cove, FH= Fortune Head, GBH= Grand Bank Head. The red box denotes map D. (D) Map of the Ediacaran-Cambrian GSSP at the Fortune Head Ecological Reserve in Fortune, Newfoundland. Star denotes the location of the field holotype of *G. scintillus*. GSSP denotes the GSSP section.

4.4. Systematic ichnology

Both ichnospecies of *Gyrolithes* are preserved as endichnial structures excavated in the siltstone and infilled with very fine-grained sand from above. The burrows may either be connected or unconnected to overlying sandstone beds, the latter having been described as a “floating preservation” style (Droser et al., 2002). They occur throughout member 2 of the CIF (Figure 4.2).

Most specimens in this study are from the Global Stratotype Section and Point (GSSP) for the Cambrian System in the Fortune Head Ecological Reserve. Scientific permits are required to study the section and the collecting of fossil specimens from outcrop is forbidden. All specimens figured in this paper, including the holotype of *Gyrolithes scintillus* isp. nov., remain *in situ* in Fortune Head Ecological Reserve where they are protected by provincial law. This situation is similar to the regulations at the nearby Mistaken Point Ecological Reserve, which contains *in situ* field holotypes for the soft-bodied Ediacaran megafossils *Hapsidophyllas flexibilis* Bamforth and Narbonne, 2009 and *Beothukis mistakensis* Brasier and Antcliff, 2009.

Ichnogenus *Gyrolithes* de Saporta, 1884

- 1849 *Gyrolithen* Debey.
- 1884 *Gyrolithes* de Saporta.
- 1884 *Siphodendron* de Saporta.
- 1895 *Syringodendron* Fuchs.
- 1927 *Xenohelix* Mansfield.
- 1969 *Conispiron* Vialov.
- 1994 *Spirocircus* Mikuláš and Pek.

Type Ichnospecies

Gyrolithes davreuxi de Saporta, 1884 (Häntzschel, 1962)

Diagnosis

Rarely branched, spiraled burrows; helix essentially vertical, consisting of dextral, sinistral, or reversing coils, which are not in contact (Uchman and Hanken, 2013, modified from Bromley and Frey, 1974).

Discussion

Debey (1849) loosely termed vertical spiral burrows “*Gyrolithen*”, which were later assigned to *Gyrolithes* by de Saporta in 1884 (Bromley and Frey, 1974). Burrow can be smooth, ornamented, or possess a wall. Lack of clarification regarding *Gyrolithes* ichnotaxobases may have resulted in a proliferation of ichnospecies. Uchman and Hanken (2013) revised all current ichnospecies of *Gyrolithes*, and reduced the number of valid ichnospecies from 18 to 13. They proposed that the burrow width (d) to whorl radius (R) ratio be used to distinguish ichnospecies of *Gyrolithes* and plotted all available data on the morphometric parameters of *Gyrolithes* ichnospecies on a R:d diagram. They then synonymized any overlapping ichnospecies, given they had similar burrow margin features.

This method was then further refined by De Renzi et al. (2017), who applied a mathematical approach to the problem. They used the burrow radius (r), whorl radius (R), whorl height (h), and the slope of the helix (σ) to mathematically describe *Gyrolithes* (Figure 4.3).

In their approach De Renzi et al. (2017) worked with circular helices (i.e., helices whose measured values, r, R, and h, do not change with depth). They erected three dimensionless parameters to describe these circular helices:

$$\kappa=r/R \dots\dots\dots(4.1)$$

$$\delta=h/(2r) \dots\dots\dots(4.2)$$

$$\beta=h/(2\pi R)=\tan(\sigma) \dots\dots\dots(4.3)$$

These three parameters are related by $\delta=(\pi/\kappa)\beta$. As a result, only two of these parameters are necessary to accurately describe the morphology of a circular helix. Herein, κ and δ are the employed parameters.

However, many *Gyrolithes* are in fact conic helices, with whorl radius’ and heights that change with depth. This is observed for example in *G. polonicus* (Jensen, 1997) and *G. krameri* (Mayoral, 1986). Raup’s (1966) seminal paper on shell coiling dealt with conical helices, and he erected four dimensionless parameters to describe these. Since the burrow radius does not change within these trace fossils, Raup’s (1966) parameters which deal solely with burrow radius (r) can be omitted when describing *Gyrolithes*. In turn, Raup’s (1966) “D” (distance from axis) is similar to, and is herein replaced by, De Renzi et al. (2017) “K”. Therefore, the only parameter which must be added to accurately describe conical helices is a variation of Raup’s (1966) “T” (translation rate). Raup’s T assumes that both the height between whorls (h) and the whorl radius

(R) will change. This is true for conic helices with a constant helix angle (θ). However, conic helices may have either a constant helix angle, or a constant pitch (height between whorls). For conic helices with a constant pitch (h), Raup's T does not work. As such, this parameter has been modified to reflect the conical angle, as this must remain constant in all forms of conic helices.

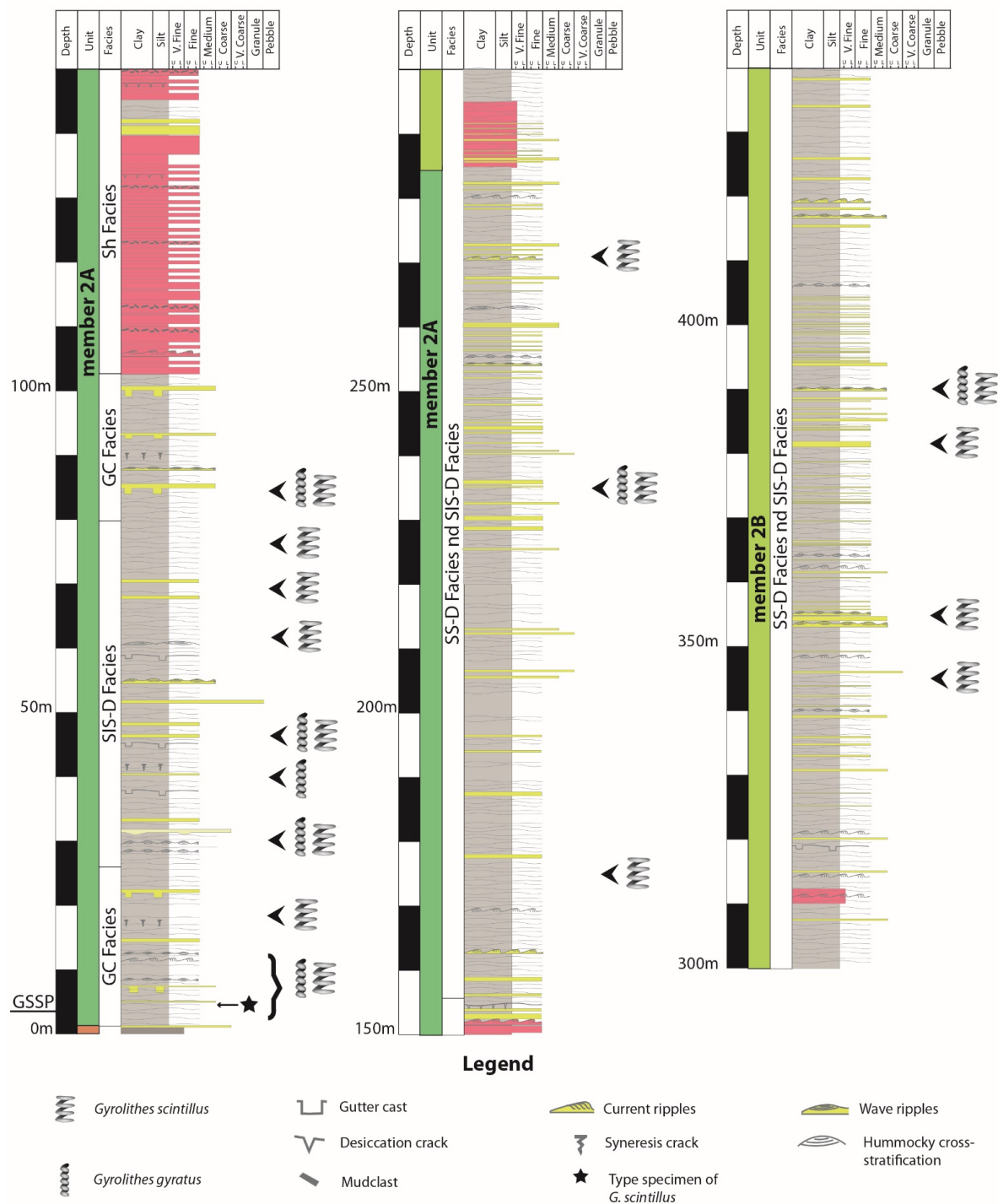
$$\tan\lambda=(R_1-R_2)/h_1 \dots\dots\dots (4.4)$$

For circular helices, $\tan\lambda$ is 0, and is not a useful parameter. In turn, β , while a useful term to describe circular helices, is not useful for conic helices. This results in three dimensionless parameters to describe circular helices (κ , δ , and β) and conic helices (κ , δ , and $\tan\lambda$) each. The relationship between these dimensionless parameters and the overall morphology of the burrow can be visualized with a computer-generated model of *Gyrolithes* (Figure 4.4). The surface of a helix with measured burrow radius (r), whorl radius (R_n), and inter-whorl height (h), is given by the parameterization:

$$\begin{aligned} x &= \left(r\cos\theta + R_1 - \frac{n\phi(R_1 - R_2)}{2\pi} \right) \cos(n\phi), \\ y &= \left(r\cos\theta + R_1 - \frac{n\phi(R_1 - R_2)}{2\pi} \right) \sin(n\phi), \text{ and} \\ z &= (R_1 - R_2) - \left(\frac{nh\phi}{2\pi} \right) + r\sin(\theta) \end{aligned}$$

Where n is the number of spirals, θ is the polar angle, and ϕ is the azimuthal angle where θ and ϕ are between 0 and 2π . When $R_1=R_2$, where $\tan\lambda=0$, the parameterization describes a circular helix. When $R_1 \neq R_2$ the parameterization describes a conical helix. This surface is modified from a parameterization of a seashell in von Seggern (2007). Since the parameters κ , δ , β , and $\tan\lambda$ are all ratios, they are independent of size, and instead describe the shape of the ichnofossil. As a result, they are pertinent ichnotaxobases (Bromley, 1990; Bertling et al., 2006), and present an effective method for distinguishing ichnospecies of *Gyrolithes*. The parameter κ incorporates the morphometric parameters used by Uchman and Hanken (2013) to differentiate ichnospecies, and should continue to be used as the primary parameter to distinguish ichnospecies of *Gyrolithes*.

Uchman and Hanken (2013) suggested three “lineages” of *Gyrolithes* ichnospecies based on the relationship between the burrow diameter ($2r$) and the whorl radius (R). The *davreuxi* “lineage” contains wide, proportional forms ratios are contained within the *krameri* “lineage”, and the *variabilis* “lineage” contains narrow forms. While these “lineages” are not true



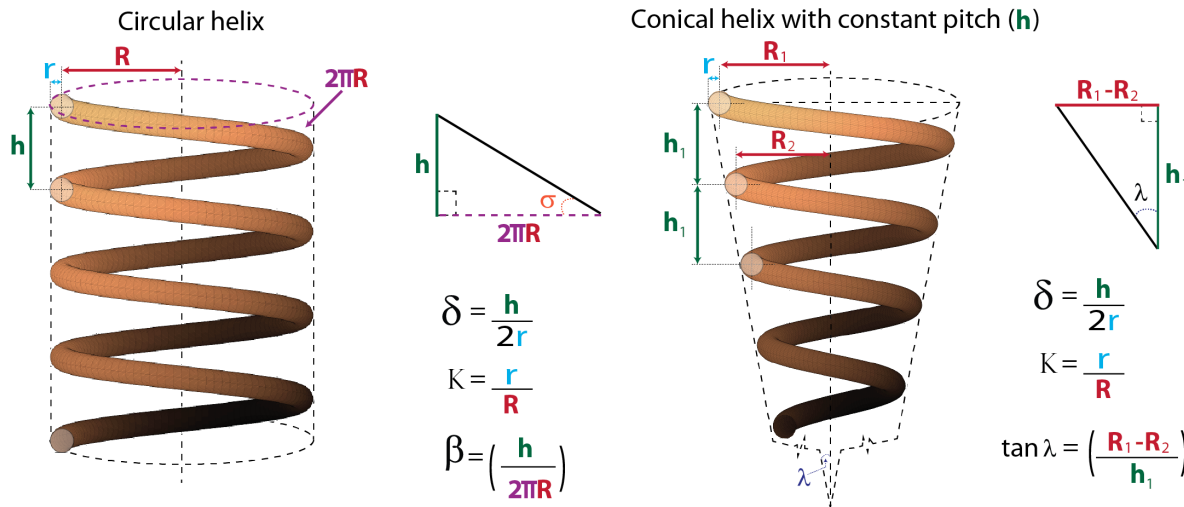


Figure 4.3 Left: a circular helix, with measured variables (r , R , and h) and dimensionless parameters (κ , δ , and β) annotated. Right: a conical helix with constant pitch (h), with measured variables (r , R , and h) and dimensionless parameters (κ , δ , and $\tan \lambda$) annotated.

evolutionary lineages (i.e., do not imply that the producers were phylogenetically related), they may provide information of the turning radius of the producer.

Jensen (1997) suggested all vertical spiral burrows should be synonymized under the ichnogenus *Gyrolithes*. Uchman and Hanken (2013) argued to retain the continental ichnogenus *Ichnogyrus* Bown and Kraus (1983). As a result, they added the phrase “...coils which are not in contact.” to the diagnosis of the ichnogenus *Gyrolithes* in order to retain *Ichnogyrus* as a separate ichnogenus. Compression or other taphonomic processes may cause the coils to appear in contact, when it may not have been originally the case. Where possible, these taphonomic overprints must be carefully evaluated and filtered out of the ichnotaxonomic classification. *Daimonhelix* a palaeocastor dwelling burrow restricted to the Oligocene to Miocene (Martin and Bennett, 1977), shows spacing between whorls and is characterized by very tight coils ($\kappa \cong 1$). However, additional architectural elements, such as an ascending or descending tunnels and a terminal chamber (Meyer, 1999), differentiates *Daimonhelix* from *Gyrolithes*.

In rare cases, vertical helical burrows have also been classified as *Skolithos* Haldeman, 1840 (Hofmann, 1979; Volohonsky et al., 2008), although some have suggested these may be better suited in *Gyrolithes* (Kim et al., 2005). With coiling absent from diagnoses of *Skolithos* (Alpert, 1974), it is not advisable to retain any helical burrows under this ichnogenus and doing so would only further compound taxonomic issues. It is herein suggested that all helical *Skolithos* be reassigned to *Gyrolithes* if $\delta > 1$ or *Ichnogyrus* if $\delta \leq 1$.

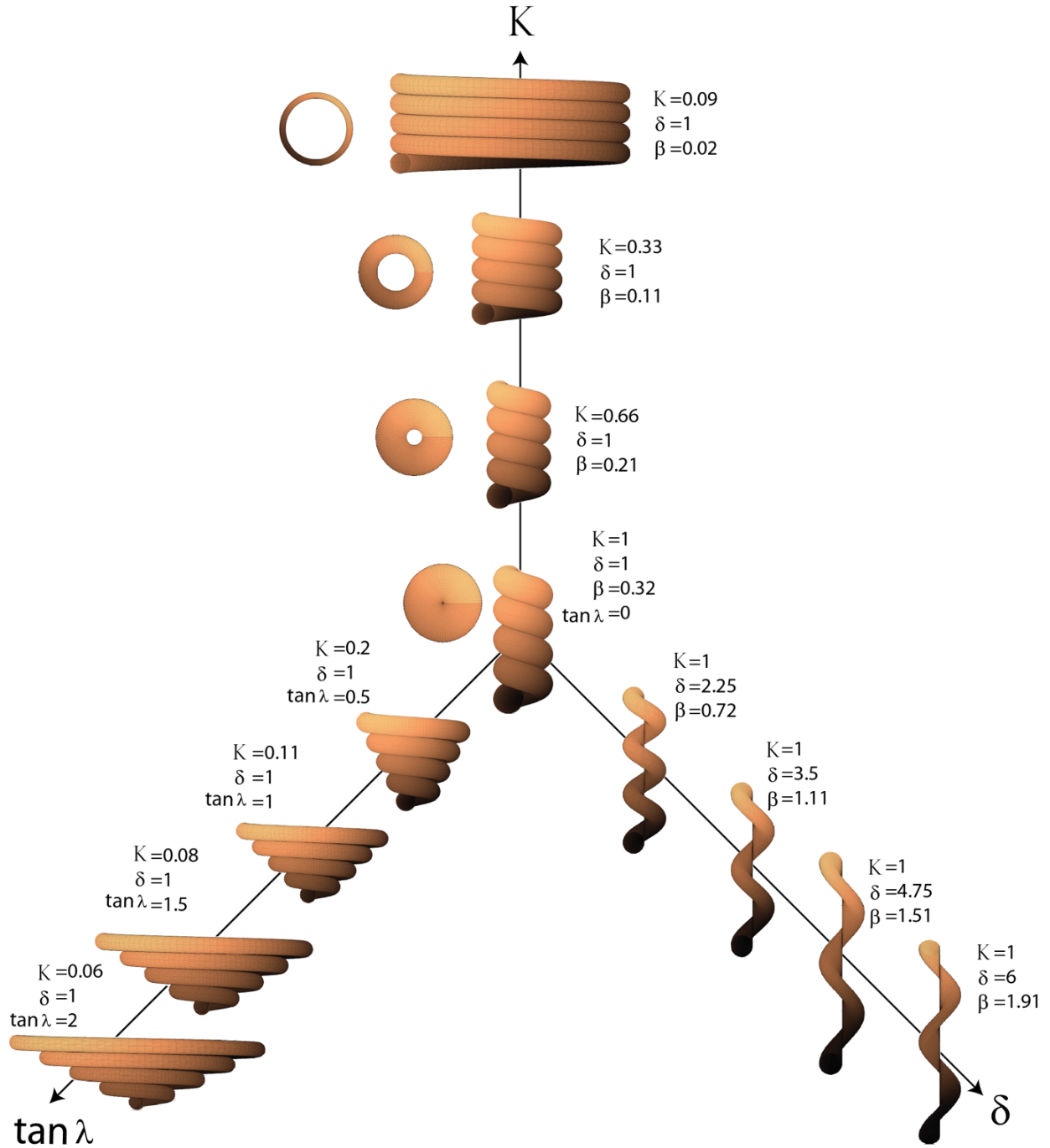


Figure 4.4 Computer-generated *Gyrolithes*, showing the morphological effects of changes in κ , δ , and $\tan \lambda$. β is related to κ and δ by the equation $\beta = \delta(\kappa/\pi)$.

***Gyrolithes scintillus* new ichnospecies**
Figures 4.5 A-C, E

- ? 1986 *Gyrolithes polonicus* Paczeńska, 1986, plate III, fig. 2, fig. 3.
? 1996 *Gyrolithes polonicus* Paczeńska, 1996, plate XII, fig. 1A, fig. 2.
1999 *Gyrolithes* isp. Jensen and Mens, 1999, p. 190, fig. 2, fig. 3.
? 2013 *Gyrolithes* Höglström et al., 2013, p. 102, fig. 5H.
2014 *Gyrolithes* isp. Tarhan and Droser, 2014, p. 318. fig. 9B.
2016 *Gyrolithes* isp. Mángano and Buatois, 2016, p. 90, fig. 3.9C.
2017 *Gyrolithes polonicus*: Herringshaw et al., p. 375, fig. 3B.

Etymology

From the Latin word scintillum (“spark”). An extension of the metaphor of the Cambrian explosion.

Material and holotype

24 specimens were photographed and measured in the field, and numerous field identifications were made. Field holotype is located in the Fortune Head Ecological Reserve (denoted by a star in Figure 4.1), 3.45 m above the base of member 2, and can be seen in Figure 4.5A.

Type horizon and location. — Siltstones and sandstones near the basal Cambrian Global Stratotype Section and Point at Fortune Head Newfoundland, 3.45 m above the base of member 2 of the Chapel Island Formation.

Diagnosis

Unlined, smooth, wide-form, variably coiled *Gyrolithes*. Low burrow radius to whorl radius ratio i.e., wide-form ($\kappa=0.1-0.4$; avg. 0.3), variable height between whorls to burrow width ratio i.e., variably coiled ($\delta=1.5-5.83$; avg. 3.58), and low height between whorls to whorl circumference ratio i.e., shallow whorl incline ($\beta=0.2-0.6$; avg. 0.3).

Description

Unbranched, passively infilled, circular helical burrows, oriented vertical to oblique to the bedding plane, consisting of coils which are not in contact. Burrows are circular in cross-section, with radii (r) ranging from 0.25-1 mm, with an average of 0.51 mm. Whorl radius (R) was measured from the middle of the burrow, and is 0.70-4.65 mm with an average of 2.10 mm. Height between whorls (h) ranged from 1.4-8 mm, with an average height of 3.69 mm.

Figure 4.5

Fortunian (earliest Cambrian) *Gyrolithes* at the Ediacaran-Cambrian GSSP. All photographs are taken perpendicular to bedding. All scale bars are 1 cm long. **(A)** Field holotype of *Gyrolithes scintillus*. Location of the specimen is denoted in Figure 4.1. **(B)** Oblique specimen of *Gyrolithes scintillus*, forming a compound burrow with *Palaeophycus* isp. **(C)** A smaller *Gyrolithes scintillus*, maintaining similar κ values. **(D)** *Gyrolithes gyratus*. **(E)** *Gyrolithes scintillus*, with 7 whorls present, penetrating 2 cm into the sediment. **(F)** Four specimens of *Gyrolithes gyratus*.



Figure 4.5 Caption on previous page.

Complete specimens show up to 7 whorls, with an average of 3 whorls. This average is likely biased towards smaller values, as several top whorls were possibly truncated by erosion. Two specimens (Figure 4.5 B) form compound burrows with *Palaeophycus*, extending from the bottommost helix. Burrow depth is 5-27.9 mm, with an average burrow depth of 10.44 mm. Assuming an originally circular burrow shape, the difference between burrow radius on the y and x axes can be equated to sedimentary compression, and was found to be 30%.

Remarks

Although recent workers have included these specimens in *G. polonicus* (e.g., Herringshaw et al., 2017), *Gyrolithes scintillus* has a higher number of whorls, and penetrates much deeper into the substrate than *G. polonicus*. Moreover, *G. polonicus* has κ values between 0.39 and 0.50, while *G. scintillus* averages at 0.26 (with a range of 0.11-0.40). This places *G. polonicus* within group 2, and *G. scintillus* within group 1. In multiple specimens where more than one whorl can be found with *G. polonicus*, the second whorl has a decreased whorl radius (e.g., Jensen, 1997 fig. 35 E), suggesting that it forms a conic helix shape. In contrast, the whorls in *G. scintillus* maintain a consistent radius, forming a circular helix shape. Additionally, *Gyrolithes polonicus* only has 2 to 3 whorls, whereas *G. scintillus* can have up to 9 whorls. Furthermore, *G. polonicus* has documented striations (Jensen, 1997; Uchman and Hanken, 2013). Despite excavation in a firmground, with exquisite preservation of very fine details (Droser et al., 2002; Buatois et al., 2014), *G. scintillus* does not show striations. In turn, *Gyrolithes lorcaensis* (Uchman and Hanken, 2013) also has much larger κ values (0.38-0.50) than *G. scintillus*.

Many Cambrian *Gyrolithes* have been classified only at ichnogeneric level as *Gyrolithes* isp. (Liñán, 1984; Jensen and Grant, 1998; Jensen and Mens, 1999; Högström et al., 2013). Many of these specimens share morphological traits with *G. scintillus* and may be better reassigned to this ichnospecies (e.g, Jensen and Mens, 1999; Högström et al., 2013). Some *Gyrolithes* previously classified as *G. polonicus* (Paczeńska, 1986, 1996) may be better classified as *G. scintillus*. We are unable to substantiate the *G. polonicus* documented at the GSSP by Gehling et al. (2001), based on the available photograph and the fact that the specimen has been apparently removed by coastal erosion.

***Gyrolithes gyratus* (Hofmann, 1979)**

Figure 4.5 (D, F), 4.6 (A), 4.8

*1979 *Skolithos gyratus* isp. nov.: Hofmann, 1979, pl. 15, A-E.

1987 *Skolithos annulatus*: Narbonne et al., p. 1287, fig. 6H.

2017 *Skolithos annulatus*: Herringshaw et al., p. 375, fig. 3A.

Material

Seven specimens photographed and measured in the field, plus numerous field identifications.

Location: Siltstones and sandstones of member 2 of the Chapel Island Formation, on the Burin Peninsula, Newfoundland. A *G. gyratus*-rich horizon is situated from 3-10 m above the base of member 2 at Fortune Head.

Diagnosis

Unlined, smooth, narrow-form, tightly coiled *Gyrolithes*. High burrow radius to whorl radius ratio i.e., narrow-form ($\kappa=0.5-1$; avg. 0.8), low height between whorls to burrow width ratio i.e., tightly coiled ($\delta=1.3-2.5$; avg. 1.6), and low height between whorls to whorl circumference ratio i.e., shallow whorl incline ($\beta=0.3-0.4$; avg. 0.4).

Description

Specimens are unbranched, passively infilled, circular helical burrows. They are oriented vertical to the bedding plane, and consist of coils which are variably in contact. Burrows are circular in cross-section, with radii (r) ranging from 0.2-0.38 mm, with an average radius of 0.27 mm. Whorl radius (R) is 0.25-0.4 mm with an average length of 0.34. Height between whorls (h) ranges between 0.5-1 mm, with an average height of 0.82 mm. Burrows have between 5 and 15 whorls, with an average of 10 whorls. Overall burrow depth ranges between 4 and 14.9 mm, with an average depth of 8.7 mm. Burrow (r) radius was measured along both the x and y axis when possible. Assuming an original circular cross-section, the difference between the y-axis and x-axis burrow radius can be attributed to compression, and an average compression ratio of 33% was calculated.

Remarks

Kim et al. (2005) reassigned *Skolithos gyratus* (Hofmann) to *Gyrolithes*, a decision endorsed here, since spiraling is absent from the definition of *Skolithos*. Vertical burrows at Fortune Head have previously been included in *Skolithos annulatus* (Howell) (Narbonne et al., 1987; Gehling

et al., 2001; Babcock et al., 2014; Herringshaw et al., 2017), but Mángano and Buatois (2016) have suggested that they may more properly belong in *Gyrolithes*. Our detailed study supports this, and it is herein proposed that they be reclassified to *Gyrolithes* as *G. gyratus*. *Gyrolithes gyratus* is unlike other *Gyrolithes* with its remarkable small size, high number of whorls, and large κ value. The helical nature of *G. gyratus* differentiates it from *Skolithos*. The variable presence of spacing between whorls ($\delta > 1$) distinguishes *G. gyratus* from *Ichnogyrus*, which consistently lacks spacing between whorls ($\delta \leq 1$). *Gyrolithes gyratus* is distinguished from *S. helicoidalis* (Volohonsky) by their δ values, as *S. helicoidalis* shows consistent spacing between whorls ($\delta > 1$).

In cross-section, *G. gyratus* appears as several oval-shaped segments nested one upon the other. The segments can be in contact with one another or separated (Figure 4.6). Three possible burrow morphologies that may account for this expression are envisioned: (1) a vertical burrow with a series of successive horizontal probes (A in Figure 4.6), (2) a compressed annulated vertical burrow, such as *Skolithos annulatus* (B in Figure 4.6), and (3) a small helical burrow (C in Figure 4.6). In the first case (A- a vertical burrow with horizontal probes), it would be expected that multiple other expressions of this burrow would be observed given its complex three-dimensional structure and the sheer volume of burrows observed. The absence of these expressions makes this explanation unlikely.

Previous authors considered these segments as the annulations of *Skolithos annulatus* (B in Figure 4.6). The annulations in *Skolithos annulatus* are horizontal “ring-like annulations” with minimal to absent expansion between them (Alpert, 1974) and in the holotype these annulations are irregularly spaced (Howell, 1957, p. 21, fig. 1). This is in stark contrast with the segments in *Gyrolithes gyratus*, which all have similar thicknesses and are evenly spaced. Given that these beds have been compressed by roughly 30%, it is possible to re-create what a hypothetical *Skolithos annulatus* might look like after compression at Fortune Head (Figure 4.7). Each segment in the compressed *Skolithos annulatus* is only very slightly more convex after compression. The resulting burrow would not show separated segments in cross-section, eliminating compression as evidence for the spacing between the segments in *G. gyratus* along with their high convexity.

The nested segments all maintain an internally consistent dip (Figure 4.8). One possible explanation for this could be that *S. annulatus* (B in Figure 4.6) buckled during compression,

preferentially bending upon the annulations (as an analogy, envision a corrugated tube being compressed). However, it is statistically unlikely that every segment would buckle in the same direction if force was applied from above. Directional stress may perhaps account for this phenomenon. However, the observation of two adjacent burrows with both dextrogyre (dextral) and levogyre (sinistral) patterns refutes this hypothesis (Figure 4.8). The observed morphology is, however, consistent with the compression of a helical burrow. Each whorl would originally be dipping in a similar direction within the same burrow, but not necessarily between two different burrows.

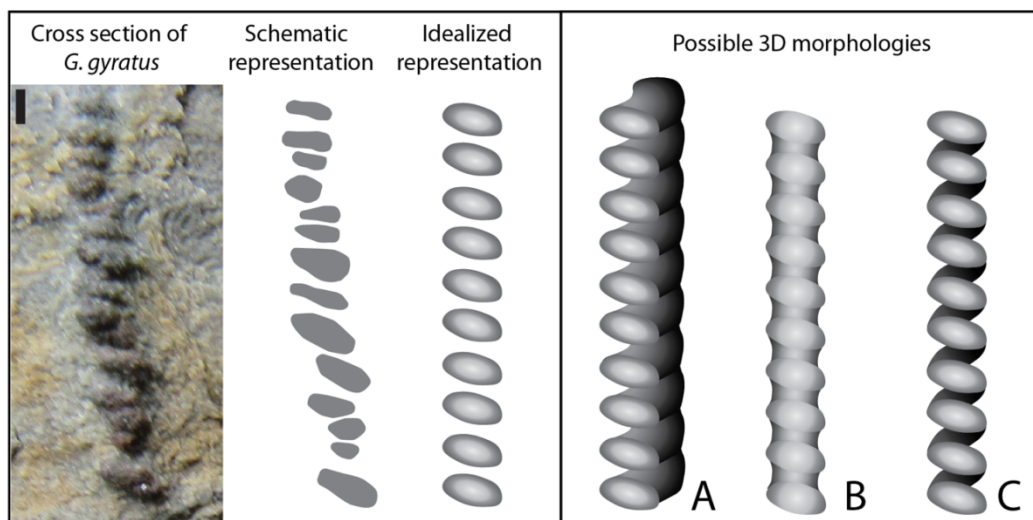


Figure 4.6. Left box: Field photo of *G. gyratus* [Specimen 18] with white line depicting burrow outline, viewed in cross-section. To the right is an idealized illustration of a cross section of *G. gyratus*, based upon field observations. Right box: Possible three-dimensional morphologies (A to C) which could result in the cross-section seen in the box to the left. (A) A vertical shaft with horizontal probes (B) A *Skolithos annulatus*, with directional stress compressing the burrow and inclining the annulations (C) The preferred interpretation as a small, tightly coiled *Gyrolithes*. See text for explanation.

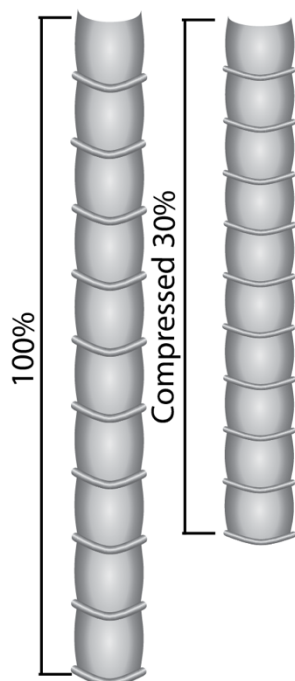


Figure 4.7. Illustration of the effect of local compression in the Chapel Island Formation on a hypothetical *Skolithos annulatus* modelled after the holotype shown in Howell (1957, p. 21, fig. 1).

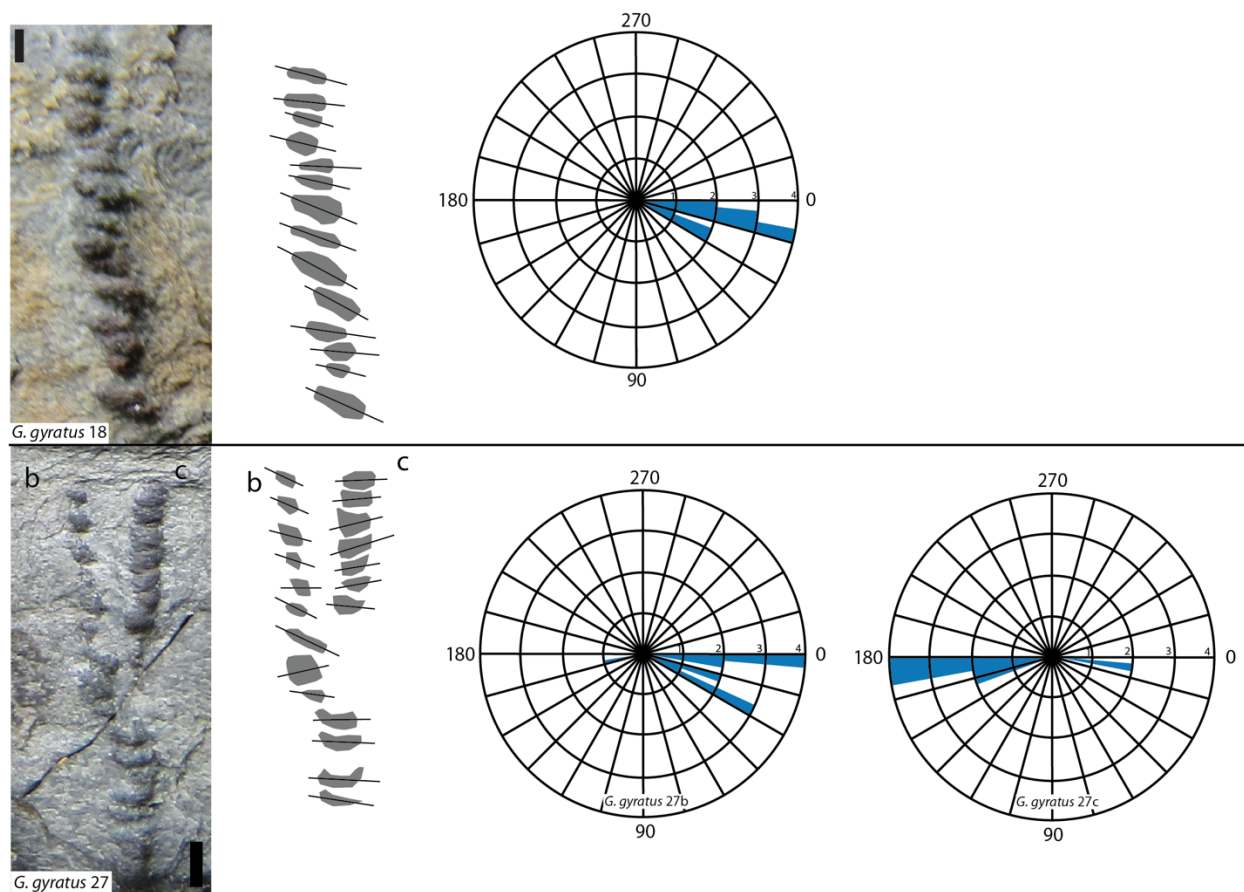


Figure 4.8. The dips of each whorl within three specimens of *G. gyratus*. From left to right: A field photographs of *G. gyratus*. Scale bar =1 mm. Sketches of the field photographs of *G. gyratus*, with dip ticks for each whorl superimposed. Dips were calculated from an imaginary horizontal plane striking right. A rose diagram, illustrating the strong trend seen in the dips of *G. gyratus*.

Table 4.1 Measured values (r , R , and h) and calculated parameters (κ , δ , and β) for the specimens of *G. gyratus* and *G. scintillus* used in this study. Specimen 2, outlined by a darker green infill, denotes the type specimen of *G. scintillus*. FH= Fortune Head, GBH= Grand Bank Head. Height measurements start two meters below the base of member 2, and match the stratigraphic column seen in Fig. 4.2.

<i>Gyrolithes</i> specimens on the Burin Peninsula, Newfoundland, Canada.										
Sample	Site	Height (m)	r	R	h	$K (r/R)$	$\delta (h/2*r)$	$\beta (h/(2*\pi*R))$	Depth	# of whorls
<i>Gyrolithes gyratus</i>										
18	FH	2.3	0.38	0.38	1	1	1.33	0.42	12	14
19b	FH	2.3	0.38	0.38		1			4.5	5
19d	FH	2.3	0.2	0.25	0.50	0.8	1.25	0.32	5	8
19e	FH	2.3	0.25	0.25		1			4	
27b	FH	2.3	0.2	0.4	1.00	0.50	2.50	0.40	14.9	14
27c	FH	2.3	0.25	0.35	0.90	0.71	1.80	0.41	5.8	7
37	FH	7.2	0.25	0.38	0.7	0.67	1.33	0.30	14.8	15
Average:			0.27	0.34	0.82	0.81	1.64	0.37	8.71	10.50
<i>Gyrolithes scintillus</i>										
2	FH	4.2	1	4.4	5.00	0.23	2.50	0.18	17	4
22a	FH	4.7	0.5	1.25		0.40				1
22b	FH	4.7	0.5	1.3	2.50	0.38	2.00	0.31	9.25	3
22c	FH	4.7	0.4	2	2.60	0.20	3.25	0.21	6.5	2
23	FH	5.3	0.5	1.3	4.6	0.38	4.6	0.56	5.5	2
15a	FH	5.3?	1	3	3.00	0.33	1.50	0.16	8.75	3
15b	FH	5.3?	0.45	2.9	5.25	0.16	5.83	0.29	10	3
4	FH	8.03	0.2	0.7	1.4	0.29	3.5	0.32	5.5	5
5	FH	8.05	0.4	1.35	2	0.30	2.5	0.24	5.1	3
3	FH	14.8	1	3	3.60	0.33	1.80	0.19	21	5
1a	FH	15	0.4	1.5	2.20	0.27	2.75	0.23	14	3
1b	FH	15	0.4	1.5	3.00	0.27	3.75	0.32		
31	FH	15.1	0.5	2.5	4.2	0.20	4.20	0.27	27.90	7.00
7a	FH	42	0.25	1		0.25			5.5	
7b	FH	42	0.25	1.25		0.20			5	
7c	FH	42	0.25	1.6		0.16			7.75	3
6	FH	51.7	0.6	4.65		0.13				1
11	FH	52	0.5	2	3.00	0.25	3.00	0.24	7.5	3
26	FH	unknown	0.75	2.25	8.00	0.33	5.33	0.57	15	2
9	FH	unknown	0.5	1.9	4.10	0.26	4.1	0.34	14	3
10	FH	unknown	0.35	1.4	4	0.25	5.71	0.45		
12	FH	unknown	0.3	2.75	3.50	0.11	5.83	0.20	10.5	3
13	FH	unknown	0.75	2.25	5	0.33	3.33	0.35	6.75	2
25	GBH	unknown	0.6	2.65	3.10	0.23	2.58	0.19	6.25	3
Average:			0.51	2.10	3.69	0.26	3.58	0.30	10.44	3.05

4.5. Discussion

4.5.1. Morphometric parameters of *Gyrolithes*

While the parameters κ , δ , β , and $\tan\lambda$ are valid ichnotaxobases for distinguishing and describing *Gyrolithes* ichnospecies, further refinement to this method is needed. First, there is ambiguity with respect to where the measurement of the whorl radius (R) ends. Some workers measure the radius from the center of the whorl to the inside of the burrow wall, some to the middle, and some to the end. This in turn affects the calculated parameters. It is suggested that all future whorl radius measurements are taken to the centre of the burrow (see Figure 4.3), as defined by Uchman and Hanken (2013) as well as De Renzi et al. (2017). Due to this the whorl radius (R) will always be greater than or equal to the burrow radius (r) and the range of all possible κ values is between 0 and 1.00.

Additionally, in order for this classification to function properly, it is imperative that future observations include burrow radius (r), whorl radius (R), and whorl height (h), for every specimen. Once this has been done, the dimensionless parameters can be calculated and averaged out. When the relationship between values for the burrow radius (r), whorl radius (R), and whorl height (h) are unknown, the values for κ , δ , β , and $\tan\lambda$ can only be inferred.

Unfortunately, previous studies typically expressed morphometric parameters as a range. In this study, it was assumed that the minimum value for burrow radius was found in the specimen with the minimum value for whorl radius, and likewise for maximum values. Possible κ values for all retained *Gyrolithes* ichnospecies were calculated following this assumption, and their ranges plotted (Figure 4.9)

Two artefacts of data collection can be seen, likely because κ values were inferred from given burrow and whorl radii ranges and not calculated on a per-specimen basis. First, there are two ichnospecies, *G. okinawensis* Myint and Noda, 2000 and *G. variabilis* Mayoral and Muñiz, 1995, which have κ values greater than one, and as such exceed the range of possible κ values. Second, the ranges of these same two ichnospecies are too wide to be properly usable as distinguishing features.

Similar to Uchman and Hanken's (2013) "lineages", the range of possible κ values can be easily divided into three groups (Figure 4.9). However, the ichnospecies included in these groups are in some cases drastically different from the Uchman and Hanken (2013) "lineages". This is

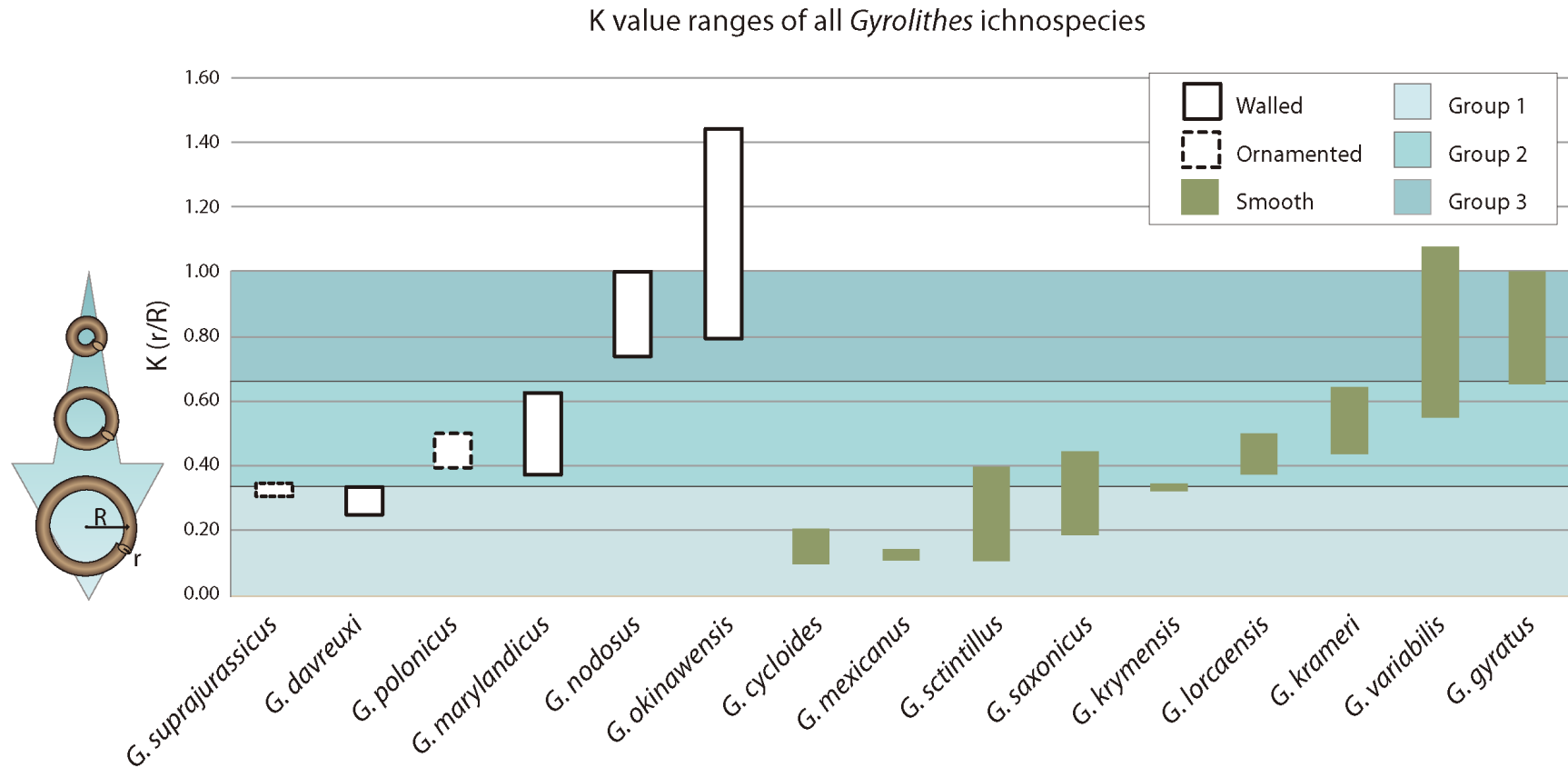


Figure 4.9 The ranges of κ values for all *Gyrolithes* ichnospecies. Smooth *Gyrolithes* are grouped into three groups recognized by Uchman and Hanken (2013). The first group contains ichnospecies which are loosely coiled, in theory corresponding with the *davreuxi* “lineage”. The second group contains ichnospecies which are moderately coiled, in theory corresponding with the *krameri* “lineage”. The third group are those with tight coils, in theory corresponding with the *variabilis* “lineage”.

especially evident in the groups with small κ values, group 1 herein and the *davreuxi* “lineage” in Uchman and Hanken (2013). The ichnospecies included in the *davreuxi* “lineage” of Uchman and Hanken (2013) maintain a similar burrow radius (roughly 3.5-7.5 mm) with a wide variety of whorl radius’ (roughly 11-65 mm). This in turn, gives them a wide variety of possible κ values, which do not necessarily coincide with an exceptionally small κ value. As a result, the *davreuxi* “lineage” is rather a “lineage” of similar burrow radii, rather than a grouping of similar κ values. This underscores the need for future work to include measurements of discrete values for κ , δ , β , and $\tan\lambda$ per specimen. As a result, the groups proposed herein may change with more detailed data collection.

Group 1 is proposed to encompass ichnospecies with κ values between 0 and 0.33, and Group 2 is proposed to include any ichnospecies with κ values between 0.33 and 0.66. Group 3 is proposed to encompass ichnospecies with κ values between 0.66 and 1.

These lineages co-occurred during the early Cambrian, with *G. scintillus* in group 1, *G. polonicus* in group 2, and *G. gyratus* in group 3, and are not herein suggested as evolutionary lineages. Rather, they are suggested as an additional means of distinguishing ichnospecies, and may prove useful when determining possible tracemakers or ethologies of *Gyrolithes* in the future.

There are cases where the range of κ values for an ichnospecies spans through the field of two groups. A producer may easily create a whorl larger than its turning radius. However, it may never create a whorl smaller than its turning radius. Therefore, the larger κ value better represents the turning radius of the producer, and the ichnospecies should be assigned to the lineage with the larger κ value.

4.5.2. Cambrian occurrences of *Gyrolithes*

The ichnogenus *Gyrolithes* is widespread across the lower Cambrian (Table 4.2), and may serve as a valuable tool to aid in the delineation of the Ediacaran-Cambrian boundary. While some Cambrian occurrences of *Gyrolithes* have been attributed to *G. polonicus* (Paczeńska, 1986, 1996; Jensen, 1997; Systra and Jensen, 2006), many authors have avoided ichnospecific classification (Liñán, 1984; Jensen and Grant, 1998; Jensen and Mens, 1999; Högström et al., 2013). A re-examination of the r:w ratio of Cambrian *Gyrolithes* yields possible additional specimens of *G.*

scintillus (Jensen and Mens, 1999; Höglström et al., 2013). Pickerill and Peel (1990) documented three poorly preserved specimens of *G. saxonicus* from Greenland. However, these are in need of re-examination. Here, they are tentatively classified as *G. polonicus* based on the incomplete whorl and presence of striations. Jensen (1997) suggested that *Gyrolithes* isp found from southwestern Spain (Liñán, 1984) is better classified as *G. polonicus*, a decision endorsed here on the basis of the specimen's κ value

4.5.3. Tracemaker

The majority of Permian to Recent *Gyrolithes* were likely produced by decapod crustaceans (Uchman and Hanken, 2013), an interpretation supported by their common intergradation with galleries typically produced by decapod crustaceans, such as *Thalassinoides*, *Ophiomorpha*, and *Spongeliomorpha* (Bromley and Frey, 1974). Cambrian *Gyrolithes* considerably predate the evolution of decapod crustaceans, which first appeared in the Late Devonian (Schram, 1981) but became abundant only as a result of the Mesozoic Marine Revolution (Buatois et al., 2016). Rather, they were likely produced by a coelomate worm-like organism. One possibility is a polychaete worm tracemaker (Powell, 1977), an interpretation that probably applies to their horizontal equivalents *Helicodromites* and *Helicolithus* (Gingras et al., 2008; Knaust and Bromley, 2013). Horizontal to oblique corkscrew burrows exhibiting small width (0.5-1.1 cm) and whorl radius (0.9-2.0 cm) are produced by the capitellid polychaete *Notomastus lobatus* in modern shallow-marine sediments (Powell, 1977). Alternatively, Van der Horst (1934, 1940) described helical burrows formed by the enteropneust *Saccoglossus inhacensis* in a tidal flat on the island of Inhaca, Mozambique. These helical burrows are mostly vertical to sub-vertical, but may in some cases create horizontal helices (Van der Horst 1940). They reach a maximum depth of 7cm with burrow diameters between 0.1-0.2 cm, and the specimens figured by Van der Horst (1934) have κ values between 0.40 and 0.44. Due to their overall small size, Powell (1977) dismissed enteropneusts as the tracemaker of *Gyrolithes*. However, *G. scintillus* and *G. gyratus* are the smallest *Gyrolithes* discovered to date, and are similar in size to the helical burrows of *Saccoglossus inhacensis*. The oldest enteropneust fossils likely come from the Burgess Shale (508 Ma) (Conway Morris, 1979; Boulter, 2003; Caron et al. 2013), although due to their low preservation potential, an earlier evolutionary origin of enteropneusts can not be dismissed (Maletz, 2014). Additionally, recent estimates (Hedges and Kumar, 2009, p. 71) placed the

Table 4.2 Summary of recorded Cambrian *Gyrolithes* occurrences.

Period	Stratigraphy	Location	Ichnospecies	Reference
Stage 4	Mickwitzia Sandstone Member, File Haidar Fm.	Västergötland, South Central Sweden	<i>G. polonicus</i>	Jensen (1997)
Stage 3	Bastion Fm.	northeast Greenland	? <i>G. polonicus</i> (<i>G. saxonicus</i> in original study)	Cowie and Spencer (1970); Pickerill and Peel (1990)
	Kaplonosy Fm.	Southern Lublin region southeastern Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
	Radzyń Fm.	Southern Lublin region southeaster Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
	Member 3, Arumbera Fm.	Amadeus Basin, Central Australia.	? <i>G. polonicus</i> (<i>G. polonicus</i> in original study)	Walter et al. (1989); Baghiyan-Yazd (1998)
	Bastion Fm.	northeast Greenland	? <i>G. polonicus</i> (<i>G. saxonicus</i> in original study)	Cowie and Spencer (1970); Pickerill and Peel (1990)
Stage 2	Kaplonosy Fm.	Southern Lublin region southeastern Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
	Radzyń Fm.	Southern Lublin region southeaster Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
	Taebila Member, Voosi Fm.	eastern Latvia and western Estonia	<i>G. scintillus</i> (<i>G. isp.</i> in original study)	Jensen and Mens (1999) ; Jensen and Mens (2001)
	Lower Breidvika and Manndrapselva Members, Vestertana Group	northeastern Finnmark, northern Norway	<i>G. scintillus</i> (<i>G. isp.</i> in original study)	Banks (1970); Högström et al. (2013) ; Jensen et al. (2017)
Fortunian	Lower interval, Dividalen Group	East of Kilpisjärvi, Northern Finland	<i>G. polonicus</i>	Systra and Jensen (2006)
	Lower Siltstone Member, Torneträsk Formation, Dividalen Group	Torneträsk area, northern Sweden	<i>G. isp.</i>	Jensen and Grant (1998)
	Upper interval, Maiva Member, Sävovare Fm.	Laisvall-Storuman area, Northern Sweden	<i>G. isp.</i>	Moczydlowska et al. (2001)
	Mazowsze Fm.	Southern Lublin region, southeastern Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1985, 1986, 1996)
	Chapel Island Fm.	Burin Peninsula, Newfoundland, Canada.	<i>G. scintillus</i> and <i>G. gyratus</i>	Narbonne et al. (1987) , Tarhan and Droser (2014) , Mángano and Buatois (2016) , Herringshaw et al. (2017) .

**Bolded sources contain a photograph of Gyrolithes. These photographs were used to reassess the ichnospecific determination of the specimens.

divergence of polychaetes at 581 Ma, consistent with the Early Cambrian age of the Fortune Head *Gyrolithes*.

In short, available information collectively implies that a worm-like organism, possibly a polychaete, enteropneust, or some other unknown affinity, was the most likely producer of the Fortune Head *Gyrolithes*.

4.5.4. Ethology

Gyrolithes has been assigned various ethologies, including feeding, dwelling, and farming burrows. In both decapod crustacean- and polychaete-produced burrows it has been suggested that *Gyrolithes* acted as a feeding burrow (Fodinichnia), spiraling to profit from nutrient rich localized infaunal areas (Netto et al., 2007; Gingras et al., 2008). However, this ethology is unlikely for the Fortune Head *Gyrolithes* — they show no evidence of active infill or fecal pellets.

The most common ethology assigned to *Gyrolithes* is that of stable structures that served as domiciles to protect their inhabitants (Domichnia). The Fortune Head *Gyrolithes*, as open burrows passively infilled from above, make good candidates for dwelling burrows (Bromley, 1990; Buatois and Mángano, 2011). It has also been suggested that both *Gyrolithes* and *Helicodromites* burrows functioned as bacterial farming structures (Agrichnia), spiraling to increase the sediment to burrow margin ratio (Felder, 2001; Netto et al., 2007; Poschmann, 2015). The Fortune Head *Gyrolithes* also share many features with typical agrichnial burrows, as they were open and later cast by the overlying sand layer (Seilacher, 1977; Bromley, 1990; Buatois and Mángano, 2011). In order to determine if the Fortune Head *Gyrolithes* are dwelling or farming burrows, the behaviour of the organism (the reason it spiraled) must be investigated.

Most post-Permian *Gyrolithes* burrows occur in marginal marine environments (Gernant, 1972; Powell, 1977; Beynon et al., 1988; Buatois et al., 2005; Netto et al., 2007). This has led many authors to suggest that the spiral morphology of *Gyrolithes* helps in mitigating salinity fluctuations (Beynon and Pemberton, 1992; Netto et al., 2007). While deep infaunalization has been shown to protect the tracemaker from salinity fluctuations (Rhoads, 1975), it is unclear why a helical morphology would provide an advantage. In fact, spiraling in post-Permian *Gyrolithes* may simply be an artefact of a decapod crustacean producer, serving as a ramp to aid the trace-maker to crawl up and down (Felder, 2001). In contrast, Cambrian *Gyrolithes* have been reported

from normal marine settings and in Fortune Head this ichnotaxon occurs within a wave-dominated shelf. Therefore, it is unlikely that the Fortune Head *Gyrolithes* spirals are a result of salinity fluctuations.

It has also been proposed that the helical morphology is a response to high-population densities (Gingras et al., 2008). This is also an unlikely cause for the Fortune Head *Gyrolithes*, given that the burrows are relatively sparse.

If interpreted as a dwelling burrow, the helical morphology could serve as an in-sediment anchor (Gingras et al., 2008), protecting the burrower from fast currents as well as predation (Felder, 2001). This is consistent with the Fortune Head *Gyrolithes*, which occur in sediments with abundant erosional and wave-generated structures (Myrow, 1992).

Farming burrows imply that the organism inhabiting the structure used it at the same time to cultivate bacteria (Bromley, 1990). As a farming burrow, the spiral morphology in *Gyrolithes* could serve to maximize the burrow margin area (Felder, 2001; Poschmann, 2015), providing a sharp redox gradient across the burrow boundary, facilitating bacterial gardening. While there is discussion about the amount of dissolved oxygen in Cambrian oceans (Sperling et al., 2013) it is generally accepted that the sediments were strongly oxygen-stratified. Matgrounds most likely effectively sealed the sediment-water interface and in turn created highly reducing sediments (Seilacher, 1999; Callow and Brasier, 2009; Boyle et al., 2014; Mángano and Buatois, 2014). Open burrows connected to the sediment water interface would create ideal redox conditions in their (Aller and Aller, 1998), to attract bacteria which the *Gyrolithes* organism could then use as a source of food (Papasprou et al., 2006). This is not unusual behaviour in polychaetes; neoichnological work shows bacterial farming within the burrow of *Arenicola marina* (Grossmann and Reichardt, 1991; Kristensen, 2005). In turn, enteropneusts filter out microbes from consumed sediment (Dobbs and Guckert, 1988).

Therefore, based on available evidence the most plausible scenario for the Fortune Head *Gyrolithes* is that they functioned as a protective, permanent domicile with the main purpose of farming bacteria. The helical morphology would serve a double purpose: as a sediment holdfast in a high-energy environment, and as an optimal shape for maximizing surface area for bacterial gardening.

4.5.5. Onshore-offshore trends

The interpretation of Cambrian *Gyrolithes* from Fortune Head as dwelling structures produced to cultivate bacteria is consistent with the onshore-offshore model. According to this model, the fossil record exhibits a pattern of onshore origination of evolutionary innovations and their later expansion to deeper water (e.g., Jablonski et al., 1983; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). This pattern has been recognized in the trace-fossil record as well (Seilacher, 1986; Bottjer et al., 1988; Droser and Bottjer, 1989; Buatois and Mángano, 2016). No onshore-offshore trend has been identified for the ichnogenus *Gyrolithes*, which is essentially a shallow-marine ichnotaxon. However, graphoglyptids, the archetypal trace fossils displaying farming strategies, occurred in shallow water in the early Cambrian, but later migrated to the deep sea (Crimes and Anderson, 1985; Jensen and Mens, 1999). Because farming strategies are typical of food-depleted settings, it has been suggested that their onshore-offshore pattern may reflect limited food supply in early Cambrian shallow-marine ecosystems (Buatois and Mángano, 2003). The farming strategy of the *Gyrolithes* tracemaker may be interpreted within this framework. Interestingly, at least in one of these Cambrian occurrences *Gyrolithes* is associated with the graphoglyptid *Dendroraphe* (Jensen and Mens, 1999).

4.5.6. *Gyrolithes* and the Cambrian explosion

Because the base of the *Treptichnus pedum* Zone is used to delineate the base of the Cambrian Period, most attention in the Ediacaran-Cambrian ichnologic literature has focused on this ichnotaxon (e.g., Vannier et al., 2010; Buatois et al., 2013; Buatois, 2017). The significance of *T. pedum* relies on the fact that this ichnospecies represents the onset of complex and systematic burrowing patterns allowing the exploitation of the infaunal ecospace. Whereas Ediacaran ichnofaunas are overwhelmingly dominated by simple and non-specialized, superficial or very shallow-tier grazing trails, the onset of the Cambrian is characterized by the appearance of more sophisticated burrows recording a diverse set of producers that show the ability of the benthos to penetrate into the sediment (e.g., Seilacher, 1999; Jensen, 2003; Vannier et al., 2010; Buatois et al., 2014; Buatois and Mángano, 2016; Mángano and Buatois, 2014, 2016).

In this regard, *Gyrolithes scintillus* and *G. gyratus* are typical representatives of the Cambrian explosion. In fact, whereas *T. pedum* is a horizontal burrow with obliquely oriented branches, the Fortunian ichnospecies of *Gyrolithes* are true vertical burrows. Given their

stratigraphic occurrence at and immediately above the Ediacaran-Cambrian boundary, they represent the earliest vertical burrows recorded to date.

4.6. Conclusions

Cambrian *Gyrolithes* have previously been regarded as shallow burrows restricted to one ichnospecies of dwelling burrow, *Gyrolithes polonicus*. Research at the Ediacaran-Cambrian GSSP at Fortune Head shows two ichnospecies of *Gyrolithes*: *G. scintillus* n. isp and *G. gyratus* (Hofmann). These ichnospecies illustrate a more diverse assemblage of Cambrian *Gyrolithes*, which penetrate deeper into the substrate and may represent a wider variety of ethologies than previously thought. These ichnospecies occur concurrent with the appearance of *T. pedum* in the section, and represent the first true vertical burrowing (up to 2.8 cm in depth) in the very earliest Fortunian. This study underscores the need for a detailed re-examination of all other *T. pedum* IAZ components, in order to evaluate the factors promoting infaunalization during the Cambrian explosion.

- (1) The ichnofossil previously described as *Gyrolithes. isp* or *G. polonicus* at the GSSP has been reassigned to the new ichnospecies *G. scintillus*. This encompasses passively infilled, vertical helical burrows, with an average κ (r/R) value of 0.26.
- (2) The ichnofossil previously described as *Skolithos annulatus* at the GSSP is reassigned to *Gyrolithes gyratus* as it shows a distinct helical morphology.
- (3) The revised morphometric parameters of Uchman and Hanken (2013) and De Renzi et al. (2017) are sufficiently robust to include all vertical spiral burrows. Uchman and Hanken's (2013) "lineages" are slightly revised as groups, and assigned specific κ value ranges: group 1 for those *Gyrolithes* where $0 < \kappa < 0.33$; group 2 for those *Gyrolithes* where $0.33 < \kappa < 0.66$; and group 3 for those *Gyrolithes* where $0.66 < \kappa < 1$.
- (4) In addition to serving as a protective domicile, burrows may have provided a strong redox gradient, facilitating bacterial gardening. This suggests that Cambrian shallow marine settings may have been relatively nutrient deficient, which aligns with the onshore-offshore model proposed for graphoglyptids (agricrinal burrows).
- (5) *Gyrolithes scintillus* and *G. gyratus* represent some of the earliest true vertical burrows in Earth evolution. As constituents of the *T. pedum* IAZ, *G. scintillus* and *G. gyratus* aid in

documenting the onset of the Cambrian explosion. They may serve as useful biostratigraphic guides for the base of the Cambrian.

4.7. Acknowledgments

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CHAPTER 5

5. Conclusions

A redefinition of the *Treptichnus pedum* Ichnofossil Assemblage Zone in the Chapel Island Formation was achieved through a thorough systematic study of observed ichnofauna, and the creation of ichnologic sections. Possible modes of life for the ichnofauna were researched and hypothesized upon, allowing for an analysis of ecospace utilization in the section to be conducted.

In total twenty ichnospecies were documented: *Archaeonassa fossulata*, *Bergaueria* isp., *Bergaueria perata*, *Cochlichnus anguineus*, *Conichnus conicus*, *Dimorphichnus* cf. *obliquus*, *Gordia* isp., *Gyrolithes gyratus*, *Gyrolithes scintillus*, *Helminthoidichnites tenuis*, *Helminthopsis tenuis*, *Monomorphichnus* isp. A, *Monomorphichnus* isp. B, *Monomorphichnus* isp. C, *Palaeophycus* isp., *Palaeophycus tubularis*, *Treptichnus coronatum*, *Treptichnus* isp., *Treptichnus pedum*, and *Trichichnus* cf. *simplex*. This corresponds to an ichnodiversity of thirteen. Seven categories of architectural design (ichnodisparity) were recorded: simple horizontal burrows, plug-shaped burrows, passively filled horizontal to oblique burrows, horizontal burrows with horizontal to vertical branches, vertical helical burrows, and trackways and scratch marks.

A few ichnofauna documented by previous studies were either reassigned or not observed. Uncontroversial specimens of *Curvolithus*, *Didymaulichnus*, *Phycodes*, or *Psammichnites* were not found within the *T. pedum* IAZ. It is hypothesized that many *Palaeophycus* were misclassified as *Planolites*, and many treptichnids misclassified as *Arenicolites*. In turn, *Skolithos annulatus* has been reassigned to *Gyrolithes gyratus*.

From hypothesized modes of life, five ichnoguilds were erected. The *Bergaueria* isp. ichnoguild is characterized by semi-infaunal to very shallow infaunal, attached facultatively motile predators. The *Dimorphichnus* cf. *obliquus* ichnoguild contains surficial, fast, fully motile grazers, predators, or surficial detritus feeders. The *Gyrolithes scintillus* ichnoguild consists of very shallow tier, slow fully motile organisms that use non-conventional feeding styles (other) such as chemosynthesis or microbial gardening. The *Helminthoidichnites tenuis* ichnoguild

includes semi-infaunal, slow, fully motile grazers. Finally, the *Treptichnus pedum* ichnoguild comprises very shallow tier, slow, fully motile organisms, with suspension, mining, or predatory feeding styles.

In this body- fossil poor interval, the *T. pedum* IAZ in the CIF illustrates a transitional period in Earth's history, between the Ediacaran and Cambrian faunas. This is observed through the ichnoguild and ecospace analysis conducted in this study. Ediacaran modes of feeding persisted into the lowermost Fortunian, such as chemosynthesis and mat-grazing, documented by the *Gyrolithes scintillus* and *Helminthoidichnites tenuis* ichnoguilds respectively. More modern feeding styles appear, such as predation and deposit-feeding, represented by the *Bergaueria* isp, *Dimorphichnus* cf. *obliquus*, and *Treptichnus pedum* ichnoguilds. While shallow-tier ichnofauna persist (*H. tenuis* ichnoguild), burrowers begin to penetrate deeper into the substrate than previously recorded. This is represented first by the *T. pedum* ichnoguild, then by the even deeper *G. scintillus* ichnoguild. Finally, the appearance of the *Dimorphichnus* cf. *obliquus* ichnoguild signifies the appearance of fast fully motile organisms, likely primitive arthropods, and may represent the first documented evidence of arthropods.

This transitional period is exemplified by the trace fossils *Gyrolithes scintillus* and *Gyrolithes gyratus*. These vertical, helical burrows penetrate up to 3 cm into the substrate, and are hypothesized to profit from the strong redox gradient between their burrow walls and the sediment to farm bacteria. In addition, morphological analysis of the ichnogenus allowed for revised morphometric parameters, as well as a 3D digitization of the ichnogenus to be constructed. Through the implementation of these revised morphometric parameters, the novel ichnospecies *G. scintillus* was erected. In turn, *Skolithos annulatus* from the CIF was shown to have a helical nature, and re-assigned to *Gyrolithes gyratus*.

This study demonstrates that a careful analysis of ichnotaxa may yield important information regarding modes of life and evolutionary innovations, especially in periods or facies that are body fossil poor. Through the study and correlation of ichnofauna in Fortunian sections worldwide, a more complete image of innovations surrounding the Ediacaran-Cambrian boundary may be achieved. Additionally, this study emphasizes the importance of re-evaluating ichnotaxonomic determination worldwide, which in turn may yield a more robust *T. pedum* IAZ. This may aid in mitigating some of the issues researchers are facing in correlation. Possible

members of a global *T. pedum* IAZ include *Dimorphichnus*, *Gyrolithes*, *Monomorphichnus*, *Treptichnus* and *Trichichnus*.

The revision of the ichnotaxonomy of the CIF *T. pedum* IAZ has revealed several novel modes of interacting with the seafloor and reflect the evolutionary innovations characteristic of the Cambrian. Deeper, penetrative burrows (*Gyrolithes*, *Treptichnus*, and *Trichichnus*) reflect the Cambrian Substrate Revolution, documenting the transition from Ediacaran matgrounds to Cambrian mixgrounds. Meanwhile, arthropod scratch marks such as *Dimorphichnus* cf. *obliquus* and *Monomorphichnus* reflect the evolution of novel body plans and their interaction with the substrate. The ichnofauna of the CIF *T. pedum* IAZ document pivotal information which is uncaptured by the body fossil record, and demonstrates a more transitional nature of the Ediacaran and Cambrian boundary.

CHAPTER 6

6. Appendix

Appendix A Global occurrences of *T. pedum* IAZ ichnotaxa between 635 Ma and 521 Ma.

Max. age (Ma)	Min. age (Ma)	Ichnotaxon	Reference; Original reference	Unit	Country
ARCHAEONASSA					
635	541	<i>Archaeonassa fossulata</i>	Buatois & Mángano (unpub); Narbonne & Aitken (1990)	Blueflower	Canada
635	541	<i>Archaeonassa</i> isp.	Carbone & Narbonne (2014)	Ingta	Canada
635	541	<i>Archaeonassa</i> isp.	Hofmann & Mountjoy (2010)	Upper Miette	Canada
556	541	<i>Archaeonassa fossulata</i>	Jenkins (1995) and Glaessner (1969)	Rawnsley Quartzite	Australia
550	541	<i>Archaeonassa</i> isp.	Crimes & Germs (1982)	Vingerbreek	Namibia
541	529	<i>Archaeonassa fossulata</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Archaeonassa fossulata</i>	Buatois & Mángano (unpub); Germs (1972)	Zamnarib	Namibia
529	521	<i>Archaeonassa fossulata</i>	Buatois & Mángano (unpub); Liñán (1984)	Julia	Spain
529	521	<i>Archaeonassa</i> isp.	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Archaeonassa</i> isp.	Buatois & Mángano (unpub); Li & Yang (1988)	Shiyantou	China
BERGAUERIA					
635	541	<i>Bergaueria</i> isp.	Zhu (1997)	Xiaowaitoushan	China
635	541	<i>Bergaueria sucta</i>	Menon et al. (2013)	Fermeuse	Canada
635	541	<i>Bergaueria</i> isp.	Grazhdankin & Krayushkin (2007)	Verhovka and Erga	Russia
541	529	<i>Bergaueria</i> isp.	Crimes & Anderson (1985)	Chapel Island M2	Canada
541	529	<i>Bergaueria</i> isp.	Buatois & Mángano (unpub); McIlroy & Brasier (2017)	Lower Breivik	Norway
541	529	<i>Bergaueria langi</i>	Fernandez-Remolar et al. (2005)	Upper Ibor	Spain
541	529	<i>Bergaueria perata</i>	Jensen & Grant (1998)	Tornetrask Lower Siltstone	Sweden
541	521	<i>Bergaueria</i> isp.	Pacześna (1996)	Mazowsze	Poland
529	521	<i>Bergaueria</i> isp.	Weber et al. (2007)	Shiyantou	China
529	521	<i>Bergaueria</i> isp.	Mángano et al. (2000); Liñán (1984)	Julia	Spain

COCHLICHNUS					
541	529	<i>Cochlichnus anguineus</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Cochlichnus anguineus</i>	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Cochlichnus anguineus</i>	Crimes & Anderson (1985)	Chapel Island member 2	Canada
541	529	<i>Cochlichnus anguineus</i>	Buatois & Mángano (unpub); MacNaughton & Narbonne (1999)	Upper Ingta	Canada
541	529	<i>Cochlichnus anguineus</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	529	<i>Cochlichnus anguineus</i>	Banks (1970)	Lower Breivik	Norway
541	529	<i>Cochlichnus</i> isp.	Farmer et al. (1992)	Lower Breivik	Norway
541	529	<i>Cochlichnus</i> isp.	Liñán (1984)	Tierna	Spain
541	521	<i>Cochlichnus anguineus</i>	Shahkarami et al. (2017)	Soltanieh	Iran
529	521	<i>Cochlichnus anguineus</i>	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Cochlichnus anguineus</i>	Goldring & Jensen (1996)	Bayan Gol	Mongolia
529	521	<i>Cochlichnus</i> isp.	Liñán (1984)	Julia	Spain
CONICHNUS					
547	541	<i>Conichnus</i> isp.	Darroch et al. (2016)	Unnamed Schwarzrand	Namibia
541	529	<i>Conichnus conicus</i>	Narbonne et al. (1987)	Chapel Island	Canada
529	521	<i>Conichnus</i> isp.	Hiscott et al. (1984)	L'Anse-au-Clair	Canada
DIMORPHICHNUS					
541	529	<i>Dimorphichnus</i> isp.	Parcha & Singh (2010)	Phe	India
541	529	<i>Dimorphichnus</i> isp.	McIlroy & Brasier (2017)	Lower Breivik	Norway

GORDIA					
635	541	<i>Gordia arcuata</i>	Vidal et al. (1994)	Estenilla	Spain
635	541	<i>Gordia</i> isp.	Vidal et al. (1994)	Estenilla	Spain
635	541	<i>Gordia marina</i>	Vidal et al. (1994)	Estenilla	Spain
635	541	<i>Gordia marina</i>	Narbonne & Hofmann (1987)	Siltstone Unit 1	Canada
556	541	<i>Gordia marina</i>	Glaessner (1969)	Rawnsley Quartzite	Australia
551	541	<i>Gordia</i> isp.	Crimes & Anderson (1985)	Chapel Island member 1	Canada
541	529	<i>Gordia arcuata</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	529	<i>Gordia marina</i>	Crimes & Anderson (1985)	Chapel Island member 2	Canada
541	529	<i>Gordia</i> isp.	Geyer & Uchman (1995)	Rosenhof	Namibia
541	529	<i>Gordia</i> isp.	Geyer & Uchman (1995)	Rosenhof	Namibia
541	521	<i>Gordia marina</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	521	<i>Gordia</i> isp.	Weber et al. (2013)	Chulaktau	Kazakhstan
529	521	<i>Gordia</i> isp.	Liñán (1984)	Julia	Spain
529	521	<i>Gordia marina</i>	Crimes & Anderson (1985)	Random	Canada
GYROLITHES					
541	529	<i>Gyrolithes</i> isp.	Farmer et al. (1992)	Lower Breivik	Norway
541	529	<i>Gyrolithes</i> isp.	Jensen & Grant (1998)	Tornetrask Lower Siltstone	Sweden
541	529	<i>Gyrolithes</i> isp.	Moczydłowska et al. (2001)	Upper Maiva	Sweden
541	529	<i>Gyrolithes polonicus</i>	Crimes & Anderson (1985)	Chapel Island member 2	Canada
541	529	<i>Gyrolithes polonicus</i>	Systra & Jensen (2006)	Dividalen	Finland
541	529	<i>Gyrolithes polonicus</i>	Buatois & Mángano (unpub); McIlroy & Brasier (2017)	Lower Breivik	Norway
541	529	<i>Gyrolithes scintillus</i>	Laing et al. (2018); Gehling et al. (2001)	Chapel Island	Canada
541	529	<i>Gyrolithes scintillus</i>	Laing et al. (2018); Jensen & Mens (1999)	Lontova	Latvia
541	529	<i>Gyrolithes gyratus</i>	Laing et al. (2018); Gehling et al. (2001); Narbonne et al. (1987)	Chapel Island member 2	Canada
541	521	<i>Gyrolithes scintillus</i>	Laing et al. (2018); Banks (1970)	Upper Breivik	Norway
541	521	<i>Gyrolithes scintillus</i>	Laing et al. (2018); Paczeńska (1996)	Mazowsze	Poland
529	521	<i>Gyrolithes</i> isp.	Liñán (1984)	Julia	Spain

HELMINTHOIDICHNITES					
635	541	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (unpub); Kowalski (1987)	Brzegi Shale	Poland
635	541	<i>Helminthoidichnites</i> isp.	Carbone & Narbonne (2014)	Blueflower	Canada
635	541	<i>Helminthoidichnites</i> isp.	Carbone & Narbonne (2014)	Ingta	Canada
635	541	<i>Helminthoidichnites</i> isp.	Corsetti & Hagadorn (2003)	Hynes Tongue	USA
635	541	<i>Helminthoidichnites tenuis</i>	Aitken (1989)	Blueflower	Canada
635	541	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (unpub); Narbonne & Aitken (1990)	Blueflower	Canada
635	541	<i>Helminthoidichnites tenuis</i>	Carbone & Narbonne (2014)	Blueflower	Canada
635	541	<i>Helminthoidichnites tenuis</i>	MacNaughton et al. (2000)	Blueflower	Canada
635	541	<i>Helminthoidichnites tenuis</i>	Aitken (1989)	Ingta	Canada
635	541	<i>Helminthoidichnites tenuis</i>	MacNaughton & Narbonne (1999)	Lower Ingta	Canada
635	541	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (unpub); Fritz & Crimes (1985)	Lower Stelkuz	Canada
635	541	<i>Helminthoidichnites tenuis</i>	Hofmann & Mountjoy (2010)	Upper Miette	Canada
635	529	<i>Helminthoidichnites tenuis</i>	Aitken (1989)	Ingta; Blueflower	Canada
556	541	<i>Helminthoidichnites tenuis</i>	Jenkins (1995)	Rawnsley Quartzite	Australia
556	541	<i>Helminthoidichnites</i> isp.	Droser et al. (1999)	Ediacara	Australia
551	541	<i>Helminthoidichnites tenuis</i>	Weber et al. (2007)	Shibantan	China
550	541	<i>Helminthoidichnites tenuis</i>	Hagadorn & Waggoner (2000)	Lower Wood Canyon	USA
550	541	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (unpub); Corsetti & Hagadorn (2003)	Wyman	USA
547	541	<i>Helminthoidichnites tenuis</i>	Seilacher et al. (2005); Gibson (1989)	Floyd Church	USA
541	529	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Helminthoidichnites</i> isp.	Buatois & Mángano (unpub); Webby (1984)	Copper Mine Range Beds	Australia
541	529	<i>Helminthoidichnites</i> isp.	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Helminthoidichnites tenuis</i>	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Helminthoidichnites tenuis</i>	MacNaughton & Narbonne (1999)	Upper Ingta	Canada
541	529	<i>Helminthoidichnites tenuis</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	521	<i>Helminthoidichnites tenuis</i>	Shahkarami et al. (2017)	Soltanieh	Iran
529	521	<i>Helminthoidichnites tenuis</i>	Hofmann & Patel (1989)	Ratcliffe Brook	Canada

HELMINTHOPSIS					
635	541	<i>Helminthopsis abeli</i>	Hofmann & Mountjoy (2010)	Upper Miette	Canada
635	541	<i>Helminthopsis hieroglyphica</i>	Han & Pickerill (1995); Narbonne & Aitken (1990)	Blueflower	Canada
635	541	<i>Helminthopsis</i> isp.	Buatois & Mángano (unpub); Webby (1970)	Fowlers Gap Beds	Australia
635	541	<i>Helminthopsis</i> isp.	Buatois & Mángano (unpub); Narbonne & Aitken (1990)	Blueflower	Canada
635	541	<i>Helminthopsis</i> isp.	Carbone & Narbonne (2014)	Blueflower	Canada
635	541	<i>Helminthopsis</i> isp.	Fritz & Crimes (1985)	Lower Stelkuz	Canada
635	541	<i>Helminthopsis</i> isp.	Buatois & Mángano (unpub); Hofmann & Mountjoy (2010)	Upper Miette	Canada
566	541	<i>Helminthopsis</i> isp.	Cope (1983)	Coomb Volcanic	UK
551	541	<i>Helminthopsis</i> isp.	Buatois & Mángano (unpub); Paczeńska (1996)	Lublin	Poland
547	541	<i>Helminthopsis</i> isp.	Gibson (1989)	Floyd Church	USA
541	529	<i>Helminthopsis abeli</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Helminthopsis</i> isp.	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Helminthopsis tenuis</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	521	<i>Helminthopsis tenuis</i>	Shahkarami et al. (2017)	Soltanieh	Iran
529	521	<i>Helminthopsis abeli</i>	Crimes & Anderson (1985)	Chapel Island member 3	Canada
529	521	<i>Helminthopsis abeli</i>	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Helminthopsis abeli</i>	Crimes & Jiang (1986)	Shiyantou	China
529	521	<i>Helminthopsis abeli</i>	Weber et al. (2007)	Shiyantou	China
529	521	<i>Helminthopsis tenuis</i>	Crimes & Anderson (1985)	Chapel Island member 3	Canada

MONOMORPHICHNUS					
550	541	<i>Monomorphichnus</i> isp.	Waggoner & Hagadorn (2002)	Wood Canyon	USA
541	529	<i>Monomorphichnus</i> isp.	Parcha & Singh (2010)	Phe	India
541	529	<i>Monomorphichnus bilinearis</i>	McIlroy & Brasier (2017)	Lower Breivik	Norway
541	529	<i>Monomorphichnus</i> isp.	Crimes & Anderson (1985)	Chapel Island member 2	Canada
541	529	<i>Monomorphichnus</i> isp.	Fernandez-Remolar et al. (2005)	Upper Ibor	Spain
541	529	<i>Monomorphichnus</i> isp.	Jensen et al. (2002)	Wood Canyon	USA
541	529	<i>Monomorphichnus lineatus</i>	Crimes & Anderson (1985)	Chapel Island member 2	Canada
541	529	<i>Monomorphichnus lineatus</i>	Brasier et al. (1979)	Pusa Shales	Spain
541	521	<i>Monomorphichnus multilineatus</i>	Alpert (1976)	Upper Deep Spring	USA
541	521	<i>Monomorphichnus bilinearis</i>	MacNaughton & Narbonne (1999)	Backbone Ranges	Canada
541	521	<i>Monomorphichnus</i> isp.	Weber et al. (2013)	Chulaktau	Kazakhstan
529	521	<i>Monomorphichnus bilinearis</i>	Crimes & Anderson (1985)	Chapel Island member 3	Canada
529	521	<i>Monomorphichnus bilinearis</i>	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Monomorphichnus bilinearis</i>	Liñán (1984)	Julia	Spain
529	521	<i>Monomorphichnus</i> isp.	Crimes & Anderson (1985)	Chapel Island member 3	Canada
529	521	<i>Monomorphichnus</i> isp.	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Monomorphichnus</i> isp.	Buatois & Mángano (unpub); Nowlan et al. (1985)	Vampire	Canada
529	521	<i>Monomorphichnus</i> isp.	Goldring & Jensen (1996)	Bayan Gol	Mongolia
529	521	<i>Monomorphichnus</i> isp.	Kowalski (1987)	Upper Czarna	Poland
529	521	<i>Monomorphichnus</i> isp.	Alvaro et al. (1993)	Embid	Spain
529	521	<i>Monomorphichnus</i> isp.	Liñán (1984)	Julia	Spain
529	521	<i>Monomorphichnus lineatus</i>	Fritz & Crimes (1985)	Boya	Canada
529	521	<i>Monomorphichnus lineatus</i>	Crimes & Anderson (1985)	Chapel Island member 3	Canada
529	521	<i>Monomorphichnus lineatus</i>	Crimes et al. (1977)	Herreria Member 1	Spain

PALAEOPHYCUS					
635	541	<i>Palaeophycus</i> isp.	Buatois & Mángano (unpub); Hofmann & Mountjoy (2010)	Upper Miette	Canada
635	541	<i>Palaeophycus</i> isp.	Moczyłowska et al. (2001)	Lower Maiva	Sweden
635	541	<i>Palaeophycus striatus</i>	Buatois & Mángano (unpub); Walter et al. (1989)	Elkera	Australia
635	541	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Webby (1970)	Fowlers Gap Beds	Australia
635	541	<i>Palaeophycus tubularis</i>	Carbone & Narbonne (2014)	Blueflower	Canada
635	541	<i>Palaeophycus tubularis</i>	Narbonne & Aitken (1990)	Blueflower	Canada
635	541	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Fritz & Crimes (1985)	Lower Stelkuz	Canada
635	529	<i>Palaeophycus</i> isp.	Parcha & Singh (2010)	Phe	India
635	521	<i>Palaeophycus</i> isp.	Sour-Tovar et al. (2007)	Puerto Blanco	Mexico
630	529	<i>Palaeophycus tubularis</i>	Bartley et al. (1998)	Platonovskaya	Russia (Asian)
555	541	<i>Palaeophycus</i> isp.	Banks (1970)	Manndraperelv	Norway
551	541	<i>Palaeophycus</i> isp.	Weber et al. (2007)	Shibantan	China
551	541	<i>Palaeophycus</i> isp.	Buatois & Mángano (unpub); Paczeńska (1996)	Lublin	Poland
551	541	<i>Palaeophycus tubularis</i>	Weber et al. (2007)	Gaojiashan	China
550	542	<i>Palaeophycus</i> isp.	Geyer & Uchman (1995)	Nasep	Namibia
550	541	<i>Palaeophycus</i> isp.	Waggoner & Hagadorn (2002)	Wood Canyon	USA
541	529	<i>Palaeophycus</i> isp.	Geyer & Uchman (1995)	Rosenhof	Namibia
541	529	<i>Palaeophycus</i> isp.	Buatois & Mángano (unpub); Fernandez-Remolar et al. (2005)	Middle Ibor	Spain
541	529	<i>Palaeophycus</i> isp.	Jensen & Grant (1998)	Tornetrask Lower Siltstone	Sweden
541	529	<i>Palaeophycus</i> isp.	Moczyłowska et al. (2001)	Upper Maiva	Sweden
541	529	<i>Palaeophycus</i> isp.	Walker & Driese (1991)	Unicoi	USA
541	529	<i>Palaeophycus</i> isp.	Jensen et al. (2002)	Wood Canyon	USA
541	529	<i>Palaeophycus tubularis</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Webby (1984)	Copper Mine Range	Australia

				Beds	
541	529	<i>Palaeophycus tubularis</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	529	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Paczeńska (1996)	Wlodawa	Poland
541	521	<i>Palaeophycus ferrovittatus</i>	Hofmann (1983)	Backbone Ranges	Canada
541	521	<i>Palaeophycus</i> isp.	Weber et al. (2013)	Chulaktau	Kazakhstan
541	521	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Fritz & Crimes (1985)	Stelkuz	Canada
541	521	<i>Palaeophycus tubularis</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	521	<i>Palaeophycus tubularis</i>	Grazhdankin & Krayushkin (2006)	Padun	Russia (European)
529	521	<i>Palaeophycus</i> isp.	Kowalski (1987)	Middle Czarna	Poland
529	521	<i>Palaeophycus</i> isp.	Loughlin & Hillier (2010)	St.Non's Sandstone	UK
529	521	<i>Palaeophycus</i> isp.	Walker & Driese (1991)	Nichols	USA
529	521	<i>Palaeophycus striatus</i>	Hofmann & Patel (1989)	Ratcliffe Brook	Canada
529	521	<i>Palaeophycus tubularis</i>	Buatois & Mángano (unpub); Fritz & Crimes (1985)	Boya	Canada
529	521	<i>Palaeophycus tubularis</i>	Crimes & Anderson (1985)	Chapel Island 5	Canada
529	521	<i>Palaeophycus tubularis</i>	Hiscott et al. (1984)	L'Anse-au-Clair	Canada
529	521	<i>Palaeophycus tubularis</i>	Hofmann & Patel (1989)	Ratcliffe Brook	Canada
529	521	<i>Palaeophycus tubularis</i>	MacNaughton & Narbonne (1999)	Vampire	Canada
529	521	<i>Palaeophycus tubularis</i>	Nowlan et al. (1985)	Vampire	Canada
529	521	<i>Palaeophycus tubularis</i>	Goldring & Jensen (1996)	Bayan Gol	Mongolia

TREPTICHNUS					
551	541	<i>Treptichnus</i> isp.	Gheling et al. (2001); Crimes & Anderson (1985)	Chapel Island 1	Canada
550	541	<i>Treptichnus</i> isp.	Jensen et al. (2000)	Huns	Namibia
550	541	<i>Treptichnus pedum</i>	Jensen et al. (2007)	Domo Extremeno	Spain
547	541	<i>Treptichnus</i> isp.	Seilacher et al. (2005); Gibson (1989)	Floyd Church	USA
541	529	<i>Treptichnus pedum</i>	Parcha & Singh (2010)	Phe	India
541	529	<i>Treptichnus bifurcus</i>	Jensen et al. (2007)	Rio Huso	Spain
541	529	<i>Treptichnus coronatum</i>	Crimes & Anderson (1985)	Chapel Island 2	Canada
541	529	<i>Treptichnus coronatum</i>	MacNaughton & Narbonne (1999)	Upper Ingta	Canada
541	529	<i>Treptichnus</i> isp.	Crimes & Anderson (1985)	Chapel Island 2	Canada
541	529	<i>Treptichnus</i> isp.	Liñán (1984)	Julia	Spain
541	529	<i>Treptichnus</i> isp.	Buatois & Mángano (unpub); Fernandez-Remolar et al. (2005)	Middle Ibor	Spain
541	529	<i>Treptichnus</i> isp.	Buatois & Mángano (unpub); Jensen et al. (2007)	Rio Huso	Spain
541	529	<i>Treptichnus</i> isp.	Geyer & Uchman (1995)	Rosenhof	Namibia
541	529	<i>Treptichnus</i> isp.	Jensen & Grant (1998)	Tornetrask Lower Siltstone	Sweden
541	529	<i>Treptichnus lublinensis</i>	McIlroy & Brasier (2017)	Lower Breivik	Norway
541	529	<i>Treptichnus pedum</i>	Narbonne et al. (1987)	Chapel Island	Canada
541	529	<i>Treptichnus pedum</i>	Buatois et al. (2013)	Dolkraals	South Africa
541	529	<i>Treptichnus pedum</i>	Liñán (1984)	Julia	Spain
541	529	<i>Treptichnus pedum</i>	Buatois et al. (2013)	Kalk Gat	South Africa
541	529	<i>Treptichnus pedum</i>	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Treptichnus pedum</i>	Banks (1970)	Lower Breivik	Norway
541	529	<i>Treptichnus pedum</i>	McIlroy & Brasier (2017)	Lower Breivik	Norway
541	529	<i>Treptichnus pedum</i>	Hagadorn & Waggoner (2000)	Lower Wood Canyon	USA
541	529	<i>Treptichnus pedum</i>	Corsetti & Hagadorn (2003)	Middle Deep Spring	USA
541	529	<i>Treptichnus pedum</i>	Wilson et al. (2012)	Nomtsas	Namibia

541	529	<i>Treptichnus pedum</i>	Buatois & Mángano (unpub); Kowalski (1987)	Osiek Sandstone	Poland
541	529	<i>Treptichnus pedum</i>	Brasier et al. (1979)	Pusa Shales	Spain
541	529	<i>Treptichnus pedum</i>	Buatois & Mángano (unpub); Germs (1972)	Rosenhof	Namibia
541	529	<i>Treptichnus pedum</i>	Crimes & Germs (1982)	Rosenhof	Namibia
541	529	<i>Treptichnus pedum</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	529	<i>Treptichnus pedum</i>	Buatois et al. (2013)	Stofkraal	South Africa
541	529	<i>Treptichnus pedum</i>	Jensen & Grant (1998)	Tornetrask Lower Siltstone	Sweden
541	529	<i>Treptichnus pedum</i>	MacNaughton & Narbonne (1999)	Upper Ingta	Canada
541	529	<i>Treptichnus pedum</i>	Jensen et al. (2002)	Wood Canyon	USA
541	529	<i>Treptichnus pedum</i>	Weber et al. (2007)	Zhongyicun	China
541	529	<i>Treptichnus pollardi</i>	Carbone & Narbonne (2014)	Ingta	Canada
541	529	<i>Treptichnus pollardi</i>	Buatois & Mángano (unpub); Webby (1970)	Lintiss Vale Beds	Australia
541	529	<i>Treptichnus pollardi</i>	Buatois & Mángano (2004)	Puscoviscana	Argentina
541	529	<i>Treptichnus pollardi</i>	Geyer & Uchman (1995)	Rosenhof	Namibia
541	529	<i>Treptichnus tripleurum</i>	Buatois & Mángano (unpub); Geyer & Uchman (1995)	Zamnarib	Namibia
541	521	<i>Treptichnus pedum</i>	Sour-Tovar et al. (2007)	Puerto Blanco	Mexico
541	521	<i>Treptichnus bifurcus</i>	Pacześna (1996)	Mazowsze	Poland
541	521	<i>Treptichnus coronatum</i>	MacNaughton & Narbonne (1999)	Backbone Ranges	Canada
541	521	<i>Treptichnus isp.</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	521	<i>Treptichnus lublinensis</i>	Pacześna (1996)	Mazowsze	Poland
541	521	<i>Treptichnus pedum</i>	Carbone & Narbonne (2014)	Backbone Ranges	Canada
541	521	<i>Treptichnus pedum</i>	MacNaughton & Narbonne (1999)	Backbone Ranges	Canada
541	521	<i>Treptichnus pedum</i>	Gehling et al. (2001)	Chapel Island	Canada
541	521	<i>Treptichnus pedum</i>	Weber et al. (2013)	Chulaktau	Kazakhstan
541	521	<i>Treptichnus pedum</i>	Dzik (2005)	Kessyusa	Russia (Asian)
541	521	<i>Treptichnus pedum</i>	Buatois & Mángano (unpub); Pacześna (1996)	Mazowsze	Poland
541	521	<i>Treptichnus pedum</i>	Corsetti & Hagadorn (2003)	Upper Deep Spring	USA

541	521	<i>Treptichnus pedom</i>	Droser et al. (1999)	Uratanna	Australia
541	521	<i>Treptichnus pollardi</i>	Shahkarami et al. (2017)	Soltanieh	Iran
541	521	<i>Treptichnus tripleurum</i>	Dzik (2005)	Kessyusa	Russia (Asian)
541	521	<i>Treptichnus triplex</i>	Pacześna (1996)	Mazowsze	Poland
529	521	<i>Treptichnus bifurcus</i>	Goldring & Jensen (1996)	Bayan Gol	Mongolia
529	521	<i>Treptichnus isp.</i>	Goldring & Jensen (1996)	Bayan Gol	Mongolia
529	521	<i>Treptichnus isp.</i>	Fritz & Crimes (1985)	Boya	Canada
529	521	<i>Treptichnus isp.</i>	Crimes & Anderson (1985)	Chapel Island 3	Canada
529	521	<i>Treptichnus isp.</i>	Crimes & Anderson (1985)	Chapel Island 5	Canada
529	521	<i>Treptichnus isp.</i>	Crimes & Anderson (1985)	Random	Canada
529	521	<i>Treptichnus isp.</i>	Li & Yang (1988)	Shiyantou	China
529	521	<i>Treptichnus pedom</i>	Goldring & Jensen (1996)	Bayan Gol	Mongolia
529	521	<i>Treptichnus pedom</i>	Buatois & Mángano (unpub); Fritz & Crimes (1985)	Boya	Canada
529	521	<i>Treptichnus pedom</i>	Buatois & Mángano (unpub); Nowlan et al. (1985)	Vampire	Canada
529	521	<i>Treptichnus pollardi</i>	Zhu (1997)	Shiyantou	China

CHAPTER 7

7. References

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