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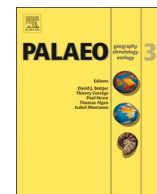


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Gyrolithes from the Ediacaran-Cambrian boundary section in Fortune Head, Newfoundland, Canada: Exploring the onset of complex burrowing

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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 in 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, suggesting that shallow early Cambrian sediments may have been relatively poor in organics and thus further supporting the model for onshore-offshore migration of gardening burrows.

1. 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.

2. Geologic and stratigraphic setting

Sedimentary units spanning the Ediacaran-Cambrian boundary on the Burin Peninsula of Newfoundland, Nova Scotia, and New Brunswick (Fig. 1A) were deposited within a transtensional regime, infilling 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

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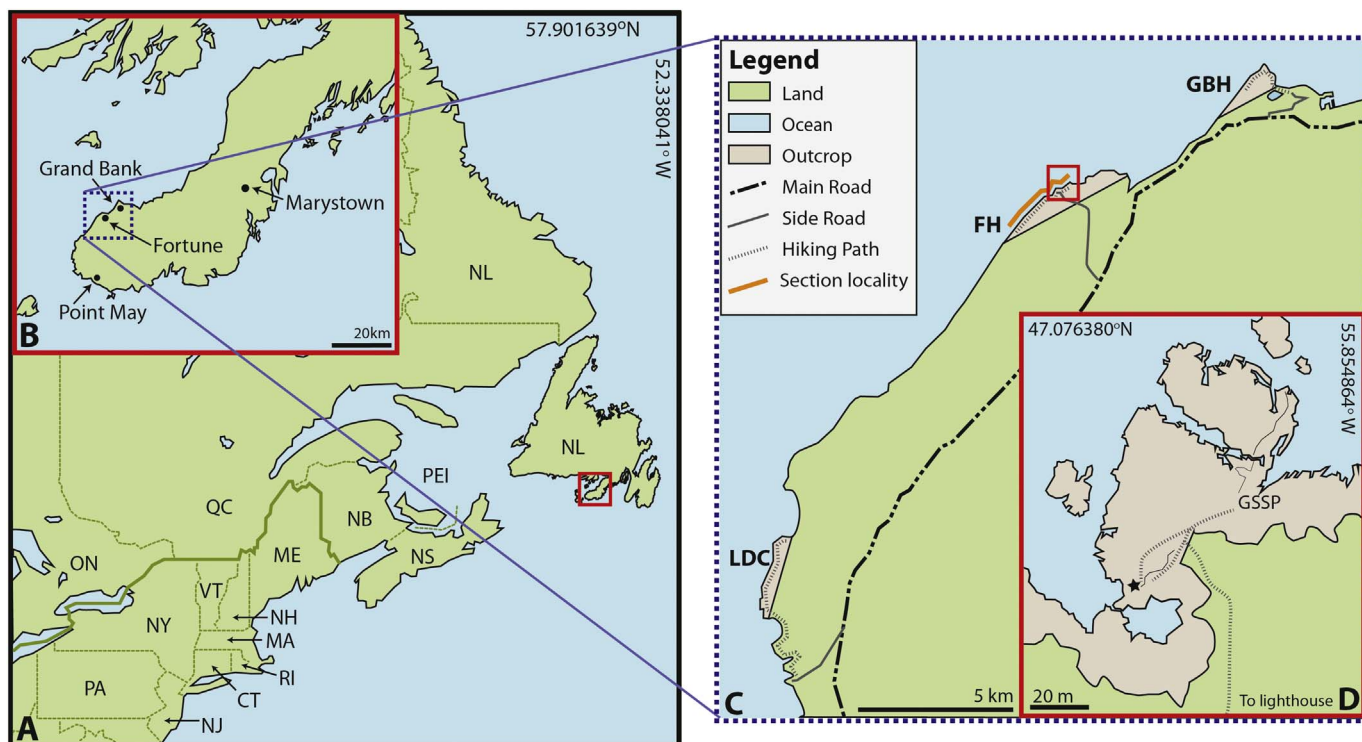


Fig. 1. (A) Map of eastern Canada and the United States. The red box denotes Burin Peninsula, shown in map B. (B) Map of the Burin Peninsula, Newfoundland. The blue dashed box is highlighting the field locality, on the northwestern corner of the Peninsula, shown in map C. (C) Map of outcrop localities 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 Global Stratotype Section and Point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 Bengston 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-grained 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 record 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 (Fig. 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 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).

3. 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 (Fig. 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 Antcliffe, 2009.

Ichnogenus GYROLITHES de Saporta 1884

1849 *Gyrolithes* Debey.

1884 *Gyrolithes* de Saporta.

1884 *Siphodendron* de Saporta.

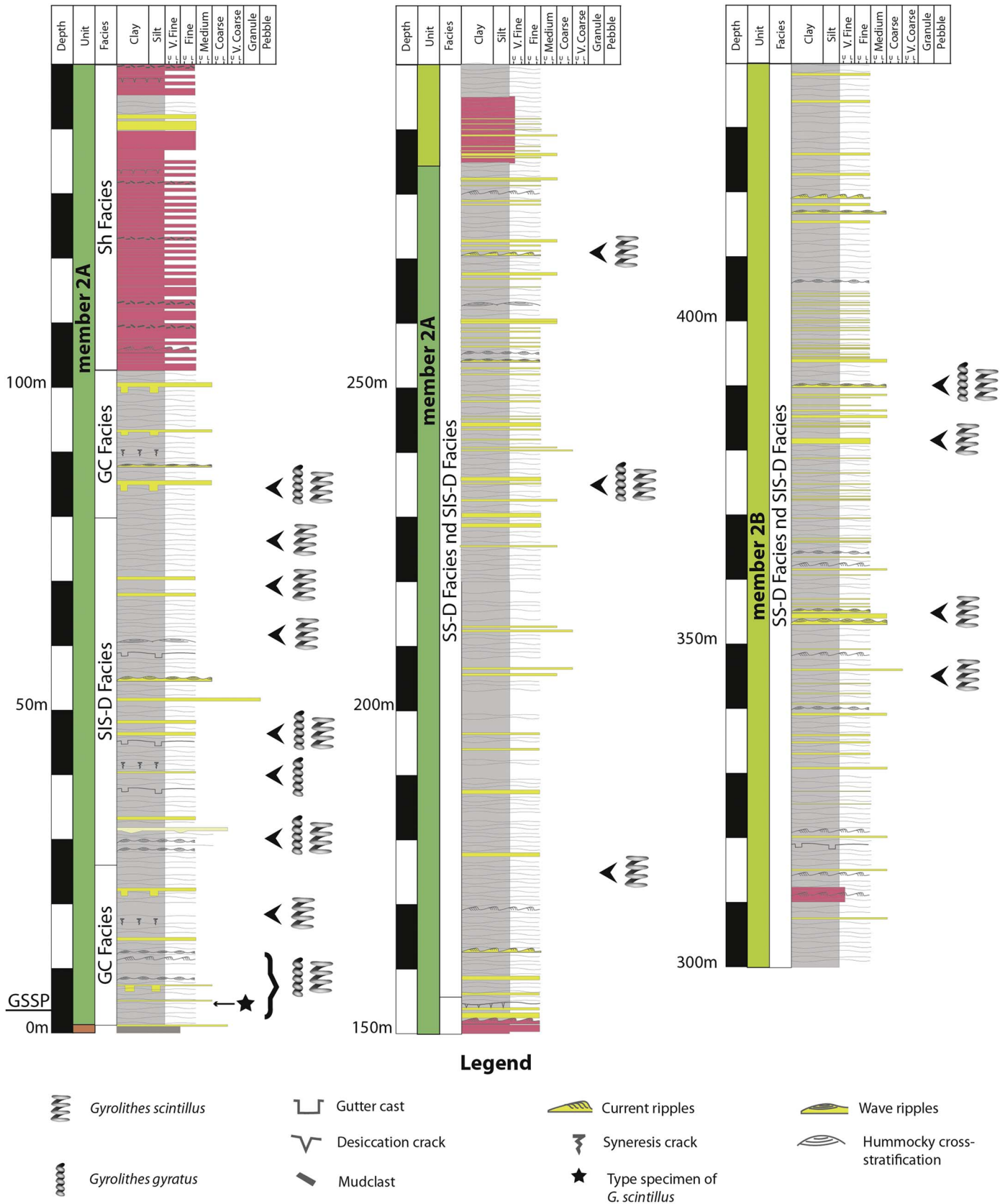


Fig. 2. A stratigraphic column of member 2 of the CIF showing *G. scintillus* and *G. gyratus* occurrences at both Fortune Head and Grand Bank Head outcrops. The star denotes the stratigraphic position (3.45 m above the base of member 2) of the *G. scintillus* holotype. The first appearance of *G. scintillus* and *G. gyratus* occur 0.2 m and 0.5 m above the base of member 2, respectively. An interval rich in both ichnospecies occurs between 3.5 m to 8 m above the base of member 2. In-depth facies descriptions can be found in Myrow (1987).

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* (Fig. 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:

$$\kappa = r/R \tag{1}$$

$$\delta = h/(2r) \tag{2}$$

$$\beta = h/(2\pi R) = \tan(\sigma) \tag{3}$$

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 radii 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.

$$\tan\lambda = (R_1 - R_2)/h_1 \tag{4}$$

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* (Fig. 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:

$$x = \left(r \cos \theta + R_1 - \frac{n\phi(R_1 - R_2)}{2\pi} \right) \cos(n\phi),$$

$$y = \left(r \cos \theta + R_1 - \frac{n\phi(R_1 - R_2)}{2\pi} \right) \sin(n\phi), \text{ and}$$

$$z = (R_1 - R_2) - \left(\frac{nh\phi}{2\pi} \right) + r \sin(\theta)$$

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 R₁ = R₂ (where $\tan\lambda = 0$) the parameterization describes a circular helix. When R₁ ≠ R₂ 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*

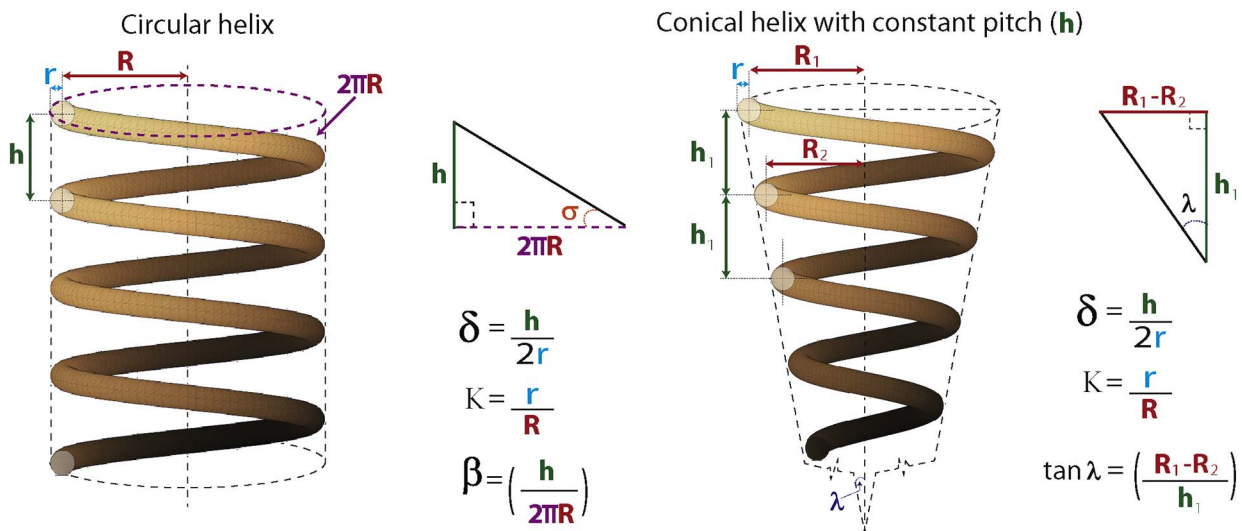


Fig. 3. Left: a circular helix, with measured variables (r, R, and h) and dimensionless parameters (κ, δ, and β) annotated. Right: a conical helix with constant pitch (h), with measured variables (r, R, and h) and dimensionless parameters (κ, δ, and $\tan\lambda$) annotated.

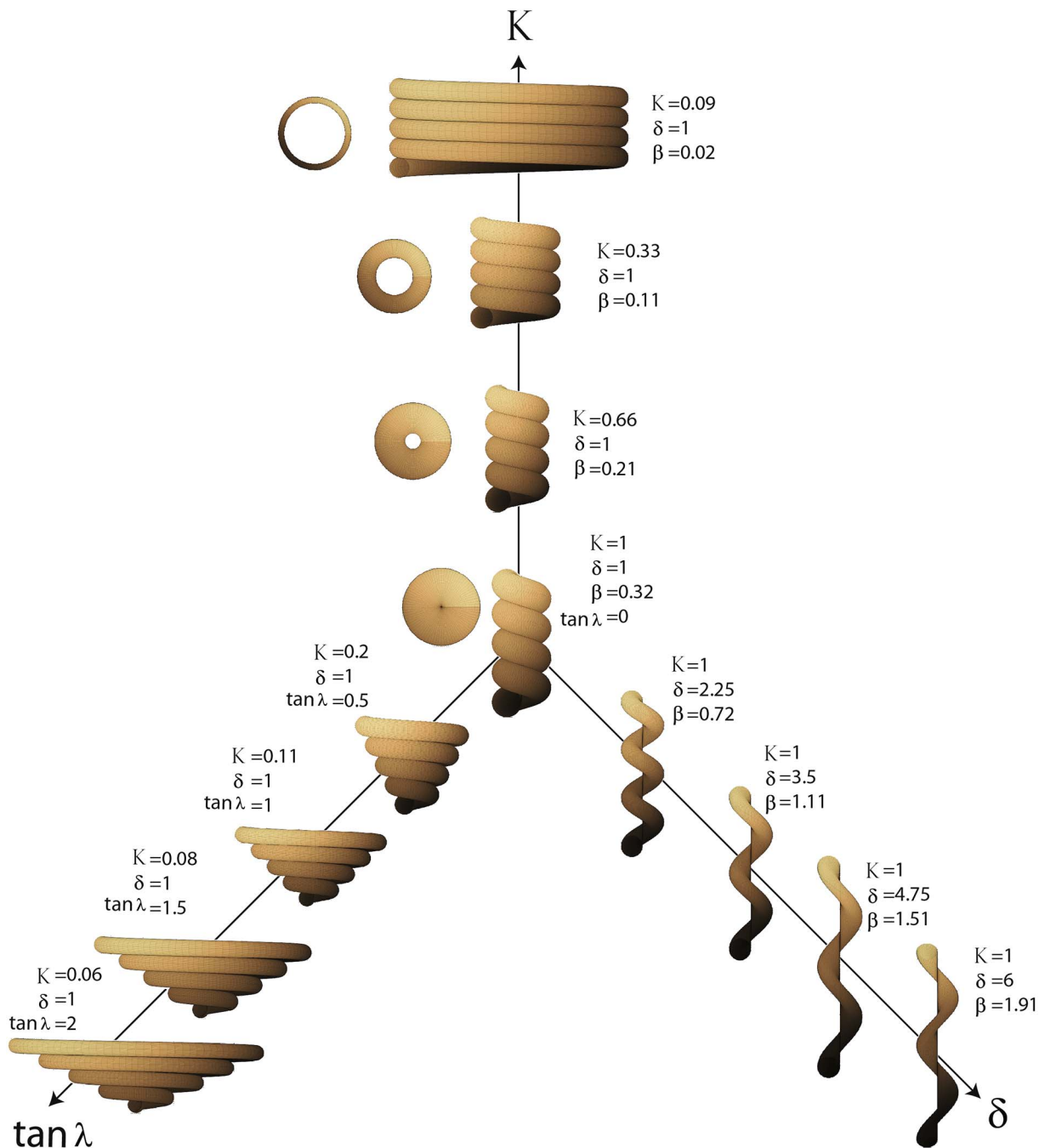


Fig. 4. Computer-generated *Gyrolithes*, showing the morphological effects of changes in κ , δ , and $\tan \lambda$. β is related to κ and δ by the equation $\beta = \delta(\kappa/\pi)$.

ichnospecies based on the relationship between the burrow diameter ($2r$) and the whorl radius (R). The *davreuxi* “lineage” contains wide forms, proportional forms are contained within the *krameri* “lineage”, and the *variabilis* “lineage” contains narrow forms. While these “lineages” are not true 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 narrow coils ($\kappa \cong 1$). However, additional architectural elements, such as an ascending or descending tunnels and a terminal chamber differentiates *Daimonhelix* from *Gyrolithes* (Meyer, 1999).

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 $\delta \leq 1$.



Fig. 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 Figs. 1 and 2. (B) Oblique specimen of *Gyrolithes scintillus*, with an elongated horizontal extension. (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*.

GYROLITHES SCINTILLUS new ichnospecies

Fig. 5A–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* Högström 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., 2017, p. 375, fig. 3B.

Etymology: From the Latin word scintillam (“spark”). An extension

Table 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. 2.

Gyrolithes specimens on the Burin Peninsula, Newfoundland, Canada.										
Sample	Site	Height (m)	r	R	h	K (r/R)	δ (h/2*r)	β (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

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 (Table 1). Field holotype is located in the Fortune Head Ecological Reserve (denoted by a star in Fig. 1), 3.45 m above the base of member 2, and can be seen in Fig. 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. 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 (Fig. 5B) have elongated bottom compartments, 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). 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 ichnogenic 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 regarded 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)

Figs. 3D, F; 4A; 6

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

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

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

Material: Seven specimens photographed and measured in the field, plus numerous field identifications (Table 1).

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 to 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 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 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* (Vohohonsky) 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 (Fig. 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 Fig. 6), (2) a compressed annulated vertical burrow, such as *Skolithos annulatus* (B in Fig. 6), and (3) a small helical burrow (C in Fig. 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.

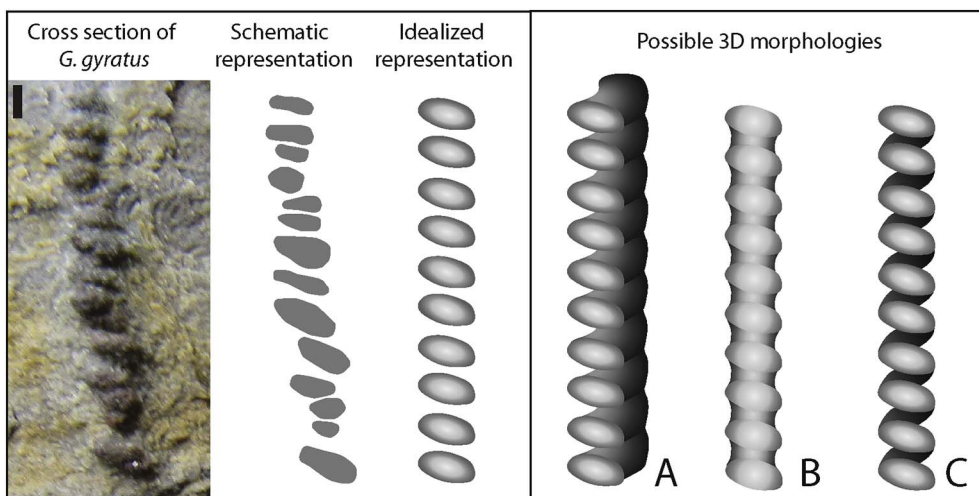


Fig. 6. Left box: Field photo of *G. gyratus* [Specimen 18] (scale = 1 mm), with a schematic representation of the specimen to the right. On the far right is an idealized illustration of a cross section of *G. gyratus*, based upon field observations. Right box: Possible three-dimensional morphologies (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.

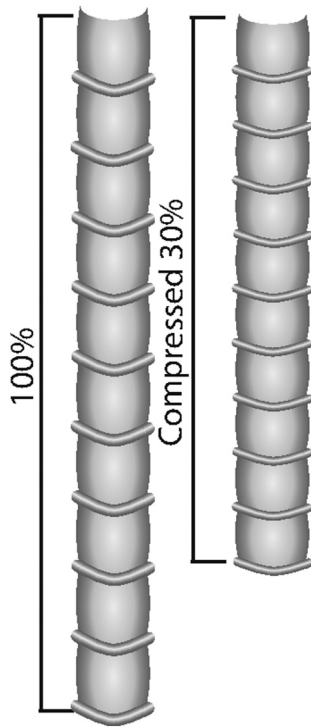


Fig. 7. Illustration of the effect of local compression in the Chapel Island Formation on a hypothetical *Skolithos annulatus* modelled after the holotype shown in Howell (1957, p. 21, fig. 1).

Previous authors considered these segments as the annulations of *Skolithos annulatus* (B in Fig. 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 (Fig. 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 (Fig. 8). One possible explanation for this could be that *S. annulatus* (B in Fig. 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 (Fig. 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.

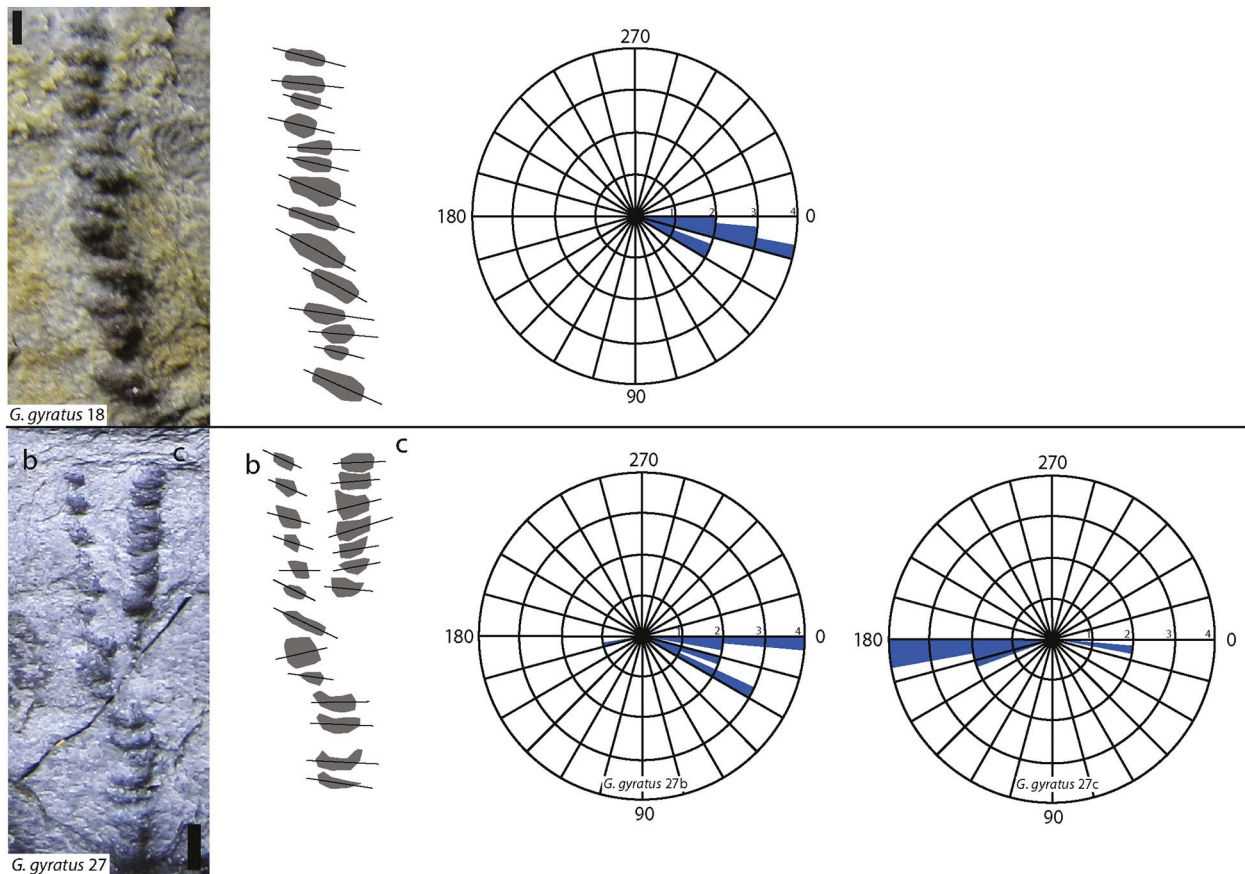


Fig. 8. The dips of each whorl within three specimens of *G. gyratus*. From left to right: Field photographs of *G. gyratus*. Scale bar = 1 mm. Sketches of the field photographs of *G. gyratus*, with dip ticks for each whorl superimposed. Dips were calculated from an imaginary horizontal plane striking right. A rose diagram, illustrating the strong trend seen in the dips of *G. gyratus*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

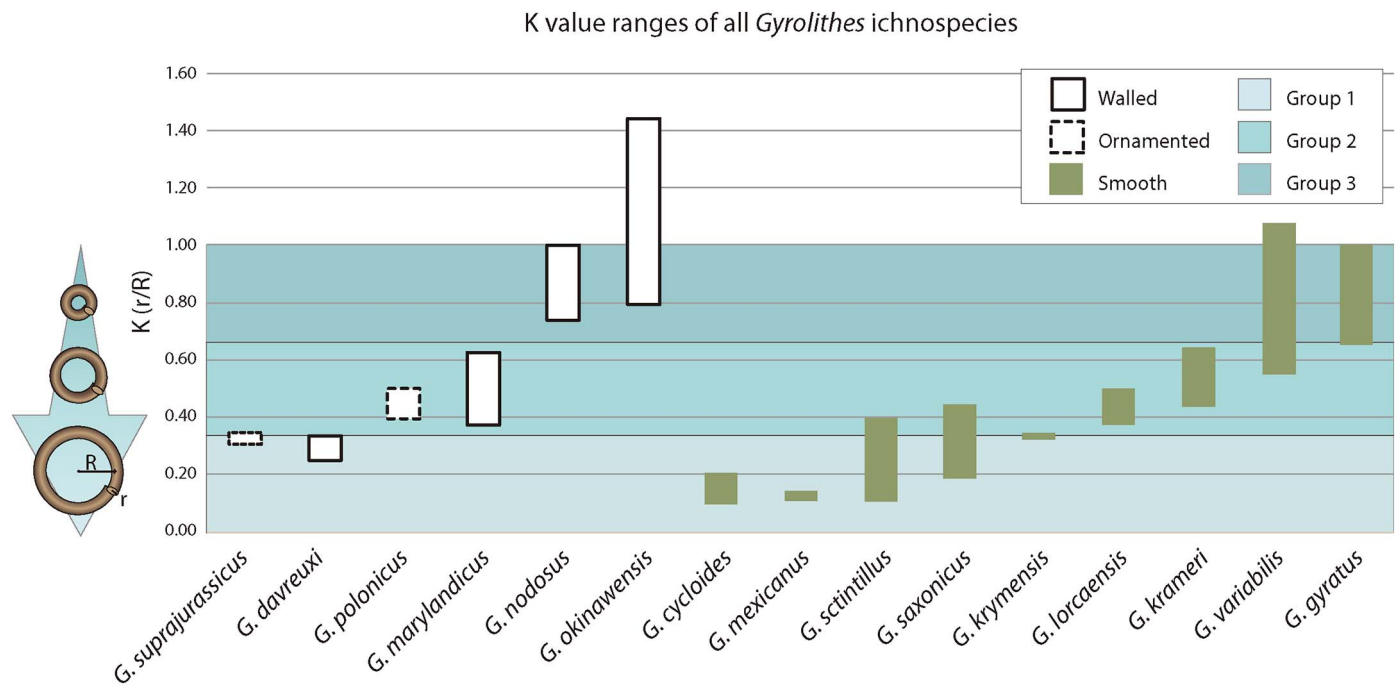


Fig. 9. The ranges of κ values for all *Gyrolithes* ichnospecies. Smooth *Gyrolithes* are grouped into three groups recognized by Uchman and Hanken (2013). The first group contains wide-form ichnospecies, in theory corresponding with the *davreuxi* “lineage”. The second group contains proportional-form ichnospecies, in theory corresponding with the *krameri* “lineage”. The third group is those with narrow forms, in theory corresponding with the *variabilis* “lineage”.

4. Discussion

4.1. 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 center of the burrow (see Fig. 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.

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 (Fig. 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 (Fig. 9). However, the ichnospecies included in these groups are in some cases drastically different from the Uchman and Hanken (2013) “lineages”. This is 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.

4.2. Cambrian occurrences of *Gyrolithes*

The ichnogenus *Gyrolithes* is widespread across the lower Cambrian (Table 2), and may serve as a valuable tool to aid in the delineation of the Ediacaran-Cambrian boundary. While some Cambrian occurrences

Table 2
Summary of recorded Cambrian *Gyrolithes* occurrences. Bolded sources contain a photograph of *Gyrolithes*. These photographs were used to reassess the ichnospecific determination of the specimens.

Period	Stratigraphy	Location	Ichnospecies	Reference
Stage 4	Mickwitzia Sandstone Member, File Haidar Fm. Bastion Fm.	Västergötland, South Central Sweden northeast Greenland	<i>G. polonicus</i>	Jensen (1997)
			? <i>G. polonicus</i> (<i>G. saxonicus</i> in original study)	Cowie and Spencer (1970); Pickerrill and Peel (1990)
Stage 3	Kaplonosy Fm. Radzyń Fm.	Southern Lublin region southeastern Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
			<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
Member 3. Arumbera Fm. Bastion Fm.	Member 3. Arumbera Fm. Bastion Fm.	Amadeus Basin, Central Australia. northeast Greenland	? <i>G. polonicus</i> (<i>G. polonicus</i> in original study)	Walter et al. (1989); Baghiyan-Yazd (1998)
			? <i>G. polonicus</i> (<i>G. saxonicus</i> in original study)	Cowie and Spencer (1970); Pickerrill and Peel (1990)
Stage 2	Kaplonosy Fm. Radzyń Fm.	Southern Lublin region southeastern Poland	<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
			<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1996)
Fortunian	Taebia Member, Voosi Fm. Lower Breidvika and Manndrapselva Members, Vestertana Group	eastern Latvia and western Estonia northeastern Finnmark, northern Norway	<i>G. scintillus</i> (<i>G. isp.</i> in original study)	Jensen and Mens (1999); Jensen and Mens (2001)
			<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 Lower Siltstone Member, Tometråsk Formation, Dividalen Group	East of Kilpisjärvi, Northern Finland Tometråsk area, northern Sweden	<i>G. polonicus</i>	Sytra and Jensen (2006)
			<i>G. isp.</i>	Jensen and Grant (1998)
Fortunian	Upper interval, Maiva Member, Sävovare Fm. Mazowsze Fm.	Laisvall-Storuman area, Northern Sweden Southern Lublin region, southeastern Poland	<i>G. isp.</i>	Moczyłowska et al. (2001)
			<i>G. scintillus</i> (<i>G. polonicus</i> in original study)	Paczeńska (1985, 1986, 1996)
Fortunian	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).

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 κ values of Cambrian *Gyrolithes* yields possible additional specimens of *G. scintillus* (Jensen and Mens, 1999; Högström 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.

4.3. 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 *Spongiomorpha* (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 7 cm with burrow diameters between 0.1 and 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 cannot be dismissed (Maletz, 2014). Additionally, recent estimates (Hedges and Kumar, 2009, p. 71) placed the 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*.

4.4. 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 (Domicichnia). 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, 1987).

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 burrows (Aller and Aller, 1998), attracting 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 domiciles 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. 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 Jr 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* Seilacher 1977 (Jensen and Mens, 1999).

4.6. *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.

5. 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 feeding strategies 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 (τ/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 (agricrhnial 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.

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