

## Original Article

**Cite this article:** Ebbestad JOR, Hybertsen F, Högström AES, Jensen S, Palacios T, Taylor WL, Agić H, Høyberget M, and Meinhold G (2022) Distribution and correlation of *Sabellidites cambriensis* (Annelida?) in the basal Cambrian on Baltica. *Geological Magazine* 159: 1262–1283. <https://doi.org/10.1017/S0016756821001187>

Received: 15 December 2020

Revised: 17 September 2021

Accepted: 18 October 2021

First published online: 9 December 2021

**Keywords:**

*Sabellidites*; Ediacaran–Cambrian boundary; biostratigraphy; correlation; Baltica; East European Platform

**Author for correspondence:**

Jan Ove R. Ebbestad,

Email: [jan-ove.ebbestad@em.uu.se](mailto:jan-ove.ebbestad@em.uu.se)

# Distribution and correlation of *Sabellidites cambriensis* (Annelida?) in the basal Cambrian on Baltica

Jan Ove R. Ebbestad<sup>1</sup> , Frida Hybertsen<sup>2,3</sup>, Anette E. S. Högström<sup>4</sup> , Sören Jensen<sup>5</sup>, Teodoro Palacios<sup>5</sup> , Wendy L. Taylor<sup>6</sup> , Heda Agić<sup>7</sup> , Magne Høyberget<sup>8</sup> and Guido Meinhold<sup>9,10,11</sup> 

<sup>1</sup>Museum of Evolution, Uppsala University, Norbyvägen 16, 752 36 Uppsala, Sweden; <sup>2</sup>Department of Earth Sciences, Uppsala University, 752 36 Uppsala, Sweden; <sup>3</sup>Department of Palaeobiology, Swedish Museum of Natural History, Box 500 07, 104 05 Stockholm, Sweden; <sup>4</sup>Arctic University Museum of Norway, UiT the Arctic University of Norway, 9037 Tromsø, Norway; <sup>5</sup>Área de Paleontología, Facultad de Ciencias, Universidad de Extremadura, Avenida de Física s/n, 06006 Badajoz, Spain; <sup>6</sup>Department of Geological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa; <sup>7</sup>Department of Earth Science, University of California at Santa Barbara, Santa Barbara, CA 93106, USA; <sup>8</sup>Magne Høyberget, Rennesveien 14, 4513 Mandal, Norway; <sup>9</sup>Department of Sedimentology & Environmental Geology, Geoscience Centre, University of Göttingen, Goldschmidtstraße 3, 37077 Göttingen, Germany; <sup>10</sup>School of Geography, Geology and the Environment, Keele University, Keele, Staffordshire, ST5 5BG, UK and <sup>11</sup>Institute of Geology, TU Bergakademie Freiberg, Bernhard-von-Cotta-Str. 2, D-09599 Freiberg, Germany

**Abstract**

*Sabellidites cambriensis* is a tubular non-mineralized metazoan that appears as compressed ribbon-shaped imprints with transverse wrinkling, thick walls and an even tube diameter of up to 3 mm. The distribution of *Sabellidites* is investigated in three Ediacaran–Cambrian sections on the Digermulen Peninsula in Arctic Norway, spanning the Manndrapselva Member of the Ståhpogieddi Formation and the lower member of the Breidvika Formation. Here, the Ediacaran–Cambrian boundary is located in the lower part of the upper parasequence (third cycle) of the Manndrapselva Member. Specimens of *Sabellidites* are rare but consistently present close to the lowest level of *Treptichnus pedum* and upsection, whereas the taxon is common and abundant in the lower part of the lower member of the Breidvika Formation, with an upper record at c. 55 m above the base. The range is comparable with that of the GSSP section in Newfoundland, Canada, establishing *Sabellidites* as an index fossil for the lowermost Cambrian. In the Manndrapselva Member, *Sabellidites* co-occurs with the acritarch *Granomarginata*, indicative of the lowermost Cambrian *Granomarginata* Zone, whereas in the Breidvika Formation it co-occurs with *Asteridium*. *Sabellidites* is widely distributed in Baltica, through the Rovnian and Lontovan regional stages but confined to the Fortunian global stage. In its lower range, *Sabellidites* is associated with a *Treptichnus pedum* trace fossil association and a depauperate leiosphaerid acritarch assemblage, followed by a *Granomarginata* assemblage. In its upper range, *Sabellidites* co-occurs with acritarchs of the *Asteridium–Comasphaeridium* Zone and the tubular foraminiferan *Platysolenites*. In Baltica, *Sabellidites* is a useful index fossil.

**1. Introduction**

Metazoan macrofossils become ubiquitous in the fossil record during the Ediacaran Period, from c. 575 Ma, signifying a novel development of marine ecosystems, stepwise oxygenation of Earth's oceans and global diversification of bilaterian metazoans (Droser & Gehling, 2015; Budd & Jensen, 2017; Darroch *et al.* 2018; Zhang *et al.* 2019; Wood *et al.* 2019 and references therein). Ediacaran shelly, soft-bodied, micro- and trace fossil assemblages are known from some 30 localities around the world (McCall, 2006; Fedonkin *et al.* 2007; Smith *et al.* 2016; Muscente *et al.* 2019; Shahkarami *et al.* 2020) representing various palaeoenvironments, depositional depths and palaeolatitudes, and often with a particular set of fossil organisms. Three distinct assemblages, the Avalon, White Sea and the Nama (oldest to youngest), are generally recognized (Waggoner, 2003; Laflamme *et al.* 2013) with the Miaohu biota potentially representing a fourth type (Muscente *et al.* 2019). These associations have also been interpreted as bio-communities, forming the basis for biozones that could be useful for inter-regional correlation (Muscente *et al.* 2019).

Ediacara-type organisms are rarely found in Cambrian strata (Jensen *et al.* 1998; Budd & Jensen, 2017), and the more diverse metazoan-dominated assemblages with shelly taxa appearing in the Cambrian have long been seen as clearly distinct and without continuity from the

older assemblages (see discussions in Erwin & Valentine, 2013; Budd & Jensen, 2017; alternatively Yang *et al.* 2016). While the dynamics and mechanisms of the Ediacaran–Cambrian transition are widely discussed (see for instance Laflamme *et al.* 2013; Smith *et al.* 2016; Darroch *et al.* 2018; Linnemann *et al.* 2019; Muscente *et al.* 2019), it is evident that there is an intimate and sustained relationship between the development of the Ediacaran biota and the evolution of bilaterian metazoans (Budd & Jensen, 2017; Buatois *et al.* 2018; Cai *et al.* 2019; Wood *et al.* 2019 and references therein).

Associated with the decline of the Ediacaran soft-bodied biota is the appearance of unique terminal Ediacaran assemblages/biota (Muscente *et al.* 2019), among which a group of mineralized to lightly mineralized or non-mineralized tubular fossils are prominent (Cohen *et al.* 2009; Tarhan *et al.* 2014; Schiffbauer *et al.* 2016; Selly *et al.* 2020); these are sometimes referred to as the ‘wormworld’ biota (Schiffbauer *et al.* 2016; Darroch *et al.* 2018). Several of these tubes are potentially useful taxa for biostratigraphy, and a few tubular forms span the Ediacaran–Cambrian boundary (Tarhan *et al.* 2014; Darroch *et al.* 2018; Cai *et al.* 2019; Muscente *et al.* 2019; Selly *et al.* 2020).

The tubular non-mineralized metazoan *Sabellidites cambriensis* Yanishevsky, 1926 has been considered one of the ‘wormworld’ taxa straddling the Ediacaran–Cambrian boundary. It is a regional index fossil for Baltica, but sabelliditids also occur in the Avalonian region of Newfoundland, Canada, where the Ediacaran–Cambrian boundary stratotype section is located. Furthermore, *Sabellidites* has been reported from Siberia, China, Australia and Spain (see online Supplementary Material). However, as is demonstrated herein, the notion that *Sabellidites cambriensis* is a diagnostic index fossil of a Terminal Ediacaran Stage (Muscente *et al.* 2019) cannot be supported.

In the present study, the distribution of *Sabellidites cambriensis* in three Ediacaran–Cambrian sections on the Digermulen Peninsula in Arctic Norway is investigated in the context of associated records of trace fossils and organic-walled microfossils. Sedimentary successions spanning the Ediacaran–Cambrian boundary are well exposed on the NE side of the Digermulen Peninsula and are seemingly continuous. Trace fossils, Ediacaran-type soft-bodied metazoans, sphaeromorphic acritarchs and vendotaenids are known from the upper Ediacaran part, while *Sabellidites cambriensis* has earlier been reported from the lower Cambrian Breidvika Formation (Banks, 1970; Vidal, 1981; Farmer *et al.* 1992; Crimes & McIlroy, 1999; McIlroy & Logan, 1999; Högström *et al.* 2013; McIlroy & Brasier, 2017). Combined with sedimentological and trace fossil evidence, the distribution of *Sabellidites cambriensis* at the Ediacaran–Cambrian boundary is tightly constrained and allows correlation across Baltica and with the Avalonian Newfoundland successions.

## 2. Geological setting

### 2.a. General setting

The Digermulen Peninsula is located in Finnmark in the northeastern part of Norway, outlined by Tanafjorden to the SE and Langfjorden to the NW (Fig. 1a). It is c. 35 km long and 18 km wide at the base of the fjords, ending to the NE in the pointed Digermulen headland. Its highest point is 639 m above sea level, but the mountain plateau forms a denudated expanse, with steep transitions to the coast and several incised valleys. The strata are well exposed and dip slightly to the west with the

strike sub-parallel to the coastline. They form part of the Lower Allochthon Gaissa Thrust Belt of the Finnmark Caledonides (Rice, 2014). Siliciclastic rocks dominate, belonging to the Smalfjorden, Nyborg, Mortensnes, Ståhpogieddi and Breidvika formations, forming the Cryogenian to basal Cambrian Vestertana Group (Fig. 1b). Both the Smalfjorden and Mortensnes formations contain diamictites related to a glacial regime, with the Nyborg Formation representing an inter-glacial deposit. The Ståhpogieddi and Breidvika formations are post-glacial marine sequences. Above this follow the Duolbagáisá, Kistedalen and Bearalgáisá formations, constituting the younger marine lower Cambrian (Stage 3) to Lower Ordovician (Tremadocian) Digermulen Group (Reading, 1965) (Fig. 1b). The rocks have undergone tectonometamorphic deformation related to the Scandian Orogeny (Meinhold *et al.* 2019a,b, 2020), resulting in a postmature overprint of 200–250 °C with very localized, low epizonal metamorphic conditions of ~300 °C (Meinhold *et al.* 2019b).

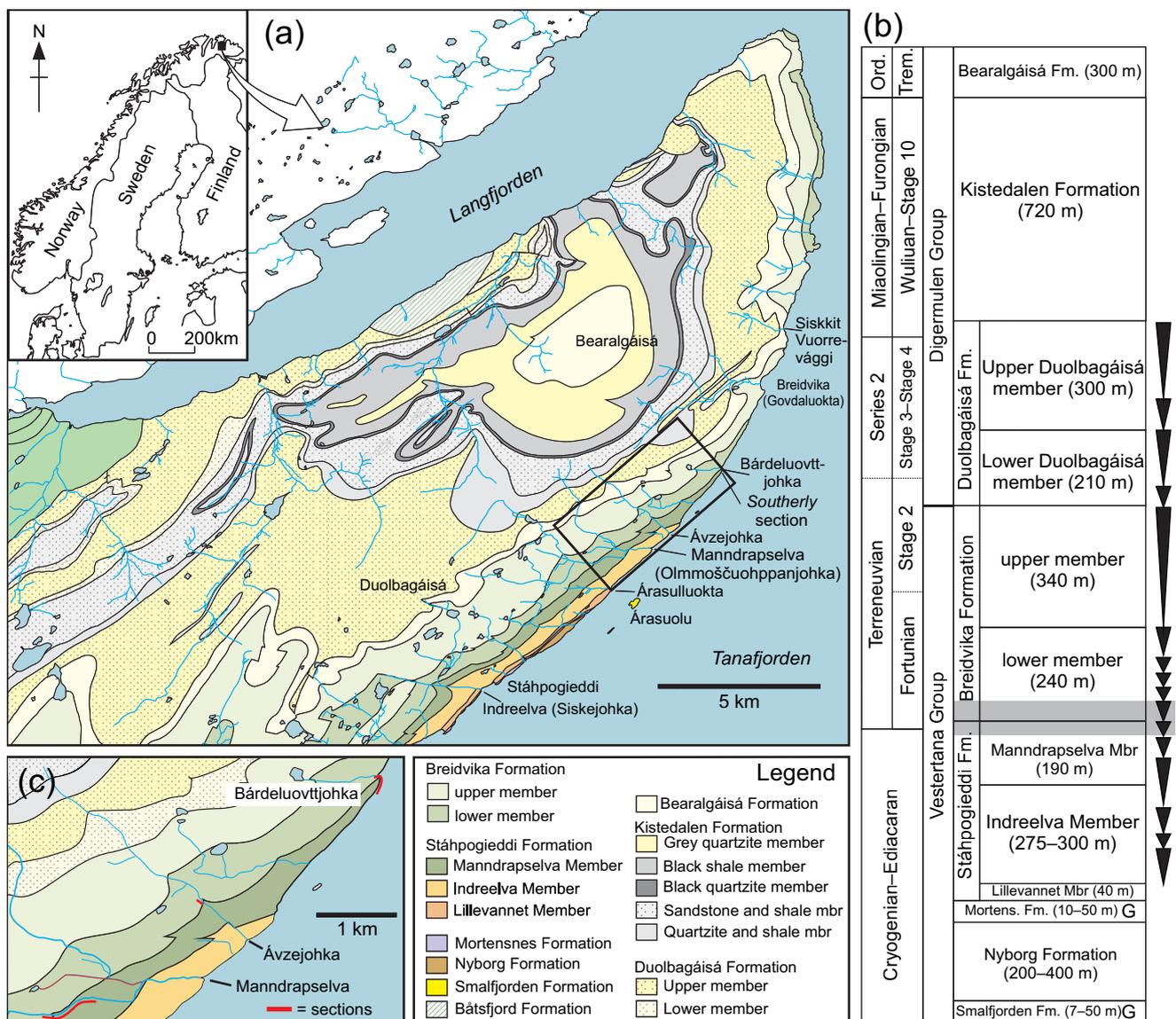
The Cryogenian–Ordovician succession on the Digermulen Peninsula is c. 3000 m thick and is the only fossiliferous site in Scandinavia with sedimentation across the Ediacaran–Cambrian transition, seemingly without any significant breaks (Högström *et al.* 2013). Age constraints on the Vestertana Group are based on glacial unconformities and the presence of trace and body fossils (Banks *et al.* 1971; Högström *et al.* 2013; McIlroy & Brasier, 2017; Jensen *et al.* 2018b).

### 2.b. The Ediacaran–Cambrian boundary beds on the Digermulen Peninsula

The post-glacial shallow marine succession of the Vestertana Group starts with the Ståhpogieddi Formation, which is divided into the Lillevannet, Indreelva and Manndrapselva members (Fig. 1b). In the latter unit, Reading (1965) recognized three sets of resistant quartzite bands in his ‘red quartzitic sandstone member’, and although the modern name was used already by Banks (1970), the member was formally named the Manndraperelva Member by Banks *et al.* (1971), now referred to as the Manndrapselva Member in accordance with the modern spelling (Siedlecka *et al.* 2006). It is estimated to be c. 190 m thick, with three parasequences (McIlroy & Brasier, 2017), that probably represent fourth order units. They are referred to as cycles herein to conform to previous literature.

The basal cycle shows a gradual transition from the underlying Indreelva Member into reddish sandstone (c. 33 m thick), followed by two coarsening-upward regressive cycles c. 60 m and c. 36 m thick, respectively (Banks *et al.* 1971; McIlroy & Brasier, 2017; Meinhold *et al.* 2019a; this study). Each of the parasequences consists of mudstone and fine sandstone beds of various thickness and lateral extension, with the sandstone beds becoming thicker towards the top of each parasequence and ending in a set of massive sandstones (see Banks *et al.* 1971; McIlroy & Brasier, 2017, fig. 2 for sedimentological details).

In the field (NE side of the peninsula), the massive sandstone units in each parasequence form weathering resistant ridges that have a reddish lower part and a whitish upper part. The uppermost sandstone package of the third cycle of the Manndrapselva Member is c. 9 m thick (red and white quartzite), but the boundary to the lower member of the succeeding Breidvika Formation is somewhat arbitrarily placed at the top of the last red sandstone (Reading, 1965), which is at the transition to the whitish



**Fig. 1.** (a) Geology of the Digermulen Peninsula (based on Siedlecka *et al.* 2006), with the study area marked by a rectangle. (b) Stratigraphy of the Vestertana and Digermulen groups with estimated thickness of strata (Banks *et al.* 1971; McIlroy & Brasier, 2017, fig. 1d). Stage divisions are based on Nikolaisen & Henningsmoen (1985, 1990), Högström *et al.* (2013), McIlroy & Brasier (2017) and Palacios *et al.* (2020). The horizontal grey bar shows the interval studied herein. The black triangles reflect upwards-coarsening parasequences (based on McIlroy & Brasier, 2017). Ord. – Ordovician; Trem. – Tremadocian; G – glaciogenic diamicites. (c) Detailed map of the study area with the studied sections marked by red bars.

sandstone in the middle of this set (see field photos and logs for further details). The name Breidvika Formation was first used by Føyn (1960) but described in detail by Reading (1965), who recognized two members, 240 m and 340 m thick, respectively (McIlroy & Brasier, 2017); these are treated as informal (Högström *et al.* 2013). The lowermost part of the lower member of the Breidvika Formation appears similar to the upper parasequence of the underlying Manndrapselva Member, forming a c. 30 m thick parasequence ending in a c. 5 m thick sandstone set with a red to white transition within.

Whereas the depositional environment of the Manndrapselva Member broadly represents the offshore to wave-dominated lower shoreface, the lower member of the Breidvika represents a near-shore shelf and offshore facies (McIlroy & Brasier, 2017). The rocks

of the lower member consist of alternating mudstone and thin sandstone beds interpreted as tempestites (Banks *et al.* 1971; McIlroy & Brasier, 2017).

The Ediacaran–Cambrian boundary is indicated by palaeopascichnids in the second cycle, and trace fossils and organic-walled microfossils close to the base of the third cycle of the Manndrapselva Member; the latter, together with the succeeding lower member of the Breidvika Formation, encompasses the Fortunian Stage of the Terreneuvian Series (Högström *et al.* 2013; McIlroy & Brasier, 2017; Jensen *et al.* 2017, 2018a,b). McIlroy & Logan (1999) and McIlroy & Brasier (2017) reported the conical skeletal fossil *Ladatheca cylindrica* (Grabau, 1900), in association with the tubular foraminiferan *Platysolenites anti-quissimus* (Eichwald, 1860), from the boundary interval between

the lower and upper members of the Breidvika Formation. In the Avalonian successions in Newfoundland, the *Ladatheca cylindrica* Zone lies in the upper part of the Fortunian Stage, although the taxon extends through the overlying *Watsonella crosbyi* Zone in Newfoundland, where it co-occurs with *Platysolenites antiquissimus*. The top of the Fortunian (and the base of the succeeding Stage 2) has been proposed to lie within the *Watsonella crosbyi* Zone (Landing *et al.* 2013).

### 2.c. The Ediacaran–Cambrian boundary beds in Baltica

The traditional Baltic and East European stratigraphical terminology encompasses horizons, series and suites, which are broadly used as regional stages, groups and formations, respectively (Mens *et al.* 1987, 1990). The base of the Cambrian has been placed at the base of the Lontovan Regional Stage (Sokolov, 1984, 1997), but is more commonly placed at the base of the Rovnian Stage (Mens *et al.* 1987, 1990; Nielsen & Schovsbo, 2011; Meidla, 2017), which has been inferred to approximate with the Global Stratotype Section and Point (GSSP) for the base of the Cambrian in Newfoundland, Canada (Landing, 1994). The basal two stages, the Rovnian and Lontovan, are of importance in relation to the succession on the Digermulen Peninsula (Fig. 2).

The Rovno layers were named by Kir'yanov (1968) for strata in Ukraine that are characterized by abundant sabelliditids and the predominance of simple, smooth acritarchs. The lower boundary was drawn at the appearance of sabelliditids. Subsequently, the layers were taken to comprise the Rovno Horizon in the East European Platform characterized by the widespread occurrence of *Sabellidites cambriensis* and the absence of *Platysolenites* (Kir'yanov, 1969), encompassing the *Sabellidites cambriensis* Zone (Mens *et al.* 1987, 1990). However, in the traditional usage (Areñ & Lenzion, 1978; Mens *et al.* 1987, 1990), *Platysolenites* co-occurs with *Sabellidites* in the uppermost part of the *Sabellidites cambriensis* Zone. The *Sabellidites cambriensis* Zone is rarely referred to in more recent studies in Baltica (but see Meidla, 2017), while it is used as a biozone in the GSSP section in Newfoundland (Landing *et al.* 1989) (Fig. 2).

Definitions of the Lontova beds and the *Platysolenites antiquissimus* Zone were developed in the 1920s and 1930s by the Estonian geologist Armin Öpik (Mens & Pirrus, 1977, 1997; Mens *et al.* 1987, 1990) for the 'Blue clay' of Estonia. The stratotype for the formation and stage is in the Kunda quarry in NE Estonia. The base of the *Platysolenites* Zone was drawn at the appearance of the acritarchs *Granomarginata*, *Tasmanites tenellus* and leiosphaerids and not by the first occurrence of *Platysolenites* (Mens *et al.* 1987, 1990). Moczyłowska (1991) refined the acritarch stratigraphy, proposing the *Asteridium tornatum*–*Comasphaeridium velvetum* Zone to encompass the Lontovan Stage, and a *Platysolenites antiquissimus* Interval-Zone with the lower boundary at the first occurrence of *Platysolenites*. Thus, it corresponds to the *Asteridium tornatum*–*Comasphaeridium velvetum* Zone and includes the upper part both of the traditional *Sabellidites cambriensis* Zone and the uppermost part of the Rovnian Stage (Moczyłowska, 1991, fig. 11). The upper boundary corresponds to the base of the *Skiagia ornata*–*Fimbriaglomerella membranacea* Zone (Moczyłowska, 1991) (Fig. 2).

On the Digermulen Peninsula most of the Rovnian Stage encompasses the third cycle of the Manndrapselva Member, while the upper part of the Rovnian and all of the Lontovan Stage are encompassed by the Breidvika Formation (Fig. 2) (see also McLroy & Brasier, 2017, fig. 2).

## 3. Material and methods

### 3.a. Sample collection

Sampling for this study was carried out during fieldwork by the Digermulen Early Life Research Group (DELRG) in 2011 and 2016–2018 on the Digermulen Peninsula. Three localities were chosen for closer examination with sections spanning the third cycle of the Manndrapselva Member and the lower member of the Breidvika Formation (Fig. 1c). For all sites, the transition from red to white quartzite marking the formation boundaries was used as a reference datum. In addition, a few horizons with conglomerate developed as channel fills(?) below distinct trace fossils of cf. *Psammichnites circularis* could be correlated between the southernmost and northernmost sections.

A total of 90 samples were collected for this study (online Supplementary Material Table S1), and the sample numbers are indicated in the logs. Additional samples, e.g. for trace fossils, microfossils and provenance analysis, were collected from the same sections, and some of these are also indicated in the logs. All recovered samples are stored in the palaeontological collection of The Arctic University Museum of Norway in Tromsø (museum number prefix TSGf).

### 3.b. Sections

The sections are described from the south to the north. Each are situated c. 2 km apart along strike (Fig. 1c). The general strike direction is c. 220–225° and the strata dip at c. 20° to the NNW. The northernmost section was described and partly sampled by Högström *et al.* (2013). All sections span the third cycle of the Manndrapselva Member and the lower member of the Breidvika Formation, although it is difficult to safely reach the third cycle in the Avžejohka section. The succession between the lower boundary of the Breidvika Formation and the top of the first thick red/white quartzite unit is referred to as the first parasequence of that formation. This quartzite unit serves as another marker bed in all three sections.

The Manndrapselva section runs alongside the Manndrapselva River (Olmmoščuohppanjohka in Sami). Around 70 m were logged, mainly along the right-side bank of the river (relative to the direction of flow) (Fig. 3). A scratch circle was described from the lower part of the third cycle of the Manndrapselva Member in this section by Jensen *et al.* (2018a) (Fig. 3a). A patchy conglomerate with small pebbles occurs a few centimetres below a surface with the trace fossil cf. *Psammichnites circularis* (Figs 3b, c, 7b, e) and allows for a precise correlation with the northernmost section. At about mid-section the river follows the top of the third cycle of the Manndrapselva Member along strike (Fig. 3d, e). Below this level the outcrop is essentially continuous, while larger parts of the section upstream are covered where the landscape is flatter (Fig. 3f). Consequently, the log was divided into parts subsequently combined into one final log, and the gaps were interpolated.

The Avžejohka section runs alongside, and partly inside, a ravine at the Avžejohka rivulet (Fig. 4). The lower part of the lower member of the Breidvika Formation is well exposed and was easily sampled along the steep cliff on the right bank of the rivulet (relative to the direction of flow) (Fig. 4a), and good exposures continue upstream through the entire unit. Although the Manndrapselva Member is exposed deep in the ravine, it is inaccessible for sampling and logging (Fig. 4b), and for practical reasons the top of the white quartzite serves as the reference level for the log here. A total of 55 m was logged.

Series Stages	Biozones eastern Avalonia			Biozones Baltica		Series Stages
	Trace fossils	Shelly fossils	Acritarch	Other	Acritarch	
Series 2		<i>Sunnagina imbricata</i>	<i>Skiagia</i>	<i>Rusophycus</i>	<i>Skiagia ornata</i> – <i>Fimbriaglomerella membranacea</i>	Domi.
Terreneuvian	Stage 2	<i>Cruziana tenella</i>	no fauna	<i>Platysolenites antiquissimus</i>	<i>Asteridium tornatum</i> – <i>Comasphaeridium velvetum</i>	Lontovan
		<i>Rusophycus avalonensis</i>	<i>Watsonella crosbyi</i>			
	<i>Ladatheca cylindrica</i>		no fauna			
	Fortunian	<i>Treptichnus pedum</i>	<i>Sabellidites cambriensis</i>	<i>leiosphaerids</i>	<i>Sabellidites cambriensis</i>	
Ediacaran						Kot-linian

**Fig. 2.** Traditional trace fossil and acritarch zonation of the Rovnian and Lontovan (Terreneuvian, Cambrian) in Baltica compared to the Terreneuvian biozones in the GSSP section in Newfoundland (eastern Avalonia). The acritarch zonation for Baltica is based on Moczyłowska (1991), while the other zones follow Nielsen & Schovsbo (2011). The biozones for Newfoundland are based on Palacios *et al.* (2018). Domi. – Dominopolian.

The Bårdeluoovttjohka section is a coastal outcrop south of the outlet of the Bårdeluoovttjohka rivulet (Fig. 5). Here the third cycle of the Manndrapselva Member is accessible while well-exposed outcrops of the lower member of the Breidvika Formation crop out near the river and can be followed upstream on the right side of the river (relative to the direction of flow) (Fig. 5a, b). The Breidvika Formation is also exposed along the coast on the north side of the river, albeit with a displacement relative to the southern section. The steepness of the cliffs at the shore does not allow continuous access to the Manndrapselva Member to the south along the coastline, and the section discussed by Jensen *et al.* (2018a, fig. 6a) lies *c.* 250 m south of the main section logged herein. However, the thick sandstone unit seen in Figure 5c is a good marker bed for correlation between the two sites, and the top of the third cycle is clearly visible. The rocks are exposed to the sea, and the more resistant sandstone beds stand out. Högström *et al.* (2013) described the trace fossil *Treptichnus pedum* from just above a massive light coloured sandstone unit (Fig. 5c–e), where also several horizons of small channel fill(?) conglomerates are seen. Jensen *et al.* (2018a) reported the occurrence of *Treptichnus pedum* some 10 m below this level in the section to the south. In addition, the acritarch *Granomarginata prima* was found a few metres above the 2013 *Treptichnus pedum* level (Högström *et al.* 2013), while *Asteridium tornatum* was found in the basal part of the lower member of the Breidvika Formation, some 35 m higher in the section (Palacios *et al.* 2018).

#### 4. Sabellidites

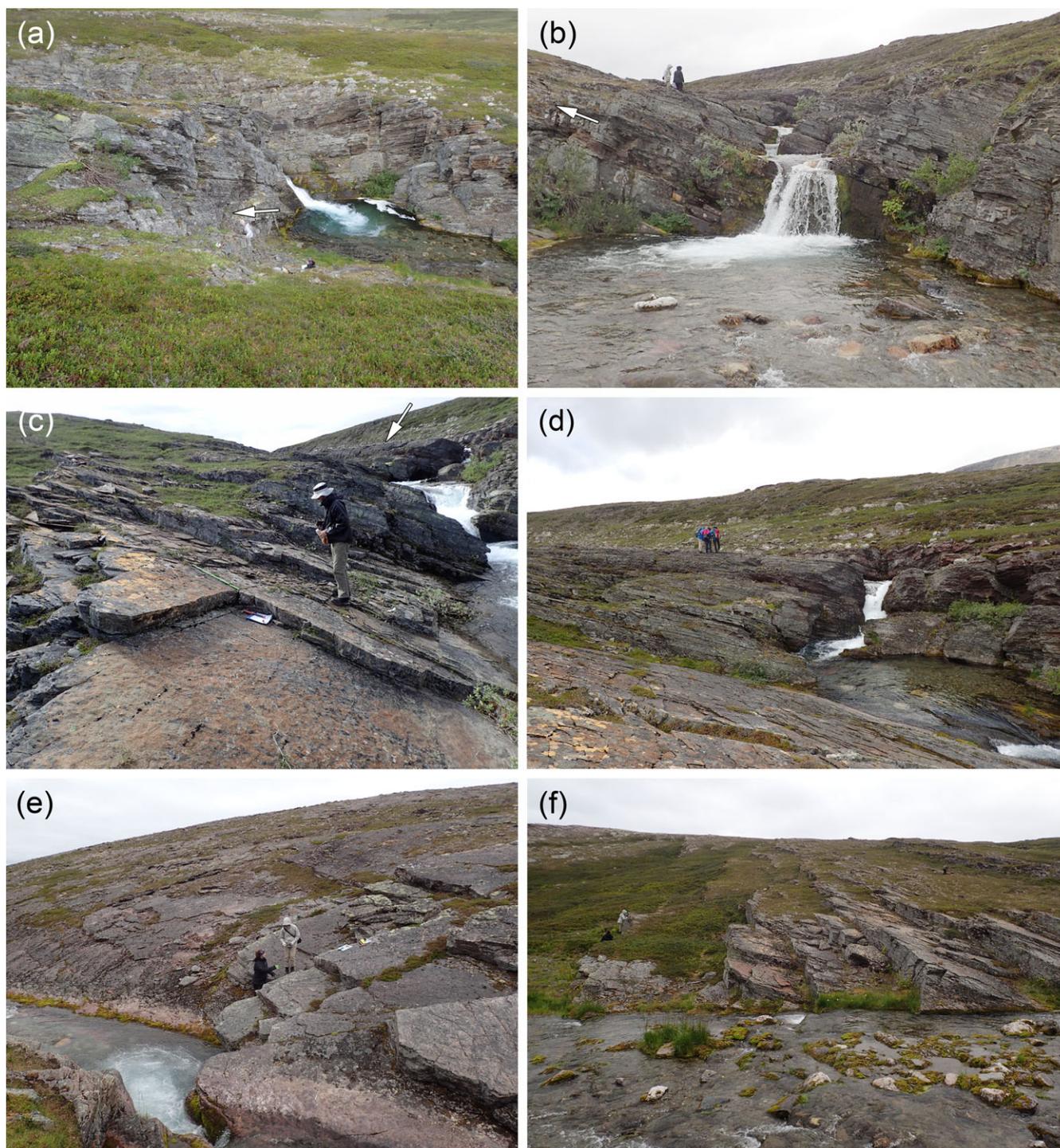
*Sabellidites cambriensis* Yanishevsky, 1926 appears as compressed ribbon-shaped carbonaceous fossils in the fissile mudstone in the succession on the Digermulen Peninsula. The taxon was first described from the soft clay of the Cambrian Lontova Formation (Lomonosov Formation in Russian terminology) near St Petersburg, Russia, by Yanishevsky (1926) and placed in the family Sabelliditidae by Sokolov (1965). The holotype was refigured by Sokolov (1997, pl. 15, fig. 1). Yanishevsky (1926) also described *Serpulites petropolitanus* from the same beds, a taxon

now placed in synonymy with the tubular foraminiferan *Platysolenites antiquissimus* (see McLroy *et al.* 2001).

*Sabellidites* was diagnosed and described by Sokolov (1965, 1967, 1968, 1972) as long (70–120 mm), flexible tubes with coarse to fine transverse wrinkling, thick walls and a constant tube diameter of 0.5–2.0 mm (rarely reaching 2.8–3.0 mm). *Sabellidites cambriensis* is the type species by original designation and monotypy. Other compressed and ribbon-shaped Cambrian tubular fossils in the family comprise *Sokoloviina* Kir'yanov, 1968 (smooth or flanged tube; see also Slater *et al.* 2018), *Paleolina* Sokolov, 1965 (long, thin-walled tubes, 0.2–1.0 mm wide, often preserved with a crumpled appearance) and *Parasabellidites* Sokolov, 1967 (finely wrinkled tubes with a distinct fibrous structure and periodical constrictions). Sokolov (1965) placed other sabelliditid-like forms in the family Saarinidae Sokolov, including *Saarina* and *Calyptrina*, which can be found in both the Cambrian and the Ediacaran. A morphological similarity between *Saarina* and *Cloudina* has been noted upon (e.g. Selly *et al.* 2020).

*Sabellidites*, *Parasabellidites* and *Paleolina* were included in the analyses by Muscente *et al.* (2019 and the supplementary information therein, p. 5), and placed in the form category Sabelliditomorpha, 'being long, slender tube- and ribbon-shaped forms with regularly spaced, narrow transverse annulations or segmentation'.

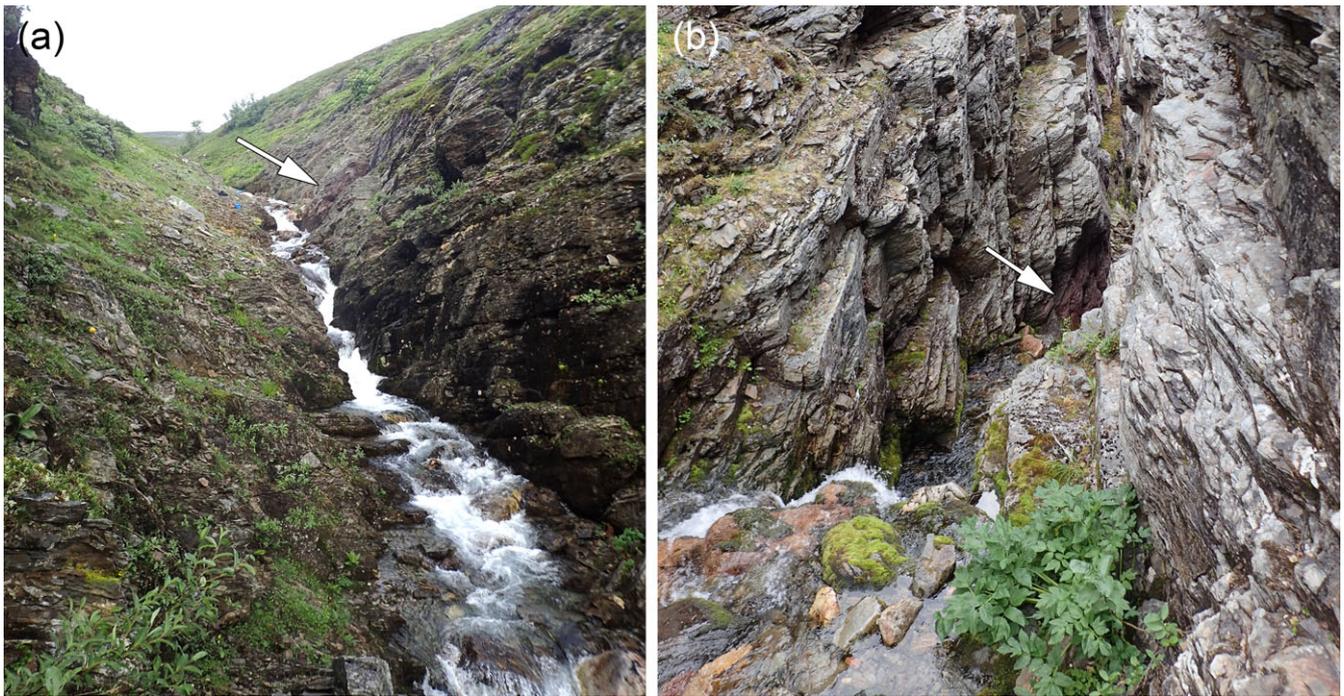
Based on overall morphology the specimens recorded in the present study are attributed to *Sabellidites cambriensis*, although the three sections offer a range of preservations, mostly due to different weathering effects (Fig. 6). Typical specimens are preserved as black opaque, but shiny tubes of various lengths and widths also occur. The fossils are often more compressed in the fissile mudstone than in the siltier or sandier beds. The thick appearance of the walls is usually a distinct feature (Fig. 6a). The transverse annulations are rarely distinct in specimens from the Digermulen Peninsula, and the surface tends to be fractured and broken up into irregular reticulate fragments, partly following the transverse annulations (Fig. 6a, b). If the upper surface is peeled off, the tube will appear smooth to various degrees, as the non-annulated inner wall is exposed (Fig. 6c, d, f). In the specimen shown in Figure 6c,



**Fig. 3.** Field photos from the Manndrapselva section. (a) Lower part of the third cycle of the Manndrapselva Member. Arrow indicates approximate position of scratch circle. (b) Approximately  $-15$  m in section. Arrow indicates approximate level of conglomerate, just above massive beds of quartzite. The people are standing on the surface with the trace fossil cf. *Psammichnites circularis*. (c) Surface with ripple marks and cf. *Psammichnites circularis*. Arrow points to the top of the Manndrapselva Member, as seen in next figure. Person standing on the surface with cf. *Psammichnites circularis*. (d) Upper part of Manndrapselva Member, with people standing near top surface. (e) Upper part of the red quartzite marking the top of the Manndrapselva Member. The river runs to the left in the photo. (f) Lower part of lower member of the Breidvika Formation, with partly covered section to the left.

the upper part shows the inner side, gradually fading downward in the image so that the lowermost part of the specimen only shows an external mould with faint traces of the black material. The inner surface in the specimen in Figure 6d, f is uneven in the lower part of the image and smooth in the upper part, reflecting various

degrees of deterioration. Specimens may also appear as rusty impressions only (possibly iron hydroxide), as illustrated in Figure 6e, g where a 'normal' specimen is compared to a 'rusty' specimen. Both specimens are from approximately the same level in the Manndrapselva section. The stratigraphically highest



**Fig. 4.** Field photos from the Avzejohka section. (a) View upstream, with arrow pointing to thick red/white quartzite bed at the top of the first parasequence in the lower member of the Breidvika Formation. (b) View downstream with arrow pointing to the red quartzite marking the top of the third cycle of the Manndrapselva Member.

recovered specimens are also ‘rusty’ (Fig. 6h). Some specimens show partly a ‘normal’ preservation, and partly a ‘rusty’ preservation (Fig. 6i). This type of preservation and the fact that ‘rusty’ and ‘normal’ specimens appear in the same intervals suggest that these are preservational variants of *Sabellidites*. It may therefore be difficult to distinguish atypical fragments of *Sabellidites* unless several specimens are available to demonstrate the variability.

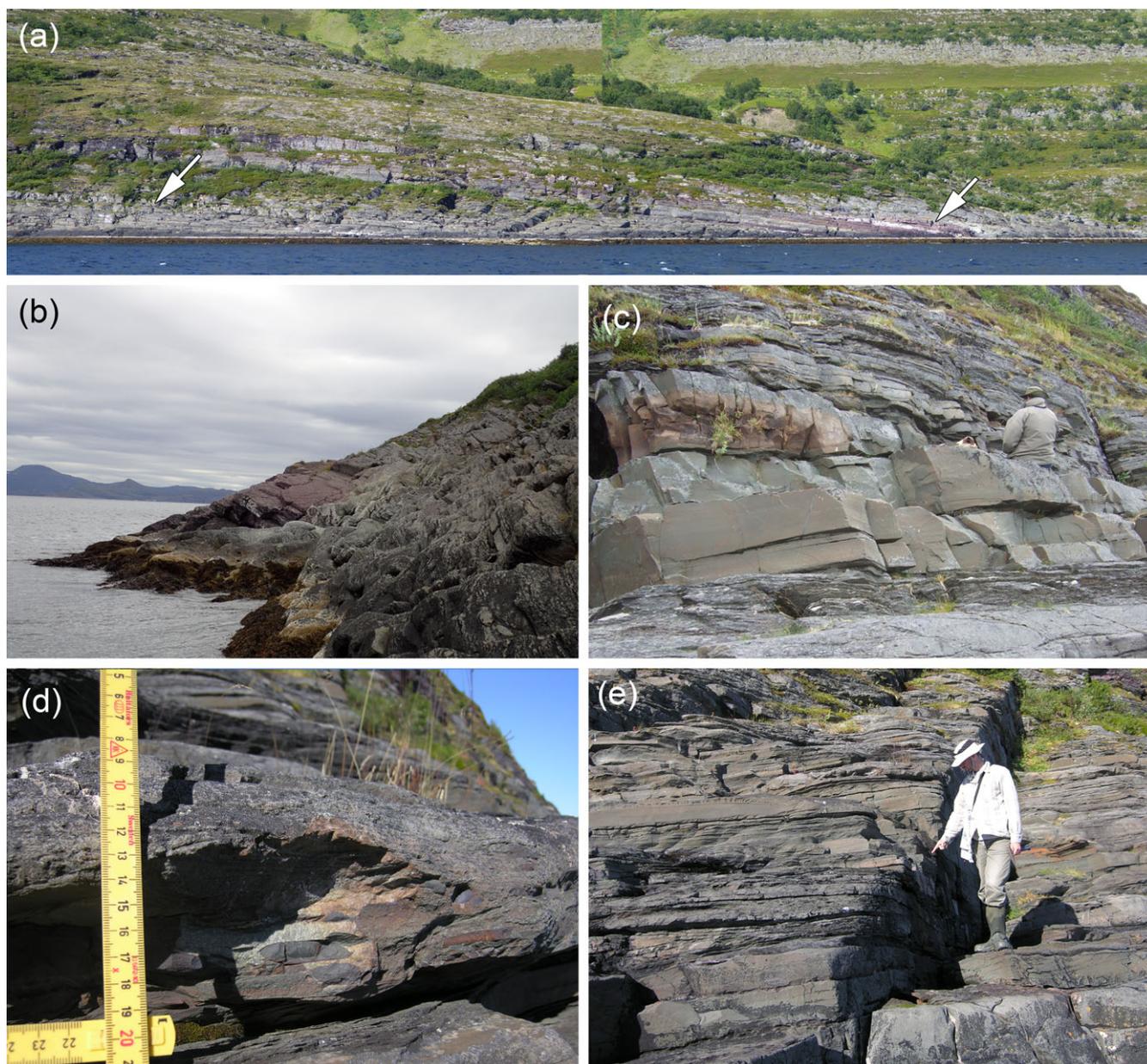
### 5. Trace fossils

Banks (1970), in his pioneering study on Finnmark trace fossils, proposed the occurrence of *Treptichnus pedum* low in the Breidvika Formation as a potential indicator of Cambrian age. Trace fossils have remained the principal focus in discussions on the placement of the base of the Cambrian in the Digermulen succession (Farmer *et al.* 1992; Högström *et al.* 2013; McIlroy & Brasier, 2017; Jensen *et al.* 2018a,b). The current status is summarized below, with the addition of new material (Fig. 7) and their distribution (Fig. 8).

*Treptichnus pedum* and *Gyrolithes* *isp.* first appear within the lower 10 m of the third cycle of the Manndrapselva Member in a section south of Bårdeluovttjohka (Jensen *et al.* 2018a). These *Treptichnus pedum* are relatively small and with limited development of probes (Jensen *et al.* 2018a, fig. 6c). At comparable stratigraphical levels in the Manndrapselva section a trace fossil with angular turns and local thickenings that could be positions of probes (Fig. 7f) is potentially a *Treptichnus*. Larger and more extensively developed *Treptichnus pedum* are found higher in the third cycle, both at the Manndrapselva and Bårdeluovttjohka sections (Fig. 7a, d, e; Högström *et al.* 2013, fig. 5d). At a slightly higher stratigraphical level in both sections, trace fossils are found that

form tightly circling bilobed positive epireliefs, in some instances giving the appearance of closed loops (Fig. 7b, e). This material is similar to the circling parts of the type material of *Taphrhelminthopsis circularis* (which we believe is better attributed to *Psammichnites*, cf. Mángano *et al.* 2019) from the lower Cambrian of northern Spain. Trace fossils showing the full range of the circling and irregular paths of the type material of this ichnospecies appear in the lower member of the Breidvika Formation. The Manndrapselva material is tentatively compared with *Psammichnites circularis*, although taxonomic treatment of this ichnospecies is currently under investigation (Mángano *et al.* 2019). In addition to the already mentioned forms, the upper part of the third cycle also yields three-lobed trace fossils and *Bergaueria* *isp.* (Banks, 1970; Högström *et al.* 2013; McIlroy & Brasier, 2017).

In comparison with the trace fossil successions in the Chapel Island Formation on the Burin Peninsula in Newfoundland, Canada, the upper part of the third cycle of the Manndrapselva Member clearly is Cambrian in age (Högström *et al.* 2013; McIlroy & Brasier, 2017). The presence of cf. *Psammichnites circularis* raises the question of whether this level could already correspond to the *Rusophycus avalonensis* Zone, for which this ichnospecies is characteristic. However, the cf. *Psammichnites circularis* does not show the full morphological range of the ichnospecies, and the first *Rusophycus* appears some 70 m higher in the lower member of the Breidvika Formation (Banks, 1970; Högström *et al.* 2013), along with *Monomorphichnus* (Fig. 7i) appearing at 47 m in the same unit. The upper part of the third cycle of the Manndrapselva Member is therefore better assigned to the *Treptichnus pedum* Zone, with the *Rusophycus avalonensis* Zone corresponding to the lower member of the Breidvika Formation.

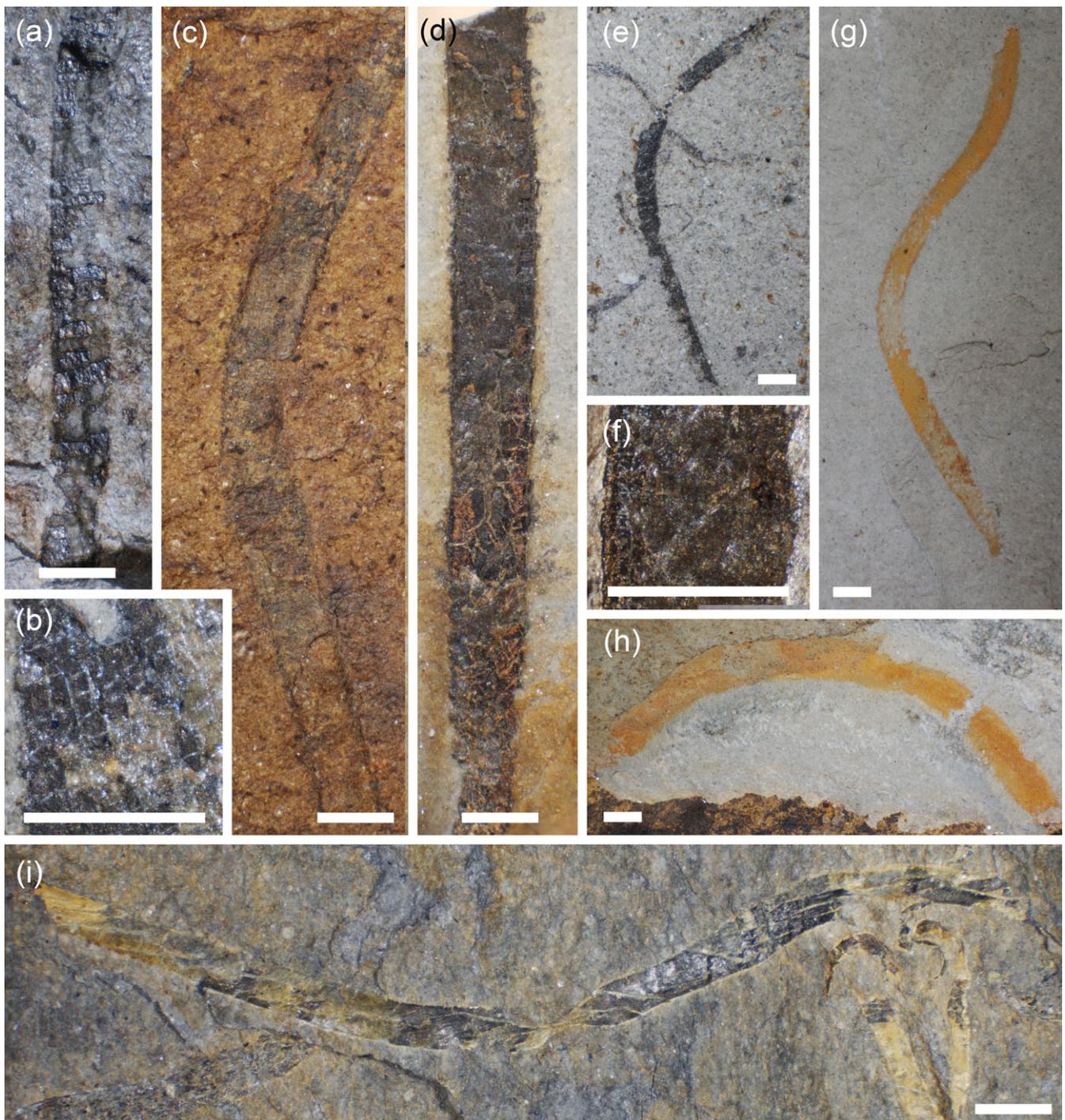


**Fig. 5.** Field photos from the Bårdeluovttjohka section. (a) Composite panorama of the section. Left arrow points to the massive sandstone bed at 18–20 m below the top of the third cycle of the Manndrapselva Member, with *Treptichnus pedum* occurring just above this bed (see log in Fig. 7a). The arrow to the right points to the top of the third cycle of the Manndrapselva Member. (b) Upper section of the coastal outcrop near Bårdeluovttjohka River. Arrow points to the top of the red boundary quartzite. (c) Massive sandstone bed with Teodoro Palacios sitting at the *Treptichnus pedum* level. (d) Local flat-pebble conglomerate just above the thick sandstone bed. (e) Section at the thick sandstone bed. Guido Meinhold standing on top of the massive sandstone and pointing to the surface with cf. *Psammichnites circularis*.

Returning to trace fossils in the lower part of the third cycle, both *Treptichnus pedum* and *Gyrolithes* extend a few metres below the GSSP level on the Burin Peninsula (Gehling *et al.* 2001; Laing *et al.* 2018). Additional trace fossils low in the third cycle are *Helminthopsis* isp., found at comparable stratigraphical levels both in the Manndrapselva section (Fig. 7c) and the section south of Bårdeluovttjohka (Fig. 7h). These *Helminthopsis*, which are preserved as positive hyporeliefs, locally show a rectangular cross-section. On large exposures these *Helminthopsis* can be seen to occur with, and apparently integrate with, trace fossils that are less winding but otherwise identical in dimensions (Fig. 7g, h); such intergradations of *Helminthopsis* are not uncommon (e.g. Carbone & Narbonne, 2014). A fragment of what seems to be a

similar form both in size and cross-section was reported as *Cochlichnus* isp. 3 from the Fortunian Khmelnitski Formation of Ukraine (Palij *et al.* 1983). In the Chapel Island Formation, the first occurrence of *Helminthopsis* is c. 8 m above the GSSP level. Although *Helminthopsis* is recorded elsewhere from the uppermost Ediacaran, the Manndrapselva material is relatively large (c. 5 mm wide), and the trace fossil association from the lower part of the third cycle of the Manndrapselva Member most likely represents the *Treptichnus pedum* Zone.

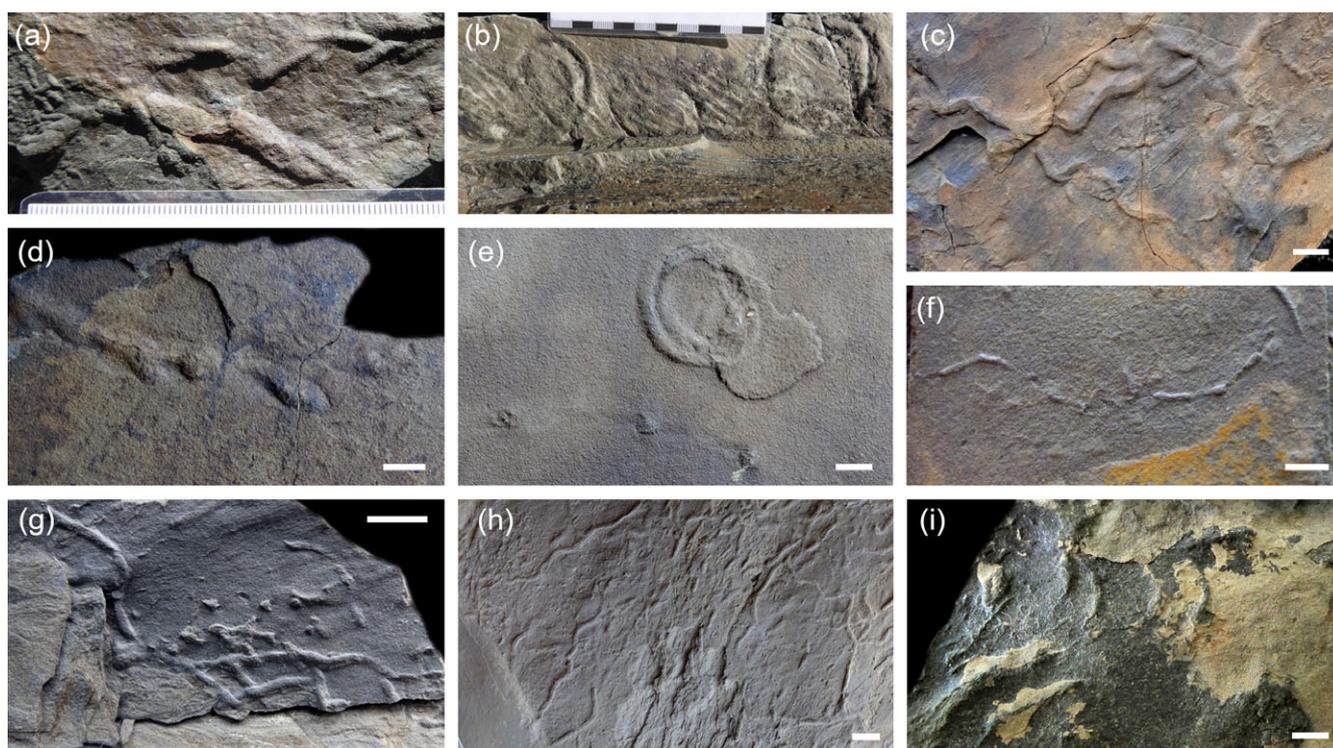
No trace fossils have been found in the sandstone-dominated upper part of the second cycle. Palaeopascichnids from the upper part of the heterolithic portion of the second cycle demonstrate a latest Ediacaran age, which is also consistent with



**Fig. 6.** Specimens of *Sabellidites* from the Digermulen Peninsula, illustrating variations in their preservation. (a) TSGf 18538 (sample D16-F03) displaying typical preservation in slightly sandy matrix. Bårdeluovtjohka section,  $-10.3$  m. (b) TSGf 18500a (sample D16-F51), detail of large specimen showing the fractured surface. Manndrapselva section, 17 m. (c) TSGf 18466 (sample D16-F14), specimen showing smooth inner surface of the tube fading into external mould (lower part). Manndrapselva section, 17.5 m. (d) TSGf 18511 (sample D17-JO4), specimen showing the smooth inner surface. Detail seen in Figure 6f. Avzejohka section,  $-27.9$  m. (e) TSGf 18500b (sample D16-F51), small curved 'normal' specimen. Manndrapselva section, 17 m. (f) TSGf 18511 (sample D17-JO4), detail of smooth inner surface. (g) TSGf 18502 (sample D16-F53/54), 'rusty' specimen to compare with specimen in Figure 6e from nearly the same level. Manndrapselva section, 17 m. (h) TSGf 18516 (sample D17-JO9), 'rusty' specimen from the highest recorded stratigraphical level. Avzejohka section, 54 m. (i) TSGf 18541 (sample D16-F06), long, twisted specimen with partly 'rusty' sections. Bårdeluovtjohka section,  $-15.5$  m. Scale bars = 1 mm.

trace fossils from this unit (McIlroy & Brasier, 2017; Jensen *et al.* 2018b). It should be noted that earlier reports of treptichnids from the second cycle are revised. Material consisting of a series of aligned sediment pods that are connected by a faintly visible horizontal ridge (Högström *et al.* 2013, fig. 5a) by them

compared with treptichnids is better interpreted as having been formed through a sinusoidal vertical movement (Jensen *et al.* 2017). What is considered the first authentic treptichnid (Högström *et al.* 2013, fig. 5b; cf. Fig. 7c) is now known to derive from the third cycle.



**Fig. 7.** (a–h) Trace fossils from the third cycle of the Manndrapselva Member and (i) the lower member of the Breidvika Formation: (a, b, i) from the Bårdeluovttjohka section, (g, h) from an adjacent section 200 m to the south, (c–f) from the Manndrapselva section. Metres and other comparisons refer to sections in Figure 8. Fine-scale divisions in millimetres. Scale bars = 10 mm. Specimens without TSGf numbers are photographed in the field. (a) *Treptichnus pedum* on bed sole, –18 m. (b) cf. *Psammichnites circularis* on bed top, –17 m. (c) *Helminthopsis* isp., on bed sole, –27 m. (d) Lower view of *Treptichnus pedum* on parting of flaggy sandstone, –16 m. (e) Top view of cf. *Psammichnites circularis* and, near bottom, intersection of vertical portions of *Treptichnus pedum*, on parting of flaggy sandstone, –16 m. (f) Trace fossil with faint angular turns on bed sole, –28 m. (g) Trace fossils on bed sole, approximately same level as *Gyrolithes* isp. (h) *Helminthopsis* isp. and other trace fossils on bed sole, 1 m below *Treptichnus pedum*. (i) *Monomorphichnus* isp., on bed sole, 47 m.

## 6. Stratigraphical distribution of *Sabellidites* on the Digermulen Peninsula

### 6.a. Results

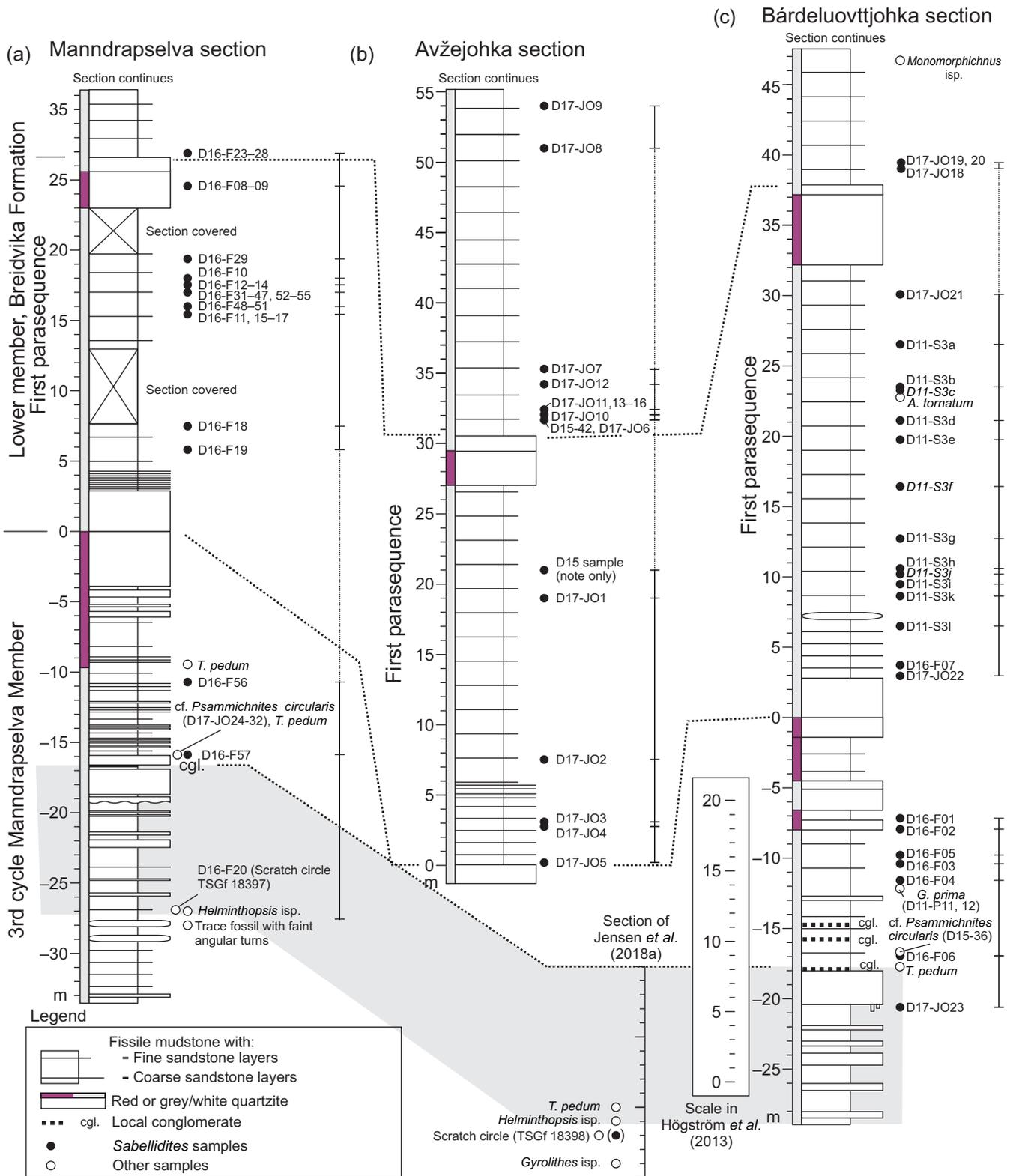
About 70 m of the Manndrapselva section were logged (Fig. 8a). The lower parts of the lower member of the Breidvika Formation are partly covered by vegetation, which prevented sampling. The flat landscape and low dip of the strata preferentially exposed upper surfaces of the beds, while lower surfaces with trace fossils are more difficult to find. In total, 46 samples with *Sabellidites cambriensis* were recovered. In the lower part of the section (Manndrapselva Member) specimens are rare and non-gregarious. The trace fossil *Treptichnus pedum* was registered at c. 9 m and 16 m below the reference level (= 0 m) in the section (Fig. 7d, e), together with *Sabellidites cambriensis*. The 9 m level below the reference level correlates with the position of *Treptichnus pedum* recorded by Höglström *et al.* (2013) from the Bårdeluovttjohka section. Specimens of *Sabellidites* are more common already in the lower part of the lower member of the Breidvika Formation, often with abundant specimens on the bedding surfaces. The stratigraphically youngest samples were found just above the upper boundary of the first parasequence in the Breidvika Formation (Fig. 8).

The Avzejohka section offered the best exposures of the fissile mudstone (Fig. 8b), with 18 samples collected. Some of the surfaces were covered with *Sabellidites* specimens. *Sabellidites* is common

within the first 5 m above the thick red/white quartzite and with a few specimens occurring more than 25 m above the quartzite.

Farmer *et al.* (1992) recorded *Sabellidites* at 9 m and 16 m above the base of the lower member of the Breidvika Formation in the Bårdeluovttjohka section, while Höglström *et al.* (2013) extended the stratigraphic range in the first parasequence. For the present study, nearly 70 m of the section was logged. A total of 26 samples were collected (including 12 samples from the 2011 expedition). Specimens are found stratigraphically lower in the Bårdeluovttjohka section, and *Treptichnus pedum* is also recorded at a lower level than in the Manndrapselva section (Jensen *et al.* 2018a, fig. 7c; but see above). The acritarch *Granomarginata prima* is found at c. 12 m below the reference level and *Asteridium tornatum* at c. 23 m above the reference level (data from Höglström *et al.* 2013; Palacios *et al.* 2018).

The sections correlate well across the c. 5 km distance between the southernmost and northernmost outcrop, with a similar distribution and abundance of *Sabellidites*. Specimens are rare in the third cycle of the Manndrapselva Member, but they are consistently present from c. 6.5 m above the lowest level of *Treptichnus pedum* and upwards (Fig. 8). A single specimen was registered by Jensen *et al.* (2018a) c. 2 m below the lowest *Treptichnus pedum* specimen in the outcrop to the south of the Bårdeluovttjohka section (Fig. 8c). *Sabellidites* is common and abundant in the first 5 m above the base of the first parasequence of the Breidvika Formation with two specimens recognized further



**Fig. 8.** Correlation of the three sections discussed herein, with marker beds, sample numbers and other key features. (a) Manndrapselva section. (b) Avžejohka section. (c) Bárdeluovttjohka section. The grey area indicates correlation of the Ediacaran–Cambrian transition beds between the sections. Samples only recorded in the field do not carry sample numbers.

15 m upsection (Figs 6h, 8b). The observed upper range of *Sabellidites* is thus at c. 55 m into the lower member of the Breidvika Formation.

## 7. Distribution and correlation of *Sabellidites cambriensis*

### 7.a. General remarks

Nielsen & Schovsbo (2011, p. 223) adopted the Rovnian and Lontovan stages developed in Eastern Europe (Mens *et al.* 1987, 1990) for the lower Cambrian of Scandinavia, with the Kotlinian being the uppermost stage of the Ediacaran. A detailed overview of the distribution of *Sabellidites* in a number of sections on Baltica and elsewhere is found in the online Supplementary Material.

The Rovnian Stage stratotype is taken at level 100–152.7 m of core 4 at Klevan in the Rivne region of Ukraine, being 29 to 53 m thick in the area (Kir'yanov, 1969) (Fig. 9b, locality 11a), with an additional reference section at the outcrop along the Ternava River (a tributary of the Dniester River) at the village of Kitaygorod, Khmelnytsky region, Ukraine (Fig. 9b, locality 11c) (Konstantinenko & Kir'yanov, 2013). The Rovnian Stage is characterized by a mass-occurrence of *Sabellidites* occurring without *Platysolenites antiquissimus* (Kir'yanov, 1968, 1969) but with a low-diversity leiosphaerid acritarch assemblage (Konstantinenko & Kir'yanov, 2013).

The stratotype of the Lontovan Stage is in the Kunda quarry in NE Estonia with additional data from the Lontova drill core (interval 14.0 to 88.3 m) (Mens & Pirrus, 1977, 1997). The Lontovan Stage has been considered equivalent in age to provisional Stage 2 of the Terreneuvian (Nielsen & Schovsbo, 2011; Meidla, 2017 and references therein). However, it seems to be older and corresponds mostly to the Fortunian, and to Stage 2 only in part (Moczyłowska & Yin, 2012; Palacios *et al.* 2018, 2020; Slater *et al.* 2018).

Two acritarch assemblages and subzones were originally recognized in the basal Cambrian of the East European Platform and considered typical for the Rovnian and Lontovan stages (Mens & Posti, 1984; Mens *et al.* 1990; Jankauskas & Lenzion, 1992; Raevskaya, 2005 and references therein). The low-diversity *Asteridium–Comasphaeridium* assemblage Zone was developed as the first recognizable zonation for the Polish part of the East European Platform and Baltoscandian successions, and considered equivalent to the latest Rovno and Lontova horizons (Moczyłowska, 1991). The zone is characterized by *Asteridium tornatum*, *Comasphaeridium velvetum*, *Granomarginata prima* and *Granomarginata squamacea*. Jachowicz-Zdanowska (2013) recorded microfossils, believed to be older but including *Granomarginata*, in the *Pulvinosphaeridium antiquum–Pseudotasmanites* assemblage Zone on the Brunovistulicum Terrane in southern Poland and northeastern Czech Republic (west of the Teisseyre–Törnquist Zone). Szczepanik & Żylińska (2016) placed this zone in the earliest Fortunian.

The post-Lontovan *Skiagia–Fimbriaglomerella* Zone corresponds to the Dominopolian Stage and the occurrence of the first trilobites in Baltoscandia of the *Schmidtellus mickwitzi* Zone (Moczyłowska, 1991; Nielsen & Schovsbo 2011; Palacios *et al.* 2020). In the review by Moczyłowska & Yin (2012), the *Asteridium–Comasphaeridium* Zone took a wider scope and encompasses the entire Fortunian Stage and extends into the undefined Stage 2, thus including both the Rovnian and Lontovan in terms of Baltic stages.

The acritarchs *Granomarginata prima* and *Granomarginata squamacea*, together with rare *Asteridium tornatum*, are present at the base of a Lontovan Stage on the East European Platform (Volkova *et al.* 1979, 1983; Moczyłowska, 1991). The first two occur in the Fortunian type section in Newfoundland, but here the name-bearing taxa of the assemblage zone are missing (Palacios *et al.* 2018, 2020). Nearly the entire Terreneuvian and most of Stage 2 instead encompass the *Granomarginata* Zone, and identification of the *Asteridium–Comasphaeridium* assemblage Zone can only be made when the index fossils of these small acanthomorphic acritarchs are present (Palacios *et al.* 2018, 2020). *Granomarginata* itself may be older (Agić *et al.*, 2021) and the Cambrian occurrences may represent the tail end of a more typical Ediacaran assemblage.

The Vendian (Period) has been used in East European literature since the mid-1960s, with the Vendian–Cambrian boundary usually placed at the base of the Lontovan Regional Stage (Sokolov, 1984, 1997). Estonian and many Ukrainian workers on the other hand preferred to place the boundary at the base of the Rovnian Stage, especially following the definition of the basal Cambrian GSSP (Mens *et al.* 1990; Kir'yanov, 2006; Velikanov, 2009; Velikanov & Melnychuk, 2013; Meidla, 2017). The Vendian of older Polish literature, with the upper boundary placed at the base of the Lontovan, is often replaced by Ediacaran in more modern studies without adjustments of the Ediacaran–Cambrian boundary level (see discussion pertaining to this in Section 7b and 7d).

### 7.b. *Sabellidites cambriensis* as an index fossil for the lowermost Cambrian

*Sabellidites cambriensis* has been recognized as a lowermost Cambrian zonal fossil since the mid-1960s and is widely used in correlation across Scandinavia and the East European Platform and with Siberia (Sokolov, 1965, 1997; Kir'yanov, 1969; Martinsson, 1974; Mens, 1980, 1987; Bergström & Ahlberg, 1981; Lenzion, 1983; Bergström & Gee, 1985; Mens *et al.* 1987, 1990). A general sequence with *Sabellidites cambriensis* in the oldest strata (Rovno), followed by, or slightly overlapping with, *Platysolenites antiquissimus*, and the appearance of a more diverse shelly fauna in the succeeding strata (Lontovan) became well established. The lower Cambrian facies on the East European Platform shows a strong lateral continuity (Rozanov & Zhuravlev, 1992), which facilitates a broad correlation across the region.

However, in the 1990s and onwards the stratigraphical value of both *Sabellidites cambriensis* and *Platysolenites* became questioned. It was argued that the lack of associated diagnostic organic-walled microfossils (OWM) for the older strata, long ranges of the macroscopic taxa, strong facies dependence and diachronic facies distribution gave a low biostratigraphical value (e.g. Vidal & Moczyłowska, 1992, 1995; Nielsen & Schovsbo, 2011; Paczeńska, 2014; Szczepanik & Żylińska, 2016), and the once widespread use of *Sabellidites* for correlation was disbanded.

Although the arguments against the stratigraphical usefulness to some extent are valid, they do not render *Sabellidites cambriensis* and *Platysolenites* biostratigraphically uninteresting. The evolutionary faunal sequence during earliest Cambrian time in Baltica is consistent and was developed in broadly the same type of widespread dominantly siliciclastic facies within a relatively short time interval; the Rovnian and Lontovan succession in Baltica span perhaps 10–15 Ma (Nielsen & Schovsbo 2011, p. 287). The flooding of an essentially flat craton (peneplain) in earliest Cambrian



**Fig. 9.** (a) Map of Newfoundland, Canada, with location of the GSSP section at Fortune Head on the Burin Peninsula. (b) Simplified map of northern and eastern Europe with main localities discussed herein and in the online Supplementary Material, surface and subsurface occurrences of lower Palaeozoic rocks and major structural elements. Location of core drilling sites and distribution of Palaeozoic rocks based on Zoricheva (1963), Rozanov (1980, 1987), Kuzmenko & Burzin (1996), Mens & Pirrus (1997), Silaupa *et al.* (2005), Maslov *et al.* (2008), Nielsen & Schovsbo (2011) and Podkovyrov *et al.* (2017). Boundaries of the Baltic shield based on Torsvik & Rehnström (2003), Gee *et al.* (2006) and Mazur *et al.* (2018).

time was stepwise and proceeded by a series of rapid transgressive–regressive cycles with initially large clastic supplies to the basins, followed by less clastic supply as the sea level rose (Nielsen & Schovsbo, 2011). The peri-cratonic deposits are thick and

complete, while epi-cratonic deposits lack the oldest strata and the facies are much reduced in thickness. *Sabellidites* and *Platysolenites* are found in the fine-grained facies, representing periods of drowning and sea level highstand. This may pose a

problem as the facies may develop differently along the platform and also be diachronous.

The distribution of OWM and small carbonaceous fossils (SCF) is therefore crucial. These are often restricted to certain facies or rocks with certain organic content (Woltz *et al.* 2021), but this is not the same as their occurrence being facies dependent. As pelagic organisms, they may be reliable index fossils and especially useful for correlation, regardless of their distribution being better represented in particular fine-grained facies. As such, it is possible to state that the distribution of these fossils, for the purpose of biostratigraphy, are independent of facies. Thus, the co-occurrence of assemblages with *Sabellidites* and/or *Platysolenites*, trace fossils and certain OWM and potentially SCF is therefore important for dating and correlation of the sedimentary rocks in Baltica regardless of facies.

The terminal Ediacaran and very earliest Cambrian has a depauperate microfossil record with mainly leiosphaerids, although new studies have demonstrated a higher diversity (Jachowicz-Zdanowska, 2011, 2013; Szczepanik & Żylińska, 2016; Arvestål & Willman, 2020; Agić *et al.*, 2021). The lowest Cambrian strata are followed by an assemblage with the first small acanthomorphic acritarchs of the *Asteridium–Comasphaeridium* assemblage Zone, where *Asteridium* is a good marker for the start of Cambrian-type OWM assemblages. Note that the occurrence of *Asteridium* does not necessarily indicate the lowermost possible Cambrian.

As not all the stratigraphical components (i.e. *Sabellidites*, *Platysolenites*, trace fossils, OWM, SCF, shelly fossils) are present or well documented in all sections, correlation across Baltica is still challenging (see online Supplementary Material). However, *Sabellidites* is a useful taxon to include, as it is a distinct component of the earliest Cambrian evolutionary fauna, has a wide distribution and is fairly easy to recognize. The supposed Ediacaran range of *Sabellidites cambriensis* is equivocal for a number of reasons. *Sabellidites cambriensis* is found just below both the GSSP and *Treptichnus pedum* on Newfoundland and possibly just below *Treptichnus pedum* also on the Digermulen Peninsula, and as such is present in the Ediacaran. However, at both sites the co-occurrences of these two taxa are less than 5 m apart, and defining confident intervals for the extremely close stratigraphic proximity in these several hundred metre thick sequences is essentially irrelevant for the distribution. For practical purposes, it is found that they both first occur at the very base of the Cambrian and that the distribution of *Sabellidites cambriensis* therefore is truly basal Cambrian. It is thus not a diagnostic index fossil of a Terminal Ediacaran Stage as suggested by Muscente *et al.* (2019), but essentially of the basal Cambrian.

Stratigraphically old occurrences of *Sabellidites cambriensis* on the East European Platform cited in the literature are largely erroneous as pointed out by Sokolov (1997), although sabelliditid-like forms such as the saarinids *Calyptrina* and *Saarina* are found already in the Redkino Stage (Gnilovskaya, 1996; Sokolov, 1997) (see online Supplementary Material).

In Poland, the original lower Cambrian boundary was traditionally placed at the base of the Włodawa Formation, encompassing the old usage Rovno *Sabellidites* Zone (Areń & Lenzion, 1978; Lenzion, 1983). Subsequent works, however, followed the Russian usage of the Vendian, with the upper boundary near the top of the Włodawa Formation. Thus the *Sabellidites* Zone, associated with a low-diversity leiosphaerid acritarch assemblage, was placed in the uppermost Vendian of the Russian usage (Moczyłowska & Vidal, 1986; Moczyłowska, 1991, 1998). Therefore, the ensuing

*Asteridium–Comasphaeridium* assemblage Zone encompassed the lower Cambrian, including the top of the Rovnian and the entire Lontovan and the *Platysolenites* Zone.

Later, however, the Vendian was simply equated with the Ediacaran in Poland (see for instance Moczyłowska, 2008; Paczeńska, 2014), therefore by default assigning an Ediacaran age for the *Sabellidites* Zone. Furthermore, the *Asteridium–Comasphaeridium* Zone was taken to encompass the entire Fortunian Stage and extend into the undefined Stage 2 (Moczyłowska & Yin, 2012), thus encompassing both the Rovnian and Lontovan in terms of the traditional Baltic stages. This view contrasts markedly with that in which a basal Fortunian leiosphaerid assemblage occurs prior to the *Asteridium–Comasphaeridium* Zone in both the Newfoundland type section and in Baltica (Nielsen & Schovsbo, 2011; Szczepanik & Żylińska, 2016; Palacios *et al.* 2018, 2020; Slater *et al.* 2018). With addition of the stratigraphical data on the distribution of *Sabellidites cambriensis* in Newfoundland and on the Digermulen Peninsula it seems clear that the taxon has an insignificant Ediacaran range, and a more extensive Ediacaran distribution of this taxon in Poland or elsewhere is most likely not the case (see also online Supplementary Material).

The sections with *Sabellidites cambriensis* on the Digermulen Peninsula described herein are the only outcrops in Baltica that offer a comprehensive record of the stratigraphical distribution of this taxon around the Ediacaran–Cambrian transition. The succession is directly comparable to that at Fortune Head on Newfoundland, with *Sabellidites* co-occurring with a diverse trace fossil association and OWM in a section seemingly without significant sedimentary breaks. The lower range of *Sabellidites* on the Digermulen Peninsula is firmly established, whereas the observed upper range may still prove to overlap with that of *Platysolenites antiquissimus*, as seen elsewhere in Baltica.

### 7.c. *Platysolenites*

The tubular foraminiferan *Platysolenites* has been regarded as a long-ranging taxon in Scandinavia, believed to be extending from the sub-trilobitic succession (Lontovan Stage) into the trilobite-bearing *Holmia kjerulfi* assemblage Zone (Vergalian–Rausvian stages) (Skjeseth, 1963; Bergström, 1981; Nielsen & Schovsbo, 2011). This assumption is partly based on two minute and doubtful fragments found in the Redalen Member of the Ringstrand Formation in the Mjøsa area of Norway reported by Vogt (1924). A much-cited correlation of this finding within the younger Brennsætersaga Member of the Ringstrand Formation by Skjeseth (1963) is probably erroneous and its occurrence is likely older, i.e. in the *Skiagia–Fimbriaglomerella* assemblage Zone (see discussion in Høyberget *et al.* 2019).

Rare specimens attributed to *Platysolenites antiquissimus* have been reported from the Sõru Formation (Dominopolian Stage, *Rusophycus parallelum* Zone) and basal Lükati Formation of western Estonia (Dominopolian Stage, *Skiagia–Fimbriaglomerella* assemblage Zone) (Mens & Pirrus, 1977, 1997; Mens, 2003), which then represent the highest stratigraphical occurrence in Baltica.

In Newfoundland, McIlroy *et al.* (2001) reported one specimen of *Platysolenites* in the West Centre Cove Member of the Bonavista Formation, comprising the upper *Aldanella attleborensis* interval of the *Sunnaginia imbricata* Zone (Fletcher, 2006). This is close to the upper part of the Terrenewian (Palacios *et al.* 2011) and only slightly older than the Lükati Formation and Mjøsa occurrences. Kouchinsky *et al.* (2017) found *Platysolenites antiquissimus*

in carbonate facies in the Anabar Uplift on the Siberian Platform, where it ranges from low in the *Anabarites trisulcatus* Zone of the Nemakit–Daldyn Formation through the overlying Emyaksin/Medvezhya formations, its upper range possibly being within the Stage 2 – Stage 3 transition beds, which is close to the range in the Lükati Formation. Thus, the youngest records of *Platysolenites* seem to extend at least to the end of the Terreneuvian, being slightly younger on the Siberian Platform than most of the occurrences in Baltica (Lontovan and lowermost Dominopolian stages).

The earliest occurrences of *Platysolenites* in Newfoundland are within the lowermost *Watsonella crosbyi* Zone, while its range starts earlier in Siberia in the lower part of the Fortunian (*Anabarites trisulcatus* Zone) (Kouchinsky *et al.* 2017). On the Digermulen Peninsula the oldest occurrence is within the lower part of the upper member of the Breidvika Formation, co-occurring with specimens of *Ladatheca* (McIlroy & Logan, 1999; McIlroy & Brasier, 2017), which places the occurrence temporally very near to that in Newfoundland. In other parts of Finnmark, *Platysolenites* is found in beds attributed to the upper part of the lower member of the Breidvika Formation (see Högström *et al.* 2013).

*Platysolenites* is also found in Cambrian strata of California, Avalonian England and Wales, and southwestern Spain (Firby-Durham, 1977; Vidal *et al.* 1999; McIlroy *et al.* 2001) generally associated with helcionelloid molluscs (Gubanov, 2002).

Moczydłowska (1991) proposed a *Platysolenites antiquissimus* Interval-Zone, ranging from its first occurrence to the *Schmidtellus mickwitzii* Zone (*Skiagia-Fimbriaglomerella* assemblage Zone). Based on other occurrences discussed herein (see online Supplementary Material) and in McIlroy *et al.* (2001), the distribution of *Platysolenites* is largely restricted to the Lontovan Stage of Baltica and it is a useful marker across this palaeocontinent.

#### 7.d. Correlation of *Sabellidites cambriensis* in Baltica

The sections illustrated in Figure 10 are used to draw broad inferences on the correlation of *Sabellidites cambriensis* in Baltica (for discussion of sections see online Supplementary Material). It should be emphasized that the range and occurrences of macrofossils in the cores is partly a matter of chance and the OWM record is therefore of great importance. Additionally, diagnostic OWM zones are unknown in several successions, and these are marked as ‘arbitrary’ in Figure 10. Clearly, more detailed studies are needed to assess the biostratigraphical potential of *Sabellidites*, evaluated in the context of other macrofossils, OWM and the SCF record within each region. The correlation of *Sabellidites cambriensis* outside Baltica is not discussed further here, but it would be helpful to understand more about its distribution in the type sequences on Newfoundland.

*Sabellidites cambriensis* co-occurs in its oldest range with simple leiosphaerids and *Granomarginata* in Newfoundland, the Digermulen Peninsula, Poland and Ukraine (*Granomarginata*/leiosphaerids in Fig. 10). These two OWM components are reported with *Sabellidites* in other areas of Baltica, but usually also include *Asteridium*, although precise ranges are often unknown.

*Platysolenites* and *Sabellidites* show partly overlapping ranges in Estonia, the Moscow Basin, Ukraine and the East European Platform of Poland, whereas they do not overlap in Newfoundland, Scandinavia, Polish territories west of the Teisseyre–Tornquist Zone and Belarus. The situation in the

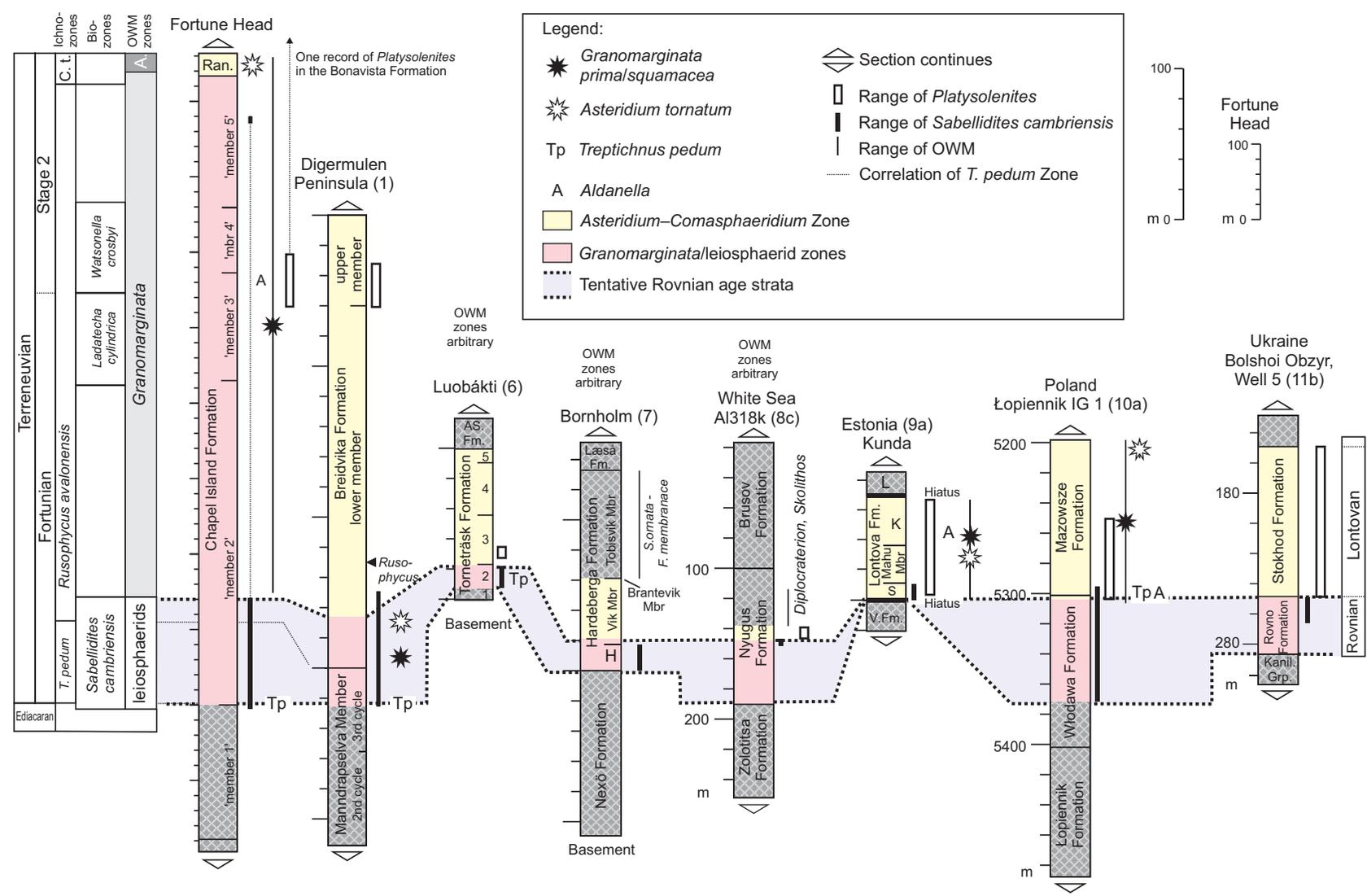
White Sea area is unresolved. A single *Sabellidites* specimen in ‘member 5’ on Newfoundland occurs well above the earliest record of *Platysolenites*, although the main distribution is within ‘member 2’ and directly comparable with the range observed on the Digermulen Peninsula. On the other hand, *Platysolenites* also occurs stratigraphically above the highest *Sabellidites* record, in the upper Terreneuvian Bonavista Formation, giving it a range close to that seen elsewhere in Baltica, i.e. in the Lontovan (see the Fortune Head column in Fig. 10). The main difference is that the thicker succession in Newfoundland would give a larger overlap of the ranges than in the more condensed successions elsewhere, but with only two single occurrences this assumption is at the moment conjectural.

*Aldanella* co-occurs with *Platysolenites* in Newfoundland, at one locality in Northern Norway, in Estonia and in Poland. In Poland the uppermost range of *Sabellidites* may overlap with the occurrences of *Aldanella*, while in Estonia the recorded occurrences are c. 40 m apart. The presence of OWM is noted in all areas, although the precise range of OWM taxa relative to *Sabellidites* and *Platysolenites* is not always clear and more studies are needed.

The northernmost occurrences in Scandinavia, outside of the Digermulen Peninsula, are in the Luobäkti section (see online Supplementary Material). Jensen & Grant (1998) suggested an early Cambrian age for the entire succession, contrasting the earlier notion that it was late Precambrian (Vidal, 1981); Nielsen & Schovsbo (2011) placed it entirely within the Dominopolian (*Skiagia-Fimbriaglomerella* Zone). Stodt *et al.* (2011) suggested that the oldest beds, the lower c. 10 m, correlate with the Ediacaran Lillevannet and Manndrapselva members in Finnmark, which poses challenges. The much discussed Vakkejokk breccia overlying the *Treptichnus pedum* level in the area may represent a proximal impact ejecta layer (Ormö *et al.* 2017), and if this is correct it is only of use in the local correlation. *Sabellidites* occurs in the lower siltstone member (see online Supplementary Material), which suggests a position in the basal Lontovan following the arguments presented here (unit 2 in Fig. 10), with *Platysolenites* in the lower part of the red and green mudstone (unit 3 in Fig. 10). The top part of the upper siltstone member of the Torneträsk Formation (unit 5 in Fig. 10, called the Grammajukku Formation by Nielsen & Schovsbo, 2011) contains *Holmia kjerulfi* and stratigraphically higher trilobites (Vergalian–Rausvian), which then gives the upper age constraint at this section. Without a diagnostic OWM record (Vidal & Moczydłowska, 1996) a firm correlation of this section is difficult, especially for the lowermost part of the succession (Stodt *et al.* 2011).

The Bornholm succession contains abundant *Sabellidites* in the Hadeborg Member but no other fossils. The boundary with the underlying Nexø Formation is sharp and conformable but may represent a sequence boundary (Nielsen & Schovsbo, 2011). A Lontovan or older age for this occurrence is inferred (Nielsen & Schovsbo, 2011), and the older option (Rovnian) is tentatively preferred here owing to the lack of *Platysolenites*.

The wide spatial distribution of the *Sabellidites*-bearing level in the White Sea area is even more extensive than on the Digermulen Peninsula, but the widespread occurrence of *Sabellidites* in a narrow stratigraphical interval is comparable. The presence of *Asteridium* and *Granomarginata* in the upper range of *Sabellidites* is confirmed in drill cores, but the ranges of the OWM relative to the ranges of *Sabellidites* and *Platysolenites* and the position relative to the Padun Group is unknown. At the moment the Padun Group succession is attributed to the lower



**Fig. 10.** Tentative correlation of a selection of basal lower Cambrian sections in Baltica compared to the GSSP section at Fortune Head on the Burin Peninsula, Newfoundland in Canada. Note that this section is half the vertical scale in order to fit within the figure. The section names and locality numbers correspond to those found on the map (Fig. 9) and are referred to in the text and in the online Supplementary Material. Metres are indicated for the drill cores, to facilitate comparison. The distribution and ranges of the various taxa are discussed in the text and in the online Supplementary Material. Stratigraphical column, left-hand side: C. t. – *Cruziana tenella*; A. – *Asteridium tornatum-Comasphaeridium velvetum* assemblage Zone. Fortune Head: Ran. – Random Formation. Luobákhti section: 1 – Lower sandstone member; 2 – Lower siltstone member; 3 – Red and green siltstone member; 4 – Upper sandstone member; 5 – Upper siltstone member; AS – Alum Shale Formation. Bornholm: H – Hadeberg Member. Estonia, Kunda section: V. Fm. – Voronka Formation; S – Sämi Member; K – Kestla Member; L – Lükati Formation.

Cambrian (Lontovan) (Kuznetsov *et al.* 2014), although the lower part of the Nyugus and Zolotitsa formations may very well prove to be older.

The Estonian section serves as a model for the St Petersburg area and central Moscow Basin. The upper range of *Sabellidites* overlaps with *Platysolenites*, which is found throughout the Lontova Formation coinciding with the appearance of acritarchs of the *Asteridium–Comasphaeridium* Zone. The Lomonosov Formation of the St Petersburg area contains *Platysolenites* and *Granomarginata*, but seemingly not *Asteridium* (Podkovyrov *et al.* 2017). A comparable distribution is seen in, for instance, the Toropets core in the Moscow Basin where *Sabellidites* in the Danilov beds (approximately equivalent with the Nekrasovo Formation) co-occurs with *Asteridium* in its lowest range and with *Platysolenites* in its upper range (Kirsanov, 1974). Both *Asteridium* and *Platysolenites* range into the overlying Rusanov beds (= Lezha Formation), where other sabelliditids are also present.

The Polish sections are re-interpreted here, placing the Ediacaran–Cambrian boundary at the lowest occurrence of *Sabellidites* in the Włodawa Formation with reference to the Łopiennik core (see online Supplementary Material). The distribution of fossils is quite similar to that seen in the comparably thick sequences of Newfoundland and the Digermulen Peninsula, starting with *Sabellidites* and simple leiosphaerids before the appearance of *Granomarginata*. In the Mazowsze Formation, *Sabellidites* generally co-occurs with acritarchs of the *Asteridium–Comasphaeridium* Zone, resembling the situation seen in the Estonian successions. Other OWM and SCF, presumed to be of late Ediacaran age, occur just 6 m below the lowest occurrence of *Sabellidites* in the Włodawa Formation of the Łopiennik IG 1 core (Moczyłowska, 2008; Moczyłowska *et al.* 2015). They represent depauperate assemblages dominated by mainly Proterozoic prokaryotes, including some long-ranging taxa like *Ceratophyton*, known from the upper Ediacaran and lower Cambrian. Two specimens identified as the Tonian (c. 800 Ma) taxon *Valkyria borealis* (Moczyłowska, 2008, fig. 8a, b) also resemble the early Cambrian problematicum *Baltinema rana* (Slater *et al.* 2017, fig. 11a–m). The Włodawa specimens have shorter lateral protrusions and lack a longitudinal stripe within the main body characteristic of *Valkyria* (Butterfield *et al.* 1994) and are truncated, so more specimens need to be examined to confidently distinguish between *Valkyria* and *Baltinema*. *Palaeopascichnus delicatus* has been reported from the underlying Lublin Formation, but the figured specimen (Paczeńska 1986, pl. 1, fig. 2) is unusual in having a marginal border. Paczeńska (1989) listed *Harlaniella* from the Lublin Formation, but this material has not been figured or described.

Although not exhibited in the section of Ukraine in Figure 10, where only the Bolshoi Obzyr drill core section is shown, the biostratigraphy appears similar to that of Poland, with *Sabellidites* occurring with leiosphaerids, *Granomarginata* and simple trace fossils followed by co-occurrence with *Platysolenites*. In the Ukrainian succession, the overlap of the ranges of sabelliditids and *Platysolenites* is short.

### 7.e. Rovnian and Lontovan

The *Asteridium–Comasphaeridium* Zone has since the 1990s been the first recognized OWM zone in the lower Cambrian of Baltica and characteristic of the Lontovan, originally including the occurrence of *Granomarginata* in the East European Platform of Poland (Moczyłowska, 1991). *Granomarginata* is widespread and

common in the Terreneuvian across the globe but also found infrequently in the upper Ediacaran (Agić *et al.*, 2021). In Newfoundland, the oldest occurrence is well below the first occurrence of the *Asteridium tornatum* and the *Asteridium–Comasphaeridium* Zone as interpreted by Palacios *et al.* (2018), who established a *Granomarginata* Zone.

However, this distribution of a *Granomarginata* Zone in Baltica is not clear-cut (Fig. 10). On the Digermulen Peninsula, *Granomarginata* is found with *Sabellidites* close to the Ediacaran–Cambrian boundary, while in Newfoundland *Granomarginata* appears just above *Sabellidites* and leiosphaerids. Furthermore, *Asteridium* appears in the upper range of *Sabellidites* on the Digermulen Peninsula, but both occurrences are well below that of *Platysolenites*. The distribution of *Sabellidites* and OWM in the Ukraine is comparable to that in Newfoundland, with a simple leiosphaerid assemblage followed by an assemblage with *Granomarginata*, whereas *Asteridium* seems to first appear in the Dominopolian (Talsy) Stage (Volkova *et al.* 1979, 1983; Konstantinenko & Kir'yanov, 2013); *Sabellidites* co-occurs with the first two assemblages, and *Platysolenites* with the *Granomarginata* assemblage (correlated with the Lontovan). In the East European part of Poland, it is not clear that the range of *Granomarginata* is lower than the Lontovan, while it seems to range into the Rovnian in the Polish territories west of the Teisseyre–Tornquist Zone where it occurs with simple leiosphaerids (Jankauskas & Lenzion, 1992; Jachowicz-Zdanowska, 2013; Szczepanik & Żylińska, 2016).

The base of the Lontovan is not well constrained or defined, but it may be possible to reach a better biostratigraphical resolution for the stage. A *Granomarginata* Zone may either be distinguished as a lower zone, apart from the *Asteridium–Comasphaeridium* Zone, or included as a lowermost subzone of the latter zone. The base of the stage would also encompass the lower range of *Platysolenites* (the *Platysolenites* Interval-Zone *sensu* Moczyłowska, 1991) and the upper range of *Sabellidites*, giving an overlapping range zone of the two. Additional sabelliditids like *Paleolina* and *Sokoloviina*, a shelly fauna including *Aldanella* and well-developed OWM of the *Asteridium–Comasphaeridium* Zone further distinguish the stage.

The assemblage zone itself is inadequate to establish the lower boundary of the Lontovan, for which OWM first appearance datum and range zones are needed (Szczepanik & Żylińska, 2016; Palacios *et al.* 2018). The tentative correlation of the local stages in Figure 10 is based on the assumption that the base of the Rovnian coincides with the base of the *Treptichnus pedum* Zone, and that the base of the Lontovan essentially corresponds to the first occurrence of *Platysolenites* following the *Platysolenites* Interval-Zone of Moczyłowska (1991), and close to the base of the *Asteridium–Comasphaeridium* Zone.

However, both on the Digermulen Peninsula and Newfoundland, the occurrence of *Platysolenites* and *Asteridium* (as an index species for the *Asteridium–Comasphaeridium* Zone) does not follow this pattern, and the base of the Lontovan would be high up in the *Platysolenites* level in those sections if the first occurrence of *Platysolenites* is used to define the base of this zone. This conundrum is difficult to resolve as long as the first appearance of *Asteridium* or *Comasphaeridium* is not well known in several areas, or the distribution differs as it does in Newfoundland. Thus, because of the lack of adequate fossil data from many sections, the placement of the Rovnian–Lontovan boundary in Baltica still remains somewhat arbitrary.

## 8. Summary

*Sabellidites cambriensis* is a worm-like metazoan, consisting of long (70–120 mm) flexible tubes with coarse to fine transverse wrinkling, thick walls and a constant tube diameter up to 3 mm in width. It is a regional index fossil for Baltica but has been reported also from Siberia, China, Australia and Spain. The distribution of *Sabellidites cambriensis* was studied in three Ediacaran–Cambrian sections on the Digermulen Peninsula in Arctic Norway, in the context of associated records of trace fossils and OWM. The succession encompasses the upper parasequence (third cycle) of the Manndrapselva Member of the Ståhpogieddi Formation and the first parasequence of the lower member of the Breidvika Formation. The Ediacaran–Cambrian boundary is located in the lower part of the third cycle of the Manndrapselva Member. Specimens of *Sabellidites* are rare but consistently present close to the lowest level of *Treptichnus pedum* and upwards, whereas the taxon is common and abundant in the lower part of the lower member of the Breidvika Formation; the youngest record is at c. 55 m above the base.

The acritarch *Granomarginata prima* co-occurs with *Sabellidites* and *Treptichnus pedum* in their lower ranges, while *Asteridium tornatum* co-occurs with *Sabellidites* in the lower part of the lower member of the Breidvika Formation. Thus, the third cycle encompasses the *Granomarginata* Acritarch Zone, while the Breidvika Formation encompasses the *Asteridium–Comasphaeridium* Acritarch Zone. Contrary to other sections in Baltica, the range of the foraminiferan *Platysolenites antiquissimus* is neither close to, nor does it overlap with that of *Sabellidites* on the Digermulen Peninsula, but occurs much higher in the Breidvika Formation. The succession of fossils on the Digermulen Peninsula is directly comparable to that of the GSSP section at Fortune Head on Newfoundland, except for the *Asteridium–Comasphaeridium* Zone, which appears higher in the Newfoundland succession.

Correlation between several sections in Baltica is attempted, with the distribution of *Sabellidites* in Newfoundland and on the Digermulen Peninsula as a proxy. It is shown that *Sabellidites* essentially is an index fossil for the lowermost Cambrian. Broadly speaking, the taxon co-occurs in the Rovnian Stage with a distinct trace fossil association that can be attributed to the *Treptichnus pedum* Ichnozone, and OWM including leiosphaerids and *Granomarginata*. Its upper range is in the base of the Lontovan, overlapping with or being close to the lower range of the *Platysolenites* range zone. The Lontovan is otherwise characterized by OWM of the *Asteridium–Comasphaeridium* Zone. However, as not all the stratigraphical components (i.e. *Sabellidites*, *Platysolenites*, trace fossils, OWM, SCF, small shelly fossils) are present or well documented in all sections, the correlation across Baltica is still challenging.

**Acknowledgements.** The Digermulen Early Life Research Group acknowledges funding to Anette E. S. Högström from the Norwegian Research Council (NRC, project number 231103). Travel support was given to Frida Hybertsen by the Department of Earth Sciences, Palaeobiology, Uppsala University. T. P. & S. J. acknowledge funding from 'Ministerio de Economía, Industria y Competitividad' grant CGL 2017-87631-P. Help with literature was provided by Sofia Bakayeva, Alexander P. Gubanov and Małgorzata Moczyłowska, for which we are grateful. Mats Eriksson provided access to the type collection in Lund. Insightful comments by Arne Thorshøj Nielsen and two anonymous reviewers greatly improved the manuscript.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0016756821001187>

## References

- Agić H, Högström AES, Jensen S, Ebbestad JOR, Vickers-Rich P, Hall M, Matthews JJ, Meinhold G, Høyberget M and Taylor WL (2021) Late Ediacaran occurrences of the organic-walled microfossils *Granomarginata* and flask-shaped *Lagoenaforma collaris* gen. et sp. nov. *Geological Magazine*. <https://doi.org/10.1017/S0016756821001096>
- Areñ B and Lenzion K (1978) Stratigraphic and lithological characteristics of the Vendian and Lower Cambrian. *Prace Instytutu Geologicznego* **90**, 7–49.
- Arvestål EHM and Willman S (2020) Organic-walled microfossils in the Ediacaran of Estonia: biodiversity on the East European Platform. *Precambrian Research* **341**, 105626. doi: [10.1016/j.precamres.2020.105626](https://doi.org/10.1016/j.precamres.2020.105626).
- Banks NL (1970) Trace fossils from the late Precambrian and Lower Cambrian of Finnmark, Norway. In *Trace Fossils* (eds TP Crimes and JC Harper), pp. 19–34. *Geological Journal Special Issue* 3.
- Banks NL, Edwards MB, Geddes WP, Hobday DK and Reading HG (1971) Late Precambrian and Cambro–Ordovician sedimentation in East Finnmark. *Norges Geologiske Undersøkelse* **269**, 197–236.
- Bergström J and Ahlberg P (1981) Uppermost Lower Cambrian biostratigraphy in Scania. *Geologiska Föreningen i Stockholm Förhandlingar* **103**, 193–214.
- Bergström J and Gee DG (1985) The Cambrian in Scandinavia. In *The Caledonide Orogen – Scandinavia and Related Areas* (eds DG Gee and BA Sturt), pp. 247–71. London: John Wiley & Sons Ltd.
- Bergström J (1981) Lower Cambrian shelly faunas and biostratigraphy in Scandinavia. In *Short Papers for the Second International Symposium on the Cambrian System 1981* (ed. ME Taylor), pp. 22–5. United States Geological Survey Open-File Report 81-743.
- Buatois LA, Almond J, Mángano MG, Jensen S and Germs GB (2018) Sediment disturbance by Ediacaran bulldozers and the roots of the Cambrian explosion. *Scientific Reports* **8**, 1–9.
- Budd GE and Jensen S (2017) The origin of the animals and a 'Savannah' hypothesis for early bilaterian evolution. *Biological Reviews* **92**, 446–73.
- Butterfield NJ, Knoll AH and Swett K (1994) Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils and Strata* **34**, 1–84.
- Cai Y, Xiao S, Li G and Hua H (2019) Diverse biomineralizing animals in the terminal Ediacaran Period herald the Cambrian explosion. *Geology* **47**, 380–4.
- Carbone C and Narbonne GM (2014) When life got smart: the evolution of behavioral complexity through the Ediacaran and early Cambrian of NW Canada. *Journal of Paleontology* **88**, 309–30.
- Cohen PA, Bradley A, Knoll AH, Grotzinger JP, Jensen S, Abelson J, Hand K, Love G, Metz J, McLoughlin N, Meister P, Shepard R, Tice M and Wilson JP (2009) Tubular compression fossils from the Ediacaran Nama group, Namibia. *Journal of Paleontology* **83**, 110–22.
- Crimes TP and McIlroy D (1999) A biota of Ediacaran aspect from Lower Cambrian strata on the Digermulen Peninsula, Arctic Norway. *Geological Magazine* **136**, 633–42.
- Darroch SA, Smith EF, Laflamme M and Erwin DH (2018) Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution* **33**, 653–63.
- Droser ML and Gehling JG (2015) The advent of animals: the view from the Ediacaran. *Proceedings of the National Academy of Sciences* **112**, 4865–70.
- Eichwald E (1860) *Lethaea rossica ou palaeontologie de la Russie. Premier Volume. Première Section de l'ancienne Période*. Stuttgart: Schweizerbart, 1657 pp.
- Erwin DH and Valentine J (2013) *The Cambrian Explosion: The Reconstruction of Animal Biodiversity*. Greenwood Village, Colorado: Roberts and Company, 406 pp.
- Farmer J, Vidal G, Moczyłowska M, Strauss H, Ahlberg P and Siedlecka A (1992) Ediacaran fossils from the Innerelv Member (late Proterozoic) of the Tanafjorden area, northeastern Finnmark. *Geological Magazine* **129**, 181–95.
- Fedonkin MA, Gehling JG, Grey K, Narbonne GM and Vickers-Rich P (2007) *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*. Baltimore, Maryland: The Johns Hopkins University Press, 326 pp.
- Firby-Durham JB (1977) *Platysolenites* from the Lower Cambrian of California. *Proceedings of the Russian Academy of Sciences, Geological Series* **9**, 146–9.

- Fletcher TP** (2006) Bedrock Geology of the Cape St. Mary's Peninsula, Southwest Avalon Peninsula, Newfoundland (includes parts of NTS map sheets 1M/1, 1N/4, 1N/16 and 1K/13), Map 2006-02. Government of Newfoundland and Labrador, Department of Natural Resources, Geological Survey, Open File NFLD/2925.
- Føyn S** (1960) Tanafjord to Laksefjord. In *Aspects of the Geology of Northern Norway. Guide to Excursion No. A 3. 21st International Geological Congress, Norden 1960* (ed. JA Dons), pp. 45–57. Norges Geologiske Undersøkelse vol. 212a.
- Gee DG, Bogolepova OK and Lorenz H** (2006) The Timanide, Caledonide and Uralide orogens in the Eurasian high Arctic, and relationships to the palaeocontinents Laurentia, Baltica and Siberia. In *European Lithosphere Dynamics* (eds DG Gee and RA Stephenson), pp. 507–20. Geological Society of London, Memoir no. 32.
- Gehling JG, Jensen S, Droser ML, Myrow PM and Narbonne GM** (2001) Burrowing below the basal Cambrian GSSP, Fortune Head, Newfoundland. *Geological Magazine* **138**, 213–8.
- Gnilovskaya MB** (1996) New saarinides of the Vendian of the Russian platform. *Proceedings of the Russian Academy of Sciences* **348**, 89–93 (in Russian).
- Grabau AW** (1900) Palaeontology of the Cambrian terranes of the Boston Basin. *Occasional Papers of the Boston Society of Natural History* **4**, 601–94.
- Gubanov AP** (2002) Early Cambrian palaeogeography and the probable Iberia–Siberia connection. *Tectonophysics* **352**, 153–68.
- Högström AES, Jensen S, Palacios T and Ebbestad JOR** (2013) New information on the Ediacaran–Cambrian transition in the Vestertana Group, Finnmark, northern Norway, from trace fossils and organic-walled microfossils. *Norwegian Journal of Geology* **93**, 95–106.
- Høyberget M, Ebbestad JOR and Funke B** (2019) Re-evaluation of the stratigraphically important olenellid trilobite *Holmia* cf. *mobergi* from the Cambrian Series 2, Stage 3 and its implications for the lower Cambrian stratigraphy in the Mjøsa area, Norway. *Norwegian Journal of Geology* **99**, 1–29.
- Jachowicz-Zdanowska M** (2011) Organic microfossil assemblages from the late Ediacaran rocks of the Małopolska Block, southeastern Poland. *Geological Quarterly* **55**, 85–94.
- Jachowicz-Zdanowska M** (2013) Cambrian phytoplankton of the Brunovistulicum – taxonomy and biostratigraphy. *Polish Geological Institute Special Papers* **28**, 1–150.
- Jankauskas TV and Lendzion K** (1992) Lower and Middle Cambrian acritarch-based biozonation of the Baltic Syncline and adjacent areas (East European Platform). *Przegląd Geologiczny* **40**, 519–25.
- Jensen S, Gehling JG and Droser ML** (1998) Ediacara-type fossils in Cambrian sediments. *Nature* **393**, 567–9.
- Jensen S and Grant SWF** (1998) Trace fossils from the Dividalen Group, northern Sweden: implications for Early Cambrian biostratigraphy of Baltica. *Norsk Geologisk Tidsskrift* **78**, 305–17.
- Jensen S, Högström AES, Almond J, Taylor WL, Meinhold G, Høyberget M, Ebbestad JOR, Agić H and Palacios T** (2018a) Scratch circles from the Ediacaran and Cambrian of Arctic Norway and the Republic of South Africa, with a review of scratch circle occurrences. *Bulletin of Geosciences* **93**, 287–304.
- Jensen S, Högström AES, Høyberget M, Meinhold G, McIlroy D, Ebbestad JOR, Taylor WL, Agić H and Palacios T** (2018b) New occurrences of *Palaeopascichnus* from the Ståhpogieddi Formation, Arctic Norway, and their bearing on the age of the Varanger Ice Age. *Canadian Journal of Earth Sciences* **55**, 1253–61.
- Jensen S, Högström AES, Høyberget M, Meinhold G, Palacios T, Taylor WL, Ebbestad JOR and Agić H** (2017) Trace fossils across the Ediacaran–Cambrian boundary on the Digermulen Peninsula, Arctic Norway. In *International Symposium on the Ediacaran–Cambrian Transition, 20–22 June 2017, St John's, Newfoundland, Canada. Abstract Volume* (ed. D McIlroy), p. 48. Newfoundland: Memorial University.
- Kir'yanov VV** (1969) Scheme of the stratigraphy of the Cambrian deposits of Volyn. *Geological Journal* **29**, 48–62 (in Ukrainian).
- Kir'yanov VV** (2006) Stratigraphy of the oldest Cambrian sediments of the East European and Siberian platforms. *Geological Journal* **2006**, 115–22.
- Kir'yanov VV** (1968) Palaeontological remains and stratigraphy of the Baltic Group deposits in Volhynia-Podolia. In *Paleontology and Stratigraphy of the Lower Paleozoic in Volyn-Podolia* (eds TA Ishchenko, VV Kiriakov and VS Krandievsky), pp. 5–25. Kiev: National Academy of Sciences of Ukraine (in Russian).
- Kirsanov VV** (1974) On the question of stratigraphy on the border layers of the Vendian and Cambrian in the central areas of the East European Platform. In *Biostratigraphy and Paleontology of Lower Cambrian in Europe and North Asia* (eds IT Zuravleva and A Yu Rozanov), pp. 5–21. Moscow: Russian Academy of Sciences, Institute of Geology and Geophysics, Siberian Branch (in Russian).
- Konstantinenko LI and Kir'yanov VV** (2013) The Cambrian System. In *Stratigraphy of Upper Proterozoic and Phanerozoic of Ukraine. Volume 1, Stratigraphy of Upper Proterozoic, Paleozoic and Mesozoic of Ukraine* (ed. PF Gozhyk), pp. 155–66. Kiev: National Academy of Sciences of Ukraine, Institute of Geological Sciences (in Ukrainian).
- Kouchinsky A, Bengtson S, Landing E, Steiner M, Vendrasco M and Ziegler K** (2017) Terreneuvian stratigraphy and faunas from the Anabar Uplift, Siberia. *Acta Palaeontologica Polonica* **62**, 311–440.
- Kuzmenko Yu T and Burzin MB** (1996) *Stratigraphic Scheme of the Vendian Deposits of the Moscow Syncline. Explanatory Note*. Moscow: Regional Interdepartmental Stratigraphic Commission, 46 pp. (in Russian).
- Kuznetsov NB, Belousova EA, Alekseev AS and Romanyuk TV** (2014) New data on detrital zircons from the sandstones of the lower Cambrian Brusov Formation (White Sea region, East-European Craton): unravelling the timing of the onset of the Arctida–Baltica collision. *International Geology Review* **56**, 1945–63.
- Lafamme M, Darroch SAF, Tweedt SM, Peterson KJ and Erwin DH** (2013) The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat? *Gondwana Research* **23**, 558–73.
- Laing BA, Buatois LA, Mángano MG, Narbonne GM and Gougeon RC** (2018) *Gyrolithes* from the Ediacaran–Cambrian boundary section in Fortune Head, Newfoundland, Canada: exploring the onset of complex burrowing. *Palaeogeography, Palaeoclimatology, Palaeoecology* **495**, 171–85.
- Landing E** (1994) Precambrian–Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. *Geology* **22**, 179–82.
- Landing E, Geyer G, Brasier MD and Bowring SA** (2013) Cambrian evolutionary radiation: context, correlation, and chronostratigraphy—overcoming deficiencies of the first appearance datum (FAD) concept. *Earth-Science Reviews* **123**, 133–72.
- Landing E, Myrow PM, Benus AP and Narbonne GM** (1989) The Placentian series: appearance of the oldest skeletalized faunas in southeastern Newfoundland. *Journal of Paleontology* **63**, 739–69.
- Lendzion K** (1983) Biostratigraphy of Cambrian sediments in the Polish part of the Eastern European platform. *Kwartalnik Geologiczny* **27**, 669–94.
- Linnemann U, Ovtcharova M, Schaltegger U, Gärtner A, Hautmann M, Geyer G, Vickers-Rich P, Rich T, Plessen B, Hofmann M, Zieger J, Krause R, Kriesfeld L and Smith J** (2019) New high-resolution age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion. *Terra Nova* **31**, 49–58.
- Mángano MG, Buatois LA, Jensen S, MacNaughton R, Marcos A, Piñuela L, García-Ramos JC and Gougeon R** (2019) Ichnotaxonomic conundrums and the calibration of the Cambrian explosion: the case of *Psammichnites-Taphrhelminthopsis*. In *Short Abstracts Presented to the International Meeting on the Ediacaran System and the Ediacaran–Cambrian Transition, Guadalupe, Extremadura, Spain, 17–24 October 2019* (eds JJ Álvaro and S Jensen), p. 16. Estudios Geológicos 75.
- Martinsson A** (1974) The Cambrian of Norden. In *Lower Palaeozoic Rocks of the World, Vol. 2, Cambrian of the British Isles, Norden and Spitsbergen* (ed. CH Holland), pp. 185–283. London: Wiley-Interscience.
- Maslov AV, Grazhdankin DV, Podkovyrov VN, Ronkin YL and Lepikhina OP** (2008) Composition of sediment provenances and patterns in geological history of the late Vendian Mezen Basin. *Lithology and Mineral Resources* **43**, 260–80.
- Mazur S, Krzywiec P, Malinowski M, Lewandowski M, Aleksandrowski P and Mikołajczak M** (2018) On the nature of the Teisseyre–Tornquist Zone. *Geology, Geophysics and Environment* **44**, 17–30.
- McCall GJH** (2006) The Vendian (Ediacaran) in the geological record: enigmas in geology's prelude to the Cambrian explosion. *Earth-Science Reviews* **77**, 1–229.

- McIlroy D and Brasier MD** (2017) Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway. In *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier* (eds AT Brasier, D McIlroy and N McLoughlin), pp. 351–68. Geological Society of London, Special Publication no. 488.
- McIlroy D, Green OR and Brasier MD** (2001) Palaeobiology and evolution of the earliest agglutinated Foraminifera: *Platysolenites*, *Spirosolenites* and related forms. *Lethaia* **34**, 13–29.
- McIlroy D and Logan GA** (1999) The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaiois* **14**, 58–72.
- Meidla T** (2017) Ediacaran and Cambrian stratigraphy in Estonia: an updated review. *Estonian Journal of Earth Sciences* **66**, 152–60
- Meinhold G, Jensen S, Høyberget M, Arslan A, Ebbestad JOR, Högström AES, Palacios T, Agić H and Taylor WL** (2019a) First record of carbonates with spherulites and cone-in-cone structures from the Precambrian of Arctic Norway, and their palaeoenvironmental significance. *Precambrian Research* **328**, 99–110.
- Meinhold G, Roberts NMW, Arslan A, Jensen S, Ebbestad JOR, Högström AES, Høyberget M, Agić H, Palacios T and Taylor WL** (2020) U–Pb dating of calcite in ancient carbonates for age estimates of syn- to post-depositional processes: a case study from the upper Ediacaran strata of Finnmark, Arctic Norway. *Geological Magazine* **157**, 1367–72.
- Meinhold G, Wemmer K, Högström AES, Ebbestad JOR, Jensen S, Palacios T, Høyberget M, Agić H and Taylor WL** (2019b) A late Caledonian tectonothermal event in the Gaissa Nappe Complex, Arctic Norway: fine-fraction K–Ar evidence from the Digermulen Peninsula. *GFF* **141**, 289–94.
- Mens K** (2003) Early Cambrian tubular fossils of the genus *Onuphionella* from Estonia. *Proceedings of the Estonian Academy of Sciences, Geology* **52**, 87–97.
- Mens K, Bergström J and Lendzion K** (1987) *The Cambrian System on the East European Platform (Correlation Chart and Explanatory Notes)*. Tallinn: Valgus, 119 pp. (in Russian).
- Mens K, Bergström J and Lendzion K** (1990) The Cambrian System on the East European Platform; correlation chart and explanatory notes. *International Union of Geological Sciences Publication* **25**, 1–73.
- Mens K** (1980) Lontovo Stage. In *Palaogeography and Lithology of Vendian and Cambrian of the Western Part of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds BM Keller and A Yu Rozanov), pp. 25–9. Moscow: Russian Academy of Sciences (in Russian).
- Mens K and Pirrus E** (1977) *Stratotype Sections of the Cambrian of Estonia*. Tallin: Valgus, 68 pp. (in Russian).
- Mens K and Pirrus E** (1997) Cambrian. In *Geology and Mineral Resources of Estonia* (eds A Raukas and A Teedumäe), pp. 39–51. Tallinn: Estonian Academy Publishers.
- Mens K and Posti E** (1984) Distribution and correlation significance of organic remains in the Baltic Series of Estonia. In *Stratigraphy of Ancient Paleozoic Deposits of the Baltic* (eds R Männil and K Mens), pp. 5–17. Tallinn: Estonian Academy of Sciences, Institute of Geology (in Russian).
- Mens K** (1987) Lontovo Stage. In *Palaogeography and Lithology of Vendian and Cambrian of the Western Part of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds A Yu Rozanov and K Łydka), pp. 32–7. Warsaw: Institute of Geological Sciences of the Polish Academy of Sciences and Moscow: Russian Academy of Sciences.
- Moczydłowska M** (1991) Acritarch biostratigraphy of the Lower Cambrian and the Precambrian–Cambrian Boundary in Southeastern Poland. *Fossils and Strata* **29**, 1–127.
- Moczydłowska M** (2008) New records of late Ediacaran microbiota from Poland. *Precambrian Research* **167**, 71–92.
- Moczydłowska M** (1998) Lower Cambrian acritarch biochronology in Baltoscandia. In *Guide to Excursions in Scania and Västergötland, Southern Sweden. IV Field Conference of the Cambrian Stage Subdivision Working Group. International Subcommission on Cambrian Stratigraphy. Sweden, 24–31 August 1998* (ed. P Ahlberg), pp. 9–16. Lund Publications in Geology vol. 141.
- Moczydłowska M, Budd GE and Agić H** (2015) Ecdysozoan-like sclerites among Ediacaran microfossils. *Geological Magazine* **152**, 1145–8.
- Moczydłowska M and Vidal G** (1986) Lower Cambrian acritarch zonation in southern Scandinavia and southeastern Poland. *Geologiska Föreningen i Stockholms Förhandlingar* **105**, 201–23.
- Moczydłowska M and Yin LM** (2012) Phytoplanktic microfossils record in the lower Cambrian and their contribution to stage chronostratigraphy. In *Cryogenian–Ediacaran to Cambrian Stratigraphy and Paleontology of Guizhou, China* (eds YL Zhao, M Zhu, J Peng, RR Gaines and RL Parsley), pp. 49–58. *Journal of Guizhou University, Natural Sciences* **29**, supplement 1.
- Muscante AD, Bykova N, Boag TH, Buatois LA, Mángano MG, Eleish A, Prabhu A, Pan F, Meyer MB, Schiffbauer JD, Fox P, Hazen RM and Knoll AH** (2019) Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. *Nature Communications* **10**, 1–15.
- Nielsen AT and Schovsbo NH** (2011) The Lower Cambrian of Scandinavia: depositional environment, sequence stratigraphy and palaeogeography. *Earth-Science Reviews* **107**, 207–310.
- Nikolaisen F and Henningsmoen G** (1985) Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninsula, Finnmark, northern Norway. *Norges Geologiske Undersøkelse Bulletin* **400**, 1–49.
- Nikolaisen F and Henningsmoen G** (1990) Lower and Middle Cambrian trilobites from the Digermul peninsula, Finnmark, northern Norway. *Norges Geologiske Undersøkelse Bulletin* **419**, 55–95.
- Ormö J, Nielsen AT and Alwmark C** (2017) The Vakkejokk Breccia: an Early Cambrian proximal impact ejecta layer in the North-Swedish Caledonides. *Meteoritics & Planetary Science* **52**, 623–45.
- Paczeńska J** (1986) Upper Vendian and Lower Cambrian ichnocoenoses of the Lublin region. *Biuletyn Instytutu Geologicznego* **355**, 31–47.
- Paczeńska J** (1989) Polski i globalny zapis biozdarzenia na granicy prekambriumu. *Przegląd Geologiczny* **11**, 542–6.
- Paczeńska J** (2014) Lithostratigraphy of Ediacaran deposits in the Lubelskie-Podlasie sedimentary basin (eastern and south-eastern Poland). *Biuletyn Państwowego Instytutu Geologicznego* **460**, 1–24.
- Palacios T, Högström AES, Ebbestad JOR, Agić H, Høyberget M, Jensen S, Meinhold G and Taylor WL** (2020) Acritarchs from the Duolbagaisá Formation (Cambrian Series 2, Miaolingian) on the Digermulen Peninsula, Finnmark, Arctic Norway: towards a high-resolution Cambrian chronostratigraphy. *Geological Magazine* **157**, 2051–66.
- Palacios T, Jensen S, Barr SM, White CE and Myrow PM** (2018) Organic walled microfossils from the Ediacaran–Cambrian boundary stratotype section, Chapel Island and Random formations, Burin Peninsula, Newfoundland, Canada: global correlation and significance for the evolution of early complex ecosystems. *Geological Journal* **53**, 1728–42.
- Palacios T, Jensen S, White CE and Barr SM** (2011) New biostratigraphical constraints on the lower Cambrian Ratcliffe Brook Formation, southern New Brunswick, Canada, from organic-walled microfossils. *Stratigraphy* **8**, 45–60.
- Palij VM, Posti E and Fedonkin MA** (1983) Soft-bodied Metazoa and animal trace fossils in the Vendian and Early Cambrian. In *Upper Precambrian and Cambrian Palaeontology of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds A Urbanek and A Yu Rozanov), pp. 56–74. Warsaw: Institute of Geological Sciences of the Polish Academy of Sciences and Moscow: Geological Institute of the Russian Academy of Sciences.
- Podkovyrov VN, Maslov AV, Kuznetsov AB and Ershova VB** (2017) Lithostratigraphy and geochemistry of Upper Vendian–Lower Cambrian Deposits in the Northeastern Baltic Monocline. *Stratigraphy and Geological Correlation* **25**, 1–20.
- Raevskaya E** (2005) Diversity and distribution of Cambrian acritarchs from the Siberian and East Europe and platforms – a generalized scheme. *Carnets de Géologie Memoire* **2005**, 39–44.
- Reading HG** (1965) Eocambrian and Lower Palaeozoic geology of the Digermul Peninsula, Tanafjord, Finnmark. *Norges Geologiske Undersøkelse* **234**, 67–191.
- Rice AHN** (2014) Restoration of the External Caledonides, Finnmark, North Norway. In *New Perspectives on the Caledonides of Scandinavia and*

- Related Areas* (eds F Corfu, D Gasser and DM Chew), pp. 271–99. Geological Society of London, Special Publication no. 390.
- Rozanov A Yu** (1980) Rovno Stage. In *Palaeogeography and Lithology of Vendian and Cambrian of the Western Part of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds BM Keller and A Yu Rozanov), pp. 24–5. Moscow: Russian Academy of Sciences (in Russian).
- Rozanov A Yu** (1987) Rovno Stage. In *Palaeogeography and Lithology of Vendian and Cambrian of the Western Part of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds A Yu Rozanov and K Lydka), pp. 29–32. Warsaw: Institute of Geological Sciences of the Polish Academy of Sciences and Moscow: Geological Institute of the Russian Academy of Sciences (in Russian).
- Rozanov A Yu and Zhuravlev A Yu** (1992) The Lower Cambrian fossil record of the Soviet Union. In *Origin and Early Evolution of the Metazoa* (eds JH Lipps and PW Signor), pp. 205–82. New York: Springer.
- Schiffbauer JD, Huntley JW, O’Neil GR, Darroch SAF, Laflamme M and Cai Y** (2016) The latest Ediacaran Wormworld Fauna: setting the ecological stage for the Cambrian Explosion. *GSA Today* **26**, 4–11.
- Selly T, Schiffbauer JD, Jacquet SM, Smith EF, Nelson LL, Andreasen BD, Huntley JW, Strange MA, O’Neil GR, Thater CA, Bykova N, Steiner M, Yang B and Cai Y** (2020) A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA. *Journal of Systematic Palaeontology* **18**, 357–79.
- Shahkarami S, Buatois LA, Mángano MG, Hagadorn JW and Almond J** (2020) The Ediacaran–Cambrian boundary: evaluating stratigraphic completeness and the Great Unconformity. *Precambrian Research* **345**, 105721. doi: [10.1016/j.precamres.2020.105721](https://doi.org/10.1016/j.precamres.2020.105721).
- Siedlecka A, Reading HG, Williams GD and Roberts D** (2006) Langfjorden, Preliminary Bedrock Geology Map 2236 II, Scale 1:50000. Trondheim: Norges Geologiske Undersøkelse.
- Silaua S, Fokin P, Lazauskienė J and Stephenson JA** (2005) The Vendian–Early Palaeozoic sedimentary basins of the East European Craton. In *European Lithosphere Dynamics* (eds DG Gee and RA Stephenson), pp. 449–62. Geological Society of London, Memoirs no. 32.
- Skjeseth S** (1963) Contributions to the geology of the Mjøsa Districts and the classical sparagmite area in southern Norway. *Norges Geologiske Undersøkelse* **220**, 1–126.
- Slater BJ, Harvey THP and Butterfield NJ** (2018) Small Carbonaceous Fossils (SCFs) from the Terreneuvian (lower Cambrian) of Baltica. *Palaeontology* **61**, 417–39.
- Slater BJ, Harvey THP, Guilbaud R and Butterfield NJ** (2017) A cryptic record of Burgess Shale-type diversity from the early Cambrian of Baltica. *Palaeontology* **60**, 117–60.
- Smith EF, Nelson LL, Strange MA, Eyster AE, Rowland SM, Schrag DP and Macdonald FA** (2016) The end of the Ediacaran: two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA. *Geology* **44**, 911–14.
- Sokolov BS** (1967) Ancient Pogonophora. *Reports of the Russian Academy of Sciences* **177**, 201–4 (in Russian).
- Sokolov BS** (1968) Vendian and Early Cambrian Sabelliditida (Pogonophora) of the USSR. In *Problems of Paleontology. Proceedings of the International Geology Congress, 23rd Session. Reports of Soviet Geologists. International Paleontology Union Symposium, Moscow*, pp. 73–9 (in Russian).
- Sokolov BS** (1972) Vendian and Early Cambrian Sabelliditida (Pogonophora) of the USSR. In *Proceedings of the International Paleontological Union, 23rd International Geological Congress (Prague 1968)*, pp. 79–84.
- Sokolov BS** (1984) Vendian System: its position in the stratigraphic column. In *Stratigrafiya. Doklady k 27-omu Mezhdunarodnomu Geologicheskomu Kongressu*, pp. 111–27 (in Russian).
- Sokolov BS** (1997) *Essays on the Advent of the Vendian System*. Moscow: KMK Scientific Press, 142 pp. (in Russian).
- Sokolov BS** (1965) The oldest Early Cambrian deposits and sabelliditids. In *All-Union Symposium on the Paleontology of the Precambrian and Cambrian: Abstracts* (ed. BS Sokolov), pp. 78–91. Novosibirsk: Russian Academy of Sciences, Institute of Geology and Geophysics, Siberian Branch (in Russian).
- Stodt F, Rice AHN, Björklund L, Bax G, Halverson GP and Pharaoh TC** (2011) Evidence of late Neoproterozoic glaciation in the Caledonides of NW Scandinavia. In *The Geological Record of Neoproterozoic Glaciations* (eds E Arnaud, GP Halverson and G Shields-Zhou), pp. 603–11. Geological Society of London, Memoirs no. 36.
- Szczepanik Z and Żylińska A** (2016) The oldest rocks of the Holy Cross Mountains, Poland – biostratigraphy of the Cambrian Czarna Shale Formation in the vicinity of Katuszow. *Acta Geologica Polonica* **66**, 267–81.
- Tarhan LG, Hughes NC, Myrow PM, Bhargava ON, Ahluwalia AD and Kudryavtsev AB** (2014) Precambrian–Cambrian boundary interval occurrence and form of the enigmatic tubular body fossil *Shaanxilithes ningqiangensis* from the Lesser Himalaya of India. *Palaeontology* **57**, 283–98.
- Torsvik TH and Rhenström EF** (2003) The Tornquist Sea and Baltica–Avalonia docking. *Tectonophysics* **362**, 67–82.
- Velikanov VA** (2009) Problematic issues Vendian stratigraphy of Ukraine. *Geologichnyy Zhurnal* **328**, 7–13 (in Ukrainian).
- Velikanov VA and Melnychuk VG** (2013) The Vendian System: introduction. In *Stratigraphy of Upper Proterozoic and Phanerozoic of Ukraine. Volume 1, Stratigraphy of Upper Proterozoic, Paleozoic and Mesozoic of Ukraine* (ed. PF Gozhyk), pp. 49–51. Kiev: Institute of Geological Sciences, National Academy of Sciences of Ukraine (in Ukrainian).
- Vidal G** (1981) Micropaleontology and biostratigraphy of the Upper Proterozoic and Lower Cambrian sequence in east Finnmark, northern Norway. *Norges Geologiske Undersøkelse* **362**, 1–53.
- Vidal G and Moczyłowska M** (1992) Patterns of phytoplankton radiation across the Precambrian–Cambrian boundary. *Journal of the Geological Society, London* **149**, 641–54.
- Vidal G and Moczyłowska M** (1995) The Neoproterozoic of Baltica – stratigraphy, palaeobiology and general geological evolution. *Precambrian Research* **73**, 197–216.
- Vidal G and Moczyłowska M** (1996) Vendian–Lower Cambrian acritarch biostratigraphy of the central Caledonian fold belt in Scandinavia and the palaeogeography of the Iapetus–Tornquist seaway. *Norsk Geologisk Tidsskrift* **76**, 147–68.
- Vidal G, Palacios T, Moczyłowska M and Gubanov AP** (1999) Age constraints from small shelly fossils on the early Cambrian terminal Cadomian Phase in Iberia. *GFF* **121**, 137–43.
- Vogt T** (1924) Forholdet mellem sparagmitsystemet og det marine Underkambrium ved Mjøsen. *Norsk Geologisk Tidsskrift* **7**, 281–384.
- Volkova NA, Kir’yanov VV, Piscun LV, Pashkyavichene LT and Jankauskas TV** (1979) Plant microfossils. In *Upper Precambrian and Cambrian Palaeontology of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds BM Keller and A Yu Rozanov), pp. 4–38. Warsaw: Institute of Geological Sciences of the Polish Academy of Sciences and Moscow: Geological Institute of the Russian Academy of Sciences (in Russian).
- Volkova NA, Kir’yanov VV, Piscun LV, Pashkyavichene LT and Jankauskas TV** (1983) Plant microfossils. In *Upper Precambrian and Cambrian Palaeontology of the East-European Platform. Contribution of the Soviet-Polish Working Group on the Precambrian–Cambrian Boundary Problem* (eds A Urbanek and A Yu Rozanov), pp. 7–46. Warsaw: Institute of Geological Sciences of the Polish Academy of Sciences and Moscow: Geological Institute of the Russian Academy of Sciences (in Russian).
- Waggoner B** (2003) The Ediacaran biotas in space and time. *Integrative Comparative Biology* **43**, 104–13.
- Woltz CR, Porter SM, Agić H, Dehler CM, Junium CK, Riedman LA, Hodgskiss MSW, Wörndle S and Halverson GP** (2021) Total organic carbon and the preservation of organic-walled microfossils in Precambrian shale. *Geology* **49**, 556–60.
- Wood R, Liu AG, Bowyer F, Wilby PR, Dunn FS, Kenchington CG, Hoyal Cuthill JF, Mitchell EG and Penny A** (2019) Integrated records of environmental change and evolution challenge the Cambrian Explosion. *Nature Ecology and Evolution* **3**, 528–38.
- Yang B, Steiner M, Zhu M, Li G, Liu J and Liu P** (2016) Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: implications for chronostratigraphy and metazoan evolution. *Precambrian Research* **285**, 202–15.

**Yanishevsky ME** (1926) On the remains of tubular worms from the Cambrian Blue Clay (preliminary report). *Annuaire de la Société Paléontologie de Russie* 4, 99–113 (in Russian).

**Zhang F, Xiao S, Romaniello SJ, Hardisty D, Li C, Melezhik V, Pokrovsky B, Cheng M, Shi W, Lenton TM and Anbar AD** (2019) Global marine redox changes drove the rise and fall of the Ediacara biota. *Geobiology* 17, 594–610.

**Zoricheva AI** (1963) Upper Proterozoic and Lower Paleozoic formations. North of the Russian Platform. In *Geology of the USSR. Vol. 2. Arkhangelsk, Vologda Regions Part 1. Geological Description* (eds AI Zoricheva and SI Volkov), pp. 79–99. Moscow: Russian State Geological Committee (in Russian).